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WORLDWIDE SPREAD OF THE LESSER SNEAKING ANT, *CARDIOCONDYLA MINUTOR* (HYMENOPTERA: FORMICIDAE)

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ABSTRACT

Cardiocondyla (Hymenoptera: Formicidae) ants are small and inconspicuous species. All *Cardiocondyla* are native to the Old World, but 5 species have been broadly dispersed through human commerce, achieving widespread distributions in both the Old World and the New World. Here I examine the worldwide spread of *Cardiocondyla minutior*. I compiled published and unpublished *C. minutior* specimen records from > 300 sites. I documented the earliest known *C. minutior* records for 56 geographic areas (countries, island groups, major Caribbean islands, and US states), including several for which I found no previously published records: Austral Islands, Barbados, Cuba, Dominican Republic, Grenada, Honduras, Îles Éparses, Jamaica, Madagascar, and Mayotte. *Cardiocondyla minutior* appears to be originally from the Indo-Malayan region, where all its closest relatives are found. Surprisingly, there are few records of *C. minutior* from this region. Instead, most Old World records of *C. minutior* come from Pacific and Indian Ocean islands where there are few or no native ants, e.g., the Chagos Archipelago, Hawaii, Îles Éparses, Easter Island, the Marquesas Islands, the Seychelles, and the Society Islands. *Cardiocondyla minutior* is becoming widespread in tropical and subtropical parts of the New World. The success of *Cardiocondyla* species in exotic locales may be due, in part, to their ability to co-exist with dominant invasive ants, such as the Argentine ant, *Linepithema humile*.

Key Words: biogeography, biological invasion, exotic species, invasive species, island fauna

RESUMEN

Las hormigas del género *Cardiocondyla* (Hymenoptera: Formicidae) son especies pequeñas y poco visibles. Todas las *Cardiocondyla* son nativas al Viejo Mundo, pero 5 especies se han dispersado ampliamente a través del comercio por humanos, obteniendo una amplia distribución tanto en el Viejo Mundo como el Nuevo Mundo. Aquí examiné la dispersión mundial de *Cardiocondyla minutior*. He compilado registros publicados y no publicados de especímenes de *C. minutior* en más de 300 sitios. He documentado los primeros registros conocidos de *C. minutior* para 56 áreas geográficas (países, grupos de islas, las principales islas del Caribe, y los estados de Estados Unidos), incluyendo varios para los cuales no he encontrado registros publicados previamente: Islas Australes, Barbados, Cuba, República Dominicana, Grenada, Honduras, Îles Éparses, Jamaica, Madagascar y Mayotte. *Cardiocondyla minutior* parece ser originario de la región Indo-Malaya, donde se encuentran todas sus especies relativas más cercanas. La variación morfológica en los especímenes de *C. minutior* procedentes de Sri Lanka, Okinawa, India, Nepal y de los obtenidos en el resto del mundo provee más evidencia que *C. minutior* es nativa del Sur de Asia. Sorprendentemente, hay pocos registros de *C. minutior* de esta región. En cambio, la mayoría de los registros del Viejo Mundo de *C. minutior* provienen de las islas del Océano Pacífico e Índico, donde hay pocas o ninguna hormiga nativa, por ejemplo, el archipiélago de Chagos, Hawaii, Îles Éparses, Isla de Pascua, las Islas Marquesas, las Seychelles, y las Islas de la Sociedad. *Cardiocondyla minutior* se está dispersando ampliamente en las zonas tropicales y subtropicales del Nuevo Mundo. El éxito de las especies *Cardiocondyla* en lugares exóticos puede ser debido, en parte, a su capacidad para coexistir con las hormigas invasoras dominantes, como la hormiga argentina, *Linepithema humile*.

Palabras Clave: biogeografía, invasión biológica, especies exóticas, especies invasoras, fauna de islas

Cardiocondyla (Hymenoptera: Formicidae) ants are small and inconspicuous species, which Deyrup et al. (2000) dubbed “sneaking ants.” All

Cardiocondyla are native to the Old World, but 5 species have achieved widespread distributions in the New World as well, spread by human com-

merce: *Cardiocondyla emeryi* Forel, *Cardiocondyla mauritanica* Forel, *Cardiocondyla minutior* Forel, *Cardiocondyla obscurior* Wheeler, and *Cardiocondyla wroughtonii* Forel. In earlier reviews, Wetterer (2012a, b) examined the spread *C. emeryi* and *C. mauritanica*. Here I examine the worldwide geographic spread of *C. minutior* (Fig. 1).

Taxonomy, Identification, and Biology

Forel (1899) described *Cardiocondyla nuda minutior* (= *C. minutior*) from Hawaii. Wilson & Taylor (1967), however, designated *C. minutior* to be a junior synonym of *C. nuda*. Although Creighton (1950) tentatively treated *C. minutior* as a distinct subspecies of *C. nuda*, Creighton & Snelling (1974) wrote: "It now seems clear that the senior author was mistaken in treating Forel's variety *minutior* as a subspecies in 1950. At that time there were few long nest series of *nuda* available for study; hence it was not certain how the single nest series which had yielded workers of the typical *nuda* and others of the variety *minutior* ought to be handled. Subsequent studies have shown that the above situation is normally encountered in any long nest series of *nuda*. It follows that *minutior* must be treated as a synonym of *nuda*, as shown by Wilson and Taylor (1967)." Even after synonymy in 1967, some authors continued to use the name *C. nuda minutior* (e.g., Whitcomb et al. 1972). Heinze (1997, 1999), however, revived *C. minutior* as a full species. Seifert (2003) confirmed *C. minutior* as a valid species and determined *Cardiocondyla tsukuyomi* Terayama (described from Okinawa) to be a junior synonym of *C. minutior*. Seifert (2003) found genuine *C. nuda* records restricted to Australia, New Guinea, and Oceania. With the revival of *C. minutior* as a valid name, Fisher & Cover (2007) removed *C. nuda* from the list of ants known from North America.

One character which *C. minutior* shares with *C. nuda* is a flat dorsal mesosoma in profile with no distinct metanotal groove. This contrasts with the tramp species *C. emeryi*, *C. obscurior*, and *C. wroughtonii*, which have a distinct metanotal groove. It is relatively simple to distinguish *C. nuda* from *C. minutior*. In *C. nuda*, the postpetiolar sternite is convex and the height of petiole about equal to height of postpetiole. In *C. minutior*, the postpetiolar sternite is nearly flat and the maximum height of petiole greater than maximum height of postpetiole. Workers of *C. minutior* are generally smaller (total length = 1.5-1.7 mm) than those of *C. nuda* (total length = 1.6-2.0 mm), no doubt the basis of its Latin name "*minutior*," meaning smaller or lesser.

Seifert (2003) noted "intraspecific variability in *C. minutior* is rather low within the huge range of its distribution, extending over the Neotropic, Polynesian, Australasian, Indo-Australasian, and Oriental regions. Samples from central Sri Lanka have significantly smaller eyes, those from Okinawa, N. India, and Nepal shorter heads but all these deviating populations are in the vast majority of other characters consistent with the overall average."

Seifert (2003) placed *C. minutior* in the '*C. minutior* species group' along with six other species: *Cardiocondyla breviscapus* Seifert from In-

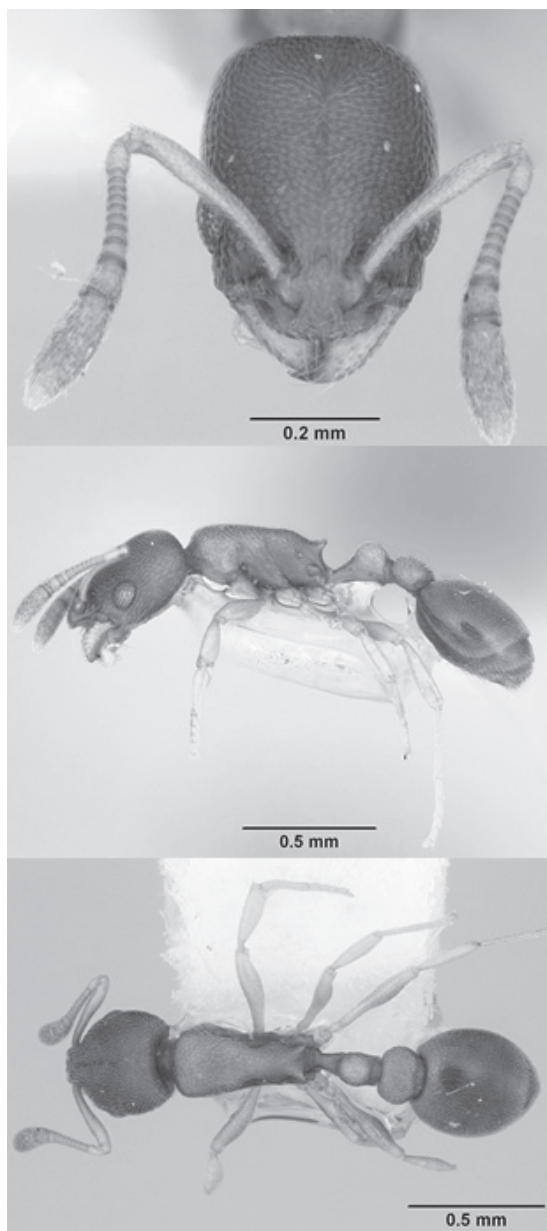


Fig. 1. *Cardiocondyla minutior*. Worker from Hilo, Hawaii, (1) head, (2) lateral view, (3) dorsal view (photos by A. Nobile, Antweb.org).

dia, *Cardiocondyla carbonaria* Forel from India, *Cardiocondyla opaca* Seifert from India, *Cardiocondyla britteni* Crawley found on butter beans in England (probably imported from India), *Cardiocondyla goa* Seifert from India, and *Cardiocondyla tjibodana* Karavajev known from Indonesia, Malaysia, the Mariana Islands, and Belize. Oettler et al. (2010) found that *C. minutior* and *C. tjibodana* are genetically almost identical, and both are quite distinct from *C. nuda*.

Cardiocondyla minutior is one of several *Cardiocondyla* species known to have dimorphic males (Heinze et al. 2004; Oettler et al. 2010). Winged males disperse, typically after mating within their natal colony. Wingless males typically do not disperse from their natal colony. Instead, they fight other wingless males, typically resulting in the death of all but one resident male.

METHODS

Using published and unpublished records, I documented the worldwide range of *C. minutior*. 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 M. Deyrup) and the Smithsonian Institution (SI, identified by M. Smith). W. P. Mackay sent me all *Cardiocondyla* specimens in his personal collection; M. Deyrup re-identified these specimens. In addition, I used on-line databases with collection information on specimens by Antweb.org, the Essig Museum of Entomology (essigdb.berkeley.edu), and the Global Biodiversity Information Facility (www.gbif.org). I received unpublished *C. minutior* records from P. Ward (California, Colombia, Cuba, and Fiji). Finally, I collected *C. minutior* specimens on Pacific and West Indian islands.

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, 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 *C. minutior* 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. Stefan Cover confirmed identification for all specimens in the MCZ.

RESULTS

I compiled published and unpublished *C. minutior* specimen records from >300 sites (Fig. 2). I documented the earliest known *C. minutior* records for 56 geographic areas (countries, island groups, major Caribbean islands, and US states), including several for which I found no previously published records: Austral Islands, Barbados, Cuba, the Dominican Republic, Grenada, Honduras, Îles Éparses, Jamaica, Madagascar, and Mayotte (Tables 1 and 2).

Published records of *C. minutior* appear to be quite reliable, particularly in areas outside its purported native range, because authors reporting this relatively obscure taxon no doubt first determined the specimens were not the much more widely reported *C. nuda*. I found no cases where a specimen identified as *C. minutior* was later re-identified as a different species. Seifert (pers. comm.), however, wrote of his own identification: "You should know that all these determinations were achieved by an enormous measuring and analytical expense. Nobody (including me) can separate *minutior* and *tjibodana* by simple eye inspection. Both species possibly hybridize at localities where they were brought into contact. This is not verified but only suggested as the determinations are not very stable in some localities." Seifert (pers. comm.) further warned that although *C. tjibodana* is only widespread in Indonesia and Malaysia, "findings of *tjibodana* from Belize, the Mariana Islands and Solomon Islands indicate that it has also some tramp species potential." It is therefore possible that some of my mapped records of *C. minutior* are actually misidentified *C. tjibodana*. Alternatively, given their genetic closeness and possible inter-breeding, perhaps *C. minutior* and *C. tjibodana* are not actually distinct species.

Re-Identification

Between 1967 and 1997, *C. minutior* was considered a junior synonym of *C. nuda*. Since the revival of *C. minutior*, some authors have re-identified published records of '*C. nuda*' as actually *C. minutior*. For example, Herrera & Roque-Albedo (2007) reported *C. nuda* from many islands in the Galapagos and no *C. minutior*, but Herrera & Heraty (2011) reported no *C. nuda* from the same islands, replacing all these records with *C. minutior*.

Before synonymy in 1967, there were several published records of *C. nuda minutior* from the New World (e.g., Wheeler 1932, Smith 1933, 1944, 1967, Vivar 1957), but none of *C. nuda*. It appears that subsequent published records of *C. nuda* from the New World may actually all be *C. minutior*. I confirmed with M. Deyrup, J. King, Z. Prusak, and J. A. Rodríguez (pers. comm.) that



Fig. 2. Worldwide distribution records of *Cardiocondyla minutior*. Circle = *C. minutior* record. + = unconfirmed New World '*C. nuda*' record.

they now consider all specimens they reported as '*C. nuda*' from Florida, the Bahamas, and Mexico (e.g., Deyrup et al. 1988, 1998, 2000; Deyrup & Trager 1986; Deyrup 1994; Ferster & Prusak 1994; King 2007; Rodríguez 2008) as actually *C. minutior*. Torres & Snelling (1997) listed many records of *C. nuda* from Puerto Rico, but Snelling & Torres, in an unpublished book manuscript, changed all records of *C. nuda* to *C. minutior*. Oddly, although Fernández & Palacio (1995) listed *C. nuda* in Colombia, Fernández & Sendoya (2004) listed neither *C. nuda* nor *C. minutior* from anywhere in the Neotropics.

Mark Deyrup (pers. comm.) examined New World *Cardiocondyla* specimens in W. P. Mackay's collection and found specimens from 11 sites to be *C. minutior*: from Columbia (7 sites), Florida (1), Georgia (1), and Nicaragua (2), including 8 that Mackay (1995) previously listed as *C. nuda*. Deyrup re-identified 1 specimen that Mackay (1995) listed as *C. nuda* (from New Iberia, Louisiana) as *Cardiocondyla venustula* Wheeler. Finally, Deyrup was uncertain of the identity of 1 queen that Mackay (1995) listed as *C. nuda* (from Dauphin Island, Alabama).

I have mapped 11 unconfirmed records of '*C. nuda*' from the New World as *C. minutior* records ("+" in Fig. 2), i.e., Alabama (one record: Mackay 1995), Columbia (5 records: Mackay 1995, Armbrrecht et al. 2001, and gbf), Georgia

(one record: Smith 1979), Louisiana (2 records: Dash 2004), South Carolina (one record: Davis 2009), and Texas (Creighton & Snelling 1974). Only 2 New World areas with published records '*C. nuda*' lack any confirmed *C. minutior* records: Alabama and South Carolina (Table 2).

Wholesale replacement of the name *C. minutior* for '*C. nuda*' in the New World cannot be repeated in the Asia and Oceania, where true *C. nuda* occurs. In addition, several other species in the Old World have been misidentified as *C. nuda*. For example, many published records of '*C. nuda*' from the Palearctic are actually *C. mauritanica* (Seifert 2003, Wetterer 2012b). Starr et al. (2007) wrote: "In Hawaii, specimens of this species were previously called *C. nuda* in error, so all previous records of *C. nuda* are now considered *C. minutior* (Krushelnicky pers. comm.)." Seifert (2003), however, noted that some specimens from Pacific region identified previously as '*C. nuda*' are actually *Cardiocondyla kagutsuchi* Terayama, a species from East Asia and Oceania that has been recently reported from Hawaii (e.g., Seifert 2003; Buczkowski & Krushelnicky 2012). Jürgen Heinze (pers. comm.) wrote: "in my opinion, *C. kagutsuchi* is the most widespread *Cardiocondyla* inland at least in Hawai'i and Kauai. What has been referred to as *C. nuda* or *C. venustula* is mostly *C. kagutsuchi*. They occur even in na-

TABLE 1. EARLIEST KNOWN RECORDS FOR *CARDIOCONDYLA MINUTIOR* FROM 29 OLD WORLD AREAS. UNPUBLISHED RECORDS INCLUDE COLLECTOR, MUSEUM OR WEB SOURCE, AND SITE. MCZ = MUSEUM OF COMPARATIVE ZOOLOGY. UCB = ESSIG MUSEUM OF THE UNIVERSITY OF CALIFORNIA, BERKELEY. + = NO KNOWN PUBLISHED RECORD.

	Earliest record
Hawaii	1893 (Forel 1899)
Nicobar Islands	≤1894 (Forel 1903)
Bismarck Arch.	1896-1897 (Forel 1901)
India	1902 (Forel 1903)
Easter Island	1916-1917 (Wheeler 1922)
Marquesas Islands	1927 (Seifert 2003)
Society Islands	1928 (Seifert 2003)
Line Islands, Kiribati	1934 (Wheeler 1936)
Mariana Islands	1946 (Clouse 2007)
FS Micronesia	1950 (Clouse 2007)
Japan	1952 (Seifert 2003)
Palau	1952 (Clouse 2007)
Line Islands, US	1952 (Clouse 2007)
Indonesia	1959 (J.L. Gressitt, MCZ): Biak Island
Nepal	1961 (Seifert 2003)
Seychelles	1968 (Seifert 2003)
Chagos Archipelago	1971 (Seifert 2003)
Sri Lanka	1988 (Seifert 2003)
Fiji	1997 (J.K. Wetterer, MCZ): Suva
Egypt	1998 (Bakr et al. 2007)
Vietnam	1998 (Eguchi et al. 2011)
Ogasawara Islands	≤1999 (Terayama 1999 as <i>C. tsukuyomi</i>)
New Zealand	2000 (Harris & Berry 2001)
+Madagascar	2001 (R. Harin'Hala, Antweb.org): Montagne d'Ambre NP
New Caledonia	≤2006 (Jourdan & Mille 2006)
+Austral Islands	2006 (P. Krushelnycky, UCB): Rimatara
Taiwan	≤2009 (Terayama 2009)
+Mayotte	2010 (S. Gasnier, Antweb.org): Combani
+Îles Éparses	2011 (B.L. Fisher, Antweb.org): Europa Island

tional parks far from the coast at elevations of 1000m and more and in some areas are the only ants around. *C. venustula* appears much rarer.” I therefore only mapped Hawaiian records specifically identified as *C. minutior*.

Seifert (2003) listed site records of *C. minutior* from the Marquesas Islands (Kopaafaa, Hiva Oa; 1927; collected by A. M. Adamson & E. P. Mumford) and the Society Islands (Hitiaa, Tahiti; 1928; collected by A. M. Adamson) from the Museum of Comparative Zoology that match reports by Wilson & Taylor (1967) of *C. emeryi*, suggesting that these are *C. minutior* specimens previously misidentified as *C. emeryi*. Eguchi et al. (2011) reported that the specimens that Eguchi et al. (2005) listed as *C. emeryi* were actually *C. minutior*.

Forel (1903) reported *C. nuda minutior* (= *C. minutior*) from Kondul Island in the Nicobar Islands, but Mohanraj et al. (2010) incorrectly reported Forel’s (1903) record as *C. nuda*.

DISCUSSION

Most Old World records of *C. minutior* have come from oceanic islands with few or no native ants, e.g., Hawaii, Easter Island, the Marquesas Islands, the Society Islands, the Seychelles, and the Chagos Archipelago. *Cardiocondyla minutior*, however, appears to be originally from the Indo-Malayan region, where all its closest relatives are found (Seifert 2003). *Cardiocondyla minutior* specimens from Sri Lanka, Okinawa, India, and Nepal are morphologically more variable than those collected in the rest of the world (Seifert 2003), providing further evidence that *C. minutior* is native to this region. There are surprisingly few records of *C. minutior* from the Indo-Malayan region (Fig. 2), though this may simply be a testament to how inconspicuous and difficult to identify these ants are. Many, if not most, published records of *C. nuda* from the Indo-Malayan region (e.g., Thailand; Jaitrong & Nabhitabhata 2005)

TABLE 2. EARLIEST KNOWN RECORDS FOR *CARDIOCONDYLA MINUTOR* FROM 27 NEW WORLD AREAS. * = EARLIEST RECORD UNCONFIRMED. ** = SOLE RECORD UNCONFIRMED. ABS = ARCHBOLD BIOLOGICAL STATION. WPMC = W.P. MACKAY COLLECTION. ALL OTHER ABBREVIATIONS AS IN TABLE 1.

	Earliest record
Florida	1924 (Seifert 2003)
Costa Rica	1956 (Vivar 1957)
Louisiana	≤1960 (Moser & Blum 1960 as <i>C. nuda</i>)*
Texas	≤1967 (Smith 1967)
California	≤1967 (Smith 1967)
Colombia	1973 (W.P. Mackay, WPMC): Bucaramanga
Trinidad	1976 (Seifert 2003)
Georgia	≤1979 (Smith 1979 as <i>C. nuda</i>)*
Puerto Rico	1979 (Seifert 2003)
Galapagos	≤1982 (Lubin 1984 as <i>C. nuda</i>)*
+Jamaica	1984 (J.T. Longino, Antweb.org): Great River
Alabama	1987 (Mackay 1995 as <i>C. nuda</i>)**
Nicaragua	1989 (F. Reinboldt, WPMC): Solentiname
Bahamas	1994 (Deyrup et al. 1998 as <i>C. nuda</i>)
Brazil	1995 (Heinze et al. 1998)
Mexico	1996 (J.A. Rodríguez, pers. comm.): Res. Ecol. San Felipe Bacalar
South Carolina	1999-2000 (Davis 2009 as <i>C. nuda</i>)**
Tobago	2000 (Seifert 2003)
French Guiana	2000-2002 (Delabie et al. 2009)
+Cuba	2001 (P.S. Ward, pers. comm.): Baracoa
+Barbados	2003 (J.K. Wetterer, MCZ): East Point
+Grenada	2003 (J.K. Wetterer, MCZ): St. George's
+Dominican Rep.	2003 (M. Deyrup, ABS): Santo Domingo Botanical Garden
Guadeloupe	2008 (Maitre et al. 2012)
Guatemala	2009 (J.T. Longino, Antweb.org): 5 km SE Antigua
+Honduras	2010 (J.T. Longino, Antweb.org): Zamorano

may be based on misidentifications of *C. minutior*. In this case, the dates of the earliest known records of *C. minutior* in the Old World appear to provide little guidance concerning where this species originated.

The success of *Cardiocondyla* species in exotic locales may be due, in part, to their ability of co-exist with dominant invasive ants (Heinze et al. 2006). Ito (1953) reported *C. minutior* occurring in an area occupied by the Argentine ant, *Linepithema humile* (Mayr, 1868), in Opauala, Hawaii and speculated that *C. minutior* “was perhaps tolerated or overlooked by the Argentine ant because of its minute size.” Wilson & Taylor (1967) noted 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*” (possibly referring to *C. minutior*, which they had newly synonymized with *C. nuda*). Ward (2005) reported that both *C. mauritanica* and *C. minutior* “are able to survive in sites invaded by the Argentine ant,” *L. humile*.

Five species of *Cardiocondyla* have become cosmopolitan tramps and have achieved widespread distributions in both the Old World and

the New World: *C. emeryi*, *C. mauritanica*, *C. minutior*, *C. obscurior*, and *C. wroughtonii* (Seifert 2003). Several additional *Cardiocondyla* species have begun to spread outside their native range, including *C. kagutsuchi*, *C. tjibodana*, and *C. venustula*. None of these species, however, 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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