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Male Polymorphism in the Ant Species Cardiocondyla minutior (Hymenoptera: Formicidae)

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Males [**MM**] of the myrmicine ant species *Cardiocondyla minutior* (Forel 1899) may be either winged and similar to normal ant **MM** in morphology and behavior, or aggressive, wingless and workerlike in external appearence ('ergatoid'). Compared to other ant **MM**, spermatogenesis appears to be prolonged in both male morphs, though the testes had completely degenerated in winged **MM** 20d after eclosion. A comparative investigation supports the hypothesis that only ergatoid **MM** are produced in those *Cardiocondyla* species that have on average large colony sizes, whereas both male morphs co-occur in species with small colony size.

Key words: *Cardiocondyla minutior* (Forel 1899) - Myrmicinae - male polymorphism - alternative reproductive tactics

HEINZE J [Inst Zool I, Univ Erlangen-Nürnberg, D-91058 Erlangen]: **Männchen-Polymorphismus bei der Ameisen-Art Cardiocondyla minutior (Hymenoptera: Formicidae).**- Entomol Gener **23**(4): 251-258; Stuttgart 1999-03. - - - [Abhandlung]

Männchen der Myrmicinae-Species *Cardiocondyla minutior* (Forel 1899) sind entweder geflügelt und ähneln in Morphologie und Verhalten den **MM** anderer Arten, oder aber sie sind aggressiv, flügellos und in ihrem Aussehen arbeiterinnenähnlich ('ergatoid'). Verglichen mit anderen Ameisen-**MM** ist der Zeitraum der Spermatogenese bei beiden Morphen verlängert, wenngleich die Hoden bei geflügelten **MM** 20 Tage nach dem Schlüpfen degeneriert waren. Ein Vergleich verschiedener *Cardiocondyla*-Species unterstützt die Hypothese, wonach ergatoide **MM** bei Arten mit im Durchschnitt größeren Kolonien auftreten, beide **MM**-Morphen aber bei Arten mit kleinerer Koloniegröße.

Schlüsselbegriffe: *Cardiocondyla minutior* (Forel 1899) - Myrmicinae - Männchen-Polymorphismus - Alternative reproduktive Taktiken

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1 Introduction

Male polymorphism is a widespread phenomenon among aminals. In species such diverse as mites, dung beetles, and elephants, some **MM** are endowed with strong horns, tusks, or elongated mandibles, whereas these characters are absent or significantly less well developed in others [RADWAN 1993, KURT et al 1995, EMLEN 1997]. Typically, the armed **MM** are territorial and fight to increase their chances to mate, whereas the other morph mimics females [**FF**] or engages in sneak copulations [GROSS 1996].

In ants, a striking male polymorphism is known from the 4 genera *Technomyrmex*, *Hypoponera*, *Formicoxenus*, and *Cardiocondyla* [LOISELLE & FRANCOEUR 1988]. Here, some **MM** are very similar in morphology to normal, winged **MM** of related taxa, i.e, they have small heads, long and slender antennae, large eyes and ocelli, strong wing muscles, etc. Other **MM,** however, are wingless, have a more or less aberrant morphology of caput, alitruncus and gaster, and may closely resemble workers in their appearance ('ergatoid **MM**'). Ergatoid **MM** of several species of the genus *Cardiocondyla* EMERY 1869 have concealed genitals, and therefore have repeatedly been mistaken for **FF,** and described as social parasites living in the nests of other species of the genus *Cardiocondyla* (referred to by the synonyms: *Emeryia* Forel 1890, *Xenometra* Emery 1917) [e.g: BERNARD 1957, but see: BARONI URBANI 1973, MARIKOVSKII & YAKUSHKIN 1974].

Similar to the **MM** of other ant genera, winged **MM** of *Cardiocondyla* are not aggressive and after attempting to mate with virgin queens in their nests for a certain period of time they emigrate and presumably try to copulate with virgin queens from other colonies. At least during this stage of their life cycle, their testes have fully degenerated, and like the **MM** of other Hymenoptera winged *Cardiocondyla* **MM** then have only a limited sperm supply. In contrast, ergatoid **MM** attack and kill freshly eclosing ergatoid rivals and occasionally also engage in fighting with adult ergatoid **MM** [STUART et al 1987, KINOMURA & YAMAUCHI 1987, HEINZE et al 1993, YAMAUCHI & KINOMURA 1993, HEINZE et al 1998]. Successful ergatoid **MM** thus remain the only adult ergatoid male in their colony for days or even weeks, during which they mate with all eclosing virgin queens. Surprisingly, spermatogenesis continues throughout the whole lifetime of ergatoid **MM** [HEINZE & HÖLLDOBLER 1993].

In most of the approximately 50 known species of *Cardiocondyla*, only workers and queens have been described [BOLTON 1995, RADCHENKO 1995]. Winged **MM** have been reported from *C emeryi*, *C nigra* (also referred to as *C batesii nigra*), and *C wroughtonii*. Ergatoid **MM** are known from eight or nine species (*C ectopia*, *C elegans*, *C. emeryi*, *C mauritanica* (= *C nuda*?), *C nigra*, *C nuda*, *C papuana*, *C stambuloffii*, *C ulianini* (= *C elegans*, DLUSSKY et al 1990), and *C wroughtonii)*. Both male morphs thus currently have been formally described only from three species [KUGLER 1983, BOLTON 1995]. Ergatoid and winged **MM** also co-occur in 2 additional, undescribed species from Okinawa [YAMAUCHI & KINOMURA 1993].

At least in those of the *Cardiocondyla* species with only ergatoid **MM**, which have been carefully studied, it is unlikely that winged **MM** have accidentally been missed. The occurrence of only ergatoid **MM** in some species and of both male morphs in others thus needs to be explained. In fig wasps, which show a male polymorphism similar to *Cardiocondyla*, HAMILTON [1979] noted that species with large broods tend to have wingless **MM**, whereas species with small broods have winged **MM**. He suggested that winged **MM** are favored in the latter species because they may disperse and mate with virgin **FF** from those broods which by chance did not contain **MM**. In species with large broods, non-dispersing **MM** inseminate all the virgin **FF** in their vicinity, dispersing winged **MM** rarely find a brood without resident **M**, and therefore are selected against.

According to a model developed explicitly for *Cardiocondyla* by TSUJI et al [1994], dimorphism is evolutionarily stable when the survival rate and / or the copulation ability of wingless **MM** are very small. An increase in the survival rate or copulation ability of ergatoid **MM** leads to their exclusive occurrence.

Tab 1: Colony size in the ant genus *Cardiocondyla* Emery 1869 [Hymenoptera: Formicidae].- For details see text.

Species	Nest Site	Locality	Sample Size	Workers	Dealate Queens	Reference
Polymorphic Males						
C emeryi [b]	soil	Texas	1	34	3	CREIGHTON & SNELLING 1974
C minutior	soil	Hawaii	Unknown	20 - 30		PHILLIPS 1934
C minutior [a]	soil	Itabuna, Brazil	9	< 30	1 - 2	own data
C nigra [a d]	soil	Tunisia	Unknown	30 - 50		SANTSCHI 1907
C wroughtonii [a]	arboreal	Okinawa	36 / 54[c]	37 ± SD 31	7.0 ± SD 4.9	KINOMURA & YAMAUCHI 1987
C wroughtonii	arboreal	Una, Brazil	15	14.5 ± SD 11	4.1 ± SD 3.4	own data
C wroughtonii	twigs	Florida	1	Ca. 20	not determined	own data
C sp (hiyake-hadaka-ari) [a]	soil	Okinawa	5	Mean 54.4	mean 3.2	K YAMAUCHI & K KINOMURA, unpubl
C sp (hime-hadaka-ari) [a]	soil	Okinawa	32	45 ± SD 29	2.9 ± SD 2.2	K YAMAUCHI & K KINOMURA, unpubl
Ergatoid Males						
C ectopia [a]	soil	California	1	75	2	CREIGHTON & SNELLING 1974
C elegans [a]	soil	Kazakhstan	5	269 ± SD 60	1	MARIKOVSKII & YAKUSHKIN 1974
C nuda	soil	Texas	1	38	2	CREIGHTON & SNELLING 1974
C nuda[f]	soil	La Palma	11	20 - 200	several	HEINZE et al 1993
C nuda	soil	Okinawa	14 / 12[c]	mean 71.5	2.8	K YAMAUCHI & K KINOMURA, unpubl

[a] colony size used for statistical test in text [b] only part of a polydomous colony [c] sample size of colonies investigated for average worker number / average queen number [d] referred to as *Cardiocondyla batesii* [e] referred to as *Cardiocondyla ulianini*
[f] *C nuda* from from palaearctic areas is probably a separate species, *C mauretanica*

As it appears that the survival rate of ergatoid **MM** depends on colony size - in very large colonies, several ergatoid **MM** may eventually co-occur [HEINZE et al 1993] - both models suggest that species with male polymorphism should on average have smaller colonies than species with only ergatoid **MM.**

Here, a new case of male polymorphism is described for *C minutior* (Forel 1899), and data are presented on colony sizes in various species of the genus *Cardiocondyla*.

2 Material and methods

Cardiocondyla minutior is a widely distributed tramp species in the Pacific islands and the neotropical region [B BOLTON, pers comm]. It was originally described from Hawaii as a variety of the cosmotropical *C nuda* (FOREL 1899) and later synonymized with the latter [WILSON & TAYLOR 1967]. Recently, however, *C minutior* was elevated to species rank [HEINZE 1997]. In addition to morphological differences in the worker caste, which were already reported by FOREL [1899] and WHEELER [1922] and summarized by SMITH [1944], such as smaller size and more acute epinotal spines, *C minutior* most notably differs from *C nuda* in the presence of winged **MM**.

A total of nine colonies of *C minutior* were collected in April 1995 and March 1998 from their nests under stones on a gravel road on the area of CEPLAC, Itabuna, Brazil. In the laboratory, the colonies were housed in plastic boxes with a plaster floor as previously described [HEINZE et al 1998]. Ergatoid and winged **MM** were regularly reared in two colonies from 1995 in the laboratory over more than two years. All measurements were made using a Wild M8 binocular microscope with an ocular micrometer at 100x magnification.

For histology, winged **MM** were fixed in alcoholic Bouin solution, embedded in Durcupan (Fluka) and serially sectioned at approx 1µm with glass knives and a Reichert microtome. The sagittal sections were stained with toluidine blue solution (0.1% toluidine blue in 0.1% sodium borate).

For comparison, material of *C emeryi* from Barbados [HEINZE & TRENKLE 1997], *C nuda* from Barranco de Las Angustias, La Palma, Canary Islands [HEINZE et al 1993], and *C wroughtonii* from a coconut plantation at Lemos Maia Exp Station, Una / Bahia, Brazil, was examined.

3 Results

3.1 Description of the male morphs of *C minutior*

The ergatoid male (Measurements from 7 **MM** , in mm): Thorax length [TL] 0.49-0.55; thorax width [TW] 0.25-0.27, head width [HW] 0.35-0.43, length of scapus [SL] 0.26-0.29, eye diameter [ED] 0.09-0.11, length of petiolus [PL] 0.18-0.22, height of petiolus in lateral view [PH] 0.13-0.18, width of petiolus in dorsal view [PW] 0.12-0.17, length of postpetiolus [PPL] 0.12, height of postpetiolus in lateral view [PPH] 0.13-0.18, width of postpetiolus in dorsal view [PPW] 0.20-0.25, length of hind femur [LHF] 0.28-0.32, length of hind tibia [LHT] 0.25-0.27. Coloration yellowish, shining, gaster somewhat darker. Eyes small, ocelli absent. Antennae with 11 segments (in 2 of 7 investigated individuals, one antenna each had 12 segments). Mandibula with 4-5 teeth, alitruncus with only slightly angular shoulders; sutures of alitruncus present to a variable degree (Fig 1), scutellum visible as a separate sclerite in some specimens, but absent in others. Petiolus approx 2/3 as wide as postpetiolus.

The winged male: (Measurements from 10 winged **MM** , in mm) TL 0.65-0.73; TW 0.33-0.35; HW 0.37-0.41, SL 0.37-0.39, ED 0.12-0.15, PL 0.27-0.31, PH 0.13-0.16, PW 0.11-0.16, PPL 0.15-0.18, PPH 0.12-0.14, PPW 0.19-0.0.24, LHF 0.42-0.46, LHT 0.34-0.38, length of praeala 1.52-1.60, length of postala 1.12-1.18 mm. Coloration dark reddish brown to reddish black, with the pedes, the scapi, the petiolus and postpetiolus slightly lighter. Caput with large, oval, convex eyes, ocelli present; antennae typically with 13 segments (of 12 individuals investigated in this respect, one had 2 antennae with 11 segments each, and another had 2 antennae with 12 segments each); clypeus without indentation and longitudinal carinae. Mandibula with 4-5 teeth, the apical tooth much larger than the others. Alitruncus with well differentiated sclerites, but without Mayrian forrows. Propodeum with 2 spines. Wing venation reduced, but in contrast to winged **MM** of *C emeryi* [KUGLER 1983] the cubital cell is posteriorly closed. Petiolus approx 2/3 as wide as postpetiolus.

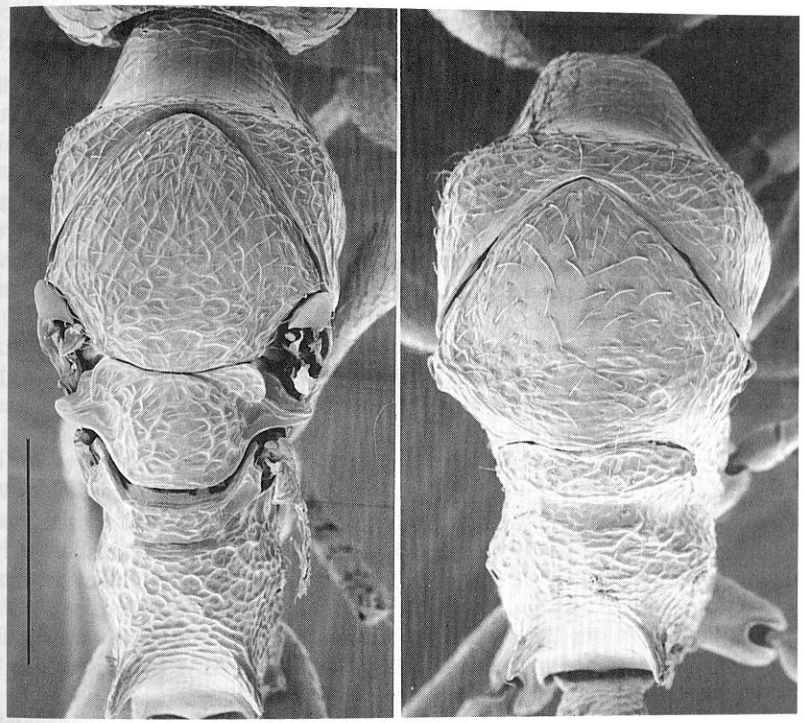

Fig 1: Thorax (in dorsal view) of males of the ant species *Cardiocondyla minutior* (Forel 1899) from Brazil [Hymenoptera: Formicidae: Myrmicinae].- **Left** of a winged male (the wings were removed for better visibility of the thorax structure), **right** of an ergatoid male (in addition to the lack of wing remnants, ergatoid **MM** differing from winged ones also in coloration, a much simpler thorax structure, the shape and size of the caput etc).- The bar on the left equals 0.2 mm.

Diagnosis: *C minutior* ergatoid **MM** differ from those of *C wroughtonii* (and *C papuana*) in that they do not have elongated mandibulae. In dorsal view, the petiolus does not have a distinct, broad node, hence in this respect *C minutior* ergatoid **MM** are similar to those of *C emeryi* and *C nuda*, but differ from those of *C elegans* and others. *C minutior* ergatoid **MM** differ from those of *C emeryi* in that their pronotal shoulders are not strongly angular and the absence of ocelli. The antennae of ergatoid **MM** of *C nuda* are 12-segmented, but 11-segmented in most investigated ergatoid **MM** of *C minutior*.

The winged **MM** of *C minutior* differ from those of *C nigra*, *C emeryi*, and *C wroughtonii* in coloration, which is yellowish in the latter 3 species.

Deposition of specimens: Both male morphs, workers, and queens have been sent to the Museum of Comparative Zoology, Cambridge, Mass / USA, and the British Museum of Natural History, London.

Histology: Four winged **MM** of different ages were investigated histologically to determine the development of their testes. In the two 14d old **MM**, testes with spermatogenic tissue were well developed and no sperm cells were present in the seminal vesicles. Testes had degenerated in **MM** 20d and 25d after eclosion, and the seminal vesicles were filled with sperm.

As expected, dissection showed that the testes were well developed and the seminal vesicles were filled in an ergatoid **M** at least seven weeks old, suggesting that spermatogenesis continues in ergatoid **MM** for an even more strongly extended period after eclosion.

Colony size: Because of the small size of *Cardiocondyla* it is often extraordinarily difficult to locate their nests [CREIGHTON & SNELLING 1974: report on an unsuccessful search], especially in those species where nest chambers may reach down in the soil to a depth of 1.3-1.5m [MARIKOVSKII & YAKUSHKIN 1974: *C elegans*], [A TINAUT & J HEINZE, unpublished: *C nigra*]. Exact data on colony composition especially of ground-nesting species are therefore difficult to obtain and published colony sizes are probably too low. On the other hand, in laboratory culture, colonies may quickly reach unnaturally large sizes due to the restriction of budding in artificial nests. Hence, worker numbers given for laboratory colonies of *C wroughtonii* [STUART et al 1987: 376 ± SD 200 workers] are astonishingly large compared to data from field colonies collected in Brazil and Okinawa (Tab 1). In fact, many of the laboratory colonies studied by STUART et al [1987] were derived from a single colony found in Florida, consisting of a queen and less than 20 workers [STUART, pers comm].

Tab 1 gives an overview on what is currently known about *Cardiocondyla* colony sizes in species with polymorphic **MM** and species with only ergatoid **MM**. Worker numbers per colony overlap between the two groups, but average colony size appears to be considerably smaller in species with polymorphic **MM**. For the statistical analysis of differences in colony size I used only one data point per species, excluding the smaller or less accurate data sets (*C emeryi*, *C wroughtonii* from Brazil and Florida, *C nuda* from Texas and La Palma). Mean colony size of species with ergatoid **MM** was significantly larger than mean colony size of species with polymorphic **MM** (Mann-Whitney U-test, $n_1 = 5$, $n_2 = 3$, $U = 0$, $p = 0.025$).

4 Discussion

Cardiocondyla minutior exhibits a striking male polymorphism which is similar to that in *C emeryi*, *C wroughtonii* and *C nigra*. Both male morphs can easily be distinguished from the described **MM** of other *Cardiocondyla* species by morphological traits or coloration. Thorax morphology, especially the expression of the scutellum, varied among ergatoid **MM**, and in both male morphs the number of antennal segments differed between individuals. It is therefore likely that a new and more detailed morphological examination will become necessary with the investigation of **MM** from other populations of *C minutior* and / or the discovery of **MM** in additional *Cardiocondyla* species than could be provided here and in previous comparative analyses [KUGLER 1983].

As in other *Cardiocondyla*, ergatoid **MM** of *C minutior* are highly aggressive and attack and kill their ergatoid rivals, especially young callows, whereas the winged **MM** do not fight. Both male morphs are capable of inseminating nestmate queens, but whereas ergatoid **MM** apparently do not emigrate from their maternal nests, winged **MM** disperse several days after eclosion [HEINZE et al 1998].

According to dissections, the testes of ergatoid **MM** of *C minutior* do not degenerate shortly after eclosion, but instead spermatogenesis probably continues throughout their whole lives as in ergatoid **MM** of other *Cardiocondyla* species [HEINZE & HÖLLDOBLER 1993, HEINZE et al 1998]. Surprisingly, the testes were still well developed and functional in 14 days old winged **MM**, though no sperm was found in their seminal vesicles. Testes had degenerated and all sperm had been transferred into the seminal vesicles by day 20 after eclosion. This stands in contrast to previous observations that in winged **MM** of *C wroughtonii* and *C emeryi* the testes degenerate within a week or so after eclosion [HEINZE & HÖLLDOBLER 1993, HEINZE et al 1998]. The winged **MM** of *C minutior* available for histological analyses eclosed in the absence of virgin queens and therefore did not have a chance to mate in the maternal nest. It was suggested that the presence of virgin queens probably affects the timing of dispersal in winged **MM** in *C emeryi* [HEINZE et al 1998] and one might speculate whether a more general influence of the availability of virgin queens on the maturation of **MM** could explain the observed prolonged spermatogenesis in winged **MM** of *C minutior*. More data are needed to clarify whether the timing of reproduction depends on the availability of virgin queens.

HAMILTON [1979] observed that in fig wasps, species with large broods tend to have wingless **MM**, whereas species with small broods have both winged and wingless **MM**. Strong evidence in support of this proposed correlation between brood size and male morph was recently found in a comparative analysis using data from 114 species of fig wasps [COOK et al 1997]. A model developed by TSUJI et al [1994] similarly predicts that average colony size influences male morph. Average colony sizes indeed appear to be larger in *Cardiocondyla* species with ergatoid **MM** than in species with polymorphic **MM**. Though very small colonies of *Cardiocondyla* have been observed to produce very large broods, [MARIKOVSKII & YAKUSHKIN 1974: young alate queens may by far outnumber all other adults per colony], brood size in general is presumably positively correlated with colony size. Hence, the pattern described for fig wasps appears to hold also for *Cardiocondyla*. It must be noted, however, that as yet nothing is known on the phylogeny of *Cardiocondyla* species, and therefore it is unclear whether different species represent independent data points.

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