

Worldwide spread of the pharaoh ant, *Monomorium pharaonis* (Hymenoptera: Formicidae)

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Abstract

The pharaoh ant, *Monomorium pharaonis* (LINNAEUS, 1758), has long been considered the most ubiquitous house ant in the world. *Monomorium pharaonis* is particularly notorious as a pest in hospitals, where it is known as a vector for disease. I compiled and mapped specimen records of *M. pharaonis* from > 1200 sites to document its known worldwide distribution and evaluate hypotheses concerning its geographic origin. I documented the earliest known *M. pharaonis* records for 225 geographic areas (countries, island groups, major islands, US states, Canadian provinces, and Russian federal districts), including many for which I found no previously published records: Austral Islands, Central African Republic, Delaware, Dominican Republic, Gabon, Guatemala, Hainan Island, Haiti, Iraq, Ivory Coast, Maine, Missouri, Montana, Nebraska, New Hampshire, Pakistan, Palmyra Atoll, Rhode Island, Tunisia, and West Virginia. In tropical areas, *M. pharaonis* occurs both indoors and out, but in temperate areas, it is found almost exclusively indoors. It is by far the most common tropical ant found in heated buildings of Europe and North America.

Monomorium pharaonis appears to have originated in tropical Asia, where widespread outdoor records have been reported. Also, *Monomorium longi* FOREL, 1902 and *Monomorium wroughtoni* FOREL, 1902, the two species thought to be most closely related to *M. pharaonis*, are endemic to tropical Asia. Although *M. pharaonis* was first described from Egypt, I found no evidence supporting the popular, but apparently mistaken, idea that *M. pharaonis* is native to Africa.

Numerous authors contend that *M. pharaonis* populations are rapidly expanding. My analyses, however, suggest that *M. pharaonis* had already spread over much of the world > 100 years ago. Much of the purportedly recent population increases of *M. pharaonis* may be an artifact of greater sampling and dissemination of information.

Key words: Disease vector, exotic species, hospital pest, house pest, pest ant, urban pest.

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Introduction

The pharaoh ant, *Monomorium pharaonis* (LINNAEUS, 1758), has long been considered the most ubiquitous household ant in the world. More than a century ago, VIEHMEYER (1906) wrote of *M. pharaonis*: "Coming from the East Indies, this ant has conquered almost the entire Earth. It has spread through commerce into almost all larger cities." SMITH (1979) concluded that in North America, *M. pharaonis* is "probably found in every town or city of commercial importance especially in hotels, large apartment buildings, groceries, or other places where food is commercially handled." In addition to its ubiquity, SMITH (1979) asserted that *M. pharaonis* "is the most persistent and difficult of all our house-infesting ants to control or eradicate."

BERNDT & EICHLER (1987) compiled information on numerous aspects of *M. pharaonis* biology. In the present study, I document the known worldwide distribution of *M. pharaonis* and consider hypotheses on its geographic origin.

Identification and taxonomy

Monomorium pharaonis workers vary in color, even within a colony, from uniform yellow to yellow with a dark

brown rear of the gaster (Figs. 1 - 4). Several other *Monomorium* species are also known as tramp ants, transported worldwide through human commerce, including *M. destructor* (JERDON, 1851), *M. floridana* (JERDON, 1851), *M. monomorium* BOLTON, 1987, *M. sechellense* EMERY, 1894, and *M. subopacum* (SMITH, 1858). Of these tramp species, *M. pharaonis* resembles only *M. destructor* in color, but has a much narrower range of worker size (*M. pharaonis*: 2.2 - 2.4 mm length; *M. destructor*: 1.8 - 3.5 mm length; BOLTON 1987). *Monomorium pharaonis* also can be easily distinguished from *M. destructor* because the head, alitrunk, petiole, and postpetiole of the workers are matte (not shiny) in *M. pharaonis*, but are almost entirely smooth and shiny in *M. destructor*.

Junior synonyms of *M. pharaonis* include *Formica antiguensis* FABRICIUS, 1793 (from Antigua; synonymized by ROGER 1862), *Myrmica domestica* SHUCKARD, 1838 (from England; synonymized by ROGER 1862), *Myrmica continua* SMITH, 1858 (from Sri Lanka; synonymized by MAYR 1886), *Myrmica fragilis* SMITH, 1858 (from Singapore; synonymized by MAYR 1886), and *Atta minuta* JERDON,



Figs. 1 - 4: *Monomorium pharaonis*. (1) Head of worker from Luzon, Philippines; (2) lateral view of the same worker; (3) dorsal view of the same worker; (4) worker foraging indoors on gouda cheese in Lower Austria, Austria (1 - 3 by D.M. Sorger, copyright NHMW Image Database & www.antbase.net; 4 by B.C. Schlick-Steiner & F.M. Steiner).

1851 (from India; synonymized by EMERY 1892). Finally, WROUGHTON (1892) mistakenly considered *Myrmica vastator* SMITH, 1857 (from Singapore) to be a synonym of *Myrmica basalis* SMITH, 1858 (= *M. destructor*), based on mislabeled specimens in the British Museum. DONISTHORPE (1932), however, concluded "it is clear that the type of *M. vastator* SMITH is at Oxford, and that the species is really *M. pharaonis* L."

Methods

To document the worldwide geographic distribution of *M. pharaonis*, I used both published and unpublished records. Because *M. pharaonis* has been such a widespread household pest for so long, the literature on this species is vast and diverse. For example, FORMIS Ant Bibliography (WOJCIK & PORTER 2008) listed *Monomorium pharaonis* among the key words for > 1200 publications, and the actual number of references that include *M. pharaonis* records is no

doubt several times this number. I obtained hundreds of these papers, written in a diversity of languages, but my attempts to acquire many publications were unsuccessful. Still, my compilation does give a broad picture of the tremendous worldwide spread of *M. pharaonis*.

I obtained unpublished site records from specimens in the collections of the Museum of Comparative Zoology (MCZ) and the Smithsonian Institution (SI). In addition, I used on-line databases of the Australian National Insect Collection (ANIC), the California Academy of Science (CAS), Landcare Services (New Zealand), the Essig Museum of UC Berkeley, hormigas.org (compiled by K. Gómez & X. Espadaler), the Nebraska State Insect Records (NSIR), and Fauna Europaea (RADCHENKO 2004). RADCHENKO (2004) was a particularly rich source of first records for geographic areas of Europe, but unfortunately included no collection information. I also received unpublished site records from H. Zettel (Indonesia, Philippines),

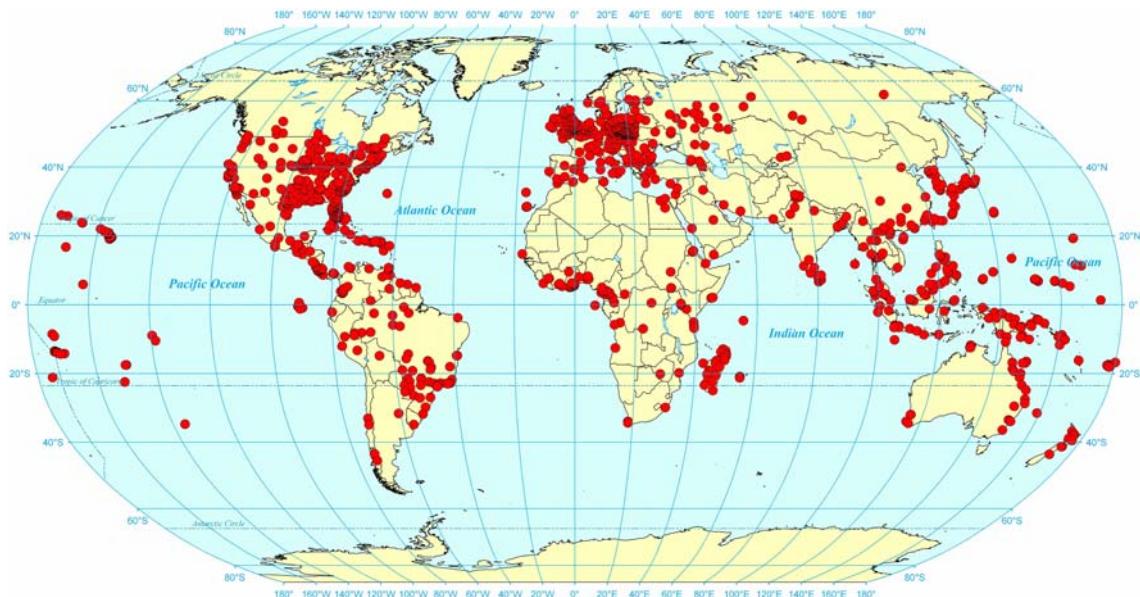


Fig. 5: Worldwide distribution records of *Monomorium pharaonis*.

R. Sullivan (Rhode Island), B.C. Schlick-Steiner & F.M. Steiner (Austria), A.M. Schmidt (Denmark, Ghana, Hungary, Ivory Coast, Japan, Norway, Panama, Poland, Switzerland, and Thailand), M.F. O'Brien (Michigan), H.L. McCreary, Jr. (Maine), M. Lush (Australia), M. Ivie (Montana), J. Huber (Ontario, Quebec), British Columbia, India, Florida), B. Guénard (Quebec), J. Glasier (Alberta), A. Francoeur (Brazil, British Columbia, Ontario, Quebec, Massachusetts), R. Fagerlund (New Mexico), G.M. Dlussky (Samoa), S. Dash (Delaware), G.A. Covert (Ohio), D.S. Chandler (New Hampshire), and H. Bharti (India). Finally, I collected *M. pharaonis* specimens at several locales in Florida, Oceania, and the West Indies. Stefan Cover confirmed identification for all specimens in the MCZ.

I obtained geographic coordinates for collection sites from published references, specimen labels, maps, or geography web sites (e.g., earth.google.com, www.tageo.com, and www.fallingrain.com). I listed records according the current national borders, e.g., a record from Rijeka (formerly Fiume; KORLEVIC 1886) is included under Croatia, though this city was in Hungary at the time of collection. Perhaps because of its perceived ubiquity, relatively few papers provide specific site records for *M. pharaonis*. If a site record listed a geographic region rather than a "point locale," and I had no other record for this region, I used the coordinates of the largest town within the region or, in the case of small islands and natural areas, the center of the region. I did not map records of *M. pharaonis* on boats or intercepted in transit by quarantine inspectors.

In several cases, I inferred the collection date from additional sources, e.g., MAYR (1862) reported *M. pharaonis* from the Novara Expedition, which visited South Africa and Australia in 1857 and 1858, respectively. A *M. pharaonis* specimen from Montenegro in Mayr's personal collection (ZIMMERMANN 1934) must predate Mayr's death in 1908.

Results

I compiled and mapped specimen records of *M. pharaonis* from > 1200 sites. I documented the earliest known *M. pharaonis* records for 225 geographic areas (countries, is-

land groups, major islands, US states, Canadian provinces, and Russian federal districts), including many for which I found no previously published records: Austral Islands, Central African Republic, Delaware, Dominican Republic, Gabon, Guatemala, Hainan Island, Haiti, Iraq, Ivory Coast, Maine, Missouri, Montana, Nebraska, New Hampshire, Pakistan, Palmyra Atoll, Rhode Island, Tunisia, and West Virginia (Tabs. 1 - 6). I included a record for "Central America" (Tab. 4) because it predated any records I found for any individual country in Central America. The range of *M. pharaonis* appears to be greater than that of any other major tramp ant (e.g., see WETTERER 2005, 2008, 2009a, b, WETTERER & al. 2009).

The highest concentration of published records came from Western and Central Europe and the Eastern US (Fig. 5). I found records of *M. pharaonis* in Europe from 54 countries, autonomous islands, and Russian federal states (Tab. 5). In summarizing the known distribution of *M. pharaonis* in Europe, BERNDT & EICHLER (1987) reported that they had *M. pharaonis* records from all except 18 European countries or autonomous islands. Here, I report *M. pharaonis* records for ten of these: Alderney, Greece, Guernsey, Ireland, Luxembourg, Netherlands, Norway, Portugal, Romania, and Turkey. I found no records for the remaining eight: Albania, Andorra, Faroe Islands, Iceland, Jersey, Liechtenstein, Monaco, and San Marino. In addition, I found no *M. pharaonis* records for Malta and Bosnia & Herzegovina. I agree with BERNDT & EICHLER (1987) that these lack of records are probably due to incomplete sampling rather than absence. I found records of *M. pharaonis* from 48 US states plus Washington D.C. (i.e., all except Alaska and Nevada) and from all seven Russian federal districts: Central, Far East, Northwestern, Siberian, Southern, Urals, and Volga.

I have rarely encountered *M. pharaonis* in my ecological studies on islands in the Pacific, Atlantic, and the West Indies. For example, I collected *M. pharaonis* only once in Hawaii, at tuna bait just outside a military base on the Big Island (WETTERER & al. 1998). In several months of collecting in Trinidad, I found *M. pharaonis* just once, on the University of West Indies campus.

Tab. 1: Earliest known records for *Monomorium pharaonis* from Asia (but see Tab. 5 for records from the Russian Federation) and neighboring islands. MCZ = Museum of Comparative Zoology.

	Earliest record
India	≤ 1851 (JERDON 1851 as <i>Atta minuta</i>)
Singapore	≤ 1857 (SMITH 1857 as <i>Myrmica vastator</i>)
Sri Lanka	≤ 1858 (SMITH 1858 as <i>Myrmica contigua</i>)
Philippines	≤ 1862 (MAYR 1862)
Indonesia	≤ 1866 (MAYR 1867)
Malaysia	1865 - 1867 (MAYR 1872)
Israel / Palestine	≤ 1880 (ANDRÉ 1881)
Russia: Urals	≤ 1884 (REUTER 1884)
Burma / Myanmar	1885 - 1887 (EMERY 1889)
PNG	≤ 1901 (FOREL 1901)
Georgia	≤ 1905 (RUZSKY 1905, in EICHLER 1974)
China	≤ 1907 (FOREL 1907)
Turkey (Asian)	1910 (FOREL 1911)
Vietnam	≤ 1920 (SANTSCHI 1920)
Iran	≤ 1927 (MENOZZI 1927)
Japan	≤ 1927 (TERANISHI 1927)
Hong Kong	≤ 1928 (WHEELER 1928)
Taiwan	≤ 1929 (WHEELER 1929)
Thailand	1930 (Alexander, MCZ): Chiang Mai
Christmas Island	1934 (DONISTHORPE 1935)
+ Hainan Island	1935 (J.L. Gressitt, MCZ): Ta Hian
+ Iraq	1950 (N.A. Weber, MCZ): Baghdad
Bangladesh	≤ 1967 (ALAM 1967, in HANNAN 2003)
North Korea	1971 (COLLINGWOOD 1976)
South Korea	≤ 1982 (KIM & KIM 1982)
Saudi Arabia	≤ 1985 (COLLINGWOOD 1985)
Lebanon	≤ 1987 (KUGLER 1988)
Russia: Far East	≤ 1987 (BERNDT & EICHLER 1987)
Kazakhstan	≤ 1987 (BERNDT & EICHLER 1987)
Armenia	≤ 1994 (ARAKELIAN 1994)
Kyrgyzstan	≤ 1996 (TARBINSKY 1996, in SCHULTZ & al. 2006)
Russia: Siberia	≤ 2005 (BLINOVA 2005)
+ Pakistan	2007 (S. & Z. Valliani, MCZ): Karachi

Tab. 2: Earliest known records for *Monomorium pharaonis* from Africa and neighboring islands. Abbreviations as in Tab. 1, and CAS = California Academy of Sciences.

	Earliest record
Egypt	≤ 1758 (LINNAEUS 1758, type locale)
South Africa	1857 (MAYR 1862)
Algeria	≤ 1862 (ROGER 1862)
Eritrea	≤ 1877 (EMERY 1877)
Sudan	≤ 1884 (MAGRETTI 1884)
Madagascar	≤ 1891 (FOREL 1891)
Tanzania	≤ 1893 (MAYR 1893)
Liberia	≤ 1895 (MAYR 1895)
Togo	≤ 1895 (MAYR 1895)
Cameroon	≤ 1896 (MAYR 1896)
Iles Eparses	≤ 1897 (FOREL 1897)
Seychelles	1905 (FOREL 1907)
Congo (Zaire)	≤ 1913 (FOREL 1913)
Senegal	≤ 1914 (SANTSCHI 1914)
São Tome	≤ 1920 (SANTSCHI 1920)
Djibouti	≤ 1922 (WHEELER 1922)
Uganda	≤ 1922 (WHEELER 1922)
Kenya	1922 (BOLTON 1987)
Somalia	1926 (MENOZZI 1930)
Ghana	1934 (G.A. Buckman, MCZ): Accra
Equatorial Guinea	1939 - 1940 (MENOZZI 1942)
+ Tunisia	≤ 1940 (F. Santschi, MCZ): Kairouan
Mozambique	≤ 1945 (BOLTON 1987)
Zimbabwe	≤ 1945 (BOLTON 1987)
Guinea	1946 (BERNARD 1952)
+ Gabon	1956 (J.A. Barra, MCZ): Plateau d'Ipassa
Nigeria	≤ 1957 (SUDD 1957)
Morocco	≤ 1962 (CAGNIANT 1962)
+ Ivory Coast	1963 (W.L. Brown, MCZ): 17 km W. of Abidjan
Canary Islands	1977 (BARQUÍN 1981)
Angola	≤ 1987 (BOLTON 1987)
Madeira	1995 (WETTERER & al. 2007)
+ CAR	2001 (B.L. Fisher, CAS): Mabéa Bai
Mascarene Islands	2001 (BLARD & al. 2003)

Tab. 3: Earliest known records for *Monomorium pharaonis* from Australia and Oceania. SI = Smithsonian Institution, TP = Te Papa Museum, UCB = University of California, Berkeley.

	Earliest record
Australia	1858 (MAYR 1862)
Samoa	≤ 1876 (MAYR 1876)
Tonga	≤ 1876 (MAYR 1876)
Hawaii	≤ 1899 (FOREL 1899)
Marshall Islands	≤ 1903 (SNEE 1903)
Society Islands	1906 - 1907 (WHEELER 1908a)
Fiji	1915 (MANN 1921)
Solomon Islands	1916 (MANN 1919)
Wake Island	1923 (TIMBERLAKE 1926)
Johnston Atoll	1923 (TIMBERLAKE 1926)
Vanuatu	1930 (BOLTON 1987)
Marquesas Islands	1931 (WHEELER 1932)
Palau	1936 (CLOUSE 2007)
Mariana Islands	1936 (CLOUSE 2007)
FS Micronesia	1937 (CLOUSE 2007)
New Zealand	1941 (collector unknown, TP): St Helens Hospital
Palmyra Atoll	1948 (N.L.H. Krauss, SI): in house
Gilbert Islands	1957 (CLOUSE 2007)
Tokelau Islands	≤ 2005 (ABBOTT & al. 2006)
+ Austral Islands	2006 (P.D. Krushelnicky, UCB): Rurutu

Tab. 4: Earliest known records for *Monomorium pharaonis* from the West Indies, South America, Central America, and surrounding islands. Abbreviations as in Tabs. 1 and 3.

	Earliest record
Antigua	≤ 1793 (FABRICIUS 1793 as <i>Formica antiguensis</i>)
Brazil	≤ 1854 (SMITH 1855 as <i>Myrmica domestica</i>)
Argentina	≤ 1859 (ROGER 1859)
Chile	1859 (MAYR 1862)
Cuba	≤ 1863 (WHEELER 1913)
French Guiana	1868 (RADOSZKOWSKY 1883)
Central America	≤ 1872 (MAYR 1872)
Mexico	≤ 1889 (VELASCO 1889)

Uruguay	≤ 1890 (BERG 1890)
Costa Rica	≤ 1890 (EMERY 1890)
Bolivia	≤ 1894 (EMERY 1894)
Trinidad	1894 (H. Caracciolo, SI): Port of Spain
Colombia	≤ 1899 (FOREL 1899)
Bahamas	1904 (WHEELER 1905)
Galapagos	1905 - 1906 (WHEELER 1919)
+ Guatemala	≤ 1908 (W.A. Kellerman, MCZ): Los Amates
Puerto Rico	1908 (WHEELER 1908b)
Guyana	1911 (WHEELER 1916)
Virgin Islands	1917 (H. Morrison, SI): St. Thomas, Magen Bay
Panama	1923 (J. Zetek, SI): Ancon
+ Haiti	1925 (G.N. Wolcott, SI): Port-au-Prince
Venezuela	1935 (N.A. Weber, MCZ): Ciudad Bolívar
Peru	1940 (W.K. Weyrauch, SI): Tingo María
Aves Island	≤ 1973 (LEVINS & al. 1973)
Paraguay	≤ 1980 (FOWLER 1980)
Nicaragua	≤ 1993 (MAES & MACKAY 1993)
Honduras	≤ 1993 (MAES & MACKAY 1993)
+ Dominican Rep.	2003 (L. Davis, MCZ): Monseñor Nouel
Ecuador	≤ 2004 (FERNÁNDEZ & SENDOYA 2004)
Suriname	≤ 2004 (FERNÁNDEZ & SENDOYA 2004)
Brazil	≤ 1854 (SMITH 1855 as <i>Myrmica domestica</i>)
Argentina	≤ 1859 (ROGER 1859)
Chile	1859 (MAYR 1862)

Although most outdoor records of *M. pharaonis* come from the tropics, there are a few temperate records from outdoors. BONDROIT (1918) reported that *M. pharaonis* occurs in open country on Corsica (~41° N). KLIMSTRA (1950) reported *M. pharaonis* in southeastern Iowa (~41° N) in a pasture > 400 m from the nearest building. KOHN & VLCEK (1984) found *M. pharaonis* living year-round in a refuse dump in the Czech Republic (~39° N), attributing this "to favourable temperature conditions created by decaying of the waste materials in the dump."

Erroneous records

In the 19th century, there was considerable confusion in North American records between *M. pharaonis* and the

Tab. 5: Earliest known records for *Monomorium pharaonis* from Europe, the Russian Federation, and surrounding islands.

	Earliest record
England	1828 (BOSTOCK 1836 & SHUCKARD 1838 as <i>Myrmica domestica</i>)
Spain	≤ 1835 (WALTL 1835, in EICHLER 1978)
Ireland (Eire)	≤ 1855 (STELFOX 1927)
France	≤ 1856 (NYLANDER 1856 as <i>Myrmica domestica</i>)
Russia: Volga	≤ 1862 (MAYR 1862)
Germany	≤ 1862 (MAYR 1862)
Denmark	≤ 1862 (ROGER 1862)
Netherlands	1877 (BOER & VIERBERGEN 2008)
Balearic Islands	≤ 1879 (EMERY & FOREL 1879)
Finland	1883 (REUTER 1884)
Romania	≤ 1884 (REUTER 1884)
Russia: Northwest- ern	≤ 1884 (REUTER 1884)
Croatia	1885 (KORLEVIC 1886)
Poland	≤ 1892 (NASONOV 1892)
Guernsey	≤ 1895 (LUFF 1895)
Scotland	≤ 1895 (SERVICE 1896)
Alderney	≤ 1901 (LUFF 1901)
Czech Republic	1902 (EICHLER 1978)
Switzerland	1902 (INEICHEN 1997, in LUESCHER & al. 2008)
Ukraine	≤ 1905 (RUZSKY 1905, in EICHLER 1974)
Russia: Southern	≤ 1905 (RUZSKY 1905, in EICHLER 1974)
Russia: Central	≤ 1905 (RUZSKY 1905, in EICHLER 1974)
Luxembourg	≤ 1906 (WASMANN 1906)
Italy	≤ 1908 (MANTERO 1908, in BARONI URBANI 1971)
Montenegro	≤ 1908 (ZIMMERMANN 1934)
Sweden	≤ 1908 (AURIVILLIUS 1908, in WOJCIK & PORTER 2008)
Belgium	≤ 1909 (BONDROIT 1909)
Wales	≤ 1915 (DONISTHORPE 1915)
Corsica	≤ 1916 (EMERY 1916)
Gibraltar	1931 (JAMESON 1932)
Bulgaria	1933 (POPOV 1939)

Greece	1934 (MENOZZI 1936)
Latvia	≤ 1939 (JACOBSON 1939)
Vatican City	≤ 1946 (MARTINI 1946, in EICHLER 1978)
Ireland (Northern)	≤ 1948 (O'FARRELL & BUTLER 1948)
Crete	≤ 1951 (BOLTON 1987)
Austria	≤ 1962 (EICHLER 1962, in EICHLER 1978)
Hungary	≤ 1962 (EICHLER 1962, in EICHLER 1978)
Norway	1975 (MEHL 1978)
Belarus	≤ 1985 (BLINOV 1985)
Slovakia	≤ 1989 (WERNER 1989)
Serbia	≤ 1992 (PETROV & COLLINGWOOD 1992)
Macedonia	≤ 1992 (PETROV & COLLINGWOOD 1992)
Portugal	≤ 1998 (COLLINGWOOD & PRINCE 1998)
Slovenia	≤ 2000 (BRAČKO 2000)
Turkey (European)	2001 (AKTAÇ & KIRAN 2006)
Albania	≤ 2004 (RADCHENKO 2004)
Cyprus	≤ 2004 (RADCHENKO 2004)
Estonia	≤ 2004 (RADCHENKO 2004)
Kaliningrad	≤ 2004 (RADCHENKO 2004)
Lithuania	≤ 2004 (RADCHENKO 2004)
Moldova	≤ 2004 (RADCHENKO 2004)
Sardinia	≤ 2004 (RADCHENKO 2004)
Sicily	≤ 2004 (RADCHENKO 2004)

Tab. 6: Earliest known records for *Monomorium pharaonis* from North America & Bermuda. CNC = Canadian National Collection, INHS = Illinois Natural History Survey, MEC = Montana Entomology Collection, NSIR = Nebraska State Insect Records, OSUC = Ohio State University Collection, SI = Smithsonian Institution, UNH = University of New Hampshire Insect Collection.

US	Earliest record
Mississippi	≤ 1864 (MARLATT 1896)
New York	≤ 1882 (LINTNER 1882, in LINTNER 1896)
Kansas	≤ 1884 (SMITH 1934)
Washington DC	≤ 1884 (REUTER 1884)
Vermont	≤ 1885 (PERKINS 1884)
Florida	≤ 1888 (SCHWARZ 1888)
Texas	1888 (C.V. Riley, SI): Columbus
New Jersey	≤ 1890 (SMITH 1890)

Colorado	≤ 1890 (ASHMEAD 1890)
Pennsylvania	≤ 1896 (SKINNER 1897)
Massachusetts	≤ 1896 (KING 1901)
New Mexico	1899 (COCKERELL 1900)
Louisiana	≤ 1900 (FOSTER 1908)
Maryland	1903 (collector unknown, SI): Baltimore
Connecticut	≤ 1904 (WHEELER 1904)
Minnesota	1904 (WASHBURN 1906)
Illinois	≤ 1905 (FORBES 1905)
Georgia	1906 (C.F. Cofer, SI): Perry
Wisconsin	1908 (BURRILL & SMITH 1918)
+ Nebraska	1908 (A.C. Brown, NSIR): Scribner
North Carolina	1909 (SMITH 1910)
California	≤ 1910 (WOODWORTH 1910)
Arkansas	≤ 1912 (HUNTER & PIERCE 1912)
Indiana	≤ 1914 (BALDWIN 1914)
Kentucky	≤ 1917 (GARMAN 1917)
Ohio	1917 (M.R. Smith, OSUC): Columbus
South Dakota	≤ 1920 (SEVERIN 1920, in WHEELER & WHEELER 1987)
North Dakota	1924 (C.N. Ains, SI): Fargo
Alabama	1927 (A.H. Sturtevant, SI): Kushla
Iowa	1928 (L. Ulch, NSIR): Elberon
South Carolina	≤ 1934 (SMITH 1934)
Idaho	≤ 1934 (COLE 1934)
Michigan	1937 (R. Hutson, SI): East Lansing
Washington	≤ 1938 (HATCH 1938)
Tennessee	≤ 1938 (DENNIS 1938)
+ Missouri	1940 (collector unknown, INHS): St Louis
Virginia	1940 (C.M. O'Kay, SI): Arlington
Utah	1953 (GRUNDMANN & PETERSON 1953)
+ New Hampshire	1961 (J.G. Conklin, UNH): Gilford
+ Montana	1963 (F.W. Wiegand, MEC): Bozeman
Oklahoma	≤ 1964 (YOUNG & HOWELL 1964)
Arizona	≤ 1973 (HUNT & SNELLING 1975)
Wyoming	≤ 1976 (LAVIGNE & TEPEDINO 1976)
+ Delaware	≤ 2002 (S. Dash, pers. comm.): Wilmington

Oregon	≤ 2002 (SYSTMA 2004)
+ Maine	≤ 2007 (H.L. McCreary, Jr., pers. comm.): Portland
+ Rhode Island	2008 (R. Sullivan, pers. comm.): Pawtucket
+ West Virginia	≤ 2009 (collector unknown, SI): Charlestown
Canada & Bermuda	
Ontario	≤ 1880 (BETHUNE 1881, in LINTNER 1896)
Quebec	≤ 1883 (PROVANCHER 1883)
Bermuda	≤ 1928 (OGILVIE 1928)
British Columbia	1940 (W. Downes, CNC): Victoria
Manitoba	1943 (AYRE 1977)
Alberta	1946 (SHARPLIN 1966)

native North American thief ant *Solenopsis molesta* (SAY, 1836), a species described as commonly found in houses in Indiana, but which can also be a major agricultural pest (HAYES 1920). Smith, Roger, Mayr, Forel, Dalla Torre, and other European researchers incorrectly assumed that *M. pharaonis* and *S. molesta* were synonyms. This problem persisted even after EMERY (1894) determined that *M. pharaonis* and *S. molesta* were separate species. As WHEELER (1917) wrote: "The European myrmecologists were misled by their inability to believe that a small *Solenopsis*, closely allied to the European *S. fugax* LATR., could become a household pest." I therefore excluded all 19th century North American records of *M. pharaonis* by European scientists who had not examined the specimens (e.g., SMITH 1871), as well as reports of *M. pharaonis* as a major agricultural pest, records that almost certainly refer to *S. molesta* rather than *M. pharaonis*. For example, FITCH (1856, in FORBES 1905) reported *M. pharaonis* as a major pest of corn in New York. *Monomorium pharaonis* is easily distinguished from a thief ant because *M. pharaonis* (like all *Monomorium*) has a three-segmented antennal club, whereas all thief ants have a two-segmented club, as SAY (1836) correctly described for *S. molesta*.

WHEELER (1906) speculated that VERRILL's (1902) record of *Monomorium minutum* MAYR, 1855 (= *M. monomorium*) from Bermuda was actually *M. pharaonis*, but this was not confirmed and WETTERER & WETTERER (2004) verified the presence of *M. monomorium* in Bermuda. HOLGERSEN (1944) reported *M. pharaonis* from Norway, but MEHL (1978) reported that the specimens were actually *Solenopsis westwoodi* FOREL, 1894. PASSERA (1994) listed *M. pharaonis* from Andorra citing EICHLER (1978) as the source, but EICHLER (1978) actually reported "Keine Angaben" (= no information) from Andorra.

Some specimens in the MCZ, previously identified as *M. pharaonis*, were actually *M. destructor* (see WETTERER 2009b). It is possible that some reports of *M. pharaonis* in the literature also were misidentified *M. destructor*. I did not find any *M. pharaonis* specimens in the MCZ misidentified as *M. destructor*. Because *M. pharaonis* is much

more widely-known as a pest than *M. destructor*, it seems unlikely that many reports of *M. destructor* in the literature were actually misidentified *M. pharaonis*. One exception is the record of *M. destructor* at Archbold Biological Station, Florida in EISNER & al. (1980), which was actually *M. pharaonis* (M. Deyrup, pers. comm.).

Discussion

WILSON & TAYLOR (1967) wrote of *Monomorium pharaonis*: "this little species is probably the most widely distributed of all ant species." My current analysis lends credence to this claim. In addition to being ubiquitous in cities around the world, *M. pharaonis* has also been recorded in tropical sites far from human habitation, e.g., it is the only ant record I know from the supremely isolated Aves Island, an uninhabited islet in the central Caribbean claimed by both Venezuela and Dominica (LEVINS & al. 1973).

Native versus exotic range

In the 1890s, when most of the world's ant fauna was still very poorly documented, *M. pharaonis* was already known from a diversity of locales scattered across Asia, Africa, Oceania, Central and South America, the West Indies, Europe, and North America (Tabs. 1 - 6). EMERY (1893), however, proposed *M. pharaonis* originated in tropical Asia because "in collections from the East Indies, *M. pharaonis* almost always is represented, but in South American and African collections, it usually is not. Indeed, I have received such specimens from Neotropical and African regions almost exclusively from coastal areas and islands, indicating a more recent introduction." Similarly, RUZSKY (1905, in EICHLER 1974) considered "the Sunda Islands [of Malaysia and Indonesia] as the home of the Pharaoh ant because they are very common not only in homes but also live outdoors." Most subsequent researchers also have considered *M. pharaonis* as being originally from tropical Asia (e.g., VIEHMEYER 1906, JACOBSON 1939, WILSON & TAYLOR 1967, BOLTON 1987, ARAKELIAN 1994, DLUSSKY 1994). STITZ (1939, in SUDD 1962) reported that *M. pharaonis* nested away from houses only in the East Indies, where it is found nesting in soil and under stones. Indeed, I found widespread outdoor records of *M. pharaonis* from tropical Asia, further supporting the contention that *M. pharaonis* is native to this region. For example, in 1972, W.L. Brown, Jr. collected *M. pharaonis* at the Kampong Sotek base camp in the forest of Kalimantan, Indonesia (specimen in the MCZ). THIENTHAWORN (2004) surveyed ants in the leaf litter and on trees in rural Ratchaburi, Thailand and found *M. pharaonis* at 17 of 19 sites. SAKCHOOWONG & al. (2009) collected *M. pharaonis* at five of six sites in Thong Pha Phum National Park, Thailand.

Not all researchers agree, however, that *M. pharaonis* originated in tropical Asia. Notably, BERNARD (1952, 1968) found *M. pharaonis* in the forest of Guinea, West Africa and based on this and on his contention that its closest relatives in the subgenus *Pharaophanes* were mainly African, proposed that *M. pharaonis* was originally from the forests of West Africa, "not Egypt or India as various authors have suggested." This argument may have convinced Marion Smith, who changed his mind on this issue: SMITH (1951) wrote *M. pharaonis* was "probably from India," but SMITH (1965) said it was "thought to be native to Africa." Combining these opinions, SMITH (1979) wrote that *M. pha-*

raonis "probably originating from Africa or tropical Asia." BOLTON (1987), however, discarded the subgenus *Pharaophanes*, and placed *M. pharaonis* in the *M. pharaonis* complex with two close relatives, *Monomorium longi* FOREL, 1902 and *Monomorium wroughtoni* FOREL, 1902, both from India, lending additional support to a tropical Asian origin for *M. pharaonis*, and undercutting the central argument for a tropical African origin. Nonetheless, some authors continue to list the geographic origin of *M. pharaonis* as tropical Africa (e.g., FOWLER & al. 1994).

WILLIAMS (1990) wrote that *M. pharaonis* "probably originated in North Africa and the Middle East." However, except for the fact that LINNAEUS (1758) first described *M. pharaonis* from Egypt, I found no evidence supporting the popular idea that *M. pharaonis* is native to this subtropical region. In fact, *M. pharaonis* appears to be rare in Egypt, e.g., ALFIERI (1931) reported *M. pharaonis* from just one site in Egypt, while reporting *Monomorium destructor* (as *Monomorium gracillimum* (SMITH, 1861)) from 55 sites. In addition, there are very few records of *M. pharaonis* from any part of subtropical North Africa and the Middle East.

Finally, RILEY (1889) believed that *M. pharaonis* originated in Europe and ARNOLD (1916) proposed that *M. pharaonis* probably originated in South America. Although *M. pharaonis* is certainly widespread in both these regions, the scarcity of outdoor records in Europe and the lack of any close relatives in the New World render these possibilities as unlikely.

On-going research on the genetic diversity of *M. pharaonis* at sites around the world aims to evaluate hypotheses concerning the geographic origin of this cosmopolitan species (A.M. Schmidt, pers. comm.).

Common names

In the past, authors used many different common names for *M. pharaonis*, including the little yellow ant, the common house ant, the hospital ant, the ship ant, the common red house ant, the red domestic ant, and the little red ant. Unfortunately, none of these common names relate to any unique feature of *M. pharaonis* and all could be applicable to many other ant species in different parts of the world.

In recent years, the most popular common name for *M. pharaonis* has been the pharaoh ant and its equivalent in other languages (e.g., Pharaameisen, formiga-do-faraó, formiga faraónica, fourmi pharaon, mrówka faraona, faraomier, faraomyre), based on its Latin name. LINNAEUS (1758) apparently chose this name because the type specimens came from Egypt. Interestingly, "pharaoh" means "great house," and originally referred to the king of Egypt's palace, not the king himself. I found no basis for the often-repeated contention that LINNAEUS (1758) thought this ant was one of the pharaoh's biblical plagues. Because *M. pharaonis* is probably not native to Egypt, this common name is misleading and may explain why so many popular accounts of this ant present it as an Africa native. Because the common name pharaoh ant never refers to any ant species other than *M. pharaonis*, I think this name should be retained for this "great-house" ant.

Impact

In most parts of the world, *M. pharaonis* is rarely collected outdoors and I found only a few anecdotal reports of its ecological importance in nature. For example, MCCLEL-

LEND & JONES (2008) reported *M. pharaonis* on petrel chicks on Laysan Island. *Monomorium pharaonis*, however, can be a very serious indoor pest. For example, SMITH (1855) wrote that in Brazil, "we have heard of houses, in this country, being deserted in consequence of their being infested by *Myrmica domestica* (= *M. pharaonis*). BURRILL & SMITH (1919) reported they had "seen several flats vacated because of the ravages of this pest." HARTNACK (1939) considered *M. pharaonis* the most common house ant in North America. OI & al. (1994) found *M. pharaonis* foraging at 51.7% baits placed on the exterior building walls in an apartment complex near Gainesville, Florida, and at 11.6% of baits placed inside the apartments. DUFFIELD (2006) reported that at least 30% of the buildings of Howard University in Washington DC had active *M. pharaonis* colonies.

Monomorium pharaonis is particularly notorious as a pest in hospitals, where it is known as a vector for diseases, workers being so small that they can crawl through gauze covering wounds, transporting pathogens among patients directly or via previously sterile equipment and supplies. BEATSON (1972) isolated numerous pathogenic bacteria from *M. pharaonis* workers in hospitals, including *Pseudomonas*, *Salmonella*, *Streptococcus*, and *Staphylococcus*. BEATSON (1972) found that "patients who develop suppurating lesions are likely to suffer attack by ants that apparently feed on the discharge inside dressings. Workers are able to locate such patients very quickly and also those with a fever or profuse sweating. In intensive-care units the problem can be acute if the ants establish nests in the structure, since workers get into drip-tubes and resuscitation equipment. In baby-units worker ants have bitten the infants around the eyelids. In central sterile supply department stores foraging workers regularly get inside sterile packs. Nearly all the hospitals I visited had found ants in these packs." STEINBRINK (1978) reported *M. pharaonis* infesting incubators for premature babies in a children's hospital, preferentially feeding on the babies' cheeks, lips, behind their ears, and on their necks and causing skin lesions. WEIDNER (1982) reported: "one hospital had three ants aspirated from a patient's tracheostomy (a permanent hole in the neck for breathing)." The problem of *M. pharaonis* in hospitals varies greatly in different parts of the world, and may increase at lower latitudes. For example, studies found *M. pharaonis* infestations at 12% of hospitals in England (EDWARDS & BAKER 1981), 25% in Texas (WEIDNER 1982), and 72% in Brazil (LISE & al. 2006).

Monomorium pharaonis may be beneficial to humans in some circumstances. In the 13th century, Chinese farmers brought *M. pharaonis* colonies into their barns to control pest insects (BERENBAUM 1994). MARLATT (1896) wrote that a "common insect visitor in houses, and a very annoying one also to the careful housekeeper, the little red ant (*Monomorium pharaonis*), is also known to be a very active and effective enemy of the bedbug. Mr. Theo. Pergande, of this office [UDSA Division of Entomology] informs me that during the Civil War, when he was in the Union army, he occupied at one time barracks at Meridian, Miss., which had been abandoned some time before. The premises proved to be swarming with bedbugs; but very shortly afterwards the little red house ant discovered the presence of the bedbugs and came in enormous numbers, and Mr. Pergande witnessed the very interesting and please-

ing sight of the bedbugs being dismembered or carried away bodily by these very minute ants, many times smaller than the bugs which they were handling so successfully." Perhaps inspired by this sight, Pergande went on to become prominent ant biologist, working as an entomologist for the U.S. government. JAMESON (1932) reported on the introduction of *M. pharaonis* to exterminate bugs in British army barracks in Gibraltar: "A considerable degree of success was attained. Bugs decreased rapidly, and ants were observed attacking bugs and taking them to their nest. The subsequent disappearance of the ants can probably be attributed to the fact that the bug population was eventually so diminished as no longer to afford sufficient food supply to the ant colony."

Continued spread

Monomorium pharaonis has life-history traits that facilitate successful colony establishment through human commerce. Colonies are polygynous (with multiple queens) and polydomous (divided among multiple nest sites). Colonies are constantly seeking new nest sites, and can quickly move parts of the colony into cargo. Small colony fragments separated from the main colony, even fragments lacking a queen but with workers and eggs, are capable of reconstituting a functioning colony (PEACOCK & al. 1955). In the absence of a queen, workers can raise the larvae to be new queens. These queens can lay unfertilized eggs, which develop into males. The queen then can mate with her sons to produce more workers and queens.

In the past, *M. pharaonis* spread around the world primarily by ship (see WEBER 1939). For example, VIEHMEYER (1923) recorded *M. pharaonis* collected in the cabin of a Nile steamer in Sudan. FOREL (1928) wrote that *M. pharaonis* "swarms in every steamer ... I have even found a colony of these ants in the handle of a knife which came off the blade while I was dining." MORLEY (1953) called *M. pharaonis* "lord of the ocean-going ants, and dominant on nearly every ocean steamer." Now, air travel allows the possible spread of *M. pharaonis* to virtually anywhere in the world. For example, WETTERER (1998) reported that a computer monitor was delivered to Hawaii Volcanoes National Park from Texas by express airmail with several hundred *M. pharaonis* inside the cardboard walls of the box.

There are many reports suggesting that *M. pharaonis* populations worldwide are rapidly expanding. For example, WISNIEWSKI (1981) wrote that in Poland: "the number of localities and buildings in which the ant was observed had increased very rapidly in the years between 1970 and 1980. By mid-1979, the species was present in 149 localities all over the country. The causes of this increase included the transport of goods, tourism, business travel and changes in place of residence of large numbers of the population." BOLTON (1987) wrote of *M. pharaonis*: "The past few decades have seen an incredible increase in the range and population density of this species in temperate zones of the world, corresponding to a large extent with the spread of high-density apartment blocks and central heating systems." KNIGHT & RUST (1990) noted that EBLING (1975) knew of only two populations of *M. pharaonis* in California, but "in the subsequent eleven years the Pharaoh ant has greatly extended its range throughout California."

Certainly increases in international travel have allowed freer movement to *M. pharaonis* around the world. My ana-

lyses, however, suggest that *M. pharaonis* had already spread over much of the world more than 100 years ago. I believe that the greater concentration of *M. pharaonis* records from temperate Europe and North America (Fig. 5) is largely an artifact of greater sampling and dissemination of information, as is much of the apparently recent range expansion of *M. pharaonis*. For example, I found no published records of *M. pharaonis* from Pakistan, but a June 2007 survey in Karachi yielded *M. pharaonis* in nine of 25 apartments surveyed (see Tab. 1). In addition, I expect that there are many repositories of unpublished information on the occurrence of *M. pharaonis* (and other pest species) kept by a variety of local, state, and national agencies. For example, I found no published records of *M. pharaonis* from Nebraska, yet the Nebraska State Insect Records website listed 57 records from the state dating back to 1908. Finally, I expect that hundreds of museums large and small around the world have undocumented *M. pharaonis* specimens in their collections. No doubt, many of these museums also harbor within their walls live specimens of this "great-house" ant, almost certainly the most widely dispersed ant species in the world.

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Zusammenfassung

Die Pharaoameise, *Monomorium pharaonis* (LINNAEUS, 1758), wird seit langem als die weltweit am weitesten verbreitete Ameisenart betrachtet, die in Häusern vorkommt. Die Pharaoameise ist insbesondere als ein Schädling in Spitäler berüchtigt, wo sie ein Überträger von Krankheiten ist. Um die weltweite Verbreitung von *M. pharaonis* darzustellen und Hypothesen den geographischen Ursprung der Art betreffend zu evaluieren, habe ich veröffentlichte und unveröffentlichte Nachweise von > 1200 Fundorten zusammengetragen. Ich dokumentiere die frühesten bekannten Nachweise der Art für 225 geographische Gebiete (Länder, Inselgruppen, große Inseln, US-Bundesstaaten, kanadische Provinzen und Russische Föderationssubjekte), einschließlich vieler, für die ich keine bisher veröffentlichten Nachweise gefunden habe: Austral-Inseln, Delaware, Dominikanische Republik, Elfenbeinküste, Gabun, Guatemala, Hainan, Haiti, Irak, Maine, Missouri, Montana, Nebraska, New Hampshire, Pakistan, Palmyra, Rhode Island, Tunesien, West Virginia und Zentralafrikanische Republik. In tropischen Regionen kommt *M. pharaonis* sowohl in Ge-

bäuden als auch im Freien vor, aber in gemäßigten Gebieten wird sie fast ausschließlich in Gebäuden angetroffen. Die Pharaoameise ist die weitaus häufigste Art in beheizten Gebäuden von Europa und Nordamerika.

Monomorium pharaonis scheint aus dem tropischen Asien zu stammen, von wo zahlreiche Freilandfunde vorliegen. Außerdem sind *Monomorium longi* FOREL, 1902 und *Monomorium wroughtoni* FOREL, 1902, also jene zwei Arten, die man für nächstverwandt mit *M. pharaonis* hält, Endemiten des tropischen Asiens. Obwohl *M. pharaonis* aus Ägypten erstbeschrieben wurde, habe ich keine Bestätigung der weit verbreiteten aber offenbar falschen Annahme gefunden, *M. pharaonis* könnte aus Afrika stammen.

Zahlreiche Autoren berichten von einer raschen aktuellen Ausbreitung der Pharaoameise. Meine Analysen hingegen legen nahe, dass die Art bereits vor > 100 Jahren über weite Teile der Erde verbreitet war. Viele der berichteten rezenten Populationszuwächse von *M. pharaonis* könnten ein Artefakt von zunehmender Besammlungsintensität und Informationsweitergabe sein.

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