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Worldwide spread of the African big-headed ant, *Pheidole megacephala* (Hymenoptera: Formicidae)

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Abstract

Originally from Africa, *Pheidole megacephala* (FABRICIUS, 1793) has become a widespread household and agricultural pest in many tropical and subtropical areas. To evaluate the worldwide spread of *P. megacephala*, I compiled published and unpublished specimen records from > 1600 sites. I documented the earliest known *P. megacephala* records for 141 geographic areas (countries, island groups, major islands, and US states), including many locales for which I found no previously published records: Anguilla, Antigua, Aruba, Barbados, Barbuda, British Virgin Islands, California, Central African Republic, Curaçao, Dominica, Galapagos Islands, Gambia, Guyana, Mali, Maryland, Montserrat, Nevis, Nicaragua, Pakistan, Peru, Rwanda, St. Kitts, St. Lucia, Trinidad, and the Turks & Caicos Islands. Many old published records of *P. megacephala* from the Mediterranean region are misidentifications of a local native species, *Pheidole pallidula* (NYLANDER, 1849). All higher latitude records from Europe are probably either indoor records or misidentifications of *P. pallidula*.

Invasive ant species with powerful stings, such as *Solenopsis invicta* BUREN, 1974, have received much media attention. Because *Pheidole megacephala* does not injure humans, this species is often not recognized as a substantial threat. In fact, in areas where it occurs at high density, few native invertebrates persist and *P. megacephala* may be responsible for driving many terrestrial invertebrate species extinct.

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

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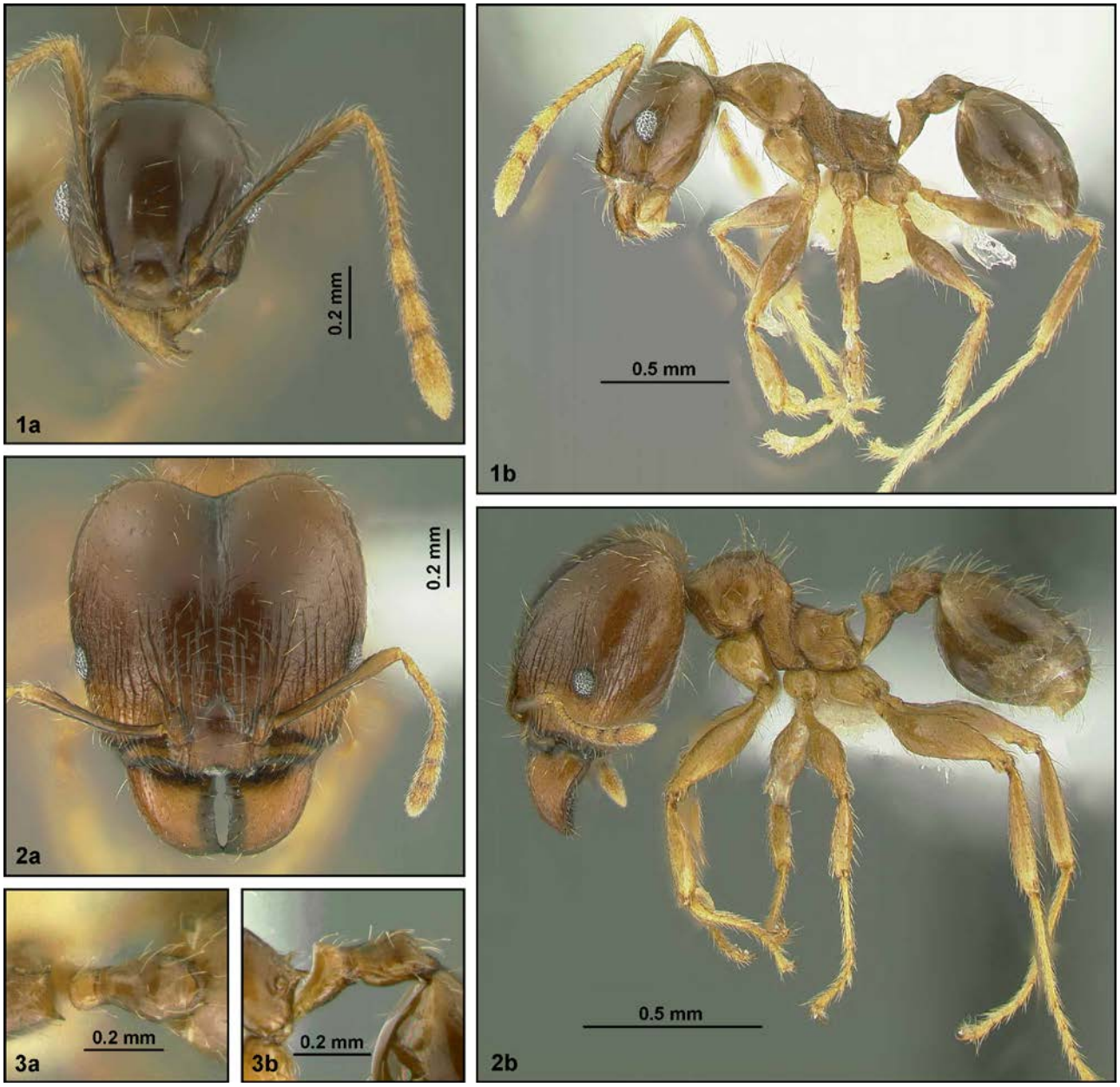
Introduction

"Tramp" ants are species that associate with humans and are spread by human commerce. They travel the world hidden in our plant products, packaging material, building supplies, and heavy machinery such as logging and military equipment. For the most part, tramp ants thrive only in disturbed environments and do not penetrate intact natural habitats. But as humans and their disturbance spread, so do the tramp ants. The ecological importance of most tramp ant species remains undocumented. Several species, however, are known to have dramatic impacts. In past reviews, I have examined the worldwide spread of 19 tramp ant species, some of which appear to have little impact, and others which have great ecological and economic impact (WETTERER 2005, 2008, 2009a, b, c, 2010a, b, c, d, 2011a, b, c, 2012, WETTERER & PORTER 2003, WETTERER & al. 2009, WETTERER & RADCHENKO 2011). Here, I examine the spread of the African big-headed ant, *Pheidole megacephala* (FABRICIUS, 1793), an invasive ant species that appears to have great negative effect on native invertebrates.

Identification and taxonomy

Like most *Pheidole* species, *P. megacephala* shows complete dimorphism (i.e., distinct minor and major workers with few, if any, intermediates) with majors having disproportionately large heads compared to minors (Figs. 1 - 2). Workers of *P. megacephala* are brown, usually with the head and abdomen darker than the mesosoma (Figs. 1 - 2). Total body length is ~ 2 mm for minors and ~ 3.5 mm for majors. For most *Pheidole*, majors are essential for species identification. In *P. megacephala*, however, minors can be easily distinguished from all other *Pheidole* found outside Africa. The post-petiole in *P. megacephala* minors is longer than it is broad, has a prominent ventral convexity visible in side view, and is bell-shaped, broadening towards the gaster when viewed from above (S. Cover, pers. comm., see Fig. 3). Major workers have a heart-shaped head that is smooth and shiny on posterior half (Fig. 2). In *P. megacephala*, minors typically do most of the foraging and majors primarily remain inside the nest, milling seeds and other food items with their powerful mandibles. Outside Africa and the Mediterranean area, the identification of *P. megacephala* is usually fairly simple. In its African range, however, subtle variation within and among closely related *Pheidole* species makes positive identification of *P. megacephala* more difficult.

FABRICIUS (1793) described *Pheidole megacephala* from "Isle de France", the 18th century name for Mauritius, part of the Mascarene Islands in the Indian Ocean east of



Figs. 1 - 3: *Pheidole megacephala.* (1) Minor worker from Nananu-i-Ra, Fiji; (1a) = head; (1b) = lateral view. (2) Major worker from Nananu-i-Ra, Fiji; (2a) = head; (2b) = lateral view. (3) Post-petiole of minor worker in Figure 1; (3a) = dorsal view; (3b) = lateral view. (Photos by G. Alpert).

Madagascar. Currently recognized junior synonyms of *P. megacephala* include *Myrmica trinodis* LOSANA, 1834 from Italy, *Formica edax* FORSKÅL, 1775 from Egypt, *Oecophthora perniciosa* GERSTÄCKER, 1859 from Mozambique, *Oecophthora pusilla* HEER, 1852 from Madeira, *Pheidole janus* SMITH, 1858 from Sri Lanka, *Myrmica laevigata* SMITH, 1855 from Great Britain, *Pheidole laevigata* MAYR, 1862 from Brazil, *Myrmica suspiciosa* SMITH, 1859 from Aru Island, and *Atta testacea* SMITH, 1858 from Brazil.

In addition to the nominal subspecies, there are several other recognized subspecies of *Pheidole megacephala*, all described from Africa or Madagascar: *P. megacephala costauriensis* SANTSCHI, 1915 from Ghana, *P. megacephala duplex* SANTSCHI, 1937 from Angola, *P. megacephala ilgi* FOREL, 1907 from Ethiopia, *P. megacephala impressifrons* (replacement name for *P. megacephala impressiceps* WASMANN, 1904) from South Africa, *P. megacephala melancholica* SANTSCHI, 1912 from Ivory Coast, *P. megacephala nkomoana* FOREL, 1916 from the Democratic Republic of the Congo (formerly Zaïre), *P. megacephala rotundata* FOREL, 1894 from Mozambique, *P. megacephala scabrior* FOREL, 1891 from Madagascar, *P. megacephala speculifrons* STITZ, 1911 from Tanzania, and *P. megacephala talpa* GERSTÄCKER, 1871 from Kenya. The taxonomic boundaries among *P. megacephala*, its subspecies, and closely related *Pheidole* in Africa are uncertain (e.g., see TAYLOR 2010). It seems likely that some or all named *P. megacephala* subspecies in Africa are actually distinct species.

In addition to uncertainties concerning taxonomic limits of *Pheidole megacephala* and closely related taxa, *P. megacephala* also may be confused with several other wide-

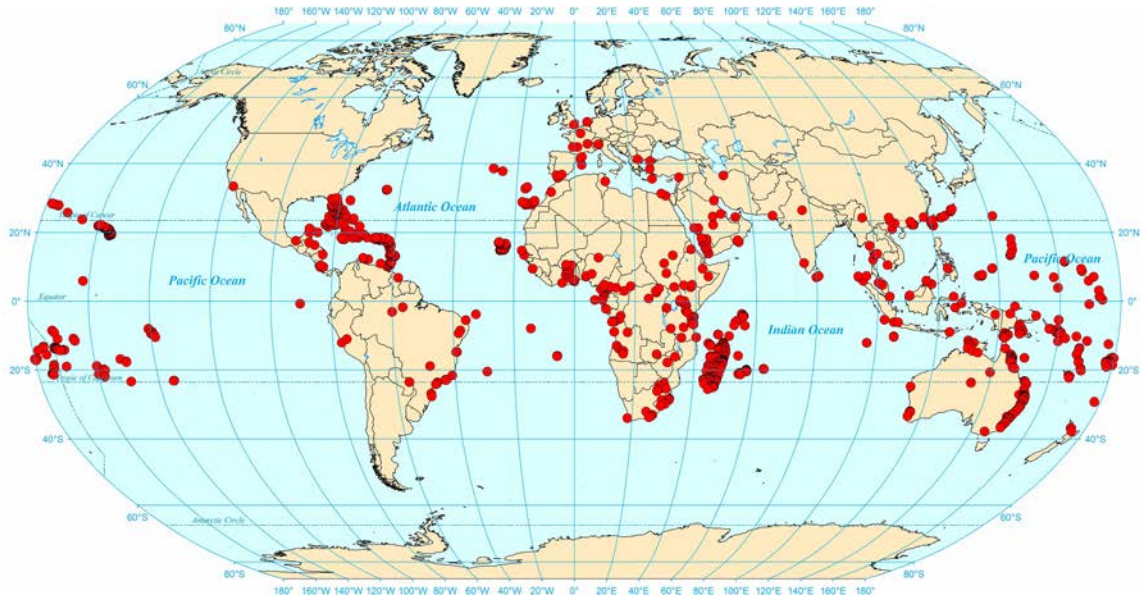


Fig. 4: Worldwide distribution records of *Pheidole megacephala*.

spread *Pheidole* species with similar size and coloration, notably *Pheidole punctulata* MAYR, 1866 (in Africa), *Pheidole pallidula* (NYLANDER, 1849) (in the Mediterranean region), and *Pheidole teneriffana* FOREL, 1893 (worldwide). As noted above, one can distinguish *P. megacephala* minors from *P. punctulata*, *P. pallidula*, and *P. teneriffana* by their bell-shaped postpetiole with a prominent ventral convexity. In addition, in *P. teneriffana* majors, sculpturing covers the entire dorsal surface of the head, but in *P. megacephala*, sculpturing is confined to the anterior half of the head, making the two species simple to differentiate (S. Cover, pers. comm.).

Methods

Using published and unpublished records, I documented the worldwide range of *Pheidole megacephala*. I was conservative and did not include records identified as subspecies of *P. megacephala* other than the nominal *P. megacephala megacephala*. I obtained unpublished site records from museum specimens in the collections of Archbold Biological Station (ABS, identified by M. Deyrup), the British Natural History Museum (BMNH; identified by B. Bolton), the Museum of Comparative Zoology (MCZ; identified by S. Cover), and the Smithsonian Institution (SI; identified by J.K. Wetterer). In addition, I used on-line databases with collection information on specimens by Antweb (www.antweb.org) and the Global Biodiversity Information Facility (www.gbif.org). I also received unpublished records from P.D. Rajan (India) and G. Dlussky (Samoa). Finally, I collected *P. megacephala* specimens on numerous islands of the Pacific (Fiji, Hawaii, Samoa, Solomon Islands, Tonga, and Vanuatu), Atlantic (Azores, Bahamas, Bermuda, Cape Verde, and Madeira), and Caribbean (Anguilla, Antigua, Aruba, Barbados, Barbuda, Curaçao, Dominica, Guadeloupe, Jamaica, Montserrat, Nevis, Puerto Rico, St. Kitts, St. Lucia, St. Martin, St. Vincent, Tobago, Trinidad, Turks & Caicos Islands, and the Virgin Islands), and in Florida. 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, www.fallingrain.com). 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 *Pheidole megacephala* on boats, found in newly imported goods, or intercepted in transit by quarantine inspectors, e.g., FOREL (1907c) recorded *P. megacephala* intercepted in Hamburg transported with orchids shipped from Bangkok. Published records usually included collection dates. In a number of cases, publications did not include the collection dates for specimens, but I was able to determine the date based on information on the collector's travel dates or limit the date by the collector's date of death. For example, Rev. W. H. Fluck collected a wide range of zoological specimens in Nicaragua in 1903, and this seems to be the likely date of his ant specimens at the MCZ.

Results

I compiled *Pheidole megacephala* specimen records from > 1600 sites worldwide (Fig. 4). I documented the earliest known *P. megacephala* records for 141 geographic areas (countries, island groups, major Caribbean islands, and US states; Tabs. 1 - 5), including many locales for which I found no previously published records: Anguilla, Antigua, Aruba, Barbados, Barbuda, California, Central African Republic, Curaçao, Dominica, Galapagos Islands, Gambia, Guyana, Maryland, Montserrat, Nevis, Nicaragua, Pakistan, Peru, St. Kitts, St. Lucia, and Trinidad.

Many old published records of *Pheidole megacephala* from the Mediterranean region were misidentifications of *P. pallidula*. SAUNDERS (1888) reported *P. megacephala* from Gibraltar and Tangiers, but later SAUNDERS (1890) instead reported *P. megacephala* race *pallidula* (= *P. pallidula*) from Gibraltar based on the same collection. BER-

Tab. 1: Earliest known records of *Pheidole megacephala* from Sub-Saharan Africa and adjacent islands of the Indian Ocean. Unpublished specimen records (+) include collector's name, source, and site.

	Earliest record
Mascarene Islands	≤ 1793 (FABRICIUS 1793)
Mozambique	≤ 1859 (GERSTÄCKER 1859 as *Oecophthora perniciosa*)
Tanzania	≤ 1893 (MAYR 1893)
Îles Éparses	1893 (EMERY 1895)
Cameroon	≤ 1896 (MAYR 1896)
Ethiopia	≤ 1897 (EMERY 1897)
Madagascar	≤ 1897 (FOREL 1897)
Sudan	1901 (MAYR 1904)
Comoro Islands	1903 - 1905 (FOREL 1907a)
South Africa	1905 (DIXEY & LONGSTAFF 1907)
Seychelles	1905 (FOREL 1907b)
Congo (Republic)	≤ 1909 (SANTSCHI 1909)
Kenya	1911 - 1912 (SANTSCHI 1914)
Angola	1913 (SANTSCHI 1925)
Senegal	≤ 1914 (SANTSCHI 1914)
Congo (Dem. Rep.)	1915 (WHEELER 1922a)
São Tomé & Príncipe	≤ 1920 (SANTSCHI 1920)
Malawi	≤ 1929 (SMEE 1929 in PRINS & al. 1990)
Guinea	1935 (SANTSCHI 1939)
South Sudan	1939 (WEBER 1943)
Equatorial Guinea	1939 - 1940 (MENOZZI 1942)
Ghana	≤ 1951 (STRICKLAND 1951)
Nigeria	≤ 1962 (SUDD 1962)
Zambia	≤ 1970 (SHEPPE & OSBORNE 1971)
Ivory Coast	1978 (BABACAUH 1982)
Eritrea	1996 - 1997 (HAILE & HOFSVANG 2001)
Gabon	2000 (FISHER 2004)
+ Rwanda	2005 (G. Bizimungu, TAYLOR 2010): Bicumbi
+ Mali	2007 (D. King, TAYLOR 2010): Bamako
+ Central African Republic	2008 (P. Annoyer, TAYLOR 2010): Bangui
+ Gambia	2009 (R.W. Goff, TAYLOR 2010): Abuko Nature Reserve

Tab. 2: Earliest known records of *Pheidole megacephala* from the Mediterranean, Atlantic Islands, Western Europe, and Arabia. * = early records from the Mediterranean may be misidentifications of *Pheidole pallidula*.

Mediterranean	**Earliest record**
* Egypt	≤ 1775 (FORSKÅL 1775 as *Formica edax*)
* Italy	≤ 1834 (LOSANA 1834 as *Myrmica trinodis*)
* Spain	≤ 1856 (ROSENHAUER 1856)
* Algeria	≤ 1883 (ANDRÉ 1883)
* Morocco	≤ 1888 (SAUNDERS 1888)
* Tunisia	1889 (FOREL 1890)
* Corsica	1899 (BIGNELL 1901)
* Syria	1914 (WHEELER & MANN 1916)
Turkey	≤ 1950 (DONISTHORPE 1950)
Greece	1982 - 1988 (COLLINGWOOD 1993)
Macedonia	1987 (PETROV 1994 in KARAMAN 2010)
Atlantic Islands	
Madeira	1850 (HEER 1852 as *Oecophthora pusilla*)
Azores	1865 (GODMAN 1870 as *Pheidole pusilla*)
Canary Islands	1871 (HEYDEN 1872 as *Pheidole pusilla*)
Saint Helena	≤ 1873 (MELLISS 1875 as *Pheidole pusilla*)
Cape Verde	≤ 1885 (JOHNSON 1885 as *Oecophthora pusilla*)
Bermuda	1889 (DAHL 1892a as *Pheidole pusilla*)
Ascension	1889 (DAHL 1892b as *Pheidole pusilla*)
Western Europe	
England	≤ 1855 (SMITH 1855 as *Myrmica laevigata*)
France	≤ 1967 (BERNARD 1968)
Netherlands	1977 (BOER & VIERBERGEN 2008)
Arabia	
Saudi Arabia	1975 (COLLINGWOOD 1985)
Oman	1984 (COLLINGWOOD & AGOSTI 1996)
Kuwait	1988 (COLLINGWOOD & AGOSTI 1996)
Yemen	1991 (COLLINGWOOD & AGOSTI 1996)
United Arab Emirates	≤ 1996 (COLLINGWOOD & AGOSTI 1996)

NARD (1960) questioned whether all records of *P. megacephala* from North African desert were misidentifications "because my own catch in 40 communities in a variety of desert contain only *P. pallidula*, common to the Mediterranean". MARTÍNEZ & ESPADALER (1986) found no *P. megacephala* among the *Pheidole* specimens they examined from Spain. BRAČKO (2006) reported that earlier records of *P. megacephala* from Croatia were actually *P. pallidula*. The same may be true of most or all *P. megacephala* records from other parts of Mediterranean region.

SANTSCHI (1919) listed *Pheidole teneriffana* in Samoa, but in a later list, SANTSCHI (1928) did not include this species. WILSON & TAYLOR (1967) concluded that the *P. teneriffana* specimens listed by SANTSCHI (1919) were actually *P. megacephala*.

Tab. 3: Earliest known records of *Pheidole megacephala* in Asia and neighboring islands. ANIC = Australian National Insect Collection. BMNH = British Natural History Museum. MCZ = Museum of Comparative Zoology.

	Earliest record
Sri Lanka	≤ 1858 (SMITH 1858 as *Pheidole janus*)
Indonesia	1857 (SMITH 1859 as *Myrmica suspiciosa*)
Singapore	1879 (F. Smith, BMNH): site unknown
Burma / Myanmar	1885 - 1887 (EMERY 1889)
Malaysia	1901-1902 (BINGHAM 1905)
India	≤ 1903 (FOREL 1903)
Papua-New Guinea	1907 (R. Bradley & J.H. Burrett, MCZ): Konedobu
Philippines	≤ 1907 (FOREL 1907c)
Taiwan	≤ 1909 (WHEELER 1909)
China	1923 (K. Okamoto, MCZ): Xiamen
Hong Kong	≤ 1928 (WHEELER 1928)
Cambodia	1930 (KARAWAJEW 1935)
Vietnam	1931 (KARAWAJEW 1935)
Christmas Island	1933 (H. Donisthorpe, BMNH): Shore Terraces
Thailand	1970 (D. Ratanaprapa, ANIC): Bangahen
Japan	1972 (SONOBE 1973)
Iran	2005 (GHAHARI & al. 2009)
Cocos (Keeling) Islands	2005 (NEVILLE & al. 2008)
+ Pakistan	2007 (S. & Z. Valliani, MCZ): Karachi

Tab. 4: Earliest known records of *Pheidole megacephala* in Australia and Oceania. Abbreviations as in Table 3.

	Earliest record
Hawaii	≤ 1879 (SMITH 1879 as *Pheidole pusilla*)
Australia	1887 (Turner, BMNH): Cairns
Society Islands	1907 (WHEELER 1908)
Fiji	1915 (MANN 1925)
Line Islands	1922 (WILSON & TAYLOR 1967)
Mariana Islands	1924 (CLOUSE 2007)
Samoa	1924 (SANTSCHI 1928)
Cook Islands	1924 (WILSON & TAYLOR 1967)
Marquesas Islands	1925 (CHEESMAN & CRAWLEY 1928)
Vanuatu	1929 (L.E. Cheesman, BMNH): Espiritu Santo
Tonga	1930 (WETTERER 2002)
Solomon Islands	1932 (R.A. Lever, BMNH): Tulagi
Austral Islands	1934 (WHEELER 1936)
Gambier Islands	1934 (WHEELER 1936)
Palau	1938 (CLOUSE 2007)
Swains Island	1940 (WILSON & TAYLOR 1967)
New Zealand	1942 (BERRY & al. 1997)
Gilbert Islands	1944 (CLOUSE 2007)
US Pacific Territories	1948 (N. KRAUSS, SI): Palmyra
FS Micronesia	1950 (CLOUSE 2007)
Marshall Islands	1950 (CLOUSE 2007)
Tokelau Islands	≤ 1959 (DALE 1959)
Kermadec Islands	1960 (TAYLOR 1971)
New Caledonia	1964 (P. Cochereau, ANIC): Noumea
Niue	1964 (TAYLOR 1967)
Wallis & Futuna	1965 (WILSON & HUNT 1967)

Discussion

In the late 19th century, when the ant fauna in most of the world was still very poorly studied, *Pheidole megacephala* was already recorded from sites across Africa, islands of the Indian Ocean, the Atlantic islands, East Asia, Australia, Hawaii, South America, Central America, and the West Indies (Tabs. 1 - 5). In many parts of the world, the earliest collection date for *P. megacephala* does not appear to indicate the earliest arrival of the ant, but often corresponds to the date of the first thorough ant surveys. Thus, reconstructing the spread of *P. megacephala* out from its original native range is not possible using a chronology of historical specimen records.

WHEELER (1922a) concluded: "In all probability *Pheidole megacephala* is of Ethiopian or Malagasy origin, as it shows a great development of subspecies and varieties in these two regions and nowhere else." I have found no subsequent study that questions this conclusion. MOREAU (2008) sequenced DNA from ~ 140 *Pheidole* species and found *P. megacephala* most closely related to three unidentified species from Madagascar and two unidentified species from Ghana. Further evidence of the origin of *P. megacephala* in the African region comes from its symbionts, including *Orasema fraudulenta* (REICHENSPERGER, 1913), a eucharitid wasp parasitoid of *P. megacephala* recorded from Ethiopia and Yemen (HERATY 1994) and *P. neokohli* WILSON, 1984, a workerless ant that parasitizes colonies of *P. megacephala melancholica* in Africa (WILSON 1984).

Climate appears to be the most important factor in determining the geographic limits of *Pheidole megacephala*. *Pheidole megacephala* is known primarily from tropical lowland regions, but ranges into more temperate latitudes in the Azores (up to 38.5° N; DONISTHORPE 1936), Australia (up to 37.8° S; CLARK 1941), New Zealand (up to 37.8° S; TAYLOR 1961), and South Africa (up to 37.8° S; WHEELER 1922b). Higher latitude records from Europe (Fig. 4, Tab. 2) are probably all either indoor records or misidentifications of *P. pallidula*. Many published records of *P. megacephala* from Mediterranean region also seem likely to be misidentifications of *P. pallidula* (BERNARD 1960).

Tab. 5: Earliest known records of *Pheidole megacephala* from continental South, Central, and North America. CAS = California Academy of Sciences. SI = Smithsonian Institution. Other abbreviations as in Table 3.

	Earliest record
Brazil	≤ 1858 (SMITH 1858 as *Atta testacea*)
Honduras	≤ 1899 (FOREL 1899b)
Mexico	≤ 1899 (FOREL 1899b)
+ Nicaragua	~ 1903 (W.H. Fluck, MCZ): Wounta
Belize	1906 (WHEELER 1907)
Costa Rica	≤ 1908 (FOREL 1908)
+ Guyana	1920 (W.M. Wheeler, MCZ): Georgetown
+ California	1928 (S. Haweis, SI): Catalina Island
Florida	1932 (SMITH 1933)
+ Peru	1939 (W. Weyrauch, SI): Valle Chanchamayo
Venezuela	≤ 1994 (JAFFE & LATTKE 1994)
+ Galapagos Islands	2008 (H. Herrera, Antweb): Puerto Ayora, Santa Cruz
+ Maryland	2009 (K. Howell, CAS): National Aquarium, Baltimore

Pheidole megacephala (as *O. pusilla*) first came to worldwide attention as a result of an outbreak in the houses of Funchal, the largest town on the subtropical Atlantic island of Madeira (HEER 1852). By 1892, *P. megacephala* was also found on many other Atlantic islands as well, including Bermuda, the Azores, Canary Islands, Cape Verde, Ascension Island, and St. Helena (Tab. 2).

The earliest *Pheidole megacephala* records from the Pacific come from Hawaii (SMITH 1879, BLACKBURN & KIRBY 1880, FOREL 1899a). At the start of the 20th century, *P. megacephala* was known in the Pacific only from Hawaii and Australia (WETTERER 2007). Over the course of the 20th century, however, *P. megacephala* spread throughout tropical parts of the Pacific region. After its arrival on one island in a group, *P. megacephala* usually spread to many nearby islands, particularly inhabited ones. In the Hawaiian Islands, BLACKBURN & KIRBY (1880) reported that *P. megacephala* was "one of the commonest ants in Oahu and probably elsewhere". It was subsequently reported from Kaua'i, Molokai, Maui, Niihau, and the Big Island (WHEELER 1934, KRAUSS 1944, BEARDSLEY & TUTHILL 1959). A 1923 expedition to the uninhabited northwestern islands of Hawaii found *P. megacephala* only on Midway (BRYAN 1926). Decades later, *P. megacephala* was first collected on Laysan (BUTLER 1961), and only recently it was reported for the first time from the uninhabited islands of Kure Atoll, Pearl and Hermes Atoll, French Frigate Shoals (NISHIDA 2001), and Kaho'olawe (STARR & al. 2004). *Pheidole megacephala* still has not been reported from some of the northwestern Hawaiian Islands, including Necker Island, Nihoa, Lisianski Island, Johnson Atoll, and Wake Island.

WARD & al. (2006) reported that quarantine inspectors in New Zealand intercepted *Pheidole megacephala* coming into the country far more common than any other ant species, with 890 records between 1955 and 1995. Only a few Pacific island groups still lack records of *P. megacephala*. For some tropical islands (e.g., Nauru, Tuvalu, Phoenix Islands, and Tuamotu Islands), this may be due to a lack of collection information. The scarcity of records from temperate regions suggests that *P. megacephala* may not be able to establish outdoor populations on more temperate Pacific islands (e.g., Bonin Islands, Pitcairn Island, Easter Island, and Juan Fernández Islands).

Tab. 6: Earliest known records of *Pheidole megacephala* in the West Indies. Abbreviations as in Tables 3 and 5.

	Earliest record
US Virgin Islands	1878 (FOREL 1881)
Bahamas	1886 (T. Pergande, SI): Abaco
Saint Vincent	≤ 1893 (FOREL 1893)
Jamaica	≤ 1901 (FOREL 1901)
Cuba	≤ 1905 (WHEELER 1905)
Puerto Rico	1908 (SMITH 1936)
Haiti	1912 - 1913 (WHEELER & MANN 1914)
Tobago	1918 (A. Treadwell, MCZ): Pigeon Point
Dominican Republic	1927 (MENOZZI & RUSSO 1930)
Curaçao	1936 (WEBER 1948)
+ Antigua	1937 (H.E. Box, MCZ): site unknown
+ St. Lucia	1978 (S.A. Marshall, MCZ): site unknown
+ British Virgin Islands	1984 (S.E. & P.M. Miller, MCZ): Buntin Ghut
Guadeloupe	1989 (J.P.E.C. Darlington, MCZ): Souquet
St. Martin	≤ 1994 (JAFFE & LATTKE 1994)
+ Barbados	2003 (J.K. Wetterer, MCZ): Holetown
+ Trinidad	2003 (J.K. Wetterer, MCZ): St. Augustine
+ Curaçao	2004 (J.K. Wetterer, MCZ): Otrabanda
+ Dominica	2004 (J.K. Wetterer, MCZ): Roseau
+ Anguilla	2006 (J.K. Wetterer, MCZ): Meads Bay
+ Aruba	2007 (J.K. Wetterer, MCZ): San Nicolas
+ Montserrat	2007 (J.K. Wetterer, MCZ): Woodlands Bay
+ St. Kitts	2007 (J.K. Wetterer, MCZ): Turtle Beach
+ Nevis	2007 (J.K. Wetterer, MCZ): Charlestown
+ Barbuda	2007 (J.K. Wetterer, MCZ): Codrington
+ Turks & Caicos Islands	2010 (J.K. Wetterer, MCZ): Grace Bay, Providenciales

In recent ant surveys in the West Indies, I found *Pheidole megacephala* on virtually every island I visited, and in many cases, my records are the first published reports

from these islands (Tab. 5). It is unclear whether this is due entirely to poor sampling in the past, or whether *P. megacephala* has only recently spread to many of these islands.

Habitat

Pheidole megacephala tends to be more common in open, disturbed habitats with weedy vegetation that can support high densities of plant-feeding Hemiptera, which the ants tend for honeydew. Typically, *P. megacephala* is largely absent in intact natural forest, even in Hawaii, which lacks any native ant competitors (WETTERER 1998). This absence may be due to a general scarcity of plant-feeding Hemiptera in forested areas. In New Caledonia, JOURDAN (1997) found a variety of exotic ants, including *Paratrechina longicornis* (LATREILLE, 1802) and *Wasmannia auropunctata* (ROGER, 1863), in intact forest and shrub habitats, but found *P. megacephala* only in areas heavily disturbed by human activities. In Fiji, MANN (1925) noted: "Especially in the cultivated districts, it was one of the commonest ants." WETTERER & VARGO (2003) commonly found *P. megacephala* in disturbed coastal areas, but not in relatively undisturbed mountainous areas. In Tonga, WETTERER (2002) found *P. megacephala* in high densities over vast areas in relatively flat, disturbed habitats on the islands of Tongatapu and 'Eua. Yet, on Tongatapu, *P. megacephala* also dominated in Toloa Forest Reserve, a flat, relatively intact natural area. The forested eastern slope of 'Eua, too steep for cultivation, however, had not been invaded by *P. megacephala*. In Australia, *P. megacephala* is most often dominant in disturbed areas (e.g., MAJER 1985, HETERICK 1997, HETERICK & al. 2000), but has also invaded some areas of regenerating and intact forest (HOFFMANN & al. 1999, VANDERWOUDE & al. 2000, CALLUM & MAJER 2009). In the West Indies, *P. megacephala* was particularly common in relatively dry, scrubby habitat, such as the vegetation that covers much of Anguilla and St. Martin (J.K. Wetterer, unpubl.).

In Hawaii, *Pheidole megacephala* is common in the lowlands, at elevations up to 900 m (PERKINS 1913, GAGNÉ 1979, REIMER 1994). MEDEIROS & al. (1986) found *P. megacephala* at elevations up to 1220 m on the Big Island, and up to 1250 m on Maui. WETTERER (1998) found *P. megacephala* in very high densities in and around the geothermal area near the park headquarters in Hawai'i Volcanoes National Park (1200 - 1220 m elevation). The geothermal areas and park buildings appear to serve as warm "habitat islands" that allow *P. megacephala* to extend its ranges to higher elevations. WETTERER & al. (1998) found *P. megacephala* at a disturbed site on Mauna Kea (1770 m elevation). REIMER & al. (1990) reported that *P. megacephala* is also limited by rainfall, and rarely found in very dry (< 38 - 50 cm annual rainfall) or wet areas (> 250 cm annual rainfall). BEARDSLEY & al. (1982) found that periods of heavy rainfall were often followed by a great drop in the numbers of *P. megacephala* in pineapple fields.

Impact

Lack of intercolony aggression may allow *Pheidole megacephala* to attain extremely high densities in exotic locales. FOURNIER & al. (2009) found no aggression among *P. megacephala* workers from different parts of Australia, indicating large-scale unicoloniality.

The impact of *Pheidole megacephala* on other invertebrates is often catastrophic. PERKINS (1913) wrote of *P. megacephala* that: "No native Hawaiian Coleoptera insect can resist this predator, and it is practically useless to attempt to collect where it is well established." ZIMMERMAN (1970) wrote that in Hawaii, "the endemic insect faunas of the lowlands of all the islands mostly have been exterminated throughout the range of the voracious introduced predatory ant *Pheidole megacephala*". In Australia, YOUNG (2000) reported: "The rainforest at Howard Springs Nature Park is dominated by the coastal brown ant [*P. megacephala*], which has eliminated almost all species of native ants, other insect species, snails, spiders and centipedes."

Pheidole megacephala seems to be particularly aggressive towards other ant species. WHEELER (1922a) wrote that *P. megacephala* "ruthlessly destroys and replaces the native ant-faunas". Colonies of *P. megacephala* can exclude other dominant ants, such as *Anoplolepis gracilipes* (SMITH, 1857) and *Linepithema humile* (MAYR, 1868) (FLUKER & BEARDSLEY 1970, JONES & al. 2001). WETTERER (1998) found extremely high densities of *P. megacephala* and *A. gracilipes* occupying mutually exclusive territories in the geothermal area next to the headquarters of Hawaii Volcanoes National Park. Similarly, WETTERER & WETTERER (2004) found *P. megacephala* and *L. humile* occupying mutually exclusive territories in Bermuda and in houses of Madeira. WILSON & TAYLOR (1967) noted that *P. megacephala* generally does not co-occur with other dominant *Pheidole* species, such as *P. fervens* and *P. oceanica*. When I collect live ants with an aspirator, *P. megacephala* workers will quickly cut to pieces other ants, particularly ponerines, in the collection vial (J.K. Wetterer, unpubl.).

Pheidole megacephala often dominates over extensive areas. In some areas, *P. megacephala* may be virtually the only ant present. For example, at one site in Hawaii, JONES & al. (2001) found that *P. megacephala* made up 96.6% of the ants collected. In three heavily infested gardens in Perth, Australia, HETERICK & al. (2000) found that 99.9% of the ants collected in pitfall traps (6885 of 6889) were *P. megacephala*. CALLUM & MAJER (2009) estimated *P. megacephala* biomass in invaded Australian bushland "was larger than that of all other ant species combined by several orders of magnitude". In many places I have collected (e.g., widespread areas on the Pacific islands of Tonga, the Atlantic islands of Cape Verde, and the West Indian islands of Anguilla and St. Martin), I found *P. megacephala* under almost every rock and log and virtually no other ants (WETTERER 2002, 2007).

In 2003, *Pheidole megacephala* was the most common ant I encountered on the nine inhabited islands of Cape Verde. On Monte Gordo, the highest mountain of the island of São Nicolau, Cape Verde, I found no ants but *P. megacephala* at all locales sampled except for sites within 100 m of the mountain's peak. Here, where *P. megacephala* had not yet spread, a small pocket of other ant species survived, including an endemic species known only from this mountain, *Monomorium boltoni* (ESPADALER & AGOSTI, 1987). By now, it seems likely that *P. megacephala* has already spread to the top of Monte Gordo, overrunning what appears to be the last refuge of *M. boltoni*. I may be the last person to have seen *M. boltoni* alive.

Pheidole megacephala may negatively impact vertebrates, both directly and indirectly. BANKO & BANKO (1976)

concluded that in Hawaii, *P. megacephala* "played an indirect though paramount role in the reduction and extinction of all insectivorous birds. *Pheidole* was particularly effective in displacing an exceptionally wide variety of insects, even causing species extinctions in the Coleoptera and Lepidoptera, the two orders of insects which are most important as food to a majority of insectivorous birds of the Hawaiian Islands."

Pheidole megacephala is well known as both an indoor and agricultural pest. As a household pest, it commonly nests inside buildings and feeds on human foodstuffs. In cooler temperate areas, *P. megacephala* may be found nesting exclusively indoors. *Pheidole megacephala* reportedly attacks and chews through electrical wires, communications cables, and irrigation tubing. MELLISS (1875) reported *P. megacephala* (as *P. pusilla*) from St. Helena, writing: "Without exception it is the most abundant insect at St. Helena, where it exists in swarms on both high and low land. Most houses are plagued with it, more especially in wet weather, when it is driven indoors. It attacks everything and even finds its way into beds, hats, brushes, and clothing."

WHEELER (1922a) wrote that *Pheidole megacephala* "has become a great pest in and about dwellings and plantations as it assiduously cultivates coccids on many economic plants". *Pheidole megacephala* can be a substantial agricultural pest on many crops, including pineapples, sugarcane, bananas, coffee, and coconuts, through enhancing populations of the plant-feeding Hemiptera, such as mealybugs, scale insects, and aphids. The ants protect Hemiptera from predators and parasites while feeding on honeydew that the Hemiptera produce. Hemiptera cause crop damage both through sapping plants of nutrients and by increasing the occurrence of diseases, including viral and fungal infections.

The rapid spread and rise to dominance of *Pheidole megacephala* is well illustrated on the main Tongan island of Tongatapu. Although *P. megacephala* specimens were collected on Tongatapu by Maddison in 1975, contemporary collections from Tongatapu by Litsinger (in 1973 - 1974) and Watt (in 1975 - 1977) did not include *P. megacephala*, suggesting that *P. megacephala* populations in the 1970's were limited. By 1995, however, *P. megacephala* dominated vast areas of Tongatapu, where it occurred in almost every log and under almost every rock (WETTERER 2002).

For at least 125 years, *Pheidole megacephala* has maintained its status as the dominant ant in the lowlands of Hawaii. Great outbreaks of *P. megacephala*, however, are often followed by population crashes. The tremendous population explosion of *P. megacephala* on Madeira in the 1850s has long since crashed. WETTERER & al. (2006) estimated that *P. megacephala* now occupies only ~ 0.6% of the land area of Madeira. WHEELER (1910) described an outbreak of *P. megacephala* on the tiny tropical Caribbean island of Culebrita: "I was astonished to find [Culebrita] completely overrun with *Ph. megacephala*. This ant was nesting under every stone and log, from the shifting sand of the sea-beach to the walls of the light-house on the highest point of the island. The most careful search failed to reveal the presence of any other species... It is highly probable that *Ph. megacephala*... had exterminated all the other ants which must have previously inhabited Culebrita" (WHEELER 1910). Later surveys of Culebrita, however, found that the *P. megacephala* populations had greatly diminished (TORRES & SNELLING 1997). MAJER (1985) and MAJER & DE KOCK (1992) documented a rise and decline of *P. megacephala* abundance during post-mining succession in Australia and South Africa.

A great negative impact of *Pheidole megacephala* on native species is not inevitable everywhere. Many authors have long assumed that *P. megacephala* has exterminated most or all of the native ants of Madeira (WETTERER 2006). However, after 150 or more years of residence on Madeira, *P. megacephala* has come to occupy only a tiny range and appears to have had little long-term impact (WETTERER & al. 2006). Most of Madeira may be too cool for *P. megacephala* to dominate. Also, Madeira's vast natural areas may generally lack weedy vegetation that can support high densities of plant-feeding Hemiptera critical for the ecological dominance of invasive ants. Finally, a dominant native ant, *Lasius grandis* FOREL, 1909, inhabiting ~ 84% of Madeira, may actively exclude *P. megacephala*.

A few ant species actually appear to be more common in areas dominated by *Pheidole megacephala*. For example, in the West Indies and Cape Verde, I often found *Cardiocondyla emeryi* FOREL, 1881 associated with high densities of *P. megacephala* (J.K. Wetterer, unpubl.). It may be that *C. emeryi* benefits from *P. megacephala* indirectly, through elimination of competing ant species.

Invasive ant species with powerful stings, such as *Solenopsis invicta* BUREN, 1974, have received much media attention. Because *Pheidole megacephala* does not injure humans, this species is often not recognized as a substantial threat. In fact, in areas where it occurs at high density, few native invertebrates persist and *P. megacephala* may be responsible for driving many terrestrial invertebrate species extinct.

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References

ANDRÉ, E. 1883: Les fourmis. In: ANDRÉ, E. (Ed.): Species des Hyménoptères d'Europe et d'Algérie. Tome Deuxième. – Edmond André, Beaune, 919 + 48 pp.

BABACAUH, K.D. 1982: Role des communautes d'insectes et de l'eau dans la dissemination de *Phytophthora palmivora* (BUTL.) BUTL. emend. BRAS. et GRIFF. dans les cacaoyeres de la Cote d'Ivoir. – Café-Cacao-Thé 26: 31-36.

BANKO, W.E. & BANKO, P.C. 1976: Role of food depletion by foreign organisms in historical decline of Hawaiian forest birds. In: Proceedings of the First Conference of Natural Sciences. – Hawai'i Volcanoes National Park, Hawai'i, pp. 29-34.

BEARDSLEY, J.W., SU, T.H., MCEWEN, F.L. & GERLING, D. 1982: Field investigations on the interrelationships of the big-headed ant, the gray pineapple mealybug, and pineapple mealybug wilt

disease in Hawaii. – Proceedings of the Hawaiian Entomological Society 24: 51-67.

BEARDSLEY, J.W. & TUTHILL, L.D. 1959: Additions to the known insect fauna of Niihau. –Proceedings of the Hawaiian Entomological Society 17: 56-61.

BERNARD, F. 1960: Notes écologiques sur diverses fourmis sahariennes. – Travaux de l'Institut de Recherches Sahariennes 19: 51-63.

BERNARD, F. 1968: Faune de l'Europe et du Bassin Méditerranéen. 3. Les fourmis (Hymenoptera Formicidae) d'Europe occidentale & septentrionale. – Masson, Paris, 411 pp.

BERRY, J.A., GREEN, O.R. & SHATTUCK, S.O. 1997: Species of *Pheidole* WESTWOOD (Hymenoptera: Formicidae) established in New Zealand. – New Zealand Journal of Zoology 24: 25-33.

BIGNELL G.C. 1901: Corsican ants. – Entomologist's Monthly Magazine 37: 127-128.

BINGHAM, C.T. 1905: Report on the aculeate Hymenoptera. – Fasciculi Malayeneses Zoology 3: 19-60.

BLACKBURN, T. & KIRBY, W.F. 1880: Notes on species of aculeate Hymenoptera occurring in the Hawaiian Islands. – Entomologist's Monthly Magazine 17: 85-89.

BOER, P.D. & VIERBERGEN, B. 2008: Exotic ants in the Netherlands (Hymenoptera: Formicidae). – Entomologische Berichten 68: 121-129.

BRAČKO, G. 2006: Review of the ant fauna (Hymenoptera: Formicidae) of Croatia. – Acta Entomologica Slovenica 14: 131-156.

BRYAN, E.H. Jr. 1926: Insects of Hawaii, Johnston Island and Wake Island. – Bernice P. Bishop Museum Bulletin 31: 1-94.

BUTLER, G.D. 1961: Insects and other arthropods from Laysan Island. – Proceedings of the Hawaiian Entomological Society 17: 279-387.

CALLUM, S.K. & MAJER, J.D. 2009: Impacts of an incursion of African big-headed ants, *Pheidole megacephala* (FABRICIUS), in urban bushland in Perth, Western Australia. – Pacific Conservation Biology 15: 102-115.

CHEESMAN, L.E. & CRAWLEY, W.C. 1928: A contribution towards the insect fauna of French Oceania – Part III. Formicidae. – Annals & Magazine of Natural History (10)2: 514-525.

CLARK, J. 1941: Notes on the Argentine ant and other exotic ants introduced into Australia. – Memoirs of the National Museum of Victoria 12: 59-70.

CLOUSE, R.M. 2007: The ants of Micronesia (Hymenoptera: Formicidae). – Micronesica 39: 171-295.

COLLINGWOOD, C.A. 1985: Hymenoptera: Fam. Formicidae of Saudi Arabia. – Fauna of Saudi Arabia 7: 230-302.

COLLINGWOOD, C.A. 1993: A comparative study of the ant fauna of five Greek islands. – Biologia Gallo-hellenica 20: 191-197.

COLLINGWOOD, C.A. & AGOSTI, D. 1996: Formicidae (Insecta: Hymenoptera) of Saudi Arabia (Part 2). – Fauna of Saudi Arabia 15: 300-385.

DAHL, F. 1892a: Die Landfauna von Bermuda. – Ergebnisse der Plankton-Expedition 1889 der Humboldt-Stiftung 1: 105-112.

DAHL, F. 1892b: Die Landfauna von Ascension. – Ergebnisse der Plankton-Expedition 1889 der Humboldt-Stiftung 1: 204-209.

DALE, P.S. 1959: Notes on some insects and other invertebrate collected in the Tokelau Islands. – New Zealand Journal of Zoology 2(4): 1-8.

DIXEY, F.A. & LONGSTAFF, G.B. 1907: Entomological observations and captures during the visit of the British Association to South Africa in 1905. – Transactions of the Entomological Society of London 1907: 309-381.

DONISTHORPE, H. 1936: The ants of the Azores. – Entomologist's Monthly Magazine 72: 130-133.

DONISTHORPE, H. 1950: A first installment of the ants of Turkey. – Annals and Magazine of Natural History (12)3: 1057-1067.

EMERY, C. 1889: Formiche di Birmania e del Tenasserim raccolte da Leonardo Fea (1885-87). – Annali del Museo Civico di Storia Naturale 27: 485-520.

EMERY, C. 1895: Mission scientifique de M. Ch. Alluaud dans le territoire de Diego-Suarez (Madagascar-Nord) (Avril-août 1893). – Annales de la Société Entomologique de Belgique 39: 336-345.

EMERY, C. 1897: Formiche raccolte da Don Eugenio dei Principi Ruspoli, durante l'ultimo suo viaggio nelle regioni dei Somali e dei Galla. – Annali del Museo Civico di Storia Naturale Giacomo Doria (Genova) (2)18(38): 595-605.

FABRICIUS, J.C. 1793: Entomologia Systematica Emendata & Aucta. Secundum Classes, Ordines, Genera, Species, Adjectis Synonimis, Locis Observationibus, Descriptionibus. Tome 2. – C.G. Proft, Hafniae (Copenhagen), 519 pp.

FISHER, B.L. 2004: Diversity patterns of ants (Hymenoptera: Formicidae) along an elevational gradient on Monts Doudou in southwestern Gabon. – California Academy of Sciences, Memoirs 28: 269-286.

FLUKER, S.S. & BEARDSLEY, J.W. 1970: Sympatric associations of three ants: *Iridomyrmex humilis*, *Pheidole megacephala*, and *Anoplolepis longipes* in Hawaii. – Annals of the Entomological Society of America 63: 1290-1296.

FOREL, A. 1881: Die Ameisen der Antille St. Thomas. – Mittheilungen des Münchener Entomologischen Vereins 5: 1-16.

FOREL, A. 1890: Fourmis de Tunisie et de l'Algerie orientale recoltees et decrites par Auguste Forel. – Annales de la Société Entomologique de Belgique 34: 61-76.

FOREL, A. 1893: Formicides de l'Antille St. Vincent, récoltées par Mons. H. H. Smith. – Transactions of the Entomological Society of London 1893: 333-418.

FOREL, A. 1897: Ameisen aus Nossi-Bé, Majunga, Juan de Nova (Madagaskar), den Aldabra-Inseln und Sansibar, gesammelt von Herrn Dr. A. Voeltzkow aus Berlin. – Abhandlungen herausgegeben von der Senckenbergischen Naturforschenden Gesellschaft 21: 185-208.

FOREL, A. 1899a: Heterogyna (Formicidae). – Fauna Hawaiiensis 1: 116-122.

FOREL, A. 1899b: Biologia Centrali-Americana; or, contributions to the knowledge of the fauna and flora of Mexico and Central America. Insecta. Hymenoptera. 3. Formicidae. – R.H. Porter, London, 160 pp.

FOREL, A. 1901: Variétés myrmécologiques. – Annales de la Société Entomologique de Belgique 45: 334-382.

FOREL, A. 1903: Les fourmis des îles Andamans & Nicobares. Rapports de cette faune avec ses voisines. – Revue Suisse de Zoologie 11: 399-411.

FOREL, A. 1907a: Ameisen von Madagaskar, den Comoren und Ostafrika. – Wissenschaftliche Ergebnisse. Systematische Arbeiten 2: 75-92.

FOREL, A. 1907b: Fourmis des Seychelles, Amirantes, Farquhar & Chagos. – Transactions of the Linnean Society of London Zoology (2)12: 91-94.

FOREL, A. 1907c: Formiciden aus dem Naturhistorischen Museum in Hamburg. II. Teil. Neueingänge seit 1900. – Mitteilungen aus dem Naturhistorischen Museum in Hamburg 24: 1-20.

FOREL, A. 1908: Fourmis de Costa-Rica récoltées par M. Paul Biolley. – Bulletin de la Société Vaudoise des Sciences Naturelles 44: 35-72.

FORSKÅL, P. 1775: Descriptiones animalium, avium, amphibiorum, piscium, insectorum, vermium; quae in itinere orientali observavit Petrus Forskal. – Moeller, Hauniae (Copenhagen), 164 pp.

FOURNIER, D., DE BISEAU, J.C. & ARON, S. 2009: Genetics, behaviour and chemical recognition of the invading ant *Pheidole megacephala*. – Molecular Ecology 18: 186-199.

GAGNÉ, W.C. 1979: Canopy-associated arthropods in *Acacia koa* and *Metrosideros* tree communities along an altitudinal transect on Hawaii Island. – Pacific Insects 21: 56-82.

GERSTÄCKER, A. 1859: [Untitled] – Monatsberichte der Königlichen Preussischen Akademie der Wissenschaften zu Berlin 1858: 261-264.

GHAHARI, H., COLLINGWOOD, C.A., TABARI, M. & OSTOVAN, H. 2009: Faunistic notes on the Formicidae (Insecta: Hymenoptera) of rice fields and surrounding grasslands in northern Iran. – Munis Entomology & Zoology 4: 184-189.

GODMAN, F.D.C. 1870: Natural history of the Azores or Western Islands. – John Van Voorst, London, 358 pp.

HAILE, A. & HOFSVANG, T. 2001: Survey of lepidopterous stem borer pests of sorghum, maize and pearl millet in Eritrea. – Crop Protection 20: 151-157.

HEER, O. 1852: Ueber die Haus-Ameise Madeiras. – Zuercherische Jugend von der Naturforschenden Gesellschaft 54: 1-24.

HERATY, J.M. 1994: Classification and evolution of the Oraseminae in the Old World, with revisions of two closely related genera of Eucharitinae (Hymenoptera: Eucharitidae). – Royal Ontario Museum, Life Sciences Contributions 157: 1-174.

HETERICK, B. 1997: The interaction between the coastal brown ant, *Pheidole megacephala* (FABRICIUS) and other invertebrate fauna of Mt Coot-tha (Brisbane, Australia). – Australian Journal of Ecology 22: 218-221.

HETERICK, B.E., CASELLA, J. & MAJER, J.D. 2000: Influence of Argentine and coastal brown ant (Hymenoptera: Formicidae) invasions on ant communities in Perth gardens, Western Australia. – Urban Ecosystems 4: 277-292.

HEYDEN, L. v. 1872: Bericht über die von den Herren Dr. Noll und Dr. Grenacher auf Tenerife gesammelten Insekten. – Bericht über die Senckenbergische Naturforschende Gesellschaft in Frankfurt am Main 1872: 74-90.

HOFFMANN, B.D., ANDERSEN, A.N. & HILL, G.J.E. 1999: Impact of an introduced ant on native rain forest invertebrates: *Pheidole megacephala* in monsoonal Australia. – Oecologia 120: 595-604.

JAFFE, K. & LATTKE, J.E. 1994: Ant fauna of the French and Venezuelan islands in the Caribbean. In: WILLIAMS, D.F. (Ed.): Exotic ants: biology, impact, and control of introduced species. – Westview Press, Boulder, CO, pp. 181-190.

JOHNSON, J.Y. 1885: Madeira, its climate and scenery. Handbook for invalids and other visitors with chapters on the fauna, flora, geology and meteorology. 3rd edn. – Dulau & Co., London, 303 pp.

JONES, V.P., WESTCOTT, D.M., FINSON, N.N. & NISHIMOTO, R.K. 2001: Relationship between community structure and southern green stink bug (Heteroptera : Pentatomidae) damage in macadamia nuts. – Environmental Entomology 30: 1028-1035.

JOURDAN, H. 1997: Are serpentine biota free from successful biological invasions? Southern New Caledonian ant community example. In: JAFFRÉ, T., REEVES, R.D. & BECQUER, T. (Eds.): Proceedings of the 2nd international conference on serpentine ecology. – ORSTOM, Nouméa, pp. 107-108.

KARAMAN, M. G. 2010: An introduction to the ant fauna of Macedonia (Balkan Peninsula), a check list (Hymenoptera, Formicidae). – Natura Montenegrina 8: 151-162.

KARAWAJEW, W. 1935: Neue Ameisen aus dem Indo-Australischen Gebiet, nebst Revision einiger Formen. – Treubia 15: 57-118.

KRAUSS, N.L.H. 1944: Notes on insects and other arthropods from the Islands of Molokai and Maui, Hawaii. – Proceedings of the Hawaiian Entomological Society 12: 81-94.

LOSANA, M. 1834: Saggio sopra le formiche indigene del Piemonte. – Memorie della Reale Accademia delle Scienze di Torino 37: 307-333.

MAJER, J.D. 1985: Recolonization by ants of rehabilitated mineral sand mines on North Stradbroke Island, Queensland, with particular reference to seed removal. – Australian Journal of Ecology 10: 31-48.

MAJER, J.D. & DE KOCK, A.E. 1992: Ant recolonization of sand mines near Richards Bay, South Africa: an evaluation of progress with rehabilitation. – South African Journal of Science 88: 31-35.

MANN, W.M. 1925: Ants collected by the University of Iowa Fiji-New Zealand Expedition. – Studies in Natural History, Iowa University 11(4): 5-6.

MARTINEZ, M.D. & ESPADALER, X. 1986: Revisión de las hormigas ibéricas de la colección M. Medina y nuevos datos de distribución. – Actas de las VIII Jornadas de la Asociación Española de Entomología 1986: 1022-1034.

MAYR, G. 1893: Formiciden von Herrn Dr. Fr. Stuhlmann in Ost-Afrika gesammelt. – Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten 10: 193-201.

MAYR, G. 1896: Beiträge zur Kenntnis der Insektenfauna von Kamerun. 5. Formiciden gesammelt von Herrn Yngve Sjöstedt. – Entomologisk Tidskrift 17: 225-252.

MAYR, G. 1904: Formiciden aus Ägypten und dem Sudan. – Results of the Swedish Zoological Expedition to Egypt and the White Nile 1(9): 1-11.

MEDEIROS, A.C., LOOPE, L.L. & COLE, F.R. 1986: Distribution of ants and their effects on endemic biota of Haleakala and Hawaii Volcanoes National Park: a preliminary assessment. In: Proceedings of the 6th Conference of Natural Sciences. – Hawai'i Volcanoes National Park, pp. 39-52.

MELLISS, J.C. 1875: St. Helena: a physical, historical, and topographical description of the Island, including its geology, fauna, flora, and meteorology. – Reeve, London, 426 pp.

MENOZZI, C. 1942: Formiche dell'isola Fernando Poo e del territorio del Rio Muni (Guinea Spagnol). 24. Beitrag zu den wissenschaftlichen Ergebnissen der Forschungsreise H. Eidmann nach Spanisch-Guinea 1939 bis 1940. – Zoologischer Anzeiger 140: 164-182.

MENOZZI, C. & RUSSO, G. 1930: Contributo alla conoscenza della mirmecofauna della Repubblica Dominicana (Antille). – Bollettino del Laboratorio di Zoologia Generale e Agraria della R. Scuola Superiore d'Agricultura 24: 148-173.

MOREAU, C.S. 2008: Unraveling the evolutionary history of the hyperdiverse ant genus *Pheidole* (Hymenoptera: Formicidae). – Molecular Phylogenetics and Evolution 48: 224-239.

NEVILLE, P.J., O'DOWD, D.J. & YEN, A.L. 2008: Issues and implications for research on disturbed oceanic islands illustrated through an ant survey of the Cocos (Keeling) Islands. – Journal of Insect Conservation 12: 313-323.

NISHIDA, G.M. 2001: NOWRAMP 2000 Terrestrial arthropod report. – U.S. Fish and Wildlife Service, Honolulu, Hawaii. 33 pp.

PERKINS, R.C.L. 1913: Introduction. – Fauna Hawaiiensis 1(6): 1-227.

PRINS, A.J., ROBERTSON, H.G. & PRINS, A. 1990: Pest ants in urban and agricultural areas of southern Africa. In: VANDER MEER, R.K., JAFFE, K. & CEDENO, A. (Eds.): Applied myrmecology: a world perspective. – Westview Press, Boulder, CO, pp. 25-33.

REIMER, N.J. 1994: Distribution and impact of alien ants in vulnerable Hawaiian ecosystems. In: WILLIAMS, D.F. (Ed.): Exo-

tic ants. Biology, impact, and control of introduced species. – Westview Press, Boulder, CO, pp. 11-22.

REIMER, N.J., BEARDSLEY, J.W. & JAHN, G. 1990: Pest ants in the Hawaiian Islands. In: VANDER MEER, R.K., JAFFE, K. & CEDENO, A. (Eds.): Applied myrmecology, a world perspective. – Westview Press, Boulder, pp. 40-50.

ROSENHAUER, W.G. 1856: Die Tiere Andalusiens. – Verlag von Theodor Blaesing, Erlangen, 429 pp.

SANTSCHI, F. 1909: Formicides nouveaux ou peu connus du Congo Français. – Annales de la Société Entomologique de France 78: 349-400.

SANTSCHI, F. 1914: Formicides de l'Afrique occidentale et australe du voyage de Mr. le Professeur F. Silvestri. – Bollettino del Laboratorio di Zoologia Generale e Agraria della R. Scuola Superiore d'Agricultura 8: 309-385.

SANTSCHI, F. 1919: Cinq notes myrmécologiques. – Bulletin de la Société Vaudoise des Sciences Naturelles 52: 325-350.

SANTSCHI, F. 1920: Études sur les maladies & les parasites du cacaoyer & d'autres plantes cultivées à S. Thomé. X. Fourmis de S. Thomé. – Société Portugaise des Sciences Naturelles. Librairie Ferin, Lisbon, 4 pp.

SANTSCHI, F. 1925: Mission Rohan-Chabot en Angola et Rhodesia (1912-1914). – Imprimerie Nationale 4(3): 159-168.

SANTSCHI, F. 1928: Formicidae (Formis). – Insects of Samoa 5: 41-58.

SANTSCHI, F. 1939: Résultats scientifiques des croisières du Navire-École Belge "Mercator" vol. 2. XIV. Formicidae. – Memoires du Musee Royale d'Histoire Naturelle de Belgique (2)15: 159-167.

SAUNDERS, E. 1888: On a collection of ants from Gibraltar and Tangier. – Entomologist's Monthly Magazine 25: 17.

SAUNDERS, E. 1890: Aculeate Hymenoptera collected by J. J. Walker, Esq., R.N., F.L.S., at Gibraltar and in North Africa. (Part I - Heterogyna). – Entomologist's Monthly Magazine 26: 201-205, 289-291.

SHEPPE, W. & OSBORNE, T. 1971: Patterns of use of a flood plain by Zambian mammals. – Ecological Monographs 41: 179-205.

SMITH, F. 1855: Essay on the genera and species of British Formicidae. – Transactions of the Entomological Society of London (2)3: 113-135.

SMITH, F. 1858: Catalogue of hymenopterous insects in the collection of the British Museum. Part VI. Formicidae. – British Museum, London, 216 pp.

SMITH, F. 1859: Catalogue of hymenopterous insects collected by Mr. A. R. Wallace at the Islands of Aru and Key. – Journal of the Proceedings of the Linnean Society of London, Zoology 3: 132-178.

SMITH, F. 1879: Descriptions of new species of aculeate Hymenoptera collected by the Rev. Thos. Blackburn in the Sandwich Islands. – Journal of the Linnean Society of London Zoology 14: 674-685.

SMITH, M.R. 1933: Additional species of Florida ants, with remarks. – Florida Entomologist 17: 21-26.

SMITH, M.R. 1936: The ants of Puerto Rico. – Journal of Agriculture of the University of Puerto Rico 20: 819-875.

SONOBE, R. 1973: Ant fauna of the Sesoko Island, Okinawa. – Sesoko Marine Science Laboratory Technical Report 2: 15-16.

STARR, F., STARR, K. & LOOPE, L.L. 2004: New arthropod records from Kaho'olawe. – Occasional Papers Bernice P. Bishop Museum 79: 50-54.

STRICKLAND, A.H. 1951: The entomology of swollen shoot of cacao I. The insect species involved, with notes on their biology. – Bulletin of Entomological Research 41: 725-748.

SUDD, J.H. 1962: The natural history of *Monomorium pharaonis* (L.) (Hym., Formicidae) infesting houses in Nigeria. – Entomologist's Monthly Magazine 98: 164-166.

TAYLOR, B. 2010: Ants of Africa. Tenth Edition. – <http://antbase.org/ants/africa>, retrieved on 13 December 2010.

TAYLOR, R.W. 1961: Notes and new records of exotic ants introduced into New Zealand. – New Zealand Entomologist 2(6): 28-37.

TAYLOR, R.W. 1967: Entomological survey of the Cook Islands and Niue. 1 – Hymenoptera-Formicidae. – New Zealand Journal of Science 10: 1092-1095.

TAYLOR, R.W. 1971: The ants (Hymenoptera: Formicidae) of the Kermadec Islands. – Insects of New Zealand 10: 81-82.

TORRES, J.A. & SNELLING, R.R. 1997: Biogeography of Puerto Rican ants: a non-equilibrium case? – Biodiversity & Conservation 6: 1103-1121.

VANDERWOUDE, C., BRUYN, L.A.L. DE & HOUSE, A.P.N. 2000: Response of an open-forest ant community to invasion by the introduced ant, *Pheidole megacephala*. – Austral Ecology 25: 253-259.

WARD, D.F., BEGGS, J.R., CLOUT, M.N., HARRIS, R.J. & O'CONNOR, S. 2006: The diversity and origin of exotic ants arriving in New Zealand via human-mediated dispersal. – Diversity and Distributions 12: 601-609.

WEBER, N.A. 1943: The ants of the Imatong Mountains, Anglo-Egyptian Sudan. – Bulletin of the Museum of Comparative Zoology 93: 263-389.

WEBER, N.A. 1948: Studies on the fauna of Curaçao, Aruba, Bonaire and the Venezuelan islands: 14. Ants from the Leeward group and some other Caribbean localities. – Natuurwetenschappelijke Studiekring voor Suriname en Curacao 5: 78-86.

WETTERER, J.K. 1998: Nonindigenous ants associated with geothermal and human disturbance in Hawai'i Volcanoes National Park. – Pacific Science 52: 40-50.

WETTERER, J.K. 2002: Ants of Tonga. – Pacific Science 56: 125-135.

WETTERER, J.K. 2005: Worldwide distribution and potential spread of the long-legged ant, *Anoplolepis gracilipes*. – Sociobiology 45: 77-97.

WETTERER, J.K. 2006: Quotation error, citation copying, and ant extinctions in Madeira. –Scientometrics 67: 351-372.

WETTERER, J.K. 2007: Biology and impacts of Pacific islands invasive species. 3. The African big-headed ant, *Pheidole megacephala* (Hymenoptera: Formicidae). – Pacific Science 61: 437-456.

WETTERER, J.K. 2008: Worldwide spread of the longhorn crazy ant, *Paratrechina longicornis* (Hymenoptera: Formicidae). – Myrmecological News 11: 137-149.

WETTERER, J.K. 2009a: Worldwide spread of the ghost ant, *Tapinoma melanocephalum* (Hymenoptera: Formicidae). – Myrmecological News 12: 23-33.

WETTERER, J.K. 2009b: Worldwide spread of the destroyer ant, *Monomorium destructor* (Hymenoptera: Formicidae). – Myrmecological News 12: 97-108.

WETTERER, J.K. 2009c: Worldwide spread of the penny ant, *Tetramorium bicarinatum* (Hymenoptera: Formicidae). – Sociobiology 54: 811-830.

WETTERER, J.K. 2010a: Worldwide spread of the flower ant, *Monomorium floricola* (Hymenoptera: Formicidae). – Myrmecological News 13: 19-27.

WETTERER, J.K. 2010b: Worldwide spread of the wooly ant, *Tetramorium lanuginosum* (Hymenoptera: Formicidae). – Myrmecological News 13: 81-88.

WETTERER, J.K. 2010c: Worldwide spread of the pharaoh ant, *Monomorium pharaonis* (Hymenoptera: Formicidae). – Myrmecological News 13: 115-129.

WETTERER, J.K. 2010d: Worldwide spread of the graceful twig ant, *Pseudomyrmex gracilis* (Hymenoptera: Formicidae). – Florida Entomologist 93: 535-540.

WETTERER, J.K. 2011a: Worldwide spread of the tropical fire ant, *Solenopsis geminata* (Hymenoptera: Formicidae). – Myrmecological News 14: 21-35.

WETTERER, J.K. 2011b: Worldwide spread of the membraniferous dacetine ant, *Strumigenys membranifera* (Hymenoptera: Formicidae). – Myrmecological News 14: 129-135.

WETTERER, J.K. 2011c: Worldwide spread of the yellow-footed ant, *Nylanderia flavipes* (Hymenoptera: Formicidae). – Florida Entomologist 94: 582-587.

WETTERER, J.K. 2012: Worldwide spread of Roger's dacetine ant, *Strumigenys rogeri* (Hymenoptera: Formicidae). – Myrmecological News 16: 1-6.

WETTERER, J.K., BANKO, P.C., LANIAWE, L.P., SLOTTERBACK, J.W. & BRENNER, G.J. 1998: Nonindigenous ants at high elevations on Mauna Kea, Hawai'i. – Pacific Science 52: 228-236.

WETTERER, J.K., ESPADALER, X., WETTERER, A.L., AGUIN-POMBO, D. & FRANQUINHO-AGUIAR, A.M. 2006: Long-term impact of exotic ants on the native ants of Madeira. – Ecological Entomology 31: 358-368.

WETTERER, J.K. & PORTER, S.D. 2003: The little fire ant, *Wasmannia auropunctata*: distribution, impact, and control. – Sociobiology 42: 1-41.

WETTERER, J.K. & RADCHENKO, A. 2011: Worldwide spread of the ruby ant, *Myrmica rubra* (Hymenoptera: Formicidae). – Myrmecological News 14: 87-96.

WETTERER, J.K. & VARGO, D.L. 2003: Ants (Hymenoptera: Formicidae) of Samoa. – Pacific Science 57: 409-419.

WETTERER, J.K. & WETTERER, A.L. 2004: Ants (Hymenoptera: Formicidae) of Bermuda. – Florida Entomologist 87: 212-221.

WETTERER, J.K., WILD, A.L., SUAREZ, A.V., ROURA-PASCUAL, N. & ESPADALER, X. 2009: Worldwide spread of the Argentine ant, *Linepithema humile* (Hymenoptera: Formicidae). – Myrmecological News 12: 187-194.

WHEELER, W.M. 1905: The ants of the Bahamas, with a list of the known West Indian species. – Bulletin of the American Museum of Natural History 21: 79-135.

WHEELER, W.M. 1907: A collection of ants from British Honduras. – Bulletin of the American Museum of Natural History 23: 271-277.

WHEELER, W.M. 1908: Ants from Moorea, Society Islands. – Bulletin of the American Museum of Natural History 24: 165-167.

WHEELER, W.M. 1909: Ants of Formosa and the Philippines. – Bulletin of the American Museum of Natural History 26: 333-345.

WHEELER, W.M. 1910: Ants: their structure, development and behavior. – Columbia University Press, New York, XXV + 663 pp.

WHEELER, W.M. 1922a: The ants collected by the American Museum Congo Expedition. – Bulletin of the American Museum of Natural History 45: 39-269.

WHEELER, W.M. 1922b: A synonymic list of the ants of the Ethiopian region. – Bulletin of the American Museum of Natural History 45: 711-1004.

WHEELER, W.M. 1928: Ants collected by Professor F. Silvestri in China. – Bollettino del Laboratorio di Zoologia Generale e Agraria della R. Scuola Superiore d'Agricultura 22: 3-38.

WHEELER, W.M. 1934: Revised list of Hawaiian ants. – Occasional Papers Bernice P. Bishop Museum 10: 1-21.

WHEELER, W.M. 1936: Ants from the Society, Austral, Tuamotu and Mangareva Islands. – Occasional Papers Bernice P. Bishop Museum 12(18): 3-17.

WHEELER, W.M. & MANN, W.M. 1914: The ants of Haiti. – Bulletin of the American Museum of Natural History 33: 1-61.

WHEELER, W.M. & MANN, W.M. 1916: The ants of the Phillips Expedition to Palestine during 1914. – Bulletin of the Museum of Comparative Zoology 60: 167-174.

WILSON, E.O. 1984: Tropical social parasites in the ant genus *Pheidole*, with an analysis of the anatomical parasitic syndrome (Hymenoptera: Formicidae). – Insectes Sociaux 31: 316-334.

WILSON, E.O. & HUNT, G.L. 1967: Ant fauna of Futuna and Wallis Islands, stepping stones to Polynesia. – Pacific Insects 9: 563-584.

WILSON, E.O. & TAYLOR, R.W. 1967: Ants of Polynesia. – Pacific Insects Monograph 14: 1-109.

YOUNG, G. 2000: The coastal brown or big headed ant. – Agnote 152: 1-4.

ZIMMERMAN, E.C. 1970: Adaptive radiation in Hawaii with special reference to insects. –Biotropica 2: 32-38.