Doctoral Thesis

Taxonomy of the Ant Genus *Odontomachus* (Hymenoptera: Formicidae: Ponerinae) in the Indo-Chinese and Indo-Malayan Subregions

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論 文 名　　インドシナ亜区及びインドマレー亜区におけるアギトアリ属 *Odontomachus*（膜翅目：アリ科：ハリアリ亜科）の分類学的研究（英文）

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Abstract

Ants (Insecta: Hymenoptera: Formicidae) are dominant terrestrial invertebrates, accounting for approximately 10% of total animal biomass in major terrestrial ecosystems of the world, and play various functions in the ecosystems as predator of small invertebrates, mechanical decomposers, seed dispersers, soil mixers, etc. On the other hands, not a few species have been known as invasive species negatively affecting native ecosystems, agriculture, public health and social infrastructure. So, Formicidae is often one of the major target taxon of biodiversity researches and conservation programs, and thus there is a strong need for the species-level classification of Formicidae.

Although species recognition and classification of ants (Insecta: Hymenoptera: Formicidae) had been long conducted almost completely based on the morphology of the worker until recently, in recent years, cryptic species diversity of ants has been increasingly discovered, and many new species have been described using integrated taxonomy. A cryptic species complex is a group of multiple species which are difficult to delimitate from each other based on morphology, but are different biological species. However, species diversity of ants in the tropics and subtropics has not yet been revealed well by integrated taxonomy.

The present study aims to revise the classification of Indo-Chinese and Indo-Malayan species of the ant genus *Odontomachus* (the subfamily Ponerinae) by integrated taxonomy. *Odontomachus* was world-widely and comprehensively revised by Brown (1976) based on the morphology of the worker, and many species and intraspecific names were synonymized. However, his view had been later questioned by some taxonomists (Yoshimura *et al.*, 2007; Satria *et al.*, 2015). Therefore, *Odontomachus* may be a good target taxon for considering usefulness of integrated taxonomy.

In the chapter II, the morphology of male genitalia was microscopically observed and compared among five Sumatran species of *Odontomachus*, and among three species of the *Anochetus rugosus* species group; *Anochetus* is the sister group of *Odontomachus*. The species recognition and classification of ants had been long conducted almost completely based on the morphology of the worker. On the other hands, the morphology of male genitalia has been poorly examined for most of ant taxa despite of male genitalia being likely associated with mechanical reproductive isolation. The present study revealed that remarkable interspecific morphological

differences appear in the male genitalia among multiple species which are very similar to each other in the morphology of the worker, and confirmed the usefulness of male genitalia and associated sclerites for delimitating multiple cryptic species of *Odontomachus* and *Anochetus*.

In the chapter III, species delimitation were revealed by integrated taxonomy consisting of DNA barcoding, molecular phylogenetic analyses, morphological examination and biogeographic consideration, based on a total of 97 specimens of the ant genus *Odontomachus* collected from Indo-Chinese and Indo-Malayan subregions and adjacent areas. Partitioning with 40 MOTUs was proposed by ABGD and PTP analyses based on a dataset of CO1 sequences. Monophyly of each of these MOTUs were then confirmed by Maximum-Likelihood (ML) and Bayesian Inference (BI) phylogenetic trees of COI and 28S gene markers. If a MOTU were paraphyletic toward other MOTU, those MOTUs should be combined into one MOTU. Consequently, those MOTUs were combined into 35. Finally, those 35 MOTUs were combined into 12 species of which each can be recognized with morphological diagnositic characterisitics; 11 of them are found from the Indo-Chinese and/or Indo-Malayan subregions. The present study reconfirm the following previous taxonomic treatments: Yoshimura *et al*. (2007) reviving *Odontomachus kuroiwae* from a synonym of *O. monticola* sensu Brown (1974); Satria *et al*. (2015) reviving *Odontomachus procerus* from a synonym of *O. latidens* sensu Brown (1974); Terayama & Ito (2014) and Satria *et al*. (2015) recognizing *O. pararixosus* and *O. minangkabau*, respectively, as cryptic species of *O. rixosus*. Furthermore, *Odontomachus* sp. 1 is an independent species corresponding to one of the synonyms of *O. monticola*, and *Odontomachus* sp. 2 is new to science.

In the chapter IV, a total of 14 species were recognized in the Indo-Chinese and Indo-Malayan subregions after morphologically examining the specimens of the "species" which were unable to be included in the present integrated taxonomy because of unavailable of fresh specimens suitable for DNA barcoding. Key to species based on the worker, description of the new species (*Odontomachus* sp. 2), redescriptions of 13 species were provided, and three cases of synonyms were solved.

In the chapter V, three distribution patterns of the species, i.e., widely spread (4 species), restricted to the Indo-Malayan subregion (2 species), and endemic to a small geographic range (6 species), were recognized and discussed below. Reliable records, except the original description, were unavailable for the remaining two species.

Future trials of the integrated taxonomy including the morphological examination of male genitalia and numerical morphometry will also found further cryptic species among the arrays of MOTUs. DNA barcode library based on the precise species-level classification provided by the integrated taxonomy may promote us identifying alate ants collected by such traps into species, and obtaining valuable biological information such as seasonal and daily timing of mating flight which should be strongly associated with reproductive isolation and consequently speciation.

The present study is a model case of the taxonomic revisions dealing with highly speciose taxa in the tropics and subtropics.

Contents

Chapter I

General Introduction

I-1. Taxonomic History of the Ant Genus *Odontomachus*

The genus *Odontomachus* was established by Latreille in 1804 with *Formica haematoda* Linnaeus, 1758 as the type species. The genus is currently assigned to the *Odontomachus* genus group in the tribe Ponerini, the subfamily Ponerinae based on the results of a recent molecular phylogenetic analysis (Schmidt, 2013; Schmidt & Shattuck, 2014). Other names have been used by previous authors for this taxon; the synonymys were then resolved by Brown (1976) in his revision of the genus *Odontomachus* of the world. The full synonym list is given in Bolton (2016). The taxonomic history of the genus is summarized in the Table 1-1.

The genus *Odontomachus* is most closely related to the genus *Anochetus* (Schmidt, 2013). The worker caste (non-reproductive female caste, hereafter referred to as "worker") and the queen caste (reproductive female caste, hereafter referred to as "queen") of the two genera share a unique morphological appearance with bizzare head bearing long and straight mandibles at the middle of the anterior margin of head (Schmidt & Shattuck, 2014). However, the genus *Odontomachus* can be easily distinguished from the genus *Anochetus* as follows: nuchal carina of the posterior face of head V-shaped in the former, but roundly arched in the latter (blue arrows in Figs. 1-1C, 1-1D); apophyseal lines well recognized as a pair of dark lines in the former (red arrows in Figs. 1-1A, 1-1C), but unrecognized in the latter; propodeal teeth absent in the former, but usually present in the latter; dorsal apex of petiolar node pointed in the former, but not pointed (variable in shape) in the latter (Schmidt & Shattuck, 2014).

Brown (1976) recognized 51 valid species, and classified them into 12 species groups which are defined well by the morphology of the worker: the *O. assiniensis* group (Afrotropical region), *O. bradleyi* group (Neotropical region), *O. cornutus* group (Brazilian subregion), *O. coquereli* group (Malagasy subregion), *O. haematodus* group (mainly in New World), *O. hastatus* group (Neotropical region), *O. infandus* group (Philippines and Austro-Malayan subregion), *O. mormo* group (Neotropical region), *O. rixosus* group (Indo-Chinese and Indo-Malayan subregions), *O. ruficeps* (Austro-Malayan and Australian subregions), *O. saevissimus* group (Austro-Malayan subregion), and *O. tyrannicus* group (Austro-Malayan subregion). Recently Sorger & Zettel (2011), in their revision of the Philippine *Odontomachus*, established two more species groups which are also defined well by the morphology of the worker: the *O. malignus* group (Indo-Malayan and Austro-Malayan subregions) and *O. silvestrii* group (Indo-Chinese subregion).

Since Brown (1976), several regional revisions and taxonomic notes of the genus have been presented by Wang (1993) (China), Yoshimura *et al*. (2007) (Japan), Wilson (1959) (Melanesia), Fisher & Smith (2008) (Madagascar), Sorger & Zettel (2011) (Philippines), Terayama & Ito (2014) (Malay Peninsula, Malaysia), MacGown *et al*. (2014) (United States), and Satria *et al*. (2015) (Sumatra Island, Indonesia). Currently, a total 72 extant and 3 fossil species of the genus *Odontomachus* are recognized. The majority of the species are known from pantropical and pansubtropical zones, though the Neotropical and Oriental regions seem to be the centers of the species richness. A few species extend into the temperate zones, specifically in the southwestern United States, northeastern China, central Argentina, and southwestern Australia (Schmidt & Shattuck, 2014; Bolton, 2016; Larabee *et al.*, 2016)

I-2. Life History of the Ant Genus *Odontomachus*

The genus *Odontomachus* usually nests in the soil, under leaf litter, under stones, and under rotten logs and stumps, and forages on the ground surface of forests (Brown, 1976; Ito *et al.*, 1996; Satria *et al*., 2015). On the other hand, some species showing “exceptional habitat preferences” were recorded. *O. simillimus* can be found in disturbed areas and sometimes nests under the paved floors around houses; *Odontomachus malignus* inhabits intertidal zones, and nests in the bare limestone in which nest entrances are usually located below the high tide mark (Wilson, 1959; Brown, 1976; Olsen, 2009; Sorger & Zettel, 2011); *O. hastatus* nests arboreally (Camargo & Oliveira, 2012).

The structure of the mouthparts with the linear mandibles in *Odontomachus* and *Anochetus* (Figs. 1A and 1B) is known to be associated with hunting and defending behaviours. During foraging, *Odontomachus* workers usually open and hold their mandibles at 180° (Ehmer and Holldobler, 1996). Whenever a small invertebrate prey touches the trigger hairs standing on the inner margin of mandibles, the mandibles strike will released with extreme force and speed, finally capturing the prey. This spring-loaded mechanism of mandibles is widely known as the “trap-jaws”, and seen exclusively in *Anochetus* and *Odontomachus* in the subfamily Ponerinae, although the genus *Harpegnathos* also has linear mandible, but its mechanism is different from that of *Odontomachus* and *Anochetus* (Gronenberg, 1996; Paul 2001).

Odontomachus species are able to close their mandibles within 0.13 ms with the speed ranging from 35 to 64 m/s. This speed is the fastest ever descibed for any animal taxa (Gronenberg, 1995; Patek *et al.*, 2006; Spagna *et al.*, 2008). The trap-jaw mechanism makes *Odontomachus* spp. a more effective predator, and most of them are generalist predators of arthropods, especially termites (Ehmer & Holldobler, 1995). Although some species are known to have a wide range of food preferences, including honeydew from homopteran insects (Schemske, 1982) and fruits and arils (Pizo & Oliveira, 1998; Passos & Oliveira, 2002, 2003, 2004). The effect of relocation of fruits and removal of the aril by *Odontomachus* likely increases the dipersion and germination success in some plant species. The genus *Odontomachus* has an important role as seed vectors on the floor of tropical forests, with its relatively large size individuals of this genus moved diaspores up to 13 m (Passos & Oliveira, 2003).

The worker and the queen of *Odontomachus* also use mandible snapping for defending themselves. The female adults produce a big sound by snapping their mandible, and fling intruders away from the nest entrance; this behaviour is known as “bouncer defense” (Carlin, 1981; Carlin & Gladstein, 1989). The mandible snapping will also propel the worker’s body into the air known as an “escape jump”, this escape mechanism increase the probability of surviving predatory attacks by this genus (Gronenberg, 1996; Larabee & Suarez, 2015).

I-3. Importance of Integrated Taxonomy

In recent years cryptic species complexes have been increasingly discovered in various animal taxa; a cryptic species complex is a group of multiple species which are difficult to delimitate from each other based on morphology, but are different biological species

(Beheregaray & Caccone, 2007; Bickford *et al*., 2007). Because precise delimitation of different cryptic species is often critical in identification and management of biological resources (Griffiths *et al*., 2009; Rutishauser, 2013;), control of pests, vectors and infectiuous disease agents (Antonini *et* al., 2009; Ashfaq & Herbert, 2016; Paterson *et al.*, 2016), treatment of biotoxins (Palencia *et al*., 2010), this is one of the biggest challenges in modern taxonomy (Bickford *et al*., 2007).

Species recognition and classification of ants (Insecta: Hymenoptera: Formicidae) had been long conducted almost completely based on the morphology of the worker until recently (Bolton, 2003). However, in recent years, the higher classification of ants has been drastically modified by molecular phylogenetic analyses with huge datasets (Lapolla *et al*., 2010; Ward *et al*., 2010; Schmidt & Shattuck, 2014; Ward *et al*., 2015; Borowiec, 2016; Economo *et al*., 2015). At the same time, cryptic species complexes have been increasingly discovered, and many new species have been described (Seifert, 1991, 1992, 1996, 1997, 2003, 2004, 2008; Schlick-Steiner *et al.*, 2005; Schlick-Steiner *et al.*, 2006; Seifert *et al.*, 2009; Yashiro *et al.,* 2010; Klarica *et al*., 2011; Bernasconi *et al.*, 2011; Terayama & Ito, 2014; Seifert *et al.*, 2014; Seifert & Csösz, 2015; Satria *et al.*, 2015). Because, in most ant species, normal mating may not occur without swarming (nuptial flight) and/or sexual calling by virgin queens (Oberstadt & Heinze, 2003), the presence/absence of reproductive isolations among multiple cryptic species is difficult to observed in natural and laboratory conditions. An alternative is the use of "integrated taxonomy" which aims to recognize and delimitate cryptic species by a combination of traditional comparative-morphological examination, DNA barcoding, and, if necessary, other modern analyses, e.g., karyotyping, cuticular hydrocarbon analysis and quantitative morphometry. DNA barcoding was established by Hebert *et al.* (2003) as a method to identify unknown samples by comparing its sequences of standardized gene markers, such as "Folmer Region" of mitochondrial CO1 gene, with the sequence library of identified species, and it is also a powerful method for delimitating multiple putative species within a cryptic species complex. Therefore, in recent years, DNA barcoding has been widely used for taxonomic studies in various animal taxa (e.g., Hebert *et al.*, 2004, for bird; Clare *et al*., 2007 for bat; Hajibabaei *et al.*, 2006, for butterflies; Ekrem *et al.*, 2007, for non-biting midgets (Chironomidae); Trivedi *et al*., 2016 for reptilia; Vences *et al*., 2005 for amphibians; Lakra *et al.,* 2011 for fishes; Wong *et al*., 2009 for sharks; Bitanyi *et al*., 2011 for antelops; Fennesy *et al*., 2016). However, precise recognition of multiple species within cryptic species complexes can not be always achieved with DNA barcoding alone (e.g., Meyer & Paulay, 2005 for cowries or cypraeid marine gastropods; Wiemers & Fiedler, 2007 for blue butterflies; Elias *et al.*, 2007 for tropical butterflies). It is partly because intra- and interspecific variations in the sequences are often largely overlapped (Meyer & Paulay, 2005).

Cryptic species diversity has been successfully revealed using integrated taxonomy in various ant taxa: *Acropyga* by Blaimer *et al*. (2016), *Amyrmex* by Ward & Brady (2009), *Anochetus* and *Odontomachus* by Fisher & Smith (2008); Satria *et al*. (2015), *Cardiocondyla* by Seifert (2008), *Colobopsis* and *Dinomyrmex* by Ward *et al*. (2016), *Formica* by Seifert (1992, 1996, 1997) and Bernasconi *et al*. (2011); *Lasius* by Seifert (1991); *Leptanilloides* by Ward (2007), *Leptogenys* by Lattke (2011), *Melophorus* by Andersen *et al*. (2016), *Messor* by Schlick-Steiner, Steiner, Konrad *et al.* (2006); *Myrmica* by Seifert *et al*. (2009), *Nylanderia* by Zhao *et al*. (2012), *Tetramorium* by Schlick-Steiner, Steiner, Moder *et al.* (2006), etc. Furthermore, integrated taxonomy may reveal the proper combination among castes, subcastes and/or sexes, and solve the synonymies.

As mentioned above, the genus *Odontomachus* was world-widely and comprehensively revised by Brown (1976) based on the morphology of the worker. He is a so-called "lumper", that is to say that he conservatively delimitate species and synonymized many species names into one. His view had been later questioned by some taxonomists. Yoshimura *et al*. (2007) revised East Asian populations of the genus based on morphological characters, including those of the male genitalia, and then revived *O. kuroiwae* which was synonymized by Brown (1976) under *O. monticola*. Satria *et al*. (2015) revised Sumatran populations of the genus by morphology and DNA barcoding, and revived *O. procerus* which was synonymized by Brown (1976) under *O. latidens*. Terayama & Ito (2014), based on morphological characters of the worker and phenotypes of the queen, deliminated a cryptic species, *O. pararixosus*, in *O. rixosus* sensu Brown (1976). These facts suggest that the species diversity of the genus *Odontomachus* has not yet been fully revealed, despite their large-sized body, bizzare habitus, and dominance in the ground-dwelling ant faunas.

I-4. Purposes of the Present Research Project

In the present study I focus on the Indo-Chinese and Indo-Malayan species of the genus *Odontomachus*, and clarify usefulness of male genitalia in uncovering cryptic species (Chapter II), delimitate the species by integrated taxonomy (Chapter III), and describe/redescribe the species and made necessary taxonomic treatments (Chapter IV).

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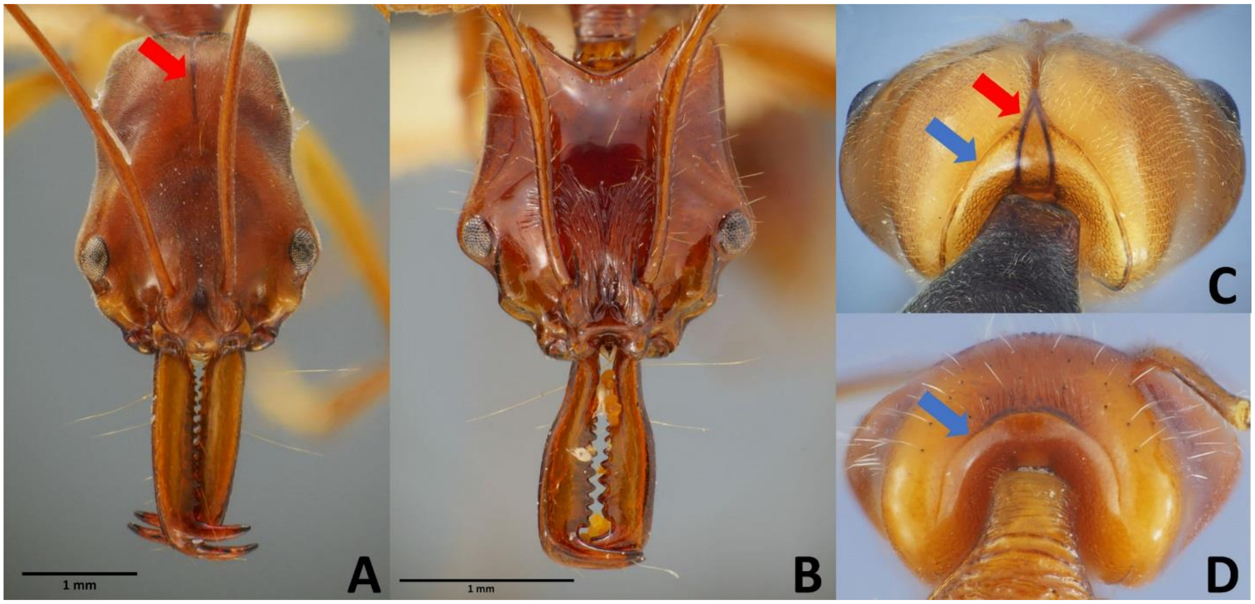

Figure 1-1. Head of the worker in full-face view (A, B) and in posterior view (C, D). A, *Odontomachus*, with a red arrow indicating median furrow; B, *Anochetus*; C, *Odontomachus,* with a red arrow indicating apophyseal lines and a blue arrow indicating nuchal carinae; D, *Anochetus*, with a blue arrow indicating nuchal carinae.

Table 1-1. Taxonomic history of the genus *Odontomachus*

Year	Major Events	References
1804	The genus *Odontomachus* established	Latreille, 1804
1835	Placed in the tribe Ponérites	Lepeletier de Saint-Fargeau, 1835
1857	Placed in the subfamily Poneridae	F. Smith,1857
1862	Placed in the subfamily Odontomachidae	Mayr, 1862
1905	Changed Odontomachidae as family	Ashmead, 1905
1893	Placed in the subfamily Ponerinae, the family Formicidae	Dalla Torre, 1893
1893	Placed in the tribe Odontomachini	Forel, 1893
1976	Placed in the subtribe Odontomachiti, the tribe Ponerini	Brown, 1976
2014	Places in the *Odontomachus* genus group of the tribe Ponerini, the subfamily Ponerinae, the family Formicidae	Schmidt & Shattuck, 2014

Chapter II

Usefulness of Male Genitalia in Uncovering Cryptic Species of the Ant Genera *Odontomachus* and *Anochetus* (Hymenoptera: Formicidae: Ponerinae)

II-1. Introduction

The family Formicidae, so-called "ants", is a monophyletic taxon belonging to the superfamily Vespoidea of the order Hymenoptera (Goulet & Huber, 1993), and consists of a total of 15,431 named species (Bolton, 2016; Antwiki, 2017). The species recognition and classification of ants had been long conducted almost completely based on the morphology of the worker (non-reproductive female caste), because workers are active outside their hidden nests, and thus they are able to be found and captured more easily than queens and males. On the other hand, the male has been described for just 27% of the named species of ants (Boudinot, 2015). However, it is likely that the male has taxonomically important morphological characters, because the morphology of the male is usually quite different from the two female castes, the worker and the queen (reproductive female caste) (Yoshimura & Onoyama, 2002; Boudinot, 2015). Special attention should be also paid to the morphology of male genitalia because it is likely to be associated at least partly with mechanical reproductive isolation.

Recently Boudinot (2013) comprehensively examined the morphology of the male genitalia of Formicidae, and provide diagnostic characteristics of the major lineages. Terminology of male genitalia revised by him is now widely accepted by myrmecologists. On the other hand, usefulness of the morphology of male genitalia in uncovering cryptic species has been increasingly reported, e.g., Western Palearctic *Tetramorium* (Myrmicinae) by Schlick-Steiner *et al.* (2006); Iberian *Cataglyphis* (Formicinae) by Tinaut (1990); Oriental and Australian *Tetraponera* (Pseudomyrmecinae) by Ward (2001); Greater Antilles and Central American *Zatania* (Formicinae) by LaPolla *et al.* (2012).

Therefore, as a part of my comprehensive taxonomic revision of *Odontomachus* and *Anochetus*, the present study aims to clarify usefulness of male genitalia in uncovering cryptic species by focusing on Sumatran species of *Odontomachus* and the *Anochetus rugosus* group.

II-2. Materials and Methods

II-2-1. Material Examined

II-2-1-1. The five species of Sumatran *Odontomachus*

Odontomachus latidens Mayr, 1867: Indonesia: Sumatra: Aceh: Leuser Ecosystem (ca. 1100 m alt.), 20.IX.2012, R. Satria leg., 1 male (colony: GK-38-12; individual: SEMUT141225E).

Odontomachus minangkabau Satriat *et al.*, 2015: Indonesia: West Sumatra: Padang: Andalas University Forest, Robby J. leg., 22.IX.2014, 1 paratype male (colony: RS01-PDG-14; individual: SEMUT150101A).

Odontomachus procerus Emery, 1893: Indonesia: West Sumatra: 50 Kota District, Mt. Sago (ca. 1000 m alt.), 06.IX.2012, R. Satria leg., 1 male (colony: SAGO-01-12; individual: SEMUT141215B).

Odontomachus rixosus F. Smith, 1857: Indonesia: Bali: Jembrana District: Pekutatan: Pulukan, 23.X.2012, R. Satria leg., 2 males (colony: PKN-01-12; individual: SEMUT150103A, SEMUT150224D).

Odontomachus simillimus F. Smith, 1858: Indonesia: Bali: West Bali: Mendaya: Dusun PK Jelati, 05-06.V.1998, R. Satria leg., 1 male (colony: PKJ-27-12; individual: SEMUT141217C).

II-2-1-2. *Anochetus rugosus* Group

Anochetus rugosus group were proposed by Brown (1978) based on the following diagnostic charasteristics in the worker: mandible with a single margin bearing a series of prminent teeth ; mesonotal disc with a raised anterior rim; and petiole in frontal view bluntly pointed or narrowly rounded at apex. Satria *et al.* (2017) revised the groups, and recognized four species based on morphology: *A. muzziolii* Menozzi, 1923; *A. mixtus* Radchenko, 1993; *A. princeps* Emery, 1884; *A. rugosus* (F. Smith, 1857). Males of the following three species were examined in the present study (the male of *A. muzziolii* is still unknown).

Anochetus mixtus Radchenko, 1993: Vietnam: Hanoi: Ba Vi N.P., 21°04'33"N, 105°22'02"E, ca. 710 m alt., 29.II.2016, R. Satria leg., 2 males (colony: RS-100-BV16; individual: SEMUT20160520A, SEMUT20160525H).

Anochetus princeps Emery, 1884: Vietnam: Dak Lak: Chu Yang Shin N.P.: Area 1359, 12˚23'02.5"N, 108˚20'41.7"E, ca. 1268 m alt., 04.III.2016, R. Satria leg., 2 males (colony: RS-10-CYS16; individual: SEMUT20160701A, SEMUT20160525I).

Anochetus rugosus (F. Smith, 1857): Indonesia: West Sumatra: Pasaman: Rimbo Panti, 6.IV.2014, R. Satria leg. leg., 2 males (colony: RS02-PAS-14; individual: SEMUT20160711B, SEMUT20160627A).

II-2-2. Specimen Preparation, Observation and Imaging

The genitalia of each male preserved in 80% ethanol were slide-mounted by following the steps below. The apical part of the gaster, including the genitalia, was cut off and washed with ca. 500 µL TE (pH 8.0) in a sterile disposable dish. The gastral apex was then transferred into 105 µL of dissolving buffer [100 µL of 10% Chelex-TE solution and 5 µL Qiagen Proteinase K (Qiagen, Germany)], and incubated at 56˚C for ca. 24−27 hours, then heated at 99˚C for 10 minutes to inactivate the Proteinase K. The apical part of the gaster was then picked up using a sterile disposable inoculating loop and transferred into a 1.5 mL microcentrifuge tube filled with in 99% ethanol for dehydration, and then male genitalia was separated from unnecessary parts and cleaned in a small dish filled with 99% ethanol. The genitalia were dissected into several main components using forceps in a small amount of Euparal (WALDECK GmbH & Co. KG) on a slide glass, and covered with a coverslip. These slide-mounted specimens were examined with a Nikon Eclipse E600 microscope and Nikon SMZ1270 stereo microscope.

Multi-focused montage images were produced using Helicon Focus Pro (Helicon Soft Ltd., http://www.heliconsoft.com/) from a series of source images taken by a Panasonic Lumix DMC-GX8 and Canon EOS KissX5 digital camera attached to a Nikon ECLIPSE E600 microscope. Artifacts/ghosts and unnecessary parts (unfocused appendages, insect pin, etc.) surrounding or covering target objects were erased and cleaned up using the retouching function of Helicon Focus Pro, and the color balance, contrast and sharpness were adjusted using Adobe Photoshop CS6.

Morphological terminology follows Boudinot (2013) and Yoshimura & Fisher (2011).

II-3. Results

II-3-1. Male Genitalia of Five Sumatran Species of *Odontomachus*

Odontomachus minangkabau was described by Satria *et al*. (2015) as a cryptic species of *O. rixosus*; the two species were very similar to each other in the morphology of the worker and queen except of the body size, the striation near the median furrow and striation on the pronotal disc (see also Chapter IV). The validity of the species-level status of *Odontomachus minangkabau* was well supported by the morphologhy of male genitalia: posterior spine of abdominal tergite VIII long and slender, weakly curved in *O. minangkabau* (Fig. 2-2D), and very weakly curved in *O. rixosus* (Fig. 2-2C); apical lobe of abdominal sternite IX much longer than disc, and slightly narrowed in basal half, with apical margin weakly convex in *O. minangkabau*, and gently tapering to almost truncate apex in *O. rixosus*; telomeral apex in lateral view much longer than high in *O. minangkabau*, and longer than high in *O. rixosus*; ventral margin of valviceps with 28–29 denticles in *O. minangkabau*, and with 21−22 denticles in *O. rixosus*.

Emery (1893) described *O. latidens* subsp. *procerus* from the Malay Peninsula based on the queen, and then Emery (1900) described *O. latidens* subsp. *sumatranus* from Sumatra based on the worker and queen. Both of the two forms were regarded as varieties of *O. latidens*, and were synonymized by Brown (1976) with the nominotypical subspecies of *O. latidens* (type locality: Java). Later, however, Satria *et al*. (2015) treated *O. latidens* and *O. procerus* as valid species, but *O. latidens* subsp. *sumatranus* as junior synonym of *O. procerus*. Their treatments were also suported by the morphology of male genitalia: the posterior spine of abdominal tergite VIII short and thick, very weakly curved in *O. latidens*, but long, slender and very weakly curved in *O. procerus*; disc of abdominal sternite IX not clearly differentiated from apical lobe, gradually merging into apical lobe, with basal margin almost straight in *O. latidens*, but the disc almost circular, much longer than apical lobe in *O. procerus*. The descriptions of the male genitalia of the five Sumatran species of *Odontomachus* were given below.

***Odontomachus latidens* Mayr, 1867** (Figs. 2-1A, 2-2A−C)

Posterior spine of abdominal tergite VIII short and thick, very weakly curved (Fig. 2-2A); pygostyle digitiform, with long setae in apical 2/3; disc of abdominal sternite IX not clearly differentiated from apical lobe, gradually merging into apical lobe, with basal margin almost straight; apical lobe gently tapering apicad, with apical margin truncated; telomeral apex in lateral view longer than high; distiventral apex of valviceps weakly produced; basiventral corner of valviceps not produced; ventral margin of valviceps with 27−30 denticles.

***Odontomachus minangkabau* Satria *et al*., 2015** (Figs. 2-1B, 2-2D−F)

Posterior spine of abdominal tergite VIII long and slender, weakly curved (Fig. 2-2D); pygostyle with long setae in its apical third; disc of abdominal sternite IX much broader than long, with posterolateral corner expanding laterad and posterolateral corner distinctly angled; apical lobe much longer than disc and slightly narrowed in basal half, with apical margin weakly convex; telomeral apex in lateral view much longer than high; distiventral apex of valviceps strongly produced; basiventral corner of valviceps distinctly produced; ventral margin of valviceps with 28–29 denticles.

***Odontomachus procerus* Emery, 1893** (Figs. 2-1C, 2-2B, 2-2G−I)

Posterior spine of abdominal tergite VIII long and slender, very weakly curved (Fig. 2-2B); pygostyle with long setae in its apical 2/3; disc of abdominal sternite IX almost circular, much longer than apical lobe, of which almost parallel lateral margins and weakly convex apex; telomeral apex in lateral view longer than high; distiventral apex of valviceps weakly produced; basiventral corner of valviceps not produced; ventral margin of valviceps with 27–31 denticles.

***Odontomachus rixosus* F. Smith, 1857** (Figs. 2-1D, 2-2J−L)

Posterior spine of abdominal tergite VIII long and slender, very weakly curved (Fig. 2-2C); pygostyle with long setae in its apical third; disc of abdominal sternite IX much broader than long, with posterolateral corner expanding laterad; apical lobe much longer than disc and gently tapering to almost truncate apex; telomeral apex in lateral view longer than high; distiventral apex of valviceps strongly produced; basiventral corner of valviceps distinctly produced; ventral margin of valviceps with 21−22 denticles.

***Odontomachus simillimus* F. Smith, 1858** (Figs. 2-1E, 2-2M−O)

Posterior spine of abdominal tergite VIII long and slender, very weakly curved (but variable in shape within species) (Fig. 2-2E); pygostyle digitiform, with long setae in apical half; disc of abdominal sternite IX broader than long, almost as long as apical lobe, with straight basal margin; apical lobe slightly narrower in basal half, with apical margin weakly convex; telomeral apex in lateral view as long as high; distiventral apex of valviceps strongly produced; basiventral corner of valviceps distinctly produced; ventral margin of valviceps with 34–36 denticles.

II-3-2. Male Genitalia of Three Species of the *Anochetus rugosus* Group

Anochetus mixtus, *A. princeps* and *A. rugosus* were distinguished well from each other in the morphology of male genitalia: abdominal sternite IX much longer than broad with obtuse posterolateral corners in *A. mixtus*, much longer than broad, without posterolateral corners in *A. princeps*, and slightly longer than broad, without posterolateral corners in *A. rugosus*; dorsal outline of paramere weakly convex in *A. mixtus* and *A. princeps*, and straight, gradually sloping downward to angulate distidorsal part in *A. rugosus*; distiventral part of valviceps produced but shorter than broad, truncate distally in *A. mixtus*, forming an acute, pointed and slightly downcurved projection which is much longer than broad in *A. princeps*, and forming a subrectangular lobe which is longer than broad in *A. rugosus*; valviceps with 23−24 denticles on the ventral margin in *A. mixtus*, with 13−14 denticles on the ventral margin, and with ca. 10 denticles on the dorsodistal margin in *A. princeps*, and with 19 denticles on the strongly concave ventral margin and 9 denticles on the distal margin of the lobe in *A. rugosus*. The descriptions of the male genitalia of the three *Anochetus* species were given below.

***Anochetus mixtus* Radchenko, 1993** (Figs. 2-3A−C)

Abdominal tergite VIII without a median spine; abdominal sternite IX longer than broad, triangular, tapering toward subrectangular apex, with obtuse but distinct posterolateral corners; dorsal outline of paramere weakly convex; distiventral part of valviceps produced but shorter than broad, truncate distally; ventral margin of valviceps very weakly concave, with 23−24 denticles; distal and dorsal margins straight, without denticles.

***Anochetus princeps* Emery, 1884** (Figs. 2-3D−F)

Abdominal tergite VIII without a median spine; abdominal sternite IX longer than broad, triangular, tapering toward subrectangular apex, without posterolateral corners; dorsal outline of paramere weakly convex; distiventral part of valviceps forming an acute, pointed and slightly downcurved projection which is much longer than broad; ventral margin to the apex of projection weakly concave, with 13−14 denticles; dorsodistal margin to the apex very weakly sinuate, with ca. 10 denticles.

***Anochetus rugosus* (F. Smith, 1857)** (Figs. 2-3G−I)

The abdominal tergite VIII without a median spine; abdominal sternite IX slightly longer than broad, triangular, tapering toward subrectangular apex, without posterolateral corners; dorsal outline of paramere straight, gradually sloping downward to angulate distidorsal part; distiventral part of valviceps forming a subrectangular lobe which is longer than broad; ventral margin of valviceps to the anterodistal corner of the lobe strongly concave, with 19 denticles; distal margin of the lobe very short and straight, with 9 denticles; dorsodistal margin of valviceps weakly sinuate, without denticles.

II-4. Discussion

In *Odontomachus* many species-level diagnostic charateristics are present in abdominal tergite VIII, abdominal strenite IX and paramere, and often very useful for deliminating multiple species which are very similar to each other in the morphology of the female castes, i.e., the worker and the queen (the present study; Yoshimura *et al.*, 2007; MacGown *et al.*, 2014). However, the valviceps seems to be less useful for deliminating the five Sumatran species (the present study), but alternative results were obtained by MacGown *et al.* (2014) from Nearctic species of *Odontomachus*.

In *Anochetus*, many species-level diagnostic charateristics are present in abdominal sternite IX, paramere and valviceps. The shape of valviceps of this species group is extremely useful for deliminating multiple species which are very similar to each other in the morphology of the female castes. For example, the shape of valviceps is qualitatively quite different between *Anochetus mixtus* and *A. princeps* (Figs. 2-3C, 2-3F).

As a conclusion, the usefulness of male genitalia and associated sclerites for delimitating multiple cryptic species of *Odontomachus* and its sister group, *Anochetus*, was confirmed by the present study as well as a few previous studies. Therefore, the integrated taxonomy including the morphological examination of male genitalia should be effective for comprehensively revising the species delimitation of *Odontomachus* (see the chapter I and III).

Alate ants (males and newly emerged queens) collected by malaise traps, light traps, etc. have been usually ignored in biodiversity assessments and inventries, and have not been used in taxonomic studies of ants because alate ants, especially males, can not be sorted and identified precisely into species based on the morphology if the conspecific male-worker-queen comprementarity is unknown. However, DNA barcode library based on the precise species-level classification provided by the integrated taxonomy may promote us identifying alate ants collected by such traps into species, and obtaining valuable biological information such as seasonal and daily timing of mating flight which should be strongly associated with reproductive isolation and consequently speciation (Torres *et al.*, 2001; Kaspari, Pickering & Windsor, 2001; Kaspari, Pickering, Longino & Windsor, 2001; Feitosa *et al.*, 2016).

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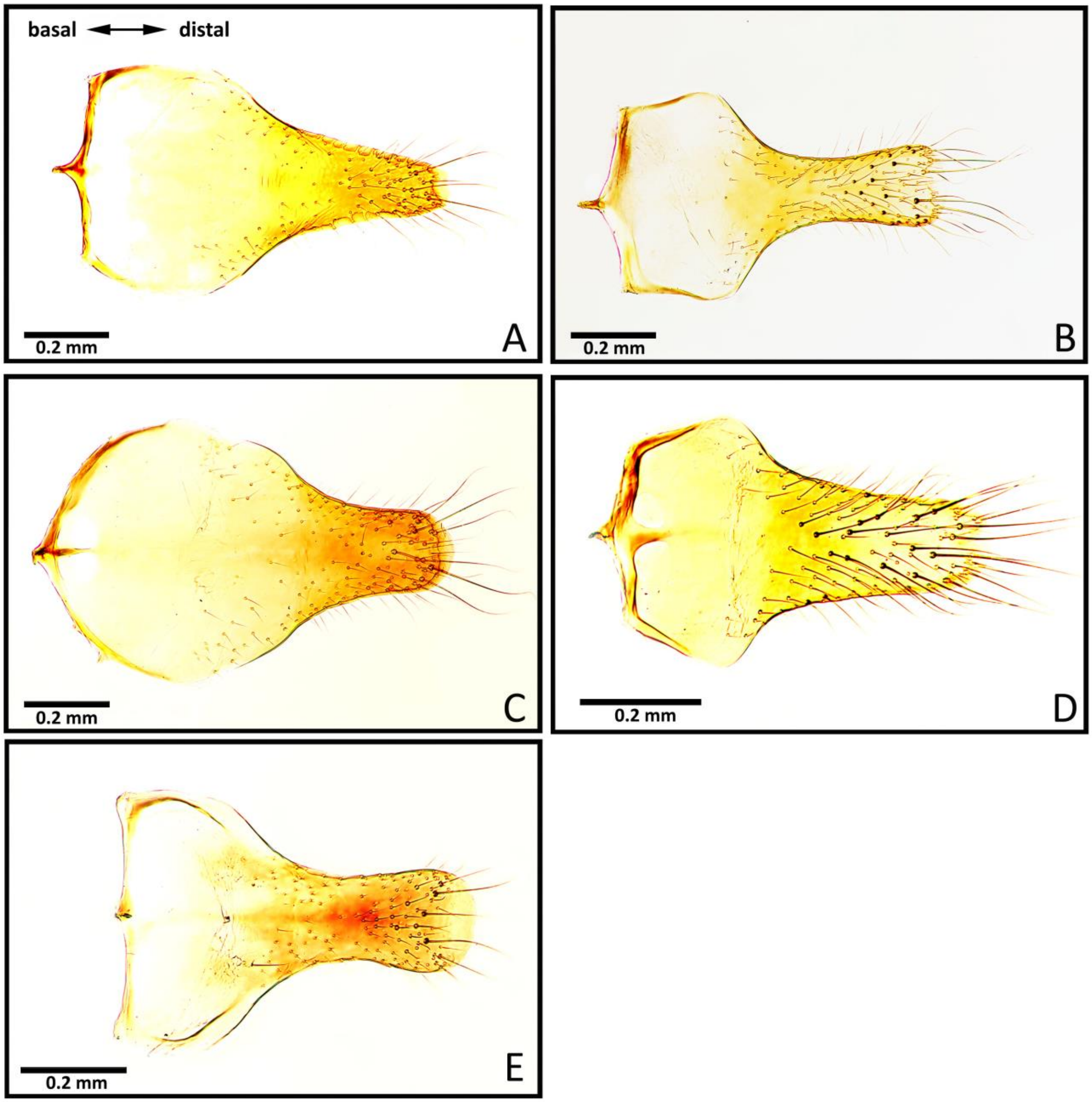

Figure 2-1. Male *Odontomachus*, abdominal sternite IX, ventral view: A, *O. latidens* Mayr, arrows indicating direction (GK-38-12; SEMUT150224E); B, *O. minangkabau* Satria *et al*. (paratype; RS01-PDG-14; SEMUT150224A); C, *O. procerus* Emery (SAGO-01-12; SEMUT150224B); D, *O. rixosus* F. Smith (PKN-01-12; SEMUT150224D); E, *O. simillimus* F. Smith(colony: PKJ-33-12; individual: SEMUT150224C).

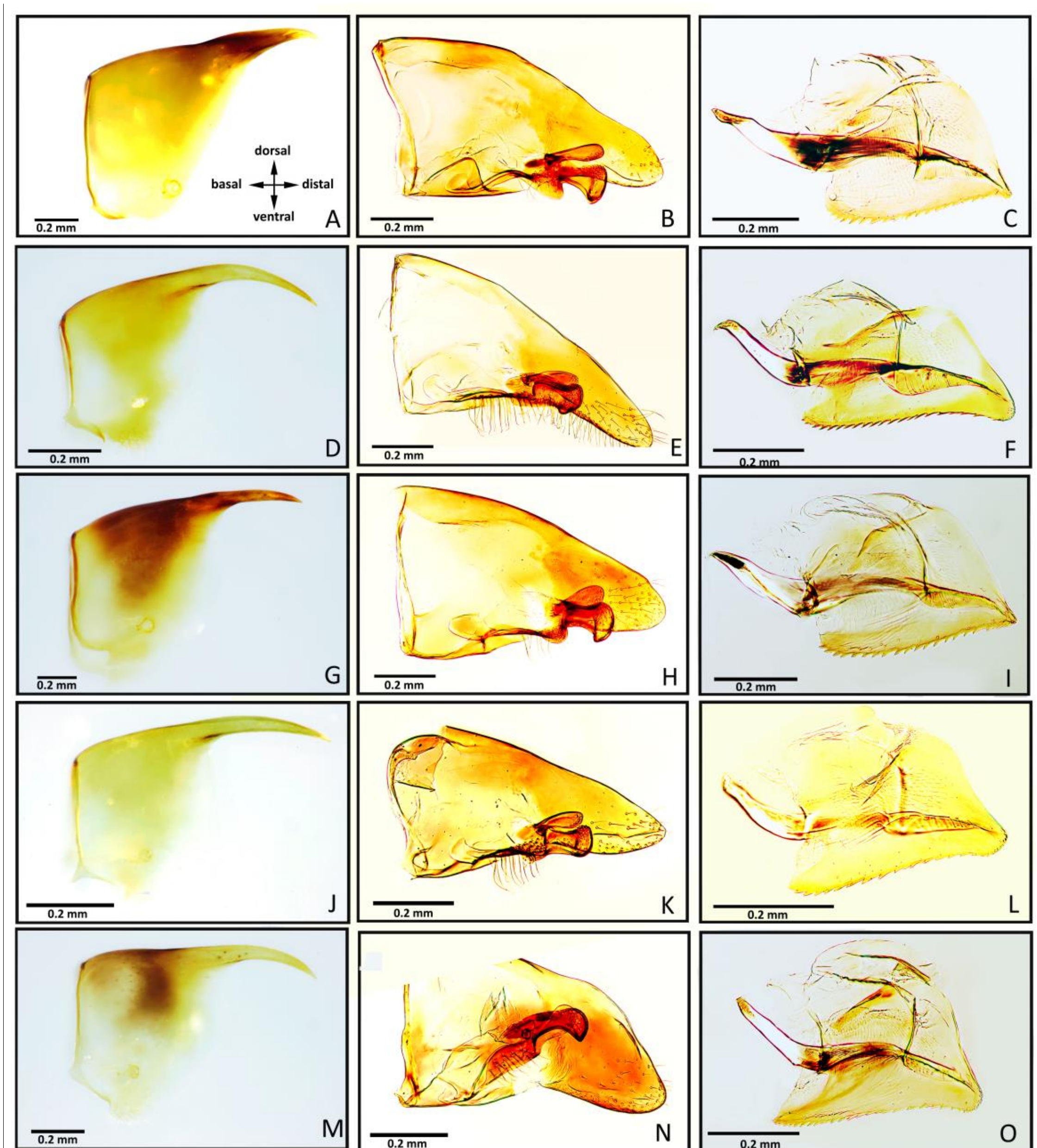

Figure 2-2. Male *Odontomachus*, with arrows in A indicating direction: A, D, G, J, M, abdominal tergite VIII, lateral view; B, E, H, K, N, paramere and volsella, right-hand side, inner view; C, F, I, L, O, penisvalvae right-hand side, inner view. A, B, C, *Odontomachus latidens* Mayr (GK-38-12; SEMUT150224E); D, E, F, *Odontomachus minangkabau* Satria *et al*. (paratype; RS01-PDG-14; SEMUT150224A); G, H, I, *Odontomachus procerus* Emery (SAGO-01-12; SEMUT150224B); J, K, L, *Odontomachus rixosus* F. Smith (PKN-01-12; SEMUT150224D); M, N, O, *Odontomachus simillimus* F. Smith (colony: PKJ-33-12; individual: SEMUT150224C).

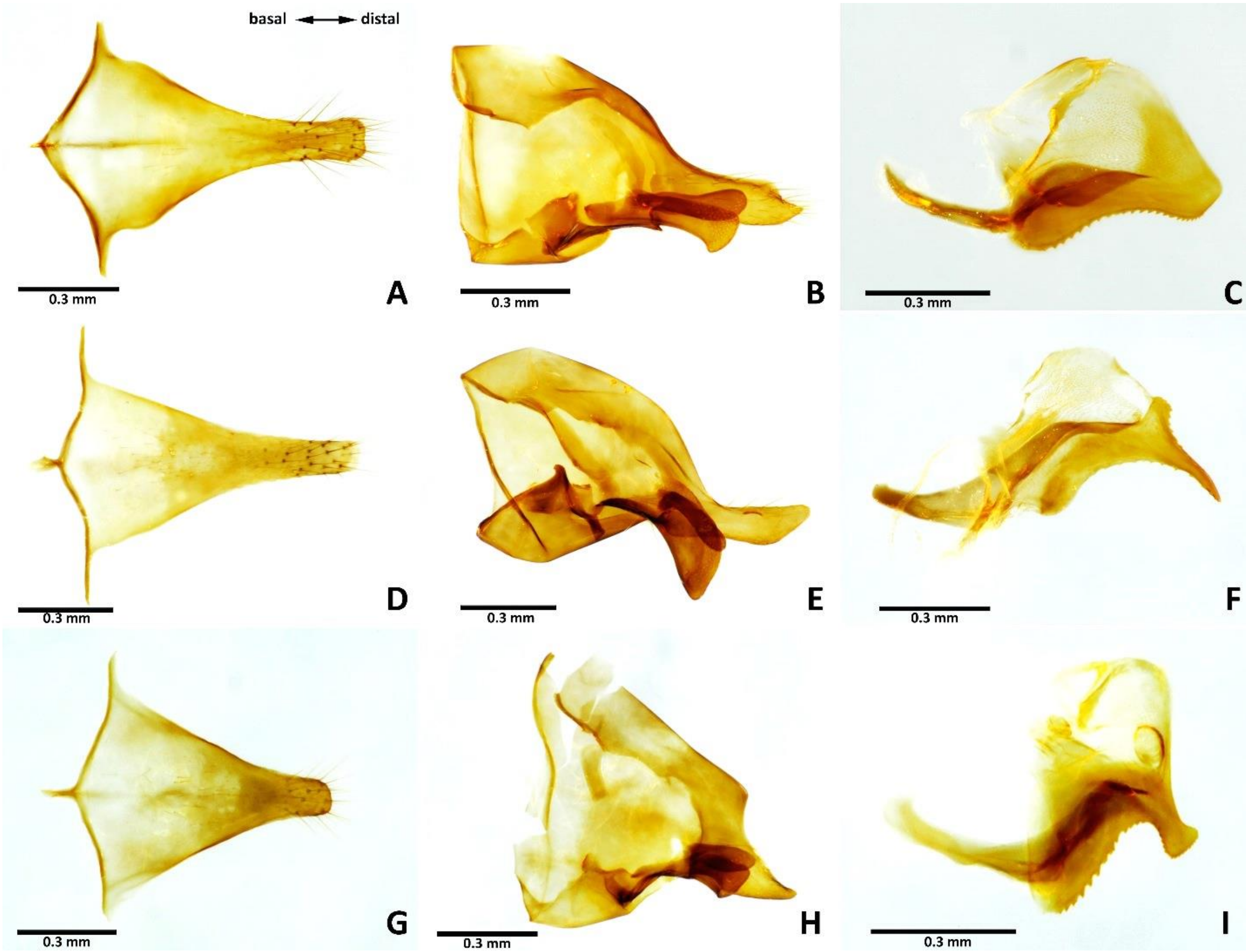

Figure 2-3. Male *Anochetus*, with arrows in A indicating direction: A, D, G, abdominal sternite IX, ventral view; B, E, H, paramere and volsella, right-hand side, inner view; C, F, I, penisvalvae, left-hand side, outer view; A−C, *Anochetus mixtus* Radchenko (colony: RS-100-BV16; individual: SEMUT20160525H); D−F, *Anochetus princeps* Emery (colony: RS-39-CYS16; individual: SEMUT20160525I); G−I, *Anochetus rugosus* (F. Smith) (colony: RS02-PAS-14; individual: SEMUT20160627A).

Chapter III

Delimitation of the Indo-Chinese and Indo-Malayan Species of the Genus *Odontomachus* by "Integrated Taxonomy"

III-1. Introduction

III-1-1. Taxonomy and Cryptic Species

Taxonomy is the science dedicated to recognizing species in nature, to describe and name them, and to improve the classification in which every species are hierarchically arranged. Identification is a practical aspect of taxonomy, i.e., to examine features of a specimen in your hand and to know its scientific name (at species-level or higher-taxonomic-level) by referring to the classification in which knowledge of named species has been accumulated and archieved. Therefore, without taxonomy and identification, biologists will be unable to report their findings, or obtain and exchange the scientific information on their target organisms.

The species is the basic unit in taxonomy, and the "biological species concept" (Mayr, 1942) is now widely accepted by taxonomists. On the other hand, taxonomists have recognized species mostly or completely based on comparative morphological approach until recently. This is partly because their available sources of information were usually dead specimens in museum collections. However, since DNA sequencing has become a common technique, cryptic species complexes have been increasingly discovered in various animal taxa; a cryptic species complex is a group of multiple species which are difficult to differentiated from each other based on morphology, but are different biological species (Beheregaray & Caccone, 2007; Bickford *et al.*, 2007). Precise species delimitation is critical in discovery and management of biological resources (Griffiths *et al*., 2009; Rutishauser, 2013), effective control of pests, vectors and infectiuous disease agents (Antonini *et al.,* 2009; Ashfaq & Herbert, 2016; Paterson *et al*., 2016), treatment of biotoxins (Palencia *et al*., 2010), etc., and thus is one of the biggest challenges in modern taxonomy (Bickford *et al*., 2007).

III-1-2. Usefulness of "Integrated Taxonomy" for Uncovering Cryptic Species Complexes in Ants

The species recognition and classification of ants (Insecta: Hymenoptera: Formicidae) has been long conducted almost completely based on the morphology of the worker until recently (Bolton, 2003). However, in recent years, the higher classification of ants has been drastically modified by phylogenetic analyses with huge molecular datasets (Lapolla *et al*., 2010; Ward *et al*., 2010; Schmidt & Shattuck, 2014; Ward *et al*., 2015; Borowiec, 2016; Economo *et al*., 2015). At the same time, cryptic species complexes have been increasingly discovered, and many new species have been described (Seifert, 1991, 1992, 1996, 1997, 2003, 2004, 2008; Seifert *et al.*, 2009; Schlick-Steiner, Steiner, Konrad *et al.*, 2006; Schlick-Steiner, Steiner, Moder *et al.*, 2006; Yashiro *et al.,* 2010; Klarica *et al*., 2011; Bernasconi *et al.*, 2011; Seifert *et al*., 2014; Terayama & Ito, 2014; Seifert & Csösz, 2015; Satria *et al.*, 2015). Because in most ant species, normal mating may not occur without swarming (nuptial flight) and/or sexual calling by virgin queens (Oberstadt & Heinze, 2003), the presence/absence of reproductive isolations among multiple cryptic species is hardly observed in natural and laboratory conditions. An alternative is the use of the "Integrated Taxonomy" which aims to recognize and delimitate cryptic species by a combination of traditional morphological examination, DNA barcoding, and, if necessary, other modern analyses, e.g., karyotyping, cuticular hydrocarbon analysis and quantitative morphometry.

DNA barcoding was established by Hebert *et al.* (2003) as a method to identify unknown samples by comparing sequences to standardized gene markers, such as the "Folmer Region" of mitochondrial CO1 gene, with the sequence library of identified species. It is also a powerful method for delimitating multiple putative species within a cryptic species complex. Therefore, in recent years, DNA barcoding has been widely used for taxonomic studies in various animal taxa (e.g., Bitanyi *et al*., 2011, for antelops; Fennesy *et al*., 2016, for giraffes;

Clare *et al*., 2007, for bats; Hebert *et al.*, 2004, for birds; Trivedi *et al*., 2016, for reptilia; Vences *et al*., 2005, for amphibians; Wong *et al*., 2009, for sharks; Lakra *et al.,* 2011, for fishes; Hajibabaei *et al*., 2006, for butterflies; Ekrem *et al*., 2007, for non-biting midgets (Chironomidae)). However, precise recognition of multiple species within cryptic species complexes can not be always achieved with DNA barcoding alone (e.g., Meyer & Paulay, 2005, for cowries or cypraeid marine gastropods; Wiemers & Fiedler, 2007, for blue butterflies; Elias *et al.*, 2007, for tropical butterflies). It is partly because intra- and interspecific variations in the sequences often overlap (Meyer & Paulay, 2005).

Cryptic species diversity has been successfully revealed using integrated taxonomy in various ant taxa: *Acropyga* by Blaimer *et al*. (2016); *Amyrmex* by Ward & Brady (2009), *Anochetus* and *Odontomachus* by Fisher & Smith (2008); *Odontomachus* by Satria *et al*., 2015); *Cardiocondyla* by Seifert (2008); *Colobopsis* and *Dinomyrmex* by Ward *et al*. (2016); *Formica* by Seifert (1992, 1996, 1997) and Bernasconi *et al*. (2011); *Lasius* by Seifert (1991); *Leptanilloides* by Ward (2007); *Leptogenys* by Lattke (2011); *Melophorus* by Andersen *et al*. (2016); *Messor* by Schlick-Steiner, Steiner, Konrad *et al.* (2006); *Myrmica* by Seifert *et al*. (2009); *Nylanderia* by Zhao *et al*. (2012); *Tetramorium* by Schlick-Steiner, Steiner, Moder *et al.* (2006) and Steiner *et al.* (2010); etc. Furthermore, integrated taxonomy may reveal the proper combination among castes, subcastes and/or sexes, and help resolve synonymies.

III-1-3. Application of "Integrated Taxonomy" for delimitating Indo-Chinese Indo-Malayan species of *Odontomachus*

The genus *Odontomachus* was established by Latreille in 1804 with *Formica haematoda* Linnaeus, 1758 as the type species. The genus is currently assigned to the *Odontomachus* genus group in the tribe Ponerini, the subfamily Ponerinae, based on the result of a recent molecular phylogenetic analysis (Schmidt, 2013; Schmidt & Shattuck, 2014). Brown (1976) world-widely and comprehensively revised the genus *Odontomachus*, and recognized 51 valid species and classified them into 12 morphologically well-defined species groups. Currently, 72 extant species and 3 fossil were recognized; a majority of the species are from pantropical and pansubtropical zones, and a few species extend into the temperate zones; Neotropical and Oriental regions seem to be the centers of the species richness (Bolton, 2016).

Brown is a so-called "lumper", that is to say that Brown (1976) conservatively delimitates species and synonymized many species and intraspecific names into one. His view has been later questioned by some taxonomists. Yoshimura *et al*. (2007) revised East Asian populations of the genus based on morphological characters, including those of the male genitalia, and then revived *O. kuroiwae* which was synonymized by Brown (1976) under *O. monticola*. Satria *et al*. (2015) revised Sumatran populations of the genus by morphological approach and DNA barcoding, and revived *O. procerus* which was synonymized by Brown (1976) under *O. latidens*. Terayama & Ito (2014), based on morphological characters of the worker and phenotypes of the queen, deliminated a cryptic species, *O. pararixosus*, in *O. rixosus* sensu Brown (1976). These facts suggest that the species diversity of the genus *Odontomachus* has not yet been fully revealed, despite their large-sized body, bizzare habitus, and dominance in the ground-dwelling ant faunas.

Therefore, the purpose of the present study is to delimitate Indo-Chinese and Indo-Malayan species of *Odontomachus* by integrated taxonomy.

III-2. Materials and Methods

III-2-1. Material Examined

A total of 97 specimens of the ant genus *Odontomachus* collected from Indo-Chinese and Indo-Malayan subregions and adjacent areas were used for DNA sequencing. In addition, a specimen of *Anochetus mixtus* Radchenko, 1993 and a specimen of *A. princeps* Emery, 1884 were also sequenced and used as outgroups in molecular phylogenetic analyses. The *Odontomachus* specimens are listed in Table 3-1 under the names of species finally recognized and identified as the result of the present integrated taxonomy.

The type materials examined for identifying the species recognized by the present integrated taxonomy are shown in Table III-2.

III-2-2. DNA Extraction, PCR and Sequencing

Wet specimens (preserved in 80% or 100% ethanol) were used for DNA barcoding. A hind leg for each worker, or apex of gaster including genitalia for each male was washed with about 500 µL TE (pH 8.0) in a sterilized disposable dish and was broken into several fragments by sterilized forceps. These were then transferred into 105 µL of extraction buffer (100 µL of

10% Chelex-TE solution and 5 μL Qiagen Proteinase K) and incubated at 56˚C for 24–27h, and then heated at 99˚C for 10 minutes for inactivating Qiagen Proteinase K in the extraction buffer. In addition, the QIAGEN DNeasy Blood & Tissue Kit (QIAGEN, www.qiagen.com) was used for extracting DNA from some wet specimens; incubation at the extraction step was performed at 56˚C for 24h.

The standard DNA barcoding region near the 5' terminus of the CO1 gene (Folmer region) was amplified using the primer set LCO-EG (TTTCAACAAATCACAAAGAYATYGG) and HCO-EG (TAAACTTCAGGRTGACCRAAAAATCA), and 28S ribosomal DNA gene by using the primer set D2B (GTCGGGTTGCTTGAGAGTGC) and D3Ar (TCCGTGTTTCAAGACGGGTC). Each PCR contained 5 μL of 2xPCR 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 DNA polymerase KOD FX Neo (TOYOBO KFX-2015), and 0.5 μL of DNA template. The PCR thermal regime consisted of one cycle of 2 min at 94 °C; five cycles of 10 sec at 98 °C, 30 sec at 45 °C and 45 sec at 68 °C; 40 cycles of 10 sec at 98 °C, 30 sec at 48.5 °C and 45 sec at 68 °C; and a final cycle of 7 min at 68 °C. After confirming the PCR amplification on a 2.0% agarose gel, the amplified products were incubated at 37°C for 30 min and 80°C for 20 min with IllustraTM 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 an automated sequencer (ABI PRISM 3100, Applied Biosystems). Sequences assembly was conducted using ChromasPro 1.7.6 (Technelysium Pty Ltd., Australia). The sequences of each gene were aligned using MUSCLE (Edgar, 2004) built in MEGA 6.06 (Tamura *et al*. 2013), and then the sequences were exported as a single Fasta file.

III-2-3. MOTU-Partitioning by ABGD and PTP Analyses

Species delimitation in the present study was conducted with online MOTU-partitioning programs, ABGD and PTP. ABGD (Puillandre *et al*., 2012) applies clustering algorithms to recognize MOTUs (molecular operational taxonomic units) based the genetic distances among aligned sequences, using a two-phased procedure; ABGD first divides sequences into groups based on a statistically inferred barcode gap and then recursively applies the same procedure to the groups obtained in the first step (Puillandre *et al*., 2012; Kekkonen & Herbert, 2014). The first round of ABGD analysis was performed using the CO1 dataset at the web interface (http://wwwabi.snv.jussieu.fr/public/abgd/; web version '05/31/17 - 09:25AM'), by setting relative gap width and other parameters as default (Pmin: 0.001; Pmax: 0.1; Steps: 10; X: 1.5; Nb bins: 20), and selecting all of the three substitution model, i.e., JC69, K2P and p-distance. Because the first round found just a single group, the second round was performed by setting the relative gap width as 1.0, 0.8 and 0.5 (but setting other parameters as default).

PTP (Zhang *et al*. 2013) is a tree-based approach for the delimitation of species. This analysis only needs an input tree (nexus or newick format) which is not required to be ultrametric and bifurcating. The analysis is performed at the web interface (http://species.h-its.org/ptp/; accessed on 24/06/2017). A Bayesian inference tree constructed based on the CO1 dataset was used as an initial input tree (see below).

III-2-4. Phylogenetic Analyses

The Maximum Likelihood (ML) and Bayesian Inference (BI) analyses were run for the 28S and COI datasets separately. The Kakusan4 version 4.0 (Tanabe, 2011) was used to select the optimum substitution model for each codon position (1^{st}, 2^{nd}, and 3^{rd} positions). The model selection criteria employed here were AICc4 (Sugiura, 1978) for ML and BIC4 (Schwarz, 1978) for BI.

For the ML analyses of COI, the model TIM (Posada, 2003)+G (gamma shape parameter), TVM (Posada, 2003)+G, and GTR (Tavaré, 1986)+G models were selected by Kakusan4 as the optimal models for the 1^{st}, 2^{nd}, and 3^{rd} codon positions, respectively. For the BI analyses of COI, GTR+G, HKY85 (Hasegawa *et al.*, 1985)+G, SYM (Zharkikh, 1994)+G were selected as the optimal substitution models. For the ML analyses of 28S, HKY85+G, J2 (Jobb, 2011)+G, TN93(Tamura & Nei, 1993)+G were selected as the optimal substitution models. For the BI analyses of 28S, the model HKY85+G, GTR+G, and HKY85 models were selected as the optimal substitution models.

Then the phylogenetic trees by ML and BI were constructed using TREEFINDER (Jobb, 2011) and MrBayes version 3.1.2 (Ronquist & Huelsenbeck, 2003), respectively. Bootstrap test was 1,000 repeats for the ML. In BI analysis, two independent runs of four Markov Chains Monte Carlo (MCMC) were conducted for 1,000,000 generations. Then one tree was sampled every 100 generations. The first 1,000 trees were discarded as burn-in. The phylogenetic trees from BI analyses were displayed by using Figtree (http://tree.bio.ed.ac.uk/software/figtree/).

III-2-5. Morphological Observation

Specimens used for DNA extraction, or specimens which were colony-mates of the specimens used for DNA extraction, were dry-mounted, and examined with a Nikon SMZ1000 stereomicroscope. The parts of the bodies were directly measured using a Nikon SMZ1000 stereomicroscope under suitable magnifications, or using ImageJ 1.49m (National Institute of mental Health, USA, available at http://imageJ.nih.gov/ij/) based on the photographs taken using a Panasonic Lumix DMC-GX8 digital camera attached to the Nikon AZ100 microscope, or using a Canon EOS 60D digital camera with a MPE Canon 65 mm lens.

III-2-6. Overview of Integrated Taxonomy used in the Present Study

Integrated taxonomy consisting of the following steps was designed by referring Puillandre *et al.* (2012), Zhang *et al.* (2013), Kekkonen & Hebert (2014) and Leavitt *et al.* (2015).

MOTU-partitioning. MOTUs (molecular operational taxonomic units) are recognized by ABGD analysis (Puillandre *et al.,* 2012) and PTP/bPTP analysis (Zhang *et al*. 2013). MOTU-partitioning are then evaluated by following criteria.

Phylogenetical Criterion. Monophyly of each MOTU will be confirmed by Maximum-Likelihood (ML) and Bayesian Inference (BI) phylogenetic trees of COI and 28S gene markers. If a MOTU is paraphyletic toward other MOTU, those MOTUs should be combined and treated as one MOTU in the next step.

Mophological Criterion. Each MOTU is compared with phylogenetically closest MOTU(s). If morphologically undistinguishable, those MOTUs are treated as multiple “genetically distinct groups” of a single species. On the other hand, if morphologically distinguishable, each of those MOTUs is treated a different species (but see below).

Distribution Criterion (optional). If an MOTU is represented by a few localities and allopatric to phylogenetically closest MOTU(s), those MOTUs may be considered to be combined into one on the conservative presumption that the observed divergences of sequences and morphology apparent between them reflect phylogeographic variation in a single species.

III-3. Results

III-3-1. MOTU-Partitioning by ABGD and PTP Analyses

The number of MOTUs proposed by ABGD analyses varied from 5 to 52, mostly depending on the substitution model selected (Table III-3). Under Juke-Cantor model (JC69), the value of relative gap width (X) also affected the number of MOTUs. Under the partitionings with more than 41 MOTUs, samples from different sites were mostly recognized as different MOTUs. On the other hand, under the partioning with less than 10 MOTUs, morphologically well-defined and already named species were combined into a single MOTU, for example *O. kuroiwae* and *O. monticola* being combined under the partitioning with 10 MOTUs. Thus, a real number of species was assumed to fall between 11 and 40 MOTUs. Because PTP analysis produced a single result with 40 MOTUs (Fig. 3-1), the PTP partitioning was compared with the ABGD partitioning with 40 MOTUs (Table 3-6). A total of 30 MOTUs (75%) were identically recognized by both analysis. Thus, the ABGD partitioning with 41 MOTUs and the PTP partitioning with 40 MOTUs were selected as working hypotheses for the evaluations by phylogenetical criterion.

III-3-2. Evaluation by Phylogenetical Criterion

The 41 MOTUs from ABGD analisys and 40 MOTUs from PTP analysis were evaluated by using the Maximum-Likelihood and Bayesian Inference phylogenetic analyses. The monophyly of each of the 28 ABGD-based MOTUs and 24 PTP-based MOTUs was supported with higher supporting values by CO1-based ML and BI (bootstrap value $\geq$ 73; posterior probability $\geq$ 0.95).

Paraphyletic MOTUs with their sister MOTUs were combined as follows: ABGD17–21 into CLM17/CBI17; ABGD25–26 into CLM21/CBI21; ABGD27–28 into CBI22; ABGD31–33 into CBI25; and ABGD32–33 into CML28. On the other hand, PTP18–19 were combined into CLM19/CBI19; PTP21–22 into CLM21/CBI21; PTP23–24 into CLM22; PTP23–26 into CBI22; PTP29–31 into CBI25; PTP30–31 into CLM28; PTP36–37 into CLM33/CBI33; and PTP38–39 into CLM34/CBI34. The total MOTUs which supported by monophyly of COI-based ML and BI was 35 MOTUs and 32 MOTUs, respectively.

Only three monophyletic groups (S1–3) were strongly supported by 28S-based ML, and only a single monophyletic group was supported by BI. Under these results, morphologically well-defined and already named species were combined into one, for example, *O. silvestri* and *O. rixosus* being combined. Thus, evaluation by 28S-based phylogenetic criterion was not adopted and is not discussed further in Chapter III.

III-3-3. Evaluation by Morphological and Distribution Criteria

The 35 ML-based MOTUs and 32 BI-based MOTUs were combined into 13 forms (M1–M13) based on comparative morphological examination of the worker, and the queen and male if available (see "Discussion" for details).

The monophyly of each of 10 forms (M4–13) was supported strongly by CO1-based ML (bootstrap value $\geq$ 98) and BI (posterior probability $\geq$ 0.98), and that of M3 weakly supported (bootstrap value = 70, posterior probability = 0.72). Although the monophyly of each of M1 and M2 was not supported, that of the form consinsting of M1 and M2 was strongly supported by ML (bootstrap value =93; but not supported by BI).

III-4. Discussions

III-4-1. Final Confirmation of the Putative Species

There is a large difference between the number of MOTUs evaluated by molecular-based analyses and the number of forms proposed by morphological examination (32 or 35 MOTUs vs 13 forms). Therefore, I adopt the partitioning with 13 forms as a conservative hypothesis, and recognized the 12 putative species after M1 and M2 are combined. The status of each putative speices is confirmed below by comparing them with the type materials. CO1-based intraspecific variation and interspecific divergence are shown in the Table 3-5.

Under this conservative partitioning, however, a new cryptic species was recognized, and the species-level status of *O. kuroiwae*, *O. pararixosus, O. procerus* and *O. minangkabau* was reconfirmed. Because of fresh specimens suitable for DNA sequencing were unfortunately unavailable for the species described from the mainland China and the Philippines, it is likely that undiscovered cryptic species still remain in the area. Rather comprehensive taxon sampling, improvement of DNA barcoding and application of other methods such as karyotyping and quantitative morphometry will be needed for improve the resolution and reliability of the integrated taxonomy approach, and for resolving questionable cases such as those of *Odontomachus* sp. 1 and *O. simillimus*.

***Odontomachus* sp. 1**

MOTUs: ABGD1–12; PTP1–11. *Forms*: M1–2.

Phylogenetically closest species: *Odontomachus monticola*.

Delimitation from phylogenetically closest species based on the worker morphology: Body larger in forms M2 of *Odontomachus* sp. 1 (HL 3.41–3.82 mm, HW 2.62–3.07 mm, WL 4.52–4.96 mm) than in *O. monticola* (HL 2.82–3.33 mm, HW 2.25–2.62 mm, WL 4–4.30 mm) and almost as large as forms M2 of *Odontomachus* sp. 1; anterodorsal slope of pronotum of the worker weakly steep in both M1 and M2, but relatively steep in *O. monticola*; vertex of head of the worker extensively striate in both M1 and M2, but smooth and shiny in *O. monticola*; pronotal disc of the worker with transverse striation in *Odontomachus* sp. 1, but concentric in *O. monticola*; mesopleuron entirely finely striated in M2, but largely smooth and shiny, with anterior 1/3 and posteriormost parts finely striate in *Odontomachus monticola* and M1.

Distribution: Japan, Taiwan, Vietnam. Sympatric to *O. monticola* in Vietnam.

Remarks: Although the monophyly of each of M1 (Japan and Taiwan) and M2 (Vietnam) was not supported, that of the "M1+M2" was strongly supported by ML. In the present study, the two are tentatively combined into a single species "*Odontomachus* sp. 1" on the conservative presumption that the observed divergence in morphology between them reflects geographic variation (Kekkonen & Hebert 2014). M1 and M2 agree well with the type series of *O. monticola* var. *formasae* Forel, 1912 and *O. monticola* var. *hainanensis* Stitz, 1925, respectively. Intensive sampling in southern China (including the Hainan Island) will allow us confirming the status of *Odontomachus* sp. 1.

Odontomachus monticola

MOTUs: ABGD13–21; PTP12–16. *Form*: M3.

Phylogenetically closest species: *Odontomachus* sp. 1.

Delimitation from phylogenetically closest species based on the worker morphology: See under *Odontomachus* sp. 1.

Distribution: Vietnam. Sympatric to *Odontomachus* sp. 1 in Vietnam.

Remarks: Dorsal outline of propodeum is faintly concave in ABGD18, but almost straight in the remainder.

Odontomachus kuroiwae

MOTUs: ABGD22–24; PTP17–20. *Form*: M4.

Phylogenetically closest species: *Odontomachus* sp. 1, *Odontomachus monticola*.

Delimitation from phylogenetically closest species based on the worker morphology: Body smaller in *O. kuroiwae* (HL 2.18–2.61 mm, HW 1.70–2.05 mm, WL 2.67–3.02 mm) than in forms M1 and M2 of *Odontomachus* sp. 1 and *O. monticola* (HL 2.82–3.82 mm, HW 2.25–3.07 mm, WL 4–4.96 mm) ; pronotal disc smooth and shiny, with anterior lobe finely striate in *O. kuroiwae*, but with concentric striation in *O. monticola* and transverse in *Odontomachus* sp. 1; body reddish brown in *O. kuroiwae* and in M1 of *Odontomachus* sp. 1 from Japan, but brown to dark brown in *O. monticola* and M2 of *Odontomachus* sp. 1 from Vietnam and Taiwan.

Distribution: Japan. Allopatric to *Odontomachus monticola*; sympatric to *Odontomachus* sp. 1 in Japan.

Remarks: *Odontomachus kuroiwae* was recognized with three MOTUs by ABGD and PTP analyses (Fig. 3-1). The populations from Okinawa Island show a large variation in COI sequences (maximum intrapopulation divergence in K2P = 2.8 %), but these MOTUs are identical to each other in the morphology. So it is treated as a single species.

Odontomachus kuroiwae was revived from a synonym of *O. monticola* sensu Brown (1974) by Yoshimura *et al*. (2007). The treatment was reconfirmed by the present integrated taxonomy.

***Odontomachus* sp. 2**

MOTUs: ABGD25–26; PTP21–22. *Form*: M5.

Phylogenetically closest species: *Odontomachus* sp. 1, *Odontomachus monticola*, *Odontomachus kuroiwae*.

Delimitation from phylogenetically closest species based on the worker morphology: Body smaller in *Odontomachus* sp. 2 (HL 2.81–3.05 mm, HW 2.23–2.34 mm, WL 3.30–3.50 mm) than in form M2 of *Odontomachus* sp. 1 (HL 3.41–3.82 mm, HW 2.62–3.07 mm, WL 4.52–4.96 mm), almost as large as *O. monticola* and form M1 of *Odontomachus* sp. 1, and slightly larger than in *O. kuroiwae* (HL 2.18–2.61 mm, HW 1.70–2.05 mm, WL 2.67–3.02 mm); the major axis of compound eye consists of 14 ommatidia in *Odontomachus* sp. 2 and in M1 of *Odontomachus* sp. 1, but 17 in *O. monticola*, 15 in *O. kuroiwae* and 19–21 in M2 of *Odontomachus* sp. 1; anterodorsal slope of pronotum of the worker relatively steep in *O. monticola* and *Odontomachus* sp. 2, but weakly steep in *O. kuroiwae* and *Odontomachus* sp. 1; pronotal disc with concentric striation in *O. monticola* and *Odontomachus* sp. 2, but transverse in *Odontomachus* sp. 1 or smooth and shiny in *O. kuroiwae*; mesopleuron largely smooth and shiny, with anterior 1/3 and posteriormost parts finely striate in *O. kuroiwae*, *O. monticola*, M1 of *Odontomachus* sp. 1 and *Odontomachus* sp. 2, but entirely finely striated in M2 of *Odontomachus* sp. 1; body brown to dark brown in *O. monticola* and *Odontomachus* sp. 2, nearly black in M2 of *Odontomachus* sp. 1, or reddish brown in *O. kuroiwae* and M1 of *Odontomachus* sp. 1.

Distribution: Vietnam. Allopatric to *Odontomachus* sp. 1, *Odontomachus monticola*, *Odontomachus kuroiwae*.

Remarks: This species is probably undescribed, and is tentatively referred to as *Odontomachus* sp. 2. This species seems to be restricted to the Central Highland of Vietnam (so far known from Dak Lak and Lam Dong provinces). The Central Highland of Vietnam was surrounded by Truong Son (Annamite) mountain ranges, and this area is known for its high level of endemism (Averyanov *et al*., 2003).

Odontomachus silvestrii

MOTUs: ABGD27–28; PTP23–26. *Form*: M6.

Phylogenetically closest species: This species is quite distant from the other species (CO1-based minimal interspecific distance: 7.5% in K2P).

Delimitation from phylogenetically closest species based on the worker morphology: The subapical teeth longer than broad, with acute apex in *O. silvestrii*, but with truncate apex, in other species except for *O. floresensis*; petiolar node in lateral view much thicker in *O. silvestrii* than in the other species.

Distribution: Vietnam and China.

Odontomachus rixosus

MOTUs: ABGD29–33; PTP27–31. *Form*: M7.

Phylogenetically closest species: *Odontomachus pararixosus*.

Delimitation from phylogenetically closest species based on the worker morphology: Gastral tergite I without erect setae in *O. rixosus*, but with several erect setae in *O. pararixosus*.

Distribution: Indo-Malayan subregion (Western part of Indonesia, Malaysia, Brunei and Phillipines), India, Myanmar, Thailand, Vietnam, Cambodia, Laos and north to Yunnan Province (China). Allopatric to *O. pararixosus* (but surrounding the range of *O. pararixosus*).

Remarks: *Odontomachus rixosus* is widespread though the Indo-Malayan subregion, and extended extends to southern China (discussed in the Chapter IV), and shows a large intraspecific variation in COI sequences (maximum intraspecific divergence in K2P = 3.3 %), with distinct local MOTUs, e.g., ABGD31/PTP29 from the Phu Quoc Island, ABGD29/PTP27, ABGD30/PTP28 and ABGD32/PTP30 from the Sumatra Island; ABGD33/PTP31 from the Simeulue Island.

Odontomachus minangkabau and *O. pararixosus* were described as cryptic species of *O. rixosus* sensu Brown (1974) by Satria *et al*. (2015) and Terayama & Ito (2014), respectively. Those treatments were reconfirmed by the present integrated taxonomy.

Odontomachus pararixosus

MOTUs: ABGD34; PTP32. *Form*: M8.

Phylogenetically closest species: *Odontomachus rixosus*.

Delimitation from phylogenetically closest species based on the worker morphology: See under *O. rixosus*.

Distribution: Malaysia (Ulu Gombak). Allopatric to *O. rixosus* (but surrounded by the range of *O. rixosus*).

Odontomachus minangkabau

MOTUs: ABGD35; PTP33. *Form*: M9.

Phylogenetically closest species: *Odontomachus pararixosus*, *Odontomachus rixosus*.

Delimitation from phylogenetically closest species based on the worker morphology: Body larger in *O. minangkabau* (HL 3.13–3.55 mm, HW 2.05–2.34 mm, WL 4.15–4.65 mm) than in *O. pararixosus* and *O. rixosus* (HW 1.70–2.19 mm, HL 2.40–3.03 mm, WL 3.33–4.00 mm); masticatory margin of mandible with 11–14 denticles in *O. minangkabau*, but less than 10 denticles in *O. pararixosus* and *O. rixosus*; median part of vertex along median furrow faintly striate transversely in *O. minangkabau*, but smooth and shiny or with rough texture in *O. pararixosus* and *O. rixosus*; striation of pronotal disc transverse in *O. minangkabau*, but concentric in *O. pararixosus* and *O. rixosus*.

Delimitation from phylogenetically closest species based on the male morphology: Gastral tergite I in lateral view long in *O. minangkabau* than in *O. rixosus*; head, pronotum, mesoscutum and mesopleuron pale yellowish in *O. minangkabau*, but yellowish to yellowish brown in *O. rixosus*; posterior spine of abdominal tergite VIII long and slender, weakly curved (Fig. 2-2D) in *O. minangkabau*, but very weakly curved (Fig. 2-2C) in *O. rixosus*; apical lobe of abdominal sternite IX much longer than disc, and slightly narrowed in basal half, with apical margin weakly convex in *O. minangkabau*, but gently tapering to almost truncate apex in *O. rixosus*; telomeral apex in lateral view much longer than high in *O. minangkabau*, but longer than high in *O. rixosus*; ventral margin of valviceps with 28–29 denticles in *O. minangkabau*, but with 21−22 denticles in *O. rixosus*.

Distribution: Indonesia (Sumatra Island). Sympatric to *O. rixosus* and allopatric to *O. pararixosus*.

Odontomachus procerus

MOTUs: ABGD36; PTP34. *Form*: M10.

Phylogenetically closest species: *Odontomachus latidens* (but posterior probability = 0.72, bootstrap value = 63).

Delimitation from phylogenetically closest species based on the worker morphology: The masticatory margin of the mandible with 6–9 distinct denticles in *O. procerus*, but with small denticles or sometimes without denticles except for preapical angle in *O. latidens*; gastral tergite I without setae in *O. procerus*, but with short erect setae in *O. latidens*.

Delimitation from phylogenetically closest species based on the worker morphology: Body relatively dark in *O. procerus,* butrelatively light in color in *O. latidens*; subpetiolar process in lateral view anteroposteriorly shorter than dorsoventrally high and triangular in *O. procerus*, but anteroposteriorly as long as dorsoventrally high and lobate in *O. latidens*; the posterior spine of abdominal tergite VIII long, slender and very weakly curved in *O. procerus*, but short and thick, very weakly curved in *O. latidens*; disc of abdominal sternite IX almost circular with the disc much longer than apical lobe in *O. procerus*, but not clearly differentiated from apical lobe, gradually merging into apical lobe, with basal margin almost straight in *O. latidens*.

Distribution: Indonesia (Sumatra) and Malaysia (Malay Peninsula, Sabah and Sarawak). Sympatric to *O. latidens* (but only a western Sumatran specimen was examined by the present integrated taxonomy).

Remarks: *Odontomachus procerus* was revived by Satria *et al*. (2015) from a synonym of *O. latidens* sensu Brown (1974). The treatment was reconfirmed by the present integrated taxonomy.

Odontomachus latidens

MOTUs: ABGD37; PTP35. *Form*: M11.

Phylogenetically closest species: *Odontomachus procerus*.

Delimitation from phylogenetically closest species based on the worker morphology: See under *O. procerus*.

Distribution: Indonesia (Sumatra and Java) and Peninsular Malaysia. Sympatric to *O. procerus* (but only a northern Sumatran specimen was examined by integrated taxonomy, and shown in Fig. 3-4).

Odontomachus simillimus

MOTUs: ABGD38–39; PTP36–39. *Form*: M12.

Phylogenetically closest species: This species is quite distant from the other species (CO1-based minimal interspecific distance: 9.7% in K2P).

Distribution: Widespread in tropical Southeast and South Asia, Melanesia and Madagascar

Remarks: The Simeulue population (ABGD38/PTP36–37) and Bali population (ABGD39/PTP38–39) were identified as *O. simillimus*. This species is native to Southeast and South Asia, Australia and Pacific islands, and introduced to several remote areas including Seychelles and the Caribbean according to antmaps.org (Janicki *et al.*, 2016). The Simeulue and Bali populations show a large genetic divergences in COI sequences (minimal interpopulation divergence in K2P = 4%). Fisher and Smith (2008) also reported a large genetic divergences of COI among the islands of Seychelles, i.e., an introduced area. Therefore, it is likely that *O. simillimus* will be recognized as a cryptic species complex by future integrated taxonomy based on a comprehensive sampling from its entire range.

Odontomachus floresensis

MOTUs: ABGD40; PTP40. *Form*: M13.

Phylogenetically closest putative species: This species is quite distant from the other species (CO1-based minimal interspecific distance: 10.1% in K2P).

Distribution: Indonesia (Flores Island).

III-4-2. The Future Prospect of This Study

The present study as well as Sorger & Zettel (2011) highlight that large-sized and dominant ground-dwelling ant genera such as *Odontomachus* still have hidden cryptic species. Therefore, the species-level classification of ants in tropical and subtropical Asia should be evaluated again by integrated taxonomy. The identities of species with widespread distribution in a zoogeographic subregion or more, and/or the species with many different names (synonyms) should be carefully examined also using integrated taxonomy.

Several theometical and methodological problems still remain in the present integrated taxonomy. The phylogenetic criterion was based on the “Phylogenetic Species Concept” (de Queiroz & Donogue, 1988; Wheeler, 1999; Mishler & Theriot, 2000) which requires members of a species to form a monophyletic unit. However, species are not always monophyletic because new species might be often formed from peripherally isolated populations of the mother species, i.e., through peripheral speciation (Hoskin *et al.*, 2011; Rettelbach *et al.*, 2016; see also the chapter V). Therefore, the design of the integrated taxonomy approach used in the present study needs to be reconsidered.

In recent years cryptic species diversity of European ant taxa were intensively revealed by integrated taxonomy, and numerical morphometry was applied as an indispensable part to their methodology (Seifert, 2009; Steiner *et al.*, 2010). As mentioned above, there is a large difference between the number of MOTUs evaluated by molecular-based analyses and the number of forms proposed by morphological examination (32 or 35 MOTUs vs 13 forms). Numerical morphometry will be able to detect rather minor but constant morphological differences among the MOTUs, and consequently to find further cryptic species among the arrays of MOTUs. Furthermore, numerical morphometry is indispensable to correspond the representative specimens of cryptic species proposed by integrated taxonomy to the type materials of relevant species because no damage is allowed for the type materials. That is to say that numerical taxonomy is the only practical method to link cryptic species to the present Zoological Nomenclature based on the Type Concept (Seifert, 2009).

The usefulness of male genitalia and associated sclerites for delimitating multiple cryptic species of *Odontomachus* was also confirmed by the chapter II as well as a few previous studies. However, unfortunately, colonies containing males have so far been obtained for only a part of MOTUs. Future trials of the integrated taxonomy including the morphological examination of male genitalia will also found further cryptic species among the arrays of MOTUs.

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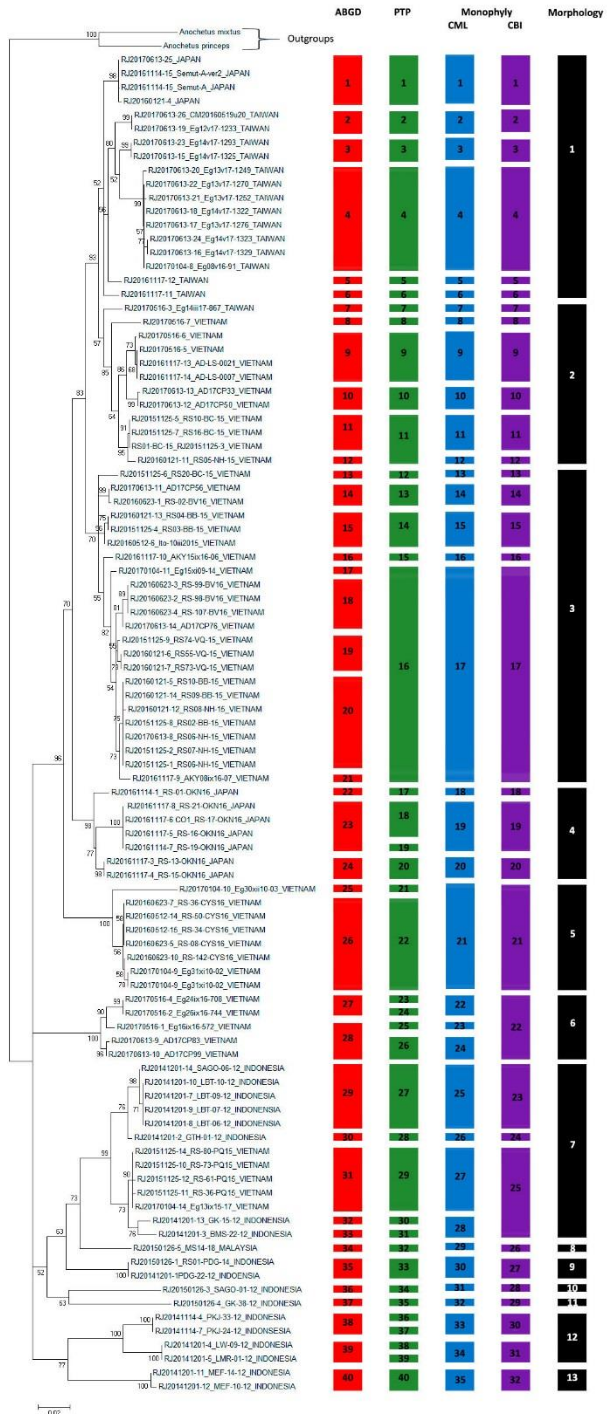

Fig. 3-1. MOTU partitioning proposed by ABGD (in red) and PTP (in green) analyses. The monophyly of each MOTUs as evaluated by COI-based Maximum-likelihood (CML) (in blue) and COI-based Bayesian Inference (CBI) (in purple), and then by morphology (M) (in black).

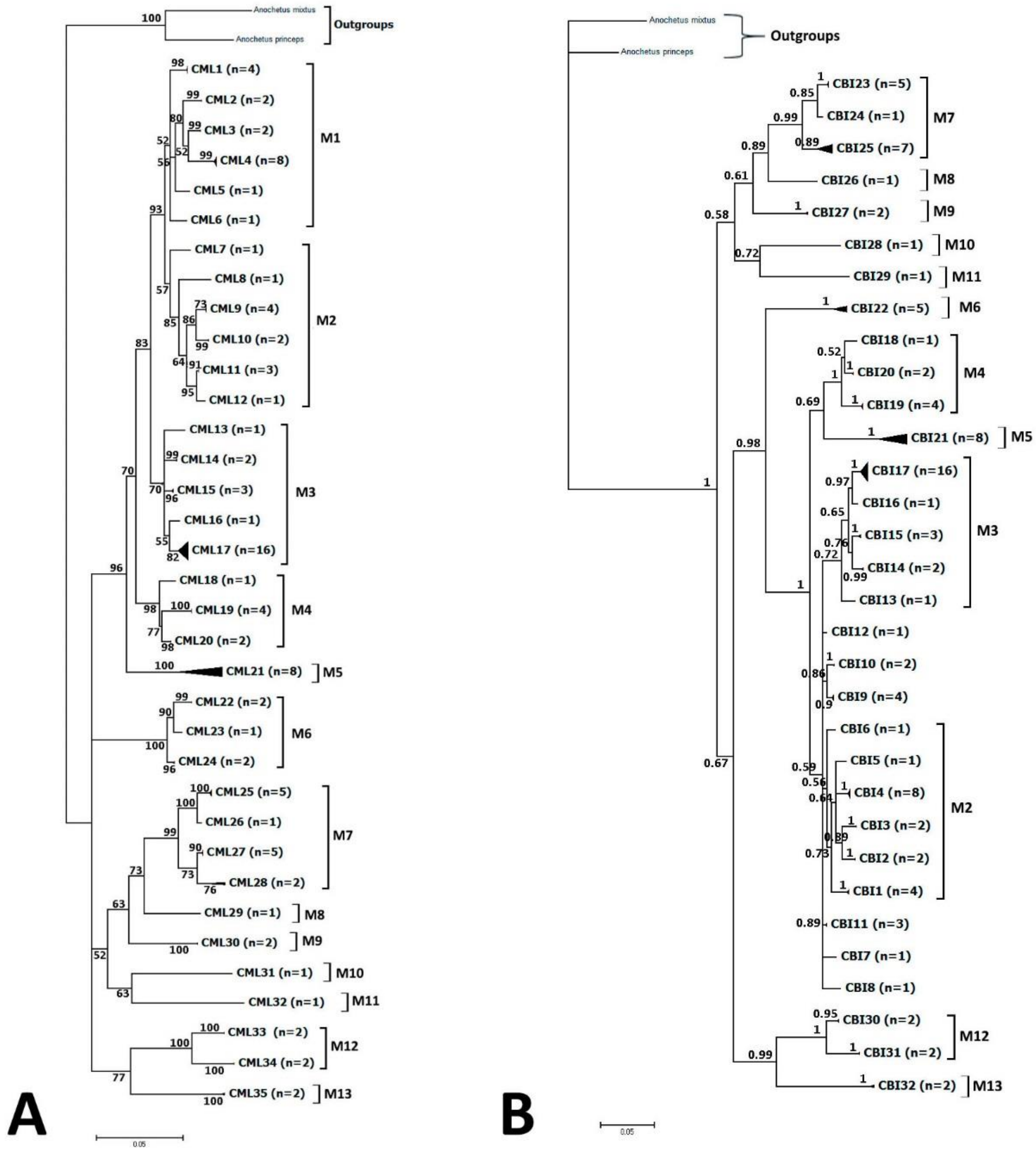

Fig. 3-2. COI-based Maximum-likelihood Tree (A) and COI-based Bayesiean Inference analyses (B). MOTUs recognized by morpholoy criterion were shown as M1–13.

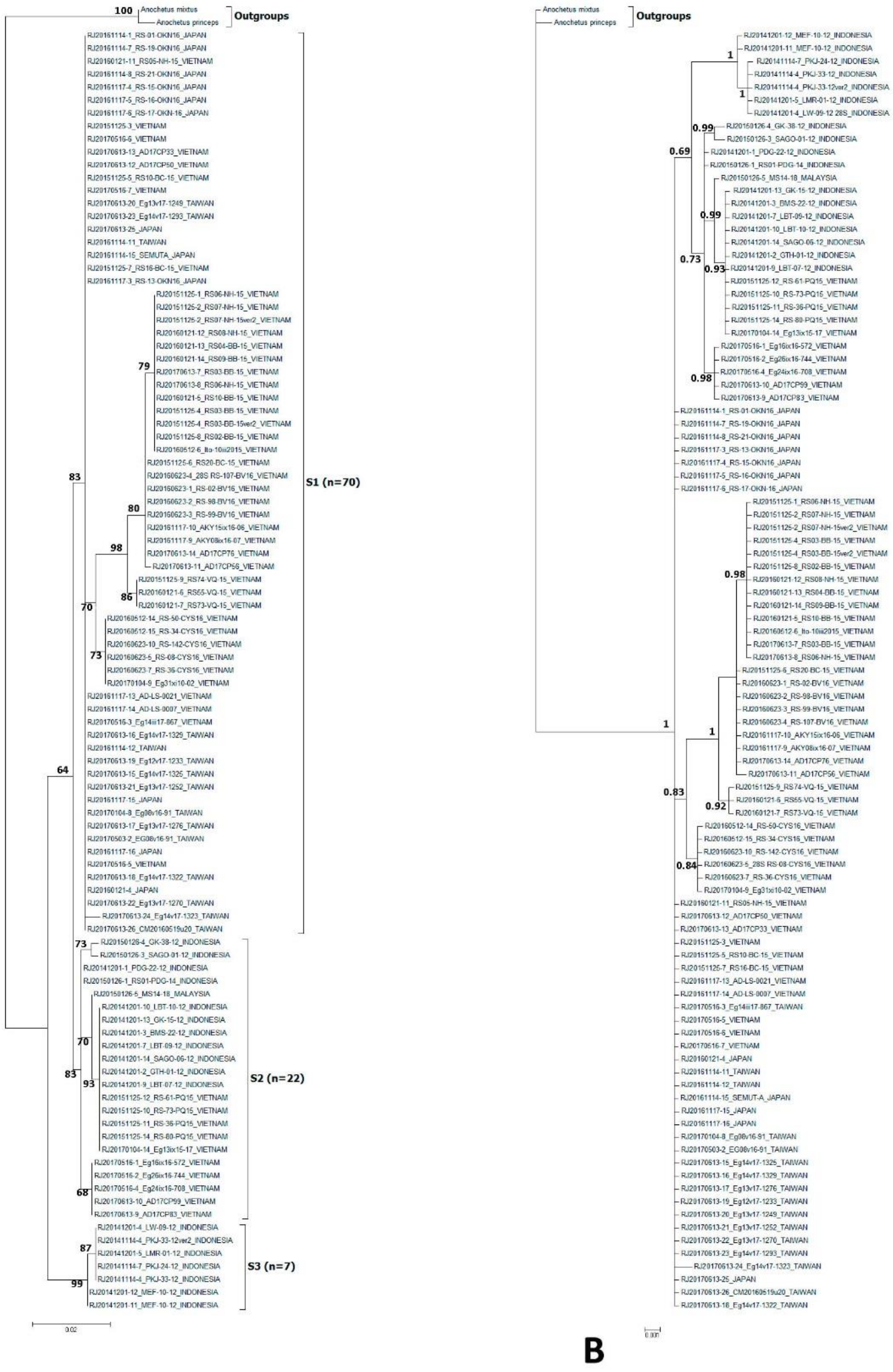

Fig. 3-3. Phylogenetic tree based on 28S gene marker. A, Maximum-likelihood analyses; B, Bayesian Inference analyses. The label of specimen for RJ20161114-1_RS-01-OKN16_JAPAN and RJ20170516-6_VIETNAM is information for Individual-code_Colony-code_Locality and Individual-code_locality, respectively.

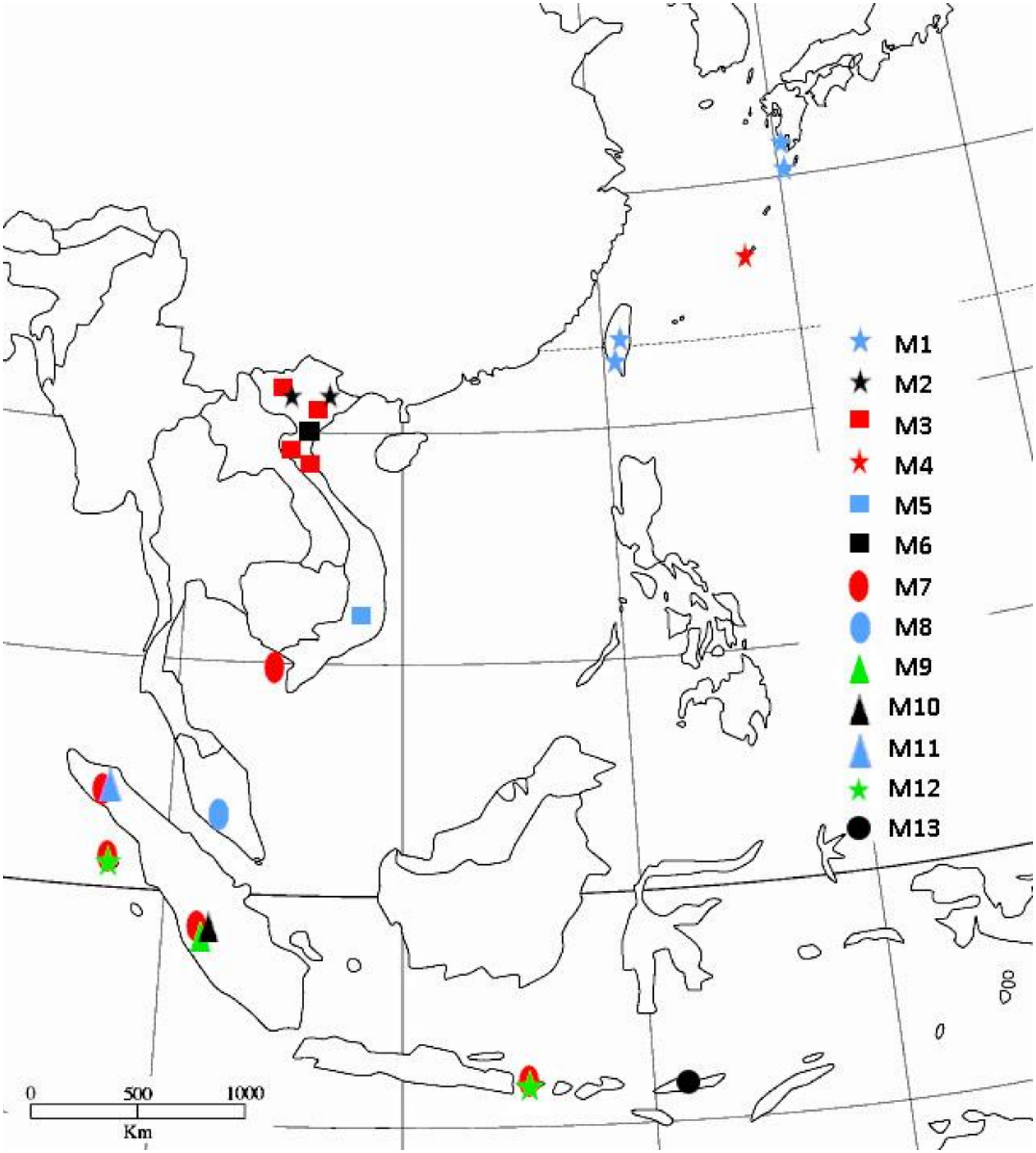

Fig. 3-4. The distribution map of the forms M1–13.

Table 3-1. Information of examined materials of Indo-Chinese and Indo-Malayan *Odontomachus*

Colony code/ Individual code	Caste	Locality	Date
RJ20170613-25	Worker	JAPAN: Kagoshima-Ken: Yakushima Island: Ano-Yindo, 650m alt.	25.VIII.2016
RJ20160121-4	Worker	JAPAN: Kagoshima-Ken: Yakushima Island: Kotodake-forest	3.III.2013
RJ20161114-15	Worker	JAPAN: Kagoshima-Ken: Kagoshima-shi: Eboshi-dake	7.VIII.2012
Eg14v17-1323/ RJ20170613-24	Worker	TAIWAN: Nantou County: Xitou Forest, N 23.67279°, E 120.79935°, 1160 m alt.	14.V.2017
Eg14v17-1293/ RJ20170613-23	Worker	TAIWAN: Nantou County: Xitou Forest, N23.67263°, E120.79935°, 1162 m alt.	14.V.2017
Eg13v17-1270/ RJ20170613-22	Worker	TAIWAN: Nantou County: Xitou Forest, N23.67015°, E120.78741°, 1179 m alt.	13.V.2017
Eg14v17-1322/ RJ20170613-18	Worker	TAIWAN: Nantou County: Xitou Forest, N23.67269°, E120.79946°, 1159 m alt.	14.V.2017
Eg13v17-1276/ RJ20170613-17	Worker	TAIWAN: Nantou County: Xitou Forest, N23.66958°, E120.78717°, 1193 m alt.	13.V.2017
Eg14v17-1323/ RJ20170613-24	Worker	TAIWAN: Nantou County: Xitou Forest, N23.67279°, E120.79935°, 1160 m alt.	14.V.2017
Eg14v17-1329/ RJ20170613-16	Worker	TAIWAN: Nantou County: Xitou Forest, N23.67287°, E120.79922°, 1163 m alt.	14.V.2017
Eg13v17-1249/ RJ20170623-20	Worker	TAIWAN: Nantou County: Sun Moon Lake, N23.84222°, E120.92863°, 792 m alt.	13.V.2017
Eg13v17-1252/ RJ20170613-21	Worker	TAIWAN: Nantou County: Sun Moon Lake, N23.84211°, E120.92847°, 790 m alt.	13.V.2017
Eg12v17-1233/ RJ20170613-19	Worker	TAIWAN: Nantou County: Sun Moon Lake, Huisun Forest, N24.08774°, E121.03181°, 756 m alt.	12.V.2017
Eg08v16-91/ RJ20170104-8	Worker	TAIWAN: Nantou County: Sun Moon Lake, Huisun Forest, Wushe, N24.01268˚, E121.12967˚, ca. 1160 m alt.	08.V.2016
RJ20161114-12	Worker	TAIWAN: Pingtung County: Kenting N.P.: Nanrenshan ecological reserve area	26.VII.2016
RJ20161114-11	Worker	TAIWAN: Pingtung County: Kenting N.P.: Kenting forest recreation area: Area II	26.VII.2016
Eg14iii17-867/ RJ20170516-3	Worker	VIETNAM: Cao Bang: Nguyen Binh: Quang Tanh: Phia Oac, N22.59554°, E105.8846°, 1300 m alt.	14.III.2017

RJ20170516-7	Worker	VIETNAM: Quang Ninh: Tay Yen Tu	22.III.2017
RJ20170516-5	Worker	VIETNAM: Lang Son: Van Lang Dist.	16.III.2017
RJ20170516-6	Worker	VIETNAM: Lang Son: Van Lang Dist.	16.III.2017
AD-LS-0021/ RJ20161114-13	Worker	VIETNAM: Lang Son: Van Lang Dist., N20˚23'26", E105˚52'08", ca 967 m alt.	21.VI.2017
AD-LS-0007/ RJ20161114-14	Worker	VIETNAM: Lang Son: Hun Lien H.R., N21˚50'25", E106˚55'55", ca 98 m alt.	12.VI.2017
AD17CP50/ RJ20170613-12	Worker	VIETNAM: Ninh Binh: Nho Quan: Cuc Phuong N.P., N20˚21'00", E105˚35'36"−34'41", ca. 366 m alt.	23.III.2017
AD17CP33/ RJ20170613-13	Worker	VIETNAM: Ninh Binh: Nho Quan: Cuc Phuong N.P., N20˚21'00", E105˚35'36"−34'41", ca. 366 m alt.	23.III.2017
AD17CP50/ RJ20170613-11	Worker	VIETNAM: Ninh Binh: Nho Quan: Cuc Phuong N.P., N20˚21'00", E105˚35'36"−34'41", ca. 366 m alt.	23.III.2017
RS10-BC-15/ RJ20151125-5	Worker	VIETNAM: Na Hang: Ban Chu, N22˚20'56"–21'06", E105˚25'35–36", ca. 200–225 m alt.	13.III.2015
RS16-BC-15/ RJ20151125-7	Worker	VIETNAM: Na Hang: Ban Ban, N22˚21'49"–22'06", E105˚26'21–37", ca. 355–450 m alt.	14.III.2015
RS01-BC-15/ RJ20151125-3	Worker	VIETNAM: Na Hang: Ban Chu, N22˚20'56"–21'06", E105˚25'35–36", ca. 200–225 m alt.	11.III.2015
RS05-NH-15/ RJ20160121-11	Worker	VIETNAM: Na Hang: Bac Vang, N22°28'49–51", E105°25'09–11", ca. 110–135 m alt.	10.III.2015
AD17CP76/ RJ20170613-14	Worker	VIETNAM: Ninh Binh: Nho Quan: Cuc Phuong N.P., N20˚21'00", E105˚35'36"−34'41", ca. 366−232 m alt.	23.III.2017
RS20-BC-15/ RJ20151125-6	Worker	VIETNAM: Na Hang: Ban Chu, N22˚20'56"–21'06", E105˚25'35–36", ca. 200–225 m alt.	13.III.2015
RS08-NH-15/ RJ20160121-12	Worker	VIETNAM: Na Hang: Ban Chu, N22˚20'56"–21'06", E105˚25'35–36", ca. 200–225 m alt.	10.III.2015
RS06-NH-15/ RJ20170613-8	Worker	VIETNAM: Na Hang: Ban Chu, N22˚20'56"–21'06", E105˚25'35–36", ca. 200–225 m alt.	10.III.2015
RS07-NH-15/ RJ20151125-2	Worker	VIETNAM: Na Hang: Ban Chu, N22˚20'56"–21'06", E105˚25'35–36", ca. 200–225 m alt.	10.III.2015
RS06-NH-15/ RJ20151125-1	Worker	VIETNAM: Na Hang: Ban Chu, N22˚20'56"–21'06", E105˚25'35–36", ca. 200–225 m alt.	10.III.2015
RJ20160512-6	Male	VIETNAM: Na Hang: Ban Chu, N22˚20'56"–21'06", E105˚25'35–36", ca. 200–225 m alt.	10.III.2015
AKY15ix16-06/ RJ20170512-8	Worker	VIETNAM: Thanh Hoa: Ben En National Park, N19˚34'30-45", E105˚31'54"-32’10", ca 20-80 m alt.	15.IX.2016
RS04-BB-15/	Worker	VIETNAM: Na Hang: Ban Bung, N22°17'02–18'02",	12.III.2015

RJ20160121-13		E105°24'52"–25'58", ca. 50–365 m alt.	
RS03-BB-15/ RJ20151125-4	Worker	VIETNAM: Na Hang: Ban Bung, N22°17'02–18'02", E105°24'52"–25'58", ca. 50–365 m alt.	12.III.2015
RS10-BB-15/ RJ20160121-5	Worker	VIETNAM: Na Hang: Ban Bung, N22°17'02–18'02", E105°24'52"–25'58", ca. 50–365 m alt.	12.III.2015
RS09-BB-15/ RJ20160121-14	Worker	VIETNAM: Na Hang: Ban Bung, N22°17'02–18'02", E105°24'52"–25'58", ca. 50–365 m alt.	12.III.2015
RS02-BB-15/ RJ20160121-8	Worker	VIETNAM: Na Hang: Ban Bung, N22°17'02–18'02", E105°24'52"–25'58", ca. 50–365 m alt.	12.III.2015
RS-02-BV16/ RJ20160623-1	Worker	VIETNAM: Hanoi: Ba Vi N.P., N21˚03'35.7", E105˚21'47.8", ca. 1019 m alt.	25.III.2016
RS-99-BV16/ RJ20160623-3	Worker	VIETNAM: Hanoi: Ba Vi N.P., N21˚03'35.7", E105˚21'47.8", ca. 1019 m alt.	25.III.2016
RS-98-BV16/ RJ20160623-2	Worker	VIETNAM: Hanoi: Ba Vi N.P., N21˚03'35.7", E105˚21'47.8", ca. 1019 m alt.	25.III.2016
RS-107-BV16/ RJ20160623-4	Worker	VIETNAM: Hanoi: Ba Vi N.P., N21˚03'34",E105˚21'49.6", ca. 710 m alt.	29.II.2016
AKY08ix16-07/ RJ20161114-10	Worker	VIETNAM: Thanh Hoa: Xuan Lien Nature Reserve, N19°58'36-41", E105˚10'04-29", ca 280-300 m alt.	8.IX.2016
Eg15xi09-14/ RJ20170104-11	Worker	VIETNAM: Hue: Bach Ma N.P., 16˚12'16−22"N, 107˚51'26−28"E, 875−930 m alt.	15.XI.2009
RS55-VQ-15/ RJ20160121-6	Worker	VIETNAM: Ha Tinh: Vu Quang N.P.: TK189, near Tram Kiem Lam Co, N18°16'21–35", E105°22'00–07", ca. 125–285 m alt.	21.III.2015
RS74-VQ-15/ RJ20151125-9	Worker	VIETNAM: Ha Tinh: Vu Quang N.P.: TK189, near Tram Kiem Lam Co, N18°16'21–35", E105°22'00–07", ca. 125–285 m alt.	21.III.2015
RS73-VQ-15/ RJ20160121-7	Worker	VIETNAM: Ha Tinh: Vu Quang N.P.: TK189, near Tram Kiem Lam Co, N18°16'21–35", E105°22'00–07", ca. 125–285 m alt.	21.III.2015
RS-01-OKN16/ RJ20161114-1	Worker	JAPAN: Okinawa-ken: Okinawa: Chibana: Chibanajoshi, N26˚21'47.5", E127˚48'37.9", ca 69 m alt	25.X.2016
RS-16-OKN16/ RJ20161114-5	Worker	JAPAN: Okinawa-ken: Okinawa: Kunigami: Yona, N26˚45'17.8", E128˚13'31.8", ca 187 m alt.	26.X.2016
RS-17-OKN16/ RJ20161114-6	Worker	JAPAN: Okinawa-ken: Okinawa: Kunigami: Yona, N26˚44'49.6", E128˚14'17.1", ca 321 m alt.	26.X.2016
RS-21-OKN16/ RJ20161114-8	Worker	JAPAN: Okinawa-ken: Okinawa: Kunigami: Yona, N26˚43'55.2", E128˚13'24.7", ca 312 m alt.	26.X.2016
RS-19-OKN16/ RJ20161114-7	Worker	JAPAN: Okinawa-ken: Okinawa: Kunigami: Yona,	26.X.2016

		N26˚43'40.3", E128˚11'44.6", ca 217 m alt.	
RS-13-OKN16/ RJ20161114-3	Worker	JAPAN: Okinawa-ken: Okinawa: Nago-shi: Nago, N26˚35'19.4", E127˚59'34.5", ca 93 m alt.	25.X.2016
RS-15-OKN16/ RJ20161114-4	Worker	JAPAN: Okinawa-ken: Okinawa: Nago-shi: Nago, N26˚35'18", E127˚59'36.4", ca 95 m alt.	25.X.2016
Eg30xii10-03/ RJ20170104-10	Worker	VIETNAM: Lam Dong: Bidoup-Nui Ba NP: nr. Giang Ly Forestry station, 12˚10'46−55"N, 108˚40'59−41'16"E, ca. 1400−1500 m alt.	30.XII.2010
Eg31xi10-02/ RJ20170104-9	Worker	VIETNAM: Lam Dong: Bidoup-Nui Ba NP: nr. Giang Ly Forestry station, 12˚10'58−11'17"N, 108˚40'45−58"E, ca. 1400−1550 m alt.	31.XII.2010
RS-36-CYS16/ RJ20160623-7	Worker	VIETNAM: Dak Lak: Chu Yang Shin: Area 1359, N12˚24'42.9", E108˚21'08", ca. 900 m alt.	05.II.2016
RS-08-CYS16/ RJ20160623-5	Worker	VIETNAM: Dak Lak: Chu Yang Shin: Area 1359, N12˚23'02.5",E108˚20'41.7", ca. 1215−1245 m alt.	04.III.2016
RS-142-CYS16/ RJ20160623-10	Worker	VIETNAM: Dak Lak: Chu Yang Shin: Area 1342, N12˚25'36.3−36.6", E108˚19'17−25.8", ca. 826−846 m alt.	06.III.2016
RS-50-CYS16/ RJ20160512-14	Worker	VIETNAM: Dak Lak: Chu Yang Shin: Area 1342, N12˚25'10.5", E108˚22'09.3", ca. 991 m alt.	06.III.2016
RS-34-CYS16/ RJ20160512-15	Worker	VIETNAM: Dak Lak: Chu Yang Shin: Area 1342, N12˚24'42.9", E108˚21'08", ca. 900 m alt.	05.III.2016
Eg31xi10-02/ RJ20170104-9	Worker	VIETNAM: Lam Dong: Bidoup-Nui Ba NP: nr. Giang Ly Forestry station, 12˚10'58−11'17"N, 108˚40'45−58"E, ca. 1400−1550 m alt.	31.XII.2010
Eg26ix16-744/ RJ20170516-2	Worker	VIETNAM: Nghe An Prov.: Pu Mat, N.P., N 18.95560°, E 104.68393°, 222 m alt. (near Tram Kiem Lam Khe Choang)	26.IX.2016
Eg24ix16-708/ RJ20170516-4	Worker	VIETNAM: Nghe An Prov.: Pu Mat, N19.17543°, E104.62068°, 154 m alt. (Sang Le Forest)	24.IX.2016
Eg16ix16-572/ RJ20170516-1	Worker	VIETNAM: Thanh Hoa prov.: Ben En N.P., N19.54140°, E105.49043°, 46 m alt. (near Xuan Thai Forestry sta.)	16.IX.2016
AD17CP83/ RJ20170613-9	Worker	VIETNAM: Ninh Binh: Nho Quan: Cuc Phuong N.P., N20˚21'00", E105˚35'36"−34'41", ca. 212 m alt.	24.III.2017
AD17CP99/ RJ20170613-10	Worker	VIETNAM: Ninh Binh: Nho Quan: Cuc Phuong N.P., N20˚20'58"−21'20", E105˚35'40", ca. 481 m alt.	25.III.2017
SAGO-06-12/ RJ20141201-14	Worker	INDONESIA: West Sumatra: 50 Kota District: Mt. Sago	06.IX.2012
GTH-01-12/ RJ20141201-2	Worker	INDONESIA: West Sumatra: 50 Kota District: Harau, Gantiang	10.IX.2012
LBT-10-12/ RJ20141201-10	Worker	INDONESIA: West Sumatra: Tanah Datar District: Barulak	05.IX.2012

LBT-09-12/ RJ20141201-7	Worker	INDONESIA: West Sumatra: Tanah Datar District: Barulak	05.IX.2012
LBT-07-12/ RJ20141201-9	Worker	INDONESIA: West Sumatra: Tanah Datar District: Barulak	05.IX.2012
LBT-06-12/ RJ20141201-8	Worker	INDONESIA: West Sumatra: Tanah Datar District: Barulak	05.IX.2012
GK-15-12/ RJ20141201-13	Worker	INDONESIA: Aceh: Leuser Ecosystem, ca. 980 m alt.	19.IX.2012
BMS-22-12/ RJ20141201-3	Worker	INDONESIA: Aceh: W. Simeulue Island: Babul Makmur	15.IX.2012
RS-36-PQ15/ RJ20151125-11	Worker	VIETNAM: Kien Giang: Phu Quoc: Bai Thom: Xom Moi: K7, N10˚21'50", E103˚59'29", ca. 35 m alt.	09.IX.2015
RS-73-PQ15/ RJ20151125-10	Worker	VIETNAM: Kien Giang: Phu Quoc: Ganh Dau: Xom Moi, N10˚21'25–33", E103˚52'33–38", ca. 35–70 m alt.	13.IX.2015
RS-61-PQ15/ RJ20151125-12	Worker	VIETNAM: Kien Giang: Phu Quoc: Ganh Dau: Xom Moi, N10˚21'25–33", E103˚52'33–38", ca. 35–70 m alt.	13.IX.2015
RS-80-PQ15/ RJ20151125-14	Worker	VIETNAM: Kien Giang: Phu Quoc: Ganh Dau: Xom Moi, N10˚21'25–33", E103˚52'33–38", ca. 35–70 m alt.	13.IX.2015
Eg13ix15-17/ RJ20170104-14	Worker	VIETNAM: Kien Giang: Phu Quoc: Ganh Dau: Xom Moi, N10˚20'55", E103˚55'00", ca. 50 m alt.	13.IX.2015
MS14-18/ RJ20150126-5	Worker	MALAYSIA: Ulu Gombak	III.2014
RS01-PDG-14/ RJ20150126-1	Worker	INDONESIA: West Sumatra: Padang: Andalas University’s forest	22.IX.2014
PDG-22-12/ RJ20141201-1	Worker	INDONESIA: West Sumatra: Padang: Andalas University’s forest	10.X.2012
SAGO-01-02/ RJ20150126-3	Worker	INDONESIA: West Sumatra: Mt. Sago, 50 Kota District, ca. 1000 m alt.	06.IX.2012
GK-38-12/ RJ20150126-4	Worker	INDONESIA: Aceh: Leuser Ecosystem, ca. 1100 m alt.	20.IX.2012
PKJ-33-12/ RJ20141114-4	Worker	INDONESIA: Bali: W. Bali, Mendaya, Dusun PK Jelati	22.X.2012
PKJ-24-12/ RJ20141114-7	Worker	INDONESIA: Bali: W. Bali, Mendaya, Dusun PK Jelati	22.X.2012
LW-09-12/ RJ20141201-4	Worker	INDONESIA: Aceh: Simeulue Island, Babul Makmur	15.IX.2012
LMR-01-12/ RJ20141201-5	Worker	INDONESIA: Aceh: Simeulue Island, Alafan: Lamerem	15.IX.2012
MEF-14-12/ RJ20141201-11	Worker	INDONESIA: Flores: Nusa Tenggara Timur: Sikka: Maumere	16.X.2012

MEF-10-12/RJ20141201-12	Worker	INDONESIA: Flores: Nusa Tenggara Timur: Sikka: Maumere	16.X.2012
RS-100-BV16/ RJ20160512-1	Worker	VIETNAM: Hanoi: Ba Vi N.P., 21°04’33”N, 105°22’02”E, ca. 710 m alt.	29.II.2016
RS-41-CYS16/ RJ20160512-2	Worker	VIETNAM: Dak Lak: Chu Yang Shin N.P.: Area 1359: 12˚24’42.9”N, 108˚21’08”E	05.III.2016

Table 3-2. The type materials of the genus *Odontomachus*. The number of specimens examined is given in parentheses. The abbreviations of the type depositories are as belows: BMNH, The National History Museum, London, UK; IZCAS, Institute of Zoology, Chinese Academy of Sciences, Beijing, China; NIAES, National Institute for Agro-Environmental Sciences, Tsukuba, Japan; MSNG, Museo Civico di Storia Naturele "Giacomo Doria", Genoa, Italy; MZB, Zoological Museum Bogoriense, Bogor, Indonesia; SEHU, Laboratory of Systematic Entomology, Hokkaido University, Hokkaido, Japan.

Taxon names	Caste	Categories	Depositories	Type locality
Odontomachus circulus Wang, 1993	Worker	Holotype	IZCAS	CHINA: Yunnan
Odontomachus kuroiwae (Mastumura, 1912)	Worker	Lectotype	SEHU	JAPAN: Okinawa
Odontomachus kuroiwae (Mastumura, 1912)	Worker	Paralectotype (n=1)	SEHU	JAPAN: Okinawa
Odontomachus latidens subsp. *procerus* Emery, 1893	Queen	Holotype	MSNG	MALAYSIA: Perak
Odontomachus latidens subsp. *sumatranus* Emery, 1900	Worker	Syntype (n=9)	MSNG	INDONESIA: North Sumatra: Si-Rambe
Odontomachus latidens subsp. *sumatranus* Emery, 1900	Queen	Syntype (n=2)	MSNG	INDONESIA: North Sumatra: Si-Rambe
Odontomachus minangkabau Satria *et al.,* 2015	Worker	Holotype	MZB	INDONESIA: West Sumatra: Padang
Odontomachus monticola Emery, 1892	Worker	Lectotype	MSNG	MYANMAR: Carin Checù
Odontomachus monticola Emery, 1892	Worker	Paralectotype (n=1)	MSNG	MYANMAR: Carin Checù
Odontomachus monticola Emery, 1892	Worker	Paralectotype (n=2)	MSNG	MYANMAR: Carin Asciuii Cheba
Odontomachus monticola Emery, 1892	Worker	Syntype (n=2)	MSNG	MYANMAR: Carin Checù
Odontomachus monticola Emery, 1892	Queen	Syntype (n=1)	MSNG	MYANMAR: Carin Checù

Odontomachus monticola var. *formosae* Forel, 1912	Worker	Syntype (n=1)	BMNH	TAIWAN: Pilam
Odontomachus monticola var. *major* Forel, 1913	Worker	Syntype (n=1)	BMNH	TAIWAN: Taihorin
Odontomachus pararixosus Terayama *et* Ito, 2014	Worker	Holotype	NIAES	MALAYSIA: Ulu Gombak
Odontomachus rixosus F. Smith, 1857	Worker	Syntype (n=1)	BMNH	SINGAPORE
Odontomachus tensus Wang, 1993	Worker	holotype	IZCAS	CHINA: Yunnan

Table 3-3. Results of the Automatic Barcode Gap Discovery (ABGD) analyses.

Subst. Model	X	Partition	Prior Intraspecific divergence (*P*)							
			0.0359	**0.2154**	**0.0129**	**0.0077**	**0.0046**	**0.0028**	**0.0017**	**0.001**
Jukes-Cantor (JC69)	1	Initial					1	41	41	41
		Recursive							50	50
	0.8	Initial	1	5	11	11	11	41	41	41
		Recursive		6	25	29	40	42	52	52
	0.5	Initial	1	5	12	12	12	41	41	41
		Recursive		6	25	31	40	42	52	52
K2P (K80)	1	Initial	1	7	7	7	7	41	41	41
		Recursive		9	9	13	13		48	48
	0.8	Initial	1	7	7	32	32	41	41	41
		Recursive		10	10	35	40	42	52	52
	0.5	Initial	1	7	16	32	32	41	41	41
		Recursive		10	27	35	40	42	52	52
P-distance	1	Initial								1
		Recursive								1
	0.8	Initial				1	34	28	28	28
		Recursive						32	32	32
	0.5	Initial	1	8	8	26	34	28	28	28
		Recursive		10	10	27		32	32	32

Table 3-4. CO1-based intraspecific variation and interspecific divergence (K2P). Interspecific variation were not calculated for the species in which a single was available. Numbers of specimens used for calculation were given in the round parentheses.

Species	Intraspecific		Interspecific	
	Max	Min	Min	Max
Anochetus mixtus (n=1)			8.60%	19.80%
Anochetus princeps (n=1)			8.60%	19.60%
Odontomachus floresensis (n=2)	0.30%	0.30%	10.10%	16.40%
Odontomachus kuroiwae (n=3)	2.80%	1.50%	3.50%	15.20%
Odontomachus latidens (n=1)			10.10%	16.60%
Odontomachus minangkabau (n=1)			6.90%	15.40%
Odontomachus monticola (n=14)	3.30%	0.20%	3.30%	16%
Odontomachus pararixosus (n=1)			5.80%	15.20%
Odontomachus procerus (n=1)			9.40%	17.70%
Odontomachus rixosus (n=9)	3.30%	0.2%	5.80%	15.40%
Odontomachus silvestrii (n=4)	1.70%	0.20%	7.50%	16.40%
Odontomachus simillimus (n=2)	4%	4%	9.70%	19%
Odontomachus sp. 1 (n=19)	4.60%	0.20%	3.30%	17%
Odontomachus sp. 2 (n=4)	4.60%	0.20%	4.90%	19.80%

Table 3-5. The minimum pairwise K2P distances of the Folmer region of the CO1 gene among the Indo-Malayan and Indo-Chinese species of *Odontomachus*. The identical sequence excluded from analysis. Number of sequences is shown in parenthesis.

No.	Species	1	2	3	4	5	6	7	8	9	10	11	12	13
1	*A. mixtus* (n=1)													
2	*A. princeps* (n=1)	0.086												
3	*O. floresensis* (n=2)	0.143	0.141											
4	*O. kuroiwae* (n=3)	0.144	0.150	0.114										
5	*O. latidens* (n=1)	0.164	0.156	0.143	0.121									
6	*O. minangkabau* (n=1)	0.154	0.139	0.119	0.101	0.109								
7	*O. monticola* (n=1)	0.155	0.155	0.120	0.047	0.123	0.097							
8	*Odontomachus* sp. 1 (n=19)	0.157	0.162	0.126	0.049	0.132	0.106	0.043						
9	*Odontomachus* sp. 2 (n=4)	0.174	0.175	0.137	0.066	0.143	0.107	0.065	0.074					
10	*O. pararixosus* (n=1)	0.152	0.135	0.127	0.100	0.103	0.077	0.097	0.106	0.113				
11	*O. procerus* (n=1)	0.177	0.170	0.129	0.108	0.115	0.094	0.113	0.120	0.109	0.109			
12	*O. rixosus* (n=9)	0.145	0.141	0.110	0.098	0.110	0.073	0.091	0.101	0.107	0.062	0.096		
13	*O. silvestrii* (n=5)	0.148	0.158	0.119	0.095	0.127	0.111	0.081	0.090	0.109	0.107	0.132	0.097	
14	*O. simillimus* (n=2)	0.187	0.168	0.108	0.120	0.131	0.115	0.121	0.128	0.138	0.105	0.138	0.101	0.110

Table 3-6. A summary of the present integrated taxonomy.

<table>
<tr><th colspan="2">MOTUs</th><th colspan="3">Monophyly</th><th rowspan="2">Morphology</th><th rowspan="2">Identification</th></tr>
<tr><th>ABGD</th><th>PTP</th><th>CO1-based ML</th><th>COI-Based BI</th><th>28S-based ML</th></tr>
<tr><td>ABGD-1</td><td>PTP-1</td><td>CML1</td><td>CBI1</td><td rowspan="27">S1</td><td rowspan="6">M1</td><td rowspan="12">Odontomachus sp. 1</td></tr>
<tr><td>ABGD-2</td><td>PTP-2</td><td>CML2</td><td>CBI2</td></tr>
<tr><td>ABGD-3</td><td>PTP-3</td><td>CML3</td><td>CBI3</td></tr>
<tr><td>ABGD-4</td><td>PTP-4</td><td>CML4</td><td>CBI4</td></tr>
<tr><td>ABGD-5</td><td>PTP-5</td><td>CML5</td><td>CBI5</td></tr>
<tr><td>ABGD-6</td><td>PTP-6</td><td>CML6</td><td>CBI6</td></tr>
<tr><td>ABGD-7</td><td>PTP-7</td><td>CML7</td><td>CBI7</td><td rowspan="6">M2</td></tr>
<tr><td>ABGD-8</td><td>PTP-8</td><td>CML8</td><td>CBI8</td></tr>
<tr><td>ABGD-9</td><td>PTP-9</td><td>CML9</td><td>CBI9</td></tr>
<tr><td>ABGD-10</td><td>PTP-10</td><td>CML10</td><td>CBI10</td></tr>
<tr><td>ABGD-11</td><td rowspan="2">PTP-11</td><td>CML11</td><td>CBI11</td></tr>
<tr><td>ABGD-12</td><td>CML12</td><td>CBI12</td></tr>
<tr><td>ABGD-13</td><td>PTP-12</td><td>CML13</td><td>CBI13</td><td rowspan="9">M3</td><td rowspan="9">O. monticola</td></tr>
<tr><td>ABGD-14</td><td>PTP-13</td><td>CML14</td><td>CBI14</td></tr>
<tr><td>ABGD-15</td><td>PTP-14</td><td>CML15</td><td>CBI15</td></tr>
<tr><td>ABGD-16</td><td>PTP-15</td><td>CML16</td><td>CBI16</td></tr>
<tr><td>ABGD-17</td><td rowspan="5">PTP-16</td><td rowspan="5">CML17</td><td rowspan="5">CBI17</td></tr>
<tr><td>ABGD-18</td></tr>
<tr><td>ABGD-19</td></tr>
<tr><td>ABGD-20</td></tr>
<tr><td>ABGD-21</td></tr>
<tr><td>ABGD-22</td><td>PTP-17</td><td>CML18</td><td>CBI18</td><td rowspan="4">M4</td><td rowspan="4">O. kuroiwae</td></tr>
<tr><td rowspan="2">ABGD-23</td><td>PTP-18</td><td rowspan="2">CML19</td><td rowspan="2">CBI19</td></tr>
<tr><td>PTP-19</td></tr>
<tr><td>ABGD-24</td><td>PTP-20</td><td>CML20</td><td>CBI20</td></tr>
<tr><td>ABGD-25</td><td>PTP-21</td><td rowspan="2">CML21</td><td rowspan="2">CBI21</td><td rowspan="2">M5</td><td rowspan="2">Odontomachus sp. 2</td></tr>
<tr><td>ABGD-26</td><td>PTP-22</td></tr>
<tr><td rowspan="2">ABGD-27</td><td>PTP-23</td><td rowspan="2">CML22</td><td rowspan="4">CBI22</td><td rowspan="5">S2</td><td rowspan="4">M6</td><td rowspan="4">O. silvestrii</td></tr>
<tr><td>PTP-24</td></tr>
<tr><td rowspan="2">ABGD-28</td><td>PTP-25</td><td>CML23</td></tr>
<tr><td>PTP-26</td><td>CML24</td></tr>
<tr><td>ABGD-29</td><td>PTP-27</td><td>CML25</td><td>CBI23</td><td>M7</td><td>O. rixosus</td></tr>
</table>

<table>
<tr><td>ABGD-30</td><td>PTP-28</td><td>CML26</td><td>CBI24</td><td rowspan="8"></td><td rowspan="4"></td><td rowspan="4"></td></tr>
<tr><td>ABGD-31</td><td>PTP-29</td><td>CML27</td><td rowspan="3">CBK25</td></tr>
<tr><td>ABGD-32</td><td>PTP-30</td><td rowspan="2">CML28</td></tr>
<tr><td>ABGD-33</td><td>PTP-31</td></tr>
<tr><td>ABGD-34</td><td>PTP-32</td><td>CML29</td><td>CBI26</td><td>M8</td><td>O. pararixosus</td></tr>
<tr><td>ABGD-35</td><td>PTP-33</td><td>CML30</td><td>CBI27</td><td>M9</td><td>O. minangkabau</td></tr>
<tr><td>ABGD-36</td><td>PTP-34</td><td>CML31</td><td>CBI28</td><td>M10</td><td>O. procerus</td></tr>
<tr><td>ABGD-37</td><td>PTP-35</td><td>CML32</td><td>CBI29</td><td>M11</td><td>O. latidens</td></tr>
<tr><td rowspan="2">ABGD-38</td><td>PTP-36</td><td rowspan="2">CML33</td><td rowspan="2">CBI30</td><td rowspan="5">S3</td><td rowspan="4">M12</td><td rowspan="4">O. simillimus</td></tr>
<tr><td>PTP-37</td></tr>
<tr><td rowspan="2">ABGD-39</td><td>PTP-38</td><td rowspan="2">CML34</td><td rowspan="2">CBI31</td></tr>
<tr><td>PTP-39</td></tr>
<tr><td>ABGD-40</td><td>PTP-40</td><td>CML35</td><td>CBI32</td><td>M13</td><td>O. floresensis</td></tr>
</table>

Chapter IV.

Taxonomic Revision of Indo-Chinese and Indo-Malayan Species of the Ant Genus *Odontomachus* Latreille, 1804 (Hymenoptera: Formicidae: Ponerinae)

IV-1. Introduction

The genus *Odontomachus* was established by Latreille in 1804 with *Formica haematoda* Linnaeus, 1758 as the type species. The genus is currently assigned to the *Odontomachus* genus group in the tribe Ponerini, the subfamily Ponerinae based on the result of a recent molecular phylogenetic analysis (Schmidt, 2013; Schmidt & Shattuck, 2014). The full synonym list is given in Bolton (2016), and the taxonomic history of the genus is summarized in the Table 1-1. *Odontomachus* is easily recognized among other Ponerine ants by large size, bizzare head with long and straight mandibles, *nuchal carina of the posterior face of head V-shaped, *apophyseal lines well recognized as a pair of dark lines, absent of propodeal teeth, and pointed dorsal apex of petiolar node, and distinguishable from its syster group, the genus *Anochetus*, by the characteristics marked with asterisks (Brown, 1976).

Brown (1976), in his revision of the genus *Odontomachus* of the world, recognized 51 valid species, and classified them into 12 species groups which are defined well by the morphology of the worker: *O. assiniensis* group (Afrotropical region), *O. bradleyi* group (Neotropical region), *O. cornutus* group (Brazilian subregion), *O. coquereli* group (Malagasy subregion), *O. haematodus* group (mainly in New World), *O. hastatus* group (Neotropical region), *O. infandus* group (Philippines and Austro-Malayan subregion), *O. mormo* group (Neotropical region), *O. rixosus* group (Indo-Chinese and Indo-Malayan subregions), *O. ruficeps* (Austro-Malayan and Australian subregions), *O. saevissimus* group (Austro-Malayan subregion), and *O. tyrannicus* group (Austro-Malayan subregion). Recently Sorger & Zettel (2011), in their revision of the Philippine *Odontomachus*, established two more species groups which are also defined well by the morphology of the worker: *O. malignus* group (Indo-Malayan and Austro-Malayan subregions) and *O. silvestrii* group (Indo-Chinese subregion).

Since Brown (1976), several regional revisions and taxonomic notes of the genus have been presented by Wang (1993) (China), Yoshimura *et al*. (2007) (Japan), Wilson (1959) (Melanesia), Fisher & Smith (2008) (Madagascar), Sorger & Zettel (2011) (Philippines), Terayama & Ito (2014) (Malay Peninsula, Malaysia), MacGown *et al*. (2014) (United States), and Satria *et al*. (2015) (Sumatra Island, Indonesia). Currently, a total 72 extant and 3 fossil species of the genus *Odontomachus* were recognized. The majority of the species has been known from pantropical and pansubtropical zones, though the Neotropical and Oriental regions seem to be the centers of the species richness. A few species extend into the temperate zones, specifically in the southwestern United States, northeastern China, central Argentina, and southwestern Australia (Schmidt & Shattuck, 2014; Bolton, 2016; Larabee *et al.*, 2016). Currently, 72 extant species and 3 fossil were recognized; a majority of the species has been known from pantropical and pansubtropical zones, and a few species extend into the temperate zones; Neotropical and Oriental regions seem to be the centers of the species richness (Bolton, 2016).

Brown is a so-called "lumper", that is to say that Brown (1976) conservatively delimitate species and synonymized many species and intraspecific names into one. His view had been later questioned by some taxonomists. Yoshimura *et al*. (2007) revised East Asian populations of the genus based on morphological characters, including those of the male genitalia, and then revived *O. kuroiwae* which was synonymized by Brown (1976) under *O. monticola*. Satria *et al*. (2015) revised Sumatran populations of the genus by morphological approach and DNA barcoding, and revived *O. procerus* which was synonymized by Brown (1976) under *O. latidens*. Terayama & Ito (2014), based on morphological characters of the worker and phenotypes of the queen, deliminated a cryptic species, *O. pararixosus*, in *O. rixosus* sensu Brown (1976). These facts suggest that the species diversity of the genus *Odontomachus* has not yet been fully revealed, despite their large-sized body, bizzare habitus, and dominance in the ground-dwelling ant faunas.

Therefore, in the chapter III, the delimitation of the Indo-Chinese and Indo-Malayan species of *Odontomachus* was clarified by integrated taxonomy, a combination of DNA barcoding, phylogenetic analyses, morphological examination and phylogeographic consideration. As the results, a total of 12 species were recognized, and the following 11 species were known from the Indo-Chinese and Indo-Malayan subregions: *O. kuroiwae*, *O. latidens*, *O. minangkabau*, *O. monticola, O. pararixosus*, *O. procerus*, *O. rixosus*, *O.* silvestrii, O. *simillimus*, *Odontomachus* sp. 1, *Odontomachus* sp. 2.

Therefore, in the present chapter, the species-level classification of the Indo-Chinese and Indo-Malayan species of *Odontomachus* is revised by referring to the results of the chapter III, and also by morphologically examining, the following six species described from from the Indo-Chinese and Indo-Malayan subregions and its adjacent areas were unable to be included in the analyses because of lack of fresh specimens suitable for DNA barcoding: *O. circulus, O. fulgidus, O. granatus, O. malignus, O. tensus,* and *O. xizangensis*.

IV-2. Materials and Methods

IV-2-1. Material Examined

The present study was conducted based on the type and non-type materials from the Indo-Chinese and Indo-Malayan subregions, and adjacent areas (for details see "Type material examined" and "Non-type material examined" of each species). Abbreviations of specimen depositories are as follows.

ACEG	Collection managed by Katsuyuki Eguchi, Systematic Zoology Laboratory, Department of Biological Sciences, Tokyo Metropolitan University.
AUMNS	Department of Biology, Faculty of Mathematics and Natural Sciences, Andalas University, West Sumatra, Indonesia.
BMNH	The Natural History Museum, London, U.K.
IEBR	Institute of Ecology and Biological Resources, Hanoi, Vietnam
IZCAS	Institute of Zoology, Chinese Academy of Sciences, Beijing, China
MZB	Museum Zoological Bogoriense, Bogor, Indonesia.

MSNG	Museo Civico di Storia Naturele "Giacomo Doria", Genoa, Italy.
MCZC	Museum of Comparative Zoology, Cambridge, MA, U.S.A.
MIZ	Museum and Institute of Zoology, Polish Academy of Sciences, Warsaw, Poland
NHMW	Naturhistorisches Museum, Vienna, Austria.
NIAES	The National Institute for Agro-Environmental Sciences, Tsukuba, Japan
RSC	Collection managed by Rijal Satria.
SEHU	Laboratory Systematic Entomology Collection, Hokkaido University, Hokkaido, Japan.
SKYC	Collection managed by Prof. Seiki Yamane, Kagoshima, Japan.

Images of the type specimens provided in AntWeb v5.17.5 (http://www.antweb.org) were examined to reconfirm our species recognition when the need arose (for details of the images see Type materials and Images examined for each species).

IV-2-2. Specimen Preparation, Observation and Imaging

Point-mounted specimens of the worker, queen, and male were examined and measured with a Nikon SMZ1000 stereomicroscope under suitable magnifications. Multi-focused montage images were produced using Helicon Focus Pro (Helicon Soft Ltd., http://www.heliconsoft.com/) from a series of source images taken by a Panasonic Lumix DMC-GX8 and Canon EOS KissX5 digital camera attached to a Nikon ECLIPSE E600 microscope, or by a Canon EOS 60D digital camera with a MPE Canon 65 mm lens. Artifacts/ghosts and unnecessary parts (unfocused appendages, insect pin, etc.) surrounding or covering target objects were erased and cleaned up using the retouching function of Helicon Focus Pro, and the color balance, contrast and sharpness were adjusted using Adobe Photoshop CS6.

IV-2-3. Measurement and Terminology

The following parts of the bodies were measured using ImageJ 1.49m (National Institute of mental Health, USA, available at http://imageJ.nih.gov/ij/) based on the photographs taken using a Panasonic Lumix DMC-GX8 digital camera attached to the Nikon AZ100 microscope, or using a Canon EOS 60D digital camera with a MPE Canon 65 mm lens. The abbreviations used for the measurements and indices are as follows:

CI	Cephalic Index. HW/HL × 100.
EL	Eye Length. Diameter of major axis of eye measured in lateral view.
EW	Eye Width. Diameter of minor axis of eye in lateral view (male only).
IFLW	Inter-Frontal Lobe Width. Maximum distance between outermost margins of frontal lobe (worker and queen). The frontal lobe is equivalent to the median arch of the torulus in Keller (2011).
FWL	Forewing Length. Maximum length of forewing (alate queen and male).
HL	Head Length. Maximum length of head in full-face view, measured from anteriormost point of clypeus to midpoint of a line drawn across posterior margin of head (including ocelli in male).
HW	Head Width. Maximum width of head in full-face view at eye level.
MDI	Mandible Index. MDL/HL × 100.
MDL	Mandible Length. Maximum length of mandible measured from mandibular insertion to apicalmost point of mandible (worker and queen).
OL	Ocellus Length. Diameter of major axis of median ocellus (queen and male).
OED	Ocellus-Eye Distance. Maximum distance between lateral ocellus and compound eye (male only).
PTH	Petiole Height. Maximum height of petiole from ventralmost point of subpetiolar process to an imaginary line tangential to apex as measured in lateral view.
PTHI	Petiole Height Index. PTH/PTL × 100.
PTL	Petiole Length. Maximum length of petiole measured in lateral view.
SI	Scape Index. SL/HW × 100.
SL	Scape Length. Maximum length of antennal scape excluding basal constriction.

WL Weber Length. Maximum diagonal distance of mesosoma in lateral view, measured from base of anterior slope of pronotum to posteriormost point of propodeal lobe.

Morphological terminology follows Brown (1976), Yoshimura *et al*. (2007), Yoshimura & Fisher (2007), and Boudinot (2013).

IV-3. Taxonomy

IV-3-1. Taxonomic remarks and synopsis of Indo-Chinese and Indo-Malayan species of *Odontomachus*

A total of 14 species were recognized in the Indo-Chinese and Indo-Malayan subregion. *Odontomachus circulus* Wang, 1993 was synonymized with *O. monticola* Emery, 1892, *O. tensus* Wang, 1993 with *O. rixosus* F. Smith, 1857, and *O. granatus* Wang, 1993 with *O. silvestrii* Wheeler, 1927.

The 14 species were assigned into four species groups sensu Brown (1976) and Sorger & Zettel (2011): 11 species belonging to the *O. rixosus* group; *O. simillimus* F. Smith, 1858 to the *O. haematodus* group; *O. malignus* F. Smith, 1859 to the *O. malignus* group, and *O. silvestrii* Wheeler, 1927 to the *O. silvestrii* group.

Since Brown (1976) established the *Odontomachus rixosus* group consisting of three species, *O. latidens*, *O. monticola* and *O. rixosus*, his view had been questioned by some taxonomists (Wang, 1993; Yoshimura *et al*., 2007; Terayama & Ito, 2014; Satria *et al*., 2015). The present study is the first comprehensive revision for the *Odontomachus rixosus* group after Brown (1976). Based on the result of integrated taxonomy (the chapter III) and comparative morphological examinations (for the species that known from the type series only), 11 species including a new species were recognized.

Brown (1976) assumed that "*Odontomachus monticola*" is a widespread species showing a wide range of morphological variations, such as sculpture on the vertex of head and pronotal disc, and synonymized the following taxa under *O. monticola* Emery, 1892: *O. monticola* var. *formosae* Forel, 1912; *O. monticola* var. *major* Forel, 1913; *O. monticola* var. *hainanensis* Stitz, 1925; and *O. kuroiwae* (Matsumura, 1912). Later, Yoshimura *et al*. (2007) revived *O. kuroiwae* as a valid species. The resuts of the present integrated taxonomy (the chapter III) strongly supported the treatment by Yoshimura *et al*. (2007). Furthermore, *Odontomachus* sp. 1

recognized as an independent species by the present integrated taxonomy seems to correspond to *O. monticola* var. *formosae* Forel, 1912, *O. monticola* var. *major* Forel, 1913 and *O. monticola* var. *hainanensis* Stitz, 1925. Further intensive sampling in southern China (including the Hainan Island) will allow us confirming the status of *Odontomachus* sp. 1. So, the striation on the vertex of head and pronotal disc are one of the important morphological characters to distinguished species in the *O. rixosus* group.

Odontomachus fulgidus Wang, 1993

Odontomachus kuroiwae (Matsumura, 1912)

Odontomachus latidens Mayr, 1867

Odontomachus malignus F. Smith, 1859

- *Odontomachus tuberculatus* Roger, 1861
- *Odontomachus retrolatior* Viehmeyer, 1914

Odontomachus minangkabau Satria *et al*., 2015

Odontomachus monticola Emery, 1892

- *Odontomachus monticola* var. *longi* Forel, 1900
- *Odontomachus monticola* var. *formosae* Forel, 1912
- *Odontomachus monticola* var. *major* Forel, 1913
- *Odontomachus monticola* var. *punctulatus* Forel, 1900
- *Odontomachus monticola pauperculus* Wheeler, 1921
- *Odontomachus monticola* var. *hainanensis* Stitz, 1925
- *Odontomachus latidens striata* Menozzi, 1930
- *Odontomachus circulus* Wang, 1993 **syn. nov.**

Odontomachus pararixosus Terayama *et* Ito, 2014

Odontomachus procerus Emery, 1893

- *Odontomachus latidens* subsp. *sumatranus* Emery, 1900

Odontomachus rixosus F. Smith, 1857

- *Odontomachus rixosus* var. *obscurior* Forel, 1900
- *Odontomachus rixosus* var. *conifera* Forel, 1913
- *Odontomachus tensus* Wang, 1993 **syn. nov.**

Odontomachus silvestrii Wheeler, 1927

- *Odontomachus silvestrii* var. *substriatus* Wheeler, 1927

Odontomachus granatus Wang, 1993 **syn. nov.**

Odontomachu simillimus F. Smith, 1858

Ponera pallidicornis F. Smith, 1860

Odontomachus haematodus var. *fuscipennis* Forel, 1913

Odontomahus haematoda var. *breviceps* Crawley, 1915

Odontomachus xizangensis Wang, 1993

Odontomachus sp. 1

Odontomachus sp. 2

IV-3-2. Key to species groups known from the Indo-Chinese and Indo-Malayan subregions, based on the worker caste

1. Subapical tooth truncate or blunt at apex (red arrow in Fig. 4-1B or blue arrow in Fig 4-1C). ... 2
- Subapical tooth acute at apex (black arrow in Fig. 4-1A). ... 3

2. Subapical tooth with blunt at apex (blue arrow in Fig. 4-1C); palp formula 4, 3; pronotal disk with long standing setae. ... *O. haematodus* group (*O. simillimus*)
- Subapical tooth truncate at apex (red arrow in Fig. 4-1B); palp formula 4, 4; pronotal disk without long standing setae. ... *O. rixosus* group

3. Head posteriorly with a pair of small and distinct tubercles; mesosoma in lateral view short and stout; mesopleuron with very sparse pubescence. ... *O. malignus* group (*O. malignus*)
- Head without tubercles; mesosma in lateral view long and slender; mesopleuron entirely covered by very dense pubescence. ... *O. silvestrii* group (*O. silvestrii*)

IV-3-3. Key to species of the *Odontomachus rixosus* species group, based on the worker caste

1. Subapical tooth shorter than broad with truncate apex; minimum distance between margin of ocular ridge and margin of compound eye less than half the length of major axis of compound eye. … 2
- Subapical tooth longer than broad with truncate apex; minimum distance between margin of ocular ridge and margin of compound eye less than half the length of major axis of compound eye. … 10

2. Pronotal disc smooth and shiny (Figs. 4-3C, 4-4C). … 3

- Pronotal disc with distinct concentric striation or fine transverse striation (Figs. 4-14C, 4-28E, 4-29E, 4-31E). … 4

3. Body and legs yellowish brown. … *O. fulgidus*

- Body reddish brown; legs orange. … *O. kuroiwae*

4. Pronotal disc with fine transverse striation. … 5

- Pronotal disc with distinct concentric striation. … 6

5. Dorsum of head with fine longitudinal striation; mesopleuron with carinate anterodorsal margin, and indistinctly separated from mesonotum (red arrow in Fig. 4-29D); mesosoma with fine dense pubescence; mesopleuron entirely striated or entirely finely sculptured. … *Odontomachus* sp. 1

- Dorsum of head smooth and shiny; mesopleuron with weakly carinate anterodorsal margin, clearly separated by distinct dorsal carina from mesonotum and metapleuron (red arrown in Fig. 4-19C); mesosoma with fine sparse pubescence; mesopleuron generally smooth and shiny, with anterior third and posteriormost parts faintly sculptured. … 5

5. Masticatory margin of mandible with very small denticles or sometimes without denticles (only preapical angle is recognizable); propodeal dorsum anteriorly with a very weak median longitudinal depression; gastral tergite I with short erect setae; subpetiolar process in lateral view lobate and directed ventrally (Fig. 4-2B). … *O. latidens*

- Masticatory margin of mandible with 6–9 distinct denticles which are reduced in size toward base of mandible; propodeal dorsum anteriorly without a median longitudinal depression; gastral tergite I without erect setae; subpetiolar process in lateral view triangular and directed posteriorly (Fig. 4-2A). … *O. procerus*

6. Body reddish brown. … *O. xizangensis*

- Body dark brown. … 9

9. Long axis of compouned eye with 17−18 ommatidia; subpetiolar process in lateral view lobate and directed anteriorly; body relatively opaque. … *O. monticola*

- Long axis of compound eye with 10−12 ommatidia; subpetiolar process in lateral view triangular and directed ventrad; body relatively shiny. … *Odontomachus* sp. 2

10. Gastral tergite I with long standing setae. … *O. pararixosus*

- Gastral tergite I without any long standing setae. …11

11. Size large (HL 3.13–3.55 mm; WL 4.15–4.65 mm); median part of vertex immediately along median furrow transversely striate; masticatory margin of mandible with more than 10 denticles; pronotal disc densely and transversely striate. … *O. minangkabau*

- Size small (HL 2.56–3.03 mm; WL 3.35–4.00 mm); median part of vertex immediately along median furrow smooth and shiny or sometimes with rough texture, but not transversely striate; masticatory margin of mandible with 10 or fewer denticles; pronotal disc usually with concentric striation (but rarely with transverse striation). … *O. rixosus*

IV-3-4. Description/redescription of the Indo-Chinese and Indo-Malayan species of the *Odontomachus rixosus* species group

Odontomachus rixosus species group

Diagnosis of the worker. Head in full-face view slightly longer than broad, with posterior margin weakly concave to almost stright; masticatory margin with a single series of distinct denticles; subapical teeth truncate at apex; palp formula 4, 4; mesopleuron without anteroventral ridge; pronotal disc and gastral tergite I without erect setae (except for *O. latidens* and *O. pararixosus*).

Odontomachus fulgidus Wang, 1993

(Fig. 4-3)

Odontomachus fulgidus Wang, 1993: 222, fig. 3, worker, type locality: China (Guizhou).

Type material examined. *Odontomachus fulgidus* — holotype (worker; IZCAS), China: Guizhou Province; paratype (1 worker; IZCAS), same data as holotype.

Worker measurements and indices. *Odontomachus fulgidus* — holotype: HW 1.61 mm, HL 2.06 mm, SL 1.78 mm, IFLW 0.46 mm, EL 0.26 mm, MDL 1.02 mm, WL 2.48 mm, PTL 0.37 mm, PTH unmeasured, CI 78, SI 110, MDI 49, PTHI incalculable.

Worker description. Body relatively small (HL 2.06 mm; WL 2.48 mm). Head in full-face view slightly longer than broad, with posterior margin weakly concave; head posteriorly without a pair of small and distinct tubercles; median furrow on vertex present as dark line; each side of median furrow not swollen dorsad; frontal lobes followed by strong frontal carinae which are slightly divergent posteriad; minimum distance between margin of ocular ridge and margin of compound eye half as long as major axis of compound eye; masticatory margin with 8–9 distinct denticles;

subapical tooth shorter than broad, with truncate apex. Mesosoma in lateral view relatively slender; pronotum including anteromedian lobe short, in lateral view with anterodorsal slope relatively steep; mesopleuron with anterodorsal margin weakly carinate, clearly separated by distinct dorsal carina from mesonotum and metapleuron; mesopleuron without anteroventral ridge, with anterodorsal margin weakly carinate, clearly separated by distinct dorsal carina from mesonotum and metapleuron; propodeum in lateral view with its dorsum almost straight, and gradually sloping posteriad, with posterior face steeply sloping; propodeal dorsum without median longitudinal depression; petiolar node conical, with sharply pointed apical spine; node excluding apical spine in lateral view with anterior and posterior faces weakly convex; apical spine of petiole with needle-shaped, less than 1/4 as long as petiolar height, and weakly curved posteriad; subpetiolar process as long as high, lobate, directed ventrad. Gastral tergite I in lateral view much short, with anterior face moderately long and vertical.

Head in full-face view largely smooth and shiny; area bordered by frontal carina and ocular ridge striate; area around eye smooth and shiny; frontal lobe with fine striation and shiny; extraocular furrow smooth and shiny; median part of vertex along median furrow smooth and shiny; lateral and ventral faces of head smooth and shiny; median disc of clypeus smooth and shiny. Pronotal disc in dorsal view smooth and shiny, with anterior lobe finely transversely striate; mesopleuron entirely smooth and shiny; propodeum with transverse striation which is a much sparser and stronger than that on mesonotum and metapleuron. Petiolar node entirely smooth and shiny.

Vertex with a pair of long erect setae; frontal lobe without seta; pronotal disc without long erect setae; gastral tergite I without any erect setae; head, mesosoma, petiole and gaster with fine sparse appressed pubescence, for length and density of pubescence same on the head, mesosoma, petiole and gaster.

For color see Fig. 4-3; body and appendages yellowish-brown, with head, mesosoma and gaster slightly darker.

Species recognition. This species is morphologically very similar to *O. kuroiwae*, but it can be easily distinguished from the latter by the following characteristics of the worker: body smaller in *O. fulgidus* (HL 2.06 mm; WL 2.48 mm) than in *O. kuroiwae* (HL 2.18–2.61 mm, WL 2.67–3.02 mm); gastral tergite I in lateral view much shorter in the former than in the latter; pronotal disc smooth and shiny in the former, but smooth and shiny or particularly striated in the latter; body and appendages yellowish brown in the former, but reddish brown in the latter.

Distribution. So far known from the type locality China (Guizhou Province).

Bionomics. The information of nesting and habitat preference of this species still unknown.

***Odontomachus kuroiwae* (Matsumura, 1912)**

(Figs. 4-4, 4-5, 4-6, 4-7A, 4-7C)

Myrtoteras kuroiwae Matsumura, 1912: 192 pl.54, fig 1,worker, type locality: Japan. In *Myrmoteras* by Mastumura and Uchida, 1926:51. In *Odontomachus* by Creighton, 1939; Terayama 2004: 21; Yoshimura *et al*., 2007: 93, figs. 2, 4, 6, male, queen.

Odontomachus monticola var. *formosae*: Teranishi, 1940: 61.

Odontomachus monticola: Brown, 1976: 105, 157−159 (in part); Ogata, 1987: 126 (in part), figs. 123−133, male.

Type material examined. *Odontomachus kuroiwae* — Lectotype (worker; SEHU), Japan: Okinawa; paralectotype (1 worker; SEHU), same data as lectotype.

Non-type materials examined. Japan: Okinawa-ken: Okinawa: Chibana: Chibanajoshi, N26˚21'47.8", E127˚48'38.2", ca. 58 m alt., along the road, 25. X.2016, R. Satria leg., RS-02-OKN16, 6 workers, 2 queens (RSC); same loc., 25. X.2016, R. Satria leg., RS-04-OKN16, 4 workers (RSC); same loc., N26˚21'47.7", E127˚48'38.1", ca. 60 m alt., along the road, 25. X.2016, R. Satria leg., RS-05-OKN16, 7 workers (RSC); same loc., N26˚21'47.5", E127˚48'37.9", ca. 69 m alt., along the road, 25. X.2016, R. Satria leg., RS-01-OKN16, 8 workers, 2 queens, 1 male (RSC); same loc., Nago-shi: Nago, N26˚35'19.4", E127˚59'34.5", ca. 93 m alt., along the road, 25. X.2016, R. Satria leg., RS-13-OKN16, 6 workers (RSC); same loc, 24.IV.1994, Sk. Yamane leg., 1 worker (RSC); same loc., N26˚35'19.2", E127˚59'34.5", ca. 84 m alt., along the road, 25. X.2016, R. Satria leg., RS-14-OKN16, 5 workers (RSC); same loc., N26˚35'18", E127˚59'36.4", ca. 95 m alt., along the road, 25. X.2016, R. Satria leg., RS-15-OKN16, 5 workers, 2 queens (RSC); same loc., Kunigami: Yona, N26˚45'17.8", E128˚13'31.8", ca. 187 m alt., along the road, 26. X.2016, R. Satria leg., RS-16-OKN16, 5 workers (RSC); same loc., N26˚44'49.6", E128˚14'17.1", ca. 321 m alt., along the road, 26. X.2016, R. Satria leg., RS-17-OKN16, 7 workers, 1 queen (RSC); same loc., N26˚43'40.3", E128˚11'44.6", ca. 217 m alt., along the road, 27. X.2016, R. Satria leg., RS-19-OKN16, 5 workers (RSC); same loc., N26˚43'55.2", E128˚13'24.7", ca. 312 m alt., along the road, 27. X.2016, R. Satria leg., RS-20-

OKN16, 7 workers, 1 queens (RSC); same loc., N26˚43'55.2", E128˚13'24.7", ca. 312 m alt., along the road, 27. X.2016, R. Satria leg., RS-21-OKN16, 8 workers (RSC).

Worker measurements and indices. Non-types (n=10): HW 1.70–2.05 mm, HL 2.18–2.61 mm, SL 2.03–2.37 mm, FLW 0.47–0.57 mm, EL 0.29–0.38 mm, MDL 1.26–1.48 mm, WL 2.67–3.02 mm, PTL 0.45–0.59 mm, PTH 0.9–1.09 mm, CI 75–80, SI 116–123, MDI 53–58, PTHI 180–208.

Worker description. Body relatively small (HL 2.18–2.61 mm, WL 2.67–3.02 mm). Head in full-face view slightly longer than broad, with posterior margin weakly concave; head posteriorly without a pair of small and distinct tubercles; median furrow on vertex present as dark line; each side of median furrow not swollen dorsad; frontal lobes followed by strong frontal carinae which are slightly divergent posteriad and then become nearly parallel; minimum distance between margin of ocular ridge and margin of compound eye half as long as major axis of compound eye; masticatory margin with 7–9 distinct denticles; subapical tooth shorter than broad, with truncate apex; palp formula 4, 4. Mesosoma in lateral view relatively stout; pronotum including anteromedian lobe short, in lateral view with anterodorsal slope relatively steep; mesopleuron without anteroventral ridge, with anterodorsal margin weakly carinate, clearly separated by distinct dorsal carina from mesonotum and metapleuron; propodeum in lateral view with dorsum almost straight, with posterior face steeply sloping; propodeal dorsum without median longitudinal depresion. Petiolar node conical, with sharply pointed apical spine; node excluding apical spine in lateral view with anterior face weakly convex and posterior face straight; apical spine needle-shaped, less than 1/4 as long as petiolar height, weakly curved posteriad (but shape variable within species); subpetiolar process triangular, directed posteriorly, with the maximum length of anterior-posterior axis shorter than that of dorsal-ventral axis. Gastral tergite I in lateral view relatively short, with anterior face moderately long and vertical.

Head in full-face view largely smooth and shiny; area bordered by frontal carina and ocular ridges striate; area around eye smooth and shiny; frontal lobe smooth and shiny; extraocular furrow faintly striate; median part of vertex along median furrow smooth and shiny; lateral and ventral faces of head smooth and shiny; median disc of clypeus smooth and shiny. Pronotal disc in dorsal view smooth and shiny, with anterior lobe finely transversely striate; lateral face of pronotum finely striate; mesonotum finely transversely striate; mesopleuron largely smooth and shiny, with anteriormost and posteriormost parts finely striate; metapleuron and propodeum with transverse striation which is a little sparser and stronger than that on pronotum and mesonotum. Petiolar node largely smooth and shiny, with basal area faintly striate.

Vertex with a pair of long erect setae; frontal lobe without seta; pronotal disc without long erect setae; gastral tergite I without erect setae. Head, mesosoma, petiole and gaster with fine appressed pubescence which is sparser and short on gaster.

For color see Fig. 4-4; body reddish brown, with darker mesosoma and gaster; legs orange; antennae reddish brown.

Queen measurements and indices. Non-types (n=5): HW 1.90–2.08 mm, HL 2.36–2.61 mm, SL 2.32–2.44 mm, IFLW 0.56–0.60 mm, EL 0.37–0.44 mm, MDL 1.34–1.46 mm, WL 2.98–3.22 mm, PTL 0.54–0.57 mm, PTH 1.23–1.29 mm, CI 79–81, SI 117–124, MDI 56–58, PTHI 221–230.

Queen description. Queen similar in general appearance to worker. Vertex near ocelli not swollen dorsad; ocular ridge well developed; distance between lateral ocelli as long as distance between lateral and median ocelli, and as long as major axis of median ocellus; ocelli in lateral view protruded dorsad. Mesosoma with main sclerites associated with wing function (Figs. 4-5D, 4-5E), in dorsal view short and stout; anterodorsal slope of pronotum in lateral view steep; anterodorsal outline of mesoscutum in lateral view relatively gentle; mesoscutum without posteromedian depression; parapsidal furrow very weak and slightly curved; dorsal outline of metascutellum in lateral view almost straight; anterior third of mesopleuron with deep, oblique furrow; propodeum in lateral view relatively short, with dorsum almost straight and gradually sloping posteriad; propodeum in dorsal view with lateral outlines parallel posteriad. Petiolar node excluding apical spine in lateral view with anterior face almost straight to weakly convex, and posterior face weakly convex; apical spine short and stout, and weakly curved posteriad; subpetiolar process triangular, directed ventrally, with the maximum length of anterior-posterior axis as long as that of dorsal-ventral axis. Gastral tergite I in lateral view relatively short, with anterior face moderately long and vertical.

Head in full-face view largely smooth and shiny; area bordered by frontal carinae and ocular ridges striate; frontal lobe weakly striate; extraocular furrow faintly striate; median part of vertex along median furrow smooth and shiny; lateral face largely smooth and shiny with posterior parts very faintly striate; venter of head smooth and shiny; median disc of clypeus with rough texture. Pronotum densely and weakly striate transversely; mesoscutum largely smooth and shiny, with faint striae on anterior part and posteromedian depression; mesopleuron largely smooth and shiny, with anteriormost and posteriormost parts faintly striate; mesoscutellum faintly striate; propodeum strongly and sparsely striate transversely. Petiolar node excluding spine largely smooth and shiny, with basal part faintly striate.

Pair of long erect setae present on vertex near lateral ocelli; frontal lobe, pronotal disc and gastral tergite I without erect setae. Head, mesosoma, petiole and gaster with sparse subdecumbent to decumbent pubescence which is extremely short on gaster; mesopleuron very sparsely pubescent.

For color pattern see Fig 4-5. Body reddish brown; gaster a little darker than head and mesosoma; all legs orange.

Male measrurements and indices. Non-type (n=1): HW 1.45 mm, HL 1.15 mm, SL 0.36 mm, EL 0.86 mm, EW 0.52 mm, OL 0.25 mm, OED 0.18 mm, WL 2.94 mm, FWL 5.43 mm, PTL 0.57 mm, PTH 0.74 mm, CI 126, SI 25, PTHI 129.

Male description. Body relatively small (HL 1.15 mm, WL 2.94 mm). Major axis of median ocellus longer than minimum distance between lateral ocellli; antenna 13-segmented; scape very short, 1/2 as long as antennal segment III; II 1/2 as long as scape; III to XIII each extremely long; palp formula 6, 4; dorsal outline of clypeus in lateral view weakly convex. Mesosoma in lateral view relatively slender and long; dorsal outline of pronotum in lateral view almost straight; anterodorsal outline of mesoscutum in lateral view gently sloping; mesoscutum without median depression; parapsidal furrow weak and almost straight; oblique mesopleural furrow relatively shallow and narrow; ventrolateral part of katepisternum without furrow; propodeum in lateral view with dorsal outline weakly convex; metapleuron separated from propodeum indistinctly by suture; wing venation as in Figs. 4-7A and 4-7C. Petiolar node in lateral view tapering gently to bluntly pointed apex, with anterior and posterior slopes weakly convex; subpetiolar process in lateral view lobate and slender, with the maximum length of anterior-posterior axis as long as that of dorsal-ventral axis; petiolar sternum without posteroventral process. Gastral tergite I in lateral view long. Gastral tergite I in lateral view long; posterior spine of abdominal tergite VIII short and slender, very weakly curved; pygostyle with long setae in its apical third; disc of abdominal sternite IX much broader than long, with posterolateral corner expanding laterad and posterolateral corner distinctly angled; apical lobe much longer than disc and slightly narrowed in basal half, with apical margin almost straight; telomeral apex in lateral view very much longer than high; distiventral apex of valviceps weaklyly produced; basiventral corner of valviceps not produced; ventral margin of valviceps weakly concave with 23–24 denticles.

Head including area between lateral ocelli entirely smooth and shiny. Pronotum in lateral view smooth and shiny; mesoscutum in dorsal view smooth and shiny; scuto-scutellar suture with sparse, strong, longitudinal striation; mesopleural anepisternum and katepisternum and metapleuron smooth and shiny; propodeum in dorsal view with rough texture and shiny. Petiole smooth and shiny.

Head, mesosoma, legs, petiole and gaster with fine dense subdecumbent to decumbent pubescence; mandible, vertex near ocelli and gaster except gastral tergite I with several long erect setae.

For color pattern see Fig. 4-6; body and appendage basically pale orange.

Species recognition. The *Odontomachus kuroiwae* is very similar in general appearance to *O. fulgidus* (see remarks under *O. fulgidus*).

Distribution. Japan (Okinoerabu Island to Okinawa Island).

Bionomics. This species nests under the leaf litter, rotting wood, and under the stone.

Remarks. *Odontomachus kuroiwae* was revived as a valid species by Yoshimura *et al*. (2007) based on morphology of worker, queen and male (including male genitalia), and his view was reconfirmed by the present integrated taxonomy (the chapter III). The delimitation between *O. kuroiwae* and *O. fulgidus* has not yet been clarified by integrated taxonomy because of lack of fresh specimens of the latter species suitable for DNA barcoding.

***Odontomachus latidens* Mayr, 1867**

(Figs. 2-1B, 2-2A, 2-2F, 2-2K, 4-2A, 4-8, 4-9, 4-10)

Odontomachus latidens Mayr, 1867: 48, queen, type locality: Indonesia (Java). Emery, 1887: 428; Emery, 1892: 560 (w); Crawley, 1924: 388; Karavaiev, 1925: 292 (w); Chapman & Capco, 1951: 45; Brown, 1976: 157; Imai, Brown, *et al.* 1984: 67 (k); Satria *et al*., 2015 (m).

Non-type materials examined. Indonesia: Sumatra: Aceh: Leuser Ecosystem (ca. 1100 m alt.), 20.IX.2012, R. Satria leg., GK-38-12, 29 workers, 5 queens (SKYC, RSC); North Sumatra: Danau Toba, Parapat (900 m alt.), 20.VIII.2002, Sk. Yamane leg., 2 workers (SKYC, RSC). Java: Banten: Cibodas, 29.11.2009, M. Ohashi leg., 1 queen (SKYC, RSC); same loc. Mt. Gede, Dec-1999, F. Ito leg., 1 worker (SKYC, RSC); Yogyakarta: G. Merapi, Kaliadem (800–1000 m alt.), 31.XII.2002, F. Yamane leg., JV02/03-SKY-39, 2 workers, 1 queen (SKYC, RSC). **Malaysia**: Malay Peninsula: Pahang: near Genting H.L., Bunga Buah (ca. 1000 m alt.), 6.VII.1999, Sk. Yamane leg., 1 worker (SKYC, RSC).

Worker measurements and indices. Non-types (n=10): HW 2.43–3.13 mm, HL 3.23–4.05 mm, SL 2.83–3.65 mm, IFLW 0.60–0.76 mm, EL 0.31–0.40 mm, MDL 1.67–2.09 mm, WL 3.50–4.30 mm, PTL 0.50–0.69 mm, PTH 1.26–1.58 mm, CI 73–77, SI 109–123, MDI 51–55, PTHI 226–280.

Worker description. Body relatively large (HL 3.23–4.05 mm, WL 3.50–4.30 mm). Head in full-face view slightly longer than broad, with posterior margin weakly concave (sometimes almost straight); head posteriorly without a pair of small and distinct tubercles; median furrow on vertex present as dark line; each side of median furrow hardly humped; frontal lobes followed by strong frontal carinae which are slightly divergent posteriad and then become nearly parallel; minimum distance between margin of ocular ridge and margin of compound eye half as long as major axis of compound eye; masticatory margin with very small denticles, or only with preapical angle (without denticles); subapical tooth shorter than broad, with truncate apex; palp formula 4, 4. Mesosoma in lateral view stout; pronotum including anteromedian lobe short, in lateral view with anterodorsal slope relatively steep; mesopleuron without anteroventral ridge, with anterodorsal margin weakly carinate, clearly separated by distinct dorsal carina from mesonotum and metapleuron; propodeum in lateral view with dorsum slightly convex, and gradually sloping posteriad, with posterior face steeply sloping; propodeal dorsum anteriorly with very weak median longitudinal depression. Petiolar node conical, with sharply pointed apical spine; node excluding apical spine in lateral view, excluding apical spine with anterior face weakly convex or weakly and bluntly angulate, and posterior face weakly convex; apical spine needle-shaped, less than 1/4 as long as petiolar height, sometimes weakly curved posteriad (but shape variable within species); subpetiolar process anteroposteriorly shorter than dorsoventrally high, lobate, directed ventrally. Gastral tergite I in lateral view relatively short, with anterior face moderately long and vertical.

Head in full-face view largely smooth and shiny; area bordered by frontal carinae and ocular ridges striate; frontal lobe smooth and shiny; extraocular furrow smooth and shiny; median part of vertex along median furrow smooth and shiny; lateral and ventral faces of head smooth and shiny; median disc of clypeus almost smooth and shiny. Pronotal disc and mesonotum in dorsal view densely and transversely striate; posterolateral face of pronotum partly smooth and shiny; mesopleuron largely smooth and shiny, with anteriormost and posteriormost parts finely striate; metapleuron moderately striate in its anterior 2/3, and smooth and shiny or faintly striate in its posterior 1/3; propodeum with transverse striation which is a little sparser and stronger than pronotum and mesonotum. Petiolar node largely smooth and shiny, but sometimes with basal area faintly striate.

Vertex with a pair of long erect setae; frontal lobe without seta; pronotal disc without long erect setae; gastral tergite I with erect setae (but often missing artificially) which are 2/3 as long as setae on vertex. Head, mesosoma, petiole and gaster with fine appressed pubescence which is sparse and very short on head and gaster.

For color pattern see Fig. 4-8; body reddish brown to brown; gaster a little darker than head and mesosoma; all legs yellowish brown.

Queen measurements and indices. Non-types (n=7): HW 2.89–2.99 mm, HL 3.60–3.95 mm, SL 3.35–3.55 mm, IFLW 0.70–0.76 mm, EL 0.50–0.52 mm, OL 0.13–0.20 mm, MDL 1.97–2.05 mm, WL 4.55–4.75 mm, FWL 10.48–11.17 mm, PTL 0.69–0.71 mm, PTH 0.94–1.85 mm, CI 76–80, SI 116–118, MDI 50–58, PTHI 131–277.

Queen description. Queen similar in general appearance to worker. Vertex near ocelli not swollen; ocular ridge clearly developed; distance between lateral ocelli as long as distance between lateral and median ocelli, and as long as major axis of median ocellus; ocelli in lateral view protruded dorsad. Mesosoma with main sclerites associated with wing function (Figs. 4-9B, 4-9C), in dorsal view short and stout; anterodorsal slope of pronotum in lateral view steep; anterodorsal outline of mesoscutum in lateral view relatively steep; mesoscutum with very weak posteromedian depression; parapsidal furrow very weak and slightly curved; dorsal outline of metascutellum in lateral view weakly convex; mesopleuron without oblique furrow; propodeum in lateral view relatively short, with dorsum very weakly convex and gradually sloping posteriad; propodeum in dorsal view with lateral outlines convergent posteriad. Wing venation as in Figs. 4-9E and 4-9F. Petiolar node excluding apical spine in lateral view with anterior face almost straight to weakly convex, and posterior face weakly convex; apical spine short and relatively slender, and sometimes weakly curved posteriad (but variable in shape within species); subpetiolar process triangular, directed ventrally, with the maximum length of anterior-posterior axis as long as that of dorsal-ventral axis. Gastral tergite I in lateral view relatively short, with anterior face moderately long and vertical.

Head in full-face view largely smooth and shiny; area bordered by frontal carinae and ocular ridges striate; frontal lobe smooth and shiny; extraocular furrow faintly striate; median part of vertex along median furrow smooth and shiny; lateral face and venter of head smooth and shiny; median disc of clypeus almost smooth and shiny. Pronotum densely and weakly striate transversely; mesoscutum largely smooth and shiny, with faint striae on posteromedian depression and along posterior margin; mesopleuron largely smooth and shiny, with anteriormost and posteriormost parts faintly striate; mesoscutellum smooth and shiny; propodeum strongly and sparsely striate transversely. Petiolar node excluding spine largely striate faintly.

Pair of long erect setae present on vertex near lateral ocelli; frontal lobe and pronotal disc without erect setae; gastral tergite I with erect setae (but often missing artificially) which are shorter than setae on vertex near ocelli. Head, mesosoma, petiole and gaster with sparse subdecumbent to decumbent pubescence which is extremely short on gaster; mesopleuron very sparsely pubescent.

For color pattern see Fig 4-9. Body reddish brown to brown; gaster a little darker than head and mesosoma; all legs yellowish brown.

Male measurements and indices. Non-types (n=7): HW 1.60–1.65 mm, HL 1.26–1.31 mm, SL 0.26–0.28 mm, EL 0.88–0.91 mm, EW 0.50–0.51 mm, OL 0.20–0.22 mm, OED 0.26–0.28 mm, WL 3.55–3.70 mm, FWL 7.05–7.25 mm, PTL 0.63–0.64 mm, PTH 0.97–1.03 mm, CI 123–128, SI 16–18, PTHI 151–164.

Male description. Body relatively large (HL 1.26–1.31 mm, WL 3.55–3.70 mm). Major axis of median ocellus smaller than minimum distance between lateral ocelli; antenna 13-segmented; scape very short, 1/3 as long as antennal segment III; II 1/2 as long as scape; III to XIII each extremely long; palp formula 6, 4; dorsal outline of clypeus in lateral view weakly convex. Mesosoma in lateral view relatively slender and long; dorsal outline of pronotum in lateral view weakly convex; anterodorsal outline of mesoscutum in lateral view relatively steeply sloping; mesoscutum with short weak median longitudinal depression; parapsidal furrow weak and slightly curved; oblique mesopleural furrow relatively shallow and narrow; ventrolateral part of katepisternum with a very weak longitudinal furrow; propodeum in lateral view with dorsal outline roundly convex; metapleuron separated from propodeum indistinctly by a suture; wing venation similar to queen (see Figs. 4-9E and 4-9F for queen wings). Petiolar node in lateral view tapering gently to rounded apex with anterior slope straight, and posterior slope much steeper and shallowly concave; subpetiolar process in lateral view lobate and slender, with the maximum length of anterior-posterior axis shorter than dorsal-ventral axis; petiolar sternum without posteroventral process. Gastral tergite I in lateral view long; posterior spine of abdominal tergite VIII short and thick, very weakly curved (Fig. 2-2A); pygostyle digitiform, with long setae in apical 2/3; disc of abdominal sternite IX not clearly differentiated from apical lobe, gradually merging into apical lobe, with basal margin almost straight; apical lobe gently tapering apicad, with apical margin truncated; telomeral apex in lateral view longer than high; distiventral apex of valviceps weakly produced; basiventral corner of valviceps not produced; ventral margin of valviceps with 27−30 denticles.

Head largely smooth and shiny, with area between lateral ocelli faintly striate. Pronotum in lateral view smooth and shiny; mesoscutum in dorsal view faintly and longitudinally striate or sometimes smooth and shiny; scuto-scutellar suture with sparse, strong, longitudinal rugae; mesopleural anepisternum and katepisternum smooth and shiny; propodeum with sparse, strong, longitudinal striate. Petiole smooth and shiny.

Head, mesosoma, legs, petiole, and gaster with fine dense subdecumbent to decumbent pubescence; mandible, vertex near ocelli and gaster except gastral tergite I with several long erect setae.

For color pattern see Fig. 4-10; head including scape, mesosoma, legs yellowish brown; funiculus dark brown; petiole and gaster darker than head and mesosoma.

Species recognition. The identities of *O. latidens* and *O. procerus* are discussed under *O. procerus*.

Distribution. Known from Indonesia (Sumatra and Java) and Peninsular Malaysia.

Bionomics. *Odontomachus latidens* inhabits secondary and primary forests in the highlands (ca. 800–1300 m alt.), and nests in the soil near the base of living trees. The colony GK-38-12, from Leuser Ecosystem, Aceh Province, was collected nesting together with *Pheidole tandjongensis* Forel, 1913 (colony GK-39-12). Details concerning the nature of their relationship are unknown.

Odontomachus minangkabau **Satria** ***et al.*****, 2015**

(Figs. 2-2D, 2-2I, 2-2N, 4-11, 4-12, 4-13)

Odontomachus minangkabau Satria *et al.*: 28, figs. 14, 15, 16, worker, queen, male, type locality: Indonesia (Sumatra).

Type material. *Odontomachus minangkabau* — holotype (worker; MZB), Indonesia: West Sumatra: secondary forest within the campus of Andalas University, Padang [RS01-PDG-14, R. Jannatan leg., 22.ix.2014]; paratypes (17 workers, 1 queen, 5 males; MZB, MHNG, MCZC & RSC) same data as the holotype.

Non-type material examined. Indonesia: Jambi, Kerinci Seblat N. P., 8.XI.2006, Syaukani leg., 2 workers (SKYC); same loc., 10.XI.2006, Syaukani leg., SYAU06-39, 7 workers (SKYC). Lampung: Sumber Jaya, Bodong Jaya, 16.IX.2007, Sk. Yamane leg., Su07-SKY-159, 19 workers (SKYC). West Sumatra: Maninjau, 7–9.VIII.1985, S. & Sk. Yamane leg., 3 workers (SKYC); same loc., 7.VIII.1985, S. & Sk. Yamane leg., 2 workers (SKYC); same loc., 16-18.VIII.1985, S. & Sk. Yamane leg., 1 worker (SKYC); Padang, 30.XI.1983, K. Nakamura leg., 83-PD-2, 1 worker (SKYC); Padang, HPPB UNAND, 14.IX.2011, R. Satria leg., 15 worker (SKYC); same loc., 10.X.2012, R. Satria leg., PDG-22-12, 30 workers, 2 queens (SKYC, RSC); same loc., 11.IX.2012, R. Satria leg., PDG-12-12, 11 workers (SKYC, RSC); Lubuk Gadang, 21-

23.VIII.1985, Sk. Yamane leg., SNS col., 4 workers (SKYC); Sako nr Tapan, 4–5.IX.1985, Sk. Yamane leg., 2 workers (SKYC); Ulu Gadut nr Padang, 27–30.VIII.1985, Sk. Yamane leg., 2 workers (SKYC); Ulu Gadut, Satar house, E. Suzuki leg., 1 worker (SKYC); Ulu Gadut, Pinang-pinang, 29.IV.1997, F. Ito leg., 1 worker (SKYC); same loc., 13.VIII.1989, E. Suzuki leg., 1 worker (SKYC).

Materials used for DNA barcoding. Colony PDG-22-12 (RJ20141201-1, LC056047), colony RS01-PDG-14 (RJ20150126-2, LC056051).

Worker measurements and indices. *Odontomachus minangkabau* — holotype: HW 2.27 mm, HL 3.4 mm, SL 3.55 mm, IFLW 0.63 mm, EL 0.46 mm, MDL 1.95 mm, WL 4.6 mm, PTL 0.86 mm, PTH 1.38 mm, CI 66, SI 156, MDI 57, PTHI 159; paratypes (n=9): HW 2.05–2.34 mm, HL 3.13–3.55 mm, SL 3.30–3.65 mm, IFLW 0.56–0.64 mm, EL 0.42–0.50 mm, MDL 1.85–2.00 mm, WL 4.15–4.65 mm, PTL 0.78–0.86 mm, PTH 1.25–1.40 mm, CI 65–69, SI 153–161, MDI 53–61, PTHI 158–173.

Worker description. Body relatively large (HL 3.13–3.55 mm, WL 4.15–4.65 mm). Head in full-face view much longer than broad, with posterior margin weakly concave; head posteriorly without a pair of small and distinct tubercles; median furrow on vertex present as dark line; each side of median furrow not swollen dorsad; frontal lobes followed by strong frontal carinae which are nearly parallel; minimum distance between margin of ocular ridge and margin of compound eye less than half of major axis of compound eye; masticatory margin with 11–14 denticles; subapical tooth 2.5 times as long as broad, with truncate apex; palp formula 4, 4. Mesosoma in lateral view relatively slender; pronotum including anteromedian lobe long, in lateral view with anterodorsal slope gentle; mesopleuron without anteroventral ridge, with anterodorsal margin weakly carinate, clearly separated by distinct dorsal carina from mesonotum and metapleuron; propodeum in lateral view with dorsum almost straight, with posterior face gently sloping; propodeal dorsum anteriorly without median longitudinal depression. Petiolar node conical, with sharply pointed apical spine; node excluding apical spine in lateral view with anterior face weakly convex or weakly and bluntly angulate and posterior face weakly convex; apical spine needel-shaped, less than 1/4 as long as petiolar height, sometimes weakly curved posteriad (but shape variable within species); subpetiolar process lobate, directed ventrally with the maximum length of anterior-posterior axis as long as dorsal-ventral axis. Gastral tergite I in lateral view long, with anterior face relatively short and vertical.

Head in full-face view largely smooth and shiny, area bordered by frontal carinae and ocular ridges striate; frontal lobe with rough texture and shiny; faint striation extended from extraocular furrow through part of temporal ridges till part of posterolateral face of vertex; median part of vertex along median furrow faintly striate transversely; lateral face of head largely smooth and shiny, with its posterior third faintly striate; venter of head smooth and shiny; median disc of clypeus smooth and shiny. Pronotal disc and mesonotum densely and weakly striate transversely; posterolateral face of pronotum partly smooth and shiny; mesopleuron largely smooth and shiny, with its anterior 1/3 and posteriormost parts finely striate; metapleuron and propodeum with transversal striation which is a little sparser and stronger than that of pronotum and mesonotum. Petiolar node largely smooth and shiny, with basal area faintly striate.

Vertex with a pair of long erect setae; frontal lobe sometimes with a seta; pronotal disc without long erect setae; gastral tergite I without erect setae. Head, mesosoma, petiole and gaster with fine appressed pubescence which is sparse and very short on head and sparse and extremely short on gaster.

For color pattern see Fig. 4-11; body dark reddish brown, with head paler; coxae and femora yellowish brown; tibiae and tarsi reddish brown.

Queen measurements and indices. *Odontomachus minangkabau* — paratype (n=1): HW 2.36 mm, HL 3.29 mm, SL 3.35 mm, IFLW 0.65 mm, EL 0.54 mm, OL 0.15 mm, MDL 1.80 mm, WL 4.80 mm, FWL unmeasured (due to the dealation) PTL 0.88 mm, PTH 1.61 mm, CI 72, SI 142, MDI 55, PTHI 183.

Non-type (n=1): HW 2.37 mm, HL 3.30 mm, SL 3.50 mm, FLW 0.66 mm, EL 0.52 mm, OL 0.15 mm, MDL 1.72 mm, WL 4.70 mm, FWL 9.50 mm, PTL 0.88 mm, PTH 1.60 mm, CI 72, SI 147, MDI 52, PTHI 182.

Queen description. Queen similar in general appearance to worker. Vertex near ocelli not swollen; ocular ridge clearly developed; distance between lateral ocelli shorter than distance between lateral and median ocelli, and as long as major axis of median ocellus; ocelli in lateral view protruded dorsad. Mesosoma with main sclerites associated with wing function (Figs. 4-12B, 4-12C), in dorsal view long and slender; anterodorsal slope of pronotum in lateral view gentle; anterodorsal outline of mesoscutum in lateral view relatively steep; mesoscutum with very weak median longitudinal depression; parapsidal furrow very weak and slightly curved; dorsal outline of metascutellum in lateral view almost straight; anterior third of mesopleuron with fine, oblique furrow; propodeum in lateral view relatively long, with its dorsum almost straight and gradually sloping posteriad; propodeum in dorsal view with lateral outlines convergent posteriad. Wing venation as in Figs. 4-12E and 4-12F. Petiolar node excluding apical spine in lateral view with anterior and posterior faces weakly convex; apical spine relatively stout and slightly curved posteriad; subpetiolar process lobate, directed ventrally, with the maximum length of anterior-posterior axis as long as dorsal-ventral axis. Gastral tergite I in lateral view long, with anterior face relatively short and vertical.

Head in full-face view largely smooth and shiny, area bordered by frontal carinae and ocular ridges striate; frontal lobe with rough texture and shiny; extraocular furrow faintly striate; median part of vertex along median furrow faintly striate transversely; lateral face of head largely smooth and shiny with posterior parts faintly striate; venter of head smooth and shiny; median disc of clypeus smooth and shiny. Pronotum densely and finely striate transversely; mesoscutum weakly and longitudinally striate; mesopleuron largely smooth and shiny, with anterior third and posteriormost part faintly striate; mesoscutellum smooth and shiny; propodeum strongly and sparsely striate transversely. Petiolar node largely smooth and shiny, with its basal area faintly striate.

Pair of long erect setae present on vertex near ocelli; frontal lobe, pronotal disc, and gastral tergite I without erect setae. Head, mesosoma, petiole and gaster with sparse, subdecumbent to decumbent pubescence which is extremely short in gaster; mesopleuron with very sparse subdecumbent to decumbent pubescence.

For color pattern see Fig. 4-12; head, mesosoma, petiole and gaster reddish brown to dark brown; femora yellowish brown; tibiae reddish brown.

Male measeurements and indices. *Odontomachus minangkabau* — paratypes (n=5): HW 1.41–1.44 mm, HL 1.21–1.24 mm, SL 0.28–0.29 mm, EL 0.85–0.89 mm, EW 0.45–0.49 mm, OL

0.21–0.23 mm, OED 0.18–0.21 mm, WL 3.28–3.40 mm, FWL 6.17–6.46 mm, PTL 0.68–0.71 mm, PTH 0.95–1.07 mm, CI 115–119; SI 15–17, PTHI 139–157.

Male description. Body relatively large (HL 1.21–1.24 mm, WL 3.28–3.40 mm). Major axis of median ocellus as long as minimum distance between lateral ocellli; antenna 13-segmented; scape very short, 1/3 as long as antennal segment III; II 1/2 as long as scape; III to XIII each extremely long; palp formula 6, 4; dorsal outline of clypeus in lateral view straight. Mesosoma in lateral view relatively slender and long; dorsal outline of pronotum in lateral view almost straight; anterodorsal outline of mesoscutum in lateral view gentle; mesoscutum without median depression; parapsidal furrow weak and almost straight; oblique mesopleural furrow relatively shallow and narrow; ventrolateral part of katepisternum without furrow; propodeum in lateral view with dorsal outline roundly convex; metapleuron separated from propodeum indistinctly by suture; wing venation similar to queen (see Figs. 4-12E and 4-12F for queen wings). Petiolar node in lateral view tapering gently to bluntly pointed apex, with anterior slope weakly convex, and posterior slope straight; subpetiolar process in lateral view lobate and slender , with the maximum length of anterior-posterior axis as long as dorsal-ventral axis; petiolar sternum without posteroventral process. Gastral tergite I in lateral view long; posterior spine of abdominal tergite VIII long and slender, weakly curved (Fig. 2-2D); pygostyle with long setae in its apical third; disc of abdominal sternite IX much broader than long, with posterolateral corner expanding laterad and posterolateral corner distinctly angled; apical lobe much longer than disc and slightly narrowed in basal half, with apical margin weakly convex; telomeral apex in lateral view much longer than high; distiventral apex of valviceps strongly produced; basiventral corner of valviceps distinctly produced; ventral margin of valviceps with 28–29 denticles.

Head including area between lateral ocelli entirely smooth and shiny. Pronotum in lateral view smooth and shiny; mesoscutum in dorsal view smooth and shiny; scuto-scutellar suture with sparse, strong, longitudinal striation; mesopleural anepisternum and katepisternum smooth and shiny; metapleuron smooth and shiny; propodeum in dorsal view with rough texture and shiny. Petiole smooth and shiny.

Head, mesosoma, legs, petiole and gaster with fine dense subdecumbent to decumbent pubescence; mandible, vertex near ocelli and gaster except gastral tergite I with several long erect setae.

For color pattern see Fig. 4-13; body basically pale yellow; antennae, area around ocelli, anteromedian and lateral parts of mesoscutum, metanotum and dorsum of propodeum blackish; tibiae, petiole and gaster yellowish brown.

Species recognition. *Odontomachus minangkabau* is morphologically most similar to *O. rixosus* and *O. pararixosus*. However, it is distinguishable from the latter two by the following characteristics of the worker: body larger in *O. mimangkabau* (HL 3.13–3.55 mm, WL 4.15–4.65 mm) than in the latter two (HL 2.56–3.03 mm, WL 3.35–4.00 mm in *O. rixosus*; HL 2.40–2.66 mm, WL 3.33–3.48 mm in *O. pararixosus*); masticatory margin of mandible with 11–14 denticles in *O. mimangkabau*, but less than 10 denticles in the latter two; SI larger in *O. mimangkabau* (SI 153–161) than in the latter two (SI 131–150 in *O. rixosus*; SI 136–148 in *O. pararixosus*); median part of vertex along median furrow faintly striate transversely in *O. mimangkabau*, but smooth and shiny or with rough texture in the latter two; colors of head, mesosoma, petiole and gaster darker in *O. mimangkabau* than in the latter two; gastral tergite I without erect setae in *O. mimangkabau* and *O. rixosus*, but with several long erect setae in *O. pararixosus*. Furthermore, *Odontomachus minangkabau* is easily distinguished from *O. rixosus* by the following characteristics of the male: gastral tergite I in lateral view long in the former, but short in the latter; head, pronotum, mesoscutum and mesopleuron pale yellowish in the former, but yellowish to yellowish brown in the latter. Furthermore, *Odontomachus minangkabau* is easily distinguished from *O. rixosus* by the following characteristics of the male: posterior spine of abdominal tergite VIII weakly curved in *O. minangkabau* (Fig. 2-2D), and very weakly curved in *O. rixosus* (Fig. 2-2C); apical lobe of abdominal sternite IX slightly narrowed in basal half, with apical margin weakly convex in *O. minangkabau*, and gently tapering to almost truncate apex in *O. rixosus*; telomeral apex in lateral view much longer than high in *O. minangkabau*, and longer than high in *O. rixosus*; ventral margin of valviceps with 28–29 denticles in *O. minangkabau*, and with 21−22 denticles in *O. rixosus*.

Distribution. Sumatra Island, Indonesia.

Bionomics. *Odontomachus minangkabau* inhabits secondary and primary lowland forests, and nests in the soil near the base of living trees.

Odontomachus monticola Emery, 1892

(Figs. 4-6B, 4-6D, 4-14, 4-15, 4-16, 4-17)

Odontomachus monticola Emery, 1892: 560 (in key), worker, type locality: Myanmar; Yasumatsu, 1962: 93; Brown, 1976: 105, 157−159 (in part); Ogata, 1987: 126 (in part). Figs. 120-122; Wang, 1993: 220−225; Terayama, 1999: 173, 174; Yoshimura *et al.*, 2007: 102−109, figs. 3, 5, 7, 8, 9.

Odontomachus monticola r. *punctulatus* Forel, 1900: 58, worker, type locality: India. Revived a status as species by Bingham, 1903: 49; Wheeler, 1928: 8; Wheeler, 1930: 61; Wu, 1941: 149. Synonymy under *Odontomachus monticola* by Brown, 1976: 105.

Odontomachus monticola var. *longi* Forel, 1900: 58, worker, type locality: India (Assam). Subspecies of *Odontomachus monticola*: Emery, 1911: 114. Synonymy under *Odontomachus monticola* by Brown, 1976: 105.

Odontomachus monticola pauperculus Wheeler, 1921: 530−531, worker, type locality: China. Synonymy under the *Odontomachus monticola* by Yasumatsu, 1962: 93.

Odontomachus latidens subsp. *striata* Menozzi, 1930b: 329, worker, type locality: China. Synonymy under *Odontomachus monticola* by Brown, 1976: 105.

Odontomachus circulus Wang, 1993: 220, fig. 1, worker, type locality: China. **Syn. Nov.**

Type material examined. *Odontomachus monticola* — lectotype (worker; MCSN), Myanmar: Carin Checù; paralectotypes (5 Workers, 1 queen; MCSN), same data as lecotype. *Odontomachus circulus*— holotype (worker; IZCAS), China: Yunnan.

Non-type materials examined. Hongkong: Taipo Kau New Territory, 26.VI.1999, Sk. Yamane leg., 1 worker (RSC). **Laos:** Phong Sali: Muang Khoua, 22–24.VIII.2005, Y. Ochiai leg., 1 worker (RSC); Oudomxai: Namo: Mainaatan, 950 m alt., 21–26.VIII.2004, Y. Ochiai leg., 1 worker (RSC). **Thailand:** Loei Province: Phu Rure Dist.: Phu Luang W.S., 10.IV.2008, Sk. Yamane leg., TH08-SKT-23, 3 workers, 1 queen (RSC); same loc., 14.IV.2010, W. Jaitrong leg., TH-08-WJT-624, 3 workers (RSC); same loc., same date, W. Jaitrong leg., TH-08-WJT-622, 3 workers (RSC); same loc., Kok Nok Kaba, 11.IV.2008, W. Jaitrong leg., TH08-WJT-626, 2 workers, 1 queen (RSC); Chiang Mai Prov.: Mae Sala Luang, 8.III.2008, W. Jaitrong leg., TH08-TWJ-607, 2 workers, 1 queen (RSC); same loc., same date, W. Jaitrong leg., TH08-TWJ-625, 5 workers (RSC); Tak Prov., near Myanmar border, Tung Yai W.S., 23.V.1999, W. Jaitrong leg, 1 worker (RSC); same loc., 20.V.2000, W. Jaitrong leg., 1 worker (RSC). **Vietnam:** Tuyen Quang: Na Hang: Ban Bung, N22°17'02–18'02", E105°24'52"–25'58", ca. 50–365 m alt., limestone forest, 12.III.2015, R. Satria leg., RS01-BB-15, 5 workers (RSC); same loc., same date, R. Satria leg., RS02-BB-15, 5 workers (RSC); same loc., same date, R. Satria leg., RS03-BB-15, 5 workers, 1 queen (RSC); same loc., same date, R. Satria leg., RS04-BB-15, 6 workers (RSC); same loc., same date, R. Satria leg., RS09-NH-15, 6 workers (RSC); same loc., same date, R.

Satria leg., RSRS10-BB-15, 9 workers (RSC); same loc., Ban Chu, 13.III.2015, R. Satria leg., RS20-BC-15, 5 workers (RSC); same loc., Bac Vang, N22°28'49–51", E105°25'09–11", ca. 110–135 m alt., limestone forest, 10.III.2015, R. Satria leg., RS06-NH-15, 7 workers (RSC); same loc., same date, R. Satria leg., RS07-NH-15, 9 workers (RSC); same loc., same loc., 10.III.2015, R. Satria leg., RS08-NH-15, 9 workers (RSC); same loc., 10.III.2015, F. Ito leg., MS15-2, 1 male (RSC); Ha Tinh: Vu Quang NP: TK189, near Tram Kiem Lam Co, N18°16'21–35", E105°22'00–07", ca. 125–285 m alt., 21.III.2015, R. Satria leg., RS55-VQ-15, 3 workers (RSC); same loc., TK182, near Tram Kiem Lam Co, N18°17'06–36", E105°22'39–46", ca. 60–240 m alt., 23.III.2015, R. Satria leg., RS73-VQ-15, 6 workers, 1 queen (RSC); same loc., same date, R. Satria leg., RS74-VQ-15, 3 workers (RSC); Nghe An Prov.: Que Phong Dist.: Ban Xan, 700 m alt., 16.IV.1999, B.T. Viet leg., 1 worker (RSC); Ha Tai: Ba Vi N.P. (ca. 1100 m alt.), 21°03'N, 105°22'E, 19.IV.2002, K. Eguchi leg., EG02-VN-035, 2 workers (RSC); same loc., ca. 700 m alt., 19.IV.2002, K. Eguchi leg., EG02-VN-029, 2 workers (RSC); Vinh Phuc Prov.: Tam Dao, 7.VIII.1998, H. Okido leg., 1 worker (RSC); same loc., same date, Sk. Yamane leg., 2 workers (RSC); same loc., ca. 950 m alt., 21°27'N, 105°38'E, 5–6.XI.2001, Sk. Yamane leg., 1 worker (RSC); same loc., N21˚03'35.7", E105˚21'47.8", ca. 1019 m alt., 25.III.2016, R. Satria leg., RS-02-BV16, 5 workers (RSC); same loc., N21˚04'33",E105˚22'2.0", R. Satria leg., RS-98-BV16, 10 workers, 1 queen (RSC); same loc., same date R. Satria leg., RS-99-BV16, 2 workers (RSC); same loc., same date, R. Satria leg., RS-107-BV16, 3 workers (RSC): Ninh Binh Prov.: Nho Quan Dist.: Cuc Phuong N.P., 10.XI.2001, Sk. Yamane leg., 1 worker (RSC); Thanh Hoa: Ben En National Park: N19˚34'30-45", E105˚31'54"-32’10", ca. 20-80 m alt., 15.IX.2016, A. Yamada leg., AKY15ix16-06, 5 workers (RSC); same loc., Xuan Lien Nature Reserve, N19˚58'36-41", E105˚10'04-29", ca. 280-300 m alt., 15.IX.2016, AKY08ix16-07, 7 workers (RSC).

Worker measurements and indices. *Odontomachus monticola* — lectotype: HW 2.56 mm, HL 3.19 mm, SL 3.12 mm, IFLW 0.67 mm, EL 0.41 mm, MDL 1.89 mm, WL unmeasured, PTL 0.62 mm, PTH unmeasured, CI 80, SI 122, MDI 59, PTHI incalculable; paralectotypes (n=5): HW 2.25–2.62 mm, HL 2.82–3.33 mm, SL 2.51–3.17 mm, IFLW 0.59–0.68 mm, EL 0.31–0.4 mm, MDL 1.57–2.01 mm, WL 4 mm (n=1), PTL 0.51–0.64 mm (n=2), PTH 1.51 mm (n=1), CI 78–80, SI 111–124, MDI 56–62, PTHI 236 (n=1). *Odontomachus circulus* — holotype: HW 2.61

mm, HL 3.27 mm, SL 3.28 mm, IFLW 0.67 mm, EL 0.46 mm, MDL 1.92 mm, WL 4.30 mm, PTL unmeasured, PTH unmeasured, CI 80, SI 125, MDI 59, PTHI incalculable.

Non-types (n=10): HW 2.27–2.69 mm, HL 2.88–3.39 mm, SL 2.92–3.18 mm, IFLW 0.60–0.68 mm, EL 0.37–0.39 mm, MDL 1.81–1.98 mm, WL 3.59–4.11 mm, PTL 0.62–0.71 mm, PTH 1.23–1.49 mm, CI 76–80, SI 117–128, MDI 55–62, PTHI 193–209.

Worker description. Body relatively small (HL 2.82−3.39 mm; WL 3.59−4.30 mm). Head in full-face view slightly longer than broad, with posterior margin weakly concave; head posteriorly without a pair of small and distinct tubercles; median furrow on vertex present as a dark line; each side of line not swollen dorsad; frontal lobes followed by frontal carinae which are slightly divergent posteriad and then become nearly parallel; minimum distance between margin of ocular ridge and margin of compound eye half as long as major axis of compound eye; masticatory margin with 8–12 distinct denticles; subapical tooth shorter than broad, with truncate apex; palp formula 4, 4. Mesosoma in lateral view relatively stout; pronotum including anteromedian lobe short, in lateral view with anterodorsal slope relatively steep; mesopleuron without anteroventral ridge, with anterodorsal margin weakly carinate, clearly separated by distinct dorsal carina from mesonotum and metapleuron; propodeum in lateral view with dorsum almost straight, with posterior face steeply sloping; propodeal dorsum without median longitudinal depression. Petiolar node conical and slender, with sharply pointed apical spine; node excluding apical spine in lateral view symmetrically raised with anterior face almost straight followed by weakly convex or weakly and bluntly angulate and posterior face almost straight followed by weakly convex; apical spine needle-shaped, less than 1/4 as long as petiolar height, sometimes weakly curved posteriad (but shape variable within species); subpetiolar process lobate, directed ventrally, with the maximum length of anterior-posterior axis as long as dorsal-ventral axis. Gastral tergite I in lateral view relatively short, with anterior face moderately long and vertical.

Head in full-face view largely smooth and shiny; area bordered by frontal carinae and ocular ridges striate; area around eye smooth and shiny; frontal lobe clearly striate; extraocular furrow smooth and shiny; median part of vertex along median furrow smooth and shiny; lateral face of head very faintly striated, and venter of head smooth and shiny; median disc of clypeus smooth and shiny. Pronotal disc in dorsal view with concentric striation; posterolateral face of pronotum clearly striate; mesopleuron largely smooth and shiny, with anterior third and posteriormost parts finely striate; metapleuron and propodeum with transverse striation, which is a little sparser and stronger than pronotum and mesonotum. Petiolar node largely smooth and shiny, with basal area finely striate.

Vertex with a pair of long erect setae; frontal lobe without seta; pronotal disc without long erect setae; gastral tergite I without erect setae. Head, mesosoma, petiole and gaster with fine appressed pubescence which is sparse and very short on head and gaster.

For color pattern see Figs. 4-14, 4-15; body brown to dark brown; gaster a little darker than head and mesosoma; all legs orange.

Queen measurements and indices. *Odontomachus monticola* — syntype (n=1): HW 2.51 mm, HL 3.13 mm, SL 3.09 mm, IFLW 0.68 mm, EL 0.46 mm, MDL 1.88 mm, WL 4.2 mm, PTL 0.66 mm, PTH unmeasured, CI 80, SI 123, MDI 60, PTHI incalculable.

Queen description. Queen similar in general appearance to worker. Vertex near ocelli not swollen dorsad; ocular ridge clearly developed; distance between lateral ocelli sligtly shorter than distance between lateral and median ocelli, and 1.5 times as long as major axis of median ocellus; ocelli in lateral view protruded dorsad. Mesosoma with main sclerites associated with wing function (Figs. 4-16D, 4-16E), in dorsal view short and slender; anterodorsal slope of pronotum in lateral view steep; anterodorsal outline of mesoscutum in lateral view relatively gentle; mesoscutum without posteromedian depression; parapsidal furrow very weak and slightly curved; dorsal outline of metascutellum in lateral view convex; anterior third of mesopleuron with fine, oblique furrow; propodeum in lateral view relatively long, with dorsum almost straigth and gradually sloping posteriad; propodeum in dorsal view with lateral outlines convergent posteriad. Petiolar node excluding apical spine in lateral view with anterior face almost straight to weakly convex, and its posterior face weakly convex; apical spine short and relatively slender, and weakly curved posteriad (but variable in shape within species); subpetiolar process triangular, directed ventrally, with the maximum length of anterior-posterior axis as long as dorsal-ventral axis. Gastral tergite I in lateral view relatively short, with anterior face moderately long and vertical.

Head in full-face view largely smooth and shiny; area bordered by frontal carinae and ocular ridges striate; frontal lobe finely striate; lateral face of head very faintly striate and venter of head smooth and shiny; median disc of clypeus with rough texture. Pronotum densely and weakly striate transversely; mesoscutum largely smooth and shiny, with rough texture on anteromedian and posteromedian margins; mesopleuron largely smooth and shiny, with anteriormost and posteriormost parts faintly striate; mesoscutellum faintly longitudinally striate; propodeum strongly and sparsely striate transversely. Petiolar node excluding spine largely smooth and shiny, with basal part faintly striate.

Pair of long erect setae present on vertex near lateral ocelli; frontal lobe, pronotal disc and gastral tergite I without erect setae. Head, mesosoma, petiole and gaster with sparse subdecumbent to decumbent pubescence which is extremely short on gaster; mesopleuron very sparsely pubescent.

For color pattern see Fig. 4-16. Body reddish brown to brown; gaster a little darker than head and mesosoma; all legs yellowish brown.

Male measurements and indices. Non-types (n=2): HW 1.51 mm, HL 1.24 mm, SL 0.26 mm, EL 0.85 mm, EW 0.48 mm, OL 0.23 mm, OED 0.25 mm, WL 3.23 mm, FWL 6.49 mm, PTL 0.67 mm, PTH 0.83 mm, CI 122, SI 17, PTHI 124.

Male description. Body relatively small (HL 1.24 mm, WL 3.23 mm). Major axis of median ocellus smaller than minimum distance between lateral ocellli; antenna 13-segmented; scape very short, 1/3 as long as antennal segment III; II 1/2 as long as scape; III to XIII each extremely long; palp formula 6, 4 (this number vary within spcies: 6, 4 or 5, 4 in Yoshimura *et al*., 2007); dorsal outline of clypeus in lateral view weakly convex. Mesosoma in lateral view relatively slender and long; dorsal outline of pronotum in lateral view almost straight; anterodorsal outline of mesoscutum in lateral view gently sloping; mesoscutum without median depression; parapsidal furrow weak and almost straight; oblique mesopleural furrow relatively shallow and narrow; ventrolateral part of katepisternum without furrow; propodeum in lateral view with dorsal outline roundly convex; metapleuron separated from propodeum indistinctly by suture; wing venation as in Figs. 4-6B and 4-6D. Petiolar node in lateral view tapering gently to bluntly pointed apex, with anterior slope weakly convex, and posterir slope almost straight; subpetiolar process in lateral view triangular, with the maximum length of anterior-posterior axis as long as dorsal-ventral axis; petiolar sternum without posteroventral process. Gastral tergite I in lateral view long; posterior spine of abdominal tergite VIII short and thick, very weakly curved; pygostyle with long setae in its apical third; disc of abdominal sternite IX as long as broad, subrectangular, with lateralside parallel; apical lobe as long as disc and slightly narrowed in basal half, with apical margin weakly convex; telomeral apex in lateral view much longer than high; distiventral apex of valviceps strongly produced; basiventral corner of valviceps distinctly produced; ventral margin of valviceps with 23 denticles.

Head including area between lateral ocelli entirely smooth and shiny. Pronotum in lateral view smooth and shiny; mesoscutum in dorsal view smooth and shiny; scuto-scutellar suture with sparse, strong, longitudinal striation; mesopleural anepisternum and katepisternum smooth and shiny; metapleuron smooth and shiny; propodeum in dorsal view with rough texture and shiny. Petiole smooth and shiny.

Head, mesosoma, legs, petiole and gaster with fine dense subdecumbent to decumbent pubescence; mandible, vertex near ocelli and gaster except gastral tergite I with several long erect setae.

For color pattern see Fig. 4-17; body and appendage basically pale yellow, except antennal segments III to XIII dark brown.

Species recognition. *Odontomachus monticola* is morphologically most similar to *O. xizangensis* and *Odontomachus* sp. 2. However, it is distinguishable from the latter two by the following characteristics of the worker: body relatively larger in *O. monticola* (HL 2.82−3.39 mm, WL 3.59−4.30 mm) than in *O. xizangensis* (HL 2.15–2.30 mm, WL 3.20–3.37) and *Odontomachus* sp. 2 (HL 2.81–3.05 mm, WL 3.30–3.50 mm); the major axis of compound eye consist of 17–18 ommatidia in *O. monticola*, but less than 14 in the latter two; the body dark brown in *O. monticola* and *Odontomchus* sp. 2, but reddish brown in the *O. xozangensis*. Furthermore, *O. monticola* is easily distinguished from *O. xizangensis* and *Odontomachus* sp. 2 by the following characters of the queen: the distance between lateral ocelli slightly shorter than distance between lateral and median ocelli in *O. monticola* and *Odontomachus* sp. 2, but as long as the distance between lateral and median ocelli in *O. xizangensis*; the distance between lateral ocelli 1.5 times as long as major axis of median ocellus in *O. monticola*, but more than twice as long as major axis of median ocellus in *O. xizangensis*, and twice as long as major axis of median ocellus in *Odontomchus* sp. 2; propodeum in lateral view long, with its dorsal outlines almost straight in *O. monticola* and *O. xizangensis*, but short, with its dorsal outlines weakly convex in *Odontomachus* sp. 2; subpetiolar process in lateral view triangular in *O. monticola* and *O. xizangensis*, but lobate in *Odontomachus* sp. 2.

Distribution. China, Vietnam, Laos, Myanmar, Thailand and India.

Bionomics. *Odontomachus monticola* inhabits secondary and primary forests in lowlands and highlands, and nests under leaf litter, in the soil near the base of living tree, and under stones, rotten logs and stumps.

Remarks. The status of *Odontomachus monticola* was discussed by Yasumatsu (1962), Brown (1976) and Yoshimura *et al.*, (2007). Brown (1976) assumed that "*Odontomachus monticola*" is a widespread species showing a wide range of morphological variations, such as sculpture on the vertex of head and pronotal disc, and synonymized *O. monticola* var. *formosae* Forel, 1912, *O. monticola* var. *major* Forel, 1913 and *O. monticola* var. *hainanensis* Stitz, 1925 (with fine striation on vertex and transverse striation on pronotal disc), and *O. kuroiwae* (Matsumura, 1912) (with smooth and shiny on vertex and pronotal disc) under *O. monticola* Emery, 1892 (with smooth and shiny on vertex and concentric striation on pronotal disc).

Later Yoshimura *et al.* (2007) revised the genus *Odontomachus* in Japan, and revived *O. kuroiwae* from synonymies under *O. monticola* based on the morphological character of the worker, queen and male, including the morphology of male genitalia. This view was reconfirmed by the present integrated taxonomy (the chapter III). Yoshimura *et al.* (2007) examined the striation of propodeal disc of specimens obtained from the full range of *O. monticola*, and confirmed that the concentric and transverse forms of pronotal disc striation do not occur as a result of allometry, and that the two forms show particular geographical distribution patterns: the concentric form, or circular form in Yoshimura *et al.* (2007), occurs in Myammer, Laos and N. Vietnam; the transverse form occurs in China, Taiwan, and Japan; the leclotype and the all paralectotypes of *O. monticola* designated by Yoshimura *et al.* (2007) belongs to the former.

Wang (1993), in his revision of Chinese *Odontomachus*, described a new species, *O. circulus*, and delimitate it from *O. monticola* by the pronotal disc with concentric striation in the former but with transverse striation in the latter. However, as pointed out by Yoshimura *et al.* (2007), it is likely that *O. monticola* sensu Wang (1993) is the transverse form and probably corresponds to *O. monticola* var. *formosae* or *O. monticola* var. *hainanensis* (see under remakrs of *Odontomchus* sp. 1). Therefore, after careful examinations of the holotype of *O. circulus* and the lectoype and paralectotypes of *O. monticola*, the conspecificity of the two was confirmed and synonymized in the present study.

The transverse form seems to correspond *Odontomachus* sp. 1 recognized by the present integrated taxonomy. However, *Odontomachus* sp. 1 consists of two allopatric forms: the form known from Vietnam was characteized by body relatively large (HL 3.41–3.82 mm, WL 4.52–4.96 mm), dorsal outline of propodeum in lateral view weakly convex, subpetiolar process in lateral view lobate, area around compound eye with fine striation, body with dense pubescence, body brown to dark brown; the form known from Japan and Taiwan by body relatively small (HL 2.72–2.77 mm, WL 3.39–3.47 mm), dorsal outline of propodeum in lateral view almost straight, subpetiolar process in lateral view triangular, area around compound eye smooth and shiny, body with sparse pubescence, body reddish brown to brown. The "Vietnamese form" agrees well with *Odontomachus monticola* var. *hainanensis* Stitz, and the "Japanese/Taiwanese form" agree well to *Odontomachus monticola* var. *formosae* Forel, 1912 and *O. monticola* var. *major* Forel, 1913; these views are made by examining directly the syntypes of *O. m. formosae* and *O. m. major*, and by referring the original descriptions and the images of the type specimens of *O. m. hainanensis* (voucher FOCOL1061), *O. m. formosae* (FOCOL0334; FOCOL0333; FOCOL0332; CASENT0907427; CASENT090065) and *O. m. major* (FOCOL0330; FOCOL0329; FOCOL0328; FOCOL0328; CASENT0907429; CASENT0900657) provided in www.antweb.org. The status of these forms will be confirmed by integrated taxonomy after fresh specimens from Hainan and southern mainland China being available.

Wheeler (1921) described *Odontomachus monticola* subsp. *paperculus* from Mokanshan (= Moganshan) County, Chekiang (Zhejiang) Prov., China. According to the original description, this species was chracterized by body size smaller than *O. monticola*; pronotum smooth and shiny; color of the body brownish red and legs brownish yellow, while this species seems to be similar to *O. kuroiwae* and *O. fulgidus*. However, the status of *O. m. paperculus* was unable to be solved in the present study, because, unfortunately, the depository of the type specimen(s) is still unknown, and fresh specimens suitable for DNA barcoding are unavailable. So, by following

Brown (1976), *O. monticola* subsp. *pauperculus* is tentatively treated as a synonym under *O. monticola* in the present study.

Odontomachus pararixosus **Terayama *et* Ito, 2014**

(Fig. 4-18)

Odontomachus pararixosus Terayama and Ito, 2104: 181, figs. 1, 2, worker, type locality: Malaysia.

Type material examined. *Odontomachus pararixosus* — holotype (worker; NIAES), Malaysia: Ulu Gombak, 29.viii.2009, F. Ito leg. (colony code: FI109-83).

Non-type materials examined. Malaysia: Ulu Gombak, iii.2014, F. Ito leg., colony MS14-7, 1 worker (RSC); same loc., same date, F. Ito leg., colony MS14-18, 1 worker (RSC).

Material used for DNA barcoding. Colony MS14-18 (individual no. RJ20150126-5, accession no. LC056045).

Worker measurements and indices. *Odontomachus pararixosus* — holotype: HW 1.78 mm, HL 2.59 mm, SL 2.54 mm, IFLW 0.45 mm, EL 0.36 mm, MDL 1.55 mm, WL 3.33 mm, PTL 0.64 mm, PTH unmeasured, CI 69, SI 143, MDI 60, PTHI incalculable; paratypes (n=6): HW 1.70–1.88 mm, HL 2.40–2.66 mm, SL 2.52–2.54 mm, IFLW 0.42–0.45 mm, EL 0.36–0.38 mm, MDL 1.46–1.57 mm, WL 3.40–3.48 mm, PTL 0.63 mm (n=1), PTH unmeasured, CI 68–71, SI 136–148, MDI 57–62, PTHI incalculable.

Non-type (n=1): HW 1.83 mm, HL 2.62 mm, SL 2.56 mm, IFLW 0.47 mm, EL 0.37 mm, MDL 1.53 mm, WL 3.48 mm, PTL 0.64 mm, PTH 1.11 mm, CI 70, SI 140, MDI 58, PTHI 173.

Worker description. Body relatively small (HL 2.40–2.66 mm, WL 3.33–3.48 mm). Head in full-face view much longer than broad, with posterior margin almost straight; head posteriorly without a pair of small and distinct tubercles; median furrow on vertex present as dark line; each side of line not swollen dorsad; frontal lobes followed by strong frontal carinae which are nearly parallel; minimum distance between margin of ocular ridge and margin of compound eye less than half major axis of compound eye; masticatory margin with 6–9 distinct denticles; subapical tooth ca. 2.5 times as long as broad, with truncate apex; palp formula 4, 4. Mesosoma in lateral view relatively slender; pronotum including anteromedian lobe long, in lateral view with anterodorsal slope gentle; mesopleuron without anteroventral ridge, with anterodorsal margin weakly carinate, clearly separated by distinct dorsal carina from mesonotum and metapleuron;

propodeum in lateral view with dorsum almost straight, with posterior face steeply sloping; propodeal dorsum without median longitudinal depression. Petiolar node conical, with sharply pointed apical spine; node excluding apical spine in lateral view with anterior and posterior faces weakly convex; apical spine needle-shaped, weakly curved; subpetiolar process lobate, directed ventrally, with the maximum length of anterior-posterior axis as long as dorsal-ventral axis. Gastral tergite I in lateral view long, with anterior face relatively short and vertical.

Head in full-face view largely smooth and shiny; area bordered by frontal carinae and ocular ridges striate; frontal lobe smooth and shiny; extraocular furrow faintly striate; median part of vertex along median furrow smooth and shiny or sometimes with rough texture; lateral face and venter of head smooth and shiny; median disc of clypeus smooth and shiny. Pronotum in dorsal view with fine concentric striation; mesonotum finely striate transversely; mesopleuron largely smooth and shiny, with anterior third and posteriormost parts finely striate; metapleuron and propodeum with transverse striation which is a little sparser and stronger than on pronotum and mesonotum. Petiolar node largely smooth and shiny, with basal area faintly striate.

Vertex with a pair of long erect setae; frontal lobe with erect seta; pronotal disc without long erect setae; gastral tergite I with long suberect setae. Head, mesosoma, petiole and gaster with fine appressed pubescence which is sparse and extremely short on gaster.

For color see Fig. 4-18; body orange-brown, with darker mesosoma and gaster; leg yellowish brown to orange-brown, with coxae and femora paler.

Species recognition. *Odontomachus pararixosus* morphologically is very similar to *O. rixosus* and *O. minangkabau*; the delimitation among these species is discussed under *O. minangkabau*.

Distribution. Malaysia (Ulu Gombak).

Bionomics. This species inhabits the forest, and nests in rotten wood or under accumulations of leaf litter. The colonies of *O. pararixosus* were observed by Terayama & Ito (2014), and they found that only the brachypterous queens in all colonies without any dealate queens.

Odontomachus procerus Emery, 1893

(Figs. 2-1C, 2-2B, 2-2G, 2-2L, 4-2B, 4-19, 4-20, 4-21)

Odontomachus latidens subsp. *procerus* Emery, 1893: 203, queen, type locality: West Malaysia. Chapman & Capco, 1951: 45. Synonymy under *Odontomachus latidens* by Brown, 1976: 104.

Odontomachus latidens subsp. *sumatranus* Emery, 1900: 671, fig. 4, worker, queen, type locality: Indonesia (Sumatra). Synonymy under *Odontomachus latidens* by Brown, 1976: 104.

Type materials and images examined. "*Odontomachus latidens* subsp. *procerus*" — holotype (queen; MCSN), Peninsular Malaysia: Perak. "*O. latidens* subsp. *sumatranus*" — syntypes (11 workers, 2 queens; MCSN, NHMW), Indonesia: North Sumatra: Si-Rambe (XII.9D-III.91, E. Modigliani leg.).

Images of the type material of the following species provided in AntWeb v5.17.5 (http://www.antweb.org) were also examined: "*O. latidens* subsp. *procerus*", queen (CASENT0903998); "*O. latidens* subsp. *sumatranus*", worker (CASENT0903999).

Non-type materials examined. Indonesia: West Sumatra: Mt. Sago, 50 Kota District (ca. 1000 m alt.), 06.IX.2012, R. Satria leg., SAGO-01-02, 31 workers (SKYC, RSC); Alahan Panjang, 4.I.1992, F. Ito leg., FI92-252, 2 workers (SKYC, RSC). **Malaysia:** Sabah: Sayap Kinabalu, ca. 1000 m alt, 13.VII.1996, Sk. Yamane leg., 2 workers (SKYC, RSC); same loc., 13.VII.1996, K. Eguchi leg., 1 worker (SKYC, RSC); Poring, Kinabalu (550–600 m alt), 17.III.1995, Sk. Yamane leg., 1 worker (SKYC, RSC); Muaya, 27–28.VIII.2012, K. Matsunaga leg., 12 workers (SKYC, RSC); same loc., 19.X.2012, K. Matsunaga leg., 1 worker (SKYC, RSC). Sarawak: Bt. Entimau (610 m alt), 23.IV.1994, Mahmud leg, 1 worker (SKYC, RSC).

Materials used for DNA barcoding. Colony SAGO-01-12 (individual no. RJ20150126-3, accession no. LC056052).

Worker measurements and indices. *Odontomachus latidens* subsp. *sumatranus* — syntypes (n=9): HW 2.69–2.93 mm, HL 3.55–4.00 mm, SL 3.65–4.00 mm, IFLW 0.68–0.75 mm, EL 0.36–0.40 mm, MDL 2.12–2.33 mm, WL 4.40–4.70 mm, PTL 0.59–0.73 mm, PTH 1.35–1.60 mm, CI 72–81, SI 133–148, MDI 56–62, PTHI 206–228.

Non-types (n=10): HW 2.66–3.13 mm, HL 3.65–4.40 mm, SL 3.80–4.10 mm, FLW 0.69–0.81 mm, EL 0.41–0.47 mm, MDL 1.97–2.49 mm, WL 4.15–4.90 mm, PTL 0.63–0.76 mm, PTH 1.45–1.82 mm, CI 71–77, SI 126–144, MDI 52–63, PTHI 203–252.

Worker description. Body relatively large (HL 3.55–4.40 mm, WL 4.15–4.90 mm). Head in full-face view slightly longer than broad, with posterior margin almost straight; head posteriorly without a pair of small and distinct tubercles; median furrow on vertex present as a dark line; each side of line hardly swollen dorsad; frontal lobes followed by strong frontal carinae which are slightly divergent posteriad and then become nearly parallel; minimum distance between margin of ocular ridge and margin of compound eye less than half of major axis of compound eye; masticatory margin with 6–9 distinct denticles; subapical tooth shorter than broad, with truncate apex; palp formula 4, 4. Mesosoma in lateral view relatively stout; pronotum including anteromedian lobe short, in lateral view with anterodorsal slope relatively steep; mesopleuron without anteroventral ridge, with anterodorsal margin weakly carinate, clearly separated by distinct dorsal carina from mesonotum and metapleuron; propodeum in lateral view with dorsum slightly convex, with posterior face steeply sloping; propodeal dorsum without median longitudinal depression. Petiole node conical, with sharply pointed apical spine; node excluding apical spine in lateral view with anterior face weakly convex or weakly and bluntly angulate, and posterior face weakly convex; apical spine needle-shaped, less than 1/4 as long as petiolar height, sometimes weakly curved posteriad (but shape variable within species); subpetiolar process triangular, directed posteriorly, with maximum length of anterio-posterior axis shorter than dorsal-ventral axis. Gastral tergite I in lateral view relatively long, with anterior face relatively short and vertical.

Head in full-face view largely smooth and shiny; area bordered by frontal carinae and ocular ridges striate; frontal lobe smooth and shiny; extraocular furrow smooth and shiny; median part of vertex along median furrow smooth and shiny; lateral face and venter of head smooth and shiny; median disc of clypeus smooth and shiny. Pronotal disc and mesonotum in dorsal view densely and transversely striate; posterolateral face of pronotum partly smooth and shiny; mesopleuron largely smooth and shiny, with anterior fourth and posteriormost parts finely striate; metapleuron moderately striate in its anterior 2/3, and smooth and shiny or faintly striate in its posterior 1/3; propodeum with transverse striation which is a little sparser and stronger than on pronotum and mesonotum. Petiolar node largely smooth and shiny, but sometimes with basal area faintly striate.

Vertex with a pair of long erect setae; frontal lobe without seta; pronotal disc without long erect setae; gastral tergite I without erect setae. Head, mesosoma, petiole and gaster with fine appressed pubescence which is sparse and very short on head and gaster.

For color pattern see Fig. 4-19; head, mesosoma and gaster dark brown; all legs yellowish brown.

Characteristics seen in the syntypes of "*O. latidens* subsp. *sumatranus*". The morphological characteristics, excluding coloration, are almost completely the same between the syntypes of "*O. latidens* subsp. *sumatranus*" and the non-type workers. However, in the syntypes the head, mesosoma and gaster are reddish brown and all legs are yellowish brown.

Queen measurements and indices. *Odontomachus procerus* — holotype: HW 3.30 mm, HL 4.40 mm, SL 4.30 mm, IFLW 0.85 mm, EL 0.56 mm, OL 0.18 mm, MDL 2.46 mm, WL 5.68 mm, FWL 10.78 mm, PTL unmeasured, PTH unmeasured, CI 75, SI 130, MDI 55, PTHI incalculable. *Odontomachus latidens* subsp. *sumatranus* — syntypes (n=2, dealate): HW 2.93 mm, HL 3.90 mm, SL 4.00 mm, IFLW 0.78 mm, EL 0.46–0.50 mm, OL 0.16–0.17 mm, MDL 2.29 mm, WL 4.90 mm, FWL unmeasured (due to the dealation), PTL 0.79–0.81 mm, PTH 1.87–1.92 mm, CI 75, SI 136, MDI 59, PTHI 229–243.

Queen description. Queen similar in general appearance to worker. Vertex near ocelli not swollen dorsad; ocular ridge clearly developed; distance between lateral ocelli as long as distance between lateral and median ocelli, and as long as major axis of median ocellus; ocelli in lateral view protruded dorsad. Mesosoma with main sclerites associated with wing function (Fig. 4-20B), in dorsal view short and stout (slightly deformed by pinning); anterodorsal slope of pronotum in lateral view steep; anterodorsal outline of mesoscutum in lateral view relatively steep; mesoscutum with very weak anteromedian depression (but posteromedian part of mesoscutum is deformed by pinning in holotype and syntypes); parapsidal furrow very weak and slightly curved; dorsal outline of metascutellum in lateral view weakly convex; mesopleuron with fine, oblique furrow; propodeum in lateral view long with its dorsum almost straight and gradually sloping posteriad; propodeum in dorsal view with lateral outlines covergent posteriad. Wing venation as in Fig. 4-20D. Petiolar node excluding apical spines in lateral view with anterior and posterior faces weakly convex; apical spine short and relatively slender, and weakly curved posteriad; subpetiolar process lobate, directed ventrally, with the maximum length of anterior-posterior axis as long as dorsal-ventral axis. Gastral tergite I in lateral view relatively short, with anterior face moderately long and vertical.

Head in full-face view largely smooth and shiny; area bordered by frontal carinae and ocular ridges striate; frontal lobe smooth and shiny; extraocular furrow faintly striate; median part of vertex along median furrow smooth and shiny; lateral face and venter of head largely smooth and shiny, but posterolateral and posteroventral faces faintly striate; median disc of clypeus smooth and shiny. Pronotum densely and weakly striate transversely; mesoscutum largely smooth and shiny, with faintly striate in anterior face and anteromedian depression; area along posterior margin of mesoscutum weakly striate; mesopleuron largely smooth and shiny, with anteriormost and posteriormost parts faintly striate; mesoscutellum smooth and shiny; propodeum strongly and sparsely striate transversely. Petiolar node excluding apical spine largely smooth and shiny.

Pair of long erect setae present on vertex near lateral ocelli; frontal lobe and pronotal disc without erect setae; gastral tergite I without erect setae. Head, mesosoma, petiole and gaster with sparse subdecumbent to decumbent pubescence which is extremely short on gaster; mesopleuron very sparsely pubescent.

For color pattern see Fig. 4-20; head, mesosoma, petiole and gaster dark reddish brown; all legs light reddish brown.

Male measurements and indices. Non-types (n=8): HW 1.55–1.70 mm, HL 1.35–1.43 mm, SL 0.26–0.30 mm, EL 0.80–0.97 mm, EW 0.45–0.51 mm, OL 0.20–0.22 mm, OED 0.23–0.31 mm, WL 3.90–4.15 mm, FWL 6.86–7.64 mm, PTL 0.79–0.81 mm, PTH 0.93–1.08 mm, CI 114–121, SI 13–18, PTHI 117–128.

Male description. Body relatively large (HL 1.35–1.43 mm, WL 3.90–4.15 mm). Major axis of median ocellus as long as minimum distance between lateral ocelli; antenna 13-segmented; scape very short, 1/4 as long as antennal segment III; II 1/2 as long as scape; III to XIII each extremely long; palp formula 6, 4; dorsal outline of clypeus in lateral view weakly convex. Mesosoma in lateral view relatively stout and long; dorsal outline of pronotum in lateral view almost straight; anterodorsal outline of mesoscutum in lateral view gently sloping; mesoscutum without median depression; parapsidal furrow weak and almost straight; oblique mesopleural furrow relatively shallow and narrow; ventrolateral part of katepisternum with a very weak longitudinal furrow; propodeum in lateral view with its dorsal outline roundly convex; metapleuron separated from propodeum indistinctly by suture; wing venation similar to queen (see Fig. 4-20D for queen wings). Petiolar node broadly conical, with blunt apex, with anterior slope of petiolar node in lateral view almost straight, and posterior slope weakly convex; subpetiolar process in lateral view triangular and much slender, with the maximum length of anterior-posterior axis shorter than dorsal-ventral axis; petiolar sternum without posteroventral process. Gastral tergite I in lateral view long; posterior spine of abdominal tergite VIII long and slender, very weakly curved (Fig. 2-2G); pygostyle with long setae in its apical 2/3; disc of abdominal sternite IX almost circular, much longer than apical lobe, of which almost parallel lateral margins and weakly convex apex; telomeral apex in lateral view longer than high; distiventral apex of valviceps weakly produced; basiventral corner of valviceps not produced; ventral margin of valviceps with 27–31 denticles..

Head including area between lateral ocelli entirely smooth and shiny. Pronotum in lateral view with rough texture and shiny; mesoscutum with rough texture and shiny; scuto-scutellar suture with sparse, strong, longitudinal rugae; mesopleural anepisternum and katepisternum smooth and shiny; propodeum with sparse, strong, longitudinal striate. Petiole smooth and shiny.

Head, mesosoma, legs, petiole and gaster with fine dense subdecumbent to decumbent pubescence; mandible, vertex near ocelli and gaster except gastral tergite I with several long setae.

For color pattern see Fig. 4-21; petiole and gaster darker than head and mesosoma; scape yellowish brown and antennal segments III to XIII darker than scape.

Species recognition. *Odontomachus procerus* is very similar in general appearance to *O. latidens*, but it is distinguishable from the latter by the masticatory margin of the mandible with 6–9 distinct denticles that are reduced in size toward the base of the mandible (vs. very small denticles or sometimes without denticles, and only preapical angle recognized in the latter); the gastral tergite I without erect setae (vs. with short erect setae that are shorter than those on vertex near ocelli in the latter. *Odontomachus procerus* and *O. latidens* also distinguishable from each other by the male morphology: body relatively dark (vs. relatively light in color in the latter); subpetiolar process in lateral view triangular, with the maximum length of anterior-posterior axis shorter than dorsal-ventral axis, (vs. lobate, anterior-posterior axis as long as dorsal-ventral axis, in the latter). The delimitation of these two species based on the morphology of male genitalia was disscussed in Chapter II.

Distribution. Indonesia (Sumatra) and Malaysia (Malay Peninsula, Sabah and Sarawak).

Bionomics. *Odontomachus procerus* inhabits secondary and primary forests in the highlands (between 800 and 1300 m alt., but one specimen in SKYC was collected from Sabah at an elevation of 550-610 m alt.), and it nests in the soil near the base of living trees. The colony SAGO-01-12 collected in Sago Mountain, West Sumatra, was collected nesting together with *Pheidole inornata* (colony SAGO-02-12). Details concerning the nature of their relationship are unknown.

***Odontomachus rixosus* F. Smith, 1857**

(Figs. 2-2D, 2-2C, 2-2H, 2-2M, 4-22, 4-23, 4-24, 4-25)

Odontomacus rixosus F. Smith, 1857: 64, worker, type locality: Singapore. Forel, 1900: 58; Viehmeyer, 1916: 116; Crawley, 1924: 388 (q); Karavaiev, 1925: 293; Chapman & Capco, 1951: 45; Wheeler & Wheeler, 1952: 651 (l); Brown, 1976: 163; Imai, Brown *et al*, 1984: 67 (k). Bolton, 1995: 297; Sorger & Zettel, 2011: 157.

Odontomachus rixosus var. *conifera* Forel, 1913: 19, worker, queen, type locality: Indonesia (Java). Chapman & Capco, 1951: 45. Synonymy by Brown, 1976: 105.

Odontomachus rixosus var. *obscurior* Forel, 1900: 58, worker, type locality: Myanmar. Viehmeyer, 1916: 116 (q); Chapman & Capco, 1951: 45. Synonymy by Brown, 1976: 105.

Odontomachus tensus Wang, 1993: 223, fig. 4, worker, type locality: China (Yunnan). **Syn. Nov.**

Type materials and images examined. *Odontomachus rixosus* — syntype (1 worker; BMNH), Singapore. "*Odontomachus tensus*" — holotype (worker; IZCAS); China: Yunnan; paratype (1 worker, 1 queen; IZCAS) same data as holotype.

Images of the type material of the following species provided in AntWeb v5.17.5 (http://www.antweb.org) were also examined for reconfirming our species recognition: *O. rixosus*, worker (CASENT0900656); "*O. rixosus conifera*", worker (CASENT0907432); "*O. rixosus obscurior*", worker (CASENT0907431).

Non-type materials examined. Indonesia: Sumatra: Aceh: Leuser Ecosystem (ca. 980 m alt.), R. Satria leg., GK-01-12, 12 workers (SKYC, RSC); same loc. (ca. 980 m alt.), 19.IX.2012, R. Satria leg., GK-15-12, 16 workers (SKYC, RSC); same loc.(ca. 1000 m alt.), 21.IX.2012, R.

Satria leg., GK-42-12, 14 workers (SKYC, RSC); same loc. (ca. 980 m alt), 19.IX.2012, R. Satria leg., GK-01-12, 2 workers (SKYC, RSC); same loc., (ca. 980 m alt.), 20.IX.2012, GK-20-12, 4 workers (SKYC, RSC); same loc., (ca. 1000 m alt.), 21.IX.2012, R. Satria leg., GK-40-12, 12 workers, 2 queen (SKYC, RSC); West Sumatra: Ulu Gadut nr Padang, 27–30.VIII.1985, Sk. Yamane leg., SNS coll., 8 workers (SKYC); Lubuk Gadang, 21–23.VIII.1985, Sk. Yamane leg., SNS coll. , 2 workers (SKYC); Padang: Ulu Gadut: Pinang-pinang, 22.III.1997, F. Ito leg., F197-385, 3 workers (SKYC); same loc., 18.II.2007, Sk. Yamane leg., 1 worker (SKYC); Andalas University's forest (ca. 200–600 m alt.), 02.IX.2012, R. Satria leg., PDG-01-12, 6 workers (SKYC, RSC); same loc., 14.IX.2011, 9 workers (SKYC, RSC); same loc., 02.VIII.2012, R. Satria leg., PDG-01-12, 5 workers (SKYC, RSC); 50 Kota District: Mt. Sago, 06.IX.2012, R. Satria leg., SAGO-06-12, 3 workers (SKYC, RSC); Harau, Gantiang, 10.IX.2012, R. Satria leg., GTH-01-12, 8 workers, 3 queen (SKYC, RSC); Tanah Datar District: Barulak, 05.IX.2012, R. Satria leg., LBT-03-12, 4 wokrkers (SKYC, RSC); same loc., 07.IX.2012, R. Satria leg., LBT-11-12, 8 workers (SKYC, RSC); Solok District: Mt. Talang (general collection), 23–28.VIII.2012, R. Satria leg. 4 workers (SKYC, RSC); Jambi: Merangin: Sungai Manau: Kerinci Seblat N.P., 7.XI.2006, Syaukani leg., SYAU06-75, 7 workers, 1 queen (SKYC); Lampung: Sumber Jaya: Bodong Jaya, 16.IX.2007, Sk. Yamane leg., SU07-SKY-149, 4 workers (SKYC); same loc., 18.IX.2007, Sk. Yamane leg., SU07-SKY-204, 9 workers (SKYC); W. Lampung: Sumber Jaya (800–900 m alt), 16.IX.2007, Sk. Yamane leg., SU07-SKY-158, 8 workers (SKYC). Simeulue Island: Luan Boya, 16.IX.2012, R. Satria leg., LLB-01-12, 29 workers, 2 queens (SKYC.RSC); Lewak: Alafan, 13.IX.2012, R. Satria leg., LW-08-12, 17 workers, 4 queens (SKYC, RSC); same loc., 13.IX.2012, R. Satria leg., LW-10-12, 11 workers, 1 queen (SKYC, RSC); E. Simeulue Island: Sinabang, 15.IX.2012, R. Satria leg., SNB-03-12, 24 workers (SKYC, RSC); W. Simeulue Island: Babul Makmur, 15.IX.2012, R. Satria leg., 13 workers, 1 queen (SKYC, RSC); same loc, same date, BMS-21-12, 10 workers (SKYC, RSC). Bali: Mendaya: Dusun PK Jelati, 6.V.1998, K. Eguchi leg., EG98-BALI-739, 3 workers (SKYC); Jembrana District: Pekutatan: Pulukan, 23.X.2012, R. Satria leg., PKN-01-12, 38 workers, 7 queens (SKYC, RSC). Mentawai Islands: Siberut Island: Simabuggei, 22.II.2007, Sk. Yamane leg., SU07-SKY-078, 5 workers (SKYC). **Malaysia.** Sabah: Poring: Kinabalu (550–600 m alt), 19.III.1995, Sk. Yamane leg., 1 worker (SKYC); same loc. (450–500 m), 21.XI.1996, K. Eguchi leg., EG96-BOR-269, 1 worker (SKYC); same loc. (600–700 m alt), 16.III.1995, Sk. Yamane leg., 2 workers (SKYC); same loc., (700–800 m alt), Sk. Yamane leg., 5 workers (SKYC); Poring Hot spring (600 m alt), 20.IX.1993, T. Kikuta leg., 2 workers (SKYC); Poring (600 m alt), 26.X.1996, T. Kikuta leg., 6.X2606-(2)Aa, 5 workers (SKYC), 6X2606-(8)Ba, 4 workers (SKYC); Sayap Kinabalu, ca. 1000 m alt., 15.VII.1996, K. Eguchi leg., Eg96-BOR-057, 3 workers, 1 male (SKYC); same loc., same date, HN-140, 1 workers (SKYC); same loc., same date, HD-112, 1 worker (SKYC); same loc., same date, HN-153, 1 worker (SKYC), same loc., same date, Eg96-BOR-056, 3 workers (SKYC); same loc., same date, HD-95, 1 worker (SKYC); same loc., same date, HD-97, 1 worker (SKYC); same loc., same date, S-17, 1 worker (SKYC); same loc., same date, HD-116, 1 worker (SKYC); same loc., 14.VII.1996, Sk. Yamane leg., 3 workers (SKYC); same loc., 15.VIII.1996, Sk. Yamane leg., SB96-SKY-5, 1 worker (SKYC); same loc., 14.VII.1996, Sk. Yamane leg., HC-4, 1 worker (SKYC); Sg. Kalang, Tenom, 800–1000 m alt., 23.III.1997, Sk. Yamane leg., 1 worker (SKYC); Danum valley, 2.XI.1996, K. Eguchi leg., Eg96-BOR-125, 6 workers (SKYC); same loc., 6.XI.1996, K. Eguchi leg., EG96-BOR-203, 3 workers (SKYC); Tawau hills N. P. HQ., 7-12.VII.1996, Sk. Yamane leg. , 1 worker (SKYC); Tambunan village resort centre, 05.XI.2000, Sk. Yamane leg., SB00-SKY-04, 1 queen (SKYC); Crocker range N.P., Mahua Waterfall area (ca. 1000 m alt.), 05.XI.2000, B.T. Viet leg., 1 worker (SKYC); same loc., 04.XI.2000, K. Eguchi leg., Eg00-BOR-110, 1 worker (SKYC). Sarawak: Bako Nat. Park., 21-22.IV.1993, Sk. Yamane leg., 3 workers (SKYC); Niah N. P., 9.I.1993, Sk. Yamane leg., 5 workers (SKYC); Mulu (lowland), 11.XI.1993, Sk. Yamane leg., 2 workers (SKYC); Miri, Tower region, Lambir N. P., 16.II.1995, Abd. Rahman leg., 1 worker (SKYC). Malay Peninsula: Selangor: Ulu Gombak, 12.III.1999, F. Ito leg., F199-139, 3 workers (SKYC); same loc., VII-X.1992, F. Ito leg., 1 worker (SKYC); same loc., (ca. 250 m alt.), 05.VII.1999, Sk. Yamane leg., 2 workers (SKYC); Selangor (ca. 250 m alt.), 5.VII.1999, Sk. Yamane leg., 2 workers (SKYC). **Thailand:** Chacheongsao: Khao Ang Reu Nai W.S. near Headquarters (secondary forest), 22.VIII.2003, Sk. Yamane leg., TH03-SKY-97, 18 workers, 1 queen (SKYC). Chanthaburi: Khao Soi Dao W.S. (rainforest), 3.VI.2001, Sk. Yamane leg., TH01-SKY-07, 8 workers, 2 queens (SKYC); same loc., 20.VII.1997, Sk. Yamane leg., 11 workers (SKYC); same loc., 19–20.VII.1997, H. Okido leg., 8 workers (SKYC); Nam Thok Phlio N.P. (300–500 m alt.), 21.IX.2003, Sk Yamane leg., 3 workers (SKYC). Nakom Ratchasima: Sakaerat lowland forest (DEF), 09.VII.1999, Sk. Yamane leg., 4 workers (SKYC); Khao Nan N.P., Klong Klai stn., 13.III.2007, Sk. Yamane leg., 2 workers (SKYC); Khao Nan

N.P., Papra stn., 14.III.2007, Sk. Yamane leg., 2 workers (SKYC). Songkhla: Hatyai, Prince of Songkhla University forest, 17.III.2007, Sk. Yamane leg., TH07-SKY-72, 3 workers (SKYC); same loc., 17.III.2007, Sk. Yamane leg., TH07-SKY-72, 3 workers (SKYC); Khao Nam Kang N.P., 25.VII.1997, Sk. Yamane leg., 1 worker (SKYC); Pattani: Sa i Kho, 25.VIII.1998, Sk. Yamane leg., 1 worker, 1 queen (SKYC). Trang: Khao Chong (river side), 25.VIII.1998, Sk. Yamane leg., 3 workers (SKYC). Suratthani: Khlongsane W.S. (evergreen forest), 14.X.2011, W. Jaitrong leg., 1 worker (SKYC). **Vietnam:** Kien Giang: Phu Quoc: Bai Thom: Xom Moi: K7, N10˚21'50", E103˚59'29", ca. 35 m alt., 09.IX.2015, R. Satria leg., colony RS-36-PQ15, 7 workers, 1 queen (RSC); Ganh Dau: Xom Moi, N10˚21'25–33", E103˚52'33–38", ca. 35–70 m alt., 11.IX.2015, R. Satria leg., colony RS-61-PQ15, 5 workers (RSC); same loc., same date, R. Satria leg., colony RS-68-PQ15, 5 workers, 1 queen (RSC); same loc., same date, R. Satria leg., colony RS-70-PQ15, 7 workers (RSC); same loc., same date, R. Satria leg., colony RS-71-PQ15, 5 workers (RSC); same loc., same date, R. Satria leg., colony RS-72-PQ15, 6 workers (RSC); same loc., 13.IX.2015, R. Satria leg., colony RS-73-PQ15, 6 workers, 1 queen (RSC); same loc., same date, R. Satria leg., colony RS-74-PQ15, 7 workers (RSC).

Material used for DNA barcoding. Colony BMS-22-12 (RJ20141201-3, accession no. LC056035), colony GK-15-12 (RJ20141201-13, LC056036), colony GTH-01-12 (RJ20141201-2, LC056038), colony LBT-06-12 (RJ20141201-8, LC056039), colony LBT-07-12 (RJ20141201-9, LC056040), colony LBT-09-12 (RJ20141201-7, LC056041), colony LBT-10-12 (RJ20141201-10, LC056042), colony SAGO-06-12 (RJ20141201-14, LC056053), colony PDG-13-12 (RJ20141114-1, LC056046), colony PKN-01-12 (RJ20141114-2, LC056050), colony RS-61-PQ15 (individual no. RJ20151125-12), colony RS-73-PQ15 (RJ20151125-10), colony RS-36-PQ15 (individual no. RJ20151125-11), colony RS-80-PQ15 (RJ20151125-14), colony RS-61-PQ16 (RJ20151125-12), colony RS-73-PQ16 (RJ20151125-10), colony RS-36-PQ16 (RJ20151125-11), colony RS-80-PQ16 (RJ20151125-14).

Worker measurements and indices. *Odontomachus rixosus* — syntype (n=1, gaster missing): HW 2.10 mm, HL 2.98 mm, SL 2.93 mm, IFLW 0.64 mm, EL 0.36 mm, MDL 1.64 mm, WL 4.00 mm, PTL 0.72 mm, PTH 1.21 mm, CI 70, SI 139, MDI 55, PTHI 168. *Odontomachus tensus* — holotype: HW 1.78 mm, HL 2.59 mm, SL 2.46 mm, IFLW 0.41 mm, EL 0.33 mm, MDL 1.41 mm, WL 3.16 mm, PTL 0.54 mm, PTH 0.97 mm, CI 68.72, SI 138.20, MDI 54.44, PTHI 179.63; paratypes (n=2); but n=1 in WL, PTL, PTH, PTHI): HW 1.77–1.84 mm, HL 2.52–2.63 mm, SL 2.47–2.52 mm, IFLW 0.47–0.53 mm, EL 0.32–0.34 mm, MDL 1. 42–1.54 mm, WL 3.28 mm, PTL 0.57 mm, PTH 1.07 mm, CI 70, SI 137–139, MDI 56–58, PTHI 188.

Non-types (n=10): HW 1.77–2.19 mm, HL 2.56–3.03 mm, SL 2.56–3.03 mm, IFLW 0.45–0.56 mm, EL 0.31–0.42 mm, MDL 1.45–1.67 mm, WL 3.35–4.00 mm, PTL 0.57–0.69 mm, PTH 1.09–1.26 mm, CI 64–73, SI 131–150, MDI 55–57, PTHI 171–196.

Worker description. Body relatively small (HL 2.56–3.03 mm, WL 3.35–4.00 mm). Head in full-face view much longer than broad, with posterior margin weakly concave; head posteriorly without a pair of small and distinct tubercles; median furrow on vertex present as dark line; each side of line not swollen dorsad; frontal lobes followed by strong frontal carinae which are nearly parallel; minimum distance between margin of ocular ridge and margin of compound eye less than half major axis of compound eye; masticatory margin with 6–10 denticles (7 in a syntype of *O. rixosus* examined; 7 in a syntype of *O. rixosus conifer* [ANTWEB CASENT 0907432]; 6 in a syntype of *O. rixosus obscurior* [ANTWEB CASENT 0907431]); subapical tooth ca. 2.5 times as long as broad, with truncate apex; palp formula 4, 4. Mesosoma in lateral view relatively slender; pronotum including anteromedian lobe long, in lateral view with anterodorsal slope gentle; mesopleuron without anteroventral ridge, with antero sloping; propodeal dorsum without median longitudinal depression. Petiolar node conical, with sharply pointed apical spine; node excluding apical spine in lateral view with anterior and posterior faces weakly convex; apical spine needle-shaped, less than 1/4 as long as petiolar height, sometimes weakly curved posteriad (but shape variable within species); subpetiolar process lobate, directed ventrally, with maximum length of anterior-posterior axis as long as dorsal-ventral axis. Gastral tergite I in lateral view long, with anterior face relatively short and vertical.

Head in full-face view largely smooth and shiny; area bordered by frontal carinae and ocular ridges striate; frontal lobe smooth and shiny; extraocular furrow faintly striate; median part of vertex along median furrow smooth and shiny or sometimes with rough texture; lateral face and venter of head smooth and shiny; median disc of clypeus smooth and shiny. Pronotum in dorsal view finely concentrically striate; mesonotum finely striate transversely; mesopleuron largely smooth and shiny, with anterior third and posteriormost parts finely striate; metapleuron and propodeum with transverse striation which is a little sparser and stronger than on pronotum and mesonotum. Petiolar node largely smooth and shiny, with basal area faintly striate.

Vertex with a pair of long erect setae; frontal lobe with erect seta; pronotal disc without long erect setae; gastral tergite I without erect setae. Head, mesosoma, petiole and gaster with fine appressed pubescence which is sparse and very short on head and petiole and is sparse and extremely short on gaster.

For color see Figs. 4-22, 4-23; body orange-brown, with darker mesosoma and gaster; leg yellowish brown to orange-brown, with coxae and femora paler.

Queen measurements and indices. Non-types (n=10): HW 1.87–2.17 mm, HL 2.53–2.96 mm, SL 2.49–2.76 mm, IFLW 0.42–0.57 mm, EL 0.39–0.50 mm, OL 0.12–0.18 mm, MDL 1.45–1.63 mm, WL 3.50–4.05 mm, FWL 6.46–8.33 mm, PTL 0.65–0.70 mm, PTH 1.40–1.56 mm, CI 72–76, SI 124–136, MDI 52–58, PTHI 214–229.

Queen description. Queen similar in general appearance to worker. Vertex near ocelli not swollen dorsad; ocular ridge clearly developed; distance between lateral ocelli shorter than or as long as distance between lateral and median ocelli, and as long as major axis of median ocellus; ocelli in lateral view protruded dorsad. Mesosoma with main sclerites associated with wing function (Figs. 33B, 33C), in dorsal view long and slender; anterodorsal slope of pronotum in lateral view gentle; anterodorsal outline of mesoscutum in lateral view relatively gentle; mesoscutum without posteromedian depression; parapsidal furrow very weak, and slightly curved; dorsal outline of metascutellum in lateral view covex; anterior third of mesopleuron with fine, oblique furrow (sometimes without any furrow); propodeum in lateral view long, with dorsum almost straight and gradually sloping posteriad; propodeum in dorsal view with lateral outlines convergent posteriad. Wing venation as in Figs. 4-24E and 4-24F. Petiolar node excluding apical spine in lateral view with anterior and posterior faces weakly convex; apical spine short and stout, and sometimes weakly curved posteriad; subpetiolar process lobate, directed ventrally, with the maximum length of anterior-posterior axis as long as dorsal-ventral axis. Gastral tergite I in lateral view long, with anterior face relatively short and vertical.

Head in full-face view largely smooth and shiny; area bordered by frontal carinae and ocular ridges striate; frontal lobe almost smooth and shiny; extraocular furrow faintly striate; median part of vertex along median furrow smooth and shiny or sometimes with rough texture; lateral face and venter of head smooth and shiny; median disc of clypeus smooth and shiny. Pronotum densely and weakly striate transversely (often dorsolateral part smooth and shiny); mesoscutum faintly longitudinally striate (but sometime largely smooth and shiny, and faintly striate along posterior margin of mesoscutum); mesopleuron largely smooth and shiny, with anterior third and posteriormost parts faintly striate; mesoscutellum smooth and shiny; propodeum strongly and sparsely striate transversely. Petiolar node largely smooth and shiny, with its basal area faintly striate.

Pair of long erect setae present on vertex near lateral ocelli; frontal lobe with a erect seta; pronotum and gastral tergite I without erect setae. Head, mesosoma, and petiole with sparse subdecumbent to decumbent pubescence which is extremely short in head and gaster; mesopleuron very sparsely pubescent.

For color see Fig. 4-24; head, mesosoma, petiole and gaster reddish brown; all coxae and femora yellowish brown; tibiae reddish brown.

Male measurements and indices. Non-types (n=10): HW 1.19–1.35 mm, HL 1.04–1.14 mm, SL 0.20–0.26 mm, EL 0.70–0.84 mm, EW 0.37–0.46 mm, OL 0.16–0.22 mm, OED 0.16–0.18 mm, WL 2.63–2.93 mm, FWL 4.52–5.58 mm, PTL 0.56–0.64 mm, PTH 0.78–0.90 mm, CI 107–120, SI 15–20, PTHI 135–152.

Male description. Body relatively small (HL 1.04–1.14 mm, WL 2.63–2.93 mm). Major axis of median ocellus as long as minimum distance between lateral ocelli; antenna 13-segmented; scape very short; 1/3 as long as antennal segment III; II 1/2 as long as scape; III to XIII each extremely long; palp formula 6, 4; dorsal outline of clypeus in lateral view weakly convex. Mesosoma in lateral view relatively slender and long; dorsal outline of pronotum in lateral view almost straight; anterodorsal outline of mesoscutum in lateral view gently sloping; mesoscutum without median depression; parapsidal furrow very weak and almost straight; oblique mesopleural furrow relatively shallow and wide; ventrolateral part of katepisternum with very weak longitudinal furrow; propodeum in lateral view with dorsal outline roundly convex; metapleuron separated from propodeum indistinctly by suture; wing venation similar to queen (see Figs. 4-24E and 4-24F for queen wings). Petiolar node in lateral view tapering gently to bluntly pointed apex, with anterior slopes weakly convex, and posterior slope almost straight; subpetiolar process in lateral view anteroposteriorly shorter than dorsoventrally high, lobate and slender; petiolar sternum without posteroventral process. Gastral tergite I in lateral view short; posterior spine of abdominal tergite VIII long and slender, very weakly curved (Fig. 2-2J); pygostyle with long setae in its apical third; disc of abdominal sternite IX much broader than long, with posterolateral corner expanding laterad; apical lobe much longer than disc and gently tapering to almost truncate apex; telomeral apex in lateral view longer than high; distiventral apex of valviceps strongly produced; basiventral corner of valviceps distinctly produced; ventral margin of valviceps with 21−22 denticles.

Head including area between lateral ocelli entirely smooth and shiny. Pronotum in dorsal view smooth and shiny; mesoscutum smooth and shiny; scuto-scutellar suture with sparse, strong, longitudinal rugae; mesopleural anepisternum and katepisternum smooth and shiny; metapleuron smooth and shiny; propodeum in dorsal view with rough texture and shiny. Petiole smooth and shiny.

Head, mesosoma, legs, petiole and gaster with fine sparse subdecumbent to decumbent pubescence; mandible, vertex near ocelli, and gaster except gastral tergite I with long erect setae.

For color pattern see Fig. 4-25; males from Thailand always darker than those from the other localities.

Species recognition. The striation of the pronotal disc of the worker shows variation: fine and transverse in the syntype workers of *O. rixosus* and *O. rixosus conifer* (ANTWEB CASENT 0907432), but fine and concentric in *O. rixosus obscurior* (ANTWEB CASENT 0907431).

The delimitations among *O. rixosus, O. pararixosus* and *O. minangkabau* were reconfirmed in the present integrated taxonomy (the chapter III). *Odontomachus rixosus* is very similar in general appearance to *O. pararixosus*, but is distinguishable from the latter by the following characteristics of the worker: weakly notched posterior head margin in the former, but almost straight in the latter; the apical spine of the petiolar node needle-shaped in the former, but acutely triangular in the latter; and the gastral tergite I without long suberect setae in the former, but with setae in the latter.

Wang (1993) described *Odontomachus tensus* based on worker collected from China (Yunnan province), and he mentioned that “this species is near to *Odontomachus fulgidus* but differs from the latter in the following characters: pronotal dorsum covered with fine, dense, circular striation; SI>135; third tooth of mandible longer and narrower". After careful examinations of the holotype and 1 paratype worker of *Odontomachus tensus* and 1 syntype worker of *Odontomachus rixosus*, the conspecificity of the two was confirmed and synonymized in the present study. It is likely that Wang (1993) described *O. tensus* without referring to the original description and the type specimen of *O. rixosus*.

Distribution. *Odontomachus rixosus* is distributed throughout tropical Asia: Indo-Malayan subregion (Western part of Indonesia, Malaysia, Brunei and Phillipines), India, Myanmar, Thailand, Vietnam, Cambodia, Laos and north to Yunnan Province (China).

Bionomics. *Odontomachus rixosus* inhabits plantations, secondary and primary forests in lowlands, and nests under leaf litter, in the soil near the base of living trees, and under rotten logs and stumps. This species frequently forms compound colonies with *Pheidole tandjongensis* (GK-01-12/GK-02-12, GK-20-12/GK-55-12, LBT-11-12/LBT-12-12, SAGO-06-12/SAGO-05-12, PDG-01-12/PDG-02-12, SU07-SKYC-204, TH03-SKY-91, TH03-SKY-152, TH91-RX-01, MP05-SKY-56, SU07-SKY-158, TH00-SKY-59, and SU07-SKY-078) and with *P. inornata* Eguchi, 2001 (GTH-01-12/GTH-02-12, SOO-SKY-04, TH01-SKY-07, and SB06-SKY-78). Details concerning the nature of the relationship between *O. rixosus* and *Pheidole* spp. are unknown.

Odontomachus xizangensis **Wang, 1993**

(Figs. 4-26, 4-27)

Odontomacus xizangensis Wang, 1993: 222, Fig. 2, worker, type locality: China (Xizang Province).

Type materials examined. *Odontomacus xizangensis* — holotype (worker; IZCAS) China: Xizang Prov.; paratypes (8 workers; IZCAS), same data as holotype.

Non-type materials examined. China: Xizang Prov.: Medog Co. (1100 m alt), 1982.I.21, Han Yinheng leg., 3 queens (IZCAS, for these queen not labeled as "paratype", but have same data as holotype) .

Note: The workers labeled as the "holotype" or the "paratype" of *Odontomachus xizangensis* in the collection of IZCAS were collected on "1982.i.21" according to the data labels (Figs. 4-26). However, Wang (1993) mentioned the collection date as "1982.i.15" in the original description of Odontomachus xizangensis. Later, Dr. Wang Min Sheng (pres. comm., March, 2016) confirmed that he deposited all of the type specimens of Chinese *Odontomachus* spp. described by Wang (1993) in the collection of IZCAS. So, in the present study, the workers labeled as the "holotype" or the "paratypes" in IZCAS are treated as the real type series of *O. xizangensis*.

Worker measurements and indices. *Odontomachus xizangensis* — holotype: HW 2.19 mm, HL 2.70 mm, SL 2.71 mm, IFLW 0.58 mm, EL 0.33 mm, MDL 1.64 mm, WL 3.37 mm, PTL 0.51 mm, PTH unmeasured, CI 81, SI 124, MDI 61, PTHI incalculable; paratypes (n=3): HW 2.15–2.30 mm, HL 2.69–2.78 mm, SL 2.62–2.77 mm, FLW 0.58 mm, EL 0.32–0.33 mm, MDL 1.60–1.62 mm, WL 3.20–3.27 mm, PTL 0.51 mm, PTH 1.13 mm (n=1), CI 80–82, SI 118–123, MDI 58–60, PTHI 221 (n=1).

Worker description. Body relatively small (HL 2.69–2.78 mm, WL 3.20–3.37 mm). Head in full-face view slightly longer than broad, with posterior margin weakly concave; head posteriorly without a pair of small and distinct tubercles; median furrow on vertex present as a dark line, each side of line hardly swollen; frontal lobes followed by strong frontal carina which are slightly divergent posteriad; minimum distance between margin of ocular ridge and margin of compound eye more than half of major axis of compound eye; masticatory margin with 6–8 distinct denticles; subapical tooth shorter than broad, with truncate apex; palp formula 4, 4. Mesosoma in lateral view stout; pronotum including anteromedian lobe short, in lateral view with anterodorsal slope relatively steep (the pronotum slightly deformed by pinning); mesopleuron without anteroventral ridge, with anterodorsal margin weakly carinate, clearly separated by distinct dorsal carina from mesonotum and metapleuron; propodeum in lateral view with dorsum almost straight, with anterior face steeply sloping; propodeal dorsum without any median longitudinal depression. Petiolar node conical, with sharply pointed apical spine; node excluding apical spine in lateral view with anterior and posterior faces weakly convex; apical spine short, less than 1/4 as long as petiolar height and weakly curved posteriad; subpetiolar process lobate, directed ventrally, with the maximum length of anterior-posterior axis as long as dorsal-ventral axis. Gastral tergite I in lateral view relatively short, with anterior face relatively short and vertical.

Head in full-face view largely smooth and shiny; area bordered by frontal carinae and ocular ridges striate; frontal lobe finely striate; extraocular furrow faintly striate; median part of vertex along median furrow smooth and shiny; posterolateral face of head faintly striate; venter of head smooth and shiny; median disc of clypeus with rough texture. Pronotal disc in dorsal view with concentric striation (pronotum of all type specimens damaged by pinning). Mesonotum finely striate; mesopleuron largely smoth and shiny, with anterior third and posteriormost parts finely striate; metapleuron and propodeum with transverse striation which is a little sparser and stronger than on pronotum and mesonotum; petiolar node entirely smooth and shiny.

Vertex with a pair of long erect setae; frontal lobe without seta; pronotal disc without long erect setae; gastral tergite I without erect setae. Head, mesosoma, petiole and gaster with fine appressed pubescence which is sparse and very short on gaster.

For color see Fig 4-26; body and appendages reddish-brown, with darker mesosoma and gaster; all legs reddish brown.

Queen measurements and indices. Non-type (n=1): HW 2.3 mm, HL 2.71 mm, SL 2.71 mm, IFLW 0.58 mm, EL 0.33 mm, MDL 1.61 mm, WL 3.38 mm, PTL 0.55 mm, PTH 1.42 mm, CI 85, SI 118, MDI 60, PTHI 258.

Queen description. Queen similar in general appearance to worker. Vertex near ocelli not swollen dorsad; ocular ridge clearly developed; distance between lateral ocelli as long as distance between lateral and median ocelli, and more than 2 times of major axis of median ocellus; ocelli in lateral view protruded dorsad. Mesosoma with main sclerites associate with wing function (Figs. 4-27C, 4-27D), in dorsal view short and stout; anterodorsal slope of pronotum in lateral view relatively steep; anterodorsal outline of mesoscutum in lateral view relatively gentle (mesoscutum deformed by pinned); mesoscutum without any posteromedian depression; parapsidal furrow very weak and almost straight; dorsal outline of metascutellum in lateral view convex; mesopleuron with shallow, oblique furrow; propodeum in lateral view relatively short, with dorsum almost straight and gradually sloping posteriad; propodeum in dorsal view with lateral outlines convergent posteriad. Petiolar node excluding apical spine in lateral view with anterior face almost straight to weakly convex and posterior face almost straight; apical spine short and stout, and weakly curved posteriad; subpetiolar process triangular, directed ventrally, with the maximum length of anterior-posterior axis as long as dorsal-ventral axis. Gastral tergite I in lateral view relatively short, with anterior face moderately long and vertical.

Head in full-face view largely smooth and shiny; area bordered by frontal carinae and ocular ridges striate; frontal lobe weakly striate; extraocular furrow faintly striate; median part or vertex along median furrow smooth and shiny; lateral face and venter of head smooth and shiny; median disc of clypeus with rough texture. Pronotum densely and weakly striate transversely; mesoscutum largely smooth and shiny, with faint striae on posterior and lateral margin; mesopleuron largely smooth and shiny with anteriormost and posteriormost parts faintly striate; mesoscutellum largely faintly striate; propodeum strongly and sparsely striate transversely; petiolar node ecluding apical spine largely smooth and shiny, with basal part faintly striate.

Pair of long erect setae present on vertex near lateral ocelli; frontal lobe and pronotal disc without any erect setae; gastral tergite I without any erect setae; head, mesosoma, petiole and gaster with sparse subdecumbent and decumbent pubescence which is extremely short on gaster; mesopleuron with very sparsely pubescence.

For color see Fig. 4-27. Body reddish brown, with legs more paler.

Species recognition. See under *Odontomachus monticola*.

Distribution. So far known from the type locality: Xizang Province (China).

Bionomics. This species inhabits in higlands (Wang, 1993).

***Odontomachus* sp. 1**

(Figs. 4-28, 4-29, 4-30)

Odontomachus monticola var. *formosae* Forel, 1912: 46, worker, queen, male, type locality: Taiwan. Subspecies of *Odontomachus monticola*: Santschi, 1925: 82. Synonymy under *Odontomachus monticola* by Yasumatsu, 1962: 93.

Odontomachus monticola var. *major* Forel, 1913: 183, worker, type locality: Taiwan. Synonymy under *Odontomachus monticola* by Brown, 1976: 105.

Odontomachus monticola var. *hainanensis* Stitz, 1925: 115, fig. 3, worker, type locality: China (Hainan). Synonymy under *Odontomachus monticola* by Brown, 1976: 105.

Odontomachus simillimus F. Smith (misidentification): Radchenko, 1993: 11

Type materials and images examined. *Odontomachus monticola var. formosae* — syntype (1 worker, BMNH), Taiwan: Pilam. *Odontomachus monticola var. major*— syntype (1 worker, BMNH), Taiwan: Taihorin.

Non-type materials examined. China: E. Guangxi: Da Yao Shan, 23.IX.1998, J.R. Fellowes leg., 1 worker (RSC); Guangxi: Xing An County: Gao Zhai (300 m alt.), 15.IX.2000, Sk. Yamane leg., 1 worker (RSC). **Japan**: Kagoshima-ken: Kagoshima-shi: Eboshi-dake, 7.VIII.2012, R. Satria leg., 2 workers, Individual no. RJ20161114-15 (SEMUT-A) and RJ20161117-16 (SEMUT-B), (RSC); same loc., Oura Cho, 17.X.1993, H. Okido leg., 1 worker (RSC); same loc., Eboshi-gake, 5.XI.2008, Sk. Yamane leg., 1 worker (RSC); same loc., Osumi Is.: Kuchinoerabu-jima, 20.VII.1989, S. Handa leg., 1 worker (RSC); Yakushima: Hanayama Natur. Forest (1170 m alt.), 26.IV.1986, A. Moroto leg., 1 worker (RSC); same loc., Kotodake Forest, 3.III.2013, R. Satria leg., leg., 2 workers (RSC); same loc., Ano-Yindo, 650m alt. 25.viii.2016, Sk. Yamane leg., worker; individual no. RJ20170613-25. **Taiwan**: Pingtung: Kenting N.P.: Kenting forest recreation area: Area II, 26.VII.2016, A. Yamada leg., 1 worker, individual no. RJ20161117-11 (RSC); Nanrenshan ecological reserve area, 26.VII.2016, A. Yamada leg., 1 worker, individual no. RJ20161117-12 (RSC); Nantou County: Xitou Forest, N 23.67279°, E 120.79935°, 1160 m alt., 14.V.2017, K. Eguchi leg., colony Eg14v17-1323, individual no. RJ20170613-24, 1 worker (ACEG); same loc., N 23.67392°, E 120.79906°, 1179 m alt., 14.V.2017, K. Eguchi leg., colony Eg14v17-1293, individual no. RJ20170613-23, 1 worker (ACEG); same loc., N 23.67263°, E 120.79935°, 1162 m alt., 14.V.2017, K. Eguchi leg., colony Eg14v17-1325, individual no. RJ20170613-15, 1 worker (ACEG); same loc., N 23.67015°, E 120.78741°, 1179 m alt., 13.V.2017, K. Eguchi leg., colony Eg13v17-1270, individual no. RJ20170613-22, 1 worker (ACEG); same loc., N 23.67269°, E 120.79946°, 1159 m alt., 14.V.2017, K. Eguchi leg., colony Eg14v17-1322, individual no. RJ20170613-18, 1 worker (ACEG); same loc., N 23.66958°, E 120.78717°, 1193 m alt., 13.V.2017, K. Eguchi leg., colony Eg13v17-1276; individual no. RJ20170613-17, 1 worker (ACEG); same loc., N 23.67279°, E 120.79935°, 1160 m alt., 14.V.2017, K. Eguchi leg., colony Eg14v17-1323; individual no. RJ20170613-24, 1 worker (ACEG); same loc., N 23.67287°, E 120.79922°, 1163 m alt., 14.V.2017, K. Eguchi leg., colony Eg14v17-1329; individual no. RJ20170613-16, 1 worker (ACEG); same loc., Sun Moon Lake, N 23.84222°, E 120.92863°, 792 m alt., 13.V.2017, K. Eguchi leg., colony Eg13v17-1249, individual no. RJ20170623-20, 1 worker (ACEG); same loc., N 23.84211°, E 120.92847°, 790 m alt., 13.V.2017, K. Eguchi leg., colony Eg13v17-1252, individual no. RJ20170613-21, 1 worker (ACEG); same loc., Huisun Forest, N 24.08774°, E 121.03181°, 756 m alt., 12.V.2017, K. Eguchi leg., colony Eg12v17-1233, individual no. RJ20170613-19, 1 worker (ACEG); same loc., Wushe, N24.01628˚, E121.12967˚, ca. 1160 m alt., 8.V.2016, K. Eguchi leg., Eg08v16-91, 2 workers (ACEG, RSC). **Vietnam:** Lang Son: Hun Lien H.R., N21˚50'25", E106˚55'55", ca. 98 m alt., 12.VI.2016, A. Dang leg., colony AD-LS-0007, 4 workers (RSC); Van Lang Dist., N20˚23'26", E105˚52'08", ca. 967 m alt., 12.VI.2016, A. Dang leg., colony AD-LS-0021, 3 workers (RSC); Tuyen Quang: Na Hang: Ban Chu, N22˚20'56"–21'06", E105˚25'35–36", ca. 200–225 m alt., 11.III.2015, R. Satria leg., colony RS01-BC-15, 6 workers (RSC); same loc., 13.III.2015, R. Satria leg., colony RS10-BC-15, 9 workers (RSC); Na Hang: Ban Ban, N22˚21'49"–22'06", E105˚26'21–37", ca. 355–450 m alt., 14.III.2015, R. Satria leg., colony RS16-BC-15, 8 workers (RSC); Nghe An Prov.: Que Phong Dist.: Thong-Thu Com: Ban Loc, 9.IV. 1999, B.T. Viet leg., 1 worker (RSC); same loc., Pu Hoat: Ban Om, 400 m alt., 2.XII.1999, B.T. Viet leg., code-015, 1 worker (RSC); Vinh Vuc Prov.: Tam Dao, 9.VIII.1998, Sk. Yamane leg., 1 worker (RSC); Ha Tai: Ba Vi (ca. 400–600 m alt.) 21˚03'N, 105˚, 22'E, 18.IV.2002, Sk. Yamane leg., 1 worker (RSC); same loc., same date, K. Eguchi leg., 1 worker (RSC); same loc., 20–21.V.2005, B.T. Viet leg., 1 worker (RSC); Cao Bang: Nguyen Binh: Quang Tanh: Phia Oac, N 22.59554°, E 105.8846°, 1300 m alt., 14.III.2017, K. Eguchi leg., colony Eg14iii17-867, 5 workers (RSC, ACEG); Quang Ninh: Tay Yen Tu, 22.III.2017, A. Yamada leg., worker; individual no. RJ20170516-7, 1 worker (RSC); same loc., Lang Son: Van Lang Dist., 16.III.2017, A. Yamada leg., individual no. RJ20170516-5, 1 worker (RSC); same loc., same date, A. Yamada leg., individual no. RJ20170516-6, 1 worker (RSC); Ninh Binh: Nho Quan: Cuc Phuong N.P., N20˚21'00", E105˚35'36"–34'41", ca. 366 m alt., 23.III.2017, An Dang leg., colony AD17CP50, individual no. RJ20170613-12, 1 worker (RSC); same loc., 23.III.2017, An Dang leg., colony AD17CP33, individual no. RJ20170613-13, 1 worker (RSC); same loc., 23.III.2017, An Dang leg., colony AD17CP50, individual no. RJ20170613-11, 1 worker (RSC).

Material used for DNA barcoding. Colony RS16-BC-15 (individual no. RJ20151125-7); colony RS01-BC-15 (individual no. RJ20151125-3), colony RS10-BC-15 (individual no. RJ20151125-5), colony AD-LS-0007 (individual no. RJ20161117-14), colony AD-LS-0021 (individual no. RJ20161117-13).

Worker measurements and indices. Non-types from Vietnam (n=10): HW 2.62–3.07 mm, HL 3.41–3.82 mm, SL 3.53–3.89 mm, IFLW 0.71–0.74 mm, EL 0.39–0.46 mm, MDL 2.00–2.29 mm, WL 4.52–4.96 mm, PTL 0.76–0.87 mm, PTH 1.42–1.72 mm, CI 76–80, SI 115–134, MDI 57–60, PTHI 184–197.

Non-types from Taiwan and Japan (n=7): HW 2.16–2.17 mm, HL 2.72–2.77 mm, SL 2.63–2.67 mm, IFLW 0.55–0.56 mm, EL 0.32–0.34 mm, MDL 1.62–1.67 mm, WL 3.39–3.47 mm, PTL 0.55–0.58 mm, PTH 1.17–1.19 mm, CI 78–79, SI 121–123, MDI 58–61, PTHI 201–216.

Worker description. Size varied from large to small that reflects the geographic variation between Japan-Taiwan form and Vietnam Form. Body relatively large (Vietnamese form, HL 3.41–3.82 mm, WL 4.52–4.96 mm) and relatively small (Japanese/Taiwanese form, HL 2.72–2.77 mm, WL 3.39–3.47 mm). Head in full-face view slightly longer than broad, with posterior margin weakly concave; head posteriorly without a pair of small and distinct tubercles; median furrow on vertex present as dark line, but vaguely seen because of dense striation on the vertex; neither side of line swollen dorsad; frontal lobes followed by frontal carinae which are divergent posteriad; minimum distance between margin of ocular ridge and margin of compound eye less than half major axis of compound eye; masticatory margin with 8–12 distinct denticles; subapical tooth as long as broad, with truncate apex; palp formula 4, 4. Mesosoma in lateral view stout; pronotum including anteromedian lobe short, in lateral view with anterodorsal slope weakly steep; mesopleuron without anteroventral ridge, and its anterodorsal margin without carina, and indistinctly separated from mesonotum; propodeum in lateral view with dorsum slightly convex, with posterior face steeply sloping; propodeal dorsum without median longitudinal depression. Petiolar node conical, with sharply pointed apical spine; node excluding apical spine in lateral view with anterior face weakly convex, and posterior face almost straight to weakly convex; apical spine short and stout, sometimes weakly curved posteriad (but shape variable within species); subpetiolar process lobate or triangular, directed ventrally, with the maximum length of anterior-posterior axis as long as dorsal-ventral axis. Gastral tergite I in lateral view relatively short, with anterior face moderately long and vertical.

Head in full-face view extensively striate; area between eye and frontal lobe smooth and shiny, and area around eye smooth and shiny or finely striate, dorsum of vertex faintly striate; frontal lobe finely striate; lateral face and venter of head finely striate; median disc of clypeus faintly striate. Pronotal disc and mesonotum in dorsal view with fine, dense, transverse striation; posterolateral face of pronotum with fine striation; mesopleuron finely striate or generally smooth and shiny with anteriormost and posteriormost finely striate; metapleuron finely striate; propodeum with transverse striation which is a little sparser and stronger than pronotum, mesonotum, and metapleuron. Petiolar node largely smooth and shiny, with its basal area faintly striate.

Vertex with a pair of long erect setae; frontal lobe without seta; pronotal disc without long erect setae; gastral tergite I without long erect setae. Head, petiole and gaster with fine decumbent to appressed pubescence; mesosoma with fine suberect to subdecumbent pubescence which is sparser than head, petiole and gaster.

For color or pattern see Figs. 4-28, 4-29; body reddish brown (Fig. 4-29) to dark brown (nearly black) (Fig., 4-28); all legs reddish brown to brown.

Queen measurements and indices. Non-type from Taiwan (n=1): HW 2.34 mm, HL 2.91 mm, SL 2.81 mm, IFLW 0.62 mm, EL 0.42 mm, OL 0.13 mm, MDL 1.76 mm, WL 3.98 mm, PTL 0.64 mm, PTH 1.47 mm, CI 80, SI 120, MDI 60, PTHI 229.

Queen description (based on a specimen from Taiwan). Queen similar in general appearance to the worker. Vertex near ocelli not swollen; ocular ridge clearly developed; distance between lateral ocelli sligtly longer than distance between lateral and median ocelli, and 2 times as long as major axis of median ocellus; ocelli in lateral view protruded dorsad. Mesosoma with main sclerites associated with wing function (Figs. 4-30D, 4-30E), in dorsal view medium and slender; anterodorsal slope of pronotum in lateral view gentle; anterodorsal outline of mesoscutum in lateral view relatively gentle; mesoscutum without posteromedian depression; parapsidal furrow very weak and slightly curved; dorsal outline of metascutellum in lateral view almost straight; anterior third of mesopleuron with fine, oblique furrow; propodeum in lateral view relatively long, with dorsum almost straigth and gradually sloping posteriad; propodeum in dorsal view with lateral outlines convergent posteriad. Petiolar node in lateral view, excluding apical spine with anterior face almost straight to weakly convex, and its posterior face weakly convex; apical spine short and relatively slender, and weakly curved posteriad (but variable in shape within species); subpetiolar process anteroposteriorly as long as dorsoventrally high, triangular, directed ventrally. Gastral tergite I in lateral view relatively short, with anterior face moderately long and vertical.

Head in full-face view extensively striate, with striation on vertex and lateral part of head finer than area bordered by frontal carinae and ocular ridges; area between eye and frontal lobe, and area around eye smooth and shiny; frontal lobe finely striate; venter of head smooth and shiny; median disc of clypeus with rough texture. Pronotum densely and weakly striate transversely; mesoscutum largely smooth and shiny, with fine striation on anterior margins; mesopleuron largely smooth and shiny, with anteriormost and posteriormost parts faintly striate; mesoscutum faintly longitudinally striate; propodeum strongly and sparsely striate transversely. Petiolar node excluding spine largely smooth and shiny, with basal part faintly striate.

Pair of long erect setae present on vertex near lateral ocelli; frontal lobe, pronotal disc and gastral tergite I without erect setae. Head, mesosoma, petiole and gaster with sparse subdecumbent to decumbent pubescence which is extremely short on gaster; mesopleuron very sparsely pubescent.

For color pattern see Fig 4-30. Body reddish brown to brown; gaster a little darker than head and mesosoma; all legs reddish brown.

Species recognition. *Odontomachus* sp. 1 is easily separated from other species member of *Odontomachus rixosus* group by the following characteristics: subapical tooth as long as broad, with truncate apex; vertex of head with fine striation; pronotal disc with transverse striation.

Distribution. Northern part of Vietnam, China, Taiwan and Japan (Kagoshima prefectures, including osumi islands and Fukuoka).

Bionomics. This species nests in the soil in secondary forest, plantation, forest edges and other open or semi-open forests.

Remarks. See the remarks of *O. monticola*.

***Odontomachus* sp. 2**

(Figs. 4-31, 4-32)

Non-type materials examined. Vietnam: Tay Nguyen: Dak Lak: Chu Yang Shin: Area 1359, N12˚23'07.2−10.5", E108˚20'41.9−42.1", ca. 1215−1245 m alt., 04.III.2016, R. Satria leg., colony RS-08-CYS16, 8 workers, 2 queens (RSC); same loc., N12˚24'42.9", E108˚21'08", ca.

900 m alt., 05.III.2016, R. Satria leg., colony RS-34-CYS16, 10 workers (RSC); same loc., same date, R. Satria leg., colony RS-36-CYS16, 10 workers (RSC); same loc., N12˚25'10.5",E108˚22'09.3", ca. 991 m alt., 06.III.2016, R. Satria leg., colony RS-50-CYS16, 4 workers (RSC); same loc., same date, R. Satria leg., 1 queen (RSC); same loc., N12˚25'36.3−36.6", E108˚19'17−25.8", ca. 826−846 m alt., 08.III.2016, R. Satria leg., colony RS-142-CYS16, 7 workers, 2 queens (RSC); same loc., same date, R. Satria leg., 1 queen (RSC).

Material used for DNA barcoding. Colony RS-08-CYS16 (individual no. RJ20160623-5), colony RS-34-CYS16 (individual no. RJ20160623-6), colony RS-36-CYS16 (individual no. RJ20160623-7).

Worker measurements and indices. Non-types (n=10): HW 2.23–2.34 mm, HL 2.81–3.05 mm, SL 2.61–2.72 mm, IFLW 0.59–0.62 mm, EL 0.31–0.34 mm, MDL 1.60–1.75 mm, WL 3.30–3.50 mm, PTL 0.54–0.55 mm, PTH 1.15–1.24 mm, CI 78–79, SI 112–118, MDI 55–57, PTHI 209–225.

Worker description. Body relatively small (HL 2.81–3.05 mm; WL 3.30–3.50 mm). Head in full-face view slightly longer than broad, with posterior margin weakly concave; head posteriorly without a pair of small and distinct tubercles; median furrow on vertex present as a dark line; each side of median furrow not swollen dorsad; frontal lobe followed by frontal carinae slightly divergent posteriad; minimum distance between margin of ocular ridge and margin of compound eye half as long as major axis of compound eye; masticatory margin with 8–10 distinct denticles; subapical tooth shorter than broad, with truncate apex; palp formula 4, 4. Mesosoma in lateral view stout; pronotum including anteromedian lobe short, in lateral view with anterodorsal slope steep; mesopleuron without anteroventral ridge, with anterodorsal margin weakly carinate, clearly separated by distinct dorsal carina from mesonotum and metapleuron; propodeum in lateral view with dorsum akmost straight, with posterior face steeply sloping; peopodeal dorsum without median longitudinal depression. Petiolar node conical and slender, with sharply pointed apical spine; node excluding apical spine in lateral view symmetrically raised with anterior and posterior faces almost straight; apical spine short and stout, weakly curved posteriad; subpetiolar process , triangular, directed ventrad, with maximum length of anterior-posterior axis as long as dorsal-ventral axis. gastral tergite I in lateral view relatively short, with anterior face moderately long and vertical.

Head in full-face view largely smooth and shiny; area bordered by frontal carinae and ocular ridges striate; area around eye smooth and shiny; frontal lobe clearly striate; extraocular furrow faintly striate; median part of vertex along median furrow smooth and shiny; lateral face and venter of head smooth and shiny; median disc of clypeus with rough texture. Pronotal disc in dorsal view with concentric striation; posterolateral face of pronotum clearly striate; mesopleuron largely smooth and shiny, with anteriormost and posteriormost parts finely striate; metapleuron and propodeum with transverse striation, which is a little sparser and stronger than pronotum and mesonotum. Petiolar node largely smooth and shiny, with basal finely striate.

Vertex with a pair of long erect setae; frontal lobe without seta; pronotal disc without long erect setae; gastral tergite I without erect setae. Head, mesosoma, petiole and gaster with fine appressed pubescence which is sparse and very short on head and gaster.

For color pattern see Fig. 4-31; brown to dark brown; gaster a little darker than head and mesosoma; all legs orange.

Queen measurements and indices. Non-types (n=3): HW 2.43–2.62 mm, HL 2.93–3.22 mm, SL 2.78–2.81 mm, IFLW 0.64–0.69 mm, EL 0.43–0.44 mm, MDL 1.77–1.82 mm, WL 3.80–3.90 mm, PTL 0.62–0.64 mm, PTH 1.48–1.57 mm, CI 81–83, SI 107–114, MDI 57–60, PTHI 235–253.

Queen description. Queen similar in general appearance to worker. Vertex near ocelli not swollen dorsad; ocular ridge clearly developed; distance between lateral ocelli longer than distance between lateral and median ocelli, and 2 times as long as major axis of median ocellus; ocelli in lateral view protruded dorsad. Mesosoma with main sclerites associated with wing function (Figs. 4-32D, 4-32E), in dorsal view short and stout; anterodorsal slope of pronotum in lateral view steep; anterodorsal outline of mesoscutum in lateral view relatively gentle; mesoscutum with without posteromedian depression; parapsidal furrow very weak and slightly curved; dorsal outline of metascutellum in lateral view almost straight; anterior third of mesopleuron with fine, oblique furrow; propodeum in lateral view relatively short, with dorsum very weakly convex and gradually sloping posteriad. Petiolar node excluding apical spine in lateral view with anterior face almost straight to weakly convex and posterior face almost straight; apical spine short and relatively slender, and weakly curved posteriad; subpetiolar process triangular, directed ventrally, with the maximum length of anterior-posterior axis as long as dorsal-ventral axis. Gastral tergite I in lateral view relatively short, with anterior face moderately long and vertical.

Head in full-face view largely smooth and shiny; area bordered by frontal carinae and ocular ridges striate; frontal lobe finely striate; extraocular furrow faintly striate; median part of vertex along median furrow smooth and shiny; lateral face of head very faintly striate, and venter of head smooth and shiny; median disc of clypeus with rough texture. Pronotum densely and weakly striate transversely; mesoscutum largely smooth and shiny, with faint striae on posteromedian depression and along anterior and posterior margins; mesopleuron largely smooth and shiny, with anteriormost and posteriormost parts faintly striate; mesoscutum faintly longitudinally striate; propodeum strongly and sparsely striate transversely. Petiolar node excluding spine largely smooth and shiny, with basal part faintly striate.

Pair of long erect setae present on vertex near lateral ocelli; frontal lobe, pronotal disc and gastral tergite I without erect setae. Head, mesosoma, petiole and gaster with sparse subdecumbent to decumbent pubescence which is extremely short on gaster; mesopleuron very sparsely pubescent.

For color pattern see Fig. 4-32. Body brown to dark brown; gaster a little darker than head and mesosoma; all legs brown, but paler than body.

Species recognition. See the recognition of *Odontomachus monticola*.

Distribution. Southern part of Vietnam.

Bionomics. This species inhabits secondary and primary highland forests, and nests under the rotting wood, under the stone and leaf litter.

IV-3-5. Redescription of the Indo-Chinese and Indo-Malayan species of the *Odontomachus haematodus* species group

Odontomachus haematodus species group

Diagnosis of the worker. Head in full-face view slightly longer than broad, with posterior margin strongly concave; masticatory margin with small denticle or edentate; subapical teeth blunt and shoort; palp formula 4, 3; mesopleuron with anteroventral ridge; pronotal disc and gastral tergite I with several long erect setae.

***Odontomachus simillimus* F. Smith, 1858**

(Figs. 2-1A, 2-2E, 2-2J, 2-2O, 4-33, 4-34, 4-35)

Odontomachus simillimus F. Smith, 1858: 80, pl. 5, figs 8, 9, queen, type locality: Fiji Islands; Wilson, 1959: 499; Brown, 1976: 165–166; Fisher & Smith, 2008: 15; Sorger & Zettel, 2011: 157–161, figs. 43–45.

Odontomachus haematodus Linnaeus, 1758: Wheeler, 1924: 243 (misidentification); Dammermann, 1948: 369 (misidentification) (see Wilson, 1959; Brown, 1976; Yamane, 2013).

Odontomahus haematoda var. *breviceps* Crawley, 1915: 239, worker, type locality: Christmas Island. Synonymy by Brown, 1976: 106.

Odontomachus haematodus var. *fuscipennis* Forel, 1913: 19, worker, queen, male, type locality: Sri Lanka (Peradenyia). Synonymy by Wilson, 1959: 499.

Ponera pallidicornis F. Smith, 1860: 73, male, type locality: Indonesia (Makassar). In *Euponera* (*Brachyponera*) by Donisthorpe, 1932: 458. In *Odontomachus* by Brown, 1976: 106. Synonymy by Brown, 1976: 106.

Type materials and Images examined. Images of the type material of the following species provided in AntWeb v5.17.5 (http://www.antweb.org) were examined to confirm our species recognition: *O. simillimus*, queen, Ceylon (CASENT0900650); "*O. haematoda braeviceps*", worker (CASENT0901486); "*O. haematoda fuscipennis*", worker (CASENT0907433); "*Ponera pallidicornis*", male (CASENT0901350).

Non-type materials examined. Indonesia: Sumatra: Aceh: Simeulue Island, Babul Makmur, 15.IX.2012, R. Satria leg., 4 workers (SKYC); same loc., 16.IX.2012, R. Satria leg., 1 worker (SKYC); West Sumatra: Padang, 24.III.1989, K. Nakamura leg., 89-PD-15 (KN), 1 worker (SKYC, RSC); same loc., Teluk kabung near Padang, 14.III.1985, Sk. Yamane leg., 1 worker (SKYC, RSC); Maninjau, 16–18.VIII.1985, Sk. Yamane leg., Sumatra Nature Study (SNS col.), 1 worker (SKYC); Solok, Mt. Talang, 23–28.X.2010, R. Satria leg., 3 workers, 1 queen (SKYC, RSC). Lampung: Krakatau Islands, P. Rakata Besar, 19.VII.1982, Sk. Yamane leg., 8 workers (SKYC, RSC); same loc., P. Sertung, 08.VII.1982, Sk. Yamane leg., 8 workers (SKYC, RSC); same loc., P. Rakata kecil, Sk. Yamane leg., 17.VII.1982, 4 workers (SKYC, RSC); same loc., P. Sertung, Sk. Yamane leg., 08.VII.1982, 2 workers, 1 queens (SKYC, RSC); same loc., P. Pencang, Sk. Yamane leg., 05.VII.1982, 1 worker (SKYC). Java: West Java: Jasinga near Bogor, 05.XI.1985, Sk. Yamane leg., 11 workers (SKYC, RSC); ITB campus (ca. 700 m alt.), 28.XII.2002, Sk. Yamane leg., 4 workers (SKYC); Bogor, 09.XI.1985, 5 workers (SKYC); Bogor (botanical garden), 03.VIII.1992, Sk. Yamane leg., 1 worker (SKYC, RSC); Carita, 03.VIII.1982, Sk. Yamane leg., 1 worker (SKYC); Yogyakarta: Campus of Gajah Mada Univ.

(100 m alt.), 29.XII.2002, Syaukani leg., 3 workers (SKYC, RSC); same loc., F. Yamane leg., 1 worker (SKYC); same loc., Sk. Yamane leg., JV02/03-SKY-26, 4 workers (SKYC); Borobudur near Yogyakarta, 07.I.2003, Sk. Yamane leg., 4 workers (SKYC, RSC); same loc., F. Yamane leg., 1 worker (SKYC, RSC); East Java: Surabaya, Taman Binatang, 04.I.2003, F. Yamane leg., 1 queen (SKYC, RSC); same loc., Syaukani leg., 1 worker (SKYC, RSC); same loc., Sk. Yamane leg., 2 workers (SKYC, RSC); Batu, Bumiaji, Air Panas Cargar (1600 m alt.), 03.I.2003, Sk. Yamane leg., 9 workers (SKYC, RSC). Bali: Denpasar, 09.III.1987, K. Nakamura leg., 1 worker (SKYC, RSC); W. Bali, Mendaya, Dusun PK Jelati, 05-06.V.1998, I.K.T. Ginarsa leg., 3 workers (SKYC, RSC); same loc., Sk. Yamane leg., 3 workers (SKYC); same loc., 22.X.2012, PKJ-22-12, 6 workers, 1 queen (SKYC, RSC); same loc., R. Satria leg., PKJ-12-12, 4 workers (SKYC, RSC); same loc., R. Satria leg., PKJ-24-12, 11 workers, 8 queens (SKYC, RSC); same loc., R. Satria leg., PKJ-33-12, 4 workers, 1 queen (SKYC, RSC); Denpasar, 24.IV.1998, I.K.T. Ginarsa leg., 5 workers (SKYC). Sulawesi: South Sulawesi: Ujung Pandang, Bantimurung, 18.VIII.1992, Sk. Yamane leg., 9 workers (SKYC). West Nusa Tenggara: W. Lombok, Kopi house near Semaya, 26.X.1998, K. Eguchi leg., EG98-LMB-1042, 4 workers (SKYC, RSC); Same loc., I.K.T. Ginarsa leg., 1 worker (SKYC). Irian Jaya (or Papua): Genyem near Jayapura, 02.v.1998, K. Eguchi leg., 1 queen (SKYC). **Malaysia:** Borneo: Sabah: Kota Kinabalu, 20.III.1995, Sk. Yamane leg., 4 workers (SKYC); Near Keningau (210 m alt.), 24.II.1997, Sk. Yamane leg., 1 worker (SKYC); Sepilok Forest, 29.I.1997, K. Eguchi leg., Eg97-BOR-514, 7 workers (SKYC); Lahad Datu, Lower Segama, 26.V.2005, Alveron leg., 9 workers (SKYC); Manggatal, Taman Fajar, 15.X.1996, K. Eguchi leg., 1 queen (SKYC). Sarawak, Niah N.P., 28.I.1993, Sk. Yamane leg., 1 worker (SKYC); Bako, Nat. Park, 21-22.IV.1993, Sk. Yamane leg., 3 workers (SKYC). Malay Peninsula: Selangor: Ulu Gombak, 12.XII.1992. K. Tomiyama leg., 1 worker (SKYC); same loc., (ca. 250 m alt.), 4.VII.1999, Sk. Yamane leg., 4 workers (SKYC); Pahang: Endu Rompin N.P., 10.VI.2005, Bakhtiar, Ruslan, Fauzi leg., SEM10 (nesting in soil), 2 workers (SKYC); Negeri Sembilan: Pasoh, 14.XII.1992. K. Tomiyama leg., 4 workers (SKYC). **Philippines:** Luzon, Olongapo, Subic Bay (FZ), 09-20.XI.2005, S. Onoda leg., 7 workers (SKYC). **Singapore:** 4.II.1995, Sk. Yamane leg., 9 workers (SKYC). **Sri Lanka:** Central Province: Kandy, Campus of University Peradeniya, 12.IV.2001, Sk. Yamane, 4 workers, 2 queens (SKYC). Sabaragamuwa: Ratnapura, 11.IV.2001, Sk. Yamane leg., 3 workers, 2 queens

(SKYC). Western Province: Gampaha Dist., Pilikuttuwa, 10.IV.2001, Sk. Yamane leg., 7 workers (SKYC).

Worker measurements and indices. Non-types (n=10): HW 1.72–2.26 mm, HL 2.12–2.73 mm, SL 1.97–2.43 mm, IFLW 0.50–0.65 mm, EL 0.34–0.42 mm, MDL 1.15–1.50 mm, WL 2.66–3.29 mm, PTL 0.46–0.57 mm, PTH 1.02–1.28 mm, CI 76–83, SI 106–116, MDI 52–56, PTHI 212–236.

Worker description. Body relatively small (HL 2.12–2.73 mm; WL 2.66–3.29 mm). Head in full-face view slightly longer than broad, with posterior margin strongly concave; head posteriorly without a pair of small and distinct tubercles; median furrow on vertex present as dark line; each side of line weakly humped; frontal lobes followed by weak frontal carinae which are divergent posteriad; minimum distance between margin of ocular ridge and margin of compound eye less than half of major axis of compound eye; mandible relatively stout; masticatory margin with small denticles or edentate; subapical tooth shorter than broad, blunt at apex; palp formula 4, 3. Mesosoma in lateral view stout; pronotum including anteromedian lobe short, in lateral view with anterodorsal slope steep; mesopleuron with conspicuous anteroventral ridge, with anterodorsal margin distinctly carinate, clearly separated by distinct dorsal carina from mesonotum and metapleuron; propodeum in lateral view with dorsum slightly, with posterior face steeply sloping; propodeal dorsum without median longitudinal depression. Petiolar node conical, with sharply pointed apical spine; node in lateral view, excluding apical spine almost straight anteriorly and very weakly convex posteriorly; apical spine short and slender, 1/4 as long as petiolar height, sometimes weakly curved posteriad; subpetiolar process, triangular, directed posteriorly, with the maximum length of anterior-posterior axis longer than dorsal-ventral axis. Gastral tergite I in lateral view short, with anterior face long and vertical.

Head in full-face view extensively striate; area bordered by frontal carinae and ocular ridges striate; frontal lobe finely and faintly striate; extraocular furrow striate; median part of vertex along median furrow striate; lateral face weakly striate; venter of head completely or largely smooth and shiny; median disc of clypeus with rough texture. Pronotal disc in dorsal view densely with concentric striation; mesonotum densely striate transversely; mesopleuron largely smooth and shiny, but with anterior third and posteriormost parts finely striate; metapleuron moderately striate; lateral face of propodeum with transverse striation which is a little sparser and stronger than mesonotum; dorsum and posterior face of propodeum coarsely and transversely striate. Petiolar node weakly striate anteriorly and laterally; posterior face of node weakly striate or sometimes smooth and shiny.

Vertex with a pair of long erect setae; frontal lobe without seta; pronotal disc and gastral tergite I with long erect setae, as long as setae on vertex. Head (except its venter), mesosoma, petiole and gaster with dense subdecumbent to decumbent pubescence; venter of head with sparse appressed pubescence.

For color pattern see Fig. 4-33; body reddish brown to dark brown (nearly black).

Queen measurements and indices. Non-types (n=10): HW 2.07–2.17 mm, HL 2.49–2.69 mm, SL 2.22–2.39 mm, IFLW 0.60–0.68 mm, EL 0.45–0.52 mm, OL 0.08–0.11 mm, MDL 1.31–1.45 mm, WL 3.19–3.29 mm, FWL 6.56–6.86 mm, PTL 0.56–0.60 mm, PTH 1.40–1.48 mm, CI 80–85, SI 102–114, MDI 50–55, PTHI 232–256.

Queen description. Queen n general appearance similar to worker. Vertex near ocelli swollen; ocular ridge faintly developed; distance between lateral ocelli as long as distance between lateral and median ocelli, and 3.5 times as long as major axis of median ocellus; ocelli in lateral view not protruded dorsad. Mesosoma with main sclerites associated with wing function (Figs. 4-34B, 4-34C), in dorsal view short and stout; anterodorsal slope of pronotum in lateral view relatively steep; anterodorsal outline of mesoscutum in lateral view relatively gentle; mesoscutum without posteromedian depression; parapsidal furrow very weak and slightly curved; dorsal outline of metascutellum in lateral view convex; mesopleuron without oblique furrow; propodeum relatively short, in lateral view with dorsum weakly convex and sloping gradually posteriad; propodeum in dorsal view with lateral outlines convergent posteriad. Wing venation as in Figs. 4-34E and 4-34F. Petiolar node excluding apical spine in lateral view with anterior face faintly to weakly concave and posterior face faintly convex; apical spine very short and slender, and curved posteriad; subpetiolar process lobate, directed ventrally, with the maximum length of anterior-posterior axis longer than dorsal-ventral axis. Gastral tergite I in lateral view relatively short, with anterior face long and vertical.

Head in full-face view extensively striate; area between eye and frontal lobe, and area around eye smooth and shiny; frontal lobe finely and faintly striate; extraocular furrow striate; median part of vertex along median furrow striate; lateral face weakly striate; venter of head completely or largely smooth and shiny; median disc of clypeus with rough texture. Pronotum weakly striate transversely; mesoscutum with dense longitudinal striation; striation finer on mesoscutum than on pronotum and propodeum; mesopleuron largely smooth and shiny, but with anteriormost and posteriormost parts faintly striate; mesoscutellum smooth and shiny; propodeum strongly striate transversely. Petiolar node excluding apical spine entirely striate, but striation on anterior and posterior faces weaker than that on lateral face.

Pair of long erect setae present on vertex near lateral ocelli; frontal lobe without erect seta; pronotal disc and gastral tergite I with long erect setae, as long as setae on vertex near lateral ocelli. Head, mesosoma, petiole and gaster with dense subdecumbent to decumbent pubescence, except mesopleuron very sparsely pubescent.

For color pattern see Fig. 4-34; body reddish brown to dark brown (nearly black).

Male measurements and indices. Non-types (n=10): HW 1.16–1.28 mm, HL 0.95–1.14 mm, SL 0.17–0.21 mm, EL 0.59–0.68 mm, EW 0.34–0.40 mm, OL 0.15–0.18 mm, OED 0.21–0.26 mm, WL 2.66–2.99 mm, FWL 4.60–5.48 mm, PTL 0.46–0.64 mm, PTH 0.81–0.95 mm, CI 104–129, SI 14–17, PTHI 147–176.

Male description. Body relatively small (HL 0.95–1.14 mm; WL 2.66–2.99 mm). Major axis of median ocellus smaller than minimum distance between lateral ocelli; antenna 13-segmented; scape very short, 1/3 as long as antennal segment III; II 1/2 as long as scape; III to XIII each extremely long; palp formula 6, 3; dorsal outline of clypeus in lateral view strongly convex. Mesosoma in lateral view relatively stout and short; dorsal outline of pronotum in lateral view strongly convex; anterodorsal outline of mesoscutum in lateral view steeply slooping; mesoscutum without median depression; parapsidal furrow weak and almost straight; oblique mesopleural furrow relatively deep and wide; ventrolateral part of katepisternum with weak longitudinal furrow; propodeum in lateral view with dorsal outline angulate (arrow in Fig. 4-35D); metapleuron distinctly separated from propodeum by a suture; wing venation similar to queen (see Figs. 4-34E, 4-34F for queen wings). Petiolar node in lateral view tapering to blunt apex, with anterior slope in lateral view very weakly sinuate, and posterior slope straight and steeper; subpetiolar process in lateral view triangular and thick, with the maximum length of anterior-posterior axis as long as dorsal-ventral axis; petiolar sternum with conspicuously angulate process posteroventraly. Gastral tergite I in lateral view short; posterior spine of abdominal tergite VIII long and slender, very weakly curved (but variable in shape within species) (Fig. 2-2M); pygostyle digitiform, with long setae in apical half; disc of abdominal sternite IX broader than long, almost as long as apical lobe, with straight basal margin; apical lobe slightly narrower in basal half, with apical margin weakly convex; telomeral apex in lateral view as long as high; distiventral apex of valviceps strongly produced; basiventral corner of valviceps distinctly produced; ventral margin of valviceps with 34–36 denticles.

Head including area between lateral ocelli largely smooth and shiny, with clypeus faintly striate; venter of head faintly striate and shiny. Pronotum largely smooth and shiny, with lateral part faintly striate; mesoscutum faintly rugoso-reticulate and opaque; scuto-scutellar suture with very sparse, weak, longitudinal rugae; mesopleuron with anepisternum smooth and shiny, and katepisternum largely smooth and shiny, but with faint and rough texture in posteriormost part; propodeum including posterior slope with rough texture. Petiole faintly striate to rugose.

Head, mesosoma, legs, petiole, and gaster with fine dense subdecumbent to decumbent pubescence; apex of mandible, vertex near ocelli, pronotum and gaster with several long erect setae.

For color pattern see Fig. 4-35; head, mesosoma, legs, petiole, gaster blackish brown; antenna yellowish brown; frons and clypeus largely yellowish brown, with lateral part of clypeus and the areas in front of antennal insertions rather yellow; mandible yellow.

Species recognition. *Odontomachus simillimus* is easily separated from the other Asian species of the genus *Odontomachus* by the following characteristics of the worker: subapical teeth blunt and short; palp formula 4, 3; pronotal disc and gastral tergite I with several long erect setae. The morphology of male genitalia of this species was disscussed in Chapter II.

Distribution. The majority of the members of the *O. haematodus* species group are distributed in the New World and one species in Africa, but only *O. simillimus* is distributed widely in tropical Southeast and South Asia, Melanesia and Madagascar.

Bionomics. *Odontomachus simillimus* is a common species in gardens and green patches in residential zones, plantations, and secondary forests. Nests are usually found in the soil near the base of living trees, and under shelters (such as stumps, rotten logs and rocks), but sometimes under paved floors around houses.

In Bali, two compound colonies of *O. simillimus* and *Pheidole ghigii* Emery, 1900 were found near the base of living trees in a cacao plantation (PKJ-22-12/PKJ-23-12, PKJ-24-12/PKJ-25-12). However, the coexistence between the two species seems to be occasional; any compound colony of the two species has not yet been found in Krakatau and Sumatra; any other ant partner of *O. simillimus* has not yet been found.

IV-3-6. Redescription of the Indo-Chinese and Indo-Malayan species of the *Odontomachus malignus* species group

Odontomachus malignus species group

Diagnosis of the worker. Head in full-face view much longer than broad; palp formula 4, 4; head posteriorly with a pair of conspicuous tubercles; subapical tooth long and acute at apex.

Odontomachus malignus F. Smith, 1859

Odontomachus malignus F. Smith, 1859: 144, worker, type locality: New Guinea; Roger, 1861: 28; Roger, 1863: 21; Emery, 1887: 429; Dalla Torre, 1893: 51; Viehmeyer, 1914a: 112; Wheeler, W.M. 1919: 61; Santschi, 1932: 13; Wilson, 1959: 495; Brown, 1976: 104, 159; Bolton, 1995: 296; Sorger & Zettel, 2011: 155.

Odontomachus retrolatior Viehmeyer, 1914: 113, worker, type locality: New Guinea.. Synonymy by Brown, 1976: 104.

Odontomachus tuberculatus Roger, 1861: 28, worker, type locality: ASIA (no locality given); Mayr, 1862: 711; Roger, 1863b: 22; Mayr, 1872: 149. Subspecies of *malignus*: Mann, 1919: 305. Synonymy by Emery, 1887b: 429; Emery, 1911d: 113; Wilson, 1959a: 495.

Type images examined. Images of the type material of the following species provided in AntWeb v5.17.5 (http://www.antweb.org) were examined: "*O. malignus*", worker (CASENT0901334); "*O. tuberculatus*", worker (CASENT0915471); "*O. malignus* var. *retrolatior*", worker (FOCOL0402, FOCOL1081, FOCOL1082).

Worker description (partly modified from Sorger & Zettel (2011) by referring to the images provided by www.antweb.org.) Head in full-face view much longer than broad, with posterior margin weakly concave; head posteriorly with a pair of small and distinct tubercles; median furrow on vertex present as dark line; frontal lobe followed by frontal carinae slightly divergent posteriad; mandible relatively slender; subapical tooth with acute apex; palp formula 4, 4.

Mesosoma in lateral view relatively slender; pronotum including anteromedian lobe long, in lateral view with anterodorsal slope gentle; mesopleuron without anteroventral ridge, with anterodorsal margin weakly carinate, clearly separated by distinct dorsal carina from mesonotum and metapleuron; propodeum in lateral view with dorsum slightly concave, and with posterior face steeply sloping. Petiolar node conical, with sharply pointed apical spine; node in lateral view, excluding apical spine with anterior and posterior faces weakly convex; apical spine needle-shaped, less than 1/4 as long as petiolar height, weakly curved posteriad (but shape variable within species). Gastral tergite I in lateral view long, with anterior face relatively short and vertical.

Head in full-face view largely smooth and shiny, but with striate area bordered by frontal carinae and ocular ridges; extraocular furrow finely striate. Pronotum in dorsal view with delicate sculpture; mesopleuron largely smooth and shiny, with anterior 1/3 and posteriormost parts finely striate; metapleuron and propodeum with transverse striation which is a little sparser and stronger than on pronotum and mesonotum. Petiolar node largely smooth and shiny, but with basal area faintly striate.

Vertex with a pair of long erect setae; pronotal disc with long erect setae. Head, mesosoma, petiole and gaster with fine appressed pubescence.

For color see Sorger & Zettel, 2011; almost unifromly reddish brown, with paler head.

Species recognition. This species is easily distinguished from the other *Odontomachus* species by the following characteristics of the worker: palp formula 4, 4; vertex of head with a pair of small and distinct tubercles; subapical tooth acute.

Distribution. *Odontomacus malignus* is widespread in the Western Pacific, Borneo (Indonesia and Malaysia), Philippines, Sulawesi, Palau, New Guinea, New Britain, and Solomon Islands (Wilson, 1959; Brown, 1976; Olsen, 2009; Sorger & Zettel, 2011).

Biology. *Odontomachus malignus* has unusual habitat preference if compared with the other *Odontomachus* species; the colonies build their nests underground in intertidal or littoral zones (Wilson, 1959; Brown, 1976; Olsen, 2009; Sorger & Zettel, 2011) and mangrove zones close to the open sea (Sorger & Zettel, 2011).

IV-3-7. Redescription of the Indo-Chinese and Indo-Malayan species of the *Odontomachus silvestrii* species group

***Odontomachus silvestrii* species group**

Diagnosis of the worker. Head in full-face view much longer than broad, with posterior margin weakly concave and shallow temporal ridge; subapical teeth longer than broad, with acute apex; palp formula 4, 4; mesosoma much slender; petiolar node excluding apical spine in lateral view with anterior face strongly convex and long gentle slope, and posterior face weakly convex (see Figs. 4-2C, 4-36B); body with very dense and fine appressed pubescence.

***Odontomachus silvestrii* Wheeler, 1927**

(Figs. 4-2C, 4-36, 4-37, 4-38)

Odontomachus silvestrii Wheeler, 1927: 85, fig. 1, worker, type locality: Vietnam; Brown, 1976a: 106, 165; Wang, M. 1993a: 220 (in key); Radchenko, 1993a: 77; Bolton, 1995b: 297.

Odontomachus silvestrii var. *substriatus* Wheeler, 1927: 86, worker, type locality: Vietnam. Synonymy by Brown, 1976: 106.

Odontomachus granatus Wang, 1993: 224, fig. 5, worker, type locality: China. **Syn. Nov.**

Type material examined. "*Odontomachus granatus*" — holotype (worker; IZCAS), China: Yunnan Province: Jinping Co. 400m.

Non-type materials examined. Vietnam: Ninh Binh: Cuc Phuong, 4.VI.1966, R. Bielawski and B. Pisarski leg., 1 worker (MIZ); same loc., "Cay Dang Co Thu trail", 14.VI.2005, K. Eguchi leg., EG14vi05-12, 1 worker (ACEG); same loc., 20°14'N, 105°36'E, 320 m alt., 10.XI.2001, K. Eguchi leg., EG01-VN-199, 1 worker (ACEG); same loc., 10.XI.2001, Sk. Yamane leg., VN01-SKY-63, 4 workers (RSC); same loc., same date, Sk. Yamane leg., 1 worker (RSC); same loc., 11.VIII.1998, H. Okido leg., 1 worker (RSC); same loc., 10–11.VIII.1998, Sk. Yamane leg., 1 worker, 1 queen (RSC); Ha Tai: Ba Vi N.P., 21°08'N, 105°22'E (ca. 400–600 m alt.), 18.IV.2002, K. Eguchi leg., Eg02-VN-002, 3 workers (RSC, ACEG); same loc., 21°03'N, 105°22'E (ca. 800 m alt.), 21.VI.2002, K. Eguchi leg., 1 worker (ACEG); Hue: Bach Ma N.P., 16°12'16–22"N, 107°51'26–28"E, 875–930 m alt., 15.XI.2009, Eg15xi09-14, 2 workers, 1 queen (ACEG, RSC); Nghe An Prov.: Que Phong Dist.: Thong-Thu Com: Ban Loc, 9.II.1999, B.T. Viet leg., 1 worker (RSC); same loc., Tuong Duong dist.: Sang Le forest, 19°11'N, 104°37–38'E, <220 m alt., 2.IV.2006, EG02iv06-17, 1 worker (RSC); Lao Cai: Sa Pa: Y Linh Ho, ca. 1100 m alt., 1.V.2002,

K. Eguchi leg., EG02-VN-216, 3 workers (RSC, ACEG); same loc., 1.V.2002, K. Eguchi leg., EG02-VN-209, 2 workers (RSC); Vin Phuc Prov.: Tam Dao, 900 m alt., 7.VIII.1998, Sk. Yamane leg., 1 worker (RSC).

Worker measurements and indices. "*Odontomachus garanatus*" — holotype: HW 2.19 mm, HL 3.00 mm, SL 3.59 mm, IFLW 0. 66 mm, EL 0.45 mm, MDL 1.81 mm, WL 4.34 mm, PTL unmeasured, PTH unmeasured, CI 73, SI 164, MDI 60, PTHI incalculable.

Non-types (n=5): HW 2.00–2.09 mm, HL 2.77–2.82 mm, SL 3.40–3.46 mm, IFLW 0.56–0.60 mm, EL 0.41–0.43 mm, MDL 1.83–1.88 mm, WL 3.94–4.19 mm, PTL 0.80–0.88 mm, PTH 1.20–1.24 mm, CI 72–75, SI 165–170, MDI 66–67, PTHI 140–150.

Worker description. Body relatively large (HL 2.77–2.82 mm; WL 3.94–4.19 mm). Head in full-face view much longer than broad, with posterior margin weakly concave and shallow temporal ridge; head posteriorly without a pair of small and distinct tubercles; median furrow on vertex present as dark line; each side of line not swollen dorsad; frontal lobes followed by strong frontal carinae which are slightly divergent posteriad; minimum distance between margin of ocular ridge and margin of compound eye less than half major axis of compound eye; masticatory margin with 13–14 distinct denticles; subapical tooth ca. 2.5 times as long as broad, with acute apex; palp formula 4, 4. Mesosoma in lateral view relatively much slender; pronotum including anteromedian lobe long, in lateral view with anterodorsal slope gentle; mesopleuron without anteroventral ridge, and anterodorsal margin without carina, and indistinctly separated from mesonotum; propodeum in lateral view with dorsum almost straight and gradually sloping posteriad, and with posterior face steeply sloping; propodeal dorsum without median longitudinal depression. Petiolar node conical, with sharply pointed apical spine; node excluding apical spine in lateral view with anterior face strongly convex and long gentle slope, and posterior face weakly convex (Figs. 4-2C, 4-36B); apical spine needle-shaped, less than 1/5 as long as petiolar height, weakly curved posteriad; subpetiolar process lobate, directed ventrally, with the maximum length of anterior-posterior axis as long as dorsal-ventral axis. Gastral tergite I in lateral view long, with anterior face relatively short and gently sloping.

Head in full-face view opaque, largely with dense and very fine striation, except area between frontal carina and compound eye, and area around eye smooth and shiny; frontal lobe very finely striate; posterolateral part of head with very fine striation; venter of head smooth and shiny; median disc of clypeus with rough texture. Pronotum in dorsal view with dense and very fine concentric striation; metapleuron and propodeum with transverse striation which is a little sparser and stronger than on mesonotum and mesopleuron. Petiolar node largely smooth and shiny, with basal area faintly striate.

Vertex with a pair of long erect setae; frontal lobe without erect seta; pronotal disc without long erect setae; gastral tergite I without erect setae. Head, mesosoma, petiole and gaster with very dense and fine appressed pubescence.

For color see Fig. 4-36; body reddish-brown; leg yellowish brown to orange-brown, with coxae and femora paler.

Queen measurements and indices. Non-type (n=1): HW 2.43 mm, HL 3.14 mm, SL 3.5 mm, IFLW 0.65 mm, EL 0.56 mm, OL 0.18 mm, MDL 2.03 mm, WL 4.71 mm, PTL unmeasured, PTH unmeasured, CI 77, SI 144, MDI 64, PTHI incalculable.

Queen description. Queen in general appearance similar to worker. Vertex near ocelli not swollen; ocular ridge clearly developed; distance between lateral ocelli shorter than distance between lateral and median ocelli, and as long as major axis of median ocellus; ocelli in lateral view protruded dorsad. Mesosoma with main sclerites associate with wing function (Figs. 4-37B, 4-37C), in dorsal view long and slender; anterodorsal slope of pronotum in lateral view relatively gentle; anterodorsal outline of mesoscutum in lateral view relatively gentle; mesoscutum without any posteromedian depression; parapsidal furrow very weak and weakly curved; dorsal outline of metascutellum in lateral view weakly angulate; mesopleuron with shallow, oblique furrow; propodeum in lateral view relatively long, with dorsum almost straight and gradually sloping posteriad; propodeum in dorsal view with lateral outlines convergent posteriad. Petiolar node in lateral view, similar to worker. Gastral tergite I in lateral view relatively short, with anterior face very short.

Head in full-face view opaque, largely with dense and very fine striation, except area between frontal carina and compound eye, and area around eye smooth and shiny; frontal lobe finely striate; posterolateral part of head with very fine striation; venter of head smooth and shiny; median disc of clypeus with rough texture. Pronotum in dorsal view with dense and very finely tranversely striate; mesoscutum and mesoscutellum with dense punctures; mesopleuron entirely with fine striation; propodeum strongly and sparsely striate transversely, stronger and sparser than pronotum. Petiolar node largely smooth and shiny.

Pair of long erect setae present on vertex near lateral ocelli; frontal lobe and pronotal disc without any erect setae; gastral tergite I without any erect setae; Head, mesosoma, petiole and gaster with very dense and fine decumbent to subdecumbent pubescence; mesopleuron entirely cover by very dense and fine decumbent to subdecumbent pubescence.

For color see Fig. 4-37: body reddish-brown; leg yellowish brown to orange-brown, with coxae and femora paler.

Species recognition. This species can be easily distinguished from the other Asian *Odontomachus* based on the following characters: subapical teeth longer than broad with acute apex; mesosoma much slender; petiolar node excluding apical spine in lateral view with anterior face strongly convex and long gentle slope, and posterior face weakly convex (see Figs. 4-2C, 4-36B); Gastral tergite I in lateral view long, with its anterior face short and gently sloping; body with very dense and fine appressed pubescence.

Brown (1976) synonimyzed *O. silvestrii* var. *subtriatus* Wheeler, 1927 under *O. silvestrii* Wheeler, 1927 which the locality of both species from Northern Vietnam. He concluded that the punctures on the body of *O. silvestrii* var. *subtriatus*, is corresponding to dense pubescence.

Wang (1993) described *O. granatus*, and distinguished it from O. silvestrii by the following characteristics of the worker: SI smaller in *O. silvestrii* (SI 150) than in *O. granatus* (SI >170); the gastral dorsum sculptured in *O. silvestrii* but smooth and shiny in *O. granatus*. After creful examinations of the holotype of *O. granatus* (in IZCAS, Beijing, China) and non-type specimens of *O. silvestrii* from Vietnam, the conspecificity of the two was strongly supported based on the entire similarity; SI was not significantly different between the two (see under the measurements of *O. silvestrii*). On the other hand, as mentioned by Wang (1993), gastral dorsum is vaguely smooth and shiny in *O. granatus* which are correspondingly with the very dense of pubescence. In the present study *O. granatus* is treated as a synonym of *O. silvestrii*, although the independence of *O. granatus* can not be ruled out.

Distribution. China and Vietnam

Bionomics. This species inhabits in secondary and primary of highland and lowland forests, and nests underground near streams.

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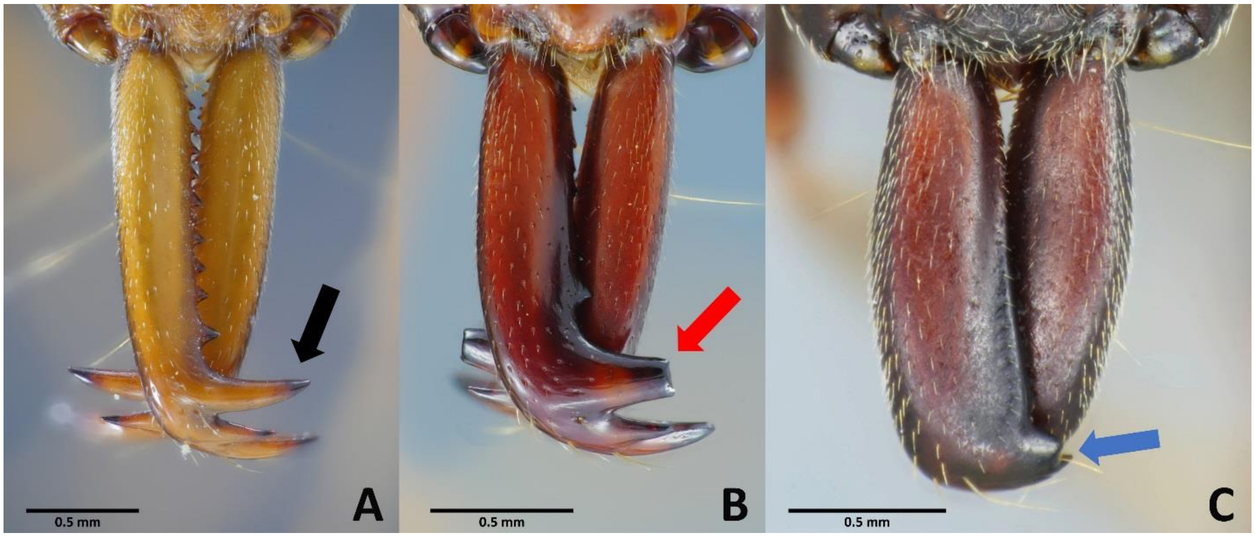

Figure 4-1. Mandibles of the genus *Odontomachus*: A, *O. silvestrii* Wheeler, with a black arrow indicating acute apex of subapical tooth; B, *O. kuroiwae* (Matsumura), with a red arrow indicating truncate apex of subapical tooth; C, *O. simillimus* F. Smith, with a blue arrow indicating blunt apex of subapical tooth.

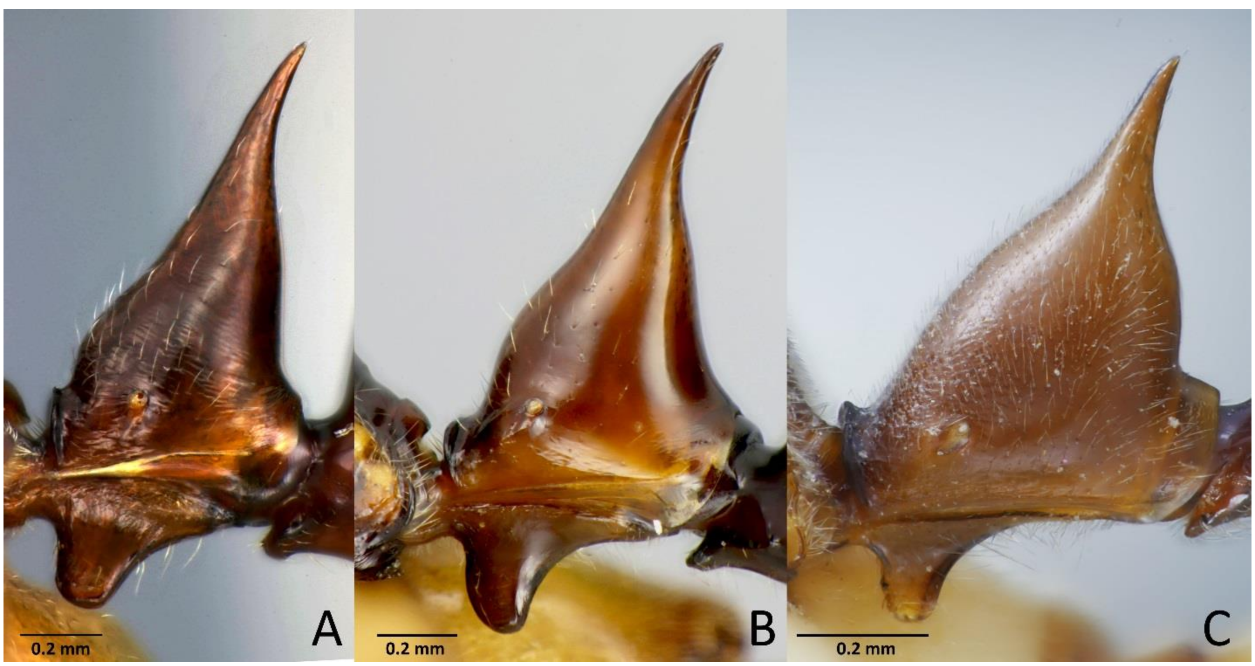

Figure 4-2. Petiole in lateral view, worker: A, *Odontomachus latidens* Mayr (colony: GK-38-12; individual: SEMUT150101B); B, *O. procerus* Emery (SAGO-01-12; SEMUT141217B); C, *O. silvestrii* Wheeler (SEMUT20170503C).

Figure 4-3. *Odontomachus fulgidus* Wang, worker (holotype): A, head in full-face view; B, profile in lateral view; C, mesosoma in dorsal view; D, label.

Figure 4-4. *Odontomachus kuroiwae* (Matsumura), worker (colony: RS-04-OKN16; individual: SEMUT20161208): A, head in full-face view; B, mesosoma in lateral view; C, mesosoma in dorsal view; D, petiole and gaster in lateral view.

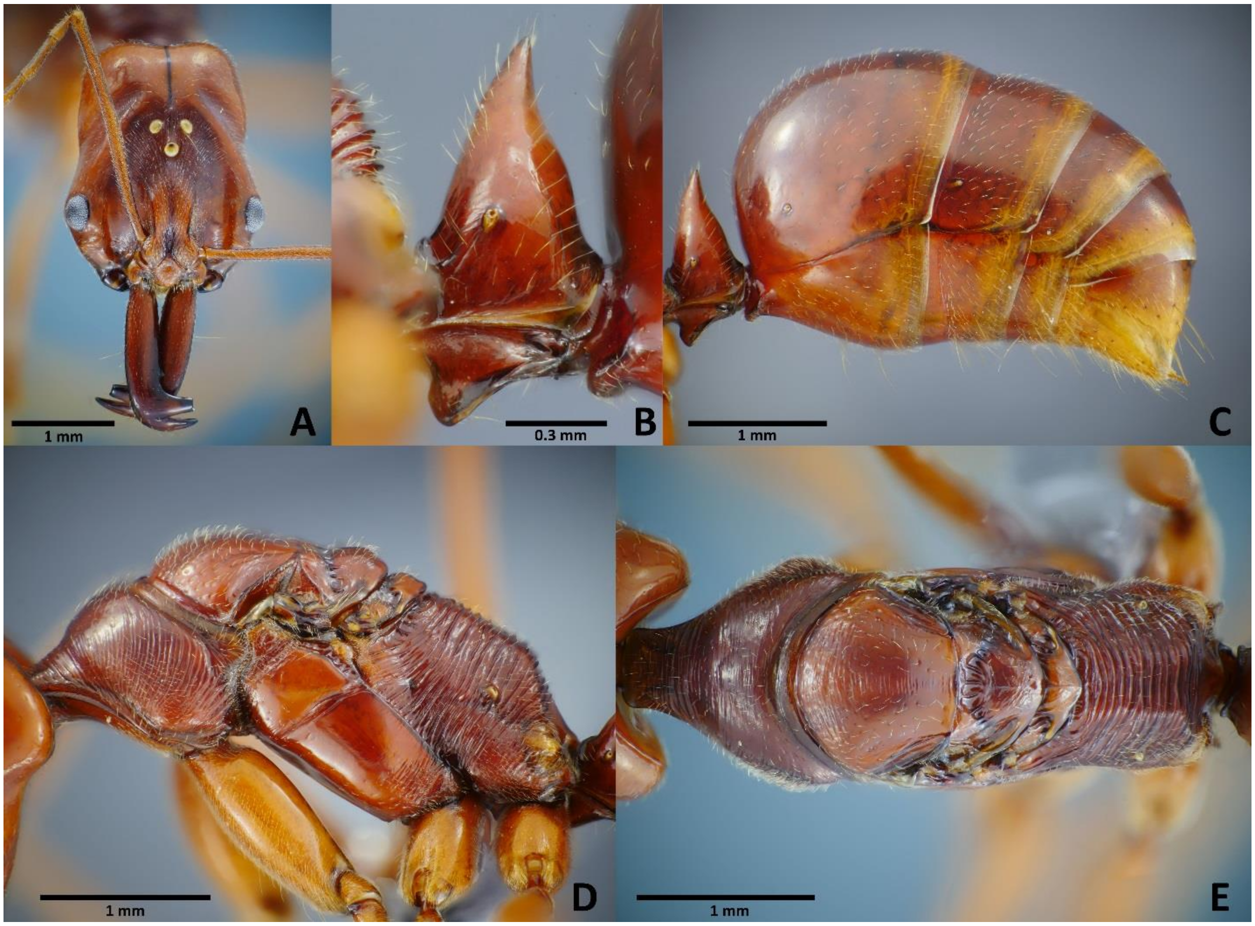

Figure 4-5. *Odontomachus kuroiwae* (Matsumura), queen (colony: RS-17-OKN16; individual: SEMUT20170310): A, head in full-face view; B, petiole in lateral view; C, gaster in lateral view; D, mesosoma in lateral view; E, mesosoma in dorsal view.

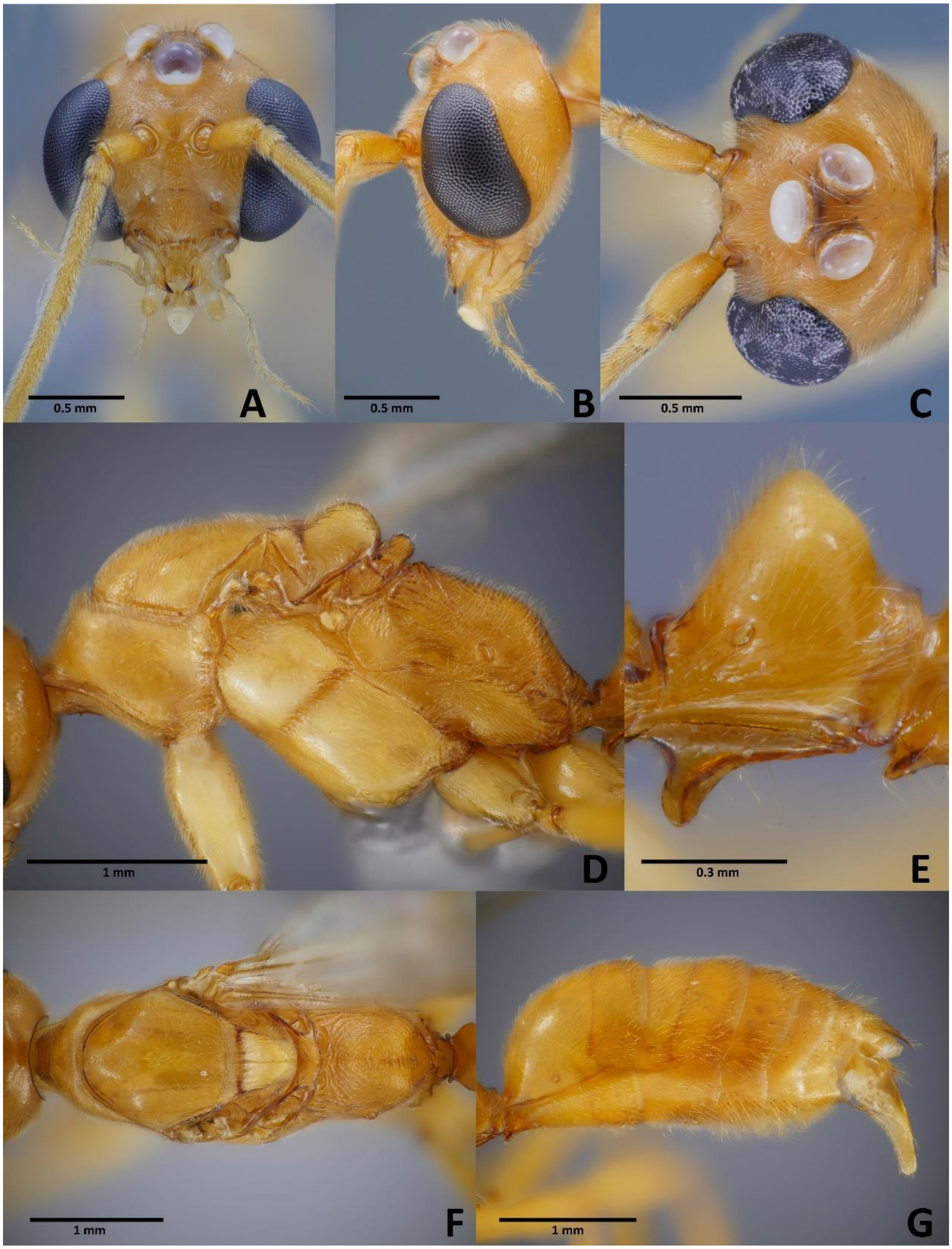

Figure 4-6. *Odontomachus kuroiwae* (Matsumura), male (colony: RS-01-OKN16; individual: SEMUT20170430A): A, head in full-face view; B, head in lateral view; C, head in dorsal view; D, mesosoma in lateral view; E, petiole in lateral view; F, mesosoma in dorsal view; G, gaster in lateral view.

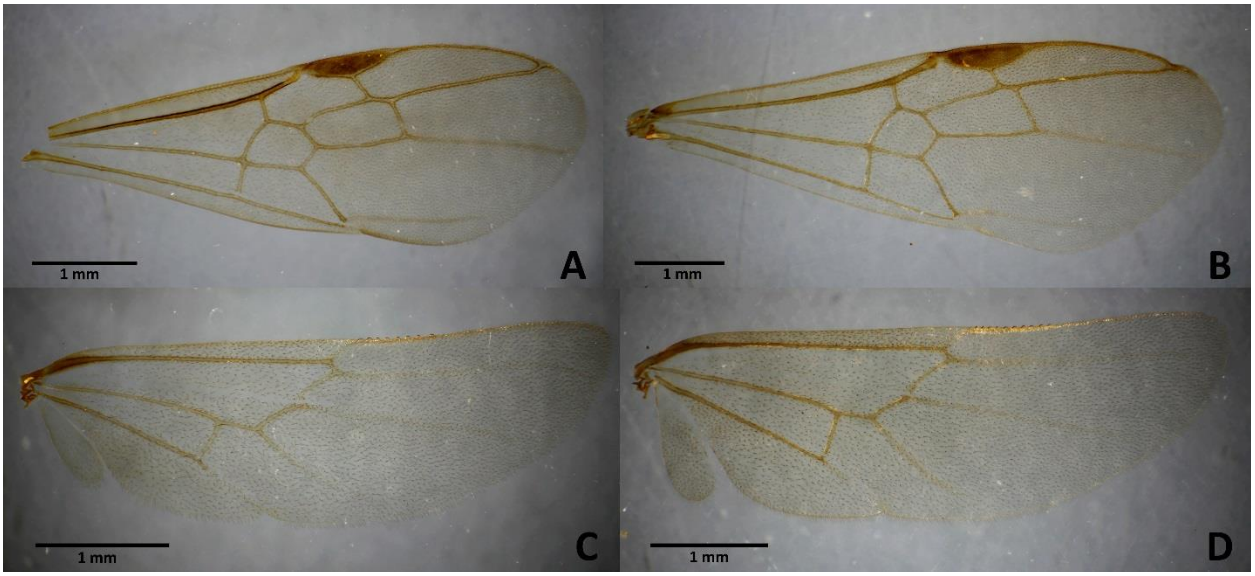

Figure 4-7. Male *Odontomachus*, wing venation: A, C, *O. kuroiwae* (Matsumura) (colony: RS-01-OKN16; individual: SEMUT20170430A); B, D, *O. monticola* Emery (colony: MS15-2; individual: SEMUT20170430B).

Figure 4-8. *Odontomachus latidens* Mayr*,* worker (colony: GK-38-12; individual: SEMUT150101B): A, head in full-face view, with an arrow indicating subapical tooth of mandible; B, mesosoma in dorsal view; C, mesosoma in lateral view, with an arrow indicating mesopleuron without its anteroventral ridge; D, petiole and gaster in lateral view.

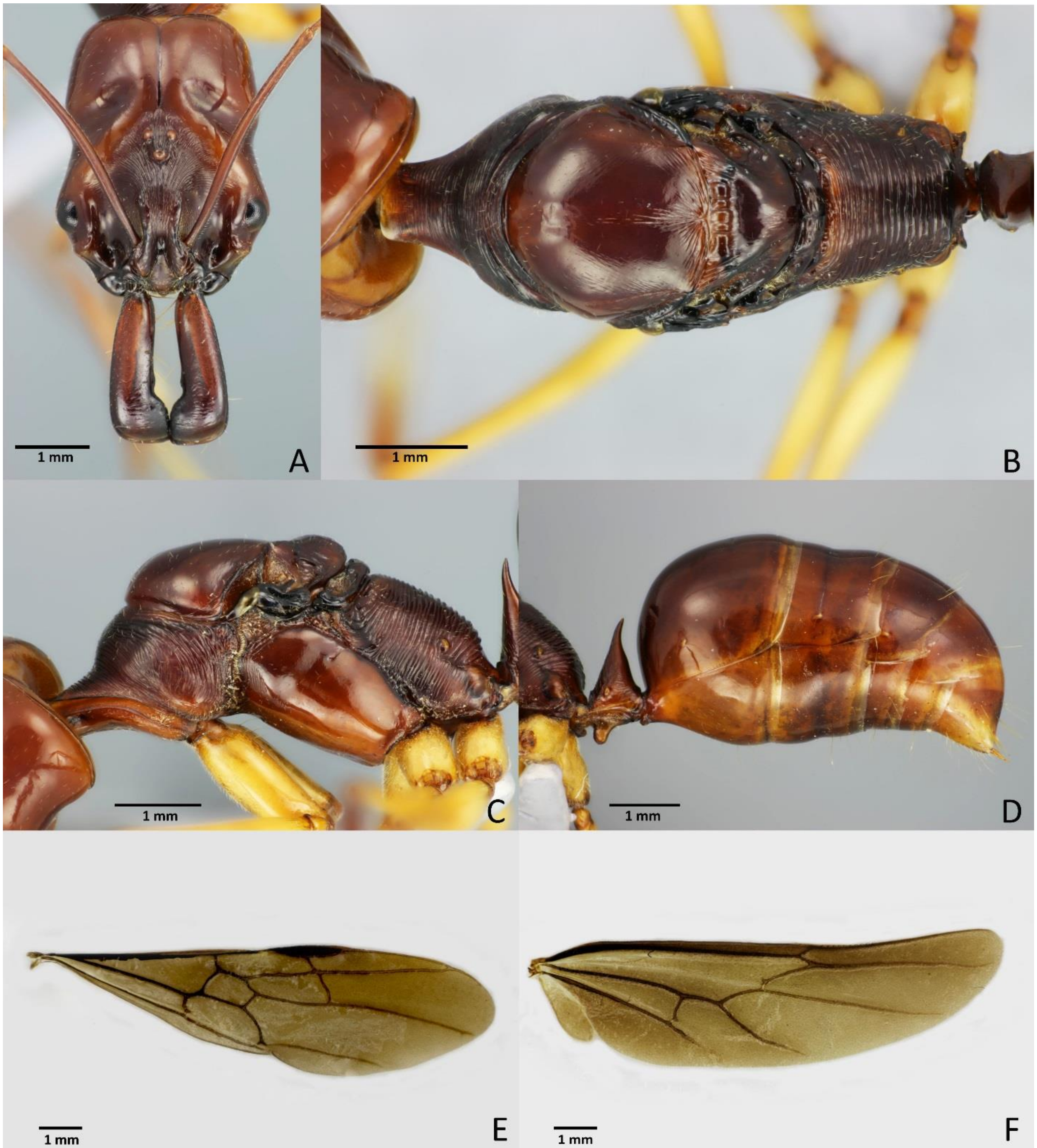

Figure 4-9. *Odontomachus latidens* Mayr, queen (colony: GK-38-12; individual: SEMUT150101C): A, head in full-face view; B, mesosoma in dorsal view; C, mesosoma in lateral view; D, petiole and gaster in lateral view; E, forewing; F, hindwing.

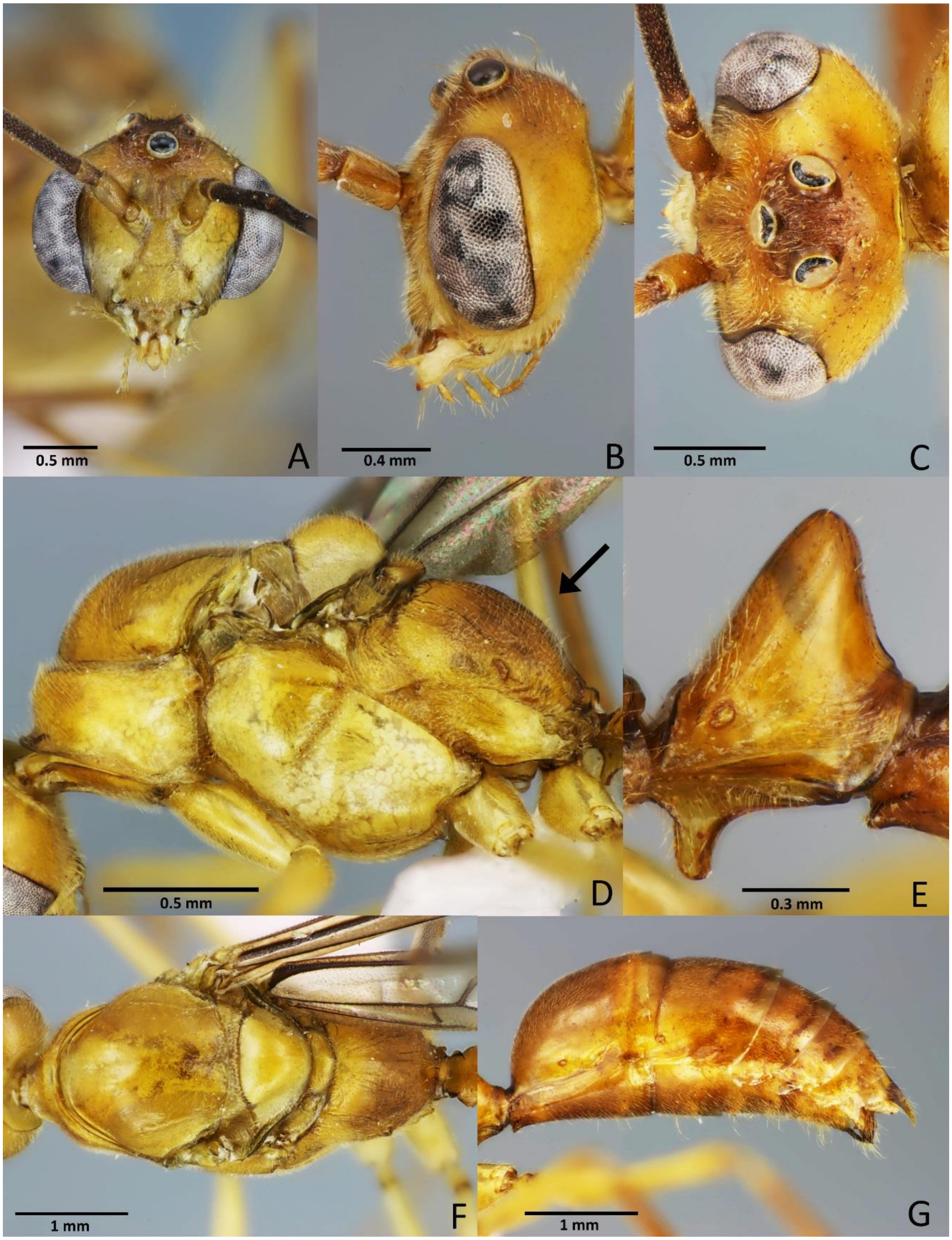

Figure 4-10. *Odontomachus latidens* Mayr, male (colony: GK-38-12; individual: SEMUT141225E): A, head in full-face view; B, head in lateral view; C, head in dorsal view; D, mesosoma in lateral view, with an arrow indicating an roundly convex dorsal outline; E, petiole in lateral view; F, mesosoma in dorsal view; G, gaster in lateral view.

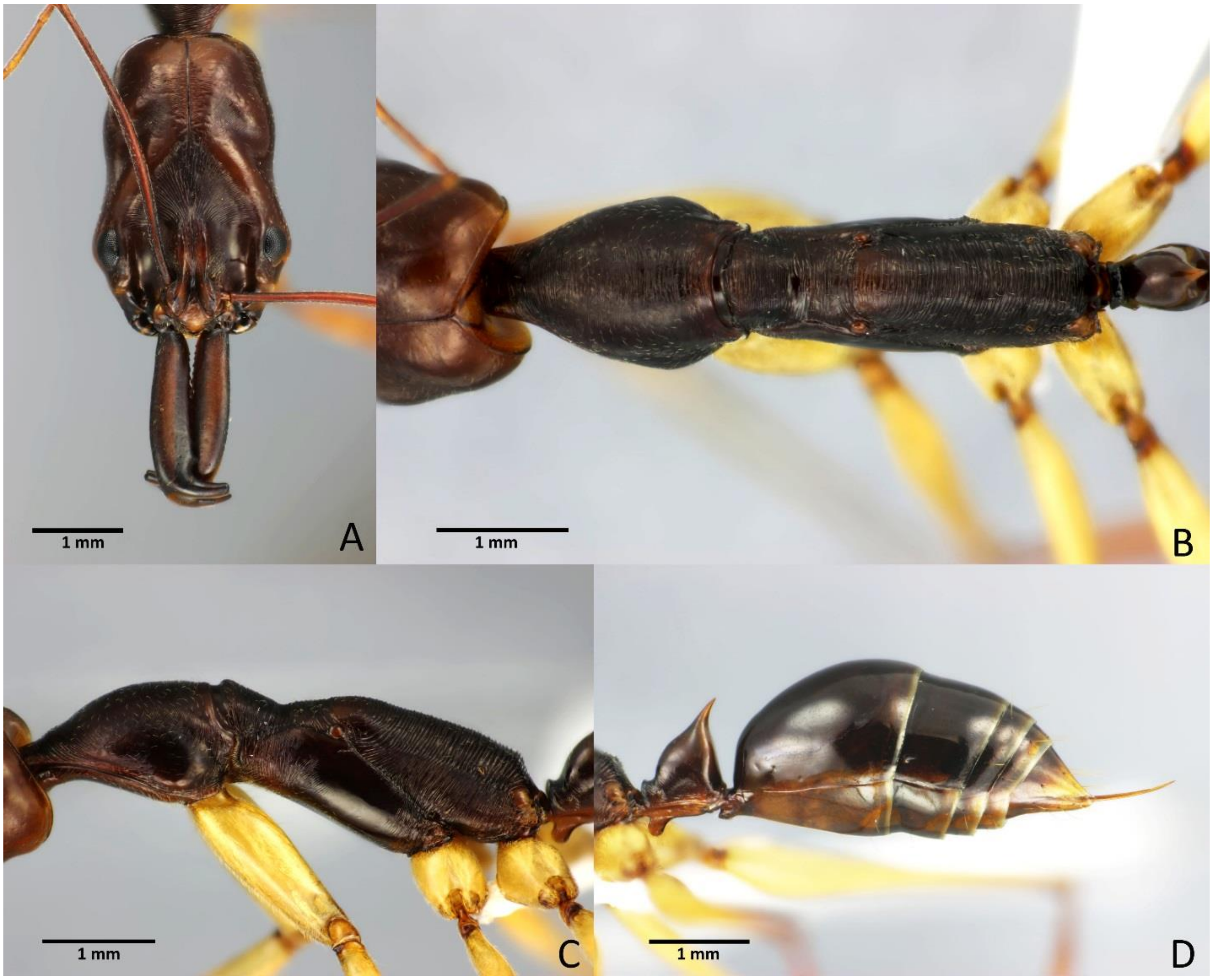

Figure 4-11. *Odontomachus minangkabau* Satria *et al*., worker (holotype; colony: RS01-PDG-14; individual: SEMUT141224B): A, head in full-face view; B, mesosoma in dorsal view; C, mesosoma in lateral view; D, petiole and gaster in lateral view.

Figure 4-12. *Odontomachus minangkabau* Satria *et al*., queen (paratype; colony: RS01-PDG-14; individual: SEMUT141224H): A, head in full-face view; B, mesosoma in dorsal view; C, mesosoma in lateral view; D, petiole and gaster in lateral view; E, forewing; F, hindwing.

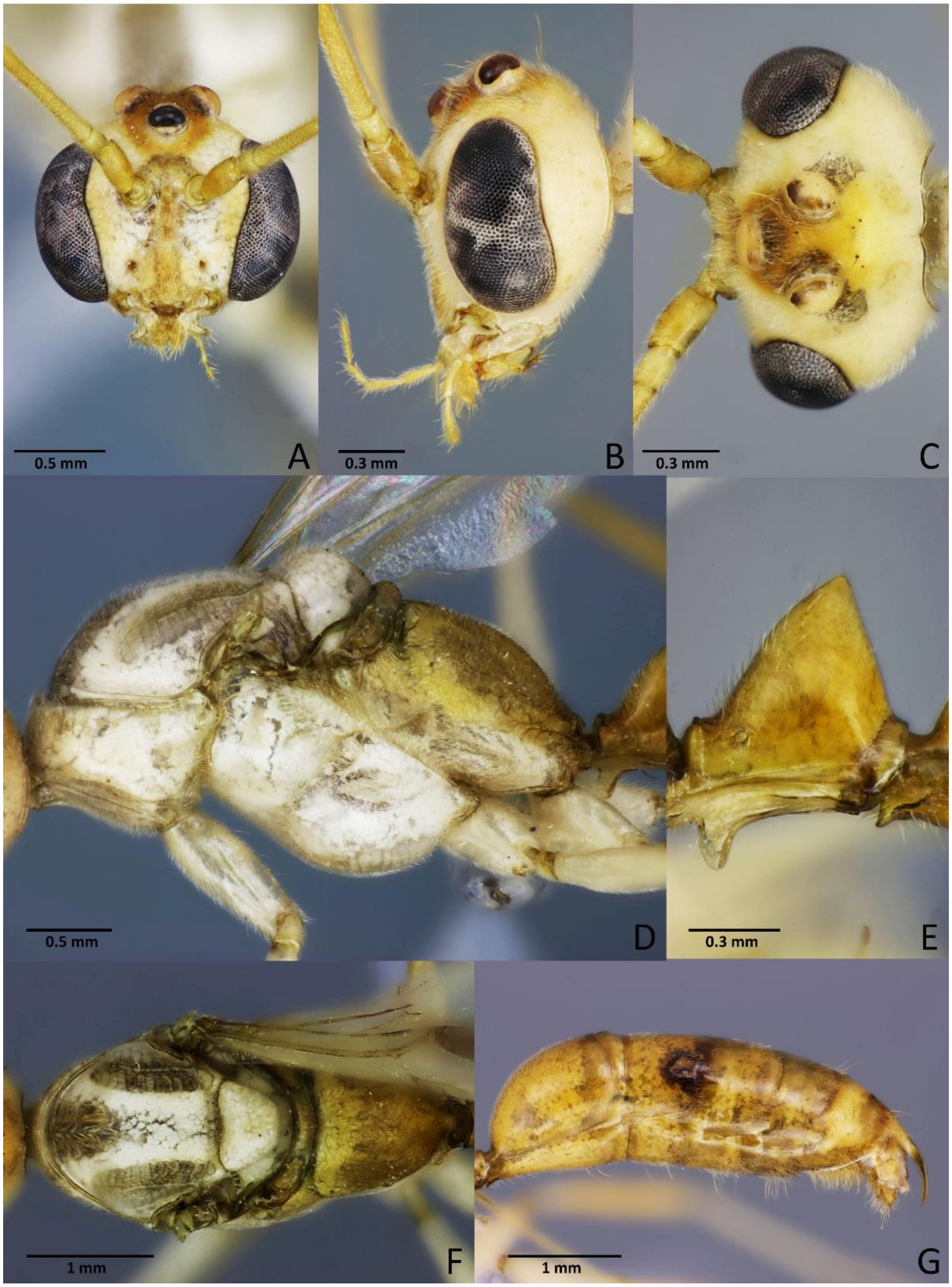

Figure 4-13. *Odontomachus minangkabau* Satria *et al*., male (paratype; colony: RS01-PDG-14; individual: SEMUT150101A): A, head in full-face view; B, head in lateral view; C, head in dorsal view; D, mesosoma in lateral view; E, petiole in lateral view; F, mesosoma in dorsal view; G, gaster in lateral view.

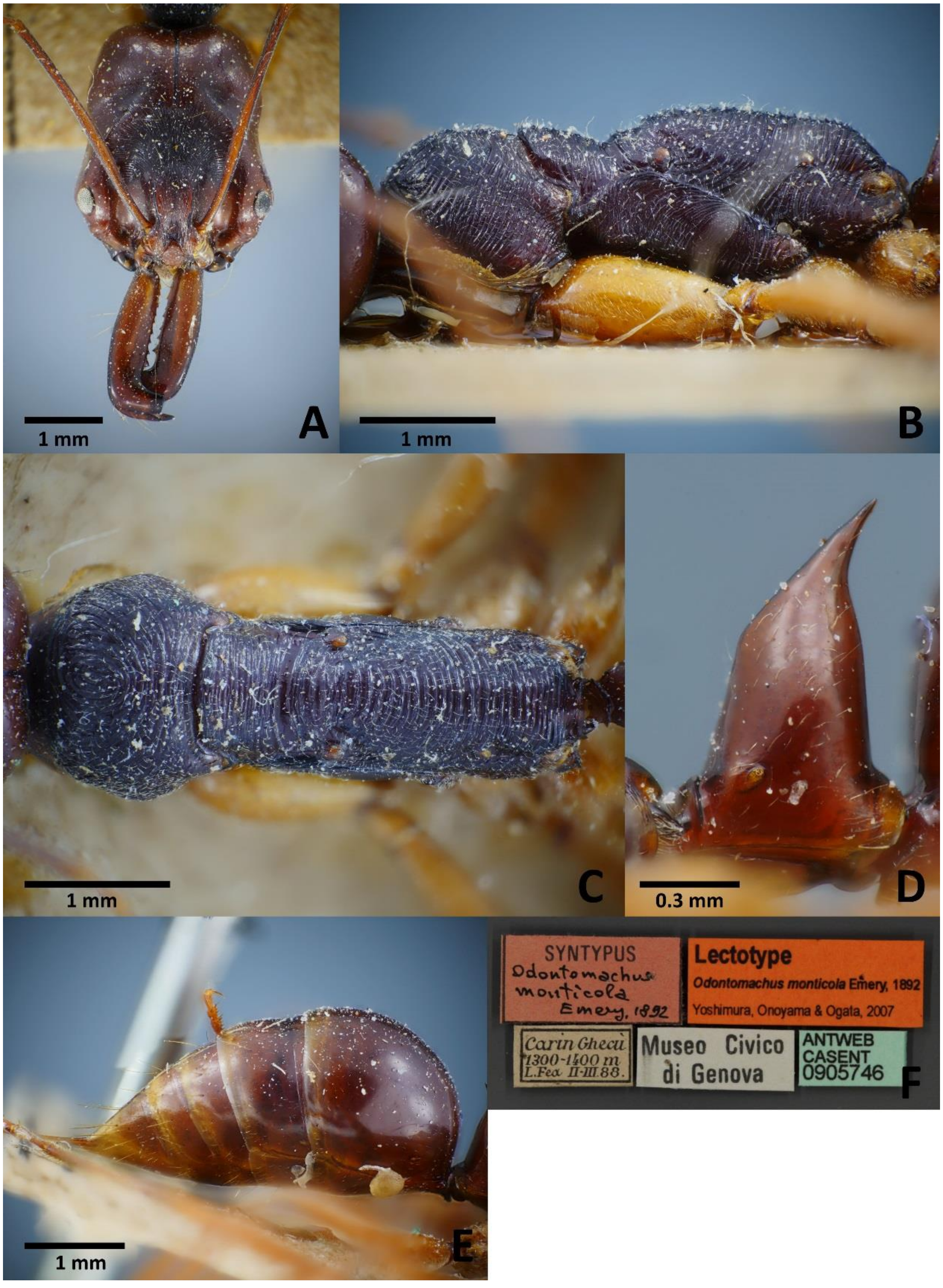

Figure 4-14. *Odontomachus monticola* Emery, worker (lectotype): A, head in full-face view; B, mesosoma in lateral view; C, mesosoma in dorsal view; D, petiole in lateral view; E, mesosoma in lateral view; G, label.

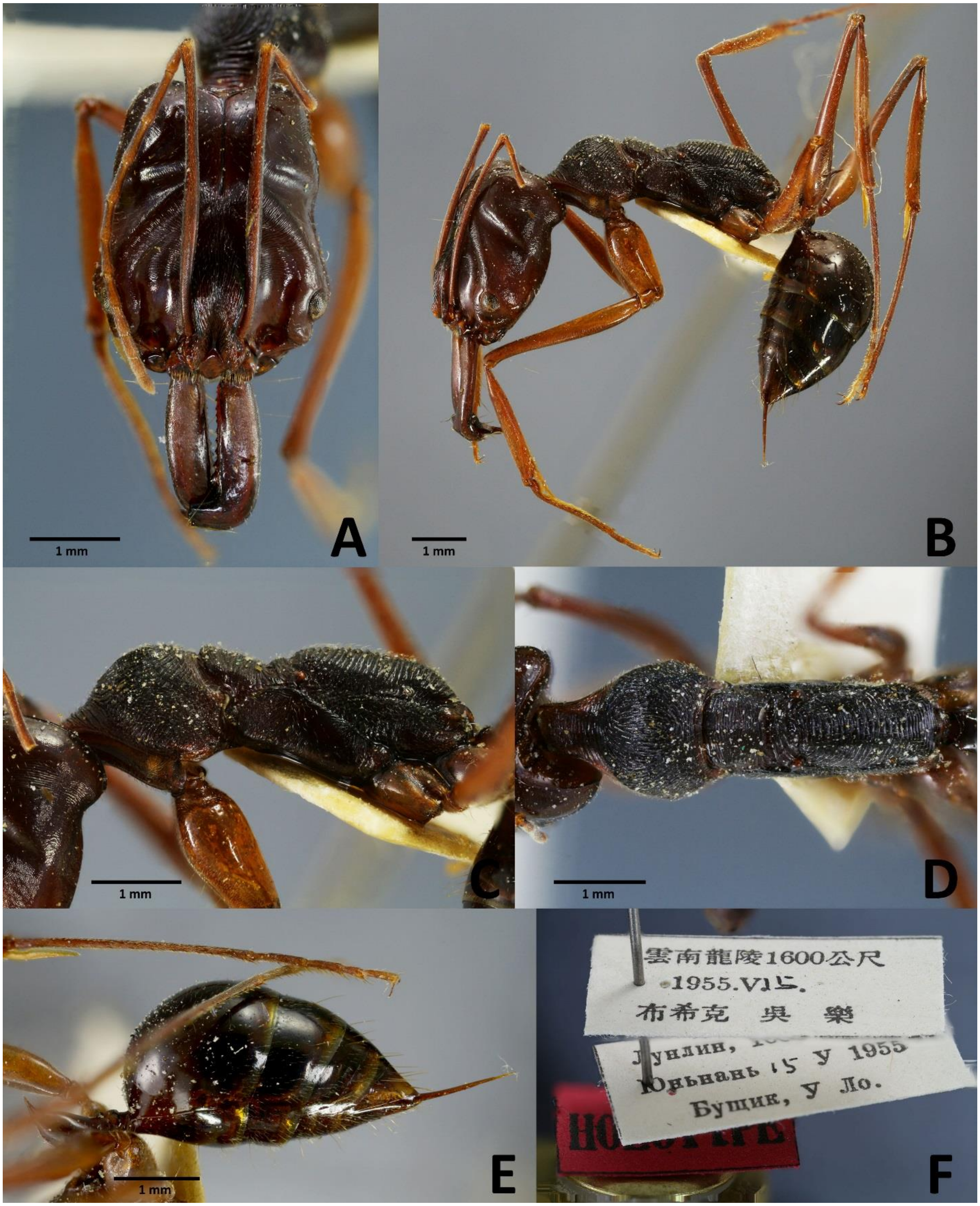

Figure 4-15. *Odontomachus circulus* Wang, worker (holotype): A, head in full-face view; B, profile in lateral view; C, mesosoma in lateral view; D, mesosoma in dorsal view; E, gaster in lateral view; F, label.

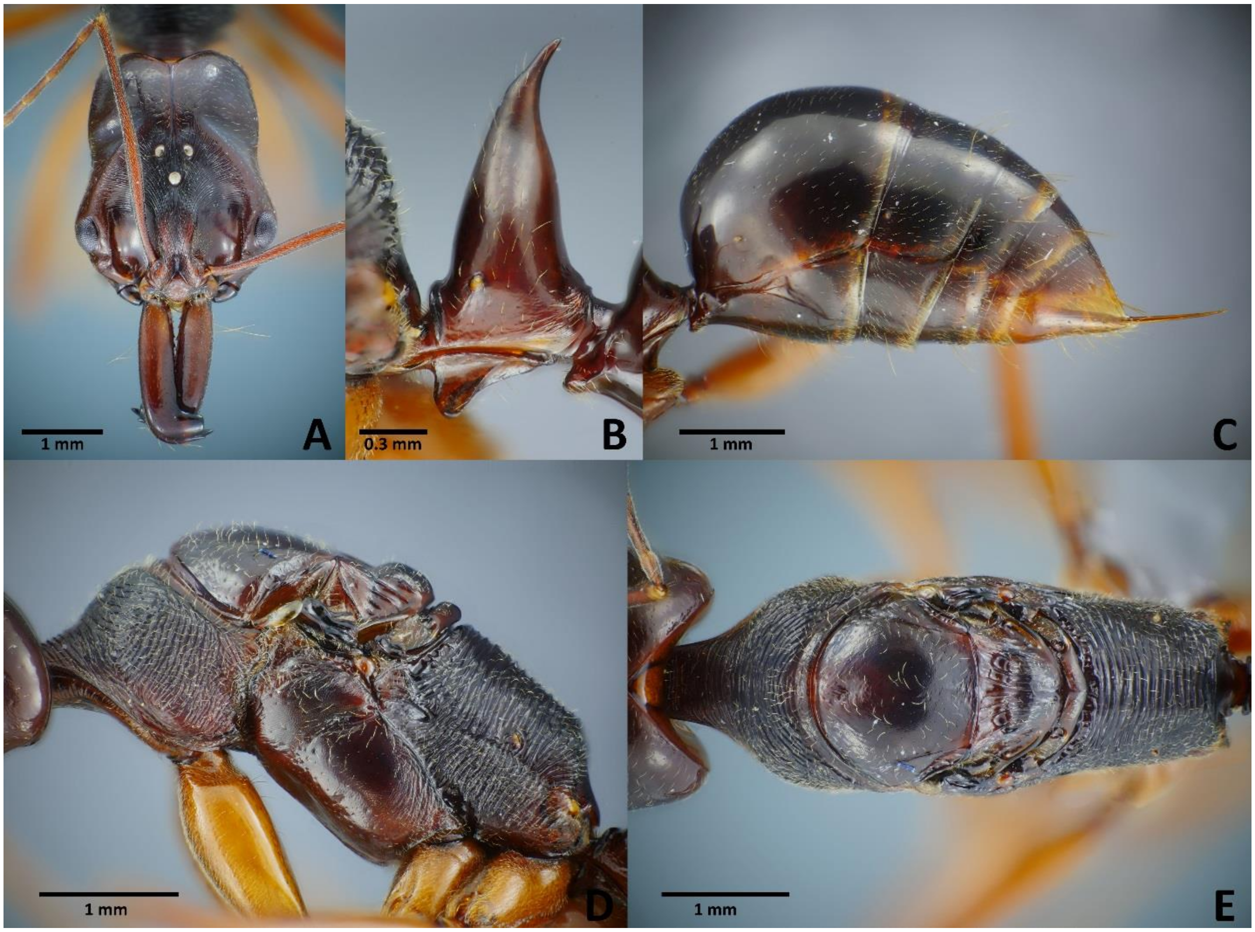

Figure 4-16. *Odontomachus monticola* Emery, queen (colony: RS-98-BV16; individual: SEMUT20161219C): A, head in full-face view; B, petiole in lateral view; C, gaster in lateral view; D, mesosoma in lateral view; E, mesosoma in dorsal view.

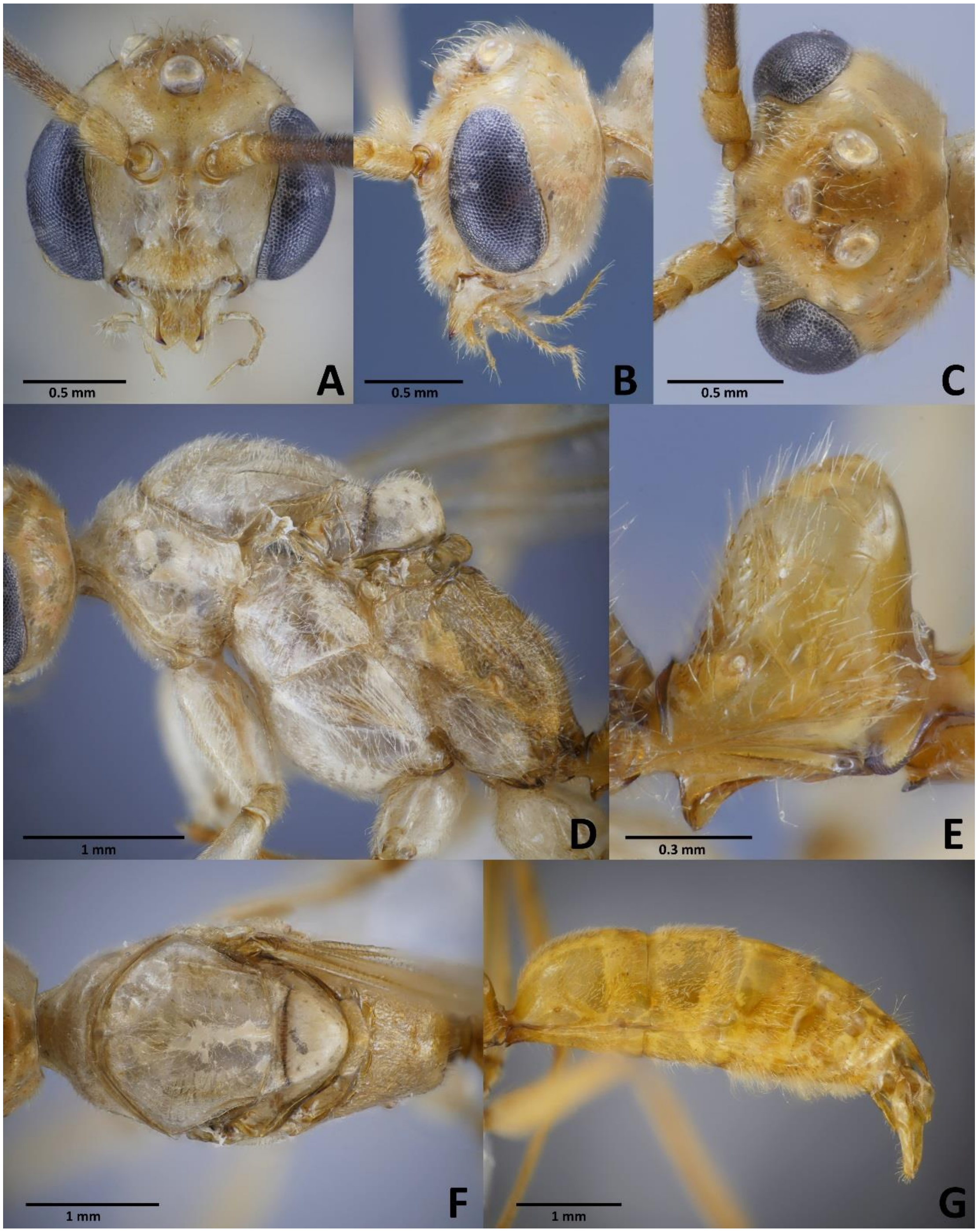

Figure 4-17. *Odontomachus monticola* Emery, male (colony: MS15-2; individual: SEMUT20170430B): A, head in full-face view; B, head in lateral view; C, head in dorsal view; D, mesosoma in lateral view; E, petiole in lateral view; F, mesosoma in dorsal view; G, gaster in lateral view.

Figure 4-18. *Odontomachus pararixosus* Terayama and Ito, worker (holotype): A, head in full-face view; B, profile in lateral view; C, mesosoma in lateral view; D. mesosoma in dorsal view; E, petiole and gaster in lateral view; F, label.

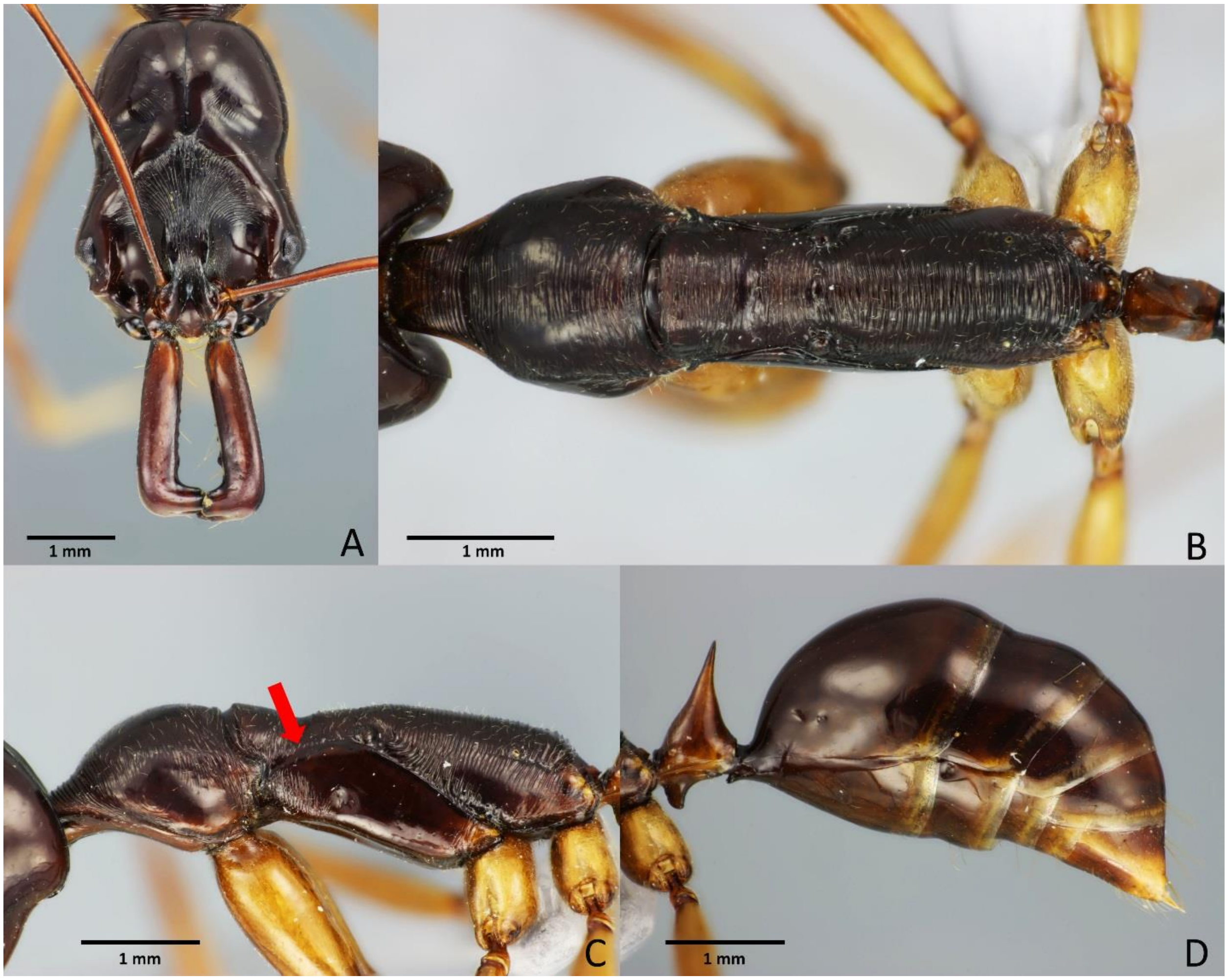

Figure 4-19. *Odontomachus procerus* Emery, worker (colony: SAGO-01-12; individual: SEMUT141230L): A, head in full-face view; B, mesosoma in dorsal view; C, mesosoma in lateral view, with an arrow indicating anterodorsal margin of mesopleuron distinctly carinate; D, petiole and gaster in lateral view.

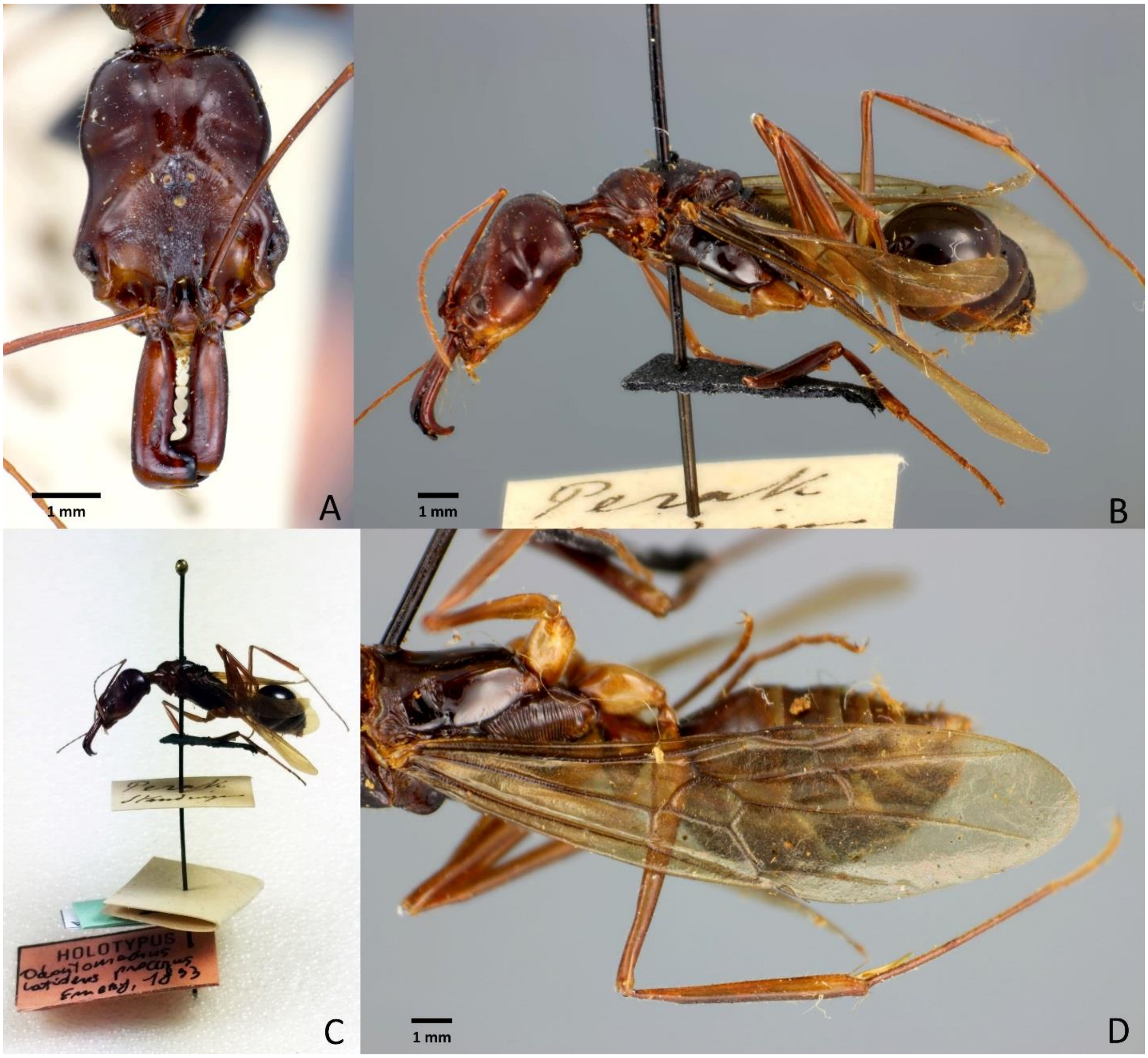

Figure 4-20. *Odontomachus procerus* Emery, queen (holotype; ANTWEB CASENT0903998): A, head in full-face view; B, profile in lateral view; C, label; D, forewing.

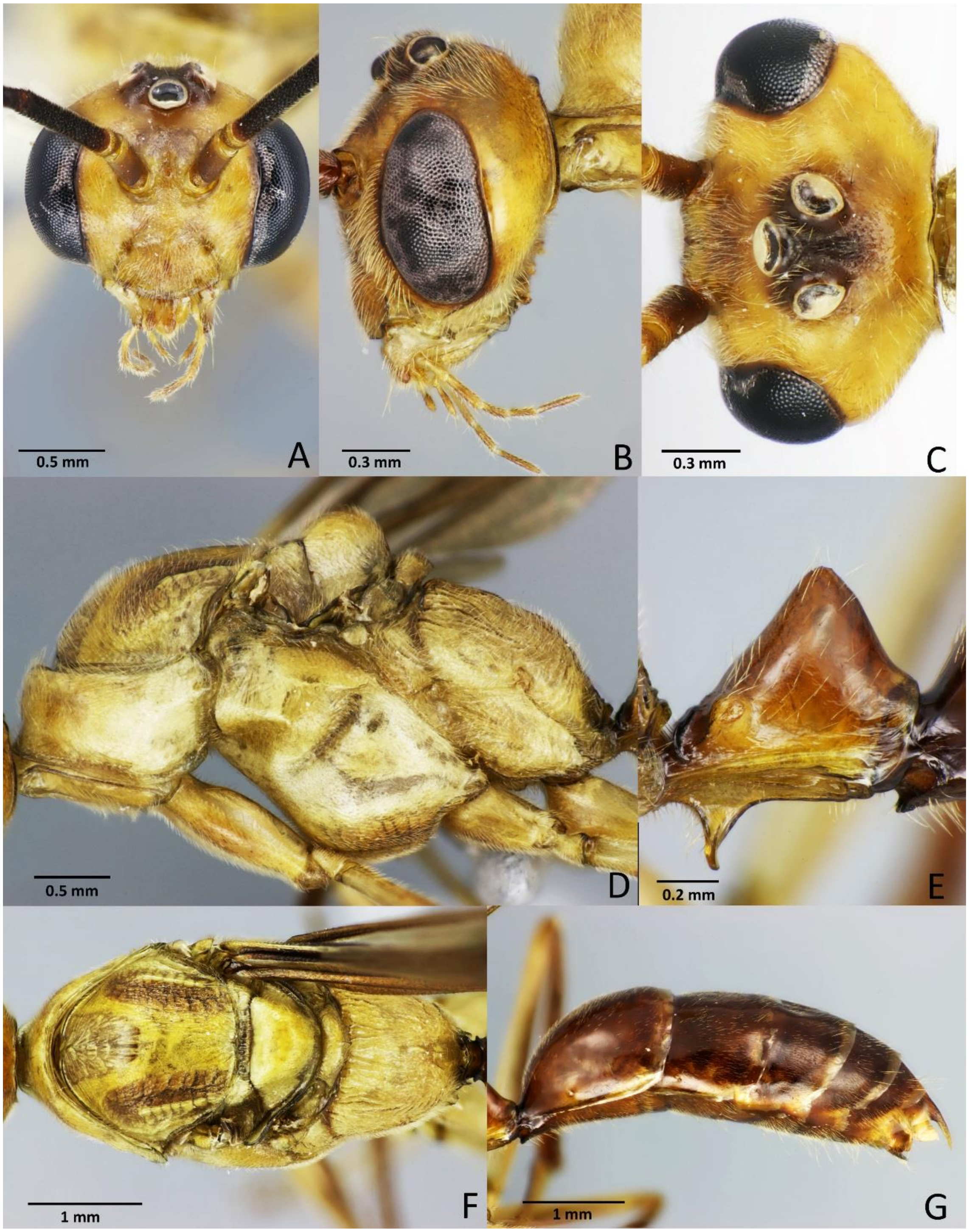

Figure 4-21. *Odontomachus procerus* Emery, male (colony: SAGO-01-12; individual: SEMUT141215B): A, head in full-face view; B, head in lateral view; C, head in dorsal view; D, mesosoma in lateral view; E, petiole in lateral view; F, mesosoma in dorsal view; G, gaster in lateral view.

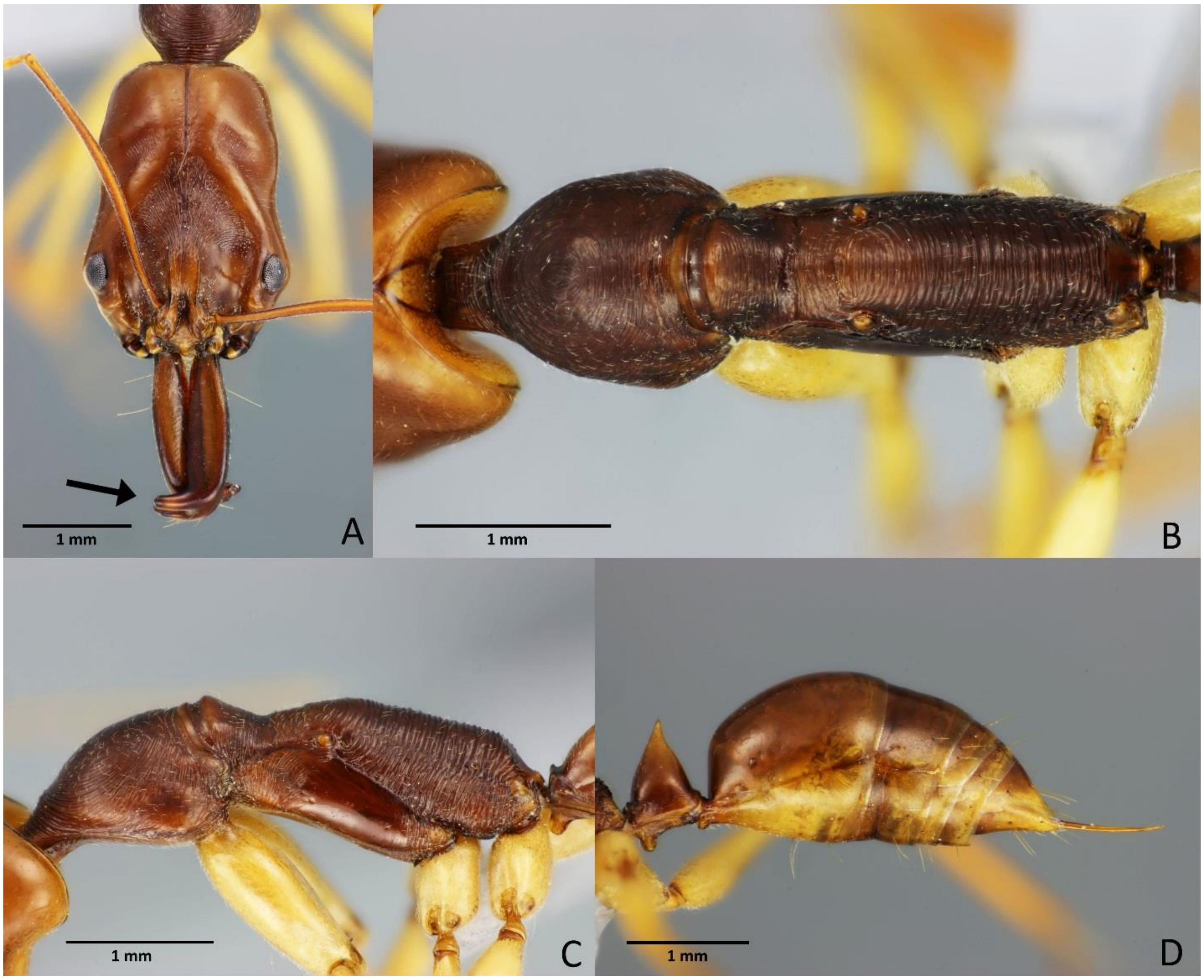

Figure 4-22. *Odontomachus rixosus* F. Smith, worker (colony: PDG-13-12; individual: SEMUT141230K): A, head in full-face view, with an arrow indicating subapical tooth of mandible; B, mesosoma in dorsal view; C mesosoma in lateral view; D petiole and gaster in lateral view.

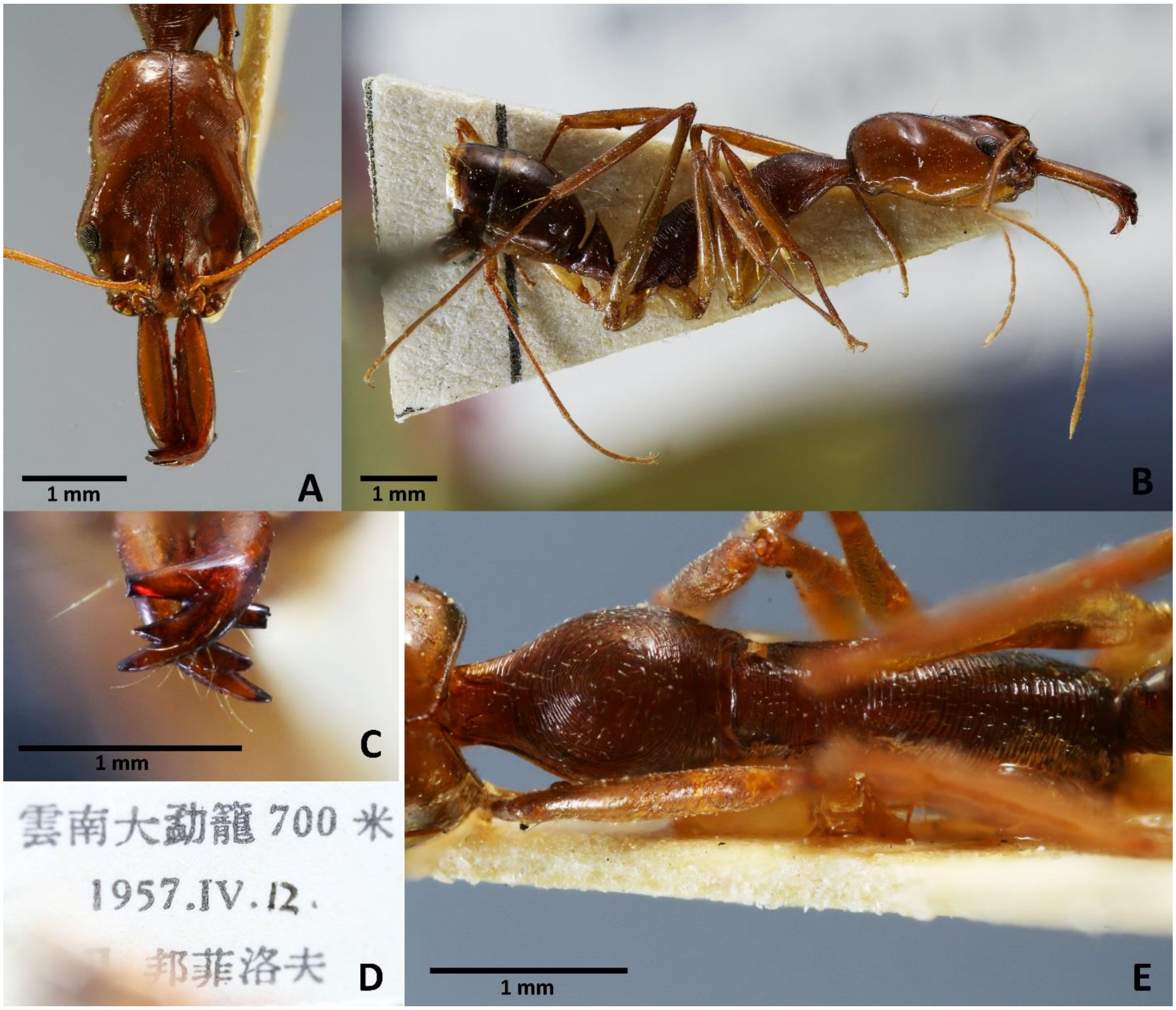

Figure 4-23. *Odontomachus tensus* Wang, worker (holotype): A, head in full-face view; B, profile in lateral view; C, apex of mandibles; D, label; E, mesosoma in dorsal view.

Figure 4-24. *Odontomachus rixosus* F. Smith, queen (colony: GTH-01-12; individual: SEMUT150102A): A, head in full-face view; B, mesosoma in dorsal view; C, mesosoma in lateral view; D, petiole and gaster in lateral view; E, forewing; F, hindwing.

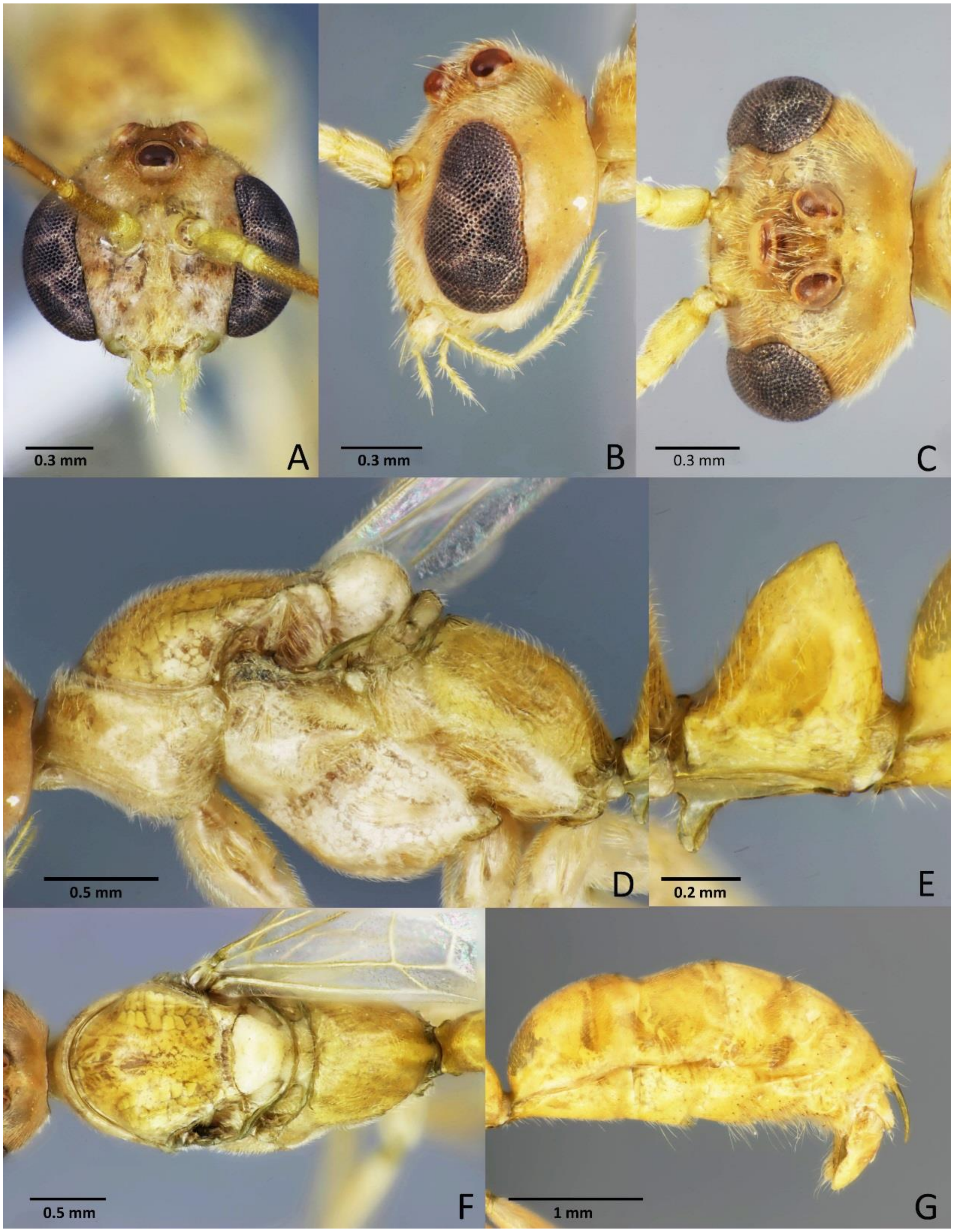

Figure 4-25. *Odontomachus rixosus* F. Smith, male (colony: PKN-01-12; individual: SEMUT150103A): A, head in full-face view; B, head in lateral view; C, head in dorsal view; D, mesosoma in lateral view; E, petiole in lateral view; F, mesosoma in dorsal view; G, gaster in lateral view.

Figure 4-26. *Odontomachus xizangensis* Wang, worker (holotype): A, head in full-face view; B, profile in lateral view; C, mesosoma in lateral view; D. mesosoma in dorsal view; E, petiole and gaster in lateral view; F, label.

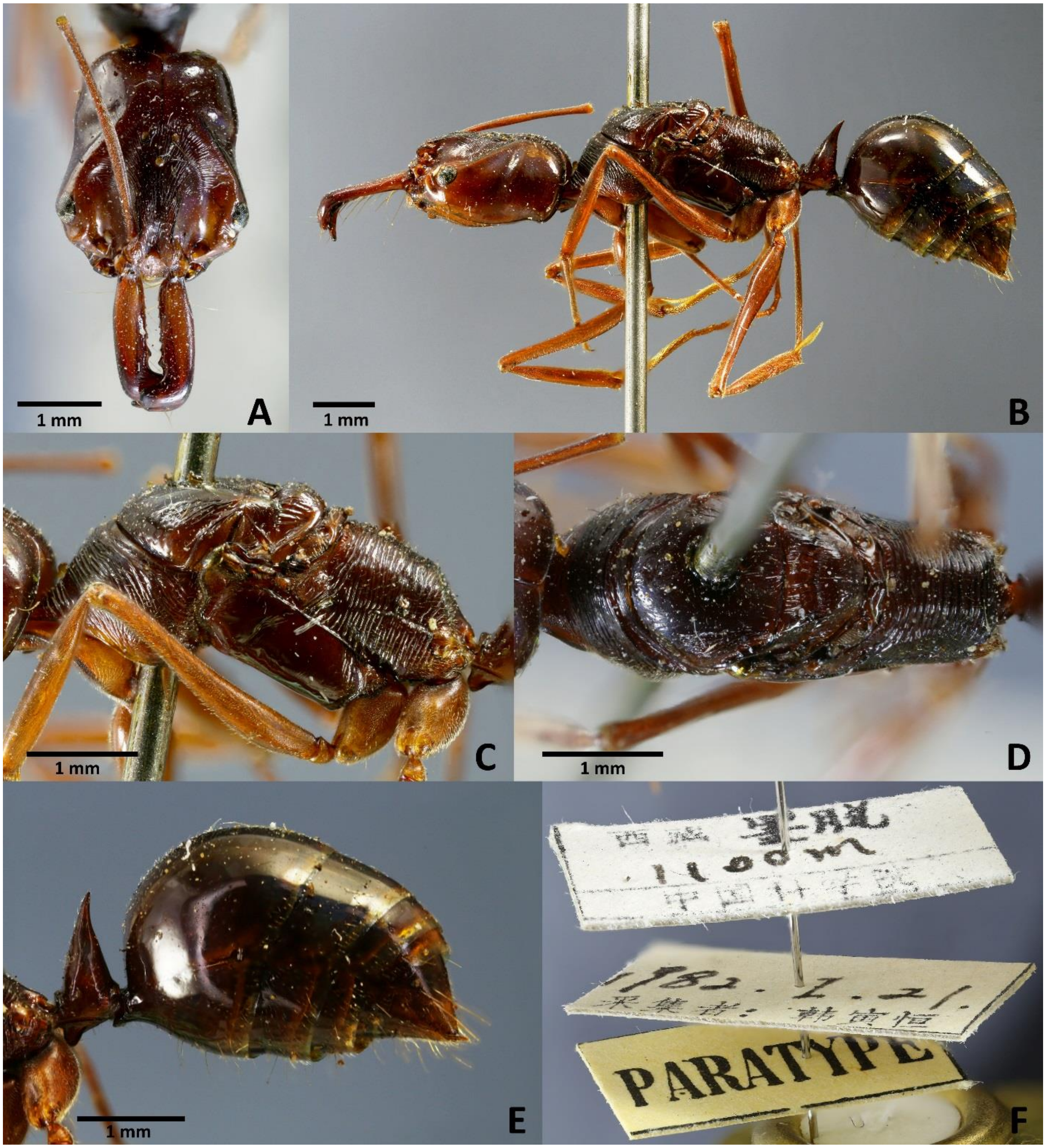

Figure 4-27. *Odontomachus xizangensis* Wang, queen (paratype): A, head in full-face view; B, profile in lateral view; C, mesosoma in lateral view; D. mesosoma in dorsal view; E, petiole and gaster in lateral view; F, label.

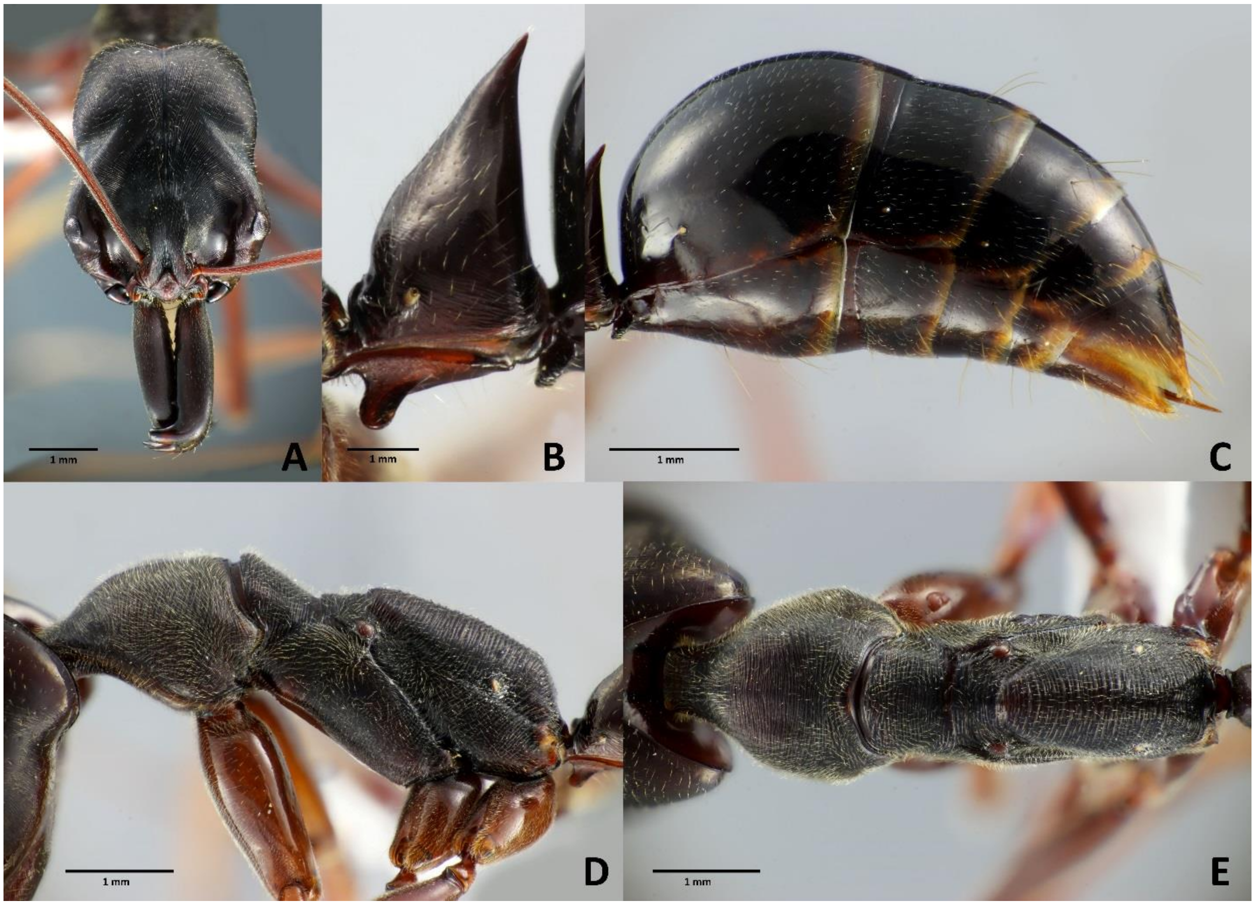

Figure 4-28. *Odontomachus* sp. 1, worker from Vietnam (colony: RS16-BC-15; individual: SEMUT151222A): A, head in full-face view; B, petiole in lateral view; C, gaster in lateral view; D, mesosoma in lateral view; E, mesosoma in dorsal view.

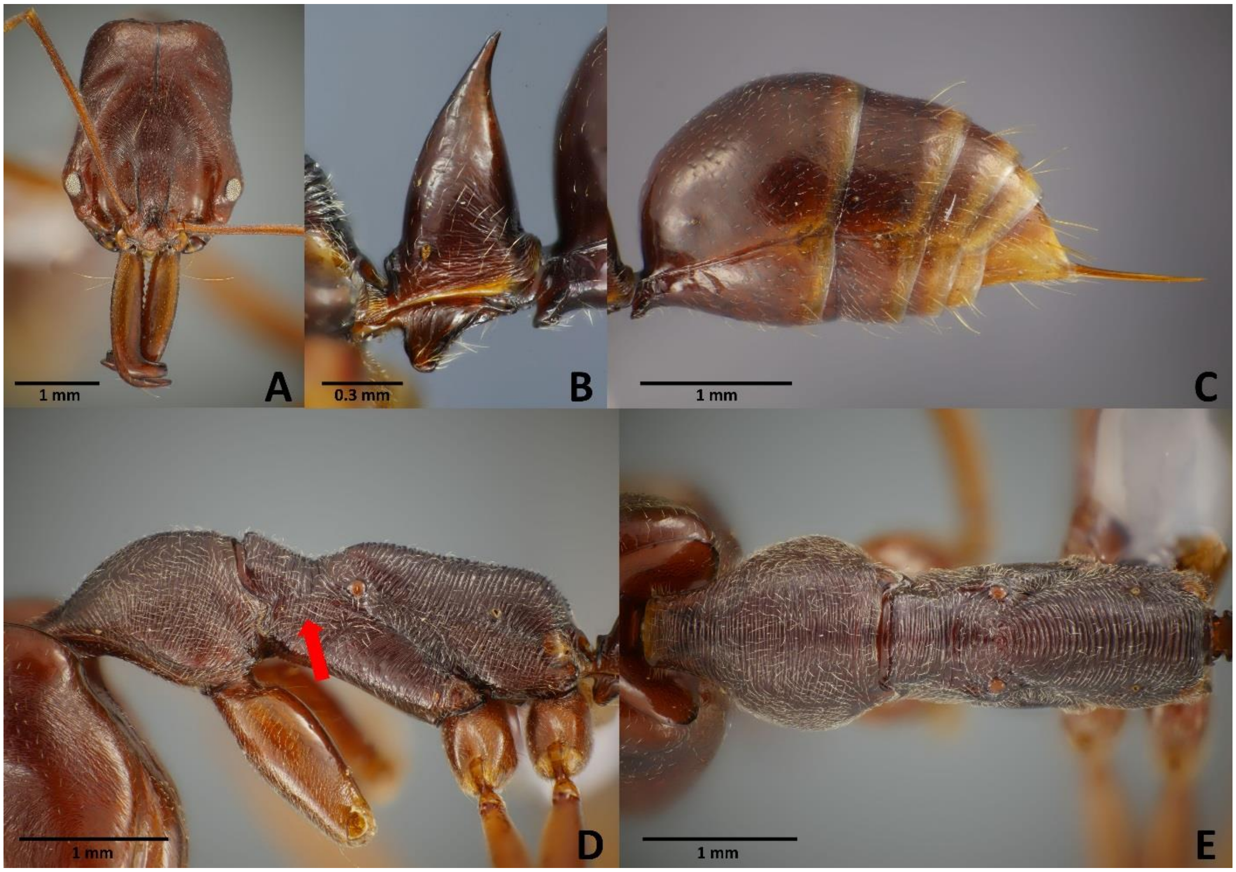

Figure 4-29. *Odontomachus* sp. 1, worker from Taiwan and Japan (individual: RJ20161117-15 (SEMUT-A)): A, head in full-face view; B, petiole in lateral view; C, gaster in lateral view; D, mesosoma in lateral view, with an arrow idndicating anterodorsal margin of mesopleuron indistinctly carinate; E, mesosoma in dorsal view.

Figure 4-30. *Odontomachus* sp. 1, queen from Taiwan (SEMUT20161222D): A, head in full-face view; B, petiole in lateral view; C, gaster in lateral view; D, mesosoma in lateral view; E, mesosoma in dorsal view.

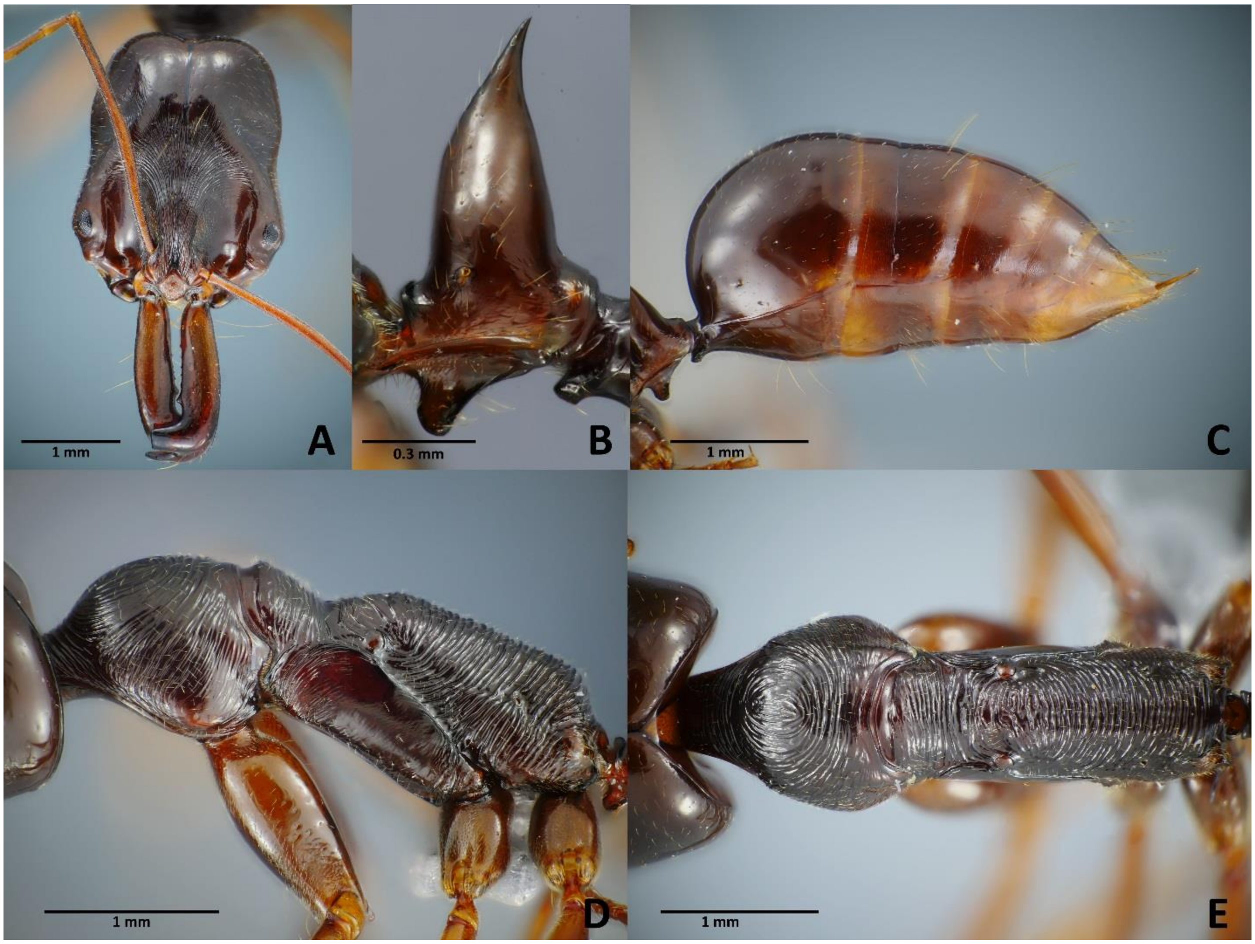

Figure 4-31. *Odontomachus* sp. 2, worker (colony: RS-74-CYS16; SEMUT20161216): A, head in full-face view; B, petiole in lateral view; C, gaster in lateral view; D, mesosoma in lateral view; E, mesosoma in dorsal view.

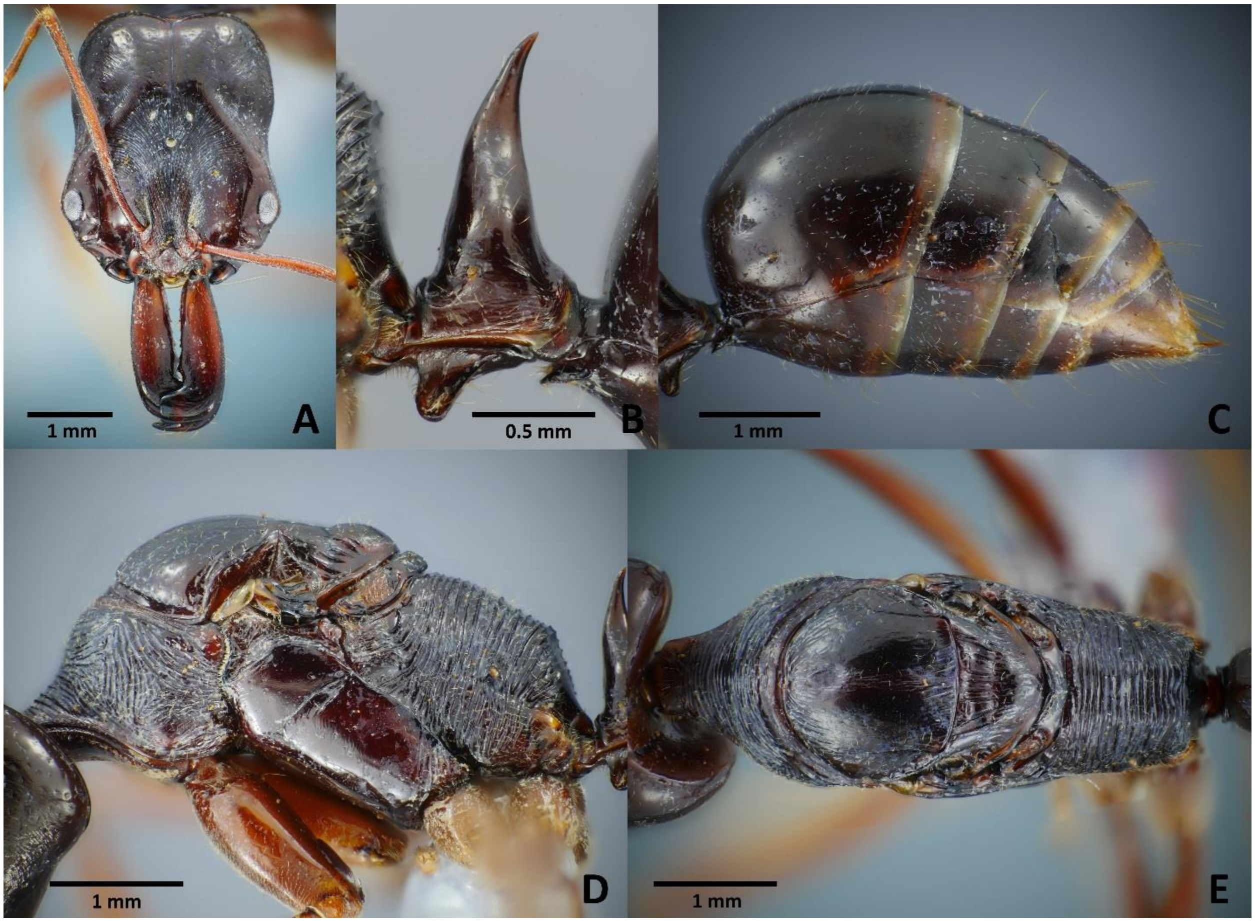

Figure 4-32. *Odontomachus* sp. 2, queen (colony: RS-142-CYS16; SEMUT20160317A): A, head in full-face view; B, petiole in lateral view; C, gaster in lateral view; D, mesosoma in lateral view; E, mesosoma in dorsal view.

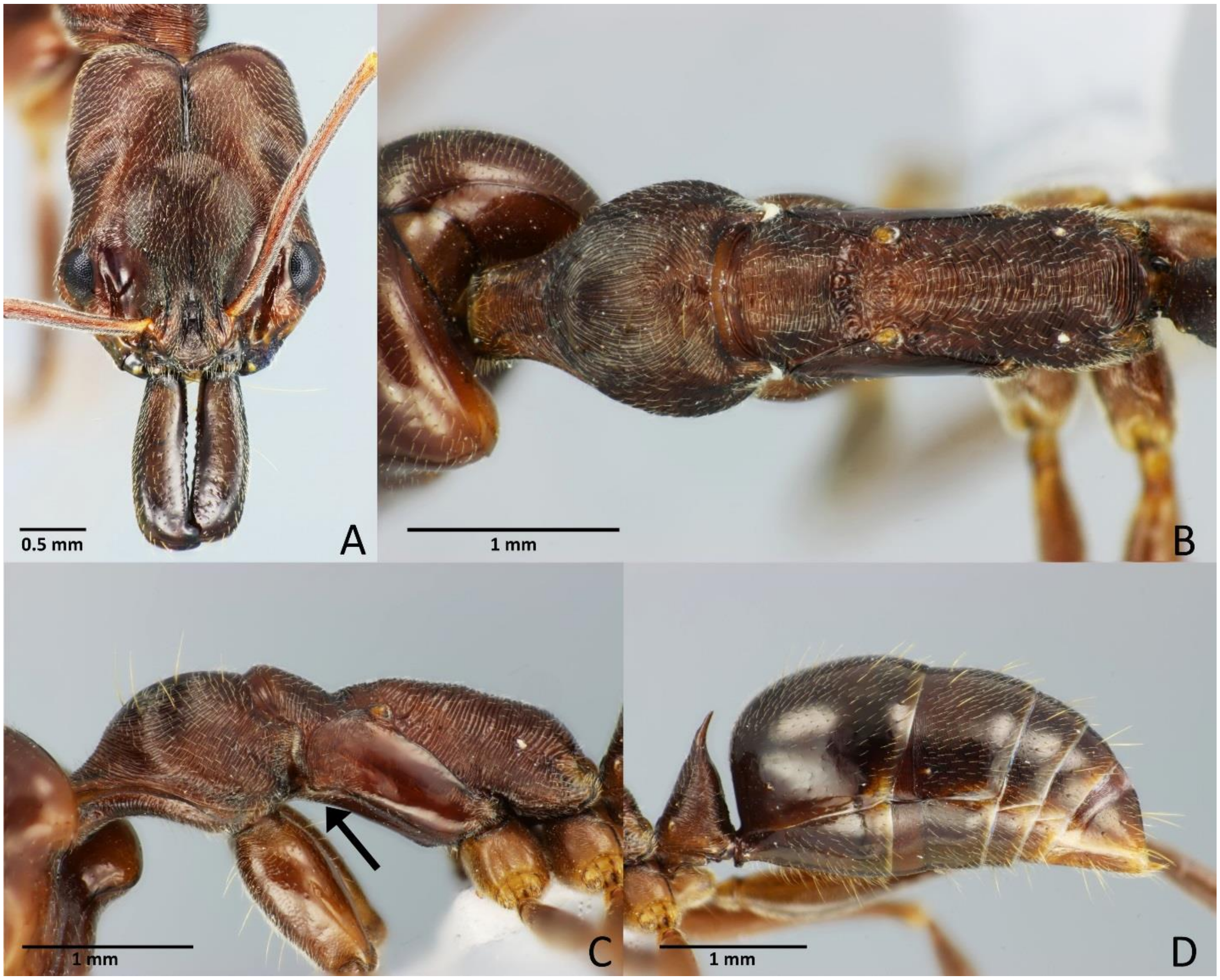

Figure 4-33. *Odontomachus simillimus* F. Smith, worker (colony: PKJ-22-12; individual: SEMUT150102D): A, head in full-face view; B, mesosoma in dorsal view; C, mesosoma in lateral view, with an arrow indicating mesosoma with its anteroventral ridge; D, petiole and gaster in lateral view.

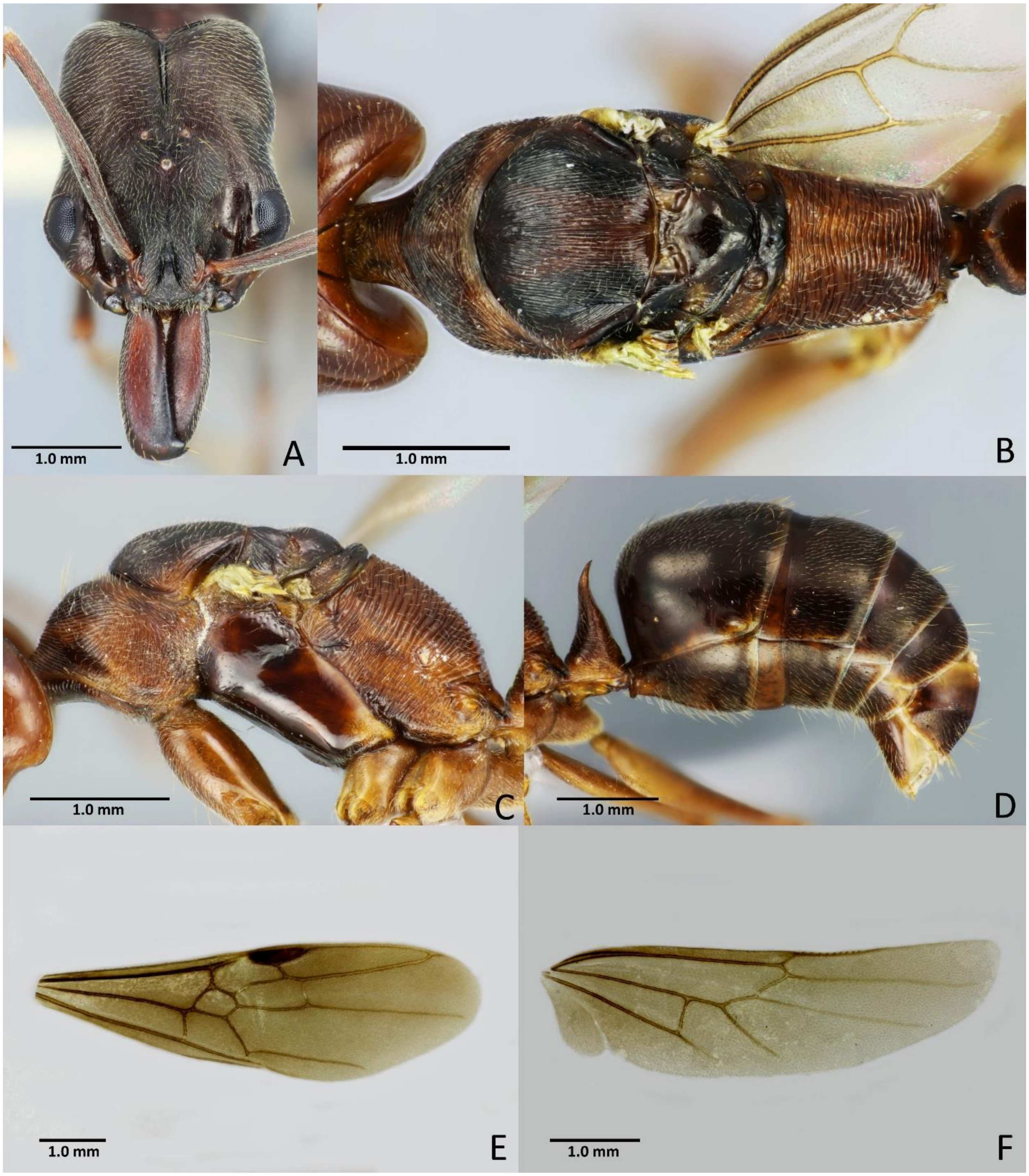

Figure 4-34. *Odontomachus simillimus* F. Smith, queen (colony: PKJ-27-12; individual: SEMUT150102C): A, head in full-face view; B, mesosoma in dorsal view; C, mesosoma in lateral view; D, petiole and gaster in lateral view; E, forewing; F, hindwing.

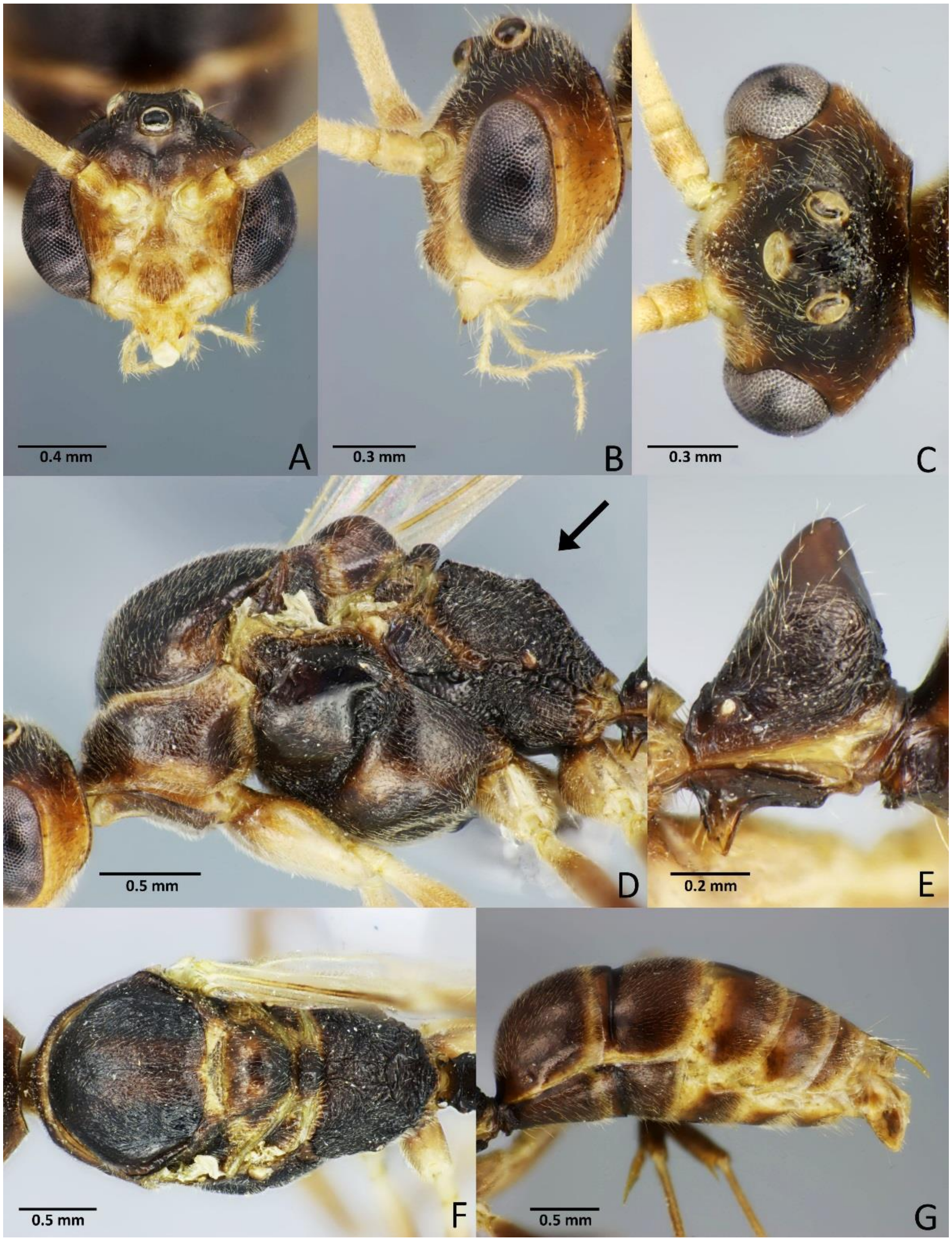

Figure 4-35. *Odontomachus simillimus* F. Smith, male (colony: PKJ-27-12; individual: SEMUT141217C): A, head in full-face view; B, head in lateral view; C, head in dorsal view; D, mesosoma in lateral view, with an arrow indicating an angulate dorsal outline; E, petiole in lateral view; F, mesosoma in dorsal view; G, gaster in lateral view.

Figure 4-36. *Odontomachus silvestrii* Wheeler, worker (individual: SEMUT20170418): A, head in full-face view; B, petiole in lateral view; C, gaster in lateral view; D, mesosoma in lateral view; E, mesosoma in dorsal view.

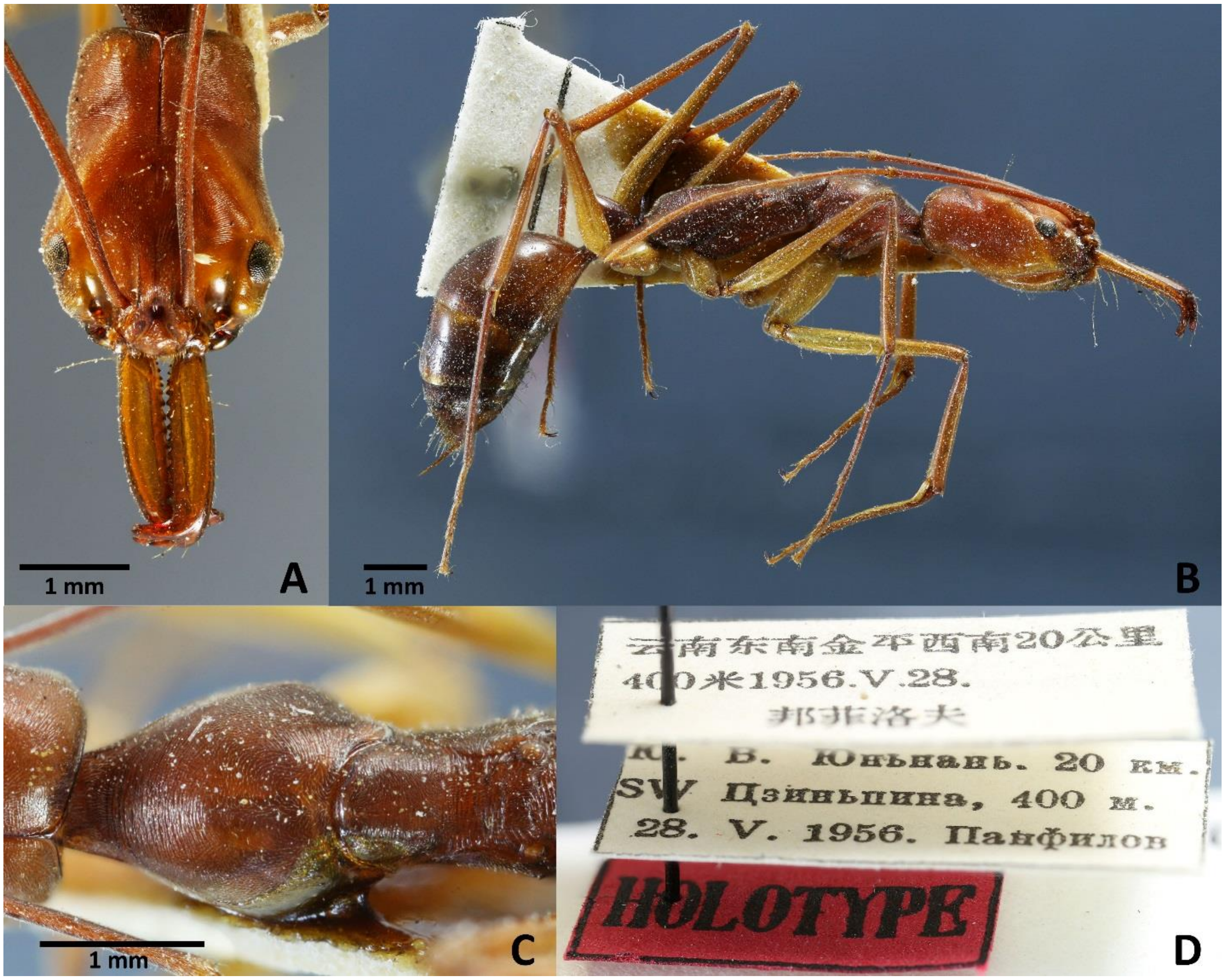

Figure 4-37. *Odontomachus granatus* Wang, worker (holotype): A, head in full-face view; B, profile in lateral view; C, pronotum in dorsal view; D, label.

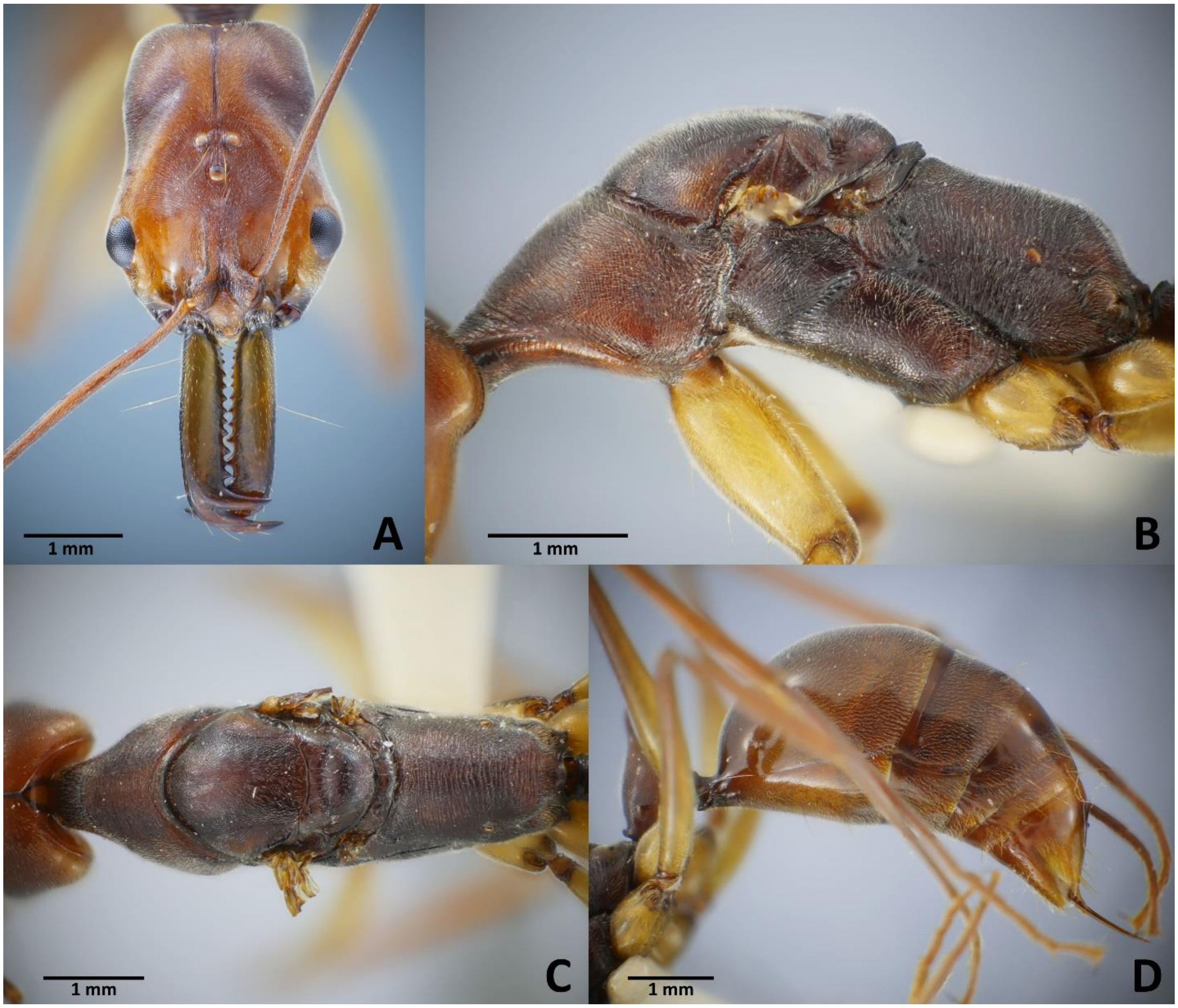

Figure 4-38. *Odontomachus silvestrii* Wheeler, queen (individual: SEMUT20170503A): A, head in full-face view; B, mesosoma in lateral view; C, mesosoma in dorsal view; E, gaster in lateral view.

Chapter V

General Discussion

V-1. Phylogeny of Indo-Chinese and Indo-Malayan Species of the Genus *Odontomachus*

The present 28S-based Maximum-likelihood analyses showed that Indo-Chinese and Indo-Malayan species of *Odontomachus* species are divided into three clades, despite the Bayesian Inference analyses not supporting the division: the clade “S1” consisting of *O. monticola*, *O. kuroiwae, Odontomachus* sp. 1 and *Odontomachus* sp. 2 which are mainly distributed in Indo-Chinese subregion extending to the north until Southern of Japan; the clade “S2” consisting of *O. latidens, O. minangkabau, O. pararixosus*, *O. procerus* and *O. rixosus* which are mainly distributed in Indo-Malayan subregion, and *O. silvestrii*, i.e., the single representative species of the *O. silvestrii* species group; and the clade “S3” consisting of *O. simillimus*, i.e, the Asian representative of the *O. haematodus* species group, and *O. floresensis*, i.e., a representative of the *O. infandus* species group. Therefore it is likely that the *O. rixosus* species group sensu to Brown (1976), the most speciose species group in Asia, is not monophyletic. Future improvement of our elucidation of the species-level diversity by integrated taxonomy may allow us revealing the intrageneric phylogenetic structure based on rather comprehensive and worldwide molecular dataset.

V-2. Distribution patterns of *Odontomachus* in Indo-Chinese and Indo-Malayan subregions

A total of 14 species of the genus *Odontomachus* belonging to five species group are recognized in Indo-Chinese and Indo-Malayan subregions. Three distribution patterns of the species, i.e., widely spread, restricted to the Indo-Malayan region, and endemic to a small geographic range, are recognized and discussed below (however, the species known only from type materials or recognized with a few specimens are ommitted from the following discussion).

V-2-1. Species with wide distribution

Odontomachus monticola is distributed widely in continental Asia: Nepal, India, Bangladesh, Myanmar (the type locality), Thailand, Laos, Vietnam, China and Taiwan (Brown, 1976; Jaitrong & Nabhitabhata, 2005; Yoshimura *et al*., 2007; Guenard & Dunn, 2012; Eguchi *et al*., 2014). The records from Borneo and Philippines shown in www.antmaps.org are unreliable as mentioned below. Pfeiffer *et al.* (2011) recorded *Odontomachus monticola* in their list of Bornean species of ants based on "picture or location data from Borneo" provided by www.antweb.org. After my re-examination of the the picture of the Bornean specimen identified as *Odontomachus monticola* (CASENT0179010), however, I recognized the species should be *O. rixosus* or closely related to *O. rixosus* based on the following characters: head in full-face view slightly longer than broad; frontal lobe with long erect seta; mesosoma in lateral view long and slender; Gastral tergite I in lateral view long. The www.antmaps.org recorded *O. monticola* from the Philippines. However, Sorger & Zettel (2011) and General & Alpert (2012) never mentioned the presence of *O. monticola* in their revision of the Philippine ants.

In *Odontomachus monticola* recognized by the present integrated taxonomy (in Chapter III), a large genetic variation (maximum intraspecific variation: 2.9 % in K2P) (Table 3-5), and a very small morphological variation are observed. Therefore, it is likely that cryptic species still remain undiscovered.

Odontomachus rixosus is widespread in Indo-Malayan subregion (Jaitrong & Nabhitabhata, 2005; Satria *et al.*, 2015) and Philippines (Sorger & Zettel, 2011), and interestingly has a geographically isolated population in Yunnan Province, China, i.e., "*O. tensus* Wang, 1993" synonymized with *O. rixosus* in Capter IV. However, the genetic profile of the Yunnan population is still unknown due to the unavailability of fresh specimens suitable for integrated taxonomy. Therefore, the possibility of the Yunnan population being another cryptic species cannot be entirely ruled out.

The *Odontomachus haematodus* species group is monophyletic based on the recent molecular phylogenetic analysis of the genus *Odontomachus* (Larabee *et al.*, 2016). The majority of the members of the *Odontomachus haematodus* species group are distributed in the New

World with two exceptions, i.e., one species in Africa, and *O. simillimus* widespread in tropical Southeast and South Asia (Satria *et al.*, 2015), Melanesia (Wilson, 1959) and Madagascar (Fisher & Smith, 2008). *Odontomachus simillimus* is a common species found in gardens and green patches in residential zones, plantations, and secondary forests. Therefore, its distribution has probably been widened at least partly by regional commerce and other human activities, because of the habitat preferences of *O. simillimus* (Economo & Sarnat, 2012). A few representative specimens of *Odontomachus simillimus* were used for the present integrated taxonomy, even though a relatively large genetic variation was recognized (maximum intraspecific variation: 4.0% in K2P) (Table 3-4), and the coloration of the body moderately varies within species (see the Chapter IV). Fisher & Smith (2008) also reported a large genetic divergences of COI among the islands of Seychelles, i.e., an introduced area (maximum intraspecific variation: 3.2% in K2P). Therefore, it is likely that *O. simillimus* is a cryptic species complex, and thus future integrated taxonomic studies are needed for this widespread species based on a comprehensive sampling from its entire native range.

V-2-2. Species with Indo-Malayan distribution

The following two species show Indo-Malayan distribution: *Odontomachus latidens* in Sumatra, Java and Peninsular Malaysia (Satria *et al.*, 2015); *Odontomachus procerus* in Sumatra, north and northwestern Borneo and Malay Peninsula (Satria *et al.*, 2015; the present study). Unfortunately sequence data for showing the degree of intraspecific divergences among these land masses is not yet available for the two species, the time scale of their expansions and isolations cannot be discussed here. These two species are closely related each other, and the interspecific K2P distance is 11.5% (in chapter III). Previous studies (Brower, 1994; Quek *et al*., 2004) estimated that nucleotide substitution rate of COI is around 1.3-2.3% per million years in several arthropod groups including Insecta. When extrapolating this value to our case, the two species have been genetically isolated for several to ten million years.

V-2-3. Endemic species

Odontomachus kuroiwae is restricted in Okinawa Island and Okinoerabu Island, Japan (Yoshimura *et al*., 2007) where a humid subtropical climate is prevalent. According to Osozawa, Shinjo *et al.* (2012) and Osozawa Su, *et al*. (2013), endemism seen in some islands or island groups of the Ryukyus reflects the complicated geological and bioclimatic history of the

Ryukyus extending between Kyushu and Taiwan mainly in the Pleistocene. Probably since 1.55 Mya, the Amami-Okinawa island group has been separated from the Yaeyama Is. by the Kerama strait; at the same priod, the Kuroshio warm current also began to flow into the Okinawa trough through the Yonaguni gateway, and effectively isolated Yaeyama Is. and Amami–Okinawa Island groups from Taiwan and the mainland China (Osozawa, Shinjo *et al*. 2012). The range of *Odontomachus kuroiwae* was surrounded by one of its phylogenetically close relatives, *Odontomachus* sp. 1 (southern Kyushu of Japan, Taiwan, and Vietnam). *Odontomachus* sp. 1 in the present study has two geographic variants: Japanese-Taiwanese forms and Vietnamese forms; and the other relatives, *O. monticola*, are distributed in northern and northern central Vietnam. (discussed in the Chapter III and IV). So, it is likely that ancestral populations of these species have been partly or completely isolated in the Ryukyus and adjacet areas during the Pleistocene, and subsequently some of them have already been raised to "species" with their own genetic profile and morphological characteristics. Similar biogeographical patterns in this area have been known in various taxa of insects, such as the genus *Papilio* (Butterflies); *Parides* (Butterflies); *Anotogaster* (Dragonfly); and *Pyrocoelia* (Firefly) (Ozawa, Su *et al*., 2013).

Odontomachus minangkabau from Sumatra and *O. pararixosus* from Malay Peninsula were described as cryptic species of *O. rixosus*, and these are closely related to each other. *O. rixosus* itself has a wide distribution in Indo-Malayan subregions, including Philippines. The interspecific K2P divergence were calculated based on CO1 dataset: 7.3% between *O. rixosus* and *O. minangkabau*, and 6.2% between *O. rixosus* and *O. pararixosus* (Chapter III). When extrapolating the known substitution rate of COI (1.5−2.3% sequence divergence per million years; Brower, 1994; Quek *et al*., 2004) to our case, *O. minangkabau* and *O. pararixosus* have been genetically isolated from *O. rixosus* for approximately 3 to 5 million years. This means the genetic diversification and subsequent speciation have been affected by the geological and/or bioclimatic events in the Pliocene and Pleistocene.

Odontomachus sp. 2 has so far been found only from Chu Yang Shin N. P., Dak Lak Province, Central Highland of Vietnam, and closely related to *O. monticola* which is known from northern and northern central Vietnam (K2P divergence: 6.5 %). The two species seem to be geographically separated by the Truong Son Ranges (above 2000 m alt.). According to Averyanov *et al*. (2003), the western border of Truong Song Ranges act as a major biogeographic barrier between moist upland zone in the eastern side (Vietnamese side) and the drier monsoon zone in the westernside (Laos side). The distribution patterns of the two species agree well with their hypothesis.

Odontomachus silvestrii is restricted to northern Vietnam and southern China (Brown, 1976; as *Odontomachus granatus* in Wang, 1993; Guenard & Dunn, 2012). For the moment, molecular data is not enough for discussing the origin and biogeographical history of this phylogenetically and morphologically very distinct species.

V-3. The Future Prospect of This Study

The present study as well as Sorger & Zettel (2011) highlight that large-sized and dominant ground-dwelling ant genera such as *Odontomachus* still have hidden cryptic species. Therefore, the species-level classification of ants in tropical and subtropical Asia should be evaluated again by integrated taxonomy. The identities of species with widespread distribution in a zoogeographic subregion or more, and/or the species with many different names (synonyms) should be carefully examined also using integrated taxonomy.

Alate ants (males and newly emerged queens) collected by malaise traps, light traps, etc. have been usually ignored in biodiversity assessments and inventries, and have not been used in taxonomic studies of ants because alate ants, especially males, can not be sorted and identified precisely into species based on the morphology if the conspecific male-worker-queen complementarity is unknown. However, DNA barcode library based on the precise species-level classification provided by the integrated taxonomy may promote us identifying alate ants collected by such traps into species, and obtaining valuable biological information such as seasonal and daily timing of mating flight which should be strongly associated with reproductive isolation and consequently speciation (Torres *et al.*, 2001; Kaspari, Pickering & Windsor, 2001; Kaspari, Pickering, Longino & Windsor, 2001; Feitosa *et al.*, 2016).

Several theometical and methodological problems still remain in the present integrated taxonomy. The phylogenetic criterion was based on the "Phylogenetic Species Concept" (de Queiroz & Donogue, 1988; Wheeler, 1999; Mishler & Theriot, 2000) which requires members of a species to form a monophyletic unit. However, species are not always monophyletic because new species might be often formed from peripherally isolated populations of the mother species, i.e., through peripheral speciation (Hoskin *et al.*, 2011; Rettelbach *et al.*, 2016; see also the chapter V). Therefore, the design of the integrated taxonomy approach used in the present study needs to be reconsidered.

In recent years cryptic species diversity of European ant taxa were intensively revealed by integrated taxonomy, and numerical morphometry was applied as an indispensable part to their methodology (Seifert, 2009; Steiner *et al.*, 2010). As mentioned above, there is a large difference between the number of MOTUs evaluated by molecular-based analyses and the number of forms proposed by morphological examination (32 or 35 MOTUs vs 13 forms). Numerical morphometry will be able to detect rather minor but constant morphological differences among the MOTUs, and consequently to find further cryptic species among the arrays of MOTUs. Furthermore, numerical morphometry is indispensable to correspond the representative specimens of cryptic species proposed by integrated taxonomy to the type materials of relevant species because no damage is allowed for the type materials. That is to say that numerical taxonomy is the only practical method to link cryptic species to the present Zoological Nomenclature based on the Type Concept (Seifert, 2009).

The usefulness of male genitalia and associated sclerites for delimitating multiple cryptic species of *Odontomachus* was also confirmed by the chapter II as well as a few previous studies. However, unfortunately, colonies containing males have so far been obtained for only a part of MOTUs. Future trials of the integrated taxonomy including the morphological examination of male genitalia will also found further cryptic species among the arrays of MOTUs.

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Appendices

Publications

Main papers:

Satria, R., Kurushima, H., Herwina, H., Yamane, S., and Eguchi, K. (2015) The trap-jaw ant genus *Odontomachus* Latreille from Sumatra, with a new species description. *Zootaxa*, 4048: 1−36.

Satria, R., Viet, B.T. and Eguchi, K. (2017) New synonymy and redescription of *Anochetus mixtus* Radchenko, 1993, and distinction from the other members of the *Anochetus rugosus* group (Hymenoptera: Formicidae: Ponerinae). *Asian Myrmecology*, 9, e009001: 1−16.

Other papers:

Satria, R., Sasaki, O., Bui, T.V., Oguri, E., Syoji, K., Fisher, B.L., Yamane, S., and Eguchi, K. (2016) Description of the first oriental species of the ant genus *Xymmer* (Hymenoptera: Formicidae: Amblyoponinae). *Zootaxa*, 4168 (1): 141−150.

Eguchi, K., Mizuno, R., Ito, F., **Satria, R.**, Dang, V.A., Bui, T.V., and Phung, T.H.L. (2016) First discovery of subdichthadiigyne in *Yunodorylus* Xu, 2000 (Formicidae: Dorylinae). *Revue suisse de Zoologie*, 123 (2): 307−314.

Japanese summary

インドシナ亜区及びインドマレー亜区におけるアギトアリ属 *Odontomachus*
（膜翅目：アリ科：ハリアリ亜科）の分類学的研究（英文）

リジャル サトリア

首都大学東京・理工学研究科・生命科学専攻

アリ類（昆虫綱：膜翅目：アリ科）は、世界の主要な陸上生態系においてバイオマスの約10%を占める優占的な陸上無脊椎動物群であり、小型無脊椎動物の捕食者、機械的分解者、種子分散者、土壌攪拌者などとして、生態系の中で様々な機能を持っている。一方で、在来生態系、農業や公衆衛生、社会インフラに多大な悪影響を及ぼす侵略的外来種となっている種もいる。したがって、生物多様性研究や保全プログラムにおいて、アリ類は主要なターゲットとなっており、アリ類の分類に対するニーズは高い。

アリ類の分類は働きアリの形態形質に基づき行われてきた。しかし、近年、従来の比較形態学的手法に DNA barcoding などの新しい解析手法を組み合わせた「Integrated Taxonomy（統合的分類学）」というアプローチが提案されて以降、アリ類においても隠蔽種群（形態学的には区別できない複数の生物学的種の集まり）の発見と、新種記載が相次いでいる。一方で、熱帯・亜熱帯地域に生息するアリ類の種多様性の解明に Integrated Taxonomy を用いた事例は未だ少ない。

そこで、インドシナ亜区及びインドマレー亜区に産するアギトアリ属（ハリアリ亜科）を対象として、Integrated Taxonomy により種分類体系の再検討を行うことを、本研究の目的とした。この属は、形態学的情報に基づき、Brown (1976) によって包括的に再検討され、その過程で、多くの種名、種内分類群名が新参シノニムとされた。しかし、彼の種認識に対しては否定的な見解も発表されていることから（Yoshimura *et al.*, 2007; Satria *et al.*, 2015）、Integrated Taxonomy の有用性を検討する上でも最適な対象分類群である。

本論文の第２章では、スマトラに産する５種のアギトアリ属、およびアギトアリ属の姉妹群であるヒメアギトアリ属の *Anochetus rugosus* 種群を対象として、光学顕微鏡を用いて雄の交尾器の形態を詳しく観察した。アリ類における種認識は、多くの場合、働きアリの形態に基づく。一方で、雄交尾器の形態は生殖的隔離に関連する可能性があるのにも関わらず、アリ類の大半の分類群において、十分な比較検討が行われてこなかった。本研究により、働きアリの形態が非常に類似する種間でも雄交尾器の形態には顕著な差異が生じることが明らかとなり、アギトアリ属やヒメアギトアリ属において、雄交尾器の形態が種識別形質として有用であることが示された。

第３章では、インドシナ亜区、インドマレー亜区、および周辺地域から集められたアギトアリ属 97 サンプルを対象として、DNA barcoding、分子系統解析、形態比較、分布様式の検討を組み合わせた Integrated Taxonomy を用いて種の識別を行った。まず、ミトコンドリア CO1 遺伝子の塩基配列を PCR とダイレクトシーケンス法で決定し、得られたデータをもとに ABGD 解析および PTP 解析を行うことで（DNA barcoding）、40 の MOTU が識別できた。ついで、最尤法及びベイズ法による分子系統解析を行い、得られた系統樹に基づき、各 MOTU の単系統性を評価した。単系統性が支持された場合は、独立した MOTU として扱い、単系統性が支持されなかった場合は、単系統群となるまで近隣の MOTU と統合した。その結果、35 の MOTU に統合できた。最後に、これらの MOTU について詳細な形態比較を行った結果、形態学的識別形質を有する 12 の種に統合できた。そのうち、インドシナ亜区、インドマレー亜区からは 11 種が確認された。Brown (1976) は *O. kuroiwae* を *O. monticola* のシノニムとしたが、Yoshimura *et al.* (2007) は前者を独立した種として扱った。本研究は Yoshimura *et al.* (2007) の見解を支持した。また、Brown (1976) は *O. procerus* を *O. latidens* のシノニムとしたが、Satria *et al.* (2015) は両者を別種とした。本研究の最終的な解析結果も Satria *et al.* (2015) を支持した。*O. pararixosus* と *O. minangkabau* は、*O. rixosus* の隠蔽種として、Terayama & Ito (2014) と Satria *et al.* (2015) によって、それぞれ記載されたが、それらの見解も本研究の最終的な解析結果によって支持された。さらに、*O.* sp. 1 は *O. monticola* のシノニムのうちの１つに対応し、独立種であり、*O.* sp. 2 は新種であることが明らかとなった。

第４章では、DNA barcoding に適した標本が得られなかった“種”の標本の形態を詳細に検討することにより、インドシナ亜区、インドマレー亜区から合計 14 種が識別できた。その結果に基づき、働きアリの形態形質に基づく検索表の作成、１新種の記載（*Odontomachus* sp. 1）、13 種の再記載、シノニムの解決（３つの種名を新参シノニムと認定し、無効名とした）を行った。

第５章では、各種の採集地点の位置情報を元に、分布様式の類型化を行った。その結果、４種が「広域分布（インドシナ亜区＋インドマレー亜区、インドマレー亜区＋オーストロマレー亜区、あるいはそれ以上広域）」、２種が「インドマレー亜区内広域分布」、6 種が「局所分布」を示した。残りの２種に関しては、模式産地以外に信頼できる分布記録がない。

将来的に全ての種について雄を含むコロニー・サンプルを入手し、雄（特に交尾器）の形態比較、また形態測定学的解析を取り入れた Integrated Taxonomy を行うことにより、さらなる隠蔽種の発見が可能となると思われる。さらに、再検討された種分類体系に基づき DNA barcode ライブラリーが整備されれば、ライトトラップやマレーゼトラップにより得られる多数の有翅生殖虫（雄アリ、有翅女王）の種同定が可能となり、結果として、繁殖フェノロジーなど生殖的隔離や種分化に関連する情報を得ることも可能となる。

本研究は、熱帯・亜熱帯地域において種の多様性が著しく高いアリ類を対象とした系統分類学的研究のモデルケースとなるものである。