Notes on *Camponotus keihitoi* Forel, 1913, A Japanese Carpenter Ant with Metapleural Glands (Hymenoptera: Formicidae)

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Abstract The metapleural gland was found in the female castes of the Japanese carpenter ant *Camponotus (Myrmentoma) keihitoi* Forel, 1913. Many other interesting characteristics are noted for this species, including the presence of the first discoidal cell on the forewing of the queen and male. The queen and male of this species are described in detail for the first time. This temperate species is recorded from Amami-ôshima, the Central Ryukyu Islands located in subtropical Japan for the first time.

Key words. Carpenter ant, metapleural gland, discoidal cell, queen and male descriptions, distribution, biology.

Introduction

Camponotus keihitoi Forel, 1913 is a relatively small carpenter ant found in Japan (Honshu and southward), the Korean Peninsula and China (Yunnan) (Terayama & Satoh 1990; Liu et al. 2020). This species inhabits forests and forest edges and nests in dead twigs on trees, decayed wood etc. (Terayama et al., 2014). Although it has been treated as belonging to the subgenus Myrmentoma Forel, 1912, some features such as very weak median indentation on the anterior clypeal margin, remarkably poor body pilosity, enlarged forefemur etc. indicate its peculiar status in the subgenus. Radchenko (1997) mentioned that C. keihitoi is very similar to C. (Myrmentoma) quadrinotatus Forel, 1886, but this view should be reexamined. We carefully examined queens and males of this species and found additional features peculiar to it among the Japanese carpenter ants, i. e., the presence of metapleural glands in the worker and queen, presence of the first discoidal cell on the forewing of the queen and male, etc. This species is the first Japanese carpenter ant having metapleural glands, though a few Camponotus species have been known to have this condition outside Japan (e.g., Datta and Rauchaudhuri 1985; Shattuck 2005). The queen and male ants of this species are described in detail for the first time. Information on its distribution and biology is also presented, adding some new localities in Japan.

Material and methods

We collected many winged queens and males attracted to light that were strongly suspected to be *Camponotus keihitoi* based on their morphology. However, we failed to get winged ants from colonies of *C. keihitoi* so that worker-queen/male combination could not be established. Molecular data (COI) compared between winged ants collected in Kagoshima, mainland Kyushu and a worker collected on Tsushima (an island close to northern Kyushu) and identified as *C. keihitoi* revealed their conspecificity (see below).

Morphological observations were made with a Nikon SMZ18 stereomicroscope. Important body parts were measured with a micrometer to a second decimal place in mm except for the total body length.

TL: total body length roughly measured in stretched

specimens to first decimal place in mm.

HW: head width in full-face view, excluding eyes.

Hwe: head width in full-face view, including eyes (male).

HL: head length in full-face view measured from anterior clypeal margin to posterior margin of head.

EL: maximum eye length (= major eye diameter).

SL: length of antennal scape excluding basal condyle.

PrW: maximum pronotal width in dorsal view except in the male where the thoracic cuticle is often fragile and deformed in dried specimens.

PtW: maximum petiolar width in dorsal view.

CI: cephalic index (HW/HL \times 100).

SI: scape index (SL/HW \times 100).

Abbreviations and symbols. w: worker, aq: alate (winged) queen, dq: dealate queen, m: male. *: new record in distribution.

Mounted specimens examined will be deposited in Sk. Yamane Collection (SKYC; Kitakyushu, Japan) and the Institute of Tropical Agriculture, Kyushu University (KUEC; Fukuoka, Japan).

DNA sequencing. To confirm the morphological identification of C. keihitoi, we conducted COI analyses on three winged ants collected in Kagoshima (mainland Kyushu) and suspected to be C. keihitoi, and one worker collected on Tsushima and identified as C. keihitoi. Genomic DNA was extracted from tissues rich in mitochondria (e.g., legs) using DNeasy Blood & Tissue Kit (Qiagen, Maryland, USA). A 658 bp region of the mitochondrial genome, the 5' region of cytochrome oxidase I (COI), was amplified via polymerase chain reaction (PCR) using primers "LCO" and "HCO" (Folmer et al. 1994). Reactions were carried out at 10 µl volumes in a PCR Thermal Cycler MP (Takara Bio Inc.) under the following conditions: a first cycle of 94°C for 1 min, followed by 5 cycles of 94°C for 1 min, annealing at 48°C for 90 sec, and 72°C for 90 sec, and then 30 cycles of 94°C for 1 min, annealing at 51°C for 90 sec, and finally 72°C for 90 sec for the COI. PCR products were visualized on a 1% agarose E-Gel 96-well system (Invitrogen) and then purified with 1.0 ul of ExoSAP-IT (GE Healthcare Life Sciences). All products were sequenced in both directions using BigDye Terminator v3.1 (Applied Biosystems) on an ABI 3100 Avant DNA Sequencer (Applied Biosystems) at the Faculty of Science,

Kyushu University, Fukuoka. DNA sequence data for the four individuals were generated and deposited at DNA Data Base of Japan, DDBJ (with accession numbers: LC726278 for *C. keihitoi* worker from Tsushima, LC726279 for *C. keihitoi* queen from Kagoshima, LC726280 and LC726281 for *C. keihitoi* males from Kagoshima). Contigs were assembled using Vector NTI Advance TM ver. 11 (Invitrogen Corp.) and subsequently aligned and checked visually. Genetic distances were estimated using the Kimura-2 parameter (K2P, Kimura, 1980) distances with MEGA 5 (Tamura *et al.* 2011).

The COI sequences of the two populations were nearly identical to each other (99.7–99.8% identity). Thus, we confirmed the conspecificity of the Tsushima and Kagoshima populations.

Results

Camponotus keihitoi Forel, 1913

Camponotus fallax var. keihitoi Forel, 1913: 663 (worker, queen). Japan.

Camponotus (Myrmentoma) caryae var. keihitoi: Emery, 1925: 188.

Camponotus (Myrmentoma) keihitoi: Terayama and Satoh, 1990: 532 (raised to species; senior synonym of *C. teranishii* Wheeler, 1928); Bolton, 1995: 106.

For more information, see AntWiki (2022): Camponotus keihitoi.

Specimens examined. HONSHU. Shizuoka-ken: w, Iwatashi, Okegaya-numa, 17.v.2013, Sk. Yamane. KYUSHU. Tsushima: w, Kôrei-zan, 19.ix.2020, fragile stony slope, Sk. Yamane leg. (JP20-SKY-110); w, Shira-take, 22.ix.2020, dead stump, Sk. Yamane (JP20-SKY-149); w, Taterasan, 21.ix.2020, dead/rotting wood, S. Hosoishi (SH20-Tsu-43). Miyazaki-ken: aq & m, Aya-chô, Ômoridakerindô, 3.viii.2022, light-attracted, T. Kinoda. Kagoshima-ken (mainland): aq, Kagoshima-shi, Chûzan-chô, 13.vii.1990, Y. Yamanouchi; w, Kagoshima-shi, Yamada-chô, 18.v.1995, H. Ôkido; w, Kagoshima-shi, Kôrimoto, 13.v.2005, K. Eguchi; aq & m, Minamiôsumi-chô, near Hetsuka, 23.vii.2020, light-attracted, Sk. Yamane; aq & m, 27-28.vii.2020, same loc., K. Kawamura. ÔSUMI ISLANDS. Yaku-shima: m, Anbô~Yakusugiland, 24.vii.2022, light-attracted, K. Kanai. Kuchinoerabu-jima: aq, Tashiro-Yumugi, 25.vii.2016, lightattracted, Sk. Yamane; m, Nagasako, 26.vii.2016, lightattracted, Sk. Yamane. AMAMI ISLANDS. Amami-ôshima: w, Yuwan-dake, 2.xi.2008, Sk. Yamane; dq, Sumiyô, Sutarumatasen, 31.vii.2021, Sk. Yamane.

Queen description. Figs. 1A–D, 2A–B. Measurements (n = 6). TL 6.8–8.0, HW 1.51–1.61, HL 1.61–1.73, EL 0.48–0.49, SL 1.26–1.32, PrW 1.28–1.48, PtW 0.70–0.76; CI 91.5–96.4, SI 81.9–84.9. Palpal formula: 6 maxillary, 4 labial; relative length of segments: 3>4>5 = 6>2>1 for maxillary palp; 4>3>2>1 for labial palp. Head in full-face view longer than broad, with straight posterior margin, weakly convex lateral margins that slightly diverge posteriad, and broadly rounded posterolateral corner. Frontal lobe flat, anteriorly clearly demarcated from clypeus; frontal carinae

only slightly raised, short, diverging and extending posteriad to level of midlength of eye. Mid-line of cranium weak, only reaching level of posterior extremity of frontal carina. Malar space (space between anterior cranial margin and anterior margin of eye) long, longer than major diameter of eye. Clypeus trapezoidal, broader than long, weakly convex medially, protruded anteriorly as short ('narrow') lobe that has straight anterior margin and weakly angled anterolateral corner. Eye large with its major diameter slightly longer than distance between antennal bases; ocelli small, arranged in low triangle. Mandible elongate-triangular, with five teeth on masticatory margin that decrease in size toward base; basal margin without denticles. Antennal scape long, surpassing posterior margin of head by its 1/3 length; pedicel and flagellar segments 1-9 slightly longer than broad; apical segment twice as long as broad. With mesosoma in dorsal view, pronotum short, distinctly narrower than head; mesoscutum almost as broad as pronotum, much longer than broad, evenly rounded anteriorly; notaulix absent; parapsidal lines faint, slightly diverging anteriad, reaching slightly more than half length of mesoscutum; transscutal line distinct; mesoscutellum narrower than mesoscutum, broader than long, narrowed posteriad; metanotum short ('narrow'), flanked by deep sutures; propodeum as broad as mesoscutellum, its declivity not margined laterally. With mesosoma in profile view, pronotum with posteroventral corner bluntly angulate; mesopleuron divided into upper and lower sections by weak, sinuate line; metapleuron demarcated from mesopleuron but fused with propodeum; metapleural gland orifice located near posteroventral portion of metapleuron close to propodeum; lateral face of propodeum roundly merging into dorsum and declivity; spiracle opening oblong. Prosternal process low-triangular (this process is located between bases of coxae on venter of prothorax); metasternal process absent. Petiole in profile view acutely tapered apicad, with posterior slope straight but anterior slope variously curved; petiole in posterior view round, slightly broader than high with weakly convex dorsal margin. With gaster in profile view, anterodorsal corner rounded; apical band of tergites and sternites semitransparent; apical opening (acidopore) of terminal segment without outstanding nozzle, with a few short inconspicuous hairs encircling it. Wing venation mostly as in typical Camponotini, but exceptionally with first discoidal cell on forewing; jugal (anal) lobe absent.

Entire body covered with microscopic sculpture and moderately shiny. Clypeus, in addition to background microsculpture, with sparse large punctures from which erect hairs arise. Mandible basally with irregular dense sculpture; its apical 2/3 strongly and longitudinally striate.

Head with pair of long erect hairs just in front of posterior ocelli (rarely additional erect hairs present in ocellar area that are much shorter and inconspicuous); another pair present close to posterior portion of frontal carinae; venter of head lacking erect hairs. Clypeus with more than 20 erect hairs of variable length in fresh specimens. Mandible with many erect hairs that are much shorter than those on clypeus. Antenna lacking erect hairs except for those located at apex of scape. Mesoscutum at most with four erect hairs; mesoscutellum

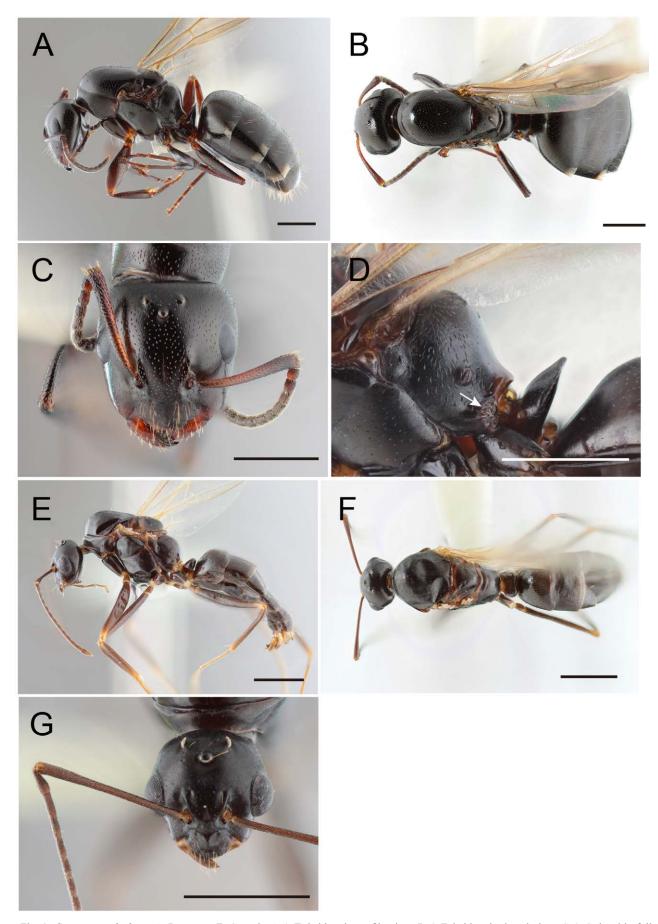


Fig. 1. *Camponotus keihitoi*. A–D, queen; E–G, male. A & E, habitus in profile view; B & F, habitus in dorsal view; C & G, head in full-face view; D, posterior portion of mesosoma in profile view, showing metapleural gland orifice (arrow).

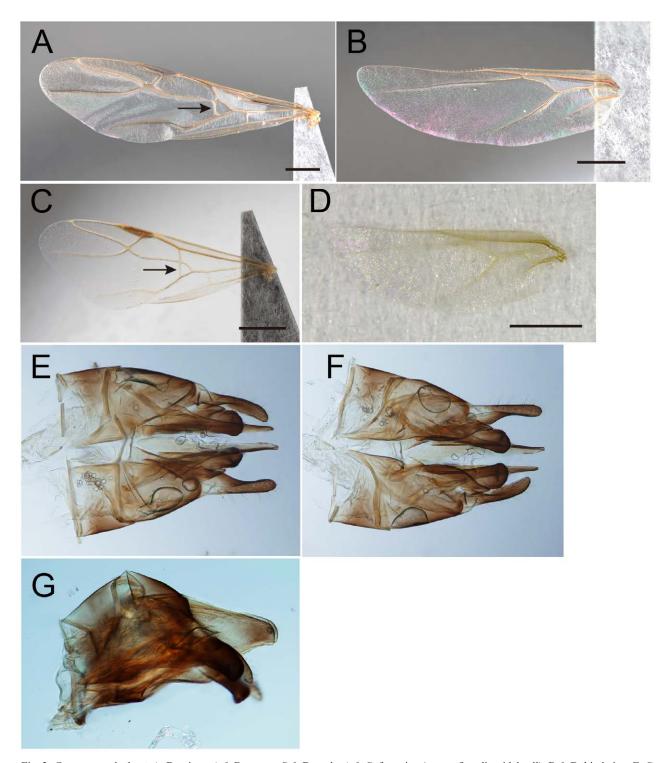


Fig. 2. Camponotus keihitoi. A–D, wings. A & B, queen; C & D, male. A & C, forewing (arrow: first discoidal cell); B & D, hindwing. E–G, male genitalia. E, dorsal; F, ventral; G, lateral.

with pair of long erect hairs anteriorly; propodeum without erect hairs. Metapleural gland orifice covered with short decumbent hairs. Petiole without long erect hairs but with many microscopic erect hairs on dorsal and lateral margins. First gastral tergite and sternite without long erect hairs except for those located along their posterior margins; other tergites and sternites with several long erect hairs in addition to those located along posterior margins. All legs without long erect hairs except for spurs at apices of femora and tibiae; tarsi with

suberect shorter hairs. Body entirely dark reddish brown to blackish brown; lamellate apical bands on gastral tergites and sternites semitransparent with whitish appearance.

Male description. Figs. 1E-G, 2C-G. Measurements (n = 4), TL 4.8-5.1, HW 0.80-0.84, HWe 0.95-1.00, HL 0.88-1.00, EL 0.33-0.37, SL 1.06-1.14, PtW 0.37-0.43; CI 82.0-90.6, SI 131.6-138.8. Palpal formula: 6 maxillary, 4 labial; relative length of segments: 3>4>5>2 = 6>1 for maxillary palp; 4=3>2>1 for labial palp. General habitus as in

typical Camponotini male. Head in full-face view longer than broad, when including eyes almost as long as broad or slightly broader than long (HWe/HL 1.00-1.08), narrower anteriorly than posteriorly, with weakly and broadly convex posterior margin. Frontal lobe ill developed so that antennal socket entirely exposed; frontal carinae slightly raised, diverging posteriad, short, not attaining level of posterior margin of eye; median line of cranium weak, obsolete in front of anterior ocellus; malar space relatively long, slightly shorter than minor diameter of eye. Clypeus sharply demarcated from frons; its major part (disc) distinctly elevated, transverse, anteriorly protruding from level of anterior margin of cranium; anterior clypeal margin straight. Eye large, distinctly protruding from lateral margin of head; ocelli arranged in low triangle. Mandible elongate-triangular, with large triangular apical tooth; remaining portion of masticatory margin edentate; basal corner evenly curved; basal margin longer than masticatory margin. With mesosoma in dorsal view, pronotum almost invisible, mesoscutum much broader than head, slightly longer than broad; mesoscutellum demarcated from mesoscutum with deep furrow, narrower than the latter, narrowed posteriad; metanotum short (transversely linear), flanked by anterior and posterior deep sulci; dorsum and posterior declivity of propodeum continuous. Mesosoma in profile view with steep anterior slope and weakly curved dorsal outline; pronotum with steep anterior slope and small posteroventral process; mesopleuron divided into upper and lower sections, separated from metapleuron by deep sulcus; metapleuron fused with lateral face of propodeum, with small upper section; metapleural gland orifice absent; opening of propodeal spiracle elongate. With thorax in ventral view, prosternal process a low, longitudinal keel; metasternal process absent. Petiole in dorsal view much broader than long, in profile view thick and low with rounded apex; in posterior view with dorsal margin concave medially.

Dorsum of head very densely and minutely punctate and rather dull; on clypeus and surrounding areas sculpture slightly coarser; mandible extensively punctate with interspaces smooth and shiny; venter of head superficially punctate and shiny; antenna entirely microsculptured and matt. Mesosoma and gaster extensively with superficial punctures and more or less shiny. Coxae, femora and tibiae superficially sculptured and weakly shiny; tarsi entirely matt.

Vertex with pair of long erect hairs close to posterior ocelli (sometimes with a few additional hairs); shorter pair of erect hairs present at level of posterior extremity of frontal carinae; clypeus with several long erect hairs; outer margin of mandible with softer and shorter hairs; antenna almost devoid of erect hairs except those located at tip of scape. Venter of head without erect hairs. Dorsum of mesosoma sparsely with very minute appressed hairs; mesonotum at most with one or two erect hairs; mesoscutellum with several erect hairs; propodeum without such hairs. Petiole with many short erect hairs. Gastral tergites sparsely covered with rather long appressed hairs; tergites and sternites 3–6 with long erect hairs. Body almost entirely dark reddish to blackish brown; genitalia much paler.

Structure of male genitalia as in Fig. 2E-G. Apical

(ninth) abdominal tergite reduced; pair of pygostyles (cerci) present, bearing erect hairs in their apical one-third; ninth sternite apically convex, not emarginate medially. Cupula in dorsal view very large, deeply concave medially, in ventral view detached medially, with each portion mesally produced posteriad as lobe. Paramere composed of large basimere and slender telomere, the latter being apically round and slightly extending beyond apex of volsella; volsella strongly sclerotized in apical half; its apex enlarged and flattened. Penisvalvae longest of three pairs of valvae, fused on dorsal face, separated on ventral face, with parallel lateral margins and truncate apex

Important morphological features observed in this species. Important character states are listed below, based on previous information and the present observations.

- 1) Size variation moderate: (0.92–1.22 mm in head width). (w)
- 2) Median concavity on anterior margin of clypeus faint. (w, q)
- 3) Erect hairs on head dorsum few, with only one pair behind line connecting posterior margins of eyes. (w, q)
- 4) Antennal scape without erect hairs. (w, q, m)
- 5) Ventral face of head without erect hairs. (w, q, m)
- 6) Dorsum of mesosoma without erect hairs. (w)
- 7) Metanotal groove present but weak, often obsolete in small individuals. (w)
- 8) Propodeum dorsally narrowed forming rather acute longitudinal ridge. (w)
- 9) Dorsum of propodeum without erect hairs. Mesonotum often with a few erect hairs. (q, m)
- 10) Metapleural glands present. In smaller workers metapleural gland orifice less prominent, but decumbent hairs covering the orifice clearly seen. (w, q)
- 11) Petiole lacking long erect hairs, but numerous microscopic erect hairs present. (w, q)
- 12) Acidopore not protruding as distinct nozzle, with peripheral hairs very short and inconspicuous. (w, q)
- 13) Femur of foreleg conspicuously widened. (w, q).
- 14) Forewing with first discoidal (discal) cell. (q, m)

Taxonomic remarks. Queens of this species can be differentiated from those of the other Japanese Camponotus species by the following combination of characteristics: 1) body entirely dark reddish to blackish brown, 2) body less than 7.5 mm in total length, 3) ventral face of head without erect hairs, 4) mesoscutum generally with only one or two erect hairs, 5) metapleural glands present (peculiar to this species), 6) propodeum without erect hairs (this feature is only shared with Camponotus devestivus Wheeler, 1928), 7) petiole in profile view acutely tapered apically. 8) forewing with first discoidal cell (peculiar to this species).

Males of this species are separated from those of the other Japanese *Camponotus* species by the following combination of characteristics: 1) entire body dark reddish to blackish brown, 2) total body length less than 5.5 mm, 3) venter of head without erect hairs, 4) erect hairs on mesoscutum generally two or less, 5) propodeum without erect hairs (probably peculiar to this species; *C. devestivus* males generally with two or three erect hairs), 6) forewing with first discoidal cell (peculiar to this species).

Distribution. Honshu and nearby islands (Eno-shima, Saru-shima, Jôga-shima), Izu Islands (Ô-shima), Shikoku, Kyushu, Gotô Islands (Fukue-jima), Tsushima, Ôsumi Islands (Yaku-shima, Kuchinoerabu-jima*), Amami Islands* (Amami-ôshima); Korean Peninsula, China (Yunnan). Distribution records except for localities with * (new records) and Tsushima (AntWiki 2022) are after Terayama et al. (2014).

Biological notes. In Kyushu and the Ryukyu Islands, southern Japan, this species is not common, and we have located only three colonies on Tsushima, an island lying between Kyushu and the Korean Peninsula. These nests were found in a crevice of a rocky slope, dead stump and rotting wood, respectively. In southern Kyushu and the Ryukyus no nest has been found, though foraging workers and winged ants (new queens and males) attracted to light have been occasionally sampled. As the winged ants were collected during July, nuptial flights seem to occur in this season in southern Kyushu and southward. Although Terayama et al. (2014) mentioned that nuptial flights of this species are conducted in October, and winged ants leave their natal nests during the daytime, we have never collected winged ants in this time zone in at least southern Kyushu and the Ryukyus. According to the web-site 'Animaria-no-zakkichô' (https:// animaria.net; accessed 7 August 2022), in all the observed cases in Honshu winged ants left their natal nests in the nighttime between 18:30 and 02:00.

Discussion

Camponotus keihitoi is one of the least studied carpenter ants in Japan for morphology and biology. Characteristics to recognize this species have been presented for the worker caste (Japan Ant Database Group, 2003; Terayama et al., 2014), but these descriptions are superficial overlooking some important characters. In the original description by Forel (1913) the subgenus to which C. keihitoi belongs was not stated. Emery (1925) later treated it as a species of the subgenus Myrmentoma, which contained diverse species roughly sorted into three species groups. Camponotus keihitoi was places in the C. caryae Fitch, 1855 group together with C. quadrinotatus Forel, 1886. These two Japanese species were considered by Radchenko (1996) to be closely related to each other. However, they are quite different except in their general habitus as mentioned above.

One of the peculiar features possessed by *C. keihitoi* is the metapleural gland seen in the worker and queen (Fig. 1D). The lack of this gland is shared by most species of Camponotini (Hölldobler and Engel-Siegel 1984; Yoshimura and Onoyama 2002; Yek and Mueller 2010). All the *Polyrhachis* species lack it, and in *Camponotus* very few species are known to have it, e.g., *C. horseshoetus* Datta and Rauchaudhuri, 1985 from India (Datta and Rauchaudhuri 1985), and *C. thadeus* Shattuck, 2005 from New Guinea (Shattuck 2005). It is quite doubtful that the possession of this gland indicates phylogenetic closeness. Rather, it occurs sporadically in different subgenera or species groups; for example, *C. thadeus* is the only species with this gland among the compact *C. aureopilus* Viehmeyer, 1914 species group, remaining eight

species in the group having no metapleural gland. This means Radchenko's assertion cannot be rejected by this character alone.

Another notable feature in *C. keihitoi* is the presence of the first discoidal (discal) cell on the forewing of the queen and male (Fig. 2A, C). The wing venation in the genus *Camponotus* is generally stable. In at least Japanese species, only *C. keihitoi* has this small cell on the forewing. We have not found any exception for this condition in *C. keihitoi* so that this is one of the most reliable recognition characteristics of this species; in one male specimen from Yaku-shima this cell was much reduced leaving a minute triangular area but it is still clearly recognized. Among Southeast Asian *Camponotus* and *Polyrhachis* faunas species with this cell sporadically occur in various species groups. Again, this feature cannot be considered to be phylogenetically suggestive. Rather we think this is expressed in a small number of non-related species based on a latent gene that is generally suppressed.

As has been shown in the result section *C. keihitoi* has many other interesting features, some of which are shared by other Japanese *Myrmentoma* species but others being peculiar to *C. keihitoi*. Due to the possession of these features, queen and male samples of this species collected with light trapping, Malaise trapping and FIT can be easily identified. However, the phylogenetic evaluation of them is another thing. To have a better (but not decisive) insight about species with unsettled status we need more morphological and molecular information from a wide range of species groups in *Camponotus*.

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References

AntWiki, 2022. Camponotus keihitoi. (Last edited 25 February 2022.)

Bolton, B., 1995. A New General Catalogue of the Ants of the World. Harvard University Press, Cambridge, Massachusetts & London, England. 504 pp.

Datta, S.K. and D. Rauchaudhuri, 1985. A new species of ant (Hymenoptera: Formicidae) from Nagaland, north-east India. *Science and Culture*, **51**: 271–273.

Folmer, O., M. Black, W. Hoeh, R. Lutz and R. Vrijenhoek, 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, **3**: 294–299.

Emery, C., 1925. In Wytsman, P. Genera Insectorum. Hymenoptera, Fam. Formicidae, subfam. Formicinae. Fasc 183: 302 pp. Bruxcelles.

Forel, A., 1913. Quelques formis des Indes, du Japon et d'Afrique. *Revue Suisse de Zoologie*, **21**: 659–673.

Hölldobler, B. and H. Engel-Siegel, 1984. On the metapleural gland of ants. *Psyche*, **91**: 201–224.

Japanese Ant Database Group, 2003. Super Visual Encyclopedia: Ants of Japan. Gakken, Tokyo. 196 pp. (In Japanese.)

Kimura, M., 1980. A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution*, **16**:

- 111-120.
- Lee, C.C., Y. M. Weng, L. C. Lai, A. V. Suarez, W. J. Wu, C. C. Lin and C. C. S. Yang, 2020. Analysis of recent interception records reveals frequent transport of arboreal ants and potential predictors for ant invasion in Taiwan. *Insects*, 11, 356 (13 pp.)
- Liu, C., G. Fischer, F. Hita Garcia, Sk. Yamane, Q. Liu, Y. Q. Peng, E. P. Economo, B. Guénard and N. E. Pierce, 2020. Ants of the Hengduan Mountains: a new altitudinal survey and updated checklist for Yunnan Province highlight an understudied insect biodiversity hotspot. *ZooKeys*, 978: 1–171.
- Radchenko, A.G., 1997. A review of ants of the subgenus *Myrmentoma*, genus *Camponotus* (Hymenoptera, Formicidae), from Asian Palaearctic. *Entomological Review*, 77: 1050–1059. (Translated from *Zoologicheskii Zhurnal*, 76 (6), 1997.)
- Shattuck, S., 2005. Review of the *Camponotus aureopilus* speciesgroup (Hymenoptera, Formicidae), including a second

- Camponotus with a metanotal gland. Zootaxa, 903: 1–20.
- Tamura, K., D. Peterson, N. Peterson, G. Stecher, M. Nei and S. Kumar, 2011. MEGA5: Molecular Evolutionary Genetics Analysis using Maximum Likelihood, Evolutionary Distance, and Maximum Parsimony Methods. *Molecular Biology and Evolution* 28: 2731–2739.
- Terayama, M. and T. Satoh, 1990. Taxonomic notes on two Japanese species of Formicidae. *Japanese Journal of Entomology*, **58**: 532.
- Yek, S.H. and U. G. Mueller, 2010. The metapleural gland of ants. *Biological Reviews* 2010: doi: 10.1111/j.1469-185X.2010.00170.x
- Yoshimura, M. and K. Onoyama, 2002. Male-based keys to the subfamilies and genera of Japanese ants (Hymenoptera: Formicidae). *Entomological Science*, **5**: 421–443.

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