

The *Geomyces* Fungi: Ecology and Distribution

MARK A. HAYES

*White-nose syndrome (WNS) is a devastating disease affecting hibernating bats, first documented in winter 2006 in eastern North America. Over 5.5 million bats of several species may have died as a result of this disease. The fungus *Geomyces destructans* is now considered the causal agent of WNS, and this species may have been recently introduced into North American bat hibernation habitats. This overview summarizes the ecology and distribution of *Geomyces* fungi. Species in this genus are common in the soils of temperate and high-latitude ecosystems and are capable of withstanding and thriving in cold, low-nutrient polar environments. These species are dispersed by wind, groundwater, arthropods, birds, and mammals and are carried by humans, their clothing, and their equipment. These characteristics present significant challenges to biologists, managers, and others charged with controlling the spread of WNS and *G. destructans* in other parts of North America and the biosphere.*

*Keywords: bats, *Geomyces*, hibernation, North America, white-nose syndrome*

White-nose syndrome (WNS) is a devastating disease affecting hibernating bats that was first documented in February 2006 in eastern North America (Blehert et al. 2009, Gargas et al. 2009, Meteyer et al. 2009). During the initial two-year period after the disease emerged, certain bat populations experienced more than 75% declines (Blehert et al. 2009, Frick et al. 2010), and over 5.5 million bats of several species died in the period from 2006 through 2011, which has led to regional population collapse and may lead to the extinction of some of these species (USFWS 2012). WNS has had a particularly destructive impact on species that hibernate in large congregations in the eastern United States and Canada (Blehert et al. 2009, Castle and Cryan 2010, Frick et al. 2010, Blehert et al. 2011). The fungal species *Geomyces destructans* is now considered to be the causal agent of WNS (Lorch et al. 2011).

Initially, WNS (the disease) and *G. destructans* (the causal agent) were known to occur only in eastern North America. However, *G. destructans* has recently been described using fungal culture identification techniques and DNA sequencing associated with cave environments and bats in Belgium, the Czech Republic, Estonia, France, Germany, Hungary, the Netherlands, Poland, Slovakia, Switzerland, and Ukraine (Martínková et al. 2010, Wibbelt et al. 2010, Puechmaille et al. 2011a, Šimonovičov et al. 2011, Pikula et al. 2012). The disease WNS, which is diagnosed by a characteristic pattern of fungal skin infection and the presence of *G. destructans* (Meteyer et al. 2009, Cryan et al. 2010), has recently been

documented in one European bat species (the greater mouse-eared bat, *Myotis myotis*) in the Czech Republic (Pikula et al. 2012). However, the mass mortality in bats associated with *G. destructans* has not been observed in Europe (Wibbelt et al. 2010, Puechmaille et al. 2011a). Several hypotheses have been proposed to explain the mass mortality observed in eastern North America. This fungus may be an invasive species recently introduced into bat hibernation habitats in North America (Warnecke et al. 2012), or it may be a virulent strain of a fungus with global distribution (see Puechmaille and colleagues [2011b] for a review of these hypotheses).

Much has been written about WNS and *G. destructans* since the new species description by Gargas and colleagues (2009). However, outside of journals specializing in mycology, microbiology, and polar biology, there is a lack of readily accessible information on the ecology and distribution of *Geomyces* species. The purpose of this overview is to provide an introduction to fungi of the genus *Geomyces* that will help provide perspective on the ecology and distribution of these fungi for those charged with understanding the dynamics of WNS and with making associated conservation and management recommendations and decisions.

The *Geomyces* fungi

A remarkable diversity of fungal species occur in soils. The vast majority of the approximately 80,000 described fungal

species may occur in soils at some time during their life cycle (Bridge and Spooner 2001), and there are undoubtedly many more species of soil fungi to be discovered (Hawksworth 1991, Bridge and Spooner 2001). Kirk and colleagues (2008) listed four species in the genus *Geomyces*, and the description of *G. destructans* by Gargas and colleagues (2009) brings the number of known species to five. Members of this genus produce small, unicellular, oval- or pear-shaped spores (arthroconidia) from existing hyphae in branched, tree-like clusters, supported on conidiophores (Sigler and Carmichael 1976, Currah 1985, Sigler et al. 2000, Rice and Currah 2005). Fungi often reproduce using propagules, which are structures that break away from the fungal body, and are dispersed by wind or water or on animals and form new fungal masses. Arthroconidia are asexual propagules that form when the tips of hyphae break apart along the cross-walls separating cells within hyphae (Kendrick 2000, Larone 2002). Conidiophores are specialized hyphal structures on which arthroconidia are formed and supported (Larone 2002). Species in the *Geomyces* have conidiophores that tend to appear clear, translucent, or glassy (Rice and Currah 2005; see figure 1).

Despite the small number of described species, *Geomyces* fungi have a global distribution, and the known species in the genus are especially common in the soils of temperate and high-latitude ecosystems (Kirk et al. 2008), but they may also be widespread in marine environments. Species in this genus tend to be *keratinophilic* (keratin loving) and *psychrophilic* (cold loving); they can be salt tolerant, and they are known to take advantage of cellulose as a food resource. The *Geomyces* fungi occur in diverse ecosystems and are often the most common fungal group found in cold environments. Members of this genus are found from wheat field soils in Germany (Domsch et al. 2007) and Arctic permafrost (Ozerskaya et al. 2009) to the soils of Antarctica (Arenz et al. 2006) and are even associated with Antarctic marine macroalgae (Loque et al. 2010) and deep-sea ecosystems (Burgaud et al. 2009, Connell et al. 2009).

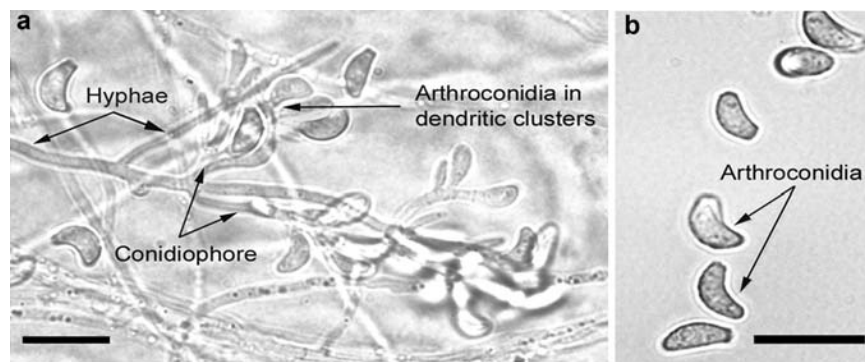


Figure 1. Micrographs showing hyphae, conidiophores, and arthroconidia of *Geomyces destructans*. (a) Hyphae, conidiophores, and arthroconidia in dendritic clusters. (b) Individual arthroconidia. The scale bars each represent 10 micrometers. Modified with permission from Gargas and colleagues' (2009) figure 3.

The *Geomyces* species most commonly identified using culture and DNA sequencing is *Geomyces pannorum* (Kirk et al. 2008). This species is associated with diverse substrates, from the debris at a reclaimed coal mine in Alberta, Canada (Chieffo 1983), to frozen forest leaf litter (Carreiro and Koske 1992). *Geomyces pannorum* is also one of the fungal species commonly found in the Lascaux caves in France, where this species is associated with the carbon compounds available in the pigments used in the 15,000-year-old paintings in these caves (Bastian et al. 2009).

The *Geomyces* fungi are common in cold environments that strike humans as extremely inhospitable. In Kashmir, India, *G. pannorum* commonly occurs in glacier bank soils at over 3000 meters (m) in elevation, in areas that have never experienced July temperatures in excess of 10 degrees Celsius ($^{\circ}\text{C}$; Deshmukh 2002). Ozerskaya and colleagues (2009) reviewed the fungi associated with permafrost and concluded that species with significant adaptive potential, such as *Geomyces*, occur frequently in permafrost. Members of the *Geomyces* were the most common species identified during surveys of the soil fungi at different sites in Antarctica (Mercantini et al. 1989, Arenz and Blanchette 2011), and *G. pannorum* was isolated from dust samples collected from the work, recreation, and living quarters of an Antarctic research expedition's base camp (Mercantini et al. 1993). *Geomyces* species can take advantage of diverse food resources, including wood, and thriving *Geomyces* colonies are now common in the wood huts built by the Scott and Shackleton expeditions to the South Pole from 1901 to 1911 (Arenz et al. 2006, 2011, Blanchette et al. 2010, Farrell et al. 2011). Microorganisms trapped in the Fox Permafrost Tunnel in Fairbanks, Alaska, have been radiocarbon dated to between 14,000 and 30,000 years old and have a current stable temperature of approximately -3.0°C (Katayama et al. 2008). Members of the genus *Geomyces* are one of the two most common types of fungi identified in this permafrost and ice (Katayama et al. 2008). *Geomyces* species also survive in arctic cryopegs, which are water bodies that occur beneath or within large masses of

ice. Cryopegs are characterized by water that, because of its high mineral content, remains unfrozen even at temperatures significantly below the freezing point of distilled water. Cryopegs that occur along the shoreline of the East Siberian Sea have water temperatures of -9°C to -11°C and very high salinity. During a study of these water bodies, *G. pannorum* was isolated and cultured from the majority of water samples from the cryopegs, showing that this species survives and grows successfully under low-temperature and high-salt conditions (Kochkina et al. 2007). *Geomyces pannorum* is capable of tolerating and growing in salinities three times those of seawater (Poole and Price 1971).

Geomyces fungi living in low-nutrient polar environments survive in the soil as dormant propagules that grow and reproduce when new organic matter is introduced into the ecosystem (Bergero et al. 1999). Remarkably, *G. pannorum* is capable of growing and producing reproductive structures at 0°C on silica gels that have no added organic compounds (Bergero et al. 1999). *Geomyces pannorum* is capable of hydrolyzing starch and produces extracellular lipase, chitinase, and urease, which allows this species to consume and metabolize diverse food sources in cold, low-nutrient environments (Fenice et al. 1997). *Geomyces pannorum* can also change fatty acid profiles and metabolic pathways in response to low ambient temperatures (Finotti et al. 1993, 1996). Fungi found in permafrost and polar conditions must also be capable of surviving and reproducing in environments with very low levels of biologically available water (Bergero et al. 1999, Ozerskaya et al. 2009). Despite being surrounded by abundant ice or permafrost, these fungi are exposed to water resources that are often not available for cellular metabolism when water is frozen. Species of the genus *Geomyces* have physiological adaptations that allow them to live productively in very cold temperatures when liquid water is scarce, and low ambient temperatures trigger physiological changes that promote survival, growth, and reproduction. When exposed to low temperatures, *G. pannorum* elevates the levels of unsaturated fats and other chemicals that have cryoprotectant properties and thus promote continued cell and membrane function (Finotti et al. 1996, Ozerskaya et al. 2009). These fungi also synthesize glycerol to help maintain cellular water balance in cold conditions (Ozerskaya et al. 2009).

Dispersal

The *Geomyces* fungi are known to be dispersed by air, water, bird feathers, animal hair, arthropods, and humans and their equipment. *Geomyces* was one of the most common taxa isolated from a variety of animal-based materials commonly observed in the Antarctic, including penguin, skua, and petrel dung and feathers (Frate and Caretta 1990). During a survey of the microfungi of the Windmill Islands region of Antarctica, *Geomyces* fungi were found in soils that had significant penguin and seal activity but also at sites with little or no bird or mammal activity (Azmi and Seppelt 1998). There appears to be an increase in fungal diversity at sites with significant human disturbance, and human visitors to Antarctica may introduce foreign and invasive fungal species (Azmi and Seppelt 1998). During biological sampling on Signey Island, a small sub-Antarctic island in the South Orkney Islands, air-borne sampling devices were positioned to collect animal material and fungal propagules carried by the prevailing westerly winds (Marshall 1998). During this research, bird feather fragments, seal hair, and viable *G. pannorum* propagules were the most commonly collected biological materials. Birds and the wind may transport fungal propagules between locations in the Antarctic region and nearby landmasses and continents (Marshall 1998).

Geomyces propagules can also be carried on the hair of mammals. In the Tver Oblast region of Russia, *G. pannorum* is commonly found in soils and on the fur of burrowing mammals, such as shrews and voles, and may be more commonly found on mammal fur than in soil (Shchipanov et al. 2003). Speculating about how various soil fungi colonized the Lascaux caves in France, Bastian and colleagues (2009) proposed that spores and fragments of hyphae may have been brought into the cave through groundwater seepage and may be associated with arthropods that use the cave for part of their life cycle. In one study, *G. pannorum* was found on species in nine arthropod orders, suggesting that flying arthropods could be an important mode of dispersal for *Geomyces* (Greif and Currah 2007).

Geomyces in marine environments and the atmosphere

Marine fungi can be found associated with most marine animals, from sponges to vertebrates (Loque et al. 2010). Although there is abundant information on the fungi associated with terrestrial ecosystems, there is little information on fungi in marine ecosystems and, until recently, no data on fungi–algae associations in the Antarctic (Loque et al. 2010). In a study of the fungi associated with Antarctic macroalgae species, the most common fungi isolated were identified as *G. pannorum*, which suggests that this *Geomyces* species may have an important decomposition and nutrient-cycling role in cold marine ecosystems (Loque et al. 2010). One of the macroalgae sampled was *Adenocystis utricularis*, which occurs along rocky shorelines. *A. utricularis* accumulates relatively large amounts of water in its bladders, which acts as ballast. The fungal species associated with *A. utricularis* were found in the water associated with these bladders. Loque and colleagues (2010) speculated that the water in the bladders may provide a relatively undisturbed habitat for microfungi species to survive. Interestingly, the fungal isolates found in this study are very similar to those isolated from the grass clothing of the Tyrolean Iceman, the 5300-year-old mummy found in 1991 at an elevation of 3210 m in the Central Eastern Alps (Rollo et al. 1995, Loque et al. 2010). This suggests that these same fungal species have inhabited cold regions and that they have been dispersed by humans since at least the Neolithic Period.

Geomyces fungi have also been found in deep-sea environments. In a study of microfungi from cold deep-sea hydrothermal vents, viable *G. pannorum* were identified (Burgaud et al. 2009). Burgaud and colleagues (2009) hypothesized that deep-sea fungi, including *Geomyces* species, may have been introduced into cold deep-sea environments as a result of exchanges with polar and coastal areas and that these fungi might be distributed throughout marine environments by oceanic currents. *Geomyces* has also been found associated with the deep-sea environment around an active volcano on the Vailulu'u seamount near Samoa, which is 1000 m deep and has water temperatures of approximately 80°C (Connell et al. 2009).

Large quantities of microorganisms are known to be transported by aerosol particles, dust, flying animals, and machines into the atmosphere and are commonly found in clouds (Margesin and Miteva 2011). It has recently been estimated that the mass of bacteria annually transported into the atmosphere by air currents and wind may be as high as 1.8×10^9 kilograms annually; viable microbial cells may spend days or weeks in the atmosphere before being deposited into other terrestrial or aquatic ecosystems by air movement or precipitation (Burrows et al. 2009). Given the global distribution of the *Geomyces* fungi and the amount of microbial material in the atmosphere, it would be plausible to hypothesize that *Geomyces* propagules regularly occur and may be transported among landmasses and continents through the atmosphere and in clouds.

Conclusions

Geomyces fungi are capable of withstanding and thriving in cold, low-nutrient environments. Members of the genus are capable of modifying their metabolism in response to challenging abiotic conditions, including very cold temperatures and low levels of biologically available water. *Geomyces* propagules are dispersed by air currents and wind, by groundwater seepage into caves and soils, on arthropods, on the feathers of birds, on the fur of mammals, and perhaps in clouds and in the atmosphere. Given that the bat species affected by WNS are all insectivorous, flying arthropods may play a key role in the dispersal of *G. destructans*. *Geomyces* propagules are also carried by humans and their clothing and equipment, and *Geomyces* can be more abundant in areas disturbed by humans. It has recently been shown that *Geomyces* fungi may be common in polar and temperate marine environments, including those associated with tropical deep-sea systems. Furthermore, current evidence suggests that the viable propagules of these fungi may be transported long distances by air and ocean currents. Biologists, managers, and others charged with controlling the spread of WNS and the causal agent *G. destructans* into other parts of North America and to other locations in the biosphere will be challenged by a fungal species with broad adaptive potential, capable of surviving and thriving in diverse terrestrial and perhaps even aquatic and marine environments.

Acknowledgments

Robert J. Reinsvold encouraged the development of this review and helped shape its content. Paul M. Cryan, David S. Blehert, Lea R. Bonewell, and Pauline Nol made thoughtful comments during various phases of this project. Three anonymous reviewers provided feedback that improved the content of the manuscript.

References cited

Arenz BE, Blanchette RA. 2011. Distribution and abundance of soil fungi in Antarctica at sites on the Peninsula, Ross Sea Region and McMurdo Dry Valleys. *Soil Biology and Biochemistry* 43: 308–315.

- Arenz BE, Held BW, Jurgens JA, Farrell RL, Blanchette RA. 2006. Fungal diversity in soils and historic wood from the Ross Sea Region of Antarctica. *Soil Biology and Biochemistry* 38: 3057–3064.
- Arenz BE, Held BW, Jurgens JA, Blanchette RA. 2011. Fungal colonization of exotic substrates in Antarctica. *Fungal Diversity* 49: 13–22.
- Azmi OR, Seppelt RD. 1998. The broad-scale distribution of microfungi in the Windmill Islands region, continental Antarctica. *Polar Biology* 19: 92–100.
- Bastian F, Alabouvette C, Saiz-Jimenez C. 2009. The impacts of arthropods on fungal community structure in Lascaux Cave. *Journal of Applied Microbiology* 106: 1456–1462.
- Bergero R, Girlanda M, Varese GC, Intili D, Luppi AM. 1999. Psychrooligotrophic fungi from Arctic soils of Franz Joseph Land. *Polar Biology* 21: 361–368.
- Blanchette RA, Held BW, Arenz BE, Jurgens JA, Baltes NJ, Duncan SM, Farrell RL. 2010. An Antarctic hot spot for fungi at Shackleton's historic hut on Cape Royds. *Microbial Ecology* 60: 29–38.
- Blehert DS, et al. 2009. Bat white-nose syndrome: An emerging fungal pathogen? *Science* 323: 227.
- Blehert DS, Lorch JM, Ballman AE, Cryan PM, Meteyer CU. 2011. Bat white-nose syndrome in North America. *Microbe* 6: 267–273.
- Bridge P, Spooner B. 2001. Soil fungi: Diversity and detection. *Plant and Soil* 232: 147–154.
- Burgaud G, Le Calvez T, Arzur D, Vandenkoornhuysse P, Barbier G. 2009. Diversity of culturable marine filamentous fungi from deep-sea hydrothermal vents. *Environmental Microbiology* 11: 1588–1600.
- Burrows SM, Butler T, Jöckel P, Tost H, Kerkweg A, Pöschl U, Lawrence MG. 2009. Bacteria in the global atmosphere—Part 2: Modeling emissions and transport between different ecosystems. *Atmospheric Chemistry and Physics* 9: 9281–9297.
- Carreiro MM, Koske RE. 1992. Effect of temperature on decomposition and development of microfungal communities in leaf litter microcosms. *Canadian Journal of Botany* 70: 2177–2183.
- Castle KT, Cryan PM. 2010. White-nose syndrome in bats: A primer for resource managers. *Park Science* 27: 20–25.
- Chieffo D. 1983. The influence of various environments and nutritional factors on the growth and survival of *Geomyces pannorum* in a reclaimed coal mine spoil. Master's thesis. University of Calgary, Canada.
- Connell LB, Barrett A, Templeton AS, Staudigel H. 2009. Fungal diversity associated with an active deep sea volcano: Vailulu'u Seamount, Samoa. *Geomicrobiology Journal* 26: 597–605.
- Cryan PM, Meteyer CU, Boyles JG, Blehert DS. 2010. Wing pathology of white-nose syndrome in bats suggests life-threatening disruption of physiology. *BMC Biology* 8 (art. 135). (26 June 2012; www.biomedcentral.com/1741-7007/8/135)
- Currah RS. 1985. Taxonomy of the *Onygenales*: *Arthrodermataceae*, *Gymnoasaceae*, *Myxotrichaceae* and *Onygenaceae*. *Mycotaxon* 24: 1–216.
- Deshmukh SK. 2002. Incidence of dermatophytes and other keratinophilic fungi in the glacier bank soils of the Kashmir valley, India. *Mycologist* 16: 165–167.
- Domsch KH, Gams W, Anderson T-H. 2007. *Compendium of Soil Fungi*, 2nd ed. Academic Press.
- Farrell RL, Arenz BE, Dunsan SM, Held BW, Jurgens JA, Blanchette RA. 2011. Introduced and indigenous fungi of the Ross Island historic huts and pristine areas of Antarctica. *Polar Biology* 34: 1669–1677.
- Fenice M, Selbmann L, Zucconi L, Onofri S. 1997. Production of extracellular enzymes by Antarctic fungal strains. *Polar Biology* 17: 275–280.
- Finotti E, Moretto D, Marsella R, Mercantini R. 1993. Temperature effects and fatty acid patterns in *Geomyces* species isolated from Antarctic soil. *Polar Biology* 13: 127–130.
- Finotti E, Paolino C, Lancia B, Merchantini R. 1996. Metabolic differences between two Antarctic strains of *Geomyces pannorum*. *Current Microbiology* 32: 7–10.
- Frate G, Caretta G. 1990. Fungi isolated from Antarctic material. *Polar Biology* 11: 1–7.

- Frick WF, Pollock JF, Hicks AC, Langwig KE, Reynolds DS, Turner GG, Butchkoski CM, Kunz TH. 2010. An emerging disease causes regional population collapse of a common North America bat species. *Science* 329: 679–682.
- Gargas A, Trest MT, Christensen M, Volk TJ, Blehert DS. 2009. *Geomyces destructans* sp. nov. associated with bat white-nose syndrome. *Mycotaxon* 108: 147–154.
- Greif MD, Currah RS. 2007. Patterns in the occurrence of saprophytic fungi carried by arthropods caught in traps baited with rotted wood and dung. *Mycologia* 99: 7–19.
- Hawksworth DL. 1991. The fungal dimension of biodiversity: Magnitude, significance and conservation. *Mycological Research* 95: 641–655.
- Katayama T, Tanaka M, Douglas TA, Cai Y, Tomita F, Asano K, Fukuda M. 2008. Microorganisms trapped within permafrost ice in the Fox Permafrost Tunnel, Alaska. Paper presented at the 2008 American Geophysical Union Fall Meeting; 15–19 December 2008, San Francisco, California.
- Kendrick B. 2000. *The Fifth Kingdom*, 3rd ed. Focus.
- Kirk PM, Cannon PF, Minter DW, Stalpers JA, eds. 2008. *Dictionary of the Fungi*. CAB International.
- Kochkina GA, Ivanushkina NE, Akimov VN, Gilichinskij DA, Ozerskaya SM. 2007. Halo- and psychrotolerant *Geomyces* fungi from Arctic cryopegs and marine deposits. *Mikrobiologia* 76: 31–38.
- Larone DH. 2002. *Medically Important Fungi: A Guide to Identification*, 4th ed. American Society of Mycology Press.
- Loque CP, Medeiros AO, Pellizzari FM, Oliveira EC, Rosa CA, Rosa LH. 2010. Fungal community associated with marine macroalgae from Antarctica. *Polar Biology* 33: 641–648.
- Lorch JM, et al. 2011. Experimental infection of bats with *Geomyces destructans* causes white-nose syndrome. *Nature* 480: 376–378.
- Margesin R, Miteva V. 2011. Diversity and ecology of psychrophilic microorganisms. *Research in Microbiology* 162: 346–361.
- Marshall WA. 1998. Aerial transport of keratinaceous substrate and distribution of the fungus *Geomyces pannorum* in Antarctic soils. *Microbial Ecology* 36: 212–219.
- Martínková N, et al. 2010. Increasing incidence of *Geomyces destructans* fungus in bats from the Czech Republic and Slovakia. *PLoS ONE* 5 (art. e13853).
- Mercantini R, Marsella R, Cervellati MC. 1989. Keratinophilic fungi isolated from Antarctic soil. *Mycopathologia* 106: 47–52.
- Mercantini R, Marsella R, Moretto D, Finotti E. 1993. Keratinophilic fungi in the Antarctic environment. *Mycopathologia* 122: 169–175.
- Meteyer CU, Buckles EL, Blehert DS, Hicks AC, Green DE, Shearn-Bochler V, Thomas NJ, Gargas A, Behr MJ. 2009. Histopathologic criteria to confirm white-nose syndrome in bats. *Journal of Veterinary Investigation* 21: 411–414.
- Ozerskaya S, Kochkina G, Ivanushkina N, Gilichinsky DA. 2009. Fungi in permafrost. Pages 85–95 in Margesin R, ed. *Permafrost Soils*. Soil Biology, vol. 16. Springer.
- Pikula J, Bandouchova H, Novotný L, Meteyer CU, Zukal J, Irwin NR, Zima J, Martínková N. 2012. Histopathology confirms white-nose syndrome in bats in Europe. *Journal of Wildlife Diseases* 48: 207–211.
- Poole NJ, Price PC. 1971. The occurrence of *Chrysosporium pannorum* in soils receiving incremental cellulose. *Soil Biology and Biochemistry* 3: 161–166.
- Puechmaile SJ, et al. 2011a. Pan-European distribution of white-nose syndrome fungus (*Geomyces destructans*) not associated with mass mortality. *PLoS ONE* 6 (art. e19167).
- Puechmaile SJ, Frick WF, Kunz TH, Racey PA, Voight CC, Wibbelt G, Teeling EC. 2011b. White-nose syndrome: Is this emerging disease a threat to European bats? *Trends in Ecology and Evolution* 26: 570–576.
- Rice AV, Currah RS. 2005. *Oidiiodendron*: A survey of the named species and related anamorphs of *Myxotrichum*. *Studies in Mycology* 53: 83–120.
- Rollo F, Sassaroli S, Ubaldi M. 1995. Molecular phylogeny of the fungi of the iceman's grass clothing. *Current Genetics* 28: 289–297.
- Shchipanov NA, Aleksandrov DY, Aleksandrova AV. 2003. Small mammals disperse micromycete spores. *Doklady Biological Sciences* 390: 225–230.
- Sigler L, Carmichael JW. 1976. Taxonomy of *Malbrachea* and some other hyphomycetes with anthroconidia. *Mycotaxon* 4: 349–488.
- Sigler L, Lumley TC, Currah RS. 2000. New species and records of saprophytic ascomycetes (*Myxotrichaceae*) from decaying logs in the boreal forest. *Mycoscience* 41: 495–502.
- Šimonovičová A, Pangallo D, Chovanová K, Lehotská B. 2011. *Geomyces destructans* associated with bat disease WNS detected in Slovakia. *Biologia* 66: 562–564.
- [USFWS] US Fish and Wildlife Service. 2012. North American bat death toll exceeds 5.5 million from white-nose syndrome. USFWS. (26 April 2012; www.fws.gov/whitenosesyndrome/pdf/wms_mortality_2012_nr_final.pdf)
- Warnecke L, Turner JM, Bollinger TK, Lorch JM, Misra V, Cryan PM, Wibbelt G, Blehert DS, Willis CKR. 2012. Inoculation of bats with European *Geomyces destructans* supports the novel pathogen hypothesis for the origin of white-nose syndrome. *Proceedings of the National Academy of Sciences* 109: 6999–7003.
- Wibbelt G, et al. 2010. White-nose syndrome fungus (*Geomyces destructans*) in bats, Europe. *Emerging Infectious Diseases* 16: 1237–1242.

Mark A. Hayes (mark.hayes@state.co.us) wrote this overview while affiliated with the School of Biological Sciences at University of Northern Colorado, in Greeley. He is currently affiliated with Colorado Parks and Wildlife in Denver, Colorado. He studies the ecology of bats and their roost environments.