Worldwide Spread of the Moorish sneaking Ant, *Cardiocondyla mauritanica* (Hymenoptera: Formicidae)

by

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ABSTRACT

Cardiocondyla spp. are small, inconspicuous ants, native to the Old World. Until recently, *Cardiocondyla mauritanica* Forel, 1890 was a little known species recorded almost exclusively from the semi-arid subtropics of North Africa, the Middle East, and neighboring islands. In contrast, *Cardiocondyla nuda* Mayr, 1866 was considered a cosmopolitan tramp species, spread broadly around the world through human commerce. A recent taxonomic reanalysis by B. Seifert, however, found genuine *C. nuda* restricted to Australia, New Guinea, and Western Oceania, and that published records of '*C. nuda*' from outside this region were based on misidentifications of other species, notably *C. mauritanica*. In addition, *Cardiocondyla ectopia*, known from North America, was found to be a junior synonym of *C. mauritanica.* Here, I examine the worldwide spread of *C. mauritanica*.

I compiled published and unpublished *C. mauritanica* specimen records from >250 sites, documenting the earliest known records for 47 geographic areas (countries, island groups, major islands, and US states), including several for which I found no previously published records: Barbados, Bonaire, Curaçao, Grenada, Saba, and Saudi Arabia.

Cardiocondyla mauritanica is found primarily in semi-arid and urban environments. *Cardiocondyla mauritanica* shows an apparently continuous distribution and geographic variation in morphology from northwest Africa to India suggesting that *C. mauritanica* is native throughout this subtropical expanse. Old World records of *C. mauritanica* far from this range come from Ascension, Zimbabwe, and several Indo-Pacific islands. The sole temperate record of *C. mauritanica* comes from Ukraine. *Cardiocondyla mauritanica* was first found in the New World in 1967, and has spread through the southwestern US, northern Mexico, Florida, and the West Indies. Part of the

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success of *C. mauritanica* in exotic locales may relate to its ability to co-exist with dominant invasive ants, such as the Argentine ant, *Linepithema humile* (Mayr, 1868).

Key words: biogeography, biological invasion, exotic species, invasive species

INTRODUCTION

Cardiocondyla (Hymenoptera: Formicidae) ants are small, inconspicuous species, native to the Old World. Until recently, *Cardiocondyla mauritanica* Forel, 1890 was a little known species recorded almost exclusively from North Africa, the Middle East, and neighboring islands. In contrast, *Cardiocondyla nuda* Mayr, 1866 was long considered a cosmopolitan tramp species, spread broadly around the world through human commerce. Seifert (2003), however, concluded that genuine *C. nuda* in fact has a fairly restricted range in Australia, New Guinea, and Oceania. All specimens from outside this region previously identified as '*C. nuda*' that he re-examined were actually less familiar species, notably *C. mauritanica*. Seifert (2003) also recognized that *Cardiocondyla ectopia* Snelling, 1974, known from many sites in North America, was actually a junior synonym of *C. mauritanica*, and concluded "the cosmopolitan *C. mauritanica* is one of the most abundant and most widely distributed *Cardiocondyla* species of the world and comprises about 12% of all investigated samples." Here, I examine the worldwide spread of *C. mauritanica*.

Taxonomy

Forel (1890) described *Cardiocondyla nuda mauritanica* (= *C. mauritanica*) from Tunisia. Ortiz & Tinaut (1987) raised *C. mauritanica* to a full species. Junior synonyms include *Cardiocondyla emeryi nitida* Bernard, 1948 from Libya, *Cardiocondyla ectopia* Snelling, 1974 from North America, and *Leptothorax caparica* Henin, Paiva & Collingwood, 2001 from Portugal.

Seifert (2003) placed C. *mauritanica* in the "*C. nuda* species-group" along with *C. nuda*, *Cardiocondyla atalanta* Forel, 1915 from Australia, *Cardiocondyla strigifrons* Viehmeyer, 1922 from Indonesia, *Cardiocondyla kagutsuchi* Terayama, 1999 from East Asia and Oceania, and *Cardiocondyla paranuda* Seifert, 2003 from Tunisia. *Cardiocondyla mauritanica* appears to be most

closely related to *C.* cf. *kagutsuchi* (Seifert 2008, Oettler *et al.* 2010). Whereas *C. mauritanica* males are all wingless, *C.* cf. *kagutsuchi* has both winged and wingless males (Oettler *et al.* 2010).

Cardiocondyla mauritanica was sometimes misidentified as *C. nuda* because *C. mauritanica* has a relatively indistinct metanotal groove (i.e., a dorsal furrow separating the propodeum from the promesonotum). This groove is only suggested in *C. nuda*, but it is well developed in several common *Cardiocondyla* species, including three widespread "tramp" species, spread by human commerce: *Cardiocondyla emeryi* Forel, 1881, *Cardiocondyla obscurior* Wheeler, 1929, and *Cardiocondyla wroughtonii* Forel, 1890. Nonetheless, it is fairly simple to distinguish *C. mauritanica* from *C. nuda*. In *C. mauritanica*, the lower surface of the postpetiole is nearly flat and the height of the postpetiole less than that of the petiole. In *C. nuda*, however, the lower surface of the postpetiole bulges out, giving it a convex profile and a taller postpetiole with a height equal to that of the petiole. Another widespread *Cardiocondyla* species lacking a distinct metanotal groove is *Cardiocondyla minutior* Forel. Seifert (2003) presented a range of allometric measures that allow the identification of these and all other described *Cardiocondyla* species.

Deyrup *et al.* (2000) coined the common name "sneaking ant" for *Cardiocondyla*, apparently due to their inconspicuous nature. "Mauritanica" is Latin for "Moorish." The term "Moor," derived from the Mauri people of northwestern Africa, has long been used in Europe as a colloquial term for all inhabitants of North Africa. Two other North African ants share this specific name: *Aphaenogaster mauritanica* Dalla Torre, 1893 from "Barbaria" (northern Algeria) and *Cataglyphis mauritanicus* Emery, 1906 from Tunisia and Algeria. I have used the common name "Moorish sneaking ant," analogous to the common names for other North African *mauritanica* species, e.g., the Moorish gecko, *Tarentola mauritanica* (L., 1758) and the Moorish viper, *Macrovipera mauritanica* (Duméril & Bibron, 1848).

METHODS

Using published and unpublished records, I documented the worldwide range of *C. mauritanica.* I obtained unpublished site records from museum specimens in the collections of 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), the Asociación Ibérica de Mirmecología (www.formicidae.org), the Global Biodiversity Information Facility (www.gbif.org), Myrmecology Forum (antfarm.yuku.com), BugGuide (bugguide.net), Fauna Europaea (Radchenko 2004), and Ants of Egypt (Taylor 2010). I received unpublished *C. mauritanica* records from J. Heinze (Bonaire) and B. Seifert (Malta, Saudi Arabia). Finally, I collected *C. mauritanica* in California, Florida, Madeira, and on several West Indian islands (all identified by S. Cover).

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.geonames.org, 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. 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 other 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 *C. mauritanica* specimen records from >250 sites worldwide (Fig. 1). I documented the earliest known *C. mauritanica* records for 47 geographic areas (countries, island groups, major islands, and US states; Tables 1-3), including Saudi Arabia plus several West Indian islands for which I found no previously published records: Barbados (one urban park site; leg. J.K. Wetterer), Bonaire (one garden site; leg. J. Heinze), Curaçao (five sites: four urban and one zoo; leg. J.K. Wetterer), Grenada (17 sites: seven disturbed forest, five urban, three beaches, one mangrove, and one sugarcane; leg. J.K. Wetterer), and Saba (one coastal site; leg. G.D. Alpert). To date, *C. mauritanica* has never been collected in Mauritania, a country whose name derives from the same source.

Cardiocondyla ants are notoriously difficult to identify to species. In the past, many authors have used the name '*C. nuda*' as a catchall for several *Cardiocondyla* species with a relatively indistinct metanotal groove. Fortunately,

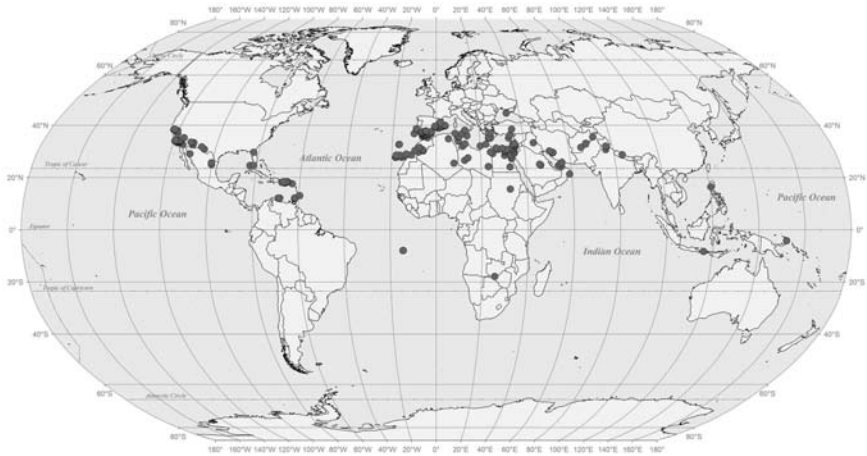

Fig. 1. Worldwide distribution records of *Cardiocondyla mauritanica*.

C. mauritanica has not been used as a catchall name, and published records of *C. mauritanica* and its junior synonym in the New World, *C. ectopia*, appear to be reliable. Authors reporting these relatively obscure taxa no doubt first determined the specimens were not *C. nuda*. I found no cases where a specimen that was identified as *C. mauritanica* was later re-identified as a different species, though Seifert (2008) incorrectly listed *C. mauritanica* from Kiribati through a typographical error (B. Seifert, pers. comm.). Except for this one record, I included all published records of *C. mauritanica*. Still, the difficulties of separating closely related species of *Cardiocondyla* should not be underestimated. As Seifert (pers. comm.) wrote: "The clustering of *kagutsuchi-mauritanica-nuda-atalanta* is stable in multivariate analyses but even an experienced '*Cardiocondyla* man' like me cannot identify each specimen by simple eye inspection. You must measure." Fortunately, except for Seifert's (2003) three Indo-Pacific records, there have been no other reports of *C. mauritanica* from within the known geographic ranges of *C. kagutsuchi*, *C. nuda*, and *C. atalanta*.

MISIDENTIFICATIONS

Emery (1884) identified specimens from Tunisia as *C. nuda*, but Emery (1891) re-identified them as *C. mauritanica*. Seifert (2003) re-examined specimens reported as *C. nuda* and found many Palearctic records of '*C.*

Table 1. Earliest known records for *Cardiocondyla mauritanica* from the Old World subtropics of Southern Europe, North Africa, the Middle East, South Asia, and neighboring islands. SI = Smithsonian Institution. + = no previously published records.

Location	Earliest record
Tunisia	1891 (A. Forel, SI): oasis by Gabes
Algeria	≤1904 (Forel 1904)
Libya	1906 (Mayr 1908)
Cyprus	≤1909 (Emery 1909)
Egypt	≤1911 (Forel 1911, Karavajev 1911)
Iraq	1918 (Seifert 2003)
Israel	1922-1928 (Menozzi 1933)
Canary Islands	1949 (Espadaler & Bernal 2003)
Afghanistan	1953 (Seifert 2003)
Iran	1974 (Seifert 2003)
Pakistan	1974 (Seifert 2003)
Balearic Islands	1976 (Gómez & Espadaler 2006)
India	1978 (Seifert 2003)
Spain	1982 (Ortiz & Tinaut 1987)
Turkey	1984 (Seifert 2003)
Malta	1984 (Seifert 2003)
Pantelleria	1987 (Mei 1995)
Crete	1990 (Seifert 2003)
Portugal	1991 (Seifert 2003)
Nepal	1991 (Seifert 2003)
Morocco	1991 (Seifert 2003)
Greece	1994 (Seifert 2003)
United Arab Emirates	1995 (Seifert 2003)
Jordan	1996 (Seifert 2003)
Madeira	2002 (Wetterer *et al*. 2007a)
Sicily	≤2004 (Radchenko 2004)
Gibraltar	≤2008 (Guillem 2008)
+Saudi Arabia	2009 (M.R. Sharaf, B. Seifert pers. comm.): Riyadh

nuda' were actually based on misidentification of *C. mauritanica* (e.g., Pisarski 1967, Bolton 1982, Heinze *et al*. 1993). A number of other studies have also re-examined specimens first reported as *C. nuda* and found them to be *C. mauritanica* (e.g., Barquín 1981 re-identified by Espadaler & Bernal 2003). Cagniant (1962) listed *C. nuda* as the only *Cardiocondyla* known from Morocco, but Cagniant & Espadaler (1993) and Cagniant (2006) listed *Cardiocondyla batesii* Forel, 1894, *C. emeryi*, and *C. mauritanica*. Comín & Furió (1986) reported *C. batesii* from Majorca, later re-identified as *C. mauritanica* (see Gómez & Espadaler 2006). It seems likely that additional published records of *C. nuda* and *C. batesii* from the Mediterranean region and the Middle East are actually *C. mauritanica*, e.g., records of *C. nuda* from

Table 2. Earliest known records for *Cardiocondyla mauritanica* from Old World tropical and temperate areas.

Location	Earliest record
Sudan	≤1911 (Karavajev 1911)
Oman	1989 (Seifert 2003)
Ascension	1990 (Ashmole & Ashmole 1997)
Zimbabwe	1995 (Seifert 2003)
Ukraine	1995 (Seifert 2003)
Indonesia	1999 (Seifert 2003)
Philippines	1999 (Seifert 2003)
Papua New Guinea	≤2003 (Seifert 2003)

Table 3. Earliest known records for *Cardiocondyla mauritanica* from the New World. Unpublished records include collector, museum source, and site. MCZ = Museum of Comparative Zoology. SI = Smithsonian Institution.

Location	Earliest record
California	1967 (Snelling 1974 as *C. ectopia*)
Arizona	1975 (C. Chandler, SI): Phoenix
Florida	1981 (Seifert 2003)
Puerto Rico	1982 (Seifert 2003)
Mexico	≤1986 (Rojas-Fernández 2001 as *C. ectopia*)
Texas	≤1992 (O'Keefe *et al*. 2000 as *C. ectopia*)
+Grenada	2003 (J.K. Wetterer, MCZ): Grenville
+Curaçao	2004 (J.K. Wetterer, MCZ): Piscadera
+Barbados	2006 (J.K. Wetterer, MCZ): Bridgetown
+Bonaire	2006 (J. Heinze, pers. comm.): Kralendijk
+Saba	2008 (G.D. Alpert, MCZ): South coast

Morocco (Delye & Bonaric 1973), Saudi Arabia (Collingwood 1985), Yemen (Collingwood & Agosti 1996), Egypt (Mohamed *et al*. 2001), and southern Europe (Radchenko 2004). Izhaki *et al*. (2009) listed *C. nuda* in a table of ants collected at Mount Carmel, Israel, but instead listed *C. nuda mauritanica* in a figure, no doubt meaning *C. mauritanica* in both cases.

Cardiocondyla mauritanica is not the only species that has been misidentified as *C. nuda*. For example, Seifert (2003) reported that many Japanese-Pacific specimens reported as *C. nuda* were actually *C. kagutsuchi*. Wilson & Taylor (1967) designated *C. minutior* as a junior synonym of *C. nuda*, but Heinze (1997, 1999) revived *C. minutior* as a full species. Between 1967 and 1997, when *C. minutior* was considered a junior synonym of *C. nuda*, most authors reported records of *C. minutior* as *C. nuda*. Based of web photos, B.

Seifert (pers. comm.) determined that specimen CASENT 0102306 from Diego Garcia, identified as *C. nuda* on antweb.com, is almost certainly *C. minutior*.

DISCUSSION

The earliest records of *C. mauritanica* come from subtropical North Africa, the Middle East, and neighboring islands (Table 1). The only *C. mauritanica* record older than 1967 from outside the Old World subtropics comes from an urban site in neighboring Sudan (Fig. 1; Table 2). Seifert (2003) found that "*C. mauritanica* specimens from India (Punjab, Himachal Pradesh) have slightly narrower postpetiole and slightly shorter spines. Furthermore, there is a certain trend from NW Africa east to India to have the petiole node lower and more rounded in profile (not quadrate as in the Tunisian type population)." This cline of geographic variation suggests that *C. mauritanica* is native throughout this region, spanning much of the subtropics of North Africa, the Middle East, and South Asia. Espadaler & Bernal (2003) considered *C. mauritanica* to be also native to the Canary Islands at the far western edge of this range.

It is uncertain how far the native range of *C. mauritanica* extends. Reyes-López *et al*. (2008) considered *C. mauritanica* to be an exotic in southern Spain. If this is true, it could explain why all known records of *C. mauritanica* from Spain are recent (Table 1). Gómez & Espadaler (2006) wrote that *C. mauritanica* "seems to be rapidly extending its range from North Africa and southern Spain to the north along the West Mediterranean coast (K. Gómez & X. Espadaler, unpubl.) and the Balearic Islands." Wetterer *et al*. (2007a) found *C. mauritanica* only at urban sites in Madeira and considered it exotic there. Wetterer *et al*. (2007b) proposed that, given its widespread occurrence in isolated, uninhabited arid parts of Ascension, it seemed possible that *C. mauritanica* was native to Ascension. After mapping the worldwide distribution of *C. mauritanica*, however, I now realize that Madeira is very close to the apparent native range of *C. mauritanica*, while Ascension, in the middle of the South Atlantic, is very distant from any populations of this species in North Africa, making it very unlikely that Ascension is part of its native range (Fig. 1). Other Old World records of *C. mauritanica* far from its native range come

from Zimbabwe and several Indo-Pacific islands (Fig. 1). The sole temperate record of *C. mauritanica* comes from Ukraine (Seifert 2003).

Cardiocondyla mauritanica was first found in the New World in 1967 (Table 3), but it has since spread extensively through the southwestern US, northern Mexico, Florida, and the West Indies (Fig. 1). Whereas in the Old World, there are few records of *C. mauritanica* from the tropics, I have found this species at numerous tropical sites in the West Indies.

ECOLOGY

Most records of *C. mauritanica* come from semi-arid areas or urban sites, agreeing with Seifert's (2003) conclusion that "it is mainly a species of semi-deserts and other xerothermous habitats" and Ward's (2005) observation that *C. mauritanica* "occur in disturbed (mostly urban) habitats in California, where they nest in sidewalks and along roadways." Seifert (2003) noted that in tropical East Asia and Oceania, "*C. kagutsuchi* seems to replace *C. mauritanica*. The fact that *C. mauritanica*, a most widely distributed cosmopolitan tramp species, could not substantially penetrate the range of *C. kagutsuchi* is intriguing." It may be that *C. mauritanica* is less well adapted for the humid tropical climate of this region.

Cardiocondyla mauritanica has habitat preferences that overlap broadly with those of the Argentine ant, *Linepithema humile* (Mayr, 1868), an invasive ant from the subtropics of South America. Wetterer *et al*. (2000) found that *C. mauritanica* (as *C. ectopia*) and *L. humile* were the only non-native ants on Santa Cruz Island, off the coast of Southern California.

Part of the success of *C. mauritanica* and other *Cardiocondyla* species in exotic locales may be due to their ability of co-exist with dominant invasive ants (Heinze *et al*. 2006). Ward (2005) reported that both *C. mauritanica* and *C. minutior* "are able to survive in sites invaded by the Argentine ant." Gulmahamad (1997) observed *C. mauritanica* (as *C. ectopia*) "co-existing with the Argentine ant at four different geographical locations in southern California. At one site, it was surviving in a nest with the entrance located only 8 cm from the nest of the Argentine ant and only 3 cm from an active trail of this species." Gulmahamad (1997) proposed several factors that promoting this co-existence, notably *C. mauritanica*'s use of chemical defenses against *L. humile*. Gómez & Espadaler (2006) reported *C. mauritanica* "on

several irrigated housing estates in Ibiza, Mallorca and Menorca, usually in coexistence with the Argentine ant, *Linepithema humile*." Gómez & Espadaler (2006) noted that *C. mauritanica* "seems to be the first case to join the Argentine ant in its invasion, with no apparent problems in gardens infested by *Linepithema*... both species are highly aggressive to each other. In encounters between foraging ants of the two species, the *C. mauritanica* worker initially crouches down to the floor and remains quiet while the Argentine worker antennates it. If pulled, the *Cardiocondyla* worker repeatedly fiercely stings the Argentine ant until it retreats... Thereafter, recruitment by the Argentine ant is not triggered and its vast numeric prevalence has no local effect."

The ability to co-exist with dominant invasive ants extends to other *Cardiocondyla* species as well. Wilson & Taylor (1967) reported that *L. humile* "excludes other larger ant species, including the formidable *Pheidole megacephala*. One species found to be compatible with it on Hawaii is the diminutive *Cardiocondyla nuda*" (probably referring to *C. minutior*, which they had designated a junior synonym of *C. nuda*). Wetterer (2012) noted that *C. emeryi* appears to be more common in areas dominated by African big-headed ant, *Pheidole megacephala* (Fabricius, 1793). At sites with high densities of *P. megacephala* on islands of the Pacific, Atlantic, and the West Indies, I usually also found *C. emeryi*, but few other ants. It may be that dominant ants such as *L. humile* and *P. megacephala* benefit *Cardiocondyla* species indirectly, through elimination of competing ant species.

Six species of *Cardiocondyla* are now known to be cosmopolitan, having achieved broad distributions in both the Old World and the New World (from largest to smallest in order of head size, from Seifert 2003): *C. venustula*, *C. mauritanica*, *C. obscurior*, *C. minutior*, *C. wroughtonii*, and *C. emeryi*. By far, the most widespread and common is *C. emeryi* (Wetterer 2012). None of these species are known to have significant ecological impacts, and it seems unlikely that any of these inconspicuous sneaking ants will ever become significant pests as they continue to spread, largely unnoticed, around the world.

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