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## The Ants of the Genus *Odontomachus* (Insecta: Hymenoptera: Formicidae) in Japan

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Species of the ant genus *Odontomachus* in Japan are revised. Type comparison and detailed morphological analysis show that *O. kuroiwa* (Matsumura, 1912) is an independent species from *O. monticola* Emery, 1892 and that the former species is distributed in Okinawa Island and Okinoerabu Island in the Ryukyu Islands. Lectotypes of both species are designated. All three castes of *O. kuroiwa* and *O. monticola* are characterized. All castes of *O. kuroiwa*, and the worker and male of *O. monticola*, are illustrated with scanning electron micrographs and light micrographs. The queen of *O. kuroiwa* is described for the first time. *Odontomachus kuroiwa* and *O. monticola* are morphologically distinguished and taxonomically discussed. Our morphological analysis suggested that *O. monticola* consists of a complex of several species. Additional notes on the morphology and distribution of both species in Japan are also given.

**Key Words:** Insecta, Hymenoptera, Formicidae, *Odontomachus kuroiwa*, *Odontomachus monticola*, worker, queen, male, taxonomy.

### Introduction

The genus *Odontomachus* contains large-sized ants belonging to the tribe Ponerini of the subfamily Ponerinae (Bolton 2003). The genus is characterized by linear mandibles, a nuchal carina running on the posterior dorsal surface of the head, a slender body, and a conical petiole. These ants are rather common on the floor of tropical forests (Ward 2000). Brown (1976) made a world-wide taxonomic revision of the genus and listed 51 valid species. Bolton (1995) cited 60 species and two fossil species in his catalogue. The latest list of Japanese ants (Terayama 2004) showed two species of the genus in Japan, *O. monticola* Emery, 1892 and *O. kuroiwa* (Matsumura, 1912).

The first record of *Odontomachus* in Japan was made by Matsumura (1912) from Okinawa Island in the Ryukyu Islands. He described the material as a new species, *Myrtoteras kuroiwa* Matsumura, 1912, the generic name being a misspelling of *Myrmoteras*, as the author later acknowledged (Matsumura and Uchida 1926). This species was later synonymized under *O. monticola formosae* Forel, 1912 (Teranishi 1940). Up until now this genus has been recorded in the southern part of

Kyushu and the Nansei Islands, including Yaku, Kuchinoerabu, Okinoerabu, and Okinawa Islands. In his revision of *Odontomachus*, Brown (1976) lumped the East Asian and Indochinese populations into a single species, *O. monticola*. The Japanese population had long been referred to *O. monticola* (see Ogata 1987).

*Odontomachus monticola* is a member of the *rixosus* species group, which includes two other species (*O. latidens* Mayr, 1867 and *O. rixosus* Smith, 1857) and probably further three Chinese species (*O. circulus* Wang, 1993, *O. rizangensis* Wang, 1993, and *O. fulgidus* Wang, 1993). *Odontomachus monticola* is separated from *O. rixosus* by a lower subapical tooth of the mandible and a shorter antennal scape, and from *O. latidens* by a smaller body and a petiolar node with a rounded anterior margin (Brown 1976). *Odontomachus monticola* in the sense of Brown (1976) shows a wide variation in morphology, and “wide-range variations” are observed even in the characters used as diagnostic characters among the three species, e.g., the shape of the subapical tooth and the shape of the petiolar node.

Morisita (1987, 1989) noticed that the population of *O. monticola* in the Okinawa Islands is different from that in other parts of Japan and thus there are two “forms” in Japan. Terayama (1999) followed Morisita’s view and distinguished the Okinawa population, regarded as an unidentified species with the Japanese name “Okinawa-agito-ari”, from *O. monticola* with the Japanese name of “Agito-ari”. Terayama (2004) listed this unidentified species as *O. kuroiwae* in his catalogue; however, neither a basis for his identification nor a reason for reviving the name from synonymy under *O. monticola* was provided.

The problem of the identities of Japanese *Odontomachus* “*monticola*” and *O. kuroiwae* has persisted. The present study aims to clarify the taxonomic status of these two species based on a detailed examination. We have compared the type specimens of relevant *Odontomachus* taxa and made a morphological analysis of all the castes of specimens from Japan and Southeast Asia. Several described varieties and a race of *O. monticola* are all deemed to be nominal subspecies under the Article 45.6 or 45.6.4 of ICZN (1999).

## Materials and Methods

Specimens in the following collections were examined (abbreviations after Brandão 2000): KUEC, Institute of Tropical Agriculture and Entomological Laboratory, Kyushu University, Fukuoka, Japan; MCSN, Museo Civico di Storia Naturale, Genoa, Italy; MHNG, Muséum d’Histoire Naturelle, Geneva, Switzerland; SEHU, Laboratory of Systematic Entomology, Hokkaido University, Sapporo, Japan. The material in Yoshimura’s collection is referred to by “MY” with colony No. -specimen No.

Observations and measurements were made under Nikon and Olympus stereoscopic microscopes with a direct-reading digital micrometer apparatus (Kogaku Co.; precise to 0.001 mm); the values are rounded to the nearest 0.01 mm and presented in mm. Observations of specimens sputter-coated with gold were made under scanning electron microscopes (JEOL JSM-6301F and JEOL JSM5600LV). Photographs of wings and male genitalia were taken using an automatic photograph system (PM-10ADS). Dissection of male genitalia and abdominal sternum IX was made chiefly in 70% alcohol. The terminal part including the genitalia was

macerated in a hot solution of 5% KOH for 15 minutes. The KOH treatment was repeated once and the treated materials were put under Neo-Shigaral (Shiga Kontyu Fukyusha) for photography.

The following measurements and indices (illustrated in Fig. 1) are cited in the

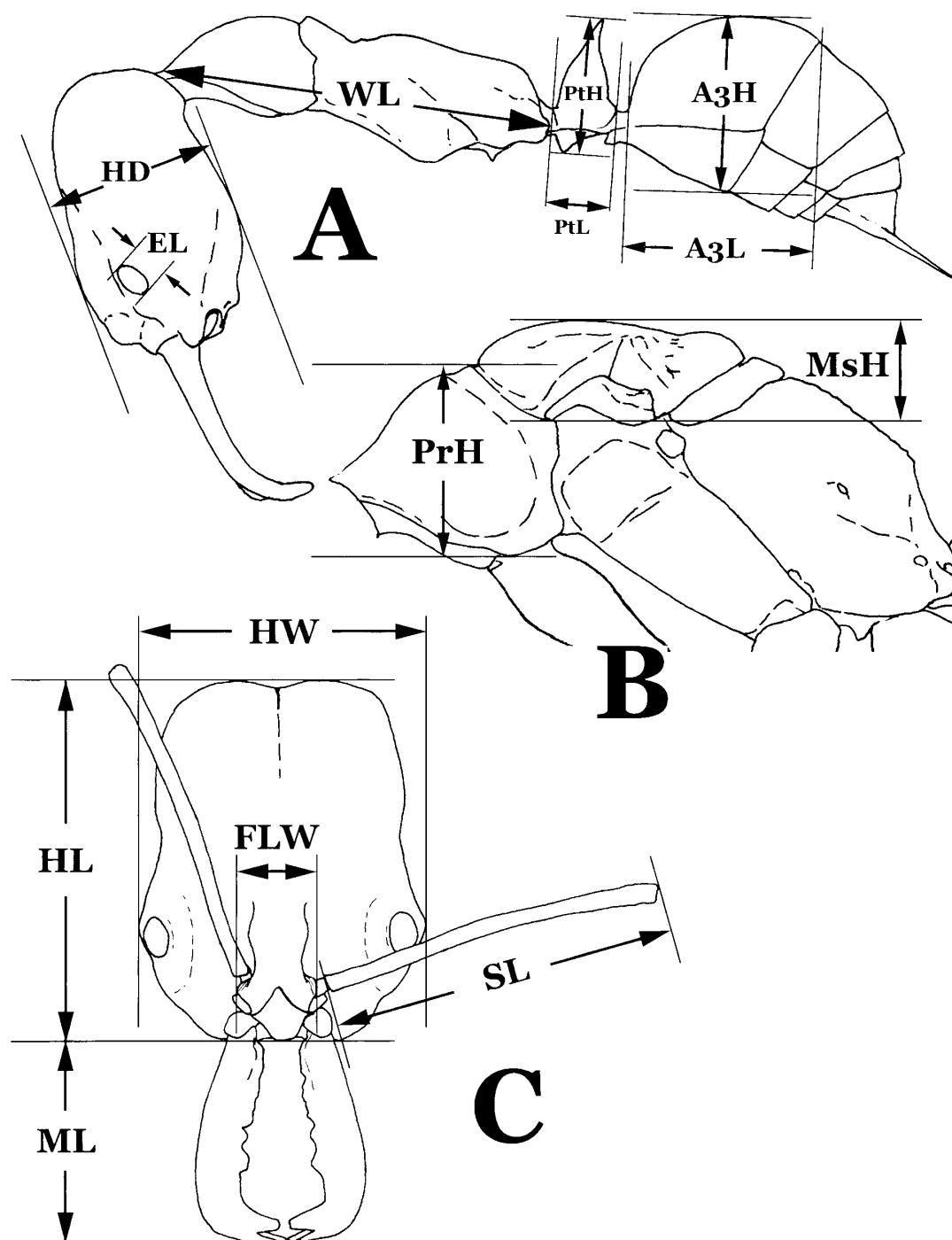


Fig. 1. Measurements for *Odontomachus* species, worker (A, C) and queen (B). A, Head to abdomen, lateral view; B, mesosoma, lateral view; C, head, full-face view. Abbreviations are explained in "Materials and Methods".

text: head length (HL), maximum length of head in full-face view from anterior-most point of clypeus to midpoint of line drawn across posterior margin of head (including ocelli in male); head width (HW), maximum width of head in full-face view, including eyes; head depth (HD), maximum depth of head in lateral view measured perpendicular to full-face view plane; mandible length (ML), maximum length in full-face view between anterior-most point of head and apical-most point of mandibles when mandibles completely closed (worker and queen); cephalic index (CI),  $HW/HL \times 100$ ; scape length (SL), length of scape excluding radicle (worker and queen); scape index (SI),  $SL/HW \times 100$ ; width of frontal lobes (FLW), maximum width between outer-most margins of frontal lobes in full-face view (worker and queen); eye length (EL), maximum length of eye measured in lateral view; pronotum height (PrH), maximum height of pronotum in lateral view (queen and male); mesoscutum height (MsH), maximum height of mesoscutum in lateral view (queen and male); mesoscutum index (MsI),  $MsH/PrH \times 100$ ; Weber's length of mesosoma (WL), maximum diagonal distance in lateral view, from base of anterior slope of pronotum to propodeal lobe; petiole length (PtL), maximum longitudinal length of petiole in lateral view, from anterior base to posterior border; petiole height (PtH), maximum height of petiole in lateral view, from dorsal border of petiole to ventral border of subpetiolar process; petiole height index (PtHI),  $PtH/PtL \times 100$ ; length of abdominal segment III (A3L), longitudinal length of abdominal segment III measured in lateral view along same line as ventral margin of tergum of AIII, excluding the helcium; height of abdominal segment III (A3H), maximum height of abdominal segment III in lateral view.

The terminology used herein basically follows Brown (1976), Wootton (1979), Gauld and Bolton (1988), Huber and Sharkey (1993), and Bolton (1994). Several characters used in discriminating the species were given special attention as mentioned below.

*Ocellus.* In males, the major axis length of the lateral ocelli relative to the ocello-ocular space is a useful character to distinguish the Japanese species, as it also is among three North American species of *Odontomachus* (Deyrup *et al.* 1985).

*Mandible.* There is some difficulty in judging one character state of the mandible. Terayama (1999: 173) focused on the ratio of subapical tooth length to width (in his key, the term "preapical teeth" is erroneously used) in separating the workers of the two Japanese species, but it is difficult to apply this character. We found that the apex of the subapical tooth could be worn down in most workers, and only in a few specimens intact subapical teeth were observed (Figs 2F, 3F). In practice, the workers of the two species cannot be separated by the relative length of the subapical tooth, although this character is available for the queens, most of which have intact subapical teeth (Fig. 4F). In males, some degree of variation was observed.

*Palp formula.* Segmentation of the maxillary and labial palpi (abbreviated as PF) varies within the genus. Brown (1976) showed PF=4, 3 in the *haematodus* group, but 4, 4 in the rest of the genus in workers. In males we found two types of PF: 6, 4 and 5, 4. The cause of this observed difference in the number of maxillary palp segments is probably frequent fusion between the apical two segments.

*Petiole.* Variation was found in the shape of the node in workers even within the same population. The subpetiolar process also varies in all the examined species. Petiolar characters were helpful to recognize species in most cases, but

they may be more variable than in other taxa of the Ponerini.

**Male Genitalia.** The male genitalia of *Odontomachus* species have an elongate abdominal sternum IX (=subgenital plate) and a winged aedeagus (Ogata 1987). The shape of the paramere is a useful character for distinguishing the species in Japan. The utility of the characters of the male genitalia may be extended to other species of *Odontomachus*.

## Systematics

### *Odontomachus kuroiwa* (Matsumura, 1912)

[Japanese name: Okinawa-agito-ari (Terayama 1999: 174)]  
(Figs 2, 4, 6, 7E–H, 8B)

*Myrtoter* [sic] *kuroiwa* Matsumura, 1912: 191–192, pl. 54, fig. 1 [type locality: Okinawa, Japan].

*Myrmoter* *kuroiwa*: Matsumura and Uchida 1926: 51.

*Odontomachus kuroiwa*: Creighton 1939: 40; Terayama 2004: 21.

*Odontomachus monticola* var. *formosae*: Teranishi 1940: 61. [Non Forel, 1912]

*Odontomachus monticola*: Brown (1976): 105, 157–159 (in part); Ogata 1987: 126 (in part), figs 123–133 (male). [Non Emery, 1892]

*Odontomachus* sp.: Terayama 1999: 173, 174.

*Odontomachus* sp. 2: Japanese Ant Database Group 2003: 192.

**Material examined.** Lectotype (here designated): worker, Okinawa, 25 October 1907, K. Kuroiwa leg. (SEHU) [Label data: OKinawa [sic] (Riukiu), Oct. '07, 425 Japan Matsum (Onoyama 1982)]. Paralectotype: 1 worker, same data as lectotype (SEHU).

Other material. [Japan] Amami Islands, Kagoshima Prefecture: 6 workers, Koshiyama, Okinoerabu Island, 15 May 1995, T. Iwai leg. Okinawa Island, Okinawa Prefecture: 1 worker, Hedo, 3 March 1984, K. Onoyama leg.; 1 worker, Mt. Nishime, Kunigami village, 27 March 1984, F. Sato leg.; 2 workers, Kunigami village, 12 March 1995, T. Iwai leg.; 6 workers, 3 queens, 5 males, Mt. Yonaha, 7 July 2001, M. Yoshimura leg. (MY 855); 1 worker, Izumi, 27 June 1974, K. Onoyama leg.; 1 worker, Motobu town, 22 October 1977, N. Tsurusaki leg.; 2 workers, same locality, 5 August 1994, H. Okido leg.; 3 queens, same locality, 5 August 1994, H. Okido leg.; 3 males, same locality, 24 June 2002, M. Yoshimura leg. (MY 972); 1 worker, Mt. Yae, Motobu town, 7 March 1984, K. Onoyama leg.; 1 worker, Nago Castle ruins, Nago city, 5 March 1984, K. Onoyama leg.; 1 worker, 1 male, same locality, 7 July 2001, K. Onoyama leg.; 1 worker, 1 queen, same locality, 18 June 2002, M. Yoshimura leg. (MY 971); 1 worker, 3 males, same locality, 25 June 2002, M. Yoshimura leg. (MY 973); 1 worker, Nago city, 27 June 1974, K. Onoyama leg.; 1 worker, Yonashiro town, 22 December 1973, W. C. Sedgwick leg.; 1 male, Naha city, 20 June 1983, Y. Fukumoto leg.

**Redescription.** *Worker* (Fig. 2). Lectotype (mounted on its back, hence several measurements cannot be given): HL 2.50, HW 1.84, ML 1.33, CI 73.6, PtL 0.52, A3L 1.63, A3H 1.52. One paralectotype: HL 2.43, HW 1.83, HD 1.32, ML 1.40, CI 75.3, SL 2.33, SI 127.3, FLW 0.61, EL 0.33, WL 2.91, PtL 0.53, PtH 0.98, PtHI 184.9, A3L 1.52,

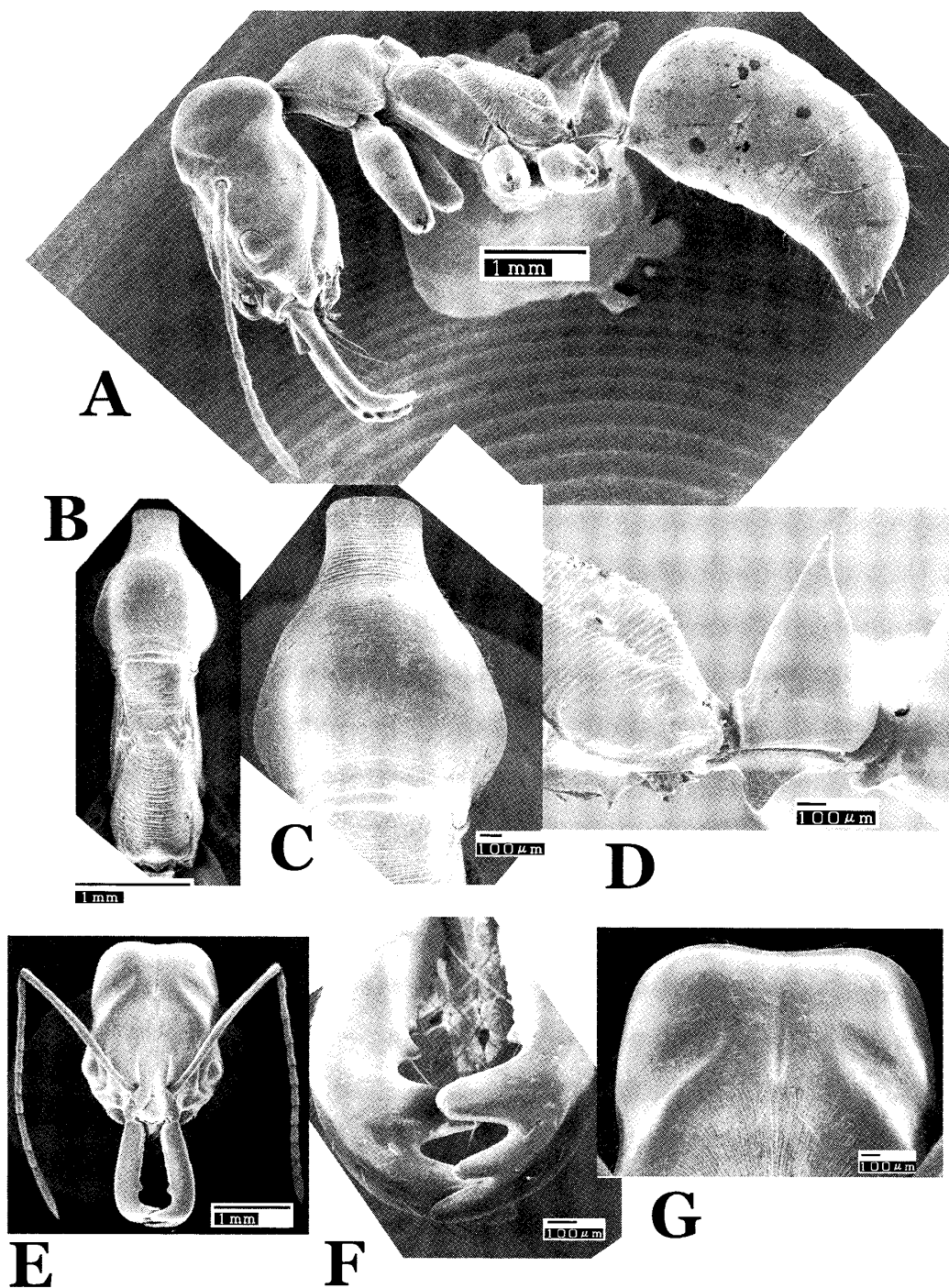


Fig. 2. *Odontomachus kuroiwae*, worker, MY 855-5 (A, D) and MY 855-6 (B, C, E-G), Mt. Yonaha, Okinawa, Japan. A, Head to abdomen, lateral view; B, mesosoma, dorsal view; C, pronotal disc, dorsal view; D, metanotum, propodeum, and petiole, lateral view; E, G, head, full-face view; F, mandible, oblique ventral view.

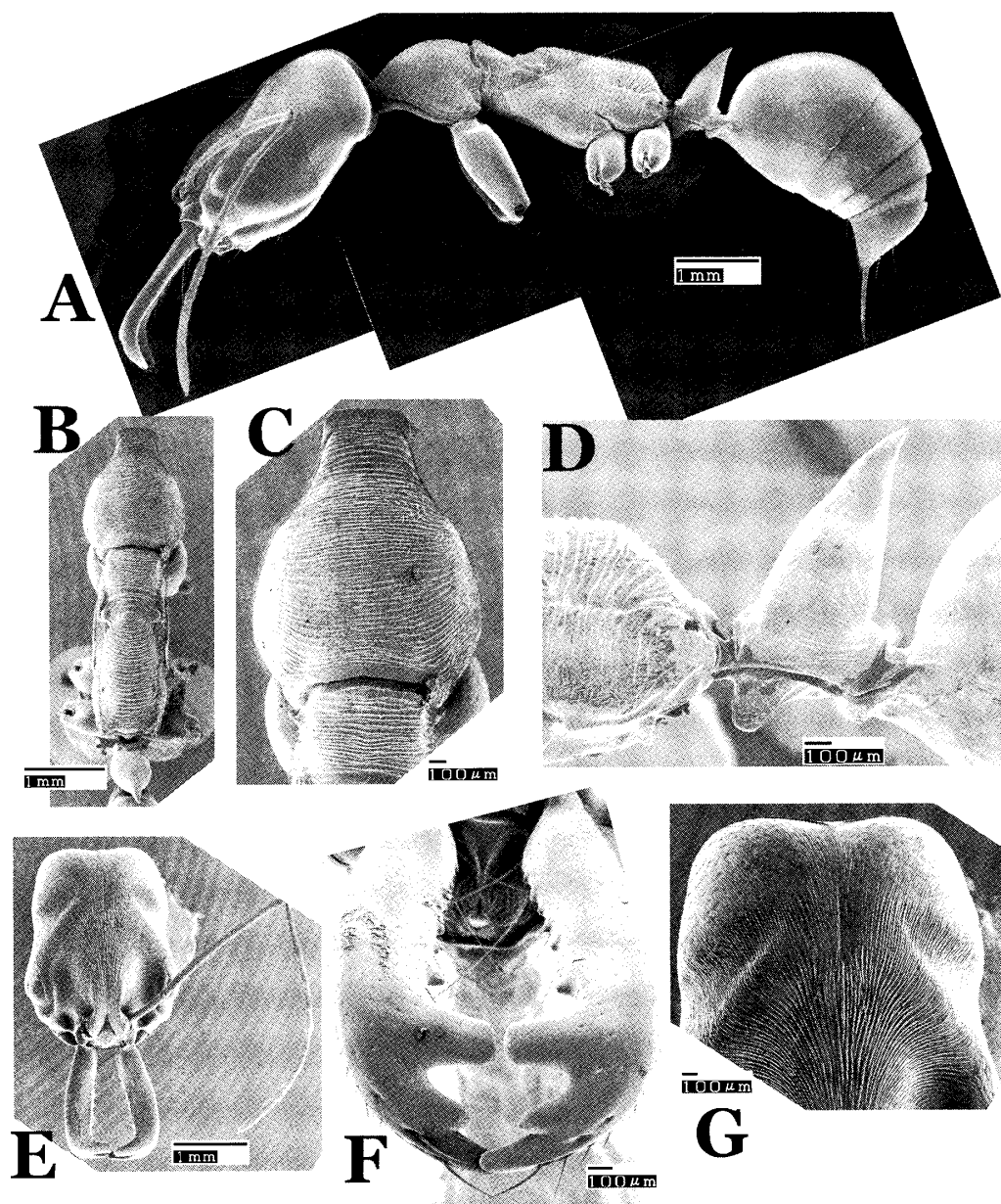


Fig. 3. *Odontomachus monticola*, worker, MY 1053-21, Hirakawa-cho, Kagoshima city, Japan. A, Head to abdomen, lateral view; B, mesosoma, dorsal view; C, pronotal disc, dorsal view; D, metanotum, propodeum, and petiole, lateral view; E, G, head, full-face view; F, mandible, oblique ventral view.

A3H 1.44. Twenty other individuals: HL 2.13–2.63, HW 1.63–2.06, HD 1.21–1.50, ML 1.11–1.45, CI 74.6–78.3, SL 1.96–2.41, SI 110.1–126.7, FLW 0.37–0.58, EL 0.26–0.37, WL 2.64–3.19, PtL 0.47–0.62, PtH 0.85–1.13, PtHI 149.1–194.8, A3L 1.29–1.75, A3H 1.39–1.69.

Head in full-face view constricted by distinct extraocular furrow in posterior half. Posterior margin of head in full-face view slightly concave. Mandible elongate and linear, its length about half of HL. Teeth of mandible divided into apical group and preapical group: apical group consisting of large and acute apical teeth,



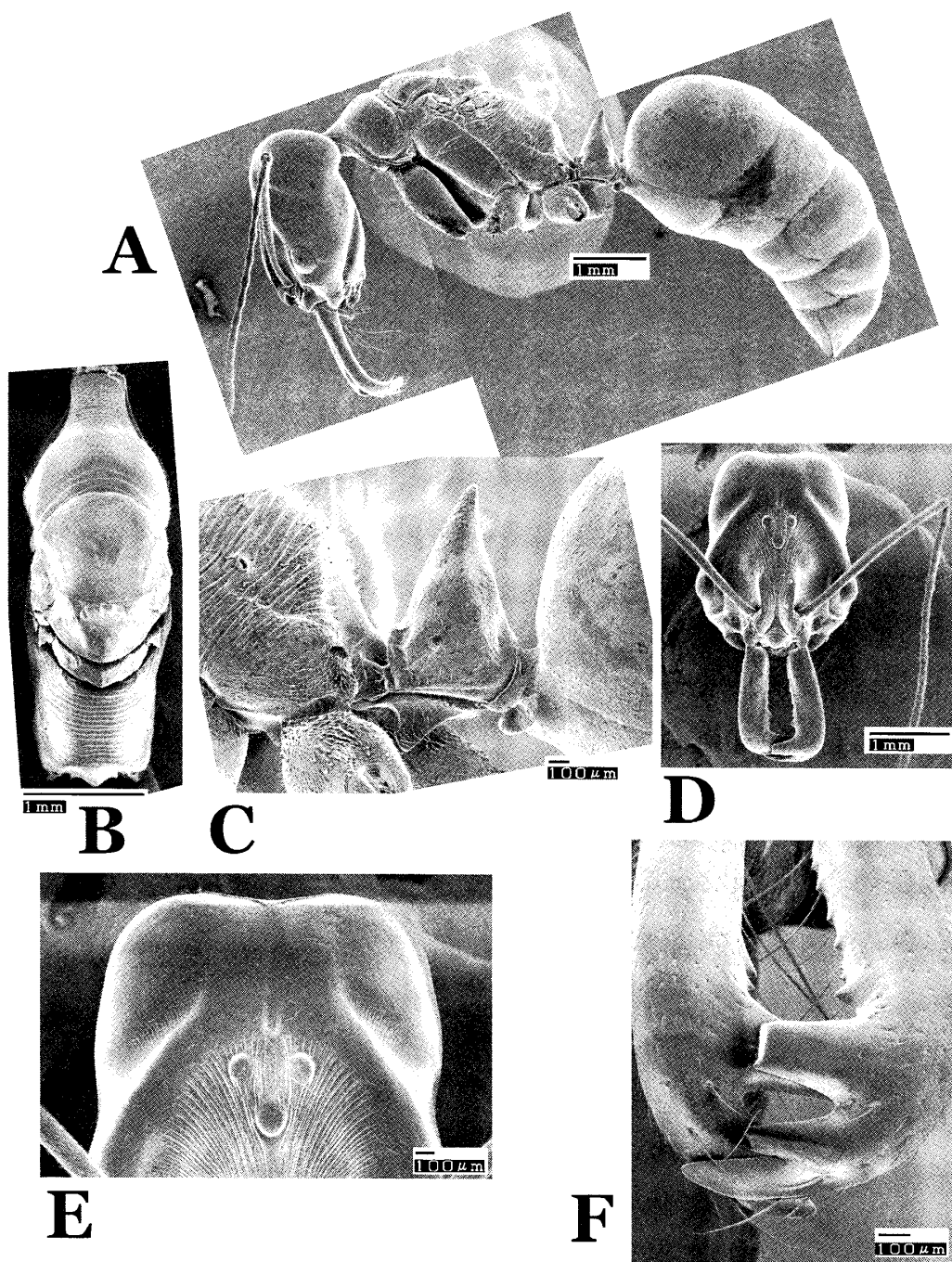


Fig. 4. *Odontomachus kuroiwae*, queen, MY 855-8 (A, C) and MY 855-7 (B, D-F), Mt. Yonaha, Okinawa, Japan. A, Head to abdomen, lateral view; B, mesosoma, dorsal view; C, petiole, lateral view; D, E, head, full-face view; F, mandible, oblique ventral view.

smaller intercalary teeth, and wide and short, truncate, subapical teeth; anteroapical corner of subapical tooth with a small dent (observed only in newly emerged individuals), but this subject to varying degree of wear; preapical group consisting of 7–9 small denticles (Fig. 2F). PF 4, 4 (1 dissected, 1 observed by SEM). Scape slender and long, exceeding posterior margin of head. Mesosoma slender. With mesosoma



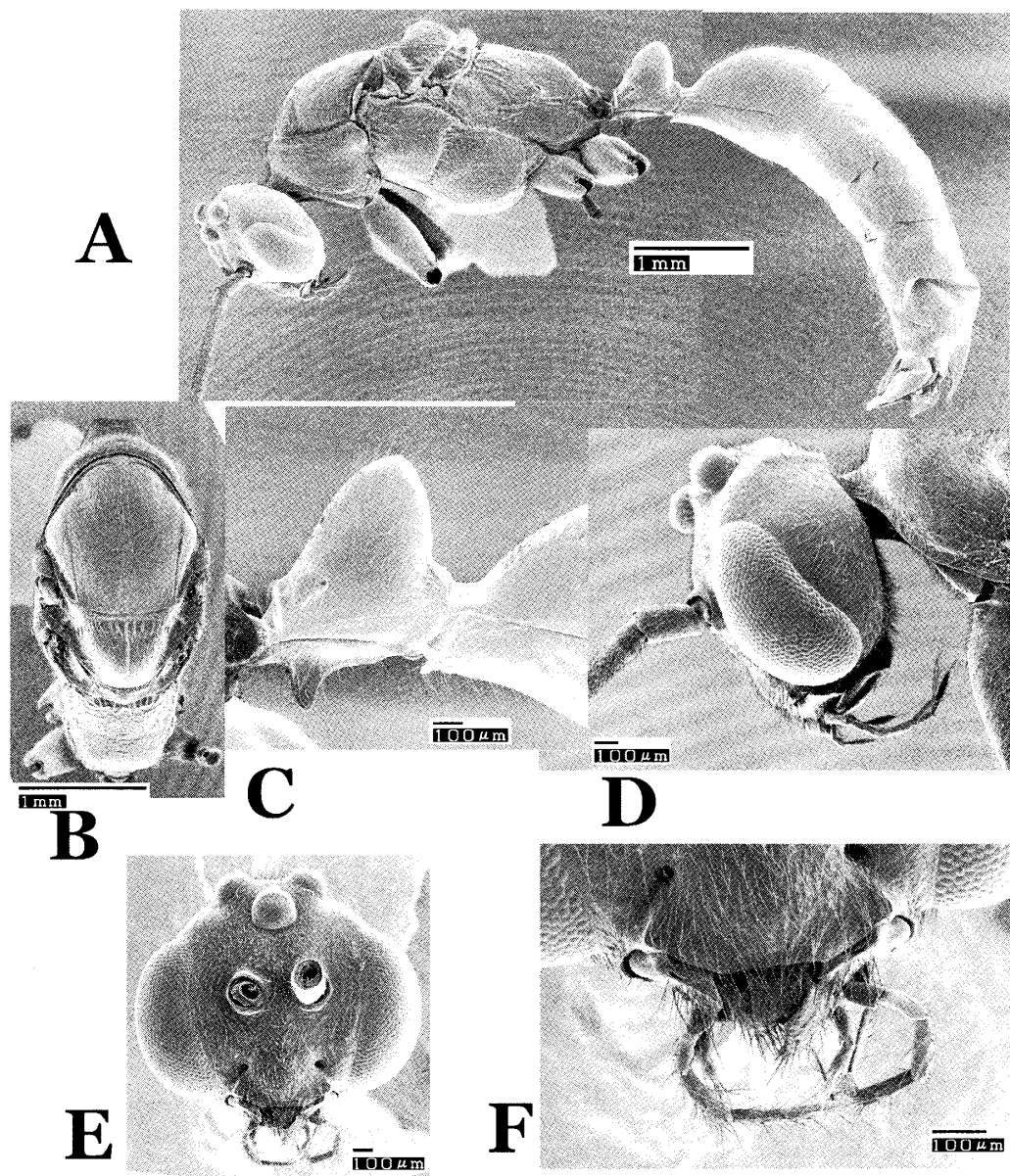


Fig. 5. *Odontomachus monticola*, male, MY 1053-24, Yaku Island, Kagoshima, Japan. A, Head to abdomen, lateral view; B, mesosoma, dorsal view; C, petiole, lateral view; D, head, lateral view; E, head, full-face view; F, mouthparts, full-face view.

in lateral view, anterior margin of pronotum gently raised, its dorsal margin gradually continuous with anterior neck. With mesosoma in dorsal view, mesepisternum without lateral projection. Anterior portion of mesonotum slightly convex in lateral view. Propodeum elongated posteriorly, dorsum nearly straight in lateral view. Pair of processes on metasternum narrow and strongly raised, their height greater than their basal width (Fig. 2D). With petiole in lateral view, node distinctly and immediately narrowed dorsally; width of nodal base about twice that of base of petiolar apical spine; anterior margin of node gently convex and never angulate at juncture with anterior margin of apical spine; apical spine short and

blunt. True petiolar peduncle reduced to anterior collar. Subpetiolar process developed but variable, its ventral apex in lateral view blunt.

With head in full-face view, ocular ridge and area posterior to extraocular furrow smooth and without striae, extraocular furrow weakly striated. With head in lateral view, area posterior to extraocular furrow smooth and shining. In dorsal view, anterior and posterior parts of pronotum transversely striated, and center of pronotal disc often smooth and glossy. Whole mesonotum and propodeum in dorsal view transversely striated. In lateral view, most of mesepisternum smooth. Petiolar tergite in lateral view smooth. Dorsal surface of abdominal tergite III glossy, not striated.

Pronotal dorsum with sparse pubescence. Dorsal surface of abdominal tergite III without setae.

Head, mesosoma, petiole, and legs brown to reddish brown. Gaster generally darker.

*Queen* (Fig. 4). Five individuals: HL 2.54–2.67, HW 2.02–2.15, HD 1.42–1.52, ML 1.34–1.52, CI 79.2–81.4, SL 2.35–2.51, SI 114.4–121.5, FLW 0.53–0.67, EL 0.39–0.44, PrH 0.96–1.11, MsH 0.48–0.66, MsI 48.0–59.5, WL 3.32–3.55, PtL 0.61–0.65, PtH 1.20–1.34, PtHI 192.1–216.1, A3L 1.94–2.34, A3H 2.01–2.29.

Generally similar to workers but with usual caste differences. Distinct ocelli situated on midlength of head in full-face view. Subapical tooth of mandible narrow and long, longer than its own basal width. Apex of subapical tooth truncate, its anteroapical corner with a small dent. Mesoscutum and scutellum weakly developed; scutellum not raised dorsally in lateral view, metanotum not convex in lateral view. Mesepisternum in lateral view with weak oblique furrow. Petiolar peduncle, node, and subpetiolar process in lateral view similar to those of workers.

With head in full-face view, ocular ridge and area posterior to extraocular furrow without striae and glossy. With head in lateral view, area posterior to extraocular furrow unstriated and glossy. Whole pronotum in dorsal view transversely striated, but striae often weak. Some parts of mesoscutum and scutellum in dorsal view with weak longitudinal striae, these often vestigial. Most of mesepisternum smooth, but posteroventral part weakly striated. Petiolar tergite in lateral view smooth. Dorsal surface of abdominal tergite III not striated, without setae.

Body color similar to that of workers.

*Male* (Figs 6, 7E–H, 8B). Nine individuals: HL 1.15–1.28, HW 1.42–1.59, HD 0.77–0.99, CI 116.7–128.3, EL 0.85–0.98, PrH 0.80–0.99, MsH 0.46–0.55, MsI 52.9–63.9, WL 2.79–3.21, PtL 0.55–0.68, PtH 0.71–0.90, PtHI 115.6–132.4, A3L 1.30–1.45, A3H 1.10–1.41.

Head in full-face view subglobose and wider than long when eyes and ocelli included. Posterior margin of head with large, prominent ocelli. Major axis of lateral ocellus distinctly longer than ocello-ocular space. Eye prominent, its length in full-face view nearly as long as head length excluding ocelli. Posterior margin of eye in lateral view slightly concave at midlength. Mandibles in full-face view (when fully opened) triangular and edentate; their masticatory faces not opposite, facing obliquely forward, expanded at their base, with 1 straight, stout seta at midlength. PF 5, 4 or 6, 4 (1 dissected, 1 observed with SEM, and 11 observed *in situ*). Anterior margin of clypeus in full-face view convex, nearly straight in middle. Anterior tentorial pits distinct. Antenna long and filiform, consisting of 13 segments. Antennal scape short. Occipital carina distinct. Mesosoma well developed. Pronotum in lat-

eral view relatively thick, nearly twice as thick as mesoscutum. Scutellum slightly convex dorsally. Metanotum slightly convex posteriorly. Petiole low, with petiolar tergite longer than high. Subpetiolar process well developed, its apex sharper than that of queens. Anterior margin of abdominal tergite III steeply raised.

Paramere long, exceeding apical margin of abdominal sternum IX by half of paramere length. Paramere in lateral view bent ventrally at 2 points at around 1/4 and 3/4 of its length. Abdominal sternum IX expanded in basal half in ventral view, this expansion most pronounced in basal 1/4.

Apical margin of forewing relatively more rounded than in male of *O. monticola* (compare Fig. 8A and 8B). On forewing, costa (C), radius (R) and radial sector 1 (Rs1), and 2r-m and cu-a cross-veins clearly present. Media (M) reduced from meeting point with 2r-m cross-vein, cubitus (Cu) and anals (A) also reduced from their own meeting point. Rs2 entirely absent, but often with vestiges of branch on 2r-m cross-vein.

On hind wing, R+ Rs, R and M+ Cu, and r-m and cu-a cross-veins clearly present. Rs, M, Cu, and distal 1/4 of A nearly vestigial. Jugal lobe developed.

Body almost uniformly yellowish brown.

**Distribution.** Japan: Okinoerabu Island in the Amami Islands (Kagoshima Prefecture) and Okinawa Island (Okinawa Prefecture). The record from Kuchinoerabu Island (Kagoshima Prefecture) in Japanese Ant Database Group (2003) is incorrect; the collection site was actually Okinoerabu Island.

**Comments.** There are two specimens in Matsumura's collection at SEHU (Onoyama 1982). Both are workers labeled as "Okinawa Pref., Japan, x.1907, K. Kuroiwa leg." We have chosen the specimen labeled as "*Myrmoteras Kuroiwa* n sp" as lectotype.

The male genitalia shown by Ogata (1987) as those of *Odontomachus monticola* are correctly identified as those of *O. kuroiwa*, as the distinctly elongate paramere shows.

In synonymizing *O. kuroiwa* with *O. monticola*, Brown (1976) reasoned as follows: (1) the variations of the striae on the vertex and the pronotal disc of *Odontomachus* workers may depend in part on allometric factors [this was also pointed out by Yasumatsu (1962)]; (2) body size tends to be smaller in eastern and southern populations, which may reflect geographical variation within a single species; (3) thus the geographically variable surface sculpture of the body in workers may be no more than a size-related expression of variation within a single species. His concept was probably based on the idea that *O. monticola* is a polytypic species with a wide range of distribution from Indochina to East Asia; however, our observations show that *O. kuroiwa* and *O. monticola* are separate species. First, striation on the head and pronotum is undeveloped even in larger-sized workers and in mature colonies of *O. kuroiwa*. Furthermore, differences in the shape of the petiolar apical spine in workers, the striation pattern on the posterior part of the head in workers and queens, and the shape of the subapical tooth of the mandible in workers and queens easily and consistently serve to separate *O. kuroiwa* from *O. monticola*. Reduction of the sculpture on the head and pronotal disc was confirmed in the holotype of *O. monticola longi* Forel, 1900 collected from Assam in India (Forel 1900); however, the narrower and longer subapical tooth (even when worn down) clearly separates *O. kuroiwa* from that specimen, which has complete subapical teeth and intercalary teeth. Although Teranishi (1940) regarded *O. kuroiwa*

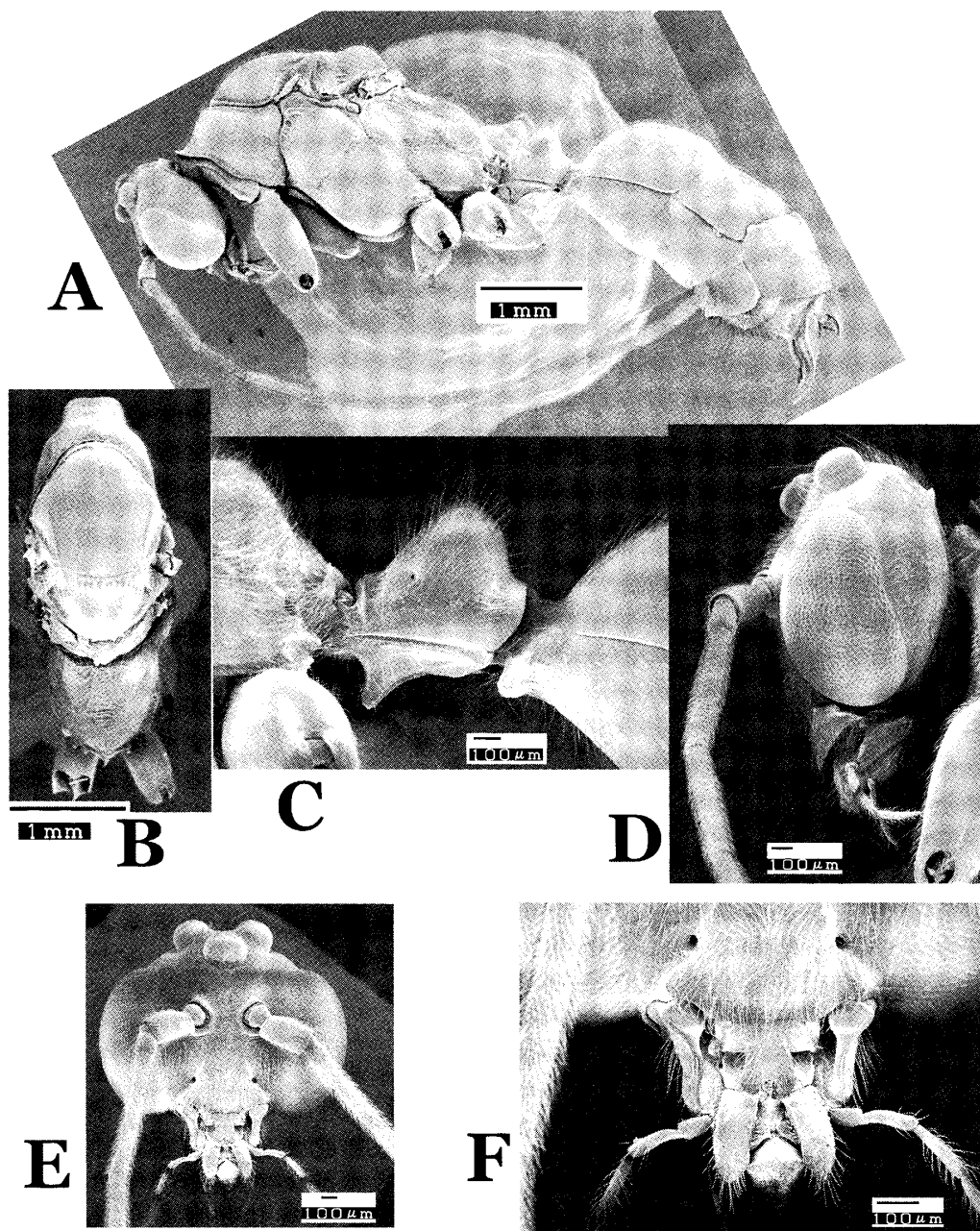


Fig. 6. Males of *Odontomachus kuroi wae*, MY 855-10 (A, C, D) and MY 855-9 (B, R, F), Mt. Yonaha, Okinawa, Japan. A, Head to abdomen, lateral view; B, mesosoma, dorsal view; C, petiole, lateral view; D, head, lateral view; E, head, full-face view; F, mouthparts, full-face view.

as a junior synonym of *O. monticola formosae*, separation of those two taxa is further supported by distinct and stable morphological differences in the male: *O. kuroi wae* can be recognized by the elongate parameres of the genitalia (Fig. 7) and the low petiolar node (Figs 5C, 6C).

As was true for *Odontomachus monticola* and *O. pauperculus* (Brown 1976), the HW/HL plots of *O. monticola* and *O. kuroi wae* seem to share a common regression axis (Fig. 10A). Brown (1976) believed that this congruence supported his hypothe-

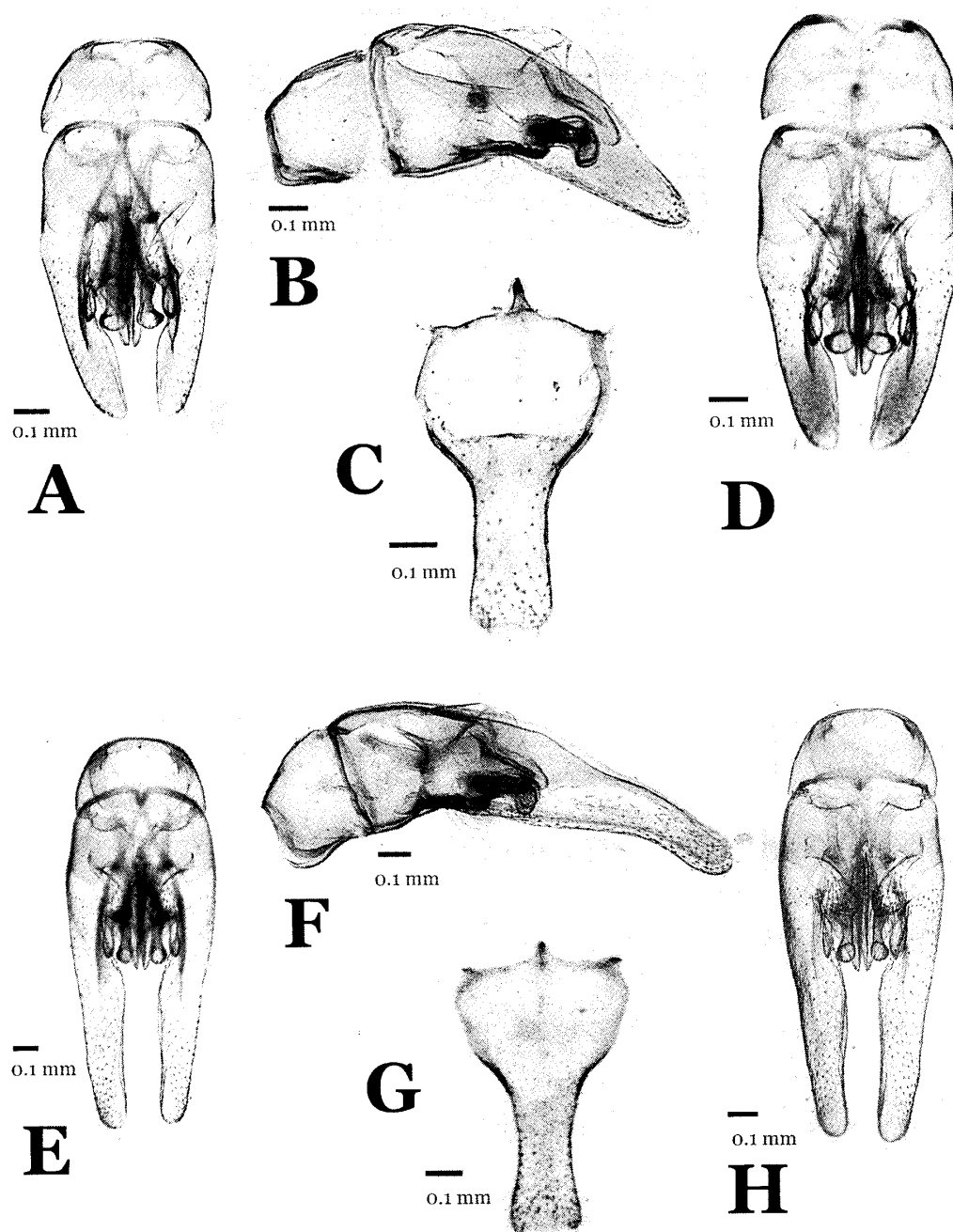


Fig. 7. Male genitalia of *Odontomachus* spp. in dorsal (A, E), lateral (B, F), and ventral (D, H) views, and abdominal sternum IX in ventral view. A-D, *Odontomachus monticola*, MY 1053-23, Hirakawa-cho, Kagoshima city, Japan; E-H, *Odontomachus kuroiwae*, MY 855-12, Mt. Yonaha, Okinawa, Japan.

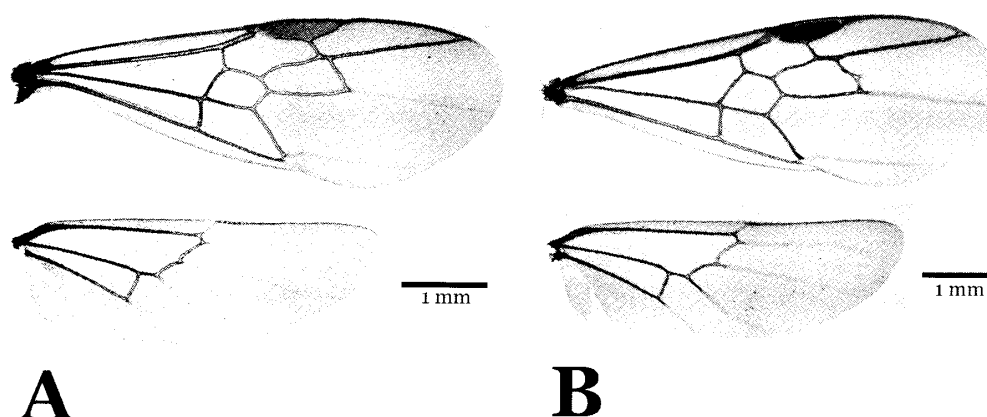


Fig. 8. Male wings of *Odontomachus* spp. A, *Odontomachus monticola*, MY 1053-23, Hirakawa-cho, Kagoshima City, Japan; B, *Odontomachus kuroiwae*, MY 855-9, Mt. Yonaha, Okinawa, Japan.

sis that differences in striation are due to allometric factors. However, this does not justify synonymizing the species, because plots of other measurements, PtH/PtL and MsH/PrH, of these two species in Japan do not share a common regression axis (Fig. 10B, C). The stable morphological differences mentioned above, i.e., in striation and petiole morphology in workers, in petiole and genital morphology in males, and in the measurements shown (Fig. 10B, C) all demonstrate that *O. monticola* and *O. kuroiwae* are separate species.

***Odontomachus monticola* Emery, 1892**

[Japanese name: Agito-ari]

(Figs 3, 5, 7A–D, 8A, 9)

*Odontomachus monticola* Emery, 1892: 560 (in key) [type locality: Burma (i.e., Myanmar)]; Yasumatsu 1962: 93; Brown 1976: 105, 157–159 (in part); Ogata 1987: 126 (in part), figs 120–122 (worker); Wang 1993: 220–225; Terayama 1999: 173, 174; Japanese Ant Database Group 2003: 193.

*Odontomachus monticola* r. *punctulatus* Forel, 1900: 58 [deemed a subspecies under Art. 45.6 of ICZN (1999); type locality: Assam, India].

*Odontomachus punctulatus*: Bingham 1903: 49.

*Odontomachus monticola* var. *longi* Forel, 1900: 58 [deemed a subspecies under Art. 45.6.4 of ICZN (1999); type locality: Assam, India].

*Odontomachus monticola* var. *formosae* Forel, 1912: 46 [deemed a subspecies under Art. 45.6.4 of ICZN (1999); type locality: Taiwan].

*Odontomachus monticola formosae*: Yano 1932: 340 (in part).

*Odontomachus monticola* var. *major* Forel, 1913: 183 [deemed a subspecies under Art. 45.6.4 of ICZN (1999); type locality: Taiwan].

*Odontomachus monticola pauperculus* Wheeler, 1921: 530–531 [type locality: Mokan-shan, China].

*Odontomachus monticola* var. *hainanensis* Stitz, 1925: 115 [deemed a subspecies under Art. 45.6.4 of ICZN (1999); type locality: Hainan, China].



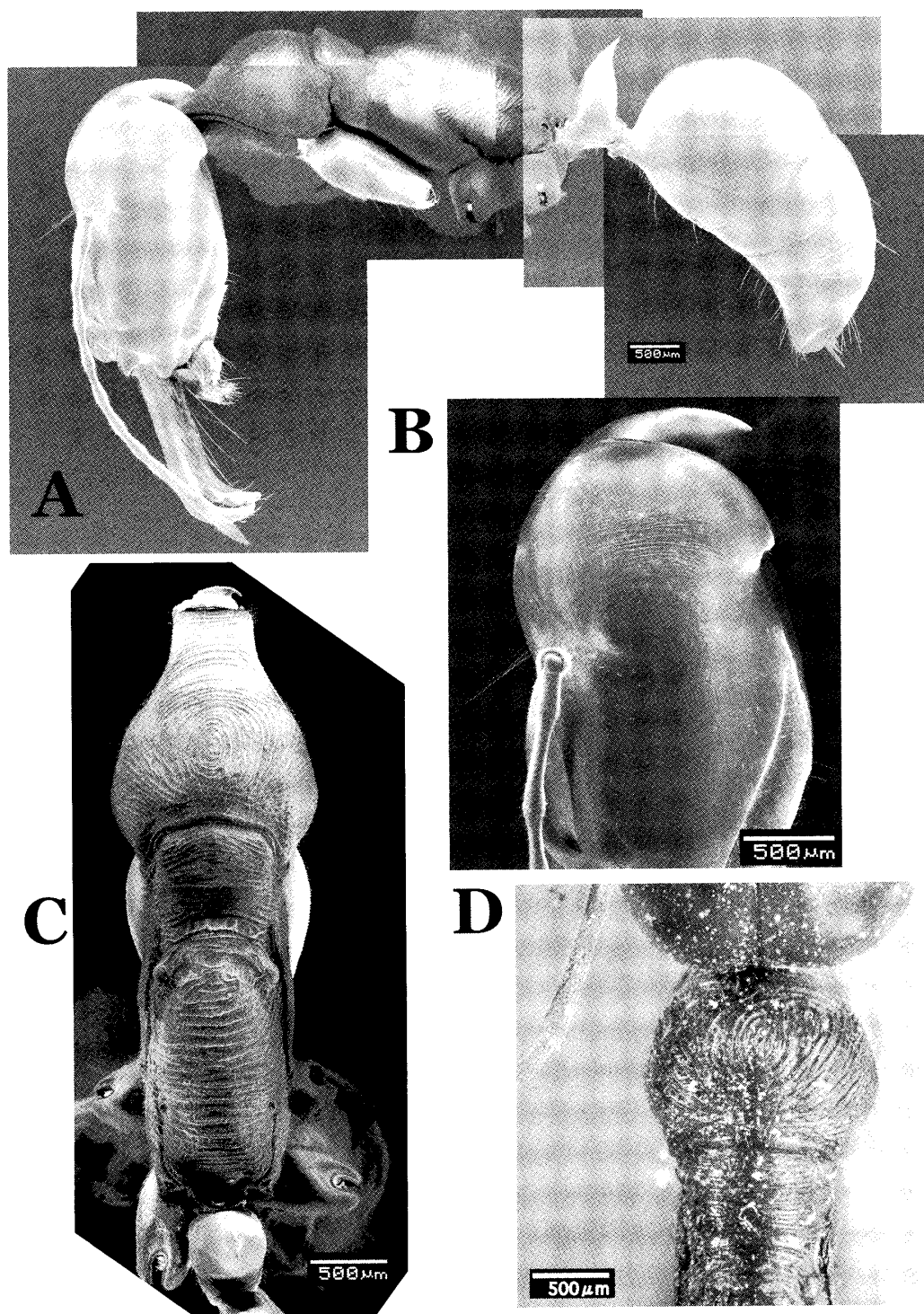


Fig. 9. Workers of *Odontomachus monticola*, MY 1221-5 (A, B) and MY 1221-6 (C), Vietnam, and lectotype (D), Myanmar. A, Head to abdomen, lateral view; B, head, lateral view; C, mesosoma and petiole, dorsal view; D, pronotal disc, dorsal view.



*Odontomachus latidens striata* Menozzi, 1930: 329 [type locality: Hong Kong, China].

**Material examined.** Lectotype (here designated): worker, Carin Checù, Burma (Myanmar), 1300–1400 m, February to March 1888, L. Fea leg. (MCSN). Paralectotypes: 1 worker, same data as lectotype (MCSN); 1 worker, same data as lectotype (MHNG); 2 workers, Carin Asciuii Chebà, Burma (Myanmar), 800–1400 m, December 1887, L. Fea leg. (MCSN).

Holotype of *Odontomachus monticola punctulatus* Forel, 1900: worker, Assam, 7 October 1861? [labeled as LXI'X/7] (MHNG).

Holotype of *Odontomachus monticola longi* Forel, 1900: worker, Garo Hill, ? [labeled as CI/6], Long leg. (MHNG).

Syntypes of *Odontomachus monticola formosae* Forel, 1912: 2 workers, Pilam, Formosa (Taiwan), January 1908, H. Sauter leg. (MHNG).

Syntypes of *Odontomachus monticola major* Forel, 1913: 1 worker, Taihorin, Formosa (Taiwan), H. Sauter leg. (MCSN); syntypes?, 3 workers, Taihorin, Formosa [labeled as No. 25a] (MHNG).

Other material. [Japan] Kyushu mainland, Kagoshima Prefecture: 1 worker, Shimofukumoto-cho, Kagoshima city, 15 May 1994, H. Okido leg.; 3 males, Hirakawa-cho, Kagoshima city, 27 August 1994, N. Kawakubo leg.; 1 worker, same locality, 3 May 1995, H. Okido leg.; 2 workers, same locality, 26 April 1995, H. Okido leg.; 1 worker, 1 queen, Oura-cho, 17 October 1998, H. Okido leg.; 1 male, same locality, 8 May 1994, H. Okido leg.; 1 worker, Makurazaki city, 14 April 1990, S. Yamane leg. Osumi Islands, Kagoshima Prefecture: 2 workers, Tanegashima Island, 5 May 1984, H. Harada and M. Yano leg.; 2 workers, Kuchinoerabu Island, 20 October 1994, H. Okido leg.; 2 workers, same locality, 20 July 1989, S. Yamane leg.; 3 workers, Yaku Island, 10 April 1970, T. Abe leg.; 6 workers, 2 males, same locality, 22 October 1978, K. Ogata leg. (TAKU); 1 worker, same locality, 19 August 1983, S. Yamane leg.; 1 worker, same locality, 21 August 1983, S. Yamane leg.; 1 male, same locality, 22 July 1988, S. Yamane leg.; 1 worker, same locality, 22 October 1994, H. Okido leg. [China] One worker, Victoria Park, Hong Kong Island, 27 June 1999, S. Yamane leg. [Vietnam] Two workers, Tam Dao, 900 m alt., Vinh Phuc Province, 7 August 1998, S. Yamane leg.; 6 workers, 21°28'20"N, 105°38'36"E, Tam Dao, 2 November 2004, M. Yoshimura leg. (MY1221); 1 worker, Ban Xan, 1012 m alt., Que Phong District, Nghe An Province, 19 April 1999, B. T. Viet leg.; 1 worker, Sapa, 1500 m alt., Lao Cai Province, 28 May 1997, R. Matsumoto leg. [Laos] One worker, V. D. Salvuza leg. (MCSN). [Myanmar] One dealate queen, Carin Asciuii Chebà, Burma (Myanmar), 800–1400 m alt., December 1887, L. Fea leg. (MCSN); 2 workers, Carin Chebà, Burma (Myanmar), 900–1100 m alt., 5 December 1888? [labeled as VXII-88], L. Fea leg. (MCSN).

Other material labeled as “typus” of *Odontomachus monticola formosae* (see comments): 3 queens, Taihorin, Formosa (Taiwan) [labeled as No. 65] (MHNG); 1 male, Taihorin, Formosa, 7 August 1911, H. Sauter leg. (MHNG).

**Redescription.** *Worker* (Fig. 3). Lectotype: HL 2.79, HW 2.31, ML 1.65, CI 82.8, SL 2.85, SI 123.4, FLW 0.66, EL 0.33, WL 4.05, PtL 0.62, PtH 1.17, A3L 1.77, A3H 1.65. Two syntypes of *Odontomachus monticola formosae*: HL 3.02–3.23, HW 2.27–2.45, HD 1.72–1.83, ML 1.67–1.81, CI 75.2–75.9, SL 2.95–3.06, SI 124.9–130.0, FLW 0.66–0.72, EL 0.34–0.38, WL 3.78–3.96, PtL 0.65, PtH 1.30–1.34, PtHI 200.0–206.2, A3L 1.92–2.15, A3H 1.83–1.87. Twenty other individuals collected in Japan: HL 2.56–3.15, HW 2.00–2.57,

HD 1.49–1.89, ML 1.45–1.83, CI 76.6–81.6, SL 2.63–3.16, SI 117.5–132.7, FLW 0.43–0.79, EL 0.29–0.41, WL 3.34–4.21, PtL 0.60–0.78, PtH 1.15–1.52, PtHI 168.0–212.7, A3L 1.60–2.05, A3H 1.59–2.00.

Head in full-face view constricted by distinct extraocular furrow in posterior half. Posterior margin of head in full-face view slightly concave. Mandible elongate and linear, its length about half of HL. Teeth of mandible divided into apical group and preapical group: apical group consisting of large and acute apical teeth, smaller intercalary teeth, and truncate subapical teeth, last ones wide and short in newly emerged specimens, but subject to various degrees of erosion with use; preapical group consisting of 8–11 small denticles (Fig. 3F). Palp formula 4, 4 (1 dissected). Scape slender and long, exceeding posterior margin of head. Mesosoma slender to stout. With mesosoma in dorsal view, mesepisternum without lateral projection. Anterior portion of mesonotum slightly convex in lateral view. Propodeum elongated posteriorly, dorsum nearly straight in lateral view. Pair of processes on metasternum gently raised, their height less than their basal width (Fig. 3D). Petiole variable in shape. With petiole in lateral view, node often symmetrically raised with its anterior margin gently convex and often making distinct angle with margin of petiolar apical spine; apical spine long to moderate in length and sharp. True petiolar peduncle reduced to anterior collar. Subpetiolar process developed but variable, its ventral apex in lateral view blunt.

With head in full-face view, ocular ridge, extraocular furrow, and area posterior to extraocular furrow fully striate or partially lacking striae. With head in lateral view, area posterior to extraocular furrow distinctly striated or mostly smooth. Whole pronotum, mesonotum, and propodeum in dorsal view transversely or circularly striated. In lateral view, most of mesepisternum striated. Petiolar tergite in lateral view weakly striated or completely lacking striation. Dorsal surface of abdominal tergite III not striated and opaque.

Pronotal dorsum with dense pubescence. Dorsal surface of abdominal tergite III without setae.

Body almost uniformly blackish brown.

*Queen.* Three individuals of *Odontomachus monticola formosae* used by Forel (1913) [MHNG: labeled as “typus” (see comments)]: HL 3.12–3.14, HW 2.43–2.58, HD 1.73–1.79, ML 1.76–1.79, CI 77.4–82.7, SL 2.95–2.99, SI 115.9–121.4, FLW 0.69–0.71, EL 0.36–0.38, PrH 1.34–1.39, MsH 0.68–0.77, MsI 50.7–57.5, WL 4.14–4.25, PtL 0.74, PtH 1.60, PtHI 216.2, A3L 2.40–2.48, A3H 2.22–2.28. One individual collected in Japan: HL 2.75, HW 2.25, HD 1.68, ML 1.63, CI 81.8, SL 2.80, SI 124.4, FLW 0.66, EL 0.35, PrH 1.33, MsH 0.78, MsI 58.6, WL 3.77, PtL 0.73, PtH 1.60, PtHI 219.2, A3L 2.42, A3H 2.35.

Generally similar to workers but with usual caste differences. Distinct ocelli situated on midlength of head in full-face view. Subapical tooth of mandible wide and short, only as long as its own basal width. Apex of subapical tooth truncate, its anteroapical corner with a small dent. Mesoscutum and scutellum developed, scutellum raised dorsally in lateral view. Metanotum not convex in lateral view. Mesepisternum in lateral view with distinct oblique furrow. Petiolar peduncle, node, and subpetiolar process in lateral view similar to those of workers. Anterior margin of abdominal tergite III steeply raised.

With head in full-face view, ocular ridge, extraocular furrow, and area posterior to extraocular furrow fully striated to partially lacking striae. With head in lateral view, area posterior to extraocular furrow distinctly striated to mostly

smooth. Whole pronotum in dorsal view transversely striated. Mesoscutum and scutellum in dorsal view with longitudinal or transverse striae, but development of striae variable. Development of striae on mesepisternum variable. Dorsal surface of abdominal tergite III not striated.

Dorsal surface of abdominal tergite III without setae.

Body almost uniformly blackish brown.

**Male** (Figs 5, 7A–D, 8A). One individual of *Odontomachus monticola formosae* [MHNG: labeled as “typus” (see comments)]: HL 1.22, HW 1.47, HD 0.86, CI 120.5, EL 0.82, PrH 0.89, MsH 0.75, MsI 84.3, WL 3.20, PtL 0.65, PtH 0.92, PtHI 141.5, A3L 1.64, A3H 1.23. Five individuals collected in Japan: HL 1.13–1.23, HW 1.40–1.48, HD 0.80–0.90, CI 120.3–125.4, EL 0.80–0.87, PrH 0.80–0.93, MsH 0.63–0.69, MsI 72.0–82.9, WL 2.95–3.24, PtL 0.64–0.68, PtH 0.80–0.96, PtHI 121.2–150.0, A3L 1.46–1.62, A3H 1.07–1.18.

Head in full-face view subglobose and wider than long when eyes and ocelli included. Posterior margin of head with large, well-developed ocelli. Major axis of lateral ocellus as long as ocello-ocular space. Eye prominent, its length in full-face view distinctly shorter than head length excluding ocelli. Posterior margin of eye in lateral view slightly concave at midlength. Mandibles in full-face view (when fully opened) reduced, variable, and triangular; their masticatory faces not opposite, facing obliquely forward, expanded at their base, and lacking setae. PF 5, 4 or 6, 4 (1 dissected, 1 observed with SEM, and 4 observed *in situ*). Anterior margin of clypeus in full-face view convex, nearly straight in middle. Anterior tentorial pits distinct. Antenna long and filiform, consisting of 13 segments. Antennal scape short. Occipital carina distinct. Mesosoma well developed. Pronotum in lateral view relatively thin, nearly as thick as mesoscutum. Scutellum strongly convex dorsally. Metanotum convex posterodorsally. Petiole high, with petiolar tergite higher than long. Subpetiolar process well developed, its apex sharper than that of queens. Anterior margin of abdominal tergite III gently raised.

Paramere short, exceeding apical margin of abdominal sternum IX by 1/4 of paramere length. Paramere in lateral view bent ventrally at single point at around 1/3 of its length. Abdominal sternum IX expanded in basal half in ventral view, this expansion most pronounced in its basal half.

Apical margin of forewing relatively sharp (compare Fig. 8A and 8B). On forewing, costa (C), radius (R) and radial sector 1 (Rs1), and 2r-m and cu-a cross-veins clearly present. Media (M) reduced from meeting point with 2r-m cross-vein, cubitus (Cu) and anals (A) also reduced from their own meeting point. Rs2 entirely absent, but often with vestiges of branch on 2r-m cross-vein.

On hind wing, R+ Rs, R and M+ Cu, and r-m and cu-a cross-veins clearly present. Rs, M, Cu, and distal 1/4 of A nearly vestigial. Jugal lobe developed.

Body almost uniformly yellowish brown.

**Distribution.** Japan: Fukuoka (Terayama and Kitade 2005) and Kagoshima Prefectures, including Osumi Islands; Taiwan, China, Vietnam, Laos, Myanmar, and India.

**Comments.** In their world catalogues of ants, Bolton (1995) and Bolton *et al.* (2006) erroneously indicated that the type locality of *Odontomachus monticola* was “Vietnam”. All specimens labeled as syntype and “cotypus” were collected by L. Fea during his trips to Myanmar. Moreover, Emery (1892: 558) gave a preliminary notice that he intended to describe a new species collected from highlands of

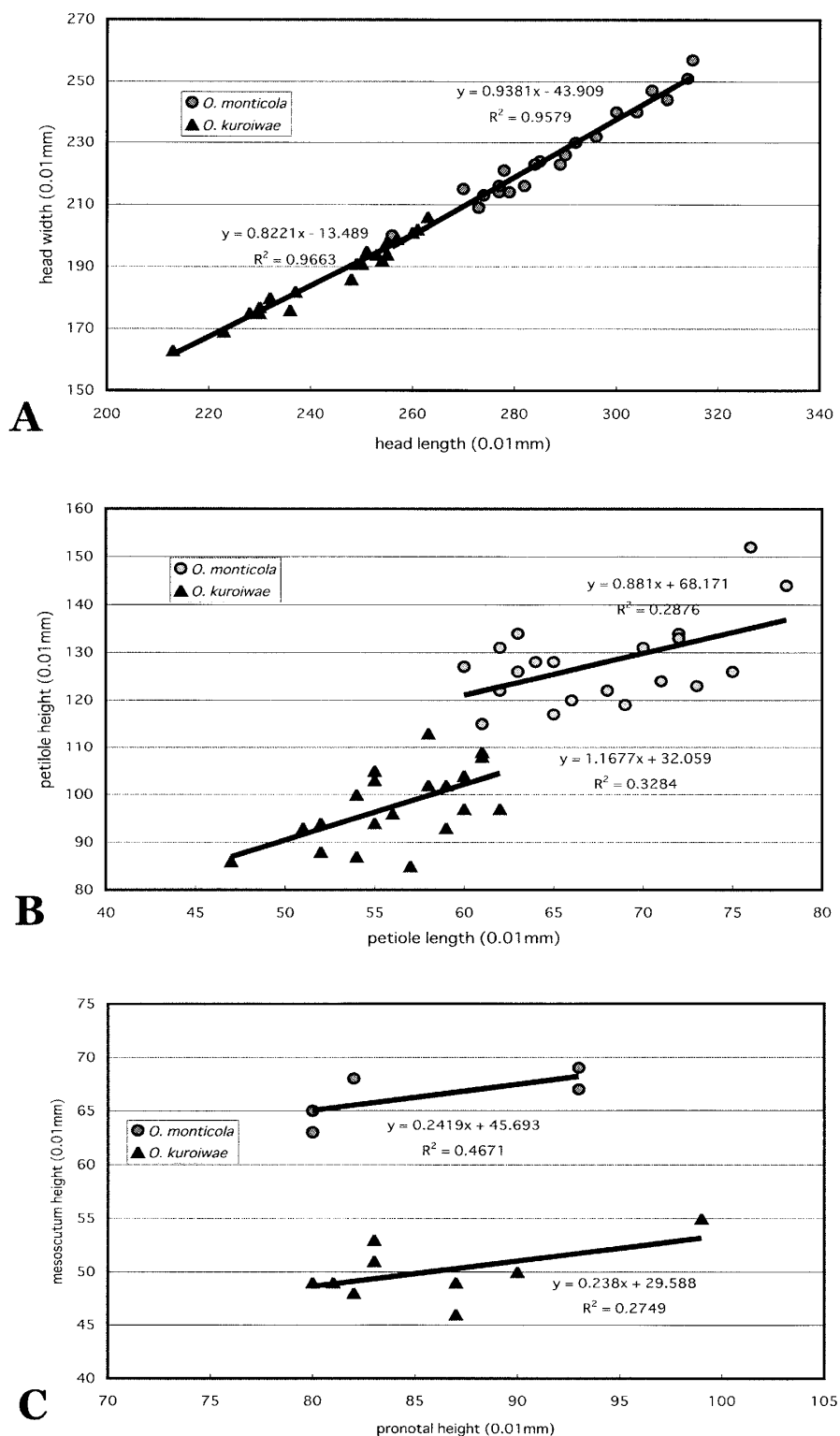


Fig. 10. Relationships and regression lines of the measurements of two *Odontomachus* species. A, HW/HL plots of workers of *O. monticola* and *O. kuroiwa*; B, Pth/PtL plots of workers of *O. monticola* and *O. kuroiwa*; C, Msh/PrH plots of males of *O. monticola* and *O. kuroiwa*. The slopes, intercepts, and  $R^2$  values of the two species are shown in each figure.

Burma as *O. monticola*. In fact, he redescribed the species in a paper that was titled “Ants of Tenasserim and Mount Carin in Burma” (Emery 1895). Therefore, Myanmar (Burma) is the correct type locality of *O. monticola*.

Forel (1912) described *Odontomachus monticola formosae* as a new variety of *O. monticola* on the basis of worker, female, and male morphologies, and he indicated the type localities of this species as Kankan, Pilan, and Kosempo in Formosa (Taiwan). Three dealate females on a single pin and one alate male labeled as “typus” were found in Forel’s collection, but the collection locality of those specimens is indicated as Thaihorin. It can be assumed that those specimens were used for his redescription of the subspecies (Forel 1913). We regard that those dealate females and an alate male are not types of Forel’s (1912) taxon.

There remain some questions concerning the identity of the taxa synonymized under *Odontomachus monticola* (see synonymy). Our direct comparison confirmed several important differences among the type lots of various nominal taxa that were synonymized under *O. monticola* by Yasumatsu (1962) and Brown (1976). The differences in characters mentioned below are concordant with differences in the pattern of surface sculpture, as in the case of *O. monticola* and *O. kuroiwae*. The taxonomic status of the taxa synonymized under *O. monticola* should be reexamined, although the full assessment of these taxa is beyond scope of this paper. Here we follow the synonymy proposed by Yasumatsu (1962) and Brown (1976), although future study may eventually reveal that more than one species are mixed in the current concept of *O. monticola*.

We have confirmed that the circular and transverse forms of pronotal sculpture recognized in *Odontomachus monticola* do not occur as a result of allometry, and that the two forms show particular geographical distribution patterns. The circular form occurs in the western area of species’ range, including Myanmar, Laos, and North Vietnam, and the transverse form occurs in the eastern part of the range, including China, Taiwan, and Japan (Fig. 11). According to the modern concept of species, sympatric distribution demonstrates isolation between two species. We did not confirm the sympatric occurrence of the two forms, but Yunnan in China and northern Vietnam are probably a region of sympatry, or at least parapatry of both of them. In fact, *O. monticola formosae*, originally described as a variety of *O. monticola*, is characterized by fine-transverse sculpture on the pronotal disc (Fig. 2C), while the pronotal sculpture in *O. monticola* s. str. is rough and circular (Fig. 9C, D). Our comparison between types of the two taxa provide two new stable differences: (1) the anterior margin of the pronotal node in lateral view is steeply raised in *O. m. monticola* (Fig. 9A), so a distinct concavity is present on dorsal margin between the node and neck, whereas the anterior margin of the pronotal node is gently raised in *O. m. formosae* (Fig. 2A), so it is continuous with the dorsal margin of the neck; (2) with the head in lateral view, striae are absent in *O. m. monticola* posterior to the extraocular furrow (except for the weak furrow running along the posterior margin of the temporal prominence) (Fig. 9B), whereas those parts are striated in *O. m. formosae*. The syntypes of *O. m. major* have features very close to those of *O. m. formosae*.

In his revision of Chinese *Odontomachus*, Wang (1993) described a new species, *O. circulus*, and distinguished it from *O. monticola* by its possession of circular pronotal sculpture, versus transverse sculpture on the pronotal disc in *O. monticola*. We did not examine these Chinese specimens, but *O. monticola* of Wang (1993)

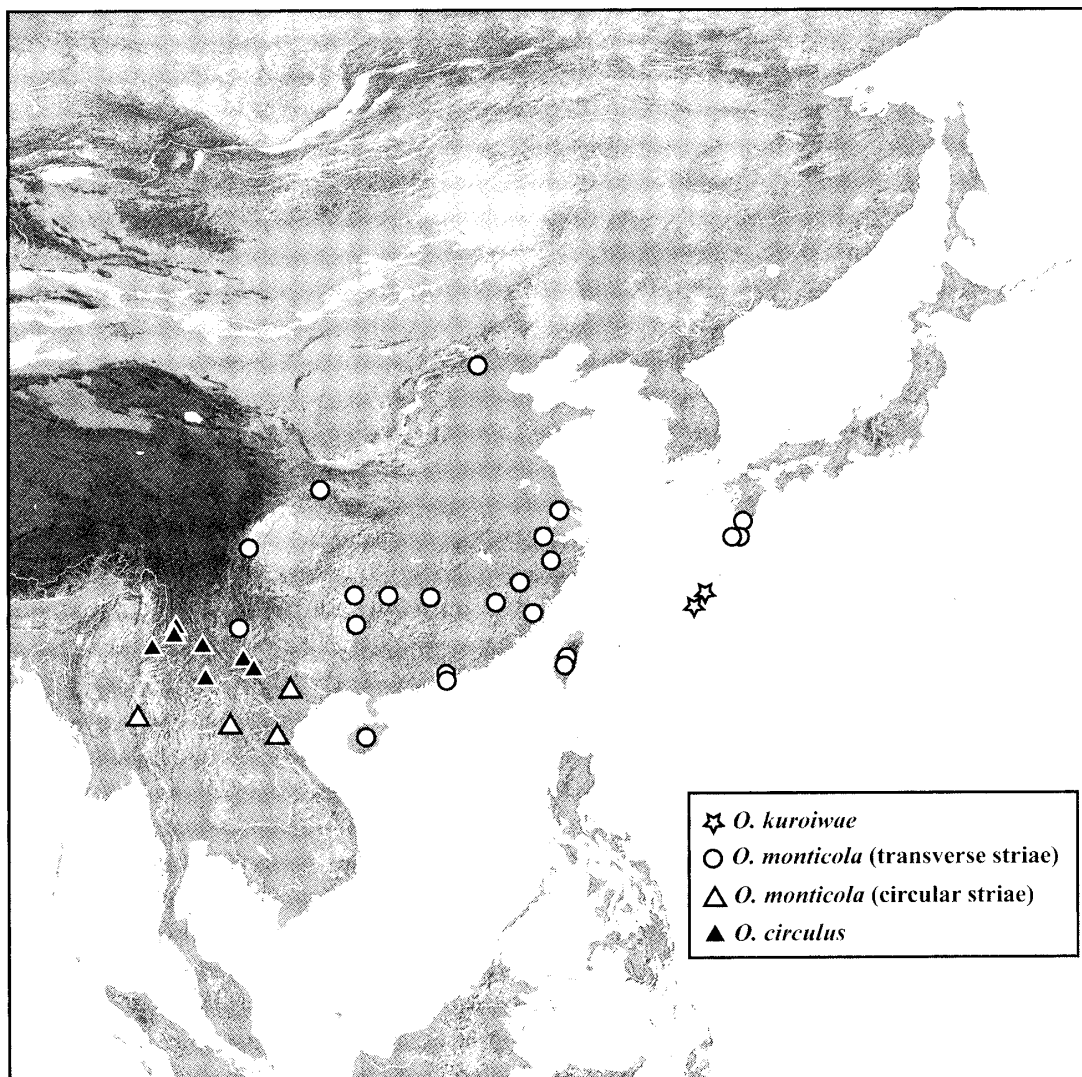


Fig. 11. Distribution map of *Odontomachus kuroiwae*, *O. monticola*, and *O. circulus*.

corresponds to the transverse form of *O. monticola*, and *O. circulus* may well be identical to the circular sculpture form of *O. monticola*. These two Chinese nominal species are parapatrically distributed (Fig. 11).

The holotypes of *Odontomachus punctulatus* and *O. monticola longi* display differences from *O. monticola* sensu Emery (1892, 1895) in the gentle anterior slope of the pronotal node in lateral view. However, materials other than the types are needed to properly decide the taxonomic status of these taxa.

### Discussion

The distributional patterns of *Odontomachus monticola* and *O. kuroiwae* in Japan are worth noting. The islands of the Ryukyus have been thought of as stepping stones between Taiwan and Kyushu or as a transitional zone of Oriental and

Palaeartic elements (e.g., Terayama and Yamane 1999). Our study suggests, however, that the range of *O. monticola* is interrupted by *O. kuroiwa* (Fig. 11). The occurrence of *O. kuroiwa* in Okinawa Island suggests two hypotheses: (1) the species was secondarily replaced north of Okinawa Island by a population of *O. monticola*, or (2) *O. kuroiwa* is a relict species that was once also distributed on the Chinese mainland, to which the Ryukyu Islands were directly connected two million to 1.7 million years ago (Kimura 1996). Terayama and Yamane (1999) suggested that separation by sea is not a very important factor for the distribution of insects, which can cross the sea with aid of their wings or by rafting; however, in this case, the existence of two seaways, the Tokara and Kerama Gaps, around one million years ago or later, seems to have allowed the divergence of *O. kuroiwa* from *O. monticola*. Detailed molecular analysis on the populations of southern Japan, Taiwan, and mainland China may clarify our knowledge on their history.

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