

Worldwide spread of the ghost ant, *Tapinoma melanocephalum* (Hymenoptera: Formicidae)

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Abstract

The ghost ant, *Tapinoma melanocephalum* (FABRICIUS, 1793), is a ubiquitous indoor and outdoor pest throughout much of the tropics and subtropics, and an increasingly common indoor pest in temperate regions. Here, I examine the taxonomy of *T. melanocephalum* and map records from > 1500 sites to evaluate its worldwide spread and probable geographic origin.

I document the earliest known *T. melanocephalum* records for 154 geographic areas (countries, major islands, island groups, US states, and Canadian provinces), including many areas for which I found no previously published records: Anguilla, Antigua & Barbuda, Barbados, Bonaire, Cambodia, Cape Verde, Cayman Islands, Comoro Islands, Curaçao, Gabon, Gambia, Grenada, Italy, Kenya, Montserrat, Nevis, Nigeria, Pakistan, Romania, St. Kitts, St. Lucia, St. Martin, Illinois, Michigan, Minnesota, Missouri, North Carolina, Virginia, and Wisconsin. *Tapinoma melanocephalum* has one of the widest distributions known for any ant species. It has spread across the Old World and New World in both the northern and southern hemispheres, though at latitudes greater than 30° it is largely restricted to living inside buildings.

In most parts of the world, *T. melanocephalum* can be reliably distinguished from other ant species. In India, Southeast Asia, and the western Pacific region, however, *T. melanocephalum* may be confused with closely related taxa, including *Tapinoma minutum* MAYR, 1862, *Tapinoma indicum* FOREL, 1895, and several seemingly intermediate forms, suggesting that *T. melanocephalum* originated in the Indo-Pacific region. Future research on the phylogeny of *Tapinoma* and on the genetic diversity of *T. melanocephalum* populations in different parts of the world should help elucidate further the native and exotic ranges of *T. melanocephalum*.

Key words: Biogeography, biological invasion, exotic species, Formicidae, invasive species.

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Introduction

Tramp ants associate with humans and are spread by human commerce. Typically, tramp ants thrive only in disturbed environments and do not penetrate intact natural habitats. But as humans and their disturbance spread, so do tramp ants. EMERY (1893a) evaluated the geographic origins of several major tramp ants using different lines of evidence. EMERY (1893a) proposed the pharaoh ant (*Monomorium pharaonis* (LINNAEUS, 1758)) originated in East 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." EMERY (1893a) proposed that the big-headed ant (*Pheidole megacephala* (FABRICIUS, 1793)) probably came from Africa, "where its closest relatives live." EMERY (1893a), however, wrote that for two species, the longhorn crazy ant (*Paratrechina longicornis* (LATREILLE, 1802)) and the ghost ant (*Tapinoma melanocephalum* (FABRICIUS, 1793)) "that have already become cosmopolitan in the tropics, I am not in the position to assign an original homeland." WETTERER (2008)

concluded the distributions of three closely related species offered good evidence that *P. longicornis* is native to Southeast Asia and Melanesia. Here, I evaluate the worldwide spread and possible geographic origin of *T. melanocephalum*.

Tapinoma melanocephalum is a ubiquitous pest through much of the tropics and subtropics. As LONGINO (2006) aptly wrote: "regardless of whether you are in Guinea, New Guinea, or Guyana, if you are sitting at a table with a sugar dispenser you are likely to see workers of *T. melanocephalum* running about on the surface." Workers are small (~ 1.5 mm) and their pale legs and abdomens often blend into the background, making them difficult to see. Their dark brown heads and thoraces often look like hovering specks, unrecognizable as ants. The barely visible "ghostly" appearance of *T. melanocephalum* no doubt explains its common name.

WILSON & TAYLOR (1967) wrote of *T. melanocephalum*: "the origin of this ubiquitous tramp species is unknown. Related species are native to various parts of Africa, southeastern Asia, and the New World subtropics and tropics." FOWLER & al. (1994) listed the assumed geo-

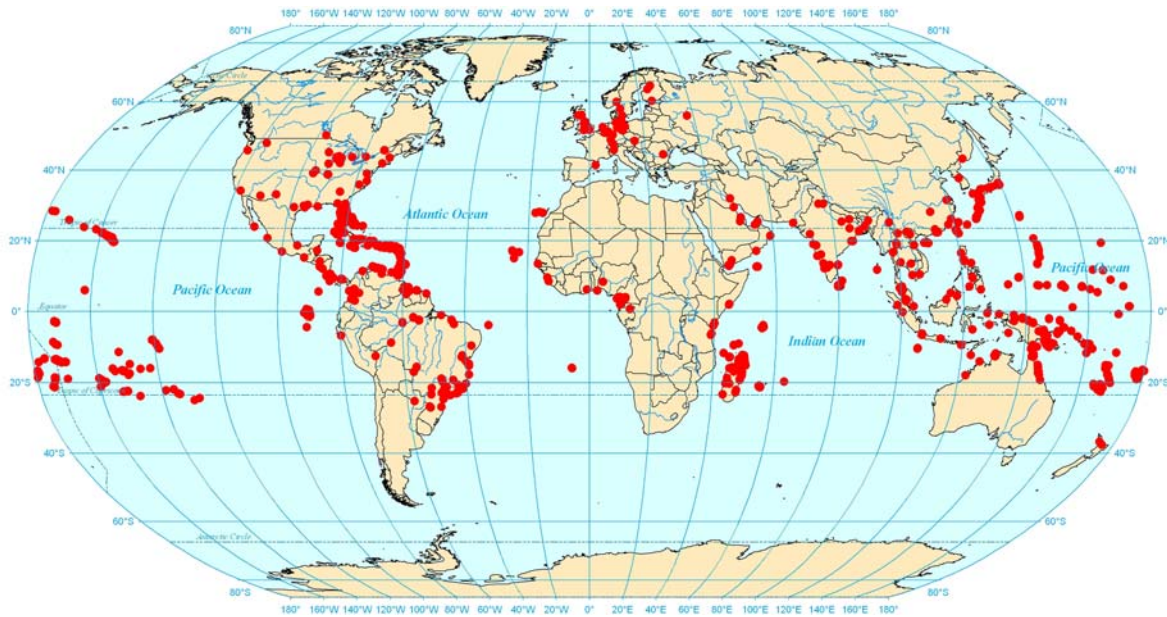


Fig. 1: Worldwide distribution of *Tapinoma melanocephalum* (some Indo-Pacific records may be misidentifications of related species).

graphic origin of *T. melanocephalum* to be tropical Africa. DLUSSKY (1994) believed *T. melanocephalum* to be of Asian origin, and in previous papers I have followed DLUSSKY (1994) in calling it an Asian species (e.g., WETTERER 2002, WETTERER & VARGO 2003).

When evaluating the native and exotic ranges of a species, researchers may consider a spectrum of distributional, historical, evolutionary, ecological, and genetic information (see WETTERER 2008). Evidence considered indicative of a species' native range includes (1) older records largely confined to a single continuous region, (2) occurrence in inland native communities, (3) high genetic diversity, (4) co-occurrence of species-specific symbionts, and (5) proximity to the ranges of closely related species. In contrast, evidence indicative of a species' exotic range includes (I) sudden appearance and spread of the species through an area discontinuous with other known populations, (II) occurrence exclusively in coastal and highly disturbed environments, (III) low genetic diversity due to a founder effect, (IV) absence of species-specific symbionts, and (V) geographic isolation from closely related species.

Methods

I documented the range of *T. melanocephalum* using both published and unpublished records. Unlike many other major pest ant species, *T. melanocephalum* is easy to identify correctly (except in the Indo-Pacific; see below), and therefore identifications in the literature are fairly reliable. I obtained unpublished site records from museum specimens in the collections of the American Museum of Natural History (AMNH), the Archbold Biological Station (ABS), the British Natural History Museum (BMNH), the Museum of Comparative Zoology (MCZ), the National Museums Liverpool (NML), the Oxford University Natural History Museum (ONHM), the Smithsonian Institute's National Museum of Natural History (SI), and the University of Minnesota Collection (UMC). In addition, I used on-line databases with specimen records from the Australia-

lian National Insect Collection (ANIC), California Academy of Science (CAS), and Essig Museum at UC Berkeley (UCB). I also received unpublished site records from J. Cook (Illinois, Texas), G. Dlussky (Samoa), X. Espadaler (France), A. Francoeur (Brazil, Colombia, Cuba, Mexico, Quebec), B. Guénard (North Carolina, Quebec), G. Heller (Canary Islands, Germany), J. LaForest (Michigan), M. Lush (Australia, Gambia), P. Mattis (Florida), P. Pellitteri (Wisconsin), F. Rigato (Italy), and B. Taylor (Nigeria). Finally, I collected *T. melanocephalum* specimens on numerous Pacific, Atlantic, and Caribbean Islands, and in Arizona and Florida (e.g., WETTERER & al. 1999, WETTERER 2002, WETTERER & O'HARA 2002, WETTERER & VARGO 2003).

I obtained geographic coordinates for sites from published references, from specimen labels, or I looked them up. For older references and specimens, some site names are no longer in use and I searched, not always successfully, to determine current names. 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. If a published source had many sites less than 10 - 20 km apart (e.g., HUDDLESTON & FLUKER 1968), I did not always plot every site. I did not map records of *T. melanocephalum* on boats or intercepted in transit by quarantine inspectors. An undated specimen collected by Theodore Pergande in Antigua must have been collected before Pergande's death in 1916.

Results

Published and unpublished specimen records of *T. melanocephalum* came from > 1500 sites in 154 different geographic areas (i.e., countries, island groups, major islands, US states, and Canadian provinces), including many areas for which I found no previously published records, e.g., Anguilla, Antigua & Barbuda, Barbados, Bonaire, Cambodia, Cape Verde, Cayman Islands, Comoro Islands, Cura-

Tab. 1: Earliest known records for *Tapinoma melanocephalum* from Asia, the Middle East, and neighboring islands. Unpublished records include collector, museum source, and site. SI = Smithsonian Institute, MCZ = Museum of Comparative Zoology, + = no known published record. Some records from India and Southeast Asia may be misidentifications of related species.

	Earliest record
India	≤ 1851 (JERDON 1851)
Singapore	≤ 1857 (SMITH 1857)
Indonesia	≤ 1860 (SMITH 1860)
Philippines	1890 (EMERY 1893d)
Malaysia	≤ 1892 (EMERY 1893e)
Sri Lanka	1892 (EMERY 1893c)
Papua New Guinea	≤ 1897 (EMERY 1897)
Burma/Myanmar	≤ 1913 (WHEELER 1913a)
Iraq	1918 (DONISTHORPE 1918)
Vietnam	≤ 1920 (SANTSCHI 1920)
China	≤ 1921 (WHEELER 1921)
Asian Russia	≤ 1926 (KARAWAJEW 1926)
Japan	≤ 1927 (TERANISHI 1927 in ONOYAMA 1980)
Taiwan	≤ 1929 (WHEELER 1929)
Christmas Island	1934 (DONISTHORPE 1935)
Yemen	1955 (E.O. Wilson, MCZ): Aden
+ Cambodia	1962 (J.L. Nickel, SI): Siem Reap, Kok Patry Station
Saudi Arabia	1978 (COLLINGWOOD 1985)
Oman	1984 (COLLINGWOOD 1985)
Kuwait	≤ 1996 (COLLINGWOOD & AGOSTI 1996)
UAE	≤ 1997 (COLLINGWOOD & al. 1997)
Thailand	≤ 2001 (MEKLOY 2001)
South Korea	≤ 2005 (ANONYMOUS 2005)
Bangladesh	2005 (HANNAN 2007)
+ Pakistan	2007 (S. & Z. Valliani, MCZ): Karachi

cao, Gabon, Gambia, Grenada, Italy, Kenya, Montserrat, Nevis, Nigeria, Pakistan, Romania, St. Kitts, St. Lucia, St. Martin, Illinois, Michigan, Minnesota, Missouri, North Carolina, Virginia, and Wisconsin (Fig. 1, Tabs. 1 - 7).

Tab. 2: Earliest known records for *Tapinoma melanocephalum* from Australia and Oceania. Some records from the western Pacific may be misidentifications of related species. Abbreviations as in Table 1.

	Earliest record
Samoa	≤ 1876 (MAYR 1876)
Tonga	≤ 1876 (MAYR 1876)
Hawaii	≤ 1887 (BLACKBURN & CAMERON 1887)
Society Islands	1906-07 (WILSON & TAYLOR 1967)
New Caledonia	≤ 1914 (EMERY 1914)
Fiji	1915 (MANN 1921)
Banaba	1923 (TIMBERLAKE 1926)
Tokelau Islands	1924 (WILSON & TAYLOR 1967)
Marquesas Islands	1925 (CHEESMAN & CRAWLEY 1928)
Vanuatu	1925 (SANTSCHI 1928b)
Australia	1932 (Darlington, MCZ): Lankelly Creek
Pitcairn Islands	1934 (WHEELER 1936)
Tuamotu Islands	1934 (WHEELER 1936)
Austral Islands	1934 (WHEELER 1936)
Line Islands	1934 (WHEELER 1936)
Cook Islands	≤ 1935 (WHEELER 1935)
Solomon Islands	≤ 1935 (WHEELER 1935)
FS Micronesia	1937 (T. Esaki, MCZ): Malem & Kolonia
Phoenix Islands	≤ 1941 (VAN ZWALUWENBURG 1943)
Mariana Islands	1945 (D.J. Borrer, SI): Agrihan
Marshall Islands	1947 (COLE 1949)
Palau	1952 (Gressitt, MCZ): Babeldaup, Ngaremeskang
Gilbert Islands	1957 (CLOUSE 2007)
New Zealand	1959 (TAYLOR 1961)
Wake Island	1959 (Y. Oshiro, MCZ): site unknown
Niue	1964 (TAYLOR 1967)
Wallis & Futuna	1965 (WILSON & HUNT 1967)
US Pacific Territories	≤ 2005 (HANDLER & al. 2007)

Tab. 3: Earliest known records for *Tapinoma melanocephalum* from Africa and neighboring islands. Abbreviations as in Table 1, and MP = Museum Paris.

	Earliest record
Madagascar	1893 (Grandidier, MP): Toamasina
Réunion	≤ 1895 (FOREL 1895)
Seychelles	≤ 1897 (FOREL 1897)
Guinea	≤ 1914 (SANTSCHI 1914)
Somalia	1926 (MENOZZI 1930)
Equatorial Guinea	1940 (MENOZZI 1942)
Mauritius	1949 (MAMET 1954)
Tanzania	≤ 1953 (WAY 1953)
Saint Helena	1967 (TAYLOR 1976)
Ghana	≤ 1970 (ROOM 1971)
+ Kenya	1973-74 (Allen & Brooks, MCZ): Mombasa
+ Gabon	1974 (W. Gotwald, MCZ): Makokou
+ Nigeria	≤ 1976 (B. Taylor, pers. comm.): Gambari
Sierra Leone	≤ 1976 (GRIFFITHS 1980)
Canary Islands	1989 (ESPADALER 2007)
Cameroon	1991 (DEJEAN & al. 1994)
+ Comoro Islands	1994 (Roger, MCZ): Dzaoudi & Moroni
+ Cape Verde	2003 (J.K. Wetterer, unpubl.): Santa Maria
+ Gambia	2007 (M. Lush, pers. comm.): Kololi

In both the Old and New World tropics, *T. melanocephalum* has been found in most maritime countries (Fig. 1), including all tropical countries of Oceania except Nauru and Tuvalu, and all island groups of the West Indies except the Turks and Caicos Islands. In tropical Asia, *T. melanocephalum* has been recorded from all countries except Brunei and Laos. In continental Africa, however, there have been relatively few records of this ant (Fig. 1).

In the continental US, most records of *T. melanocephalum* were from Florida. Although the majority of records came from disturbed habitats, some were from relatively intact habitats. For example, I collected *T. melanocephalum* nesting in a cypress tree in a relatively natural marsh area of Loxahatchee National Wildlife Refuge in Palm Beach County, Florida.

At latitudes greater than 30°, *T. melanocephalum* is largely restricted to living inside buildings. The highest latitude records came from indoor sites in Scandinavia (up to 65.0° N; SORVARI 2003), Scotland (up to 55.9° N; GOD-

Tab. 4: Earliest known records for *Tapinoma melanocephalum* from South and Central America and neighboring islands. Abbreviations as in Table 1, and BMNH = Natural History Museum in London.

	Earliest record
French Guiana	≤ 1793 (FABRICIUS 1793)
Brazil	≤ 1881 (FOREL 1881)
Galapagos	≤ 1892 (EMERY 1893b)
Mexico	≤ 1894 (PERGANDE 1896)
Belize	1905-06 (WHEELER 1907)
Costa Rica	≤ 1908 (FOREL 1908)
Guyana	1914 (G.E. Bokin, BMNH): Georgetown
Panama	1918 (no collector data, SI): Ancon
Venezuela	1936 (WEBER 1948)
Colombia	1939 (Gallego, SI): Medellin Valley
Nicaragua	1943 (Woke, SI): Chinandega
Surinam	1959 (KEMPF 1961)
Peru	≤ 1964 (PARDO 1964)
Honduras	≤ 1972 (KEMPF 1972)
Paraguay	1997 (A. Wild, pers. comm.): Asunción

FREY 1907), and Russia (up to 55.8° N; KUNASHEV & NI-YAZOVA 1998). In North America, the highest latitude records come from indoor sites in Manitoba (49.9° N; AYRE 1977), Quebec (45.5° N; B. Guénard, pers. comm.), Oregon (45.5° N; NUGENT & al. 2005), Minnesota (45.0° N; P. Clausen, pers. comm.), Wisconsin (up to 43.6° N; P. Pelletteri, pers. comm.), Michigan (43.6° N; J. LaForest, pers. comm.), and Maine (43.4° N; DEARBORN & GRANGER 2000). In the southern hemisphere, the highest latitude records came from sites in New Zealand (up to 37.6° S; TAYLOR 1961).

Nest symbionts

Although *T. melanocephalum* workers readily tend a wide range of Hemiptera, I found only one record of a purported species-specific symbiont of *T. melanocephalum*. SHEPARD & GIBSON (1972) reported salticid spiders of the genus *Cotinusa* present in 61% of *T. melanocephalum* nests on the Osa Peninsula, Costa Rica "where these ants build their nests on the lower surface of leaves in the lower forest canopy." I believe, however, that the ants were misidentified (see Discussion).

Related *Tapinoma*

In the Indo-Pacific, *T. melanocephalum* may be confused with a number of closely related taxa, including *Tapinoma minutum* MAYR, 1862 and *Tapinoma indicum* FOREL, 1895. *Tapinoma minutum* is brown with a somewhat darker abdomen; *Tapinoma indicum* is very similar to *T. minutum*,

Tab. 5: Earliest known records for *Tapinoma melanocephalum* from the West Indies. Abbreviations as in Table 1.

	Earliest record
Virgin Islands	≤ 1881 (FOREL 1881)
Jamaica	1891 (Pergande collection, SI): Kingston
St Vincent	≤ 1893 (FOREL 1893)
Puerto Rico	1899 (Busck, SI): San Juan
Bahamas	1904 (WHEELER 1905)
Trinidad & Tobago	1910 (WHEELER 1916)
Haiti	1912-13 (WHEELER & MANN 1914)
Dominica	≤ 1913 (WHEELER 1913b)
Cuba	1913 (WHEELER 1913b)
+ Antigua & Barbuda	≤ 1916 (Pergande collection, SI): Antigua
Dominican Republic	≤ 1930 (MENOZZI & RUSSO 1930)
+ Nevis	1934 (N.A. Weber, MCZ): site unknown
+ St Lucia	no date (N.A. Weber, MCZ): site unknown
+ Montserrat	1991 (J.P.E.C. Darlington, MCZ): Salem
Aruba	≤ 1994 (JAFFE & LATTKE 1994)
Martinique	≤ 1994 (JAFFE & LATTKE 1994)
Guadeloupe	≤ 1994 (JAFFE & LATTKE 1994)
+ Barbados	1998 (S. Cover & E.O. Wilson, MCZ): Graeme Hall Swamp
+ Grenada	2003 (J.K. Wetterer, MCZ): St George's
+ Curaçao	2004 (J.K. Wetterer, MCZ): Piscadera
+ Anguilla	2006 (J.K. Wetterer, MCZ): Meads Bay
+ St Martin	2006 (J.K. Wetterer, MCZ): Baie Nettle
+ St. Kitts	2007 (J.K. Wetterer, MCZ): Bird Rock
+ Cayman Islands	2008 (J.K. Wetterer, MCZ): Grand Cayman; Websters
+ Bonaire	2008 (J.K. Wetterer, MCZ): Barkadera

but with lighter color and longer antennae (though with shorter antennae than those of *T. melanocephalum*).

FOREL (1913) described *Tapinoma melanocephalum* var. *malesianum* FOREL, 1913 from sites in Sumatra and Java, as a variety with more uniform color, thinner palps, and shorter antennae than the type. Although this remains a valid subspecies of *T. melanocephalum*, its description is very similar to that of *T. indicum*. SANTSCHE (1928a) de-

Tab. 6: Earliest known records for *Tapinoma melanocephalum* from Europe. Abbreviations as in Table 1, and BMNH = Natural History Museum in London.

	Earliest record
England	1886 (BILLUPS 1887)
Scotland	1904 (GODFREY 1907)
Germany	1926 (Dorn, BMNH): Leipzig Zoo
Scandinavia	≤ 1979 (COLLINGWOOD 1979)
Finland	1991 (SORVARI 2003)
Sweden	≤ 1995 (DOUWES 1995)
France	1995 (HUGEL & al. 2003)
Switzerland	1997 (DORN & al. 1997)
European Russia	1997 (KUNASHEV & NIYAZOVA 1998)
Spain	1999 (ESPADALER & ESPEJO 2002)
Austria	2001 (STEINER & al. 2003)
Denmark	≤ 2002 (JESPERSEN & CHRISTENSEN 2003)
Netherlands	≤ 2002 (VIERBERGEN 2003)
+ Romania	≤ 2004 (RADCHENKO 2004): site unknown
Norway	≤ 2006 (BIRKEMOE 2006)
Belgium	2006 (DEKONINCK & al. 2006)
+ Italy	2006 (F. Rigato, pers. comm.): Milan

scribed *Tapinoma melanocephalum* var. *australis* SANTSCHE, 1928 from several sites in Samoa, and mentioned that Buxton also collected this variety in Vanuatu. SANTSCHE (1928b) described *Tapinoma melanocephalum* var. *australe* SANTSCHE, 1928 based on specimens collected by Buxton in "Noq Narbow," Vanuatu (= misreading of "Hog Harbour," hand-written on specimen labels in BMNH and SI), mentioning that this variety also occurred in Samoa. Both *australis* and *australe* have a dark head and thorax and light abdomen, like the *melanocephalum* type, but have narrower palps, like those of *T. melanocephalum malesianum*. From the matching descriptions, it is clear that SANTSCHE (1928a, b) described the same taxon twice, using slightly different names: *australis* and *australe*, however, as BOLTON (1995) pointed out "the type-localities of the two are different and the names must be treated as separate." Although both names were later synonymized with *T. melanocephalum* (by WILSON & TAYLOR 1967 and BOLTON 1995, respectively), taxonomic questions remain. In many surveys of Indo-Pacific ants, researchers were unable to identify satisfactorily *Tapinoma* specimens. For example, ONOYAMA (1976) recorded *Tapinoma* sp. A in Okinawa that "seems to be recorded as *melanocephalum* by several authors in Japan, but does not agree with the figure and description of *melanocephalum* by WILSON & TAY-

Tab. 7: Earliest known records for *Tapinoma melanocephalum* from the United States and Canada. Abbreviations as in Table 1, and UMC = University of Minnesota Collection.

	Earliest record
Washington DC	1894 (PERGANDE 1896)
New York	≤ 1907 (WHEELER 1907)
Florida	≤ 1930 (SMITH 1930)
+ Virginia	1932 (H.T. Vanderford, SI): Norfolk
+ Minnesota	1935 (D.G. Denning, UMC): Minneapolis
Quebec	1939 (E.R. Bellemare, A Francoeur pers. comm.): Montréal
Iowa	1947 (KING 1948)
Georgia	≤ 1951 (SMITH 1951)
New Mexico	1967 (Elson, SI): Cloudcroft
Manitoba	1977 (AYRE 1977)
California	≤ 1979 (SMITH 1979)
Ontario	≤ 1979 (SMITH 1979)
Connecticut	≤ 1979 (FROST 1979)
Kansas	1980 (DUBOIS & DANOFF-BURG 1994)
Texas	1994 (COOK & al. 1994)
+ Missouri	1995 (J. Trager, pers. comm.): Chesterfield
Arizona	1996 (WETTERER & al. 1999)
+ Illinois	≤ 1997 (J.L. Cook, pers. comm.): Chicago
Louisiana	1999 (DASH 2004)
Maine	1999 (DEARBORN & GRANGER 2000)
Washington	≤ 2000 (HEDGES 2000)
+ Wisconsin	2000 (P. Pellitteri, pers. comm.): Wisconsin Dells
+ Michigan	2004 (J. LaForest, pers. comm.): Midland; Dow Gardens
Oregon	2005 (NUGENT & al. 2005)
+ North Carolina	2007 (B. Guénard; pers. comm.): Raleigh

LOR (1967)." ONOYAMA (1976) wrote that the decisive difference was that *Tapinoma* sp. A has shorter antennae, with the scape extending beyond the occiput by about half the length of the first funicular segment, rather than by more than the length of the first two funicular segments as in *T. melanocephalum*. CLOUSE (2007) found that in Micronesia, most *Tapinoma* specimens could be unambiguously

assigned either to *T. melanocephalum* or to *T. minutum*. However, some specimens were intermediate, with antennae like *T. melanocephalum* but color like *T. minutum* or the reverse, which CLOUSE (2007) referred to as *Tapinoma* A and *Tapinoma* B, respectively. *Tapinoma* B may or may not correspond to *T. melanocephalum australis/australe* and ONOYAMA's (1976) *Tapinoma* sp. A.

FOREL (1908) described the only other valid subspecies, *T. melanocephalum coronatum* FOREL, 1908 from Costa Rica, reporting that this subspecies also occurred in Jamaica and "etc." This taxon has the same coloration and antenna length as the type, but with shorter and narrower palps, no indentation in the thorax, and less shiny head and thorax.

Discussion

Tapinoma melanocephalum has one of the widest distributions known for any ant species. It has spread across the Old World and New World in both the northern and southern hemispheres. It is tropical and subtropical; at latitudes greater than 30°, it is largely restricted to living inside buildings. The only ants with broader known distributions than *T. melanocephalum* are the longhorn crazy ant, *Paratrechina longicornis* (WETTERER 2008), and the pharaoh ant, *Monomorium pharaonis* (L.) (J.K. Wetterer, unpubl.). I expect that *T. melanocephalum* will eventually spread to the disturbed lowlands of virtually every tropical country. This species also appears to be an increasingly common indoor pest in temperate areas, and someday may be found in every major city of the world. Because *T. melanocephalum* can live anywhere that humans live, there is no limit to the latitude where indoor populations of this species may be found.

Tapinoma melanocephalum is particularly noted as a pest in homes, restaurants, hospitals, and greenhouses. For example, *T. melanocephalum* was the most common house ant in Brazil (e.g., KAMURA & al. 2007) and on Panang Island, Malaysia (LEE & al. 2002), and it was the most frequently reported pest ant in greater Miami (KLOTZ & al. 1995). WHEELER (1907) noted that *T. melanocephalum* had been "introduced into well-heated buildings in New York," and observed workers in the winter "visiting the sugar bowls on the tables of the Columbia University commons." KARAWAJEW (1926) reported *T. melanocephalum* from hotel tables both on Ambon Island, Indonesia and in Vladivostok, Russia. James Trager (pers. comm.) observed *T. melanocephalum* inside the Sachs Butterfly House in Chesterfield, Missouri, beginning shortly after it opened in 1995. *Tapinoma melanocephalum* also has been a long-term problem in the greenhouses of the Dow Estate in Midland, Michigan, where fumigation is incompatible with a butterfly exhibit (J. LaForest, pers. comm.).

Although *T. melanocephalum* does not sting and its bite is not very painful (pers. obs.), it can be a serious pest. For example, FOWLER & al. (1993) and MOREIRA & al. (2005) found that *T. melanocephalum* was the most prevalent ant in hospitals in Brazil, and had the highest potential as a vector for pathogens. In fact, MOREIRA & al. (2005) found at least 14 different types of bacteria on *T. melanocephalum* workers collected in the hospitals, including antibiotic resistant strains. *Tapinoma melanocephalum* also can be an agricultural pest because it tends populations of phloem-feeding Hemiptera, such as mealybugs, scale insects, and

aphids, for their honeydew (VENKATARAMAIAH & REHMAN 1989). Hemiptera cause damage by sapping plants of nutrients and increasing the occurrence of diseases, including viral and fungal infections. FOWLER & al. (1994) concluded that *T. melanocephalum* had a great impact on other ant species on banana plantations in Brazil. Under some conditions, *T. melanocephalum* may be beneficial as a bio-control agent. For example, OSBORNE & al. (1995) found that in greenhouses of central Florida, naturally occurring populations of *T. melanocephalum* were important in controlling a serious plant pest, the two-spotted spider mite, *Tetranychus urticae* KOCH, 1836.

Whereas *T. melanocephalum* is most prevalent in disturbed habitats, it has also been reported from natural reserves around the world, including the Baiyer River Wildlife Sanctuary in Papua-New Guinea (WHALEN & MAC-KAY 1988), Reserva Biológica de Una in Brazil (DELABIE & al. 1997), primary rainforest in Chocó, Colombia (ARM-BRECHT & al. 2001), and on many Galapagos islands (CAUSTEN & al. 2006). In the Wapoga River Area of Irian Jaya, Indonesia, SNELLING (2000) found that *T. melanocephalum* "had successfully invaded forest areas where they apparently became quickly assimilated into the native mix; their presence did not seem to adversely affect other ant species there. This apparently benign situation probably would be reversed in the presence of continued disturbance of the habitat."

Tapinoma melanocephalum colonies are polygynous and frequently relocate their nests. In a matter of hours, colonies can move into cargo, which is then shipped worldwide. In fact, LESTER (2005) reported that *T. melanocephalum* was the second most common ant species (after *Pheidole megacephala*) intercepted in freight entering New Zealand between 1997 and 2002. WEBER (1939) reported collecting *T. melanocephalum* from riverboats in Venezuela and Guyana and on a ship between Haiti and New York. *Tapinoma melanocephalum* was found on a train in France, traveling from Paris to Rennes (X. Espadaler, pers. comm.). In Le Carbet, Martinique, a *T. melanocephalum* colony moved overnight into luggage packed for departure, requiring me to shake out everything before repacking.

Many of the most recent first records reported here come from the West Indies, but this is likely an artifact of poor past collection records. For example, PERGANDE (1896) wrote that *T. melanocephalum* was "common on all of the West Indian islands," though at the time the only published West Indian records were from St Thomas and St Vincent (Tab. 5). In contrast, the many first records of *T. melanocephalum* from well-studied parts of Europe and North America dating from the past 15 years (Tabs. 6, 7) suggests a recent spread in these areas, perhaps as a result of the increasing prevalence of air commerce.

Native and exotic range

The general consensus holds that *T. melanocephalum* is from the Old World tropics. The earliest *T. melanocephalum* record from continental Africa (SANTSCHI 1914; Tab. 3) was reported long after this species was already known from many sites in Asia and the Pacific (Tabs. 1, 2), suggesting that *T. melanocephalum* may be a relatively recent arrival in Africa. In addition, site records from continental Africa remain scarce (Fig. 1). In contrast, *T. melanocephalum* has widespread records from India, South-

east Asia, and the western Pacific. The close resemblance between *T. melanocephalum* and several species in this region further indicates that *T. melanocephalum* most probably originated in the Indo-Pacific.

A few lines of evidence appear to support the hypothesis that *T. melanocephalum* originated in the Neotropics: (a) *T. melanocephalum* was first described from French Guiana (FABRICIUS 1793), (b) the salticid spider *Continusa* sp., which is the sole proposed symbiont of *T. melanocephalum*, has only been reported from Costa Rica (SHEPARD & GIBSON 1972), and (c) the subspecies *T. melanocephalum coronatum* is known only from Costa Rica and Jamaica (FOREL 1908). Closer inspection, however, calls into question all three of these lines of evidence. First, subsequent to FABRICIUS (1793), I found no other published report of *T. melanocephalum* from French Guiana. Second, SHEPARD & GIBSON (1972) found that *Continusa* spiders were extremely common in *T. melanocephalum* nests on the Osa Peninsula, but spiders have never been reported in *T. melanocephalum* nests elsewhere. It is also very unusual that SHEPARD & GIBSON (1972) found *T. melanocephalum* was common in a forest canopy and was nesting on the undersides of leaves. I am confident that the ants in this study were misidentified *Tapinoma ramulorum inrectum* FOREL, 1908. According to LONGINO (2006), *T. ramulorum inrectum* "has very distinctive nesting habits and thus is more easily identified in the field than from museum specimens. It makes small carton nests on the undersides of leaves." Finally, after FOREL (1908) described *T. melanocephalum coronatum*, no subsequent researcher has ever reported this taxon, despite extensive ant sampling particularly in Costa Rica, calling its validity into question.

A thorough taxonomic revision of *Tapinoma* would be valuable. Future research on the phylogeny of *Tapinoma* and on the genetic diversity of *T. melanocephalum* populations in different parts of the world should help elucidate further the native and exotic ranges of *T. melanocephalum*.

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Zusammenfassung

Die Ameisenart *Tapinoma melanocephalum* (FABRICIUS, 1793), auch "ghost ant" genannt, ist ein ubiquitärer Lästling innerhalb und außerhalb von Gebäuden in großen Teilen der Tropen und Subtropen und zunehmend auch ein Läst-

ling in Gebäuden temperater Gebiete. Ich erörtere hier die Taxonomie von *T. melanocephalum* und zeige Nachweise von > 1500 Fundorten, um die weltweite Ausbreitung und den wahrscheinlichen geographischen Ursprung der Art zu evaluieren.

Ich habe die frühesten bekannten Nachweise von *T. melanocephalum* für 154 geographische Gebiete (Länder, große Inseln, Inselgruppen, US-Bundesstaaten und Kanadische Provinzen) zusammengetragen, einschließlich vieler, für die ich keine bisher veröffentlichten Nachweise gefunden habe: Anguilla, Antigua & Barbuda, Barbados, Bonaire, Curaçao, Gabon, Gambia, Grenada, Illinois, Italien, Kaiman-Inseln, Kambodja, Kap Verde, Kenya, Komoren, Montserrat, Nevis, Nigeria, Pakistan, Rumänien, St. Kitts, St. Lucia, St. Martin, Michigan, Minnesota, Missouri, North Carolina, Virginia und Wisconsin. *Tapinoma melanocephalum* hat somit eine der weitesten Verbreitungen, die man von Ameisen kennt. Die Art hat sich über die Alte Welt und die Neue Welt, sowohl auf der nördlichen als auch auf der südlichen Hemisphäre, ausgebreitet. In Breitengraden höher als 30° ist die Art aber im Wesentlichen auf Vorkommen innerhalb von Gebäuden beschränkt.

Für die meisten Teile der Welt kann *T. melanocephalum* verlässlich von anderen Ameisenarten unterschieden werden. In Indien, Südostasien und der westlichen Pazifik-Region allerdings leben nahe verwandte Taxa, mit denen *T. melanocephalum* verwechselt werden kann. Dies sind *Tapinoma minutum* MAYR, 1862, *Tapinoma indicum* FOREL, 1895 sowie einige scheinbar intermediäre Formen; daraus kann geschlussfolgert werden, dass *T. melanocephalum* ursprünglich aus der Indo-Pazifischen Region stammt. Zukünftige Untersuchungen der Phylogenie von *Tapinoma* und der genetischen Vielfalt von *T. melanocephalum*-Populationen in verschiedenen Teilen der Welt sollten die Einteilung der Vorkommen in native und exotische im Detail klären können.

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