Zootaxa 5209 (2): 293–300
https://www.mapress.com/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.5209.2.9
http://zoobank.org/urn:lsid:zoobank.org:pub:EB0B447D-47B4-46FE-9974-AFAEA955659E

Review of the genera *Rondoniella* Kaszab, 1970 and *Durandius* Kaszab, 1970 (Coleoptera: Tenebrionidae), with description of *R. hosoishii* sp. nov. from an ant nest in Cambodia

MUNETOSHI MARUYAMA[1*] & KIYOSHI ANDO[2]
[1]*The Kyushu University Museum, Hakozaki 6–10–1, Fukuoka 812-8581, Japan.*
[2]*Entomological Laboratory, Faculty of Agriculture, Ehime University, Tarumi 3–5–7, Matsuyama, 790–8566 Japan.*
https:/orcid.org/0000-0003-1794-2718
[*]*Corresponding author.* *dendrolasius@gmail.com;* *https://orcid.org/0000-0003-4531-1008*

Abstract

The enigmatic tenebrionid genera *Rondoniella* Kaszab, 1970 and *Durandius* Kaszab, 1970 are briefly reviewed and diagnosed. *Rondoniella hosoishii* **sp. nov.** is described based on specimens collected from a nest of the arboreal ant *Crematogaster sewardi* in Cambodia. Because of where *R. hosoishii* **sp. nov.** was collected and its specialized morphology, the members of *Rondoniella* and its close relative *Durandius* are considered to be myrmecophilous, as was suggested in the original description. They also have reduced mouthparts, which are unknown in other tenebrionids, and they might receive food from ants by trophallaxis.

Key words: Cnemeplatiini, Indochina, Laos, myrmecophily, Pimeliinae, taxonomy, Thailand

Introduction

Although tenebrionid beetles are found in various habitats and occur worldwide, very few species live in symbiosis with ants (myrmecophily). The enigmatic tenebrionid genus *Rondoniella* (subfamily Pimeliinae, tribe Cnemeplatiini, subtribe Rondoniellina: Bouchard *et al.* 2021) was established for *R. costata* from northern Laos, which was described at the same time (Kaszab 1970). Ferrer and Moragues (2000) added *R. bremeri* from northern Thailand as a second species in the genus. Nothing is known about the biology of the members of the genus or the genus *Durandius* Kaszab, 1970, which was originally described in the same paper (Kaszab 1970) as a close relative of *Rondoniella*. Kaszab (1970) suggested their myrmecophily or termitophily based on the shield-shaped head structures, which are often observed in inquilinous beetles (Kistner 1982; Parker 2016). Recently, Dr. Shingo Hosoishi, an ant taxonomist, collected an unidentified species of *Rondoniella* from a nest of the ant *Crematogaster sewardi* Forel, 1901 in Cambodia. Judging from the collection site and the specialized morphology of *Rondoniella* species, they are considered myrmecophilous. Comparing it with authentic specimens of the congeners, the Cambodian species was found to be a new species. Moreover, we found several interesting mouthpart characteristics in *Rondoniella* species, which indicate their highly integrated relationship with ant societies. We also had an opportunity to examine specimens of *Durandius ardoini* Kaszab, 1970, the only *Durandius* species known from Cambodia. This paper briefly reviews *Rondoniella* and *Durandius*, providing the diagnoses of the known species, a description of the new species, and a key to the species.

Material and methods

Specimens were observed under binocular microscopes Olympus SXZ9 (by MM) and Leica MZ16 (by KA), photographed using a Canon camera (EOS 7D) with MP-E 65 lens, and then combined with a montage software CombineZP. Dissected parts were soaked in a 10% KOH solution and then warmed in hot water until the muscles

Accepted by M. Lillig: 19 Oct. 2022; published: 16 Nov. 2022

and other tissues were dissolved and suitable for observation. Later, they were sealed in Euparal and preserved on a glass plate, following Maruyama (2004). The holotype of the new species will be deposited in the Kyushu University Museum (KUM) (M. Maruyama). The authentic specimens were borrowed from the Hungarian Natural History Museum (O. Merkl). We did not compare the male aedeagus in this study because it is taxonomically not very informative for these tenebrionid species and due to the paucity of the specimens allowed to be dissected. The terminology used to mouthparts, wing venation and female inner reproductive organs follows Matthews and Bouchard (2008) and Tschinkel and Doyen (1980). The following abbreviations for measurements are used (all in mm): BL, body length; HL, hindtibial length; HW, head width; PL, pronotal length; PW, pronotal width; EL, elytral length; FTL, foretibial length; MTL, midtibial length; and for wing vein: AP, anal posterior; CuA, cubitus anterior; RP, radius posterior.

The specimens used in this study were collected during expeditions in Cambodia under the Memorandum of Understanding (MOU) between Japan and Cambodia, Kyushu University, Japan and the Forestry Administration, Cambodia, on cooperation concerning biological resources and information. The materials are shared between Cambodia and Japan, but the present materials are deposited in Japan, as indefinite loan from Cambodia.

Genus *Rondoniella* Kaszab, 1970

Rondoniella Kaszab, 1970: 112 (original description).

Diagnosis. In *R. costata* and *R. hosoishii* **sp. nov.** the abdomen has no membranes between the ventrites 3 to 5, and the procoxal cavities externally closed behind, these characters are common with the other genera of the tribe Cnemeplatiini. The head is triangularly flabellate in form, and covered with scale-like setae, with a sulcus on the gular plate for receiving the antenna, and also the pronotum (venter) with a shallow excavation for receiving the antennal club; these characteristics are unique.

Additional description. Mouthparts. Labrum (Fig. 8) elongate, longer than wide, sparsely setiferous anteriorly, with some imbricate villi along apical margin, without epitorma at middle; tormal arms long, without posterior extension. Mandibles (Figs 9, 10) much reduced, apices pointed, apices to inner margin weakly sclerotized, mola rudimental and very small in the basalmost portion, without transverse ridges for grinding, entirely covered with prostheca, which bears dense and microscopic setulae; scissorial lobe with apex fringed with filmy margin, neither toothed nor incurved. Ligula (Fig. 11) simple and reduced, transverse, slightly emarginate at apex. In maxilla (Fig. 12), lacinia divided, densely pubescent over all, without uncus; apical pubescence of galea long and dense; ultimate maxillary palpomere enlarged, elongate oval.

Hind wings (Fig. 13) short, apical flecks present, lacking medial fleck; venation is rather thick, without Anal Lobe (AP_{1+2} & AP_{3+4}) in anal field (as modified from Lawrence & Britton, 1991); vein CuA_{1+2} is linked; Radio-medical Loop very broadened; RP is short, lost in basal part.

Ovipositor and cuticular parts of representative female genital tubes (Figs 16, 17) are very primitive in the Tenebrionidae; gonostyle rudimental and apical; oviduct ventrally basal; primary bursa copulatrix short and large; spermathecal gland apical, very short; coxite reduced, with lobes 3 and 4 fused; paraproct slightly longer than coxite; protigeral baculus clear, baculi-1 and baculi-2 distinctively sclerotized. Defensive glands lost, bearing only short thin membrane.

Comments. The additional description of the genus is based on the specimens of *Rondoniella hosoishii* **sp. nov.** but these characteristics are most probably also shared by the other congeners because of their obvious close relationship.

Rondoniella costata Kaszab, 1970
(Fig. 1)

Rondoniella costata Kaszab, 1970: 113 (original description).

Non-type specimen examined. 1 ♂, "Nordost Thailand / Khon Kaen / ad lucem // Dr. Sastri / Saowakontha leg. / 23. 11. 1980 // *Rondoniella* / *costata* Kaszab / det. Kaszab" (Hungarian Natural History Museum).

***Diagnosis*.** This species is closely similar to *R. hosoishii* **sp. nov.** in several character states. See the diagnosis of *R. hosoishii* **sp. nov.**

***Measurements of examined specimens*.** BL, 7.35; HL, 1.13; HW, 2.275; PL, 1.675; PW, 2.775; EL, 4.85; FTL, 1.00; MTL, 1.05.

***Comments*.** This species was originally described based on a single male specimen from "Phou Khao Khouai [Khouay]" of Vien Chang, Laos. Although we could not find the holotype, we examined the specimen identified by the author of the original description. Its locality (Khon Kaen, Thailand) is close to the type locality and the morphology agreed well with the original description.

***Rondoniella hosoishii* sp. nov.**
(Figs 2–4, 8–17)

Type series. **Holotype.** ♂, "[CAMBODIA] / Plot RK14 / Ratanakiri Prov. / N13 34, E 106 55 / 6. v. 2013 / S. Hosoishi leg." (KUM). **Paratypes.** 1 ♂, 3 ♀♀, same data as the holotype (KUM).

Etymology. The specific epithet is cordially dedicated to Dr. Shingo Hosoishi (Kyushu University), who collected the type series.

Diagnosis. *Rondoniella hosoishii* **sp. nov.** is most closely similar to *R. costata* Kaszab, 1970 in color and general body shape, but distinguished from it by the lateral depression of the pronotum being narrower, the punctation on the pronotum being finer, the striae on the elytra less clear, the tibiae being broader and less punctate, the tarsi being shorter and thicker.

Description. Body cylindrical, subparallel-sided. Color grayish black-brown overall.

Male. Head triangular, rounded at apex, with lateral margins weakly bisinuate, and with posterior margin almost straight though shallowly emarginate medially; disc laterally strongly depressed, flattened around clypeus, inner part of eyes margined, angled at posterior end; eyes small, their diameter less than half of distance between eyes; surface granulate-punctate and covered with scale-like setae; both of punctation and setation becoming sparser and finer toward lateral margins.

Venter of head densely with granules and punctures, with a longitudinal and subparallel-sided elevation in middle, the elevation weakly depressed in middle, with dense and circular tubercles; ventral eyes weakly convex, situated at posterior end beside the elevation; mentum transverse, large, strongly emarginate at apex, with a pair of connecting rods at middle of posterior margin; gula roundly convex, with dense tubercles becoming gradually larger anteriad, microscopic punctures between tubercles with short setae.

Pronotum subtrapezoid, widest around anterior 1/4; anterior margin almost straight but shallowly emarginate medially; lateral margins rounded and narrowed posteriad to angled postero-lateral corners; posterior margin widely rounded, margined and slightly depressed; disc gently convex, but strongly depressed antero-laterally, with a shallow longitudinal groove medially, which is terminated at posterior round depression; surface granulate-punctate; punctation becoming smaller and finer toward antero-lateral corners where only finely punctate. Venter of prothorax with distinct prothoracic cavity for receiving antennomeres. Prothoracic hypomera weakly depressed, with large and circular tubercles. Prosternum unevenly convex, densely and irregularly tuberculate; prosternal process cuneiform, strongly bent inward. Mesoventrite densely tuberculate, subvertical posteriorly between coxae. Metaventrite weakly convex, unevenly depressed along posterior margin, evenly covered with tubercles, and without transverse sulci. Abdomen weakly convex in middle and slightly depressed laterally, densely tuberculate.

Elytra oblong oval, widest around basal 1/3, slightly narrowed from middle toward base; nine striae slightly convex, each formed by a row of granules; surface weakly granulate-punctate; epipleura uneven, reaching almost apices of elytra, densely tuberculate, not beaded beside metepisternum.

Legs short and robust, densely with small granules and large punctures; femora rather flat, gently dilated toward near middle; tibiae dilated apicad; foretibiae with ecto-apical angles strongly produced; inner margin of hindtibia with a smooth longitudinal line.

Aedeagus slender; median lobe 1.21 times as long as the length of apicale and basale combined; basale weakly divergent posteriorly, almost entirely opened ventrally, 1.26 times as long as apicale; apicale confluent at apex, dorsally with a pair of rounded notches at base, sparsely setiferous apically.

Female. Outer margin of foretibia curved; elytra widest around apical 1/4.

***Measurements of type series*.** BL, 5.75–6.05; HL, 0.95–1.02; HW, 1.72–2.13; PL, 1.42–1.71; PW, 2.10–2.47; EL, 3.80–4.02; FTL, 0.83–0.88; MTL, 0.76–0.86 (N = 5).

***Bionomics*.** All the specimens were collected from a nest of *Crematogaster sewardi* under bark of a living standing tree. See also Discussion.

Rondoniella bremeri Ferrer & Moragues, 2000

(Fig. 5)

Rondoniella bremeri Ferrer & Moragues, 2000: 100 (original description).

Non-type specimen examined. 1 ♂ (?), "THAILAND, / Erawan N.P., / Erawam Guest House // at light, No. 96, / 15. II. 1994, / leg. S. & L. Mahunka // Rondoniella / bremeri Ferrer / det. O. Merkl, 2003" (Hungarian Natural History Museum).

Diagnosis. This species is easily distinguished from the other congeners by the combination of the following characteristics: the body being pale reddish brown; the pronotum being widest near the anterior margin; the outer margin of the foretibiae being sinuate owing to rounded weak tooth at middle. The head shape is similar to those of *R. costata* and *R. hosoishii* **sp. nov.** but the other characteristics including the body color are rather similar to those of *Durandius ardoini*. The foretibial shape is intermediate between *R. costata* (and *R. hosoishi* **sp. nov.**) and *D. ardoini*; the outer margin of the former is almost straight but the that of the latter bears rounded weak tooth.

***Measurements of examined specimen*.** BL, 4.4; HL, 0.688; HW, 1.45; PL, 0.88; PW, 1.538; EL, 2.8; FTL, 0.562; MTL, 0.623.

***Comments*.** This species was described based on a single, old specimen collected in “Siam, Gylden, Pak Koh (no other data).” Ferrer and Moragues (2000: 104) stated “Pak Koh” is Laos but they mapped the place of “Pak Koh” in an old map of Thailand. “Pak Koh” is apparently in Thailand. Dr. Sasitorn Hasin of Thailand checked some old maps of Siam, Thailand and the Lanna Kingdom to find Pak Koh but could not find it. She said that the position of "Pak Koh" is quite same position as "Pak Pan Railway Station" which is a minor train station and its position is close to Den Chai train station, Den Chai District, Phrae Province.

As is often the case in Ferrer's papers, the outline of the habitus figure of the species is not very accurate. The figure of the original description overemphasises the size of the foretibiae and the widening of the anterior angles of the pronotum.

Durandius Kaszab, 1970

Durandius Kaszab, 1970: 115 (original description).

***Comments*.** Most of the characteristics of the genus *Durandius* fit well with those of the genus *Rondoniella*. Although Kaszab (1970) accounted for the genus as distinguishing characteristics, the truncated anterior margin of the head, the character states of prothoracic hypomera and of antennal form are considered to be diagnosis of the species in the genus rather than a synapomorphy. The rounded tooth of foretibia is also recognizable in that of *Rondoniella bremeri* Ferrer & Moragues. However, we confirmed that *Durandius ardoini* does not share the character state, prothoracic cavity for receiving antennomeres, which is observed in the *Rondoniella* species, and the gular shape of *D. ardoini* is also considerably different from that of *Rondoniella* species. Also, the mouthparts are less strange than in *Rondoniella*: in *Durandius ardoini* the labrum is circular, not elongate as in *Rondoniella*, and the mandibles are well developed and slightly visible in ventral view while invisible in ventral view and apparently degenerated in *Rondoniella*. At the moment it is difficult to determine whether *Durandius* is a synonym of *Rondoniella*, so we will tentatively leave *Durandius* as an independent genus. As we examined only a single specimen of *D. ardoni* and were unable to dissect and observe the mouthparts in detail.

***Durandius ardoini* Kaszab, 1970**
(Figs 6, 7)

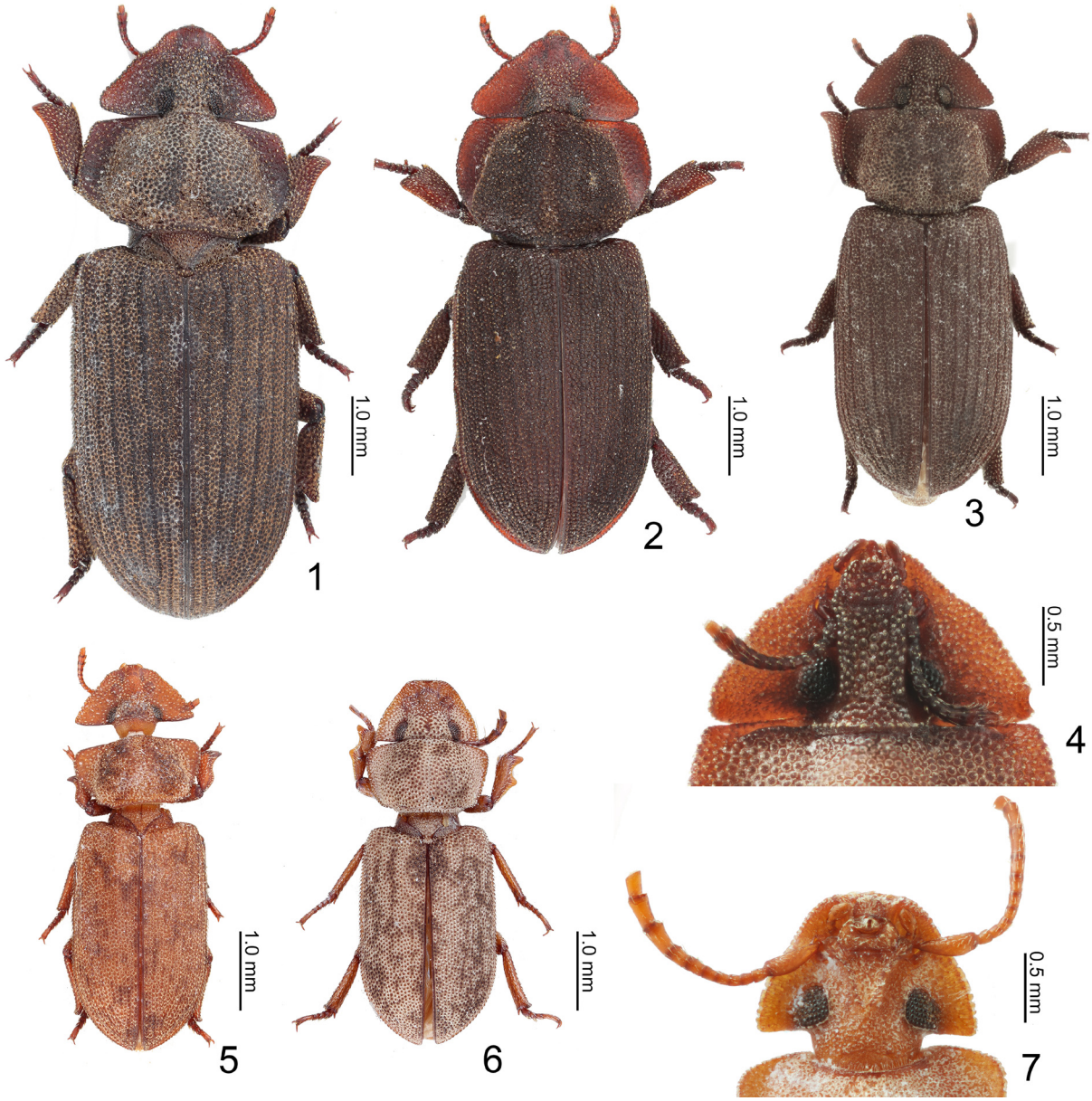
Durandius ardoini Kaszab, 1970: 116 (original description).

Type specimens examined. **Paratypes.** 1 male (?), "CAMBODGE / Dei Dos / II. 1965 // Paratypus 1969 / *Durandius* / *ardoini* / Kaszab"; 1 ex. (sex?), "II. 1965 / Dei Dos / Cambodge / H. Durand leg." (both Hungarian Natural History Museum).

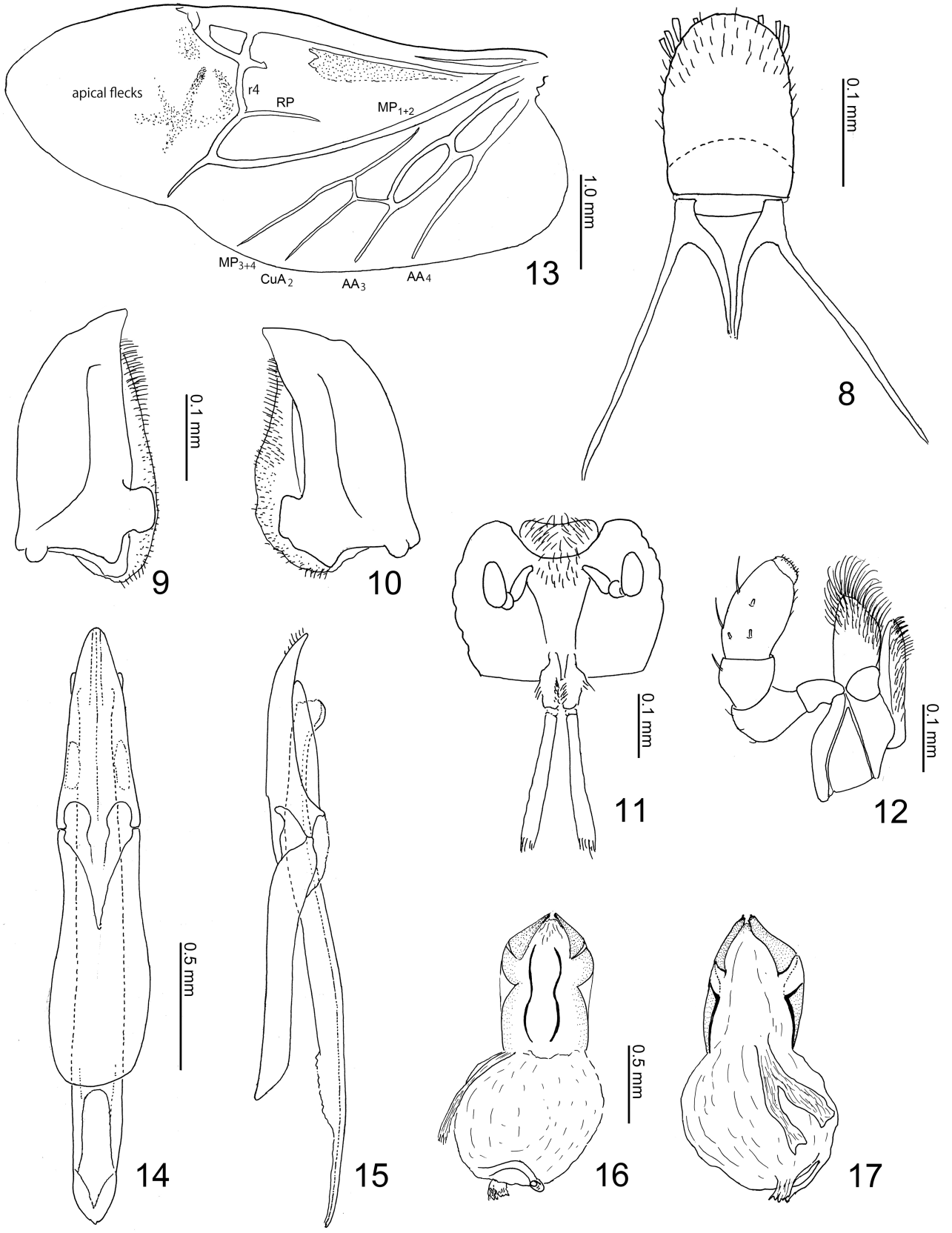
Non-type specimen examined. 1 ♀, "Cambodia (Mekong River) / Kampong Cham / 12º12'7.80"N 105º32'46.36" / 15–16 Feb. 2014" (Maruyama collection at the Kyushu University Museum).

Diagnosis. This species is easily distinguished from the members of *Rondoniella* by the combination of the following character states: the body color being light brown; the head being trapezoid, clearly truncate at the apex; the outer margin of the foretibia with distinct rounded tooth.

Measurements of examined specimens. BL, 4.5–5.0; HL, 0.77–0.81; HW, 1.31–1.33; PL, 0.95–1.01; PW, 1.56–1.62; EL, 2.76–2.85; FTL, 0.72–0.73; MTL, 0.77–0.79.



FIGURES 1–7. 1, Habitus of *Rondoniella costata* Kaszab, 1970; 2, habitus of *R. hosoishii* Maruyama & Ando **sp. nov.** (holotype male); 3, ditto (paratype female); 4, head of *R. hosoishii* **sp. nov.**, ventral view; 5, habitus of *R. bremeri* Ferrer & Moragues, 2000; 6, habitus of *Durandius ardoini* Kaszab, 1970; 7, ditto, head, ventral view.



FIGURES 8–17. *Rondoniella hosoishii* Maruyama & Ando **sp. nov.:** 8, labrum, dorsal view; 9, left mandible, dorsal view; 10, right mandible, dorsal view; 11, mentum and labium, adoral view; 12, left maxilla (cardo removed), ventral view; 13, left hindwing; 14, aedeagus (holotype), dorsal view; 15, ditto, lateral view; 16, 17, female genitalia.

A key to species of the genera *Rondoniella* and *Durandius*

1. Head trapezoidal, truncate at apex; eyes large; gular plate triangular with weak sulci for receiving antennae, and prothoracic hypomera of pronotum without excavation for receiving antennal clubs; outer margin of fortibia with distinct tooth at middle. Body length: 4.00–5.80 mm (genus *Durandius*) . . . . . *D. ardoini* Kaszab
- Head triangular, rounded at apex; eyes small; gular plate parallel-sided with distinct sulci for receiving antennae, and prothoracic hypomera of pronotum with excavation for receiving antennal clubs; outer margin of fortibia simple or with weak rounded process at middle. Body length: 4.30–7.35 mm (genus *Rondoniella*) 2
2. Body darker, grayish black-brown; elytra with punctate striae; outer margin of foretibia simple, almost straight 3
- Body paler, light brown or pale reddish brown; elytra without punctate striae; outer margin of foretibia sinuate owing to rounded weak process at middle. Body length: 4.40–4.60 mm . . . . . *R. bremeri* Ferrer & Moragues
3. Pronotum more finely punctate, with lateral depression narrower; elytral striae more ambiguous; tibiae broader and less punctate; tarsi shorter and thicker. Body length: 5.75–6.05 mm . . . . . *R. hosoishii* **sp. nov.**
- Pronotum more coarsely punctate, with lateral depression wider; elytral striae distinct; tibiae narrower and more densely punctate; tarsi longer and slenderer. Body length: 4.30–7.35 mm. . . . . *R. costata* Kaszab

Discussion

The type series of *Rondoniella hosoishii* **sp. nov.** was found in the center of a *Crematogaster sewardi* nest, under the bark of a living tree, and no aggressive or exclusive behavior by the ants toward the beetles was observed (Hosoishi pers. comm.). Considering this and the similarity of the specialised body shapes of the congeners, *Rondoniella* species are most probably myrmecophiles. Although many arboreal *Crematogaster* species are known, few studies of myrmecophiles associated with them have been conducted in Asia due to the difficulty searching for nests, which are often high in trees in living tree trunks, which are rarely excavated. Recently, new genera belonging to Scarabaeidae and Brentidae were found from a *C. difformis* nest in Borneo (Maruyama, 2010; Maruyama *et al*. 2014). *Crematogaster difformis* and *C. sewardi* belong to the *inflata* species group (Blaimer 2012). Further investigation of this group of ants is likely to reveal other interesting myrmecophiles, such as those found here.

Our study also revealed that *Rondoniella* species share very strange mouthpart structures, including degenerate mandibles, which are small, with a sub-membranous tip, and are unable to chew solid food. In other myrmecophilous insects, such as myrmecophilous crickets (Komatsu *et al*. 2018) and *Lomechusa* beetles (Hölldobler & Kwapich 2022), the species with degenerate mandibles do not feed on solid food and receive food from ants by trophallaxis. *Rondoniella* beetles are probably also fed in the same way. This should be verified by captive observation of live beetles and ants. No such case has been found in myrmecophilous tenebrionid beetles and, if verified, would be a very interesting discovery.

Durandius ardoini has morphological characteristics similar to *Rondoniella* species and it is also most probably myrmecophilous. However, it has a more "normal" mouthpart morphology, which suggests that this species has less tightly integrated relationships with its host ant. Komatsu *et al.* (2018) showed that myrmecophilous crickets with weaker mouthpart specialisation also had weaker relationships with ants, indicating that they feed on their own food. Closely related species can have strong or weak relationships with ants, as supported by the differences between *Rondoniella* and *Durandius* species.

Acknowledgements

We thank Dr. Shingo Hosoishi (Institute of Tropical Agriculture, Kyushu University) for offering the material and the biological information of the new species and Dr. Tetsukazu Yahara for establishing co-operative relationship with Cambodian government and institutes which allowed biodiversity research by the staff of Kyushu University. They also confirmed the local collaborators suggesting the type depository of new species (at least part of them will be returned when a reliable collection facility is established in Cambodia, as well as the material in the other papers by Kyushu University staff). We also thank the late Dr. Ottó Merkl (Hungarian Natural History Museum) for kindly making a loan of the important material used in this paper, and Dr. Hasin Sasitorn (Valaya Alongkorn Rajabhat University, Thailand) for a geographical information concerning the type locality of *R. bremeri*. Our thanks are also due to Dr. Wolfgang Schawaller and Dr. Luboš Purchart for critically reviewing the manuscript. The colleting

survey in Cambodia by Dr. Hosoishi was supported in part by the Global COE program (Center of Excellence for Asian Conservation Ecology as a Basis of Humannature Mutualism), MEXT, Japan funded to Kyushu University. This paper is supported by KAKENHI (19H03285) funded to MM.

References

Blaimer, B.B. (2012) A subgeneric revision of *Crematogaster* and discussion of regional species-groups (Hymenoptera: Formicidae). *Zootaxa*, 3482, 47–67.

Ferrer, J. & Moragues, G. (2000) Contribution á l'etude des Cnemmeplatiini. Description de *Rondoniella bremeri* n. sp. du Laos (Coleoptera, Tenebrionidae). *Nouvelle Revue d'Entomologie*, New Series, 17 (2), 99–105.

Hölldobler, B. & Kwapich, C.L. (2022) *The guests of ants*. Harvard University Press, Cambridge, Massachusetts, 576 pp. https://doi.org/10.4159/9780674276451

Kaszab, Z. (1970) Fünf neue Tenebrioniden aus Asien (Coleoptera). *Entomologische Arbeiten aus dem Museum Georg Frey*, 21, 112–120.

Kistner, D.H. (1982) The social insects' bestiary. *In*: Hermann, H.R. (Ed.), *Social insects*. *Vol. III*. Academic Press, New York, pp. 1–244. https://doi.org/10.1016/B978-0-12-342203-3.50008-4

Komatsu, T., Maruyama, M., Hattori, M. & Itino, T. (2018) Morphological characteristics reflect food sources and degree of host ant specificity in four Myrmecophilus crickets. *Insectes Sociaux*, 65, 47–57. https://doi.org/10.1007/s00040-017-0586-3

Lawrence, T.F. & Britton, E.B. (1991) Coleoptera (Beetles). *In*: CSIRO Division of Entomology (Ed.), *Insects of Australia: A Textbook for Students and Research workers, Second Edition*. *Vol. 2*. Melbourne University Press. Carlton, Victoria, pp. 543–683.

Maruyama, M. (2004) A permanent slide pinned under a specimen. *Elytra*, 32 (2), 276.

Maruyama, M. (2010) A new genus and species of myrmecophilous aphodiine beetle inhabiting the myrmecophytic epiphyte *Platycerium* sp. (Polypodiaceae) in the Bornean rainforest canopy. *Zookeys*, 34, 49–54. https://doi.org/10.3897/zookeys.34.281

Maruyama, M., Bartolozzi, L., Inui, Y., Tanaka, H., Hyodo, F., Shimizu-Kaya, U., Takematsu, Y., Hishi, T. & Itioka, T. (2014) A new genus and species of myrmecophilous brentid beetle (Coleoptera: Brentidae) inhabiting the myrmecophytic epiphytes in the Bornean rainforest canopy. *Zootaxa*, 3786 (1), 73–78. https://doi.org/10.11646/zootaxa.3786.1.5

Matthews, E.G. & Bouchard, P. (2008) *Tenebrionid Beetles of Australia*. Australian Biological Resources Study, Canberra, viii + 398 pp.

Parker, J. (2016) Myrmecophily in beetles (Coleoptera): evolutionary patterns and biological mechanisms. *Myrmecological News*, 22, 65–108.

Tschinkel, W.R. & Doyen, J.T. (1980) Comparative anatomy of the defensive glands, ovipositor and female genital tubes of tenebrionid beetles (Coleoptera). *International Journal of Insect Morphology and Embryology, Oxford*, 9, 321–368. https://doi.org/10.1016/0020-7322(80)90009-4