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A new data of worker polymorphism in the ant genus *Dorylus* (Hymenoptera: Formicidae: Dorylinae)

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ABSTRACT

Recently, in southern and central Vietnam, foraging columns of *D. orientalis* which contained not only "typical" workers but also a few "atypical" workers were collected. The atypical worker mentioned above is characterized by a set of the following features: (1) head narrowed anteriorly, (2) median portion of clypeus strongly projecting anteriad, and (3) antenna 8-segmented. Sequences of the 658-base standard mitochondrial DNA barcoding region were completely identical between typical and atypical workers. Therefore, the condition observed was a case of worker polymorphism within a colony. The mode of polymorphism observed has the following interesting aspects: (1) workers are clearly subdivided into two series by a set of qualitative characters; (2) the "typical series" is numerically much more dominant than the "atypical series" (the latter occupied less than 1% of the whole of the workers collected); (3) a wider size variation was observed in the former (HW, 0.48–1.41 mm; ML, 0.42–1.12 mm) than in the latter (HW, 0.44–1.13 mm; ML, 0.35–0.79 mm); and (4) within the atypical series, smaller workers are numerically much dominant. Rareness of the workers belonging to the atypical series in foraging column as well as morphological differences between the two series suggests a certain possibility that the atypical series does not adapt to foraging but to other tasks in the colony's life history.

Introduction

The ants of the genus *Dorylus* Fabricius, 1793 are known as true army ants (Gotwald, 1995; Schöning et al., 2005). *Dorylus* is subdivided into six subgenera: *Anomma* Shuckard, 1840, *Dorylus*, *Typhlopone* Westwood, 1839, *Rhogmus* Shuckard, 1840, *Alaopone* Emery, 1881 and *Dichthadia* Gerstäcker, 1863 (Bolton, 1995, 2003). The majority (55) of the species are known from the Afrotropical region, and only four from the Oriental region (Wilson, 1964): *Dorylus* (*Typhlopone*) *labiatus* Schuckard, 1840 (Indian subregion), *Dorylus* (*Alaopone*) *orientalis* Westwood, 1835 (Oriental region excluding the Malay Archipelago), *D.* (*Alaopone*) *vishnui* Wheeler, 1913 (Indo-Chinese and Indo-Malayan subregions) and *D.* (*Dichthadia*) *laevigatus* (Smith, 1857) (Myanmar to Sumatra, Java, Borneo and Sulawesi) (Wilson, 1964; present study).

Recently, in southern Vietnam, a lot of foraging workers of *D. orientalis* were captured by two underground bait-traps (60 mm in length and 15 mm in inside diameter, for the details, see Eguchi and Bui, 2009). Each of the two traps (BTN17xii08-20, BTN20xii08-19) contained not only "typical" workers, i.e., workers with the typical habitus of *D. orientalis*, but also a few "atypical" workers with a set of characteristics including (1) head narrowed anteriorly, (2) median portion of clypeus strongly projecting anteriad, and (3) antenna 8-segmented. The word "typical" used in the present paper means "to agree well with the habitus of the major worker (Meitan, Kweichow, G. Liu leg.) which was determined as *D. orientalis* by Wilson (1964: 442; see also Figs. 1–4)" (Westwood's original description is based on the male). Later, in central Vietnam, a foraging column of *D. orientalis* which contain a few atypical workers was found.

The anteriorly produced clypeus in small workers of *Dorlyrus* was first noticed by Wheeler (1922) in African species. Later Wilson (1964) also observed this condition in small workers (HW < 0.6 mm) of *D. vishnui*, and used it to separate *D. vishnui* from *D. orientalis*. However, in the columns of *D. orientalis* mentioned above, two morphologically distinct series of workers exist in the worker caste apart from the usual size/allometric polymorphism. Because the mode of the worker polymorphism observed has several interesting features, in the present paper, the morphology of the two series is described and brief comments concerning the polymorphism are provided.

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Figs. 1–4. Major worker of *Dorylus orientalis* Westwood, from China: Kweichow: Meitan [S. Liu coll., E. O. Wilson det., MCZC]: 1, head in full-face view; 2, mesosoma and waist in lateral view; 3, mesosoma and waist in dorsal view; 4, labels.

Materials and methods

Abbreviations of the specimen depositories are: VNMN, Vietnam National Museum of Nature, 18 Hoang Quoc Viet, Cau Giay, Hanoi, Vietnam; ACEG, Ant Collection of Katsuyuki Eguchi (see his contact address given under the title of this article); MCZC, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; and MHNG, Muséum d'Histoire Naturelle, Geneva, Switzerland.

Measurements are made for 69 workers of the bait#17xii08-20 using a Nikon AZ100 microscope: HL, head length measured from the level crossing the anterior margins of antennal fossae to the level crossing the posterolateral ends of head; HW, maximal head width; ClyL, clypeal length measured from the level crossing anterior margins of antennal fossae to the anteriormost point of the median part of clypeus; SL, length of antennal scape excluding basal condylar bulb; ML, diagonal length from the posteroventral corner of promesonotum to the posteriormost point of metapleuron; PW, maximal width of promesonotum; HFL, hind femur length; PtNL, maximum horizontal length of petiolar node in lateral view; PtW, maximum width of petiole viewed directly from above; PtNH, height of petiole in lateral view, measured vertically from the level of the highest point of petiolar node to the ventral margin of subpetiolar process. Indices are as follows: CI = HW / HL ∗ 100; ClyI = ClyL / HL ∗ 100; SI = SL / HW ∗ 100; MI = ML / PW ∗ 100; PtI1 = PtNL / PtW ∗ 100; PtI2 = PtNL / PtNH ∗ 100; HFI = HFL / HW ∗ 100.

The genetic relationship between "typical" and "atypical" series of the bait#17xii08-20 was confirmed by barcoding the cytochrome c oxidase subunit I (COI). A region near the 5′ terminus of the COI gene, including the 658-base standard mitochondrial DNA barcoding region, was amplified using primers LCO-EG: TTTCAACAAATCACAAAGAYAT YGG (modified from Folmer et al., 1994) and CI-14-EG: GTTTCTTTTTTT CCWCTTTC (modified from Hasegawa et al., 2002). Each PCR contained 5 μL of 2× PCR buffer, 2 μL of dNTPs (final 0.4 mM), 0.3 μL of 10 pmol/μL forward and reverse primers (final 0.3 μM), 0.2 μL of 1.0 U/μL KOD FX Neo (TOYOBO KFX-2015) and 0.5 μL of DNA template. The PCR thermal regime consisted of 1 cycle of 2 min at 94 °C; 5 cycles of 10 s at 98 °C, 30 s at 45 °C and 45 s at 68 °C; 40 cycles of 10 s at 98 °C, 30 s at 48.5 °C (CI-14) and 45 s at 68 °C; and a final cycle of 7 min at 68 °C. After confirming the PCR amplification on a 1.0% agarose gel, the amplified products were incubated at 37 °C for 30 min and 80 °C for 20 min with Illustra™ ExoStar (GE Healthcare, Buckinghamshire, UK) to remove any excess primers and nucleotides. The cycle sequencing reactions were run with ABI PRISM BigDye Terminator Cycle Sequencing Kit v.3.1 (Applied Biosystems). The sequencing reaction products were purified, concentrated by ethanol precipitation with sodium acetate, and their nucleotide sequences were determined using automated sequencers (ABI PRISM 3100, Applied Biosystems). The sequences obtained were submitted to the DDBJ database.

Results

Sequences of the 658-base standard mitochondrial DNA barcoding region were completely identical among a medium-sized worker of the typical series and a medium-sized and a small worker of the atypical series of BTN17xii08-20 (accession nos.: AB767278, AB767279, AB846958). This means that the two morphologically distinct series are conspecific. Therefore, the condition observed is a case of worker polymorphism that has not been known among the army ants.

Detailed descriptions of the two series of workers are given below, and the conspicuous differences between them are summarized in Table 1.

"Typical Series"
(Figs. 1–4, 5, 7, 9, 12)

Materials examined. China: Kweichow: Meitan [S. Liu coll., E. O. Wilson det., MCZC] (Figs. 1–4). Thailand: Trang: Khao Chong Water Fall [K. Eguchi leg., 28/Sept/2001, Eg01-TH-703]. Vietnam: Lao Cai Prov.: Sa Pa: well-developed forest, ca. 2100–2200 m alt. [K. Eguchi leg., 30/Apr/2002, Eg02-VN-189], disturbed forest, ca. 2100 m alt. [K. Eguchi leg., 25/Apr/2002, Eg02-VN-083], stream-side secondary forest, ca. 2000–2200 m alt. [K. Eguchi leg., 28/Apr/2002, Eg02-VN-148]; Van Ban: Liem Phu, 300–700 m alt. [K. Eguchi leg., 30/Sept/2006, Eg30ix06-16]; Vinh-Phuc: Tam Dao NP, 21°27′N, 105°38′E, ca. 900 m alt. [K. Eguchi leg., 5/Nov/2001, Eg01-VN-101]; Nghe An Prov.: Tuong Duong: Sang Le Forest, 19°11′N, 104°37–38′E, <210 m alt. [K. Eguchi leg., 1/Apr/2006, Eg01iv06-10]; Hue Prov.: Bach Ma NP, 16°13′08.8″N, 107°51′31.3″E, ca. 631 m alt. [K. Eguchi & Bui T. V. leg., 12/Nov/2009, bait UGBT12xi09-01, -02, -03, -04, -05, -06, -07,

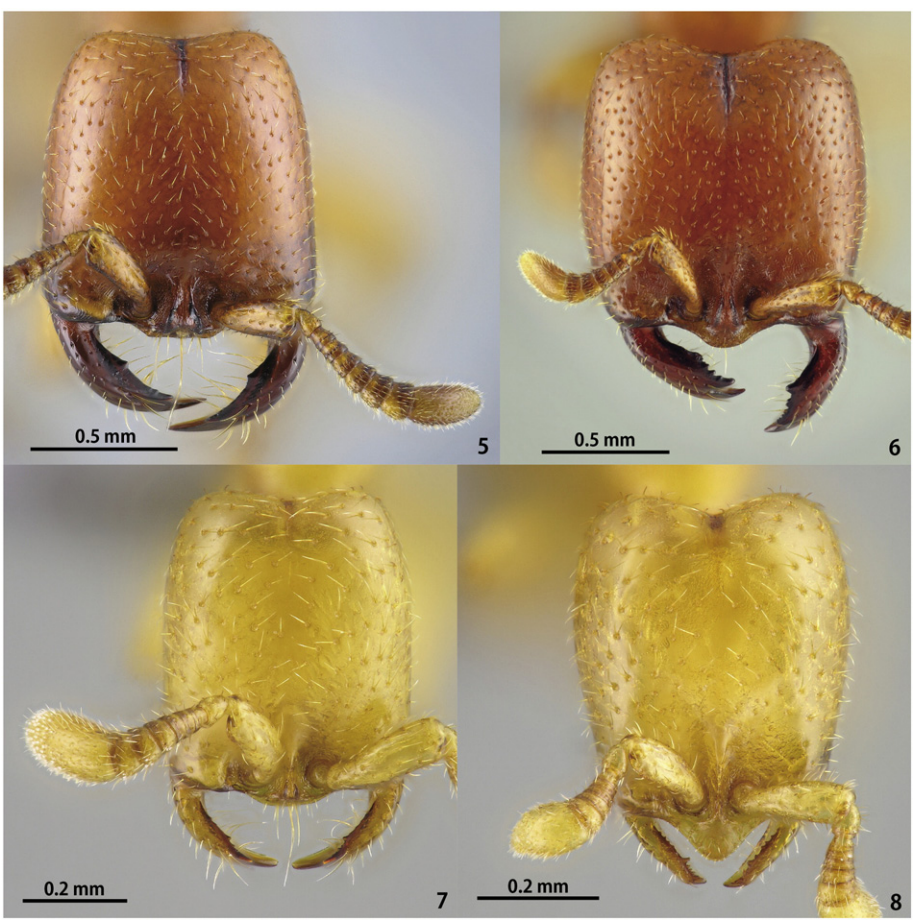
Table 1
Main differences between typical and atypical series of workers of *Dorylus orientalis* Westwood.

	Typical series	Atypical series
Head in full-face view	With sides slightly convergent posteriad (Fig. 5, 7)	With sides more or less divergent posteriad from the level of mandibular insertions to midlength of head or further (Fig. 6, 8)
Anterior clypeal margin	Weakly produced and distinctly truncated in the middle (Figs. 5 & 7)	Distinctly convex medially, with rounded or subtriangular apex (Figs. 6 & 8)
Median clypeal seta	Very long (Figs. 5 & 7)	Short or absent (Figs. 6 & 8)
Mandibular blade	Falcate	Elongate-triangular (Fig. 6) or somewhat linear (Fig. 8), but not falcate
Antenna	9-segmented (Figs. 5 & 7)	8-segmented (Figs. 6 & 8)
Mesosoma in lateral view	Relatively long and low (Fig. 9)	Relatively short and high (Fig. 10, 11)
Gaster in lateral view	Relatively long (Fig. 9)	Relatively short (Figs. 10 & 11)

The word "typical" used in the present paper means to agree well with the habitus of a major worker (Meitan, Kweichow, G. Liu leg.) determined by Wilson (1964): 442).

-08, -09, -10, -11, -12, -13, -14, -15, -16, -17, -18, -19, -20]; Ba Ria–Vung Tau Prov.: Binh Chau-Phuoc Buu NR: 10°32′46″N, 107°29′09″E, 51 m alt. [K. Eguchi & Bui T.V. leg., 17/Dec/2008, bait BTN17xii08-20], 10°32′46″N, 107°29′09″E, 56 m alt. [K. Eguchi & Bui T.V. leg., 20/Dec/2008, bait BTN20xii08-17, -18, -19].

Worker. Head in full-face view distinctly longer than broad, with sides parallel or slightly convergent posteriad from the level of mandibular insertions, with posterior margin weakly concave (Figs. 1, 5, 7); a short median longitudinal furrow present running anteriad from the posterior concavity; anterior clypeal margin weakly produced and distinctly truncated in the middle, with a very long and thick median clypeal seta and a pair of thick paracarinal setae; frontal lobes closely approximated (often confluent posteriorly in smaller workers), extending anteriad close to anterior clypeal margin (the lobes reaching anterior margin in largest workers); mandibular blade falcate; apical tooth very large; preapical tooth distinct but much smaller than apical tooth, followed by long edentate or indistinctly serrate margin and small third (basal) tooth; basal margin edentate; antenna 9-segmented; scape not reaching midlength of head when it is laid backward; relative lengths of antennal segments II–IX as in Figs. 5 and 7; IX much longer than broad, weakly flattened apically. Mesosoma in lateral view relatively long and low, with a straight dorsal outline (Figs. 2, 9), in dorsal view slightly narrowed between promesonotum and propodeum. Petiolar node in dorsal view trapezoidal, broader than long, with weakly concave anterior margin, almost straight lateral margin, and almost straight or slightly convex posterior margin; petiolar node in lateral view roundly



Figs. 5–8. *Dorylus orientalis* Westwood, worker, from Vietnam: Ba Ria–Vung Tau Prov.: Binh Chau-Phuoc Buu [bait BTN17xii08-20], head in full-face view: 5, 7, typical series; 6, 8, atypical series; 5, 6, medium-sized worker; and 7, 8, small worker.

Figs. 9–11. *Dorylus orientalis* Westwood, worker, from Vietnam: Ba Ria–Vung Tau Prov.: Binh Chau-Phuoc Buu [bait BTN17xii08-20], body in lateral view: 9, typical series, media; 10, 11, atypical series; 10, medium-sized worker; 11, small worker.

convex apically and weakly leaned posteriad; subpetiolar process rectangular, leaned anteriad. Abdominal posttergites IV, V and VI each almost as long as high.

Body covered by short decumbent to appressed hairs as shown in Figs. 1–3, 5, 7, 9 and 12, with a few long hairs on the dorsum of petiole, and gaster. Body largely smooth except for hair-pits, but anterior and posterolateral faces of promesonotum, part of mesopleuron and metapleuron, and posterolateral face of propodeum shagreened. Body reddish-brown to yellowish-brown; smaller worker lighter and rather yellowish in color.

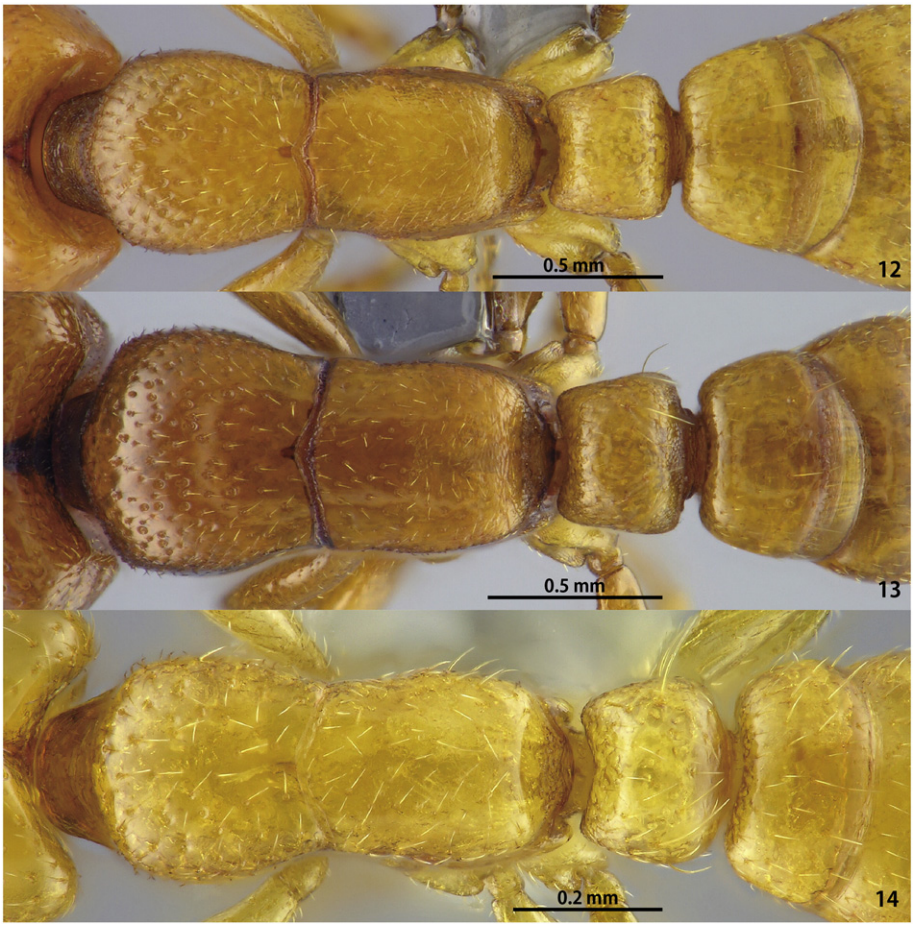
Measurements and indices (30 workers of bait#17xii08-20): HL, 0.57–1.69 mm; HW, 0.48–1.41 mm; ClyL, 0.03–0.07 mm; SL, 0.26–0.58 mm; ML, 0.42–1.12 mm; PW, 0.29–0.87 mm; HFL, 0.36–0.99 mm; PtNL, 0.19–0.54 mm; PtW, 0.21–0.60 mm; PtNH, 0.20–0.63 mm; CI, 80–97; ClyI, 3–7; SI, 40–55; MI, 128–145; PtI1, 80–97; PtI2, 81–99; HFI 70–78.

Atypical Series
(Figs. 6, 8, 10, 11, 13, 14)

Material examined. Vietnam: Ba Ria–Vung Tau Prov.: Binh Chau-Phuoc Buu NR: 10°32′46″N, 107°29′09″E, 51 m alt. [K. Eguchi & Bui T. V. leg., 17/Dec/2008, bait BTN17xii08-20], 10°32′46″N, 107°29′09″E, 56 m alt. [K. Eguchi & Bui T. V. leg., 19/Dec/2008, bait BTN20xii08-19]; Hue Prov.: Bach Ma NP, 16°13′08.8″N, 107°51′31.3″E, ca. 631 m alt. [K. Eguchi & Bui T. V. leg., 12/Nov/2009, bait UGBT12xi09-01, -08, -11, -12, -13, -17, -19].

Worker. Atypical series consists of small to medium-sized workers only (HW ranges from 0.44 to1.13 mm in the atypical series, but from 0.48 to 1.41 mm in the typical series).

Head in full-face view as long as or longer than broad, with sides more or less divergent posteriad from the level of mandibular insertions to midlength of head or further (Figs. 6, 8), with posterior margin distinctly concave; head in lateral view slightly more thickened



Figs. 12–14. *Dorylus orientalis* Westwood, worker, from Vietnam: Ba Ria–Vung Tau Prov.: Binh Chau-Phuoc Buu [bait BTN17xii08-20], body in dorsal view: 12, typical series, media; 13, 14, atypical series; 13, medium-sized worker; and 14, small worker.

dorsoventrally in medium-sized workers than in smaller workers (Figs. 10, 11); a short median longitudinal furrow present running anteriad from posterior concavity; anterior clypeal margin distinctly convex medially, with rounded apex in medium-sized workers (Fig. 6) or with subtriangular apex in smaller workers (Fig. 8); median clypeal seta short and thin in medium-sized workers (Fig. 6), and vestigial or completely absent in smaller workers (Fig. 8); paracarinal setae almost completely absent; frontal lobes vertical, approximated anteriorly, and often confluent posteriorly, not reaching anterior clypeal margin; mandibular blade elongate-triangular in medium-sized workers (Fig. 6), or somewhat linear in smaller workers (Fig. 8) but not falcate as seen in the typical workers (Figs. 5, 7); apical tooth very large; preapical tooth also developed well but smaller than apical tooth, followed by several denticles and distinct third (basal) tooth; basal margin edentate or with several denticles; antenna 8-segmented; scape not reaching midlength of head when it is laid backward; relative lengths of antennal segments II–VIII as in Figs. 6 and 8; VIII much longer than broad, weakly flattened apically. Mesosoma in lateral view relatively short and high, with a straight dorsal outline (Figs. 10, 13), in dorsal view narrowed behind promesonotum; humeral angle of promesonotum expanded laterad in medium-sized workers more than in smaller workers (Figs. 13, 14). Petiolar node in dorsal view trapezoidal, broader than long, with weakly concave anterior margin, almost straight lateral margin, and almost straight or slightly convex posterior margin; petiolar node in lateral view roundly convex and weakly leaned posteriad; subpetiolar process rectangular or round, leaned anteriad. Abdominal posttergite IV in lateral view almost as long as or a little shorter than high; posttergites V and VI a little shorter than high.

Body covered by short decumbent to appressed hairs as shown in Figs. 6, 8, 10, 11 and 13, with a few long hairs on the dorsum of petiole, and gaster. Body largely smooth with hair-pits, but anterior and posterolateral faces of promesonotum, part of mesopleuron and metapleuron, and posterolateral face of propodeum shagreened. Body reddish-brown to yellowish-brown; smaller worker lighter and rather yellowish in color.

Measurements and indices (39 workers of bait#17xii08-20). HL, 0.52–1.13 mm; HW, 0.44–1.13 mm; ClyL, 0.07–0.11 mm; SL, 0.20–0.45 mm; ML, 0.35–0.79 mm; PW, 0.28–0.72 mm; HFL, 0.31–0.79 mm; PtNL, 0.18–0.38 mm; PtW, 0.23–0.46 mm; PtNH, 0.21–0.46 mm; CI, 85–102; ClyI, 9–15; SI, 39–46; MI, 109–131; PtI1, 74–87; PtI2, 77–93; HFI 67–73.

Discussion

Worker polymorphism has been universally known in *Dorylus* spp. (Gotwald, 1995; Schöning et al., 2005). The mode of polymorphism observed by us has, however, the following interesting aspects: (1) workers are clearly subdivided into two series by a set of qualitative characters (Table 1); (2) the "typical series" is numerically much more dominant than the "atypical series" in foraging columns (the latter occupied less than 1% of the whole of the workers collected); (3) a wider size variation was observed in the former (HW, 0.48–1.41 mm; ML, 0.42–1.12 mm) than in the latter (HW, 0.44–1.13 mm; ML, 0.35–0.79 mm); and (4) within the atypical series, smaller workers are numerically much dominant.

The mode of worker polymorphism mentioned above may not be restricted to *Dorylus orientalis*. For example, Wilson (1964) mentioned

the three syntypes of *Dorylus vishnui* Wheeler as follows: "The smallest worker had 8 antennal segments, the largest 9. Other strong allometric variation occurred in the form of the clypeus and subpetiolar process." One of the present author (K. Eguchi) examined these syntypes (MCZ Type Number: MCZT_20220) and confirmed that the smallest one shows the habitus very similar to smaller individuals of the atypical series of *D. orientalis* (Figs. 8, 11). Wheeler (1922) mentioned in the definition of the genus *Dorylus* "Minima very small, with the head narrowed anteriorly and the anterior border of clypeus strongly projecting in the middle. Number of antennal segments reduced, seven being the minimum". This also recalls to us the habitus of the atypical series of *D. orientalis*.

Nothing is known about the developmental mechanism of these two series and their roles in the colony. Rareness of the workers belonging to the atypical series in foraging column as well as morphological differences between the two series suggests a certain possibility that the atypical series does not adapt to foraging but to other task in the colony's life history.

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