

RESEARCH PAPER

Taxonomic study on the queens of the Japanese ponerine genera, with a redescription of *Ectomomyrmex horni* restituted as a valid species (Hymenoptera: Formicidae)

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Abstract. Queen ants of the Japanese ponerine genera are described, with the first key to the Japanese genera based on the queen caste. Important queen characters are enumerated and caste differences are discussed for each genus. Physical and behavioral aspects of functional queens (alate/dealate queen, ergatoid, and gamergate) in the Japanese ponerines are briefly discussed. *Ectomomyrmex horni* (Forel, 1913), stat. restit., is resurrected from synonymy with *Ectomomyrmex javanus* Mayr, 1867. A redescription of *E. horni* is presented based on Japanese and Taiwanese specimens.

Key words. Hymenoptera, Formicidae, Ponerinae, ant, caste, genus character, male, queen, redescription, worker, Japan, Taiwan.

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Introduction

Classification systems of the ponerine ants (Formicidae) have recently undergone a drastic change. Relationships of taxa at genus, tribe and subfamily levels have been reestablished and reorganized with molecular and newly found morphological characters by SCHMIDT & SHATTUCK (2014), BOUDINOT (2015) and others. Much prior to these epoch-making contributions, OGATA (1987) reviewed the Japanese genera of Ponerinae based on the morphology of the worker, queen and male with many line drawings. At that time queen material was unavailable for some genera. Since this pioneer work, we have attempted to accumulate more material of and information about Japanese ponerines. Although there are still species for which the material remains incomplete, i.e., lacking the queen or male, or both, in this study we have tried to prepare keys to genera based on the queen caste, and synoptic descriptions of the queens of all the Japanese genera. In addition to these, we redescribe *Ectomomyrmex horni* (Forel, 1913), stat. restit., which is resurrected from synonymy with *E. javanus* Mayr, 1867.

Materials and methods

Materials examined and biological information used were mostly collected by the authors, and deposited at the Institute of Tropical Agriculture, Kyushu University (KUEC), Sk. Yamane Collection at the Kitakyushu Museum of Natural History and Human History (SKYC), and F. Ito Collection at Kagawa University. The classification system follows that of SCHMIDT & SHATTUCK (2014).

Measurements (in mm) and indices are as follows:

CI	Cephalic index = head width divided by head length × 100.
EL	Length of major diameter of eye (compound eye).
HW	Head width in full-face view, excluding eyes.
HWe	Head width in full-face view, including eyes in male.
HL	Head length in full-face view from anterior margin of clypeus to posterior margin of head, or to a line drawn across posterolateral corners of head.
PrW	Width of pronotum at broadest part (including posterolateral lobe in the queen and male) in dorsal view.
PtI	Petiole index = petiolar width divided by head width × 100.
PtW	Width of petiole in dorsal view.
SI	Scape index = scape length divided by head width × 100.
SL	Length of antennal scape excluding basal condyle.
TL	Roughly measured total length of body from tip of head to tip of gaster.



The number of ommatidia composing the eye (compound eye) is shown in some cases as the number of ommatidia along the longest axis of the eye. However, as the ommatidia are not always arranged along it, the counts often have errors of plus or minus two. ‘Narrow’ and ‘broad’ (with quotation marks) are used for convenience to describe the ‘width’ or ‘thickness’ of a strip or belt-like structure like the metanotal groove; this refers to the length of such structures from front to rear so that in strict sense short and long should be used. Malar space denotes the space between the anterior margin of the eye and the anterior margin of the cranium.

Abbreviations and symbols:

aq	alate (winged) queen;
dq	dealated queen;
m	male;
w	worker;
*	new locality record.

Taxonomy

Recognition of ponerine queens and useful morphological characters

Queens of ponerine ants are generally similar to workers of the same species in habitus and structure except for the caste-specific differences such as the possession of wings and associated complicated structures of the thorax, possession of large eyes and ocelli etc. The similarity between the female castes makes the recognition of ponerines among queen samples relatively easy, especially when the geographical areas treated are limited. The Japanese ponerine queens have the following combinations of characters: 1) large compound eye (simply ‘eye’ hereafter) with more than 9 ommatidia (often >15) on longest axis of eye; 2) complete set of ocelli present except for ergatoid queens and gamergates; 3) horizontal frontal lobes present; 4) waist composed of a single segment (petiole or second abdominal segment), which is never flattened transversely, and connected to propodeum and gastral segment I at lower extremities, with distinct free space in front of and behind petiole; 5) gaster of normal shape with gastral tergite II not strongly arched and vaulted; 6) helcium infraaxial; 7) generally distinct constriction present between gastral segments I and II (not seen in samples with shrunk gasters); 8) strong sting present at tip of gaster; 9) wings fully developed, or scars present at wing base in dealated queens, except for ergatoid queens and gamergate workers (functional queens in *Diacamma* Mayr, 1862) that lack wings.

Although the queen is generally similar to the worker in each species, the key to genera for the worker caste does not necessarily work well for queens without some modification. For example, in general, the eyes are very small or missing in the worker caste and their size and relative location are frequently used in keys. In worker keys to the Japanese ponerine genera the presence/absence of the division of the mesopleuron (conventional term indicating the lateral area of the mesopectus; see AIBEKOVA et al. 2022) into upper and lower sections is often used (e.g., TERAYAMA

2014); in the worker this division is only seen in *Ectomyrmex* Mayr, 1867 and more indistinctly in *Anochetus* Mayr, 1861 and *Odontomachus* Latreille, 1804, while the queens of all Japanese genera have this division except for *Leptogenys* Roger, 1861. In *Brachyponera* Emery, 1900 workers the propodeum is at a distinctly lower height than the thorax and generally strongly narrowed dorsally; this peculiar condition in the worker is much less pronounced in the queen. The above-mentioned characters are often useful in recognizing species and genera also in the queen, but they should be used in different ways.

Presence/absence of a basal pit on the mandible and an anterior fenestra on the subpetiolar process gives useful cues in separating genera in both workers and queens. The metapleuron is completely fused with or separated from the propodeal side. In most Japanese ponerine genera the metasternum of the thorax bears a small process located between the coxal bases and called metasternal process; although this process may be of taxonomic importance, it was only examined in *Brachyponera* species in this study (Figs 1D–F). Separation of the tergite from the sternite on the lateral face of the petiole is generally distinct but differentiation of the subpetiolar process from the sternite proper is often unclear (Figs 1A–C). Generally, the anteroventral portion of the gastral segment I has a small prominence called the prora, which is, however, vestigial in *Brachyponera* species (see SCHMIDT & SHATTUCK 2014). Constriction between the gastral segments I and II (abdominal segments III and IV) is variable in degree; the pretergite of the gastral tergite II is frequently concealed under the preceding tergite in mounted specimens, but the presternite is more often exposed; cinctus (girdling constriction sensu BOLTON (1994); a ‘narrow’ zone between presclerite and postsclerite) on pretergite II is conspicuous only in a few genera (see BOLTON 1994: 191, 195, 198, fig. 531); the pretergite and presternite of segment II are generally with similar sculpture, but in *Parvaponera* Schmidt & Shattuck, 2014 they have different types of sculpturation. Apicoventral portions of mid- and hindtibiae usually have a long pectinate spur, but in some genera an additional shorter simple spur is present. The jugal lobe (anal lobe) of the hindwing is lacking in five genera, i.e., *Hypoconera* Santschi, 1938, *Euponera* Forel, 1891, *Cryptopone* Emery, 1893, *Parvaponera* and *Ponera* Latreille, 1804; in the other genera the jugal lobe is more or less distinct. This character is not used in the key because material under examination often contains only dealate queens.

In most Japanese genera, the eye has minute standing hairs. In the descriptions presented below, ‘short’ and ‘long’ mean just relative lengths of the hairs because all the hairs on the eye are minute. Most hairs are erect, but only in *Brachyponera* the hairs are decumbent or apically down-curved. The standing hairs here defined are those that are clearly recognizable at 100× or less in magnification. With much higher magnifications, other types of hairs can be observed.

In the following key, we use practical characters in addition to phylogenetically important ones to make identification easier.

Key to the Japanese genera of Ponerinae based on the queen caste

- 1 Mandibles very long and linear, without differentiation of masticatory and basal margins; their bases located close to each other (Figs 6B, F). Outer margin of head with indentations in front of and behind eye (with distinct ocular prominences) (Figs 2B, F, 6B, F). 2
 - Mandibles short, generally triangular with masticatory and basal margins well defined; their bases generally widely separated. Head in full-face view with nearly parallel to shallowly convex outer margins, without lateral indentations (without ocular prominence) (Figs 6A, C–E, 7A–E). 3
- 2 Body smaller than 5 mm. Petiole subsquamiform (Fig. 2B). Midtibia apicoventrally without spur; hindtibia with pectinate spur only. *Anochetus* Mayr, 1861
 - Body larger than 8 mm. Petiolar node apex pointed (Fig. 2F). Both mid- and hindtibiae with long pectinate spur and shorter simple spur apicoventrally. *Odontomachus* Latreille, 1804
- 3 Petiole posterodorsally with pair of posteriorly directed spines (Fig. 3B). Head and mesosoma extensively covered with deep rugae. *Diacamma* Mayr, 1862
 - Petiole without such spines. Head and mesosoma smooth to variously sculptured, never extensively covered with deep rugae. 4
- 4 Mid- and hindtibiae apicoventrally with simple spur and longer pectinate spur. 5
 - Mid- and hindtibiae apicoventrally with pectinate spur only. 9
- 5 Clypeus triangularly produced anteriad (Fig. 6E). Pretarsal claws pectinate. Wings absent. *Leptogenys* Roger, 1861
 - Clypeus not distinctly produced anteriad; anterior margin straight or shallowly concave to convex. Pretarsal claws simple. Wings or wing bases present. 6
- 6 Eye very close to or almost touching posterior margin of clypeus and anterior rim of cranium (Figs 3D, 7D). Subpetiolar process with anterior fenestra. *Parvaponera* Schmidt & Shattuck, 2014
 - Distance between anterior cranial rim and eye longer, at least as long as width of antennal pedicel (Fig. 2C), generally as long as or longer than half eye width (Figs 2D, 3C). Subpetiolar process lacking both anterior fenestra and paired posterior teeth. 7
- 7 Mandible without basal pit. Both anterior and posterior faces of petiole coarsely and transversely rugose. ... *Ectomomyrmex* Mayr, 1867
 - Mandible with basal pit. Anterior and posterior faces of petiole smooth, or shallowly or finely punctate. 8

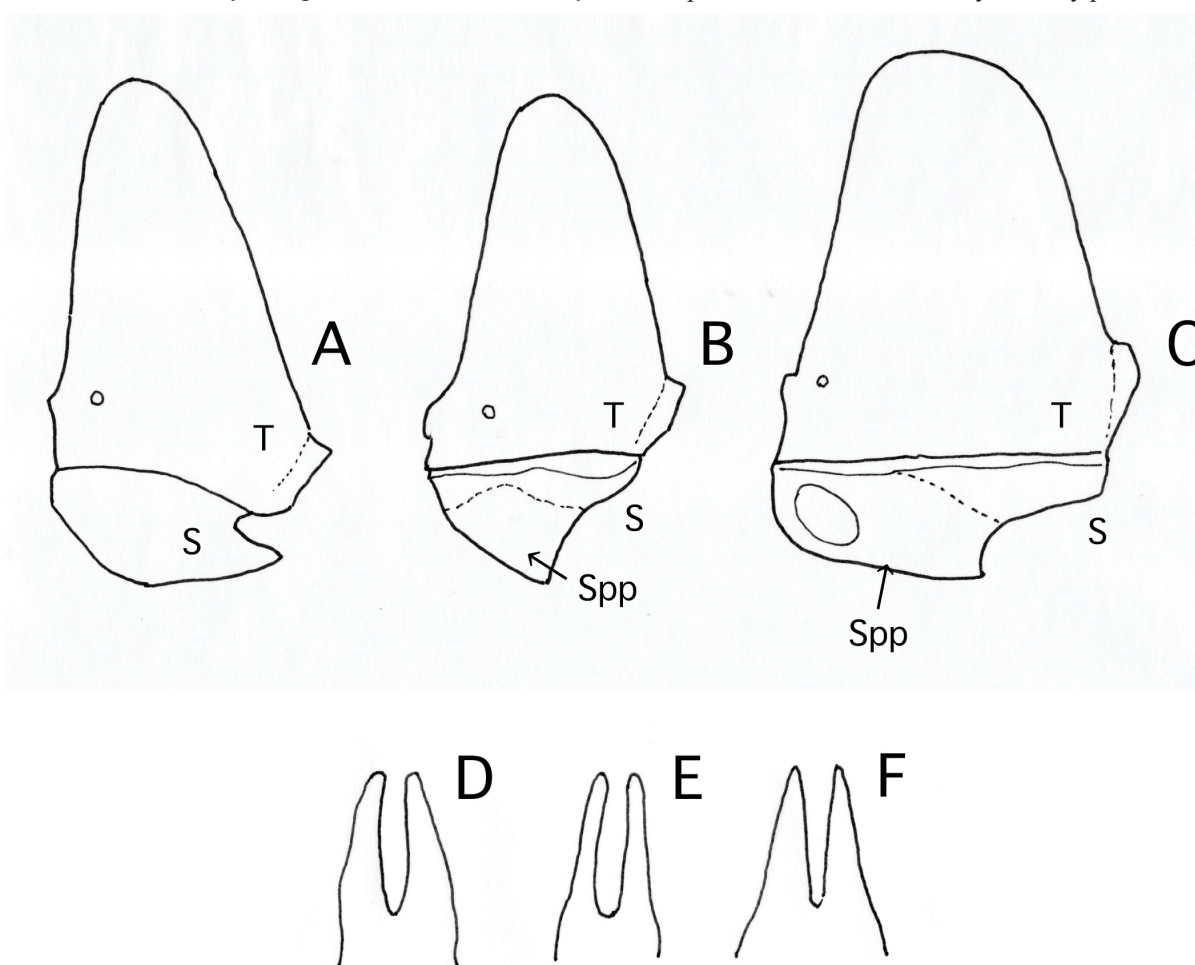


Fig. 1. A–C. Petiole (queen) in profile view. A – *Brachyponera chinensis* (Emery, 1895); B – *Cryptopone sauteri* (Wheeler, 1906); C – *Ponera kohmoku* Terayama, 1996 (S – sternite, T – tergite, Spp – subpetiolar process). D–F – metasternal process (queen) in posterior view: D – *Brachyponera chinensis*; E – *B. luteipes* (Mayr, 1862); F – *B. nakasujii* (Yashiro, Matuura, Guénard, Terayama & Dunn, 2010).

- 8 Mesopleuron extensively smooth. Sternite of petiole posteroventrally forming thin projection, with space between it and petiolar tergite. Suture between metapleuron and lateral face of propodeum more or less distinct. *Brachyponera* Emery, 1900
- Mesopleuron entirely sculptured. Venter of petiolar sternite without such posterior extension. Metapleuron and lateral face of propodeum completely fused. *Euponera* Forel, 1891
- 9 Midtibia with strong bristles on outer surface. Mandible with basal pit. *Cryptopone* Emery, 1893
- Midtibia without such strong bristles. Mandible without basal pit. 10
- 10 Subpetiolar process with anterior fenestra, generally also with paired posterior teeth. *Ponera* Latreille, 1804
- Subpetiolar process without anterior fenestra and paired posterior teeth. *Hypoponera* Santschi, 1938

Synoptic descriptions of the queen of the genera from Japan

Hypoponera genus group *Hypoponera* Santschi, 1938 (Figs 2A, 4A, 6A)

Recognition. Small ants, measuring 2.2–3.2 mm in total body length; mandible without basal pit; mid- and hindtibiae apicoventrally with pectinate spur only; subpetiolar process without anterior fenestra.

Description. Small ants, measuring 2.2–3.2 mm in total body length and 0.40–0.66 mm in head width. Head longer than broad, with posterior margin straight to very shallowly emarginate. Clypeus with anterior margin straight to shallowly concave, and with median longitudinal blunt swelling. Malar space generally shorter than half major diameter of eye, with exception of *H. beppin*, in which it is slightly longer. Eye generally large, comprising 12–16 ommatidia on its longest axis, with moderately-set to dense short hairs. Mandible with distinct teeth along masticatory margin (in at least apical 3/4) except for *H. beppin* Terayama, 1999 and probably *H. zwaluwenbergi* (Wheeler, 1933), in which basal half or more of masticatory margin serrate without distinct teeth; basal pit or groove absent. Antennal scape either fails to reach posterior margin of head or slightly extends beyond it. With mesosoma in dorsal view promesonotum slightly to distinctly narrower than head; parapsidal line generally faint and parascutal carina distinct on mesoscutum; scutoscutellar sulcus very ‘narrow’; metanotum ‘narrow’ strip defined anteriorly and posteriorly by shallow sutures. Propodeal spiracle with elongate or slit-like opening. Petiole scale-like or node-like; subpetiolar process without anterior fenestra. Prora small scale often margined with pigmented rim. Constriction between gastral segments I and II weak; most of pretergite of gastral segment II generally unexposed, while presternite often extensively exposed; cinctus cross-ribbed (forming a chain of punctures). Sting relatively short, extending from tip of gaster by length of last tergite (often

invisible from outside). Midtibia without strong bristles; ventral apices of mid- and hindtibiae with pectinate spur only. Wings fully developed except for ergatoid queens in some species; hindwing lacking jugal lobe.

Caste differences. The queen is similar to the worker in habitus and sculpture except for the mesosoma of the former having wings and associated structures on the meso- and metathorax, much larger eyes and complete set of ocelli (but see Remarks).

Remarks. The queens of the Japanese *Hypoponera* species are recognized among the Japanese genera by the character combination mentioned in Recognition above. Four Japanese species have been reported to have ergatoid queens (TERAYAMA et al. 2014): *H. nubatama* Terayama & Hashimoto, 1996, *H. opacipes* (Mayr, 1887), *H. punctatissima* (Roger, 1859) and *H. ragusari* (Emery, 1894). Caste system and behavior of one of them, *H. nubatama*, was studied by HASHIMOTO (1995), HASHIMOTO et al. (1995), TERAYAMA & HASHIMOTO (1996) and YAMAUCHI et al. (2001). This species has both winged and apterous queens (ergatoids) and also winged and apterous males; ergatoid queens are similar to workers but distinguished from the latter by much larger eyes, frequent possession of anterior ocellus and a thicker petiole (see also Discussion).

Species examined (5/8). *Hypoponera beppin* Terayama, 1999, *H. nippona* Santschi, 1937, *H. nubatama* Terayama & Hashimoto, 1996, *H. punctatissima* (Roger, 1859) (= *H. ergatandris* sensu SEIFERT 2013), *H. sauteri* Onoyama, 1989.

Odontomachus genus group *Anochetus* Mayr, 1861 (Figs 2B, 4B, 6B)

Recognition. Relatively small ants with total length measuring 3.6–3.8 mm; posterior margin of head in full-face view deeply and broadly emarginate; mandible linear and very long, apically strongly curved inwardly; petiole scale-like.

Description. Relatively small ants with total length measuring ca. 3.6–3.8 mm and head width 0.94–1.00 mm in the single Japanese species *A. shohki* Terayama, 1996. Head as long as broad, broadest at level of eye, with posterior margin deeply and broadly emarginate; lateral margin behind eye shallowly concave; nuchal carina (occipital carina) running behind ‘vertex’ continuously curved, without anterior V-shaped infolding; median furrow (line) absent on vertex. Eye with rather long sparse hairs. Ocelli situated near posterior margin of head; distance between posterior ocellus and posterior margin of head about as long as distance between posterior ocelli. Mandible linear and long, inserted medially on front of cranium, apically strongly curved inwardly; in the single Japanese species apical portion with two major teeth that are arranged vertically; the lower tooth with additional smaller tooth near base. Metanotum flanked by deep anterior and posterior furrows. Opening of propodeal spiracle oval. Petiole subsquamiform, in profile view tapering apicad. Constriction between gastral segments I and II moderate; pretergite and presternite of segment II transversely striate; cinctus distinctly defined, cross-ribbed (forming series of elongate

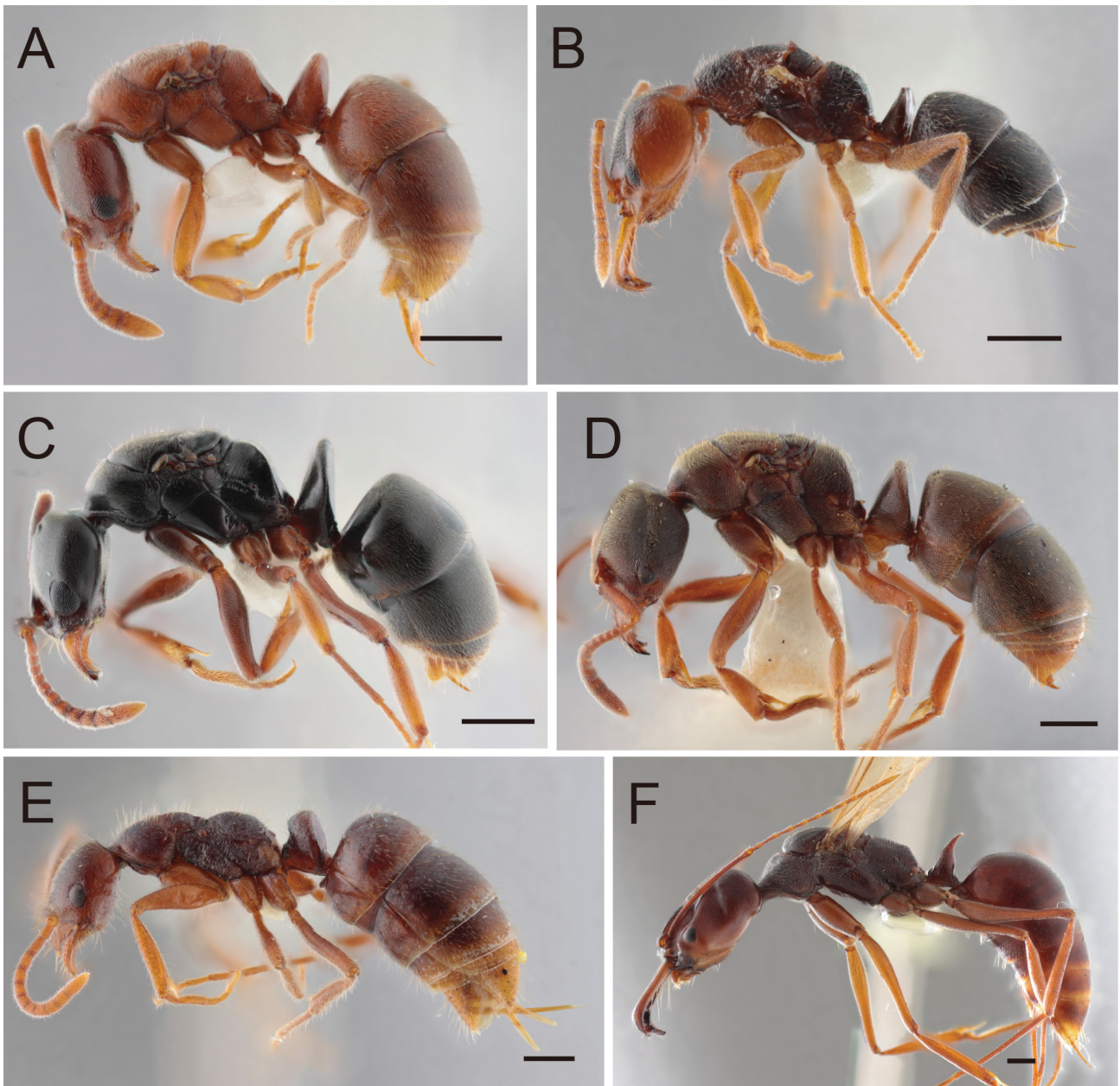


Fig. 2. Habitus (queen) in profile view. A – *Hypoponera beppin* Terayama, 1999 (Yakusugiland, Yaku-shima, Ôsumi Is., Kagoshima-ken, 22.viii.2006, Y. Kuboki leg., Litter No. 3); B – *Anochetus shohki* Terayama, 1996 (Oganzaki, Sakieda, Ishigaki-jima, Yaeyama Is., Okinawa-ken, 10.iv.2022, H. Matsumura leg., MH97, emerged in vii.2022 from captive colony); C – *Brachyponera luteipes* (Mayr, 1862) (Shirahama-rindo, Iriomote-jima, Okinawa-ken, 11.xi.2018, Sk. Yamane leg., JP18-SKY-154); D – *Euponera sakishimensis* (Terayama, 1999) (Funaura, Iriomote-jima, Yaeyama Is., Okinawa-ken, 9.v.1979, K. Ogata leg.); E – *Leptogenys confucii* Forel, 1912 (Mikyo, Tokuno-shima, Amami Is., Kagoshima-ken, 6.iii.2010, Sk. Yamane leg., M10-SKY-12); F – *Odontomachus* cf. *monticola* Emery, 1892 (Miyamura, Yaku-shima, Ôsumi Is., Kagoshima-ken, 16.ix.2008, collector unknown).

punctures). Midtibia without apical spur; hindtibia with pectinate spur only. For the structure of mesosoma, see also TERAYAMA (1996: fig. 25).

Caste differences. In *A. shohki* the queen differs from the worker in having the following characters: body larger (HW 0.94–1.00 mm in the queen vs ca. 0.85 mm in the worker); eye larger (maximum diameter 0.20 mm vs. 0.13 mm); three ocelli present; meso- and metathorax with developed wings and associated structures; mesoscutellum differentiated from mesoscutum; groove dividing mesopleuron into upper and lower sections much more conspicuous than in the worker.

Remarks. The single Japanese species *Anochetus shoh-*

ki is confined to the Central Ryukyus (Okinawa-jima) and Southern Ryukyus, and found in semi-open sites (TERAYAMA 1996; TERAYAMA et al. 2014; HISASUE & TOKUSHIGE 2021). The colonies are small with a single foundress. Many Asian species of *Anochetus* have an elongate head and an apically pointed petiole as in *Odontomachus*. In the Japanese species the hindwing lacks a jugal lobe, while in other species groups from Asia the jugal lobe is often present. Although in *A. shohki* apicoventral spurs on mid- and hindtibiae are reduced to 0 and 1, respectively, the number of spurs is highly variable in this genus (BROWN 1978). Thelytokous parthenogenesis is known in dealate queens (MIYAZAKI 2023).

Species examined (1/1). *Anochetus shohki* Terayama, 1996.

***Brachyponera* Emery, 1900**

(Figs 1A, 1D–F, 2C, 4C, 6C)

Recognition. Medium-sized ants with body length 3.8–4.6 mm; mandible with basal pit; in profile view, petiole squamiform and high with posterior portion of sternite forming spatulate lobe detached from tergite; prora apparently absent; mid- and hindtibiae with both simple and spatulate spurs.

Description. Body 3.8–4.6 mm in total length. Head 0.82–0.90 mm broad, longer than broad, with almost straight posterior margin and parallel to shallowly convex outer margins. Clypeus convex anteriorly, with anterior margin medially almost straight or very shallowly emarginate. Malar space less than $0.33\times$ major diameter of eye. Eye round, large with 13–19 ommatidia along longest axis of eye; with head in full-face view outer margin of eye slightly breaking lateral margin of head, with decumbent or apically curved hair. Mandible with basal pit, with around ten teeth of variable size along masticatory margin. Antennal scape long, surpassing posterior margin of head by more than scape diameter, with sparse short and fine hairs and appressed shorter hairs. With mesosoma in dorsal view, promesonotum narrower than head excluding eyes. Parapsidal line present on posterior half of mesoscutum; transscutal line sharply defined; scutoscullular sulcus distinct, ‘narrowed’ medially; metanotum much shorter and narrower than mesoscutellum; in profile view mesosoma with dorsal outline evenly convex; propodeum only slightly lower than thorax; dorsum of propodeum shorter than mesoscutellum; mesopleuron extensively smooth and shiny, divided into upper and lower sections by sharply defined groove; propodeal side separated from metapleuron by weak line; propodeal spiracle small, often indistinct; its opening oval to elongate-oval; venter of thorax bearing bifurcate metasternal process. Petiole squamiform and high; posterior portion of sternite forming spatulate lobe detached from node (Fig. 1A). Gastral segment I with prora vestigial or apparently lacking; gastral constriction weak, but gastral segment II with pretergite generally at least partly and presternite almost always exposed in mounted specimens; pretergite and presternite superficially minutely punctostriate; cinctus not differentiated. Mid- and hindtibiae with both simple and pectinate spurs. Hindwing with jugal lobe.

Caste differences. The queen is very similar to the worker in body size, structure and coloration except for the possession of wings and associated thoracic structures and a complete set of ocelli and larger eyes in the former; in the worker the eye has 7–12 ommatidia along its longest axis (13–19 in the queen). Petiole in profile view generally relatively broader in dorsal view, thinner (shorter) in profile view than in the worker.

Remarks. All three Japanese species have winged queens only. Hairs on the eye are decumbent or apically curved; this condition may be unique in the Japanese Ponerinae. Gastral constriction is weak; exposed portion of presclerites of gastral segment II is often large in area in stretched

samples and finely microsculptured. For queen and worker morphology see also YASHIRO et al. (2010).

In all the castes and sexes, the petiolar sternite has a backward-directed projection. OGATA (1987) considered it a paired structure of the subpetiolar process. Regarding the Vietnamese species EGUCHI et al. (2014) mentioned that the subpetiolar process [is] developed, posteroventrally with an acute angle or a pair of acute angles. However, the projection is actually not paired but a single flattened lobe with round posterior margin (YAMANE 2007). The question is if this structure is part of the subpetiolar process or part of the sternite proper. This question is very difficult to answer because separation of the process from the sternite proper is in many cases ambiguous in the ponerines. If we adopt BOLTON’s (1994) definition of subpetiolar process as an anteroventral projection on the petiole or its peduncle, then it should be located anteriorly on the sternite. According to his view, the posterior projection in *Brachyponera* does not belong to the subpetiolar process, because no anterior process is recognized and the projection almost reaches the posterior margin of the segment (Fig. 1A). The subpetiolar process is often not clearly separated from the sternite proper except for a few genera, for example *Cryptopone*, in which the process is lamellate and distinctive from the sternite proper (Fig. 1B). In *Brachyponera*, we cannot recognize the subpetiolar process sensu Bolton, instead the sternite is a single sclerite separated from the tergite by a distinct sulcus. We think this condition is unique to *Brachyponera* species.

Species examined (3/3). *Brachyponera chinensis* (Emery, 1895), *B. luteipes* (Mayr, 1862), *B. nakasujii* (Yashiro et al., 2010).

***Euponera* Forel, 1891**

(Figs 2D, 4D, 6D)

Recognition. Medium-sized ants with total body length 5.0–6.2 mm; mandible with basal pit; petiolar sternite without posterior extension; mid- and hindtibiae with both simple and spatulate spurs.

Description. The genus includes medium-sized species. In the Japanese species queen measuring 5.0–6.2 mm in total body length. Head 1.04–1.28 mm in width, in full-face view slightly longer than broad, with very shallowly emarginate posterior margin and shallowly convex lateral margins. Clypeus very weakly convex anteriorly with anterior margin entire. Malar space subequal to or slightly longer than half the major diameter of eye. Eye moderately large, with 12–15 ommatidia along its longest axis, with sparse hairs. Mandible subtriangular; masticatory margin with distinct teeth of variable length; basal pit present. Antennal scape reaching or slightly surpassing posterior margin of head, with sparse erect hairs and dense appressed pubescence. Mesosoma almost entirely densely sculptured and matte except for propodeal declivity, in dorsal view narrower than head; pronotum as broad as mesoscutum; promesonotal suture conspicuous. In profile view mesosoma with dorsal outline weakly arched; groove separating mesopleuron into upper and lower sections strong, with punctures on its bottom; metapleuron fused with propodeum; opening of propodeal spiracle slit-like. Petiole scale-like. Gastral

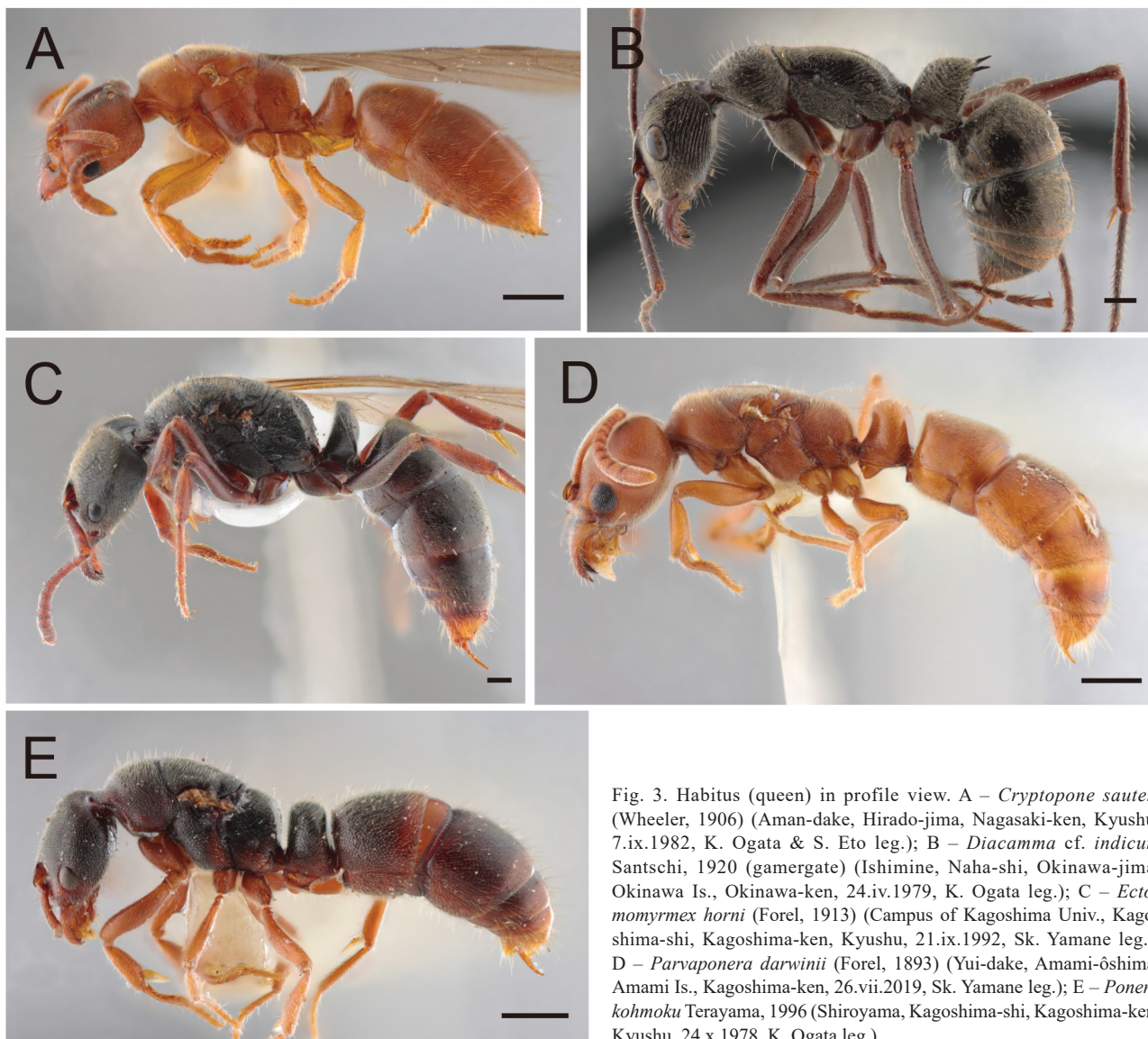


Fig. 3. Habitus (queen) in profile view. A – *Cryptopone sauteri* (Wheeler, 1906) (Aman-dake, Hirado-jima, Nagasaki-ken, Kyushu, 7.ix.1982, K. Ogata & S. Eto leg.); B – *Diacamma* cf. *indicum* Santschi, 1920 (gamergate) (Ishimine, Naha-shi, Okinawa-jima, Okinawa Is., Okinawa-ken, 24.iv.1979, K. Ogata leg.); C – *Ectomomyrmex horni* (Forel, 1913) (Campus of Kagoshima Univ., Kagoshima-shi, Kagoshima-ken, Kyushu, 21.ix.1992, Sk. Yamane leg.); D – *Parvaponera darwinii* (Forel, 1893) (Yui-dake, Amami-ôshima, Amami Is., Kagoshima-ken, 26.vii.2019, Sk. Yamane leg.); E – *Ponera kohmoku* Terayama, 1996 (Shiroyama, Kagoshima-shi, Kagoshima-ken, Kyushu, 24.x.1978, K. Ogata leg.).

constriction distinct; gastral segment II with pretergite often and presternite almost always exposed except for samples with shrunk gasters; both presclerites densely covered with fine transverse striae; cinctus differentiated from pretergite proper, very ‘narrow’, microscopically cross-ribbed. Mid- and hindtibiae with simple spur and longer pectinate spur. Hindwing jugal lobe often missing. **Caste differences.** Workers are slightly smaller than queens, with head width 0.90–1.17 mm (1.04–1.28 mm in the queen). The eye is much smaller and indistinct with a few ill-defined ommatidia. The posterovetral corner of subpetiolar process angulate in the worker, while subpetiolar process gradually sloping posteriad in the queen.

Remarks. In the Japanese members of this genus, the presternite of the gastral segment II is almost always extensively exposed in mounted specimens, and pretergite is also frequently exposed: these sclerites have dense regular striae. In the male the hindwing generally has a jugal lobe that is obsolete and somewhat difficult to recognize. See also OGATA (1987: 114, referred to as *Trachymesopus*).

Species examined (2/2). *Euponera pilosior* (Wheeler, 1928) and *E. sakishimensis* (Terayama, 1999).

Leptogenys Roger, 1861

(Figs 2E, 4E, 6E)

Recognition of ergatoid queen. Without wings and ocelli; medium-sized ants, measuring 4.9–5.1 mm in total body length; clypeus strongly and triangularly produced anteriorly; mid- and hindtibiae with both simple and longer pectinate spurs; pretarsal claws pectinate.

Description of ergatoid queen. Medium-sized ants, measuring 4.9–5.1 mm in total length and 0.75–0.82 mm in head width in the single Japanese species. Head in full-face view much longer than broad, with straight posterior margin and rounded posterolateral corner of head; head broader posteriorly than anteriorly. Frontal carina short; frontal lobe small. Clypeus strongly and triangularly produced anteriorly. Malar space slightly shorter than eye length. Eye large, 0.24 mm in major diameter, its outer margin slightly breaking lateral margin of head, apparently without standing hairs. Ocelli absent. Mandible slender and linear; masticatory margin short with large apical tooth and several small teeth; basal margin long, 3 times as long as masticatory margin, weakly curved, without denticles; outer and basal margins slightly diverging apicad. Antennal scape long, slightly

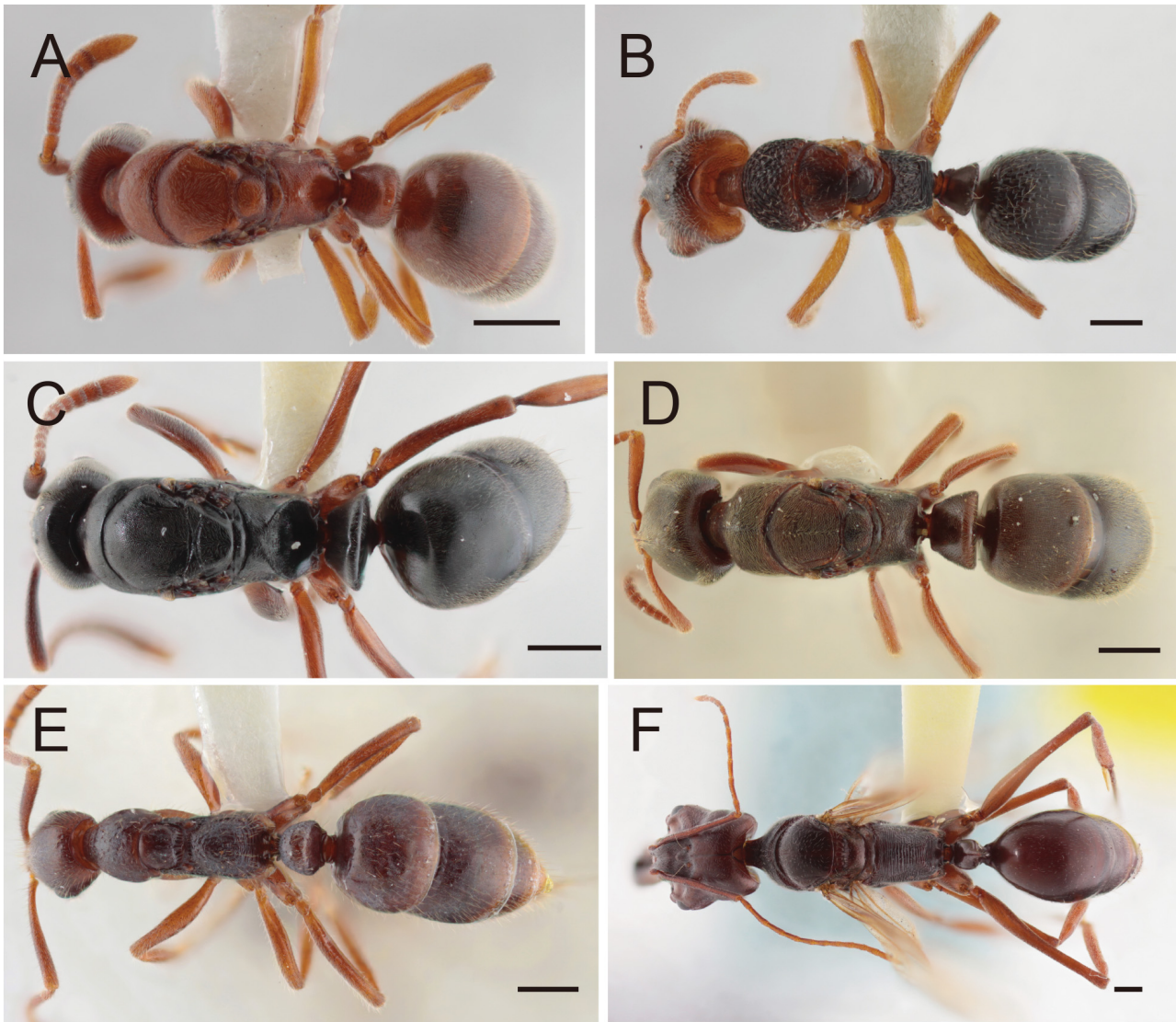


Fig. 4. Habitus (queen) in dorsal view. A – *Hypoponera beppin* Terayama, 1999; B – *Anochetus shohki* Terayama, 1996; C – *Brachyponera luteipes* (Mayr, 1862); D – *Euponera sakishimensis* (Terayama, 1999); E – *Leptogenys confucii* Forel, 1912; F – *Odontomachus* cf. *monticola* Emery, 1892. (Collection data same as in Fig. 2).

shorter than head length. With mesosoma in dorsal view pronotum narrower than head, broader than mesonotum and propodeum; mesoscutum as long as broad, longer than half length of pronotum; mesoscutellum indistinct; scuto-scutellar sulcus rather ‘broad’, comparable to metanotum, ‘widened’ medially; metanotum a ‘narrow’ impressed belt, ‘widened’ laterally; dorsum of propodeum smoothly continuous to posterior declivity, defined from the latter by different sculpturation. With mesonotum in profile view, metapleuron not clearly divided into upper and lower sections, demarcated from mesopleuron and lateral face of propodeum by distinct sulci; propodeal spiracle very small, much smaller than metathoracic spiracle, with round opening. Petiole node-like, distinctly broader than long in dorsal view, short in profile view, measuring 0.33–0.37 mm excluding very short peduncle. Gastral tergite I distinctly broader than long; prora prominent; gastric constriction moderate; cinctus inconspicuous, simple ‘narrow’ band with chain of punctures; presclerites of tergite and sternite of gastral segment II densely micropunctate. Both mid-

and hindtibiae with simple spur and longer pectinate spur. Pretarsal claws of all legs pectinate. Wings absent.

Caste differences. Worker size is similar to that of queen, 4.6–5.2 mm in total body length (4.9–5.1 mm in the queen), but head is slightly narrower (0.67–0.70 mm) than in the queen (0.75–0.82 mm). In the worker caste the following features are noted: major diameter of eye: 0.20–0.23 mm; mesonotum much shorter than half length of pronotum, completely lacking mesoscutellum; petiole in dorsal view much longer than broad, in profile view triangular, much longer than in queen, measuring 0.47–0.48 mm; gaster much slenderer than in queen; gastral tergite I about as long as broad. The worker is easily separated from the queen by the long and laterally flattened petiole and much slenderer gaster.

Remarks. Queens of *Leptogenys* species are generally ergatoids, flightless, with the petiole shorter, broader and more node-like than in workers.

Species examined (1/1). *Leptogenys confucii* (Forel, 1912).

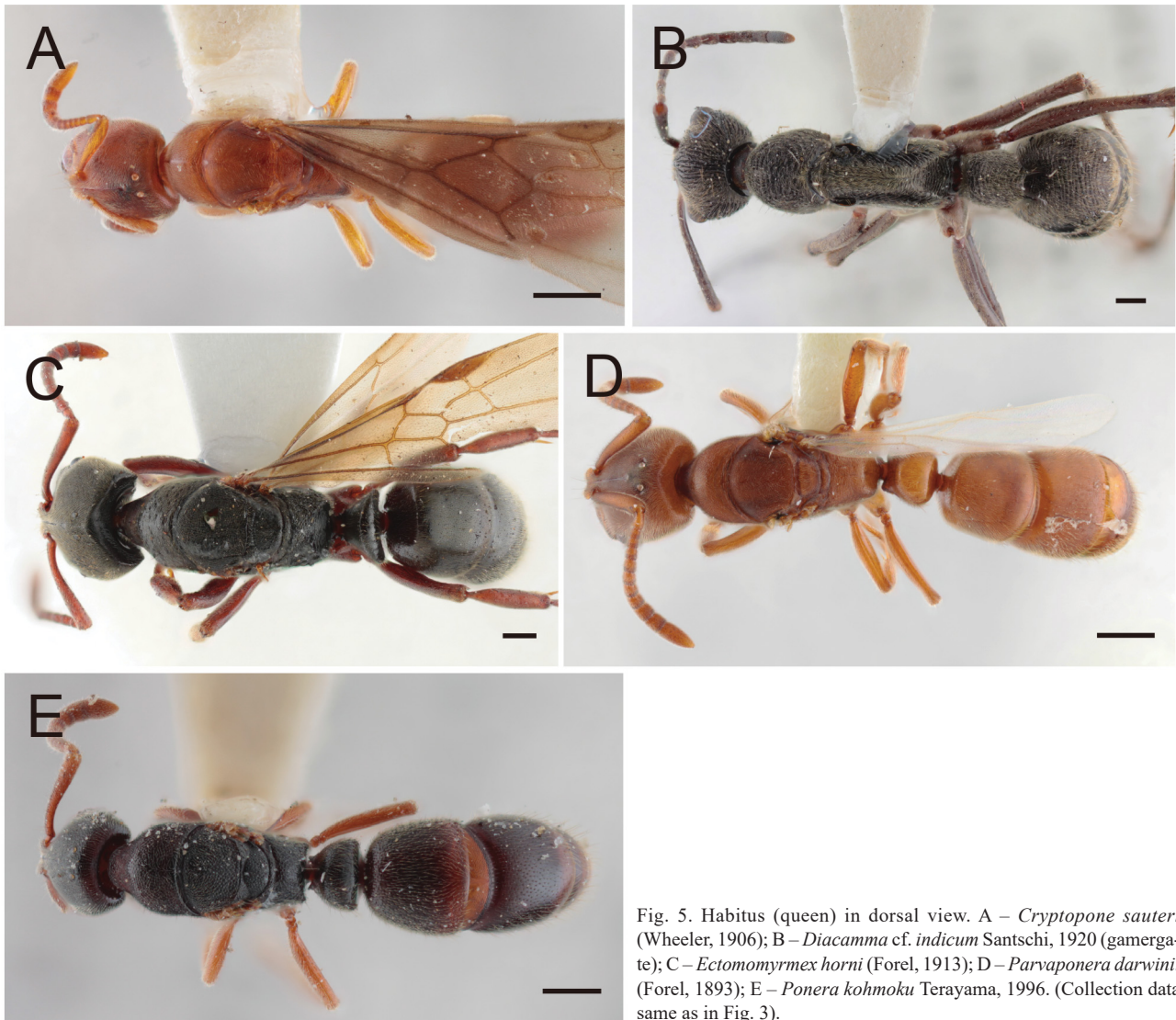


Fig. 5. Habitus (queen) in dorsal view. A – *Cryptopone sauteri* (Wheeler, 1906); B – *Diacamma* cf. *indicum* Santschi, 1920 (gamergate); C – *Ectomomyrmex horni* (Forel, 1913); D – *Parvaponera darwinii* (Forel, 1893); E – *Poner a kohmoku* Terayama, 1996. (Collection data same as in Fig. 3).

Odontomachus Mayr, 1862

(Figs 2F, 4F, 6F)

Recognition. Large ants measuring 9.4–10.2 mm in total body length; nuchal carina (occipital carina) running behind vertex turned anteriorly medially on vertex forming V-shaped infolding, merging with median line of head; mandible very long, linear, apically strongly curved inward; petiole sharply pointed apically.

Description. Large ants measuring 9.4–10.2 mm in total body length. Head longer than broad, broadest at level of eye, with posterior margin shallowly and broadly emarginate; lateral margin in front of and behind eye concave; nuchal carina (occipital carina) running behind vertex turned anteriorly medially on vertex forming V-shaped infolding, merging with median line of head. Eye with rather long sparse hairs. Ocelli situated far from posterior margin of head; distance between posterior ocellus and posterior margin of head more than three times as long as distance between posterior ocelli. Mandible linear and long, inserted medially on front of cranium, apically strongly curved inwardly; in the two Japanese species apical portion with three teeth that are arranged vertically; upper tooth truncate apically. Metanotum flanked by deep anterior and posterior

furrows. Opening of propodeal spiracle elongate. Petiole conical with pointed apex; subpetiolar process without anterior fenestra. Prora projected anteriorly as small tongue. Gastral constriction weak; pretergite of gastral segment II generally concealed under tergite I, transversely striate; presternite with same sculpturation; cinctus not differentiated. Both mid- and hindtibiae with a simple spur and a longer pectinate spur. Hindwing with jugal lobe.

Caste differences. In *O.* cf. *monticola* Emery, 1892 the worker differs from the queen in having the following characters: body slightly smaller (HW 2.01–2.24 mm in the worker vs. 2.28–2.44 mm in the queen); eye smaller (major diameter 0.30–0.33 vs. 0.38); ocelli absent; thorax without wings and simply constructed; mesoscutellum absent; groove dividing mesopleuron into upper and lower sections very faint. For more details for the entire genus see BROWN (1976).

Remarks. In the Japanese *Odontomachus* species, the antennal scape and mid- and hindtibiae bear no distinct erect hairs, while in *Anochetus shohki* these parts have erect hairs.

Species examined (2/2). *Odontomachus kuroiwae* (Matsumura, 1912) and *O.* cf. *monticola* Emery, 1892.

***Ponera* genus group**
***Cryptopone* Emery, 1893**
 (Figs 1B, 3A, 5A, 7A)

Recognition. Pale-colored and relatively small ants measuring 3.6–4.2 mm in total body length; mandible with basal pit; petiole node-like, with well-defined lamellate subpetiolar process that lacks fenestra; ventral apices of mid- and hindtibiae with pectinate spur only; midtibia with strong bristles on outer surface.

Description. Relatively small ants measuring 3.6–4.2 mm in total body length; head width varies from 0.70 to 0.82 mm. Head longer than broad, with posterior margin nearly straight, lateral margin shallowly convex, and posterolateral corner broadly round; median line distinct, starting at anterior ocellus and reaching level of antennal insertion. Clypeus with anterior margin evenly and shallowly convex. Malar space much shorter than half major diameter of eye. Eye large with 14–16 ommatidia along its longest axis, with rather dense short hairs; with head in full-face view outer margin of eye slightly breaking lateral margin of head. Mandible with basal pit; distinct teeth present along its masticatory margin. Antennal scape fails to reach posterior margin of head. With mesosoma in dorsal view promesonotum narrower than head; scutoscutellar suture very ‘narrow’. With mesosoma in profile view deep furrow (excavation) present between lower part of mesopleuron and metapleuron. Propodeal spiracle elongate. Petiole node-like, with well-defined lamellate subpetiolar process that lacks fenestra (Fig. 1B). Prora inconspicuous, represented by small swelling with lateral carinae. Constriction between gastral segments I and II weak; pretergite of gastral segment II occasionally exposed but presternite always extensively exposed in mounted samples; both sclerites very minutely punctate; cinctus differentiated, cross-ribbed (forming chain of elongate punctures). Ventral apices of mid- and hindtibiae with pectinate spur only; midtibia with strong bristles on outer surface. Hindwing without jugal lobe.

Caste differences. Workers are smaller than queens with total body length 3.0–3.5 mm and head width 0.64–0.78 mm (3.6–4.2 mm and 0.70–0.82 mm, respectively, in the queen). The eye is very small comprising one to a few ill-defined ommatidia. The upper portion of the metapleuron is extensively deeply impressed. The subpetiolar process is often less developed than in the queen. See also OGATA (1976: 118).

Remarks. In the two Japanese species the queen has a dark blotch around ocelli (sometimes the blotch extending to the vertex), while the worker lacks this. They are similar to *Parvaponera darwini* (Forel, 1893) in size and general habitus but quite different from the latter in a number of structural characters (see Remarks for *Parvaponera*).

Species examined (2/2). *Cryptopone sauteri* (Wheeler, 1906) and *C. tengu* Terayama, 1999.

***Diacamma* Mayr, 1862**
 (Figs 3B, 5B, 7B)

Recognition of gamergate (mated and egg-laying

worker). Morphological queen absent; lacking wings; large ants measuring ca. 10 mm; head, mesosoma and petiole covered with deep rugae; petiole massive, with pair of spines on posterodorsal portion.

Description of gamergate. Winged queens are not known in this genus; the physically same females can become either the worker or functional queen (gamergate) depending on social circumstances (if newly emerged females lost gemmae just after emergence from cocoons, then they become workers) (see FUKUMOTO et al. 1989, PEETERS & HIGASHI 1989). Large ants, with total body length ca. 10 mm in the Japanese species. Head, mesosoma and petiole covered with deep rugae. Head longer than broad, with weakly convex posterior margin, parallel lateral margins and broadly rounded posterolateral corners; occipital carina developed. Clypeus distinctly protruding anteriorly and tapering apically. Eye large with ca. 40 ommatidia along its longest axis, essentially without standing hairs; with head in full-face view eye distinctly breaking lateral margin of head. Mandible elongate-triangular, with small teeth along its masticatory margin; teeth on basal 1/3 of masticatory margin very small; basal pit absent. With mesosoma in dorsal view, promesonotum distinctly narrower than head; promesonotal suture distinct; metanotal groove absent. With mesosoma in lateral view, deep pit (gemma pit) present just above mesopleuron; mesopleuron not divided into upper and lower sections. Lateral face of propodeum separated from metapleuron by indistinct line; propodeal spiracle elevated from level of cuticle; its opening linear. Petiole massive, with pair of spines on posterodorsal portion; subpetiolar process developed, in profile view concave medially to form anterior and posterior spines, without anterior fenestra. Prora rather conspicuous, directed anteriorly. Gasteral constriction strong; pretergite and presternite of gastral segment II generally more or less exposed in mounted specimens, densely with fine transverse striation; cinctus ‘narrow’ zone with cross-ribs. Both mid- and hindtibiae with simple spur and longer pectinate spur.

Caste differences. Morphologically the normal worker and gamergate worker are identical except for presence/absence of gemmae, but behaviorally different.

Remarks. The Japanese species is very similar to the Indian species *Diacamma indicum*, but its status is not yet settled. According to OGATA (1987) the male hindwing has a jugal lobe.

Species examined (1/1). *Diacamma cf. indicum* Santschi, 1920.

***Ectomomyrmex* Mayr, 1867**
 (Figs 3C, 5C, 7C)

Recognition. Body dark reddish brown; relatively large ants measuring 7.0–9.0 mm in total body length; head dorsum covered with dense striae that diverge posteriorly; lateral face of head nearly flat; mandible without basal pit; subpetiolar process without anterior fenestra; mid- and hindtibiae with both simple and pectinate spurs.

Description of queen. Relatively large ants with total body length 7.0–9.0 mm and head width 1.73–2.10 mm. Head in full-face view almost as long as broad, with medially

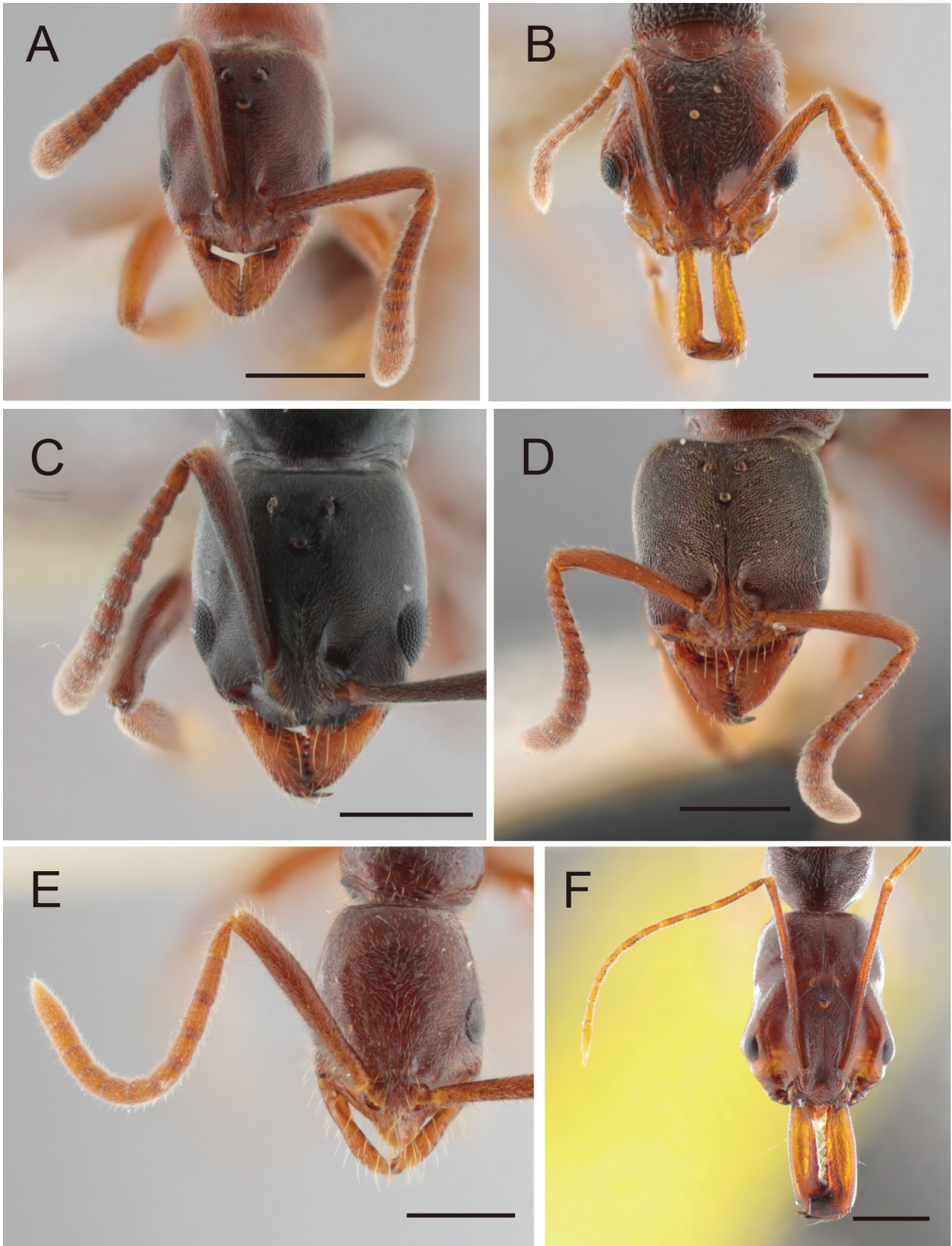


Fig. 6. Head (queen) in full-face view. A – *Hypoponera beppin* Terayama, 1999; B – *Anochetus shohki* Terayama, 1996; C – *Brachyponera luteipes* (Mayr, 1862); D – *Euponera sakishimensis* (Terayama, 1999); E – *Leptogenys confucii* Forel, 1912; F – *Odontomachus* cf. *monticola* Emery, 1892. (Collection data same as in Fig. 2).

emarginate posterior margin, roundly convex lateral margins and weakly angled posterolateral corners; lateral face of head almost flat. Clypeus weakly convex anteriorly, with anteromedian portion concave. Malar space more than half major diameter of eye. Eye moderately large comprising 16–17 ommatidia along its longest axis, with rather sparse long hairs. Mandible triangular, without basal pit; masticatory margin with ca. 10 teeth of varying size. Antennal scape slightly surpassing posterior margin of head. With mesosoma in dorsal view scutoscuteellar sulcus 'broad' with its median area rugose; parapsidal line faint; line running along posterolateral margin of mesoscutum deep and complete. With mesosoma in profile view metapleuron clearly delimited from mesopleuron with deep suture but fused with lateral face of propodeum. Propodeal spiracle with linear opening. Petiole subsquamiform; subpetiolar process not differentiated from sternite proper, ventrally round, without fenestra. Prora small and round, simple prominence. Gastral constriction moderately strong; pretergite and presternite of gastral segment II with very fine transverse striation; cinctus absent. Mid- and hindtibiae with simple spur and longer pectinate spur. Hindwing with jugal lobe. Entire body dark reddish brown to blackish brown.

Caste differences. Among the Japanese ponerine genera *Ectomomyrmex* is an exceptional genus in which the worker has a mesopleuron that is divided into upper and lower sections by a groove. In this respect the worker and queen do not differ, but the suture is broader and deeper in the queen. In other characters the queen is also similar to the worker except for queen-specific thoracic structures, large eyes and complete set of ocelli in the former.

Remarks. The two Japanese species are similar to the *Euponera* species in general habitus and habitat preference, but the latter have a basal pit on the mandible and lack the jugal lobe at the base of the hindwing; however, note that in *Ectomomyrmex* the jugal lobe is often folded under the hindwing so that it is easily overlooked.

Species examined (2/2). *Ectomomyrmex horni* (Forel, 1913) and *E. sp.*, both closely allied to *E. javanus* Mayr, 1867.

Parvaponera Schmidt & Shattuck, 2014

(Figs 3D, 5D, 7D)

Recognition. Body yellowish; medium-sized ants measuring 5.0–5.5 mm in total body length; eye almost touching anterior margin of cranium; mandible without basal pit; petiole node-like, in profile view thick, lacking anterior fenestra; mid- and hindtibiae with both simple spur and longer pectinate spur in apicoventral part.

Description of queen. Medium-sized ponerine, measuring 5.0–5.5 mm in total body length and 0.96–1.00 mm in head width. In full-face view, head (excluding eyes) almost as long as broad, slightly narrowed posteriad, with broadly emarginate posterior margin, straight lateral margin and rounded posterolateral corner. Malar space almost absent. Clypeus only shallowly convex anteriorly. Mandible elongate-triangular, without basal pit; masticatory margin with 7–8 strong teeth of varying size. Eye round with ca. 20 ommatidia along longest axis, with many rather long

erect hairs. Three ocelli arranged in right triangle. With mesosoma in dorsal view promesonotum much narrower than head; mesoscutum flat with weak parapsidal line and parascutal carina; scutoscuteellar sulcus linear for most of its length; mesoscutellum and metanotum smooth with superficial punctures. Opening of propodeal spiracle linear. Petiole node-like, in profile view thick; tergite separated from sternite with deep sulcus flanked with sharply defined carinae; subpetiolar process with anterior fenestra, but lacking posterior paired spines. Prora small, scale-like, margined with dark rim. Gastral constriction rather strong; pretergite of gastral segment II smooth with very superficial sculpture and strongly shiny; presternite densely with minute punctures and matte; cinctus not clearly defined, represented by impressed line. Mid- and hindtibiae with simple spur and longer pectinate spur in apicoventral part. Hindwing without jugal lobe.

Caste differences. The worker is much smaller (TL ca. 3.5 mm; HW 0.86 mm) than the queen. The eye is vestigial with a few ill-defined ommatidia. The median line on the cranium is less conspicuous than in the queen, in which it is well defined, starting at the anterior ocellus and reaching the posterior margin of the frontal lobes.

Remarks. The single Japanese species *P. darwinii* is very similar to *Cryptopone* species in size, general habitus and sometimes coloration, but it is easily distinguished from the latter by the following combination of characteristics: 1) mandible without basal pit, 2) midtibia without strong bristles on outer surface, and 3) subpetiolar process with anterior fenestra. Among the Japanese genera the pretergite of the gastral segment II differs in sculpturation type from the presternite solely in this genus.

Species examined (1/1). *Parvaponera darwinii* (Forel, 1893).

Ponera Latreille, 1804

(Figs 1F, 3E, 5E, 7E)

Recognition. Body color various; small ants with total length 2.2–4.4 mm; mandible without basal pit; petiole node-like to squamiform, generally thick, with anterior fenestra and often also with paired posterior processes; mid- and hindtibiae apicoventrally with pectinate spur only.

Description of queen. Small ants, measuring 2.2–4.4 mm in total body length and 0.44–0.80 mm in head width. In full-face view, head longer than broad, with almost straight to shallowly emarginate posterior margin, straight to weakly convex lateral margin and rounded posterolateral corner. Malar space slightly shorter than, subequal to, or slightly longer than half major diameter of eye. Clypeus only weakly convex anteriorly. Mandible elongate-triangular, without basal pit; three apical teeth large; basal half or more of masticatory margin serrate. Eye round with ca. 9–18 ommatidia along longest axis, with dense short hairs; with head in full-face view outer margin of eye hardly or slightly breaking lateral margin of head. Antennal scape either failing to reach posterior margin of head or slightly extending beyond it. With mesosoma in dorsal view promesonotum slightly narrower than head; mesoscutum with weak or distinct parapsidal line; parascutal carina blunt

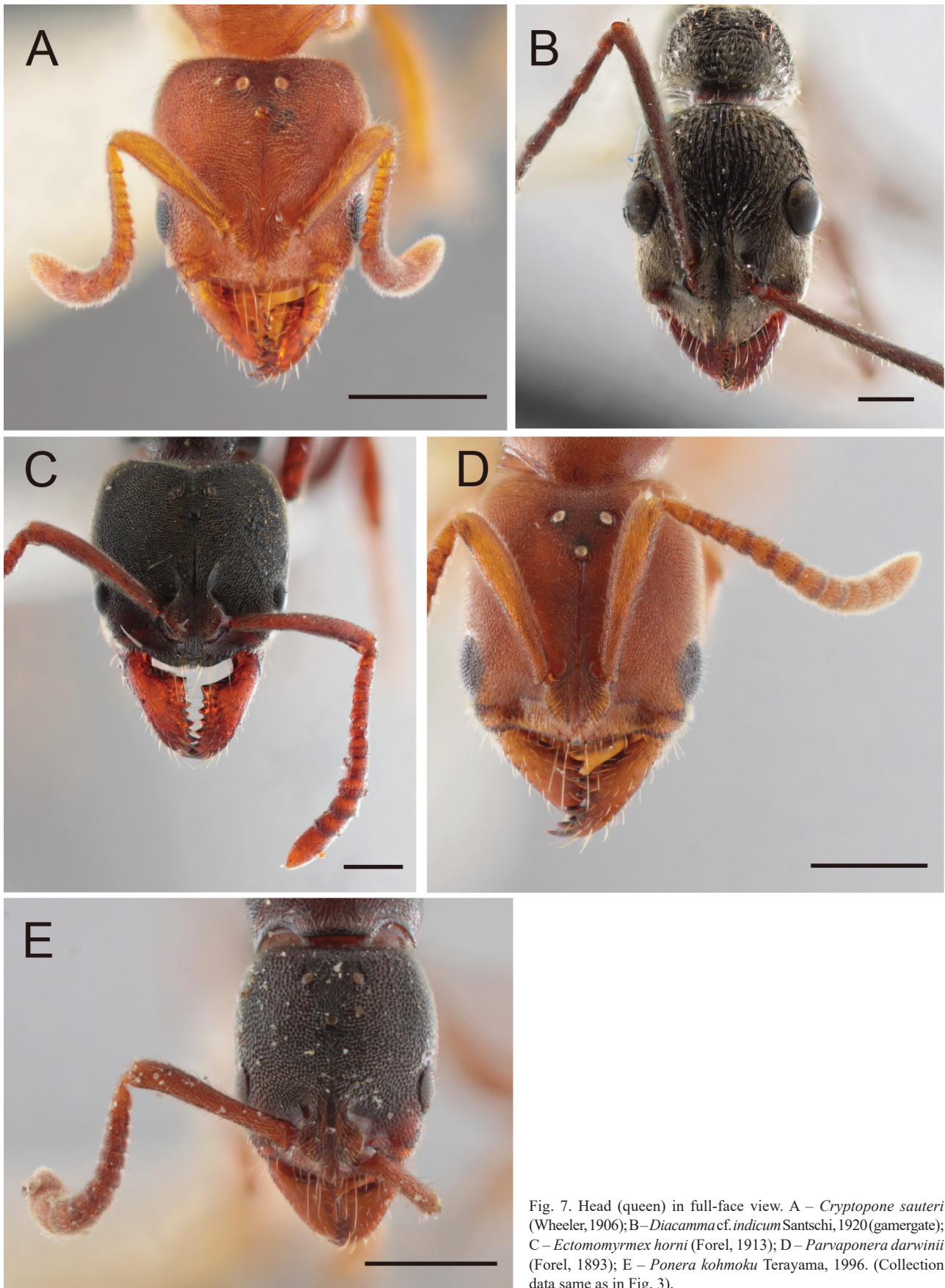


Fig. 7. Head (queen) in full-face view. A – *Cryptopone sauteri* (Wheeler, 1906); B – *Diacamma* cf. *indicum* Santschi, 1920 (gamergate); C – *Ectomyrmex horni* (Forel, 1913); D – *Parvaponera darwinii* (Forel, 1893); E – *Ponera kohmoku* Terayama, 1996. (Collection data same as in Fig. 3).

to absent. Opening of propodeal spiracle oval. Petiole node-like to squamiform, generally thick; tergite separated from sternite with deep sulcus flanked with sharply defined carinae; subpetiolar process with anterior fenestra, generally also with paired posterior spines (Fig. 1C). Prora small, thin scale margined with rim. Gastral constriction moderate; pretergite and presternite of gastral segment II punctate or irregularly striate; sculpture on presternite often stronger than on pretergite; cinctus generally distinctly defined, cross-ribbed (forming chain of coarse punctures). Mid- and hindtibiae apicoventrally with a pectinate spur only. Hindwing without jugal lobe. For the queen of *P. kohmoku* Terayama, 1996 and *P. tamon* Terayama, 1996, see TERAYAMA (1996: Figs 1–3, 10–12).

Caste differences. The worker is slightly smaller than the queen (TL: 1.6–3.5 mm vs. 2.2–4.4 mm; HW: 0.33–0.75 vs. 0.44–0.80). The eye is much smaller in the worker than in the queen, even vestigial in some species, generally consisting of one to a few ill-defined ommatidia. *Ponera kohmoku* is exceptional in this respect; the worker eye is relatively large with ca. 8 ommatidia along the longest axis of the eye (in total more than 20), but in the queen the number is much larger, i.e., 18–20 along the longest axis. In the worker the malar space is as long as the major diameter of the eye, while in the queen it is much shorter than eye length.

Remarks. *Ponera* is one of the two Japanese ponerine genera with an anterior fenestra on the petiolar sternite, the other being *Parvaponera*. However, it is easily separated from the latter by the reduced number of spurs (one) on the apicoventral part of the mid- and hindtibiae (*Parvaponera* has two), the masticatory margin of the mandible serrate in its basal half (in the latter the entire masticatory margin is provided with strong teeth), and the ‘broader’ scutoscutellar sulcus that is narrowed medially (in the latter the scutoscutellar sulcus is linear over most of its length).

Species examined (5/8). *Ponera bishamon* Terayama, 1996, *P. kohmoku* Terayama, 1996, *P. scabra* Wheeler, 1928, *P. takaminei* Terayama, 1996, *P. tamon* Terayama, 1996.

Discussion

The queens of most of the Japanese ponerine species are relatively easily identified at genus level. Most of the characters used in sorting worker specimens are also applicable to queens. However, *Brachyponera* queens lack the most remarkable feature seen in the worker, i.e., the distinct step between the promesonotum and propodeum, the former being much higher than the latter. On the other hand, *Parvaponera* queens are recognized at once by the absence of the malar space, the eye almost touching the anterior margin of the cranium. This condition is unique among the females (queens and workers) of the Japanese ponerines. In the worker caste the separation of the mesopleuron into the upper and lower sections is used to separate *Ectomomyrmex* from all the remaining genera, though this cannot be used for the queen caste because in all genera the queen has this condition. The presence/absence of the jugal lobe on the hindwing is stable in each genus in at least the Japanese fauna except for *Euponera*

and provides a useful cue in genus identification.

In this paper queen characters that are useful to distinguish among species are not discussed. For species identification, some of worker characters are also applicable to queens, e.g., the gastral pilosity (*Brachyponera*), petiolar shape (*Ponera*), color pattern (*Hypoponera*). The shape of the metasternal process has a potential efficacy in discriminating species in the ponerine ants; an example is shown in Figs 1D–F for *Brachyponera* species. The variation in wing venation can be also important. However, this issue will be discussed in detail in a separate paper.

The functional queens (egg-laying females) of the Japanese ponerine ants are sorted into three principal categories: 1) alate/dealate females that are morphologically distinguishable from workers, 2) ergatoid queens that are similar in body structure to the worker (wings absent; simple thorax; ocelli occasionally lacking), but with larger eyes, broader gaster and sometimes with modification of the thoracic structure, 3) gamergates that are morphologically identical to the worker.

In the species of the first category, the queen is generally larger than the worker in body size, and separated from the worker by the possession of large compound eyes and ocelli, wings and associated thoracic structure that is much more complex than in the worker. In body size, queens of *Cryptopone* and *Parvaponera* and of most species of *Hypoponera* and *Ponera* are almost always larger than workers, but in other genera the difference is less significant, usually with an overlap in body size between the two castes. In profile view, the petiole is generally less thick (shorter) in the queen than in the worker. Anyway, as far as the Japanese ants are concerned, the physical differentiation between the worker and queen castes is much weaker in Ponerinae than in other subfamilies, as shown by PEETERS & ITO (2015).

Among the Japanese ponerine species with ergatoid queens (category 2), *Leptogenys confucii* shows typical colony structure as reported for the Oriental congeners (ITO 1997): the single ergatoid lays eggs in a colony. The queen is the same size as the worker, with the eyes of the same size as those of workers, but the mesothorax is slightly modified, the petiole is much shorter than in the worker, and the gaster is characteristically swollen. In other cases (*Hypoponera ergatandria*, *H. nubatama*, *H. opaciceps* and *H. punctatissima*), the colonies have both ordinary queens and ergatoids, the latter having large eyes and copulating with wingless males in the same colonies (HASHIMOTO 1995, SEIFERT 2013, YAMAUCHI et al. 1996, TERAYAMA et al. 2014).

The single species belonging to category 3 is *Diacamma* sp. cf. *indicum*. All the *Diacamma* species studied for behavior have a unique reproductive strategy in which the single gamergate (mated and egg-laying worker) behaves as functional queen in the colony (SCHMIDT & SHATTUCK 2014). A few species of *Ectomomyrmex* in the Oriental tropics reproduce by both dealate queens and gamergates (ITO & OHKAWARA 1994, ITO et al. 2007). Gamergates have not yet been found in the two Japanese congeners, which have been poorly studied for reproductive structure.

Morphological and behavioral plasticity is a classical

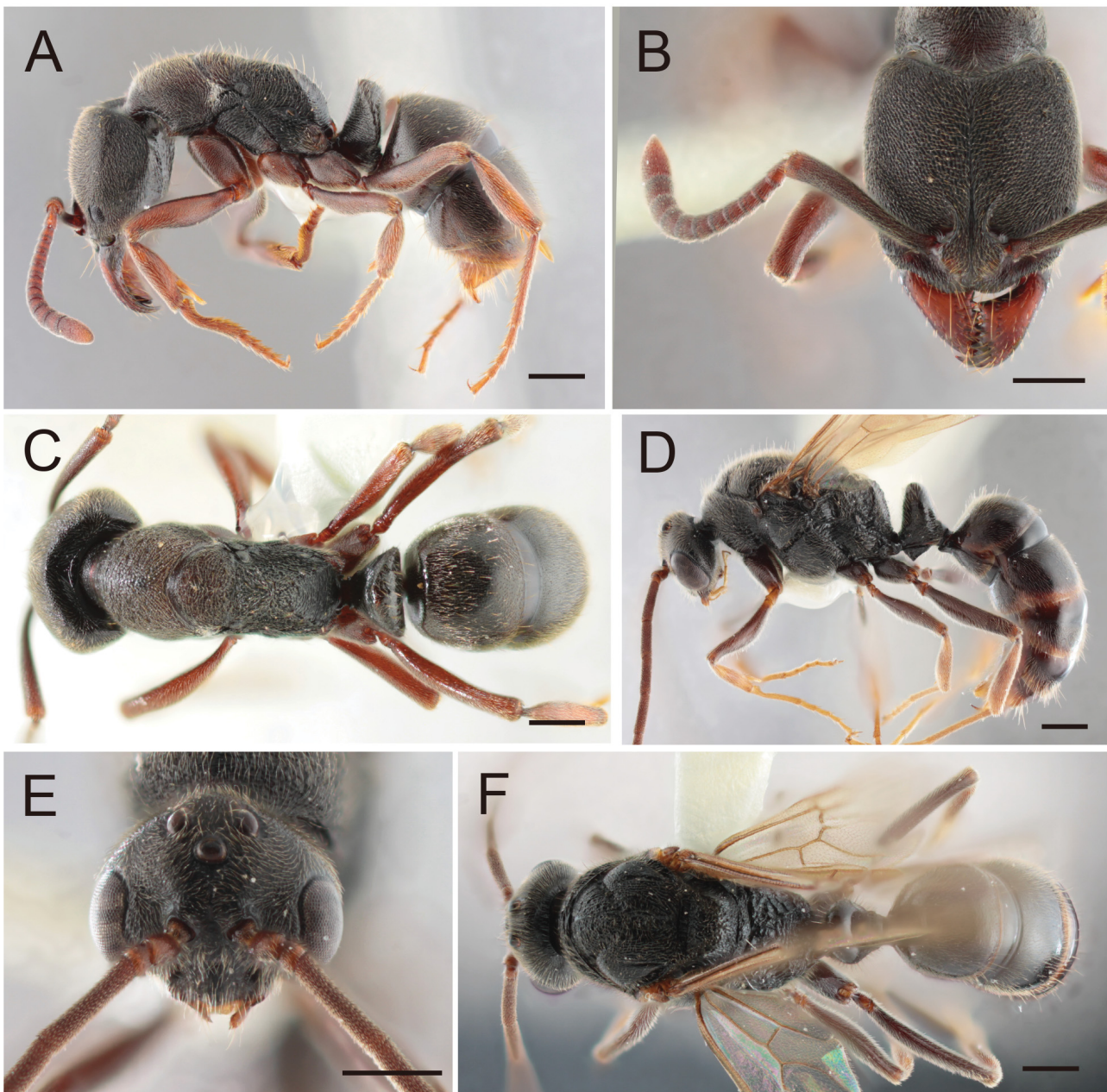


Fig. 8. *Ectomyrmex horni* (Forel, 1913). A–C – worker (Sata-misaki, Minamiôsumi-chô, Kagoshima-ken, Kyushu, 7.v.2022, Sk. Yamane leg., JP22-SKY-019); D–F – male (Campus of Kagoshima Univ., Kagoshima-shi, Kagoshima-ken, Kyushu, 20.ix.1999, collector unknown). For the queen see Figs 3C, 5C & 7C.

but still central issue in the study of the social insects (WILSON 1953, GADAU & FEWELL 2009; for the most recent topics, see BOUDINOT et al. 2021). Among the Japanese ponerines the species of *Leptogenys* and *Diacamma* have unique ‘queen’ castes. With wingless ‘queens’ and dependent colony founding their dispersal ability is restricted. All the species in other genera have ordinary queens with wings and independent colony foundation, but three species of *Hypoponera* have ergatoid queens and males as well that serve to facilitate faster colony development and budding. Three of the four species, *H. opaciceps*, *H. punctatissima* and *H. ragusari* are aliens of exotic origin (probably from Africa), only *H. nubatama* being native to mainland Japan. Interestingly, no ergatoid queen has been found in the Japanese *Ponera* species, which have

similar nesting habits. However, ergatoid queens have been known in a few Nearctic species of the genus such as *P. coarctata* (Latreille, 1802), *P. exotica* M. R. Smith, 1962 and *P. pennsylvanica* Buckley, 1886 (e.g., WHEELER 1900, SCHMIDT & SHATTUCK 2014).

Redescription of *Ectomyrmex horni*

Ectomyrmex horni (Forel, 1913), status resurrected

(Figs 3C, 5C, 7C, 8)

Pachycondyla (*Ectomyrmex*) *horni* Forel, 1913: 185; TERAYAMA (2009): 105 (in key).

Ectomyrmex javanus Mayr, 1867: YASUMATSU (1962): 94 (*E. horni* synonymized with *E. javanus*); ANTWIKI (2024) (syntype images of *Pachycondyla horni* examined).

Ectatomma [sic!] *horni*: SANTSCHI (1937): 363 (recorded from Kagoshima, Japan).

Ectomomyrmex sauteri Forel, 1912: ONOYAMA (1980: 196).

Pachycondyla javana: BOLTON (1995): 306 (*P. horni* as junior synonym of *P. javana*); YAMANE et al. (2010: 121).

Ectomomyrmex sp. B: TERAYAMA et al. (2014: 54); TERAYAMA (2021): 90 (Japanese name: Minamifuto-hariari).

Material examined. JAPAN: KYUSHU: *Kagoshima-ken* (mainland): aq, Ono-chô, Kagoshima-shi, 30.x.1990, T. Iwai; w, Kôrimoyo, Kagoshima-shi, 2.ix.1998, Sk. Yamane; aq·m, same loc., 20.ix.1999; w, Toso, Kagoshima-shi, 12.vii.2002, T. Akiyama; m, Tagayama-Kôen, Kagoshima-shi, 8.xi.2013; w, Kurokami, Sakurajima, 26.v.2021, Sk. Yamane; w, near Yôgan-Nagisa (Taishô lava), 10.viii.2022, Sk. Yamane; w, Okoga-shima, off Sakurajima, 19.v.2009, S. Onoda; w, Sata-misaki, Minamiôsumi-chô, 7.v.2022, nest in soil, Sk. Yamane (JP22-SKY-019). RYUKYU ISLANDS: *Kagoshima-ken*: AMAMI IS.: *Amami-ôshima*: w, Kinsakubaru (300 m alt.), 28.viii.2000, Sk. Yamane. *Okinawa-ken*: OKINAWA IS.: *Okinawa-jima*: w, 15.v.1991, H. Watanabe. *Kume-jima*: w, Daruma-yama, 8.x.2021, Sk. Yamane leg. YAEYAMA IS.: *Ishigaki-jima*: m, Omoto-dake, 16.x.1981, K. Konishi; w, Tomino, 6.v.2018, N. Murayama. *Taketomi-jima*: dq, 24.vii.1987, Sk. Yamane. *Iriomote-jima*: m, Komi, 6.vi.1982, K. Ôhara; w, Amitori, 21.vii.1989, Y. Nishizono; m, Komi, 12.x.1987, A. Nagatomi; w, Ôtomi-rindô, 28.iv.1998, K. Eguchi; w, Ôhara, 16.iii.2004, Sk. Yamane; w, Uehara near Univ. Ryukyus Field Stn., 11.xi.2018, Sk. Yamane. **OGASAWARA ISLANDS:** *Tokyo-to*: *Haha-jima*: w, Sakaiga-take (310–410 m alt.), 12.vii.1990, H. Watanabe; w, Sekimon, 6.vi.1998, N. Kawakubo & K. Nakashima. **TAIWAN:** *Taipei Hsien*: w, Fushan (600–670 m alt.), 22–23.ix.1997, Sk. Yamane.

Description of worker (based on Japanese and Taiwanese specimens). Measurements (n = 5: samples from Kyushu mainland and the Ryukyus). TL: 6.0–7.3 mm, HW: 1.56–1.74 mm, HL: 1.73–1.88 mm, EL: 0.20–0.24 mm, SL: 1.25–1.36 mm, PrW: 1.06–1.24 mm, PtW: 0.84–0.96 mm; CI: 91–94, SI: 75–80.

Head in full-face view slightly longer than broad, with posterior margin broadly concave, lateral margin convex and posterolateral corner roundly angled. Clypeus convex anteriorly, with anterior margin medially concave and indented; median area without longitudinal keel. Eye large, 0.20–0.24 mm in major diameter, with ca. 10 ommatidia (range: 9–11) along longest axis, located lower on head; malar space slightly shorter than or subequal to major diameter of eye. With head in full-face view antennal scape barely reaches posterior margin of head, but fails to attain posterodorsal corner; eye barely breaking lateral margin of head. Mandible elongate-triangular, with 9–10 teeth of varying size on masticatory margin; large and small teeth often alternating but not always. With mesosoma in dorsal view pronotum narrower than head; promesonotal suture distinct; propodeum as broad as mesonotum with much narrower dorsum; metanotal groove obsolete. In profile view mesosoma with dorsal outline evenly convex; pronotum anteroventrally angled, not produced as prominence, with ventral furrow that continues anteriorly to pronotal lobe; metapleuron sharply demarcated from mesopleuron but fused with lateral face of propodeum; propodeal declivity laterally distinctly margined throughout. Petiole subsquamiform, with short transverse dorsum that is vaguely defined, large outwardly curved anterior face, linear lateral face and weakly concave posterior face; sternite sharply demarcated from tergite with sulcus, anteriorly produced

ventrad. Gastral tergite I anteriorly truncate; prora scale-like with anterior concavity; gastral constriction weak; cinctus absent.

Dorsum and lateral face of head very densely striate and matte or with weak luster; striae not regular throughout, often waving and branching, mixed with small punctures. Frontal lobe laterally with distinct smooth area. Clypeus with median portion just below frontal lobe longitudinally rugulose; on anterior slope of lateral portion rugulae slightly coarser; dorsolateral portion densely micro-punctate; anteromedian concave part nearly smooth. Mesosoma almost entirely sculptured. Pronotum transversely striate on anterior lobe, densely punctate on dorsum, densely and minutely punctostriate on lateral face. Mesonotum with dense longitudinal rugulae; lower section of mesopleuron rather coarsely rugose from front to rear; metanotum with similar rugae. Dorsum of propodeum with coarse irregular sculpture; lateral face with coarse rugae as in metapleuron; declivity transversely rugose. Anterior and posterior faces of petiole transversely rugose; dorsal face superficially sculptured and shiny. Anterior vertical face of gastral segment I smooth with minute punctures from which setae arise; gastral tergites and sternites covered with dense small punctures, rather shiny; presclerites of gastral segment II with minute transverse striae, shiny.

Dorsum of head densely covered with decumbent to suberect golden hairs; clypeus anteriorly with two pairs of long hairs; venter of head with sparse erect hairs. Mandible with scattered short appressed hairs mixed with longer suberect hairs on dorsum; ventral face bearing much longer hairs. Eye with sparse but conspicuous erect hairs. Antennal scape with a few or no erect hairs on leading edge. Mesosomal dorsum densely covered with short appressed hairs and sparser erect hairs; erect/suberect hairs on propodeal declivity generally shorter than those on mesosomal dorsum. Anterior and posterior faces of petiole densely covered with fine appressed hairs; hairs on dorsal face stronger and variable in length. All gastral tergites and sternites covered with soft appressed hairs and stronger long hairs. Coxae, femora and tibiae with dense pubescence; erect hairs sparse on ventral faces of coxae and femora, almost absent on tibiae except for apical area. Body entirely dark reddish brown to blackish brown; antennal flagellum slightly paler; legs brown.

Description of queen (based on Japanese specimens). Measurements (n = 2). TL: 7.0–7.2 mm, HW: 1.73–1.80 mm, HL: 1.81–1.90 mm, EL: 0.31–0.33 mm, SL: 1.35–1.38 mm, PrW: 1.36–1.38 mm, PtW: 1.05–1.06 mm; CI: 95, SI: 76–78.

In structure, sculpture and coloration similar to the worker except for caste-specific structures. Fully winged. Eye much larger than in the worker, 0.31–0.33 mm in major diameter, with ca. 16 ommatida along longest axis of eye; malar space subequal to half major diameter of eye. Pronotum densely transversely punctostriate; mesoscutum densely longitudinally punctostriate. Scutoscutellar sulcus ‘broad’; coarse rugae running from front to rear, anteriorly defined by deep suture that continues anteriorly along lateral margin of scutum. Anterior and posterior faces of petiole

more strongly rugose than in worker; dorsum of petiole irregularly sculptured (almost smooth in worker). Antennal scape bearing sparse erect hairs on its leading edge. Hindwing with jugal lobe.

Description of male (based on Japanese specimens). Measurements ($n = 5$). TL: 5.5–6.4 mm, HW: 0.95–1.08 mm, HL: 0.93–1.03 mm, EL: 0.51–0.60 mm, SL: 0.16–0.21 mm, PrW: 1.15–1.39 mm, PtW: 0.50–0.64 mm; CI: 101–109, SI: 16–20.

Head slightly broader than long when excluding eyes, but much broader when including eyes (HWe: 1.08–1.21 mm). Clypeus broadly and slightly produced anteriorly, with median portion of anterior margin almost straight. Distance between antennal insertions shorter than diameter of antennal scape. Eye large, composed of more than 50 ommatidia along longest axis of eye, with inner margin shallowly concave; its outer margin distinctly breaking lateral margin of head. Ocelli large, arranged in low triangle; distance between anterior and posterior ocelli shorter than ocellar diameter. Mandible reduced, in profile view spatulate, in dorsal view linear. Palpal formula: 6, 4. Thorax in dorsal view as broad as head; mesoscutum with profound notaulix that merges posteriorly into median sulcus that reaches posterior margin of scutum, and with weaker parapsidal line and strong parascutal carina; scutoscutellar sulcus deep with foveae on its bottom; mesoscutellum distinctly convex dorsally; metanotum ‘narrow’ band, posteriorly more sharply defined than anteriorly. Thorax in profile view with mesopleuron divided into upper and lower sections with deep and ‘broad’ sulcus whose bottom has foveolae; metapleuron demarcated from mesopleuron. Declivity of propodeum demarcated from dorsal and lateral faces, but dorsal face merging into lateral face. Petiole globular, in profile view rather thick, weakly tapered apically, with broadly rounded apex. Gaster anteriorly not truncate; with gaster in profile view anterior slope roundly continuing to dorsum; prora scale-like; gastral constriction moderate; cinctus absent.

Entire body sculptured. Dorsum of head very densely puncto-striate; in median zone between anterior ocellus and clypeus sculpture weaker; clypeus superficially sculptured and shiny. Mesosoma entirely coarsely sculptured. Anterior face and sometimes upper half of lateral face of petiole densely and irregularly sculptured; remaining portion of petiole extensively smooth and shiny. Gastral tergites and sternites superficially and finely punctate and shiny; presclerites of gastral tergite II and sternite II minutely and transversely striate. Hindwing with jugal lobe.

Head and mesosoma with dense appressed/decumbent short hairs and longer suberect hairs. Antenna and legs covered with short appressed pubescence; coxae and femora sparsely covered with longer erect/suberect hairs. Dorsum and lateral face of petiole with many erect hairs of varying length; anterior and posterior faces with shorter slanting hairs. Body entirely dark reddish brown to blackish brown; antenna, mandible, coxae and femora brown; maxillary and labial palpi, tibiae and tarsi yellowish.

Distribution. Japan: Kyushu (YAMANE et al. 2010), Amami Islands (Amami-ōshima) (ABE 1977, YAMANE

2016), Okinawa Islands (Okinawa-jima, Henza-jima, Miyagi-jima, Tokashiki-jima, Kume-jima*) (ONOYAMA 1976, TERAYAMA et al. 2014), Miyako Islands (Miyako-jima, Irabu-jima, Shimoji-jima) (TERAYAMA et al. 2014), Tarama Island (Tarama-jima) (TERAYAMA et al. 2014), Yaeyama Islands (Ishigaki-jima, Taketomi-jima, Iriomote-jima, Hateruma-jima, Yonaguni-jima) (ABE 1974, TERAYAMA et al. 2014), Senkaku Islands (Uotsuri-jima) (AZUMA 2002; TERAYAMA et al. 2009, 2014), Ogasawara Islands (Haha-jima) (KATO 1992, OHBAYASHI et al. 2003). Taiwan (FOREL 1913, TERAYAMA 2009).

Remarks. *Ectomyrmex horni* was described by FOREL (1913) as a species of *Pachycondyla* F. Smith, 1858 closely related to *Pachycondyla (Ectomyrmex) sauteri* Forel, 1912 (junior primary homonym of *Pachycondyla sauteri* Wheeler, 1906) based on the worker and queen castes. FOREL (1913) mentioned that in the worker this species is separated from the latter mainly by a larger body (7.0–7.5 mm; 6.5 mm in *E. sauteri*) and the anteroventral corner of the pronotum bluntly angulate (produced as a tooth in *E. sauteri*). Another related species, *E. denticeps* Wheeler, 1929, was described by WHEELER (1929); this is very peculiar in having a distinct tooth at the posterolateral corner of the head (WHEELER 1929: 33, fig. 2). However, YASUMATSU (1962) mentioned that another specimen in the MCZ (not cited by Wheeler) displays a different condition of this character, suggesting that the holotype shows an anomaly.

YASUMATSU (1962) assigned all the above forms to *Ectomyrmex*, synonymized *E. horni* and *E. denticeps* with *E. javanus* Mayr, 1867, and suspected that *E. sauteri* is also a junior synonym of *E. javanus* (type locality: Java). Although ONOYAMA (1980) considered *E. horni* to be conspecific with *E. sauteri*, BOLTON (1995) treated them as different species with the former being a junior synonym of *E. javanus* (referred to as *Pachycondyla javana*). In the material from Taiwan and Japan (except for Tsushima) examined by us the body size is more similar to that of *E. horni*, though rather variable, and the anteroventral corner of the pronotum is roundly angulate as in *E. horni*. These specimens agreed well with the original description and the images of the syntype of *E. horni* on ANTWEB (2024). We have thus concluded that the material we examined belonged to *E. horni*. TERAYAMA (2020: 90) tentatively treated the Japanese population as *Ectomyrmex* sp. B, but inferred that it is most probably *E. horni*, reaching a conclusion similar to our view. At present it is not certain if *E. sauteri* and *E. horni* are conspecific or not as the available material of this species complex is still insufficient.

Apart from the status of *Ectomyrmex sauteri* and *E. denticeps*, *E. horni* is clearly separated from *E. javanus* by the following combination of worker characteristics: 1) body small with head width 1.56–1.73 mm (2.03–2.23 mm in *E. javanus*), 2) dorsum of head very densely and finely rugulose or punctorugulose; rugulae more or less regular, but frequently branching or reticulate (rugulae sharply defined and coarser, more constantly regular in *E. javanus*), 3) lateral face of head weakly punctate-rugulose, matte (more coarsely rugulose in *E. javanus*); 4) frontal

lobe laterally with distinct smooth area (smooth area lacking or much less distinct in *E. javanus*), 5) mandible generally with scattered punctures in basal half and well defined longitudinal striae in apical half, but essentially shiny (mandible opaque even if entirely without visible sculpture; striation, if any, microscopic in *E. javanus*); 6) eye with sparse but conspicuous erect hairs (essentially without erect hairs in *E. javanus*), 7) outer face of mid- and hindtibiae without erect hairs (with many erect hairs in *E. javanus*). Two worker specimens from the Ogasawara Islands have slightly longer antennal scapes (1.54, 1.59 mm) and larger scape indices (SI: 86, 93) compared with workers from the Kyushu mainland and the Ryukyu Islands. More time is needed to entirely resolve the complicated problem surrounding *E. horni* and *E. sauteri*.

The Tsushima population of the *E. javanus*-complex (= *E. japonicus* (Emery, 1902) and *E. sp. A* of TERAYAMA et al. 2014) is more similar to the Korean and some other continental populations in having mandibles that are entirely striate and matte. The workers of these populations are constantly larger than those of *E. horni*, and the dorsum of the head has more regular rugae. Larger forms from Southeast Asia generally lack erect hairs on the eye, while in other characters they have various combinations of character conditions. DNA information is prerequisite for correct sorting of samples of this complex (currently assigned to *E. javanus* or treated as different species) from entire Asia into species.

Ectomomyrmex horni inhabits sparse forests and forest edges in Japan. Workers are often found under stones but nests are constructed in soil with complicated systems of passages and chambers.

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