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White-Nose Syndrome Fungus in a 1918 Bat Specimen from France

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White-nose syndrome, first diagnosed in North America in 2006, causes mass deaths among bats in North America. We found the causative fungus, *Pseudogymnoascus destructans*, in a 1918 sample collected in Europe, where bats have now adapted to the fungus. These results are consistent with a Eurasian origin of the pathogen.

We report the earliest known historical incidence of the fungus *Pseudogymnoascus* (formerly *Geomyces*) *destructans*, detected in a museum specimen of a bat (*Myotis bechsteinii*) collected in France in 1918. This fungal pathogen causes white-nose syndrome (WNS) in bats (*1*). Since its introduction into eastern North America around 2006, WNS has devastated bat populations across the continent (*2*). *P. destructans* has also been found across the Eurasian landmass (*3,4*) without documented mass bat deaths. Epidemiologic evidence among bats and fungal genetics indicate that the fungus has been recently introduced into North American bat populations (*5*–*7*).

To clarify the epidemiologic history of WNS and to investigate physical evidence of its presence in specific locations in the past, we screened 138 19th- and 20th-century bat specimens (housed at the National Museum of Natural History [USNM], Washington, DC) from North America (n = 41), Europe (n = 83), and East Asia (n = 14) for *P. destructans* DNA (online Technical Appendix, https://wwwnc.cdc.gov/EID/article/23/9/17-0875-Techapp1.pdf). We sampled dry museum skins and intact bodies stored in 70% ethanol; some were originally fixed in formalin. We swabbed bat rostra and wings to collect potentially preserved *P. destructans* biomolecules and stored swabs in 100% ethanol until DNA extraction.

We extracted DNA in a dedicated ancient DNA laboratory at the National Zoological Park (Washington, DC) by using stringent protocols to prevent false positive results from modern DNA contamination (*8*). Before extraction, we removed swabs from the ethanol and let them air dry. We then let swabs digest overnight at 55°C in 600 μL extraction buffer (1× Tris-EDTA buffer, pH 8.0, 0.019 mmol/L EDTA, 0.01 mmol/L NaCl, 1% SDS, 10 mg/mL DTT, and 1 mg/mL proteinase K) (*8*). Later extractions omitted DTT. We extracted digested samples twice in 600 μL phenol and once in 600 μL chloroform. We removed and concentrated the aqueous phase by using Amicon Ultra-4 30 kDA molecular weight cutoff columns (Millipore Sigma, Merck, Billerica, MA, USA) to a final volume of ≈250 μL. We included 1 extraction blank for every 10–11 historical samples.

We screened extracts for *P. destructans* by using a previously described species-specific quantitative PCR targeting 103 bp (including primers) of the intergenic spacer region (*9*). Each extract was amplified in 2–8 replicate PCRs. Multiple, no-template controls (*2*,*3*) were included in each PCR setup. Positive products from experiments in which quantifiable contamination (>0.1 genome equivalents/μL sample) was observed in ≥1 negative control were discarded; these experiments were repeated with fresh reagents.

One sample (USNM 231170) tested positive in 2 of 3 PCRs. We performed a second independent extraction on this sample. The replicate extraction tested positive in 4 of 5 PCRs. Two of the USNM 231170–positive PCR products were confirmed by using Sanger sequencing and comparison to publicly available *P. destructans* sequences in GenBank. These sequences were 100% identical to *P. destructans* sequences from North America (GenBank accession nos. JX270192.1

and JX415267.1). In addition, 2 samples (USNM 15513 and 154222) yielded positive products in a single PCR each, but we were unable to replicate these results. No usable sequence was obtained from the USNM 15513 amplicon; the USNM 154222 sequence differed from the North American sequence by a single thymine deletion. DNA sequences were deposited in GenBank (accession nos. MF370925–6).

The 1 confirmed case of *P. destructans* infection among the museum samples we studied (USNM 231170, male, skin and skull) was in a Bechstein's bat (*Myotis bechsteinii*) collected on May 9, 1918, at Forêt de Russy, Centre-Val de Loire, France. This sequence is unlikely to represent *P. destructans* from a recently collected infected bat from North America because recently collected specimens have been purposefully stored with care in a separate room within the USNM mammal department, away from the historical bat collection. Furthermore, none of the historical samples of bats collected in North America, which are more likely to be cross-contaminated with potentially infected specimens compared with European specimens, tested positive for *P. destructans.*

We provide evidence of the presence of *P. destructans* ≈100 years ago in Europe. In addition, we found no evidence of *P. destructans* in bats collected in eastern North America during 1861–1971. Although false negatives are highly likely because of the age, preparation, and storage of these specimens, these results are consistent with a Eurasian origin of the current WNS epidemic and strong association of the fungus with Eurasian bats of the genus *Myotis* (*3,6,10*). Bats across Eurasia have adapted to *P. destructans* over more than a century, but the fungus was initially detected in North America during the early 21st century, and the bats on this continent have no immunity. This result extends the documented temporal occurrence of *P. destructans* as a bat-associated fungus to the early 20th century and highlights the value of archived museum specimens for epidemiologic study of emerging fungal diseases, including WNS.

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Dr. Campana is a computational genomics scientist at the Smithsonian Institution Conservation Biology Institute's Centers for Conservation Genomics. His research interests include analysis of animal and pathogen population genomics by using a combination of ancient DNA and computational genomics.

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White-Nose Syndrome Fungus in a 1918 Bat Specimen from France

Technical Appendix

Technical Appendix Table. Bat specimens screened for *Pseudogymnoascus destructans*

USNM no.	Species	Region	Collection location	Collection date	Preparation
11189	*Myotis brandtii*	East Asia	Petropavlovsk-Kamchatsky, Kamchatka Krai, Russia	Pre-1900	Fluid
155523	*Myotis brandtii*	East Asia	Petropavlovsk-Kamchatsky, Kamchatka Krai, Russia	1889 Jul	Fluid
240190	*Myotis chinensis*	East Asia	Changsha, Hunan, China	1923 Jul 26	Skin
240191	*Myotis chinensis*	East Asia	Changsha, Hunan, China	1923 Jul 26	Skin
240215	*Myotis chinensis*	East Asia	Changsha, Hunan, China	1923 Jul 26	Fluid
240216	*Myotis chinensis*	East Asia	Changsha, Hunan, China	1923 Jul 26	Fluid
240217	*Myotis chinensis*	East Asia	Changsha, Hunan, China	1923 Jul 26	Fluid
253368	*Myotis daubentonii*	East Asia	Sichuan, China	1920s	Fluid
279358	*Myotis altarium*	East Asia	Guìyáng, Guizhou, China	1945 Aug 26	Skin
279359	*Myotis altarium*	East Asia	Guìyáng, Guizhou, China	1945 Aug 26	Skin
279360	*Myotis altarium*	East Asia	Guìyáng, Guizhou, China	1945 Sep 1	Skin
279361	*Myotis altarium*	East Asia	Guìyáng, Guizhou, China	1945 Sep 1	Skin
356343	*Myotis brandtii*	East Asia	Seoul, South Korea	1952 Aug 11	Fluid
302908	*Myotis daubentonii*	East Asia	Daegu, Yeongnam, South Korea	1955 Jun 15	Fluid
5569	*Myotis mystacinus*	Europe	Bavaria, Germany	Pre-1862	Skin
5570	*Myotis mystacinus*	Europe	Bavaria, Germany	Pre-1862	Skin
12335	*Myotis daubentonii*	Europe	Gotthard, Ticino, Switzerland	Pre-1900	Skin
13516	*Myotis mystacinus*	Europe	Dresden, Saxony, Germany	1873 Jun 10	Skin
14535	*Rhinolophus euryale*	Europe	Saint-Paterne, Pays-de-la-Loire, France	Pre-1884	Fluid
15512	*Myotis mystacinus*	Europe	Skåne County, Götaland, Sweden	1883 Mar	Fluid
15603	*Rhinolophus ferrumequinum*	Europe	France	Pre-1900	Skin
15604	*Rhinolophus hipposideros*	Europe	France	Pre-1900	Skin
15605	*Myotis nattereri*	Europe	France	Pre-1900	Skin
15606	*Myotis mystacinus*	Europe	France	Pre-1900	Skin
15607	*Plecotus auritus*	Europe	France	Pre-1900	Skin
18523	*Myotis capaccinii*	Europe	Marseilles, Provence-Alpes-Côte D'Azur, France	Pre-1900	Fluid
18528	*Myotis mystacinus*	Europe	South Tyrol, Italy	Pre-1900	Fluid
85182	*Myotis daubentonii*	Europe	Uppsala, Uppsala, Sweden	1898 Aug	Fluid
85519	*Myotis mystacinus*	Europe	Belgium	Pre-1900	Skin
86574	*Myotis daubentonii*	Europe	Lecco, Lombardy, Italy	1898 Feb	Fluid
86926	*Eptesicus serotinus*	Europe	Barsac, Aquitaine-Limousin-Poitou-Charentes, France	1897 Mar 28	Fluid
101326	*Myotis myotis*	Europe	Cadillac, Aquitaine-Limousin-Poitou-Charentes, France	1899 Jun	Skin
102468	*Rhinolophus hipposideros*	Europe	Marseilles, Provence-Alpes-Côte D'Azur, France	1900 Jun	Fluid
102469	*Rhinolophus ferrumequinum*	Europe	Marseilles, Provence-Alpes-Côte D'Azur, France	Received 1900 Jun	Fluid
102470	*Myotis myotis*	Europe	Marseilles, Provence-Alpes-Côte D'Azur, France	Received 1900 Jun	Fluid
102500	*Pipistrellus pipistrellus*	Europe	Marseilles, Provence-Alpes-Côte D'Azur, France	Received 1900 Jun	Fluid
102501	*Pipistrellus kuhlii*	Europe	Marseilles, Provence-Alpes-Côte D'Azur, France	Received 1900 Jun	Fluid
102502	*Miniopterus schreibersii*	Europe	Marseilles, Provence-Alpes-Côte D'Azur, France	Received 1900 Jun	Fluid
102503	*Plecotus auritus*	Europe	Marseilles, Provence-Alpes-Côte D'Azur, France	Received 1900 Jun	Fluid

USNM no.	Species	Region	Collection location	Collection date	Preparation
113855	*Myotis myotis*	Europe	Tagerwilen, Thurgau, Switzerland	1900 Jun 9	Fluid
113858	*Myotis myotis*	Europe	Tagerwilen, Thurgau, Switzerland	1900 Jun 9	Fluid
113861	*Myotis myotis*	Europe	Tagerwilen, Thurgau, Switzerland	1900 Jun 9	Fluid
113866	*Myotis nattereri*	Europe	Thurgau, Switzerland	1900 Jun 9	Fluid
113868	*Myotis nattereri*	Europe	Thurgau, Switzerland	1900 Jun 9	Fluid
120994	*Myotis myotis*	Europe	Lipová, Ústi nad Labem, Czech Republic	1902 Sep 24	Skin
120995	*Myotis myotis*	Europe	Lipová, Ústi nad Labem, Czech Republic	1902 Sep 24	Skin
120998	*Myotis nattereri*	Europe	Moritzburg, Saxony, Germany	1902 Nov 5	Skin
120999	*Myotis nattereri*	Europe	Moritzburg, Saxony, Germany	1902 Nov 5	Skin
121000	*Myotis nattereri*	Europe	Moritzburg, Saxony, Germany	1902 Nov 5	Skin
121191	*Myotis myotis*	Europe	Andermatt, Uri, Switzerland	1902 Aug 20	Skin
152524	*Rhinolophus ferrumequinum*	Europe	Dions, Languedoc-Rousillon-Midi-Pyrénées, France	1907 Oct 10	Skin
152525	*Rhinolophus ferrumequinum*	Europe	Troubate, Pyrenees, France	1900 Jan 14	Skin
152526	*Rhinolophus ferrumequinum*	Europe	Troubate, Pyrenees, France	900 Jan 20	Skin
152528	*Rhinolophus hipposideros*	Europe	Dions, Languedoc-Rousillon-Midi-Pyrénées, France	1907 Oct 11	Skin
152529	*Rhinolophus hipposideros*	Europe	Dions, Languedoc-Rousillon-Midi-Pyrénées, France	1907 Oct 11	Skin
152533	*Rhinolophus euryale*	Europe	Grotte de Meounes, Provence-Alpes-Côte D'Azur, France	1908 Jan	Fluid
152534	*Rhinolophus euryale*	Europe	Grotte de Meounes, Provence-Alpes-Côte D'Azur, France	1908 Jan	Fluid
152535	*Rhinolophus euryale*	Europe	Grotte de Meounes, Provence-Alpes-Côte D'Azur, France	1908 Jan	Fluid
152539	*Myotis daubentonii*	Europe	Uppsala, Uppsala, Sweden	1895 May 21	Skin
152556	*Pipistrellus pipistrellus*	Europe	Santo Domingo de Silos, Castile and León, Spain	Pre-1910	Fluid
152600	*Miniopterus schreibersii*	Europe	Dions, Languedoc-Rousillon-Midi-Pyrénées, France	1907 Oct 10	Skin
152601	*Miniopterus schreibersii*	Europe	Dions, Languedoc-Rousillon-Midi-Pyrénées, France	1907 Oct 10	Skin
152602	*Miniopterus schreibersii*	Europe	Dions, Languedoc-Rousillon-Midi-Pyrénées, France	1907 Oct 10	Skin
152603	*Miniopterus schreibersii*	Europe	Dions, Languedoc-Rousillon-Midi-Pyrénées, France	1907 Oct 10	Skin
152604	*Miniopterus schreibersii*	Europe	Dions, Languedoc-Rousillon-Midi-Pyrénées, France	1907 Oct 10	Skin
152605	*Miniopterus schreibersii*	Europe	Dions, Languedoc-Rousillon-Midi-Pyrénées, France	1907 Oct 10	Skin
152606	*Miniopterus schreibersii*	Europe	Dions, Languedoc-Rousillon-Midi-Pyrénées, France	1907 Oct 10	Skin
152607	*Miniopterus schreibersii*	Europe	Dions, Languedoc-Rousillon-Midi-Pyrénées, France	1907 Oct 10	Skin
154080	*Myotis bechsteinii*	Europe	Hungary	Pre-1910	Fluid
154081	*Myotis bechsteinii*	Europe	Hungary	Pre-1910	Fluid
154221	*Rhinolophus ferrumequinum*	Europe	Nîmes, Languedoc-Rousillon-Midi-Pyrénées, France	Pre-1910	Skin
154222†	*Rhinolophus euryale*	Europe	Gard Department, Languedoc-Rousillon-Midi-Pyrénées, France	Pre-1910	Skin
172121	*Rhinolophus hipposideros*	Europe	Ax-les-Thermes, Languedoc-Rousillon-Midi-Pyrénées, France	1906 Aug 18	Skin
172127	*Myotis oxygnathus*	Europe	Near Burgos, Castile and León, Spain	1906 Oct 3	Skin
172128	*Pipistrellus kuhlii*	Europe	Saint-Gilles, Languedoc-Rousillon-Midi-Pyrénées, France	1908 May	Skin
172304	*Rhinolophus hipposideros*	Europe	Ax-les-Thermes, Languedoc-Rousillon-Midi-Pyrénées, France	1906 Oct 18	Fluid
187431	*Myotis daubentonii*	Europe	Christchurch, Isle of Wight, UK	Pre-1910	Fluid
231169	*Myotis bechsteinii*	Europe	Forêt de Russy, Centre-Val de Loire, France	1918 May 3	Skin
231170*	*Myotis bechsteinii*	Europe	Forêt de Russy, Centre-Val de Loire, France	1918 May 9	Skin
231171	*Myotis bechsteinii*	Europe	Forêt de Russy, Centre-Val de Loire, France	1918 May 9	Skin
260651	*Pipistrellus pipistrellus*	Europe	Madrid, Madrid, Spain	1934 Mar 31	Skin
260656	*Myotis myotis*	Europe	Riofrío, Castile and León, Spain	1933 May 2	Skin
260657	*Myotis myotis*	Europe	Riofrío, Castile and León, Spain	1933 Feb 5	Skin
260659	*Myotis myotis*	Europe	Almadenejos, Castile-La Mancha, Spain	1930s	Fluid
260660	*Myotis myotis*	Europe	Almadenejos, Castile-La Mancha, Spain	1930s	Fluid

USNM no.	Species	Region	Collection location	Collection date	Preparation
260663	*Miniopterus schreibersii*	Europe	Pyrénées-Orientales, Languedoc-Rousillon-Midi-Pyrénées, France	1930s	Fluid
260664	*Miniopterus schreibersii*	Europe	Pyrénées-Orientales, Languedoc-Rousillon-Midi-Pyrénées, France	1930s	Fluid
260665	*Miniopterus schreibersii*	Europe	Pyrénées-Orientales, Languedoc-Rousillon-Midi-Pyrénées, France	1930s	Fluid
260673	*Pipistrellus pipistrellus*	Europe	Ruidera, Castilla-La Mancha, Spain	1934 Jul 11	Fluid
303346	*Plecotus austriacus*	Europe	Saint-Vaast-la-Hougue, Normandy, France	1956 Aug 21	Skin
345233	*Myotis myotis*	Europe	Augsburg, Bavaria, Germany	1957 Aug 1	Fluid
345234	*Myotis myotis*	Europe	Augsburg, Bavaria, Germany	1960 Jul 17	Fluid
345235	*Myotis daubentonii*	Europe	Bavarian Forest, Bodenwöhr, Bavaria, Germany	1959 May 9	Fluid
540784	*Myotis mystacinus*	Europe	"Izbica" Cave, Slovakia	1961 Feb 12	Skin
12337	*Myotis myotis*	Europe	Gotthard, Ticino, Switzerland	Pre-1900	Skin
15513†	*Myotis bechsteinii*	Europe	Ronnemollo, Sweden	1883 Mar 5	Fluid
85518	*Myotis mystacinus*	Europe	Belgium	Pre-1900	Skin
5334	*Myotis lucifugus*	North America	West Point, New York, USA	Pre-1861	Fluid
22228	*Myotis sodalis*	North America	Centre County, Pennsylvania, USA	1892 Feb 7	Fluid
71926	*Myotis leibii*	North America	Sing Sing, New York, USA	1884 Jun 9	Fluid
84888	*Myotis septentrionalis*	North America	Markleton, Pennsylvania, USA	1898 Aug 12	Skin
96957	*Myotis septentrionalis*	North America	Wilmington, Massachusetts, USA	1898 Oct 1	Skin
114015	*Myotis septentrionalis*	North America	Plummer's Island, Maryland, USA	1902 Jun 1	Skin
117109	*Myotis septentrionalis*	North America	Plummer's Island, Maryland, USA	1902 Mar 31	Skin
140765	*Myotis septentrionalis*	North America	Peterboro, New York, USA	1900 Sep 11	Skin
187295	*Myotis lucifugus*	North America	Howes Cave, Schoharie County, New York, USA	1884 Nov 18	Fluid
187300	*Myotis lucifugus*	North America	Howes Cave, Schoharie County, New York, USA	1884 Nov 18	Fluid
187358	*Myotis lucifugus*	North America	Keene Valley, Essex County, New York, USA	1880 Jul	Skin
187853	*Myotis leibii*	North America	Sing Sing, New York, USA	1881 Jun 29	Fluid
205961	*Myotis lucifugus*	North America	Proctor, Vermont, USA	1915 Jan 11	Skin
206577	*Myotis sodalis*	North America	Proctor, Vermont, USA	1915 Apr 2	Skin
206580	*Myotis sodalis*	North America	Proctor, Vermont, USA	1915 Apr 2	Skin
206801	*Myotis lucifugus*	North America	Proctor, Vermont, USA	1915 May 4	Skin
249133	*Myotis grisescens*	North America	Dixon Cave, Mammoth Cave National Park, Kentucky, USA	1929 Jul 6	Skin
249138	*Myotis leibii*	North America	Crystal Cave, Mammoth Cave National Park, Kentucky, USA	1929 Aug 22	Skin
249139	*Myotis leibii*	North America	Mammoth Cave National Park, Kentucky, USA	1929 Aug 22	Skin
252560	*Myotis grisescens*	North America	Marvel Cave, Stone County, Missouri, USA	1927 Sep 27	Fluid
268446	*Myotis lucifugus*	North America	Laurel Caverns, Fayette County, Pennsylvania, USA	1938 Oct	Fluid
270287	*Myotis lucifugus*	North America	Dulany's Cave, Uniontown, Pennsylvania, USA	1941 Apr 20	Skin
270288	*Myotis lucifugus*	North America	Dulany's Cave, Uniontown, Pennsylvania, USA	1941 Apr 20	Skin
270289	*Myotis lucifugus*	North America	Dulany's Cave, Uniontown, Pennsylvania, USA	1941 Apr 20	Skin
282666	*Myotis lucifugus*	North America	Pecks Lake, Pike County, Pennsylvania, USA	1947 Jul 25	Fluid
282770	*Myotis lucifugus*	North America	Deposit, New York, USA	1947 Aug 11	Skin

USNM no.	Species	Region	Collection location	Collection date	Preparation
282771	*Myotis lucifugus*	North America	Deposit, New York, USA	1947 Aug 11	Skin
282772	*Myotis lucifugus*	North America	Little Broken Straw Creek, Warren County, Pennsylvania, USA	1947 Aug 19	Fluid
288567	*Myotis lucifugus*	North America	Aeolus Cave, East Dorset, Vermont, USA	1962 Jul 15	Skin
288982	*Myotis lucifugus*	North America	Bearton Reservation, Monterey, Massachusetts, USA	1963 Jul 19	Skin
288984	*Myotis lucifugus*	North America	Bearton Reservation, Monterey, Massachusetts, USA	1963 Jul 19	Skin
288986	*Myotis lucifugus*	North America	Winchendon, Massachusetts, USA	1963 Aug 6	Skin
296704	*Myotis leibii*	North America	Near Hyndford, Renfrew County, Ontario, Canada	1942 Apr 4	Skin
296705	*Myotis leibii*	North America	Near Hyndford, Renfrew County, Ontario, Canada	1942 Apr 4	Skin
314985	*Myotis leibii*	North America	Breathing Cave, Burnsville, Virginia, USA	1960 Dec 11	Skin
349702	*Myotis lucifugus*	North America	Piscataway Park, Accokeek, Maryland, USA	1971 Aug 20	Skin
505449	*Myotis lucifugus*	North America	Rohrersville Cave #3, Locust Grove, Maryland, USA	1970 Oct 24	Skin
505455	*Myotis lucifugus*	North America	John Friends Cave, Garrett County, Maryland, USA	1971 Feb 27	Skin
526781	*Myotis septentrionalis*	North America	Wilmington, Massachusetts, USA	1899 Sep 9	Skin
32317	*Myotis sodalis*	North America	Centre County, Pennsylvania, USA	1892 Feb 11	Fluid
364632	*Myotis leibii*	North America	Tawney's Cave, Giles County, Virginia, USA	1964 Aug 17	Skin

**P. destructans*-positive specimen.
†Samples that yielded non-replicated positive PCR products.