



Emeryia, *Xenometra*, *zoserka*: it's a boy, again! The misleading morphology of *Cardiocondyla* male ants

J. Heinze¹

Received: 20 June 2019 / Revised: 19 November 2019 / Accepted: 22 November 2019
© International Union for the Study of Social Insects (IUSSI) 2019

Abstract

Wingless “ergatoid” males of the ant genus *Cardiocondyla* have repeatedly been described as females of novel genera of workerless social parasites (*Emeryia* and *Xenometra*), which after recognition of their real nature were synonymized with *Cardiocondyla*. Examination of ants newly collected from Comoé National Park in Côte d’Ivoire, West Africa revealed that winged *Cardiocondyla* males have sparked a similar misidentification: the “winged female sexuals” of the supposed inquiline *Cardiocondyla zoserka* Bolton 1982, known only from the type material from Nigeria, are in fact the winged males of their presumed host, a species of the *Cardiocondyla shuckardi* group (sensu Seifert 2002). The types of *C. zoserka* are immediately recognizable by their strangely modified antennal funiculi with cup-shaped apical segments, which do not resemble any other known ant antenna. More than twenty winged individuals from two *Cardiocondyla* colonies from the flood plain of Comoé River exhibited the same strange modifications of their antennae and were otherwise also similar to the *C. zoserka* type specimens. However, these winged ants turned out to be winged males rather than winged female sexuals. The inspection of the holotype and one paratype of *C. zoserka* verified that they also were males: like the winged males from Comoé N.P., they have concealed male genitals and ocelli, which are considerably larger than those of the female sexuals of *Cardiocondyla*. All female sexuals and workers found in the colonies with the bizarre winged males from Comoé N.P. had antennae with a three-segmented club as is typical for this genus. Sequences of the mitochondrial cytochrome c oxidase subunits I (CO I) and II (CO II) of a winged male and two nestmate workers showed that they are close to *C. venustula* and *C. shuckardi* but differ from them in about 10% of the base pairs. Other samples of *Cardiocondyla* collected in Comoé N.P. belong to *C. venustula* and related species. Their males were always ergatoid or “intermorphic” (i.e., ergatoid with rudimentary wings), as previously found in other populations of *C. venustula*, and never winged with modified antennae.

Keywords Ant males · Ergatoid males · Inquiline · Social parasitism · *Cardiocondyla*

Introduction

Males lead a rather shadowy existence in the matriarchies of ants. They rarely engage in social activities in the nest, are short-lived relative to queens and workers, and in many species make their most important contributions to the society during an unobservable nuptial flight, often high in the

sky (Boomsma et al. 2005). The typical morphology myrmecologists associate with males includes large eyes and ocelli, a bulky thorax, a relatively short antennal scape, and well-developed wings. Exceptions to this generalization are rare, but they do occur in the form of wingless, ergatoid males that resemble workers or ergatoid female sexuals. Ergatoid males have only been described for a handful of genera (Loiselle et al. 1988; Heinze and Tsuji 1995; Alpert 2007; Boudinot et al. 2016) and are probably studied best in the myrmicine genus *Cardiocondyla*.

Ergatoid *Cardiocondyla* males are morphologically so aberrant that they have repeatedly duped eminent myrmecologists into describing them as females of new workerless socially parasitic taxa (Fig. 1a–c; Baroni Urbani 1973; Marikovsky and Yakushkin 1974; Seifert 2002): Forel (1890) described a wingless individual with “soldier-like”

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s00040-019-00737-5>) contains supplementary material, which is available to authorized users.

✉ J. Heinze
juergen.heinze@ur.de

¹ Zoology/Evolutionary Biology, University of Regensburg, 93040 Regensburg, Germany



Fig. 1 *Cardiocondyla* males previously mistaken for female sexuals of new taxa of workerless, socially parasitic ants (photos **a–c** taken by S. Frohschammer, **d** by Ryan Perry, antweb.org: <https://www.antweb.org/bigPicture.do?name=casent0901750&shot=p&number=1>). **a** Ergatoid male of *Cardiocondyla obscurior*—the morphologically similar ergatoid male of its sibling species *C. wroughtonii* was described as *Emeryia wroughtonii*. Scale bar 0.5 mm. **b** Erga-

toid male of *Cardiocondyla venustula*—a similar ergatoid male was described as *Xenometra monilicornis*. Scale bar 1 mm. **c** Ergatoid male of *Cardiocondyla elegans*; such a male has been described as *Xenometra gallica*. Scale bar 1 mm. **d** Holotype of *Cardiocondyla zoserka* Bolton 1982, a winged male of a species of the *C. shuckardi* group. Scale bar 1 mm

mandibles found in a colony of *C. wroughtonii* (Forel 1890) as a separate parasitic species, *Emeryia wroughtonii*. Two years later, he corrected his error after realizing that wingless individuals in colonies of another congeneric species—*C. stambuloffii* Forel 1892—were ergatoid males (Forel 1892a, b). Indeed, ergatoid males of *C. wroughtonii* and its sister species *C. obscurior* Wheeler 1929 (Fig. 1a) are known to use their long, sabre-shaped mandibles to eliminate rival males from their natal nests and in this way monopolize mating with all newly emerging female sexuals (Kinomura and Yamauchi 1987; Stuart et al. 1987; Heinze and Hölldobler 1993; Heinze 2017).

Emery (1909) considered a large ergatoid male, perhaps of a species belonging to the *C. shuckardi* Forel 1891 group (Seifert 2002; Fig. 1b) as a wingless *Cardiocondyla* queen and later placed it into the new, supposedly parasitic genus *Xenometra* (Emery 1917). Later, the ergatoid male of *C. elegans* Emery 1869 (Fig. 1c), already recognized as such

by Menozzi (1918), was described as the social parasite *Xenometra gallica* (Bernard 1957). These errors were corrected by Baroni Urbani (1973) and also by Marikovskiy and Yakushkin (1974). The latter authors, however, made a similar mistake by identifying an ergatoid *Cardiocondyla* male as a “male-like wingless queen” of *C. ulianini* Emery 1889 (Seifert 2002).

Here I show that the morphology of fully winged *Cardiocondyla* males can also give rise to erroneous species descriptions. *C. zoserka* was described by Bolton (1982) based on five winged individuals collected by E. Classey in 1972 at Gurara Falls, Abuja, Nigeria (Fig. 1d), the only known specimens of this taxon. Bolton (1982) considered them to be winged female sexuals and from the strong apical teeth of their mandibles and the unique morphology of their antennae suspected *C. zoserka* to be a workerless social parasite (inquiline) living in the nests of *C. shuckardi*. Based on samples collected 1180 km further west in Comoé National

Park, Côte d'Ivoire, and the inspection of the holotype and one paratype of *C. zoserka*, the supposed socially parasitic females are in fact the regular winged males of the colonies in which they were found.

Methods

In April 2019, fragments of approximately 50 colonies of *Cardiocondyla venustula* Wheeler 1908 and other species belonging to the *Cardiocondyla shuckardi* group (sensu Seifert 2002) were excavated from their nests in the floodplain of Comoé River near Comoé National Park Research Station, Côte d'Ivoire, West Africa (8° 46' 2" N, 3° 47' 03" W, ca. 195 m elevation) and a few other sites in Comoé National Park (for details see caption of Supplementary Fig. S1). Foragers of *Cardiocondyla* were active throughout the day even at air temperatures of more than 35 °C and soil temperatures of more than 50 °C. In the hottest places, foragers over several meters moved from one blade of grass to the next without touching the hot ground. Colonies were located by baiting foragers with cookie crumbs and following them to the entrances of their nests. Large numbers of workers, female and male sexuals, and brood were found in chambers in moist soil at depths between 15 and 30 cm on three elevated heaps of sand with *Mimosa* shrubs and small *Ficus* trees (Fig. 2), and occasionally also in wet sand under large pebbles in the floodplain.

In the laboratory of Comoé Research Station, samples were checked under a binocular microscope. Samples consisting only of workers were stored in 100% EtOH for genetic analyses (see below). Larger colony fragments with



Fig. 2 Habitat of *Cardiocondyla* ants near Comoé Research Station, Côte d'Ivoire. The small red flag indicates the site of a nest and the insert shows how colonies were excavated

winged female sexuals, dealate queens, and/or males were transferred to the University of Regensburg and since then have been kept in plastic boxes, each with a regularly moistened plaster floor and a nest consisting of three parallel, 3 mm wide and 6 cm long slits in Plexiglas®, sandwiched between two microscope slides and covered by black foil. This nest design allows the males, which in *C. venustula* and possibly also other species of the *C. shuckardi* group are territorial (Frohschammer and Heinze 2009; Jacobs and Heinze 2017), to spread out. Colonies were reared in incubators at 12 h 23 °C/12 h 28 °C day–night cycles, provided with honey and pieces of cockroaches twice per week and checked regularly for newly emerging sexuals using a Zeiss Stemi 508 binocular microscope at 10 to 40× magnification.

To compare the specimens from Côte d'Ivoire with previously collected *C. venustula*, *C. shuckardi*, and other species of *Cardiocondyla*, we analyzed sequences of the mitochondrial cytochrome c oxidase subunits I (CO I) and II (CO II) from one worker each from 38 colony fragments from Côte d'Ivoire. DNA was extracted using a CTAB protocol (Sambrook and Russell 2001), amplified by PCR using the primer combination C1-J 2183/C2-N-3661 (Simon et al. 1984) and an initial denaturation step at 94 °C for 3 min followed by 36 cycles with 45 s at 94 °C, 30 s at 50 °C, and 45 s at 72 °C, and a final step of 10 min at 72 °C. PCR products were purified in a Macherey–Nagel gel, extracted using the NucSpin extraction kit (Macherey–Nagel, Düren, Germany) and sequenced by LGC Genomics (Berlin, Germany).

Sequences of CO I/CO II (up to 1457 bp) of ants from Côte d'Ivoire and previously obtained partial sequences of CO I (mostly 814 bp) of *C. shuckardi*, *C. venustula*, and several other congeneric species (Heinze et al. 2013; Jacobs and Heinze 2019) were aligned with the software BioEdit v 7.09 (Hall, 1999) using the CLUSTAL W Algorithm (Thompson et al., 1994) and then manually corrected. For the visualization of sequence similarities among colonies, a neighbor-joining tree was constructed using Mega X (Kumar et al. 2018) following the Tajima–Nei method (Tajima and Nei 1984). In the tree shown in the Supplementary material (Fig. S1), branches reproduced in less than 60% of 500 bootstrap replicates are collapsed.

To document the peculiar modifications of the antenna of winged males, three antennae from three different winged males, two antennae from two workers, two from two female sexuals from colony CI 15, and one antenna from an ergatoid male of *C. venustula* (colony CI 51) were gold–sputtered using a Polaron SC515 SEM coating system (Fisons, Ipswich, UK) and examined in ventral view using a JSM-IT 100LV scanning electron microscope (JEOL, Tokyo, Japan) at 100–4300× magnification. Nine winged males (four from CI 15, five from CI 30) and 12 winged or dealate female sexuals (6 each from colonies CI 15 and CI 30), which enclosed in the lab from brood collected in the field and died

in the laboratory nests, were mounted. Mesosoma length, head width, and head length were measured using a Wild M10 microscope at 100× to 125× magnification. In four males and five female sexuals from CI 15, the diameters of eyes and median ocelli were measured using a Keyence VHX-500FD digital microscope at 200× magnification. As several individuals had already started to decay and were partly overgrown by mold, not all measures could be taken with the same accuracy in all individuals. This resulted in a relatively large measurement error of approximately 2% (head width of a male measured three times). Voucher specimens are stored in Senckenberg Museum of Natural History Görlitz, Germany.

Results

Most of the samples collected at Comoé N.P. were similar to *C. venustula* both based on morphology and sequences of the cytochrome c oxidase subunits I (CO I) and II (CO II) (in black in Supplementary Fig. S1). All males found in these colonies upon collection and later in the laboratory were the typical ergatoid or, in one colony, also intermorphic males as previously described for *C. venustula* (Fig. 1b; for details see last paragraph of results).

Individuals from two additional colony fragments (CI 15, CI 37) from two sand heaps in the floodplain of Comoé River differed in their sequences in about 10% (8.77–10.7%) from sequences of sympatric *C. venustula* from Comoé N.P., *C. venustula* from Puerto Rico, Kaua'i, Ethiopia, Egypt, Kenia, and South Africa, and *C. shuckardi* from Madagascar. In a NJ tree, they formed the outgroup to these sequences (in green in Supplementary Fig. S1). Of CI 37, only workers were collected and stored in EtOH. Colony fragment CI 15 and a second colony fragment from the same sand heap, CI 30 (no sequence available), in addition to workers, queens, brood, and/or winged female sexuals contained two winged individuals each (Fig. 3a, b), which differed consistently from nestmate queens and winged female sexuals (Fig. 3c, d) in the morphology of their antennae and the larger size of their ocelli and eyes. Instead, they closely resembled the description and photos of the type material of *C. zoserka* Bolton 1982 (Fig. 1d) in all characteristic features of the latter, in particular the bizarrely modified antennae, in which funicular segments 6 and 7 are dorsoventrally flattened, segment 8 is broad and slightly transversely concave, segments 9 and 10 are strongly transversely concave, and the most apical segment is swollen in dorsal view and invaginated and almost cup-shaped in ventral view (Figs. 3b, 4; for a more detailed, very accurate description see Bolton 1982).

A closer analysis of the winged individuals with bizarre antennae revealed the presence of male genitalia, i.e., they were not female sexuals but winged males. Similarly, all 30

additional winged ants with such antennae, which eclosed in the laboratory during 7 months after collection, turned out to be males. No other males, neither wingless nor winged, were reared in colonies CI 15 and CI 30. As is typical for both winged and ergatoid males of *Cardiocondyla* (Kugler 1983), their genitals are often concealed, which leads to misidentifying them as female sexuals. Nevertheless, the tips of the parameres were visible in all winged individuals with modified antennae, and the genitals were evaginated in a few of them (see Fig. 3a).

The presence of male genitals in the specimens from Comoé N.P. spurred a closer look at the type material of *C. zoserka*. Judging from photos (Fig. 1d), the holotype is a winged male and not a female sexual: the ocelli are much larger than in female sexuals of *Cardiocondyla* and the rounded tip of the gaster suggests the presence of partly retracted parameres (for the same opinion by Bernhard Seifert, Senckenberg Museum of Natural History, Görlitz, see discussion). Stefan Cover (in litt.) kindly examined the *C. zoserka* paratype deposited at the Museum of Comparative Zoology, Cambridge, Mass., and confirmed it to be a male. Unfortunately, in the paratype loaned from the British Museum of Natural History by courtesy of Suzanne Ryder the abdominal tip was shrunken and the genitals were invisible. Nevertheless, its overall morphology closely matched that of the males from Comoé N.P. and the two types of *C. zoserka* identified as males. According to Bolton (1982), the two remaining paratypes of *C. zoserka* are also similar in morphology to the holotype. Hence, it appears that all previously known specimens of *C. zoserka* are winged males and not winged female sexuals.

Winged males from Comoé N.P. were slightly smaller on average than the *C. zoserka* types (Table 1). Their head shape was similar to that of the types and appeared slightly more elongated than that of female sexuals (Fig. 3b, d). The relative diameters of their eyes and median ocelli were considerably larger than those of female sexuals. Bolton (1982) considered the enlarged apical mandibular teeth of the mandibles in the types of *C. zoserka* as indicative of a socially parasitic lifestyle. The winged males from Comoé N.P. share this character, but so do the female sexuals of this taxon and the mandibles are not strikingly different in ergatoid males, female sexuals, and workers of other species of the *C. shuckardi* group on antweb.org.

The most striking character of *C. zoserka* and the winged males from Comoé N.P. is the uniquely modified antenna (Figs. 3b, 4). Workers and female sexuals both from the colonies with winged males and from colonies of *C. venustula* had the typical antennal structure of *Cardiocondyla* with a distinct three-segmented club (Fig. 3d). SEM photos of the antenna of three winged males revealed the presence of numerous “pores” in the ventral surface of funicular segments 7–10 and the bottom of the apical cup (Fig. 4), but the

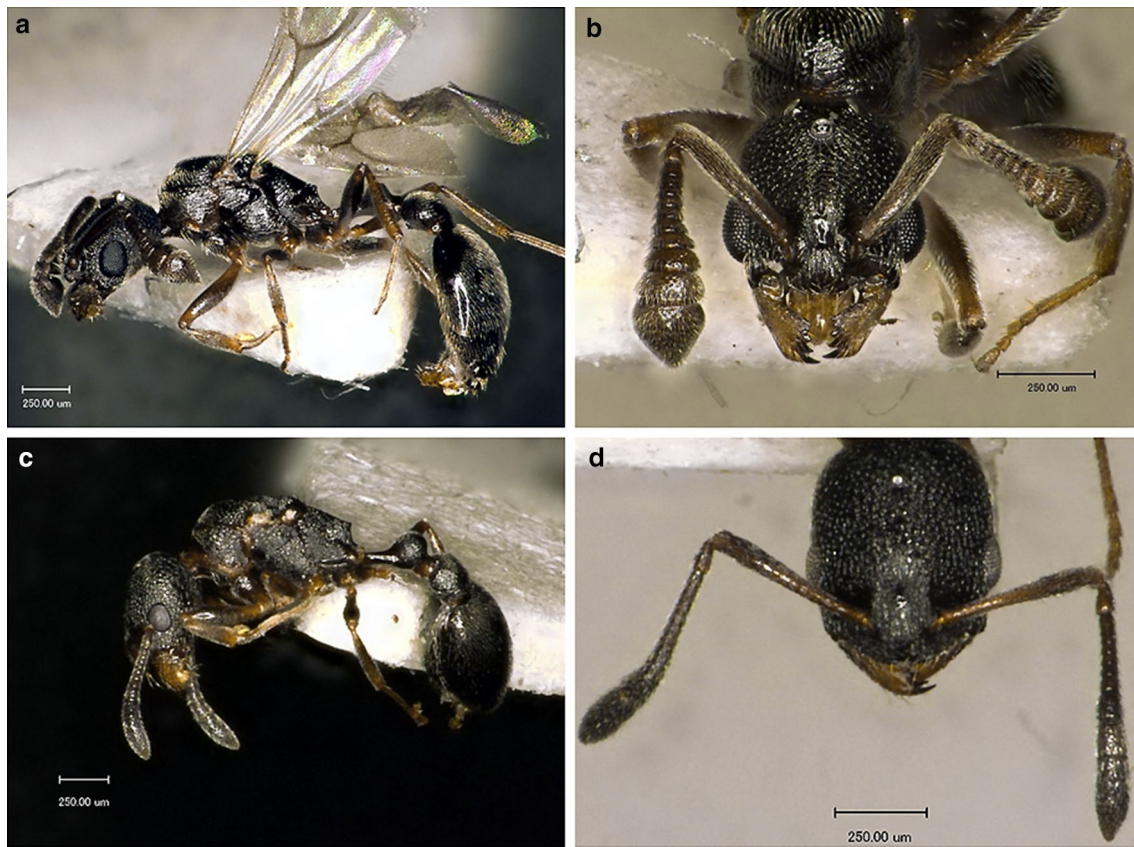


Fig. 3 Morphology of winged males and female sexuals of *Cardiocondyla* colony CI 15 from Comoé National Park, Côte d'Ivoire. Like the types of *Cardiocondyla zoserka*, the winged male has peculiar antennae. **a** Lateral view of a winged male. The evaginated male genitalia are clearly visible. **b** Frontal view of the head of the same winged male, showing the peculiar antennal modifications. **c** Lateral view of a dealate female sexual. **d** Frontal view of the head of a

winged female sexual, showing the typical antennal structure of *Cardiocondyla* with a distinct three-segmented club. The scale bars indicate 250 µm. Photos were made using a Keyence VHX-500FD digital microscope at a magnification of $\times 100$ for lateral views and $\times 150$ for frontal views; the sharpness of the composite image was increased using the Photoshop® sharpening filter

exact nature of these pores awaits further analyses. Neither the antennae of conspecific female sexuals and workers nor of an ergatoid male of *C. venustula* from Comoé N.P. had such pores.

CO I/CO II sequences of the winged male and two nestmate workers of CI 15 were identical except for different sequence lengths, suggesting that the winged males are not a separate socially parasitic species but the regular males of the colony in which they were found. Colonies CI 15, CI 30, and CI 37 from Comoé N.P. might therefore be considered as colonies of *C. zoserka*.

Concerning *C. venustula* from Comoé N.P., upon collection 18 of 19 larger colony fragments contained winged female sexuals and/or dealate queens, workers and brood. In addition, 9 of these 18 colony fragments and one fragment without female sexuals contained one to seven (median three) large and robust ergatoid males with a light brown coloration and angular shoulders typical of this species (Fig. 1b, Frohschammer and Heinze 2009; Heinze et al. 2013, 2014). One colony

fragment, CI 62, had more than seven “intermorphic” males, i.e., ergatoid males with the typical morphology of ergatoid males but in addition with rudimentary wings as previously described for *C. venustula* from South Africa (Heinze et al. 2013). Another fragment only had workers, a single, ergatoid male, and no queens. All of these colony fragments produced numerous female sexuals and ergatoid males (in the case of CI 62 together with intermorphic males), but not a single winged male during 7 months in the laboratory. Casual observations suggested that *C. venustula* males spread out in the provided multi-chambered nests and only rarely engaged in aggressive interactions, as previously observed (e.g., Frohschammer and Heinze 2009; Heinze et al. 2013; Jacobs and Heinze 2017).

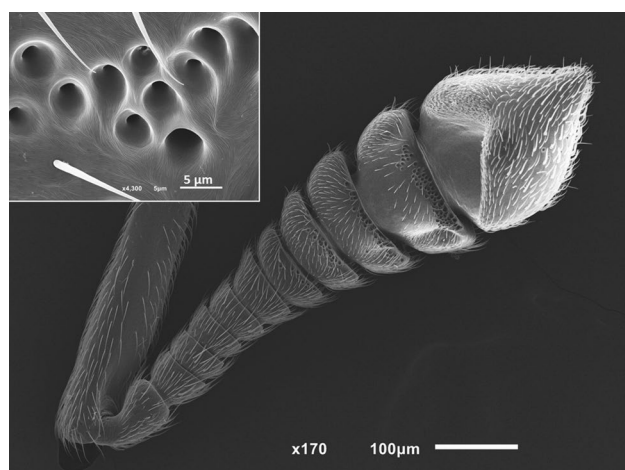


Fig. 4 SEM photo of the antenna of a winged male of *Cardiocondyla* from Comoé National Park, Côte d'Ivoire, in ventral view ($\times 200$), showing pores on the ventral side of funicular segments 7–10. The pores in the inner side of the cup-shaped apical segment 11 cannot be seen from this angle. The insert shows pores on the apical side of funicular segment 10 at a magnification of $\times 4300$. Photo: B. Lautenschläger

Discussion

Compared to the males of other social Hymenoptera, the wingless, ergatoid males of *Cardiocondyla* ants are quite exceptional. Their fights are one of the most striking cases of regular lethal combat in animals (e.g., Kinomura and Yamauchi 1987; Stuart et al. 1987; Heinze and Hölldobler 1993; Heinze 2017), and their lifelong spermatogenesis makes them unique among social Hymenoptera (Heinze and Hölldobler 1993; Boomsma et al. 2005). Their aberrant “worker-like” morphology has repeatedly misled

researchers to describe them as female sexuals, living as social parasites in *Cardiocondyla* colonies.

As the present study shows, winged *Cardiocondyla* males may also be misleading: the “winged female sexuals” of *Cardiocondyla zoserka* Bolton 1982, a presumed workerless social parasite known only from the type material, are in fact the regular winged males of their supposed host, a non-parasitic species of the *C. shuckardi* group. This conclusion is based on the morphological similarities between the type material and winged *Cardiocondyla* males collected in two colonies from Comoé N.P., Côte d'Ivoire. Winged males from Comoé N.P., but neither their female sexual nor their worker nestmates, show the same unique modifications of the antennal funiculi as the *C. zoserka* types. According to Bolton (1982), “no other ant has funiculi even remotely resembling this one, and certainly they [*C. zoserka*] cannot be confused with any other member of *Cardiocondyla*.” The winged individuals from Comoé N.P., though slightly smaller than the *C. zoserka* types, also show other distinctive characteristics of *C. zoserka*, e.g., relatively large ocelli and an enlarged apical mandibular tooth (Fig. 3b). Nevertheless, the examination of the abdominal tip of more than 30 of such individuals revealed that they all were winged males, even though their genitals were typically concealed and could not be seen easily.

The inspection of photos of the holotype of *C. zoserka* (Fig. 1d) and the direct examination of the paratype of *C. zoserka* in the Museum of Comparative Zoology by S.P. Cover suggested the presence of male genitals in both specimens, verifying that they are also males. According to Bernhard Seifert (in litt), head proportions as in the holotype of *C. zoserka* “do not occur in any *Cardiocondyla* female worldwide.” He also found that the diameter of the lateral ocelli as concluded from the photo of the holotype is about 10% of head length, while it is around 3% in female sexuals

Table 1 Measurements of winged males and female sexuals of *Cardiocondyla* from colonies CI 15 and CI 30 from Comoé N.P. For comparison, data from the description of the types of *C. zoserka* (Bolton 1982) are given

	Winged males of <i>Cardiocondyla</i> from colonies CI 15 and CI 30 (Comoé N.P.)	Female sexuals of <i>Cardiocondyla</i> from colonies CI 15 and CI 30 (Comoé N.P.)	Types of <i>C. zoserka</i> as given by Bolton (1982) ($n=5$)
Mesosoma length	0.88–0.99 mm Mean 0.92 mm ($n=8$)	0.71–0.98 mm Mean 0.84 mm ($n=11$)	0.90–1.04 mm
Head width	0.46–0.53 mm Mean 0.48 mm ($n=9$)	0.45–0.54 mm Mean 0.49 mm ($n=11$)	0.51–0.55 mm
Head length	0.55–0.62 mm Mean 0.58 mm ($n=9$)	0.54–0.66 mm Mean 0.59 mm ($n=10$)	0.62–0.68 mm
Head width/head length $\times 100$:	82–86 Mean 84 ($n=9$)	82–89 Mean 85 ($n=10$)	82–84
Eye diameter/head width	0.36–0.40 Mean 0.39 ($n=4$)	0.25–0.30 Mean 0.27 mm ($n=5$)	0.44
Ocellus diameter/head width	0.07–0.10 Mean 0.09 ($n=4$)	0.03–0.06 mm Mean 0.04 ($n=6$)	Not measured

of *Cardiocondyla*, and that the relative size of the compound eye is also much too large and it is much more vaulted than seen in female sexuals. Finally, B. Seifert (in litt.) notes that “the lateral view of the gaster does not indicate the presence of a stinger. The barely visible terminal structure in the holotype is rather blunt and should represent the tip of the retracted paramere(s).” As all five hitherto known specimens of *C. zoserka* are morphologically very similar (Bolton 1982), it can safely be concluded that they all are winged males of a species of the *C. shuckardi* group and not female sexuals of a workerless social parasite.

The taxonomy of the *C. shuckardi* group is in need of a thorough revision. Seifert (2002) synonymized several taxa with *C. venustula* and *C. shuckardi*, but sympatric samples of *C. venustula* vary so widely in gene sequences (Heinze et al. 2013, Fig. S1) that more detailed morphological and genetic analyses are needed to fully resolve species borders. Such a revision will also clarify if the colonies from Comoé N.P. are indeed *C. zoserka* or a separate, related species. Gene sequences of a winged male and two workers from colony CI 15 show that they are closely related to the *C. shuckardi* group but differ from previously studied *C. venustula* and *C. shuckardi* in about 10% of the sequence of the cytochrome c oxidase subunits I (CO I) and II (CO II).

While phylogenetic analyses suggest that a polyphenism with both winged and ergatoid males is ancestral in *Cardiocondyla* (Oettler et al. 2010; Heinze 2017), winged males have been lost in most species including all previously studied taxa of the *C. shuckardi* group (Seifert 2002; Frohshammer and Heinze 2009; Heinze et al. 2013, 2014; Jacobs and Heinze 2017; Heinze 2017). Not surprisingly, dozens of inspected males from colonies of *C. venustula* from Comoé N.P. were all ergatoid or, in one colony also “intermorphic”, i.e., combining the typical ergatoid morphology of head and mesosoma with rudimentary wings. Similar intermorphs have been observed in *C. venustula* from South Africa (Heinze et al. 2013) and in the *C. nuda* group (sensu Seifert 2002), e.g., *C. kagutsuchi* from Malaysia (Yamauchi et al. 2005) and *C. nuda* from Australia (unpublished observations). The dealate “winged male” of *C. nigra* described by Santschi (1907) also appears to be such an intermorph (Kugler, 1983). Interestingly, in contrast to all other previously studied species of *Cardiocondyla*, the two colonies from Comoé N.P. tentatively assigned to *C. zoserka* have so far produced more than 30 winged males and not a single ergatoid male.

The most striking character of the *C. zoserka* types and the winged males from Comoé N.P. is the extremely aberrant morphology of their antennae (Bolton 1982, Fig. 3b), which makes these ants immediately recognizable. Female sexuals (Fig. 3d) and workers from the colonies with winged males, and also previously studied ergatoid males of other *Cardiocondyla* species have antennae with a distinct

three-segmented club (e.g., Kugler 1983; Seifert 2002; Heinze 2017). Winged males of *C. obscurior*, *C. minorior*, *C. emeryi* and others typically have antenna without any conspicuous modification (e.g., Kugler 1983). Scanning electron microscopy of the antennae of winged males from Comoé N.P. revealed “pores” in the ventral surface of funicular segments 7–10 and the bottom of the apical cup (Fig. 4b). Such pores were absent from the antennae of conspecific female sexuals and workers and also from the antenna of an ergatoid male of *C. venustula*. The pores might suggest the presence of antennal glands. Male antennal glands are known from several Hymenoptera and probably play a role during mating (e.g., Isidoro et al. 1999; Romani et al. 2003, 2008). In ants, antennal glands have so far been found only in queens and workers of a few species (Renthal et al. 2008). During courtship and mating, *Cardiocondyla* males touch the head and body of female sexuals with their antennae (Mercier et al. 2007), and the presence of pores on the ventral surface of the funiculus of the winged males from Comoé N.P. suggests an exciting new perspective of sexual communication in this genus.

Acknowledgements Research in Comoé Park was permitted by the director of the Office Ivoirien des Parcs et Réserves (permit no. 221), the exportation of ants by a permit from the Ministère de l'Enseignement Supérieur et de la Recherche Scientifique. I thank Dr. Koné N'golo Abdoulaye, Dr. Erik Frank, and the staff of the Comoé Research Station for their help with obtaining permits and technical support. Claudia Gstöttl and Tina Wanke helped locating and excavating the colonies of *Cardiocondyla*. Tina Wanke and Birgit Lautenschläger assisted with Keyence and SEM photography and Andi Trindl and Nana Gratiashvili with DNA isolation and amplification. I thank Stefan Cover and Bernhard Seifert for their opinions about the type material of *C. zoserka* and Suzanne Ryder for providing the paratype from BMNH. The research was supported by Deutsche Forschungsgemeinschaft (He1623/42).

References

- Alpert GD (2007) A review of the ant genus *Metapone* Forel from Madagascar. In: Snelling RR, Fisher BL and Ward PS (eds) Advances in ant systematics (Hymenoptera: Formicidae): homage to E.O. Wilson—50 years of contributions, vol 80. Memoirs American Entomological Institute, Ann Arbor, pp 8–18
- Baroni Urbani C (1973) Die Gattung *Xenometra*, ein objektives Synonym. Mitt Schweizer Entomol Ges 46:199–201
- Bernard F (1957) *Xenometra* Emery, genre de fourmis parasite nouveau pour l'Ancien Monde. Bull Soc Ent Fr 62:100–103
- Bolton B (1982) Afrotropical species of the myrmicine ant genera *Cardiocondyla*, *Leptothorax*, *Melissotarsus*, *Messor* and *Cataulacus* (Formicidae). Bull Brit Mus (Nat Hist) Entomol 45:307–370
- Boomsma JJ, Baer BC, Heinze J (2005) The evolution of male traits in social insects. Annu Rev Entomol 50:395–420. <https://doi.org/10.1146/annurev.ento.50.071803.130416>
- Boudinot BE, Wachkoo AA, Bharti H (2016) The first ergatoid male of *Platythyrea* (Hymenoptera: Formicidae: Ponerinae), with contribution to colony labor suggested by observation and comparative morphology. Myrmecol News 22:59–64

- Emery C (1909) Beiträge zur Monographie der Formiciden des paläarktischen Faunengebietes. (Hym.). Teil VI. Deutsche Ent Zeitschr 1909:19–37
- Emery C (1917) Questions de nomenclature et synonymies relatives à quelques genres et espèces de Formicides (Hym.). Bull Soc Entomol Fr 1917:94–97
- Forel A (1890) *Aenictus*—*Typhlatta* découverte de M. Wroughton. Nouveaux genres de Formicides. Ann Soc Entomol Belgique 34:102–114
- Forel A (1892a) Die Ameisenfauna Bulgariens. Verh Zool Bot Ges Wien 42:305–318
- Forel A (1892b) Le mâle des *Cardiocondyla* et la reproduction consanguine perpétués. Ann Soc Ent Belg 36:458–462
- Frohschammer S, Heinze J (2009) Male fighting and “territoriality” within colonies of the ant *Cardiocondyla venustula*. Naturwissenschaften 96:159–163. <https://doi.org/10.1007/s00114-008-0460-2>
- Hall TA (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/96/NT. Nucl Acids Symp Ser 41:95–98
- Heinze J (2017) Life-history evolution in ants: the case of *Cardiocondyla*. Proc R Soc B 284:20161406. <https://doi.org/10.1098/rspb.2016.1406>
- Heinze J, Hölldobler B (1993) Fighting for a harem of queens: physiology of reproduction in *Cardiocondyla* male ants. Proc Natl Acad Sci USA 90:8412–8414. <https://doi.org/10.1073/pnas.90.18.8412>
- Heinze J, Tsuji K (1995) Ant reproductive strategies. Res Popul Ecol 37:135–149. <https://doi.org/10.1007/BF02515814>
- Heinze J, Aumeier V, Bodenstein B, Crewe RW, Schrempf A (2013) Wingless and intermorphic males in the ant *Cardiocondyla venustula*. Insectes Soc 60:43–48. <https://doi.org/10.1007/s00040-012-0263-5>
- Heinze J, Schrempf A, Wanke T, Rakotondrazafy H, Rakotondranaivo T, Fisher B (2014) Polygyny, inbreeding, and wingless males in the Malagasy ant *Cardiocondyla shuckardi* Forel (Hymenoptera, Formicidae). Sociobiology 61:300–306. <https://doi.org/10.13102/sociobiology.v61i3.300-306>
- Isidoro N, Bin F, Romani R, Pujade-Villar J, Ros-Farré P (1999) Diversity and function of male antennal glands in *Cynipoidea* (Hymenoptera). Zool Scr 28:165–174. <https://doi.org/10.1046/j.1463-6409.1999.00013.x>
- Jacobs S, Heinze J (2017) Between fighting and tolerance: reproductive biology of wingless males in the ant *Cardiocondyla venustula*. Insect Sci 24:818–828. <https://doi.org/10.1111/1744-7917.12359>
- Jacobs S, Heinze J (2019) Population and colony structure of an ant with territorial males *Cardiocondyla venustula*. BMC Evol Biol 19:115. <https://doi.org/10.1186/s12862-019-1448-6>
- Kinomura K, Yamauchi K (1987) Fighting and mating behaviors of dimorphic males in the ant *Cardiocondyla wroughtoni*. J Ethol 5:75–81. <https://doi.org/10.1007/BF02347897>
- Kugler J (1983) The males of *Cardiocondyla* Emery (Hymenoptera: Formicidae) with the description of the winged male of *Cardiocondyla wroughtoni* (Forel). Isr J Entomol 17:1–21
- Kumar S, Stecher G, Li M, Knyaz C, Tamura K (2018) MEGA X: molecular evolutionary genetics analysis across computing platforms. Mol Biol Evol 35:1547–1549. <https://doi.org/10.1093/molbev/msy096>
- Loiselle R, Francoeur A (1988) Régression du dimorphisme sexuel dans le genre *Formicoxenus* et polymorphisme comparé des sexes dans la famille des Formicidae (Hymenoptera). Naturaliste Can (Rev ècol syst) 115:367–378
- Marikovskiy PI, Yakushkin VT (1974) The ant *Cardiocondyla ulianini* Em., 1889 and the systematic position of the “parasitic ant *Xenometra*”. Izv Akad Nauk Kaz SSR Ser Biol 3:57–62
- Menzio C (1918) Primo contributo alla conoscenza della fauna mirmecologica del Modenese. Atti Soc Nat Mat Modena 4:81–88
- Mercier J-L, Lenoir J-C, Eberhardt A, Frohschammer S, Williams C, Heinze J (2007) Hammering, mauling, and kissing: stereotyped courtship behavior in *Cardiocondyla* ants. Insectes Soc 54:403–411. <https://doi.org/10.1007/s00040-007-0960-7>
- Oettler J, Suefuji M, Heinze J (2010) The evolution of alternative reproductive tactics in male *Cardiocondyla* ants. Evolution 64:3310–3317. <https://doi.org/10.1111/j.1558-5646.2010.01090.x>
- Renthal R, Velasquez D, Olmos D, Vinson SB (2008) Occurrence of antennal glands in ants. Microsc Res Techniq 71:787–791. <https://doi.org/10.1002/jemt.20620>
- Romani R, Isidoro N, Riolo P, Bin F (2003) Antennal glands in male bees: structures for sexual communication by pheromones? Apidologie 34:603–610. <https://doi.org/10.1051/apido:2003053>
- Romani R, Rosi MC, Isidoro N, Bin F (2008) The role of the antennae during courtship behaviour in the parasitic wasp *Trichopria drosophilae*. J Exp Biol 211:2486–2491. <https://doi.org/10.1242/jeb.013177>
- Sambrook J, Russell D (2001) Molecular cloning: a laboratory manual. Cold Spring Harbor Laboratory Press, New York
- Santschi F (1907) Fourmis de Tunisie capturées en 1906. Rev Suisse Zool 15:305–334
- Seifert B (2002) The ant genus *Cardiocondyla* (Insecta: Hymenoptera: Formicidae)—a taxonomic revision of the *C. elegans*, *C. bulgarica*, *C. batesii*, *C. nuda*, *C. shuckardi*, *C. stambuloffii*, *C. wroughtonii*, *C. emeryi*, and *C. minutior* species groups. Ann Nat Mus Wien 104B: 203–338. <https://www.jstor.org/stable/41767253>. Accessed 1 Nov 2019
- Simon C, Frati F, Beckenbach A, Crespi B, Liu H, Flook P (1984) Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. Ann Entomol Soc Am 87:651–701. <https://doi.org/10.1093/aesa/87.6.651>
- Stuart RJ, Francoeur A, Loiselle R (1987) Lethal fighting among dimorphic males of the ant, *Cardiocondyla wroughtonii*. Naturwissenschaften 74:548–549. <https://doi.org/10.1007/BF00367076>
- Tajima F, Nei M (1984) Estimation of evolutionary distance between nucleotide sequences. Mol Biol Evol 1:269–285. <https://doi.org/10.1093/oxfordjournals.molbev.a040317>
- Thompson JD, Higgins DG, Gibson TJ (1994) CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. Nucl Acids Res 22:4673–4680. <https://doi.org/10.1093/nar/22.22.4673>
- Yamauchi K, Asano Y, Lautenschläger B, Trindl A, Heinze J (2005) A new type of male dimorphism with ergatoid and short-winged males in *Cardiocondyla* cf. *kagutsuchi*. Insectes Soc 52:274–281. <https://doi.org/10.1007/s00040-005-0803-3>