

Review article

## Stealthy invaders: the biology of *Cardiocondyla* tramp ants

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**Abstract.** Many invasive ant species, such as the Argentine ant or the red imported fire ant, have huge colonies with thousands of mass-foraging workers, which quickly monopolise resources and therefore represent a considerable threat to the native ant fauna. *Cardiocondyla obscurior* and several other species of this myrmicine genus have similarly been transferred throughout the tropics by human activities. However, because their colonies are tiny and workers forage solitarily, *Cardiocondyla* are often not recognized as successful invaders. Here, we document that the life history of *Cardiocondyla* closely resembles that of the more conspicuous tramp species, with polygyny, intranidal mating, budding, worker sterility, low genetic variability, and possibly also unicoloniality. Given that introduced *Cardiocondyla* may locally reach a very high population density, the effects of these stealthy invaders on the native arthropod fauna should receive more attention.

**Keywords:** Invasive ants, unicoloniality, polygyny, intranidal mating, competition.

### Introduction

The accidental transfer of animal and plant species across biogeographic barriers by human commerce can have a tremendous impact on ecosystems and often also on the life history of the introduced taxon itself. Life history changes are particularly striking in several invasive social insects. For example, the German yellowjacket, *Vespula germanica*, has switched from an annual life cycle with single-queen colonies in its native range to perenniability and colonies with multiple queens in Australia and New Zealand (Harris, 1996; Goodisman et al., 2001). Invasive ants (tramp ants) show increased queen numbers and have completely lost their colo-

ny boundaries, resulting in a transition from a multicolonial social structure with independent colonies in the native range to unicoloniality, i.e., a network of non-aggressive nests, in the introduced range. The unicolonial population structure allows invasive ants to reach extremely high population densities in the new habitat and strongly enhances their competitive ability, e.g., through a highly increased foraging efficiency. Successful invasive ants have therefore frequently become ecologically dominant and reached “pest status” (Passera, 1994; Suarez et al., 1999; Holway et al., 2002; Tsutsui and Suarez, 2003).

Most of the more intensively studied invasive ants, such as the Argentine ant (*Linepithema humile*), the red imported fire ant (*Solenopsis invicta*), the crazy ants (*Anoplolepis gracilipes* and *Paratrechina longicornis*), the little fire ant (*Wasmannia auropunctata*), and the big-headed ant (*Pheidole megacephala*), have conspicuous, large colonies and effectively exploit and defend new resources by mass recruitment. However, there are also introduced ants that are often overlooked because they are much less destructive. Several species of the myrmicine genus *Cardiocondyla* are such stealthy invaders (Passera, 1994). *Cardiocondyla* are often among the first arthropod pioneers settling in disturbed areas (Hoffmann and Andersen, 2003), including recently formed volcanic islands (Ball and Glucksman, 1975; Edwards and Thornton, 2001), rehabilitated bauxite mines and ash dams (Majer et al., 1984; van Hamburg et al., 2004) and the 1.28 hectare closed greenhouse structure biosphere 2 in Arizona (Wetterer et al., 1999). At least six originally paleotropical species (*C. emeryi* Forel, 1881; *C. kagutsuchi* Terayama, 1999; *C. mauritanica* Forel, 1890; *C. minutior* Forel, 1899; *C. obscurior* Wheeler, 1929; *C. wroughtonii* (Forel, 1890)) have since long become established throughout large parts of the tropics and subtropics, including remote oceanic islands without a native ant fauna and the originally *Cardiocondyla*-free New World and New Zealand (Wilson and Taylor, 1967a; Harris and Berry, 2001; Seifert, 2003; Wetterer and

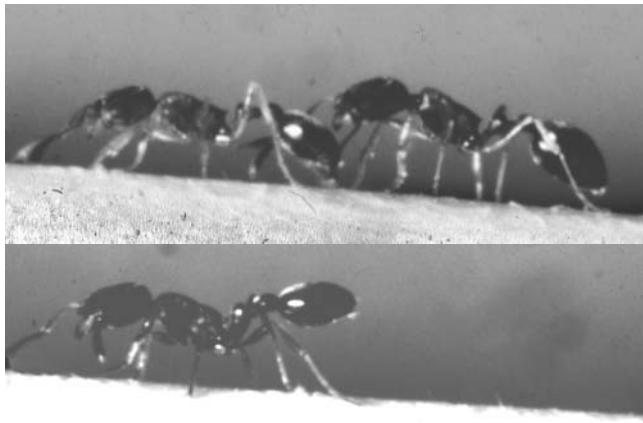
Wetterer, 2004). Forel described *Cardiocondyla* from the Caribbean Island St. Thomas and Hawaii as early as 1881 and 1899, respectively. At approximately the same time, *L. humile* became established in New Orleans (Suarez et al., 1999) and only 40 years later *S. invicta* was introduced to the United States (Vinson, 1997). Hence, *Cardiocondyla* ants have a long and successful history of biological invasions.

Despite their ubiquity, *Cardiocondyla* differ in a number of features from the better known and more prominent invasive species. *Cardiocondyla* colonies are small, with only a few dozens or hundreds of workers, which forage slowly and solitarily and only occasionally employ tandem recruitment (Wilson, 1959; Fig. 1). Their mostly subterraneous nests consist of several small chambers up to 1.5 m down in the soil (Fig. 2) and are difficult to locate, because their cryptic entrance holes have a diameter of only around 1 mm (Creighton and Snelling, 1974; Marikovsky and Yakushkin, 1974; Gulmahamad, 1997). Whereas *Linepithema*, *Solenopsis*, *Wasmannia*, and other invasive species readily make themselves noticed even by the casual observer, the occurrence of *Cardiocondyla* in a certain habitat often remains overlooked, because, in Longino's (2004) words, "studying these ants often involves putting your nose to the pavement in highly public places. It can expose you to considerable public scrutiny and perhaps even derision, and ... also carries the risk of physical harm when the habitat under investigation is the side of a busy highway."

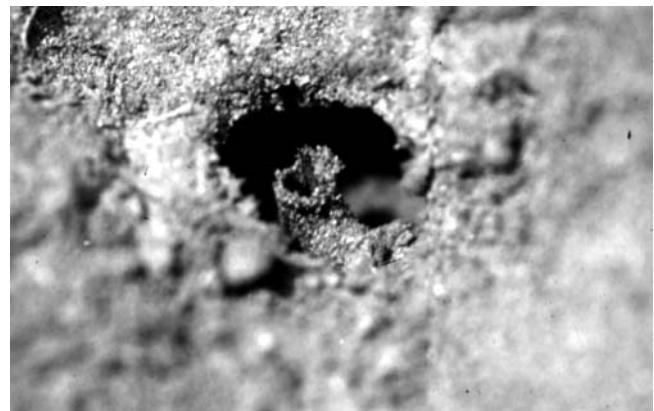
Here, we summarize data, which document that the life history of *Cardiocondyla* tramps resembles that of the more conspicuous invasive species, albeit in a miniaturized way, and we point out a number of open questions that need to be investigated in the future.

#### *Colony structure and reproduction*

Invasive ants are characterized by a suite of traits that apparently facilitate their hitchhiking with human travel and



**Figure 1.** Tandem running and tandem calling in *Cardiocondyla mauritanica* from Barranco de las Angustias, La Palma, Canary Islands. Photograph: C. Kleineidam



**Figure 2.** View of one of several nest cavities of *Cardiocondyla batesii* in Guadix, Spain, showing a chimney-like structure protecting the tunnel leading to a deeper chamber. The diameter of the nest cavity is approximately 1 cm.

establishment in new biogeographic areas (Passera, 1994; Holway and Suarez, 1999). They are dietary generalists and opportunistically utilize ephemeral nests, which forces them to migrate frequently between nest sites. Colonies are polygynous with short-lived queens that mate with males inside the nest, and sterile workers, which have completely lost their ovaries. New colonies are typically founded by budding, and it appears to be particularly important that queenless worker groups can rear new sexuals from the queens' brood and thus start new colonies (Aron, 2001). Such a life history combining polygyny and polydomy generally decreases the generation time and is thus advantageous in habitats with increasing population size such as disturbed, man-made habitats (Tsuji and Tsuji, 1996).

Invasive species of *Cardiocondyla* share most of these traits (Passera, 1994). For example, though queen numbers are known only from a limited number of species, it appears that all tramp species and their closest relatives in the tropics are polygynous (Heinze, 1999; Anderson et al., 2003; Seifert, 2003; Yamauchi, pers. comm.). More than 50 % of all colonies of *C. obscurior* collected in Brazil contained several queens (Heinze and Delabie, 2005). The large seasonal variation exhibited by both queen number and colony size indicates that the peak production of female sexuals, which mate and start reproduction in the maternal nest, is followed by the foundation of new colonies by budding. Though several endemic *Cardiocondyla* species in xeric areas of Eurasia are reportedly monogynous (Marikovsky and Yakushkin, 1974; Seifert, 2003; Schrempf et al., 2005a) and are definitively no tramp species, a phylogenetic analysis suggests that polygyny is the ancestral state in *Cardiocondyla* (Heinze et al., 2005). Additional, as yet unstudied species in the tropics might therefore also be facultatively polygynous and could eventually become established as new successful tramps.

Similarly, mating in the nest is an ancestral trait in *Cardiocondyla*. The widespread occurrence of intranidal mating in invasive ants provides an interesting analogue to Baker's

rule, which states that successful invasive plants are often self-compatible (Baker, 1955). *Cardiocondyla* is well known for its peculiar male polymorphism, with winged disperser males and wingless, ergatoid males with small eyes, sturdy antennae, and strong sabre- or shear-shaped mandibles (Forel, 1892; Kugler, 1983), which fight for access to the virgin queens eclosing in their maternal nests (Kinomura and Yamauchi, 1987; Stuart et al., 1987). All species that have as yet been studied possess ergatoid males, but winged males have been lost convergently in several species, such as in the invasive *C. mauritanica* and *C. nuda* (sensu Yamauchi and Kinomura, 1993; Heinze et al., 2005). Both male morphs readily court virgin queens by pummelling them with their antennae and mandibles (Lupo and Galil, 1985; Kinomura and Yamauchi, 1987; Heinze et al., 1993) and mate with them inside the nest.

As in other invasive species, intranidal mating raises the problem of inbreeding, which in addition to its normal detrimental effects is associated with the production of sterile, diploid males in social Hymenoptera with single-locus complementary sex determination (sl-csd), such as honeybees and fire ants (e.g., Cook and Crozier, 1995). The presence of several fertile queens per colony might to some extent decrease the probability of inbreeding in polygynous *Cardiocondyla*. In addition, the production of winged males might lead to regular or irregular episodes of outbreeding, and even the wingless, ergatoid males might contribute to gene flow between colonies by dispersal on foot, as observed in *C. emeryi* (Bolton, 1982). In contrast, most matings in monogynous *Cardiocondyla* are between sibs (Schrempf et al., 2005a; Lenoir et al., 2005). Nevertheless, diploid males have as yet not been found and there is no evidence that diploid male eggs are destroyed or eaten (A. Schrempf and S. Aron, unpubl. results), suggesting that in the genus *Cardiocondyla* sex is not determined by a simple sl-csd mechanism. This apparent stability of *Cardiocondyla* against the adverse effects of inbreeding might strongly contribute to their success as tramp ants. Species with an alternative sex determination mechanism suffer less from the loss of genetic diversity during founder effects than species with sl-csd, in which in introduced populations a significant proportion of founding colonies fail due to the production of diploid males (Ross and Fletcher, 1986).

Polygyny and intranidal mating commonly lead to dependent colony founding through budding. New colonies of *C. obscurior*, *C. minutior*, *C. emeryi*, and related taxa are readily initiated by the fragmentation of large laboratory colonies (e.g., Stuart, 1990). In the laboratory, groups of one or more queens and 20 workers quickly grow to large colonies, while founding experiments with solitary queens are usually unsuccessful (Heinze et al., 1993; A. Schrempf, unpubl. results). It is therefore likely that budding is the predominant mode of colony founding also in the field. Colony censuses of *C. obscurior* show that solitary queens are quite exceptional, while the occurrence of numerous small colonies with one or several young queens, a few workers and brood suggests frequent colony fragmentation (Heinze and Delabie, 2005). Furthermore, queenless experimental

**Table 1.** Colony founding success of *C. obscurior* worker groups from Bahia, Brazil, measured as the production of sexuals. Queenless worker groups of different size were established in the laboratory and provided with different numbers of eggs from queenright colonies. Worker number has a strong effect on founding success, which increases with the number of eggs (Yates corrected  $\chi^2$ -test, 5 vs. 20 workers, 5 eggs:  $\chi^2 = 1.78$ ,  $p = 0.182$ ; 10 eggs:  $\chi^2 = 5.49$ ,  $p = 0.019$ ; 20 eggs:  $\chi^2 = 8.33$ ,  $p = 0.004$ ).

Number of eggs	Number of workers	Sexuals eclosed in ... of 6 colonies
5	5	0
5	10	1
5	20	3
10	5	1
10	10	3
10	20	6
20	5	0
20	10	4
20	20	6

groups of 20 workers easily managed to rear sexuals from the provided 10 or 20 eggs and to thus successfully initiate a new colony (Table 1). The capability of small colony fragments to grow to complete, new societies certainly facilitates the propagation of this species with potted plants or small samples of soil or plant material. As in many other invasive ants (Passera, 1994), the queens at least of *C. obscurior* are extremely short-lived, with a life span of approximately 7 months (Schrempf et al., 2005b).

One final characteristic concerning reproduction that *Cardiocondyla* shares with other tramp ants is complete worker sterility. Workers of all investigated invasive (*C. emeryi*, *C. mauritanica*, *C. minutior*, *C. obscurior*) and non-invasive species (*C. batesii*, *C. elegans*, *C. nigra*) lack ovaries and therefore cannot even lay unfertilized eggs (unpubl. results). The absence of reproductive competence in workers is often explained as “self-policing”, i.e., selection leading to the loss of worker ovaries whenever the probabilities of successful worker reproduction are extremely low because of mutual worker policing (Ratnieks, 1988; Bourke and Franks, 1995).

#### Population structure

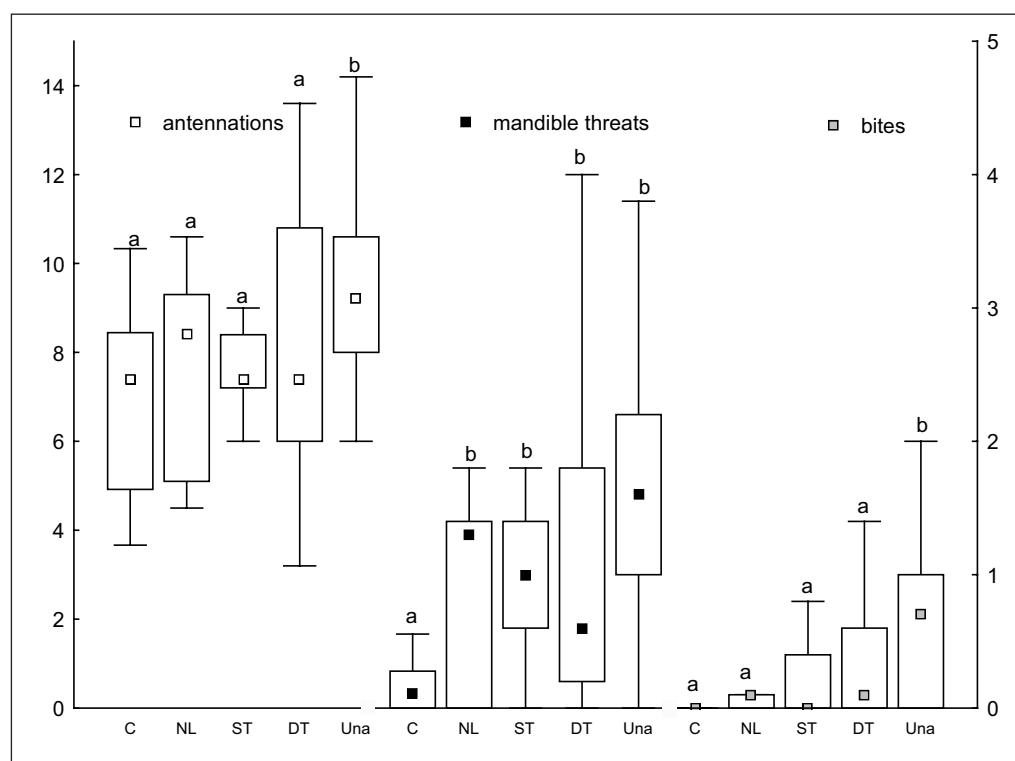
Colony budding underlies the formation of networks of interconnected nests and, in the case of *L. humile* and other tramp ants, may eventually result in uniclonality, i.e., the free exchange of individuals between all nests of a population. As yet, little is known on colony borders in introduced and native populations of *Cardiocondyla*. Colonies of the arboreal species *C. obscurior* from introduced populations

near Ilhéus, Brazil, appear to be capable of distinguishing non-nestmates and nestmates. Shortly after collection from their nests in rolled leaves on lemon trees we confronted workers from acceptor colonies with nestmates (controls) and non-nestmates from different donor colonies a) from a neighbouring leaf (NL), b) a distant leaf from the same tree (ST), c) from a different tree in the same population (DT), and d) from a 150 km distant population (Una). Like the control ants, all alien workers remained unharmed and were finally integrated into the colony after some initial aggression. Nevertheless, the frequency of antagonistic interactions differed significantly among the five combinations (median tests, d.f. = 4; inspective antennation:  $\chi^2 = 12.400$ ,  $p = 0.015$ ; biting:  $\chi^2 = 19.026$ ,  $p < 0.001$ ; mandible threats:  $\chi^2 = 31.072$ ,  $p < 0.001$ ; Fig. 3). The statistical significance results mostly from the difference between controls (nestmates) and experiments involving ants from different populations (U-tests; antennation:  $U = 62.0$ ,  $p < 0.001$ ; mandible threats:  $U = 32.0$ ,  $p < 0.0001$ ; biting:  $U = 52.5$ ,  $p < 0.0002$ ). The frequencies of antennation and biting did not differ between controls and experiments with ants from distant leaves from the same tree and different trees within the Ilhéus population (antennation, DT:  $U = 138$ ,  $p = 0.219$ ; ST:  $U = 68$ ,  $p = 0.300$ ; biting: DT,  $U = 94.5$ ,  $p = 0.012$ , not significant after Bonferroni correction; ST:  $U = 52.5$ ,  $p = 0.077$ ; Fig. 3).

In contrast, workers threatened introduced workers from these alien sources with opened mandibles more intensively than control workers (DT:  $U = 79.0$ ,  $p = 0.003$ ; ST:  $U = 16.0$ ,  $p < 0.001$ ). Stray foragers, which by chance enter alien nests in the field, might therefore not stay permanently but

flee after some initial aggression and colonies are perhaps more closed in the field than our experiments suggest. Nevertheless, nestmate recognition, including aggression against non-nestmates, apparently does not preclude unicoloniality (Chapuisat et al., 2003), and the differential occurrence of mandible threats has rarely been studied in other invasive ants. More data are therefore needed to determine whether invasive *Cardiocondyla* form independent colonies or networks of nests. Interestingly, several combinations between acceptor and donor colonies of the same population resulted in much more aggression than others (N. Eckl and A. Schrempf, unpubl. results). Here, too, further research is needed to clarify whether this variation is due to idiosyncrasies of the respective colonies, polydomy, or the existence of different genetic lineages of colonies. A similar phenomenon in *L. humile* was explained by the occurrence of multiple "supercolonies" (Jaquiéry et al., 2005), probably resulting from independent introductions.

It is currently debated whether unicoloniality is a consequence of the founder-effects accompanying species introduction. Tsutsui et al. (2000) argue that a general depletion of genetic variation (genetic bottleneck) in *L. humile* might also be associated with a loss of variation at those loci that code for the innate colony odour cues responsible for nestmate recognition. Such effects might be enhanced or complemented by selection against rare recognition alleles (Giraud et al., 2002, but see Tsutsui et al., 2003). Like in other tramp species, the genetic variability of some *Cardiocondyla* tramps appears to be low, at least in comparison with that in native populations of Eurasian species. For example, the



**Figure 3.** Number of antennations (left y-axis), mandible threats (right y-axis), and bites (right y-axis) per 5 min (median, quartiles, and range) by workers from an acceptor colony from rolled leaves of lemon trees in Ilhéus, Bahia, Brazil, directed towards individuals from donor colonies in a neighbouring leaf (NL,  $n = 10$ ), a more than 1m distant leaf of the same tree (ST,  $n = 9$ ), a more than 15m distant tree (DT,  $n = 18$ ), a 150km distant population (Una,  $n = 18$ ), and a nestmate as a control (C,  $n = 8$ ). Each experiment was conducted with five different workers from the same donor colony and data were pooled. Different letters mark experiments, in which the response towards introduced workers was significantly different

mitochondrial cytochrome oxidase genes differed in 7 of the approximately 1435 base-pairs (0.5 %) between *C. elegans* from two 200 km distant native populations in France and in 15 base pairs (1 %) between two workers of *C. ulianini* from the same native population in Kazakhstan. In contrast, introduced *C. mauritanica* from Malta, Southern Spain, La Gomera, Madeira, and California, and also *C. emeryi* from Tobago and Hawaii differed in only one or two base pairs (0.1 %) (Heinze et al., 2005). Though nothing is known about the diversity in the source populations of invasive *Cardiocondyla* species and also about their exact locations, it appears that the as yet studied populations of invasive *Cardiocondyla* do not rely on multiple introductions and high genetic diversity to adapt to the new environment, as suggested for invasive lizards (Kolbe et al., 2005).

Furthermore, the genetic similarity among *C. mauritanica* from different introduced populations worldwide indicates that they all originate from a single, genetically poor, native population or, more likely, from the same already bottlenecked, invasive population. Tramp ants might thus first become established on islands with a depauperate ant fauna, such as Hawaii, or in small patches with high human disturbance, and there build up high population densities that multiple secondary transfers to other habitats become possible. It is therefore probably more likely that the Canary Islands were colonized by *C. mauritanica* from Southern Spain or vice versa instead of both sites being invaded independently from the same native population somewhere in Southern Asia (see also Suarez et al., 2001).

### *Ecological impact*

Regardless of whether nests are closed entities or parts of large supercolonies, native and invasive *Cardiocondyla* can reach very high densities because they do not defend their foraging areas and food sources. In this respect they resemble most other ants with small colony sizes (Dobrzański, 1966; Levings and Taniello, 1981; Heinze et al., 1996). One lemon tree in a plantation can therefore easily harbour ten or more colonies of *C. obscurior*, often in immediately adjacent folded leaves (unpubl. results). Similarly, up to 1/3 of moth galls developing on *Tamarix* branches were found to be inhabited by *Cardiocondyla* (Lupo and Galil, 1985). Despite of this high colony density, the impact of introduced *Cardiocondyla* on an ecosystem is very different from that of other tramp ants, in particular those, which are regularly recognized as ecological threats. *Cardiocondyla* are ecologically subordinate (Perez Insueta et al., 2004) and therefore do not compete with conspicuous native or introduced ants with large colonies and mass recruitment. Instead, they might utilize the same niches as other subordinate myrmicine generalists or niches, which are rarely used by native ants. For example, most ants that co-occur with *Cardiocondyla* on beaches or in gardens on Atlantic and Caribbean islands are introduced *Pheidole*, *Tetramorium*, and *Monomorium* (e.g., Wetterer and O'Hara, 2002). In a coconut plantation in Brazil, *C. obscurior* lives in the same

nesting sites – aborted coconuts – as the pantropical tramp *Monomorium floricola* and a few native species widely distributed throughout disturbed New World habitats, such as *Dolichoderus lutosus* and *Pseudomyrmex elongatus* (Conceição et al., 2004). Only a small number of endemic taxa, such as *Nesomyrmex*, might eventually be replaced by *Cardiocondyla*. Several introduced *Cardiocondyla* species may co-occur in close vicinity even though they appear to utilize similar niches. For example, both *C. minutior* and *C. emeryi* nested in a small garden in Plymouth, Tobago (unpubl. results), and at least four introduced species have been reported from Hawaii (Reimer, 1990). Whether this coexistence is permanent or not is unclear. From the non-overlapping distributions of *C. emeryi* and *C. nuda* in Polynesia, Wilson and Taylor (1967a,b) concluded that at least these two species competitively displace one another. Similarly, *C. mauritanica* could not substantially invade the range of *C. kagutsuchi* (Seifert, 2003).

*Cardiocondyla* are among the few ants that co-exist with more aggressive tramp ants, such as *Linepithema* (Carpintero et al., 2004; Harris, 2002; Heterick et al., 2000; Wetterer et al., 1998). While dominant invaders may engage in long-lasting struggles for ecological supremacy, as *Pheidole megacephala* and *Linepithema humile* have done for more than half a century in Bermuda (Wetterer and Wetterer, 2004), *Cardiocondyla* appears to flourish in the shadow of the more aggressive taxa and perhaps even benefits from their destructive effects on the native ant fauna. Workers of dominant species were seen to avoid foragers of *Cardiocondyla*, apparently because the latter produce highly effective repellents in their gasters (Creighton and Snelling, 1974; Gulmahamad, 1997). However, the source and nature of such substances is not known.

### **Conclusion**

As we have shown, striking similarities exist between the life histories of *Cardiocondyla* and other invasive species. Numerous preadaptations that enable species to become successful invaders, such as polygyny, intranidal mating, worker sterility, and budding, are widespread in this genus. Though *Cardiocondyla* presumably will never present large-scale ecological threats, the ease with which colonies can be transferred even in small samples of soil or plant material and their abundance even in areas infested with ecologically dominant invasive species clearly shows that their occurrence and advance should be carefully monitored. *Cardiocondyla* have repeatedly been found in greenhouses (Della Santa, 1998) and even in apartments in temperate areas (unpubl. results). It is therefore problematic that colonies of these and other tramp ants are commercially available as pet ants from "ant stores" (Buschinger, 2004). Given that "pest control" is often more easily explicable to the public than basic research, it might be possible with this excuse to agreeably collect samples of these extremely interesting ants, even if it exposes the researcher "to considerable public scrutiny and perhaps even derision" (Longino, 2004).

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