Wingless and intermorphic males in the ant *Cardiocondyla venustula*

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Abstract The ant genus *Cardiocondyla* is characterized by a pronounced male diphenism with wingless fighter males and winged disperser males. Winged males have been lost convergently in at least two species-rich clades. Here, we describe the morphological variability of males of *C. venustula* from uThukela valley, South Africa. Winged males appear to be absent from this species. However, in addition to wingless ("ergatoid") males with widely fused thoracic sutures and without ocelli, "intermorphic" males exist that combine the typical morphology of wingless males with characteristics of winged males, e.g., more pronounced thoracic sutures, rudimentary ocelli, and vestigial wings. Similar "intermorphic" males have previously been described from one of several genetically distinct lineages of the Southeast Asian *"C. kagutsuchi*" complex (Yamauchi et al., 2005). To determine whether male morphology is associated with distinct clades also in *C. venustula*, we sequenced a 631 bp fragment of mitochondrial DNA of workers from 13 colonies. We found six haplotypes with a sequence variation of up to 5.7%. Intermorphic and wingless males did not appear to be associated with a particular of these lineages and within colonies showed the same sequence. Interestingly, two colonies contained workers with different haplotypes, suggesting the occasional migration of queens and / or workers between colonies.

Keywords *Cardiocondyla venustula* · male diphenism · ergatoid male · intracolony mtDNA variation

Introduction

Across related taxa of ants, males often differ less in appearance than the female castes. Their morphology is conservatively adapted for locating female sexuals and for mating during a nuptial flight or after alighting on the ground: they are uniformly winged, have bulky wing muscles, and relatively small heads with long antennae, large eyes and well-developed ocelli (e.g., Smith, 1943; Hölldobler and Bartz, 1985). Wingless or short-winged (brachypterous) males with a morphology that deviates from that of "standard ant males" have been described from a number of genera scattered throughout the phylogeny of ants (Dolichoderinae: *Technomyrmex albipes* group, Terron, 1972; Yamauchi et al., 1991; Bolton, 2007. Formicinae: several species of *Plagiolepis*, Le Masne, 1956; Espadaler, 2007. Cerapachyinae: *Cerapachys* sp: Bolton, 2003; Ponerinae: *Hypoponera punctatissima* group, Le Masne, 1948; Bolton and Fisher, 2011. Myrmicinae: *Anergates atratulus*, Adlerz, 1886; Heinze et al., 2007; *Cardiocondyla* spp., Kugler, 1983; Seifert, 2003; *Formicoxenus* spp., Francoeur et al., 1985; *Metapone madagascarica* Hölldobler et al., 2002; Alpert, 2007; *Pheidole acutidens,* Bruch, 1931; Wilson, 1984; *Ph*. *neokohli*, Wasmann, 1915; Wilson, 1984, *Ph.* sp., Sarnat, 2009, *Pogonomyrmex* spp., R.A. Johnson, pers. comm.; *Temnothorax caesari,* Espadaler, 1997). Their morphology varies greatly, from ordinary ant males that simply lack wings to individuals that, at a superficial glance, are almost completely identical with workers ("ergatoid males"; Loiselle and Francoeur, 1988).

Because male winglessness is associated with mating in the nest (intranidal mating) or at least on the ground in the vicinity of the nest, its occurrence in patchily distributed taxa, such as guest ants (*Formicoxenus* spp.) or inquilines (*Anergates atratulus*, *Pheidole acutidens*, *Ph. neokohli*; *Plagiolepis ampeloni, Pl. xene*) is not surprising. In several other species, mating of wingless males with winged or wingless nestmate queens in the natal nest increases the number of reproductives per nest and accelerates colony growth (e.g., *Technomyrmex albipes,* Yamauchi et al., 1991; *Cardiocondyla obscurior,* Cremer and Heinze, 2003). Intranidal mating allows males to monopolize female mating partners. It therefore selects for male fighting (e.g., *Hypoponera punctatissima,* Hamilton, 1979;

Yamauchi et al., 1996; *Cardiocondyla* spp., Kinomura and Yamauchi, 1987; Stuart et al., 1987), mate guarding (e.g., *Hypoponera nubatama,* Yamauchi et al., 2001; *H. opacior,* Foitzik et al., 2002), and increased sperm supply (*Cardiocondyla* spp., Heinze and Hölldobler, 1993; *Anergates*, Heinze et al., 2007).

Male diphenism with winged disperser males and wingless fighter males appears to be an ancestral trait in the genus *Cardiocondyla* (Oettler et al., 2010). Wingless males are characterized by relatively small eyes, the absence of ocelli, strong shear- or sickle-shaped mandibles, and a mesosoma with reduced thoracic sutures and often well-developed pronotal anterior corners (e.g., Kugler, 1987; Seifert, 2003, Heinze et al., 2010). Winged males have been lost in all hitherto studied species of a clade comprising species from Europe and Central Asia, including the *C. elegans, C. bulgarica, C. batesii,* and *C. stambuloffii* species groups (sensu Seifert, 2003; Fig. 1). The situation is more complex in the closely related *C. nuda* group: colonies of *C. mauritanica* and the "*C. kagutsuchi*" species complex from Okinawa and the Hawaiian archipelago appear to produce exclusively ergatoid males (Heinze et al., 1993; Frohschammer and Heinze, 2009a), while both winged and ergatoid males are known from other populations of "*C. kagutsuchi"* (Yamauchi et al., 2005). A third group of "*C. kagutsuchi*" colonies from Malaya regularly produce "intermorphic" and short-winged males, which combine the typical morphology of wingless males with features of winged males, i.e., they have ocelli, distinct thoracic sutures, and more or less well developed wings (Yamauchi et al., 2005).

The African *C. shuckardi* group is of considerable interest because it is situated between the clade of European and Central Asian species (with mutually tolerant, wingless males) and the *C. nuda* group (with fighting wingless males and in some taxa also winged males; Oettler et al., 2010; Fig. 1). As yet, males have been studied only in one species of this complex, *C. venustula*. A colony from a population introduced to Kaua'i, Hawai'i, produced only wingless males (Frohschammer and Heinze, 2009b), but obviously more data are needed. Here, we report on the occurrence of both wingless males and intermorphic males with vestigial wings in laboratory and field colonies of *C. venustula*

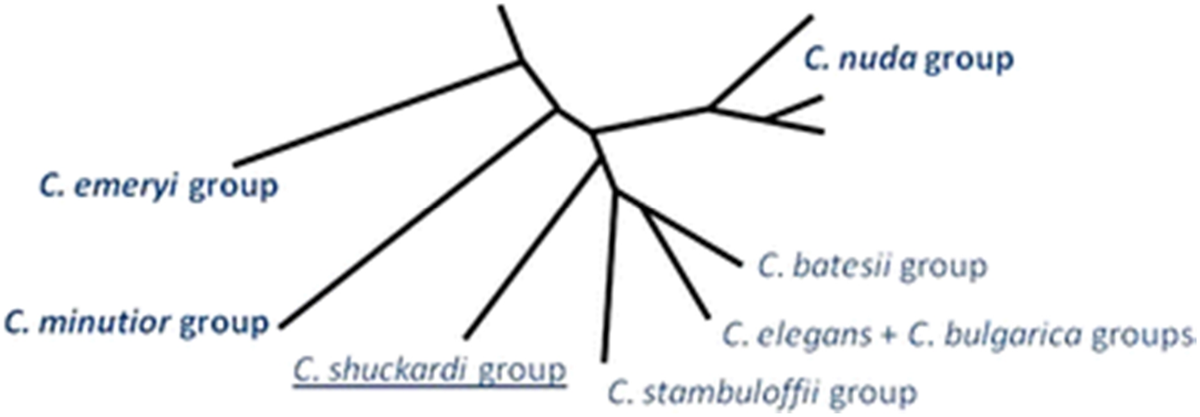

Fig. 1 : Schematic phylogeny of the Cardiocondyla species groups (sensu Seifert, *2003*) mentioned in this study. Both winged males and wingless males with shear-shaped mandibles have been reported in the species groups printed in bold, while only wingless males with shear-shaped mandibles are known from the species groups in normal font. Our study describes intermorphic and wingless males from C. venustula, a species of the underlined C. shuckardi group (based on Oettler et al., *2010*). The large branch of Southeast Asian and Wallacean species, in which wingless males have sickle-shaped mandibles, is omitted

from South Africa. We describe the morphology of these males and examine whether, as in "*C. kagutsuchi*" (Yamauchi et al., 2005), intermorphic males are produced only by particular haplotypes.

Methods

Complete colonies of *C. venustula* Wheeler 1908 were collected on a sand track and degraded patches of grassland in uThukela valley, KwaZulu Natal, South Africa in early April 2011 (April 4 – 7, 2011: 21 colonies at Hlalanathi Drakensberg resort, 28° 39’ 33” S, 29° 01’ 52” E, altitude 1284m, and April 10, 2011: 8 colonies near the entrance of Royal Natal National Park, 28° 40’ 56” S, 28° 58’ 29” E, altitude 1354m). The ants nested in small cavities in the upper layers of sandy soil down to a depth of 10 – 20cm. In addition, we collected several dealate, dispersing queens.

Colonies were cursorily inspected by eye immediately after collection but censused under a microscope only after transfer to the laboratory. Thereafter, the colonies were maintained in incubators in three-chambered plastic boxes with a plaster floor as previously described (e.g., Frohschammer and Heinze, 2009b). Males were mounted on points, and head width (behind the eyes), eye diameter, mesosoma length in lateral view ("Weber’s length," i.e., from the anterior margin of the pronotum to the postero-ventral edge of the mesosoma, Weber, 1938) and prosoma width (at the anterior corners in dorsal view) were measured at 80x magnification using a Leica Wild M10 stereo microscope. In three cases, we measured two or three intermorphic or wingless males from the same colony. To avoid dependence of data, we used the median of male measurements from these colonies for statistical analysis.

To determine whether male morphology varies with mtDNA haplotype, DNA was extracted as previously described (Heinze et al., 2005) from individual workers from 13 of those 14 colonies that had produced males and in addition from three intermorphic and two wingless males from two colonies. Because of amplification problems with our standard primers for the mitochondrial gene COI / CO II, we only amplified a 631 bp fragment using the primer combination LCO / HCO (Folmer et al. 1994) with the BioX-act short mix from Bioline (Great Britain; volume per sample 15µl with 7.5 µl BioX, $MgCl_2$ (50mM) 0,25µl, HCO (10µM) 0,6µl, LCO (10µM) 0,6µl, DNA 1µl, PCR water 5,05µl; initial step of 94°C, 39 cycles a 94°C, 75 sec, 50°C,; 60 sec 72°C,105 sec, final step 72°C, 5 minutes). PCR products were purified and sequenced by LGC Genomics (Berlin). Sequences were aligned with the software BioEdit v 7.09 (Hall, 1999) using the CLUSTAL W Algorithm (Thompson et al., 1994) and then manually corrected. Bayesian inference of phylogeny was calculated using Mr. Bayes 3.2.1 (Huelsenbeck and Ronquist, 2001) and a HKY + I model. The specific model was estimated using the platform MrModeltest GUI (available under www.softpedia.com) in conjuncture with PAUP 4.0b10 (Swofford, 1998). The analysis was performed with a MCMC length of 3.000.000 generations out of which the first 10.000 generations were discarded. The program FigTree version 1.3.1 (available under http://tree.bio.ed.ahc.uk) was used to illustrate the tree.

Results

When collected in early April, colonies of *C. venustula* from uThukela valley contained numerous alate female sexuals and dealate queens. This and the collection of large numbers of dealate dispersing queens indicate that sexuals are produced in South African fall, and that at least some mated, dealate queens attempt to found colonies away from their maternal nests. Colonies from Hlalanathi had between 0 and 37 dealate queens and between 0 and 30 alate female sexuals (n = 21, median, quartiles: dealates 1, 0, 3; alates 2, 0, 11). Colonies from the entrance of Royal Natal National Park, collected a few days later, had between 0 and 4 dealate queens, but mostly no alate female sexuals (n = 8, median, quartiles: dealates 1, 1, 1.5; alates: 0, 0, 1).

In 14 of 29 colonies, one or two adult males were present upon collection or were reared during or shortly after the transfer to the laboratory. Seven colonies (three from Hlalanathi: ZAII-1, 22, 27; four from the entrance of Royal Natal National Park: ZAII-30, 31, 32, 38) produced one or two wingless males with a simplified thorax structure and without ocelli, similar to those described from Kaua'i (Frohschammer and Heinze, 2009b). Three colonies (all from Hlalanathi) produced one to four males with vestigial or well-developed but short wings, distinct meso-metanotal and meta-epinotal sutures, and one to three clearly visible ocelli (Fig. 2, ZAII-11, 23, 24). In other aspects, these intermorphic males closely resembled the typical wingless males of *C. venustula*, i.e., they had large heads, massive, sclerotized, shear-shaped mandibles, small eyes, and strong pronotal shoulders. Four colonies (all from Hlalanathi, ZAII-6, 7, 12, 20) produced one or two males each of both types. At least one colony (from Hlalanathi) contained an intermorphic male in the field, i.e., the production of this type of males is not an artifact due to transportation or laboratory conditions. Intermorphic males were significantly larger than wingless males concerning mesosoma length (0.71 – 0.77mm, median 0.73mm vs. 0.54 – 0.71mm, median 0.64mm; Mann-Whitney U-test, $n_1 = 4$, $n_2 = 8$, $U = 0.50$, $p = 0.008$), pronotal width (0.44 – 0.50mm, median 0.48mm vs. 0.33 – 0.42mm, median 0.40mm; $U = 0$, $p = 0.007$), and head width (0.51 – 0.56mm, median 0.55mm vs. 0.45 – 0.54mm, median 0.49mm; $n_1 = 3$, $n_2 = 7$, $U = 0.5$, $p = 0.022$). They also had larger eyes than wingless males (0.28 – 0.30mm, median 0.25mm vs. 0.19 – 0.22mm, median 0.22mm, $n_1 = n_2 = 4$, $U = 0$, $p = 0.021$).

Though we did not have enough males to study their behavior in detail, the finding of males with severed legs or antennae suggested that both wingless and intermorphic males occasionally engage in aggressive interactions and also attack and kill freshly emerging males. Nevertheless, in a few colonies two adult males co-occurred for at least ten days. Both types of male copulated with virgin queens, which later shed their wings and laid eggs.

The genetic analysis of 13 colonies revealed the presence of several major haplotypes at the CO I gene, which differed from one another in 1 to 36 base pairs (0.13 – 5.71%; Fig. 3). At least two of the 13 studied colonies (colony ZAII-7 and ZAII-32) contained workers with different haplotypes. As already suggested by the production of both types of males in some colonies, a phylogenetic analysis (Fig. 3) did not support the hypothesis that wingless or intermorphic males are produced in different lineages of *C. venustula*. Male haplotypes were available only from two colonies (two intermorphic, one wingless male from ZAII-20 and one intermorphic and one wingless male from ZAII-23). The two types of males did not differ in their sequence and shared the haplotype of nestmate workers.

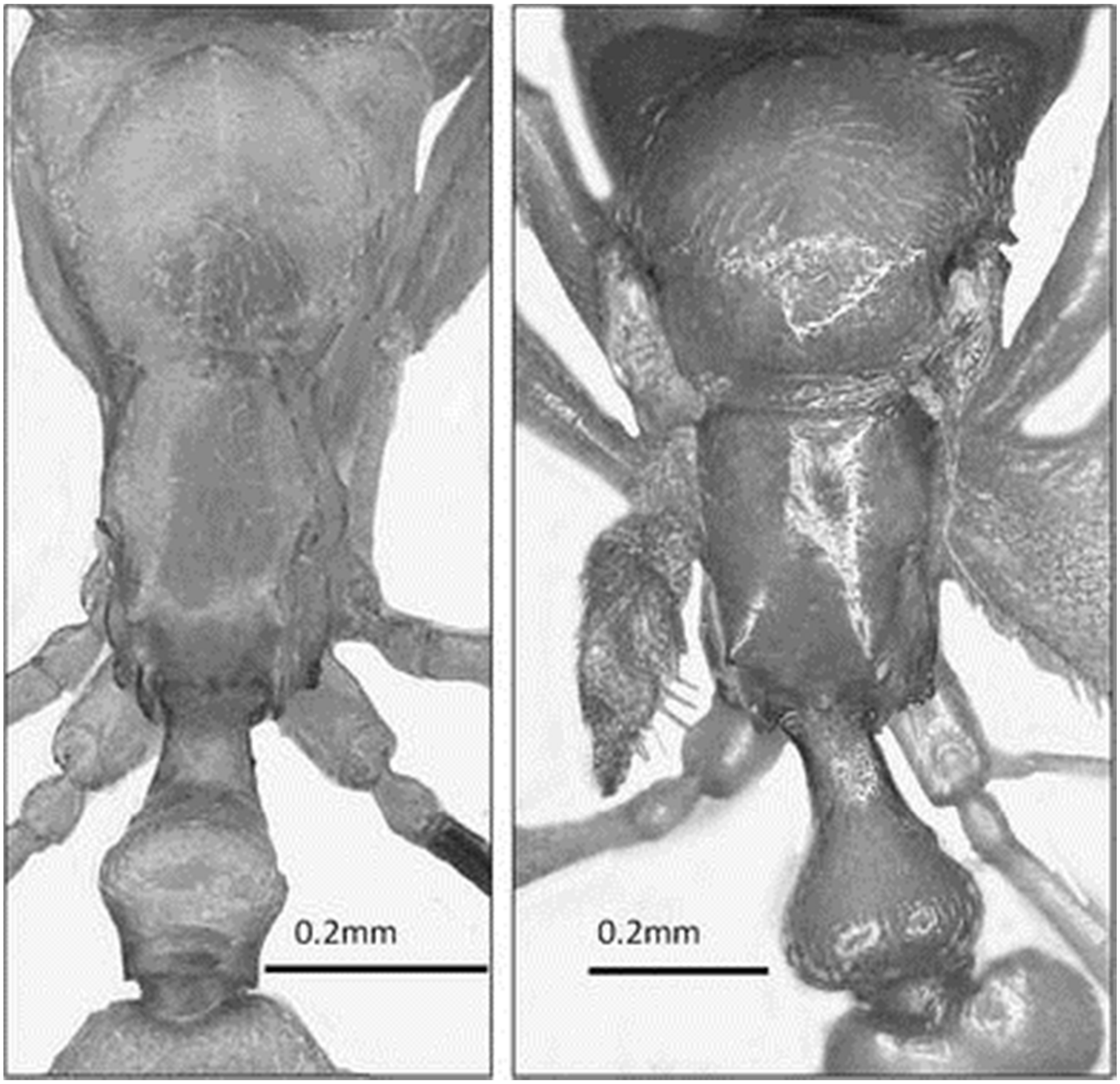

Fig. 2 : Mesosoma of wingless male (left) and intermorphic male (right) of the ant Cardiocondyla venustula from uThukela valley, KwaZulu Natal in dorsal view. Thoracic sutures and vestigial wings of the intermorphic male are clearly visible

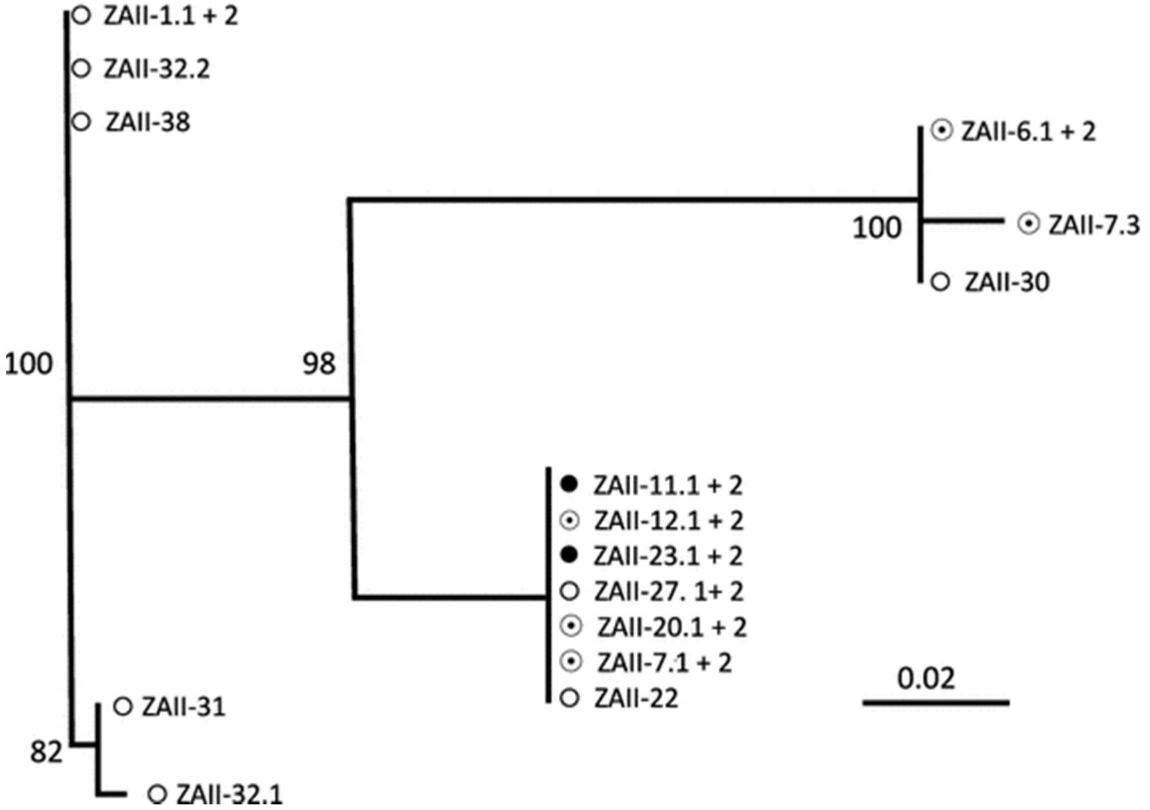

Fig. 3 : Consensus tree of workers of Cardiocondyla venustula from several colonies in uThukela valley, KwaZulu Natal, estimated by the software MrBayes from sequences of a 631 bp fragment of the CO I gene. Numbers near the nodes give posterior probabilities. In some colonies, two or three individuals were sequenced. This is indicated by the Figures 1, 2, or 3 behind the name of colony. The phenotype of males observed in these colonies is indicated by circled dots (wingless and intermorphic males), empty circle (wingless males), and filled circle (intermorphic males). As only very few males were produced per colony it is likely that most colonies rear both types of males

Discussion

Males of *C. venustula* from uThukela valley in South Africa show a remarkable variation in morphology. Several wingless males resembled the typical wingless males known from other species of *Cardiocondyla* in overall morphology, i.e., they were wingless and had large heads, strong shear-shaped mandibles, and widely fused thoracic sclerites (see, e.g., Frohschammer and Heinze, 2009b). In others, the groundplan of wingless males combined with rudimentary or shortened wings and more or less pronounced thoracic sutures and ocelli. The extent to which these features were expressed varied considerably, but the morphology of intermorphic males never approached that of standard winged ant males. Intermorphic males were considerably larger than wingless males. Molecular data and the co-occurrence of wingless and intermorphic males in several colonies indicate that, in contrast to *C.* cf. *kagutsuchi* (Yamauchi et al., 2005), the different types of *C. venustula* males are not associated with distinct genetic lineages.

Given that even the intermorphic males with the best developed wings appear to be incapable of flight, it is unlikely that the observed polyphenism is associated with different dispersal or mating tactics. Yamauchi et al. (2005) found that intermorphic males of *C.* cf. *kagutsuchi* that eclose in the presence of adult rivals have a significantly higher survival rate than wingless males. They suggested that young intermorphic males might use their short wings to protect themselves from attacks by older rivals. *C. venustula* males may similarly engage in lethal combat (Frohschammer and Heinze, 2009b) and intermorphic males might benefit from their larger size. However, because their wings are usually only small rudiments it is unlikely that they can be used as a shield.

Instead, we suggest that male polyphenism in *C. venustula* is a non-adaptive consequence of variation in factors that control the ontogeny of larvae. The variability of male phenotype in *C. venustula* might therefore resemble the sporadic occurrence of intercastes, i.e., females with a mix of features typical of “gynomorphic” ant queens and “ergatomorphic” ant workers (e.g., Heinze, 1998), only that intermorphic males have retained their specific reproductive function. Similar intermorphic males have been produced in laboratory colonies of *C. obscurior,* which had been induced experimentally to switch from the production of wingless males to winged males (Cremer et al., 2002). This again suggests a strong environmental influence on the morphology of *Cardiocondyla* males.

Though we did not aim to determine the colony and population structure of *C. venustula*, our study revealed a surprisingly large variability of mt DNA haplotypes both between and within colonies. Intracolonial mtDNA polymorphism indicates that alien colonies of *C. venustula* may fuse or that alien queens or workers may be adopted, as suggested for *C. obscurior* (Kinomura and Yamauchi, 1987). The co-occurrence of workers with different haplotypes has previously been demonstrated in a few other ants (e.g., Stille and Stille, 1992; Carew et al., 1997; Tay et al., 1997) and there is more and more direct and indirect evidence for the evolutionary puzzling occurrence of colony fusion and the adoption of alien females (e.g., Foitzik and Heinze, 2004; Johns et al., 2009; Kellner et al., 2010). Although our collecting data and dissection of queens from laboratory colonies (A.S., unpubl. data) suggest the presence of multiple, mated queens in colonies of *C. venustula*, it remains unclear whether this is stable polygyny or a temporary condition under natural conditions. In the field, young, mated queens with developing eggs might have dispersed from the maternal nest, leading to the monogynous conditions of *C. venustula* described by Wheeler (1908) at its type locality in Puerto Rico.

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