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Taxonomy of the African army ant *Dorylus gribodoi* Emery, 1892 (Hymenoptera, Formicidae) — new insights from DNA sequence data and morphology

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Abstract

Numerous species in the Old World army ant genus *Dorylus* have been described based on a single sex or caste. Our analysis of mitochondrial *cytochrome oxidase II* gene sequences of specimens from the same population reveals that *D. gribodoi* Emery males are conspecific with *D. gerstaeckeri* Emery workers, rendering *D. gerstaeckeri* a junior synonym of *D. gribodoi*. *Dorylus gribodoi* var. *insularis* Santschi, *D. gribodoi* var. *confusus* Santschi and *Dorylus lamottei* Bernard are also synonymized under *D. gribodoi*. A description of the *D. gribodoi* queen, which was collected together with workers from a nest in Ivory Coast, is provided. *Dorylus gerstaeckeri* st. *quadratus* Santschi is shown to be distinct from *D. gribodoi* and synonymised under *Dorylus kohli* Wasmann. Similar studies examining the relationship between species described based on males and others described based on workers are needed to clarify the formidable taxonomic confusion in the ecologically important but little-studied genus *Dorylus*.

Key words: Dorylinae, Formicidae, male-worker matching, West Africa

Introduction

Due to their extraordinary behaviour, army ants of the Old World genus *Dorylus* have received considerable attention from naturalists and other biologists for over 200 years (Gotwald 1995). The queens in this genus are the largest known ants and have an enormous egg-laying capacity (an estimated 3–4 million eggs per month in *D. wilverthi*, Raignier and van Boven 1955). Colonies of certain species in the subgenus *Anomma* (the fierce and famous "driver ants", Savage 1847; see also Kronauer *et al.* 2007) have the largest worker populations among all monogynous ant species (up to 9 million adult individuals in *D. nigricans*, Leroux 1982) and stage massive swarm raids on the forest floor and up in the vegetation, where they attack, kill and retrieve an extremely diverse array of prey (Gotwald 1995). Species in the subgenus *Typhlopone* often attack and destroy huge colonies of fungus-growing termites (e.g. Darlington 1985) and even of other *Dorylus* species (Leroux 1982) in tremendous battles involving millions of social insects.

Dorylus s.l. taxonomy has been in disarray for a long time and this has represented a huge impediment for studies on all aspects of the group's biology. Emery (1910) was the last author to treat the genus as a whole taxonomically and since then numerous descriptions of species, subspecies, and varieties have been added to the literature (Bolton 1995). One of the major challenges in *Dorylus* taxonomy is that most taxa have been described based only on a single caste or sex. Twenty-four species are based solely on the large and distinctive males (Bolton 2003), which fly at night and are often collected at lights. The crucially important association

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of males with conspecific workers (and queens) can be demonstrated in three ways. First, when winged males are found inside their maternal nest (Forel 1911, Santschi 1915, Raignier and van Boven 1955) or while flying off from it (Wheeler 1922, Kronauer *et al.* 2004, 2006), workers can be directly collected together with them. However, discovery of nests with males is a rare event and usually requires long-term field observations at a site. Second, as Emery (1895) observed for *D. fimbriatus*, tiny workers are sometimes carried away from the nest in the genital capsule of dispersing males. When such a male is captured and examined, the morphology of the two castes can be documented together. However, these smallest *Dorylus* workers usually have very few species-specific morphological features and are hard to distinguish even between subgenera. For example, Emery originally described small workers of an *Anomma* species as a new species in the subgenus *Alaopone* (Emery 1881, Emery 1910). This makes it difficult to recognize the conspecificity of a male carrying workers in its genital capsule with samples of larger workers collected in a different context. Third, since intraspecific genetic variation is usually low relative to interspecific variation (e.g. Hebert *et al.* 2003, 2004), comparative analyses of mitochondrial and nuclear sequence data can elucidate the relationships between single males found at light sources and putatively conspecific workers (Berghoff *et al.* 2003, Ward 2007).

Recently, gene sequence data have been used to infer a species-level phylogeny of *Dorylus* (Kronauer *et al.* 2007). Comparing pair-wise genetic distances of males and workers, the authors also demonstrated the male-worker associations for five species. However, they employed a rather conservative cut-off point so that other possible pairs of males and conspecific workers may have gone undetected in their study. Here, we re-examine the possible association between *D. gribodoi* males and *D. gerstaeckeri* workers by gathering mitochondrial *cytochrome oxidase II* sequence data for multiple specimens collected at the same site. Our results allow clarification of the taxonomy of *D. gribodoi*. Moreover, we provide a description of the *D. gribodoi* queen.

Material and methods

mtDNA analysis. In order to assess whether the *D. gribodoi* male may be conspecific with workers originally described as *D. gerstaeckeri*, we sequenced the mitochondrial *cytochrome oxidase II* (*COII*) gene for additional *D. gerstaeckeri* worker specimens from the same site in Ivory Coast where the *D. gribodoi* male specimen used in the study by Kronauer *et al.* (2007) had been collected (Taï Forest). Moreover, we sequenced *COII* for a *D. emeryi* worker from the same location as *D. emeryi* appears to be the sister taxon to *D. gribodoi* / *D. gerstaeckeri* (Kronauer *et al.* 2007). DNA was extracted from ant legs using the DNeasy® kit from QIAGEN®. A fragment from the *COII* gene was amplified in standard polymerase chain reaction (PCR), using primers tRNALeu (Kronauer *et al.* 2007) and Barbara (Simon *et al.* 1994). The annealing temperature was 45°C and we used a concentration of 2.5 mM $MgCl_2$ in the PCR cocktail. PCR products were purified using a MicroSpin® kit from Omega Bio-Tek. Automated fluorescent dye sequencing was conducted on an Applied Biosystems 3130xl Genetic Analyzer. We generated a final alignment of 564 base pairs (bp) of sequence data for the new specimens as well as for some specimens used in the previous study (Kronauer *et al.* 2007). All new sequences have been deposited in GenBank (accession numbers EU515184 - EU515187). We computed uncorrected pairwise distances between DNA sequences in MEGA 2.1 counting missing data as complete deletions (Kumar *et al.* 2001).

Morphological analyses. We examined more than 80 worker samples of *D. gerstaeckeri* Emery and the closely related *D. emeryi* Mayr, which is sympatric over most of the range of *D. gerstaeckeri*; 17 *D. gribodoi* males; one *D. gribodoi* queen and associated workers from the same nest; and the type specimens for all relevant names excluding *D. atratus* Smith 1859, the type of which is apparently lost (George Else pers. comm., Natural History Museum London).

Entomological collections cited in this study are abbreviated as follows:

CSAC Caspar Schöning personal collection, Copenhagen, Denmark.
MCSN Museo Civico di Storia Naturale 'Giacomo Doria', Genoa, Italy.
MNHN Muséum National d'Histoire Naturelle, Paris, France.
NHMB Naturhistorisches Museum Basel, Basel, Switzerland.
NHME Natuurhistorisch Museum Maastricht, Maastricht, Netherlands.
RMCA Royal Museum for Central Africa, Tervuren, Belgium.
WHGC William Gotwald Jr. personal collection, Utica, USA.

All observations were made at magnifications 6 – 50x on a Leica MS 5 stereomicroscope. We examined a suite of morphological characters commonly used in ant systematics such as pilosity, pubescence, colour, shape of the head, shape of the petiole and mandibular dentition. In addition we recorded several standard morphometric characters for some specimens using an ocular micrometer and report measurements here to the nearest 0.01 mm. The characters examined were:

HW maximum measurable head width (includes the eyes in males).
HL head length, measured in a straight line from the anteriormost point of the median clypeal margin to the mid-point of the posterior head margin.
SL maximum straight line scape length excluding the basal condyle.
HFL hind femur length.
HTL hind tibia length.
PeW maximum petiole width in dorsal view.

For the queen we also determined:

HAD distance between the apices of the lobes of the hypopygium.

Additionally, the following characters were measured in males:

EL maximum length of the eye in lateral view.
DPF distance between the anteriormost points of the parapsidal furrows.
PL prong length of the subgenital plate, measured in a straight line parallel to the longitudinal axis of the subgenital plate from the apical point of the right prong to its base (Fig. 1).
PD distance between the apices of subgenital plate prongs (see Fig. 1).
SPWB width of the subgenital plate at the baseline of the prongs (see Fig. 1).

Several specimens were imaged in an Automontage system (http://www.syncroscopy.com) by April Nobile at the California Academy of Sciences and images are available online as part of the Antweb database (http://www.antweb.org). Additional Automontage images and SEM pictures were taken at the Zoological Museum, University of Copenhagen.

Results and discussion

Pair-wise genetic distances between the *D. gerstaeckeri* workers from both Taï (Ivory Coast) and Bossou (Guinea) and the single *D. gribodoi* male specimen (from Taï) were never above 0.050, while the distances between the *D. emeryi* workers (from Taï) and all other specimens were above 0.060 (Table 1). In particular, the distance between the *D. gribodoi* male and the *D. emeryi* workers was about 6.9 times as large as that between the *D. gribodoi* male and the *D. gerstaeckeri* workers from Taï (Table 1). Moreover, the distances

between *D. gerstaeckeri* workers from the two sites were about 4.2 times as large as those between the *D. gribodoi* male and *D. gerstaeckeri* workers from Taï. These results indicate that the *D. gribodoi* male is conspecific with *D. gerstaeckeri* workers and that this relationship was not borne out in the study by Kronauer *et al.* (2007) because of substantial genetic differentiation between the Bossou and Taï populations. The currently valid classification of *Dorylus* species into subgenera does not reflect the phylogenetic relationships, because *Dorylus* s.s. and *Anomma* do not represent monophyletic groups (Kronauer *et al.* 2007). Therefore, we do not assign *D. gribodoi* to a subgenus here, because a revised subgenus classification will be presented elsewhere.

TABLE 1. Uncorrected pair-wise genetic distances (based on 564 bp of the mitochondrial *CO II* gene) between worker specimens of the closely related *D. gerstaeckeri* and *D. emeryi* (from Bossou, Guinea and Taï, Ivory Coast) and the *D. gribodoi* male (from Taï).

	D. gerstaeckeri				*D. gribodoi*	*D. emeryi*	*D. emeryi*
	Bossou 1	Bossou 2	Taï 1	Taï 2	Taï MALE	Taï1	Taï 2
D. gerstaeckeri Bossou 1	-	-	-	-	-	-	-
D. gerstaeckeri Bossou 2	0.002	-	-	-	-	-	-
D. gerstaeckeri Taï 1	0.042	0.044	-	-	-	-	-
D. gerstaeckeri Taï 2	0.042	0.044	0.000	-	-	-	-
D. gribodoi Taï DM9 MALE	0.048	0.050	0.010	0.010	-	-	-
D. emeryi Taï 1	0.082	0.082	0.065	0.065	0.073	-	-
D. emeryi Taï 2	0.080	0.080	0.061	0.061	0.069	0.004	-

For the specimens *D. gerstaeckeri* 1 (from Bossou), *D. gribodoi* male (from Taï) and *D. emeryi* 2 (from Taï), sequences had been gathered by Kronauer *et al.* (2007) (specimen numbers 10, 11 and 22, respectively, in their Table 2).

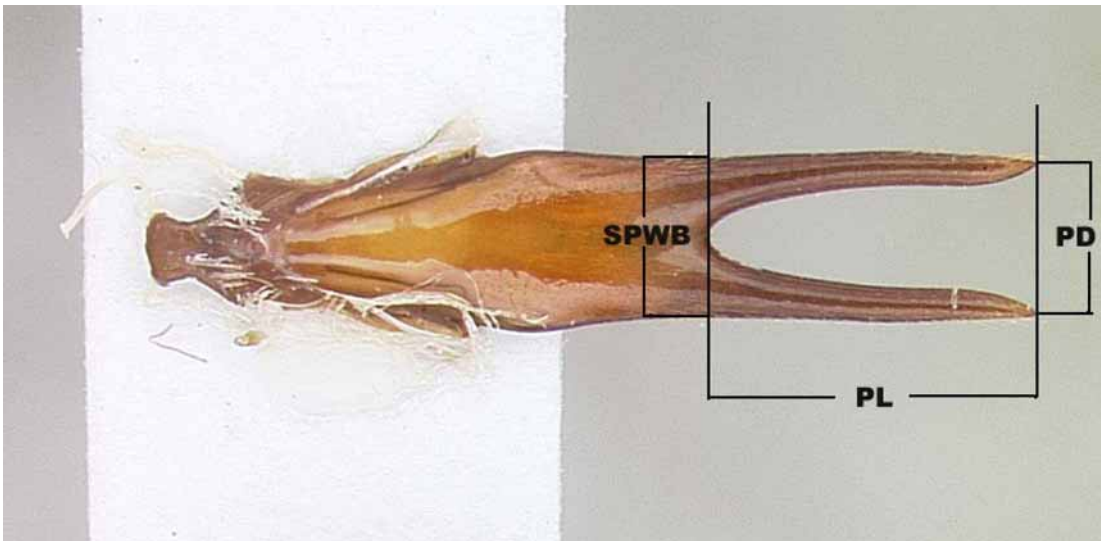

FIGURE 1. Definition of the subgenital plate measurements.

Dorylus gribodoi **Emery 1892**
(Figures 2–5, 7, 9, 11–13)

Dorylus gribodoi Emery 1892: 570. Two syntype males, West Africa [Wheeler (1922) and Bolton (1995) listed Togo as country of the type location]: Amu, collected by M. Gribodo, MCSN (examined).

Dorylus (*Anomma*) *gerstäckeri* (sic!) Emery 1895: 713 – 714. Holotype worker, Ghana: Accra, MCSN (examined), **new synonomy**.

Dorylus (*Dorylus*) *gribodoi*; Emery 1895: 723 (combination in subgenus *Dorylus*), Emery 1910: 10, Wheeler 1922: 732, Bernard 1953: 217, Bolton 1995: 179, Kronauer *et al.* 2007: 56 (examined).

Dorylus (*Anomma*) *gerstaeckeri*; Emery 1901: 415 – 436, Emery 1910: 11, Santschi 1912: 154, Santschi 1914: 332, Wheeler 1922: 736, Raignier and van Boven 1955: 85, Gotwald 1974a: 877–886, Gotwald 1974b: 705–713, Gotwald 1978: 161–169, Bolton 1995: 179, Kronauer *et al*. 2007: 56 (examined), Schöning *et al*. 2007: 125–133 (examined), Boesch and Boesch 1990: 86–99, Humle and Matsuzawa 2002: 133–148 (examined).

Dorylus gribodoi var. *confusa* Santschi 1915: 246 – 247. Five syntype males, Ivory Coast: Grand Bassam and Imbokro collected by J.H. Lohier and Posth, MNHN (examined), **new synonomy**.

Dorylus (*Dorylus*) *gribodoi* var. *confusus* Santschi 1915 ; Wheeler 1922: 732, Bolton 1995: 178.

Dorylus (*Anomma*) *gribodoi* var. *insularis* Santschi 1937: 98. Two syntype males, Equatorial Guinea: Bioko Island, collected by Conradt and J. Moser, NHMB (examined), **new synonymy**.

Dorylus (*Anomma*) *lamottei* Bernard 1953: 219. 12 syntype workers, Guinea: Mt Nimba, MNHN (examined), **new synonomy**.

Dorylus (*Anomma*) *lamottei* Bernard 1953; van Boven and Levieux 1970: 351–358. *Dorylus* (*Dorylus*) *gribodoi* var. *insularis* Santschi 1937; Bolton 1995: 179.

Dorylus gerstaeckeri complex sp. 1; Schöning *et al.* in press (examined).

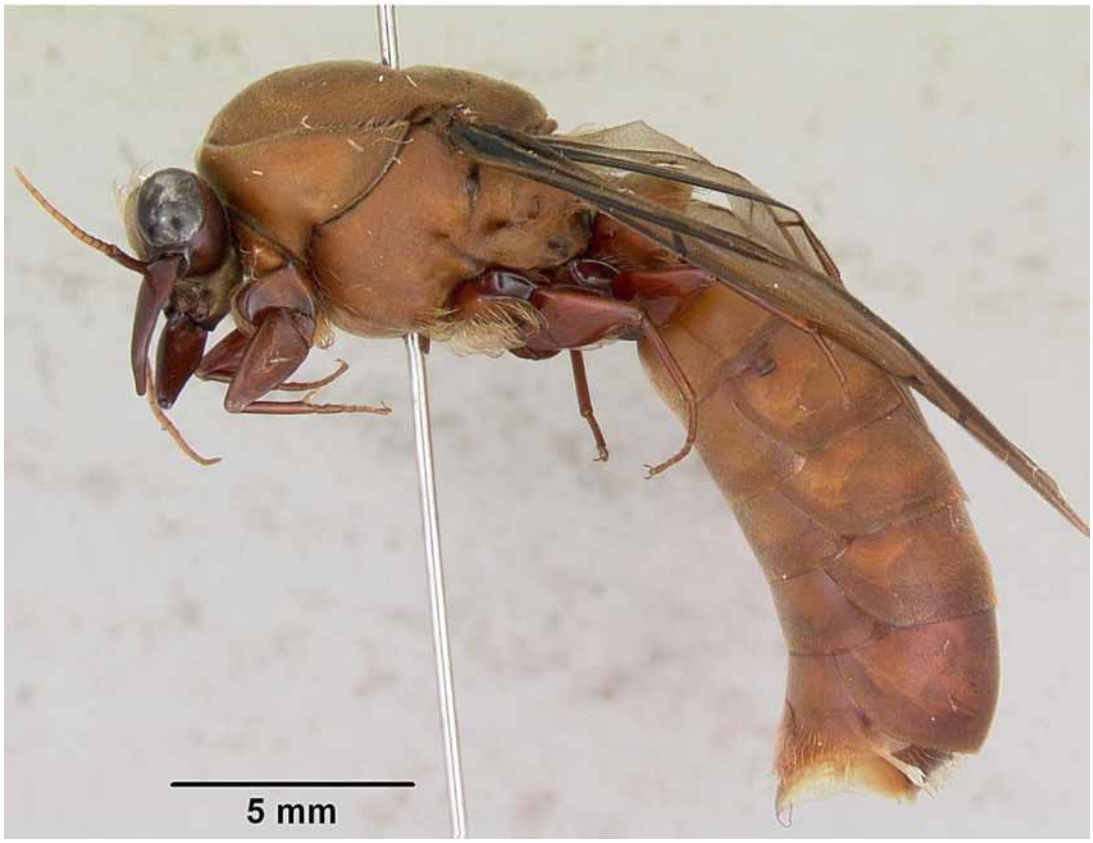

FIGURE 2. Lateral overview of a *Dorylus gribodoi* male from Taï, Ivory Coast.

Other material examined: Ghana: Kade ([N 6º4', W 0º49'], 150 m asl, W.H. Gotwald Jr., WHGC), Osenase ([N 5º57', E 0º45'], 180 m asl, D. Leston, WHGC), Tafo ([N 6º43', W 1º37', 278 m asl], W.H. Gotwald Jr., WHGC). Guinea: Bossou (N 7º38'42", W 8º30'35", 572 m asl, T. Humle, K. Koops, Y. Sugiyama, CSAC), Seringbara (N 7º37'37", W 8º28'2", 608 m asl, T. Humle, K. Koops, CSAC). Ivory Coast: Taï ([N 6°20' – 5°10', W 4°20' – 6°50'], 150 m asl, Y. Möbius, T. Deschner, C. Schöning, CSAC), Lamto ([N 6º13', W5º2'], 100m asl, queen specimen collected from nest along with workers in 1974, sample label #740701, J.M. Leroux, WHGC), Orstrom Experiment Station, nr. Abidjan ([N 5º20'28",W 4º1'41"], 70 m asl, W.L. Brown, WHGC). Liberia: Charlesville ([N 6º12'22", W 10º22'29"], 90 m asl, D. Kistner, RMCA). Nigeria: Gambari ([N 8º12'22", W 4º19'], 308 m asl, B. Bolton, WHGC), Gashaka (N 7º19'46.1", E 11º35'1.9", 560 m asl, D. Ellis, CSAC), Ibadan ([N 7º23'16", E 3º53'47"], 230 m asl, W.H. Gotwald, WHGC).

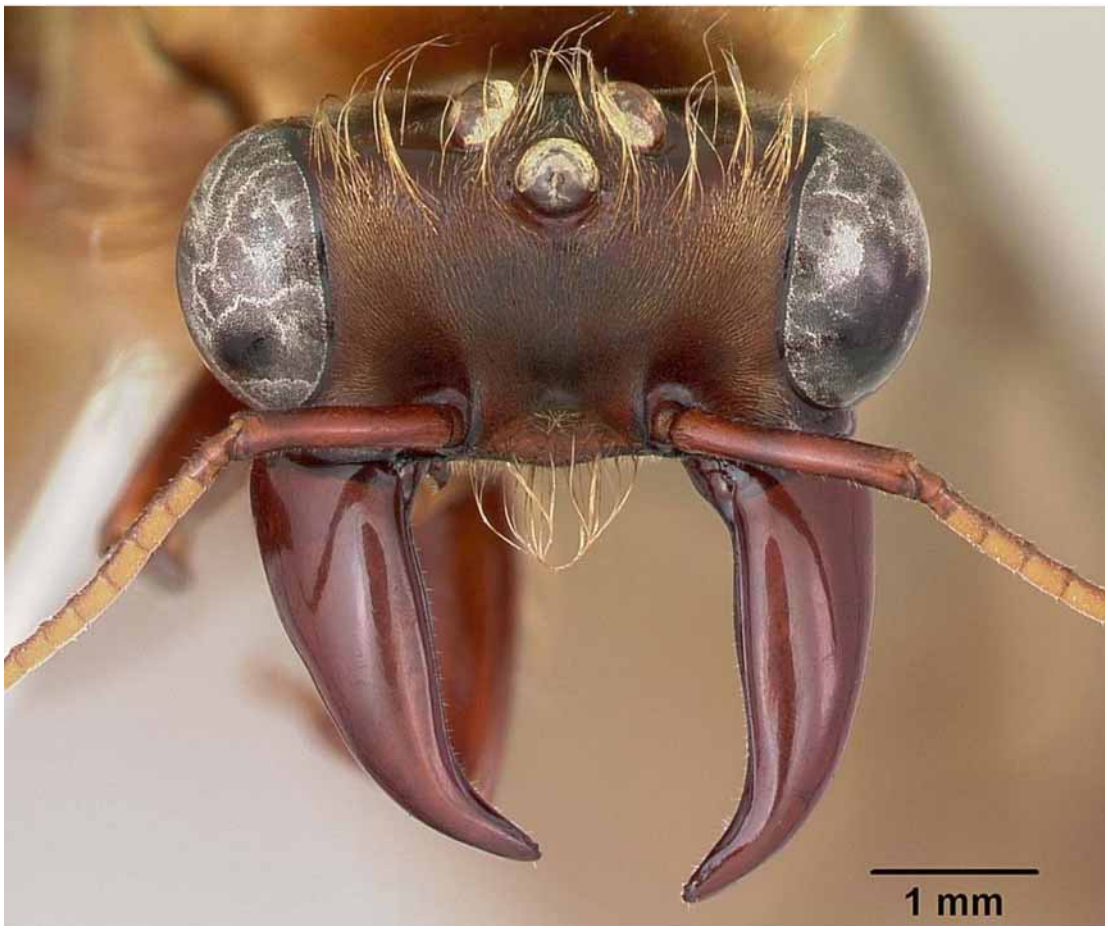

FIGURE 3. Frontal view of the head of a *Dorylus gribodoi* male from Taï, Ivory Coast.

FIGURE 4. *Dorylus gribodoi* male: genital capsule and subgenital plate.

Worker measurements: Worker caste highly polymorphic, among samples from Taï (Ivory Coast) HW varies between 0.78 mm and 2.9 mm. SL, hind leg length and mandible length notably shorter than in workers of the driver ant clade (Kronauer *et al.* 2007, Schöning *et al.* in press).

FIGURE 5. Lateral overview of a large *Dorylus gribodoi* worker from Taï, Ivory Coast.

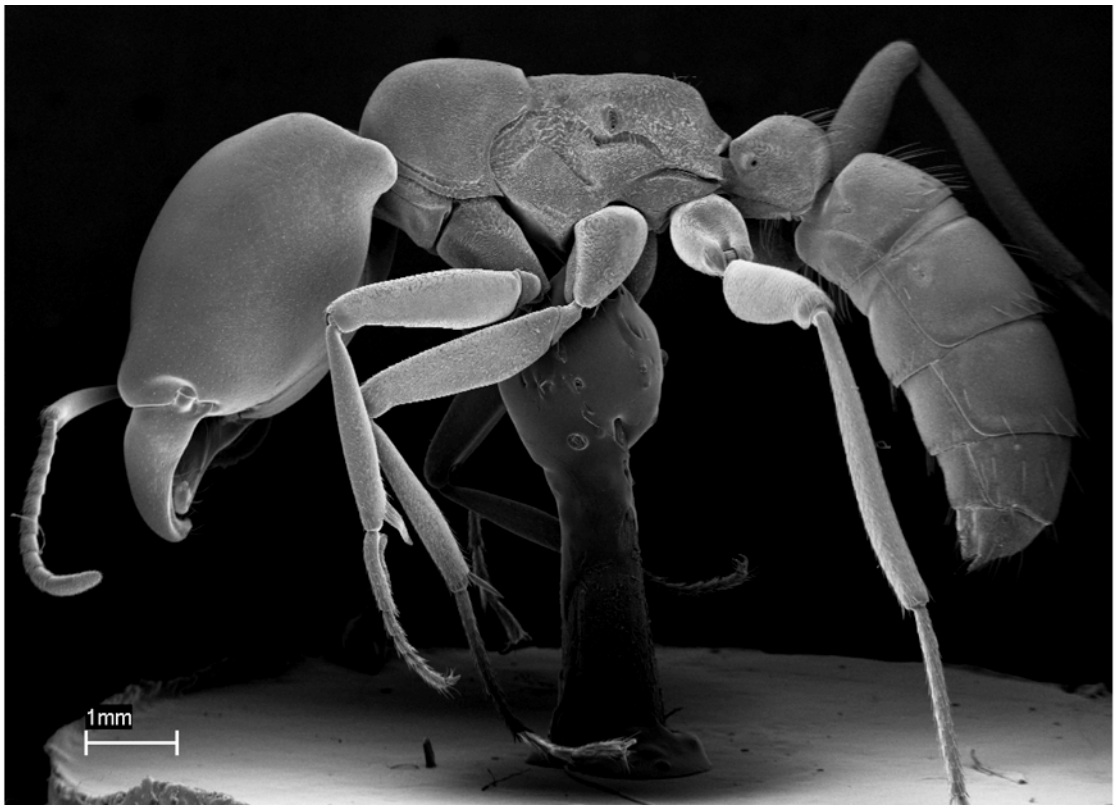

FIGURE 6. Lateral overview of a large *D. emeryi* worker from Taï, Ivory Coast.

Male measurements (n = 12, mean ± SD, range): HW 4.38 ± 0.11, 4.19 – 4.55; SL 1.57 ± 0.05, 1.48 – 1.67; HL 2.24 ± 0.07, 2.12 – 2.33; EL 1.78 ± 0.08, 1.61 – 1.88; DPF 2.77 ± 0.12, 2.57 – 2.95; PeW 3.70 ±

0.14, 3.52 – 3.90; HTL 2.29 ± 0.08, 2.07 – 2.42; PL 2.10 ± 0.08, 1.99 – 2.24; PD 1.01 ± 0.05, 0.96 – 1.09; SPWB 1.05 ± 0.07, 0.93 – 1.14.

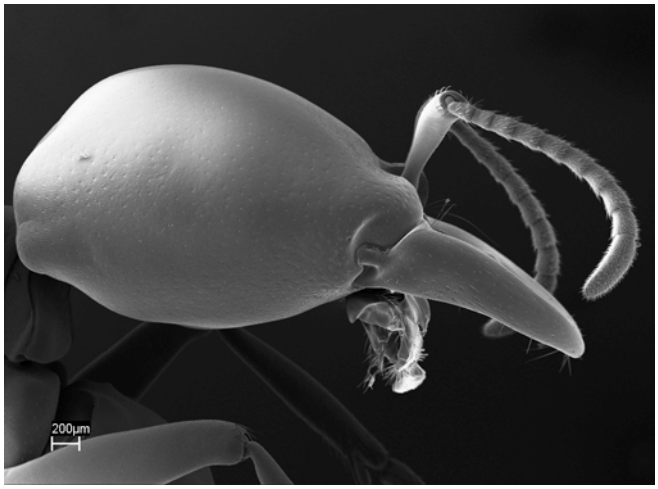

FIGURE 7. Lateral view of the head of a large *D. gribodoi* worker (HW 2.79 mm), Taï, Ivory Coast.

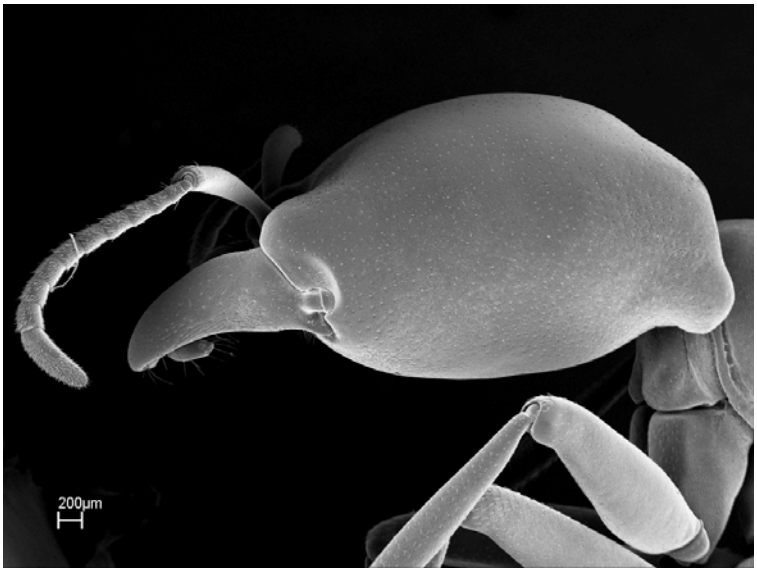

FIGURE 8. Lateral view of the head of a large *D. emeryi* worker (HW 3.62 mm) from Taï, Ivory Coast.

Queen measurements (n = 1): HW 4.58, SL 1.44, HL 3.32, PeW 4.54, HFL 2.73, HAD 2.53, maximum total length, in lateral view, from anterior surface of head to tips of hypopygial apices 40.45.

Distribution: West Africa (from Guinea and Liberia to Cameroon).

Biology: Restricted to humid habitats such as rainforest and gallery forest in mixed savanna – forest landscapes. Occurs at least up to 1600 m asl. Raids are conducted in the leaf-litter stratum (Gotwald 1974a, see also Kronauer *et al.* 2007). Workers retreat in tunnels when disturbed or exposed to sun (Gotwald 1978). Limited observations indicate that the species seems to prey almost exclusively on earthworms (Gotwald 1974b, C.S. personal observation), but this information has to be viewed with caution since variation in prey composition can be considerable in other *Dorylus* species (Schöning *et al.* 2008). Analysis of more extensive samples is therefore needed. Chimpanzees are known to feed on *D. gribodoi* at two sites (Bossou in Guinea and Taï in Ivory Coast); they either use sticks to "dip" for ant workers at trails or nests or open nests and take brood and workers with their hands (Boesch and Boesch 1990, Humle and Matsuzawa 2002, Schöning *et al.* in press). Nests are much less conspicuous than those of driver ant species and extremely difficult to find (for

humans, chimpanzees seem to do much better). It is interesting to note that *D. emeryi* is broadly sympatric with *D. gribodoi* and has nearly identical hunting behavior and habitat requirements, such that the two species may be easily confused in the field. The largest workers of *D. emeryi* are much larger (HW up to 3.92 mm, Schöning *et al.* in press).

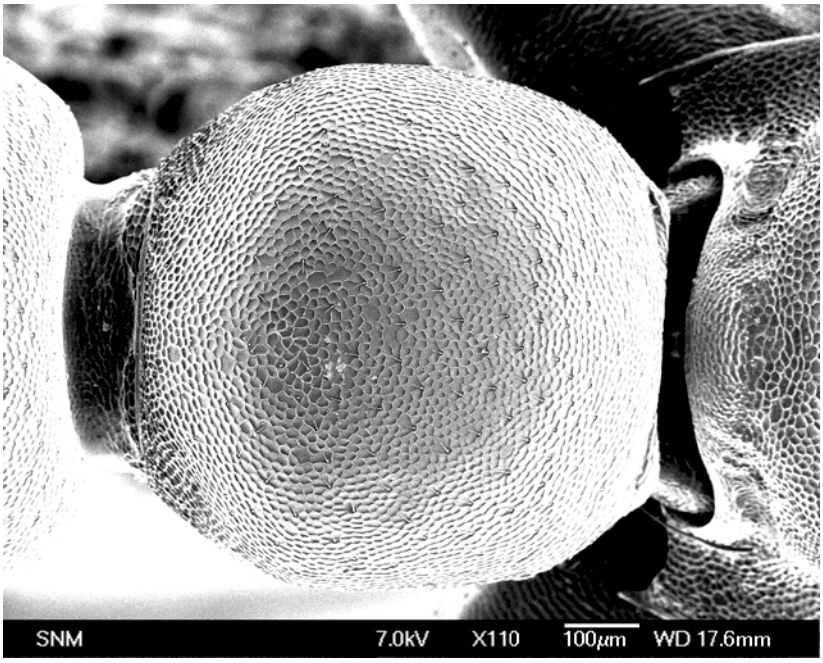

FIGURE 9. Dorsal view of the petiole of a large *D. gribodoi* worker (HW 2.85 mm) from Taï, Ivory Coast.

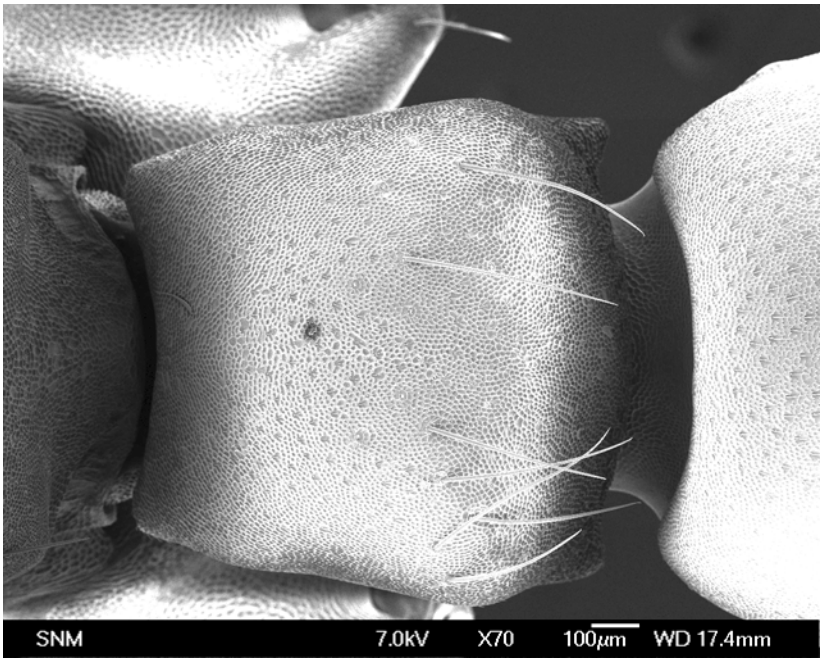

FIGURE 10. Dorsal view of the petiole of a large *D. emeryi* worker (HW 3.74 mm) from Taï, Ivory Coast.

Comments: The diagnostic features of the *D. gribodoi* male are its mandible shape (the anterior quarter notably flexed inward, Fig. 3) (Emery 1892) and the nearly flat posterior head margin (Fig. 3). In the original description Emery compared *D. gribodoi* with *D. atratus* and stated that *D. atratus* was darker than *D. gribodoi* and that its scape was longer than half the length of the funiculus. Both Smith (1859) in the original description and later Santschi (1914) mentioned that the posterior head margin of the *D. atratus* male was

convex. While the colouration of *D. gribodoi* is variable, it is not uniformly black in any of the specimens examined by us and the head shape is nearly rectangular with a flat posterior margin. Unfortunately, the *D. atratus* type specimen appears to be lost (George Else pers. comm., Natural History Museum London), so that we could not directly examine the relationship between *D. gribodoi* and *D. atratus*. However, the distinctness of the taxa appears beyond doubt. Workers of *D. gribodoi* are unique (and easily identifiable) among all *Dorylus* species in having a nearly round petiole in dorsal view (Fig. 9) and a distinct ridge on the posterior head margin that is laterally developed into tiny horns in larger specimens (> 1.5 mm HW). *Dorylus gribodoi* workers of the same size class can be separated from workers of the *D. kohli* / *D. congolensis* complex also by the posterior margin of the head being angular in lateral view and not smoothly rounded (Fig. 7). Larger *Dorylus emeryi* workers can be separated from *Dorylus gribodoi* workers of the same size class by the following features: posterior angles of head drawn out backwards and ventrally ["Die ziemlich dick-kegeligen, am Ende stark abgerundeten Hinterecken des Kopfes (den Kopf von der Seite gesehen und nach vorne gestreckt gedacht) ziemlich stark hinabgebogen und zwar schief nach hinten und unten gerichtet." (Mayr 1896)] (Fig. 8), petiole in dorsal view angled at widest point (Fig. 10), petiole has several conspicuous erect setae on dorsal surface (which are lacking in *D. gribodoi*), largest workers have massive heads with width ≤ 3.92 mm (HWmax of largest *D. gribodoi* workers 2.9 mm, see above). The unique petiole shape of *D. gribodoi* was recognized by Emery in his original description of *D. gerstaeckeri* (Emery 1895) and also by Bernard (1952) who described *D. lamottei* based on workers collected at Mount Nimba in Guinea but failed to realize that these specimens were in fact conspecific with Emery's *D. gerstaeckeri*. Bernard (1953) also identified males taken from the same location as *D. gribodoi*, but the association between these males and his *D. lamottei* workers necessarily remained unknown to him.

FIGURE 11. Lateral overview of the *D. gribodoi* queen collected from a nest at Lamto, Ivory Coast.

A *D. gribodoi* queen was collected along with workers from a nest at Lamto (Ivory Coast) by Jean-Marie Leroux and below we provide the queen description. *Dorylus gribodoi* is thus now one of the few *Dorylus* species for which workers, the male and the queen are now known.

Queen description. Habitus as in Figure 11. Head: Antenna 11-segmented (Fig. 12), funicular segments and scape yellow; head glossy, finely punctate, without conspicuous pilosity, antennal fossae deeply impressed; small (0.18 mm diameter) ocellus-like body located on the midline of head in frontal view 1.98 mm dorsad of the anterior clypeal border (Fig. 12); head impressed along the midline; mandibles with smooth medial (masticatory) border (i.e., without subapical teeth), sharply pointed apical tooth directed medially; cly-

peal margin straight with a row of short setae; labrum smoothly emarginate medially and weakly bilobed, reminiscent of the labrum in queens of the New World genus *Eciton* (see Gotwald 1969), not of other *Dorylus* queens; head deeply impressed posteriorly at pronotal insertion, posterior angles rounded, directed posteriorly (Fig. 14). Head and mandibles orange brown. Mesosoma: Similar in colour to head except for dark reddish-brown patches on dorsum of pronotum, mesonotum, and propodeum. Pronotal suture deeply impressed; mesonotum, metanotum and propodeum separated by shallow but well-defined sutures (Fig. 14); propodeum in dorsal view rectilinear (Fig. 14); mesosoma finely punctate without conspicuous pilosity. Petiole: Dark reddish-brown, finely punctate, without conspicuous setae or pilosity; posterior lateral lobes conspicuous in dorsal view (Fig. 14). Gaster: Segments reddish-brown to orange-brown, finely punctate, without conspicuous pilosity; posterior margin of pygidium in dorsal view with deep semicircular notch medially, sharp, downward pointed horns laterally (Figs. 11, 13). The two lobes of the hypopygium of the *D. gribodoi* queen terminate in apically pointed processes (Fig. 13) as in *D. kohli* (currently classified in *Anomma*) (van Boven 1968), *D. ghanensis* and *D. brevipennis* (both classified in the subgenus *Dorylus*) (van Boven 1975), whereas the two lobes are very broad posteriorly in driver ant queen hypopygia (see e.g. Figs. 20a and 20b in Raignier & van Boven 1955).

FIGURE 12. Frontal view of the head of the *D. gribodoi* queen (HW 4.58 mm).

***Dorylus kohli* Wasmann 1904**

Dorylus (*Anomma*) *kohli* Wasmann 1904: 669. Six syntype workers, DR Congo: St. Gabriel (near Kisangani), collected by P. Kohl, NHME (examined).

Dorylus gerstaeckeri st. *quadratus* Santschi 1914: 430. Holotype worker, Tanzania: Manow, collected by M. Viehmeyer, NHMB (examined), **new synonomy**.

Dorylus gerstaeckeri st. *quadratus*; Wheeler 1922: 736, Bolton 1995: 180.

Since the diagnostic features of large *D. gribodoi* workers are constant in all examined samples (from eastern Guinea to eastern Nigeria) and the *Dorylus gerstaeckeri* st. *quadratus* worker from Tanzania (more than 3000 km outside the recorded range of *D. gribodoi)* lacks these features, we exclude this form from *D. gribodoi* and place it under *D. kohli* Wasmann.

FIGURE 13. Dorsal view of the hypopygium of the *D. gribodoi* queen (HAD 2.53 mm).

FIGURE 14. Dorsal view of *D. gribodoi* queen mesosoma (PeW 4.54 mm).

The matching of males and workers by analysis of gene sequences of specimens from the same population is a promising approach for clarifying the taxonomy of army ants and other groups of ants in which these forms are rarely collected together. The discovery of more male-worker associations is essential not only for sorting out the taxonomic confusion in *Dorylus*, but also for determining the diagnostic features of the subgenera.

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