

Worldwide spread of Emery's sneaking ant, *Cardiocondyla emeryi* (Hymenoptera: Formicidae)

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Abstract

Cardiocondyla emeryi FOREL, 1881 has long been recognized as a cosmopolitan ant species, spread around the world by human commerce. To evaluate its worldwide distribution, I compiled published and unpublished *C. emeryi* specimen records from > 1000 sites. I documented the earliest known records for 109 geographic areas (countries, island groups, major islands, and US states), including several for which I found no previously published records: Antigua, Aruba, Barbuda, Bonaire, Comoro Islands, Congo (Republic), Curaçao, Dominica, Gambia, Honduras, Îles Éparses, Martinique, Montserrat, Nevis, St Lucia, St Martin, Trinidad, Turks & Caicos Islands, and Vanuatu.

Originally from Africa, *Cardiocondyla emeryi* is now one of the most widespread ants in tropical and subtropical areas. Although *C. emeryi* is usually very inconspicuous, an exceptional aspect of its ecology is that it is one of the few ant species that actually appears to be more common in areas dominated by African big-headed ant, *Pheidole megacephala* (FABRICIUS, 1793). In areas where *P. megacephala* occurs at high density, few native invertebrates persist. Yet, at sites with high densities of *P. megacephala* on islands of the Pacific, Atlantic, and the West Indies, I usually also found *C. emeryi*. It may be that *P. megacephala* benefits *C. emeryi* indirectly, through elimination of competing ant species.

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

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Introduction

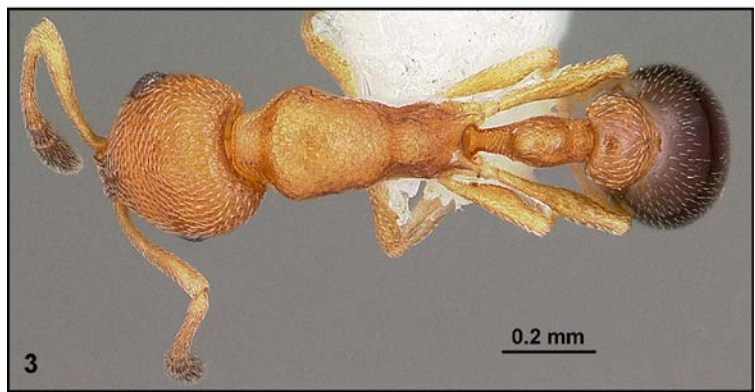
More than 100 years ago, FOREL (1911) compiled a list of 15 ant species, spread by human commerce, which had achieved or were in the process of achieving broad cosmopolitan distributions. In previous reviews, I examined the known distribution of eleven of FOREL's (1911) cosmopolitan ant species (WETTERER 2005, 2007, 2008, 2009a, b, c, WETTERER & al. 2009, WETTERER 2010a, b, c, 2011). Of these eleven, eight have become widespread 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). Three other species, though widespread, have remained relatively inconspicuous and have caused little or no noticeable impact in their native and exotic ranges: *Monomorium floricola* (JERDON, 1851), *Tetramorium bicarinatum* (NYLANDER, 1846), and *Tetramorium lanuginosum* MAYR, 1870. Here, I examine the worldwide spread of one of the remaining four species on FOREL's (1911) list: *Cardiocondyla emeryi* FOREL, 1881 (Figs. 1 - 3), perhaps the most inconspicuous ant on the list.

Taxonomy

FOREL (1881) described *Cardiocondyla emeryi* from St Thomas, US Virgin Islands, naming the species after the

eminent Italian myrmecologist, Carlo Emery. Junior synonyms of *C. emeryi* include *Cardiocondyla emeryi rasalamae* FOREL, 1891 from Madagascar, *Cardiocondyla emeryi mahdii* KARAVAIEV, 1911 from Sudan, *Cardiocondyla nuda nereis* WHEELER, 1927 from Norfolk Island, and *Cardiocondyla mauritia* DONISTHORPE, 1946 from Mauritius (SEIFERT 2003).

SEIFERT (2003) noted great geographic variation among *Cardiocondyla emeryi* populations: "The type specimens of *C. emeryi* and *C. emeryi* var. *rasalamae* show the external morphology of separate species. However, a consistency of these differences was not demonstrable on a larger scale and both taxa are assumed to represent different genotypes of the same polymorphic species. The cosmopolitan population of *C. emeryi* shows extreme polymorphism in microsculpture clearly exceeding the usual intraspecific variability known for *Cardiocondyla*." SEIFERT (2003) distinguished three forms of *C. emeryi*: SC1 (26% of specimens examined, including the types of *C. emeryi rasalamae*, *C. emeryi mahdii*, and *C. nuda nereis*), SC2 (19% of specimens examined, including the type of *C. mauritia*), and SC3 (55% of specimens examined, including the type of *C. emeryi*). SEIFERT (2003) wrote: "SC3 specimens predominate in the Caribbean and adjacent regions. They have significantly shorter scapes and wider and higher waist segments than SC1 specimens, which predominate in E and N Africa and the Near East. Inter-



Figs. 1 - 3: *Cardiocondyla emeryi*. Worker from the Seychelles, (1) head, (2) lateral view, (3) dorsal view (photos by A. Nobile, courtesy antweb.org).

mediate SC2 specimens are most abundant on the Atlantic islands and in Central Africa and show also intermediate morphometric characters. The distribution pattern of SC3 suggests American SC3 specimens to have been anthropogenically introduced from W Africa via the intensive shipping connections that were established as early as 400 years ago in connection with the transport of plant material and slaves. Some of the Atlantic islands were used as stopovers in this routes [sic]. N and E African SC1 populations developed notable morphological divergence from the W African SC3 populations in the precultural period and their anthropogenic transport to America began much later and was less strong. The spreading by human commerce all over the world should have lead to repeated local encounters and hybridising of SC3 (*C. emeryi*) and SC1 (*C. emeryi rasalamae*) populations and stopped their beginning divergence." Some exotic *C. emeryi* populations are very closely related, e.g., HEINZE & al. (2006) reported that mtDNA sequence of *C. emeryi* from Tobago and Hawaii differed by only 0.1%.

Cardiocondyla emeryi is one of several *Cardiocondyla* species known to have dimorphic males (HEINZE & al. 2005). Winged males disperse, typically after mating within their natal colony. Wingless males do not disperse from their natal colony. Instead, they fight other wingless males, typically resulting in the death of all but one resident male.

SEIFERT (2003) placed *Cardiocondyla emeryi* in the *emeryi* species-group along with three other species: *Cardiocondyla weserka* BOLTON, 1982 (from Cameroon), *Car-*

diocondyla neferka BOLTON, 1982 (from Ghana and Nigeria), and *Cardiocondyla yemeni* COLLINGWOOD & AGOSTI, 1996 (from Yemen).

DEYRUP & al. (2000) coined the common name "sneaking ant" for *Cardiocondyla*. This is probably better a common name for these inconspicuous ants than the awkward direct translation of the genus name from the Greek: "heart-knuckle ant" (kardia = heart and kondylos = knuckle or knob).

Methods

Using published and unpublished records, I documented the worldwide range of *Cardiocondyla emeryi*. I obtained unpublished site records from museum specimens in the collections of Archbold Biological Station (ABS, identified by M. Deyrup), the Museum of Comparative Zoology (MCZ, identified by S. Cover), and the Smithsonian Institution (SI, identified by M. Smith). In addition, I used on-line databases with collection information on specimens by Antweb (www.antweb.org), Asociación Ibérica de Mirmeología (www.formicidae.org), and the Global Biodiversity Information Facility (www.gbif.org). I also received unpublished records from M. Lush (Gambia), F. Hita Garcia (Kenya), and G. Dlussky (Samoa). Finally, I collected *C. emeryi* specimens in Florida and on many islands in the Pacific, Atlantic, and Caribbean.

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,

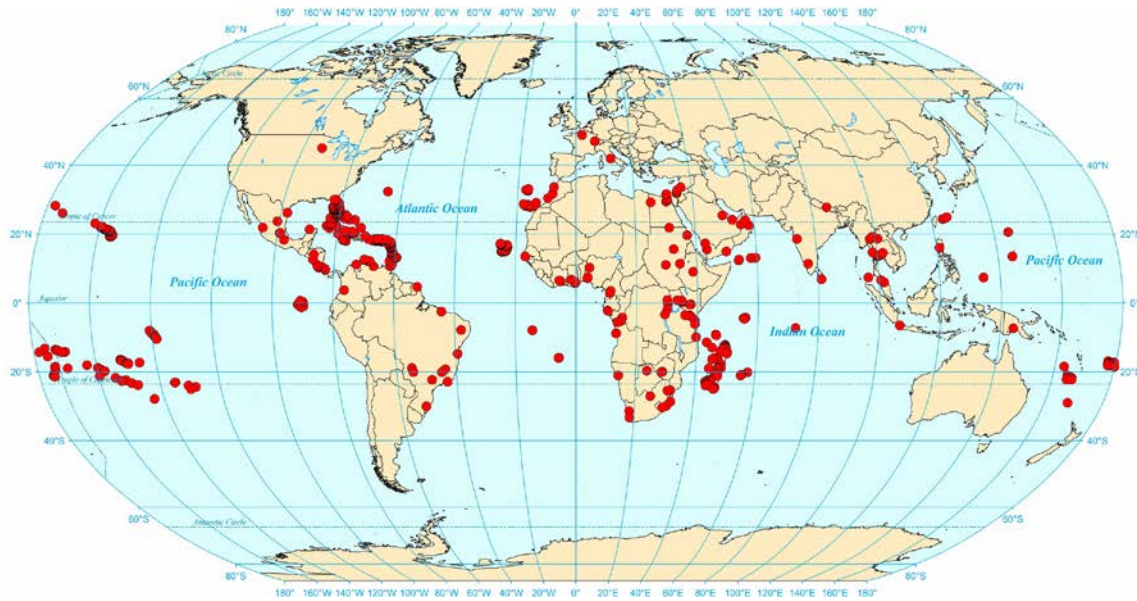


Fig. 4: Worldwide distribution records of *Cardiocondyla emeryi*.

and 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 *Cardiocondyla emeryi* on boats, found in newly imported goods, or intercepted in transit by quarantine inspectors. 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 from museum specimens, on the collector's travel dates, or limit the date by the collector's date of death.

Results

I compiled published and unpublished *Cardiocondyla emeryi* specimen records from > 1000 sites, documenting the earliest known records for 109 geographic areas (countries, island groups, major islands, and US states), including several for which I found no previously published records: Antigua, Aruba, Barbuda, Bonaire, Comoro Islands, Congo (Republic), Curaçao, Dominica, Gambia, Honduras, Îles Éparses, Martinique, Montserrat, Nevis, St Lucia, St Martin, Trinidad, Turks & Caicos Islands, and Vanuatu.

Most records of *Cardiocondyla emeryi* come from tropical areas (Fig. 4). I found only four records of *C. emeryi* from sites > 40° N latitude (Fig. 4), two from inside greenhouses (at a zoo in St. Paul, Minnesota and a butterfly house in Marin, Switzerland) and the other two (France and Italy) presumed from indoors. The next highest latitude record came from a hotel in Agadir, Morocco (33.6° N; SEIFERT 2003). Only a few presumed or known outdoor records come from latitudes greater than 30° in Syria (~ 3.5° N; WHEELER 1922a), South Africa (to 33.3° S; ADDISON & SAMWAYS 2000), Madeira (to 33.0°; WETTERER & al. 2007), Israel (to 32.7°; IZHAKI & al. 2009), Bermuda (to 32.3°; WETTERER & WETTERER 2004), Morocco (to 31.6°; CAGNIANT 2006), Egypt (to 31.6°; TAYLOR 2010), and Brazil (to 30.0°; DIEHL & ALBUQUERQUE 2007).

Possible misidentifications

WILSON & TAYLOR (1967) wrote that *Cardiocondyla emeryi* "is closely related to the better known *C. nuda* (MAYR) and has been consistently confused with that species by past authors," but they did not present any examples of misidentification. It appears that WILSON & TAYLOR (1967) were referring to use of the name *C. nuda nereis* (= *C. emeryi*), a taxon WILSON & TAYLOR (1967) synonymized, that several authors (e.g., WHEELER 1927, 1932a, b, 1934, 1935, 1936, KRAUSS 1961, FOSBERG & al. 1983) used for Pacific island populations of *C. emeryi*.

KUGLER (1983) concluded that BORGMEIER's (1937) record of *Cardiocondyla emeryi* from Rio de Janeiro, Brazil was actually *Cardiocondyla wroughtonii* (FOREL, 1890) based on the account of the male morphology.

CLOUSE (2007) wrote: "it seems clear now that Micronesian determinations of [*Cardiocondyla*] *emeryi* are actually [*C.*] *tjibodana*." For Micronesia, I found published *C. emeryi* records only from the Mariana Islands (WHEELER 1912, WEBER 1950, TERAYAMA & al. 1994). The postpetiole of *Cardiocondyla tjibodana* KARAVAIEV, 1935 is quite unlike that of *C. emeryi*, so such misidentification seems far from certain to me. Given that CLOUSE (2007) did not examine the specimens from any of the published records of *C. emeryi* from the Mariana Islands, I have provisionally retained these records.

Discussion

The same year FOREL (1881) described *Cardiocondyla emeryi* from St Thomas, US Virgin Islands, ANDRÉ (1881), who received a specimen from Forel, wrote (in French), "by comparing this specimen with the individuals that I had previously received from Jaffa [now Yafa, Israel], I found they matched perfectly, so we therefore are dealing with a cosmopolitan species." Thus, with just two known site records, the newly described *C. emeryi* was already recognized as cosmopolitan. At the time of FOREL's (1911) compilation of cosmopolitan ants, almost all *C. emeryi* rec-

Tab. 1: Earliest known records for *Cardiocondyla emeryi* from Africa and neighboring islands. Unpublished records include collector, museum source, and site. CAS = California Academy of Sciences.

	Earliest record
Saint Helena	≤ 1877 (WETTERER & al. 2007)
Madagascar	≤ 1891 (FOREL 1891 as <i>C. emeryi rasalamae</i>)
Seychelles	1892 (EMERY 1894)
Sudan	1900 (SEIFERT 2003)
Egypt	1901 (KUGLER 1983)
Madeira	≤ 1904 (FOREL 1904)
Zimbabwe	≤ 1913 (FOREL 1913a)
Congo (Zaire)	≤ 1913 (FOREL 1913b)
South Africa	1914 (ARNOLD 1916)
Tanzania	≤ 1922 (WHEELER 1922b)
Uganda	1939 (WEBER 1952)
Mascarene Islands	1941 - 1945 (DONISTHORPE 1946 as <i>C. mauritia</i>)
Canary Islands	1949 (WELLENUS 1955)
Angola	1949 (SEIFERT 2003)
Cape Verde	1953 (SEIFERT 2003)
Ascension	1958 (DUFFEY 1964)
Nigeria	1969 (KUGLER 1983)
Ghana	1969 - 1970 (ROOM 1971)
Botswana	1975 (SEIFERT 2003)
Burundi	1977 (SEIFERT 2003)
Rwanda	1977 (SEIFERT 2003)
Cameroon	1980 (SEIFERT 2003)
Kenya	≤ 1982 (BOLTON 1982)
Morocco	1992 (SEIFERT 2003)
Ethiopia	1999 - 2000 (DEGAGA & al. 2001)
Namibia	≤ 2000 (ROBERTSON 2000)
Gabon	2000 (FISHER 2004)
Ivory Coast	2005 (KONE & al. 2010)
+ Congo (Republic)	2007 (Y. Braet & E. Zassi, Taylor 2010): Brazzaville
+ Gambia	2007 (M. Lush, pers. comm.): Kololi
+ Îles Éparses	2007 (B.L. Fisher & al., CAS): Mont Chongui, Mayotte
+ Comoro Islands	2008 (B.L. Fisher & al., CAS): Mou-adja, Grande Comore

ords came from Africa and the West Indies. Outside these regions, it was reported only from Israel and India. Nonetheless, FOREL (1913b) went so far as to report, somewhat prematurely, that one encounters *C. emeryi* "in all tropical countries."

Tab. 2: Earliest known records for *Cardiocondyla emeryi* from Asia, Europe, and neighboring islands.

Asia	Earliest record
Israel	≤ 1881 (ANDRÉ 1881)
India	≤ 1903 (FOREL 1903)
Syria	≤ 1922 (WHEELER 1922a)
Japan	≤ 1971 (SONOBE 1972 in ONOYAMA 1980)
Chagos Archipelago	1971 (SEIFERT 2003)
Papua New Guinea	1972 (ROOM 1975)
Oman	1979 (COLLINGWOOD 1985)
Saudi Arabia	1983 (COLLINGWOOD 1985)
Sri Lanka	1988 (SEIFERT 2003)
Nepal	1988 (SEIFERT 2003)
Yemen	≤ 1994 (COLLINGWOOD & VAN HARTEN 1994)
UAE	1995 (COLLINGWOOD & al. 1997)
Philippines	≤ 1996 (WAY & al. 1998)
Indonesia	1996 (ITO & al. 2001)
Thailand	2002 - 2003 (SITTHICHAROENCHAI & CHANTARASAWAT 2006)
Europe	
Switzerland	1997 (DELLA SANTA 1998)
France	≤ 2004 (RADCHENKO 2004)
Italy	≤ 2004 (RADCHENKO 2004)

Tab. 3: Earliest known records for *Cardiocondyla emeryi* from Oceania. BPBM = Bishop Museum.

	Earliest record
Mariana Islands	≤ 1912 (WHEELER 1912)
Norfolk Island	1915 (WHEELER 1927 as <i>C. nuda nereis</i>)
Hawaii	1919 (O.H. Swezey, BPBM): Mount Kaala
Society Islands	1925 (CHEESMAN & CRAWLEY 1928)
Marquesas Isl.	1929 (WILSON & TAYLOR 1967)
Austral Islands	1934 (WHEELER 1936 as <i>C. nuda nereis</i>)
Tuamotu Islands	1934 (WHEELER 1936 as <i>C. nuda nereis</i>)
Pitcairn Is.	1934 (WHEELER 1936 as <i>C. nuda nereis</i>)
Gambier Islands	1934 (WHEELER 1936 as <i>C. nuda nereis</i>)
Cook Islands	1960 (KRAUSS 1961)
Samoa	1962 (WILSON & TAYLOR 1967)
Niue	1964 (TAYLOR 1967)
Wallis & Futuna	1965 (WILSON & HUNT 1967)
+ Vanuatu	1976 N.L.H. Krauss; SI: Vila, Efate
Tonga	1976 - 1977 (DLUSSKY 1994)
Fiji	1977 (DLUSSKY 1994)
New Caledonia	2000 (DELSINNE & al. 2001)
Palau	≤ 2004 (IDECHIL & al. 2007)

Tab. 4: Earliest known records for *Cardiocondyla emeryi* from the West Indies. MCZ = Museum of Comparative Zoology.

	Earliest record
US Virgin Islands	1878 (FOREL 1881)
St Vincent	≤ 1893 (FOREL 1893)
Barbados	1896 (FOREL 1912)
Bahamas	1904 (WHEELER 1905)
Bermuda	1905 (WHEELER 1906)
Jamaica	≤ 1907 (FOREL 1907)
Puerto Rico	≤ 1908 (WHEELER 1908)
Vieques	≤ 1908 (WHEELER 1908)
Guadeloupe	≤ 1912 (FOREL 1912)
Cuba	≤ 1913 (WHEELER 1913)
Dominican Republic	1928 (MENOZZI & RUSSO 1930)
St Kitts	1934 (SEIFERT 2003)
Grenada	~ 1934 (SEIFERT 2003)
+ St Lucia	1935 (H.E. Box, MCZ): Ravine Poisson
Anguilla	1980 (SEIFERT 2003)
British Virgin Islands	1993 (SEIFERT 2003)
Tobago	2000 (SEIFERT 2003)
+ Curaçao	2004 (J.K. Wetterer, MCZ): Piscadera
+ Dominica	2004 (J.K. Wetterer, MCZ): 1 km N Portsmouth
+ Trinidad	2004 (J.K. Wetterer, MCZ): D'Abadie
+ St Martin	2006 (J.K. Wetterer, MCZ): Mary's Fancy
+ Antigua	2007 (J.K. Wetterer, MCZ): Jabberwock Beach
+ Barbuda	2007 (J.K. Wetterer, MCZ): Codrington
+ Aruba	2007 (J.K. Wetterer, MCZ): Tierra del Sol
+ Montserrat	2007 (J.K. Wetterer, MCZ): Carr's Bay
+ Nevis	2007 (J.K. Wetterer, MCZ): Basseterre
+ Bonaire	2008 (J.K. Wetterer, MCZ): Plaza Resort
+ Martinique	2008 (J.K. Wetterer, MCZ): Fort-de-France
+ Turks & Caicos	2010 (J.K. Wetterer, MCZ): Town Centre, Providenciales

Over the course of the 20th century, records of *Cardiocondyla emeryi* accumulated from many tropical and subtropical regions around the world (Tabs. 1 - 5; Fig. 4). WILSON & TAYLOR (1967) noted that in Polynesia, despite extensive collections of *Cardiocondyla*, *C. emeryi* was rarely found before the early 1930s, and concluded "since *emeryi* is a distinctive species, the chances are great that it first gained a secure foothold in the islands during the thirties." I do not believe, however, that my many first records from the West Indies (Tab. 4) indicate that the spread of

Tab. 5: Earliest known records for *Cardiocondyla emeryi* from South, Central, and North America.

South & Central	Earliest record
Brazil	1928 (BORGMEIER 1937)
Galapagos	1981 (CAUSTEN & al. 2006)
Costa Rica	1989 (MACKAY 1995)
Nicaragua	1989 (MACKAY 1995)
Venezuela	1992 (MACKAY 1995)
Colombia	1995 (MACKAY 1995)
French Guiana	2004 (SERVIGNE 2004)
+ Honduras	2010 (J.T. Longino, Antweb): Francisco Morazán
North	
Florida	1911 (WHEELER 1915)
Mexico	≤ 1922 (WHEELER 1922a)
Texas	1964 (CREIGHTON & SNELLING 1974)
Minnesota	2006 (HAHN 2007)

C. emeryi to these islands is recent. Instead, I think that earlier collectors on the islands simply overlooked this species, both because it is very inconspicuous and because it is most often found in highly disturbed environments, not in forests where researchers prefer to collect. A disproportionately large number of *C. emeryi* records came from just a few parts of the world, such as Cape Verde, Florida, Madagascar, and the West Indies (Fig. 4). For example, I collected *C. emeryi* at 121 sites on the nine inhabited islands of Cape Verde. The large number of *C. emeryi* records is probably not indicative of exceptionally high densities, but is more a result of recent intensive collecting in these areas.

Given that *Cardiocondyla emeryi* is so widespread, it is surprising that there are still many tropical and subtropical regions where *C. emeryi* has not been recorded, e.g., China, Australia, and most of South America. It is striking that FOREL's (1903) two records have remained the only reports of *C. emeryi* from India.

Although *Cardiocondyla emeryi* is usually very inconspicuous, an exceptional aspect of its ecology is that it is one of the only ant species that actually appear to be more common in areas dominated by African big-headed ant, *Pheidole megacephala*. In areas where *P. megacephala* occurs at high density, few native invertebrates persist. But in Tonga, Cape Verde, and the West Indies, I often found *C. emeryi* 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. Given that both *C. emeryi* and *P. megacephala* originate in Africa, this association between the two species may have a long evolutionary history.

Other cosmopolitan ant species

With the present review, I have now examined the worldwide spread of 12 of FOREL's (1911) 15 cosmopolitan ant species. The remaining three species on FOREL's (1911) list are *Nylanderia vividula* (NYLANDER, 1846), *Odonto-*

machus haematodes (LINNAEUS, 1758), and *Tetramorium simillimum* (SMITH, 1851). All three pose taxonomic problems. The taxonomic boundaries of *N. vividula* remain unclear, and it now appears that *O. haematodes* is not a cosmopolitan tramp species, but instead several different species with regional ranges spread around the world. What FOREL (1911) considered *T. simillimum* included a second tramp species, *Tetramorium caldarium* (ROGER, 1857), which, from 1862 to 1979, was considered a junior synonym of *T. simillimum* (see BOLTON 1979). Dropping *O. haematodes* and adding *T. caldarium* to the list, twelve of the fifteen species that FOREL (1911) considered cosmopolitan originated in the Old World. Only three are native to the New World: *L. humile*, *N. vividula*, and *S. geminata*.

In the past, three *Cardiocondyla* species were considered cosmopolitan tramp species: *C. emeryi*, *C. nuda*, and *C. wroughtonii*. SEIFERT (2003), however, found many published reports of *C. nuda* and *C. wroughtonii* were based on misidentifications, with several less familiar species shoehorned into these two well-known names. For example, SEIFERT (2003) found that "Palearctic '*C. nuda*' (sensu PISARSKI 1967, BOLTON 1982, HEINZE & al. 1993) turned out to be *C. mauritanica* while Japanese-Pacific '*C. nuda*' (see TERAYAMA & al. 1992, TERAYAMA 1999) were *C. kagutsuchi*" TERAYAMA, 1999. SEIFERT (2003) concluded that *C. nuda* has a fairly restricted range and is not a tramp, but six other *Cardiocondyla* species are cosmopolitan with widespread distributions in both the Old World and the New World: *C. emeryi*, *C. mauritanica*, *C. minutior* FOREL, 1899, *C. obscurior* WHEELER, 1929, *C. venustula* WHEELER, 1908, and *C. wroughtonii*.

Over the past 100 years, about 30 ant species not on FOREL's (1911) list have become cosmopolitan, with broad ranges in both the Old World and New World (J.K. Wetterer, unpubl.). Although most of these new cosmopolitans are inconspicuous Old World species (including the five other widespread *Cardiocondyla* species), two of the greatest ecological and economic pests are New World natives: *Solenopsis invicta* BUREN, 1972 and *Wasmannia auropunctata* (ROGER, 1863). With the modern global economy, one can expect many more new cosmopolitans in the future.

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