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Worldwide spread of *Tetramorium caldarium* (Hymenoptera: Formicidae)

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Abstract

Tetramorium caldarium (ROGER, 1857) is a tramp ant species originally from Africa that has dispersed around the world through human commerce. From 1862 to 1979, *T. caldarium* was considered a junior synonym of *T. simillimum* (SMITH, 1851). To document the worldwide spread of *T. caldarium*, we compiled > 300 published and unpublished specimen site records. In addition, in order to assess their species boundaries, we examined the type specimens of *T. caldarium* and *T. simillimum*.

We documented *Tetramorium caldarium* records from 67 geographic areas (countries, island groups, major Caribbean islands, and US states), including several for which there are no previously published records: Austral Islands, Australia, Benin, Cameroon, Cayman Islands, Congo (Republic), Curaçao, Dubai, El Salvador, Gabon, Guadeloupe, Indonesia, Jamaica, Martinique, Namibia, Panama, Scotland, Senegal, South Africa, Tanzania, and Uganda. *Tetramorium caldarium* is truly cosmopolitan, with records spread across seven of the world's eight bioregions (all except the Antarctic, which has no ants). *Tetramorium caldarium* records are particularly common on Atlantic islands and from greenhouses and heated buildings in temperate Europe.

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

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Introduction

FOREL (1911) listed 15 tramp ant species, spread by human commerce, which had achieved or were in the process of achieving broad cosmopolitan distributions. Previous reviews have examined the worldwide spread of 12 of FOREL's (1911) cosmopolitan species (WETTERER 2005, 2007, 2008, 2009a, b, c, 2010a, b, c, 2011a, 2012d, e, WETTERER & al. 2009). Of these, eight have become major global pests: *Anoplolepis gracilipes* (SMITH, 1857), *Linepithema humile* (MAYR, 1868), *Monomorium destructor* (JERDON, 1851), *Monomorium pharaonis* (LINNAEUS, 1758), *Paratrechina longicornis* (LATREILLE, 1802), *Pheidole megacephala* (FABRICIUS, 1793), *Solenopsis geminata* (FABRICIUS, 1804), and *Tapinoma melanocephalum* (FABRICIUS, 1793). Four others are widespread, but have not developed into significant pests: *Cardiocondyla emeryi* FOREL, 1881, *Monomorium floricola* (JERDON, 1851), *Tetramorium bicarinatum* (NYLANDER, 1846), and *Tetramorium lanuginosum* MAYR, 1870. All 12 of these species are relatively simple to recognize outside their native ranges. The remaining three names on FOREL's (1911) list, *Nylanderia vividula* (NYLANDER, 1846), *Odontomachus haematodus* (LINNAEUS, 1758), and *Tetramorium simillimum* (SMITH, 1851), have all posed significant taxonomic problems. These three names, as used by FOREL (1911), each represented multiple species with different geographic ranges, not single species. For "*N. vividula*" and "*O. haematodus*", it now appears that none of the constituent species are actually cosmopolitan tramps. What FOREL (1911) considered "*T. simillimum*" appears to represent at least two species: *T. simillimum* and *T. caldarium* (ROGER, 1857). Even without *T. caldarium*, *T. simillimum* is still a highly variable species and might actually consist of more than one species (FHG, unpubl.). At present, *T. caldarium* is the only species in this complex whose taxonomic boundaries we can confidently define. Here, we examine the worldwide spread of *T. caldarium*.

Taxonomic history

ROGER (1857) described *Tetrogmus caldarius* (= *T. caldarium*) from a tropical hothouse growing pineapples in Rauden, Prussia (now in Poland, not Germany as listed by BOLTON 1979 and others). However, shortly after his original description, ROGER (1862) designated *T. caldarium* to be a junior synonym of *T. simillimum*, and this species remained in synonymy for more than a century, from 1862 to 1979. This situation changed with the extensive revisions of the genus *Tetramorium* undertaken by BOLTON (1976, 1977, 1979, 1980, 1985). Although BOLTON (1977) initially continued to treat *T. caldarium* as a junior synonym of *T. simillimum*, BOLTON (1979) later revived *T.*

caldarium as a valid species, based on distinct morphological differences.

Junior synonyms of *Tetramorium caldarium* include the African taxa *T. pusillum hemisi* WHEELER, 1922 from the Democratic Republic of Congo (Zaire), *T. minutum* DONISTHORPE, 1942 from Egypt, and *T. pauper transformans* SANTSCHI, 1914 from Kenya (BOLTON 1979, 1980, 1985, 1995).

BOLTON (1979) distinguished *Tetramorium caldarium* from *T. simillimum* using four characters that can differentiate the two species. Compared with *T. simillimum*, *T. caldarium* has "frontal carinae less strongly developed", "antennal scrobes feeble", "cephalic sculpture weak", and "head differently shaped" (i.e., *T. simillimum* with head broadening behind eyes and *T. caldarium* with no such broadening). Based on our examination, we concur with BOLTON (1979). The four characters listed above distinguish both species immediately throughout their whole distribution ranges. BOLTON (1979, 1980) placed both *T. caldarium* and *T. simillimum* in the *T. simillimum* species-group. Most of the other 26 members of this species group are known only from Sub-Saharan Africa, with a few species also found in the southwest of the Arabian Peninsula, Madagascar, and neighboring islands in the western Indian Ocean. Based on this species richness centered in the Afrotropical region, it is likely that *T. caldarium* and *T. simillimum* are both native to this region. This conclusion is also supported by their wide distribution ranges in Africa and their occurrence in undisturbed and anthropogenic habitats.

Tetramorium caldarium workers (Fig. 1) are similar in body size, proportions, and color to another tramp ant species, *Wasmannia auropunctata* (ROGER, 1863). *Wasmannia auropunctata*, however, is slightly smaller, has longer setae on the face and dorsum, longer propodeal spines, and a more rectangular petiole in side view. Another important key difference is the presence of a two-segmented antennal club in *W. auropunctata* compared to the three-segmented club of *T. caldarium*. The latter also has very weak frontal carinae and reduced antennal scrobes while both of these characters are strongly developed in *W. auropunctata*.

Methods

Using published and unpublished records, we documented the known worldwide range of *Tetramorium caldarium.* We obtained unpublished site records from museum specimens in the collections of the Archbold Biological Station (ABS, identified by M. Deyrup), the California Academy of Science (CAS, identified by FHG), the Natural History Museum London (BNHM, identified by B. Bolton and FHG), the Museum of Comparative Zoology (MCZ, identified by B. Bolton, S. Cover, X. Espadaler, and FHG), and the Smithsonian Institution (SI, identified by B. Bolton). In addition, we used on-line databases with collection information on specimens by Ants of Africa (TAYLOR 2012), AntWeb (www.antweb.org), the Australian National Insect Collection (ANIC), the Essig Museum of Entomology (UCB Essig), Fauna Europaea (RADCHENKO 2004), and the Global Biodiversity Information Facility (www.gbif.org). Finally, JKW collected *T. caldarium* specimens on numerous Atlantic and Caribbean islands, as well as in Florida, Dubai, and El Salvador.

We obtained geographic coordinates for collection sites from published references, specimen labels, maps, or geography web sites (e.g., earth.google.com, www.tageo.com, and www.fallingrain.com). If a site record listed a geographic region rather than a "point locale", and we had no other record for this region, we 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. We did not map records of *Tetramorium caldarium* on boats, found in newly imported goods or intercepted in transit by quarantine inspectors, e.g., *T. caldarium* specimens intercepted in 1936 in New York on a shipment from the Dominican Republic (SI and BMNH). Published records usually included collection dates. In a number of cases, publications did not include the collection dates for specimens, but we were able to determine them based on information on the collector's travel dates or limited them by the collector's date of death.

Results

We compiled *Tetramorium caldarium* specimen records from > 300 sites worldwide (Fig. 2), documenting the earliest known *T. caldarium* records for 67 geographic areas (Tabs. 1 - 3), including several for which there are no previously published records: Austral Islands, Australia, Benin, Cameroon, Cayman Islands, Congo (Republic), Curaçao, Dubai, El Salvador, Gabon, Guadeloupe, Indonesia, Jamaica, Martinique, Namibia, Panama, Scotland, Senegal, South Africa, Tanzania, and Uganda. Our only records of *T. caldarium* from France, Germany, and Monaco came from the Fauna Europaea website (RADCHENKO 2004) and lacked any specimen data. BOROWIEC (2014) reported *T. caldarium* from France, Germany, and Monaco in his catalog of European ants based on this same source (L. Borowiec, pers. comm.). We obtained a record of *T. caldarium* from Scotland on the Myrmecology Forum on antfarm.org (http://antfarm.yuku.com/reply/99651/Queen-ID-request-Small-pictures#reply-99651).

In a number of cases, specimens originally identified as *Tetramorium simillimum* were re-identified in later papers as *T. caldarium*, from e.g., Madeira (SAUNDERS 1903, WETTERER & al. 2007), the Imatong Mountains, South Sudan (WEBER 1943, BOLTON 1980), and Saint Helena (TAYLOR & WILSON 1961, BOLTON 1976, 1980). BOLTON (1977) listed three *T. simillimum* records he later re-identified as *T. caldarium*: from Tres Hermanos and Mayaguez, Puerto Rico (BOLTON 1979) and Pombas, Cape Verde (BOLTON 1980). BOLTON (1979) wrote that the only *T. caldarium* records he knew from the Oriental and Indo-Australian biogeographic regions were three series from India and one from New Caledonia (all at the MCZ).

Problematic records: MEINERT (1861) reported *Myrmica caldaria* (= *T. caldarium*) from Rosenborg Castle Gardens in Copenhagen, Denmark, but BOLTON (1995) listed MEINERT (1861) as having described the gynandromorph of *T. simillimum* and the male of *T. caldarium*. Bolton (pers. comm.) did not personally examine any Danish *Tetramorium* specimens. In the unsorted *Tetramorium* specimens at the Smithsonian, we found three specimens labeled "Copenhagen 2 / 3 - 1858" and "Copenhagen 17 / 5 - 1858" that are almost certainly specimens collected by Meinert. Stefan Cover identified these as *T. caldarium*; we therefore consider all of MEINERT's (1861) records to be *T. caldarium* (and the record of *T. simillimum* from Denmark to be an error).

Fig. 1: *Tetramorium caldarium*. (a) Head of worker from Hawaii; (b) lateral view of the same worker; (c) dorsal view of the same worker (photos by Eli Sarnat).

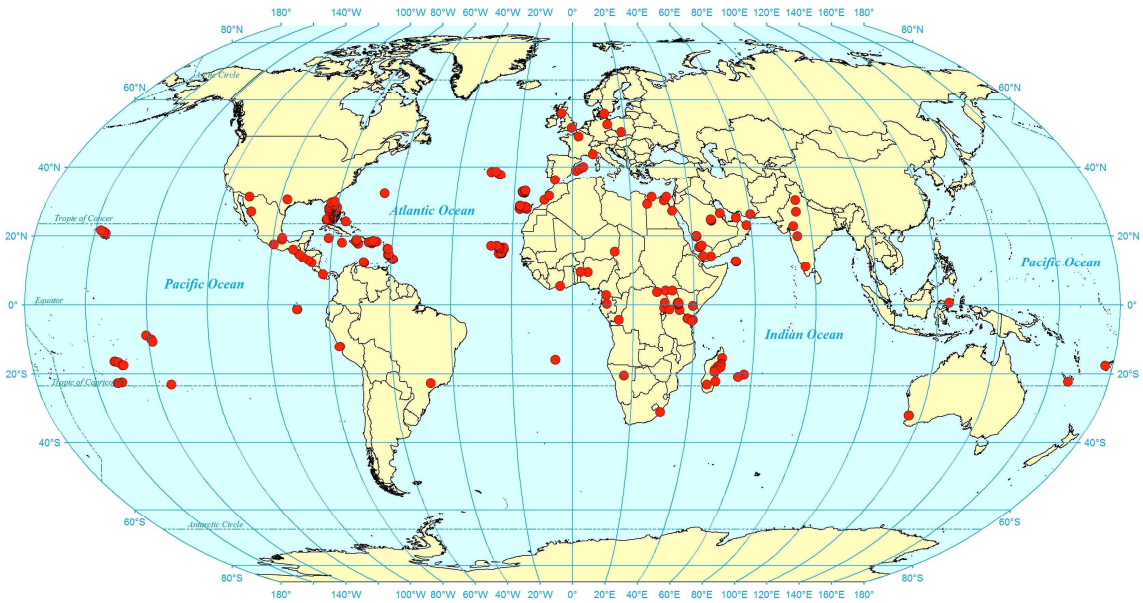

Fig. 2: Distribution records of *Tetramorium caldarium.*

Tab. 1: Earliest known records for *Tetramorium caldarium* from Africa, the Arabian Peninsula, and neighboring islands. Unpublished records include collector, museum source, and site. BMNH = Natural History Museum London. CAS = California Academy of Science. MCZ = Museum of Comparative Zoology. + = no previously published record. * = earliest record unconfirmed.

	Earliest record
Madeira	1847 - 1858 (T.V. Wollaston, BMNH): multiple sites
Kenya	1911 (SANTSCHI 1914 as *T. pauper transformans*)
Congo (Dem. Rep.)	1913 (WHEELER 1922 as *T. pusillum hemisi*)
Egypt	1935 (DONISTHORPE 1942 as *T. minutum*)
South Sudan	1939 (BOLTON 1980)
Mascarene Islands	≤ 1951 (BOLTON 1980)
Cape Verde	1953 (BOLTON 1980)
Saint Helena	1958 (BOLTON 1980)
Ivory Coast	1963 (BOLTON 1980)
Nigeria	≤ 1980 (BOLTON 1980)
+ Cameroon	1980 (D. Jackson, BMNH): Nkoemvon
Saudi Arabia	1983 (COLLINGWOOD 1985)
Oman	1984 (COLLINGWOOD & AGOSTI 1996)
Madagascar	1991 (A. Pauly, CAS): Ambatondrazaka
Canary Islands	1993 (ESPADALER & BERNAL 2003)
+ Tanzania	1993 (A.M. Varela, BMNH): Bukoba
Yemen	1993 (COLLINGWOOD & AGOSTI 1996)
Morocco	≤ 1993 (CAGNIANT & ESPADALER 1993)
+ Namibia	1998 (B.L. Fisher, CAS): Waterberg NP
+ South Africa	2000 (S. van Noort, CAS): Umtanvuna Nature Reserve
+ Uganda	2001 (A. Abera, CAS): Kamunyinga
+ Congo (Rep.)	2007 (Y. Braet & E. Zassi, TAYLOR 2012): Brazzaville
+ Gabon	2008 (A. Fotso Kuate, TAYLOR 2012): Awome
+ Senegal	2010 (F.B. Ndiaye, TAYLOR 2012): Katané
+ Benin	2012 (J.F. Vayssieres, TAYLOR 2012): Korobourou
+ Dubai	2012 (J.K. Wetterer, MCZ): Palm Deira

NOVAK & SADIL (1941) listed *Tetramorium simillimum* from Upper Silesia, which almost certainly refers to the type locale of *T. caldarium* in Silesian Prussia (ROGER 1857), now in Poland.

Tab. 2: Earliest known records for *Tetramorium caldarium* from Europe, Asia, Oceania, and neighboring islands. UCB Essig = Essig Museum of Entomology. Abbreviations as in Table 1.

Europe	**Earliest record**
Poland	≤ 1857 (ROGER 1857)
Denmark	1858 (MEINERT 1861)
England	1910 (BOLTON 1979)
Azores	1930 (A. Méquignon, AntWeb): Furnas, Sao Miguel
France	≤ 2004 (RADCHENKO 2004)
Germany	≤ 2004 (RADCHENKO 2004)
Monaco	≤ 2004 (RADCHENKO 2004)
Spain	2004 (REYES & ESPADALER 2005)
Balearic Islands	2004 (GOMEZ & ESPADALER 2006)
+ Scotland	≤ 2011 (Cantiacus, antfarm.yuku.com): Glasgow Botanic Gardens
Asia & Oceania	**Earliest record**
New Caledonia	1950 (BOLTON 1979)
India	1962 (BOLTON 1980)
+ Indonesia	1985 (R.H.L. Disney, BMNH): Dumoga-Bone NP
+ Australia	1986 (B. Heterick, pers. comm.): Bicton
Society Islands	1992 (MORRISON 1996)
Gambier Islands	1996 (MORRISON 1997)
Marquesas Islands	1996 (MORRISON 1997)
Iran	2005 (GHAHARI & COLLINGWOOD 2011)
+ Austral Islands	2006 (P.D. Krushelnycky, UCB Essig): Rimatara
Hawaii	2007 (R. Chang, AntWeb): Haleiwa
Fiji	2008 (SARNAT 2009)

Several specimens reported as *Tetramorium caldarium* on AntWeb from Madagascar and South Africa were misidentifications of local native *Tetramorium* species (FHG, unpubl.).

Discussion

BOLTON (1980) wrote that both *Tetramorium simillimum* and *T. caldarium* "have been widely distributed over the earth by human commerce. In the main their outdoor distribution is more or less restricted to the tropical and subtropical zones, but both are found fairly frequently in the temperate zones, associated with man and living in hothouses, zoos, or other constantly heated buildings". Our analyses match BOLTON's (1980: figs. 9 - 11) general assessment of widespread tropical and subtropical outdoor populations for *Tetramorium caldarium*. On Atlantic Islands (e.g., Bermuda, the Azores, Madeira, the Canary Islands, Cape Verde, and St Helena), *T. caldarium* was found much more commonly than *T. simillimum* (ESPADALER &

Tab. 3: Earliest known records for *Tetramorium caldarium* from the New World. Abbreviations as in Table 1.

	Earliest record
Puerto Rico	1908 (BOLTON 1979)
Haiti	1912 - 1913 (BOLTON 1979)
Mexico	1929 (collector unknown, MCZ): Coatepec
Brazil	1965 (BOLTON 1979)
Peru	1967 (BOLTON 1979)
Florida	1968 (BOLTON 1979)
Nicaragua	1986 (PERFECTO 1990)
+ Panama	1987 (D.M. Olson, MCZ): Cerro Pata de Macha
Bahamas	1989 - 1994 (MORRISON 1998)
Galapagos	1992 (PEZZATTI & al. 1998)
Barbados	1998 (E.O. Wilson & S.P. Cover, MCZ): Casuarina Beach Club
Bermuda	2002 (WETTERER & WETTERER 2004)
Texas	≤ 2003 (COOK 2003)
+ Curaçao	2004 (J.K. Wetterer, MCZ): Van Engelen, zoo
+ Cayman Islands	2008 (J.K. Wetterer, MCZ): Foster Village
+ Martinique	2008 (J.K. Wetterer, MCZ): Fort-de-France
+ Jamaica	2010 (J.K. Wetterer, MCZ): Mona
+ Guadeloupe	2011 (J.K. Wetterer, MCZ): Pointe-à-Pitre
Guatemala	≤ 2012 (BRANSTETTER & SAENZ 2012)
+ El Salvador	2012 (J.K. Wetterer, MCZ): San Salvador
Dominican Republic	2012 (LUBERTAZZI & ALPERT 2014)

BERNAL 2003, WETTERER & WETTERER 2004, WETTERER & al. 2004, 2006). With the exception of one record from an urban plaza in Córdoba, Spain (REYES & ESPADALER 2005), all known outdoor records of *T. caldarium* at latitudes higher than 32° come from islands in the Atlantic (Bermuda, the Azores, and Madeira; WETTERER & WETTERER 2004, WETTERER & al. 2004, 2007) and the Mediterranean (the Balearic Islands; GOMEZ & ESPADALER 2006). In addition, *T. caldarium* appears to be more common than *T. simillimum* in greenhouses and heated buildings, primarily in temperate areas. Whereas there are many recent indoor records of *T. caldarium* from temperate areas (Tab. 2), we found only one confirmed published record of *T. simillimum* from a temperate site: its type locale in England (SMITH 1851). In addition, unconfirmed temperate records of *T. simillimum* come from England (SAUNDERS 1880, EMERY 1909), Winnipeg, Canada (AYRE 1977), France (BERNARD 1968), and Estonia (RADCHENKO 2004). It is possible that most or all unconfirmed temperate records of *T. simillimum* were actually *T. caldarium*.

In contrast, in most tropical areas (except Atlantic islands), *Tetramorium simillimum* has been collected more often than has *T. caldarium.* For example, on West Indian islands, JKW frequently collected *T. simillimum*, but only rarely encountered *T. caldarium*. Unfortunately, most specimen records published as *T. simillimum* between 1862 and 1979, when *T. caldarium* was considered a junior synonym, have never been re-examined. It would be useful for researchers to confirm the species identity of all museum specimens previously identified as *T. simillimum*.

It is unclear whether the differences in the distributions of *Tetramorium simillimum* and *T. caldarium* reflect ecological differences or whether they are largely due to chance differences in where each species has been introduced. However, it appears that *T. caldarium* is a fairly arid-adapted species that does not like shade or forests or woodland in its native range in Africa, whereas *T. simillimum* is predominantly found in forested habitats (rainforests, dry forests, woodland).

Although both *Tetramorium simillimum* and *T. caldarium* are certainly widespread in disturbed environments, they remain quite inconspicuous and we found no evidence that either species has significant ecological impacts. This contrasts with the great impacts reported for the very similar appearing *Wasmannia auropunctata* (WETTERER & PORTER 2003).

With the addition of *Tetramorium caldarium* and the removal of *Nylanderia vividula* and *Odontomachus haematodus* from FOREL'S (1911) list, only two of the 14 cosmopolitan species are native to the New World: *Linepithema humile* and *Solenopsis geminata*. In addition to those on FOREL's (1911) list, almost 30 more ant species have become cosmopolitan, with broad ranges in both the Old World and New World (e.g., see WETTERER 2011b, c, d, e, 2012a, b, c, f, 2013c, 2014a, b, WETTERER & RADCHENKO 2011, WETTERER & al. 2012). Although most of these new cosmopolitans are inconspicuous Old World species, two of the greatest ecological and economic pests are New World natives: *Solenopsis invicta* BUREN, 1972 and *Wasmannia auropunctata* (WETTERER 2013a, b). With the modern global economy, one can expect more new cosmopolitans in the future.

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