瑤寺　裕

Revision of the leaf-mining jewel beetle tribe Tracheini from Japan (Coleoptera, Buprestidae, Agrilinae), with notes on the morphology-based phylogeny of genera and species

（日本産潜葉性チビタマムシ族の分類学的再検討および
形態に基づく属ならびに種の系統について）

北海道大学 大学院農学院　農学専攻
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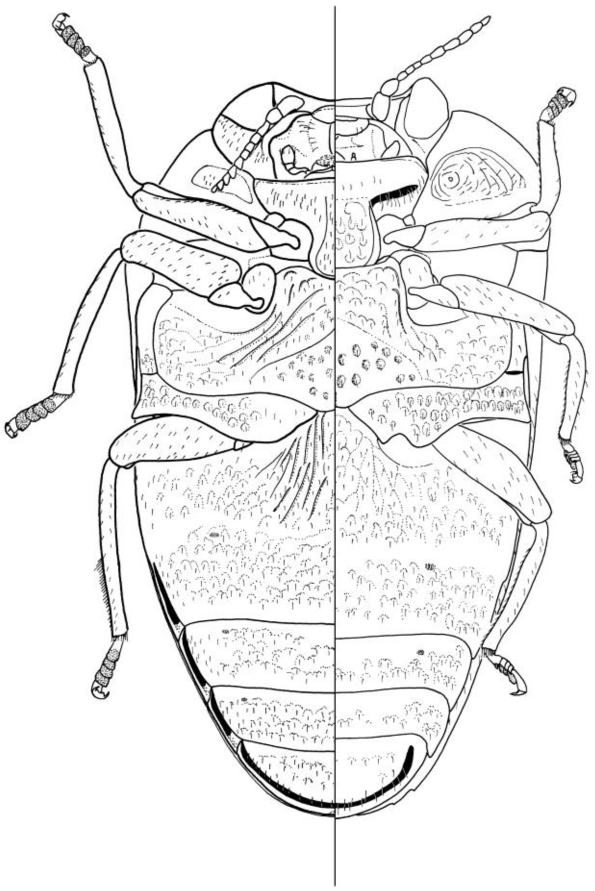

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by
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Abstract

This thesis revised the taxonomy of Japanese Tracheini (Coleoptera, Buprestidae, Aglirinae) based on morphological information and contributed to the morphology and biology for leaf-mining jewel beetles thorough detailed morphological observations, cladistic analyses, and investigations of host associations. General morphology of *Trachys* and *Habroloma* are described in detail and their diagnoses are revised. In addition, their biological information, especially on the leaf-mining habit, is reviewed. Species diagnostic characters for each genus are also reviewed, with some newly proposed useful characters for their species identifications. To systematically classifying them, species-group concepts are tentatively proposed for Japanese species of the two genera, respectively.

So far, two genera, *Trachys* Fabricius, 1801 and *Habroloma* Thomson, 1864, and 32 species of Tracheini are recorded from Japan. In Japanese *Trachys*, nineteen species in seven tentative species-groups, including five junior synonyms, are recognized: group I) *T. minutus* (Linnaeus, 1758) (= *T. minutus salicis* (Lewis, 1893) **syn. nov.**), *T. inconspicuus* Saunders, 1873, *T. pseudoscrobiculatus* Obenberger, 1940, *T. ineditus* Saunders, 1873, *T. tsushimae* Obenberger, 1922, and *T. broussonetiae* Kurosawa, 1976; group II) *T. auricollis* Saunders, 1873 and *T. toringoi* Kurosawa, 1951; group III) *T. saundersi* Lewis, 1893 (= *T. cuneiferus* Kurosawa, 1959 **syn. nov.**), *T. cupricolor* Saunders, 1873, *T. pecirkai* Obenberger, 1926, and *T. aurifluus* Solsky,1875; group IV) *T. reitteri* Obenberger, 1930 (= *T. lushanensis* Peng, 2021 **syn. nov.**); group V) *T. tokyoensis* Obenberger, 1940 (= *T. ovalis* Peng 2021 **syn. nov.** and *T. aureoles* Peng, 2021 **syn. nov.**); group VI) *T. griseofasciatus* Saunders, 1873 and *T. yanoi* Kurosawa, 1959; and group VII) *T. variolaris* Saunders, 1873, *T. robustus* Saunders, 1873, and *T. dilaticeps* Gebhardt, 1929. A new key and biological information (adult foods, hosts, and leaf-mining habits) are provided. Twenty-five plant species in ten families are recognized as hosts (five new host records).

In Japanese *Habroloma*, two subgenus, *Habroloma* and *Parahabroloma* Kurosawa, 1959 are so far recorded from Japan. In this study, eleven species and three subspecies in three species-groups (for *Parahabroloma* species), including one undescribed species, two undescribed subspecies, one junior synonym, and one removed species, are recognized: *H.* (*H.*) *bifrons* (Kiesenwetter, 1879); group I) *H.* (*P.*) *eximium eximium* (Lewis, 1893), *H.* (*P.*) *eximium eupoetum* (Obenberger, 1929) (= *H.* (*P.*) *liukiuense* (Obenberger, 1940) **syn. nov.**), *H.* (*P.*) *eximium* subsp. 1 (= *H.* (*P.*) *liukiuense* sensu

Kurosawa, 1976), and *H*. (*P*.) *griseonigrum* (Saunders, 1873); group II) *H*. (*P*.) *lewisii* (Saunders, 1873), *H*. (*P*.) *nixilla inslicola* Kurosawa, 1959, and *H*. (*P*.) *yuasai* Kurosawa, 1976; group III) *H*. (*P*.) *subbicorne* (Motschulsky, 1860), *H*. (*P*.) *marginicolle*, *H*. (*P*.) *asahinai asahinai* Kurosawa, 1959, *H*. (*P*.) *asahinai* subsp. 1, and *H*. (*P*.) sp. 1; and removed species, *H*. (*P*.) *atronitidum* Gebhardt, 1929. A new key and biological information (adult foods, hosts, and leaf-mining habits) are provided. Fourteen plant species in six families are recognized as hosts (nine new host records).

Phylogenetic relationships among genera of Tracheini and between species in Japanese *Trachys* and *Habroloma* are investigated using cladistic analyses based on morphology. The polyphyly of Tracheini and the monophyly of each subtribe are indicated. In the subtribe Tracheina, *Trachys* and *Habroloma* are recognized as a monophyletic genus, respectively. Sixteen character states (including three doubtful one) are useful to distinguish the two genera and autapomorphic character states are estimated: the delimitation of the basistipes and palpifer reduced in *Trachys*; the female coxites with the dorsal projections of baculi in *Trachys*; and the prosternum with transverse grooves above procoxal cavities in *Habroloma*. In the Japanese *Trachys*, the monophyly of the tentative species-groups III, IV, V, and VII and the paraphyly of the group I, II, VI are indicated. In addition, two additional species-groups consisted of Taiwanese species are estimated. It is needed improvements of species-group concepts: the additional divisions of group I; the assignment changing of *T. toringoi* to the estimated additional group; and the integration of group VI and VII. Host associations of Japanese *Trachys* suggest that host shifts to distant plant families are contributed to the speciation of this genus. In the Japanese *Habroloma*, the monophyly of the tentative species-group I and II and the polyphyly of the group III are indicated. It is needed the assignment changing of *H*. (*Parahabroloma*) sp.1 to the group II and improvements of the species-group concepts. Host associations of Japanese *Habroloma* suggest the following two hypotheses: 1) host shifts to distant plant families are contributed to the speciation of the members of group I and II; and 2) other factors (e. g. geographic isolation) are contributed to the speciation of the revised group III, of which species are exclusively associated with *Rubus* plants.

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Enumeration of species

Genus *Trachys*

Genus *Habroloma*

Subgenus *Habroloma*

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Chapter 1. Introduction

The leaf-mining habit independently occurs in various herbivorous insects (Connor & Taverner, 1997). The mines provided by leaf-miners have sufficient information for identifying insect species and for clarifying life history, behavior, and insect-host association (Hering, 1951; Hespenheide, 1991; Hirowatari, 2011). Biological information obtained from mines often helps taxonomists to find cryptic species and to understand phylogenetic relationships, morphological evolutions, and speciation (e.g. Kumata, 1978; Hartsough *et al*., 2007; Kobayashi *et al*., 2021).

The members of the tribe Tracheini Laporte, 1835, belonging to the subfamily Agrilinae (Coleoptera, Buprestidae), are well known as most species diverse leaf-mining jewel beetles and consisted of more than 2,000 species in twelve genera, four subtribes (Bellamy, 2003, 2008 b; Hespenheide, 2014; Migliore *et al*., 2020 a). This tribe is mainly differentiated from the tribe Apahisticini by the absence of the antennal grooves on hypomera (Hołyński, 1993), but there are some exceptions which are regarded as reasons for combining members of Tracheini and Aphanistici into a single group, the subfamily Trachyinae *sensu* Cobos (1979) (except Cylindromorphina). In addition, the monophyly of Tracheini have been suspected (Bellamy, 2000) and a comprehensive molecular study (Evans *et al*., 2015) indicates the polyphyly of this tribe. The estimated artificial tribe Tracheini, however, has been maintained due to the lacking of morphological information to revise its concept. Detailed morphological examinations seem to be still very useful for the morphologically poor knowledge jewel beetles. For example, Migliore *et al*. (2020 a) revealed the mistake of genus affiliation in Tracheini thorough detailed comparative morphology (namely, the genus *Taphroceroides* Hespenheide, 2007 that was placed in the subtribe Brachyina of the tribe Tracheini was transferred into the subtribe Cylindromorphoidina of the tribe Aphanisticini). There is no doubt that understanding of morphology of the type genus *Trachys* is an essential step to resolve the polyphyly of Tracheini, to precisely redefine this tribe, and to understand morphological chance similarities in Buprestidae attributed to the leaf-mining habit.

In Japan, two genera, *Trachys* and *Habroloma*, of the subtribe Tracheina in the tribe Tracheini are recognized. The genus *Trachys* Fabricius, 1801 is a species-rich genus and contains more than 600 described species. Members of this genus are widely distributed in the Old World except for one Australasian species (Bellamy, 2008 b; Lawrence &

Lemann, 2019). *Trachys* is known as one of the most famous leaf-mining jewel beetles associated with various dicotyledonous plants (Hering, 1951; Yano, 1952; Bílý, 2003) and is also as the type genus of the tribe Tracheini mentioned above. The genus *Habroloma* Thomson, 1864 contains more than 250 described species. Species of this genus are also widely distributed in the same biogeographic regions of *Trachys* and are dicotyledonous plant leaf-miners (Yano, 1952; Bílý, 2003). This genus occasionally treated as a subgenus of *Trachys* due to dull-defined morphological separation shown by several species (e.g. Obenberger, 1929 a; Hołyński, 2003). In the recent classification system of Buprestidae (Bellamy, 2003, 2008 b), *Trachys* and *Habroloma* are recognized as independent genera. The morphological differences between them are always discussed on the basis of the superficial morphological examinations (Théry, 1938; Cobos, 1979). Because of autapomorphic morphological information of them are not revealed, the taxonomic treatment of *Habroloma* is actually still unstable. This problem seems to be caused by the traditional taxonomy of *Trachys* and *Habroloma*, of which species are described based only on superficial morphology and not even examined male terminalia (genital segment) except a few studies.

Taxonomy of Japanese *Trachys* and *Habroloma* species has been well studied for a long time. To date, 32 species and three subspecies are recognized in Japan (Kurosawa, 1951, 1959, 1976 a; 1985 a; Akiyama & Ohmomo, 1995; Fukutomi & Ohmomo, 2013). However, it seems that some problems are remaining in taxonomy of them: previous studies, unfortunately, did not examine the structures of male and female terminalia except for a few studies (Ishiguro & Nishida, 2018; Tamadera & Yoshitake, 2018 c); the identification of Japanese species using keys is rather difficult because the keys of Kurosawa (1959) and the modified keys of Ohmomo & Fukutomi (2013) are starting from the coloration and patterns of fragile body setae and using many quantitative characters without measurement values and helpful figures; and my preliminary investigation suggests that taxonomic treatments of several species are doubtful and that one undescribed *Habroloma* species are founded.

With regard to biological information, Yano (1952, 1954 & 1955) described leaf-mimes and larval morphology for 15 Japanese *Trachys* and *Habroloma* species (Yano's studies, unfortunately, include misidentifications which are referenced in the correspondence parts of the world catalog of Buprestoidea (Bellamy, 2008 b) in error). Later, some studies recorded additional biological information (e.g. Inada & Fukutomi, 2008; Takahashi, 2008; Tamadera & Yamada, 2019). Four *Trachys* species and six *Habroloma* species have never been described their leaf-mining habits.

The aims of this study are to contribute to the morphology and biology of the tribe Tracheini and revise taxonomy of Japanese Tracheini. Specifically, this study addresses (1) to describe adult morphology of the genus *Trachys* and *Habroloma* in detail, (2) to review known useful characters for species identification of them and explore more useful ones, (3) to revise taxonomy of Japanese *Trachys* and *Habroloma*, with redescriptions of known species, new keys to species, and biological information (leaf-mining habits and host associations), and (4) to reconstruct phylogenetic relationships between genera in the tribe Tracheini as preliminary investigation and between species in *Trachys* and *Habroloma*, respectively, then discuss on their unique morphology and host associations.

Chapter 2. Material and Methods

Material and depository. This study examined dried specimens of the Japanese Tracheini, the genera *Trachys* and *Habroloma*. These specimens are preserved in the following institutions and private collections: EUM — Ehime University Museum, Matsuyama, Japan; HFCH — Hirokazu Fukutomi collection, Hakusan, Japan; KCMH — Kushiro City Museum, Hokkaido, Japan; NIAES — Institute for Agro-Environmental Sciences, NARO, Tsukuba, Japan; NSMT — National Museum of Nature and Science, Tsukuba, Japan; SEHU — Systematic Entomology, Hokkaido University, Sapporo, Japan; SOCI — Sadahiro Ohmomo collection, Inashiki, Japan; STCH — Susumu Tskahashi collection, Hokkaido, Japan; TUA — Laboratory of Entomology, Tokyo University of Agriculture, Atsugi, Japan; YTJ — Yutaka Tamadera collection, Japan; YTCU — Yûji Tsutsumiuchi collection, Usuki, Japan; WYCA — Wataru Yamada collection, Atsugi, Japan. Verbatim label data indicated by double quotation marks are provided for the holotypes. Label breaks are indicated by a slash ("/").

Observation, dissection, and terminology. Morphological observations were conducted under a Nikon SMZ745T stereomicroscope, a Nikon SMZ800 one, and a Nikon Eclipse E800 optical microscope. The illustrations of structures except terminalia were traced from photographs taken under a Nikon digital sight DS-Fi2 attached to the stereomicroscopes or the optical microscope. Dissection, observation, and illustration methods for the male and female terminalia follows Tamadera and Yoshitake (2018 c). Hind wings were carefully removed from body after macerating in hot water and then glued onto cover glasses or paper mounting cards. Furthermore, to dissect and observe another body parts in detail, whole body were cleaned in ca 10% KOH solution and supplementary decolorized in ca 3% H_2O_2 solution as appropriate. After washing distilled water, each body part was mounted on slides with glycerol or much less than 70% ethyl alcohol. Membranous parts were stained with Chlorazol Black E solution as appropriate. After observation, body parts of each specimen were stored in a polyethylene or glass genital vial filled with glycerol or mounted on a small slide glass with euparal (Maruyama, 2004). Morphological terminology mainly follows Lawrence and Ślipiński (2013) for the general structures, Tamadera and Yoshitake (2018 c) for the male and female terminalia, and Harris (1979) for the body surface sculpturing. For other morphological terms, indicate citation when using them in the section of the general morphology and terms for the genus *Trachys*.

Measurement. Measured body parts and abbreviations used in this study are shown in Fig. 1. Measurement abbreviations are as follows:

Body (Fig. 1A): LB — maximum length of body from apex of head capsule to apices of elytra; WB — maximum width of body.

Head (Fig. 1B): LC — length of clypeus along midline; LSC — length from line of suprantennal pores to apical margin of clypeus along midline; WC — minimum width of clypeus between antennal insertions.

Pronotum (Fig. 1A): AMP — width of apical margin of pronotum; BMP — width of basal margin of pronotum; LP — maximum length of pronotum along midline; WP — maximum width of pronotum.

Elytra (Fig. 1A): LE — length of elytra from basal margin of scutellar shield to apices of elytra; WE — maximum width of elytra.

Prosternum (only for *Habroloma*): BTP — basal width of trapezoidal plate; LTP — maximum length of trapezoidal plate along midline; WTP — maximum width of trapezoidal plate.

Terminalia [mainly following Tamadera & Yoshitake, 2018 c] (Figs. 1C–F): PL — maximum length of parameres; PbL — maximum length of phallobase; PbW — maximum width of proximal part of phallobase [partly modified Tamadera & Yoshitake, 2018 c]; PeL — maximum length of penis including median struts [additionally measured part]; PeW — maximum width of dorsal plate of penis except median struts [additionally measured part]; PW — maximum width of parameres; SL — maximum length of male sternite IX; SW — maximum width of male sternite IX except for struts at base; SlL — maximum length of stylus; SlW — maximum width of stylus.

Photography. Habitus photographs were taken under a Nikon digital sight DS-Fi2. Each final image was assembled from a series of photographs with different focus planes using CombineZP (Hadley, 2010). SEM photographs were taken with a JSM-6510 scanning electron microscope. Leaf-mine photographs on white background were scanned with an EPSON GT-S640 scanner within a few days after collection in the field. All images were edited using Adobe Photoshop CC 2019.

Biogeographical regions, plant nomenclature, and host determination. The biogeographical regions used in this study follow the world catalog of the superfamily

Buprestoidea of Bellamy (2008 a): Afrotropical; Madagascan (the island of Madagascar, the Comoro and Mascarine Islands); Palaearctic; Oriental; Oceania; Australasian; Nearctic; Neotropical; and Patagonian (temperate southern South America, parts of Argentina and Chile). Plant nomenclature follows Yonekura and Kajita (2003-) for Japanese plant species and WFO (2022) for other ones. The terms, 'host plant' and 'host', are meaning the larval food plant in this study and are strictly distinguished from the adult food plant. The determination of host plant is based on rearing larvae collected from the field then confirming adult emergence. The adult specimens reared from immature stages by the author are indicated their rearing numbers, 'rearing no.', in each specimen data. For example, 1 ex., Hokkaido University, Sapporo, 1.V. 2022, Y. Tamadera leg., emerged from *Ulmus davidiana*, 5.V.2022, rearing no. 2022-001. Literature records of hosts for Japanese *Trachys* often include adult food plants without distinguishing from larval food plants. Such records based only on adult foods (no indication for the larval rearing or the adult emergence from leaf-mines) are also referenced as host plants in this study, but 'adult record?' are indicated within parentheses for referenced literatures. For example, *Cydonia oblonga* Mill. [Japanese name: Marumero] (Kurosawa, 1959: adult record?).

Cladistic analysis. To clarify generic relationships of the tribe Tracheini and species relationships of Japanese *Trachys* and *Habroloma*, cladistic analyses are conducted, respectively, on the basis of adult morphology. Detailed methods for the analyses are described in the corresponding section of the chapter 4.

Chapter 3. Systematics

Subfamily Agrilinae Laporte, 1835
Tribe **Tracheini** Laporte, 1835

Notes. Type genus of the Tracheini is the genus *Trachys* Fabricius, 1801. This tribe contains the following twelve genera in four subtribes (Bellamy, 2008b; Hespenheide, 2014; Migliore *et al*., 2020 a): 1) Tracheina Laporte, 1835 — *Trachys* Fabricius, 1801, *Habroloma* Thomson, 1864, and *Neotrachys* Obenberger, 1923; 2) Brachyina Cobos, 1979 — *Brachys* Dejean, 1833, *Lius* Deyrolle, 1865, and *Taphrocerus* Solier, 1833; 3) Leiopleurina Hołyński, 1993 — *Leiopleura* Deyrolle, 1865 and *Callimicra* Deyrolle, 1865; and 4) Pachyschelina Bøving & Craighead, 1931 — *Pachyschelus* Solier, 1833, *Hylaeogena* Obenberger, 1923, *Hedwigiella* Obenberger, 1941, and *Euhylaeogena* Hespenheide, 2014.

Relative to the number of known species of the tribe Tracheini, more than 2,000 spp. (Bellamy, 2008 b), the knowledge of the biology for them are prominently limited due to the lack of sufficient surveys. Generally, immatures of the tribe Tracheini are known as leaf-miners of angiosperms. However, recent studies revealed that several species (or genera) are gall-inducers (Medianero *et al*., 2007; Ascendino and Maia, 2018) or fruit- and seed-borers (Lourenço *et al*., 2017). Most of genera, *Trachys*, *Habroloma*, *Brachys*, *Leiopleura*, *Pachyschelus*, *Hedwigiella*, and *Euhylaeogena*, are leaf-miners associated with various dicotyledonous plants (e.g. Weiss & Nicolay, 1919; Hering, 1942; Yano, 1952; Bílý, 2003; Kogan, 1963, 1964a, b; Dhileepan *et al*., 2013; Hornburg, 2014; Solís-Blanco *et al*., 2016; Hespenheide and Eiseman, 2016; Migliore *et al*., 2020 b). In addition, *Euhylaeogena thoracica* (Waterhouse, 1889) is known as a gall-inducer of *Amphilophium paniculatum* (L.) H.B.K (Bignoniaceae; Medianero *et al*., 2007). The genus *Taphrocerus* is monocot leaf-miners associated with the family Cyperaceae (Story *et al*., 1979). In addition, two species of *Brachys* and one species of *Neotrachys* (see below) are known as monocot leaf-miners (Hering, 1942; Meurgey, 2017). In Buprestidae, all other monocot leaf-miners are found only from members of the tribe Aphanisticini (*Aphanisticus*, *Cylindromorphus*, *Paracylindromorphus*, and *Germarica*), which is considered to be a related tribe of Tracheini. The genus *Neotrachys* is considered to be leaf-miners associated with ferns since their adults are collected on leaves of ferns (Hespenheide, 1980, 1982), except for *Neotrachys dominicanus* Théry, 1947 is known as a monocot leaf-miner of *Arthrostylidium venezuelae* (Steud.) McClure (Poaceae; Meurgey, 2017). In Buprestidae, fern-associated leaf-miners are very rare and only found from this genus and one genus of the tribe Aphanisticini (*Endelus*: Kurosawa, 1985a; Goolsby *et al*., 2003). In the remaining three genera of Tracheini, *Lius conicus* (Gory & Laporte, 1840) is known as fruit- and seed-borers of *Vochysia haenkeana* C. Mart. (Vochysiaceae; Lourenço *et al*., 2017). *Callimicra* sp. from Brazil is recorded by Ascendino and Maia (2018) as a gall-inducer of "*Ficus* sp. 2" (Moraceae). The genus *Hylaeogena* shows no information of the larval habits and host associations after changing of its taxonomic concept (Hespenheide, 2014; Hornburg, 2014).

Subtribe **Tracheina** Laporte, 1835

Trachisites Laporte, 1835: 166 (type genus: *Trachys* Fabricius, 1801) [part].

Traches: Théry, 1929: 268 (in Agrilini) [part].

Trachyini: Cobos, 1978: 65 (as tribe; without definition; in Trachyinae); 1979: 425 (with definition; in Trachyinae).

Trachydina: Hołyński, 1993: 15, 39 (downgrade of Trachyini *sensu* Cobos, 1979); Bellamy, 2003: 95 (catalogued).

Trachina: Bellamy, 2002 c: 414 (catalog; spelling emendation).

Trachyina: Bellamy, 2008: 2464 (World catalog; spelling emendation in Nelson *et al*., 2008).

Tracheina [justified emendation based on ICZN, 2009: 100]: Löbl & Smetana, 2013: 30 (in errata for Kubáň, 2006: 416); Evans *et al*., 2015: 12 (molecular phylogeny); Kubáň, 2016: 568 (catalog).

Type genus. *Trachys* Fabricius, 1801.

Genera included. *Trachys* Fabricius, 1801, *Habroloma* Thomson, 1864, and *Neotrachys* Obenberger, 1923

Diagnosis. The Tracheina has been estimated as polyphyletic group (Evans *et al*., 2015), but is distinguished from other subtribes of the tribe Tracheini by the absence of the antennal grooves on hypomera (Cobos, 1979; Hołyński, 1993).

Note. The presence or absence of the antennal grooves on hypomera is very useful to distinguish the subtribe Tracheina from the other subtribes of the tribe Tracheini. The absence of the antennal grooves, however, is also shared with the members of the tribe

Aphanisticini which is considered to be a related group of Tracheini. This character state is important to separate the two tribes except the subtribe Tracheina. Due to the dull-defined separation of them, Cobos (1979) treated that Tracheini and Aphanisticini are the same group (the subfamily Trachyinae). On the other hand, Hołyński (1993) separated the two tribes and added several character states to resolve the dull-defined separation in the antennal grooves as follows (cited from the key): "Propleura without sulci for antennae. If femora without sulci for tibiae, then either supraantennal pits absent, or propleural suture double" (p. 39) — Aphanisticini; "Propleura with deep sulci for antennae; or humeri without sulci for tibiae, supraantennal pits present, and propleural suture simple" (p. 39) — Tracheini. Although these character states of Hołyński (1993) are seemed to be weak for separating tribes, the latter treatment, at the present time, is widely followed in the systematics of Buprestidae (e.g. Bellamy, 2008 b; Kubáň, 2016).

3.1 Review of the genus *Trachys*

— synonymy, general morphology, and biology —

Genus ***Trachys*** Fabricius, 1801

Trachys Fabricius, 1801: 218 (no designation of type species); Westwood, 1838: 25 (type species: *Buprestis minuta* Linnaeus, 1758, fixed by subsequent designation); Thomson, 1864: 40 (redefinition); Deyrolle, 1864: 218, 237 (in key to some genera; key to Malayan spp., incl *Habroloma* spp. as same genus); Harold, 1869: 117 (gender); Gemminger & Harold, 1869: 1452 (catalog, incl. *Habroloma* as junior synonym); Kraatz, 1870: 31 (gender); Saunders, 1871: 130 (catalog, incl. *Habroloma* as junior synonym); Kerremans, 1892 a: 284 (catalog, incl. *Habroloma* as junior synonym); 1893: 121 (incl. *Habroloma*); 1892 b: 221 (key to Indian spp., incl. *Habroloma* spp. as same genus); 1900: 46 (key to Sumatran spp., incl. *Habroloma* spp. as same genus); 1903: 307 (catalog, incl. *Habroloma* as junior synonym); Klapálek, 1903: 11 (incl. *Habroloma* as subgenus); Théry, 1905: 11, 26, 148 (list and key to Malagasy spp., incl. *Habroloma* as subgenus); Jakobson, 1913: 9, 780 (catalog); Obenberger, 1918 a: 1, 2, 12, 18, 34, 64 (in key to Palaearctic genera and species, incl. *Habroloma* as subgenus); Fisher, 1921: 350, 421 (in key to Pilipino genera, incl. *Habroloma* spp. as same genus); Obenberger, 1924 b: 633 (incl. *Habroloma*); 1937 a: 1352 (World catalog); 1937 c: 52 (key to African spp., incl. *Habroloma* as subgenus); 1937 a: 1352 (catalog, incl. *Habroloma* as subgenus); Théry, 1938: 89 (comparison with *Habroloma*); 1942 a: 182 (in key to French genera); Schaefer, 1950: 460 (redescription: key to French spp.); Kurosawa, 1959: 204 (redescription; key to Japanese spp.); Descarpentries & Villiers, 1964: 250 (in key to genera of Indochina Trachydini); 1965: 723 (species-groups; key to Indochina spp.); Cobos, 1979: 423, 426 (in key; type species: *Buprestis pygmaeus* Fabricius, 1801 [sic]); Bílý, 1982: 87 (type species: *Buprestis pygmaeus* Fabricius, 1801 [sic]); Nelson, 1982: 446 (list); Bellamy, 1985: 428 (catalog); 1986: 597 (in checklist); Cobos, 1986: 277, 278 (in key; Trachyinae); Hołyński, 1993: 15, 32 (in Trachydina; incl. *Neotrachys* as subgenus); Bellamy & Nelson, 2002: 108 (in key to Nearctic genera); Bellamy, 2003: 95 (higher classification; catalog); Bílý & Kubáň, 2006: 172 (gender); Bellamy, 2006 a: 151 (gender); Kubáň, 2006: 418 (Palaearctic catalog);

Bellamy, 2006 b: 273 (gender); Bellamy, 2007: 82 (gender); MacRae *et al*., 2007: 64 (gender); Alonso-Zarazag, 2007: 187 (gender); Bellamy, 2008 b: 2464 (World catalog); ICZN, 2009: 100 (masculine gender); Kubáň, 2016: 569 (Palaearctic catalog); Lawrence & Lemann, 2019: 562, 575 (in key to Australian genera; type species: *Buprestis pygmaeus* Fabricius, 1801 [sic]).

Phytotera: Gistel, 1856: 366; Obenberger, 1937 a: 1354 (World catalog; synonymized under *Trachys*); Bellamy, 2003: 11, 95 (type species: *Buprestis minuta* Linnaeus, 1758, fixed by subsequent designation); 2008 b: 2465 (World catalog).

See Bellamy (2008b) for other references.

Type species. *Buprestis minuta* Linnaeus, 1758 by subsequent designation (Westwood, 1838).

Gender. Masculine (ICZN, 2009). For a long time, the genus *Trachys* had been treated as of feminine gender. ICZN (2009), however, has ruled that the stem of the *Trachys* is *Trache*- and the name of *Trachys* Fabricius, 1801 treats as of masculine gender on the basis of comments of researchers (Bílý & Kubáň, 2006; Bellamy, 2006; MacRae *et al*., 2007; Alonso-Zarazag, 2007). Therefore, the names of higher taxa derived from the *Trachys* are also emended.

Diagnosis. The *Trachys* may be easily distinguished from other genera of the tribe Tracheini by the combination of the following character states: hypomera without antennal grooves; prosternum with distinct marginal carinae along prosternal process; prosternal process narrow; prosternal lobe absent; elytra without lateral carinae; elytra with distinct marginal carinae only in thoracic region; elytral epipreura distinct only in thoracic region; hind wing with distinct anal field; abdominal ventrites with sternal grooves on ventrites I–V or II–V; female proctiger with a pair of ventrally curved baculi; female coxites with dorsal projections of baculi.

Distribution range and species number. Afrotropical, Madagascan, Palaearctic, Oriental, and Australasian Regions. The total number of known species of *Trachys* is ca. 650 spp. (Bellamy, 2008 b; Fukutomi & Ohmomo, 2013; Kubáň, 2016; Peng, 2021 c, d, 2022 a).

Trachys is not distributed naturally in the Nearctic and Neotropical regions, but two species, *Trachys troglodytiformis* Obenberger, 1918 and *T. minutus* (Linnaeus, 1758), are recorded from the former region as introduced species (Linsley, 1949; Weiss, 1954; Westcott & Murray, 2012).

Species examined. In addition to all nineteen Japanese species treated in the section of the taxonomy of Japanese *Trachys*, the following species were examined and compared of the external structures: six European species — *Trachy fragariae* Brisout & Barneville, 1874 (NSMT), *T. problematicus* Obenberger, 1918 (NSMT; YTJ), *T. pumilus* (Illiger, 1803) (NSMT), *T. reflexus* Gené, 1839 (NSMT), *T. scrobiculatus* Kiesenwetter, 1857 (NSMT), and *T. trogloditiformis* Obenberger, 1918 (NSMT; SEHU; YTJ); two Taiwanese species — *T. kurosawai* Bellamy, 2004 (NSMT; YTJ) and *T. ohbayashii* Kurosawa, 1954 (NSMT; YTJ); two Indochina species — *T. laoticus* Baudon, 1962 (EUM; YTJ) and *T. daoensis* Descarpentries & Villiers, 1965 (EUM; TUA; YTJ); and one Indian species — *T. bicolor* Kerremans, 1890 (SEHU). Among them, *T. trogloditiformis* and *T. problematicus* were dissected to observe the hind wing and terminalia.

General morphology of *Trachys* and terms

Traditional terms referring to the same body part for Buprestidae are indicated in brackets.

Body ovate to wedge-shaped, more or less depressed dorsoventrally, more or less setiferous with recumbent to semirecumbent short setae, in the Afrotropical, Madagascan and Oriental species rarely with several tufts consisting of erect setae on elytra or pronotum and elytra. Surface more or less sculptured on dorsal and ventral sides.

Head capsule hypognathous, clearly narrower than pronotum. Eyes moderately large, vertically subreniform, with inner margins obliquely converging downward in frontal view (Fig. 2A), weakly grooved along lower outer side of each inner margin. Occiput concealed beneath prothorax at rest, with longitudinal line of endocarina reaching upper side of frons, with “postocciput” (Fig. 3A) (Snodgrass, 1935) which is very narrow and glabrous and is condyle-shaped around area attaching with cervical sclerites; frons with a pair of “suprantennal pores” (Migliore *et al*., 2020 a) [supraantennal pits; epistomal pores] (Fig. 2B); frontoclypeal suture absent; clypeus [epistoma; frontoclypeus] (Figs. 2B, C) with or without elevated basal margin, arcuately emarginate at apical margin, with surface substrigulate; anteclypeus narrowly visible; antennal insertions somewhat confluent with very shallow subantennal grooves for receiving basal antenomeres at rest; genae very narrow; temples narrow, partly concealed beneath prothorax at rest; “gulamentum” (Lawrence *et al*., 2011; submentum in a strict sense) (Figs. 2I, 3A) transversely wide, with surface reticulate, concealed beneath prosternum at rest; gula (in a strict sense) and gular sutures (between posterior tentorial pits and occipital foramen) absent. Tentorium very slender, without dorsal arms and corpotentorium (tentorial bridge); anterior arms invaginated from gena regions below lowermost part of eyes in lateral view, but well-defined anterior tentorial pits not recognizable externally; posterior arm invaginated from postoccipital region below level of condyle-shaped part of postocciput (Fig. 3A).

Antennae eleven segmented, short in length, serrate from antenomeres VII; antenomeres VII–XI apically with sensory fossae, which are slightly extending to inner surface except antennomere XI (Fig. 2J).

Mouth parts. Labrum (Figs. 2B, 3B) small, narrowly emarginate at apical margin, with surface finely reticulate in about basal half; tormae (lateral tormal processes in Kubáň *et al*., 2001) with inwardly recurved or straight apices. Mandibles (Figs. 2D–F) short, with "mandibular holes" (Kubáň *et al*., 2001) on lateral bases, smooth and concave on surfaces of inner sides. Maxillae (Fig. 3C) with transverse cardines which are weakly enlarged posteriorly between tendons; stipites without distinct separations of basistipites and palpifers, bearing several setae laterally, with mediostipites largely membranous in basal half and sparsely setiferous on sclerotized portions; laciniae not elongated distally, densely clothed with robust setae apically; galeae rounded, densely clothed with robust setae in apical part; maxillary palps four segmented, with palpomere IV somewhat truncate at apex. Labium (Fig. 2I, 3D) with transversely subtriangular to subtrapezoidal mentum, which is somewhat produced at apex and is finely reticulate on surface; ligula short, bearing several setae; palpigers absent; labial palps two segmented; "premental sclerites" (Kolibáč, 2001) short, with enlarged apices often bearing a few setae. Epipharynx (Fig. 3B) nearly unarmed, but faintly bearing microtrichia in proximal part. Hypopharynx (Fig. 3F) well lobed distally (this character state is widely recognizable in Buprestidae), with a pair of "hypopharyngeal sclerites" (Anton & Beutel, 2012) [mental sclerites (Kolibáč, 2001; Kubáň *et al*., 2001)], each of which have well developed three processes, dorsal process, distal process, and proximal process (this study; Fig. 3E), the latter processes are not connected each other.

Prothorax. Pronotum transversely subtrapezoidal; lateral margins narrowed anteriorly from base to apicolateral angles; marginal carinae complete; apical margin simply arcuately or bisinuately emarginate, with or without median lobe; basal margin trisinuate posteriorly, with median lobe, with slightly ridged inner margin (Fig. 4B), with true edge of basal margin more or less covered on basal margins of elytra and scutellar shield (except almost invisible scutellar shield), as a result invisible at rest; surface more or less variolate-punctate with setiferous pin-prick punctures and circular to semicircular incised line sculptures [ocellate punctures]. Hypomera without antennal grooves, with depressed "hypomeral markings" (Peng, 2021 c) in apical half (Fig. 4A), declivous toward basal margins from behind hypomeral markings. Prosternum (Figs. 4A, 5A–C) without well-defined prosternal lobe [gular lobe], but if it is weakly lobed at apical margin like as *T. toringoi* (Fig. 29G), apical margin is not rimed; prosternal process short, narrow, with apparent apex contacting to metaventrite, with sparsely setiferous true apex (Fig. 5A) invisible at rest and inserted into the cavity composed of mesoventrite and metaventrite; disk with "marginal carinae" (Kurosawa, 1959) from near prosternal apical margin to apparent apex of prosternal process, with or without elevated portions along procoxal cavities (Fig. 5C). Procoxal cavities posteriorly open. Protrochantins (Figs. 4A, B) relatively largely exposed at each corner of procoxal cavity facing prosternum and hypomeron. Profurca as shown in Fig. 8A, with two short projections. ***Mesothorax***. Mesothoracic tergum as shown in Fig. 6A; mesoscutellum with very small scutellar shield, which is far narrower than mesonotum in width. Mesoventrite [mesosternum] very short in length, appearing to be completely divided longitudinally by prosternal process (Fig. 4A). Mesanepisterna [mesepisterna] and mesepimera fused with each other, with boundary sutures reduced except in upper side, where is almost concealed by elytra, with invaginations of the sutures also reduced except in the upper side. Mesocoxal cavities widely separated each other; separation in mesocoxal cavities clearly larger than in procoxal cavities. Mesotrochantins (Fig. 4A, B) very narrowly exposed at each corner of mesocoxal cavity facing mesepimeron and metaventrite. Mesendosternite (mesofurca) as shown in Fig. 8B, with two separate, short projections which are weakly enlarged apically. ***Metathorax***. Metathoracic tergum as shown in Fig. 6A; metapostnotum subdivided into "median postnotum" and "lateral postnota" (Matsuda, 1970), the latter of which are strongly raised from median postnotum and fused with sclerotized portions around first abdominal spiracles. Metaventrite [metasternum] (Fig. 4A) with apical margin of metaventral process more or less emarginate; disk with slightly inconspicuous discrimen [longitudinal suture], with metakatepisternal suture [transverse suture] joining near middle of discrimen. Metanepisterna [metepisterna] (Fig. 4A, B) longitudinally rectangle, arcuate inwardly in ventral view. Metepimera concealed by "lateral sternal projections" of abdomen (Jendek, 2001) (Fig. 4B) and elytra at rest. Metendosternite (metafurca) as shown in Figs. 8B and 8C, without developed furcal arms.

Elytra wide, suboval to wedge-shaped; humeral calluses more or less developed or not, very rarely, prominently developed and largely projecting laterally like *Trachys reflexus* Gené, 1839; marginal carinae distinct only in thoracic region (Fig. 4B), sometimes indistinctly reaching near apices (e.g. Fig. 19B); epipleura (Fig. 4B) distinct only in thoracic region, then becoming prominently linear behind thoracic region (nearly reduced); disk without lateral carinae [longitudinal carinae; sublateral carinae; post-humeral carinae]; surface more or less sculptured with setiferous pin-prick punctures and shallow circular punctures, the latter punctures bearing a non-setiferous pin-prick puncture in middle of each. ***Hind wings*** (Figs. 7A, B) elongate oval, short in length, with weak anal notches; anal field (defined by anal fold) narrow, but well-defined. Wing base as shown in Fig. 6B (terms follow Matsuda, 1970); third axillary sclerite strongly elongated in distal process which is connected with vein A; median plate formed a single plate. Venation (traditional interpretation of Good (1925) for Buprestidae is indicated in brackets): vein RA_{3+4} [a part of "Rs" + two cross veins "r"] not reunite to RA_{1+2} ["R_1"], as a result radial cell more or less open to distal end; cross-vein r3 [a part of "Rs"] moderately short, not joining vein RP ["M"]; cross-vein r4 ["r-m"] absent or barely recognized as a dull-defined, pigmented zone (Fig. 7B; e.g. figure 84B in Lawrence *et al.*, 2021); vein MP_3 ["1st A"] and MP_4 ["2d A_1"] obsolete or absent; vein CuA_2 ["2d A_2"] absent; wedge cell ["2d-2dA"] absent (open); vein AA_3 ["3d A_1"] completely separated from AA_4 ["3d A_2"], as a result first cubito-anal cell absent; vein AP reduced or vein AP_{3+4} ["4th A"] barely occurring.

Legs (Fig. 4A) slender. Coxae with pro- and mesocoxae subglobular; metacoxae transverse, with metacoxal plates broadly emarginate in about lateral half of posterior margin. Trochanters subtriangular, obliquely connecting to femoral bases. Femora slightly sulcate on inner margins, but occurring no expansions to conceal tibiae at rest. Tibiae not lodged under femora at rest; metatibiae usually with a fringe of spines on each outer margin (e.g. Fig. 13H; it is used for grooming tarsal pads), except for those of *Trachys problematicus* Obenberger, 1918 without the fringe, only with a few fine, sparse setae; tibial spurs reduced on each tibae. Tarsi short; tarsomeres I–IV ventrally with tarsal pads [pulvilli; lamella] which become larger toward distal end; tarsal claws bearing a blunt tooth at base of each (Fig. 5D).

Abdomen. ***Terga*** (Fig. 8D) well sclerotized, subdivided into tergites and laterotergites by shallow grooves. Tergite I and II strongly fused, with distinct boundary suture. Tergal "cuticularia" (Jendek, 2001) recognized near each basal margin of tergites II–VI (II with ambiguous ones). Laterotergites recognized in second to seventh abdominal segments; laterotergite III strongly and acutely produced basad. Spiracles recognized on each laterotergite, except for first abdominal spiracles recognized on sclerotized portions which are fused with metapostnotum. ***Sterna*** (Figs. 4A & 8D) divided into sternites, laterosternites, and parasternites. Sternites four segmented at a glance; sternite I and II not exposed externally, but lateral parts visible as lateral sternal projections which are reaching metanepisterna and lacking boundary suture between the projections and third abdominal segment; suture between sternites III and IV (= ventrites I and II) obliterated, but barely recognizable as somewhat interrupted sculptures on surface; sternite III (= ventrite I) with obtuse intercoxal process, with or without sternal grooves laterally;

sternites IV–VI (= ventrites II–IV) with sternal grooves laterally; sternite VII (= ventrite V) semicircular, with sternal groove along apical margin, with outside area of the groove not enlarged posteriorly. Sternal cuticularia recognized near each basal margin of sternite IV–VI. Laterosternites delimited from sternites by “sternal carinae” (Jendek, 2001) and/or sternal grooves; laterosternites I–IV of first to fourth abdominal segments without each boundary suture, always bearing “laterosternal sulci” (Jendek, 2001), in which elytra more or less fit; laterosternites V–VII present, occasionally bearing laterosternal sulci on V–VI (e.g. *T. ineditus* Saunders, 1873 and *T. tsushimae* Obenberger, 1922). Parasternites well-demarcated from laterostersites, recognized in third to seventh abdominal segments; parasternites III and VII shorter than other parasternites; “pleural membrane” (Jendek, 2001) barely recognized at proximal part before parasternite III. Spicules (for wing-folding) occurring on whole parasternites, along apical margins of laterotergite VII + tergite VII, and as patches on laterotergites II–VI (in II, very small ones at apical part) and tergite VI, tergite patches of spicules being transversely oblong to round.

Terminalia (genital segments) completely telescoped into seventh abdominal segment. ***Male***. Tergite VIII (Fig. 9A) semicircular, arcuately emarginate at basal margin, covered with small spines in apical margin, sparsely setiferous at each side of disk, with spiracle at each side of apical half. Sternite VIII (Fig. 9B) semicircular, arcuately emarginate at basal margin and densely setiferous on apical margin. Proctiger (Fig. 9C) consisting of completely fused paraproct (tergite IX) and epiproct (tergite X), transversely subreniform, densely setiferous on apical margin, with a pair of short baculi at base. Sternite IX (Fig. 10A) with broad apical margin, setiferous on each side of apical margin. Aedeagus (in a broad sense) trilobate type; tegmen (Fig. 10B) with parameres more or less setiferous in apicolateral parts, ventrally with small phallobase [basal piece]; penis [median lobe; aedeagus in a strict sense] (Fig. 10C) not completely fixed to tegmen, as a result somewhat movable toward distal side, consisting of dorsal plate and ventral membrane (the latter term is modified from the ventral plate (Tamadera & Yoshitake, 2018 c)), ventrally with slit-shaped ostium, from which endophallus is invaginated; endophallus membranous, with a few spicules, connecting with ejaculatory duct at proximal end. ***Female***. Tergite VIII and sternite VIII practically as in male (Figs. 9D, E). Ovipositor short in length; proctiger (Figs. 9F, G) basally with a pair of long, ventrally curved baculi, which is probably formed by the complete fusion of proctiger baculi and valvifers (the latter is regarded as baculi like sclerites between proctiger baculi and bases of coxites); coxites (Figs. 10D, E) transverse, setiferous on apical margin, with dorsal projections of baculi (new term in this study) which are lamina-like, outwardly raised structures and sparsely clothed with microtrichia in apical parts; styli occurring on dorsal side of coxites, somewhat flattened dorso-ventrally, setiferous apically; ventral valve (Fig. 10E) setiferous on each side of subapical part; internal part of ovipositor invaginating from vulva between coxites and ventral valve; vagina sack-shaped (Fig. 10F); spermatheca dorsally opened into about proximal half of vagina without well-defined spermathecal duct, completely membranous, tubular, basally with an unpigmented accessory portion (new term in this study; Fig. 10F) in proximal side (its function is unknown, but may be a muscle attachment point), usually without spermathecal gland, but rarely occurring (e.g. Fig. 52F).

Sexual dimorphism. Species of the genus *Trachys* usually show no distinct morphological differences between both sexes. If sexual dimorphism showing, it may be recognized in the following points: coloration of setae on frons; coloration of integument on frons and clypeus; size of antennae; and/or shape of inner margins of mesotibiae (the last one is usually very difficult to observe without removing legs from body).

Biology of *Trachys*

Life history. Generally, in Japan proper (the temperate zone), the new adults emerge in the summer (from July to August) and somewhat feed on the host leaves, then hibernate in the winter under various gaps, such as the bark of the trees, the moss on the stones, and the leaf-litter (Kurosawa, 1959). In the next spring, the adults wake up and again feed on the host leaves. After copulation and egg laying by the next summer, they finish their life. In the late spring to summer, the immatures mine into leaf tissues and develop into adults in about one month. At least, the voltinism of *Trachys* is considered to be of univoltine in the Japan proper. However, adults of several generation had been confirmed in the same year from the summer to autumn in one species under breeding condition (Ishiguro, 2014). Thus, in the field, several generations may occur in the same year. This possibility is also pointed out in Central European species by Bílý (2003).

Adult stage. The adults of *Trachys* feed externally on leaf blades and leave feeding scars on leaf-margins. Insofar as is known, adult food plants are the same as in immature stages.

Immature stages. Insofar as is known, the larvae of *Trachys* are leaf-miners associated with various dicotyledonous trees and herbs (e.g. Subramaniam, 1920; Yano, 1952; Bílý, 2003; Sahoo, 2021; Özdikmen *et al*., 2021). The eggs are laid singly on the adaxial or abaxial surfaces of the leaf blade (lamina) and are always covered in varnish-like transparent substances. Additionally, the eggs of some species are somewhat covered on powdery substances (those may be fine feces). The larvae, hatched from the eggshell surface in contact with the plant body, mine into the parenchymal layer of the leaf blade and then each larva leaves a full-depth or upper surface, blotch mine. The frass is left inside the mine. The third instar larvae (final instar, based on the number of exuviated head-capsules left inside the mine) pupate inside the mine after passing the stage of prepupa. After around ten days, the adults are emerged from mines.

3.2 Taxonomy of Japanese *Trachys*

Historical review of Japanese *Trachys*

To date, 20 species and 1 subspecies of the genus *Trachys* are recorded from Japan. Taxonomy of Japanese *Trachys* has been studied as in the following time line (showing changes in the number of species and subspecies).

1871. Saunders transferred *Brachys subbicornis* Motschulsky (1860) into *Trachys* [*T. subbicornis*].

+1 transferred sp. = 1 sp. (0 subsp.)

1873. Saunders described ten new species [*Trachys lewisii*, *T. griseonigrum*, *T. elegantulum*, *T. auricollis*, *T. griseofasciatus*, *T. robustus*, *T. cupricolor*, *T. variolaris*, *T. ineditus*, and *T. inconspicuus*].

+10 new spp. = 11 (0)

1893. Lewis described two new species [*Trachys eximium* and *T. saundersi*]; and synonymized one species under a known species [*T. subbicornis* (= *T. griseofasciatus*)].

+2 new spp. −1 synonymized sp. = 12 (0)

1903. Kerremans transferred *Brachys salicis* Lewis (1893) into *Trachys* [*T. salicis*].

+1 transferred sp. = 13 (0)

1918. Obenberger transferred four species of Saunders (1873) and Lewis (1893) into *Habroloma* [*Trachys lewisii*, *T. griseonigrum*, *T. elegantulum*, and *T. eximium*], although he regarded *Habroloma* as the subgenus of *Trachys*.

−4 transferred spp. = 9 (0)

1919. Obenberger described one new species [*Trachys clavicornis*].

+1 new sp. = 10 (0)

1922. Obenberger described one new species [*Trachys tsushimae*].

+1 new sp. = 11 (0)

1923. Obenberger described two new species [*Trachys obscuripennis* and *T. japonica*].

+2 new spp. = 13 (0)

1924 a. Obenberger described one new species [*Trachys ogumensis*].

+1 new sp. = 14 (0)

1927. Théry synonymized one species under an unrecorded species [*Trachys minutus* (= *T. obscuripennis*)].

−1 synonymized sp. +1 recorded sp. = 14 (0)

1928 a. Obenberger resurrected one species [*Trachys obscuripennis*], as a result one species removed [*T. minutus*].

+1 resurrected sp. −1 recorded sp. = 14 (0)

1934. Théry described one new species [*Trachys ornatus*].

+1 new sp. = 15 (0)

1940. Obenberger described two new species [*Trachys pseudoscrobiculatus* and *T. tokyoensis*].

+2 new spp. = 17 (0)

1947. Kurosawa & Iga synonymized one species under an unrecorded species, which was newly recognized from Japan [*Trachys minutus* (= *T. salicis*)].

+1 recorded sp. −1 synonymized sp. = 17 (0)

1950. Chûjô & Kurosawa synonymized one species under a known species [*Trachys saundersi* (= *T. obscuripennis*)].

−1 synonymized sp. = 16 (0)

1951. Kurosawa described one new species [*Trachys toringoi*].

+1 new sp. = 17 (0)

1959. Kurosawa described seven new species [*Trachys violae*, *T. cuneiferus*, *T. yoshidai*, *T. falcatae*, *T. oviformis*, *T. yanoi*, and *T. tiliae*] and two new subspecies [*T.*

pseudscrobiculatus shirozui and *T. variolaris robustissima*]; synonymized four species under known species [*T. inconspicuus* (= *T. ogumensis*), *T. ineditus* (= *T. ornatus*), *T. japonica* (= *T. tokyoensis*), and *T. variolaris* (= *T. clavicornis*)]; resurrected one species [*T. griseofasciatus*]; upgraded the status of *T. salicis* (syn. of *T. minutus*) as a subspecies [*T. minutus salicis*]; and transferred *T. subbicornis* into *Habroloma*. This revisional study includes many misidentifications which are corrected by Kurosawa (1985 a) based on examinations of type specimens in his trip to Europe in 1973 (Kurosawa, 1976 b, c).

+7 new spp. −4 synonymized spp. +1 resurrected sp. –1 transferred sp. (+2 new subsp. +1 upgraded subsp.) = 20 (3)

1980. Kurosawa synonymized one subspecies under an unrecorded species, which was newly recognized from Japan [*T. dilaticeps* (= *T. variolaris robustissima*)].

+1 recorded sp. (−1 synonymized subsp.) = 21 (2)

1985 a. Kurosawa described one new species [*Trachys broussonetiae*]; newly recorded one species [*T. pecirkai*]; resurrected one species [*T. tokyoensis*]; synonymized four species under two known species [*T. tokyoensis* (= *T. oviformis*) and *T. tsushimae* (= *T. japonica*)] and under two unrecorded species [*T. reitteri* (= *T. falcatae*) and *T. aurifluus* (= *T. tiliae*)]; corrected misidentifications of *T. japonica*, *T. ineditus*, and *T. tsushimae* and also their related synonyms in Kurosawa (1959); and removed *T. obscuripennis* from the synonymy of *T. saundersi* [he followed the status of *T. obscuripennis* in Théry (1927) (according to the notes on *T. saundersi* in Kurosawa, 1976 d)]. The taxonomic changes and corrections in Kurosawa (1985 a) were preliminary reported by Kurosawa (1976 c, d, e) in Japanese.

+1 new sp. +3 recorded spp. +1 resurrected sp. −4 synonymized spp. = 22 (2)

2008b. Bellamy emended species scientific names of members of the genus *Trachys* as of masculine gender, then ICZN (2009) has formally ruled that the name of *Trachys* treats as that gender (no changes in the number of Japanese species).

±0 = 22 (2)

2013. Fukutomi & Ohmomo synonymized two species under known species [*Trachys pseudoscrobiculatus* (= *T. violae*) and *T. inconspcuus* (= *T. yoshidai*)] and one subspecies under a nominotypical subspecies [*T. pseudscrobiculatus pseudscrobiculatus* (= *T. pseudscrobiculatus shirozui*)].

−2 synonymized spp. (−1 synonymized subsp.) = 20 (1)

This study will synonymize one species under a known species [*Trachys saundersi* (= *T. cuneiferus*)] and one subspecies under a nominotypical subspecies [*T. minutus minutus* (= *T. minutus salicis*)].

−1 synonymized sp. (−1 synonymized subsp.) = 19 (0)

Review of species diagnostic characters

This study reassesses diagnostic characters for species identification of the genus *Trachys* and also proposes some new characters here. This genus consists of numerous species including many similar ones in general appearance. To well organize species classification of this genus, Obenberger (1929) for the first time summarized diagnostic characters for species identifications of the continental Asian *Trachys* that contains the genus *Habroloma* as a subgenus under it at that time. In addition, some structures are described as useful characters for species determination, but such characters are scattered in various previous studies (e.g. Obenberger, 1918; Théry, 1942; Schaefer, 1950; Cobos, 1958 a; Kurosawa, 1959; Descarpentries & Villers, 1965; Peng, 2021 c).

Species of the genus *Trachys* occasionally show morphological intraspecific variations, which haunt our species identification, even in diagnostic characters listed below, so that the species identification based on a combination of multiple characters are required. The combination of the following characters may be useful for the reliable identification of *Trachys* species:

Structure. **Body**: dorsal and lateral contour. **Vestiture**: tufts of pronotal and elytral erect setae. **Head**: shape and depth of concavity on frons outline of head in dorsal view; visible size of eye in dorsal view; proportion of clypeus [WC/LSC ratio] (revised). **Pronotum**: apical margin of pronotum. **Scutellar shield**: visible size. **Elytra**: ridge strength of elytral humeral callus; serrations of elytral lateral margins. **Underside**: apical margin of prosternum; shape of prosternal process; marginal carinae of prosternum; elevated portions along procoxal cavities of prosternum (newly proposed); hypomeral depressed markings; sculpture of median portion of metaventrite; fringe of spines on outer margin of metatibia (newly proposed); size of inner tooth of claws; sternal grooves of abdominal ventrites (newly proposed); shape of apex of abdominal ventrite V. **Terminalia**: shape of male sternite IX and its setae (newly proposed); shape of male parameres and their setae; shape of male penis; sclerotized portion on ventral membrane of penis; transverse depression of coxites in ventral apical part; shape of female styli (newly proposed); shape of female spermatheca (newly proposed).

Coloration. Integument of dorsum, venter, maxillary palps, and basal four tarsomeres on each leg; patterns of setae on head, pronotum, and elytra.

Notes for some useful characters. The dorsal contour can be roughly divided into two types: ovate type (e.g. Fig. 11: lateral margins of elytra relatively subparallel in basal half, then relatively continuously, arcuately narrowed apicad); or wedge-shaped type (Figs. 25A, B: lateral margins of elytra narrowed posteriorly from near base to apices, as a result dorsal contour looks like a triangle).

Vestiture. The tufts of pronotal and elytral setae are rarely recognized in *Trachys* species, for example *Trachys kurosawai* Bellamy, 2004 (Théry, 1905; Obenberger, 1929, 1937 c; Kurosawa, 1954; Descarpentries & Villers, 1965, etc.). This character is clearly important to determine species of this genus, although all Japanese species have no pronotal and elytral tufts.

Head characters. The proportion of the clypeus is often described in species descriptions for *Trachys*, such as it is narrow or wide. Kurosawa (1959) was described this proportion as a width to length ratio for Japanese *Trachys* species. This ratio looks useful to identify species, but accurate measurement for the length of the clypeus is often difficult due to dull-defined separation between the clypeus and the frons. The separation shows the following states: the clypeus is somewhat separated from the frons with the elevated basal margin (Fig. 2C); or it is indistinctly separated from the frons without the elevated basal margin (Fig. 2B). Additionally, intraspecific variations in the ratio of the clypeus seem to be recognizable on each species. To figure out those variations, this study measured the ratio of the clypeus as two types of measurement ratio, WC/LC and WC/LSC. Values of these ratios indicate in Table 1 and also in each species description. As a result, it seems that WC/LSC is rather stable than WC/LC and that Kurosawa's measurement ratios should be revised since those are rather ambiguous values. Therefore, this study replaces the width to length ratio of the clypeus with the WC/LSC ratio to indicate the proportion of the clypeus.

Elytral characters. The ridge strength of the elytral humeral callus has been recognized as a useful character in Descarpentries & Villers (1964) and Peng (2021 c). The latter study calls this character as "humeral carina", but this carina is essentially different from the humeral carina as seen in the genus *Aglirus* (Jendek & Grebennikov, 2011) and the lateral carina as seen in the genus *Habroloma* (Fig. 5G). This study avoids using of the term, humeral carina, to describe this character which represents the degree of ridge strength. As Peng (2021 c) noted, this character can be easily observed in lateral view.

The serrations of the elytral lateral margins are often difficult to observe in dorsal view because the elytral semirecumbent setae somewhat cover on this character. In this study, this character is observed in obliquely ventral view (e.g. Fig. 27C).

Underside characters. The marginal carinae of the prosternum (Fig. 5B) are often described as the shape (sides) of the prosternal process. For example, Fisher (1921), Obenberger (1929), Théry (1942 a), Cobos (1958 a), Peng (2021 c), etc. described the states of the marginal carinae as the shape of prosternal process (but Obenberger's study mentioned this replacement). Such description should be avoided to prevent non-homologous comparisons with other buprestid taxa for higher classifications and confusing readers. Thus, this study separately describes the marginal carinae from the shape of the prosternal process as in Kurosawa (1959).

On the other hand, it is known that the marginal carinae of the prosternum show intraspecific variations to some extent in some species (Schaefer, 1950; Luna, 2017)
The depressed hypomeral markings (Fig. 4A) have been used for keys to *Trachys* species in a few studies (Cobos, 1986; Levey, 2012). Peng (2021 c) proposed that this character should be also described for species descriptions and it showed five types of the shape of depression with figures 4–6. In this study, this character is also recognized as relatively useful ones, but the shape of depression occasionally shows intraspecific variations to some extent. Therefore, careful examinations based on enough specimens are required in each species.

The fringe of spines on the outer margin of metatibia has never been described in the genus *Trachys*. This character usually shows the following two character states: a longer spine present in the basal part of the fringe (e.g. Fig. 13H & 44I); or the longer spine absent (e.g. Fig. 17H). We require careful observation to recognize those character states since the fringe of spines is usually inconspicuous due to its pale color. Exceptionally, *Trachys problematicus* Obenberger, 1918, distributed in Europe, has no fringe of spines on the metatibia (only bearing several sparse fine setae).

The size of the inner teeth of claw has been known that it shows very clear differences in some European species (Obenberger, 1918; Théry, 1942).

The sternal grooves of the abdominal ventrites (Fig. 4A) were already recognized as a useful character to distinguish *Trachys* from the related genus *Habroloma* by Théry (1938) and Cobos (1979). In addition to the genus level differences, this study found sufficient differences in the sternal grooves at species level. The absence or presence of the sternal grooves on the abdominal ventrite I is very important to identify species (Figs. 5E, F).

The shape of the apex of the abdominal ventrite V looks useful to identify species at a first glance. Generally, this character shows two different character states: evenly rounded to weakly subtruncate; and emarginate. Several species showing the latter state, however, have intraspecific variations: the emarginate apex of the ventrite V in those species is sometimes being almost truncate (for example, *Trachys pecirkai* Obenberger, 1926; Fig. 39I'). On the other hand, the emarginate apex of the ventrite V in *T. toringoi* Kurosawa, 1951 (Fig. 29J) is seemed to be well stable to determine this species. Therefore, careful examinations based on enough specimens are required to judge usefulness of this character in each species.

Terminalia characters. The male terminalia of *Trachys* have been the focus of several European and East Asian studies in classifying species (Schaefer, 1950; Cobos, 1958a, 1959, 1986; Levey, 2012; Luna, 2017; Ishiguro & Nishida, 2018; Tamadera & Yoshitake, 2018 c; Peng, 2021 c, d), whereas the female terminalia of this genus has been largely ignored except in a few studies (Schaefer, 1950; Verdugo, 2011; Tamadera & Yoshitake, 2018c). In this study, sufficient differences of the terminalia in both sexes are well recognized between Japanese species. In particular, this study finds taxonomic usefulness on the female spermatheca at species level. The internal part of the ovipositor has never been described for species classification of the family Buprestidae, although several studies observed this structure for higher classification of this family (Kasap & Crowson, 1975; Kolibáč, 2001; Kubáň *et al*., 2001; Karagyan, 2007).

In order to observe the internal (membranous) part of the ovipositor, whole the abdomen should be dissected carefully since the internal part is easily broken by directly pulling and extracting from externally visible terminal part of the abdomen. Due to the difficulty of observation for transparent parts on the terminalia with microscopes under incident lights, the observation of the terminalia is required using microscope under transmitted lights, especially in the female ovipositor, in the lateral subapical part of the male parameres, and in the apex of penis (see Tamadera & Yoshitake (2018 c) for these dissection and observation method).

Coloration. The characters related to the coloration cannot be neglected for *Trachys* species, although they should be more carefully considered their intraspecific variations like most of insect taxa. In *Trachys*, the coloration of the maxillary palps and basal four tarsomeres have been described as useful characters (Obenberger, 1929; Descarpentries & Villers, 1965, 1966; Peng, 2021 c, d). In addition, the patterns of setae, which has been also described traditionally, is useful when combined with characters of structures.

However, observers should pay attention to the possibility of the missing setae on specimens, because the setae were often come off the pronotum and the elytra in individuals after hibernating or in the dry specimen made by bad making processes (especially in when turning over specimens to spread specimen's legs).

Notes for non-adopted characters. The "curvature" (Peng, 2021 c: figures 3–4) refers to "the forward bending of the head and thorax plus the short basal part of the abdomen, forming a specific angle between pronotal margin and subhumeral lobe" in lateral view. This character, however, seems to be dull-defined without its measurement method (only figures). In this study, the curvature is measured as a trial in several Japanese species with a tentative measurement method (curvature is defined herein as follows: in lateral view, the angle formed by the line connecting both end points of the pronotal marginal carina and the line connecting the basal point of the elytral marginal carina and the bottom point of the marginal carina). Although it was measured in a few numbers of specimens, intraspecific variations overlapping with other species were recognized in measured species: curvature of *Trachys minutus* 123°–132° (mean 127°; n = 6); *T. auricollis* 110°–120° (mean 114°; n = 6); and *T. saundersi* 117°–129° (mean 124°; n = 6). In addition, this value is strongly affected by the position of the prothorax under dry specimen. Probably, the previous study cannot be considered intraspecific variations of this character due to the lack of multiple specimens and also not be done the prothorax position of specimens. Therefore, this study avoids describing the curvature in species descriptions.

"The extent of margin between inner and outer margins of pronotal base" is used for Chinese *Habroloma* species as a diagnostic character (Peng, 2021 a: figures 4–6). *Trachys* also shows a same kind of character as in *Habroloma*, so that it is possible that this character can be adopted to *Trachys*. However, at least, Japanese *Trachys* species show no significant differences between species because states of this character are variable individually. In addition, since this character is formed by the overlap of the pronotum and the elytra, it is strongly affected by the position of the prothorax under dry specimen. Judging from those unstable conditions, this study avoid using of this character.

Species-groups for Japanese *Trachys*

The genus *Trachys* has six species-groups established by Descarpentries & Villiers (1965) for the Indochina *Trachys* species: the *arhemus*-, *auricollis*-, *fasciuncula*-, *fleutiauxi*-, *mixtipilis*-, and *pseudolyrus*-groups. These species-groups are referenced in the latest world catalog for Buprestoidea (Bellamy, 2008 b) and then members of the *fasciuncula*-

group are revised (Wei & Shi, 2016). However, this study avoids using these concepts for Japanese species since these species-groups are dull-defined by limited character states in the elytra (e.g. the presence or absence of the elytral tuft and the patterns of the elytral setae).

More comprehensive studies based on a number of species are necessary to provide with well-defined *Trachys* species-group concepts, which are practical and also reflect phylogenetic relationships. This study, however, tentatively grouped Japanese *Trachys* species into seven groups to systematically classify them and to make it easier to species identification. Diagnoses for those tentative groups are described in the corresponding section, respectively.

Japanese species list

Group I
Trachys minutus (Linnaeus, 1758)
= subsp. *salicis* (Lewis, 1893) syn. nov.
Trachys inconspicuus Saunders, 1873
Trachys pseudoscrobiculatus Obenberger, 1940
Trachys ineditus Saunders, 1873
Trachys tsushimae Obenberger, 1922
Trachys broussonetiae Kurosawa, 1959

Group II
Trachys auricollis Saunders, 1873
Trachys toringoi Kurosawa, 1951

Group III
Trachys saundersi Lewis, 1893
= *cuneiferus* Kurosawa, 1959 syn. nov.
Trachys cupricolor Saunders, 1873
Trachys pecirkai Obenberger, 1926
Trachys aurifluus Solsky, 1875

Group IV
Trachys reitteri Obenberger, 1930
= *lushanensis* Peng, 2021 c syn. nov.

Group V
Trachys tokyoensis Obenberger, 1940
= *ovalis* Peng, 2021 c syn. nov.
= *aureoles* Peng, 2021 d syn. nov.

Group VI
Trachys griseofasciatus Saunders, 1873
Trachys yanoi Kurosawa, 1959

Group VII
Trachys variolaris Saunders, 1873
Trachys robustus Saunders, 1873
Trachys dilaticeps Gebhardt, 1929

Species descriptions

Group I (minutus)

(Fig. 11)

Species included. [Subgroup I-1] *Trachys minutus* (Linnaeus, 1758), *T. inconspicuus* Saunders, 1873, and *T. pseudoscrobiculatus* Obenberger, 1940. [Subgroup I-2] *T. ineditus* Saunders, 1873, *T. tsushimae* Obenbeger, 1922, and *T. broussonetiae* Kurosawa, 1985.

Diagnosis. Body ovate type. Apical margin of pronotum with small to very small median lobe. Elytra with unserrated lateral margins; elytral vestiture with two transverse bands consisting of unicolor setae in apical half of each elytron, without tufts consisting of erect setae. Prosternum more or less rimmed along apical margin which is not lobed; prosternal disk without elevated portions along procoxal cavities. Abdominal ventrites with sternal grooves on ventrite II–V. Female coxites ventrally without transverse depression in apical part.

Notes. The members of this group are easily distinguished from other Japanese congeners by the unserrated lateral margins of elytra (see also the key). Additionally, the members are subdivided into two subgroups (I-1and I-2) by the presence or absence of yellow setae on dorsum and by the smoothly convex or transversely ridged frons from just above each antennal insertion to the inner margin of each eye.

With regard to the character state that the unserrated lateral margins of elytra, it is very commonly recognizable in the European species examined by this study and in more than 100 Afrotropical species based on some literatures (e.g. Obenberger, 1937 c, 1938, 1939; Cobos, 1958 a).

Trachys minutus (Linnaeus, 1758)
[Japanese name: Yanagi-chibi-tamamushi]
(Figs. 2A, B, D–G, I, J, 3A–E, 4, 5A, B, D, E, 6, 7A, 8, 9A–G, 10, 11A, 12A–F, 13, 14, 63A, B, 66A, B)

Buprestis minuta Linnaeus, 1758: 410 (type locality: "Europa").

Trachys minuta: Fabricius, 1801: 218 (transferred from *Buprestis*); Schiødte, 1870: 360, 375 (larva); Kerremans, 1892 a: 287 (catalog); Heyden, 1893: 119 (list); Kerremans, 1903: 310 (catalog); Kurosawa, 1950 a: 13 (note); 1950 b: 1112, fig. 3188 (pictorial book); Chûjô & Kurosawa, 1950: 12 (Shikoku, Japan); Yano, 1952: 26 (immature stages); Iga, 1955 a: 10, pl. 4 (pictorial book); 1955b: 80, pl.24 (pictorial book) ; Kurosawa, 1959: 211 (redescription); Bílý, 1999: 38, 41 (in key of larva); Kolibáč, 2001; 140, figs. 50, 79, 80, 95, 111, 127, 143, 173, 188, 204, 219, 233, 249, 263, 276, 291, 306, 332, 333, 364 & 365 (illustrations of morphology); Niehuis, 2004: 457 (Rheinland-Pfalz and Saarland).

Trachys (*Trachys*) *minuta*: Obenberger, 1918: 20, 45, 64, figs. 24, 25 (in key; larva; catalog); 1926 b: 662 (catalog); 1937: 1361 (World catalog).

Trachys minutus [justified emendation, according to ICZN (2009)]: Heyden, 1862: 61 (larva); Théry, 1942 a: 185, 187, fig. 139 (in key; diagnosis); Schaefer, 1947: 166, tab. II (larva); 1950: 464, 466, figs. 476, 486, 487 (in key; redescription; aedeagus); Muskovits & Hegyessy, 2002: 112, 234 (in key); Verdugo, 2005: 239, 242, figs. 148, pl. 49c (in key; diagnosis; aedeagus); Štrunc, 2022: 196 (photograph).

Trachys minuta minuta: Cobos, 1986: 280, 320, pl. LI–LII (in key; aedeagus); Kubáň, 2006: 419 (Palaearctic catalog).

Trachys minutus minutus [justified emendation, according to ICZN (2009)]: Bílý, 1982: 89, figs. 101, 103, 105, & 106 (in key; note); Bellamy, 2008 b: 2503 (World catalog); Kubáň, 2016: 572 (Palaearctic catalog).

Trachys minuta var. *supraviolacea* Thomson, 1864: 41 (type locality: ?"Skandinavien"). Synonymized under *T. minutus minutus* by Bílý, 1982: 89 (recognized as subspecies level).

Trachys (*Trachys*) *minuta* ab. *supraviolacea*: Obenberger, 1937 a: 1366 (World catalog; ab. of *T. minutus*)

Trachys (*Trachys*) *minuta reflexiformis* Obenberger, 1918: 46, 65 (type locality: "Italien: Vallombrosa", Italy). Synonymized under *T. minutus minutus* by Curletti, 1987: 152.

Trachys minuta reflexiformis: Cobos, 1986: 319 (as synonym of *T. reflexus* Gené).

Brachys salicis Lewis, 1893: 337 (type locality: "Main island. On sallow at Subashiri, Miyanoshita, and Kioto", Japan); Obenberger, 1918: 72 (list); 1926 b: 663 (catalog); 1928 b: 111 (note); 1928 a: 46 (note); 1928 c: 25 (note); Bellamy, 2001: 28 (petition to conserve name; *Buprestis* [sic] *salicis* Lewis, 1893); ICZN, 2002: 211 (Opinion 2008: name conserved; *Buprestis* [sic] *salicis* Lewis, 1893). Synonymized under *T. minutus* by Kurosawa & Iga, 1947: 25.

Trachys salicis: Kerremans, 1903: 310 (transferred from *Brachys* without reason); 1912: 209 (Taiwan); Jakobson, 1913: 800 (catalog); Théry, 1927: 39 (transferred from *Brachys* without reason); 1930: 33 (with reason of transfer from *Brachys*; Hong-Kong, China); Miwa, 1931: 127 (list); Miwa & Chûjô, 1936: 25 (catalog; Japanese name: Nomi-chibi-tamamushi); Kurosawa & Iga, 1947: 25 (synonymized under *T. minutus*); Chûjô & Kurosawa, 1950: 12 (synonym of *T. minutus*; misspelling as "*salcis*").

Trachys (*Trachys*) *salicis*: Miwa & Chûjô, 1936: 25 (catalog; Japanese name: Nomi-chibi-tamamushi); Obenberger, 1937 a: 1378 (world catalog).

Trachys minuta salicis: Kurosawa, 1959: 212 (resurrected as subspecies; Japan: Hokkaido, Honshu, Sado Is., Shikoku, Kyushu); 1963: 155, pl. 78 (pictorial book); 1976 c: 3 (note); 1985 b: 34, pl. 6 (pictorial book); Cobos, 1986: 320 (listed); Akiyama & Ohmomo, 1997: 47 (checklist); 2000: 284, pl. 120 (pictorial book); Kubáň, 2006: 52, 419 (erroneous of ICZN, 2002; Palaearctic catalog).

Trachys minutus salicis [justified emendation, according to ICZN (2009)]: Bellamy, 2008 b: 2503 (World catalog); Ohmomo & Fukutomi, 2013: 166, pl. 52 (pictorial book); Lan & Ohmomo, 2015: 106 (Taiwan); Ishiguro *et al*., 2015: (host: *Corylus heterophylla*); Kubáň, 2016: 572 (Palaearctic catalog); Ishiguro & Nishida, 2018: 33, figs. 2, 3 & 6 (aedeagus).

Trachys mandjurica Obenberger, 1917: 218 (type locality: "Südmandjurien"). Synonymized under *T. minutus minutus* (Linnaeus) by Bílý, 1982: 89. Justified emendation: *T. mandjuricus*, according to ICZN (2009).

Trachys (*Trachys*) *obscuripennis* Obenberger, 1923: 65 (type locality: "Kioto (Japon)"); 1928 b: 111 (comparison with *T. minutus*); 1928 a: 47 (comparison with *T. minuta*); Miwa & Chûjô, 1936: 25 (catalog; Japanese name: Usuguro-chibi-tamamushi);

Obenberger, 1937 a: 1367 (World catalog). Synonymized under *T. minutus* by Théry, 1927: 40.

Trachys obscuripennis: Théry, 1927: 40 (misspelling as "*obscuricollis*"; synonymized under *T. minutus*); Théry, 1942 a: 187 (synonym of *T. minutus*); Chûjô & Kurosawa, 1950 a: 12 (synonymized under *T. saundersi* Lewis); Kurosawa, 1959: 213 (synonym of *T. saundersi*); 1976 d: 2 (synonym of *T. minutus* after Théry, 1927); Kubáň, 2006: 420 (Palaearctic catalog; synonym of *T. saundersi*); Bellamy, 2008 b: 2517 (World catalog: synonym of *T. saundersi*); Ohmomo & Fukutomi, 2013: 192 (catalog; synonym of *T. minutus*); Kubáň, 2016: 573 (Palaearctic catalog; synonym of *T. saundersi*).

See Bellamy (2008 b) for other references and unavailable names.

Description. Male and female. Body ovate, moderately convex dorsally (Figs. 13A, B). LB 3.03–3.80 mm (mean 3.47 mm); WB 1.69–2.15 mm (mean 1.96 mm); LB/WB 1.72–1.84 (mean 1.77) (n = 20 for all measurements except terminalia). Habitus as shown in Figs. 11A and 12A–F.

Integument. Head and pronotum black to brassy-black, occasionally being weak reddish to purplish black; elytra black, often with weak purplish, bluish or greenish tints; underside black with weak golden-bronze reflections; antennae and legs black, except for femora and tibiae sometimes with weak purplish tints in ventral side and tarsal pads brown; maxillary palps brownish-black. Dorsal and ventral surfaces moderately shiny.

Vestiture mainly consisting of white and black setae; black setae sometimes with brownish tints. Head sparsely clothed with fine, recumbent, black to pale-brown setae. Pronotum sparsely clothed with short, semirecumbent, black to pale-brown setae, with some white patches across middle. Elytra sparsely clothed with short, semirecumbent, white and black setae which are arranged on each elytron as follows: 1) white setae irregularly scattering in basal part; 2) inconspicuously undulated, interrupted white band just before middle; 3) first white transverse band at apical 1/3, moderately wavy, zigzag-shaped; 4) second white transverse band at subapical part, rather straight, often connecting to the first transverse band along sutural margin; and 5) black setae in remaining space. Underside more sparsely setiferous, with fine, recumbent, whitish setae.

Head, when viewed from above, moderately arcuately concave on frons, with oculofrontal margins rounded. Eyes, when viewed from above, slightly broadly visible, weakly convex laterally. Vertex obscurely and coarsely variolate-punctate; frons widely concave, weakly impressed along upper side of midline, smoothly convex from just above each antennal insertion to inner margin of each eye, with surface rather smooth but faintly punctate; suprantennal pores simply round; clypeus narrow (Fig. 13C), without elevated basal margin, WC/LC 1.25–1.57 (mean 1.39), WC/LSC 1.22–1.39 (mean 1.30), deeply arcuately emarginate at apical margin.

Antennae (Fig. 13D) reaching just behind apicolateral angles of pronotum when laid alongside; antennomere I stout claviform, longer than II; II ovate, longer than III; III subrectangular, slightly longer than IV; IV–VI subrectangular, subequal each other in length; VII–X triangular, moderately enlarged; XI subtriangular to sublingulate.
Mandibles without transverse ridge in middle of each outside. Maxillary palps with oval palpomere IV somewhat longer than wide (Figs. 2G, 3C).

Pronotum widest at base, WP/LP 2.57–2.96 (mean 2.75), BMP/AMP 1.53–1.67 (mean 1.59), narrower than elytra; lateral margins weakly arcuately or straightly and moderately narrowed apicad, sometimes sinuate around middle; apicolateral angles nearly right (angle); basolateral angles broadly acute (angle); apical margin bisinuately emarginate, with small median lobe; basal margin trisinuate, with median lobe moderately produced; disk weakly depressed along lateral margins, faintly depressed along basal median lobe; surface obscurely variolate-punctate, becoming denser toward apical and basal margins. Scutellar shield very small, glabrous.

Elytra widest at humeri, LE/WE 1.26–1.36 (mean 1.31), LE/LP 3.46–4.20 (mean 3.85); humeral calluses moderately developed; lateral margins subparallel in basal half and weakly constricted between humeri and middle point, and then arcuately convergent to conjointly rounded apices, without serrations; marginal carinae distinct only in thoracic region; sutural margin faintly elevated in apical half; disk weakly depressed in basal part, constricted behind humeri; surface irregularly and coarsely punctate. Lateral part of abdomen narrowly visible in dorsal view; laterosternites I–IV with laterosternal sulci.

Underside. Prosternum (Fig. 13E) rather straight at apical margin which is weakly rimmed; prosternal process wide, constricted between procoxa, with apex broadly rounded at rest; marginal carinae moderately widely separated each other at widest part of prosternal process, strongly divergent posteriad from near middle; disk rather flat on median portion, somewhat declivous laterad on outside of marginal carinae, without elevated portions along procoxal cavities. Hypomera with depressed hypomeral markings longitudinally narrowed subreniform usually, but with proportion variable (Figs. 13F, G). Metaventrite moderately sculptured with large punctures on inside of katepisternal suture and with linearly confluent sculptures on outside of the suture. Legs moderately slender; metacoxal plates weakly produced posteriorly at each lateral angle which is broadly acute (angle), with surface coarsely variolate; metatibiae bearing a fringe of spines in apical half of each outer margin, with one long spine in base of the fringe (Fig. 13H); inner tooth of each claw large (Fig. 5D). Abdominal ventrite with sternal grooves on ventrites II–V; V (Fig.13I) rounded at apex; surface variolate, in ventrite I with linearly confluent sculptures on median part.

Sexual dimorphism indistinct.

Male terminalia (n = 5 for measurements). Tergite VIII and sternite VIII as shown in Figs. 9A, B. Proctiger with a pair of short baculi at base (Fig. 9C). Sternite IX (Fig. 10A) wide, SL/SW 0.85–0.95 (mean 0.90), almost truncate at apical margin, bearing several short setae on each side of apical margin. Tegmen (Fig. 10B) slightly wide; parameres PL/PW 1.91–2.18 (mean 2.02), sparsely setiferous on apicolateral margins, with sides which are gently dilated from base to widest subapical part, but occasionally faintly expanded around subapical part, and then arcuately convergent to apices; phallobase PbL/PbW 2.33–3.11 (mean 2.68), about 1/4 length of tegmen. Penis (Fig. 10C) wide, PeL/PeW 3.85–4.95 (mean 4.20), shorter than tegmen; dorsal plate with sides (not including sides of median struts) which are subparallel from widest point of base to apical 1/5, and then strongly, arcuately convergent apicad, with roundly, weakly produced apex, basally with median struts about 1/3 length of penis; ventral plate membranous, but weakly sclerotized as an inverted Y-shaped patch in middle of subapical part.

Female terminalia (n = 5 for measurements). Tergite VIII and sternite VIII as shown in Figs. 9D, E. Ovipositor (Figs. 9F, G, 10D–F) short; proctiger basally with a pair of long, ventrally curved baculi; coxites transversely subreniform, sparsely setiferous on each side of apical margin, ventrally without transverse depression in apical part; styli subtrapezoidal, rather slender, with sides gently narrowed apicad, SlL/SlW 1.76–2.57 (mean 2.21), bearing several setae apically; ventral valve sparsely setiferous on each side of subapical part; vagina roundly sack-shaped, strongly expanded dorsally in about distal half; spermatheca slender tubular, moderate in length, widest in apical half, without spermathecal gland.

Differential diagnosis. In the species-group I, *Trachys minutus* shows some resemblances to *T. inconspicuus* Saunders, 1873 and *T. pseudoscrobiculatus* Obenberger, 1940 in the sparse body vestiture, in the frons without transverse ridges from just above antennal insertions to inner margins of eyes, and in the subparallel-sided penis. *T. minutus* is, however, readily distinguished from them by the larger body size (3.0–3.8 mm), by the oval maxillary palpomere IV, by the darker maxillary palps (brownish-black), by the more weakly produced apex of penis (than that of *T. inconspicuus*), and by the slenderer spermatheca.

Specimens examined. Non-type material. **Japan**. Hokkaido — 2 exs., Kannonzawa, Sapporo-shi, 2.VI.1980, E. Ishibashi leg. (SEHU); 1 ex., Jôzankei, Sapporo-shi, 8.VI.1997, A. Tanaka leg. (SEHU); 1 ex., Shikotsuko Lake, 27.VII.1988, A. Tanaka leg. (SEHU); 1 ex., Sapporo-shi, 4.VI.1978, A. Tanaka leg. (SEHU); 1 ex., same locality, 18.IX.1983, A. Tanaka leg. (SEHU); 1 ex., Atsubetsu, Sapporo-shi, 17.VI.2009, S. Aoyama leg. (SEHU); 3 exs., Konopporo, Sapporo-shi, 24.VII.2018, S. Aoyama leg. (SEHU); 1 ex., Teshio-gawa River, Bihuka-onsen Spa, 22, 26.V.2006, H. Takizawa leg. (SEHU); 1 ex., Toyotaki, Sapporo-shi, no date, M. Ôhara leg. (SEHU); 1 ex., same locality, 27.V.1984, K. Furukawa leg. (SEHU); 1 ex., same locality, 20.V.1990, S. Shiyake leg. (SEHU); 1 ex., same locality, 29.VIII.1990, S. Shiyake leg. (SEHU); 1 ex., Hôheikyô, Sapporo-shi, 5.VI.1996, M. Matsuda leg. (SEHU); 3 exs., Teine, Sapporo-shi, 15.V.1959, T. Kumata leg. (SEHU); 2 exs., Shirataki, Kitami, 15.VI.1974, T. Kumata, M. Kiuchi & M. Furukawa leg. (SEHU); 1 ex., same locality, 16.VI.1974, same collectors (SEHU); 2 exs., Kimobetsu, 9.VII.1991, Y. Nishijima leg. (SEHU); 1 ex., Hyakumatsu-zawa, Sapporo-shi, 10.VII.2005, H. Takizawa leg. (SEHU); 1 ex., Oiranbuchi, Sapporo, 5.VI.1938, no collector name (SEHU); 1 ex., Maruyama, Sapporo, 19.VI.1917, S. Matsumura leg. (SEHU); 1 ex., Sapporo, 12.VI.1924, Tamanuki leg. (SEHU); 1 ex., Ônuma Park, Nanae-chô, 18.VII.1954, K. Sawada leg. (SEHU); 4 exs., Ônuma, Nanae-chô, 18.VI.1954, T. Nakane leg. (SEHU); 1 ex., same locality, 13.IV.1954, T. Nakane leg. (SEHU); 2 exs., Obihiro-shi, 28.VI.1954, T. Nakane leg. (SEHU); 1 ex., Tokachi Dam, st.4, GS, 15.VI.1998, A. Nakanishi leg. (SEHU); 1 ex., Ueno, Yukawa, Hakodate, 18.VIII.1943, M. Tsuduki leg. (SEHU); 3 exs., Dansukezawa, Hakodate, 14.VI.1940, M. Tsuduki leg. (SEHU); 2 ♂♂, 4 ♀♀, Utonai-ko Lake, 26.VIII.2018, Y. Fukuda leg. (YTJ); 1 ♀, Ishikarigawa River, Oyafuru, Ishikari-shi, 27.VIII.2018, Y. Fukuda leg. (YTJ). Honshu — [Aomori] 1 ex., Mt. Osorezan – Yunomata, 1.VIII.1956, T. Nakane leg. (SEHU). [Iwate] 1 ♀, Kuroyachi, Hachimantai-hi, 14.IX.2000, M. Hayashi leg. (YTJ). [Miyagi] 1 ex., Sendai-shi, 1.VI.1951, K. Nagayama leg. (SEHU); 1 ex., same locality, 17.V.1953, K. Nagayama leg. (SEHU). [Fukushima] 1 ex., Tateiwa-mura, 20–21.V.1999, H. Takizawa leg. (SEHU); 1 ex., same locality, 28.VIII.1999, H. Takizawa leg. (SEHU); 1 ex., Mt. Iimori-yama, Aizu-Wakamatsu-shi, 11.V., K. Nagayama leg. (SEHU); 1 ex., Asahi, South Aizu, 16.VI.1949, K. Nagayama leg. (SEHU); 1 ex., Mt. Seaburi-yama, Aizu-Wakamatsu-shi, no date, K. Nagayama leg. (SEHU); 2 exs., same locality, VIII, 1952, K. Nagayama leg. (SEHU); 1ex., Mt. Ôshiromori-yama, Iwase-gun, no date, K. Nagayama leg. (SEHU); 8 exs., Higashiyama-chô, Aizu-Wakamatsu-shi, 2.V.1948, K. Nagayama leg. (SEHU); 2 exs., sama locality, no date, K. Nagayama leg. (SEHU); 9 exs., same locality, VIII, K. Nagayama leg. (SEHU). [Tochigi] 2 exs., Shiobara, Nasu-siobara-shi, 17.VI.1979, A. Tanaka leg. (SEHU); 1 ex., Kawamata, Kuriyama, Nikkô-shi, 5.VI.1999, H. Takizawa leg. (SEHU); 2 exs., Mitoshizawa, Miyori, 15.V.1999, H.

Takizawa leg. (SEHU); 1 ex., Kamimiyori, Nikkô-shi, 30.V.1948, K. Nagayama leg. (SEHU). [Gunma] 2 exs., Akagi-jinja Shrine – Miyagi-mura, 12.VI.2005, H. Takizawa leg. (SEHU); 1 ex., Mt. Ômine-yama, Tone-gun, 20.VII.1951, T. Takei leg. (SEHU). [Tokyo] 1 ex., Tama-gawa River, Akiruno-shi, 30.IV.2005, H. Takizawa leg. (SEHU). [Kanagawa] 2 ♀♀, Tanashioda, Chûô-ku, Sagamihara-shi, 23.IV.2017, J. Souma leg. (YTJ); 2 ♀♀, same locality, 3.VI.2017, J. Souma leg. (YTJ). [Niigata] 1 ex., Tainai-shi, 5.VIII.1981, A. Tanaka leg. (SEHU); 1 ex., Mt. Hakkai-san, Uonuma-shi, 12.VI.1988, A. Tanaka leg. (SEHU). [Yamanashi] 1 ex., Kirisawabashi, Nirasaki-shi, 27.VIII.2004, Y. Komiya leg. (SEHU); 1 ex., Fujigawa River Bank, Utsubunashimo, Nanbu-chô, 28.X.2005, Y. Komiya leg. (SEHU); 1 ♂, 1 ♀, Daibo, Hokushu town, Hokuto city, 5.V.2011, M. Miyao leg. (YTJ). [Nagano] 3 exs., Shimashima-dani, Matsumoto-shi, 10.VIII.1950, T. Nakane leg. (SEHU); 1 ex., Nojiri-ko Lake (Tôyô-eiwa), Shinano-machi, 21.VII.1941, T. Nakane leg. (SEHU); 1 ex., Nojiri-ko Lake (Sunama), Shinano-machi, 21–22.VIII.1943, T. Nakane leg. (SEHU); 1 ex., Nojiri-ko Lake (Sunama–Teragasaki), Shinano-machi, 8.VII.1941, T. Nakane leg. (SEHU); 1 ex., Nojiri-ko Lake (Hotel), Shinano-machi, 20.VIII.1943, T. Nakane leg. (SEHU); 1 ex., Nojiri-ko Lake (Sunama–Hotel), Shinano-machi, 24.VIII.1943, T. Nakane leg. (SEHU); 1ex., Nojiri-ko Lake (Gaijinmura), Shinano-machi, 28.V.1941, T. Nakane leg. (SEHU); 3 exs., Komanoyu, Fukushima, Kiso-machi, 5.VII.1947, T. Nakane leg. (SEHU); 1 ex., same locality, 24.VII. 1947, T. Nakane leg. (SEHU); 2 exs., same locality, 11.VI.1949, T. Nakane leg. (SEHU); 1 ex., same locality, 6.VII.1947, T. Nakane leg. (SEHU); 1 ex., Kamikôchi, 12–13.VIII.1950, T. Nakane leg. (SEHU). [Gifu] 1 ex., Kawai, Hida-shi, 2.VI.1957, T. Nakane leg. (SEHU). [Aichi] 1 ex., Gamo, Mikawa, 14.V.1948, T. Nakane leg. (SEHU). [Mie] 2exs., Hirakura, Tsu-shi, 18.VI.1955, T. Nakane leg. (SEHU); 1 ex., same locality, 23–24.VII.1950, T. Nakane leg. (SEHU); 2 exs., Yunoyama, Ise-shi, 1.VI.1947, S. Osawa leg. (SEHU); 1 ex., same locality, 31.V.1948, S. Osawa leg. (SEHU). [Shiga] 2 exs., Mt. Hira, Ômi, 29.V.1956, T. Nakane leg. (SEHU). [Osaka] 3 exs., Yamato-gawa River, Yadamura, 23.IX.1943, K. Sakaguchi leg. (SEHU). [Hyôgo] 1 ex., Muko-gawa River, 29.IV.1943, K. Sakaguchi leg. (SEHU); 1 ex., Hataganaru, Tajima, 27.V.1955, T. Nakane leg. (SEHU); 5 exs., same locality, 24.V.1955, T. Nakane leg. (SEHU); 1ex., Mt. Hyônosen, 30.VII.1952, T. Nakane leg. (SEHU). [Nara] 1 ex., Hôriki-tôge, Mt. Inamuragatake, Tenkawa-mura, 5.VI.1957, no collector name (SEHU). [Tottori] 2 exs., Hinogawa River Bank, Kohôchi, Yonago-shi, 6.VI.2005, Y. Komiya leg. (SEHU); 1 ex., Mt. Goen-san, Mt. Daisen, 5.IX.2004, H.Takizawa leg. (SEHU); 1ex., Daisen-chô, 20.VIII. 1952, T. Nakane leg. (SEHU); 1 ex., same locality, 4.IX.2004, H. Takizawa leg. (SEHU). Shikoku — [Kagawa] 1 ex., Mt. Ryûô-san, 11.V.2000, H. Takizawa leg. (SEHU).

Kyushu — [Miyazaki] 1 ex., Hyûga-shi, 9.V.1970, A. Nagai leg. (SEHU). **South Korea** — 2 exs., Mt. Sudosan (alt. 700 m), Kyongsangpuk-do, 28.V.1970, K. Yamagishi leg. (NSMT); 2 exs., Mt. Sudosan (alt. 400 m), Kyongsangpuk-do, 17–18.VII.1971, K. Yamagishi leg. (NSMT). Europe. **Italy** — 2 exs., Lago di Tenno, 5.V.1976, A. Shinohara leg. (NSMT); 2 exs., same locality, 6.V.1976, A. Shinohara leg. (NSMT). **France** — 1 ex., 76130 Mont Saint-Aignan, Bois des Compagnons, Normandie, 16.V.2010, T. Yoshida & P. Tripotin leg. (SEHU); 1 ex., Saint-Jean-de-Luz, Pyrénées-Atlantiques, 18.VIII.2005, T. Yoshida leg. (SEHU); 1 ex., Bellevue, Cestas, Gironde, 9–10.X.2004, T. Yoshida leg. (SEHU). **Romania** — 1 ex., Bârnova, 5.IX.2010, T. Yoshida leg. (SEHU).

Distributions in Japan. Hokkaido, Honshu, Shikoku, and Kyushu.
Record in literature: Sadogashima Is. (Kurosawa, 1959).

Other distributions. This species is very widely distributed in the Palaearctic Region (Bellamy, 2008 b) — Albania, Algeria, Armenia, Austria, Azerbaijan, Belarus, Belgium, Bosnia and Herzegovina, Bulgaria, China, Croatia, Czech Republic, Denmark, Estonia, Finland, France (incl. Corsica Is.), Germany, Georgia, Great Britain, Greece, Hungary, Iran, Ireland, Italy (incl. Sardina and Sicily Isls.), Korea, Latvia, Lichtenstein, Lithuania, Luxemburg, Macedonia, Moldavia, Mongolia, Netherlands, Norway, Poland, Portugal, Romania, Russia (incl. Sakhalin Is.), Serbia, Slovakia, Slovenia, Spain, Sweden, Switzerland, Syria, Taiwan, Turkey, Ukraine, and Yugoslavia — and is introduced to USA (Westcott & Murray, 2012).

Adult food plants. Same as in the larvae (host plant) mentioned below. In addition, some adults were captured on leaves of *Salix udensis* Trautv. et C.A.Mey. [Japanese name: Onoe-yanagi] and *S. schwerinii* E.L.Wolf [Japanese name: Ezono-kinu-yanagi] in Japan.

Host plants. In Japan: Salicaceae: *Salix vulpina* Andersson [Japanese name: Kitsune-yanagi] (Kurosawa & Iga, 1947 — adult record?; confirmed by this study), *S. caprea* L. [Japanese name: Bakko-yanagi] (Kurosawa & Iga, 1947 — adult record?; confirmed by this study), *S. gracilistyla* Miq. [Japanese name: Neko-yanagi] (Yano, 1952), *S. chaenomeloides* Kimura [Japanese name: Maruba-yanagi] (Kurosawa, 1976c — adult record?), *S. integra* Thunb. [Japanese name: Inukori-yanagi] (confirmed by this study), *S. shiraii* Seemen var. *shiraii* [Japanese name: Shirai-yanagi] (confirmed by this study), and *Populus suaveolens* Fisch. [Japanese name: Doronoki] (Yano, 1952); and Betulaceae: *Corylus heterophylla* Fisch. ex Besser [Japanese name: Hashibami] (Ishiguro *et al*., 2015).

In the continental region, the following four plant families are recorded as hosts: Salicaceae: *Salix alba*, *S. aurita*, *S. caprea*, *S. cinerea*, and *S. nigricans* in Europe; *S. caprea*, *S. excelsa*, *S. fragilis*, *S. pentandra*, *S. schwerinii*, *S. viminalis*, and *Populus tremula* in Siberia, Betulaceae: *Corylus avellana* in Europe, Sapindaceae: *Acer campestre* in Europe, Malvaceae: *Tilia cordata* and *Ti. platyphyllos* in Europe, and Ulmaceae: *Ulmus laevis* and *U. minor* in Europe (Bílý, 2003; Kirichenko *et al*., 2018). *T. minutus* shows the widest host range in the members of the genus *Trachys*, although the preferred hosts are definitely *Salix* species, especially broad leaves species such as *S. caprea* in Europe (Bílý, 2003), as well as in Japan.

Leaf-mining habit. Mines of *Trachys minutus* were found on *Salix vulpina* subsp. *vulpina*, *S. integra*, and *S. shiraii* var. *shiraii* by this study (Figs. 63B, 66A, B): each mine was of the full-depth type and formed a large, elongate blotch occurring usually along leaf-margin; when full-grown, it occupied about half of whole the leaf blade in the small leaf *Salix*, such as *S. integra* and *S. shiraii* var. *shiraii*; eggs, which were black (remaining eggshell) and not covered on powdery substances, were laid singly on the apex of leaf blade on the adaxial surface but rarely found on other parts of the blade on the same surface; hatched larvae left granular to thread-like frass inside the mines; adults were usually emerged from the adaxial surface of the leaves with oval adult exit holes. See also Yano (1952) for descriptions of the leaf-mines and immature stages of Japanese populations of this species. The leaf-mining habit of the Japanese populations of *T. minutus* well match in that of the European ones (Bílý, 2003; Niehuis, 2004).

Notes. Photographs of the speciemns of *Buprestis minuta* Linnaeus, 1758 taken are available from the website of the Linnean Collection (Linnean Society of London, 2022).

Taxonomic treatment of the subspecies salicis. In Kurosawa & Iga (1947), *Trachys salicis* (Lewis, 1893) was synonymized under *T. minutus*. Later, Kurosawa (1959) resurrected *T. salicis* as a subspecies, *T. minutus salicis*, since he distinguished this subspecies from the nominotypical one distributed in the continental region by the following character states: “Elytral punctures more obsolete, irregular and sparser causing elytra more shining than nominotypical race”. However, after careful examinations of the two subspecies in this study, I recognized no significant differences in the elytral punctures and the elytral shining between those subspecies (Fig. 14): the density of elytral punctures have no differences between them, but rarely being smaller in size of the disk-shaped punctures (Fig. 14F); in the elytral shining, the specimens from Japan sometimes have relatively strong luster caused by smooth surface between punctures (Fig. 14C), but such state is also sometimes recognizable in the specimens from the continental region (Fig. 14F). Judging from these results, I conclude that the differences between the two subspecies of *T. minutus* in Kurosawa (1959) are intraspecific variations. Thus, this study treats *T. minutus salicis* as a junior synonym of the nominotypical subspecies.

Taxonomic treatment of Trachys obscuripennis. In Théry (1927), *Trachys obscuripennis* Obenberger, 1923 was synonymized under *T. minutus*, although

Obenberger (1928 a, 1937, etc.) treated it as a full species. Later, Kurosawa (1950, 1959) treated *T. obscuripennis* as a junior synonym of *T. saundersi* Lewis, 1893 on the basis of the original description. After his investigations of the type specimens, Dr. Kurosawa noticed that the treatment of *T. obscuripennis* in his previous studies are incorrect, whereas the treatment in Théry (1927) is definitely correct (Kurosawa, 1976d). Finally, he removed *T. obscuripennis* from the synonymy of *T. saundersi* in Kurosawa (1985a), but he did not show a revised synonymy of *T. minutus* in that study. Due to the missing of Kurosawa's work in Japanese (Kurosawa, 1976 d) and the lack of a revised synonymy in Kurosawa (1985 a), recent catalogs for jewel beetles (Bellamy, 2008 b; Kubáň, 2016) cannot reference to Kurosawa's taxonomic correction for *T. obscuripennis*. In this study, I follow Théry's taxonomic treatment based on Kurosawa (1976 d), namely *T. obscuripennis* is a junior synonym of *T. minutus*.

Conservation name. Bellamy (2001) proposed conservation of some jewel beetle scientific names originally published as junior primary homonyms in *Buprestis* (Linnaeus, 1758). In that paper, *Buprestis salicis* Lewis, 1893 (current: *Trachys salicis*) was listed as a name to be conserved, since the name *salicis* was preoccupied by *Buprestis salicis* (Linnaeus, 1758) (current: *Antaxia salicis*). However, there is no fact that Lewis (1893) described and treated *Buprestis salicis*; actually, he described "*Brachys salicis*". Therefore, there is no need to conserve the scientific name *salicis* and it is considered to be just a misunderstanding of Bellamy (2001) and ICZN (2002), although Kubáň (2006) has already pointed out this erroneous.

Trachys inconspicuus Saunders, 1873
[Japanese name: Ume-chibi-tamamushi]
(Figs. 11B, 12G, H, 15, 16, 63C, 66C)

Trachys inconspicua Saunders, 1873 (type locality: "Japan"): 522; Lewis, 1879: 15 (catalog); Kerremans, 1885: 157 (catalog); Schönfeldt, 1887: 113 (catalog); Kerremans, 1892 a: 286 (catalog); Lewis, 1893: 338 (in list); Kerremans, 1903: 313 (catalog); Jakobson, 1913: 800 (catalog); Kurosawa, 1950 a: 13 (note); 1950 b: 1112, fig. 3187 (pictorial book); Chûjô & Kurosawa, 1950: 12 (Shikoku, Japan); Yano, 1952: 27 (immature stages); Iga, 1955 a: 10, pl.4 (pictorial book); 1955 b: 81, pl.24 (pictorial book); Kurosawa, 1959: 220 (redescription; Japan, China); 1963: 155, pl. 78 (pictorial book); 1976 c: 4 (noted); 1985 a: 166 (Korea); 1985 b: 34, pl. 7 (pictorial book; Taiwan); Akiyama & Ohmomo, 1997: 47 (checklist; Taiwan); 2000:

284, pl. 120 (pictorial book); Mühle, 2003: 48 (list); Kubáň, 2006: 419 (Palaearctic catalog); Peng, 2022 a: 268 (distribution).

Trachys (*Trachys*) *inconspicua*: Obenberger, 1918 a: 21, 43, 64 (in key); 1926 b: 661 (catalog); Miwa & Chûjô, 1936: 24 (catalog; Japanese name: Usugurro-chibi-tamamushi and Mame-tamamushi); Obenberger, 1937 a: 1360 (World catalog).

Trachys inconspicuus [justified emendation, according to ICZN (2009)]: Bellamy, 2008 b: 2492 (World catalog); Fukutomi & Ohmomo, 2013: 83 (note); Ohmomo & Fukutomi, 2013: 166, pl. 51 (pictorial book); Kubáň, 2016: 571 (Palaearctic catalog); Ishiguro & Nishida, 2018: 33, figs. 2, 3 & 6 (aedeagus); Ong & Hattori, 2019: 204, 226 (pictorial book; aedeagus).

Trachys (*Trachys*) *ogumensis* Obenberger, 1924 a: 57 (type locality: "Japan: Oguma"); 1926 b: 661 (catalog); 1937 a: 1368 (World catalog). Synonymized by Kurosawa, 1959: 220.

Trachys (*Trachys*) *ogmensis* [sic]: Miwa & Chûjô, 1936: 25 (misspelling of *ogumensis*; Japanese name: Oguma-chibi-tamamushi).

Trachys (*Trachys*) *galloisi* Obenberger, 1940: 41 (type locality: "Corea: Seoul", South Korea). Synonymized by Kurosawa, 1985 a: 166.

Trachys yoshidai Kurosawa, 1959: 222 (type locality: "Hakozaki, Fukuoka, Kyûshû, Japan"); 1976 d: 4 (note; Japanese name: Yoshida-chibi-tamamushi); 1985 b: 34 (noted in pictorial book); Akiyama & Ohmomo, 1997: 49 (checklist; Taiwan); 2000: 285, pl. 120 (pictorial book); Nagahata & Fukutomi, 2006: 36 (photograph of type specimen); Kubáň, 2006: 421 (Palaearctic catalog); Bellamy, 2008 b: 2533 (World catalog). Synonymized by Fukutomi & Ohmomo, 2013: 83.

Description. Male and female. Body broadly subovate, highly convex dorsally (Figs. 15A, B). LB 2.45–2.90 mm (mean 2.72 mm); WB 1.45–1.75 mm (mean 1.63 mm); LB/WB 1.63–1.73 (mean 1.67) (n = 20 for all measurements except terminalia). Habitus as shown in Figs. 11B, 12G, H.

Integument mainly dark-bronze, sometimes with weak purplish to reddish tints, with weak golden-bronze reflections; maxillary palps light-brown; basal four tarsomeres brown to dark-brown. Dorsal and ventral surfaces moderately shiny.

Vestiture mainly consisting of white, brown and black setae; brown setae sometimes replaced black setae completely. Head sparsely clothed with fine, recumbent, inconspicuous pale-brown setae. Pronotum sparsely clothed with short, semirecumbent, white, pale-brown and black setae which are arranged as follows: 1) white setae transversely scattering in middle, sometimes forming a short longitudinal stripe at midline; and 2) pale-brown setae mixing with black ones in remaining space. Elytra sparsely clothed with short, semirecumbent, white, pale-brown and black setae which are arranged on each elytron as follows: 1) white patches in basal part; 2) inconspicuously undulated, interrupted white band in middle; 3) first white transverse band at apical 1/3, weakly wavy, with setae relatively denser; 4) second white transverse band at subapical part, rather straight, with setae relatively denser, often connecting to the first transverse band along sutural margin; and 5) black setae mixing with pale-brown ones in remaining space. Underside more sparsely setiferous, with fine, recumbent, whitish setae.

Head, when viewed from above, moderately subtriangularly concave on frons, with oculofrontal margins rounded. Eyes, when viewed from above, slightly narrowly visible, weakly convex laterally. Vertex obscurely and coarsely variolate-punctate; frons widely concave, weakly impressed along upper side of midline, smoothly convex from just above each antennal insertion to inner margin of each eye, with surface rather smooth but faintly punctate; suprantennal pores simply round; clypeus narrow (Fig. 15C), without elevated basal margin, WC/LC 1.23–1.60 (mean 1.37), WC/LSC 1.13–1.33 (mean 1.18), deeply arcuately emarginate at apical margin.

Antennae (Figs. 15D, E) reaching just behind apicolateral angles of pronotum when laid alongside; antennomere I stout claviform, longer than II; II ovate, longer than III; III subrectangular, slightly longer than IV; IV–VI subrectangular, subequal each other in length; VII–X triangular, slightly more strongly enlarged in male than in female; XI subtriangular to sublingulate.

Mandibles without transverse ridge in middle of each outside. Maxillary palps with round palpomere IV almost as long as wide.

Pronotum widest at base, WP/LP 2.60–3.03 (mean 2.80), BMP/AMP 1.61–1.78 (mean 1.70), narrower than elytra; lateral margins weakly arcuately and moderately to strongly narrowed apicad; apicolateral angles obtuse; basolateral angles broadly acute; apical margin bisinuately shallowly emarginate, with small median lobe; basal margin trisinuate, with median lobe moderately produced; disk faintly depressed along basal median lobe or not; surface obscurely variolate-punctate, becoming denser toward apical and basal margins. Scutellar shield very small, subtriangular, glabrous.

Elytra widest at humeri, LE/WE 1.19–1.29 (mean 1.24), LE/LP 3.45–4.16 (mean 3.78); humeral calluses weakly developed; lateral margins weakly narrowed posteriorly behind humeri then subparallel or faintly narrowed to middle, and finally arcuately convergent to conjointly rounded apices, without serrations; marginal carinae distinct only in thoracic region; sutural margin faintly elevated in apical half; disk faintly depressed in basal part, weakly constricted behind humeri; surface irregularly and coarsely punctate. Lateral part of abdomen usually invisible in dorsal view; laterosternites I–IV with laterosternal sulci.

Underside. Prosternum (Fig. 15F) straight to slightly emarginate at apical margin which is weakly rimmed; prosternal process wide, constricted between procoxa, with apex broadly rounded at rest; marginal carinae moderately widely separated each other at widest part of prosternal process, strongly divergent posteriad from near middle; disk rather flattened on median portion, somewhat declivous laterad on outside of marginal carinae, without elevated portions along procoxal cavities. Hypomera with depressed hypomeral markings crescent-like shaped (Fig. 15G). Metaventrite weakly and sparsely punctate on inside of katepisternal suture and moderately sculptured with linearly confluent sculptures on outside of the suture. Legs moderately slender; metacoxal plates weakly produced posteriorly at each lateral angle which is broadly acute, with surface coarsely variolate; metatibiae bearing a fringe of spines in apical half of each outer margin, with one long spine in base of the fringe (Fig. 15H); inner tooth of each claw slightly small. Abdominal ventrites with sternal grooves on ventrites II–V; V (Fig. 15I) rounded at apex; surface variolate, in ventrite I with linearly confluent sculptures on median part.

Sexual dimorphism barely recognized on the relative size of serrate antennomeres (see above).

Male terminalia (n = 4 for measurements). Proctiger with a pair of short baculi at base. Sternite (Fig. 16A) wide, IX SL/SW 0.74–0.82 (mean 0.79), shallowly emarginate at apical margin, bearing several short setae on each side of apical margin. Tegmen (Fig. 16B) slightly wide; parameres PL/PW 1.86–2.00 (mean 1.94), sparsely setiferous on apicolateral margins, with sides which are gently dilated from base to widest subapical part, but occasionally faintly expanded around subapical part, and then arcuately convergent to apices; phallobase PbL/PbW 1.50–2.20 (mean 1.79), about 1/4 length of tegmen. Penis (Fig. 16C) wide, PeL/PeW 3.83–4.00 (mean 3.92), shorter than tegmen; dorsal plate with sides which are subparallel from widest point of base to apical 1/5, and then strongly, arcuately convergent apicad, with roundly, slightly strongly produced apex, basally with median struts about 1/3 length of penis; ventral plate membranous, but weakly sclerotized as an inverted Y-shaped patch in middle of subapical part.

Female terminalia (n = 5 for measurements). Ovipositor (Figs. 16D–F) short; proctiger basally with a pair of long, ventrally curved baculi; coxites transversely subhexagonal, sparsely setiferous on each side of apical margin, which is roundly produced at the parts inside from each stylus, ventrally without transverse depression in apical part; styli subtrapezoidal, rather slender, with sides subparallel, SlL/SlW 2.61–3.25 (mean 2.93), bearing several setae apically; ventral valve sparsely setiferous on each side of subapical part; vagina roundly sack-shaped, strongly expanded dorsally in about distal half; spermatheca moderately wide tubular, claviform, slightly short in length, widest around subapical part.

Differential diagnosis. This species is similar to *Trachys pseudoscrobiculatus* Obenberger, 1940 in the small-sized body, the round maxillary palpomere IV, and the relatively small inner tooth of claws, but it is easily distinguished from *T. pseudoscrobiculatus* by the combination of the following character states: body dark-bronze; elytral white patterns of setae distinct; elytral surface more shallowly punctate; apex of male penis distinctly produced; and female spermatheca claviform.

Specimens examined. Type material. Holotype of *Trachys yoshidai* Kurosawa, 1959: ♂ (based on Kurosawa, 1959; no dissected terminalia), "HAKOZAKI / FUKUOKA / KYÛSHÛ / 14.IX.1953 / T. YOSHIDA" (NSMT).

Non type material. **Japan**. Honshu — [Fukushima] 1 ex., Moriai, Fukushima, Fukushima Pref., 6.V.1964, K. Tazoe leg. (NSMT). [Gunma] 2 exs., Numata-shi, 16.V.1971, T. Takei leg. (SEHU). [Saitama] 2 exs., Mikajima, Tokorozawa-shi, 4.IV.2016, Y. Tamadera leg. (YTJ). [Chiba] 1 ex., Sahara, Katori-shi, 1945, M. Yasuda leg. (SEHU); 2 exs., Sakura-shi, 22.V.1989, T. Nakane leg. (SEHU). [Kanagawa] 1 ♂, 4 ♀♀, Mt. Kôbô-yama, Minamiyana, Hadano-shi, 27.IV.2015, Y. Tamadera leg. (YTJ); 3 ♂♂, 3 ♀♀, same locality, 15.VI.2015, Y. Tamadera leg. (YTJ). [Shizuoka] 1 ex., Toyosawa, Fukuroi-shi, 23.V.2016, Y. Fujisawa leg. (YTJ). [Shiga] 36 exs., Wani, near Mt. Hira, Ôtsu-shi, 26.V.1956, T. Nakane leg. (SEHU). [Kyoto] 3 exs., Kurama, 11.VII.1956, T. Nakane leg. (SEHU); 1 ex., Kyôto, 3.VI.1951, H. Ishida leg. (SEHU). [Osaka] 1 ex., Ikeda-shi, 29.V.1937, M. Azuma leg. (SEHU). [Nara] 1 ex., Mt. Kongô-san, 17.VI.1935, no collector name (SEHU). [Hiroshima] 1 ex., Mt. Noro-san, Kure-shi, 13.V.1967, T. Kosaka leg. (SEHU). Shikoku — [Ehime] 1 ex., Saretani, Nakayama-chô, Iyo-shi, 22.IV.2019, Y. Tamadera leg. (YTJ). Kyushu — [Fukuoka] 1 ex., Haki, Asakura-shi, C. Takeya leg. (SEHU). **Taiwan**. 1 ex., Nanshanchi, Taiwan, 5.V.1979, S. Fukuda leg. (NSMT); 1 ex., same locality, 27.III.1980, T. Niisato leg. (NSMT). **China**. 1 ex., "Shôtan Pref., Funang, C.-China" (Xiangtan, Hunan, Central China), IV.1945, K. Shirahata leg. (NSMT; recorded by Kurosawa, 1959 mistaking as "Shin-hua, Hu-nan").

Distributions in Japan. Honshu, Shikoku, and Kyushu.

Other localities based on literatures: Shôdoshima Is. (Fujimoto, 2019) and Tsushima Is. (Kurosawa, 1959).

Other distributions. China, South Korea, and Taiwan.

Adult food plants. Same as in the larvae mentioned below. In addition, some adults were captured on leaves of *Prunus tomentosa* Thunb [Japanese name: Yusura-ume] in Ôita Prefecture, Kyushu (Y. Tsutsumiuchi, pers. comm.).

Host plants. Rosacea: *Prunus mume* Siebold et Zucc. [Japanese name: Ume] (Yano, 1952; confirmed by this study), *P. salicina* Lindl. [Japanese name: Sumomo] (Kurosawa, 1959 — adult record?), *P. persica* (L.) Batsch [Japanese name: Momo] (Kurosawa, 1959 — adult record?), and *P. armeniaca* L. var. *ansu* Maxim. [Japanese name: Anzu] (Kurosawa, 1976c — adult record?) in Japan.

Agricultural pest record. Umeya and Okada (2003) is listed this species as pests of plum and peach leaves.

Leaf-mining habit. Mines of *Trachys inconspicuus* were found on *Prunus mume* by this study (Figs. 63C, 66C): each mine was of the full-depth type and formed an elongate blotch occurring usually along leaf-margin but rarely on other parts of the leaf blade; when full-grown, it occupied much less than an half of whole the leaf blade; eggs, which were black (remaining eggshell) and not covered on powdery substances, were laid singly on the adaxial or abaxial surfaces of the leaf blade; hatched larvae left granular frass inside the mines; adult exit holes were not confirmed in this study. See also Yano (1952) for descriptions of the leaf-mines and immature stages.

Trachys pseudoscrobiculatus Obenberger, 1940
[Japanese name: Kuro-chibi-tamamushi]
(Figs.2H, 11C, 17, 18, 63D, E, 66D)

Trachys (*Trachys*) *pseudoscrobiculata* Obenberger, 1940: 41 (type locality: "Japan: Mont Takao").

Trachys pseudoscrobiculata pseudoscrobiculata: Kurosawa, 1959: 208 (redescription; Japan, China); 1963: 155, pl. 78 (pictorial book); 1976 d: 1 (note; misspelling as "*pseudoscurobiculata*", corrected by Kurosawa, 1976 e: 7); 1985b: 34, pl. 7 (pictorial book); Akiyama & Ohmomo, 1997: 48 (checklist); 2000: 284, pl. 120 (pictorial book); Kubáň, 2006: 420 (Palaearctic catalog).

Trachys pseudoscrobiculatus pseudoscrobiculatus [justified emendation, according to ICZN (2009)]: Bellamy, 2008 b: 2512 (World catalog); Fukutomi & Ohmomo, 2013: 84 (note); Ohmomo & Fukutomi, 2013: 166, pl. 51 (pictorial book); Kubáň, 2016: 572 (Palaearctic catalog); Ishiguro & Nishida, 2018: 33, figs. 2, 3 & 6 (aedeagus).

Trachys pseudoscrobiculata shirozui Kurosawa, 1959: 209 (type locality: "Mt. Tachibana-yama, Vicinity of Fukuoka City, Fukuoka Pref., Kyûshû", Japan); 1963: 155 (noted in pictorial book); 1976 d: 1 (note; misspelling as "*pseudoscurobiculata*", corrected by Kurosawa, 1976e: 7); 1985 b: 34 (noted in pictorial book); Akiyama & Ohmomo, 1997: 48 (checklist); 2000: 284 (noted in pictorial book); Nagahata & Fukutomi, 2006: 36 (photograph of type specimen); Kubáň, 2006: 420 (Palaearctic catalog). Synonymized by Fukutomi & Ohmomo, 2013: 84.

Trachys pseudoscrobiculatus shirozui [justified emendation, according to ICZN (2009)]: Bellamy, 2008 b: 2512 (World catalog); Kubáň, 2016: 572 (Palaearctic catalog); Peng, 2022a: 270 (distribution).

Trachys violae Kurosawa, 1959: 209 (type locality: "Cape Nagasaki-hana, Kagoshima Pref.", Japan; Host: *Viola* sp.); 1963: 155 (noted in pictorial book; Japanese name: Sumire-chibi-tamamushi); 1976 d: 4 (note); 1985 b: 34, pl. 7 (pictorial book); Akiyama & Ohmomo, 1997: 49 (checklist); 2000: 285, pl. 120 (pictorial book); Nagahata & Fukutomi, 2006: 36 (photograph of type specimen); Kubáň, 2006: 421 (Palaearctic catalog); Bellamy, 2008 b: 2532 (World catalog). Synonymized under *T. pseudoscrobiculatus* by Fukutomi & Ohmomo, 2013: 84.

Description. Male and female. Body broadly ovate, slightly highly convex dorsally (Figs. 17A, B). LB 2.20–2.72 mm (mean 2.51 mm); WB 1.30–1.63 mm (mean 1.52 mm); LB/WB 1.63–1.69 (mean 1.65) (n = 13 for all measurements except clypeus and terminalia). Habitus as shown in Fig. 11C.

Integument mainly black with faint golden-bronze reflections, sometimes being brassy-black on head and pronotum; maxillary palps light-brown; basal four tarsomeres brownish-black with brown tarsal pads. Dorsal and ventral surfaces moderately shiny.

Vestiture mainly consisting of inconspicuous white and brown setae. Head and pronotum very sparsely clothed with fine, recumbent, pale-brown setae mixing with greyish-white ones. Elytra very sparsely clothed with fine, recumbent, greyish-white and pale-brown setae which are somewhat variously arranged on each elytron as follows: 1) white setae irregularly scattering in basal half; 2) first white transverse band barely recognized at apical 1/3; 3) second white transverse band often lacking, but a few white setae sometimes scattering at subapical part; and 4) pale-brown setae mixing with blackish ones in remaining space. Underside more sparsely setiferous, with fine, recumbent, whitish to yellowish setae.

Head, when viewed from above, moderately arcuately concave on frons, with oculofrontal margins rounded. Eyes, when viewed from above, narrowly visible, weakly convex laterally. Vertex obscurely and coarsely variolate-punctate; frons widely concave, weakly impressed along upper side of midline, smoothly convex from just above each antennal insertion to inner margin of each eye, with surface rather smooth but faintly punctate; suprantennal pores simply round; clypeus narrow (Fig. 17C), without elevated basal margin, WC/LC 1.15–1.78 (mean 1.53; n = 11), WC/LSC 1.01–1.35 (mean 1.15; n = 11), deeply arcuately emarginate at apical margin.

Antennae (Figs. 17D, E) reaching just behind apicolateral angles of pronotum when laid alongside; antennomere I stout claviform, longer than II; II ovate, slightly longer than III; III subrectangular, slightly longer than IV; IV–VI subrectangular, subequal each other in length; VII–X triangular, slightly more strongly enlarged in male than in female; XI subtriangular to sublingulate.

Mandibles without transverse ridge in middle of each outside. Maxillary palps with round palpomere IV almost as long as wide (Fig. 2H).

Pronotum widest at base, WP/LP 2.48–2.77 (mean 2.61), BMP/AMP 1.55–1.73 (mean 1.64), narrower than elytra; lateral margins weakly arcuately and moderately narrowed apicad; apicolateral angles nearly right; basolateral angles broadly acute; apical margin bisinuately emarginate, with small median lobe; basal margin trisinuate, with median lobe moderately produced; disk sometimes faintly depressed around apical angles; surface obscurely variolate-punctate, becoming denser toward apical and basal margins. Scutellar shield very or extremely small, occasionally almost invisible, glabrous.

Elytra widest at humeri, LE/WE 1.14–1.23 (mean 1.18), LE/LP 3.14–3.61 (mean 3.34); humeral calluses small, not developed; lateral margins subparallel in basal half and faintly constricted between humeri and middle point, and then arcuately convergent to conjointly rounded apices, without serrations; marginal carinae distinct only in thoracic region; sutural margin faintly elevated in apical 1/5 or not elevated; disk faintly depressed in basal part, weakly constricted behind humeri; surface irregularly and coarsely punctate, faintly rugose in basal half. Lateral part of abdomen narrowly visible in dorsal view; laterosternites I–IV with laterosternal sulci.

Underside. Prosternum (Fig. 17F) rather straight at apical margin which is weakly rimmed; prosternal process wide, constricted between procoxa, with apex broadly rounded at rest; marginal carinae moderately widely separated each other at widest part of prosternal process, strongly divergent posteriad from near middle; disk rather flattened on median portion, somewhat declivous laterad on outside of marginal carinae, without elevated portions along procoxal cavities. Hypomera with depressed hypomeral markings longitudinally narrowed subreniform (Fig. 17G). Metaventrite weakly and sparsely punctate on inside of katepisternal suture and moderately sculptured with linearly confluent sculptures on outside of the suture. Legs moderately slender; metacoxal plates weakly produced posteriorly at each lateral angle which is broadly acute, with surface coarsely variolate; metatibiae bearing a fringe of spines in apical half of each outer margin, without one long spine in base of the fringe (Fig. 17H); inner tooth of each claw slightly small. Abdominal ventrites with sternal grooves on ventrites II–V; V (Fig. 17I) rounded at apex; surface variolate, in ventrite I with linearly confluent sculptures on median part.

Sexual dimorphism barely recognized on the relative size of serrate antennomeres (see above).

Male terminalia (n = 5 for measurements). Proctiger with a pair of short baculi at base. Sternite IX (Fig. 18A) wide, SL/SW 0.75–1.08 (mean 0.88), slightly emarginate at apical margin, bearing several setae on each side of apical margin. Tegmen (Fig. 18B) stout; parameres PL/PW 1.57–1.89 (mean 1.75), sparsely setiferous on apicolateral margins, with sides which are gently dilated from base to widest subapical part, but occasionally faintly expanded around subapical part, and then arcuately convergent to apices; phallobase PbL/PbW 1.52–3.00 (mean 1.99), about 1/3 length of tegmen. Penis (Fig. 18C) wide, PeL/PeW 3.50–3.85 (mean 3.65), shorter than tegmen; dorsal plate with sides which are subparallel from widest point of base to beyond apical 1/3, and then strongly, slightly straightly convergent apicad, with roundly, indistinctly produced apex, basally with median struts about 1/3 length of penis; ventral plate membranous, but weakly sclerotized as a linear patch in middle of subapical part.

Female terminalia (n =2 for measurements). Ovipositor (Figs. 18D–F) short; proctiger basally with a pair of long, ventrally curved baculi; coxites transversely subhexagonal, sparsely setiferous on each side of apical margin, ventrally without transverse depression in apical part; styli subtrapezoidal, rather slender, with sides subparallel, SlL/SlW 2.78–2.80 (mean 2.79), bearing several setae apically; ventral valve sparsely setiferous on each side of subapical part; vagina sack-shaped (under incompletely inflated state), somewhat expanded dorsally in about distal half; spermatheca moderately wide tubular, moderate in length, weakly expanded in apical part with widest point, without spermathecal gland.

Differential diagnosis. This species is similar to *Trachys inconspicuus* in the small-sized body, the round maxillary palpomere IV, and the relatively small inner tooth of claws, but can be easily distinguished from *T. inconspicuus* by the combination of the following character states: body mainly black; elytral white patterns of setae indistinct or absent; elytral surface more deeply punctate; apex of male penis indistinctly produced; and female spermatheca weakly expanded in apical part.

Specimens examined. Type material. Holotype of *Trachys pseudoscrobiculatus shirozui* Kurosawa, 1959: ♂ (based on Kurosawa, 1959; no dissected terminalia), "TACHIBANAYAMA / FUKUOKA PREF. / 19.III.1933 / T. SHIROZU" (NSMT). Holotype of *Trachys violae* Kurosawa, 1959: ♀ (based on Kurosawa, 1959; no dissected terminalia), "Kyūshū / Nagasaki- / bana / (Satsuma) / 16.IX.1956 / H. Kuroko"; "スミレの / Miner / Vila [sic] Sp." (NSMT).

Non type material. **Japan**. Honshu — [Aomori] 1 ex., Hachinohe, Aomori Pref., IX.1944, K. Shirahata leg. (NSMT; recorded by Kurosawa, 1959). [Yamagata] 3 ♂♂, Arato, Shirataka-machi, Nishiokitama-gun, 8.V.2004, H. Fukutomi leg. (YTJ). [Tokyo] 2 ♂♂, Narabai-tanito, Onoji-machi, Machida-shi, Tokyo, Japan, 20.III.2019, Y. Tamadera leg. (YTJ); 1 ♂, 1 ♀, 2 exs., same locality, 13.VII.2020, Y. Tamadera leg. (YTJ). [Kanagawa] 1ex., Odawara, Kanagawa Pref., 26.IV.1957, Y. Hirano leg. (NSMT). Kyushu — [Ôita] 1 ♂, Hita-shi, 3.X.2010, H. Fukutomi leg. (YTJ). [Miyazaki] 1 ♀, Yûgakuno-mori, Kawaminami-chô, Koyu-gun, no collecting date, Y. Tsutsumiuchi leg., emerged from *Viola* sp., 21.VI.2012 (YTJ). [Kagoshima] 1 ex., Cape Sata, Kyushu, Japan, 6.VI.1960, T. Kikuchi leg. (NSMT). **China**. 1 ex., "Shinkawa Pref., Funang, C.-China" (Xinghua, Hunan, Central China), V.1945, K. Shirahata leg. (NSMT; recorded by Kurosawa, 1959 in note of *T. pseudoscrobiculatus shirozui*).

Distributions in Japan. Honshu and Kyushu.

Other distributions. China (Hunan).

Adult food plants. Same as in the larvae mentioned below. In addition, Nagahata & Fukutomi (2006) confirmed that the adults feed on leaves of *Viola kusanoana* Makino [Japanese name: Ôba-tachitsubo-sumire] and *V. keiskei* Miq. [Japanese name: Maruba-sumire]. Adult feeding scars as shown in Figs. 63D, E.

Host plants. Violaceae: *Viola grypoceras* A.Gray var. *grypoceras* [Japanese name: Tachitsubo-sumire] (Watanabe, 2013; confirmed by this study), *V. mandshurica* W.Becker [Japanese name: Sumire] (Nagahata & Fukutomi, 2006), *V. hondoensis* W.Becker et H.Boissieu [Japanese name: Aoi-sumire] (Otsuka, 2019), and *V. yedoensis* Makino [Japanese name: Noji-sumire] (Otsuka, 2019) in Japan.

Leaf-mining habit. Mines of *Trachys pseudoscrobiculatus* were found on *Viola grypoceras* var. *grypoceras* by this study (Fig. 66D): each mine was of the full-depth type and formed a blotch occurring along leaf-margin; when full-grown, it occupied more than an half of whole the leaf blade; eggs, which were pale-brown (remaining eggshell) and not covered on powdery substances, were laid singly on the abaxial surface of the leaf blade; hatched larvae left granular frass inside the mines; one adult exit hole was found on the abaxial surface of the leaf.

Notes. *Trachys pseudoscrobiculatus* is seemed to be rather related to *T. inconspicuus* than other Japanese congeners in having the similarities mentioned in the differential diagnosis. However, actually, *T. pseudoscrobiculatus* shows much closer similarities to some European *Trachys* species, for example *T. scrobiculatus* Kiesenwetter, 1857, *T. fragariae* Brisout de Barneville, 1874, and *T. problematicus* Obenberger, 1918, than to Japanese species in general appearance (the clearly small-sized body, blackish body, and prominently sparse vestiture) and in host associations (using herbaceous plants). Among such European species, *T. scrobiculatus* is considered to be the most similar species to *T. pseudoscrobiculatus* in the concaved frons outline of the head, in the clearly posteriorly diverging marginal carinae on the prosternum, in the presence of the fringe of spines on outer margin of each meatatibia, and in the degree of sparse vestiture. However, *T. pseudoscrobiculatus* is differentiated from *T. scrobiculatus* by the more strongly concaved frons outline of the head and by the host plant (Violaceae in *T. pseudoscrobiculatus*; Lamiaceae in *T. scrobiculatus*) on the basis of several literatures (Schaefer, 1950; Cobos, 1986; Muskovits & Hegyessy, 2002; Niehuis, 2004; Verdugo, 2005) and a comparison with one *T. scrobiculatus* specimen [1ex., St. Martes de Candy, France, VIII.1972. (NSMT)].

Voltinism of *Trachys pseudoscrobiculatus* may be of multivoltine since adults of several generations are found in same year from summer to autumn under breeding condition (outside temperature) (Ishiguro, 2014). Although the following report slightly lacks quantitativeness, Watanabe (2013) mentioned that active adults of *T. pseudoscrobiculatus* were confirmed in all seasons at Tokyo and Kanagawa Prefectures, Honshu, Japan (the number of individuals in Winter is small) and larvae of this species were often found on May and from September to November. Additionally, the adult of this species seems to show a long lifespan under breeding condition: ca 70 days (Watanabe, 2013); more than ten moths (Ishiguro, 2014); and 798 days (Otsuka, 2019).

Trachys ineditus Saunders, 1873
[Japanese name: Marugata-chibi-tamamushi]
(Figs. 11D, 12I, J, 19, 20, 66E)

Trachys inedita Saunders, 1873: 522 (type locality: "Japan"); Lewis, 1879: 15 (catalog); Kerremans, 1885: 157 (catalog); Schönfeldt, 1887: 113 (catalog); Kerremans, 1892 a: 286 (catalog); Lewis, 1893: 338 (in list); Kerremans, 1903: 313 (catalog); Jakobson, 1913: 800 (catalog); Théry, 1935: 132 (China); Kurosawa, 1976 c: 4

(note); 1985a: 167 (note); 1985b: 35, pl. 7 (pictorial book); Akiyama & Ohmomo, 1997: 47 (checklist); 2000: 284, pl. 120 (pictorial book); Kubáň, 2006: 419 (Palaearctic catalog).

Trachys (*Trachys*) *inedita*: Obenberger, 1918: 20, 40, 64 (in key); 1926 b: 661 (catalog); Miwa & Chûjô, 1936: 24 (catalog); Obenberger, 1937 a: 1360 (catalog).

Trachys ineditus [justified emendation, according to ICZN (2009)]: Bellamy, 2008b: 2492 (World catalog); Ohmomo & Fukutomi, 2013: 167, pl. 53 (pictorial book); Kubáň, 2016: 571 (Palaearctic catalog); Ishiguro & Nishida, 2018: 33, figs. 2, 3 & 6 (aedeagus); Ong & Hattori, 2019: 202, 226 (pictorial book; Taiwan; aedeagus); Peng, 2022 a: 268 (distribution).

Trachys inedita [auct. non Saunders]: Kurosawa, 1950 a: 13 (misidentification of *Travhys tsushimae* Obenberger); Chûjô & Kurosawa, 1950: 12; Yano, 1954: 32; Kurosawa, 1959: 227; 1963: 156, pl. 78.

Trachys medita [sic; auct. non Saunders]: Matsumura, 1931: 179 (misspelling of *inedita*; misidentification of *Travhys tsushimae* Obenberger). Corrected by Kurosawa, 1985 a: 167.

Trachys oviformis Kurosawa, 1959: 229 (type locality: "Nagasaki City", Japan); 1963: 156, pl. 78 (pictorial book). Synonymized by Kurosawa, 1985 a: 167.

Description. Male and female. Body ovate, moderately convex dorsally (Figs. 19A, B). LB 2.90–3.25 mm (mean 3.09 mm); WB 1.61–1.80 mm (mean 1.72 mm); LB/WB 1.74–1.87 (mean 1.80) (n = 20 for all measurements except terminalia). Habitus as shown in Figs. 11D, 12 I, J.

Integument mainly blackish-bronze with weak golden-bronze reflections; head in male tend to be weakly greenish on frontoclypeal region, in female with golden tints on the region; maxillary palps black, sometimes with brownish tints; basal four tarsomeres brownish-black with brown tarsal pads. Dorsal and ventral surfaces moderately shiny except for median part of metaventrite with more luster.

Vestiture mainly consisting of white, brownish-yellow and black setae. Head clothed with short, recumbent brownish-yellow setae. Pronotum clothed with short, semirecumbent brownish-yellow setae, with some small white patches across middle. Elytra clothed with short, semirecumbent, white, brownish-yellow and black setae which are arranged on each elytron as follows: 1) one or several small white patches in basal 1/5; 2) inconspicuously undulated, interrupted white band just before middle; 3) first white transverse band at apical 1/3, moderately wavy, zigzag-shaped; 4) second white transverse band at subapical part, rather straight, weakly interrupted near middle; 5) brownish-yellow setae along basal and sutural margin, in humeral region and apex, and around white patches and bands; and 6) black setae in remaining space, sometimes with brownish tints. Underside more sparsely setiferous, with fine, recumbent whitish setae, except for metacoxal plates with yellowish ones in lateral part.

Head, when viewed from above, faintly concave on frons, with oculofrontal margins rounded. Eyes, when viewed from above, broadly visible, strongly convex laterally. Vertex obscurely and coarsely variolate-punctate; frons widely, faintly concave, weakly impressed along upper side of midline, transversely ridged from just above each antennal insertion to inner margin of each eye, with surface rather smooth but faintly punctate; suprantennal pores simply round; clypeus wide (Fig. 19C), without elevated basal margin, WC/LC 1.48–1.88 (mean 1.67), WC/LSC 1.56–1.88 (mean 1.75), deeply arcuately emarginate at apical margin.

Antennae (Figs. 19D, E) reaching just behind apicolateral angles of pronotum when laid alongside; antennomere I stout claviform, longer than II; II ovate, longer than III; III–VI subrectangular, subequal each other in length; VII–X triangular, slightly more strongly enlarged in male than in female; XI subtriangular to sublingulate.

Mandibles without transverse ridge in middle of each outside. Maxillary palps with oval palpomere IV somewhat longer than wide.

Pronotum widest at base, WP/LP 2.66–2.91 (mean 2.78), BMP/AMP 1.40–1.52 (mean 1.45), narrower than elytra; lateral margins straightly and moderately to slightly weakly narrowed apicad; apicolateral angles right to obtuse; basolateral angles broadly acute to right; apical margin bisinuately shallowly emarginate, with small median lobe; basal margin trisinuate, with median lobe moderately produced; disk weakly depressed basal median lobe; surface obscurely variolate-punctate, becoming denser toward apical and basal margins. Scutellar shield very small, subtriangular, glabrous.

Elytra widest at humeri, LE/WE 1.26–1.34 (mean 1.31), LE/LP 3.64–4.1 (mean 3.84); humeral calluses weakly developed; lateral margins subparallel in basal half and weakly constricted between humeri and middle point, and then arcuately convergent to conjointly rounded apices, without serrations; marginal carinae distinct in thoracic region, indistinctly reaching near apices; sutural margin faintly elevated in apical 1/5; disk weakly depressed in basal part, constricted behind humeri; surface irregularly and coarsely punctate. Lateral part of abdomen narrowly visible in dorsal view; laterosternites I–VI with laterosternal sulci.

Underside. Prosternum (Fig. 19F) rather straight at apical margin which is weakly rimmed; prosternal process clearly wide, subparallel-sided, with apex broadly weakly rounded at rest; marginal carinae clearly widely separated each other at widest part of prosternal process, subparallel except for apical 1/5 faintly narrowed posteriorly; disk rather flattened on median portion, weakly declivous laterad on outside of marginal carinae, without elevated protions along procoxal cavities. Hypomera with depressed hypomeral markings subreniform (Fig. 19G). Metaventrite weakly punctate on inside of katepisternal suture and moderately sculptured with linearly confluent sculptures on outside of the suture, with rather smooth part along outside of the suture. Legs moderately slender; metacoxal plates slightly strongly produced posteriorly at each lateral angle which is acute, with surface coarsely variolate; metatibiae bearing a fringe of spines in apical half of each outer margin, with one long spine in base of the fringe (Fig. 19H); inner tooth of each claw large. Abdominal ventrites with sternal grooves on ventrites II–V; V (Fig. 19I) rounded or obtusely subtruncate at apex; surface variolate, in ventrite I with linearly confluent sculptures on median part.

Sexual dimorphism barely recognized on the relative size of serrate antennomeres and may be on the coloration of frontoclypeal region (see above).

Male terminalia (n = 5 for measurements). Proctiger with a pair of short baculi at base. Sternite IX (Fig. 20A) wide, SL/SW 0.72–0.79 (mean 0.75), shallowly arcuaterly emarginate at apical margin, bearing several setae on each side of apical margin. Tegmen (Fig. 20B) wide; parameres PL/PW 1.73–2.04 (mean 1.87), bearing a pair of setae on apicolateral margins, with sides which are gently dilated from base to beyond middle, then expanded continuously into angular shape to widest point of apical 1/5, and finally strongly convergent to apices; phallobase PbL/PbW 2.30–3.02 (mean 2.72), about 1/4 length of tegmen. Penis (Fig. 20C) wide, PeL/PeW 4.17–4.60 (mean 4.39), slightly shorter than tegmen; dorsal plate with sides which are parallel in basal half, and then faintly arcuately and gently convergent apicad, with round apex, basally with median struts about 1/4 length of penis; ventral plate membranous, without sclerotized portion.

Female terminalia (n = 2 for measurements). Ovipositor (Figs. 20D–F) short; proctiger basally with a pair of long, ventrally curved baculi; coxites transversely subreniform, sparsely setiferous on each side of apical margin, ventrally without transverse depression in apical part; styli subtrapezoidal, rather slender, with sides subparallel, SlL/SlW 2.54–2.67 (mean 2.61), bearing several setae apically; ventral valve sparsely setiferous on each side of subapical part; vagina sack-shaped (under incompletely inflated state); spermatheca moderately wide tubular, claviform, rather short in length, widest near apex, without spermathecal gland.

Differential diagnosis. This species may be related to *Trachys tsushimae* in having the faintly concave frons outline of the head, the subparallel-sided prosternal process, and the shape of penis (subparallel-sided in basal half, not produced at apex, and without a sclerotized patch on ventral membrane), but can be distinguished from *T. tsushimae* by the combination of the following character states: eyes larger in dorsal view and also more strongly convex laterally; inner margin of each eye more strongly rounded in dorsal view; setae coloration clearer; male parameres with somewhat sharp lateral expansion being widest at apical 1/5; and female spermatheca claviform and wider.

Specimens examined. Type material. Holotype of *Trachys oviformis* Kurosawa, 1959: ♂ (based on Kurosawa, 1959; no dissected terminalia), "NAGASAKI / KYUSHU / 26.II.1953 / H. KAMIYA" (NSMT). Paratypes (part) of *T. oviformis*: 2 exs., Nagasaki, Kyushu, 12.XI.1953, H. Kamiya leg. (NSMT).

Non type material. **Japan**. Honshu — [Miyagi] 1 ex. Gassan-ike Pond, Kamiayashi, Aoba, Sendai-shi, 28.VIII.2012, H. Yoshitake leg. (24-0479952) (NIAES; recorded by Yoshitake *et al*., 2018). [Ibaraki]: 1 ex., Tsukuba-gakuen-toshi, 3.V.1979, M. Ôhara leg. (SEHU). [Saitama] 2 ♂♂, 2 ♀♀, Kamiyamaguchi, Tokorozawa-shi, 28.VIII.2018, Y. Tamadera leg. (YTJ). [Chiba] 1 ex., Miyanogi-chô, Inage-ku, 3–4.V.1999, H. Takizawa leg. (SEHU); 6 exs., Sakura-shi, 22.V.1989, T. Nakane leg. (SEHU). [Kanagawa] 1 ♂, Mt. Kôbô-yama, Minamiyana, Hadano-shi, 25.V.2014, H. Nagano leg. (YTJ); 1 ♂, Atsugi Campus of Tokyo University of Agriculture, Funako, Atsugi-shi, 4.VI.2015, Y. Tamadera leg. (YTJ); 1 ♂, Asamizodai, Minami-ku, Sagamihara-shi, Kanagawa-ken, Japan, 16.XII.2017, J. Souma leg. (YTJ); 2 exs., Sagamigawa-kôen Park, kamigô, Ebina-shi, 16.VIII.2020, W. Yamada leg. (YTJ); 4exs., Ôshima, Midoriku, Sagamihara-shi, 29.VIII.2020, W. Yamada leg. (YTJ). [Kyoto] 8 exs., Shimogamo, Kyoto-shi, 16.V.1955, T. Kishii leg. (SEHU); 4 exs., same locality, 9.XII.1951, T. Kishii leg. (SEHU). [Hyôgo] 1 ex., Hataganaru, Tajima, 28.V.1954, T. Okutani leg. (SEHU). [Hiroshima] 1 ex., Motoujina, Hiroshima-shi, 9.V.1978, T. Kosaka leg. (SEHU). Shikoku —1 ♂, Saretani, Nakayama-machi, Iyo-shi, 22.IV.2019, Y. Tamadera leg. (YTJ).

Distributions in Japan. Honshu, Shikoku, and Kyushu.

Other locality based on literature: Awajishima Is. (Takahashi, 1999).

Other distributions. China and Taiwan.

Adult food plant. Same as in the larvae mentioned below.

Host plant. Cannabaceae: *Aphananthe aspera* (Thunb.) Planch. [Japanese name: Mukunoki] (Kurosawa, 1959 for *Trachys oviformis* — adult record?; confirmed by this study) in Japan.

Leaf-mining habit. Mines of supposed *Trachys ineditus* and one pupa were found on *Aphananthe aspera* by this study (Fig. 66E): each mine was of the full-depth type and formed a blotch occurring usually along apical leaf-margin; when full-grown, it occupied less than an half of whole the leaf blade; eggs, which were black (remaining eggshell) and not covered on powdery substances, were singly laid near the apex of leaf blade on the adaxial surface; hatched larvae left granular frass inside the mines; one adult exit hole was found on the abaxial surface of the leaf.

Notes. In Japan, *Trachys ineditus* is occasionally sympatlically distributed with *T. griseofasciatus* Saunders, 1873, which is also associated with *Aphananthe aspera*, but usually *T. ineditus* is less than *T. griseofasciatus*. *T. ineditus* is readily distinguished from *T. griseofasciatus* by the absence of serrations on the lateral margins of the elytra, etc.

Taxonomic history. For a long time, Japanese researchers had misidentified *Trachys ineditus* and its related in Japan as shown in Table 2. These misidentifications were reviewed by Kurosawa (1976 c) in Japanese and formally corrected by Kurosawa (1985 a).

Trachys tsushimae Obenberger, 1922

[Japanese name: Akagane-chibi-tamamushi]

(Figs. 11E, 12K, L, 21, 22, 63F, 66F)

Trachys (*Trachys*) *tsushimae* Obenberger, 1922: 70 (type locality: "Japan: Tsushima"); Miwa & Chûjô, 1936: 25 (catalog; Japanese name: Tsushima-chibi-tamamushi); Obenberger, 1926 b: 661 (catalog); 1937 a: 1384 (World catalog).

Trachys tsushimae: Kurosawa, 1976 d: 3 (note); 1985 a: 167 (Japan and China); 1985 b: 34, pl. 7 (pictorial book); Akiyama & Ohmomo, 1997: 49 (checklist); 2000: 285, pl. 120 (pictorial book); Kubáň, 2006: 421 (Taiwan; Palaearctic catalog); Bellamy, 2008 b: 2529 (World catalog); Ohmomo & Fukutomi, 2013: 167, pl. 53 (pictorial book); Kubáň, 2016: 574 (Palaearctic catalog); Ishiguro & Nishida, 2018: 33, figs. 2, 3 & 6 (aedeagus); Peng, 2022 a: 272 (distribution).

Trachys tsushimae [auct. non Obenberger]: Chûjô & Kurosawa, 1950: 13 (misidentification of *Trachys broussonetiae* described later by Kurosawa, 1985 a); Yano, 1952: 28; Kurosawa, 1959: 225; 1963: 156, pl. 78.

Trachys (*Trachys*) *japonica* Obenberger, 1923: 65 (type locality: "Kioto (Japan)"); 1926 b: 661 (catalog); Miwa & Chûjô, 1936: 24 (catalog; Japanese name: Nihon-chibi-tamamushi); Obenberger, 1937 a: 1360 (World catalog). Synonymized by Kurosawa, 1985 a: 167. Justified emendation: *T. japonicus*, according to ICZN (2009).

Trachys japonica [auct. non Obenberger]: Chûjô & Kurosawa, 1950: 12 (misidentification of *Trachys tokyoensis*); Yano, 1952: 29; Kurosawa, 1959: 225.

Trachys medita [sic]: Matsumura, 1931 b: 179 (pictorial book; misspelling of *inedita*; misidentification); Kato, 1933: pl. 32 (pictorial book). Corrected by Kurosawa, 1985 a: 167.

Trachys ornata Théry, 1934: 86 (type locality: "Okayama, Japon"); Kurosawa, 1959: 227 (synonymized under *Trachys ineditus* Saunders *sensu* Kurosawa, 1959). Synonymized under *T. ineditus* by Kurosawa, 1985 a: 167. Justified emendation: *T. ornatus*, according to ICZN (2009).

Trachys inedita [non Saunders, 1873]: Chûjô & Matuda, 1940: 66 (Kyushu; *T. formosanus* treated as junior synonym); Kurosawa, 1950 a: 13 (noted); Chûjô & Kurosawa, 1950: 12 (Shikoku, Japan); Yano, 1954: 32 (immature stages); Iga, 1955 a: 10, pl.4 (pictorial book); 1955b: 81, pl.24 (pictorial book); Kurosawa, 1959: 227 (redescription; Japan and China). Corrected by Kurosawa, 1985 a: 167.

Description. Male and female. Body ovate to subovate, moderately convex dorsally (Figs. 21A, B). LB 3.05–3.55 mm (mean 3.31 mm); WB 1.65–2.00 mm (mean 1.84 mm); LB/WB 1.76–1.85 (mean 1.81) (n = 20 for all measurements except terminalia). Habitus as shown in Figs. 11E, 12K, L.

Integument mainly blackish-bronze, sometimes with faint coppery tints, with golden-bronze reflections; head occasionally with faint greenish tints on frons and clypeus in both sexes; maxillary palps black, sometimes with faint brownish tints; basal four tarsomeres brownish-black with brown tarsal pads. Dorsal surface slightly strongly shiny; ventral surface moderately shiny.

Vestiture mainly consisting of white, brownish-yellow and black setae, which are usually dark in color. Head clothed with short, recumbent brownish-yellow seta Pronotum clothed with short, semirecumbent brownish-yellow setae, with several white spots, one of which on midline. Elytra clothed with short, semirecumbent, white, brownish-yellow and black setae which are arranged on each elytron as follows: 1) white setae irregularly scattering or absent in basal part; 2) inconspicuously undulated, interrupted white band just before middle; 3) first white transverse band at apical 1/3, moderately wavy, zigzag-shaped; 4) second white transverse band at subapical part, rather straight, often connecting to the first transverse band along sutural margin; 5) brownish-yellow setae along basal and sutural margin, in humeral region and apex, and around white patches and bands; and 6) black setae in remaining space. Underside more sparsely setiferous, with fine, recumbent, whitish to pale-yellowish setae.

Head, when viewed from above, faintly concave on frons, with oculofrontal margins obtusely ridged. Eyes, when viewed from above, narrowly visible, weakly convex laterally. Vertex obscurely and coarsely variolate-punctate; frons widely, faintly concave, weakly impressed along upper side of midline, transversely ridged from just above each antennal insertion to inner margin of each eye, with surface rather smooth but faintly punctate; suprantennal pores simply round; clypeus slightly narrow (Fig. 21C), without elevated basal margin, WC/LC 1.25–1.67 (mean 1.47), WC/LSC 1.24–1.67 (mean 1.44), deeply arcuately emarginate at apical margin.

Antennae (Fig. 21D) reaching just behind apicolateral angles of pronotum when laid alongside; antennomere I stout claviform, longer than II; II ovate, longer than III; III subrectangular, longer than IV; IV–VI subrectangular, subequal each other in length; VII–X triangular, moderately enlarged; XI subtriangular to sublingulate.

Mandibles without transverse ridge in middle of each outside. Maxillary palps with oval palpomere IV somewhat longer than wide.

Pronotum widest at base, WP/LP 2.48–2.72 (mean 2.61), BMP/AMP 1.43–1.54 (mean 1.49), narrower than elytra; lateral margins straightly or weakly arcuately and slightly weakly narrowed apicad; apicolateral angles obtuse; basolateral angles broadly acute; apical margin bisinuately shallowly emarginate, with small median lobe; basal margin trisinuate, with median lobe moderately produced; disk weakly depressed along basal median lobe; surface rather densely variolate-punctate throughout. Scutellar shield very small, subtriangular, glabrous.

Elytra widest at humeri, LE/WE 1.27–1.35 (mean 1.32), LE/LP 3.53–3.92 (mean 3.70); humeral calluses weakly developed; lateral margins subparallel in basal half and weakly constricted between humeri and middle point, and then arcuately convergent to conjointly rounded apices, without serrations; marginal carinae distinct in thoracic region, indistinctly reaching near apices; sutural margin not elevated or faintly elevated in apical part; disk weakly depressed in basal part, constricted behind humeri; surface irregularly and coarsely punctate. Lateral part of abdomen narrowly visible in dorsal view; laterosternites I–VI with laterosternal sulci.

Underside. Prosternum (Fig. 21E) rather straight at apical margin which is weakly rimmed; prosternal process clearly wide, subparallel-sided, with apex broadly rounded at rest; marginal carinae clearly widely separated each other at widest part of prosternal process, subparallel, weakly arcuate inwardly; disk rather flattened on median portion, weakly declivous laterad on outside of marginal carinae, without elevated protions along procoxal cavities. Hypomera with depressed hypomeral markings subreniform (Fig. 21F). Metaventrite moderately sculptured with large punctures on inside of katepisternal suture and with linearly confluent sculptures on outside of the suture. Legs moderately slender; metacoxal plates slightly strongly produced posteriorly at each lateral angle which is sharply acute, with surface coarsely variolate; metatibiae bearing a fringe of spines in apical half of each outer margin, with one long spine in base of the fringe (Fig. 21G); inner tooth of each claw large. Abdominal ventrites with sternal grooves on ventrites II–V; V (Fig. 21H) rounded or obtusely subtruncate at apex; surface variolate, in ventrite I with linearly confluent sculptures on median part.

Sexual dimorphism indistinct.

Male terminalia (n = 5 for measurements). Proctiger with a pair of short baculi at base. Sternite IX (Fig. 22A) wide, SL/SW 0.67–0.91 (mean 0.76), shallowly arcuately emarginate at apical margin, bearing with several setae on each side of apical margin. Tegmen (Fig. 22B) wide; parameres PL/PW 1.64–1.79 (mean 1.75), bearing a pair of setae on apicolateral margins, with sides which are gently dilated from base to apical half, then weakly arcuately expanded to widest point at apical 1/4, and finally strongly convergent to apices; phallobase PbL/PbW 3.10–3.95 (mean 3.39), more than 1/3 length of tegmen. Penis (Fig. 22C) wide, PeL/PeW 3.83–4.09 (mean 3.99), slightly shorter than tegmen; dorsal plate with sides which are parallel in basal half, and then faintly arcuately and gently convergent apicad, with round apex, basally with median struts about 1/4 length of penis; ventral plate membranous, without sclerotized portion.

Female terminalia (n = 5 for measurements). Ovipositor (Figs. 22D–F) short; proctiger basally with a pair of long, ventrally curved baculi; coxites transversely subreniform, sparsely setiferous on each side of apical margin, ventrally without transverse depression in apical part; styli subtrapezoidal, short, rather slender, with sides faintly narrowed apicad or subparallel, SlL/SlW 2.14–3.00 (mean 2.50), bearing several setae apically; ventral valve sparsely setiferous on each side of subapical part; vagina sack-shaped (under incompletely inflated state); spermatheca slender tubular, moderate in length, widest in apical half, without spermathecal gland.

Differential diagnosis. This species may be related to *Trachys ineditus* in having the faintly concave frons outline of the head, the subparallel-sided prosternal process, and the shape of penis (subparallel-sided in basal half, not produced at apex, and without a sclerotized patch on ventral membrane), but differs from *T. ineditus* by the combination of the following character states: eyes appear to be smaller in dorsal view and more weakly convex laterally; inner margin of each eye more weakly rounded in dorsal view; setae coloration darker; male parameres with weakly arcuate lateral expansion being widest at apical 1/4; and female spermatheca much slenderer.

Specimens examined. Non type material. **Japan**. Honshu — [Miyagi] 1 ex., Akiho, Natori, 23.VI.1951, K. Nagayama leg. (SEHU). [Fukushima] 1 ex., Iitate-mura, 7.VII.1981, A. Tanaka leg. (SEHU); 1 ex., Takikawa D., 11–13.V.2000, H. Takizawa leg.

(SEHU). [Ibaraki] 1 ex., Akiyama, Takahagi-shi, 4.VI.2015, Y. Fujisawa leg. (YTJ). [Gunma] 1 ex., Numata-shi, 3.VI.1971, T. Takai leg. (SEHU). [Saitama] 1 ex., Nishikubo-shicchi, Iruma-shi, 22.X.2004, Y. Komiya leg. (SEHU); 1 ex., Yorii-machi, 5.V.2000, H. Takizawa leg. (SEHU). [Chiba] 1 ex., Mt. Nokogiriyama, Chiba, 8.VI.1991, T. & T. Nakane leg. (SEHU); 2 exs., Ainosawa-rindô, Kiyosumi, Kamogawa-shi, 7.VI.2015, S. Shimamoto leg. (YTJ). [Tokyo] 1 ex., Mont Takao, Hachiôji, 4.V.1913, E. Gallois leg. (SEHU); 1 ex., same locality, 18.V.1913, E. Gallois leg. (SEHU); 1 ex., Nippara, Okutama-chô, 9.VI.1991, T. & T. Nakane leg. (SEHU); 2 exs., Kogesawa-rindô, Uratakao-machi, Hachiôji-shi, 14.V.2016, S. Shimamoto leg. (YTJ). [Kanagawa] 1 ex., Zushi-shi, 24.IV.1988, A. Tanaka leg. (SEHU); 1 ex., Mt. Takatori-yama, Zushi-shi, 19.VIII.1973, S. Tachikawa & M. Taguchi leg. (SEHU); 1 ex., Nagara, Hayama-machi, 19.IV.2004, H. Takizawa leg. (SEHU); 6 exs., Ôsawa-rindô, Nanasawa, Atsugi-shi, 21.V.2016, S. Shimamoto leg. (YTJ); 1 ex., Hiromachi, Koshigoe, Kamakura-shi, 5.IV.2013, W. Yamada leg. (YTJ); 3 ♂♂, 2 ♀♀, Tanitaro-rindô, Susugaya, Kiyokawa-mura, Aikô-gun, 24.IV.2011, M. Miyao leg. (YTJ); 1 ♂, 2 ♀♀, Kanasawa, Matsudashoshi, Matsuda-machi, Ashigara-jô-gun, 29.IV.2011, M. Miyao leg. (YTJ). [Yamanashi] 2 exs., Kôshû-shi, 15.V.2011, Yuki Shimizu leg. (YTJ); 1 ex., Nakahara, Katsunuma-chô, Kôshû-shi, 4.V.2011. M. Miyao leg. (YTJ); 1 ex., Ôtaki-fudôson, Katsunuma-chô, Kôshû-shi, 14.V.2011, M. Miyao leg. (YTJ); 1 ex., Enzan-hirasawa, Kôshû-shi, 3.V.2016, S. Shimamoto leg. (YTJ); 1 ♂, 2 ♀♀, 5 exs., Hishiyama, Katsunuma-chô, Kôshû-shi, 3.V.2017, J. Souma leg. (YTJ); 4 exs., same locality, 3.V.2017, M. Yamada leg. (YTJ); 2 ♂♂, Ôtaki-fudôson, Katsunuma-chô, Kôshû-shi, 14.V.2011, M. Miyao leg. (YTJ). [Nagano] 1 ex., Komanoyu, Hukushima, Kiso, 25.VII.1947, T. Nakane leg. (SEHU). [Shizuoka] 1 ex., Yugashima, Izu-shi, 15.VIII.1971, T. Kumata leg. (SEHU); 1 ♀, Ita, Numazu-shi, 31.V.2013, H. Handa leg. (YTJ). [Aichi] 1 ex., Haraiji, Mikawa, 30.IV.1950, T. Nakane leg. (SEHU); 1 ex., Mikawa-ôno, 10.V.1991, TTM. Nakane leg. (SEHU); 3 exs., Inuyama, 21.V.1950, T. Nakane leg. (SEHU); 1 ex., Ishimaki-chô, Toyohashi-shi, 13.V.2016, S. Shimamoto leg. (YTJ). [Mie] 1ex., Momozaki, Isato-chô, Kumano-shi, 14.VII.2016, Y. Tamadera leg. (YTJ). [Shiga] 1 ex., Mt. Ôike-dake, Mts. Suzuka, 27.VII.1940, K. Sakaguchi leg. (SEHU). [Kyoto] 1 ex., Kurama, Kyoto-shi, 11.VII.1956, T. Nakane leg. (SEHU); 2 exs., same locality, 17.VI.1954, T. Nakane leg. (SEHU); 3 exs., Serio, Kyoto-shi, 1.VI.1953, T. Nakane leg. (SEHU); 4 exs., same locality, 29.V.1954, T. Nakane leg. (SEHU); 12 exs., same locality, 20.VI.1951, H. Ishida leg. (SEHU); 1 ex., same locality, 12.V.1956, T. Nakane leg. (SEHU); 1 ex., Yamaso, Kyoto, 24.VI.1951, H. Ishida leg. (SEHU); 4 exs., Kyoto, 3.VI.1951, H. Ishida leg. (SEHU); 1 ex., Kibune, Kyoto-shi, 13.V.1952, T. Nakane leg. (SEHU); 1 ex., Yase, Kyoto-shi, 23.VI.1951, H.

Ishida leg. (SEHU); 1 ex., Kumogahata, Kyoto-shi, 8.VI.1954, T. Nakane leg. (SEHU); 2 exs., Ninose, Kyoto-shi, 10.V.1957, T. Nakane leg. (SEHU); 3 ♀♀, 2 exs., Nishikyô-ku, Kyoto-shi, 18.V.2015, Y. Tamadera leg. (YTJ). [Osaka] 1 ex., Myôken, 22.V.1938, M. Azuma leg. (SEHU); 1 ex., Mt. Daihi-san, Kyoto-shi, 15.VI.1941, K. Sakaguchi leg. (SEHU); 1 ex., Hattani, Myôken, 21.VIII.1949, K. Sawada leg. (SEHU); 2 exs., same locality, 11.VI.1949, K. Sawada leg. (SEHU). [Hyôgo] 1 ex., Hataganaru, Tajima, 27.V.1955, T. Nakane leg. (SEHU); 3 exs., Mt. Maya-san, Hyogo, 1.V.1936, H. Takenaka leg. (SEHU). [Nara] 1 ex., Shionoha, Mt. Ohdai, 23.VII.1953, T. K. Leg. (SEHU); 1 ex., Shionoha, Yamato, 29.VII.1935, no collector name (SEHU); 1 ex., Ikadaba, Mt. Ohdai, 21.VII.1953, T. Nakane leg. (SEHU); 2 exs., Hôriki-Tôge, Mt. Inamuragatake, 5.VI.1957, Y. Okada leg. (SEHU). [Wakayama] 1 ex., Sogawa, Kii, 2.VIII.1950, T. Nakane leg. (SEHU); 1 ex., Kawayu, Tanabe-shi, South Kii, 24.VII.1946, S. Osawa leg. (SEHU). [Tottori] 1 ex., Mt. Daisen, 21.VII.1952, T. Nakane leg. (SEHU). [Hiroshima] 2 exs., Nakatsuya, Yoshiwa, Hatsukaichi-shi, 24.V.1976, T. Kosaka leg. (SEHU); 1 ex., Hirugakusa, Sera-chô, 10.VI.1979, T. Kosaka leg. (SEHU); 1 ex., Mt. Mitsumine, Kure-shi, 29.IV.1963, T. Kosaka leg. (SEHU); 1 ex., Yoshiwa, Saeki-gun (Hatsukaichi-shi), 29.V.1977, T. Kosaka leg. (SEHU); 1 ex., Uga-kyô, Hiroshima-shi, 11.V.1974, T. Kosaka leg. (SEHU). [Prefectures unknown] 1 ex., Mt. Hyônosen, 19.VII.1940, K. Taniguchi leg. (SEHU); 1 ex., Ôsugidani, 28.V.1959, A. Nobuchi leg. (SEHU); 2 exs., Mt. Ohdai, 22.VII.1953, T. Nakane leg. (SEHU); 1 ex., same locality, 1.VIII.1953, T. Nakane leg. (SEHU); 1 ex., same locality, 23.VII.1953, T. Nakane leg. (SEHU); 1 ex., Mt. Tonbio Ha, Tano-shi, 27.V.1973, no collector name (SEHU). Awajishima Is. (Hyôgo) — 1 ex., Kashiwarayama-rindô, Chikusaki, Sumoto-shi, 13.VII.2022, Y. Tamadera leg. (YTJ). The Oki Islands (Shimane) — [Dôgo Is.] 1 ex., Goka, Okinoshima-chô, 27.V.1968, H. Kadowaki leg. (SEHU). Shikoku — [Tokushima] 2 exs., Yokose-chô, Katsuura-gun, 19.VIII.1952, M. Hirai leg. (SEHU); 1 ex., Mt. Tsurugi-san, Awa, 11.VIII.1952, M. Hirai leg. (SEHU). [Kagawa] 1 ex., Mt. Ôtaki-san, 10, 12.V.2000, H. Takizawa leg. (SEHU); 1 ex., Mt. Ryûô-san, 11.V.2000, H. Takizawa leg. (SEHU); 1 ex., Kagawa-chô, 13.V.2000, H. Takizawa leg. (SEHU). [Ehime] 1 ex., Omogo, Kumakôgen-chô, 21.VIII.1969, T. Nakane leg. (SEHU); 1 ex., Omogokei, 20.IX.1958, K. Kamijo leg. (SEHU); 1 ex., Ishizuchi, Koguchi, 1.VI.1952, N. Yato leg. (SEHU); 1 ex., Mt. Ishizuchi, 13.V.1968, T. Kosaka leg. (SEHU); 1 ex., same locality, 16.VI.1969, T. Kosaka leg. (SEHU); 2 exs., Shuku-gawa River, Kawanobori, Tobe-chô, Iyo-gun, 24.IV.2019, Y. Tamadera leg. (YTJ); 1 ♀, 5 exs., Kaminada, Futami-chô, Iyo-gun, 22.IV.2019, Y. Tamadera leg. (YTJ); 2 exs., Saretani, Futami-chô, Iyo-gun, 22.IV.2019, Y. Tamadera leg. (YTJ); 2 exs., Tamagawa-ko Lake, Ryuokashimo, Tamagawa-chô, Imabari-shi, 23.IV.2019, Y. Tamadera leg.

(YTJ); Komeno-machi, Matsuyama-shi, 2.VI.2018, Y. Hisasue leg. (YTJ). Kyushu — [Nagasaki] 1 ex., Tororo, Shimo, Amakusa, 30.VII.1984, M. Maeda leg. (head and pronotum missing) (SEHU). [Ôita] 1 ex., Mt. Kurodake, Kujû-machi, Taketa-shi, 5.VII.1981, T. & T. Nakane leg. (SEHU); 1 ex., Azamui, Minamiamabe-gun (Saiki-shi), 4.VI.1945, K. Kurosa leg. (SEHU); 2 exs., Saiki-shi, 26.V.1945, K. Kurosa leg. (SEHU). [Miyazaki] 2 exs., Mt. Takahata-yama, Kushima-shi, 14.VI.2006, Y. Komiya leg. (SEHU); 1 ex., Kitagô-onsen Spa, Nichinan-shi, 3-4.X.1986, T. & T. Nakane leg. (SEHU); 2 exs., Aya-chô, Higashimorokata-gun, 9.V.1987, T. & T. Nakane leg. (SEHU); 2 exs., same locality, 29.IV.1987, T. & T. Nakane leg. (SEHU); 1 ex., same locality, 24.IV.1986, T. & T. Nakane leg. (SEHU); 1 ex., Uryûno, Miyazaki-shi, 8.VI.1986, T. & T. Nakane leg. (SEHU); 2 exs., Hinokage-chô, 16.V.1987, T. & T. Nakane leg. (SEHU); 1 ex., Mitate, Hinokage-chô, 16.V.1987, T. Kinoda leg. (SEHU); 1 ex., Atago, Nobeoka-shi, 23.IV.1987, T. Kinoda leg. (SEHU). [Kagoshima] ex., Ônogara-rindô, Kanoya-shi, 12.VI.2006, Y. Komiya leg. (SEHU); 1 ex., Mt. Eboshi-dake (Hirakawa), 19.VI.1982, M. Ôhara leg. (SEHU); 1 ex., Kawanabe, 10.V.1981, M. Ôhara leg. (SEHU); 1 ex., Kiire-chô, 19.IV.1982, M. Miura leg. (SEHU); 1 ex., Shiroyama, Kagoshima-shi, 9.IV.1979, M. Miura leg. (SEHU); 7 exs., Tashiro, Kinkô-chô, 5.V.1982, T. & T. Nakane leg. (SEHU); 3 exs., Jigenji- chô, Kagoshima-shi, 14.IV.1981, T. Nakane leg. (SEHU); 2 exs., Iriki-chô, 1.V.1980, T. Kinoda leg. (SEHU); 1 ex., Kagoshima-shi, 21.VI.1936, H. Takenaka leg. (SEHU). Tsushima Is. (Nagasaki) — 1 ex., Kamitsushima, 20.X.1979, T. Kumata leg. (SEHU); 2 exs., Yamanoshiro-rindô, Mine-machi, 16.VI.2005, Y. Komiya leg. (SEHU); 2 exs., Sugorokuzaka, Yoshida, Mine-machi, 16.VI.2005, Y. Komiya leg. (SEHU).

Distributions in Japan. Honshu, Shikoku, Kyushu, Awajishima Is., the Oki Isls. (Dôgo Is.), and Tsushima Is.

Other localities based on literatures: Shôdoshima Is. (Fujimoto, 2007) and the Gotô Isls. (Nozakijima Is. and Fukuejima Is. (Scientific Research Group of the Gotô Islands, the Nagasaki Biological Society, 1981)).

Other distributions. China. Taiwan is removed from distribution of this species because the first record (Kubáň, 2006: “TAI”) does not show material examined data.

Adult food plants. Same as in the larvae mentioned below.

Host plants. Hydrangeaceae: *Deutzia crenata* Siebold et Zucc. [Japanese name: Utsugi] (Yano, 1954 for *Trachys ineditus*) and *D. scabra* Thunb. [Japanese name: Maruba-utsugi] (Yano, 1954 for *T. ineditus*; confirmed by this study) in Japan.

Leaf-mining habit. Mines of *Trachys tsushimae* were found on *Deutzia scabra* by this study (Figs. 63F, 66F): each mine was of the full-depth type and formed an elongate blotch occurring usually along leaf-margin; when full-grown, it occupied more or less an half of whole the leaf blade; eggs, which were black (remaining eggshell) and often sparsely covered on powdery substances, were laid singly on the adaxial surface of the leaf blade; hatched larvae left granular frass inside the mines; adult exit holes were not confirmed in this study. See also Yano (1954) treated as "*Trachys inedita*" (misidentification) for descriptions of the leaf-mines and immature stages.

Notes. In Japan, *Trachys tsushimae* is sometimes sympatlically distributed with *Trachys saundersi* Lewis, 1893, which is also associated with *Deutzia* plants, but is readily distinguished from the latter by the absence of serration on the lateral margins of the elytra, the body coloration, etc.

On the basis of the original description and figures, *Trachys tsushimae* is seemed to be closely related to *T. fusiformis*, described from Jiangxi, China (Peng, 2021 c), but is distinguishable from the latter at least in having the more strongly expanded parameres in apical half.

Taxonomic history. For a long time, Japanese researchers had misidentified *Trachys tsushimae* and its related in Japan as shown in Table 2. These misidentifications were reviewed by Kurosawa (1976d) in Japanese and formally corrected by Kurosawa (1985a).

Trachys broussonetiae Kurosawa, 1985
[Japanese name: Kôzo-chibi-tamamushi]
(Figs. 11F, 12M, N, 23, 24)

Trachys tsushimae [non Obenberger, 1922]: Kurosawa, 1950 a: 13 (note); Chûjô & Kurosawa, 1950: 13 (Shikoku, Japan); Yano, 1952: 28 (immature stages); Kurosawa, 1959: 225 (redescription; Japan, China, and Taiwan); 1963: 156, pl. 78 (pictorial book).

Trachys sp.: Kurosawa, 1976 d: 4 (note).

Trachys broussonetiae Kurosawa, 1985a: 167 (type locality: "Kinuta, Setagaya, Tokyo, Japan"); 1985 b: 35, pl. 7 (pictorial book); Akiyama & Ohmomo, 1997: 46 (checklist); 2000: 284, pl. 120 (pictorial book); Kubáň, 2006: 418 (Palaearctic catalog); Bellamy, 2008 b: 2474 (World catalog); Ohmomo & Fukutomi, 2013: 167, pl. 53 (pictorial book); Lan & Ohmomo, 2015: 106 (Taiwan); Kubáň, 2016: 570 (Palaearctic catalog); Ishiguro & Nishida, 2018: 33, figs. 2, 3 & 6 (aedeagus).

Trachys formosana [non Kerremans, 1912]: Ong & Hattori, 2019: 196 (misidentification).

Description. Male and female. Body ovate to subovate, slightly highly convex dorsally (Figs. 23A, B). LB 2.46–3.22 mm (mean 3.05 mm); WB 1.41–1.90 mm (mean 1.78 mm); LB/WB 1.67–1.77 (mean 1.72) (n = 20 for all measurements except terminalia). Habitus as shown in Figs. 11F, 12M, N.

Integument mainly blackish-bronze with weak golden-bronze reflections; maxillary palps brownish-black; basal four tarsomeres brownish-black with brown tarsal pads. Dorsal and ventral surfaces moderately shiny.

Vestiture mainly consisting of white, brownish-yellow and black setae; brownish-golden setae sometimes being paler. Head clothed with short, recumbent brownish-yellow setae. Pronotum clothed with short, semirecumbent brownish-yellow setae, with some small white patches, one of which on midline. Elytra clothed with short, semirecumbent, white, brownish-yellow and black setae which are arranged on each elytron as follows: 1) several white patches usually in basal part; 2) inconspicuously undulated, interrupted white band just before middle, almost forming two separate patches; 3) first white transverse band at apical 1/3, moderately wavy, zigzag-shaped; 4) second white transverse band at subapical part, rather straight, weakly interrupted near middle; 5) brownish-yellow setae predominant in elytron, occurring along basal and sutural margin, around white patches and bands, and in humeral region and apical region behind second transverse band; and 6) black setae in remaining space. Underside more sparsely setiferous, with fine, recumbent whitish setae.

Head, when viewed from above, slightly shallowly, triangularly concave on frons, with oculofrontal margins obtusely ridged. Eyes, when viewed from above, narrowly visible, weakly convex laterally. Vertex obscurely and coarsely variolate-punctate; frons widely concave, weakly impressed along upper side of midline, transversely ridged from just above each antennal insertion to inner margin of each eye, with surface rather smooth but faintly punctate; suprantennal pores simply round; clypeus slightly narrow (Fig.23C), with weak elevated basal margin, WC/LC 2.00–3.00 (mean 2.52), WC/LSC 1.29–1.76 (mean 1.57), deeply arcuately emarginate at apical margin.

Antennae (Fig. 23D) reaching just behind apicolateral angles of pronotum when laid alongside; antennomere I stout claviform, longer than II; II ovate, longer than III; III–VI subrectangular, subequal each other in length; VII–X triangular, moderately enlarged; XI subtriangular to sublingulate.

Mandibles with indistinct transverse ridge in middle of each outside. Maxillary palps with oval palpomere IV somewhat longer than wide.

Pronotum widest at base, WP/LP 2.49–2.73 (mean 2.57), BMP/AMP 1.57–1.73 (mean 1.64), narrower than elytra; lateral margins weakly arcuate in basal part then straightly and moderately to strongly narrowed apicad; apicolateral angles obtuse; basolateral angles broadly acute; apical margin almost straight, with very small median lobe; basal margin trisinuate, with median lobe moderately produced; disk weakly depressed along basal median lobe; surface obscurely variolate-punctate. Scutellar shield very small, subtriangular, glabrous.

Elytra widest at humeri, LE/WE 1.21–1.31 (mean 1.27), LE/LP 3.29–3.79 (mean 3.53); humeral calluses slightly weakly developed; lateral margins weakly narrowed posteriorly behind humeri then subparallel or faintly narrowed to middle, and finally slightly weakly arcuately convergent to conjointly rounded apices, without serrations; marginal carinae distinct in thoracic region, indistinctly reaching near apices; sutural margin faintly elevated in apical 1/3; disk weakly depressed in basal part, constricted behind humeri; surface irregularly and coarsely punctate. Lateral part of abdomen narrowly visible in dorsal view; laterosternites I–IV with laterosternal sulci.

Underside. Prosternum (Fig. 23E) straight to weakly emarginate at apical margin which is weakly rimmed; prosternal process wide, constricted between procoxa, with apex broadly rounded at rest; marginal carinae moderately widely separated each other at widest part of prosternal process, subparallel in apical 1/3 then gently divergent posteriad; disk rather flattened on median portion with weak depression in median apical part, somewhat declivous laterad on outside of marginal carinae, usually without elevated protions along procoxal cavities but rarely with indistinct ones. Hypomera with depressed hypomeral markings semicircular, sometimes additionally depressed laterally inside (Fig. 23F). Metaventrite moderately sculptured with large punctures on inside of katepisternal suture and with linearly confluent sculptures on outside of the suture. Legs moderately slender; metacoxal plates slightly strongly produced posteriorly at each lateral angle which is acute, with surface coarsely variolate; mesotibiae with short, robust erect spines at subapical part of each inner margin in both sexes (Fig. 23G); metatibiae bearing a fringe of spines in apical half of each outer margin, with one long spine in base of the fringe (Fig. 23H); inner tooth of each claw large. Abdominal ventrites with sternal grooves on ventrites II–V; V (Fig. 23I) rounded or obtusely subtruncate at apex; surface variolate, in ventrite I with linearly confluent sculptures on median part.

Sexual dimorphism indistinct.

Male terminalia (n = 5 for measurements). Proctiger with a pair of short baculi at base. Sternite IX (Fig. 24A) rather slender, SL/SW 0.94–1.15 (mean 1.08), deeply arcuately emarginate at apical margin, with clearly strongly produced apical angles which are clothed with several robust brownish setae. Tegmen (Fig. 24B) slender; parameres PL/PW 2.40–2.71 (mean 2.51), sparsely setiferous on apicolateral margins, with sides which are subparallel or faintly dilated from base to subapical part, and then arcuately convergent to apices; phallobase wide, PbL/PbW 2.09–2.56 (mean 2.25), more than 1/3 length of tegmen. Penis (Fig. 24C) slightly slender, PeL/PeW 4.76–5.41 (mean 5.17), shorter than tegmen; dorsal plate with sides which are gradually narrowed from widest point of base to subapical part, and then arcuately convergent apicad, with round apex, basally with median struts more than 1/3 length of penis; ventral plate membranous, but weakly sclerotized as a linear patch in middle of apical 1/4.

Female terminalia (n = 4 for measurements). Ovipositor (Figs. 24D–F) short; proctiger basally with a pair of long, ventrally curved baculi; coxites transversely subhexagonal, sparsely setiferous on each side of apical margin with three pairs of robust dark brown setae, ventrally without transverse depression in apical part; styli subtrapezoidal, slender, with sides subparallel, SlL/SlW 3.11–4.29 (mean 3.51), bearing several setae apically; vagina rather elongate sack-shaped, moderately expanded dorsally in distal half; spermatheca slender tubular, slightly short in length, widest near apex, without spermathecal gland.

Differential diagnosis. This species is similar in general appearance to *Trachys ineditus* and *T. tsushimae* in the species-group A, but differs from them by the combination of the following character states: frons outline of head more deeply, triangularly concave in dorsal view; sides of pronotum usually more strongly narrowed apicad; and marginal carinae on prosternal process gently divergent posteriad. In addition, this species is isolated from other Japanese congeners in having the male sternite IX bearing several robust brownish setae on apical angles, the relatively subparallel-sided parameres, and the female coxites bearing three pairs of robust brownish setae on each side of apical margin.

Specimens examined. Type material. Holotype: ♂ (based on Kurosawa, 1985; no dissected terminalia), "Tokyo / Kinuta / 2.I.1966 / Y. Kurosawa" (NSMT).

Non type material. **Japan**. Honshu — [Fukushima] 1 ex., Aizu-wakamatsu-shi, no date, K. Nagayama leg. (SEHU). [Tochigi] 1 ex., Itaga, Kanuma-shi, 9.VII.2000, H. Takizawa leg. (SEHU). [Gunma] 1 ex., Numata-shi, 25.V.1967, T. Takei leg. (SEHU); 1 ex., same locality, 1.V.1968, T. Takei leg. (SEHU). [Saitama] 1 ex., Yorii-machi, 5.V.2000, H. Takizawa leg. (SEHU). [Chiba] 1 ex., Miyanogi-chô, Inage-ku, 3–4.V.1999, H. Takizawa leg. (SEHU); 1 ex., Kashiwa-shi, 6.VI.1991, H. Kobayashi leg. (SEHU). [Tokyo] 1 ex., Ônita, Ôme-shi, 2.V.2004, H. Takizawa leg. (SEHU). [Kanagawa] 5 exs., Moritogawa, Hayama-chô, Miura-gun, 14.IX.2004, Y. Komiya leg. (SEHU); 9 ♂♂, 4 ♀♀, Atsugi Campus of Tokyo University of Agriculture, Funako, Atsugi-shi, 22.VI.2015, Y. Tamadera leg. (YTJ); 1 ♂, Mt. Kôbô-yama, Minamiyana, Hadano-shi, 27.IV.2015, Y.

Tamadera leg. (YTJ). [Yamanashi] 1 ex., Sanogawa-rindô, Ide, Nanbu-chô, 28.X.2005, Y. Komiya leg. (SEHU). [Gifu] 1 ex., Kawai-idani, Hida-shi, 2.VI.1957, T. Nakane leg. (SEHU). [Aichi] 1 ex., Jôkôji-chô, Seto-shi, 17.V.1942, no collector name (SEHU); 1 ex., same locality, 27.VIII.1950, T. Nakane leg. (SEHU); 2 exs., Mikawa-ôno, Shinshiro-shi, 10.V.1991, TTM. Nakane leg. (SEHU); 6 exs., Asuke-chô, Higashi-kamo-gun, 13.V.1948, T. Nakane leg. (SEHU). [Mie] 1 ex., Ôsugi-dani Valley, Ôdai-chô, 9.VI.1952, H. Ishida leg. (SEHU); 1 ex., Ise-jingû Sotomiya, Ise-shi, 21.VIII.1977, C. Ohkawa leg. (SEHU). [Kyoto] 1 ex., Arashiyama, Kyoto-shi, 5.VI.1947, M. Azuma leg. (SEHU); 1 ex., Kurama-kibune-chô, Kyoto-shi, 3.V.1956, T. Nakane leg. (SEHU). [Hyôgo] 1 ex., Kuroi, Kasuga-chô, Tamba-shi, 27.II.1962, H. Kawakami leg. (SEHU). [Wakayama] 1 ex., Ryûjin, Tanabe-shi, 15.VIII.1936, M. Azuma leg. (SEHU). [Hiroshima] 1 ex., Kabe- chô, Hiroshima-shi, 4.VI.1967, T. Kosaka leg. (SEHU). The Oki Islands (Shimane) — [Dôgo Is.] 1 ex., Saigô, 4.V.1967, H. Kadowaki leg. (SEHU). Shikoku — [Tokushima] 1 ex., Koyadaira, Awa, 2.VIII.1913, E Gallois leg. (SEHU); 1 ex., same locality, 5.VIII.1913, E. Gallois leg. (SEHU); 1 ex., same locality, 6.VIII.1913, E. Gallois leg. (SEHU). [Kagawa] 2 exs., Kagawa-chô, 13.V.2000, H. Takizawa leg. (SEHU); 2 exs., Mt. Zôzu-san, 14.V.1976, T. Kosaka leg. (SEHU). Kyushu — [Saga] Kabejima Is., Yobuko-chô, 19.VI.1984, H. Yamaguchi leg. (SEHU). [Miyazaki] 1 ex., Mt. Mukabaki-Yama, Nobeoka-shi, 14.V.1967, A. Nagai leg. (SEHU); 1 ex., Sakai-dani, Shi-iba-son, 2.VIII.1970, A. Nagai leg. (SEHU). Tsushima Is. (Nagasaki) — 1 ex., Yamanoushiro-rindô, Mine-machi, 16.VI.2005, Y. Komiya leg. (SEHU); 2 exs., Sugorokuzaka, Yoshida, Mine-machi, 16.VI.2005, Y. Komiya leg. (SEHU); 2 exs., Teterayama-rindô, Izuhara-machi, 9.VI.2005, Y. Komiya leg. (SEHU); 1 ex., Tokue, Mine-machi, 17.VI.2005, Y. Komiya leg. (SEHU); 1 ex., Mt. Ariake-yama, 28.VII.1959, Y. Ichō leg. (SEHU).

Distributions in Japan. Honshu, Shikoku, Kyushu, Oki Isls. (Dôgo Is.), and Tsushima Is.

Other localities based on literatures: Okinoshima Is. (Chikuzen) (Miyata *et al*., 1977), Kashiwajima Is. (Saga) (Nishida, 2018), and the Koshikijima Isls. (Kamikoshikijima Is. (Imasaka *et al*., 2019) and Shimokoshikijima Is. (Imasaka, 2019)).

Other distributions. China and Taiwan.

Adult food plants. Same as in the larvae mentioned below.

Host plants. Moraceae: *Broussonetia monoica* Hance (= *B. kazinoki*) [Japanese name: Hime-kouzo] (Yano, 1952 for *Trachys tsushimae*), *B. papyrifera* (L.) L'Hér. ex Vent. [Japanese name: Kajinoki] (Kurosawa, 1976 d — adult record?; confirmed by this study), *B. kaempferi* Siebold [Japanese name: Tsuru-kouzo] (Kurosawa, 1959 — adult record?), and *Morus australis* Poir. [Japanese name: Yamaguwa] (Kurosawa, 1959 — adult record?) in Japan.

Leaf-mining habit. Mines and larvae of supposed *Trachys broussonetiae* were confirmed by the author on *Broussonetia papyrifera* that the same individual as the tree from which some adults were collected. Yano (1952) described leaf-mines on *Broussonetia kazinoki* and immature stages of *T. broussonetiae* as "*Trachys tsushimae*" (misidentification): each mine forms an elongate blotch occurring along leaf-margin; eggs, which are blackish and not clothed on powdery substances, are laid singly on the adaxial surface of the leaf blade; hatched larvae leave granular frass inside the mines.

Note. *Taxonomic history*. For a long time, Japanese researchers had misidentified *Trachys broussonetiae* and its related in Japan as shown in Table 2. These misidentifications were reviewed by Kurosawa (1976 d) as "*T.* sp." and formally corrected by Kurosawa (1985 a).

Group II (auricollis)

(Fig. 25A, B)

Species included. *Trachys auricollis* Saunders, 1873 and *T. toringoi* Kurosawa, 1951.

Diagnosis. Body wedge-shaped type. Apical margin of pronotum with small to very small median lobe. Elytra with serrate lateral margins; elytral vestiture with transverse bands consisting of unicolor setae in apical half of each elytron, without tufts consisting of erect setae. Prosternum more or less rimmed along apical margin which is not lobed or not rimed along apical margin which is slightly lobed; prosternal disk without elevated portions along procoxal cavities. Abdominal ventrites with sternal grooves on ventrite I–V. Female coxites ventrally without transverse depression in apical part.

Note. Descarpentries & Villiers (1965) already established the *auricollis*-group for the Indochina *Trachys* species. Their *auricollis*-group is characterized by the well-developed ridges of humeral callus (described as "huméral caréné") on the elytra, whereas the group II established herein is characterized by the different character states mentioned in the diagnosis.

Trachys auricollis Saunders, 1873
[Japanese name: Kuzu-no-chibi-tamamushi]
(Figs. 7B, 25A, 38A–C, 27, 28, 64A, 67A)

Trachys auricollis Saunders, 1873: 520 (type locality: "Japan"); Lewis, 1879: 15 (catalog); Kerremans, 1885: 157 (catalog); Schönfeldt, 1887: 113 (catalog); Kerremans, 1892 a: 284 (catalog); Lewis, 1893: 338 (in list); Kerremans, 1903: 312 (catalog); Jakobson, 1913: 800 (catalog); Chûjô & Matuda, 1940: 65 (Kyushu, Japan); Kurosawa, 1950 a: 12 (note); 1950d: 1113, fig. 3189 (pictorial book); Chûjô & Kurosawa, 1950: 11 (Shikoku, Japan); Yano, 1952: 23 (immature stages); Iga, 1955 a: 10, pl.4 (pictorial book); 1955b: 80, pl.24 (pictorial book); Obenberger, 1958: 241 (Yunnan, China); Kurosawa, 1959: 218 (redecription); Kurosa, 1959: 460, fig. 3189 (pictorial book; larva); Kurosawa, 1963: 155, pl. 78 (pictorial book); Descarpentries & Villiers, 1965: 728 (in key; Vietnam); 1966: 136 (in key; Laos); Kurosawa, 1976c: 2 (note); Hołyński, 1981: 128 (Vietnam); Kurosawa, 1985 b: 34, pl. 6 (pictorial book); Seki & Kashizaki, 1996: 89 (Hokkaido, Japan); Akiyama & Ohmomo, 1997: 46 (checklist); 2000: 283, pl. 120 (pictorial book); Mühle, 2003: 48 (list); Kubáň, 2006: 418 (Palaearctic catalog; Fujian, China); Bellamy, 2008 b: 2470 (World catalog); Ohmomo & Fukutomi, 2013: 165, pl. 51 (pictorial book); Lan & Ohmomo, 2015: 105 (Taiwan); Kubáň, 2016: 570 (Palaearctic catalog); Ishiguro & Nishida, 2018: 33, figs. 2, 3 & 6 (aedeagus); Ong & Hattori, 2019: 194, 226 (pictorial book; aedeagus); Xiao *et al*., 2019: 1 (complete mitochondrial genome); Tamadera, 2021: 54 (Okinoshima Is, Kôchi); Peng, 2022 a: 265 (distribution).

Trachys (*Trachys*) *auricollis*: Obenberger, 1918: 19, 34, 64 (in key); 1926 b: 661 (catalog); Théry, 1927: 40 (note); Obenberger, 1929 a: 74 (in key; Japan, China, Taiwan, and India); Miwa & Chûjô, 1936: 23 (catalog; Japanese name: Kin-iro-chibi-tamamushi); Obenberger, 1937 a: 1355 (World catalog).

Trachys sauteri Kerremans, 1912: 209 (type locality: "Taihorin", Taiwan); Obenberger, 1918: 19, 35, 64; Théry, 1927: 40 (synonymized under *T. auricollis*); Obenberger, 1929 a: 74 (synonymized under *T. auricollis*); Miwa, 1931: 127 (list); Miwa & Chûjô, 1936: 23 (in synonymy of *Trachys cupricolor* Saunders, corrected by Kurosawa, 1976 d: 2). Synonymized under *T. auricollis* by Théry, 1927: 40.

Trachys freyi Théry, 1942: 272 (type locality: "Erzendjancy, Mandchourie", Manchuria); Obenberger, 1943: 10 (as synonym of *Trachys duplofasciata* Gebhart); Kubáň, 2006: 418 (Palaearctic catalog; as synonym of *Trachys aurifluus* Solsky). Synonymized under *T. auricollis* by Bellamy, 2008 b: 2470.

Trachys auricollis ab. *osawai* Kurosawa, 1959: 220 (unavailable name: Article 1.3.4 of ICZN (1999)).

Description. Male and female. Body wedge-shaped, highly convex dorsally (Figs. 27A, B). LB 3.24–4.15 mm (mean 3.89 mm); WB 1.85–2.50 mm (mean 2.29 mm); LB/WB 1.62–1.75 (mean 1.70) (n = 20 for all measurements except terminalia). Habitus as shown in Figs. 23A, 36A–C.

Integument mainly black; head and pronotum occasionally being weak brassy-black; maxillary palps light-brown; basal four tarsomeres brownish-black with brown tarsal pads. Dorsal and ventral surfaces moderately shiny.

Vestiture mainly consisting of white, yellow and black setae. Head clothed with short, recumbent, yellow to pale-yellow setae. Pronotum clothed with short, semirecumbent, yellow to pale-yellow setae, usually with two white spots near base of median lobe of basal margin. Elytra clothed with short, semirecumbent, white and black setae which are arranged on each elytron as follows: 1) white setae complicatedly scattering in basal half, partly forming a large circle near sutural margin, very rarely being black entirely; 2) first white transverse band at apical 1/3, strongly wavy, zigzag-shaped; 3) second white transverse band at subapical part, weakly wavy; and 4) black setae in remaining space. Underside more sparsely setiferous, with fine, recumbent whitish setae, except for prosternum with longer pale-yellowish setae.

Head, when viewed from above, moderately arcuately concave on frons, with oculofrontal margins ridged. Eyes, when viewed from above, slightly broadly visible, weakly convex laterally. Vertex obscurely and coarsely variolate-punctate; frons widely concave, weakly impressed along upper side of midline, transversely ridged from just above each antennal insertion to inner margin of each eye, with surface sparsely and obscurely variolate-punctate; suprantennal pores simply round; clypeus narrow (Fig. 27D), without elevated basal margin, WC/LC 1.33–1.90 (mean 1.51), WC/LSC 1.20–1.77 (mean 1.34), deeply arcuately emarginate at apical margin.

Antennae (Fig. 27E) reaching just behind apicolateral angles of pronotum when laid alongside; antennomere I stout claviform, longer than II; II ovate, longer than III; III subrectangular, slightly longer than IV; IV–VI subrectangular, subequal each other in length; VII–X triangular, moderately enlarged; XI subtriangular to sublingulate.

Mandibles without transverse ridge in middle of each outside. Maxillary palps with oval palpomere IV somewhat longer than wide.

Pronotum widest at base, WP/LP 2.86–3.54 (mean 3.17), BMP/AMP 1.60–1.81 (mean 1.74), narrower than elytra; lateral margins straightly and strongly narrowed apicad, sometimes in apical part being weakly arcuate, occasionally faintly sinuate around middle; apicolateral angles obtuse; basolateral angles acute; apical margin bisinuately emarginate, with very small median lobe; basal margin trisinuate, with median lobe moderately produced; disk weakly depressed along basal median lobe; surface obscurely, slightly densely variolate-punctate, becoming denser toward apical and basal margins. Scutellar shield moderately small, subtriangular, glabrous.

Elytra widest at humeri, LE/WE 1.22–1.34 (mean 1.28), LE/LP 3.93–4.88 (mean 4.40); humeral calluses strongly developed, often longitudinally ridged in basal 1/5 of elytra in lateral view; lateral margins constricted behind humeri and weakly narrowed posteriorly from behind humeri to middle, then more strongly, faintly arcuately narrowed to subapical part, and finally strongly arcuately convergent to conjointly, broadly rounded apices, with weak serrations in about apical half except apices (Fig. 27C); marginal carinae distinct in thoracic region, indistinctly reaching near apices; sutural margin faintly elevated in apical 1/3; disk weakly depressed in basal part, constricted behind humeri, weakly swollen in subapical part; surface irregularly and slightly densely punctate. Lateral part of abdomen narrowly visible in dorsal view; laterosternites I–IV with laterosternal sulci.

Underside. Prosternum (Fig. 27F) straight to slightly emarginate at apical margin which is weakly rimmed; prosternal process wide, constricted between procoxa, with apex broadly rounded at rest; marginal carinae moderately widely separated each other at widest part of prosternal process, strongly divergent posteriad from apical 1/3; disk rather flattened on median portion, somewhat declivous laterad on outside of marginal carinae, without elevated protions along procoxal cavities. Hypomera with depressed hypomeral markings subreniform, sometimes additionally depressed laterally inside (Fig. 27G). Metaventrite moderately sculptured with large punctures on inside of katepisternal suture and with linearly confluent sculptures on outside of the suture. Legs moderately slender; metacoxal plates weakly produced posteriorly at each lateral angle which is broadly acute, with surface coarsely variolate; mesotibiae in male (Fig. 27H) weakly emarginate in each apical inner margin with two short, robust erect spines, in female (Fig. 27I) not emarginate in each apical inner margin without the spines; metatibiae bearing a fringe of spines in apical half of each outer margin, with one long spine in base of the fringe (Fig. 27J); inner tooth of each claw large. Abdominal ventrites with very shallow, reduced sternal grooves on ventrite I, with moderate sternal grooves on ventrites II–V; V (Fig. 27K) rounded or obtusely subtruncate at apex; surface variolate, in ventrite I with linearly confluent sculptures on median part.

Sexual dimorphism recognized in structure of mesotibiae (see above).

Male terminalia (n = 5 for measurements). Proctiger with a pair of short baculi at base. Sternite IX (Fig. 28A) wide, SL/SW 0.59–0.82 (mean 0.70), triangularly emarginate at apical margin, bearing several setae on each side of apical margin. Tegmen (Fig. 28B) wide; parameres PL/PW 1.82–1.98 (mean 1.91), sparsely setiferous on apicolateral margins, with sides which are gently dilated from base to apical 2/3, then weakly arcuately and more strongly dilated to widest subapical part, and finally inwardly arcuately and clearly strongly convergent to apices; phallobase PbL/PbW 2.13–3.00 (mean 2.55), more than 1/4 length of tegmen. Penis (Fig. 28C) slightly wide, PeL/PeW 4.61–5.10 (mean 4.84), shorter than tegmen; dorsal plate with sides which are gradually narrowed from widest point of base to subapical part, and then arcuately convergent apicad, with round apex, basally with median struts about 1/3 length of penis; ventral plate membranous, but weakly sclerotized as a linear patch in middle of apical 1/4.

Female terminalia (n = 4 for measurements). Ovipositor (Figs. 28D–F) short; proctiger basally with a pair of long, ventrally curved baculi; coxites transversely subhexagonal, sparsely setiferous on each side of apical margin, ventrally without transverse depression in apical part; styli lingulate, wide, with sides subparallel, SlL/SlW 2.06–2.40 (mean 2.26), bearing several setae apically; ventral valve sparsely setiferous on each side of subapical part; vagina sack-shaped, strongly expanded dorsally in distal half; spermatheca slender tubular, moderate in length, widest in apical half, without spermathecal gland.

Differential diagnosis. This species is similar in general appearance to *Trachys toringoi* especially in the wedge-shaped body, but can be easily distinguished from *T. toringoi* by the following character states: (1) abdominal ventrite I with clearly reduced sternal grooves; (2) head and pronotum black with distinct yellow to pale-yellow setae; (3) prosternum marginal carinae much more strongly divergent posteriad; (4) frons outline of head arcuately concave; (5) male sternite IX bearing several setae on apical angles; (6) parameres relatively continuously dilated from base to widest subapical part; (7) apex of penis not produced; and (8) female styli lingulate.

Additionally, this species is similar to *Trachys saundersi* in the coloration of body and vestiture, but differs from *T. saundersi* as follows: wedge-shaped body; disk of prosternum without elevated protions along procoxal cavities; male parameres being widest at subapical part and with several setae on apicolateral margins; penis not produced at apex; female spermatheca much slenderer; and the points mentioned above in (1) and (3).

Specimens examined. Non type material. **Japan**. Hokkaido — 3 exs., Iwabe, Fukushima-chô, Matsumae-gun, 22.VI.1993, Y. Nishijima leg. (SEHU); 1 ex., same locality, 2.VIII.1993, Y. Nishijima leg. (SEHU); 1 ex., same locality, 24.VII.1995, Y. Nishijima leg. (SEHU). Honshu — [Ibaraki] 2 exs., Yatabe, Tsukuba-shi, 3.VIII.1983, A. Tanaka leg. (SEHU); 2 exs., Tsukuba-shi, 23.V.1976, A. Tanaka leg. (SEHU); 4 exs., Tsukuba-shi, 23.V.1976, A. Tanaka leg. (SEHU). [Tochigi] 1 ex., Kuriyama, Kawamata, Nikkô-shi, 5.VI.1999, H. Takizawa leg. (SEHU); 1 ex., Itaga, Kanuma-shi, 9.VII.2000, H. Takizawa leg. (SEHU). [Gunma] 1 ex., Akagi-jinja Shrine – Miyagi-mura, Maebashi-shi, 12.VI.2005, H. Takizawa leg. (SEHU); 1 ex., Kawahuru-onsen, Minakami-machi, 29–31.V.2000, H. Takizawa leg. (SEHU); 1 ex., Numata-shi, 8.V.1968, T. Takei leg. (SEHU). [Saitama] 1 ex., Yorii-machi, 5.V.2000, H. Takizawa leg. (SEHU); 1 ex., Mikajima, Tokorozawa-shi, 2.VII.2016, Y. Tamadera leg. (YTJ). [Chiba] 1 ex., Ôami, 15.VI.1980, M. Ôhara leg. (SEHU); 1 ex., Hegurigawa, Tomiura, 29–30.VII.1999, H. Takizawa leg. (SEHU); 1 ex., Miyanogi-chô, Inage-ku, Chiba-shi, 3–4.V.1999, H. Takizawa leg. (SEHU); 1 ex., Kasamori, Mobara, 2.VI.1989, T. & T. Nakane leg. (SEHU). [Tokyo] 1 ex., Mt. Takao-san, Hachiôji-shi, 17.VI.1988, leg.; 1 ex., Ônita, Ôme-shi, 2.V.2004, H. Takizawa leg. (SEHU); 1 ex., Mont Takao, Hachiôji, 8.VI.1913, E. Gallois leg. (SEHU); 1 ex., same locality, 18.V.1913, E. Gallois leg. (SEHU). [Kanagawa] 3 exs., Takatori, Zushi-shi, 19.VIII.1973, S. Tachikawa & M. Taguchi leg. (SEHU); 1 ex., Zushi-shi, 27.V.1975, A. Tanaka leg. (SEHU); 1 ex., same locality, 15.VIII.1988, A. Tanaka leg. (SEHU); 2 exs., Kurihama, Yokosuka-shi, 15.IX.1973, N. Kino et al. leg. (SEHU); 1 ex., Morito-gawa River, Hayama-chô, Miura-gun, 14.IX.2004, Y. Komiya leg. (SEHU); 1 ex., Ôsawa-rindô, Nanasawa, Atsigi-shi, 21.V.2016, S. Shimamoto leg. (YTJ); 1 ex., Tanasawa, Atsugi-shi, 8.V.2016, S. Shimamoto leg. (YTJ); 1 ex., Mt. Kôbô-yama, Hadano-shi, 5.VI.2011, M. Miyao leg. (YTJ); 2 ♀♀, Mt. Enkai-san, Mine-chô, Isogo-ku, Yokohama-shi, 25.VII.2015, N. Kaneko leg. (YTJ). [Ishikawa] 2 exs., Iwama, Ozoe, Hakusan-shi, 15.VI.2016, Y. Tamadera leg. (YTJ). [Yamanashi] 1 ex., Anayamabashi, Nirasaki-shi, 27.VIII.2004, Y. Komiya leg. (SEHU). [Nagano] 1 ex., Shimashima-dani, Matsumoto-shi, 10.VIII.1950, T. Nakane leg. (SEHU); 1 ex., Nojiri-ko Lake (Hotel), 23.VIII.1940, T. Nakane leg. (SEHU); 1 ex., same locality, 24.VIII.1940, T. Nakane leg. (SEHU); 1 ex., same locality, 18.VIII.1941, T. Nakane leg. (SEHU); 1 ex., same locality, 20.VIII.1941, T. Nakane leg. (SEHU). [Gifu] 1 ex., Yôrô-chô, 29.V.1949, T. Nakane leg. (SEHU). [Shizuoka] 1 ex., Shimoda-shi, 1.VI.1929, S. Kato leg. (SEHU). [Aichi] 1 ex., Mikawa-ôno, Shinshiro-shi, 9.V.1991, TTM. Nakane leg. (SEHU); 1 ex., same locality, 10.V.1991, TTM. Nakane leg. (SEHU). [Mie] 2 ex., Owase-chô, Matsusak-shi, 13.VII.2016, Y. Tamadera leg. (YTJ). [Kyoto] 1 ex., Mt. Tennô-zan, Oyamazaki-chô, 9.VII.1983, H. Ohira leg. (SEHU); 1 ex., Kurama, Kyoto-shi, 12.VI.1955, T. Nakane leg. (SEHU); 1 ex., Nishikyô-ku, Kyoto-shi, 18.V.2015, Y. Tamadera leg. (YTJ). [Osaka] 1 ex., Hirakata, 26.V.1935, K. Kotera leg. (SEHU); 1 ex., Hattani, Myôken, 29.VI.1949. K. Sawada leg. (SEHU); 1 ex., Mt. Inunaki-yama, 21.VIII.1938, K. Sakaguchi leg. (SEHU); 1 ex. same locality, 27.VIII.1954, Y. Yano leg. (SEHU); 4 ♂♂, Nishikyô-ku, Kyoto-shi, 18.V.2015, Y. Tamadera leg. (YTJ). [Hyôgo] 1 ex., Motoyama-mura near Kôbe, 16.VI.1938, K. Sakaguchi leg. (SEHU); 1 ex., Foot of Mt. Maya-san, Kôbe-shi, 6.VIII.1941, K. Taniguchi leg. (SEHU). [Nara] 1 ex., Mt. Ôdaigahara-san, 29.VIII.1952, O. Sato leg. (SEHU); 1 ex., Nara, 6.VI.1935, K. Kotera leg. (SEHU). [Wakayama] 1 ex., Gobô-shi, 4.V.1993, N. Ito leg. (SEHU); 1 ex., Shingû-shi, 19.VII.1946, S. Osawa leg. (SEHU); 1 ex., Shionomisaki, Higashimurogun-Kushimoto-cho, 15.IV.1941, T. Nakane leg. (SEHU); 2 exs., Kishû, VI.1931, Sakaguchi leg. (SEHU). [Hiroshima] 2 exs., Motoujina-chô, Minami-ku, Hiroshima-shi, 9.V.1978, T. Kosaka leg. (SEHU). Awashima Is. (Niigata) — 1 ex., Uchiura, Y. Maki leg. (YTJ). Sarushima Is. (Kanagawa) — 1 ex., Yokosuka-shi, 5.VI.2018, S. Taru leg. (YTJ). Awajishima Is. (Hyôgo) — 1 ex., Kashiwarayama-rindô, Chikusaki, Sumoto-shi, 13.VII.2022, Y. Tamadera leg., emerged from *Pueraria lobata*, 2.VIII.2022, rearing no. 2022-187 (YTJ). Shikoku — [Tokushima] 4 exs., Koyadaira, Awa, 7.VIII.1913, E. Gallois leg. (SEHU); 1 ex., same locality, 9.VIII.1913, E. Gallois leg. (SEHU); 3 exs., same locality, 11.VIII.1913, E. Gallois leg. (SEHU); 1 ex., same locality, 5.VIII.1913, E. Gallois leg. (SEHU); 2 exs., same locality, 20.VII.1913, E. Gallois leg. (SEHU). [Kagawa] 2 exs., Kagawa-chô, Takamatsu-shi, 13.V.2000, H. Takizawa leg. (SEHU). Okinoshima Is. (Kôchi) — 1 ex., Okinoshima, Kôchi-ken, 18–20.VII.1952, K. Sakaguchi leg. (SEHU; recorded by Tamadera, 2021). Kyushu — [Fukuoka] 2 exs., Mt. Hiko-san, Soeda-machi, 4.VI.1952, T. Nakane leg. (SEHU); 1 ex., Ushikubi, Onojô-shi, 24.VI.2018, Y. Hisasue leg. (YTJ); 1 ex., Mt. Tachibana, Higashi-ku, 7.VI.2018, Y. Hisasue leg. (YTJ); 1 ex., Kyushu Univ., Kuwabara, Nishi-ku, 4–6.VI.2019, Y. Hisasue leg. (YTJ); 1 ♂, 2 ♀♀, Gyûkubi, Onojô-shi, 26.V.2019, Y. Hisasue leg. (YTJ). [Saga] Kabejima Is.: Yobuko, V.1985, A. Matsuo leg. (SEHU). [Kumamoto] 1 ex., Nihonsugi, 23.VI.1982, Maegata leg. (SEHU). [Ôita] Azamui, Minamiamabe-gun (Saiki-shi), 4.VI.1945, K. Kurosa leg. (SEHU). [Miyazaki] 1 ex., Mi-ike-chô, Miyakonojô-shi, 6.VI.1981, M. Ôhara leg. (SEHU); 1 ex. Mimata-chô, 12.VIII.1980, T. Kinoda leg. (SEHU); 2 exs., Hinokage-chô, 16.V.1987, T. Nakane leg. (SEHU); 1 ex., Morowaku, Hinokage-chô, 27.IV.1969, A. Nagai leg. (SEHU); 3 exs., Aoshima, 10.V.1953, K. Kôno leg. (SEHU); 10 exs., Mt. Takahata-yama, Kushima-shi, 14.VI.2006, Y. Komiya leg. (SEHU); 2 exs., Miyazaki-shi, 1.VI.1986, T. & T. Nakane leg. (SEHU); 1 ex., Nagayu, Bungo, V.1910, T. Otsuka leg. (SEHU). [Kagoshima] 3 exs., Kiire-chô, Kagoshima-shi, 29.IV.1982, M. Miura leg. (SEHU); 6 exs., Sata, Minami-ôsumi-chô, 4.V.1981, M. Ôhara leg. (SEHU); 1 ex., Shibushi-shi, 9.X..1982, T. & T.

Nakane leg. (SEHU); 3 exs. Kagoshima-shi, 8.VII.1981, T. Kinoda leg. (SEHU); 1 ex., Kagoshima University, Kagoshima-shi, 13.IV.1983, T. & T. Nakane leg. (SEHU); 1 ex., Takeoka, Kagoshima-shi, 18.V.1980, T. Nakane leg. (SEHU); 1 ex., Shiroyama, Kagoshima-shi, 3.VII.1983, T. & T. Nakane leg. (SEHU); 1 ex., same locality, 21.V.1982, M. Ôhara leg. (SEHU); 1 ex., same locality, 15.IV.1979, T. Nakane leg. (SEHU); 4 exs., same locality, 1.V.1980, T. Nakane leg. (SEHU); 1 ex., same locality, 20.V.1979, T. Nakane leg. (SEHU); 1 ex., same locality, 17.IV.1981, T. Nakane leg. (SEHU); 1 ex., same locality, 11.IV.1981, T. Nakane leg. (SEHU); 2 exs., same locality, 12.VII.1981, T. Nakane leg. (SEHU); 1 ex., same locality, 24.V.1980, T. Nakane leg. (SEHU); 2 exs., same locality, 5.VI.1980, T. Kinoda leg. (SEHU); 2 exs., same locality, 7.V.1980, T. Kinoda leg. (SEHU); 1 ex., same locality, 25.VI.1981, T. Kinoda leg. (SEHU); 3 exs., same locality, 21.IV.1979, M. Miura leg. (SEHU); 3 exs., same locality, 15.IV.1967, T. Kocha leg. (SEHU); 1 ex., same locality, 15.IV.1982, M. Ôhara leg. (SEHU); 1 ex., Suzuyama, Kagoshima-shi, 7.VI.1980, T. Kinoda leg. (SEHU); 6 exs., Unagi-ike, Yamagawa-chô, Ibusuki-gun, 24.V.2006, Y. Komiya leg. (SEHU); 1 ex., Jigenji, Kagoshima-shi, 14.IV.1981, T. Nakane leg. (SEHU); 1 ex., Sata, Ôsumi-hantô Peninsula, 24.V.1952, T. Nakane leg. (SEHU). Nokoshima Is. (Fukuoka) — 2 exs., Nishi-ku, Fukuoka-ken, 4.VII.2018, Y. Hisasue leg. (YTJ). Tsushima Is. (Nagasaki) — 2 exs., Mt. Ariake-san, Nagasaki, 28.VII.1978, T. Kosaka leg. (SEHU). Ikinoshima Is. (Nagasaki) — 2 exs., Mt. Ondake, Ashibe-chô, Iki-shi, Nagasaki, 19.VI.2005, Y. Komiya leg. (SEHU). Shimokoshiki Islands: Shimokoshikijima Is. — 2 exs., Seo-kan-non-camp-jô, Simokoshiki-cho aose, Satsuma-sendai-shi, 27. IV.2019, N. Kaneko leg. (YTJ). The Ryukyus: the Ôsumi Islands — [Takeshima Is.] 2 exs., Mishima-mura, Kagoshima, 28.VIII.1984, SK. Yamane leg. (SEHU). [Yakushima Is.] 1 ex., Miyanoura, Yaku-chô, Kagoshima, 10.V.1981, SK. Yamane leg. (SEHU); 5 exs., Onoaida, Yaku-chô, Kagoshima, 28.V.2006, Y. Komiya leg. (SEHU); 1 ex., same locality, 28.IV.1982, K. Tomiyama leg. (SEHU).

Distributions in Japan. Hokkaido, Honshu, Shikoku, Kyushu, Awashima Is. (Niigata), Sarushima Is., Awajishima Is., Okinoshima Is. (Kôchi), Tsushima Is., Koshikijima Isls. (Shimokoshikijima Is.), and the Ryukyus: Ôsumi Isls. (Yakushima Is.).

Other localities based on literatures: Tobishima Is. (Sakurai, 2016), Sadogashima Is. (Kurosawa, 1959), Izu Isls. (Hachijôjima Is. (Kawabata, 2009)), Shôdoshima Is. (Fujimoto, 2019; other small islands of Kagawa Pref. are recorded by Fujimoto, 2007), Oki Isls. (Dôgo Is. (Hayashi and Kadowaki, 2012)), small islands of Saga Pref. (Takashima Is., Kashiwajima Is., Kakarajima Is., and Matsushima Is. (Kido & Oda, 2010)), , Gotô Isls. (Tairajima Is., Nakadôrijima Is., and Narushima Is. (Scientific

Research Group of the Gotô Islands, the Nagasaki Biological Society, 1981)), Amakusa Isls., Koshikijima Isls. (Kamikoshikijima Is. (Imasaki *et al*., 2020) and Nakakoshikijima Is. (Imasaka *et al*., 2021)), and the Ryukyus: Ôsumi Isls. (Tanegashima Is. (Kurosawa, 1959)).

Other distributions. This species is distributed in the Palaerctic Region (China: Fujian and Yunnan; and Taiwan) and Oriental region (Vietnam, Laos, and India).

Adult food plants. Same as in the larvae mentioned below. Adult feeding scars as shown in Fig. 64A.

Host plants. Fabaceae: *Pueraria lobata* (Willd.) Ohwi [Japanese name: Kuzu] (Yano, 1952; confirmed by this study) in Japan, and *P. montana* (Lour.) Merr. [Japanese name: Taiwan-kuzu] in Taiwan (confirmed by this study: the Kumata collection in SEHU).

Leaf-mining habit. Mines of *Trachys auricollis* were found on *Pueraria lobata* by this study (Fig. 67A): each mine was of the full-depth type and formed a large, elongate blotch occurring usually along leaf-margin; when full-grown, it is large but occupied much less than an half of whole the large leaf blade; eggs, which were pale grayish-brown (remaining eggshell) and not covered on powdery substances, were laid singly on the adaxial or abaxial surfaces of the leaf blade; hatched larvae left granular to thread-like frass inside the mines; adults were emerged from the adaxial or abaxial surfaces of the leaves with oval adult exit holes. See also Yano (1952) for descriptions of the leaf-mines and immature stages.

Notes. *Trachys auricollis* is one of the most common *Trachys* species in Japan, although in the north Honshu and Hokkaido this species is relatively uncommon.

Photographs of one syntype of *Trachys sauteri* Kerremans, 1912, treated as a junior synonym of *T. auricollis*, are available from the National Museum of Natural Science, Taichung (2022).

Trachys toringoi Kurosawa, 1951

[Japanese name: Zumi-chibi-tamamushi]

(Figs. 25B, 26D, E, 29, 30, 64B, C, 67B)

Trachys toringoi Kurosawa, 1951: 73 (type locality: "Fukiyayama near Aizu-Wakamatsu, Fukushima Pref., Japan"); Yano, 1952: 40 (in host list); Iga, 1955 a: 10, pl. 4 (pictorial book; fig. 64: misidentification of *T. aurifluus*); 1955b: 80, pl. 24 (pictorial book; fig. 532: correct image); Kurosawa, 1959, 217 (redescription; Kyushu, Japan); 1963: 155, pl. 78 (pictorial book); 1976 d: 3 (note); 1985 b: 34, pl. 6 (pictorial book;

China — examined the corresponding specimen in NSMT); Akiyama & Ohmomo, 1997: 49 (checklist); 2000: 285, pl. 120 (pictorial book); Kubáň, 2006: 421 (Palaearctic catalog); Bellamy, 2008b: 2525 (World catalog); Ohmomo & Fukutomi, 2013: 165, pl. 51 (pictorial book); Kubáň, 2016: 573 (Palaearctic catalog); Ishiguro & Nishida, 2018: 33, figs. 2, 3 & 6 (aedeagus); Peng, 2022 a: 271 (listed).

Description. Male and female. Body wedge-shaped, slightly highly convex dorsally (Figs. 29A, B). LB 3.25–3.70 mm (mean 3.50 mm); WB 1.81–2.24 mm (mean 2.03 mm); LB/WB 1.63–1.80 (mean 1.72) (n = 20 for all measurements except terminalia). Habitus as shown in Figs. 25B, 26D, E.

Integument. Head, pronotum and antennae brassy-black with golden-bronze to golden reflections, except for clypeus lighter in color and pronotum with blakish to purplish tints in apical half; elytra black, sometimes with faint bluish or purplish tints; underside black with weak golden-bronze reflections; maxillary palps light-brown; legs black, sometimes with faint purplish tints on femora and tibiae in ventral side, except for basal four tarsomeres brownish-black with brown tarsal pads. Dorsal and ventral surfaces moderately shiny.

Vestiture mainly consisting of white, golden and black setae. Head clothed with short, recumbent dark-brownish-golden to pale-golden setae but frons partly naked, rarely with white setae on temples. Pronotum clothed with short, semirecumbent, white, dark-golden and black setae which are arranged as follows: 1) white wavy transverse band in apical half; 2) dark-brownish-golden setae scattering around basal margin but occasionally absent; and 3) black setae in remaining space. Elytra clothed with short, semirecumbent, white and black setae which are arranged on each elytron as follows: 1) white setae complicatedly scattering in basal half, partly forming a small circle near sutural margin; 2) first white transverse band at apical 1/3, strongly wavy, zigzag-shaped; 3) second white transverse band at subapical part, weakly wavy; and 4) black setae in remaining space. Underside more sparsely setiferous, with fine, recumbent whitish setae.

Head, when viewed from above, deeply triangularly concave on frons which is sometimes faintly sinuated, with oculofrontal margins ridged. Eyes, when viewed from above, narrowly visible, weakly convex laterally. Vertex obscurely and coarsely variolate-punctate; frons widely concave, weakly impressed along upper side of midline, transversely ridged from just above each antennal insertion to inner margin of each eye, with surface faintly punctate with glabrous area; suprantennal pores simply round; frontoclypeal suture obsolete; clypeus narrow (Fig. 29D), without elevated basal margin, WC/LC 1.31–1.77 (mean 1.58), WC/LSC 1.21–1.50 (mean 1.36), deeply arcuately emarginate at apical margin.

Antennae (Figs. 29E, F) reaching just behind apicolateral angles of pronotum when laid alongside; antennomere I stout claviform, longer than II; II ovate, longer than III; III subrectangular, longer than IV; IV–VI subrectangular, subequal each other in length; VII–X triangular, more strongly enlarged and slightly thicker in male than in female; XI subtriangular to sublingulate.

Mandibles with strong, transverse ridge in about middle of each outside. Maxillary palps with oval palpomere IV somewhat longer than wide.

Pronotum widest at base, WP/LP 2.75–3.08 (mean 2.91), BMP/AMP 1.50–1.62 (mean 1.57), narrower than elytra; lateral margins straightly and moderately narrowed apicad; apicolateral angles obtuse; basolateral angles acute; apical margin bisinuately emarginate, with very small median lobe; basal margin trisinuate, with median lobe moderately produced; disk weakly depressed along basal median lobe, occasionally weakly depressed along lateral margins; surface obscurely variolate-punctate, becoming denser toward apical and basal margins. Scutellar shield very small, subtriangular, glabrous.

Elytra widest at humeri, LE/WE 1.20–1.33 (mean 1.28), LE/LP 3.74–4.38 (mean 4.10); humeral calluses strongly developed, often longitudinally ridged in basal part in lateral view; lateral margins weakly constricted behind humeri and weakly narrowed posteriorly from behind humeri to middle, then slightly more strongly, faintly arcuately narrowed to subapical part, and finally strongly arcuately convergent to conjointly broadly rounded apices, with weak serrations in about apical half except apices (Fig. 29C); marginal carinae distinct in thoracic region, indistinctly reaching near apices; sutural margin faintly elevated in apical 1/3; disk slightly strongly depressed in basal part, constricted behind humeri, weakly swollen in subapical part; surface irregularly and slightly densely punctate. Lateral part of abdomen narrowly visible in dorsal view; laterosternites I–IV with laterosternal sulci.

Underside. Prosternum (Fig. 29G) weakly rounded at apical margin which is not rimmed; prosternal process wide, constricted between procoxa, with apex broadly rounded at rest; marginal carinae slightly narrowly separated each other at widest part of prosternal process, weakly narrowed posteriorly in apical 1/3 then weakly divergent posteriad; disk rather flattened on median portion, weakly declivous laterad on outside of marginal carinae, without elevated protions along procoxal cavities. Hypomera with depressed hypomeral markings rounded subtrapezoidal, additionally depressed inside (Fig. 29H). Metaventrite moderately sculptured with large punctures on inside of katepisternal suture and with linearly confluent sculptures on outside of the suture. Legs moderately slender; metacoxal plates weakly produced posteriorly at each lateral angle which is broadly acute, with surface coarsely variolate; metatibiae bearing a fringe of spines in apical half of each outer margin, with one long spine in base of the fringe (Fig. X); inner tooth of each claw large. Abdominal ventrites with sternal grooves on ventrites I–V; V (Fig. X) shallowly concavely emarginate at apex, rarely weakly produced at bottom of the apical emargination; surface variolate, in ventrite I with linearly confluent sculptures on median part.

Sexual dimorphism barely recognized on the relative size of antennae (see above).

Male terminalia (n = 3 for measurements). Proctiger with a pair of short baculi at base. Sternite IX (Fig. 30A) wide, SL/SW 0.68–0.77 (mean 0.72), truncately rounded at apical margin, with sides clearly rounded, bearing a pair of setae on each side of apical margin. Tegmen (Fig. 30B) wide; parameres PL/PW 1.56–1.93 (mean 1.76), sparsely setiferous on apicolateral margins, with sides which are sinuately and gently dilated from base to apical half, then weakly arcuately expanded to widest point at apical 1/4, and finally strongly convergent to apices; phallobase PbL/PbW 2.21–2.32 (mean 2.28), more than 1/4 length of tegmen. Penis (Fig. 30C) wide, PeL/PeW 4.14–4.41 (mean 4.30), slightly shorter than tegmen; dorsal plate with sides which are gradually narrowed from widest point of base to subapical part and faintly constricted at apical 1/4, and then arcuately convergent apicad, with roundly, faintly produced apex, basally with median struts about 1/3 length of penis; ventral plate membranous, but weakly sclerotized as a linear patch in middle of apical 1/4.

Female terminalia (n = 5 for measurements). Ovipositor (Figs. 30D–F) short; proctiger basally with a pair of long, ventrally curved baculi; coxites transversely subhexagonal, sparsely setiferous on each side of apical margin, ventrally without transverse depression in apical part; styli fan-shaped, with sides gently dilated apicad, SlL/SlW 2.03–2.41 (mean 2.20), bearing several setae apically; ventral valve sparsely setiferous on each side of subapical part; vagina sack-shaped, very strongly and roundly expanded dorsally in middle; spermatheca slender tubular, rather short in length, widest near apex, without spermathecal gland.

Differential diagnosis. This species is similar in general appearance to *Trachys auricollis* especially in the wedge-shaped body, but can be easily distinguished from *T. auricollis* by the following character states: abdominal ventrite I with distinct sternal grooves; head and pronotum brassy-black without distinct yellow setae usually; prosternal marginal carinae much more weakly divergent posteriad; frons outline of head more deeply, triangularly concave; male sternite IX bearing a pair of setae on apical angles; parameres with weak lateral expansion being widest at apical 1/4; apex of penis faintly produced; and female styli fan-shaped.

Specimens examined. Type material. Holotype: ♂ (based on Kurosawa, 1951; no dissected terminalia), “FUKIYAYAMA Mt. / AIZU PROV. / FUKUSHIMA PREF. / 22.V.1945 / Y. K.” (NSMT).

Non type material. **Japan**. Honshu — [Miyagi] 1 ♂, 2 ♀♀, 1 ex., Sendai-shi, 17.V.1953, K. Nagayama leg. (SEHU); 1 ♀, Sahoyama, Sendai-shi, 2.V.1953, K. Nagayama leg. (SEHU). [Yamagata] 1ex., Koriyama, Nanyô-shi, 19.VI.1947, K. Suzuki leg. (SEHU). [Fukushima] 1 ♂, 3 exs., Oishi, VI. 1927, no collector name, “リンゴ寄生”, meaning infested apples, written on the underside of label (SEHU; recorded by Kurosawa, 1959); 1 ♂, 4 ♀♀, Mt. Gamôdake, Tadami-chô, Minamiaizu-gun, 18.VI.2016, Y. Tamadera leg. (YTJ; recorded by Tamadera and Yamada, 2019); 1 ex., same locality , 20.VI.2015, Y. Tamadera leg., captured on *Aria alnifolia* (YTJ; recorded by Tamadera and Yamada, 2019); 5 exs., same locality, 18.VI.2016, Y. Tamadera leg., captured on *A. alnifolia* (YTJ; recorded by Tamadera and Yamada, 2019); 1 ex., same locality, 19.VI.2016, Y. Tamadera leg., captured on *A. alnifolia* (YTJ; recorded by Tamadera and Yamada, 2019); 1 ex., same locality, 26.VII.2018, Y. Tamadera leg., captured on *A. alnifolia* (YTJ; recorded by Tamadera and Yamada, 2019); 1 ex., ditto, captured on *Sorbus commixta* (YTJ; recorded by Tamadera and Yamada, 2019); 1 ex., ditto, emerged from *A. alnifolia*, 28.VII.2018 (YTJ; recorded by Tamadera and Yamada, 2019); 2 exs., ditto, emerged from *A. alnifolia*, 4.VIII.2018 (YTJ; recorded by Tamadera and Yamada, 2019); 1 ex., ditto, emerged from *A. alnifolia*, 7.VIII.2018 (YTJ; recorded by Tamadera and Yamada, 2019); 1 ex., ditto, emerged from *S. commixta*, 31.VII.2018 (YTJ; recorded by Tamadera and Yamada, 2019); 2 exs., ditto, emerged from *S. commixta*, 3.VIII.2018 (YTJ; recorded by Tamadera and Yamada, 2019); 1 ex., ditto, emerged from *S. commixta*, 7.VIII.2018 (YTJ; recorded by Tamadera and Yamada, 2019); 1 ♂, 1 ♀, Mt. Yôgai-san, Tadami-cho, Minamiaizu-gun, 20.VI.2016, Y. Tamadera leg. (YTJ); 3 exs., same locality, 20.VI.2016, Y. Tamadera leg., captured on *A. alnifolia* (YTJ; recorded by Tamadera and Yamada, 2019). [Tochigi]: 2 exs., Takaku-koh, Nasu-machi, 7.VII.1992, S. Ohmomo leg. (SEHU; NSMT). [Fukui] 2 exs., Mt. Hoonji, Fukui Pref., 6.V.1973, H. Sasaji leg. (NSMT). [Nagano] 1 ex., Kitafukashi, Matsumoto City, 19.V.1995, T. Kosaka leg. (NSMT). [Gifu] 1 ex., Matsunoki, Takayama, Gifu Pref., 12.VI.1974, C. Sato leg. (NSMT). [Kyoto]: 1 ex., Kyoto, 15.X.1966, T. Kumata leg. (SEHU). [Hyôgo] 1 ex., Sekinomiya, Tajima, 1.V.1949, A Nagatomi leg. (SEHU); 2 exs., Yumura, Tajima, 27.V.1955, T. Nakane leg. (SEHU). Kyushu — [Fukuoka] 1 ex., Hirao, Fukuoka, 21.IV.1952, T. Yoshida leg. (NSMT;

recorded by Kurosawa, 1959). **China**. 1 ♀, “Shōtan Pref., Funang, C. -China” (Hunan, Central China), VII.1945, K. Shirahata leg. (NSMT; recorded by Kurosawa, 1985b).

Distributions in Japan. Honshu and Kyushu.

Other distributions. China (Hunan).

Adult food plants. Same as in the larvae mentioned below. The adults are sometimes collected on *Pyrus pyrifolia* (Burm. f.) Nakai var. *culta* (Makino) Nakai based on literatures (Tsutsumiuchi, 2000; Sugiura and Koseki, 2005).

Host plants. Rosaceae: *Malus toringo* (Siebold) Siebold ex de Vriese [Japanese name: Zumi] (Kurosawa, 1951 — adult record?), *M. asiatica* Nakai (= *M. pumila*) [Japanese name: Waringo] (Kurosawa, 1959 — adult record based only on the label data of specimen preserved in SEHU), *Chaenomeles japonica* (Thunb.) Lindl. ex Spach [Japanese name: Kusaboke] (Kurosawa, 1951 — adult record?), *Cydonia oblonga* Mill. [Japanese name: Marumero] (Kurosawa, 1959 — adult record?), *Amelanchier asiatica* (Siebold et Zucc.) Endl. ex Walp. [Japanese name: Zaifuriboku] (Kurosawa, 1959 — adult record?), *Pyrus pyrifolia* (Burm.f.) Nakai [Japanese name: Yama-nashi] (Kurosawa, 1959 — adult record?), *Aria alnifolia* (Siebold et Zucc.) Decne. [Japanese name: Azukinashi] (Tamadera & Yamada, 2019), and *Sorbus commixta* Hedl. [Japanese name: Nanakamado] (Tamadera & Yamada, 2019) in Japan.

Leaf-mining habit. Mines of *T. toringoi* were found on *Aria alnifolia* and *Sorbus commixta* by Tamadera & Yamada (2019) and this study (Figs. 64B, C, 67B). Each mine is of the full-depth type and the blotch one occurring on various portions in each tree leaf. Eggs are laid singly on the adaxial surface of each the leaf along latero-basal margin. Hatched larvae left linear frass inside the mines. Adults are emerged from either the adaxial or abaxial surfaces of the leaves with oval adult exit holes.

Agricultural pest record. Umeya and Okada (2003) is listed this species as pests of apple and peach leaves.

Notes. In Ohmomo & Fukutomi (2013), they point out that the first transverse band of the elytron is more strongly wavy in *Trachys toringoi* than in *T. auricollis*. However, I removed this character state from the diagnosis of *T. toringoi* because it shows rather small differences and is sometimes not recognizable between them.

On the basis of the original description and figures, *Trachys toringoi* is seemed to be very similar in general appearance to *T. albopilosus* described from Zhejiang, China based on one female specimen (Peng, 2021 d), but is distinguished from the latter at least by the more weakly waved second transverse band on each elytron.

Group III (saundersi)

(Figs. 25 C–F)

Species included. *Trachys saundersi* Lewis, 1893, *T. cupricolor* Saunders, 1873, *T. pecirkai* Obenberger, 1925, and *T. aurifluus* Solsky, 1875.

Diagnosis. Body ovate type. Apical margin of pronotum without median lobe. Elytra with serrate lateral margins; elytral vestiture with transverse bands consisting of unicolor setae in apical half of each elytron, without tufts consisting of erect setae. Prosternum more or less rimmed along apical margin which is not lobed; prosternal disk with elevated portions along procoxal cavities. Abdominal ventrites with sternal grooves on ventrite I–V. Female coxites ventrally without transverse depression in apical part.

Trachys saundersi Lewis, 1893

[Japanese name: Sôndâzu-chibi-tamamushi]

(Figs. 5C, 25C, 31, 32, 33, 67C)

Trachys saundersi Lewis, 1893: 337 (type locality: "Main island. Sixteen examples taken at various places on the Nakasendo", Japan); Kerremans, 1903: 310 (catalog); Kurosawa, 1950 a: 13 (note); Chûjô & Kurosawa, 1950: 11 (Shikoku, Japan); Yano, 1952: 26 (immature stages); Iga, 1955 a: 10, pl.4 (pictorial book); 1955 b: 80, pl.24 (pictorial book); Kurosawa, 1959: 213 (redescription); 1963: 155, pl. 78 (pictorial book); 1976 d: 2 (note); 1985 a: 168 (removed *Trachys obscuripennis* Obenberger, 1923 from synonymy of *T. saundersi* Lewis in Kurosawa, 1959); 1985b: 34, pl. 6 (pictorial book); Akiyama & Ohmomo, 1997: 48 (checklist); 2000: 285, pl. 120 (pictorial book); Kubáň, 2006: 420 (Palaearctic catalog); Bellamy, 2008 b: 2517 (World catalog); Ohmomo & Fukutomi, 2013: 165, pl. 51 (pictorial book); Kubáň, 2016: 573 (Palaearctic catalog); Ishiguro & Nishida, 2018: 33, figs. 2, 3 & 6 (aedeagus); Peng, 2022 a: 270 (distribution).

Trachys (*Trachys*) *saundersi*: Obenberger, 1918: 19, 35, 64 (in key; diagnosis; catalog); 1926 b: 661 (catalog); Miwa & Chûjô, 1936: 25 (list).

Trachys (*Trachys*) *mariola* Obenberger, 1929 a: 74 (type locality: "Formose", Taiwan); Miwa & Chûjô, 1936: 25 (list); Obenberger, 1937 a: 1392 (World catalog). Synonymized under *T. saundersi* by Kurosawa, 1985 a: 168.

Trachys (*Trachys*) *yunnana* Obenberger, 1929 c: 11 (type locality: "China: Yunnan"); 1937 a: 1385 (World catalog). Synonymized by Kurosawa, 1985 a: 168. Justified emendation: *T. yunnanus*, according to ICZN (2009).

Trachys (*Trachys*) *jakovlevi* Obenberger, 1929 b: 126 (type locality: "China: Yunnan"); 1937 a: 1360 (World catalog). Synonymized under *T. saundersi* by Kurosawa, 1985 a: 168.

Trachys jakovlevi: Obenberger, 1958: 242 (Yunnan, China)

Trachys (*Trachys*) *vimmeri* Obenberger, 1930: 113 (type locality: "China or."); 1937 a: 1385 (World catalog). Synonymized under *T. saundersi* by Kurosawa, 1985 a: 168.

Trachys (*Trachys*) *opsigona* Obenberger, 1937 b: 43 (type locality: "China: Kiulung"); 1937: 1368 (World catalog). Synonymized under *T. saundersi* by Kurosawa, 1985 a: 168. Justified emendation: *T. opsigonus*, according to ICZN (2009).

Trachys (*Habroloma*) *saundersi* [sic]: Jakobson, 1913: 800 (*lapsus calami*; catalog); Obenberger, 1937 a: 1414 (*lapsus calami*; World catalog); Kurosawa, 1959: 213 (in synonymy of *T. saundersi*).

Habroloma (*Habroloma*) *saundersi* [sic]: Bellamy, 2008 b: 2562 (*lapsus calami*; World catalog).

Trachys cuneifera Kurosawa, 1959: 215 (type locality: "Mt. Odayama, Aizu-Wakamatsu City, Fukushima Pref.", Japan); 1976 c: 2 (note); Seki, 1980: 34 (additional distribution record: Nagano Pref., Japan); Kurosawa, 1985 b: 34 (pictorial book); Akiyama & Ohmomo, 1997: 46 (checklist); 2000: 284, pl. 120 (in pictorial book); Kubáň, 2006: 418 (Palaearctic catalog). **Syn. nov.**

Trachys cuneiferus [justified emendation, according to ICZN (2009)]: Bellamy, 2008 b: 2478 (World catalog); Ohmomo & Fukutomi, 2013: 165, pl. 51 (pictorial book); Kubáň, 2016: 570 (Palaearctic catalog).

Trachys auricollis: Štrunc, 2022: 196 (misidentification of *T. saundersi*).

Description. Male and female. Body ovate to narrowly ovate, moderately convex dorsally (Figs. 32A, B). LB 3.15–4.55 mm (mean 4.06 mm); WB 1.60–2.45 mm (mean 2.15 mm); LB/WB 1.84–1.97 (mean 1.89) (n = 20 for all measurements except terminalia). Habitus as shown in Figs. 25C, 31.

Integument. Head and pronotum brassy-black with weak golden-bronze reflrctions, rarely with faint greenish tints; elytra black, with weak golden tints along basal and sutural margins, rarely with faint purplish tints; underside black, with faint golden-bronzy reflections; antennae and legs black, except for femora sometimes with faint purplish tints in ventral side and basal four tarsomeres brown to light-brown with brown tarsal pads; maxillary palps light-brown. Dorsal and ventral surfaces moderately shiny.

Vestiture mainly consisting of white, brownish-yellow and black setae; black setae rarely being brownish. Head clothed with short, recumbent, brownish-yellow to pale-yellow setae, sometimes with two white spots on vertex. Pronotum clothed with short, semirecumbent, brownish-yellow to pale-yellow setae, with some small white patches; pronotal setae rarely being whitish. Elytra clothed with short, semirecumbent, white, brownish-yellow and black setae which are arranged on each elytron as follows: 1) white setae irregularly scattering in basal 1/3; 2) inconspicuously, wavy white band near middle, usually connecting to anterior white patch near sutural margin; 3) first white transverse band at apical 1/3, moderately wavy, zigzag-shaped; 4) second white transverse band at apical 1/5, weakly wavy; 5) a few brownish-yellow setae sometimes in base and along basal 2/3 of sutural margin; and 6) black setae in remaining space, rarely mixing with brownish ones. Underside more sparsely setiferous, with fine, recumbent whitish setae.

Head, when viewed from above, moderately arcuately concave on frons, visible lowermost part of frons, with oculofrontal margins ridged. Eyes, when viewed from above, narrowly visible, weakly convex laterally. Vertex obscurely and coarsely variolate-punctate; frons widely concave, weakly impressed along upper side of midline, transversely strongly ridged from just above each antennal insertion to inner margin of each eye, with surface rather smooth but faintly punctate; suprantennal pores simply round; clypeus wide (Fig. 32D), without elevated basal margin, WC/LC 1.50–2.00 (mean 1.75), WC/LSC 1.33–1.65 (mean 1.54), deeply arcuately emarginate at apical margin.

Antennae (Fig. 32E) reaching just behind apicolateral angles of pronotum when laid alongside; antennomere I stout claviform, longer than II; II ovate, longer than III; III subrectangular, longer than IV; IV–VI subractangular, shorter in VI than in IV and V; VII–X triangular, moderately enlarged; XI subtriangular to sublingulate.

Mandibles with strong, transverse ridge in about middle of each outside. Maxillary palps with oval palpomere IV somewhat longer than wide.

Pronotum widest at base, WP/LP 2.85–3.17 (mean 2.96), BMP/AMP 1.43–1.60 (mean 1.53), narrower than elytra; lateral margins weakly arcuately and slightly weakly to moderately narrowed apicad; apicolateral angles obtuse to broadly acute; basolateral angles broadly acute to almost right; apical margin arcuately emarginate, without median lobe; basal margin trisinuate, with median lobe moderately produced; disk weakly depressed along lateral margins and along basal median lobe; surface obscurely variolate-punctate, becoming denser toward apical and basal margins. Scutellar shield very small, subtriangular, glabrous.

Elytra widest at humeri, LE/WE 1.36–1.45 (mean 1.41), LE/LP 4.37–4.85 (mean 4.57); humeral calluses moderately developed; lateral margins subparallel in basal half and weakly constricted behind humeri, and then weakly arcuately convergent to conjointly rounded apices, with slightly weak serrations in about apical half except apices

(Fig. 32C); marginal carinae distinct in thoracic region, indistinctly reaching near apices; sutural margin faintly elevated in apical half; disk weakly depressed in basal part, constricted behind humeri, weakly swollen in subapical part; surface irregularly and slightly densely punctate. Lateral part of abdomen narrowly visible in dorsal view; laterosternites I–IV with laterosternal sulci.

Underside. Prosternum (Fig. 32F) rather straight at apical margin which is weakly rimmed; prosternal process slightly slender, strongly constricted between procoxa, with apex broadly rounded at rest; marginal carinae narrowly separated each other, gently narrowed posteriorly in apical half then gently divergent posteriad; disk rather flattened on median portion, somewhat declivous laterad on outside of marginal carinae, with weak elevated protions along procoxal cavities. Hypomera with depressed hypomeral markings large in size, arcuate, somewhat jagged posteriorly (Fig. 32G). Metaventrite densely sculptured with large punctures on inside of katepisternal suture and moderately sculptured with linearly confluent sculptures on outside of the suture. Legs moderately slender; metacoxal plates weakly produced posteriorly at each lateral angle which is broadly acute, with surface coarsely variolate; metatibiae bearing a fringe of spines in apical half of each outer margin, with one long spine in base of the fringe (Fig. 32H); inner tooth of each claw large. Abdominal ventrites with sternal grooves on ventrites I–V; V (Fig. 32I) shallowly emarginate at apex; surface variolate, in ventrite I with linearly confluent sculptures on median part.

Sexual dimorphism indistinct.

Male terminalia (n = 4 for measurements). Proctiger with a pair of short baculi at base. Sternite IX (Fig. 33A) slightly slender, SL/SW 0.91–1.20 (mean 1.01), arcuately emarginate at apical margin, bearing several setae on each side of apical margin. Tegmen (Fig. 33B) slightly wide; parameres PL/PW 1.95–2.16 (mean 2.06), bearing a pair of setae on apicolateral margins, with sides which are gently dilated from base to apical half, then arcuately expanded to widest point at apical 1/4, and finally slightly sharply convergent to apices; phallobase PbL/PbW 2.59–2.86 (mean 2.74), about 1/3 length of tegmen. Penis (Fig. 33C) slightly wide, PeL/PeW 4.42–5.48 (mean 4.94), slightly shorter than tegmen; dorsal plate with sides which are gradually narrowed from widest point of base to subapical part, and then arcuately convergent apicad, with roundly, faintly produced apex, basally with median struts about 1/3 length of penis; ventral plate membranous, but weakly sclerotized as a linear patch in middle of apical 1/4.

Female terminalia (n = 5 for measurements). Ovipositor (Figs. 33D–F) short; proctiger basally with a pair of long, ventrally curved baculi; coxites transversely subhexagonal, sparsely setiferous on each side of apical margin, ventrally without transverse depression in apical part; styli subtrapezoidal, wide, with sides gently dilated apicad, SlL/SlW 1.27–1.86 (mean 1.47), bearing several setae apically; ventral valve sparsely setiferous on each side of subapical part; vagina elongately sack-shaped, moderately expanded dorsally in about distal 2/3; spermatheca prominently wide tubular, rather short in length, widest in basal part which is roundly expanded dorsally, without spermathecal gland.

Differential diagnosis. This species is similar to *Trachys auricollis* Saunders, 1873 in the coloration of body and vestiture, but can be easily distinguished from *T. auricollis* by the following character states: narrowly ovate body; abdominal ventrite I with distinct sternal grooves; prosternal marginal carinae more narrowly separated each other and more weakly divergent posteriad; disk of prosternum with elevated protions along procoxal cavities; male parameres with arcuate lateral expansion being widest at apical 1/4 and with a pair of setae on apicolateral margins; apex of penis faintly produced; female spermatheca much wider.

In addition, this species may be related to the three Japanese species, *T. cupricolor*, *T. pecirkai* and *T. aurifluus*, in having the elevated protions along procoxal cavities of prosternal disk, the narrowly ovate body and the presence of the swelling on the subapical part of the elytral disk, but is readily distinguished from the three species by the black elytra and by the presence of black setae in the apical part of the elytra.

Specimens examined. Type material. Holotype of *Trachys cuneiferus* Kurosawa, 1959: ♂ (no dissected terminalia; visible apex of aedeagus), "ODAYAMA MT. / MONDEN V. / KITA-AIZU D. / 30.V.1948 / Y. K. & K. HAYASHI" (NMNS).

Non type material. **Japan**. Honshu — [Fukushima] 1 ex., Takikawa D., 11–13.V.1999, H. Takizawa leg. (SEHU); 1 ex., Mt. Myôjindake, Ônuma-gun, 25.II.1948, K. Nagayama leg. (SEHU). [Chiba] 1 ex., Mt. Nokogiri-yama, Awagun-Kyonan-machi, 8.VI.1991, T. & T. Nakane leg. (SEHU); 1 ex., Ainosawa-rindô, Kiyosumi, Kamogawa-shi, 7.VI.2015, S. Shimamoto leg. (YTJ). [Tokyo] 2 exs., Mont Takao, Hachiôji, 18.V.1913, E. Gallois leg. (SEHU); 1 ex., same locality, 8.VI.1913, E. Gallois leg. (SEHU); 2 exs., same locality, 4.V.1913, E. Gallois leg. (SEHU); 1 ex., same locality, 10.V.1914, E. Gallois leg. (SEHU); 1 ex., same locality, 27.V.1917, E. Gallois leg. (SEHU). [Kanagawa] 1 ex., Mt. Ôyama, 3.V.1967, K. Masumoto leg. (SEHU); 1 ex., Gôra – Shôjinike, Hakone-chô, 15.VII.1960, T. Nakane leg. (SEHU); 1 ex., Midori-ku, Sagamihara-shi, 9.VII.2011, Y. Fujisawa leg. (YTJ); 1 ♂, 4 ♀, Mt. Ôyama, Isehara-shi, 24.V.2015, T. Hasegawa leg. (YTJ). [Toyama] 1 ex., Komoridani, Oyabe-shi, 7.VIII.1952, N. Yato leg. (SEHU). [Yamanashi] 2 exs., Funatsu-rindô, Narusawa-mura, 10.IX.2005, Y. Komiya leg. (SEHU); 9 exs., Hishiyama, Katsunuma-chô, Kôshû-shi, 3.V.2017, J. Souma leg. (YTJ); 14 exs., ditto, M. Yamada leg. (YTJ); 1 ex., Saiko, Fujikawaguchiko-chô, 2.V.2015, Y. Fukuda leg. (YTJ); 6 exs., Mt. Gangaharazuri-yama, Narago, Nanaho-machi, Ôtsuki-shi, 16.V.2014, Y. Tamadera leg. (YTJ); 1 ex., Biwakubo-sawa, Masutomi, Hokuto-shi, 23.IX.2007, G. Oishi leg. (YTJ); 5 ♀♀, Hishiyama, Katsunuma-cho, Kôshû-shi,20.V.2010, Y. Sawada leg. (YTJ); 2 ♀♀, same locality, 14.V.2011, Y. Fujisawa leg. (YTJ). [Nagano] 1 ex., Shimosuwa-machi, alt. 800–1000 m, 22.V.1979, M. Suwa leg. (SEHU); 1 ex., Kamikôchi, Matsumoto-shi, 19.VII.1963, T. Nakane leg. (SEHU); 1 ex., Komanoyu, Fukushima, Kiso-machi, 6.VII.1947, T. Nakane leg. (SEHU); 5 exs., Shimashimadani, Matsumoto-shi, 28.VII.1953, S. Ueno leg. (SEHU). [Gifu] 1 ex., Yôrô, 29.V.1949, T. Nakane leg. (SEHU); 1 ex., Oku, Mino-shi, 16.VI.1961, no collector name (SEHU). [Shizuoka] 1 ex., Nishi-usuduka, Mt. Fuji-san, Awakura, Fujinomiya-shi, 11.VI.2017, S. Shimamoto leg. (YTJ); 1 ♂, 6 ♀♀, Fumoto, Shizuoaka-shi, 14.V.2017, Y. Tamadera leg. (YTJ). [Aichi] 6 exs., Gamo, Mikawa, 14.V.1948, T. Nakane leg. (SEHU); Mikawa-ôno, Shinshiro-shi, 10.V.1991. TTM. Nakane leg. (SEHU); 1 ex., Hôraiji Temple, Shinshiro-shi, 30.IV.1950, T. Nakane leg. (SEHU); 1 ex., same locality, 20.V.1992, T. & T. Nakane leg. (SEHU); 1 ex., Ishimaki-chô, Toyohashi-shi, 13.V.2016, S. Shimamoto leg. (YTJ). [Mie] 2 exs., Yunoyama, Ise-shi, 1.VI.1947, S. Osawa leg. (SEHU); 1 ex., same locality, 31.V.1948, S. Osawa leg. (SEHU); 1 ex., Ôsugi-dani, Takigun-Ôdai-chô, 10.VI.1952, T. Nakane leg. (SEHU). [Shiga] 47 exs., Mt. Hira, Ômi, 28.V.1956, T. Nakane leg. (SEHU); 14 exs., same locality, 29.V.1956, T. Nakane leg. (SEHU); 3 exs., Mt. Hira, 3.VIII.1955, T. Nakane leg. (SEHU); 1 ex., same locality, 5.VIII.1955, T. Nakane leg. (SEHU); 3 exs., same locality, 12.V.1956, T. Nakane leg. (SEHU); 1 ex., Mt. Oikedake (Suzuka), 27.VII.1940, K. Sakaguchi leg. (SEHU). [Kyoto] 3 exs., Sakashita – Ôfuse, 16.VI.1957, T. Nakane leg. (SEHU); 1 ex., Kitashirakawa, Kyoto-shi, 9.V.1964, T. Nakane leg. (SEHU); 1 ex., Hanase, Kyoto-shi, 28.V.1958, T. Nakane leg. (SEHU); 2 exs., Kurama – Kibune, Kyoto-shi, 3.V.1956, T. Nakane leg. (SEHU); 3 exs., Kumogahata, Kyoto-shi, 8.VI.1954, T. Nakane leg. (SEHU); 1 ex., Kibune, Kyoto-shi, 20.VI.1951, H. Ishida leg. (SEHU); 1 ex., Kurama, Kyoto-shi, 17.VI.1954, T. Nakane leg. (SEHU); 7 exs., same locality, 3.V.1956, T. Nakane leg. (SEHU); 20 exs., Serio, Kyoto-shi, 20.VI.1951, H. Ishida leg. (SEHU); 1 ex., same locality, 1.VI.1952. H. Ishida leg. (SEHU); 11 exs., same locality, 1.VI.1953, T. Nakane leg. (SEHU); 3 exs., same locality, 28.V.1954, T. Nakane leg. (SEHU); 23 exs., same locality, 29.V.1954, T. Nakane leg. (SEHU); 3 exs., Mt. Daihi-zan, 27.V.1954, T. Nakane leg. (SEHU); 4 exs., same locality, 16.VII.1951, T. Nakane leg. (SEHU); 2 exs., same locality, 1.VI.1958, T. Nakane leg. (SEHU); 2 exs., same locality, 15.VI.1941, K. Sakaguchi leg. (SEHU); 6 exs., same locality, 27.V.1954, T. Nakane leg. (SEHU); 14 exs., same locality, 31.V.1958, T. Nakane leg. (SEHU); 1 ex., same locality, 29.V.1960, T. Nakane leg. (SEHU); 13 exs., Bômura, 15.VI.1957, T. Nakane leg. (SEHU); 1 ex., Nishikyô-ku, Kyoto-shi, 18.V.2015, Y. Tamadera leg. (YTJ). [Osaka] 1 ex., Hattani, Myôken, 11.VI.1949, K. Sawada leg.; 1 ex., Mino-o-shi, 6.VI.1933, Y. Yano leg. (SEHU); 1 ex., same locality, VI.1936, H. Takenaka leg. (SEHU). [Hyôgo] 1 ex., Hataganaru, Tajima, 24.V.1955, T. Nakane leg. (SEHU); 1 ex., same locality, 27.V.1955, T. Nakane leg. (SEHU). [Nara] 1 ex., Mt. Ômine-san, 23.V.1974, T. Hattori leg. (SEHU); 16 exs., Hôriki-tôge, Mt. Inamuragatake, 5.VI.1957, Y. Okada leg. (SEHU); 1 ex., Mt. Ôdaigahara, 1.VIII.1953, T. Nakane leg. (SEHU); 1 ex., same locality, 22.VII.1953, T. Nakane leg. (SEHU); 4 exs., Mt. Ôdaigahara, Ikadaba, 21.VII. 1953, T. Nakane leg. (SEHU). [Tottori] 1 ex., Daisen-chô, 18.VII.1952, T. Nakane leg. (SEHU). [Hiroshima] 1 ex., Nakatsuya, Yoshiwa, Hatsukaichi-shi, 24.V.1976, T. Kosaka leg. (SEHU). The Ogasawara Islands (Bonin Isls; Tokyo) — [Hahajima Is.] 2 exs., Hahajima Is., Ogasawara Isls., 15.VIII.1930, Yamamoto leg. (NSMT; recorded by Kurosawa, 1976d)). Awajishima Is. (Hyôgo) — 1 ex., Kashiwarayama-rindô, Chikusaki, Sumoto-shi, 13.VII.2022, Y. Tamadera leg. (YTJ). The Oki Islands (Shimane) — [Dôgo Is.] 1 ex., Goka, Okinoshima-chô, Shimane, 27.V.1968, H. Kadowaki leg. (SEHU). Shikoku — [Tokushima] 1 ex., Koyadaira, Awa, 9.VIII.1913, E. Gallois leg.; 1 ex., same locality, 11.VIII.1913, E. Gallois leg. (SEHU). [Kagawa] 1 ex., Mt. Ôtaki-san, Takamatsu-shi, 10, 12.V.2000, H. Takizawa leg. (SEHU); 1 ex., Mt. Ryûô-san, 11.V.2000, H. Takizawa leg. (SEHU). [Ehime] 6 exs., Omogokei, Kamiukenagun-Kumakôgen-chô, 21.VIII.1969, T. Nakane leg. (SEHU); 2 exs., Mt. Ishiduchi-san, Koguchi, 1.VI.1952, N. Yato leg. (SEHU); 2 exs., Mt. Ishiduchi-san, 13.V.1968, T. Kosaka leg. (SEHU). [Kôchi] 1 ex., Mt. Kodakasa-yama, Tosa, 24.IV.1936, no collector name (SEHU).

Distributions in Japan. Honshu, Shikoku, Awajishima Is., and the Oki Isls. (Dôgo Is.).

I confirmed three specimens (but actually one specimen lost) collected on Hahajima Is. in the Ogasawara Islands (Bonin Isls.), which are already recorded by Kurosawa (1976 d) as individuals imported from the Japan proper. Kurosawa (1959) was recorded from Chichijima Is. in the Ogasawara Isls., but it is probably an error as Hahajima Is. I follow Kurosawa's consideration that the record from the Ogasawara Islands is removed from the original distribution of *Trachys saundersi*.

Record based on literature: Kyushu? (Kurosawa, 1985 b).

Kurosawa (1985 b) added Kyushu as one of the distribution localities of *Trachys saundersi* without specimen data, but I could not find its voucher specimens from Kurosawa's collections in NSMT. As far as I known, it is nothing that detailed distribution records of this species from Kyushu. Thus, this study treated Kyushu is a doubtful locality.

Other distributions. China and Taiwan.

Adult food plants. Same as in the larvae mentioned below.

Host plants. Hydrangeaceae: *Deutzia crenata* Siebold et Zucc. [Japanese name: Utsugi] (Yano, 1952; confirmed by this study) and *D. gracilis* Siebold et Zucc. [Japanese name: Hime-utsugi] (Kurosawa, 1959 — adult record?) in Japan.

Leaf-mining habit. Mines of *Trachys saundersi* were found on *Deutzia crenata* by this study (Fig. 67C): each mine was of the full-depth type and formed a large, elongate blotch occurring usually along leaf-margin; when full-grown, it occupied much more than an half of whole the leaf blade; eggs, which were black (remaining eggshell) and not covered on powdery substances, were laid singly on the adaxial surface of the leaf blade; hatched larvae left granular frass inside the mines; adult exit holes were not confirmed in this study. See also Yano (1952) for descriptions of the leaf-mines and immature stages.

Notes. In Japan, *Trachys saundersi* is sometimes sympatrically distributed with *T. tsushimae* Obenberger, 1922, which is also associated with *Deutzia* plants, but is readily distinguished from the latter by the serrate lateral margins of the elytra, etc.

Trachys saundersi is often noticed about the similarity to *T. auricollis* Saunders, 1873 in general appearance (black body and occurrence of yellow setae on head and pronotum), while *T. saundersi* are not rarely done about the similarities to *T. cupricolor*, *T. pecirkai* and *T. aurifluus* since the latter three species are readily distinguishable from *T. saundersi* at first glance on the basis of the coloration of body and vestiture (see the differential diagnosis). However, *T. saundersi* actually shows more close affinity to *T. cupricolor*, *T. pecirkai* and *T. aurifluus* than to *T. auricollis* in morphological characters except for the coloration similarities. Therefore, I placed *T. saundersi* in the species-group III together with these three species.

Taxonomic treatment of Trachys cuneiferus. Kurosawa (1959) was originally described *Trachys cuneiferus* as a full-species showing intermediate character states between *T. saundersi* and *T. auricollis* Saunders, 1873. Kurosawa (1959, 1976 c) presumed that *T. cuneiferus* is a F1 hybrid between *T. auricollis* and *T. saundersi* on the basis of the following points: the similarity to *T. auricollis* in the body shape (wedge-shaped); the similarity to *T. saundersi* in the integument coloration, in the patterns of setae, and in the shape of prosternal process; and the two species were also collected together with *T. cuneiferus* at its type locality. Later, Seki (1980) recorded one additional specimen of *T. cuneiferus* from Nagano Prefecture, Honshu, which was identified by Dr. Kurosawa. At the present time, there are only the two specimens of this species including the holotype. In this study, I carefully examined the holotype of *T. cuneiferus* (Figs. 34, 35) and then revealed that the detailed morphological character states of *T. cuneiferus* match well with those of *T. saundersi*, except for the wedge-shaped body. Additionally, I confirmed that the holotype of *T. cuneiferus* is a malformed individual with deformation in the abdomen, especially in the transversely strong dent between ventrites I and II and in the strong distortion of ventrite II (Fig. 35A), as a result the sternal grooves on the ventrites I and II are completely fused. This fact strongly suggests that the wedge-shaped body of the holotype of *T. cuneiferus* is caused by the deformation of abdomen. Furthermore, on the basis of the photograph of the additional specimen of *T. cuneiferus* in figure 1 of Seki (1980), this specimen is rather similar to *T. saundersi* than to the holotype of *T. cuneiferus* because its body shape is not wedge-shaped (narrowly oval body, but the elytra very weakly narrowed posteriorly). Such state of the elytra in Seki's specimen is rarely recognizable in a few specimens of *T. saundersi* examined in this study. Judging from these facts, this study proposes that *T. cuneiferus* is treated as a junior synomym of *T. saundersi*.

Taxonomic treatment of Trachys obscuripennis. See notes of *Trachys minutus*.

Trachys cupricolor Saunders, 1873

[Japanese name: Dôiro-chibi-tamamushi]

(Figs. 25D, 36, 37, 68A)

Trachys cupricolor Saunders, 1873: 521 (type locality: Japan); Lewis, 1879: 15 (catalog); Kerremans, 1885: 157 (catalog); Schönfeldt, 1887: 113 (catalog); Kerremans, 1892 a: 285 (catalog); Lewis, 1893: 338 (in list); Kerremans, 1903: 313 (catalog); Jakobson, 1913: 800 (catalog); Kurosawa, 1950 a: 13 (note, including *Trachys pecirkai* Obenberger); Kurosawa, 1959: 220 (redescription, including *Trachys pecirkai* Obenberger; Japan and China); 1963: 156, pl. 78 (pictorial book, including *Trachys pecirkai* Obenberger); 1976 c: 2 (China removed from distribution; Taiwan); 1985 a: 166 (note); 1985b: 34, pl. 7 (pictorial book); Akiyama & Ohmomo, 1997: 47 (checklist); 2000: 284, pl. 120 (pictorial book); Kubáň, 2006: 419 (Palaearctic catalog); Bellamy, 2008 b: 2478 (World catalog); Ohmomo & Fukutomi, 2013: 166, pl. 52 (pictorial book); Kubáň, 2016: 570 (Palaearctic catalog); Ishiguro & Nishida, 2018: 33, figs. 2, 3 & 6 (aedeagus); Ong & Hattori, 2019: 198, 226 (pictorial book; aedeagus).

Trachys (*Trachys*) *cupricolor*: Obenberger, 1918: 19, 35, 64 (in key; catalog); 1926 b: 661 (catalog); 1937a: 1357 (World catalog).

Trachys cupricollis [sic]: Miwa & Chûjô, 1936: 23 (misspelling of *cupricolor*; synonymized *T. sauteri* under this species, corrected by Obenberger, 1937 a: 1357).

Description. Male and female. Body ovate to narrowly ovate, slightly lowly to moderately convex dorsally (Figs. 36A, B). LB 3.90–4.60 mm (mean 4.25 mm); WB 2.05–2.44 mm (mean 2.25 mm); LB/WB 1.84–1.95 (mean 1.89) (n = 20 for all measurements except terminalia). Habitus as shown in Fig. 25D.

Integument. Head and pronotum golden-bronze, sometimes with faint purplish tints; elytra reddish-copper except for golden-bronze basal and sutural margins, sometimes with faint purplish tints; underside dark-bronze with faint golden-bronze reflections; antennae and legs black, except for femora sometimes with faint purplish tints in ventral side and basal four tarsomeres brownish-black with brown tarsal pads; maxillary palps light brown. Dorsal surface slightly weakly shiny; ventral surface moderately shiny.

Vestiture mainly consisting of white, yellow and black setae. Head clothed with short, recumbent yellow setae, sometimes with two whitish spots on vertex. Pronotum clothed with short, semirecumbent yellow setae mixing with a few white ones, usually with a small naked part on midline. Elytra clothed with short, semirecumbent, white, brownish-yellow and black setae which are arranged on each elytron as follows: 1) white setae irregularly scattering in base part; 2) inconspicuously undulated, interrupted white band just before middle, partly forming a small circle near sutural margin; 3) first white transverse band at apical 1/3, moderately wavy, zigzag-shaped; 4) second white transverse band just behind first one, very weakly wavy, sometimes partly connecting first transvers band; 5) brownish-yellow setae in basal part and along sutural margin; 6) dark brownish-yellow setae in apical part behind second transverse band; and 7) black setae in remaining space. Underside more sparsely setiferous, with fine, recumbent, yellowish to whitish setae, except for prosternum with longer yellowish setae.

Head, when viewed from above, slightly shallowly, arcuately concave on frons which is faintly bisinuate, with oculofrontal margins weakly ridged. Eyes, when viewed from above, broadly visible, moderately convex laterally. Vertex obscurely and coarsely variolate-punctate; frons widely concave, weakly impressed along upper side of midline, both sides of which are weakly swollen, transversely ridged from just above each antennal insertion to inner margin of each eye, with surface faintly punctate; suprantennal pores simply round; clypeus wide (Fig. 36D), without elevated basal margin, WC/LC 1.69–2.42 (mean 2.00), WC/LSC 1.69–2.07 (mean 1.86), deeply arcuately emarginate at apical margin.

Antennae (Fig. 36E) reaching just behind apicolateral angles of pronotum when laid alongside; antennomere I stout claviform, longer than II; II ovate, longer than III; III subrectangular, longer than IV; IV–VI subrectangular, subequal each other in length; VII–X triangular, moderately enlarged; XI subtriangular to sublingulate.

Mandibles with weak, transverse ridge in about middle of each outside. Maxillary palps with oval palpomere IV somewhat longer than wide.

Pronotum widest at base, WP/LP 2.77–3.00 (mean 2.86), BMP/AMP 1.45–1.57 (mean 1.50), narrower than elytra; lateral margins faintly arcuately and slightly weakly narrowed apicad; apicolateral angles nearly right to obtuse, relatively rounded; basolateral angles broadly acute to right; apical margin arcuately emarginate, without median lobe; basal margin trisinuate, with median lobe moderately produced; disk weakly depressed along basal median lobe; surface obscurely variolate-punctate, becoming denser toward apical and basal margins. Scutellar shield very small, subtriangular, glabrous.

Elytra widest at humeri, LE/WE 1.39–1.45 (mean 1.42), LE/LP 4.24–4.61 (mean 4.39); humeral calluses weakly developed; lateral margins subparallel in basal half and weakly constricted behind humeri, and then weakly arcuately convergent to conjointly rounded apices, with moderate serrations in about apical half except apices (Fig. 36C); marginal carinae distinct in thoracic region, indistinctly reaching near apices; sutural margin faintly elevated in apical half; disk occasionally faintly depressed in basal part, constricted behind humeri, weakly swollen in subapical part; surface irregularly and slightly densely punctate, weakly rugulose between punctures in basal half. Lateral part of abdomen narrowly visible in dorsal view; laterosternites I–IV with laterosternal sulci.

Underside. Prosternum (Fig. 36F) rather straight at apical margin which is weakly rimmed; prosternal process slightly slender, strongly constricted between procoxal cavities, with apex broadly rounded at rest; marginal carinae slightly narrowly separated each other at widest part of prosternal process, gently narrowed posteriorly in apical half then gently divergent posteriad; disk rather flattened on median portion, weakly declivous laterad on outside of marginal carinae, with weak elevated protions along procoxal cavities. Hypomera with depressed hypomeral markings large in size, arcuate to subreniform (Fig. 36G). Metaventrite moderately sculptured with large punctures on inside of katepisternal suture and linearly confluent sculptures on outside of the suture. Legs moderately slender; metacoxal plates slightly strongly produced posteriorly at each lateral angle which is broadly acute and rather rounded, with surface coarsely variolate; metatibiae bearing a fringe of spines in apical half of each outer margin, with one long spine in base of the fringe (Fig. 36H); inner tooth of each claw large. Abdominal ventrites with sternal grooves on ventrites I–V; V (Fig. 36I) shallowly emarginate to obtusely subtruncate at apex; surface variolate, in ventrite I with linearly confluent sculptures on median part.

Sexual dimorphism indistinct.

Male terminalia (n = 5 for measurements). Proctiger with a pair of short baculi at base. Sternite IX (Figs. 37A, B) slightly slender, SL/SW 0.79–1.13 (mean 0.93), arcuately emarginate at apical margin, with slightly strongly produced apical angles which are usually clothed with several setae or rarely with a pair of setae. Tegmen (Fig. 37C) slightly wide; parameres PL/PW 1.97–2.13 (mean 2.03), bearing a pair of very short setae on apicolateral margins, with sides which are gently dilated from base to apical half, then strongly arcuately expanded to widest point at apical 1/4, and finally strongly convergent to apices; phallobase PbL/PbW 1.98–2.36 (mean 2.18), about 1/4 length of tegmen. Penis (Fig. 37D) rather slender, PeL/PeW 5.35–5.82 (mean 5.57), slightly shorter than tegmen; dorsal plate with sides which are gradually narrowed from widest point of base to subapical part, and then arcuately convergent apicad, with roundly, faintly produced apex, basally with median struts about 1/3 length of penis; ventral plate membranous, but weakly sclerotized as a linear patch in middle of apical 1/5.

Female terminalia (n = 5 for measurements). Ovipositor (Figs. 37E–G) short; proctiger basally with a pair of long, ventrally curved baculi; coxites transversely subhexagonal, sparsely setiferous on each side of apical margin, ventrally without transverse depression in apical part; styli fan-shaped, with sides dilated apicad, SlL/SlW 1.71–2.68 (mean 2.08), bearing several setae apically; ventral valve sparsely setiferous on each side of subapical part; vagina roundly sack-shaped, weakly expanded dorsally in distal 1/5; spermatheca slender tubular, extremely elongate in length (like spermathecal duct), weakly expanded in apical part, without spermathecal gland.

Differential diagnosis. This species is similar in general appearance to *Trachys pecirkai* Obenberger, 1926, but can be distinguished from *T. pecirkai* by the combination of the following character states: (1) elytra reddish-copper; (2) underside dark-bronze without purplish tints; (3) prosternal marginal carinae more broadly separated each other; (4) frons outline of head more shallowly concave; (5) male parameres with larger lateral expansion being widest at apical 1/4; (6) female spermatheca extremely elongated.

Additionally, this species is similar in general appearance to *T. aurifluus* Solsky, 1875, but differs from *T. aurifluus* as follows: pronotum usually with a small naked part on midline; first and second transverse bands on apical half of elytron more weakly wavy; female styli fan-shaped; and the points mentioned above in (1), (2), (3), (5) and (6).

Specimens examined. Non type material. **Japan**. Honshu — [Tochigi] 1 ex., Nasu, 14.VII.1982, I. Hattori leg. (24-0480140) (NIAES; recorded by Yoshitake *et al*., 2018). [Chiba] 2 ♂♂, Kimitsu-shi, 9.V.2009, K. Odagiri leg. (YTJ). [Tokyo] 1 ex., Nippara, Okutama-chô, 9.VI.1991, T. Nakane leg. (SEHU); 1 ex., Mont Takao, Hachiôji, 8.VI.1913, E. Gallois leg. (SEHU); 4 ♀♀, Mt. Mitake, 15.V.1966, Y. Ishikawa leg. (YTJ); 29 exs., near Takaosan-guchi-eki Station, Takao-chô, Hachiôji-shi, 8.IV.2018, Y. Tamadera leg., captured on *Zelkova serrata* (YTJ); 2 exs., Hikagesawa-rindô, Takao-chô, Hachiôji-shi, 3.V.2016, Y. Tamadera leg., captured on *Zelkova serrata* (YTJ); 3 ♀♀, same locality, 3.V.2016, Y. Tamadera leg., captured on *Zelkova serrata* (YTJ); 6 ♀♀, same locality, 12.V.2017, Y. Tamadera leg., captured on *Zelkova serrata* (YTJ); 1 ♂, 7 ♀♀, same locality, 8.IV.2018, Y. Tamadera leg., captured on *Zelkova serrata* (YTJ); 1 ♀, Uratakao-machi, Hachiôji-shi, 3.V.2016, Y. Tamadera leg., captured on *Zelkova serrata* (YTJ). [Kanagawa] 1 ex., Sano Riv., Fujinomachi, Kanagawa, 13.V.1979, M. Takakuwa leg. (NSMT). [Nagano] 1 ex., near Iiduna-jinja, Shimauchi, Matsumoto-shi, 21.V.2018, Y. Tamadera leg., captured on *Zelkova serrata* (YTJ). [Mie] 1 ex., Mie Univ. Forest, Ichishi-gun, Mie, 14.V.1956, H. Ichihashi leg. (NSMT; recorded by Kurosawa, 1959); 1 ex., Misogi-Vill. Mie Pref., 30.IV.1955, M. Sato leg. (NSMT; recorded by Kurosawa, 1959). [Kyoto] 1 ex., Miyama-chô-Ashiu, Nantan-shi, M. Yoshida leg. (SEHU). Shikoku — [Ehime] 1 ex., Saragamine, Shikoku, 16.V.1954, Toshiro Yano leg. (NSMT; recorded by Kurosawa, 1959). Kyushu — [Fukuoka] 1 ♀, Masubuchi Dam, Kagumeyoshi, Kogura-minami-ku, Kitakyushu-shi, 20.VI.2001, H. Fukutomi leg (HFCH).

Distributions in Japan. Honshu, Shikoku, and Kyushu.

Other distributions. Taiwan.

Adult food plant. *Zelkova serrata* (Thunb.) Makino [Ulmaceae; Japanese name: Keyaki] (Kurosawa, 1959; this study).

Host plant. Ulmaceae: *Zelkova serrata* (Thunb.) Makino [Japanese name: Keyaki] (Kurosawa, 1959 — adult record?; confirmed by this study) Formal records for larval food plants are absent, but *Zelkova serrata* is probably a host of *Trachys cupricolor* in Japan since adults of this species were generally captured on leaves of this plant and an estimated mine and larva of this species is founded in the field. In addition, I confirmed that adults of this species lay eggs on the leaves of this plant under rearing conditions.

Leaf-mining habit. An estimated mine of *Trachys cupricolor* was found on *Zelkova serrata* by this study (Fig. 68A) on the basis of collected larva that is differentiated from the other congener, *T. yanoi*, also associated with this plant by slightly greenish body color, etc.: the mine was of the full-depth type and formed a large, irregularly elongate blotch occurring somewhat along leaf-margin; eggs, which were blackish (remaining eggshell) or slightly yellowish (under rearing conditions) and not covered on powdery substances, were laid singly on the adaxial surface of the leaf blade along lateral margin (Fig. 68A) or near the apex (under rearing conditions); hatched larvae left thread-like frass inside the mines.

Note. In Japan, *Trachys cupricolor* is often sympatrically distributed with *T. yanoi*, which is also associated with *Zelkova serrata*, but is readily distinguished from the latter by the presence of the elevated protions along procoxal cavities and the reddish-copper elytra. *T. yanoi* is, however, occasionally discolored into reddish to purplish-copper after hibernation, so that we need to be careful for misidentification caused by such discolored specimens (see also the section of *T. yanoi*).

Trachys pecirkai Obenberger, 1926
[Japanese name: Kita-dôiro-chibi-tamamushi]
(Figs. 25E, 38–40, 64D, 68B)

Trachys (*Trachys*) *pecirkai* Obenberger, 1926 a: 100 (type locality: "Sibiria: Lac Baikal"); 1926 b: 663 (catalog); 1937 a: 1368 (World catalog).

Trachys pecirkai: Kurosawa, 1976 e: 7 (correction of Kurosawa, 1976 d); Akiyama, 1978: 7 (Tsushima Is.); Kurosawa, 1985 a: 166 (Japan, Korea, Siberia, and China); 1985 b: 35, pl. 7 (pictorial book); Akiyama & Ohmomo, 1997: 48 (checklist); 2000: 284, pl. 120 (pictorial book); Kubáň, 2006: 420 (Palaearctic catalog); Bellamy, 2008 b: 2508 (World catalog); Ohmomo & Fukutomi, 2013: 166, pl. 52 (pictorial book); Kubáň, 2016: 572 (Palaearctic catalog); Ishiguro & Nishida, 2018: 33, figs. 2, 3 & 6 (aedeagus).

Trachys (*Trachys*) *semenovi* Obenberger, 1929 b: 126 (type locality: "China: Ning Po"); Obenberger, 1937 a: 1379 (World catalog); Kurosawa, 1976 d: 2 (Japan). Synonymized under *T. pecirkai* by Kurosawa, 1985 a: 166.

Trachys (*Trachys*) *amuricola* Obenberger, 1929 c: 11 (type locality: "Siberia or: Amur"); Théry, 1942 b: 271 (as synonym of *Trachys aurifluus* Solsky). Synonymized under *T. pecirkai* by Kurosawa, 1985 a: 166. Justified emendation: *T. amuricolus*, according to ICZN (2009).

Trachys cupricolor [part]: Kurosawa, 1959: 243 (specimens from Hokkaido, Yamagata, and Fukushima).

Description. Male and female. Body ovate to narrowly ovate, moderately convex dorsally (Figs. 39A, B). LB 3.62–4.35 mm (mean 4.04 mm); WB 1.95–2.42 mm (mean 2.20 mm); LB/WB 1.77–1.90 (mean 1.83) (n = 20 for all measurements except terminalia). Habitus as shown in Figs. 25E, 38.

Integument. Head and pronotum dark golden-bronze, in the former darker, sometimes with purplish tints; elytra dark-purple to bronzy-purple, rarely being reddish, in basal part and apical 1/5 becoming lighter, sometimes with weak golden-bronze tints along basal and sutural margins; underside bronze with weak purplish tints; antennae and legs black, except for femora with faint bronzy to purplish tints in ventral side and basal four tarsomeres brownish-black with brown tarsal pads; maxillary palps light-brown. Dorsal surface slightly weakly shiny; ventral surface moderately shiny.

Vestiture mainly consisting of white, yellow and black setae. Head clothed with short, recumbent, yellow to pale-yellow setae; head setae rarely being whitish. Pronotum clothed with short, semirecumbent, yellow setae mixing with a few white ones, usually with a small naked part on midline; pronotal setae rarely being whitish. Elytra clothed with short, semirecumbent, white, brownish-yellow and black setae which are generally arranged on each elytron as in *Trachys cupricolor*, but white patterns of setae variable as shown in Fig. 38. Underside more sparsely setiferous, with fine, recumbent whitish setae.

Head, when viewed from above, arcuately, more deeply concave on frons, with oculofrontal margins ridged; elytra slightly more strongly developed in humeral calluses, with slightly more strong serrations in lateral margins (Fig. 39C); prosternum (Fig. 39F) with marginal carinae more narrowly separated each other at widest part of prosternal process, with disk strongly declivous on outside of marginal carinae; ratios of body parts as follows: WC/LC 1.49–2.04 (mean 1.71), WC/LSC 1.44–2.00 (mean 1.67), WP/LP 2.74–3.05 (mean 2.88), BMP/AMP 1.50–1.63 (mean 1.58), LE/WE 1.30–1.41 (mean 1.36), LE/LP 4.05–4.58 (mean 4.33). In external structures, otherwise practically as in *Trachys cupricolor*, except for structures of terminalia.

Male terminalia (n = 5 for measurements). Proctiger with a pair of short baculi at base. Sternite IX (Fig. 40A) slightly slender, SL/SW 0.77–1.20 (mean 1.00), deeply arcuately emarginate at apical margin, with strongly produced apical angles which are clothed with several setae. Tegmen (Figs. 40B, C) rather slender, weakly variable in shape of parameres; parameres PL/PW 1.71–2.70 (mean 2.24), usually without setae on apicolateral margins, with sides which are subparallel or gently dilated from base to beyond middle, then usually expanded into somewhat angular shape to widest point of apical 1/5 but the expansion rarely being rounded, and finally strongly convergent to apices; phallobase PbL/PbW 2.20–2.68 (mean 2.47), about 1/4 length of tegmen. Penis

(Fig. 40D) rather slender, PeL/PeW 4.49–6.00 (mean 5.37), slightly shorter than tegmen; dorsal plate with sides which are gradually narrowed from widest point of base to subapical part, and then arcuately convergent apicad, with roundly, faintly produced apex, basally with median struts about 1/3 length of penis; ventral plate membranous, but weakly sclerotized as a linear patch in middle of apical 1/5.

Female terminalia (n = 4 for measurements). Ovipositor (Figs. 40E–G) short; proctiger basally with a pair of long, ventrally curved baculi; coxites transversely subreniform to subhexagonal, sparsely setiferous on each side of apical margin, ventrally without transverse depression in apical part; styli fan-shaped, with sides dilated apicad, SlL/SlW 2.08–2.29 (mean 2.21), bearing several setae apically; ventral valve sparsely setiferous on each side of subapical part; vagina sack-shaped (under incompletely inflated state), expanded dorsally in middle; spermatheca slender tubular, long in length, widest in apical part, without spermathecal gland.

Differential diagnosis. This species is resemblance to *Trachys aurifluus* in the coloration of body and vestiture, but can be distinguished from *T. aurifluus* by the following character states: (1) frons outline of head usually more deeply concave; (2) pronotum usually with a small naked part on midline; (3) white transverse bands on apical half of elytra more weakly wavy; (4) underside bronze with purplish tints; (5) male parameres with slightly angulate or arcuate lateral expansion being widest at apical 1/5; (6) female styli fan-shaped; and (7) spermatheca much slenderer.

Additionally, this species is similar to *T. cupricolor*, especially in the weakly wavy first and second transverse bands on the apical half of elytron and the expanded parameres in apical half, but differs from *T. cupricolor* as follows: elytra dark-purple; male parameres with smaller lateral expansion; female spermatheca much shorter (not extremely elongated); and the points mentioned above in (1) and (4).

Specimens examined. Non type material. **Japan**. Hokkaido — 1 ex., Hokkaido, 25.IX.1931, H. Kôno leg. (NSMT); 1 ex., Maruyama, Sapporo, 1.VI.1942, no collector name (NSMT); 1 ex., Sapporo, 29.VI.1941, Y. Nishijima leg. (NSMT; recorded by Kurosawa, 1959 as *T. cupricolor*); 1 ex., Nopporo, 9.X.1931, K. Igarashi leg. (NSMT; recorded by Kurosawa, 1959 as *T. cupricolor*); 1 ex., 東川町江御 (裏面：北海道上川), 22.VI.1987, S. Araki leg. (NSMT). Honshu — [Fukushima] 1 ex., Tateiwa-mura, Minami-aizu-chô, 20–21.V.1999, H. Takizawa leg. (SEHU); 1 ex., near Ôkurakawa-hachi, Wakamiya, Inawashiro-machi, Yama-gun, 16.VIII.2018, Y. Tamadera leg. (YTJ); 1 ♂, Masuzawa, Tateiwa-mura, Minamiaizu-gun, 10.VI.2000, H. Fukutomi leg. (YTJ). [Tochigi] 1 ♀, Dorobu, Nikko-shi, 15.VII.2018, K. Matsumoto leg. (YTJ). [Gunma] 1 ex., Kawafuru, 30.V–2.VI.1999, H. Takizawa leg. (SEHU); 2 ♀♀, near Nurigawa River, Hanasaku, Katashina-mura, Tone-gun, 13.VII.2019, Y. Tamadera leg. (YTJ). [Toyko] 1 ♀, Kotsu-gawa river, Shimo-onkata, Hachiôji-shi, 12.V.2001,M. Kaneko leg. (YTJ). Kyushu — [Ôita] 1 ♂, Kyûsuikei, Kokonoe-machi, Kusu-gun, 17.VI.2001, K. Mori leg. (YTJ). Tsushima Is. (Nagasaki) — 1 ex., Mt. Ontake, 1.VIII.1977, K Matsuda leg. (NSMT; recorded by Akiyama, 1978); 1 ♂, Saho, Toyotama-machi, Tsushima-shi, 3.VI.2019, Y. Tsutsumiuchi leg. (YTJ). **Russia**. 1 ex., USSR, Primorsky reg., Ussurian reserve, 17.IX.1974, Kuznetsov leg. (NSMT). **South Korea**. 1 ex., Dang-Sa-Do I., Jeon-Nan, S. Korea, 23.V.1984, S. M. Lee leg. (NSMT). **China**. 1 ex., Manchuria, 23.VI.1940, S. Asahina leg. (SEHU); 2 exs., "Eihôchin, Funang, C.-China" (Hunan, Central China), K. Shirahata leg. (NSMT; recorded by Kurosawa, 1959 in notes of *T. cupricolor*).

Distributions in Japan. Hokkaido Honshu, Shikoku, Kyushu, and Tsushima Is.

Other distributions. China, South Korea, and Russia.

Adult food plant. Same as in the larvae mentioned below. In China, this species was captured on leaves of "*Ulmus* sp." (Kurosawa, 1959).

Host plant. Ulmaceae: *Ulmus davidiana* Planch. var. *japonica* (Rehder) Nakai [Japanese name: Harunire] (Kurosawa, 1959 for *Trachys cupricolor* incl. *T. pecirkai*; Kurosawa, 1985a — adult record?; Takahashi, 2008; confirmed by this study) in Japan.

Leaf-mining habit. Mines of *Trachys pecirkai* were found on *Ulmus davidiana* var. *japonica* by this study (Figs. 64D, 68B): each mine was of the full-depth type and formed a large, elongate blotch occurring usually along leaf-margin; when full-grown, it occupied more than an half of whole the leaf blade; eggs, which were pale grayish-yellow (remaining eggshell) and not covered on powdery substances, were laid singly on the adaxial surface of the leaf blade near latero-basal margin; hatched larvae left thread-like frass inside the mines; adults were usually emerged from the adaxial surface of the leaves with oval adult exit holes.

Note. One of the specimens collected on Tsushima Is., western Japan, in 2019 (Fig. 38E) shows some morphological differences from the typical character states of *Trachys pecirkai* in having the lager white patterns of elytral setae, the relatively wide body (LB/WB 1.80), the relatively shorter male parameres (PL/PW 1.71) and penis (PeL/PeW 4.49), and the parameres bearing a pair of distinct setae on apico-lateral part. In addition, this specimen was captured on leaves of *Ulmus parvifolia* Jacq. (Ulmaceae) [Japanese name: Akinire], which have never been recorded as an adult food plant of *T. pecirkai*, as well as a host. However, decisive differences between the specimen and *T. pecirkai* seems unrecognizable at the present time. On the other hand, the remaining one collected on Tsushima Is. in 1977 (recorded by Akiyama, 1978) shows the typical character states of *T. pecirkai* (no examination of terminalia). Thus, I consider that *T. pecirkai* is definitely distributed in Tsushima Is. based on the latter specimen and that the former specimen can be regarded as *T. pecirkai*. More specimens from Tsushima Is. are needed to determine their true identities.

Trachys aurifluus Solsky, 1875
[Japanese name: Shinanoki-chibi-tamamushi]
(Figs. 31F, 41, 42, 64E, F, 68C)

Trachys auriflua Solsky, 1875: 280 (type locality: “embouchures de l’Oussouri, dans la Sibérie orientale”); Kerremans, 1885: 157 (catalog); Marseul, 1889: 302 (redescription); Kerremans, 1892 a: 284 (catalog); Heyden, 1893: 119 (list); Kerremans, 1903: 312 (catalog); Jakobson, 1913: 800 (catalog); Théry, 1930: 33 (note); Kurosawa, 1976 c: 2 (note; Japan, North Korea, and China (Manchuria: Erzendjanzsy)); 1985 a: 166 (note); 1985 b: 34, pl. 7 (pictorial book); Volkovitsh & Alexeev, 1988: 45 (list); Akiyama & Ohmomo, 1997: 47 (checklist); 2000: 283, pl. 120 (pictorial book); Kubáň, 2006: 419 (Palaearctic catalog).

Trachys (*Trachys*) *auriflua*: Obenberger, 1918: 68 (in catalog); 1926 b: 663 (catalog); Obenberger, 1937 a: 1355 (World catalog).

Trachys aurifluus [justified emendation, according to ICZN (2009)]: Théry, 1942 b: 271 (note); Bellamy, 2008 b: 2470 (World catalog); Ohmomo & Fukutomi, 2013: 166, pl. 52 (pictorial book); Kubáň, 2016: 570 (Palaearctic catalog); Ishiguro & Nishida, 2018: 33, figs. 2, 3 & 6 (aedeagus).

Brachys orichalcea Kiesenwetter, 1879 [in Kraatz & Kiesenwetter (1879)]: 255 (type locality: Amur, Russia); Kerremans, 1885: 156 (catalog); 1892 a: 291 (catalog); 1903: 326 (catalog); Obenberger, 1926 b: 663 (catalog); 1928 b: 111 (note); 1928 a: 46 (note); 1928 c: 25 (note). Synonymized under *T. aurifluus* by Obenberger, 1937a: 1356.

Brachys aurichalcea [sic]: Marseul, 1889: 303 (misspelling of *orichalcea*).

Trachys orichalcea: Jakobson, 1913: 800 (transferred from *Brachys*, without reason); Théry, 1927: 39 (transferred from *Brachys*, without reason); 1930: 33 (with reason of transfer). Justified emendation: *T. orichalceus*, according to ICZN (2009).

Trachys tiliae Kurosawa, 1959: 245 (type locality: “Yunohana, Minami-Aizu-gun, Fukuhima Pref.”, Japan); 1963: 156, pl. 78 (pictorial book). Synonymized under *T. aurifluus* by Kurosawa, 1985 a: 166.

Trachys sp.: Yano, 1952: 40 (in host list, *Tilia japonica* and *Ti. maximowicziana* (= *miyabei*), based on a personal letter from Kurosawa on 8 Nov. 1950).

Description. Male and female. Body ovate to narrowly ovate, moderately convex dorsally (Figs. 41A, B). LB 4.26–5.08 mm (mean 4.71 mm); WB 2.22–2.71 mm (mean 2.49 mm); LB/WB 1.86–1.98 (mean 1.90) (n = 20 for all measurements except terminalia). Habitus as shown in Fig. 25F.

Integument. Head and pronotum golden-bronze; elytra dark-purple, in basal part and apical part becoming lighter, with weak golden-bronze tints along basal margin; underside dark-purple, sometimes with faint bluish tints; antennae black with weak golden-bronze reflections; maxillary palps light-brown; legs black, except for femora with faint purplish tints in ventral side and basal four tarsomeres brown to light-brown with brown tarsal pads. Dorsal surface slightly weakly shiny; ventral surface moderately shiny.

Vestiture mainly consisting of white, yellow and black setae. Head clothed with short, recumbent, yellow to pale-yellow setae. Pronotum clothed with short, semirecumbent, yellow to brownish-yellow setae. Elytra clothed with short, semirecumbent, white, brownish-yellow and black setae which are arranged on each elytron as follows: 1) white setae irregularly scattering in basal part; 2) inconspicuously undulated, interrupted white band just before middle, partly forming a small circle near sutural margin; 3) first white transverse band at apical 1/3, strongly wavy, zigzag-shaped; 4) second white transverse band just behind first one, moderately wavy, zigzag-shaped; 5) brownish-yellow setae in basal 1/5; 6) dark brownish-yellow setae in apical part behind second transverse band; and 7) black setae in remaining space. Underside more sparsely setiferous, with fine, recumbent whitish setae, except for prosternum with longer yellowish setae.

Head, when viewed from above, moderately arcuately concave on frons, with oculofrontal margins ridged. Eyes, when viewed from above, broadly visible, moderately convex laterally. Vertex obscurely and coarsely variolate-punctate; frons widely concave, weakly impressed along upper side of midline, transversely ridged from just above each antennal insertion to inner margin of each eye, with surface faintly variolate-punctate; suprantennal pores simply round; clypeus wide (Fig. 41D), with weak elevated basal margin or without it, WC/LC 1.47–2.17 (mean 1.74), WC/LSC 1.47–1.90 (mean 1.69), deeply arcuately emarginate at apical margin.

Antennae (Fig. 41E) reaching just behind apicolateral angles of pronotum when laid alongside; antennomere I stout claviform, longer than II; II ovate, longer than III; III subrectangular, longer than IV; IV–VI subrectangular, subequal each other in length; VII–X triangular, moderately enlarged; XI subtriangular to sublingulate.

Mandibles with strong, transverse ridge in about middle of each outside. Maxillary palps with oval palpomere IV somewhat longer than wide.

Pronotum widest at base, WP/LP 2.72–3.04 (mean 2.89), BMP/AMP 1.53–1.63 (mean 1.58), narrower than elytra; lateral margins faintly arcuately and moderately narrowed apicad; apicolateral angles obtuse; basolateral angles broadly acute; apical margin arcuately emarginate, without median lobe; basal margin trisinuate, with median lobe moderately produced; disk faintly depressed along basal median lobe; surface obscurely variolate-punctate, becoming denser toward apical and basal margins. Scutellar shield very small, subtriangular, glabrous.

Elytra widest at humeri, LE/WE 1.38–1.48 (mean 1.42), LE/LP 4.18–4.75 (mean 4.45); humeral calluses slightly weakly developed; lateral margins subparallel in basal half and weakly constricted between humeri and middle point, and then weakly arcuately convergent to conjointly rounded apices, with slightly strong serrations in about apical half except apices; (Fig. 41C); marginal carinae distinct in thoracic region, indistinctly reaching near apices; sutural margin faintly elevated in apical half; disk faintly depressed in basal part, constricted behind humeri, weakly swollen in subapical part; surface irregularly and slightly densely punctate, weakly rugulose between punctures in basal 1/3. Lateral part of abdomen narrowly visible in dorsal view; laterosternites I–IV with laterosternal sulci.

Underside. Prosternum (Fig. 41F) rather straight at apical margin which is weakly rimmed; prosternal process slightly slender, constricted between procoxa, with apex broadly rounded at rest; marginal carinae narrowly separated each other at widest part of prosternal process, gently narrowed posteriorly in about apical half then gently divergent posteriad; disk rather flattened on median portion, strongly declivous laterad on outside of marginal carinae, with weak elevated protions along procoxal cavities. Hypomera with depressed hypomeral markings large in size, subreniform to rounded subtrapezoidal (Fig. 41G). Metaventrite densely sculptured with large punctures on inside of katepisternal suture and moderately sculptured with linearly confluent sculptures on outside of the suture. Legs moderately slender; metacoxal plates slightly strongly produced posteriorly at each lateral angle which is slightly sharply acute and slightly rounded, with surface coarsely variolate; metatibiae bearing a fringe of spines in apical half of each outer margin, without one long spine in base of the fringe (Fig. 41H); inner tooth of each claw large. Abdominal ventrites with sternal grooves on ventrites I–V; V (Fig. 41I) shallowly emarginate to obtusely subtruncate at apex; surface variolate, in ventrite I with linearly confluent sculptures on median part.

Sexual dimorphism indistinct.

Male terminalia (n = 5 for measurements). Proctiger with a pair of short baculi at base. Sternite IX (Fig. 42A) slightly slender, SL/SW 0.93–1.09 (mean 1.02), arcuately emarginate at apical margin, bearing several setae on each side of apical margin. Tegmen (Fig. 42B) wide; parameres PL/PW 1.82–2.05 (mean 1.95), two pairs of setae on apicolateral margins, with sides which are dilated from base to widest point at apical 1/4, then rounded to subapical part, and finally strongly convergent to apices; phallobase PbL/PbW 2.32–2.59 (mean 2.46), about 1/3 length of tegmen. Penis (Fig. 42C) wide, PeL/PeW 4.53–5.36 (mean 4.95), shorter than tegmen; dorsal plate with sides which are gradually narrowed from widest point of base to subapical part, and then arcuately convergent apicad, with roundly, faintly produced apex, basally with median struts about 1/3 length of penis; ventral plate membranous, but weakly sclerotized as a linear patch in middle of apical 1/4.

Female terminalia (n = 5 for measurements). Ovipositor (Figs. 42D–F) short; proctiger basally with a pair of long, ventrally curved baculi; coxites transversely subhexagonal, sparsely setiferous on each side of apical margin, ventrally without transverse depression in apical part; styli lingulate, wide, with sides subparallel, SlL/SlW 1.90–2.55 (mean 2.23), bearing several setae apically; ventral valve sparsely setiferous on each side of subapical part; vagina roundly sack-shaped (under incompletely inflated state), moderately expanded dorsally at distal 1/3; spermatheca moderately wide tubular, somewhat claviform, moderate in length, widest near apex, without spermathecal gland.

Differential diagnosis. This species is similar in general appearance to *Trachys pecirkai* and *T. cupricolor*, but can be easily distinguished from them by the combination of the following character states: pronotum always without a small naked part on midline; first and second transverse bands on apical half of elytron more strongly wavy; underside dark-purple; male parameres gently dilated from base to widest point at apical 1/4; female spermatheca slightly claviform and wider.

Specimens examined. Type material. Holotype of *Trachys tiliae* Kurosawa, 1959: ♂ (based on Kurosawa, 1959; no dissected terminalia), "YUNOHANA / MINAMI-AIZU / FUKUSHIMA PREF. / 14.VI.1947 / Y. K." (NSMT). Paratypes (part) of *T. tiliae*: 2 exs., Naderayama, nr. Yonezawa, 11.V.1941, Y. Kurosawa leg. (NSNM).

Non type material. **Japan**. Hokkaido — 2 ♂♂, 1 ex., Kaitorima, Taisei-ku, Setana-chô, 10–11.VI.2020, A. Kashizaki leg., captured on *Tilia japonica* (YTJ). Honshu — [Yamagata] 3 exs., Mt. Nadera-yama, Yonezawa-shi, 11.V.1941, F. Yano leg. (SEHU). [Fukushima] 1 ex., Yunohana, Minami-aizu, 8.VII.1948, T. Nakane leg. (SEHU). [Saitama] 2 ♀♀, 2 exs., Mt. Futago-yama-Higashi-dake, Fujikura, Ogano-machi, Chichibu-gun, 15.V.2018, Y. Tamadera leg., captured on *Tilia japonica* (YTJ); 15.V.2018,

Y. Tamadera leg.; 2 ♂♂, 3 ♀♀, 15 exs., Mt. Futago-yama-Nishi-dake, Fujikura, Ogano-machi, Chichibu-gun, 16.V.2018, Y. Tamadera leg., captured on *Tilia japonica* (YTJ). [Ishikawa] 1 ♀, Iwama, Ozoe, Hakusan-shi, 15.VI. 2016, H. Fukutomi leg. (YTJ). [Shizuoka] 1 ♂, Misakubo-chô, Iwata-gun, 22.IX.2001, H. Fukutomi leg., captured on *Tilia japonica* (YTJ). **Russia**. 1 ex., USSR, Far East, Ussuri, 16.VI.1929, Philippov leg. (NSMT). **China**. 1 ex., "Ynichnan, Manchoukuo, May.21.1939, T. Tsuchiyama leg." (NSMT).

Distributions in Japan. Hokkaido and Honshu.

Other distributions. China, North Korea, and Russia.

Adult food plants. Same as in the larvae mentioned below.

Host plants. Malvaceae: *Tilia japonica* (Miq.) Simonk. [Japanese name: Shinanoki] (Kurosawa, 1959 — adult record?; confirmed by this study) and *Ti. maximowicziana* Shiras. [Japanese name: Ôba-bodaiju] (Kurosawa, 1959 — adult record?) in Japan.

Leaf mining habit. Mines of *Trachys aurifluus* were found on *Tilia japonica* by this study (Figs. 64E, 68C): each mine was of the full-depth type and formed a large, elongate blotch; usually, it first ran from the middle of leaf-margin to the base or apex of the leaf blade along margin, then bended inward, and finally made several U-turns to efficiently feed on limited food resources; when full-grown, it occupied more than an half of whole the leaf blade; eggs, which were black (both eggshell and remaining one) and not covered on powdery substances, were laid singly on the adaxial surface of the leaf blade along near middle of leaf-margin (Fig. 64F); hatched larvae left granular to thread-like frass inside the mines; adults were usually emerged from the adaxial surface of the leaves with oval adult exit holes.

Notes. *Trachys aurifluus* is known as the largest species in size among the Japanese congeners.

Trachys aurifluus has been considered to prefer *Ti. maximowicziana* to *Ti. japonica* as hosts in Honshu, Japan by Kurosawa (1976 c) and Ohmomo & Fukutomi (2013). In Yamagata Prefecture, Honshu, this species was frequently collected on the former plant (Sugiura & Koseki, 2005). However, *T. aurifluus* from Hokkaido, northern Japan are collected only on *Ti. japonica* (personal communication with A. Kashizaki) even though this Island is also included the distribution area of *Ti. maximowicziana*. Because of the lack of biological information due to the uncommonness of *T. aurifluus* in Japan, it seems that our understanding of the preferred host of this species is actually still limited.

Group IV (reitteri)

(Fig. 25G)

Species included. *Trachys reitteri* Obenberger, 1930.

Diagnosis. Body ovate type. Apical margin of pronotum with small median lobe. Elytra with serrate lateral margins; elytral vestiture with transverse bands consisting of unicolor setae in apical half of each elytron, without tufts consisting of erect setae. Prosternum more or less rimmed along apical margin which is not lobed; prosternal disk without elevated portions along procoxal cavities. Abdominal ventrites with sternal grooves on ventrite II–V. Female coxites ventrally without transverse depression in apical part.

Trachys reitteri Obenberger, 1930

[Japanese name: Mame-chibi-tamamushi]

(Figs. 25G, 43A–C, 44, 45, 65A, 69A)

Trachys (*Trachys*) *reitteri* Obenberger, 1930: 114 (type locality: "Korea: Čemulpo, Soeul", South Korea); Miwa & Chûjô, 1936: 25 (catalog; Japanese name: Raiteru-chibi-tamamushi); Obenberger, 1937: 1378 (World catalog).

Trachys reitteri: Kurosawa, 1976 d: 1 (note); 1985 a: 166 (note); 1985 b: 34, pl. 7 (pictorial book); Akiyama & Ohmomo, 1997: 47 (checklist); 2000: 285, pl. 120 (pictorial book); Kubáň, 2006: 419 (Palaearctic catalog); Bellamy, 2008 b: 2515 (World catalog); Ohmomo & Fukutomi, 2013: 167, pl. 52 (pictorial book); Lan & Ohmomo, 2015: 106 (Taiwan); Kubáň, 2016: 573 (Palaearctic catalog); Ishiguro & Nishida, 2018: 33, figs. 2, 3 & 6 (aedeagus); Peng, 2022 a: 270 (Hunan, China).

Trachys falcatae Kurosawa, 1959: 223 (type locality: "Sashi, Karatsu City, Saga Pref., Kyûshû", Japan); 1963: 155, pl. 78 (in pictorial book). Synonymized under *T. reitteri* by Kurosawa, 1985 a: 166.

Trachys sp. of *Falcata japonica*: Yano, 1952: 31 (immature stages).

Trachys lushanensis Peng, 2021 c: 325 (type locality: "Shimenjia, 1000 m, Mt. Lushan, 29°10'N 114°66'E, Jiujiang, Jiangxi, China"). **Syn. nov.**

Description. Male and female. Body ovate to narrowly ovate, moderately convex dorsally (Figs. 44A, B). LB 2.61–3.25 mm (mean 2.98 mm); WB 1.42–1.80 mm (mean 1.61 mm); LB/WB 1.81–1.90 (mean 1.85) (n = 20 for all measurements except terminalia). Habitus as shown in Figs. 25G, 43A–C.

Integument mainly black with weak golden-bronze reflections; maxillary palps and basal four tarsomeres light-brown. Dorsal and ventral surfaces moderately shiny.

Vestiture mainly consisting of white, yellow and black setae; yellow setae rarely being pale-yellow. Head clothed with short, recumbent yellow setae. Pronotum clothed with short, semirecumbent, white, yellow and black setae which are generally arranged as follows: 1) four, inconspicuous, black round patches across middle; 2) yellow setae in remaining space, sometimes with some white spots. Elytra clothed with short, semirecumbent, white, yellow and black setae which are arranged on each elytron as follows: 1) white setae irregularly scattering in basal part; 2) inconspicuously undulated, interrupted white band just before middle, but rarely absent; 3) first white transverse band at apical 1/3, moderately wavy, zigzag-shaped, weakly interrupted near middle; 4) second white transverse band at subapical part, faintly wavy, weakly interrupted near middle; 5) yellow setae slightly reticulately scattering in basal 2/3, around two transverse bands, in apical part, and along sutural margin; and 6) black setae in remaining space. Underside more sparsely setiferous, with fine, recumbent, pale-yellowish to whitish setae.

Head, when viewed from above, moderately subtriangularly concave on frons, with oculofrontal margins ridged. Eyes, when viewed from above, narrowly visible, weakly convex laterally. Vertex obscurely and coarsely variolate-punctate; frons widely concave, weakly impressed along upper side of midline, transversely ridged from just above each antennal insertion to inner margin of each eye, with surface faintly variolate-punctate; suprantennal pores simply round; clypeus narrow to slightly wide (Fig. 44D), with weak elevated basal margin or without it, WC/LC 1.35–1.86 (mean 1.53), WC/LSC 1.29–1.6 (mean 1.42), deeply arcuately emarginate at apical margin.

Antennae (Fig. 44E) reaching just behind apicolateral angles of pronotum when laid alongside; antennomere I stout claviform, longer than II; II ovate, longer than III; III subrectangular, slightly longer than IV; IV–VI subrectangular, subequal each other in length; VII–X triangular, moderately enlarged; XI subtriangular to sublingulate.

Mandibles without transverse ridge in middle of each outside. Maxillary palps with oval palpomere IV somewhat longer than wide.

Pronotum widest at base, WP/LP 2.65–2.89 (mean 2.75), BMP/AMP 1.50–1.64 (mean 1.58), narrower than elytra; lateral margins straightly to weakly arcuately and moderately narrowed apicad; apicolateral angles obtuse; basolateral angles broadly acute; apical margin bisinuately shallowly emarginate, with small median lobe; basal margin trisinuate, with moderately produced median lobe which is arcuately truncate along scutellar shield at rest ; disk weakly depressed along lateral margins, faintly depressed along basal median lobe or not; surface rather uniformly and densely variolate-punctate. Scutellar shield moderately small, but relatively large in *Trachys*, triangular, glabrous.

Elytra widest at humeri, LE/WE 1.31–1.41 (mean 1.37), LE/LP 3.77–4.21 (mean 3.98); humeral calluses weakly developed; lateral margins subparallel in basal half and faintly constricted between humeri and middle point, and then weakly arcuately convergent to conjointly rounded apices, with very weak serrations in about apical 1/3 except apices (Fig. 44C); marginal carinae distinct in thoracic region, indistinctly reaching near apices; sutural margin faintly elevated in apical 1/3; disk weakly depressed in basal part, constricted behind humeri; surface irregularly and coarsely punctate. Lateral part of abdomen almost invisible in dorsal view; laterosternites I–IV with laterosternal sulci.

Underside. Prosternum (Fig. 44F) rather straight at apical margin which is weakly rimmed; prosternal process clearly wide, subparallel-sided or faintly constricted between procoxa, with apex broadly rounded at rest; marginal carinae widely separated each other at widest part of prosternal process, subparallel but often weakly narrowed at middle; disk weakly swollen on median portion in prosternal process, weakly declivous laterad on outside of marginal carinae, without elevated protions along procoxal cavities. Hypomera with depressed hypomeral markings semicircular (Fig. 44G). Metaventrite moderately sculptured with large punctures on inside of katepisternal suture and with linearly confluent sculptures on outside of the suture, with rather smooth area along outside of the suture. Legs moderately slender; metacoxal plates weakly produced posteriorly at each lateral angle which is broadly acute, with surface coarsely variolate; mesotibiae (Fig. 44H) with short, robust semierect spines on subapical part of each inner margin in both sexes; metatibiae bearing a fringe of spines in apical half of each outer margin, with one long spine in base of the fringe (Fig. 44I); inner tooth of each claw large. Abdominal ventrites with sternal grooves on ventrites II–V; V (Fig. 44J) rounded or obtusely subtruncate at apex; surface variolate, in ventrite I with linearly confluent sculptures on median part.

Sexual dimorphism indistinct.

Male terminalia (n = 5 for measurements). Proctiger with a pair of short baculi at base. Sternite IX (Fig. 45A) wide, SL/SW 0.87–0.95 (mean 0.91), arcuately emarginate at apical margin, bearing several setae on each side of apical margin. Tegmen (Figs. 45B, C) wide; parameres PL/PW 2.07–2.22 (mean 2.15), sparsely setiferous on apicolateral margins, with sides which are gently dilated from base to apical half, then weakly arcuately and more strongly dilated to widest subapical part, and finally strongly convergent to apices; phallobase PbL/PbW 2.10–2.56 (mean 2.34), about 1/4 length of tegmen. Penis (Fig. 45D) wide, PeL/PeW 4.19–4.56 (mean 4.42), shorter than tegmen; dorsal plate weakly sinuate on sides which are faintly arcuately and gradually narrowed from widest point of base to apical half, then more weakly narrowed to subapical part, and finally weakly arcuately convergent apicad, with round apex, basally with median struts about 1/3 length of penis; ventral plate membranous, but weakly sclerotized as a linear patch in middle of subapical part.

Female terminalia (n = 4 for measurements). Ovipositor (Figs. 45E–G) short; proctiger basally with a pair of long, ventrally curved baculi; coxites transversely subtrapezoidal, sparsely setiferous on each side of apical margin, ventrally without transverse depression in apical part; styli subtrapezoidal, rather slender, with sides subparallel, SlL/SlW 2.00–2.80 (mean 2.43), bearing several setae apically; ventral valve sparsely setiferous on each side of subapical part; vagina elongately sack-shaped, moderately expanded dorsally in middle; spermatheca slender tubular, rather short in length, widest in apical half, without spermathecal gland.

Differential diagnosis. This species is easily distinguished from Japanese other congeners by the combination of the very weakly serrate lateral margins of the elytra and the absence of the sternal grooves on the abdominal ventrite I.

In addition, this species may be slightly related to *Trachys toykoensis* by the combination of the triangularly concaved frons outline of the head, the serrate lateral margins of the elytra, the absence of the swelling on the subapical part of the elytral disk, and the light-brown basal four tarsomeres on each leg, but can be very easily separated from *T. toykoensis* by the following character states: scutellar shield clearly larger in size; lateral margins of elytra much more weakly serrate; prosternal marginal carinae subparallel; median portion of prosternal disk weakly swollen in prosternal process; abdominal ventrite I without sternal grooves; male parameres gently dilated from base to widest subapical part; penis with sinuate sides.

Specimens examined. Type material. Holotype of *Trachys falcatae* Kurosawa, 1959: ♂ (based on Kurosawa, 1959; no dissected terminalia), "SASHI / KARATSU / SAGA PREF. / 22.VI.1950 / T. SHIBUYA" (NSMT). Paratypes of *Trachys falcatae* Kurosawa, 1959: 2 exs., Hachinohe, Aomori Pref., Japan, IX.1944, K. Shirahata leg. (NSMT); 1 ex., Tsingtao, China, 15–25.VI.1937, Yoshio Yano leg. (NSMT); 1 ex., same locality, 18–25.VI.1937, Yoshio Yano leg. (NSMT).

Non type material. **Japan**. Hokkaido — 1 ex., Miyanomori-kôen Park, Moto-machi, Otobe-chô, Nishi-gun, 10.VI.2020, A. Kashizaki leg. (YTJ). Honshu — [Tochigi] 1 ex., Itaga, Kanuma-shi, 9.VII.2000, H. Takizawa leg. (SEHU); 4 ♂♂, 1 ♀, 5 exs., Sugiyama, Ichikai-machi, Haga-gun, 16.X.2016, Y. Tamadera leg. (YTJ). [Gunma] 1 ex., Akagi-jinja

– Miyagi-mura, Maebashi-shi, 12.VI.2005, H. Takizawa leg. (SEHU); 1 ex., Shima, Nakanojô-machi, 30.VII.1958, K. Sakaguchi leg. (SEHU). [Tokyo] 1 ex., Ônita, Ôme-shi, 2.V.2004, H. Takizawa leg. (SEHU); 1 ex., Juniso, Tsunohazu, 25.VI.1913, S. Hirayama leg. (SEHU); 2 ♂♂, 3 ♀♀, Ôto-ryokuchi, Aihara-chô, Machida-shi, 26.IX.2015, Y. Tamadera leg. (YTJ). [Kanagawa] 1 ex., Moritogawa, Hayama, Miura-gun, 14.IX.2004, Y. Komiya leg. (SEHU). [Nagano] 1 ex., Shimashima-dani, Matsumoto-shi, 24.VII.1937, K. Taniguchi leg. (SEHU). [Osaka] 1 ex., Mt. Myôken-san, 22.V.1938, M. Azuma leg. (SEHU); [Hyôgo] 1 ex., Sasayama-shi, 29.VI.1952, T. Nakane leg. (SEHU); 1 ex., Kôbe-shi, no date, K. Kurosa leg. (SEHU). [Hiroshima]: 1 ex., Ujina, Hiroshima-shi, 19.VI.1966, S. Osawa leg., captured on *Wisteria floribunda* (SEHU). Kyushu — [Fukuoka] 1 ex., Moji, 19.VI.1906, S. Matsumura leg. (SEHU); 1 ex., Kyushu Univ., Kuwabara, Nishi-ku, 19–21.IX.2019, Y. Hisasue leg. (YTJ); [Ôita] 1 ex., Saeki-shi, 26.V.1945, K. Kurosa leg. (SEHU); [Miyazaki] 1 ex., Udo, Nichinan-shi, 29.VI.1974, A. Nagai leg. (SEHU); [Kagoshima] 1 ex., Kirishima-onsen spa, Kirishima-shi, 8.V.1981, T. & T. Nakane leg. (SEHU). Ikinoshima Is. (Nagasaki) — 2 exs., Mt. Ondake, Ashibe-chô, Nagasaki, 19.VI.2005, Y. Komiya leg. (SEHU). **South Korea**. 1 ex., Keijo, Korea, 13.VII.1937, Yoshio Yano leg. (NSMT; recorded by Kurosawa, 1976d); 2 exs., Mt. Sudosan, alt. 400 m, Kyongsangpuk-do, Korea, 17–18.VII.1971, K. Yamagishi leg. (NSMT; recorded by Kurosawa, 1976d).

Distributions in Japan. Hokkaido, Honshu, and Kyushu.

Other localities based on literatures: Shikoku (Kurosawa, 1959: Ehime), Tsushima Is. [?] (Shirôzu and Miyata, 1976) and Kashiwajima Is. (Saga) (Nishida, 2018).

Shirôzu and Miyata (1976) listed *Trachys reitteri* (as *falcatae* Kurosawa, 1959) in the buprestid fauna of Tsushima Is. as a doubtful distribution record referenced from Sakai (1970). The latter study was only listed this species as a recorded species from Tsushima Is. based on something literature (no reference data). As far as I known, *T. reitteri* has never been recorded from this island with specimen data.

Other distributions. Russan Far East, China, South Korea, and Taiwan.

Adult food plants. Same as in the larvae mentioned below.

Host plants. Fabaceae: *Amphicarpaea edgeworthii* Benth. [Japanese name: Yabu-mame] (Yano, 1952 for *Trachys* sp. of *Falcata japonica*; confirmed by this study), *Rhynchosia volubilis* Lour. [Japanese name: Tankiri-mame] (Kurosawa, 1959 — adult record?), *Glycine max* (L.) Merr. [Japanese name: Daizu] (Kurosawa, 1959 — adult record?), and *Pueraria lobata* (Willd.) Ohwi [Japanese name: Kuzu] (Kurosawa, 1959 — adult record?) in Japan.

Leaf-mining habit. Mines of *Trachys reitteri* were found on *Amphicarpaea edgeworthii* by this study (Figs. 65A, 69A): each mine was of the full-depth type and formed an elongate blotch occurring along leaf-margin; when full-grown, it occupied about half of whole the leaf blade; eggs, which were black (remaining shell) and not covered on powdery substances, were usually laid singly on near the apex of leaf blade on the adaxial or abaxial surfaces; hatched larvae left granular frass inside the mines; one adult specimen was emerged from the abaxial surface of the leaf with an oval adult exit hole. See also Yano (1952) treated as "*Trachys* sp. of *Falcata japonica*" for descriptions of the leaf-mines and immature stages.

Note. *Taxonomic treatment of* Trachys lushanensis. Peng (2021 c) was originally described *Trachys lushanensis* from Jiangxi, China based only one male specimen, with the following differential diagnosis comparing with *T. reitteri*:

This species strongly resembles Trachys reitteri *Obenberger, 1930, but can be separated as follows: 1) body more attenuate posteriorly in* T. lushanensis*, widest at pronotal base, wider or as wide as elytral base, while in* T. reitteri *body only slightly attenuate posteriorly, pronotal base markedly narrower than elytral base; 2) prosternal process in* T. lushanensis *strongly narrowed at apical third, while in* T. reitteri *subparallel; and 3) male aedeagus in* T. lushanensis *longer, with a pair of distinct basal knots and distinctly dilated near apices, while in* T. reitteri *very short, subcylindrical, only slightly dilated before apices, basal knots small or indistinct.* (Peng, 2021 c, p. 326)

However, these three character states in *T. lushanensis* are also recognizable on *T. reitteri* as continuous intraspecific variations, respectively. Furthermore, on the basis of the images of the holotype (figures 56–59 in Peng, 2021 c), the description for the width of the pronotal base of *T. lushanensis* seems to misidentify it as the width including the distal parts of the profemora that overhang laterally from the bases of the pronotal lateral margins. Thus, the state of the widest pronotal base is seemed to be suspicious. Judging from these facts, this study treats *T. lushanensis* as a junior synonym of *T. reitteri*.

Taxonomic treatment of Trachys cylindricus. Peng (2022) was originally described *Trachys cylindricus* from Hunan, China based only one female bad specimen (elytral setae in median part and prolegs almost missing), with the following differential diagnosis:

This species is rather unique, and it only slightly resembles Trachys reitteri *Obenberger, 1930, but it can be easily distinguished from* T. reitteri *for its much longer and much more cylindrical shape, and its prosternal process with narrowed lateral margins at middle, while* T. reitteri *is much wider and more flattened in shape, and its prosternal process has parallel lateral margins.* (Peng, 2022 a, pp. 267–268)

These character states in *Trachys cylindricus*, however, are also recognized in *T. reitteri* from Japan. With regard to the ratio of each body parts, especially in elytra, it also shows no sufficient differences between the two species even if the measurement method is standardized to Peng (2022) (because the method is slightly different from that of this (present) study; see the section of material & methods). Although *T. cylindricus* appears to be conspecific to *T. reitteri*, examinations of terminalia are needed to determine the taxonomic treatment of *T. cylindricus*.

Group V (tokyoensis)

(Fig. 25H)

Species included. *Trachys tokyoensis* Obenberger, 1940.

Diagnosis. Body ovate type. Apical margin of pronotum with small median lobe. Elytra with serrate lateral margins; elytral vestiture with transverse bands consisting of unicolor setae in apical half of each elytron, without tufts consisting of erect setae. Prosternum more or less rimmed along apical margin which is not lobed; prosternal disk without elevated portions along procoxal cavities. Abdominal ventrites with sternal grooves on ventrite I–V. Female coxites ventrally without transverse depression in apical part.

Trachys tokyoensis Obenberger, 1940

[Japanese name: Nusubito-chibi-tamamushi]

(Figs. 25H, 43D, E, 46, 47, 65B, 69B)

Trachys (*Trachys*) *tokyoensis* Obenberger, 1940: 42 (type locality: “Japan: Tokyo”).

Trachys tokyoensis: Kurosawa, 1976 d: 3 (note); 1985a: 167 (note); 1985 b: 35, pl. 7 (pictorial book); Akiyama & Ohmomo, 1997: 49 (checklist); 2000: 285, pl. 120 (pictorial book); Kubáň, 2006: 421 (Palaearctic catalog); Bellamy, 2008 b: 2525 (World catalog); Ohmomo & Fukutomi, 2013: 167, pl. 52 (pictorial book); Kubáň, 2016: 573 (Palaearctic catalog); Ishiguro & Nishida, 2018: 33, figs. 2, 3 & 6 (aedeagus).

Trachys japonica [non Obenberger, 1923]: Kurosawa, 1950 a: 13 (noted); Yano, 1952: 29 (immature stages); Kurosawa, 1959: 225 (redescription); 1963: 155, pl. 78 (pictorial book). Corrected by Kurosawa, 1985 a: 167.

Trachys ovalis Peng, 2021 c: 322 (type locality: "Nanhualing Vill., Hule, Ningguo, Anhui, China, 30°33'N 118°79'E"). **Syn. nov.**

Trachys aureoles Peng, 2021 d: 753 (type locality: "Jiulong Forest Reserve, altitude 600 m, 28°32'N 114.53'E, Wanzhai, Jianxi, China"); 2022: 263 (Hunan, China). **Syn. nov.**

Description. Male and female. Body ovate to narrowly ovate, moderately convex dorsally (Figs. 46A, B). LB 2.57–3.51 mm (mean 3.25 mm); WB 1.40–1.95 mm (mean 1.78 mm); LB/WB 1.78–1.87 (mean 1.82) (n = 20 for all measurements except terminalia). Habitus as shown in Figs. 25H, 43D, E.

Integument above mainly blackish-golden-bronze with bright-golden to dark-golden reflections; underside, antennae, and legs black with faint golden-bronze reflections, except for basal four tarsomeres light-brown; maxillary palps light-brown. Dorsal and ventral surfaces moderately shiny.

Vestiture mainly consisting of white, yellow and black setae; yellow setae occasionally being whitish. Head clothed with short, recumbent yellow to pale-yellow setae. Pronotum clothed with short, semirecumbent, yellow to pale-yellow setae mixing with a few white setae. Elytra clothed with short, semirecumbent, white, yellow and black setae which are arranged on each elytron as follows: 1) white setae irregularly scattering in basal part; 2) inconspicuously undulated, interrupted white band just before middle; 3) first white transverse band at apical 1/3, moderately wavy, zigzag-shaped; 4) second white transverse band at subapical part, faintly wavy; 5) yellow to pale-yellow setae predominant in elytron, scattering reticulately in basal 2/3, around two transverse bands, in apical part, and along sutural margin; and 6) black setae in remaining space. Underside more sparsely setiferous, with fine, recumbent, pale-yellowish to whitish setae, except for prosternum and metacoxal plates with longer yellow setae.

Head, when viewed from above, moderately triangularly concave on frons, with oculofrontal margins ridged. Eyes, when viewed from above, narrowly visible, weakly convex laterally. Vertex obscurely and coarsely variolate-punctate; frons widely concave, weakly impressed along upper side of midline, transversely ridged from just above each antennal insertion to inner margin of each eye, with surface rather smooth but faintly punctate; suprantennal pores simply round; clypeus narrow to slightly wide (Fig. 46D), without elevated basal margin, WC/LC 1.17–1.73 (mean 1.46), WC/LSC 1.17–1.55 (mean 1.38), deeply arcuately emarginate at apical margin.

Antennae (Fig. 46E) reaching just behind apicolateral angles of pronotum when laid alongside; antennomere I stout claviform, longer than II; II ovate, slightly longer than III;

III–V subrectangular, subequal each other in length; VI subrectangular, slightly shorter than V; VII–X triangular, moderately enlarged; XI subtriangular to sublingulate.

Mandibles with transverse ridge in about middle of each outside. Maxillary palps with oval palpomere IV somewhat longer than wide.

Pronotum widest at base, WP/LP 2.63–3.04 (mean 2.79), BMP/AMP 1.58–1.70 (mean 1.64), narrower than elytra; lateral margins weakly arcuately and moderately narrowed apicad; apicolateral angles obtuse; basolateral angles broadly acute; apical margin bisinuately shallowly emarginate, with small median lobe; basal margin trisinuate, with median lobe moderately produced; disk faintly depressed along basal median lobe; surface obscurely variolate-punctate, becoming denser toward apical and basal margins. Scutellar shield very small, subtriangular, glabrous.

Elytra widest at humeri, LE/WE 1.32–1.43 (mean 1.35), LE/LP 3.68–4.34 (mean 4.01); humeral calluses slightly weakly developed; lateral margins weakly narrowed posteriorly behind humeri then subparallel to middle, and finally arcuately convergent to conjointly rounded apices, with moderate serrations in about apical half except apices (Fig. 46C); marginal carinae distinct in thoracic region, indistinctly reaching near apices; sutural margin faintly elevated in subapical part; disk weakly depressed in basal part, constricted behind humeri; surface irregularly and coarsely punctate. Lateral part of abdomen narrowly visible in dorsal view; laterosternites I–IV with laterosternal sulci.

Underside. Prosternum (Fig. 46F) slightly convexly rounded at apical margin which is weakly rimmed; prosternal process wide, weakly constricted between procoxa, with apex broadly rounded at rest; marginal carinae moderately widely separated each other at widest part of prosternal process, strongly divergent posteriad from apical half; disk rather flattened on median portion, somewhat declivous laterad on outside of marginal carinae, without elevated protions along procoxal cavities. Hypomera with depressed hypomeral markings subreniform, often becoming clearly indistinct posteriorly (Fig. 46G). Metaventrite moderately sculptured with large punctures on inside of katepisternal suture and with linearly confluent sculptures on outside of the suture. Legs moderately slender; metacoxal plates weakly produced posteriorly at each lateral angle which is broadly acute, with surface coarsely variolate; metatibiae bearing a fringe of spines in apical half of each outer margin, with one long spine in base of the fringe (Fig. 46H); inner tooth of each claw large. Abdominal ventrites with sternal grooves on ventrites I–V; V (Fig. 46I) rounded or obtusely subtruncate at apex; surface variolate, in ventrite I with linearly confluent sculptures on median part.

Sexual dimorphism indistinct.

Male terminalia (n = 4 for measurements). Proctiger with a pair of short baculi at base. Sternite IX (Fig. 47A) wide, SL/SW 0.88–1.06 (mean 0.98), arcuately emarginate at apical margin, bearing several setae on each side of apical margin. Tegmen (Fig. 47B) wide; parameres PL/PW 2.00–2.13 (mean 2.06), a little setiferous on apicolateral margins, with sides which are faintly sinuately subparallel or gently dilated from base to beyond middle, then strongly arcuately expanded abruptly to widest point at apical 1/4, and finally slightly sharply convergent to apices; phallobase PbL/PbW 1.54–2.33 (mean 1.94), about 1/4 length of tegmen. Penis (Fig. 47C) rather slender, PeL/PeW 5.74–6.50 (mean 6.15), slightly shorter than tegmen; dorsal plate with sides which are gradually narrowed from widest point of base to subapical part, and then arcuately convergent apicad, with round apex, basally with median struts about 1/3 length of penis; ventral plate membranous, but weakly sclerotized as a linear patch in middle of apical 1/4.

Female terminalia (n = 5 for measurements). Ovipositor (Figs. 47D–F) short; proctiger basally with a pair of long, ventrally curved baculi; coxites transversely subreniform, sparsely setiferous on each side of apical margin, ventrally without transverse depression in apical part; styli subtrapezoidal, rather slender, with sides subparallel, SlL/SlW 2.69–3.45 (mean 2.95), bearing several setae apically; ventral valve sparsely setiferous on each side of subapical part; vagina roundly sack-shaped (under incompletely inflated state), strongly expanded dorsally in about distal half; spermatheca slightly wide tubular, rather short in length, widest at beyond middle, without spermathecal gland.

Differential diagnosis. Among Japanese congeners, this species may be slightly related to *Trachys reitteri* by the combination of the triangularly concaved frons outline of the head, the serrate lateral margins of the elytra, the absence of the swelling on the subapical part of the elytral disk, and the light-brown basal four tarsomeres on each leg, but can be very easily separated from *T. reitteri* by the following character states: scutellar shield clearly smaller in size; lateral margins of elytra much more strongly serrate; prosternal marginal carinae divergent posteriad; median portion of prosternal dick flattened; abdominal ventrite I with sternal grooves; male parameres with distinct lateral expansion being widest at apical 1/4; penis straightly narrowing apicad (not sinuate).

Specimens examined. Non type material. **Japan**. Honshu — [Tochigi] 1 ex., Itaga, Kanuma-shi, 9.VII.2000, H. Takizawa leg. (SEHU). [Tokyo] 1 ex., Miyao-jinja, Kamiongata-machi, Hachiôji-shi, 13.VII.2020, Y. Tamadera leg., captured on *Hylodesmum podocarpum* (YTJ). [Kanagawa] 1 ex., Mt. Jimba-san, Fujino, Sagamihara-shi, 31.V.1973, no collector name (SEHU); 1 ex., Kanagawa, 21.VI.1973, no collector name (SEHU); 2 exs., near Ogino-undô-kôen Park, Naka-ogino, Atsugi-shi, 28.IV.2018,

Y. Fukuda leg. (YTJ); 2 ♂♂, 2 ♀♀, Miyagase, Kiyokawa-mura, Aikô-gun, 27.IX.2019, Y. Tamadera leg., captured on *Hylodesmum podocarpum* (YTJ); 3 ♀♀, 2 exs., same locality, 15.VII.2020 Y. Tamdera leg. (YTJ). [Ishikawa] 2 ♂♂, 1 ♀, Inu, Yawata-machi, Hakusan-shi, 15.VI.2016, Y. Tamadera leg. (YTJ). [Gifu] 1 ex., Yôrô-shi, 29.V.1949, T. Nakane leg. (SEHU). [Mie] 1 ex., Ise-shi, 29.IV.1973, C. Ohkawa leg. (SEHU). [Kyoto] 1 ex., Kurama, Kyoto-shi, 13.V.-, O. Mutsuura leg. (SEHU). [Osaka] 1 ex., Ikeda-shi, 11.VI.1938, M. Azuma leg. (SEHU); 1 ex., Mino-o-shi, 17.V.1931, M. Azuma leg. (SEHU). [Nara] 1 ex., Mt. Kongô-san, Gose-shi, 25.VI.1936, H. Takenaka leg. (SEHU). [Hiroshima] 1 ex., Taishaku-kyo, 8.VI.1968, T. Kosaka leg. (SEHU). Shikoku — [Tokushima] 1 ex., Koyadaira, Awa, 7.VIII.1913, E. Gallois leg. (SEHU); 1 ex., Mt. Nakatsumine-san, 7.IX.1952, M. Hirai leg. (SEHU). [Ehime] 2 exs., Tachibana, Matsuyama, Ehime Pref., 9.VIII.1949, T. Yano leg. (NSMT; recorded by Kurosawa,1959). Kyushu — [Fukuoka] 1 ex., Mt. Kôra-san, Kurume-shi, 22.V.1983, N. Hirata leg. (SEHU). [Miyazaki] 1 ex., Udo, Nichinan-shi, 29.VII.1974, T. Nakane leg. (SEHU). [Kagoshima] 1 ex., Hanase, Tashiro, 11.IX.1985, K. Kushigemati leg. (SEHU). Ikinoshima Is. (Nagasaki) — 1 ex., Mt. Takenotsuji, Iki Is., Japan, 9.V.1962, M. Ohno leg. (NSMT).

Distributions in Japan. Honshu, Shikoku, Kyushu, and Ikinoshima Is.

Record based on literature: the Koshikijima Isls. (Kamikoshikijima Is. (Imasaki *et al*., 2020)).

Other distributions. No record.

Adult food plants. Same as in the larvae mentioned below.

Host plants. Fabaceae: *Hylodesmum podocarpum* (DC.) H.Ohashi & R.R.Mill [Japanese name: Nusubitohagi] (Yano, 1952 for *Trachys japonicus*; confirmed by this study) and *Rhynchosia volubilis* Lour. [Japanese name: Tankiri-mame] (Yano, 1952 for *Trachys japonicus*) in Japan. This species clearly prefers *H*. *podocarpum* to *R*. *volubilis*, the latter of which has never been recorded as a host except for the record of Yano (1952).

Leaf-mining habit. Mines of *Trachys tokyoensis* were found on *Hylodesmum podocarpum* by this study (Figs. 65B, 69B): each mine was of the full-depth type and formed an elongate blotch occurring along leaf-margin; when full-grown, it occupied about half of whole the leaf blade; eggs, which were blackish (remaining eggshell) and not covered on powdery substances, were usually laid singly on the adaxial surface of the leaf blade; hatched larvae left granular frass inside the mines; one adult specimen was emerged from the adaxial surface of the leaf with an oval adult exit hole. See also Yano (1952) treated as "*Trachys japonica*" for descriptions of the leaf-mines and immature stages.

Notes. *Taxonomic history*. For a long time, Japanese researchers had misidentified *Trachys tokyoensis* and other congeners in Japan as shown in Table 2. These misidentifications were reviewed by Kurosawa (1976 d) in Japanese and formally corrected by Kurosawa (1985 a).

Taxonomic treatment of Trachys ovalis. Peng (2021 c) originally described *Trachys ovalis* from Anhui, China based only one male, with the following remarks:

This species resembles Trachys tokyoensis *Obenberger, 1940 from Japan but is more oviform with the anterior half of the elytra more arcuate and wider at the base, while* T. tokyoensis *is longer, more deeply emarginate behind the humeri, and narrower in the basal part of the elytra. In addition, the apical part of the prosternal process in T. ovalis is more widely expanded with the apical angles more acute and the apex acute medially, while in T. tokyoensis it is only slightly expanded at the apical part with the apical angles and apical margin both more arcuate*. (Peng, 2021 c, p. 323)

These character states in *T. ovalis*, however, are also recognized in *T. tokyoensis* from Japan. In addition, the shape of prosternal process is known that it shows intraspecific variations in *Trachys* species (Schaefer, 1950; Luna, 2017). The differences in the prosternal process mentioned by Peng (2021 c) are seemed to be rather small and quantitative. Furthermore, the male aedeagus of *T. ovalis* (figure 52 in Peng, 2021 c) have no morphological differences from that of *T. tokyoensis*. Judging from these facts, this study proposes that *T. ovalis* is synonymized under *T. tokyoensis*.

Taxonomic treatment of Trachys aureoles. Peng (2021 d) originally described *Trachys aureoles* from Jiangxi (holotype) and Anhui, China based on six specimens, with the following differential diagnosis:

This species resembles Trachys purpuratus *Peng, 2021, but differs by its golden yellow color and the elytra quadrate only in the anterior half and more attenuate posteriorly, while* T. purpuratus *is dark purple with the elytra quadrate in the anterior two-thirds and moderately attenuate posteriorly. The prosternal process is also different between the two species; in* T. aureolus *the apical half is very widely dilated and fan-shaped, while in* T. purpuratus *the apical half is only slightly dilated and arcuate.* (Peng, 2021 d, p. 755)

Although *Trachys aureoles* were compared with *T. purpuratus*, described from Jiangxi, China (Peng, 2021 c), as sited above, the former is no doubt much more similar to *T. tokyoensis* (= *ovalis* Peng, 2021) than to *T. purputatus* based on their descriptions and images (*purpuratus*, figures 34–37 in Peng, 2021 c; *aureoles*, figures 11–14 in Peng, 2021 d). In addition, on the basis of the original description and figures of *T. aureoles*, its morphological character states are well match those of *T. tokyoensis*. Furthermore, the elytral serrations of *T. aureoles* are actually present based on figure 12 in Peng (2021 c), although the original description mentions that the distinct serrations are absent. Therefore, this study proposes that *T. aureoles* is synonymized under *T. tokyoensis*.

Group VI (griseofasciatus)

(Figs. 48A, B)

Species included. *Trachys griseofasciatus* Saunders, 1873 and *T. yanoi* Kurosawa, 1959.

Diagnosis. Body ovate type. Apical margin of pronotum without median lobe. Elytra with serrate lateral margins; elytral vestiture with transverse bands consisting of unicolor setae in apical half of each elytron, without tufts consisting of erect setae. Prosternum more or less rimmed along apical margin which is not lobed; prosternal disk without elevated portions along procoxal cavities. Abdominal ventrites with sternal grooves on ventrite I–V. Female coxites ventrally with transverse depression in apical part.

Trachys griseofasciatus Saunders, 1873

[Japanese name: Namigata-chibi-tamamushi]

(Figs. 48A, 49A, B, 50A–E, 51A–F, 52, 54A, B, 69C)

Trachys griseofasciata Saunders, 1873: 521 (type locality: "Japan"); Schönfeldt, 1887: 113 (catalog); Lewis, 1893: 338 (synonymized under *T. subbicornis* Motschulsky); Jakobson, 1913: 800 (catalog); Obenberger, 1918 a: 64 (synonym of *T. subbicornis*); Obenberger, 1937 a: 1380 (World catalog; synonym of *T. subbicornis*); Kurosawa, 1950 a: 14 (note, including *T. yanoi* Kurosawa); Chûjô & Kurosawa, 1950: 13 (Shikoku, Japan; including *T. yanoi*); Yano, 1952: 32 ("Forma B"; immature stages on *Aphananthe aspera*); Iga, 1955 a: 10, pl. 4 (pictorial book, including *T. yanoi*); 1955 b: 80, pl. 24 (pictorial book, including *T. yanoi*); Kurosawa, 1959: 235, fig. 10 (redescription); 1963: 156 (pictorial book); 1976 c: 3 (note); 1985 b: 35, pl. 7 (pictorial book); Akiyama & Ohmomo, 1997: 47 (checklist); 2000: 284, pl. 120 (pictorial book); Kubáň, 2006: 419 (Palaearctic catalog).

Trachys griseifasciata [sic]: Kerremans, 1885: 157 (misspelling; catalog); Kerremans, 1892 a: 286 (catalog); Kerremans, 1903: 313 (misspelling; cataloged as full species, neglecting or overlooking taxonomic treatment in Lewis, 1893); Miwa & Chûjô, 1936: 24 (catalog).

Trachys grisefasciata [sic]: Obenberger, 1926 b: 661 (misspelling; cataloged; synonym of *T. subbicornis*).

Trachys griseofasciatus [justified emendation, according to ICZN (2009)]: Bellamy, 2008 b: 2489 (World catalog); Ohmomo & Fukutomi, 2013: 168, pl. 54 (pictorial book); Kubáň, 2016: 571 (Palaearctic catalog); Ishiguro & Nishida, 2018: 33, figs. 2, 3 & 6 (aedeagus); Tamadera & Yoshitake, 2018 c: 334 (male and female terminalia).

Trachys subbicornis [non Motschulsky, 1860 nec Saunders, 1871]: Lewis, 1893: 338 (synonymized *T. griseofasciatus* under *T. subbicornis*); Kerremans, 1903: 310 (catalog); Obenberger, 1918: 19, 36, 64 (in key; note; in catalog); 1926 b: 661 (catalog); Miwa & Chûjô, 1936 : 25 (nec Lewis, 1893; catalog; Japanese name: Ajia-chibi-tamamushi); Obenberger, 1937 a: 1379 (World catalog); 1958: 242 (Yunnan and Szechwan, China). Corrected by Kurosawa, 1959: 236.

Trachys (*Trachys*) *subbicornoides* Obenberger, 1921: 238 (type locality: "Tonkin: Environs de Lam", Vietnam). Synonymized under *T. griseofasciatus* by Kurosawa, 1959: 236 (based only on the original description).

Description. Male and female. Body ovate to narrowly ovate, slightly lowly to moderately convex dorsally (Figs. 50A, B). LB 3.80–4.35 mm (mean 4.05 mm); WB 1.96–2.25 mm (mean 2.10 mm); LB/WB 1.86–1.98 (mean 1.93) (n = 20 for all measurements except terminalia). Habitus as shown in Figs. 48A, 49A, B.

Integument above mainly blackish-bronze with faint golden-bronze reflections; underside, antennae, and legs black with faint golden-bronze reflections, except for basal four tarsomeres brownish-black with brown tarsal pads; maxillary palps brownish-black. Dorsal surface slightly weakly shiny; ventral surface moderately shiny.

Vestiture mainly consisting of white and brown setae; brown setae usually dark but occasionally being lighter or rarely being yellowish. Head clothed with short, recumbent brown setae, which sometimes become lighter than setae on other body parts, very rarely with several white setae on vertex irregularly. Pronotum clothed with short, semirecumbent brown setae mixing with a few white setae as some spots. Elytra clothed with short, semirecumbent, white and brown setae which are arranged on each elytron as follows: 1) white setae irregularly scattering in basal 1/3; 2) inconspicuously undulated, interrupted white band in middle; 3) first white transverse band at apical 1/3, moderately wavy, zigzag-shaped; 4) second white transverse band at subapical part, weakly wavy, slightly zigzag-shaped; and 5) brown setae in remaining space. Underside more sparsely setiferous, with fine, recumbent, yellowish to whitish setae.

Head, when viewed from above, slightly shallowly, arcuately concave on frons, with oculofrontal margins rounded. Eyes, when viewed from above, broadly visible, moderately convex laterally. Vertex obscurely and coarsely variolate-punctate; frons widely concave, weakly impressed along upper side of midline, transversely ridged from just above each antennal insertion to inner margin of each eye, with surface faintly variolate-punctate; suprantennal pores simply round; clypeus wide (Figs. 50D, E), without elevated basal margin, WC/LC 2.00–2.88 (mean 2.49), WC/LSC 2.00–2.71 (mean 2.41), arcuately emarginate at apical margin.

Antennae (Figs. 51A, B) reaching just behind apicolateral angles of pronotum when laid alongside; antennomere I stout claviform, longer than II; II ovate, slightly longer than III; III subrectangular, longer than IV; IV–VI subrectangular, subequal each other in length; VII–X triangular, more strongly enlarged and slightly thicker in male than in female; XI subtriangular to sublingulate.

Mandibles with transverse ridge in about middle of each outside. Maxillary palps with oval palpomere IV somewhat longer than wide.

Pronotum widest at base, WP/LP 2.63–2.87 (mean 2.76), BMP/AMP 1.40–1.54 (mean 1.45), narrower than elytra; lateral margins faintly to weakly arcuately and slightly weakly narrowed apicad; apicolateral angles obtuse; basolateral angles right to broadly acute; apical margin arcuately emarginate, without median lobe; basal margin trisinuate, with median lobe moderately produced; disk faintly depressed along basal median lobe; surface obscurely variolate-punctate, becoming denser toward apical and basal margins. Scutellar shield very small, subtriangular, glabrous.

Elytra widest at humeri, LE/WE 1.37–1.43 (mean 1.41), LE/LP 4.05–4.37 (mean 4.20); humeral calluses slightly weakly developed; lateral margins subparallel in basal half and faintly constricted between humeri and middle point, and then arcuately convergent to conjointly rounded apices, with slightly strong serrations in about apical half except apices (Fig. 50C); marginal carinae distinct in thoracic region, indistinctly reaching near apices; sutural margin faintly elevated in apical 1/3; disk weakly depressed in basal part, constricted behind humeri, weakly swollen in subapical part; surface irregularly and coarsely punctate. Lateral part of abdomen narrowly visible in dorsal view; laterosternites I–IV with laterosternal sulci.

Underside. Prosternum (Fig. 51C) rather straight at apical margin which is weakly rimmed; prosternal process wide, constricted between procoxa, with apex broadly rounded at rest; marginal carinae moderately widely separated each other at widest part of prosternal process, faintly narrowed posteriorly in apical half then weakly divergent posteriad; disk rather flattened on median portion, somewhat declivous laterad on outside of marginal carinae, without elevated protions along procoxal cavities. Hypomera with depressed hypomeral markings semicircular to subreniform, with linearly confluent sculptures inside (Fig. 51D). Metaventrite densely sculptured with large punctures on inside of katepisternal suture and moderately sculptured with linearly confluent sculptures on outside of the suture. Legs moderately slender; metacoxal plates weakly produced posteriorly at each lateral angle which is sharply acute, with surface coarsely variolate; metatibiae bearing a fringe of spines in apical half of each outer margin, without one long spine in base of the fringe (Fig. 51E); inner tooth of each claw large. Abdominal ventrites with sternal grooves on ventrites I–V; V (Fig. 51F) rounded at apex; surface variolate, in ventrite I with linearly confluent sculptures on median part.

Sexual dimorphism barely recognized in the relative size and thickness of serrate antennomeres (see above).

Descriptions of terminalia [partly modification of Tamadera & Yoshitake (2018c: 334)]. Male terminalia (n = 5 for measurements). Proctiger with a pair of short baculi at base. Sternite IX (Fig. 52A) wide, SL/SW 0.69–0.84 (mean 0.79), arcuately emarginate on apical margin, bearing several setae on each side of apical margin. Tegmen (Fig. 52B) slender; parameres PL/PW 2.50–2.71 (mean 2.63), sparsely setiferous on apicolateral margins, with sides which are gently dilated from base to widest point at apical 1/3, then slightly narrowed to subapical part, and finally rather sharply convergent to apices; phallobase PbL/PbW 1.60–1.79 (mean 1.69), about 1/4 length of tegmen. Penis (Fig. 52C) slender, PeL/PeW 6.75–7.46 (mean 7.11), slightly shorter than tegmen; dorsal plate faintly bisinuate on sides which are gradually narrowed from widest point of base to subapical part, and then arcuately convergent apicad, with round apex, basally with median struts about 1/3 length of penis; ventral plate membranous, but weakly sclerotized as a patch in middle of apical 1/4.

Female terminalia (n = 5 for measurements). Ovipositor (Figs. 52D–F) short; proctiger basally with a pair of long, ventrally curved baculi; coxites transversely subhexagonal, sparsely setiferous on each side of apical margin, ventrally with transverse depression in apical part; styli subtrapezoidal, wide, with sides subparallel, SlL/SlW 1.67–2.20 (mean 2.05), bearing several setae apically; ventral valve sparsely setiferous on each side of subapical part; vagina sack-shaped, moderately expanded dorsally in distal half; spermatheca slender tubular, moderate in length, widest in middle, with spermathecal gland apically.

Differential diagnosis. This species is extremely similar in general appearance to *Trachys yanoi*, but may be distinguished from *T. yanoi* by the combination of the following character states: lateral margins of pronotum more slightly weakly narrowed apicad, as a result head appears to be slightly wider; clypeus wider, more than twice as WC (wide) as LSC (long); male parameres gently dilated from base to widest point at apical 1/3 (without lateral expansion).

Specimens examined. Non type material. **Japan**. Honshu —[Saitama] 7 ♂♂, 1 ♀, Kamiyamaguchi, Tokorozawa-shi, 13.VI.2015, Y Tamadera leg. (YTJ); 1 ♂, 6 ♀♀, same locality, 25.VIII.2018, Y. Tamadera leg. (YTJ). [Chiba] 1 ex., Miyanogi-chô, Inage-ku, 3–4.V.1999, H. Takizawa leg. (SEHU). [Kanagawa] 1 ♀, Nurumizu, Atsugi-shi, 30.XI.2014, Y. Tamadera leg. (YTJ). [Osaka] 1 ex., Sakai, 31.VII.1975, T. Kumata leg., host no. 1407 (SEHU); 1 ex., same locality, 2.VIII.1975, T. Kumata leg., host no. 1407 (SEHU). [Wakayama] 2 exs., Gobô-shi, 4.V.1993, N. Ito leg. (SEHU). Shikoku — [Ehime] 1 ex., Saretani, Nakayama-chô, Iyo-shi, 22.IV.2019, Y. Tamadera leg. (YTJ). Kyushu — [Nagasaki] 2♂♂, 1 ex., Suwa-jinja Temple, Nagasaki-shi, 3.XI.1953, T. Moroki leg. (SEHU); 1 ♂, same locality, 26.XII.1955, Y. Ikezaki leg. (SEHU); 1 ♂, 2 ♀♀, Aburagi-machi, Nagasaki-shi, 16.III.2017, N. Yamamoto leg. (YTJ). [Kumamoto] 1 ex., Mt. Shiraga, 4.24.1983, M. Ôhara leg. (SEHU).

Distributions in Japan. Honshu, Shikoku, and Kyushu.

Other localities in literatures: Kashiwajima Is. (Saga) (Kido & Oda, 2010).

Other distributions. China, Korea, and Vietnam.

Adult food plants. Same as in the larvae mentioned below.

Host plants. Cannabaceae: *Aphananthe aspera* (Thunb.) Planch. [Japanese name: Mukunoki] (Yano, 1952; confirmed by this study) and *Celtis sinensis* Pers. [Japanese name: Enoki] (Kurosawa, 1976 c — adult record?; confirmed by this study: the Kumata collection in SEHU) in Japan.

Leaf-mining habit. Mines of *Trachys griseofasciatus* were found on *Aphananthe aspera* by the author (Fig. 69C) and one mine specimen on *Celtis sinensis* with an emerged adult specimen collected by a great taxonomist of leaf-mining moths, deceased Dr. Toshio Kumata, was examined in this study: each mine was of the full-depth type and formed a large, elongate blotch occurring usually along leaf-margin; when full-grown, it occupied about half of whole the leaf blade; eggs, which were pale-yellow (remaining eggshell) and not covered on powdery substances, were laid singly on the adaxial surface of the leaf blade near leaf-margin; hatched larvae left granular to thread-like frass inside the mines; adults were emerged from the adaxial or abaxial surfaces of the leaves with oval adult exit holes. See also Yano (1952) treated as *Trachys griseofasciata* “Forma B” for descriptions of the leaf-mines and immature stages.

Notes. *Trachys griseofasciatus* is considered to be definitively closely related to *T. yanoi* Kurosawa, 1959 on the basis of the high morphological similarities, but can be clearly separated from *T. yanoi* by the host plant and by the larval morphology (see notes of *T. yanoi* for detailed these differences), as well as the adult character states mentioned in the differential diagnosis. Tamadera & Yoshitake (2018 c) described the width of the female stylus as a useful character to distinguish these morphologically similar species. However, this character was removed by this study from the diagnosis of *T. griseofasciatus* because it is a rather continuous difference and sometimes overlap with that of *T. yanoi*.

Taxonomic history of Trachys subbiconis *auct. non Motschulsky and* Trachys griseofasciatus *Saunders*. For a long time, the taxonomic treatments of *Trachys subbicornis* auct. non Motschulsky, 1860 and *Trachys griseofasciatus* Saunders, 1873 had been confused. Saunders (1871) transferred *Brachys subbicornis* Motschulsky, 1860 (current name, *Habroloma subbicorne* (Motschulsky, 1860)) to the genus *Trachys* (this treatment is correct because he regarded *Habroloma* is a subgenus of *Trachys*). Later, Lewis (1893) synonymized *Trachys griseofasciatus* Saunders, 1873 under *T. subbicornis* non Motschulsky, 1860 nec Saunders, 1871. However, Kerremans (1903) treated *T. subbicornis* and *T. griseofasciatus* as an independent species, respectively (without reason for his taxonomic change), and then Miwa & Chûjô (1936) cataloged them as two separate species who show different distributions in Japan, respectively. Consequently, Lewis's, Kerremans's, and Miwa & Chûjô's treatments caused confusion in the taxonomy of Japanese *Trachys* and its related genus *Habroloma*. This confusion was reviewed in detail by Kurosawa (1959) (see that study for detail), although he did not mention about Saunders (1871) and Kerremans (1903). According to Kurosawa (1959), he considered that *T. griseofasciatus* is definitely different species from *T. subbicornis* and suggested that the latter species is a *Habroloma* species but not a *Trachys* species based on their original descriptions. Finally, the taxonomic confusion was resolved by Akiyama & Ohmomo (1995) which was confirmed that the holotype of *Brachys subbicornis* Motstchulsky, 1860 is definitely a *Habroloma* species (*Habroloma subbicorne*) and the taxonomic treatment of Lewis (1893) is wrong.

Trachys yanoi Kurosawa, 1959
[Japanese name: Yano-namigata-chibi-tamamushi]
(Figs. 3F, 48B, 49C–E, 50F–K, 51G–M, 53, 54C, D, 65C, 69D)

Trachys griseofasciatus [non Saunders, 1873]: Yoshino, 1910: 610 (larva on *Zelkova serrata*); Matsumura, 1931a: 54, 82, pl. 7 (pictorial book; host: *Zelkova serrata*); Kato, 1933: pl. 32 (pictorial book; host: *Zelkova serrata*).

Trachys griseofasciata [non Saunders, 1873]: Niijima, 1913: 63, fig. 38 (larva on *Zelkova serrata*); Matsumura, 1915: 245, pl. 24 (larva on *Zelkova serrata*); Yokoyama, 1930: 85, pl. 10 (pictorial book); Matsumura, 1931 b: 179, fig. 383 (pictorial book; host: *Zelkova serrata*); 1932: 920 (larva on *Zelkova serrata*); Kurosawa, 1950 b [part]: 1112, fig. 3186 (pictorial book); Yano, 1952: 32 ("Forma A"; immature stages on *Zelkova serrata*).

Trachys subbicornis [non Motschulsky, 1860 nec Lewis, 1893]: Yuasa, 1932: 660, fig. 1294 (pictorial book; host: *Zelkova serrata*); Kamiya & Adachi, 1933: pl. 22 (pictorial book; host: *Zelkova serrata*); Yuasa, 1933: 276, figs. 8–10 in pl. 18. (larva on *Zelkova serrata*).

Trachys yanoi Kurosawa, 1959: 233, figs. 9 & 10 (type locality: Matsuyama, Ehime Pref., Japan); 1963: 156, pl. 78 (pictorial book); 1976d, 4 (note; China and North Korea); 1985 b: 35, pl. 7 (pictorial book); Akiyama & Ohmomo, 1997, 49 (checklist); 2000: 285, pl. 120 (pictorial book); Kubáň, 2006: 421 (Palaearctic catalog); Bellamy, 2008: 2533 (World catalog); Ohmomo & Fukutomi, 2013: 168, pl. 54 (pictorial book); Kubáň, 2016: 574 (Palaearctic catalog); Ishiguro & Nishida, 2018: 33, figs. 2, 3 & 6 (aedeagus); Tamadera & Yoshitake, 2018 c: 335 (male and female terminalia; mistaking type locality as "Yokohama, Kanagawa Pref."); Štrunc, 2022: 196 (photograph).

Description. Male and female. Body ovate to narrowly ovate, slightly lowly to moderately convex dorsally (Figs. 50F, G). LB 3.04–4.35 mm (mean 3.83 mm); WB 1.59–2.34 mm (mean 2.06 mm); LB/WB 1.78–1.94 (mean 1.87) (n = 20 for all measurements except terminalia). Habitus as shown in Figs. 48B, 49C–E.

Vestiture mainly consisting of white and brown setae; brown setae usually slightly lighter but coloration of setae sometimes overlapping with *Trachys griseofasciatus*.

Head usually slightly narrower, with relatively narrower clypeus (Figs. 50I–K). Pronotum with lateral margins often more strongly narrowed apicad. Ratios of body parts as follows: WC/LC 1.64–2.30 (mean 1.82), WC/LSC 1.64–1.97 (mean 1.74), WP/LP

2.64–2.95 (mean 2.82), BMP/AMP 1.44–1.60 (mean 1.53); LE/WE 1.33–1.41 (mean 1.38), LE/LP 4.00–4.44 (mean 4.22). Otherwise practically as in *T. griseofasciatus*.

Male terminalia (n = 5 for measurements). Sternite IX (Fig. 53A) narrower, SL/SW 0.86–1.03 (mean 0.94). Tegmen (Fig. 53B) slenderer; parameres PL/PW 3.11–3.37 (mean 3.20), with sides which are gently dilated from base to apical half, then weakly arcuately expanded to behind apical 1/3, and finally gradually convergent apicad; phallobase PbL/PbW 1.82–2.00 (mean 1.86). Penis (Fig. 53C) PeL/PeW 7.39–9.02 (M 8.17). Otherwise practically as in *T. griseofasciatus*.

Female terminalia (n = 5 for measurements). Ovipositor (Figs. 53D–F) with slightly narrower styli, SlL/SlW 2.25–2.75 (mean 2.55); vagina moderately expanded dorsally in middle. Otherwise practically as in *T. griseofasciatus*.

Differential diagnosis. This species is extremely closely similar in general appearance to *Trachys griseofasciatus*, but may be distinguished from *T. griseofasciatus* by the combination of the following character states: lateral margins of pronotum more slightly strongly narrowed apicad, as a result head appears to be slightly narrower; clypeus narrower, less than twice as WC (wide) as LSC (long); male parameres with very weak lateral expansion being widest behind apical 1/3.

Specimens examined. Type material. Holotype: Sex unknown (not indicated in the original description, but probably male; no dissected terminalia), “MATSUYAMA / EHIME PREF. / 24.V.1942 / Y. INOUE” (NSMT). Paratype: 1 ex., Yamadera, nr. Yamagata, 24.V.1942, Y. Kurosawa leg. (NSMT).

Non type material. **Japan**. Hokkaido — 14 exs., Akagawa-chô, Hakodate-shi, 1.XI.2014, K. Nakoshi leg., captured under the bark of *Zelkova serrata* (YTJ); 8 exs., same locality, 12.VI.2019, S. Takahashi leg. (YTJ); 10 exs., same locality, 14.VI.2022, Y. Tamadera leg., captured on *Zelkova serrata* (YTJ). Honshu — [Fukushima] 8 exs., Wakamatsu, 17.VIII.1951, K. Nagayama leg. (SEHU); 9 exs., same locality, 26.III.1948, K. Nagayama leg. (SEHU); 1 ex., same locality, 11.II.1948, K. Nagayama leg. (SEHU); 1 ex., Keizan, Kita-Aizu, 13.III.1949, K. Nagayama leg. (SEHU); 77 exs., Aizu, Fukushima, no date, K. Nagayama leg. (SEHU). [Tochigi] 1 ex., Itaga, Kanuma-shi, 9.VII.2000, H. Takizawa leg. (SEHU). [Tokyo] 1 ex., Mt. Mitake-san, Ôme-shi, 3.V.2005, Y. Komiya leg. (SEHU); 4 exs., Unasawa, 31.VII.1979, M. Miura leg. (SEHU); 4 exs., Aoyama, Tokyo, Musashi, 27.V.1946, T. Nakane leg., captured on Keyaki (*Zelkova serrata*), (SEHU); 1 ex., Sawai, Okutama, 5.VI.1936, Y. Yano leg. (SEHU); 1 ex., Mt. Nokogiriyama, Okutama, 17.VI.1936, Y. Yano leg. (SEHU); 6 ♂♂, 6 ♀♀, Mt. Takao-san, Takao-chô, Hachiôji-shi, 4.IX.2015, Y. Tamadera leg. (YTJ). [Kanagawa] 1 ex., Odawara-shi, 16.VII.1974, T. Miyata leg. (SEHU); 1 ex., same locality, 18.VII.1974, T.

Miyata leg. (SEHU); 1 ex., Maita, Yokohama, 18.V.1937, K. Iwase leg. (SEHU); 1 ex., Mt. Takatori-yama, Zushi-shi, 19.VIII.1973, S. Tachikawa & M. Taguchi leg. (SEHU). [Ishikawa] 1 ♂, 3 ♀♀, near Ishikawa Insect Museum, Inu, Yawata-machi, Hakusan-shi, 15.VI.2016, Y. Tamadera leg. (YTJ). [Gifu] 1 ex., Yôrô-chô, 29.V.1949, T. Nakane leg. (SEHU). [Shizuoka] 4 ♂♂, Mt. Goten-yama, Kanbara, Shimizu-ku, Shizuoka-shi, 30.III.2017, H. Nagano leg. (YTJ). [Aichi] 5 exs., Ishimaki-chô, Ishikawa, 9.VIII.1955, T. Nakahara leg. (SEHU). [Kyoto] 95 exs., Shimogamo, Kyoto-shi, 16.III.1955, T. Kishii leg. (SEHU); 1 ex., Hira, nr. Kyoto, 27.V.1956, T. Nakane leg. (SEHU); 3 exs., Kurama, Kyoto-shi, 12.VI.1955, T. Nakane leg. (SEHU); 2 exs., same locality, 5.V.1955, T. Nakane leg. (SEHU); 2 exs., Kibune, Kyoto-shi, 20.V.1956, T. Nakane leg. (SEHU); 1 ex., same locality, 13.V.1952, T. Nakane leg. (SEHU); 1 ex., Kyoto, 3.V.1955, T. Nakane leg. (SEHU); 2 exs., same locality, 30.IV.1960, T. Nakane leg. (SEHU). [Osaka] 2 exs., Sumiyoshi Park, 28.XI.1949, K. Sawada leg. (SEHU); 1 ex., Osaka, 7.V.1938, M. Azuma leg. (SEHU). [Hyôgo] 5 exs., Yumura, Tajima, 23.V.1955, T. Nakane leg. (SEHU); 2 exs., same locality, 27.V.1955, T. Nakane leg. (SEHU). [Nara] 1 ex., Mt. Kasugayama, 17.VI.1951, H. Ishida leg. (SEHU). [Tottori] 1 ex., Akamatsu, Daisen-chô, 5.IX.2004, H. Takizawa leg. (SEHU). Shikoku — [Tokushima] 5 exs., Mt. Benten-yama, Katanokami-chô, Tokushima-shi, 19.VIII.2021, Y. Tamadera leg. (YTJ). Kyushu — 2 ex., Masubuchi Dam, Kagumeyoshi, Kokura-minami-ku, Kitakyushu-shi, 25.VII.2022., Y. Tamadera leg. (YTJ). Tsushima Is. (Nagasaki) — 2 exs., Meboro, Kamiagata-machi, Nagasaki, 12.VI.2005, Y. Komiya leg. (SEHU). **South Korea**. 1 ♂, 3 exs., Jung-Mun, Quelpart I. (Jeju Is.), 12.VIII.1984, S. M. Lee leg. (NSMT). **China**. 1 ex., "Tenshing" (Tianjin), X.1925, von M. Suzuki leg. (NSMT; recorded by Kurosawa, 1976 d).

Distributions in Japan. Hokkaido (new record), Honshu, Shikoku, Kyushu, and Tsushima Is. (new record).

Other locality based on literature: Yashirojima Is. (Yamaguchi) (Entomological Society of Yamaguchi, 2018), Shôdoshima Is. (Fujimoto, 2019), and Kashiwajima Is. (Saga) (Nishida, 2018).

Other distributions. China and North Korea.

Adult food plant. Same as in the larvae mentioned below. Adult feeding scars as shown in Fig. 65C.

Host plant. Ulmaceae: *Zelkova serrata* (Thunb.) Makino [Japanese name: Keyaki] (Yano, 1952 for the forma A of *Trachys griseofasciatus*; Kurosawa, 1959; this study) in Japan.

Leaf-mining habit. Mines of *Trachys yanoi* were found on *Zelkova serrata* by this study (Figs. 65C, 69D): each mine was of the full-depth type and formed a large, elongate blotch occurring usually along leaf-margin; when full-grown, it occupied about half of whole the leaf blade; eggs, which were pale-yellow (remaining eggshell) and usually not covered on powdery substances, were laid singly on the adaxial surface of the leaf blade near leaf-margin; hatched larvae left granular to thread-like frass inside the mines; adults were emerged from the adaxial or abaxial surfaces of the leaves with oval adult exit holes. See also Yano (1952) treated as *Trachys griseofasciata* "Forma A" for descriptions of the leaf-mines and immature stages and Yuasa (1933) treated as *T. subbicornis* for a description of the immature stages.

Agricultural pest records. Several papers have been reported that *T. yanoi* sometimes occurs in large numbers on Honshu, for example Tokyo, Yamanashi, and Kyoto (Kurosawa, 1976d; Ohsawa, 2017). This species is recognized as an important pest of *Zelkova serrata*, which is a common plant species in Japan and is often planted in parks and streets. At the time of outbreak, infested trees by this species are caused premature leaf fall. Ohsawa (2017) and Ohsawa and Iijima (2019) are reported its life cycle, population dynamics, etc. to establish methods for reducing this plant damages caused by the jewel beetles.

Notes. With regard to the morphological differences between adults of *Trachys yanoi* and *T. griseofasciatus* Saunders, 1873, the proportion of clypeus is recognized as the most useful character to be differentiated *T. yanoi* from *T. griseofasciatus* (Kurosawa, 1959): the clypeus of *T. yanoi* is about 1.5 times as wide as long, whereas that of *T. griseofasciatus* is about twice as wide as long. In this study, it is also confirmed that the clypeus of *T. yanoi* is usually narrower than that of *T. griseofasciatus* and this character is useful to determine species, but the measured value of the proportion of clypeus in each species does not match Kurosawa's description (see also Table 1). Actually, the clypeus of *T. yanoi* is 1.64–1.97 times as wide as long (WC/LSC ratio), whereas that of *T. griseofasciatus* is 2.00–2.71 times as wide as long (WC/LSC ratio). Judging from these facts, many literature records of *T. yanoi* and *T. griseofasciatus*, based on Kurosawa's measured values for the proportion of the clypeus, probably include numerous misidentifications.

Trachys yanoi is sometimes sympatrically distributed with *T. cupricolor* Saunders, 1873, which is also associated with *Zelkova serrata*. Hibernated individuals of *T. yanoi* are often discolored the elytra into similar copper color to those of *T. cupricolor*, but such *T. yanoi* are readily distinguished from *T. cupricolor* by the absence of the prosternal elevated portions along the procoxal cavities, etc.

Taxonomic history. *Trachys yanoi* had been identified to the same species as *T. griseofasciatus* for a long time. Yano (1952), for the first time, found that *T.*

griseofasciatus can be divided into two morphological types, "Forma A" and "Forma B", in its larval stages: the forma A larva (final instar) is characterized by the light colored thoracic and abdominal sclerotized-plates, by the rugose and depressed sclerotized-plates on the abdominal segments first to seventh ("R-type" after Yano, 1952) (Figs. 54C, D), and by the host, *Zelkova serrata*, whereas the forma B is by the much darker thoracic and abdominal sclerotized-plates, by the smooth and depressed sclerotized-plates on the abdominal segments first to seventh ("S-type" after Yano, 1952) (Figs. 54 A, B), and by the host, *Aphananthe aspera*. Later, Kurosawa (1959) described forma A as a new species *Trachys yanoi* since the forma A adult is distinguishable from the forma B adult by the clypeus proportion and by the shade of integument coloration (see also the original description of *T. yanoi*) in addition to the differences of larval morphology and hosts. Through examination of type specimens of *T. griseofasciatus*, Kurosawa (1976 c) mentions that his recognition of *T. griseofasciatus* and *T. yanoi* is nothing but correct.

Group VII (variolaris)

(Figs. 48C–E)

Species included. *Trachys variolaris* Saunders, 1873, *T. robustus* Saunders, 1873, and *T. dilaticeps* Gebhardt, 1929.

Diagnosis. Body ovate type. Apical margin of pronotum without median lobe. Elytra with serrate lateral margins; elytral vestiture with thick transverse bands consisting of multicolor setae in apical half of each elytron, without tufts consisting of erect setae. Prosternum more or less rimmed along apical margin which is not lobed; prosternal disk without elevated portions along procoxal cavities. Abdominal ventrites with sternal grooves on ventrite I–V. Female coxites ventrally with transverse depression in apical part.

Trachys variolaris Saunders, 1873

[Japanese name: Dandara-chibi-tamamushi]

(Figs. 48C, 55A–E, 56, 57, 65D, 70A)

Trachys variolaris Saunders, 1873: 521 (type locality: "Japan"); Lewis, 1879: 15 (catalog); Kerremans, 1885: 157 (catalog); 1892 a: 289 (catalog); Lewis, 1893: 338 (in list); Kerremans, 1903: 314 (catalog); Jakobson, 1913: 800 (catalog); Kurosawa, 1950 a: 13 (note); 1950d: 1111, fig. 3185 (pictorial book); Chûjô & Kurosawa, 1950:

14 (Shikoku, Japan); Yano, 1952: 34 (immature stages); Iga, 1955 a: 10, pl.4 (pictorial book); 1955 b: 80, pl.24 (pictorial book); Kurosawa, 1959: 238 (redescription; Japan and China); 1963: 156, pl. 78 (pictorial book); 1976 d: 3 (note; South Korea); 1980: 47, fig. 2 (subsp. *robustissima* Kurosawa synonymized under *Trachys dilaticeps* Gebhardt); 1985 b: 36, pl. 7 (pictorial book); Akiyama & Ohmomo, 1997: 49 (checklist); 2000: 285, pl. 120 (pictorial book); Fukutomi & Hori, 2004: 15, fig. 59 (Okushiritô Is., Japan); Kubáň, 2006: 421 (Palaearctic catalog; Taiwan); Ohmomo & Fukutomi, 2013: 168, pl. 53 (pictorial book); Kubáň, 2016: 574 (Palaearctic catalog); Ishiguro & Nishida, 2018: 33, figs. 2, 3 & 6 (aedeagus); Cao & Wang, 2019: 3042 (complete mitochondrial genome); Peng, 2022a: 272 (distribution).

Trachys (*Trachys*) *variolaris*: Obenberger, 1918: 19, 36, 64 (in key; in catalog); 1926 b: 661 (catalog); Miwa & Chûjô, 1936: 26 (list); Obenberger, 1937 a: 1384 (World catalog).

Trachys variolaris variolaris: Kurosawa, 1959: 238 (redescription; Japan and China); 1963: 156, pl. 78 (pictorial book); Bellamy, 2008b: 2530 (World catalog).

Trachys variolaris [auct. non Saunders, 1873]: Ong & Hattori, 2019: 208, 226 (misidentification of *Trachys dilaticeps*; aedeagus).

Trachys (*Trachys*) *clavicornis* Obenberger, 1919: 144 (type locality: "Kiao-Tchéou (Chine)"); 1926 b: 662 (catalog); 1937 a: 1356 (World catalog); Miwa & Chûjô, 1940: 74 ("Hoki", Okayama, Japan). Synonymized under *T. variolaris* by Kurosawa, 1959: 238.

Trachys clavicornis: Obenberger, 1958: 242 (Yunnan, China).

Description. Male and female. Body ovate, lowly convex dorsally (Figs. 56A, B). LB 3.34–4.45 mm (mean 3.86 mm); WB 1.87–2.55 mm (mean 2.23 mm); LB/WB 1.69–1.79 (mean 1.74) (n = 20 for all measurements except terminalia). Habitus as shown in Figs. 48C, 55A–E.

Integument. Head and pronotum brassy-black to dark golden-bronze, sometimes with faint reddish to faint purplish tints; elytra black, sometimes with faint purplish tints; underside, antennae, and legs black with faint golden-bronze reflections, except for femora sometimes with faint purplish tints in ventral side and basal four tarsomeres light-brown; maxillary palps light-brown. Dorsal surface slightly weakly shiny; ventral surface moderately shiny.

Vestiture mainly consisting of white, yellow to brown, and black setae; black and yellow to brown setae showing various shades individually. Head densely clothed with short, recumbent, yellow to brown setae, usually with two white spots on vertex which are surrounded by brownish setae, in male setae becoming more yellow and denser on frons than in female. Pronotum densely clothed with short, semirecumbent, white, yellow to brown, and black setae which are arranged as follows: 1) four round black patches across middle; 2) a few white setae scattering around the black patches; and 3) yellow setae in remaining space, becoming brownish near the black patches. Elytra densely clothed with short, semirecumbent, white, yellow to brown, and black setae which are generally arranged on each elytron as follows: 1) white setae and yellow to brown ones irregularly scattering in basal 1/3 and sometimes at apex; 2) one yellow to brown patch just before middle near sutural margin; 3) one yellow to brown patch laterally just behind middle, sometimes forming a circle fused with the following first transverse band; 4) first transverse band consisting of yellow to brown setae at apical 1/3, becoming more brownish medially, somewhat surrounded by white setae except lateral part, moderately wavy, thick; 5) second transverse band at subapical part, consisting of darker setae than those of first band, with white setae along distal side throughout, more weakly wavy than the first transverse band; and 6) black setae in remaining space, usually predominant in elytron. Dorsal patterns of setae rarely showing prominent individual variations as in Figs. 55C–E. Underside more sparsely setiferous, with fine, recumbent, yellowish setae becoming denser and longer in lateral part of metacoxal plates.

Head, when viewed from above, slightly shallowly, arcuately concave on frons, with oculofrontal margins rounded. Eyes, when viewed from above, broadly visible, moderately convex laterally. Vertex obscurely and coarsely variolate-punctate; frons widely concave, weakly impressed along upper side of midline, transversely ridged from just above each antennal insertion to inner margin of each eye, with surface rather smooth but faintly punctate; suprantennal pores simply round; clypeus wide (Fig. 56D), with weak elevated basal margin, WC/LC 1.76–2.25 (mean 2.02), WC/LSC 1.74–2.64 (mean 2.00), deeply arcuately emarginate at apical margin.

Antennae (Fig. 56E, F) reaching just behind apicolateral angles of pronotum when laid alongside; antennomere I stout claviform, longer than II; II ovate, longer than III; III subrectangular, longer than IV; IV–VI subrectangular, subequal each other in length; VII–X triangular, more strongly enlarged and slightly thicker in male than in female; XI subtriangular to sublingulate.

Mandibles with strong, transverse ridge in about middle of each outside. Maxillary palps with oval palpomere IV somewhat longer than wide.

Pronotum widest at base, WP/LP 2.76–3.09 (mean 2.94), BMP/AMP 1.44–1.56 (mean 1.50), narrower than elytra; lateral margins weakly arcuate in basal 1/3 then straightly and moderately narrowed apicad; apicolateral angles obtuse, not reaching eyes; basolateral angles broadly acute to right; apical margin moderately arcuately emarginate, without median lobe; basal margin trisinuate, with median lobe moderately produced; disk weakly depressed along median lobe of basal margin; surface obscurely variolate-punctate, becoming denser toward apical and basal margins. Scutellar shield very small, subtriangular, glabrous.

Elytra widest at humeri, LE/WE 1.22–1.30 (mean 1.27), LE/LP 3.76–4.27 (mean 3.99); humeral calluses slightly weakly developed; lateral margins weakly narrowed posteriorly behind humeri then subparallel to middle, and finally arcuately convergent to conjointly rounded apices, with slightly strong serrations in about apical half except apices (Fig. 56C); marginal carinae distinct in thoracic region, indistinctly reaching near apices; sutural margin faintly elevated in apical 1/3; disk weakly depressed in basal part, constricted behind humeri, weakly swollen in subapical part; surface irregularly and coarsely punctate, weakly rugulose between punctures in basal half. Lateral part of abdomen narrowly visible in dorsal view; laterosternites I–IV with laterosternal sulci.

Underside. Prosternum (Fig. 56G) rather straight at apical margin which is weakly rimmed; prosternal process wide, constricted between procoxa, with apex broadly rounded at rest; marginal carinae moderately widely separated each other at widest part of prosternal process, weakly divergent posteriad from apical 1/4; disk rather flattened on median portion, somewhat declivous laterad on outside of marginal carinae, without elevated protions along procoxal cavities. Hypomera with depressed hypomeral markings large in size, subreniform, additionally depressed inside (Fig. 56H). Metaventrite densely sculptured with large punctures on inside of katepisternal suture and moderately sculptured with linearly confluent sculptures on outside of the suture. Legs moderately slender; metacoxal plates slightly strongly produced posteriorly at each lateral angle which is sharply acute with rounded apex, with surface coarsely variolate; metatibiae bearing a fringe of spines in apical half of each outer margin, without one long spine in base of the fringe (Fig. 56I); inner tooth of each claw large. Abdominal ventrites with sternal grooves on ventrites I–V; V (Fig. 56J) rounded at apex; surface variolate, in ventrite I with linearly confluent sculptures on median part.

Sexual dimorphism recognized in the setae on frons and the relative size and thickness of serrate antennomeres (see above), but slightly continuous.

Male terminalia (n = 4 for measurements). Proctiger with a pair of short baculi at base. Sternite IX (Fig. 57A) wide, SL/SW 0.67–0.91 (mean 0.77), rather roundly truncate on apical margin, bearing several setae on each side of apical margin. Tegmen (Fig. 57B) wide; parameres PL/PW 1.55–1.75 (mean 1.64), slightly densely setiferous on apicolateral margins, with sides which are gently dilated from base to apical half, then more strongly dilated to widest subapical part, and finally strongly arcuately convergent to apices; phallobase PbL/PbW 2.69–3.82 (mean 3.26), about 1/3 length of tegmen. Penis (Fig. 57C) wide, PeL/PeW 3.57–4.00 (mean 3.82), shorter than tegmen; dorsal plate weakly bisinuate on sides which are rather strongly narrowed from widest point of base to apical 3/4, then more weakly narrowed to subapical part, and finally continuously arcuately convergent apicad, with weakly pointed apex, basally with median struts about 1/3 length of penis; ventral plate membranous, but weakly sclerotized as a linear patch in middle of apical 1/3.

Female terminalia (n = 5 for measurements). Ovipositor (Figs. 57D–F) short; proctiger basally with a pair of long, ventrally curved baculi; coxites transversely subhexagonal, sparsely setiferous on each side of apical margin, ventrally with transverse depression in apical part; styli slightly fan-shaped, with sides gently dilated apicad, SlL/SlW 1.42–1.75 (mean 1.63), bearing several setae apically; ventral valve sparsely setiferous on each side of subapical part; vagina sack-shaped, constricted at middle; spermatheca prominently wide tubular, rather short in length, widest near apex, without spermathecal gland.

Differential diagnosis. This species is related to *Trachys robustus* and *T. dilaticeps* in having the characteristic patterns of setae on the pronotum and elytra, but can be distinguished from them by the combination of the following character states: pronotum usually with more distinct four black patches; lateral margins of pronotum weakly arcuate in basal 1/3 (same as in *T. dilaticeps*); elytra predominantly clothed with black setae usually; male parameres continuously dilated from base to widest subapical part (similar to that of *T. dilaticeps*); wider penis with weakly pointed apex which is not produced; female styli slightly fan-shaped (same as in *T. dilaticeps*); and spermatheca much wider (same as in *T. dilaticeps*) and bended proximally behind unpigmented accessory portion (same as in *T. robustus*).

Specimens examined. Non type material. **Japan**. Hokkaido — 5 exs., Toi, Hama-chô, Hakodate-shi, 11.VII.2022, Y. Tamadera leg. (YTJ); 1 ex., ditto, emerged from *Quercus dentata*, 1.VIII.2022, rearing no. 2022-148 (YTJ). Okushiri-tô Is. — 1 ♂., Akaishi, Okushiri-chô, 23–24.IX.2004, S. Takahashi leg., captured on *Fagus crenata* (STCH; recorded by Takahashi, 2008). Honshu — [Miyagi] 1 ex., Akiho, Natori-shi, 24.VI.1951, K. Nagayama leg. (SEHU). [Fukushima] 1 ex., Aizu-wakamatsu-Shi, 17.V.1946, K. Nagayama leg. (SEHU). [Ibaraki] 1 ex., Tsukuba-shi, 23.V.1976, A. Tanaka leg. (SEHU). [Gunma] 1 ex., Akagi-jinja – Miyagi-mura, Maebashi-shi, 12.VI.2005, H. Takizawa leg. (SEHU); 1ex., Numata-shi, 12.VI.1966, T. Takei leg. (SEHU); 1 ex., same locality, 4.V.1967, T. Takei leg. (SEHU); 1 ex., same locality, 27.V.1966, T. Takei leg. (SEHU). [Saitama] 1 ex., Nishikubo-shittchi, Iruma-shi, 22.X.2004, Y. Komiya leg. (SEHU); 1 ex., Yorii-machi, 5.V.2000, H. Takizawa leg. (SEHU); ken, Japan, 29.V.2015, G. Mashima leg; 1 ♀, Kitanominami, Tokorozawa-shi, 2.VII.2016, Y. Tamadera leg. (YTJ). [Tokyo] 1 ex., Mont Takao, Hachiôji, 18.V.1913, E. Gallois leg. (SEHU); 1 ♀, near Kogesawa-rindo, Uratakao-machi, Hachioji-shi, Tokyo-to, Japan, 12.V.2017, Y. Tamadera leg. (YTJ). [Kanagawa] 1 ex., Mt. Bukka-san, Hadano-shi, 15.IX.1973, S. Tachikawa leg. (SEHU); 1 ♂, Mt. Takamatsu-yama, Ono, Atsugi-shi, 10.V.2008, T. Ishizaki leg. (YTJ). [Niigata] 1 ♀, Mt. Sumon-odake, Tochibori, Nagaoka-shi, 29.V.2015, G. Mashima leg. (YTJ). [Yamanashi] 1 ex., Hinoharu, Hokuto-shi, 30.IV.1979, M. Ôhara leg. (SEHU); 1 ♀, Hishiyama, Katsunuma-chô, Koshû-shi, 3. V.2017, J. Souma leg. (YTJ). [Gifu] 1 ex., Suhara, Mino-shi, 2.V.1955, K. Ohbayashi leg. (SEHU); 1 ♂, Daibo, Hakushû-machi, Hokuto-shi, 5.V.2011, M. Miyao leg. (YTJ). [Aichi] 1 ex., Higashiyama, Nagoya-shi, 15.V.1946, T. Nakane leg., captured on *Quercus acutissima* (SEHU); 1 ex., same locality, 16.V.1946, T. Nakane leg. (SEHU), 1 ex., same locality, 1–10.V.1948, T. Nakane leg. (SEHU); 1 ex., same locality, 13.V.1949, T. Nakane leg. (SEHU); 1 ex., Gamo, Mikawa, 14.V.1948, T. Nakane leg. (SEHU); 1 ex., Mikawa-ôno, Shinshiro-shi, 10.V.1991, TTM. Nakane leg. (SEHU); [Mie] 1 ex., Ise-Jingû Sotomiya, Toyokawa-chô, Ise-shi, 21.XI.1976, C. Oikawa leg. (SEHU); 1 ex., Asahidani, Ise-shi, 24.VII.1977, C. Ohkawa leg. (SEHU). [Kyoto] 1 ex., Kitashirokawa, Kyoto-shi, 9.V.1964, T. Nakane leg. (SEHU); 2 exs., Fukuchiyama-shi, 5.VIII.1956, F. Takahashi leg. (SEHU); 1 ex., Kyoto, 2.V.1964, T. Nakane leg. (SEHU); 1 ex., Ninose, Kyoto-shi, 10.V.1957, T. Nakane leg. (SEHU); 1 ♀, Nishikyô-ku, Kyoto-shi, 18.V.2015, Y. Tamadera leg. (YTJ). [Osaka] 1 ex., Mino-o-shi, 30.V.1937, K. Sakaguchi leg. (SEHU). [Hyôgo] 1 ex., Harima, 23.IV.1912, T. Takamuku leg. (SEHU); 1 ex., Sasayama, 28.VI.1956, T. Nakane & T. Okutani leg. (SEHU); 1 ex., Okanomura, Taki-gun, 21.IV.1951, A. Nagatomi leg. (SEHU); 1 ex., Mt. Maya-san, Kôbe-shi, 13.V.1939, K. Taniguchi leg. (SEHU); 1 ex., Motoyama-mura near Kôbe, 2.VII.1939, K. Taniguchi leg. (SEHU). [Nara] 1 ex., Shimoikehara, Shimokitayama-mura, 10.VIII.1956, S. Kokawa leg. (SEHU). [Wakayama] 1 ex., Gobô-shi, 4.V.1993, N. Ito leg. (SEHU). [Hiroshima] 2 exs., Onomichi-shi, 16.V.1947, K. Ohbayashi leg. (SEHU); 1 ex., Hirugakusa, Sera-chô, 10.VI.1979, T. Kosaka leg. (SEHU); 1 ex., Mt. Mitsumine-san, Kure-shi, 29.IV.1963, T. Kosaka leg. (SEHU); 1 ex., Mt. Ôtsuchi-yama, Akitakata-shi, 7.V.1978, T. Kosaka leg. (SEHU). Awajishima Is. (Hyôgo) — 1 ex., Kashiwarayama-rindô, Chikusaki, Sumoto-shi, 13.VII.2022, Y. Tamadera leg. (YTJ); Shikoku — [Tokushima] 1 ex., Koyadaira, Awa, 9.VIII.1913, E. Gallois leg. (SEHU). [Kagawa] 1 ex., Kagawa-chô, Takamatsu-shi, 13.V.2000, H.

Takizawa leg. (SEHU). [Ehime] 1 ex., Iyo, 19.V.1910, S. Matsumura leg. (SEHU); 2 ♂♂, Sue-machi, Matsumoto-shi, 23.IV.2019 Y. Tamadera leg. (YTJ). Kyushu — [Fukuoka] 2 exs., Mt. Tachibana-yama, Fukuoka-shi, 18.V.1986, A. Tanaka leg. (SEHU). [Saga] 1 ex., Hill Kurigo, 16.V.1952, H. Yamaguchi leg. (SEHU); 1 ex., same locality, 30.IX.1952, H. Yamaguchi leg. (SEHU). [Miyazaki] 1 ex., Mt. Takahata-yama, Kushima-shi, 14.VI.2006, Y. Komiya leg. (SEHU); 1 ex., Hinokage-chô, 16.V.1987, T. & T. Nakane leg. (SEHU); 1 ex., Akiru, Hyûga-shi, 7.VI.1942, no collector name (SEHU). [Kagoshima] 1 ex., Sata, Minami-ôsumi-chô, 26.V.1952, T. Nakane leg. (SEHU); 2 exs., Izashiki, Sata, Minami-ôsumi-chô, 15.IV.1984, T. & T. Nakane leg. (SEHU). Tsushima Is. (Nagasaki) — 1 ex., Azamo, Izuhara-machi, 10.VI.2005, Y. Komiya leg. (SEHU). **South Korea**. 1 ex., Mt. Sudosan, Kyongsangpuk-do, Korea, alt. 400 m, 17–18.VII.1971, K. Yamagishi leg. (NSMT; recorded by Kurosawa, 1976d); 1 ex., Korea, Mt. Sudosan, Kyongsangpuk-do, alt. 700 m, 29.V.1970, K. Yamagishi leg. (NSMT; recorded by Kurosawa, 1976d). **China**. 2 exs., "Shinka Pref., Funnang, C.-China" (Xinghua, Hunan, Central China), VI.1945, K. Shirahata leg. (NSMT; recorded by Kurosawa, 1959).

Distributions in Japan. Hokkaido, Honshu, Shikoku, Kyushu, Okushiri-tô Is., Awajishima Is., and Tsushima Is.

Other record based on literature: Shôdoshima Is. (Fujimoto, 2007, included other small islands of Kagawa Pref.).

Other distributions. China and South Korea.

Taiwan is removed from distribution of this species because the first record (Kubáň, 2006) does not show material examined data. In addition, this species shown by Ong & Hattori (2019) from Taiwan are probably misidentification of *Trachys dilaticeps* based on the roundly produced apex of male penis and the large-sized body.

Adult food plants. Same as in the larvae mentioned below. In addition, Takahashi (2008) confirmed that the adults feed on leaves of *Fagus crenata* Blume [Japanese name: Buna] (Fagaceae) in Okushiritô Is. off Hokkaido, Japan.

Host plants. Fagaceae: *Quercus acutissima* Carruth. [Japanese name: Kunugi] (Kurosawa, 1959 — adult record?), *Q. variabilis* Blume [Japanese name: Abemaki] (Yano, 1952), *Q. serrata* Murray [Japanese name: Konara] (Yano, 1952), *Q. crispula* Blume [Japanese name: Mizunara] (Kurosawa, 1959 — adult record?), *Q. dentata* Thunb. [Japanese name: Kashiwa] (Kurosawa, 1959 — adult record?; confirmed by this study), *Q. glauca* Thunb. [Japanese name: Arakashi] (Yano, 1952), and *Q. salicina* Blume [Japanese name: Urajirogashi] (confirmed by this study) in Japan.

Leaf-mining habit. Mines of *Trachys variolaris* were found on *Quercus dentata* and *Q. salicina* by this study (Fig. 65D, 70A): each mine was of the full-depth type and formed a large, irregularly elongate blotch occurring usually along leaf-margin, but occasionally in medial part; when full-grown, it occupied more than half of whole the leaf blade of *Q*. *salicina* and much less than half of it of *Q*. *dentata*; eggs, which were black (remaining eggshell) and covered on powdery substances, were laid singly on the adaxial surface of the leaf blade; hatched larvae left thread-like frass inside the mines; adults were emerged from the adaxial surfaces of the leaves with oval adult exit holes. See also Yano (1952) for descriptions of the leaf-mines and immature stages.

Note. The patterns of setae of *Trachys variolaris* shows various shades in color. The predominant color of the elytral setae is usually black (Figs. 55A, B), but the black, yellow, and brown setae are occasionally subequally occurring on the elytra (Fig. 55C). Additionally, much more yellow or black colored individuals are very rarely recognized as shown in Figs. 55D, E (the former: n =1; the latter: n = 2).

Trachys robustus Saunders, 1873
[Japanese name: Sashige-chibi-tamamushi]
(Figs. 48D, 55F–J, 58, 59, 65E, 70B)

Trachys robusta Saunders, 1873: 521 (type locality: “Japan”); Lewis, 1879: 15 (catalog); Kerremans, 1885: 157 (catalog); Schönfeldt, 1887: 113 (catalog); Kerremans, 1892 a: 288 (catalog); Lewis, 1893: 338 (in list); Kerremans, 1903: 314 (catalog); Jakobson, 1913: 800 (catalog); Chûjô & Matuda, 1940: 66 (Kyushu, Japan); Kurosawa, 1950 a: 14 (note); Chûjô & Kurosawa, 1950: 13 (Shikoku, Japan); Iga, 1955 a: 10, pl.4 (pictorial book); Yano, 1955: 90 (immature stages); Iga, 1955 b: 80, pl.24 (pictorial book); Kurosawa, 1959: 241 (redescription); 1963: 156, pl. 78 (pictorial book); 1976d: 1 (note); 1980: 46 (biogeography); 1985b: 36, pl. 7 (pictorial book); Akiyama & Ohmomo, 1997: 48 (checklist); 2000: 285, pl. 120 (pictorial book); Kubáň, 2006: 420 (Palaearctic catalog); Tamadera, 2021: 54 (distribution); 2022: 65 (distribution).

Trachys (*Trachys*) *robusta*: Obenberger, 1918: 19, 36, 64 (in key; in catalog); 1926 b: 661 (catalog); Miwa & Chûjô, 1936: 25 (list); Obenberger, 1937 a: 1378 (World catalog; Japan and ? China).

Trachys robustus [justified emendation, according to ICZN (2009)]: Bellamy, 2008 b: 2516 (World catalog); Ohmomo & Fukutomi, 2013: 168, pl. 53 (pictorial book); Kubáň, 2016: 573 (Palaearctic catalog); Ishiguro & Nishida, 2018: 33, figs. 2, 3 & 6 (aedeagus); Štrunc, 2022: 196 (photograph).

Description. Male and female. Body ovate, lowly convex dorsally (Figs. 58A, B). LB 3.52–4.91 mm (mean 4.30 mm); WB 1.98–2.82 mm (mean 2.44 mm); LB/WB 1.72–1.82 (mean 1.77) (n = 20 for all measurements except terminalia). Habitus as shown in Figs. 48D, 55F–J.

Integument above mainly black; head, pronotum and underside sometimes with faint golden-bronze reflections; maxillary palps light-brown; basal four tarsomeres brown to light-brown. Dorsal surface slightly weakly shiny; ventral surface moderately shiny.

Vestiture mainly consisting of white, yellow to brown, and black setae; yellow to brown setae predominant above, showing various shades individually. Head densely clothed with short, recumbent, yellow to brown setae, usually with two white spots on vertex, in male setae becoming more yellow and denser on frons than in female. Pronotum densely clothed with short, semirecumbent, yellow, dark-brown and white setae which are arranged as follows: 1) four round dark-brown patches across middle, rather inconspicuous; 2) a few white setae scattering around the dark-brown patches; and 3) brownish-yellow setae in remaining space. Elytra densely clothed with short, semirecumbent, yellow to brown, white and black setae which are arranged on each elytron as follows: 1) white setae and yellow to brown setae rather complexly scattering in basal half; 2) first transverse band consisting of yellow to brown setae at apical 1/3, somewhat surrounded by white setae except lateral part, moderately wavy, thick; 3) second transverse band consisting of yellow to brown setae at subapical part, with white setae along distal side throughout, more weakly wavy than the first transverse band; and 4) dark brown setae in remaining space, but occasionally replaced black ones as shown in Fig. 55I. Dorsal patterns of setae rarely showing prominent intraspecific variations as in Fig. 55J. Underside more sparsely setiferous, with fine, recumbent, yellowish setae becoming denser and longer in lateral part of metacoxal plates.

Head, when viewed from above, slightly shallowly, arcuately concave on fronts, with oculofrontal margins rounded. Eyes, when viewed from above, broadly visible, moderately convex laterally. Vertex obscurely and coarsely variolate-punctate; frons widely concave, weakly impressed along upper side of midline, transversely ridged from just above each antennal insertion to inner margin of each eye, with surface rather smooth but faintly punctate; suprantennal pores simply round; clypeus wide (Fig. 58D), with weak elevated basal margin, WC/LC 1.71–2.44 (mean 2.19), WC/LSC 1.71–2.10 (mean 1.96), deeply arcuately emarginate at apical margin.

Antennae (Fig. 58E, F) reaching just behind apicolateral angles of pronotum when laid alongside; antennomere I stout claviform, longer than II; II ovate, longer than III; III subrectangular, longer than IV; IV–VI subrectangular, subequal each other in length; VII–X triangular, more strongly enlarged and slightly thicker in male than in female; XI subtriangular to sublingulate.

Mandibles with strong, transverse ridge in about middle of each outside. Maxillary palps with oval palpomere IV somewhat longer than wide.

Pronotum widest at base, WP/LP 2.81–3.09 (mean 2.95), BMP/AMP 1.44–1.56 (mean 1.50), narrower than elytra; lateral margins usually straightly and moderately narrowed apicad; apicolateral angles obtuse; basolateral angles broadly acute; apical margin moderately arcuately emarginate, without median lobe; basal margin trisinuate, with median lobe moderately produced; disk faintly to weakly depressed along basal median lobe; surface obscurely variolate-punctate, becoming denser toward apical and basal margins. Scutellar shield very small, subtriangular, glabrous.

Elytra widest at humeri, LE/WE 1.27–1.33 (mean 1.30), LE/LP 3.86–4.37 (mean 4.12); humeral calluses slightly weakly developed; lateral margins weakly narrowed posteriorly behind humeri then subparallel to middle, and finally arcuately convergent to conjointly rounded apices, with slightly strong serrations in about apical half except apices (Fig. 58C); marginal carinae distinct in thoracic region, indistinctly reaching near apices; sutural margin faintly elevated in apical 1/3; disk weakly depressed in basal part, constricted behind humeri, weakly swollen in subapical part; surface irregularly and coarsely punctate, weakly rugulose between punctures in basal half. Lateral part of abdomen narrowly to slightly broadly visible in dorsal view.

Underside. Prosternum (Fig. 58G) rather straight at apical margin which is weakly rimmed; prosternal process wide, constricted between procoxa, with apex broadly rounded at rest; marginal carinae moderately widely separated each other at widest part of prosternal process, weakly divergent posteriad from apical 1/4; disk rather flattened on median portion, somewhat declivous laterad on outside of marginal carinae, without elevated protions along procoxal cavities. Hypomera with depressed hypomeral markings large in size, subreniform, additionally depressed inside (Fig. 58H). Metaventrite densely sculptured with large punctures on inside of katepisternal suture and moderately sculptured with linearly confluent sculptures on outside of the suture. Legs moderately slender; metacoxal plates slightly strongly produced posteriorly at each lateral angle which is sharply acute with rounded apex, with surface coarsely variolate; metatibiae bearing a fringe of spines in apical half of each outer margin, without one long spine in base of the fringe (Fig. 58I); inner tooth of each claw large. Abdominal ventrites with sternal grooves on ventrites I–V; V (Fig. 58J) rounded at apex; surface variolate, in ventrite I with linearly confluent sculptures on median part.

Sexual dimorphism recognized in the setae on frons and the relative size and thickness of serrate antennomeres (see above), slightly continuous.

Male terminalia (n = 5 for measurements). Proctiger with a pair of short baculi at base. Sternite IX (Fig. 59A) wide, SL/SW 0.61–0.77 (mean 0.71), rather truncate on apical margin, bearing several setae on each side of apical margin. Tegmen (Fig. 59B) wide; parameres PL/PW 1.53–1.84 (mean 1.68), slightly densely setiferous on apicolateral margins, with sides which are faintly sinuately subparallel from base to beyond middle, then strongly arcuately expanded to widest point at apical 1/5, and finally strongly arcuately convergent to apices; phallobase PbL/PbW 2.26–2.90 (mean 2.61), more than 1/4 length of tegmen. Penis (Fig. 59C) wide, PeL/PeW 4.35–5.41 (mean 4.85), slightly shorter than tegmen; dorsal plate faintly bisinuate on sides which are gradually narrowed from widest point of base to subapical part, and then continuously arcuately convergent apicad, with round apex, basally with median struts about 1/3 length of penis; ventral plate membranous, but weakly sclerotized as a linear patch in middle of apical 1/3.

Female terminalia (n = 5 for measurements). Ovipositor (Figs. 59D–F) short; proctiger basally with a pair of long, ventrally curved baculi; coxites transversely subhexagonal, sparsely setiferous on each side of apical margin, ventrally with transverse depression in apical part; styli subtrapezoidal, slender, with sides subparallel, SlL/SlW 2.22–2.71 (mean 2.50), bearing several setae apically; ventral valve sparsely setiferous on each side of subapical part; vagina roundly sack-shaped, rather strongly expanded dorsally in distal half; spermatheca slender tubular, long in length, widest at base, without spermathecal gland.

Differential diagnosis. This species is moderately or very similar in general appearance to *Trachys dilaticeps*, but differs from *T. dilaticeps* by the combination of the following character states: (1) lateral margins of pronotum relatively straight throughout usually; (2) elytral patterns of setae less distinct usually; (3) male parameres with distinct lateral expansion being widest at apical 1/5; (4) round apex of penis not produced; (5) female styli slender subtrapezoidal; and (6) spermatheca much slenderer.

Additionally, this species is similar in general appearance to *T. variolaris*, but is distinguished from *T. variolaris* by the combination of the following character states: four round patches on pronotum normally brown and inconspicuous; more brownish setae usually occurring on elytra; male penis slenderer with rounded apex; and the points mentioned above in (1), (2), (3), and (6).

Specimens examined. Non type material. **Japan**. Honshu — [Ibaraki] 1 ex., Makizono, Tsukuba-shi, 26.VI.1977, A. Tanaka leg. (SEHU). [Chiba] 1ex., Heguri-gawa River, Tomiura, 29–30.VII.1999, H. Takizawa leg. (SEHU); 1 ex., Ôami, 8.XI.2014, M.

Ôhara leg., soil sampling (SEHU); 3 exs., Ôami, 15.VI.1980, M. Ôhara leg. (SEHU); 4 exs., Kasamori, Mobara, 2.VI.1989, T. & T. Nakane leg. (SEHU); 4 exs., Narita-shi, 14.VI.1989, T. & T. Nakane leg. (SEHU); 1 ex., Sanuki-machi, Futtsu-shi, 21.IV.1989, T. & T. Nakane leg. (SEHU); 41 exs., Sakura-shi, 22.V.1989, T. & T. Nakane leg. (SEHU); 5 exs., Mt. Nokogiri-yama, 8.VI.1991, T. & T. Nakane leg. (SEHU); 5 exs., Abe, Sodegaura-shi, 10.VI.2015, S. Shimamoto leg. (YTJ). [Tokyo] 1 ex., Tokyo, VII.1903, no collector name (SEHU). [Kanagawa] 3 exs., Zushi-shi, 9.VI.1977, A. Tanaka leg. (SEHU); 4 exs., same locality, 24.IV.1988, A. Tanaka leg. (SEHU); 2 exs., Mt. Ôgusu-yama, Yokosuka-shi, 3.IX.1973, N. Kino, T. Ishiwatari, Y. Hasegawa, & T. Nakane leg. (SEHU); 3 exs., Mt. Takatori-yama, Zushi-shi, 19.VIII.1973, S. Tachikawa & M. Taguchi leg. (SEHU); 1 ex., Kamakura-shi, 26.V.-7.VII.1946, S. Imaoka leg. (SEHU); 3 exs., Atsugi Camp. of Toyko University of Agricultue, Funako, Atsugi-shi, 12.IV.2017, Y. Tamadera leg. (YTJ). [Shizuoka] 2 ♂♂, 3 ♀♀, 6 exs., Wakamiya-jinja, Kanbara, Shimizu-ku, Shizuoka-shi, 29.III.2017, H. Nagano leg. (YTJ). [Aichi] 3 exs., Mt. Ishimaki-yama, Minamiyama, Ishimaki-chô, Toyohashi-shi, 12.V.2016, S. Shimamoto leg. (YTJ). [Kyoto] 2 exs., Shimogamo, Kyoto-shi, 20.XI.1956, no collector name (SEHU); 1 ex., same locality, 16.V.1955, T. Kishii leg. (SEHU); 8 exs., Kyoto, 9.V.1964, T. Nakane leg. (SEHU); 1 ex., Kitashirakawa, Kyoto-shi, 21.IV.1964, T. Nakane leg. (SEHU). [Wakayama] 1 ♂, 2 ♀♀, 2 exs., Shionomisaki, Kushimoto-chô, Higashimuro-gun, 4.V.2013, Y. Fujisawa leg. (YTJ). The Izu Islands — [Izu-Ôshima Is.] 3 exs., near Yôgoshi-minasaki-tenbôdai, Okada, 4.VI.2019, Y. Tamadera leg. (YTJ; recorded by Tamadera, 2022). [Niijima Is.] 7 exs., Niijima-mura, 13.X.2014, T. Hasegawa leg. (YTJ); 14 exs., Niijima Is., Izu Isls., 14–15.VI.1983, T. Niisato leg. (NSMT); 4 exs., Niijima Is., Izu Isls., 2.VI.1967, M. Ohno leg. (NSMT); 2 exs., Niijima Is., Higashi-kaigan, 12.V.1951, T. Aoki leg. (NSMT). [Shikinejima Is.] 2 exs., Jinata, Niijima-mura, 31.V.2012, W. Yamada leg. (YTJ; recorded by appendix of Tamadera, 2022). [Kôzushima Is.] 11 exs., Kôzushima Is., Izu Isls., 10–13.VI.1983, T. Niisato leg. (NSMT). Awajishima Is. (Hyôgo) — 1 ex., Mt. Mikuma-yama, Orodani, Sumoto-shi, 13.VII.2022, Y. Tamadera leg., emerged from *Castanopsis sieboldii* subsp. *sieboldii*, 2.VIII.2022, rearing no. 2022-189 (YTJ). Shikoku — [Ehime] Mt. Sano-yama, Iyo, 2.VI.1916, S. Matsumura leg. (SEHU). [Kôchi] 2 exs., Mt. Kajigamori, Ôtoyo-chô, Nagaoka-gun, 22.VII.1952, K. Sawada leg. (SEHU); 1 ex., Matsuo, Tosashimizu-shi, 21.IV.2019, Y. Tamadera leg. (YTJ); 6 exs., Ashizuri-rindô, Ashizurimisaki, Tosashimizu-shi, 21.IV.2019, Y. Tamadera leg. (YTJ). Okinoshima Is. (Kôchi) — 2 exs., Okinoshima Is., 2–4.V.2019, K. Kuroda & K. Yasuda leg. (YTJ; recorded by Tamadera, 2021); 4 exs., Tanijiri, 2.III.1952, K. Sakaguchi leg. (SEHU; recorded by Tamadera, 2021); 46 exs., Moshima, 30.III.1952, K. Sakaguchi leg.

(SEHU; recorded by Tamadera, 2021); 17 exs., Okinoshima Is., 23.VII.1952, K. Sakaguchi leg. (SEHU; recorded by Tamadera, 2021); 1 ex., Kuboura, 25.VII.1952, K. Sakaguchi leg. (SEHU; recorded by Tamadera, 2021); 7 exs., Okinoshima Is., Kochi, 30.IV.1952, M. Azuma & K. Sakaguti leg. (SEHU); 1 ex., Moshima, Okinoshima Is., 22.VII.1952, K. Sakaguti leg. (SEHU). Kyushu — [Ôita] 3 ♀♀, 4 exs., Kamaeura, Kamae, Saiki-shi, 25.IV.2017, Y. Tamadera leg. (YTJ). [Miyazaki] 1 ex., Ibii, Nichinan-shi, 4.IV.1987, T. & T. Nakane leg. (SEHU); 1 ex., Gongenzaki, Hyûga-shi, 13.X.1968, A. Nagai leg. (SEHU); 4 exs., Udo, Nichinan-shi, 29.VII.1974, T. Nakane leg. (SEHU). [Kagoshima] 1 ex.,Sugiyamadani, Minami-ôsumi-chô, Kimotsuki-gun, 5.VIII.2007, Y. Tsutsumiuchi leg. (YTJ). Tsushima Is. (Nagasaki) — 1 ex., Mt. Ariake-yama, Izuhara-machi, Nagasaki, 28.VII.1978, T. Kosaka leg. (SEHU).

Distributions in Japan. Honshu, Shikoku, Kyushu, the Izu Isls. (Izu-Ôshima Is., Niijima Is., Shikinejima Is., and Kôzushima Is.), Awajishima Is., Okinoshima Is. (Kôchi), and Tsushima Is.

Other locality based on literature: Ugurujima Is. (Kôchi) (Doi & Fujita, 2012).

Other distributions. No record.

Adult food plant. Same as in the larvae mentioned below.

Host plant. Fagaceae: *Castanopsis sieboldii* (Makino) Hatus. ex T.Yamaz. et Mashiba subsp. *sieboldii* [Japanese name: Sudajii] (Yano, 1955; confirmed by this study); *C. cuspidata* (Thunb.) Schottky [Japanese name: Tsuburajii] (confirmed by this study: the Kumata collection in SEHU).

Leaf-mining habit. Mines of *Trachys robustus* were found on *Castanopsis sieboldii* by this study (Fig. 70B): each mine was of the upper surface type (the larvae feed on tissues of the upper epidermis and palisade layer) and formed a large, elongate blotch occurring along leaf-margin; when full-grown, it occupied almost whole of the leaf blade; eggs, which were pale-yellow (remaining eggshell) and not covered on powdery substances, were laid singly on the apical part of midrib on the adaxial surface but rarely on other parts of the leaf blade; hatched larvae left granular frass inside the mines; adults were emerged from the adaxial surface of the leaves with oval adult exit holes. When mines are relatively grown to the stage of the final instar, infested leaves are occasionally fallen off as shown in Fig 65E. See also Yano (1955) for descriptions of the leaf-mines and immature stages.

Notes. The character state on the shape of pronotal lateral margins in *Trachys robustus* (it is relatively straight throughout) has been recognized as a useful one to differentiate from two similar species, *T. variolaris* Saunders, 1873 and *T. dilaticeps* Gebhardt, 1929 (Kurosawa, 1959, 1976 d; Ohmomo & Fukutomi, 2013). However, we should be careful to identify *T. robustus* based on the shape of pronotal lateral margins, because that of *T. robustus* is occasionally arcuate as in those of *T. variolaris* and *T. dilaticeps*. So that, to identify *T. robustus*, individuals without its typical characteristics should be observed the structures of terminalia. These three species are easily distinguished by the character states of male and female teminalia (see their differential diagnoses).

Trachys dilaticeps Gebhardt, 1929

[Japanese name: Ôdandara-chibi-tamamushi]

(Figs.2C, 5F, 48E, 55K–O, 60, 61, 65F, 70C, D)

Trachys (*Trachys*) *dilaticeps* Gebhardt, 1929: 103 (type locality: "China: Hangchow, Chekiang"); Obenberger, 1937 a: 1357 (World catalog).

Trachys dilaticeps: Kurosawa, 1976 c: 3 (note; Japan, Taiwan, and China); 1980: 47 (biogeography); 1985 b: 36, pl. 7 (pictorial book); Akiyama & Ohomomo, 1997: 47 (checklist): 2000: 284, pl. 120 (pictorial book); Mühle, 2003: 48 (list); Kubáň, 2006: 418 (Palaearctic catalog); Bellamy, 2008 b: 2481 (World catalog); Ohmomo & Fukutomi, 2013: 168, pl. 53 (pictorial book); Lan & Ohmomo, 2015: 106 (Taiwan); Kubáň, 2016: 570 (Palaearctic catalog); Ishiguro & Nishida, 2018: 33, figs. 2, 3 & 6 (aedeagus); Tamadera & Yoshitake, 2018 a: 16 (Tokunoshima Is.); 2018 b: 58 (Kakaromajima Is.); Tamadera *et al*., 2019: 42 (Kumejima Is.).

Trachys (*Trachys*) *mixtipilis* Obenberger, 1929 a: 94 (type locality: "Tonkin: Faï-Tsi-Long", Vietnam). Synonymized under *T. dilaticeps* by Kurosawa, 1980: 47.

Trachys mixtipilis: Descarpentries & Villiers, 1966: 587, 596 (in key); Kubáň, 2006: 418 (Palaearctic catalog; synonym of *T. dilaticeps*); Bellamy, 2008 b: 2503 (World catalog); Kubáň, 2016: 570 (Palaearctic catalog; synonym of *T. dilaticeps*).

Trachys variolaris robustissima Kurosawa, 1959: 241 (type locality: "Ambô, Yakushima Island, Japan"); 1963: 156 (pictorial book). Synonymized under *T. dilaticeps* by Kurosawa, 1980: 47.

Trachys variolaris robustissimus [justified emendation, according to ICZN (2009)]: Bellamy, 2008 b: 2531 (World catalog); Kubáň, 2016: 570 (Palaearctic catalog; synonym of *T. dilaticeps*).

Trachys robusta robustissima [sic]: Kurosawa, 1976 c: 3 (*lapsus calami*; treated as synonym of *T. dilaticeps*; Taiwan).

Description. Male and female. Body ovate, lowly convex dorsally (Figs. 60A, B). LB 3.85–4.76 mm (mean 4.38 mm); WB 2.01–2.66 mm (mean 2.41 mm); LB/WB 1.76–1.92 (mean 1.82) (n = 20 for all measurements except terminalia). Habitus as shown in Figs. 48E, 55K–O.

Integument. Head and pronotum black or brassy-black, often with golden-bronze reflections; elytra black, sometimes with faint purplish tints, sometimes with weak golden-bronze reflections; underside, antennae, and legs black, sometimes with faint golden-bronze reflections, except basal four tarsomeres brown to light-brown; maxillary palps light-brown. Dorsal surface slightly weakly shiny; ventral surface moderately shiny.

Vestiture mainly consisting of white, yellow to brown, and black setae; yellow to brown setae sometimes being paler; arrangement of setae similar to *Trachys robustus* rather than *T. variolaris*. Head rarely with a few white setae as two small spots on vertex, in male setae becoming more yellow and denser on frons than in female. Elytron in apical half with two transverse bands usually more distinct than those of *T. robustus* but less distinct than those of *T. variolaris*. Underside practically as in *T. robustus* and *T. variolaris*.

Ratios of body parts as follows: WC/LC 1.75–2.73 (mean 2.20), WC/LSC 1.75–2.33 (mean 2.09), WP/LP 2.76–3.13 (mean 3.01), BMP/AMP 1.46–1.61 (mean 1.54); LE/WE 1.30–1.42 (mean 1.35), LE/LP 3.96–4.49 (mean 4.27). External structures practically as in *Trachys variolaris* except male and female terminalia described below.

Male terminalia (n = 5 for measurements). Proctiger with a pair of short baculi at base. Sternite IX (Fig. 61A) wide, SL/SW 0.59–0.75 (mean 0.71), rather truncate on apical margin, bearing several setae on each side of apical margin. Tegmen (Fig. 61B) wide; parameres PL/PW 1.63–1.83 (mean 1.75), slightly densely setiferous on apicolateral margins, with sides which are gently dilated from base to apical half, then more strongly dilated to widest subapical part, and finally strongly arcuately convergent to apices; phallobase PbL/PbW 2.59–3.83 (mean 3.31), more than 1/4 length of tegmen. Penis (Fig. 61C) wide, PeL/PeW 4.35–4.77 (mean 4.61), slightly shorter than tegmen; dorsal plate faintly bisinuate on sides which are gradually narrowed from widest point of base to subapical part, and then arcuately convergent apicad, with roundly, faintly produced apex, basally with median struts about 1/3 length of penis; ventral plate membranous, but weakly sclerotized as a linear patch in middle of apical 1/3.

Female terminalia (n = 5 for measurements). Ovipositor (Figs. 61D–F) short; proctiger basally with a pair of long, ventrally curved baculi; coxites transversely subhexagonal, sparsely setiferous on each side of apical margin, ventrally with transverse depression in apical par; styli slightly fan-shaped, with sides gently dilated apicad, SlL/SlW 1.52–1.88 (mean 1.71), bearing several setae apically; ventral valve sparsely setiferous on each side of subapical part; vagina elongate sack-shaped, abruptly expanded dorsally at middle; spermatheca opening from the dorsal expansion of vagina, prominently wide tubular, rather short in length, widest at base, without spermathecal gland.

Differential diagnosis. This species is moderately or very similar in general appearance to *Trachys robustus*, but can be distinguished from *T. robustus* by the combination of the following character states; (1) lateral margins of pronotum weakly arcuate in basal 1/3 usually; (2) elytral patterns of setae more distinct usually; (3) male parameres continuously dilated from base to widest subapical part; (4) round apex of penis faintly produced; (5) female styli slightly fan-shaped; and (6) spermatheca much wider.

Additionally, this species is moderately or very similar in general appearance to *T. variolaris* especially in having the arcuate pronotal lateral margins in basal 1/3, but differs from *T. variolaris* by the combination of the following character states: four black patches on pronotum more inconspicuous usually; brownish setae on elytra more frequently occurring usually; male penis slenderer; female spermatheca not bended proximally behind unpigmented accessory portion; and the point mentioned above in (4).

Specimens examined. Type material. Holotype of *Trachys variolaris robustissima* Kurosawa, 1959: ♂ (based on Kurosawa, 1959; no dissected terminalia), "(Yakushima) / Ambô / 16.VII.1952 / Y. Kurosawa" (NSMT). Paratypes (part) of *Trachys variolaris robustissima*: 1 ex., Cape Sata, Kagoshima, 3.VIII.1955, Y. Nonaka leg. (NSMT).
Non type material. **Japan**. Kyushu — [Kagoshima] 1 ex., Cape Sata, Kagoshima, 27.VII.1970, T. Akiyama leg. (NSMT);1 ♀, Sugiyamadani, Minami-ôsumi-chô, Kimotsuki-gun, 15.VIII.2003., Y. Tsutsumiuchi leg. (YTJ); 1 ♂., same locality, 17.VII.2004., Y. Tsutsumiuchi leg. (YTJ); 1 ♀, same locality, 5.VIII.2007, Y. Tsutsumiuchi leg. (YTJ). The Ryukyus: Ôsumi Islands — [Yakushima Is.] 1 ex., Nakama-rindô, Nakama, 30.V.2006, Y. Komiya leg. (SEHU); 1 ex., Onoaida, Yaku-chô, 28.V.2006, Y. Komiya leg. (SEHU); 1 ex., Anbô, 11.V.1981, SK. Yamane leg. (SEHU); 1 ♀, Ryûjinno-taki Fall, Hara, Yakushima-chô, Kumage-gun, 12.V.2015, G. Kawamura leg. (YTJ). Amami Islands — [Amami-Ôshima Is.] 1 ex., Kawauchi-gawa River, Sumiyô-son, 15.IV.2005, H. Takizawa leg. (SEHU); 1 ex., Sumiyô Dam, Sumiyô-son, 18.IV.2005, H. Takizawa leg. (SEHU); 1 ex., Hatsuno, 29.IV.1964, J. Nagano leg. (SEHU); 1 ex., same locality, 26.III.1964, J. Nagano leg. (SEHU); 1 ex., Asani, 27.V.1960, no collector name (SEHU); 1 ex., Mt. Yuwa-dake (alt. 390 m), Uken-son, Kagoshima-ken, 23.III.2019, Y. Hisasue leg. (YTJ); 2 ♂♂, Amami-chûô-rindô,

Nazekoshuku, Amami-shi, 27.III.2015, N. Ito leg. (YTJ); 1 ♀, same locality, 30.III.2015, N. Ito leg. (YTJ). [Kakeromajima Is.] 1ex., Ankyaba, Setouchi-chô, Ôshima-gun, 7.VI.2016, H. Yoshitake leg. (NIAES; recorded by Tamadera & Yoshitake, 2018b); 1 ex., Chûô-rindô, 5.VI.1998, Y. Kusakabe leg. (YTJ). [Tokunoshima Is.] 2 exs., Mt. Fûgusuku-yama, Matsubara, Amagi-chô, Ôshima-gun, 16.IX.2017, H. Yoshitake leg. (YTJ; recorded by Tamadera & Yoshitake, 2018a); 1ex., Mt. Yamatogusuku-yama, Amagi, Amagi-chô, Ôshima-gun, 25.VI.2017, H. Yoshitake & Y. Tamadera leg. (YTJ; recorded by Tamadera & Yoshitake, 2018a); 2 exs., same locality, 18.IX.2017, H. Yoshitake leg. (YTJ; recorded by Tamadera & Yoshitake, 2018a); 1ex., Uenamichi-sinrin-kôen Park, Amagi, Amagi-chô, Ôshima-gun, 18.IX.2017, H. Yoshitake leg. (YTJ; recorded by Tamadera & Yoshitake, 2018a). Okinawa Islands — [Okinawajima Is.] 1 ex., Hetona, Kunigami-son, 16.III.1980, A. Tanaka leg. (SEHU); 1 ex., same locality, 12.IV.1982, A. Tanaka leg. (SEHU); 1 ♀, Yona, Kunigami-son, Kunigami-gun, 17.VI.2013, S. Komagata leg. (YTJ); 2 exs., Yona-rindô, Yona, Kunigami-son, Kunigami-gun, Okinawa-ken, 21.IV.2016, Y. Tamadera leg., captured on *Castanopsis sieboldii* (YTJ); 1 ex., Shashiki, Kunigami-son, Kunigami-gun, Okinawa-ken, 24.IV.2017, Y. Tamadera leg., captured on *Castanopsis sieboldii* (YTJ); 3 exs., near Mt. Nago-dake, Nago-shi, Okinawa-ken, 24.VI.2016, H. Shigetoh leg. (YTJ); 1 ex., Mt. Nekumachidi-dake, Ôgimi, Ôgimi-son, Kunigami-gun, Okinawa-ken, 28.VI.2016, H. Shigetoh leg. (YTJ); 1 ♀, Oku, Kunigami-son, Kunigami-gun, 21.VI.2013, S. Komagata leg. (YTJ); 1 ♀, Mt. Nishimedake, Uka, Kunigami-son, Kunigami-gun, 5.V.2015, T. Hasegawa leg. (YTJ); 1 ♀, Chinufuku-rindô, Uka, Kunigami-son, Kunigami-gun, 20.IV.2015, T. Hasegawa leg. (YTJ); 1 ♂, Aha, Kunigami-son, Kunigami-gun, Okinawa-ken, Japan, 21.IV.2016, K. Watanabe leg. (YTJ); 1 ♂, near Mt. Nagodake, Nago, Nago-shi, 24.VI.2016, H. Shigetoh leg. (YTJ). [Kumejima Is.] 1 ex., Ara-rindô, Shimajiri, Kumejima-chô, 4.VI.2018, Y. Tamadera leg. (YTJ; recorded by Tamadera *et al*., 2019); 2 exs., Darumayama-enchi Park, Nishime, Kumejima-chô, 5.VI.2018, Y. Tamadera & H. Yoshitake leg. (YTJ; recorded by Tamadera *et al*., 2019); 1 ex., same locality, 6.VII.2018, H. Yoshitake leg. (YTJ; recorded by Tamadera *et al*., 2019). Yaeyama Islands — [Ishigakijima Is.] 1 ex., Mt. Omoto-dake, 6.VII.1974, H. Takizawa leg. (SEHU); 1 ex., Omoto, 21.VI.1996, M. Hayashi leg. (YTJ); 1 ex., same locality, 15.VI.1984, T. & T. Nakane leg. (SEHU); 1 ex., Mt. Yasura-dake, Hirakubo, Ishigaki-shi, Yaeyama-gun, Okinawa-ken, 1.IV.2019, Y. Tamadera leg., captured on *Castanopsis sieboldii lutchuensis* (YTJ); 1 ex., Mt. Yarabu-dake, Sakieda, Ishigaki-shi, Yaeyama-gun, Okinawa-ken, 30.III.2019, Y. Tamadera leg., captured on *Castanopsis sieboldii lutchuensis* (YTJ); 4 exs., same locality, 19.V.2017, Y. Tamadera leg., captured on *Castanopsis sieboldii lutchuensis* (YTJ); 5 exs., same locality, 22.V.2017, Y. Tamadera leg., captured on *Castanopsis sieboldii lutchuensis* (YTJ). [Iriomotejima Is.] 1 ex., Mt. Sonai-dake, Sonai, 15.III.2002, K. Sugisima leg., emerged from *Castanopsis sieboldii*, 22. IV.2002 (SEHU); 1 ex., End of trans-island highway (near Mt. Goza), 17.V.1973, S. Hisamatsu leg. (SEHU); 1 ex., Sonai, Taketomi-chô, Yaeyama-gun, Okinawa-ken, 30.V.2017, Y. Tamadera leg., captured on *Castanopsis sieboldii* (YTJ); 1 ♀, Komi, Taketomi-chô, Yaeyama-gun, 17.III.2015, Y. Tamadera leg. (YTJ); 1 ♀, same locality, 19.III.2015, Y. Tamadera leg. (YTJ); 1 ♂, Ôtomi-rindô, Haeminaka, Taketomi-chô, Yaeyama-gun, 30.III.2016, Y. Tamadera leg. (YTJ); 1 ex., Komi-rindô, 4.X.2013, Y. Kusakabe leg. (YTJ).

Distributions in Japan. Kyushu and the Ryukyus: the Ôsumi Isls. (Yakushima Is.); Amami Isls. (Amami-Ôshima Is., Kakeromajima Is., and Tokunoshima Is.); Okinawa Isls. (Okinawajima Is. and Kumejima Is.); and Yaeyama Isls. (Ishigakijima Is. and Iriomotejima Is.).

Records based on literatures: the Gotô Isls. (Fukuejima Is. (Takakura, 1978)), Koshikijima Isls. (Kamikoshikijima Is. (Akiyama & Ohmomo, 2000, without specimen data) and Shimokoshikijima Is. (Imasaka, 2019)), and the Ryukyus: the Ôsumi Isls. (Tanegashima Is. (Kurosawa, 1959) and Kuchinoerabujima Is. (Yamaya, 1987)).

Other distributions. China, Taiwan, and Vietnam.

Adult food plants. Same as in the larvae mentioned below.

Host plants. Fagaceae: *Castanopsis sieboldii* (Makino) Hatus. ex T.Yamaz. et Mashiba subsp. *sieboldii* [Japanese name: Sudajii] (Kurosawa, 1959 — adult record?; confirmed by this study: the Kumata collection in SEHU); C. *sieboldii* subsp. *lutchuensis* (Koidz.) H.Ohba [Japanese name: Okinawajii] (Kurosawa, 1959 — adult record?; confirmed by this study) in Japan.

Leaf-mining habit. Mines of *Trachys dilaticeps* were found on *Castanopsis sieboldii* by this study (Figs. 65F, 70C, D): each mine was the upper surface type (the larvae feed on tissues of the upper epidermis and palisade layer) and formed a large, elongate blotch occurring along leaf-margin; when full-grown, it occupied almost whole of the leaf blade; eggs, which were pale-yellow to blackish-brown (remaining eggshell) and rarely sparsely covered on powdery substances, were laid singly on the apical part of midrib on the adaxial surface but rarely on other parts of the leaf blade; hatched larvae left granular frass inside the mines; one adult specimen was emerged from the adaxial surface of the leaf with an oval adult exit hole. The leaf-mining habit of *T. dilaticeps* are practically as in those of *T. robustus*.

Note. In the southern Kyushu (Kagoshima and Miyazaki Prefectures), Japan, *Trachys dilaticeps* is sympatlically distributed with *T. robustus* Saunders, 1873, which is also associated with *Castanopsis sieboldii* subsp *sieboldii*, but the population size of the former species in this area appears to be clearly smaller than that of the latter species (personal communication with Y. Tsutsumiuchi).

Key to the Japanese species of *Trachys*

1. Lateral margins of elytra without serrations. [Group I] … 7
–. Lateral margins of elytra with serrations (Figs. 62A, B). … 2
2. Body wedge-shaped type (Fig. 62C; sides of elytra narrowed posteriorly from behind humeri). [Group II] … 12
–. Body ovate type (Figs. 62D, E; sides of elytra relatively subparallel in basal half). … 3
3. Disk of prosternum with elevated portions along procoxal cavities (Fig. 62F). [Group III] … 13
–. Disk of prosternum without elevated portions along procoxal cavities (Fig. 62G). … 4
4. Abdominal ventrite I without sternal grooves (Fig. 62H). [Group IV] … 16
–. Abdominal ventrite I with sternal grooves (Fig. 62I). … 5
5. Anterior margin of pronotum with median lobe, but very small (Fig. 62K). [Group V] … 17
–. Anterior margin of pronotum without median lobe (Fig. 62L). … 6
6. Setae on elytra nearly bicolor. First and second transverse bands on apical half of elytra moderately thin, consisting of unicolor setae (Figs. 48A, B). [Group VI] … 18
–. Setae on elytra tricolor to four-color. First and second transverse bands on apical half of elytra thick, consisting of multicolor setae (Figs. 48C–E). [Group VII] … 19

Group I

7(1). Head, pronotum, and elytra not clothed with yellow setae. Frons smoothly convex from just above each antennal insertion to inner margin of each eye (Fig. 62M). [Subgroup I-1] … 8
–. Head, pronotum, and elytra distinctly clothed with yellow setae. Frons somewhat ridged transversely from just above each antennal insertion to inner margin of each eye (Fig. 62N). [Subgroup I-2] … 10
8. Body length 3.0–3.8 mm (mean 3.5 mm). Maxillary palps with oval palpomere IV longer than wide (Fig. 2G). Integument usually brassy-black on head and pronotum, black on elytra which are often tinged with bluish, purplish, or greenish tints (Figs. 12A–F). Terminalia as shown in Fig. 10. … ***T. minutus*** (Linnaeus, 1758)

–. Body length < 3.0 mm. Maxillary palps with round palpomere IV nearly as long as wide (e.g. Fig. 2H). Integument above black or dark-bronze. … 9

9. Integument above dark-bronze. Setae sparsely scattering on elytra, with white patterns distinct (Fig. 11B). Terminalia as shown in Fig. 16. … ***T. inconspicuus*** Saunders, 1873

–. Integument above black. Setae prominently sparsely scattering on elytra, with white patterns indistinct or absent (Fig. 11C). Terminalia as shown in Fig. 18.
… ***T. pseudoscrobiculatus*** Obenberger, 1940

10. Frons outline of head triangularly concave in dorsal view (Fig. 23A). Laterosternite I–IV with laterosternal sulci. Marginal carinae of prosternum gradually divergent posteriad (Fig. 23E). Terminalia as shown in Fig. 24. … ***T. broussonetiae*** Kurosawa, 1985

–. Frons outline of head faintly concave in dorsal view (e.g. Fig. 19A). Laterosternite I–VI with laterosternal sulci. Marginal carinae of prosternum subparallel (e.g. Fig. 19F). … 11

11. When viewed from above, eyes broadly visible and well convex laterally (Fig. 19A). Setae coloration usually clear (Fig. 11D). Terminalia as shown in Fig. 20.
… ***T. ineditus*** Saunders, 1873

–. When viewed from above, eyes narrowly visible and faintly convex laterally (Fig. 21A). Setae coloration usually dark (Fig. 11E). Terminalia as shown in Fig. 22.
… ***T. tsushimae*** Obenberger, 1922

Group II

12(2). Abdominal ventrites II–V with distinct sternal grooves and ventrite I with clearly reduced grooves (Fig. 27B). Marginal carinae of prosternum strongly divergent posteriad from anterior 1/3 (Fig. 27F). Front of head arcuately concave in dorsal view (Fig. 27A). Pronotum predominantly clothed with yellow to pale yellow setae (Figs. 26A–C). Terminalia as shown in Fig. 28. … ***T. auricollis*** Saunders, 1873

–. Abdominal ventrites I–V with distinct sternal grooves (Fig. 29B). Marginal carinae of prosternum weakly divergent posteriad from anterior 1/3 (Fig. 29G). Frons outline of head deeply triangularly concave in dorsal view (Fig. 29A). Pronotum usually without yellow setae (Fig. 26D). Terminalia as shown in Fig. 30.
… ***T. toringoi*** Kurosawa, 1951

Group III

13(3). Integument black on elytra (Fig. 25C) and underside also black. Apical part of elytra clothed with black setae. Terminalia as shown in Fig. 33.
… ***T. saundersi*** Lewis, 1893

–. Integument above purple to reddish-copper on elytra (Figs. 25D–F) and underside purple to bronze. Apical part of elytra clothed with dark brownish-yellow setae. … 14

14. First and second transverse bands on apical half of elytra strongly wavy (Fig. 25F). Frons outline of head slightly shallowly concave in dorsal view. Integument above dark-purple on elytra and underside dark-purple. Terminalia as shown in Fig. 42. … ***T. auriflu*us** Solsky, 1875

–. First and second transverse bands on apical half of elytra weakly wavy (Figs. 25D, E). Frons outline of head shallowly or deeply concave in dorsal view. Integument above dark-purple or reddish-copper on elytra and underside bronze or purplish-bronze. … 15

15. Frons outline of head usually deeply concave in dorsal view (Fig. 39A). Integument above usually dark-purple on elytra (Fig. 25E) and underside purplish-bronze. Marginal carinae of prosternum clearly narrowly separated each other (Fig. 39F). Terminalia as shown in Fig. 40. … ***T. pecirkai*** Obenberger, 1925

–. Frons outline of head shallowly concave in dorsal view (Fig. 36A). Integument above reddish-copper on elytra (Fig. 25D) and underside bronze. Marginal carinae of prosternum slightly narrowly separated each other (Fig. 36F). Terminalia as shown in Fig. 37. … ***T. cupricolor*** Saunders, 1873

Group IV

16(4). Marginal carinae of prosternum subparallel (Fig. 44F). Lateral margins of elytra with very weak serrations (Fig. 44C). Relative size of scutellar shield large (Fig. 44A). Terminalia as shown in Fig. 45. … ***T. reitteri*** Obenberger, 1930

Group V

17(5). Marginal carinae of prosternum strongly divergent posteriad from middle (Fig. 46F). Lateral margins of elytra with moderate serrations (Fig. 46C). Relative size of scutellar shield very small (Fig. 46A). Terminalia as shown in Fig. 47.
… ***T. tokyoensis*** Obenberger, 1940

Group VI

18(6). Clypeus clearly wide (WC/LSC ratio ≥ 2.0) Male parameres gently dilated from base to widest point at apical 1/3 without distinct lateral expansion (Fig. 52B). Hosts (incl. adult foods): *Aphananthe aspera* and *Celtis sinensis*.
… ***T. griseofasciatus*** Saunders, 1873

–. Clypeus usually moderately wide (1.5 < WC/LSC ration < 2.0, but rarely reaching 2.0). Male parameres with small lateral expansion being widest at behind apical 1/3 (Fig. 53B). Host (incl. adult food): *Zelkova serrata*.
… ***T. yanoi*** Kurosawa, 1959

Group VII

19(6). Pronotum usually with conspicuous four round black patches (Fig. 48C). Elytra predominantly clothed with black setae usually (Figs. 55A, B). Sides of pronotum weakly arcuate in basal 1/3 (Fig. 56A). Apex of male penis weakly pointed and not produced (Fig. 57C). Female spermatheca prominently wide (Fig. 57F). … ***T. variolaris*** Saunders, 1873

–. Pronotum usually with inconspicuous four round brown patches (Figs. 48D, E). Elytra subequally clothed with each color setae usually (Figs. 55F–H, K–N). Sides of pronotum weakly arcuate in basal 1/3 or rather straight throughout. Apex of male penis rounded and faintly produced or not. Female spermatheca prominently wide or slender. … 20

20. Sides of pronotum usually relatively straight throughout (Fig. 58A). Elytral patterns of setae less distinct usually (Figs. 55F–J). Male parameres with distinct lateral expansion being widest at apical 1/5 (Fig. 59B). Apex of penis not produced (Fig. 59C). Female spermatheca clearly slender (Fig. 59F). … ***T. robustus*** Saunders, 1873

–. Sides of pronotum usually weakly arcuate in basal 1/3 (Fig. 60A). Elytral patterns of setae distinct usually (Figs. 55K–O). Male parameres continuously dilated from base to widest subapical part (Fig. 61B). Apex of male penis faintly produced (Fig. 61C). Female spermatheca prominently wide (Fig. 61F). … ***T. dilaticeps*** Gebhardt, 1929

Host associations of Japanese *Trachys*

Japanese *Trachys* is associated with various eudicot plants including twelve families in five orders (see below the host list). Monophagy, defined as using a single plant genus (including specialists using a single plant species), is a common diet breadth in Japanese *Trachys* species: 13 out of 19 species are recognized as monophagous (68%). Among the remaining six species, five species are recognized as oligophagous (26%), defined as using plants of multiple genera within a single family. The remaining one species, *Trachys minutus*, is only recognized as polyphagous (6%), defined as using two or more plant families or orders, although this species clearly prefers to *Salix* plants in Japan. Japanese *Trachys* shows wide host breadth, whereas individual species show narrow host breadth. The tendencies are often confirmed in various herbivorous insects, especially in leaf-miners (e.g. Winkler *et al*., 2009; Doorenweerd *et al*., 2015).

Host list for Japanese *Trachys*

Host plant		Japanese *Trachys* [diet breadth; species-groups]
Betulaceae (Fagales)		
Corylus	……………	*Trachys minutus* [polyphagy; I]
Cannabaceae (Rosales)		
Aphananthe	……………	*Trachys griseofasciatus* [oligophagy; VI]
		Trachys ineditus [monophagy; I]
Celtis	……………	*Trachys griseofasciatus* [oligophagy; VI]
Fabaceae (Fabales)		
Amphicarpaea	……………	*Trachys reitteri* [oligophagy; IV]
Glycine	……………	*Trachys reitteri* [oligophagy; IV]
Hylodesmum	……………	*Trachys tokyoensis* [oligophagy; V]
Pueraria	……………	*Trachys auricollis* [monophagy; II]
		Trachys reitteri [oligophagy; IV]
Rhynchosia	……………	*Trachys reitteri* [oligophagy; IV]
		Trachys tokyoensis [oligophagy; V]
Fagaceae (Fagales)		
Castanopsis	……………	*Trachys dilaticeps* [monophagy; VII]
		Trachys robustus [monophagy; VII]
Quercus	……………	*Trachys variolaris* [monophagy; VII]
Hydrangeaceae (Cornales)		
Deutzia	……………	*Trachys saundersi* [monophagy; III]
		Trachys tsushimae [monophagy; I]
Malvaceae (Malvales)		
Tilia	……………	*Trachys aurifluus* [monophagy; III]
		Trachys minutus (from Europe) [polyphagy; I]
Moraceae (Rosales)		
Broussonetia	……………	*Trachys broussonetiae* [oligophagy; I]
Morus	……………	*Trachys broussonetiae* [oligophagy; I]
Rosaceae (Rosales)		
Amelanchier	……………	*Trachys toringoi* [oligophagy; II]
Aria	……………	*Trachys toringoi* [oligophagy; II]
Chaenomeles	……………	*Trachys toringoi* [oligophagy; II]
Cydonia	……………	*Trachys toringoi* [oligophagy; II]
Malus	……………	*Trachys toringoi* [oligophagy; II]
Prunus	……………	*Trachys inconspicuus* [monophagy; I]

Pyrus …………… *Trachys toringoi* [oligophagy; II]
Sorbus …………… *Trachys toringoi* [oligophagy; II]
Salicaceae (Malpighiales)
Populus …………… *Trachys minutus* [polyphagy; I]
Salix …………… *Trachys minutus* [polyphagy; I]
Sapindaceae (Sapindales)
Acer …………… *Trachys minutus* (from Europe) [polyphagy; I]
Ulmaceae (Rosales)
Ulmus …………… *Trachys minutus* (from Europe) [polyphagy; I]
Trachys pecirkai [monophagy; III]
Zelkova …………… *Trachys cupricolor* [monophagy; III]
Trachys yanoi [monophagy; VI]
Violaceae (Malpighiales)
Viola …………… *Trachys pseudoscrobiculatus* [monophagy; I]

3.3 Review of the genus *Habroloma*

— synonymy, general morphology, and biology —

Genus ***Habroloma*** Thomson, 1864

Habroloma Thomson, 1864: 42 (no designation of type species); Gemminger & Harold, 1869: 1452 (as synonym of *Trachys*); Saunders, 1871: 130 (as synonym of *Trachys*); Kerremans, 1892 a: 284 (as synonym of *Trachys*); Kerremans, 1903: 307 (as synonym of *Trachys*); Théry, 1938: 89 (comparison with *Trachys*); 1942 a: 199 (diagnosis); Schaefer, 1950: 454 (redescription; type species: *Buprestis nana* Paykull, 1799, fixed by subsequent designation); Obenberger, 1958: 240 (note); Kurosawa, 1959: 247 (redescription; subgenus *Parahabroloma*); Descarpentries &Villiers, 1964: 250 (in key to genera of Indochina Trachydini); Cobos, 1979: 421, 426 (in key; subgenus *Malobroha*); Bílý, 1982 b: 91 (diagnosis for adult and larva); Bellamy, 1985: 428 (catalog); 1986: 597 (in checklist); Cobos, 1986 a: 276, 277 (in key; Trachyinae); Hołyński, 1993: 15 (in Trachydina); Bellamy, 2003: 95 (higher classification); Kubáň, 2006: 416 (Palaearctic catalog); Bellamy, 2008: 2534 (World catalog); Kubáň, 2016: 568 (Palaearctic catalog); Lawrence & Lemann, 2019: 562, 575 (in key to Australian genera).

Trachys (*Habroloma*): Klapálek, 1903: 12; Jakobson, 1913: 800 (catalog); Obenberger, 1918 a: 17, 28, 63 (note; in key and catalog of Palaearctic spp.); Obenberger, 1924 b: 633 (as part of *Trachys*); 1926 b: 661 (catalog); Obenberger, 1937 a: 1410 (World catalog); 1937 c: 47 (key to African spp.).

See Bellamy (2008 b) for other references.

Type species. *Buprestis nana* Paykull, 1799, fixed by subsequent designation (Schaefer, 1950).

Gender. Neuter.

Diagnosis. The *Habroloma* may be easily distinguished from other genera of the tribe Tracheini by the combination of the following character states: hypomera without antennal grooves; prosternum with transverse grooves above procoxal cavities; prosternal process wide and forming into trapezoidal plate combined with prosternal marginal carinae; prosternal lobe present; elytra usually with lateral carinae; elytra with distinct marginal carinae from bases to near apices; elytral epipreura distinct from bases to near apices; hind wing without anal field; abdominal ventrites with sternal grooves on ventrites V; female proctiger with a pair of straight baculi in lateral view; female coxites without dorsal projections of baculi.

Distribution range and species number. Afrotropical, Madagascan, Palaearctic, Oriental, and Australasian Regions. The total number of known species of *Trachys* is ca. 250 spp. (Bellamy, 2008 b; Kubáň, 2016; Peng, 2020, 2021 a, b, 2022 b).

Subgenera. *Habroloma* Thomson, 1864, *Parahabroloma* Kurosawa, 1959 (type species: *Trachys eximia* Lewis, 1893), and *Malobroha* Cobos, 1979 (type species: *Trachys thomasseti* Théry, 1928).

Species examined. In addition to all eleven Japanese species treated in the section of the taxonomy of Japanese *Habroloma*, the following species were examined and compared of the external structures: two European species —*Habroloma* (*Habroloma*) *nanum* (Paykull, 1799) [type species] (NSMT; SOCI; YTJ) and *H.* (*H.*) *triangulare* (Lacordire, 1835) (NSMT). Three Indochina species — *H.* (*Parahabroloma*) *soror* Descarpentries & Villiers, 1964 (TUA; YTJ), *H.* (*P.*) *septimia* (TUA; YTJ), and *H.* (*P.*) *coomani* Descarpentries & Villiers, 1964 (EUM; TUA). One Chinese species — *H.* (*P.*) *pulchrum* Peng, 2021 (NSMT).

General morphology of *Habroloma*

Body usually wedge-shaped but rarely being ovate, more or less depressed dorsoventrally, more or less setiferous with recumbent to semirecumbent short setae, in the Oriental species rarely with several tufts consisting of erect setae on elytra or pronotum and elytra (e.g. *Habroloma baucis* (Obenberger, 1929)). Surface more or less sculptured on dorsal and ventral sides.

Head capsule hypognathous, clearly narrower than pronotum. Eyes moderately large, vertically subreniform, with inner margins obliquely converging downward in frontal view (e.g. Fig. 76C), weakly grooved along lower outer side of each inner margin. Occiput concealed beneath prothorax at rest, with longitudinal line of endocarina reaching upper side of frons, with postocciput which is very narrow and glabrous and is condyle-shaped around area attaching with cervical sclerites; frons with a pair of suprantennal pores; frontoclypeal suture absent; clypeus usually, more or less transverse, but rarely being very narrow (much longer than wide) between antennal insertions (e.g. *Habroloam* (*Parahabroloma*) *soror* Descarpentries & Villiers, 1964), usually with elevated basal margin, arcuately emarginate or rather straight at apical margin, with surface substrigulate to finely reculate; anteclypeus narrowly visible; antennal insertions somewhat confluent with very shallow subantennal grooves for receiving basal antenomeres at rest; genae very narrow; temples narrow, always concealed beneath prothorax at rest; gulamentum transversely wide, with surface reticulate, concealed beneath prosternum at rest; gula and gular sutures absent. Tentorium very slender, without dorsal arms and corpotentorium; anterior arms invaginated from gena regions below lowermost part of eyes in lateral view, but well-defined anterior tentorial pits not recognizable externally; posterior arm invaginated from postoccipital region below level of condyle-shaped part of postocciput.

Antennae eleven segmented, short in length, serrate from antenomeres VII; antenomeres VII–XI apically with sensory fossae, which are slightly extending to inner surface except antennomere XI; in the Oriental species, antennomere I rarely modified into horn-shaped segment (prominently dilated toward outer side; e.g. *Habroloma baucis* (Obenberger, 1929), *H. clymeme* (Obenberger, 1929), *H. erichtho* (Obenberger, 1929), *H. minotaurum* (Hołyński, 2003)); exceptionally, antennae of a myrmecophilous species (*H.* (*P.*) *myrmecophilum*) modified into unserrated antenomers and nearly fused with rather indistinct articulations between antenomers III–XI (after Bílý *et al*., 2008).

Mouth parts. Labrum small, narrowly emarginate at apical margin, with surface finely reticulate in about basal half; tormae with inwardly recurved or straight apices. Mandibles short, without mandibular holes on lateral bases, smooth and concave on surfaces of inner sides. Maxillae with transverse cardines; basistipites slightly oblong, bearing several setae, with surface more or less reticulate; mediostipites largely membranous in basal part and sparsely setiferous on sclerotized portions; laciniae not elongated distally, densely clothed with robust setae apically; galeae slightly trapezoidal, densely clothed with robust setae in apical part; maxillary palps four segmented, with palpomere IV somewhat truncate at apex. Labium with transversely subtriangular to semicircular mentum, which is somewhat produced at apex and is finely reticulate on surface; ligula short, bearing several setae; palpigers absent; labial palps two segmented, with apical segment much shorter than basal segment; premental sclerites short, with enlarged apices often bearing a few setae. Epipharynx nearly unarmed, but faintly bearing microtrichia in proximal part. Hypopharynx well lobed distally, with a pair of hypopharyngeal sclerites bearing well developed dorsal, distal, and proximal processes, the latter processes of which are sometimes connected each other.

Prothorax. Pronotum transversely subtrapezoidal; lateral margins narrowed anteriorly from base to apicolateral angles; marginal carinae complete; apical margin simply arcuately or bisinuately emarginate, with or without median lobe; basal margin trisinuate posteriorly, with median lobe, with slightly ridged inner margin (Fig. 71B), with true edge of basal margin more or less covered on basal margins of elytra and scutellar shield, as a result invisible at rest; disk often with apicolateral depressions behind apicolateral angles, those depressions usually with fovea or pore at the middle of each (Figs. 5H, 76A, 83A), but rarely absent (Fig. 78A); surface more or less variolate-punctate with setiferous pin-prick punctures and circular to semicircular incised line sculptures (ocellate sculptures). Hypomera without antennal grooves, with hypomeral markings consisting of strong winkles or incised linear sculptures in apical half (e.g Figs. 76G, 78H), declivous toward basal margins from behind hypomeral markings. Prosternum (Fig. 5I) with well-defined prosternal lobe, somewhat rimed along apical margin; prosternal process short, wide, with apparent apex contacting to metaventrite, with sparsely setiferous true apex invisible at rest and inserted into the cavity composed of mesoventrite and metaventrite; disk with transverse grooves above procoxal cavities (Fig. 5I), with trapezoidal plate (Fig. 5I) delimited by marginal carinae running from base of prosternal lobe to apparent apex of prosternal process. Procoxal cavities posteriorly open. Protrochantins (Figs. 71A, B) relatively largely exposed at each corner of procoxal cavity facing prosternum and hypomeron. Profurca with two short projections. ***Mesothorax***. Mesothoracic tergum with mesoscutellum with very small scutellar shield, which is far narrower than mesonotum in width. Mesoventrite very short in length, appearing to be completely divided longitudinally by prosternal process (Fig. 71A). Mesanepisterna and mesepimera fused with each other, with boundary sutures reduced except in upper side, where is almost concealed by elytra (Fig. 71A), with invaginations of the sutures also reduced except in the upper side. Mesocoxal cavities widely separated each other; separation in mesocoxal cavities clearly larger than in procoxal cavities. Mesotrochantins (Figs. 71A, B) very narrowly exposed at each corner of mesocoxal cavity facing mesepimeron and metaventrite. Mesendosternite with two separate, short projections which are enlarged apically. ***Metathorax***. Metathoracic tergum with metapostnotum subdivided into median postnotum and lateral postnota, which are fused with sclerotized portions around first abdominal spiracles. Metaventrite (Fig. 71A) with apical margin of metaventral process weakly emarginate; disk with slightly inconspicuous discrimen, with metakatepisternal suture joining near middle of discrimen. Metanepisterna (Fig.71A, B) longitudinally rectangle, arcuate inwardly in ventral view. Metepimera concealed by lateral sternal projections of abdomen (Fig. 71B) and elytra. Metendosternite without developed furcal arms.

Elytra wide, wedge-shaped to suboval; humeral calluses more or less developed; marginal carinae distinct from humeral angles to near apices (Figs. 5J, K, 71B); epipleura

(Figs. 5J, K, 71B) distinct from humeral angles to near apices, but rarely being very narrow (Cobos, 1979; subgenus *Malobroha*); disk usually with lateral carinae (Figs. 5G, 71B), but very rarely without the carinae (e.g. *H. bicarinatus* (Kerremans, 1892), *H. glyphicum* Hołyński, 2003, *T. blairi* Obenberger, 1929, and *T. aone* Obenberger, 1929) or with much shorter lateral carinae than an half of elytral length (Cobos, 1979; subgenus *Malobroha*); surface more or less sculptured with setiferous pin-prick punctures and short, linearly incised punctures. ***Hind wings*** (Fig. 7C) elongate oval, short in length, without anal notches; anal field absent. Wing base with third axillary sclerite strongly elongated in distal process which is connected with vein A; median plate formed a single plate. Venation: vein RA_{3+4} not reunite to RA_{1+2}, as a result radial cell more or less open to distal end; cross-vein r3 moderately short, not joining vein RP; cross-vein r4 absent; vein MP_3 and MP_4 absent; vein CuA_2 absent; wedge cell absent (open); vein AA_3 completely separated from AA_4, as a result first cubito-anal cell absent.

Legs (Fig. 71A) slender to slightly stout. Coxae with pro- and mesocoxae subglobular; metacoxae transverse, with metacoxal plates broadly emarginate in about lateral half of posterior margin. Trochanters subtriangular, obliquely connecting to femoral bases. Femora slightly sulcate on inner margins, but occurring no expansions to conceal tibiae at rest. Tibiae not lodged under femora at rest; metatibiae without a fringe of spines on each outer margin, only with a few fine, sparse setae; tibial spurs reduced on each tibia. Tarsi short; tarsomeres I–IV ventrally with tarsal pads which become larger toward distal end; tarsal claws bearing a blunt tooth at base of each.

Abdomen. Terga well sclerotized, subdivided into tergites and laterotergites by shallow grooves, but the subdivision very weak in second segment. Tergite I and II strongly fused, with distinct boundary suture. Tergal cuticularia recognized near each basal margin of tergites II–VI (II with ambiguous ones). Laterotergites recognized in second to seventh abdominal segments; laterotergite III strongly and acutely produced basad. Spiracles recognized on each laterotergite, except for first abdominal spiracles recognized on sclerotized portions which are fused with metapostnotum. Sterna divided into sternites, laterosternites, and parasternites. Sternites four segmented at a glance; sternite I and II not exposed externally, but lateral parts visible as lateral sternal projections which are reaching metanepisterna and lacking boundary suture between the projections and third abdominal segment; suture between sternites III and IV (= ventrites I and II) obliterated, but barely recognizable as somewhat interrupted sculptures on surface; sternite III (= ventrite I) with obtuse intercoxal process, without sternal grooves laterally; sternites IV–VI (= ventrites II–IV) without sternal grooves laterally; sternite VII (= ventrite V) semicircular, with sternal groove along apical margin (Figs. 5L, 71A), with outside area of the groove not enlarged posteriorly. Sternal cuticularia recognized near each basal margin of sternite IV–V (Fig. 71A). Laterosternites delimited from sternites by sternal carinae; laterosternites I–IV of first to fourth abdominal segments without each boundary suture, bearing laterosternal sulci, in which elytra more or less fit; laterosternites V–VII present, bearing laterosternal sulci on V–VI. Parasternites well-demarcated from laterostersites, recognized in third to seventh abdominal segments; parasternite VII shorter than other parasternites; pleural membrane barely recognized at proximal part before parasternite III. Spicules (for wing-folding) occurring on whole parasternites, along apical margins of laterotergite VII + tergite VII, and as patches on laterotergites III–VI and tergites V and VI, tergite patches of spicules being very small in tergite V and transversely oval in tergite VI.

Terminalia completely telescoped into seventh abdominal segment. ***Male***. Tergite VIII (Fig. 72A) semicircular, arcuately emarginate at basal margin, covered with small spines in apical margin, sparsely setiferous at each side of disk, with spiracle at each side of apical half. Sternite VIII (Fig. 72B) semicircular, arcuately emarginate at basal margin and densely setiferous on apical margin. Proctiger (Fig. 72C) consisting of completely fused paraproct (tergite IX) and epiproct (tergite X), transversely subreniform, densely setiferous on apical margin, with a pair of short baculi at base. Sternite IX (e.g Fig. 77A) with broad apical margin, usually bearing setae but rarely a pair of setae occurring on each side of apical margin. Aedeagus (in a broad sense) trilobate type; tegmen (e.g. Fig. 77B) with parameres more or less setiferous in apicolateral parts, with distinctly shallow dorsal notch, ventrally with small phallobase; penis (e.g. Fig. 77C) not completely fixed to tegmen, as a result somewhat movable toward distal side, consisting of dorsal plate and ventral membrane, ventrally with slit-shaped ostium, from which endophallus is invaginated; endophallus membranous, with a few spicules, connecting with ejaculatory duct at proximal end. ***Female***. Tergite VIII and sternite VIII practically as in male (Figs. 72D, E). Ovipositor short in length; proctiger (Figs. 72F, G) basally with a pair of straight baculi; valvifers probably fused with proctiger baculi, but the contacting parts to bases of coxites unpigmented and rather membranous (Fig. 72G); coxites (e.g. Figs. 77D, E) transverse, setiferous on apical margin; styli occurring on dorsal side of coxites, somewhat flattened dorso-ventrally, setiferous apically; ventral valve (e.g. Fig. 77E) often without setae, with surface more or less sculptured; internal part of ovipositor invaginating from vulva between coxites and ventral valve; vagina somewhat sack-shaped (e.g. Figs. 77F, 99G); spermatheca dorsally opened into about distal half of vagina without well-defined spermathecal duct, completely membranous, tubular, basally with unpigmented accessory portion in proximal side, without spermathecal gland.

Sexual dimorphism. Species of the genus *Habroloma* usually show no distinct morphological differences between both sexes. If sexual dimorphism showing, it may be recognized in the size of antennae.

Biology of *Habroloma*

Life history. Generally, in Japan proper (the temperate zone), the new adults emerge in the summer (from July to August) and somewhat feed on the host leaves, then hibernate in the winter under various gaps, such as the bark of the trees, the moss on the stones, and the leaf-litter (Kurosawa, 1959). In the next spring, the adults wake up and again feed on the host leaves. After copulation and egg laying by the next summer, they finish their life. In the late spring to summer, the immatures mine into leaf tissues and develop into adults in about one month. At least, the voltinism of *Habroloma* is considered to be of univoltine in the Japan proper. As in the *Habroloma*, the possibility of multivoltine is pointed out in Central European species by Bílý (2003).

Adult stage. The adults of *Habroloma* feed externally on leaf blades and leave feeding scars on leaf-margins. Insofar as is known, adult food plants are the same as in immature stages.

Immature stages. Insofar as is known, the larvae of *Habroloma* are leaf-miners associated with various dicotyledonous trees and herbs (e.g. Yano, 1952; Bílý, 2003). The eggs are laid singly on the adaxial or abaxial surfaces of the leaf blade (lamina) and are always covered in varnish-like substances. Additionally, the eggs are usually somewhat covered on powdery substances (those may be fine feces). The larvae, hatched from the eggshell surface in contact with the plant body, mine into the parenchymal layer of the leaf blade and then each larva leaves a full-depth or upper surface mine. The frass is left inside the mine or ejected outside the mine. The third instar larvae (final instar, based on the number of exuviated head-capsules left inside the mine) pupate inside the mine after passing the stage of prepupa. After around ten days, the adults are emerged from mines.

Note. Myrmecophily of Buprestidae is found only in *Habroloma* (*Parahabroloma*) *myrmecophilum* Bílý, Fikáček & Šípek, 2008, of which immatures are somewhat associated with *Oecophylla* ants.

3.4 Taxonomy of Japanese *Habroloma*

Historical review of Japanese *Habroloma*

To date, twelve species and two subspecies in two subgenera are recorded from Japan. Taxonomy of Japanese *Habroloma* has been studied as in the following time line (showing changes in the number of species and subspecies).

1913. Jakobson (treated *Habroloma* as a subgenus of *Trachys*) transferred five species of Motschulsky (1860), Saunders (1873), and Lewis (1893) into *Habroloma* [*Trachys* (*Habroloma*) *subbicornis*, *T*. (*H*.) *lewisii*, *T*. (*H*.) *griseonigrum*, *T*. (*H*.) *elegantulum*, and *T*. (*H*.) *eximium*].

+5 transferred spp. = 5 species (0 subspecies)

1918 a. Obenberger (treated *Habroloma* as a subgenus of *Trachys*) described one new species [*Trachys* (*Habroloma*) *ronino*]; and treated *T*. (*H*.) *subbicornis* as the subgenus *Trachys* based on Lewis (1893)*.

*) Lewis (1893) synonymized *Trachys griseofasciatus* Saunders, 1873 (current: *Trachys*) with *T*. *subbicornis* Motschulsky, 1860 (current: *Habroloma*). It is a wrong treatment.

+1 new sp. −1 sp. = 5 species (0 subspecies)

1940. Obenberger described two new species [*Trachys* (*Habroloma*) *kagosimana* and *T*. (*H*.) *liukiuensis*].

+2 new spp. = 7 (0)

1959. Kurosawa (treated *Habroloma* as an independent genus) established a new subgenus [the subgenus *Parahabroloma*]; described three new species [*Habroloma* (*Parahabroloma*) *shirozui*, *H*. (*P*.) *asahinai*, and *H*. (*P*.) *hikosanense*]; newly recorded one species as a new subspecies [*H*. (*P*.) *nixilla inslicola*]; downgraded the status of *H*. (*P*.) *liukiuense* as a subspecies of known species [*H*. (*P*.) *eximium liukiuense*].

+3 new spp. +1 recorded sp. −1 downgraded sp. (+1 new subsp. +1 downgraded subsp.) = 10 (2)

1976 b. Kurosawa described one new species [*Habroloma* (*Parahabroloma*) *yuasai*]; upgraded the status of *H.* (*P.*) *eximium liukiuense* as species [*H.* (*P.*) *liukiuense*]; newly recorded two species [*H.* (*H.*) *amurense* and *H.* (*P.*) *atronitidum*] and one subspecies [*H.* (*P.*) *eximum eupoetum*]; synonymized two species under two known species [*H.* (*P.*) *elegantulum* (= *H.* (*P.*) *ronino*) and *H.* (*P.*) *kagosimanum* (= *H.* (*P.*) *shirozui*)]; and corrected misidentifications of *H.* (*P.*) *kagosimanum* and *H.* (*P.*) *ronino* in Kurosawa (1959).

+1 new sp. + 1 upgraded sp. +2 recoded spp. −2 synonymized spp. (+1 recorded subsp. −1 upgraded subsp.) = 12 (2)

1995. Akiyama & Ohmomo transferred the *increate sedis* species of Kurosawa, 1959 to the subgenus *Parahabroloma* in *Habroloma* then synonymized one known species under it [*Habroloma* (*Parahabroloma*) *subbicorne* (= *H.* (*P.*) *elegantulum*)].

+1 transferred sp. −1 synonymized sp. = 12 (2)

2006. Kubáň synonymized one species under an unrecorded species [*Habroloma* (*Parahabroloma*) *marginicolle* (= *H.* (*P.*) *kagosimanum*)].

+ 1 recorded sp. −1 synonymized sp. = 12 (2)

This study will describe one new species and two new subspecies [*Habroloma* (*Parahabroloma*) sp. 1, *H.* (*P.*) *eximium* subsp. 1, and *H.* (*P.*) *asahinai* subsp. 1]; synonymize one species under a known subspecies [*H.* (*P.*) *eximium eupoetum* (= *H.* (*P.*) *liukiuense*)]; and remove one species from Japanese fauna [*H.* (*P.*) *atronitidum* from Japan is regarded as the misidentification of *H.* (*P.*) *subbicorne*].

+1 new sp. −1 synonymized sp. −1 removed sp. (+1 new subsp.) = 11 (4)

Review of species diagnostic characters

This study reassesses diagnostic characters for species identification of the genus *Habroloma* and also proposes several new characters here. As in *Trachys*, this genus consists of numerous species including many similar ones in general appearance. To well organize species classification of this genus, Obenberger (1929) for the first time summarized diagnostic characters for species identifications of the continental Asian *Trachys* that contains the genus *Habroloma* as a subgenus under it at that time. In addition, several studies are described as useful characters for species determinations (e.g. Kurosawa, 1959; Descarpentries & Villers, 1964; Peng, 2020, 2021 a).

Considering intraspecific variations, the species identification based on a combination of multiple characters are required. The combination of the following characters may be useful for the reliable identification of *Habroloma* species:

Structure. **Body**: dorsal and lateral contour. **Vestiture**: tufts of pronotal and elytral erect setae. **Head**: shape and depth of concavity on frons outline of head in dorsal view; shape of clypeus; proportion of clypeus [WC/LC ratio]. **Antennae**: shape of antennomere I. **Pronotum**: apical margin of pronotum. **Scutellar shield**: visible size. **Elytra**: ridge strength of elytral humeral callus; serrations of elytral lateral margins. **Underside**: proportion of prosternal trapezoidal plate; shape of hypomeral markings; pores in hypomeral markings; sculpture of prosternal trapezoidal plate; size of inner tooth of claws; shape of apex of abdominal ventrite V. **Terminalia**: shape of male sternite IX and its setae (newly proposed); shape of male parameres and their setae; shape of male penis (dorsal plate); depression of dorsal plate of penis (newly proposed); sclerotized portion on ventral membrane of penis (newly proposed); finely tuberculate part of ventral membrane of penis (newly proposed); shape of apical margin of coxites; shape of female styli (newly proposed); shape of female spermatheca (newly proposed).

Coloration. Integument of dorsum, venter; patterns of setae on head, pronotum, and elytra.

Notes for some useful characters. *Underside characters*. The term of the prosternal process, traditionally used in the taxonomy of the genus *Habroloma*, seems to be not indicate the true prosternal process in the coleopteran morphology. Although the prosternal process is generally defined as the posterior part from between procoxal cavities (Lawrence and Ślipiński, 2013), the prosternal process for *Habroloma* indicate a trapezoidal portion delimited by the prosternal marginal carinae (Fig. 5I). As in the replacement term for the shape of prosternal process in the genus *Trachys*, this replacement for the morphological term should be avoided to prevent non-homologous comparisons with other buprestid taxa for higher classifications. Therefore, this study uses a new term, (prosternal) trapezoidal plate, for the part of prosternal process used in taxonomy of *Habroloma*.

Terminalia characters. As in *Trachys*, the male terminalia of *Habroloma* have been the focus of several European and East Asian studies in classifying species (Schaefer, 1950; Ishiguro & Nishida, 2018; Peng, 2020, 2021a, 2022b), whereas the female terminalia of this genus has been largely ignored except Schaefer (1950). In this study, sufficient differences of the terminalia in both sexes are well recognized between

Japanese species, but the female one is more uniform in *Habroloma* than in *Trachys* (see also the correspondence note for species diagnostic characters for *Trachys*). In particular, these characters are very important to determine the tentative species-groups defined below section.

The setae of male sternite IX as useful character for identification of *Habroloma* species, but rarely show intraspecific variations: the male sternite IX of *H*. (*P*.) *subbicorne* usually have a pair of setae (Fig. 93A), but very rarely absent setae (Fig. 93E; n = 1); and that of *H*. (*P*.) *yuasai* is usually have no setae, but very rarely have a pair of setae (n = 1). Judging from these variations in the setae of male sternite IX, the presence or absence of the setae of male sternite IX is not useful for species determination based only on this character. In combination with other morphological characters, this character helps identifications *Habroloma* species.

Notes for non-adapted characters. The curvature (Peng, 2020) and the extent of margin between inner and outer margins of pronotal base (Peng, 2021 a) are not used in this study because the same reasons mentioned in the correspondence notes in the review of species diagnostic characters for *Trachys*.

Species-groups for the Japanese *Habroloma*

The concept of the species group for the genus *Habroloma* has not erected to date. More comprehensive studies based on a number of species are necessary to provide with well-defined *Habroloma* species-group concepts, which are practical and also reflect phylogenetic relationships. Because of several useful characters for grouping them are founded, this study, however, tentatively grouped Japanese *Habroloma* species into three groups to systematically classify them and to make it easier to species identification. Diagnoses for those tentative groups are described in the corresponding section, respectively.

Species list of Japanese *Habroloma*

Subgenus *Habroloma*
Habroloma (*Habroloma*) *bifrons* (Kiesenwetter, 1879)

Subgenus *Parahabroloma*
Group A (eximium)
Habroloma (*Parahabroloma*) *eximium eximium* (Lewis, 1873)

Habroloma (*Parahabroloma*) *eximium eupoetum* (Obenberger, 1929)
= *liukiuense* (Obenberger, 1940)
Habroloma (*Parahabroloma*) *eximium* subsp. 1 (= *liukiuense* auct. non Obenberger)
Habroloma (*Parahabroloma*) *griseonigrum* (Saunders, 1873)
= *chionochaetum* (Obenberger, 1929)

Group B (lewisii)
Habroloma (*Parahabroloma*) *lewisii* (Saunders, 1873)
Habroloma (*Parahabroloma*) *nixilla inslicola* Kurosawa, 1959
Habroloma (*Parahabroloma*) *yuasai* Kurosawa, 1976

Group C (subbicorne)
Habroloma (*Parahabroloma*) *subbicorne* (Motschulsky, 1860)
Habroloma (*Parahabroloma*) *marginicolle* (Fairmire, 1888)
Habroloma (*Parahabroloma*) *asahinai asahinai* Kurosawa, 1959
Habroloma (*Parahabroloma*) *asahinai* subsp. 1 (Ishigakijima Is.)
Habroloma (*Parahabroloma*) *hikosanense* Kurosawa, 1959
Habroloma (*Parahabroloma*) sp. 1 (saekii)

Removed species
Habroloma (*Parahabroloma*) *atronitidum*.

Species descriptions

Subgenus ***Habroloma*** Thomson, 1864

Habroloma* (*Habroloma*) *bifrons (Kiesenwetter, 1879)
[Japanese name: Suji-chibi-tamamushi]
(Figs. 5, 72, 73A, 76, 77)

Trachys bifrons Kiesenwetter, 1879 [in Kraatz & Kiesenwetter (1879)]: 256 (type locality: Amur, Russia); Kerremans, 1885: 157 (catalog); 1892 a: 285 (catalog); 1903: 312 (catalog); Jakobson, 1913: 800 (catalog).

Trachys (*Trachys*) *bifrons*: Obenberger, 1918 a: 68 (catalog); 1926 b: 663 (catalog); Théry, 1927: 39 (listed); Obenberger, 1937 a: 1356 (World catalog).

Habroloma bifrons: Théry, 1942 b: 271 (note).

Habroloma (*Habroloma*) *bifrons*: Kubáň, 2006: 46, 416 (Palaearctic catalog); Bellamy, 2008 b: 2540 (World catalog); Ohmomo & Fukutomi, 2013: 170, pl. 54 (pictorial book); Kubáň, 2016: 568 (Palaearctic catalog); Kubáň, 2016: 568 (Palaearctic catalog).

Trachys (*Habroloma*) *amurensis* Obenberger, 1922 a: 69 (type locality: "Sibiria orientalis: Vladivostok", Russia); 1926 b: 661 (catalog); 1937 a: 1410 (World catalog). Synonymized under *H.* (*H.*) *bifrons* by Kubáň, 2006: 46.

Habroloma (*Habroloma*) *amurensis*: Kurosawa, 1976 a: 2 (note; Japan and Korea).

Habroloma (*Habroloma*) *amurense*: Kurosawa, 1976 b: 129 (Japan and Korea); 1985: 36, pl.7 (pictorial book); Volkovitsh & Alexeev, 1988: 45 (list); Akiyama & Ohmomo, 1997: 50 (checklist); 2000: 286, pl. 120 (pictorial book).

Description. Male and female. Body ovate, moderately convex dorsally (Figs. 76A, B). LB 3.01–3.11 mm (mean 3.06 mm); WB 1.74–1.75 mm (mean 1.75 mm); LB/WB 1.72–1.78 (mean 1.75) (n = 2 for all measurements except terminalia). Habitus as shown in Figs. 73A.

Integument mainly black, with weak golden-bronze reflections. Head and pronotum with weak, dark bronzy tints; elytra with some very inconspicuous, dark purple to dark blue patches throughout as shown in Fig. 73A, 76A; tarsal pads pale brown. Dorsal surface slightly strongly shiny; ventral surface moderately shiny.

Vestiture mainly consisting of inconspicuous, white and pale brown setae. Head sparsely clothed with short, recumbent, white setae mixing with pale brown ones, but upper side of frons somewhat naked. Pronotum with short, recumbent, white and pale brown setae which are very sparsely scattering. Elytra very sparsely clothed with short, recumbent, white and pale brown setae which are arranged on each elytron as follows:1) white setae scattering throughout except for the dark purple to dark blue patches of integument, as a result, inconspicuous, wavy transverse bands occurring at just before apical 1/3 and at apical 1/5; 2) pale brown setae occurring on the patches of integument in apical 1/3 and irregularly on other parts. Underside more sparsely setiferous, with fine, recumbent, whitish setae.

Head, when viewed from above, faintly concave on frons, with oculofrontal margins rounded and not produced anteriorly. Eyes, when viewed from above, slightly broadly visible, weakly convex laterally. Vertex coarsely variolate-punctate, microsculptured between punctures; frons widely, faintly concave, weakly impressed along upper side of midline, with surface microsculptured; suprantennal pores transversely oval; clypeus wide (Fig. 76C), with elevated basal margin, WC/LC 2.06–2.07 (mean 2.07), WC/LSC 1.71–1.72 (mean 1.72), weakly arcuately emarginate at apical margin.

Antennae (Figs. 76D, E) short, just reaching level of pronotal widest point when laid laterally; antennomere I stout claviform, longer than II; II ovate, longer than III; III subrectangular, slightly longer than IV; IV–VI subrectangular, subequal each other in length; VII–X triangular, slightly more strongly enlarged in male than in female; XI triangular to subtriangular, small in size, almost same size as VI.

Pronotum widest at base, WP/LP 2.79–2.82 (mean 2.81), BMP/AMP 1.85–1.89 (mean 1.87), slightly narrower than elytra; lateral margins weakly arcuately, slightly weakly narrowed apicad; apicolateral angles nearly right (angle); basolateral angles sharply acute (angle); apical margin moderately deeply, arcuately emarginate, with small median lobe; basal margin trisinuate, with median lobe moderately produced; disk rather evenly convex medially, weakly swollen in basolateral part, weakly depressed along lateral margins, with apicolateral depressions being slightly U-shaped foveae (Fig. 76A), faintly depressed along basal median lobe; surface coarsely variolate-punctate in basal 1/3, with linear sculptures along apical margin, in other part sparsely, weakly punctate, with interspaces between punctures microsculptured. Scutellar shield small, rounded subtriangular, glabrous.

Elytra widest at base, LE/WE 1.25–1.31 (mean 1.28), LE/LP 3.65–3.81 (mean 3.73); humeral calluses small, almost not developed; lateral margins subparallel in just before basal half or faintly arcuately, weakly narrowed posteriorly from base to behind middle, then continuously arcuately, more strongly narrowed to subapical part, and finally arcuately convergent to conjointly rounded apices after faintly constricted behind subapical part, without serrations; marginal carinae distinct from base to subapical part; lateral carinae occurring from just behind humeri to subapical part, weakly sinuate behind basal parts; disk without depressions along lateral half of basal margin, faintly constricted behind humeri; surface irregularly and sparsely sculptured with shortly, linearly incised punctures, weakly rugoso-punctate around basal 2/4 of medial part, weakly rugulose near basal margin and along lateral side of lateral carinae.

Underside. Prosternum (Fig. 76F) with arcuate prosternal lobe faintly emarginate at middle of apical margin which is weakly rimmed; prosternal process wide; trapezoidal plate longer than wide, WTP/LTP 0.87–0.93 (mean 0.90), WTP/BTP 1.64–1.71 (mean 1.68), with rounded apical corners, with sides which are dilated from base to widest point around apical corners, with apex broadly, weakly arcuate; disk flattened on trapezoidal plate bearing marginal carinae along sides, evenly convex on prosternal lobe, with elevated parts along protrochantins; surface on trapezoidal plate only with setiferous pin-prick punctures, microsculptured. Hypomera with ill-defined hypomeral markings consisting of strong wrinkles and bearing pores medially (Fig. 76G). Metaventrite moderately variolate-punctate on inside of katepisternal suture and more densely variolate on outside of the suture, microsculptured. Legs moderately slender in femora and tibiae; metacoxal plates without arcuate notches on medial posterior margins, weakly produced posteriorly at each lateral angle which is broadly acute (angle), with surface moderately variolate and microsculptured; metafemora without angulate part at distal part of outer margins; metatibiae without a fringe of spines on each outer margin (Fig. 76H), but very sparsely bearing fine setae throughout; inner tooth of each claw slightly small. Abdominal ventrites with sternal groove only on ventrite V, this apical ventrite subtriangular and rounded at apex; surface variolate, in ventrite I with linearly confluent sculptures on median part.

Sexual dimorphism recognized on the relative size of serrate antennomeres (see above).

Male terminalia (n = 1for measurements). Tergite VIII and sternite VIII as shown in Fig. 72A, B. Proctiger (Fig. 72C) with a pair of short baculi at base. Sternite IX (Fig. 77A) rather slender, SL/SW 1.31, more or less emarginate at apical margin, without setae. Tegmen (Fig. 77B) slender; parameres PL/PW 3.70, bearing a pair of setae on apicolateral margins, almost parallel-sided, but with sides which are faintly dilated apicad; phallobase PbL/PbW 2.50, about 1/5 length of tegmen. Penis (Fig. 77C) wide, PeL/PeW 5.02, much shorter than tegmen; dorsal plate with sides (not including sides of median struts) which are subparallel but faintly dilated from base to apical 1/3, and then arcuately, moderately convergent apicad, with broadly rounded apex, basally with median struts nearly 1/2 length of penis; ventral membrane without sclerotized part, swollen above in apical half.

Female terminalia (n = 2 for measurements). Tergite VIII and sternite VIII as shown in Fig. 72D, E. Ovipositor (Figs. 72F, G, 77D–F) short. Proctiger with a pair of short, straight baculi at base; coxites transversely oblong, sparsely setiferous on each side of apical margin; styli very short, slightly wide, SlL/SlW 1.00–1.02 (mean 1.01), bearing several setae apically; ventral valve bearing a few setae on each side; vagina sack-shaped (under uninflated state); spermatheca slender tubular, slightly long in length, widest in middle.

Differential diagnosis. This species is very easily distinguished from Japanese other congeners by the large fossae on the pronotal apicolateral depressions, by the very sparse vestitures on dorsum, and by the unserrated elytral lateral margins.

Specimens examined. Non-type material. **Japan**. Honshu — [Tochigi] 1 ♂, 2 ♀♀, Jomin-yugari, Toyohara-otsu, Nasu, 13.VII.1996, T. Matsuzawa leg. (SOCI, YTJ). [Nagano] 1 ex., (♀ based on Kurosawa, 1976 b; no dissected terminalia), Karuizawa, 7–14.VII.1959, K. Morimoto leg. (NSMT).

Distributions in Japan. Honshu (Tochigi Prefecture).

Other records based on literatures. Nagano Prefectures in Honshu (Kurosawa, 1976 b).

Other distributions. Russian Far East and South Korea.

The specimen recorded from South Korea by Kurosawa (1976 b) is deposited in NSMT. I confirmed only pin and pined triangular card and labels for the specimen and thus insect body had been lost.

Adult food plant. Unknown.

Host plant. Unknown.

Leaf-mine. Unknown.

Note. *Habroloma* (*Habroloma*) *bifrons* is presumed associations with Geraniaceae plants (Kurosawa, 1976 a) since the members of the subgenus *Habroloma* are often used this plant families in Europe.

Subgenus ***Parahabroloma*** Kurosawa, 1959

Group I (eximium)

Species included. *Habroloma* (*Parahabroloma*) *eximium* (Obenberger, 1929) and *H*. (*P*.) *griseonigrum* (Saunders, 1873).

Diagnosis. Clypeus transverse; antennae without horn-shaped antennomere I; elytra without tufts of erect setae; metacoxal plates with arcuate notches at medial posterior margins; legs more or less stout in each femur and tibiae; male parameres moderate length; penis moderate length, with dorsal plate which is almost as wide as ventral membrane; female spermatheca moderate length.

Habroloma* (*Parahabroloma*) *eximium eximium (Lewis, 1893)
[Japanese name: Tsumaki-hirata-chibi-tamamushi Meigi-taipu-ashu]
(Figs. 71, 73B, 78, 79A, B, 80, 103B–D, 106A)

Trachys eximia Lewis, 1893: 337 (type locality: “Higo forests”, “Kiushiu”, Kumamoto Pref., Japan); Kerremans, 1903: 308 (catalog).

Trachys (*Habroloma*) *eximia*: Jakobson, 1913: 800 (catalog); Obenberger, 1918 a: 18, 31, 63 (in key; diagnosis; catalog); Obenberger, 1937 a: 1411 (World catalog).

Trachys (*Trachys*) *eximia* [sic]: Miwa & Chûjô, 1936: 23 (*lapsus calami*; catalog; Japanese name: Tsumaki-chibi-tamamushi).

Habroloma eximia: Kurosawa, 1950 a: 14, fig. 24c (note); Iga, 1955 a: 11 (in key; pictorial book); 1955 b: 82 (in key; pictorial book).

Habroloma (*Parahabroloma*) *eximia eximia*: Kurosawa, 1959: 263, 264, fig. 15c (redescription); 1963: 156, pl. 78 (pictorial book); 1976 a: 3 fig. 18c (note); Mühle, 2003: 47 (in checklist).

Habroloma (*Parahabroloma*) *eximium eximium*: Kurosawa, 1985: 36, pl.7 (pictorial book); Akiyama & Ohmomo, 1997: 50 (checklist); 2000: 286, pl. 120 (pictorial book); Kubáň, 2006: 417 (Palaearctic catalog); Bellamy, 2008 b: 2547 (World catalog); Ohmomo & Fukutomi, 2013: 171, pl. 54 (pictorial book); Kubáň, 2016: 569 (Palaearctic catalog).

Description. Male and female. Body wedge-shaped, slightly weakly convex dorsally (Figs. 78A, B). LB 2.90–3.59 mm (mean 3.30 mm); WB 1.63–2.08 mm (mean 1.89 mm); LB/WB 1.69–1.8 (mean 1.75) (n = 5 for all measurements except terminalia). Habitus as shown in Figs.73B, 79A, B.

Integument. Head and pronotum dark brass, with dark reddish to brownish tints on basal half of pronotum; elytra dark brass, but with dark reddish to brownish tints in post-scutellar triangular region reaching basal half and near humeral callus and in apical 1/5; underside, antennae, and legs black, often with weak golden-bronze reflections, except for tarsal pads pale brown. Dorsal and ventral surfaces moderately shiny.

Vestiture mainly consisting of yellowish-white and brown setae. Head clothed with short, recumbent, pale yellowish-white to pale yellowish-brown setae, but upper side of frons naked. Pronotum clothed with short, semirecumbent, pale yellowish-white and plae yellowish-brown setae which are arranged as follows: 1) pale yellowish-white setae occurring in apical half, becoming slightly denser apicolaterally; and 2) pale yellowish-brown setae in basal half. Elytra clothed with short, semirecumbent, pale yellowish-white and dark brown setae which are arranged on each elytron as follows: 1) dark brown triangular mark in post-scutellar region of elytra reaching basal half and near humeral callus, sometimes with reddish tints; 2) dark brown apical patch in about apical 1/5, sometimes with reddish tints; 3) inconspicuous small brown patch between triangular mark and apical patch mentioned above; and 4) pale yellowish-white setae in remaining space, slightly more densely occurring along triangular mark and apical patch. Underside more sparsely setiferous, with fine, recumbent, whitish setae.

Head, when viewed from above, shallowly concave on frons with a small incision at middle, with oculofrontal margins ridged and moderately produced anteriorly. Eyes, when viewed from above, narrowly visible, weakly convex laterally. Vertex coarsely variolate-punctate; frons widely concave, weakly impressed along upper side of midline, with surface coarsely variolate-punctate around the naked part which is microsculptured; suprantennal pores transversely oval; clypeus wide (Fig. 78D), with elevated basal margin, WC/LC 2.72–3.27 (mean 3.01), WC/LSC 2.11–2.60 (mean 2.23), moderately arcuately emarginate at apical margin.

Antennae (Fig. 78E, F) short, not reaching level of pronotal widest point when laid laterally; antennomere I stout claviform, longer than II; II ovate, longer than III; III subrectangular, longer than IV; IV–VI subrectangular, subequal each other in length; VII–X triangular, slightly more strongly enlarged in male than in female; XI triangular to subtriangular.

Pronotum widest at sub-basal part, WP/LP 2.99–3.37 (mean 3.21), BMP/AMP 1.78–1.87 (mean 1.84), slightly wider than elytra; lateral margins showing variations in shape: evenly arcuately narrowed apicad; or weakly arcuately to rather straightly narrowed anteriorly from basal widest point to apical 1/3, then arcuately convergent apicad;

apicolateral angles nearly right (angle); basolateral angles sharply acute (angle); apical margin moderately deeply, arcuately emarginate, with faint median lobe; basal margin trisinuate, with median lobe moderately produced; disk depressed laterally, faintly depressed along basal median lobe, with ill-defined apicolateral and basolateral depressions, without pores in the apicolateral depressions; surface rather densely variolate-punctate throughout. Scutellar shield small, triangular, glabrous.

Elytra widest at base, LE/WE 1.26–1.34 (mean 1.31), LE/LP 3.98–4.3 (mean 4.14); humeral calluses weakly developed; lateral margins gradually narrowed posteriorly from base to around middle, then more strongly and faintly arcuately narrowed to subapical part, and finally arcuately convergent to conjointly rounded apices, serrated with two to four denticles at subapical part (Fig. 78C); marginal carinae distinct from base to subapical part; lateral carinae occurring from behind humeri to subapical part, faintly sinuate in basal parts; disk moderately depressed along lateral half of basal margin; surface irregularly and sparsely sculptured with shortly, linearly incised punctures, weakly rugulose between the punctures.

Underside. Prosternum (Fig. 78G) with arcuate prosternal lobe broadly, faintly emarginate at apical margin which is faintly rimmed; prosternal process wide; trapezoidal plate wider than long, WTP/LTP 1.28–1.34 (mean 1.32), WTP/BTP 1.31–1.41 (mean 1.38), with rounded apical corners, with sides which are dilated from base to widest point around apical corners, with apex broadly, faintly arcuate; disk flattened on trapezoidal plate bearing marginal carinae along sides, evenly convex on prosternal lobe; surface on trapezoidal plate with setiferous pin-prick punctures and ocellate sculptures. Hypomera with large, transversely oval hypomeral markings consisting of linearly incised punctures. Metaventrite moderately variolate-punctate on inside of katepisternal suture and more densely variolate on outside of the suture. Legs stout in femora and tibiae; metacoxal plates with arcuate notches on medial posterior margins, weakly produced posteriorly at each lateral angle which is broadly acute (angle) and rounded, with surface moderately variolate; metafemora obtusely angulate at about distal 1/3 of outer margins; metatibiae without a fringe of spines on each outer margin (Fig. 78I), but very sparsely bearing fine setae throughout; inner tooth of each claw large. Abdominal ventrites with sternal groove only on ventrite V, of which apex is rounded; surface variolate, in ventrite I with linearly confluent sculptures on median part.

Sexual dimorphism recognized on the relative size of serrate antennomeres (see above).

Male terminalia (n = 1 for measurements). Proctiger with a pair of short baculi at base. Sternite IX (Figs. 80A, D) rather slender, SL/SW 1.14, more or less emarginate at apical margin, without setae. Tegmen (Figs. 80B, E) slender; parameres PL/PW 3.39, bearing two to three setae on each apicolateral margin, with sides which are gently dilated from base to widest part around apical 1/3, then faintly arcuately narrowed to subspical part, and finally strongly arcuately convergent apicad; phallobase PbL/PbW 2.00, about 1/5 length of tegmen. Penis (Figs. 80C, F) wide, PeL/PeW 5.53, shorter than tegmen; dorsal plate with sides (not including sides of median struts) which are subparallel from base to subapical part, and then strongly, arcuately convergent apicad, with roundly produced apex, basally with median struts about 1/2 length of penis; ventral membrane weakly sclerotized as a liner patch in middle of subapical part, with finely tuberculate part in apical half around the sclerotized patch.

Female terminalia (n = 1 for measurements). Ovipositor (Figs. 80G–I) short. Proctiger with a pair of short, straight baculi at base; coxites transversely subtrapezoidal with arcuate apical margin, sparsely setiferous on each side of apical margin; styli short, slightly slender, faintly curved inwardly, SlL/SlW 2.67, bearing several setae apically; ventral valve without setae; vagina sack-shaped (under uninflated state); spermatheca slender tubular, moderate in length, widest much before middle.

Differential diagnosis.

Specimens examined. Non-type material. Kyushu — [Fukuoka] 4 ♂♂, 9 ♀♀, Fukakurakyô, Ochiai, Soeda-machi, Tagawa-gun, 27.IV.2017, Y. Tamadera leg. (YTJ). [Ôita] . [Kagoshima] 1 ex., Kurino, 5.V.1955, Y. Takemura leg. (SEHU).

Distributions in Japan. Kyushu.

Other records based on literatures. Honshu (Saito, 1991) and Shikoku (Kurosawa, 1959).

Yakushima Is. is often included distribution area of *Habroloma* (*Parahabroloma*) *eximium eximium*, but actually suspicious adult feeding scars are only founded from leaves of *Symplocos lancifolia* (Kurosawa, 1976 a) and this s have never been recorded from this island. This study, therefore, removed Yakushima Is. from distributions of this nominotypical subspecies.

Other distributions. Unknown.

Adult food plants. Same as in the larvae mentioned below.

Host plants. Symplocaceae: *Symplocos myrtacea* Siebold et Zucc. [Japanese name: Hainoki] (confirmed by this study); *S. lancifolia* Siebold et Zucc. [Japanese name: Shirobai] (Kurosawa, 1959 — adult record?; confirmed by this study).

Symplocos theophrastifolia Siebold et Zucc. [Japanese name: Kanzaburô-no-ki] is not recognized as a host of *Habroloma eximium eximium*, but I confirmed that a female individual of this nominotypical subspecies oviposited on this plant leaf under the rearing condition and finally its larva grown up to third instar (n = 1).

Leaf-mining habit. Mines of *Habroloma* (*Parahabroloma*) *eximium eximum* were found on *Symplocos myrtacea* and *S. lancifolia* by this study (Figs. 103B–D, 10A): each mine was of the upper surface type and was linear and blotchy; when full-grown, it occupied almost whole the leaf blade; eggs, which were matte black (remaining eggshell) and covered on powdery substances, were laid singly on the base of leaf-blade on the adaxial surface; hatched larvae firstly crossed the base of midrib — this behavior seems to cause early defoliation of the infested leaves — and left linear mines and then second to third instars (final instar) left blotch mines; frass were powdery to granular and were left inside the mines; adults were emerged from the both surfaces of the leaves with oval adult exit holes.

In my field survey (Fukuoka and Ôita, Kushu), mines of this subspecies were always found on defoliated leaves even in the stage of the first instar, although eggs before hatching were always done on the living leaves on trees. The defoliated leaves gradually withered, and finally whole of the leaves completely withered when mines were full-grown. As a result, this subspecies does not form green island (Hering, 1951) on infested leaves.

Habroloma* (*Parahabroloma*) *eximium eupoetum (Obenberger, 1929 a)
[Japanese name: Tsumaki-hirata-chibi-tamamushi Taiwan-Yaeyama-ashu]
(Figs. 73C, 79C–G, 81)

Trachys (*Habroloma*) *eupoeta* Obenberger, 1929 a: 61 (type locality: "Formose" [sic]); Miwa & Chûjô, 1936: 26 (catalog; Japanese name: Akage-mame-tamamushi); Obenberger, 1937 a: 1421 (World catalog); Kurosawa, 1959: 264 (noted in *H.* (*P.*) *eximia*).

Habroloma (*Parahabroloma*) *eximium eupoeta*: Kurosawa, 1976 b: 132 (downgraded as subspecies; Ishigakijima Is. Ryukyus, Japan); Kubáň, 2006: 417 (Palaearctic catalog); Kubáň, 2016: 569 (Palaearctic catalog; China — Fujian and Hunan); Peng, 2022 b: 305 (Fujian and Hunan, China).

Habroloma (*Parahabroloma*) *eximium eupoetum*: Kurosawa, 1985: 36 (noted in pictorial book); Akiyama & Ohmomo, 1997: 50 (checklist); 2000: 286, pl. 120 (pictorial book); Bellamy, 2008 b: 2547 (World catalog); Ohmomo & Fukutomi, 2013: 171, pl. 54 (pictorial book).

Habroloma (*Parahabroloma*) *eximia eupoeta*: Mühle, 2003: 47 (in checklist).

Trachys (*Habroloma*) *liukiuensis* Obenberger, 1940: 39 (type locality: "Archipel Liu-Kiu: Ku-kien-san", Japan). **Syn. nov.**

Habroloma (*Parahabroloma*) *liukiuense*: Kubáň, 2006: 417 (Palaearctic catalog); Bellamy, 2008 b: 2552 (World catalog); Kubáň, 2016: 569 (Palaearctic catalog; Taiwan).

Description. Male and female. Body wedge-shaped, slightly weakly convex dorsally. LB 3.04–3.47 mm (mean 3.30 mm); WB 1.71–2.02 mm (mean 1.90 mm); LB/WB 1.72–1.78 (mean 1.74) (n = 5 for all measurements except terminalia). Habitus as shown in Figs. 73C, 79C–G.

Differs from nominotypical subspecies as follows: weakly produced oculofrontal margins of head in dorsal view; dorsum vestiture with reddish-brown, orange-yellow, or yellow setae forming same patterns of the nominotypical subspecies. Ratios of body parts as follows: WC/LC 2.65–2.86 (mean 2.76), WC/LSC 2.08–2.3 (mean 2.16), WP/LP 3.06–3.29 (mean 3.18), BMP/AMP 1.66–1.78 (mean 1.73); LE/WE 1.29–1.33 (mean 1.30), LE/LP 3.97–4.24 (mean 4.11), WTP/LTP 1.37–1.58 (mean 1.48), WTP/BTP 1.36–1.54 (mean 1.47).

Terminala as shown in Fig. 81. Female coxites slightly more densely setiferous on each side of apical margin. Ratios as follows (n=1 ♂, 1 ♀ for all measurements): SL/SW 1.07, PL/PW 3.76, PbL/PbW 2.00, PeL/PeW 5.57. Otherwise practically as in the nominotypical subspecies.

Specimens examined. Non-type material. **Japan**. The Ryukyus: Yaeyama Isls. — [Ishigakijima Is.] 1 ♂, Mt. Omotodake fumoto, Ôhama, Ishigaki-shi, Okinawa-ken, 21.III.2002, H. Fukutomi leg. (YTJ). [Iriomotejima Is.] 2 ♂♂, Ôtomi-rindô, Haeminaka, Taketomi-chô, Yaeyama-gun, Okinawa-ken, 26.III.2016, Y. Tamadera leg; 1 ♂, 1 ♀, same 28.III.2016, Y. Tamadera leg. (YTJ); 2 ♂♂, 3 ♀♀, same locality, 30.III.2016, Y. Tamadera leg. (YTJ). **Taiwan**. 1 ♂, Yangmingshan, Taipei Hsien, 24.VIII.1966, H. Kamiya leg. (NSMT); 1 ex., Yangmingshan, Taipei Hsien, 1–2.VII.1977, H. Takizawa leg. (NSMT).

Distributions in Japan. The Ryukyus: Yaeyama Isls. (Ishigakijima Is. and Iriomotejima Is.).

Other distributions. China, Hainan Is., and Taiwan.

Adult food plants. Adults of this subspecies are captured on leaves of *Symplocos cochinchinensis* (Lour.) S. Moore [Japanese name: Aoba-no-ki] in Iriomotejima Is, Japan and also on leaves of host mentioned below.

Host plant. Symplocaceae: *Symplocos prunifolia* Siebold et Zucc. var. *tawadae* Nagam. [Japanese name: Nagaba-kurobai] (Kurosawa, 1976 b — adult record?) in

Ishigakijima Is, Japan.

Leaf-mining habit. Unknown.

Note. *Taxonomic treatment of* Habroloma (Parahabroloma) liukiuense. To date, the detailed type locality of *Habroloma* (*Parahabroloma*) *liukiuense* (Obenberger, 1940), "Ku-Kien-San" in the Ryukyus, have been regarded as an unknown locality name (Kurosawa, 1976 a). In addition, because of more large-sized body in the type specimen, Kurosawa (1976 a) suspected that the type of *H*. (*P*.) *liukiuense* is different species from the species (subspecies) identified as *H*. (*P*.) *eximium liukiuense* sensu Kurosawa (1959) in Amami-Ôshima Is. and Okinawajima Is. Since the type specimen is, unfortunately, a bad specimen with elytral setae peeling off, Kurosawa (1976 b) treated it as the same of his identified species, *H*. (*P*.) *liukiuense* sensu Kurosawa, tentatively.

Recently, I realized that the unknown locality name, "Ku-Kien-San" indicates Iriomotejima Is. in the Yaeyama Isls., Ryukyus, based on an old atlas (Alden, 1888). In the Yaeyama Isls., *H*. (*P*.) *eximium eupoetum* (Obenberger, 1929 a) is distributed and it is differentiated from *H*. (*P*.) *liukiuense* sensu Kurosawa (1976 b) by the more large-sized body and clearer elytral triangular pattern of setae. In addition to the locality, the morphological information is also suggested that the true *H*. (*P*.) *liukiuense* (Obenberger, 1940) is a junior synonym of *H*. (P.) *eximium eupoetum* (Obenberger, 1929) and furthermore the misidentified species as *H*. (*P*.) *liukiuense* sensu Kurosawa (1976 b) is recognized as an unnamed taxon. This study, thus, synonymizes *H*. (*P*.) *liukiuense* with *H*. (*P*.) *eximium eupoetum* and describes the misidentified taxon as a new subspecies below.

***Habroloma* (*Parahabroloma*) *eximium* subsp. 1**

[Japanese name: Okinawa-tsumaki-hirata-chibi-tamamushi]

(Figs. 73D, 79H–J, 82, 103E, F, 106B)

Habroloma (*Parahabroloma*) *eximia liukiuensis* [auct. non Obenberger, 1940]: Kurosawa, 1959: 265 (description); 1963: 156 (noted in pictorial book); Chûjô, 1970: 21 (distribution).

Habroloma (*Parahabroloma*) *liukiuensis* [auct. non Obenberger, 1940]: Kurosawa, 1976 a: 4 (noted on problem of type locality).

Habroloma (*Parahabroloma*) *liukiuense* [auct. non Obenberger, 1940]: Kurosawa, 1976 b: 132 (as species); 1985: 36, pl.7 (pictorial book); Akiyama & Ohmomo, 1997: 51 (checklist); 2000: 287, pl. 120 (pictorial book); Ohmomo & Fukutomi, 2013: 171, pl. 55 (pictorial book); Tamadera and Yoshitake, 2018 a: 16 (distribution).

Description. Male and female. Body wedge-shaped, slightly weakly convex dorsally. LB 2.79–3.25 mm (mean 3.11 mm); WB 1.56–1.88 mm (mean 1.77 mm); LB/WB 1.72–1.80 (mean 1.76) (n = 6 for all measurements except terminalia). Habitus as shown in Figs. 73D, 79H–J.

Differs from nominotypical subspecies and subsp. *eupoetum* as follows: oculofrontal margins of head in dorsal view more weakly produced anteriorly than those of the nominotypical subspecies; dorsum vestiture with orange-yellow or yellow setae forming same patterns of other subspecies, but each pattern usually being more indistinct due to mixing with yellow setae in white patterns; and small-sized body. Ratios of body parts as follows: WC/LC 2.84–4.00 (mean 3.29), WC/LSC 2.13–3.06 (mean 2.54), WP/LP 3.00–3.29 (mean 3.16), BMP/AMP 1.74–1.85 (mean 1.80); LE/WE 1.28–1.36 (mean 1.32), LE/LP 3.94–4.47 (mean 4.16), WTP/LTP 1.21–1.37 (mean 1.28), WTP/BTP 1.37–1.62 (mean 1.48).

Terminala as shown in Fig. 82. Female coxites slightly more densely setiferous on each side of apical margin. Ratios as follows (n = 1 ♂, 1 ♀ for all measurements): SL/SW 1.07, PL/PW 3.81, PbL/PbW 2.11, PeL/PeW 5.93. Otherwise practically as in the nominotypical subspecies.

Specimens examined. The Ryukyus: Amami Isls. — [Amami-Ôshima Is.] 3 exs., Mt. Yuwandake, Uken-son, 18.IV.2005, Y. Komiya leg. (SEHU); 1 ex., Chinase Rindô, Chinase, Naze-shi, 17.IV.2005, Y. Komiya leg. (SEHU); 2 exs., Mt. Yuidake, Setouchi-chô, 15.IV.2005, H. Takizawa leg. (SEHU); 1 ex., Gusuku, Sumiyô-chô, 26.V.1960, no collector name (SEHU); 1 ♂, Yuwan, Uken-son, Ôshima-gun, Kagoshima-ken, Japan, 29.III.2015, Y. Fujisawa leg. (YTJ); 1 ♂, 1 ♀, same locality, 19.IV.2017, Y. Tamadera leg. (YTJ); 2 ♂♂, Kamiya, Sumiyô-cho, Ôshima-gun, 27.V.2016, Y. Tamadera leg. (YTJ); 1 ♂, 2 ♀♀, near Kinsakubaru, Nazeasado, Amami-shi, 1.VII.2016, S. Shimamoto leg. (YTJ). [Okinoerabujima Is.] 1 ♀, Kamishiro, China-chô, Ôshima-gun, 25.IV.2016, Y. Tamadera leg. (YTJ); 1 ♂, Tamina, China-chô, Ôshima-gun Kagoshima-ken, Japan, 27.IV.2016, Y. Tamadera leg. (YTJ); 1 ♀, ditto, K. Watanabe leg. (YTJ). [Tokunoshima Is.] 1 ex., Tete-rindô, Tete, Tokunoshima-chô, 24.VI.2017, Y. Tamadera leg. (YTJ; recorded by Tamadera and Yoshitake, 2018a), 6 exs., Yama-kubiri-rindô, Todoroki, Tokunoshima-chô, 24.VI.2017, Y. Tamadera leg. (YTJ; recorded by Tamadera and Yoshitake, 2018a); 20 exs., same locality, 27.VI.2017, Y. Tamadera leg. (YTJ; recorded by Tamadera and Yoshitake, 2018a); 2 exs., Mt. Fûgusuku-yama, Matsubara, Amagi-chô, Ôshima-gun, 16.IX.2017, H. Yoshitake leg. (YTJ; recorded by Tamadera and Yoshitake, 2018a); 6 exs., Mt. Yamatogusuku-yama, Amagi, Amagi-chô, Ôshima-gun, 25.VI.2017, Y. Tamadera & H. Yoshitake leg. (YTJ; recorded by Tamadera and Yoshitake, 2018a); 2exs., Uenamichi-sinrin-kôen Park, Amagi, Amagi-chô, Ôshima-gun, 18.IX.2017, H. Yoshitake leg. (YTJ; recorded by Tamadera and Yoshitake, 2018a). [Okinoerabujima Is.] 7 exs., Mt. Ôyama, 17.VII.1981, M. Ôhara leg. (SEHU). Okinawajima Isls. — [Okinawajima Is.] 1ex., Yona, Kunigami-son, 18.IX.1978, M. Kinjo leg. (SEHU); 1 ♂, 2 ♀♀, Taiho, Ôgimi-son, Kunigami-gun, 30.III.2001, H. Fukutomi leg. (YTJ).

Distributions in Japan. The Ryukyus: Amami Isls. (Amami-Ôshima Is., Tokunoshima Is., and Okinoerabujima Is.); and Okinawa Isls., (Okinawajima Is.).

Other distributions. Unknown.

Adult food plants. Same as in the larvae mentioned below. In addition, some adults were captured on leaves of *Symplocos liukiuensis* Matsum. [Japanese name: Aobana-hainoki] in Okinoerabujima Is., Japan (confirmed by this study) and also on leaves of *S. okinawensis* Matsum. [Japanese name: Ryûkyû-hainoki] in Okinawajima Is., Japan (Kurosawa, 1976a).

Host plant. Symplocaceae: *Symplocos formosana* Brand [Japanese name: Amashiba] (confirmed by this study).

Leaf-mining habit. Mines of *Habroloma* (*Parahabroloma*) *eximium* subsp.1 were found on *Symplocos formosana* by this study (Figs. 103F, 106B): mines, eggs, frass, and adult exit holes showed almost same states as those of the nominotypical subspecies, but differ from the latter as follows: after crossing the base of midrib, hatched larva linearly mined along the midrib toward middle and then left blotch mines (based on the population of Amami-Ôshima Is).

Note. This subspecies had been treated as *Habaroloma* (*Parahabroloma*) *liukiuense* sensu Kurosawa (1976 b). Based on the reasons mentioned in the note of *H.* (*P.*) *eximium eupoetum*, this study regarded this taxon as an unnamed one.

Kurosawa (1976 b) treated this taxon (populations of Amami and Okinawa Isls.) as a full species based on the small-sized body and indistinct elytral triangular pattern of setae. However, this character states occasionally show individual variations and become ambiguous between subsp. *eupoetum* and this taxon. In addition, male and female terminalia show no significant differences to separate species. Judging from the morphological examinations, this taxon (populations of Amami and Okinawa Isls.) is regarded as a subspecies of *H.* (*P.*) *eximum*.

Habroloma* (*Parahabroloma*) *griseonigrum (Saunders, 1873)
[Japanese name: Hai-iro-hirata-chibi-tamamushi]
(Figs. 73E, 83, 84, 106C)

Trachys griseonigra Saunders, 1873: 520 (type locality: "Nagasaki", Japan); Lewis, 1879: 15 (catalog); Kerremans, 1885: 157 (catalog); Schönfeldt, 1887: 113 (catalog); Kerremans, 1892 a: 286 (catalog); Lewis, 1893: 338 (in list); Kerremans, 1903: 308 (catalog).

Trachys (*Habroloma*) *griseonigra*: Jakobson, 1913: 800 (catalog); Obenberger, 1918 a: 18, 32, 63 (in key; diagnosis; catalog); 1926 b: 661 (catalog); Obenberger, 1937 a: 1411 (World catalog).

Trachys (*Trachys*) *griseonigra* [sic]: Miwa & Chûjô, 1936: 24 (*lapsus calami*; catalog; Japanese name: Hai-iro-chibi-tamamushi).

Habroloma griseonigra: Kurosawa, 1950 a: 14, fig. 24b (note); 1950 b: 1111, fig. 3183 (pictorial book); Chûjô & Kurosawa, 1950: 14 (Shikoku, Japan); Yano, 1952: 37 (immature stages); Iga, 1955 a: 11, pl.4 (pictorial book); 1955 b: 82, pl.24 (pictorial book).

Habroloma (*Parahabroloma*) *griseonigra*: Kurosawa, 1959: 261, fig.15b (redescription); 1976 a: 3, fig. 17 (note); Mühle, 2003: 47 (in checklist).

Habroloma (*Parahabroloma*) *griseonigrum*: Kurosawa, 1985: 37, pl. 7 (pictorial book); Akiyama & Ohmomo, 1997: 51 (checklist); 2000: 286, pl. 120 (pictorial book); Kubáň, 2006: 417 (Palaearctic catalog); Kubáň, 2016: 569 (Palaearctic catalog).

Habroloma (*Parahabroloma*) *griseonigrum griseonigrum*: Bellamy, 2008 b: 2549 (World catalog); Ohmomo & Fukutomi, 2013: 171, pl. 55 (pictorial book).

Trachys (*Habroloma*) *chionochaeta* Obenberger, 1929 a: 54 (type locality: "Formosa"); Obenberger, 1937 a: 1419 (World catalog); Akiyama & Ohmomo, 1997: 51 (*lapsus calami*, as synonym of *H*. (*P*.) *griseonigrum*); Kubáň, 2006: 417 (*lapsus calami*, as synonym of *H*. (*P*.) *griseonigrum*). **Syn. nov.**

Trachys (*Habroloma*) *chinochaeta* [sic]: Miwa & Chûjô, 1936: 26 (misspelling; catalog; Japanese name: Ginge-mame-tamamushi).

Habroloma (*Parahabroloma*) *griseonigrum chionochaeta*: Kurosawa, 1976: 132 (downgraded as subspecies); Akiyama & Ohmomo, 1997: 51 (in synonymy of *H*. (*P*.) *griseonigrum*); Kubáň, 2006: 417 (in synonymy of *H*. (*P*.) *griseonigrum*).

Habroloma (*Parahabroloma*) *griseonigrum chionochaetum*: Bellamy, 2008 b: 2549 (World catalog); Kubáň, 2016: 569 (Palaearctic catalog; in synonymy of *H*. (*P*.) *griseonigrum*); Ong & Hattori, 2019: 210, fig. 102 (pictorial book; aedeagus).

Description. Male and female. Body wedge-shaped, weakly convex dorsally (Figs. 83A, B). LB 2.74–3.25 mm (mean 3.03 mm); WB 1.76–2.07 mm (mean 1.93 mm); LB/WB 1.55–1.59 (mean 1.57) (n = 5 for all measurements except terminalia). Habitus as shown in Figs.73E.

Integument mainly black; head becoming dark brass from lower side of frons to clypeus; pronotum becoming dark brass along basal half of lateral margins; scutellar shield sometimes with weak bronzy tints; underside sometimes with golden-bronze reflections on prosternal trapezoidal plate and metaventrite and along posterior margins of metacoxal plates; antennae and legs sometimes with golden-bronze reflections; tarsal pads pale brown. Dorsal and ventral surfaces moderately shiny.

Vestiture mainly consisting of white, yellow, and black setae. Head clothed with short, recumbent, white and yellow setae which are arranged as follows: 1) white setae usually occurring on vertex, sometimes mixing with pale yellow setae; 2) yellow setae on frons, becoming denser toward apical margin of frons, but occasionally frons setae almost replacing white setae. Pronotum clothed with short, semirecumbent, pale white and black setae which are arranged as follows: 1) four black patches across middle, sometimes mixing with a few yellowish setae, the two median patches reaching basal margin of pronotum; 2) white setae in remaining space, becoming denser apicolaterally, forming three stripes between black patches. Elytra clothed with short, semirecumbent, white, yellow, and black setae which are arranged on each elytron as follows: 1) black, broad, oblique stripe from middle of basal margin to behind middle of sutural margin, but separated from sutural margin by white to pale yellow setae; 2) black patch at apical 1/3, separated from sutural margin by white to pale yellow setae; 3) three black spots at just behind middle of outside lateral carina, at behind middle of inside lateral carina, and at behind apical 1/3 of outside lateral carinae; 4) a few pale yellow setae along basal 2/3 of sutural margin; and 5) white setae in remaining space, occasionally mixing with a few pale yellow setae, becoming denser along outside of the black oblique stripe and before and behind the black patch. Underside more sparsely setiferous, with fine, recumbent, whitish setae, becoming slightly denser on medial part of hypomeral markings, and lateral parts of metacoxal plates.

Head, when viewed from above, shallowly concave on frons with a small incision at midline, with oculofrontal margins sharply ridged and slightly strongly produced anteriorly. Eyes, when viewed from above, slightly broadly visible, moderately convex laterally. Vertex coarsely variolate-punctate; frons widely concave, weakly impressed along upper side of midline, with surface coarsely variolate-punctate except upper side around midline; suprantennal pores simply round; clypeus wide (Fig. 83D), with weakly elevated basal margin, WC/LC 2.59–2.97 (mean 2.72), WC/LSC 1.71–2.00 (mean 1.86), moderately arcuately emarginate at apical margin, with sides distinctly dilated apicad.

Antennae (Fig. 83E, F) short, in male just reaching level of pronotal widest point when laid laterally, in female not reaching; antennomere I stout claviform, longer than II; II ovate, longer than III; III subrectangular, slightly longer than IV; IV–VI subrectangular, subequal each other in length; VII–X triangular, slightly more strongly enlarged in male than in female; XI weakly elongate triangular.

Pronotum widest at sub-basal part, WP/LP 3.21–3.41 (mean 3.26), BMP/AMP 1.85–1.92 (mean 1.88), usually slightly wider than elytra, but ocassinally almost same as elytral width; lateral margins evenly, strongly arcuately narrowed apicad; apicolateral angles nearly right (angle); basolateral angles sharply acute (angle); apical margin moderately deeply, arcuately emarginate, with inconspicuous, faint median lobe which is almost straight line at glance; basal margin trisinuate, with median lobe moderately produced; disk rather evenly convex, faintly depressed along basal median lobe, with ill-defined apicolateral depressions bearing small round pore on the middle of each, which is mostly hidden by dense pronotal setae; surface rather densely variolate-punctate throughout. Scutellar shield small, triangular, glabrous.

Elytra widest at base, LE/WE 1.14–1.19 (mean 1.16), LE/LP 3.63–4.01 (mean 3.75); humeral calluses weakly developed; lateral margins slightly strongly narrowed posteriorly from base to conjointly, truncately rounded broad apices, behind middle part faintly arcuate, serrated with two to four denticles at subapical part (Fig. 83C); marginal carinae distinct from base to subapical part; lateral carinae occurring from behind humeri to subapical part, weakly sinuate behind basal parts; disk moderately depressed along lateral half of basal margin, weakly constricted behind humeri; surface irregularly and sparsely sculptured with shortly, linearly incised punctures.

Underside. Prosternum (Fig. 83G) with arcuate prosternal lobe faintly emarginate at middle of apical margin which is weakly rimmed; prosternal process wide; trapezoidal plate as wide as long, WTP/LTP 1.33–1.52 (mean 1.43), WTP/BTP 1.31–1.49 (mean 1.40), with rounded apical corners, with sides which are dilated from base to widest point around apical corners, with apex broadly, faintly arcuate; disk flattened on trapezoidal plate bearing marginal carinae along sides, evenly convex on prosternal lobe; surface on trapezoidal plate with setiferous pin-prick punctures and ocellate sculptures. Hypomera with large, transversely oval hypomeral markings consisting of linearly incised punctures (Fig. 83H). Metaventrite moderately variolate-punctate on inside of katepisternal suture and moderately variolate on outside of the suture. Legs stout in femora and tibiae;

metacoxal plates with arcuate notches on medial posterior margins, weakly produced posteriorly at each lateral angle which is sharply to broadly acute (angle), with surface moderately variolate; metafemora obtusely angulate at about distal 1/3 of outer margins; metatibiae without a fringe of spines on each outer margin (Fig. 83I), but very sparsely bearing fine setae throughout; inner tooth of each claw large. Abdominal ventrites with sternal groove only on ventrite V, of which apex is broadly rounded; surface variolate, in ventrite I with linearly confluent sculptures on median part.

Sexual dimorphism recognized on the relative size of serrate antennomeres (see above).

Male terminalia (n = 1 for measurements). Proctiger with a pair of short baculi at base. Sternite IX (Fig. 84A) rather slender, SL/SW 1.20, rounded at apical margin, without setae. Tegmen (Fig. 84B) slender; parameres PL/PW 3.79, bearing a few, very short setae on apicolateral margins, with sides which are subparallel or gently dilated from base to middle, then weakly arcuately dilated to widest part in about apical 1/4, then weakly arcuately narrowed to subapical part, and finally strongly arcuately convergent apicad; phallobase PbL/PbW 1.67, about 1/5 length of tegmen. Penis (Fig. 84C, D) slender, PeL/PeW 8.11, shorter than tegmen; dorsal plate with sides (not including sides of median struts) which are subparallel in basal 3/4, and then arcuately convergent apicad, with strongly produced apex which is truncated, with a pair of long V-shaped lines in apical 3/4 (Fig. 84C), basally with median struts longer than 1/3 length of penis; ventral membrane weakly sclerotized as a liner patch in middle of subapical part, with finely tuberculate part in apical 1/3 around the sclerotized patch.

Female terminalia (n = 1 for measurements). Ovipositor (Figs. 84E–G) short. Proctiger with a pair of short, straight baculi at base; coxites transversely subtrapezoidal, broadly, weakly protruded at median part of apical margin between styli, sparsely setiferous on each side of apical margin; styli short, rather slender, SlL/SlW 2.50, bearing several setae apically; ventral valve without setae; vagina sack-shaped (under incompletely inflated state); spermatheca slender tubular, moderate in length, widest around middle.

Differential diagnosis. This species is readily distinguished from Japanese other congeners by the unique white patterns of elytral setae, the anteriorly dilated clypeus, the roundly truncated elytral apices, the truncately produced apex of slender penis; and the weakly protruded median part of coxites.

Specimens examined. Non-type material. **Japan**. Honshu — [Saitama] 1 ex., Yorii-machi, 5.V.2000, H. Takizawa leg. (SEHU). [Tokyo] 1 ex., Ônita, Ôme-shi, 2.V.2004, H. Takizawa leg. (SEHU); 1 ex., same locality, 25.V.1991, H. Takizawa leg. (SEHU); 1 ex., Tamagawa River, Akiruno-shi, 30.IV.2005, H. Takizawa leg. (SEHU); 2 ♀♀, Mt. Takao-san, Takao-chô, Hachiôji-shi, 13.V.2016, H. Shigeto leg. (YTJ). [Kanagawa] 3 ♀♀, Mt. Kôbô-yama, Minamiyana, Hadano-shi, 27.IV.2015, Y. Tamadera leg. (YTJ); 3 ♂♂, Bôsainooka-park, Nurumizu, Atsugi-shi, 5.IV.2017, Y. Tamadera leg. (YTJ); 1 ♂, Atsugi Campus of Tokyo University of Agriculture, Funako, Atsugi-shi, 14.IV.2017, Y. Tamadera leg. (YTJ). [Gifu] 1 ex., Oku-Mino, VI.1961, M. Nagai leg. (SEHU). [Aichi] 1 ex., Higashiyama, Nagoya-shi, 10.V.1946, T. Nakane leg., on *Quercus acutissima* (SEHU); 1 ex., same locality, 14.V.1946, T. Nakane leg., on *Quercus acutissima* (SEHU); 1 ex. ditto, T. Nakane leg. (SEHU); 1 ex., same locality, 20.V.1946, T. Nakane leg. (SEHU); 1 ex., same locality, 28.V.1948, S. Osawa leg. (SEHU); 1 ex., Mikawa-ôno, Shinshiro-shi, 10.V.1991, TTM. Nakane leg. (SEHU). [Kyoto] 1 ex., Kibune, Kyoto-shi, 29.IV.1957, T. Nakane leg. (SEHU); 7 exs., Arashiyama, Kyoto-shi, 23.IV.1954, T. Kishii leg. (SEHU); 1 ex., same locality, 24.IV.1954, T. Kishii leg. (SEHU). [Osaka] 1 ex., Mino-o, 5.V.1942, K. Sakaguchi leg. (SEHU); 1 ex., same locality, 22.IV.1933, S. Fukki leg. (SEHU). [Nara] 1 ex., Mt. Kasuga-yama, 5.V.1951, K. Sawada leg. (SEHU); 2 exs., same locality, 20.V.1951, K. Sawada leg. (SEHU). [Hiroshima] 1 ex., Tanojiri, Tsutsuga, Yamagata-gun, 22.IV.1978, T. Kosaka leg. (SEHU). Shikoku — [Ehime] 2 ♀♀, Yuyama, Yanagi, Matsuyama, 20.VI.2001, H. Kan leg. (YTJ). [Kôchi] 2 exs., Yakyô, Nankoku-shi, 10.IX.1945, K. Sakaguchi leg. (SEHU). [Fukuoka] 1 ex., Haki, Asakura-shi, 26.V.1952, C. Takeya leg. (SEHU). [Miyazaki] 1 ex., Akidome, Hyûga-shi, 10.X.1942, no collector name (SEHU); 1 ex., Mt. Hokkedake, 10.VI.1986, T. & T. Nakane leg. (SEHU). **Taiwan**. 1 ♂, Ren' ai Township, Nantou County, 16.V.2016, Y. Tamadera leg. (YTJ); 1 ♀, same locality, 19.V.2016, Y. Tamadera leg. (YTJ); 2 exs., same locality (alt. 700–1100 m), 24.III.2018, Y. Fukuda leg. (YTJ).

Distributions in Japan. Honshu, Shikoku, and Kyushu.

Other distributions. China and Taiwan.

Adult food plant. Same as in the larvae mentioned below.

Host plant. Fagaceae: *Quercus glauca* Thunb. [Japanese name: Arakasi] (Yano, 1952; confirmed by this study), *Q. serrata* Murray [Japanese name: Konara] (Kurosawa, 1959 — adult record?), *Q. acutissima* Carruth. [Japanese name: Kunugi] (Kurosawa, 1959 — adult record?), and *Q. acuta* Thunb. [Japanese name: Akagashi] (Kurosawa, 1959 — adult record?) in Japan.

Leaf-mining habit. Mines of *Habroloma* (*Parahabroloma*) *griseonigrum griseonigrum* were found on *Quercus glauca* by this study (Fig. 106C): each mine was of the full-depth type and formed an elongate blotch occurring along leaf-margin to some extent; when full-grown, it occupied much less than half of whole the leaf blade; eggs, which were black (remaining eggshell) and covered on powdery substances, were laid singly on the leaf margin on the adaxial surface; hatched larvae left powdery to granular frass inside the mines; adults were usually emerged from the adaxial surface of the leaves with oval adult exit holes. See also Yano (1952) for descriptions of the leaf-mines and immature stages of this species.

Note. *Taxonomic treatment of* Habroloma (Parahabroloma) griseonigrum chionochaetum. Obenberger (1929 a) was described *Trachys* (*Habroloma*) *chionochaetus* from Taiwan. Later, Kurosawa (1976 b) regarded it as a subspecies of *H*. (*Parahabroloma*) *grieonigrum*. In the Japanese buprestid checklist of Akiyama & Ohmomo (1997), *H*. (*P*.) *griseonigrum chionochaetum* was listed in a synonymy of *H*. (*P*.) *griseonigrum* as a junior synonym of the nominotypical race. According to the brief synonymy information of Akiyama & Ohmomo (1997), the taxonomic change of subsp. *chionochaetum* was conducted by Kurosawa (1985 b) in a pictorial book. However, Kurosawa (1985 b) does not mention the taxonomic change and is nothing but omitting the knowledge of subspecies from note on *H*. (*P*.) *griseonigrum*. Majority of studies and catalogs, unfortunately, referenced the mistake of Akiyama & Ohmomo (1997), but actually formal taxonomic treatment of *H*. (*P*.) *griseonigrum chionochaetum* is not changed.

After carful comparison of *H*. (*P*.) *griseonigrum chionochaetum* (Taiwan) and Japanese nominotypical subspecies, I revealed that they have no significant morphological differences. Therefore, this study proposes that *H*. (*P*.) *griseonigrum chionochaetum* is synonymized with the nominotypical subspecies.

Group II (lewisii)

Species included. *Habroloma* (*Parahabroloma*) *lewisii* (Saunders, 1873), *H*. (*P*.) *nixilla insulicola* Kurosawa, 1959, and *H*. (*P*.) *yuasai* Kurosawa, 1976.

Diagnosis. Clypeus somewhat transverse; antennae without horn-shaped antennomere I; elytra without tufts of erect setae; metacoxal plates without arcuate notches at medial posterior margins; legs more or less stout in each femur and tibiae; male parameres elongate; penis elongate, with rod-shaped dorsal plate which is much narrower than ventral membrane; female spermatheca elongate.

Note. *Habroloma* (*Parahabroloma*) *compactiforme* Peng (2022 b), described from Fujian, China, is probably assigned to this species-group based on the original description and images of male aedeagus.

The male aedeagus in the members of this group is easily broken thorough removing it from the tegmen (the dorsal plate and ventral plate of the penis are often separated). I promote no separation (dissection) of the aedeagus into the tegmen and penis.

Habroloma* (*Parahabroloma*) *lewisii (Saunders, 1873)
[Japanese name: Ruisu-hirata-chibi-tamamushi]
(Figs. 74A, 85, 86, 104A, B, 107A)

Trachys lewisii Saunders, 1873: 519 (type locality: "Japan"); Lewis, 1879: 15 (catalog); Schönfeldt, 1887: 113 (catalog); Kerremans, 1892 a: 286 (catalog); Lewis, 1893: 338 (in list); Kerremans, 1903: 308 (catalog).

Trachys lewisi [sic]: Kerremans, 1885: 157 (misspelling; catalog); Obenberger, 1926 b: 661 (misspelling; catalog);

Trachys (*Trachys*) *lewisi* [sic]: Miwa & Chûjô, 1936: 24 (*lapsus calami*; misspelling; catalog).

Trachys (*Habroloma*) *lewisii*: Obenberger, 1918 a: 18, 32, 63, fig. 10 (in key; diagnosis; misspelling as "*lewisi*" in catalog).

Trachys (*Habroloma*) *lewisi* [sic]: Jakobson, 1913: 800 (misspelling; catalog); Obenberger, 1937 a: 1411 (misspelling; World catalog).

Habroloma lewisi [sic]: Théry, 1935: 132 (misspelling; in list); Obenberger, 1958: 241 (misspelling; Yunnan and "Szecwan" [sic], China).

Habroloma lewisii: Kurosawa, 1950 a: 14, fig. 25 (note); Chûjô & Kurosawa, 1950: 15 (Shikoku, Japan); Yano, 1952: 38 (immature stages); Iga, 1955 a: 11, pl.4 (pictorial book); 1955 b: 82, pl.24 (pictorial book).

Habroloma (*Parahabroloma*) *lewisii*: Kurosawa, 1959: 265, fig. 17 (redescription; Japan, Korea, and China); 1963: 156, pl. 78 (pictorial book); 1976 a: 4, fig. 19 (note); Akiyama & Ohmomo, 1997: 51 (cheklist); 2000: 287, pl. 120 (pictorial book); Kubáň, 2006: 417 (Palaearctic catalog); Bellamy, 2008 b: 2564 (World catalog); Ohmomo & Fukutomi, 2013: 170, pl. 54 (pictorial book); Kubáň, 2016: 569 (Palaearctic catalog; China — Fujian, Hainan, Hunan, Sichuan, and Yunnan); Peng, 2022 b: 306 (distribution).

Habroloma (*Parahabroloma*) *lewisi* [sic]: Kurosawa, 1985b: 36, pl. 7 (misspelling; pictorial book).

Description. Male and female. Body wedge-shaped, moderately convex dorsally (Figs. 85A, B). LB 3.15–3.43 mm (mean 3.28 mm); WB 1.81–2.00 mm (mean 1.93 mm); LB/WB 1.69–1.74 (mean 1.71) (n = 5 for all measurements except terminalia). Habitus as shown in Fig. 74A.

Integument. Head and pronotum dark brass to dark bronze; elytra dark brass, with two large, blue to purple marks occupying on basal 2/3 except for the part along sutural margin and medial half of basal margin; underside, antennae, and legs black, sometimes with weak golden-bronze reflections, except for tarsal pads pale brown. Dorsal surface slightly strongly shiny; ventral surface moderately shiny.

Vestiture mainly consisting of white, brownish-yellow, and black setae. Head clothed with short, recumbent, brownish-yellow setae, sometimes mixing with a few white setae. Pronotum with oval naked part in middle of each lateral half, clothed with short, semirecumbent, pale white and brownish-yellow setae which are arranged as follows: 1) four white patches occurring on behind apicolateral angles and on medial side of each naked part; 2) brownish-yellow setae in remaining space, forming a median stripe. Elytra clothed with short, semirecumbent, white, brownish-yellow, and black setae which are arranged on each elytron as follows: 1) brownish-yellow setae along about medial half of basal margin, throughout sutural margin, from apical 1/3 of lateral carina to elytral apex; 2) white band along the purplish blue mark, shortly interrupted by brownish-yellow setae along lateral carina, its posterior part is recognizable as modified first transverse band; 3) second white transvers band at subapical part, rather straight, shortly interrupted by brownish-yellow setae along lateral carina, white setae more densely occurring than other color setae; and 4) black setae in the dark purplish-blue mark and in remaining space of apical 1/3. Underside more sparsely setiferous, with fine, recumbent, whitish setae, except for prosternal trapezoidal plate and lateral parts of metacoxal plate with yellowish to brownish setae.

Head, when viewed from above, shallowly, subtriangularly concave on frons, with oculofrontal margins ridged and slightly weakly produced anteriorly. Eyes, when viewed from above, narrowly visible, weakly convex laterally. Vertex coarsely variolate-punctate; frons widely concave, weakly impressed along upper side of midline, with surface coarsely variolate-punctate except upper side around midline; suprantennal pores simply round; clypeus wide (Fig. 85D), with elevated basal margin, WC/LC 2.21–2.82 (mean 2.50), WC/LSC 1.75–2.15 (mean 1.89), weakly arcuately emarginate at apical margin.

Antennae (Fig. 85E, F) short, not reaching level of pronotal widest point when laid laterally; antennomere I stout claviform, longer than II; II ovate, longer than III; III subrectangular, slightly longer than IV; IV–VI subrectangular, subequal each other in length; VII–X triangular, slightly more strongly enlarged in male than in female; XI sublingulate. Pronotum widest at subbasal part, WP/LP 2.73–3.06 (mean 2.94), BMP/AMP 1.85–1.95 (mean 1.90), faintly wider than elytra or almost same as elytral width; lateral margins rather subparallel and weakly arcuate in basal 1/3, and then relatively straightly, strongly narrowed apicad ; apicolateral angles nearly right (angle); basolateral angles sharply acute (angle); apical margin moderately deeply, arcuately emarginate, with very small median lobe; basal margin trisinuate, with median lobe moderately produced; disk depressed laterally, faintly depressed along basal median lobe, with apicolateral depressions bearing round pore on the middle of each; surface slightly sparsely variolate-punctate, except for the naked parts impunctate. Scutellar shield small, triangular, glabrous.

Elytra widest at base, LE/WE 1.23–1.26 (mean 1.25), LE/LP 3.38–3.76 (mean 3.63); humeral calluses weakly developed, weakly ridged; lateral margins gradually narrowed posteriorly from base to just before apical 1/3, then moderately arcuately convergent to conjointly rounded apices, serrated with two to three denticles at subapical part (Fig. 85C); marginal carinae distinct from base to subapical part; lateral carinae occurring from just behind humeri to subapical part, strongly sinuate behind basal parts; disk moderately depressed along lateral half of basal margin, constricted behind humeri; surface irregularly and sparsely sculptured with shortly, linearly incised punctures.

Underside. Prosternum (Fig. 85G) with arcuate prosternal lobe faintly emarginate at middle of apical margin which is weakly rimmed; prosternal process wide; trapezoidal plate slightly longer than wider, WTP/LTP 0.97–1.2 (mean 1.14), WTP/BTP 1.29–1.42 (mean 1.38), with rounded apical corners, with sides which are dilated from base to widest point around apical corners and weakly constricted in basal part, with apex broadly, faintly arcuate; disk flattened on trapezoidal plate bearing marginal carinae along sides, evenly convex on prosternal lobe; surface on trapezoidal plate only with setiferous pin-prick punctures. Hypomera with slightly narrow, transversely oval hypomeral markings consisting of linearly incised punctures (Fig. 85H). Metaventrite moderately variolate-punctate on inside of katepisternal suture and moderately variolate on outside of the suture. Legs slightly stout in femora and tibiae; metacoxal plates without arcuate notches on medial posterior margins, weakly produced posteriorly at each lateral angle which is broadly acute (angle), with surface moderately variolate; metafemora obtusely angulate at about distal 1/3 of outer margins; metatibiae without a fringe of spines on each outer margin (Fig. 85I), but very sparsely bearing fine setae throughout; inner tooth of each claw large. Abdominal ventrites with sternal groove only on ventrite V, of which apex is faintly angulately rounded; surface variolate, in ventrite I with linearly confluent sculptures on median part.

Sexual dimorphism recognized on the relative size of serrate antennomeres (see above).

Male terminalia (n = 1 for measurements). Proctiger with a pair of short baculi at base. Sternite IX (Fig. 86A) rather slender, SL/SW 1.04, more or less emarginate at apical margin, without setae. Tegmen (Fig. 86B) elongate and slender; parameres slightly long, PL/PW 4.63, bearing a few setae on apicolateral margins, with sides which are gently dilated from base to subapical part, then arcuately convergent apicad; phallobase PbL/PbW 1.36, about 1/7 length of tegmen. Penis (Fig. 86C, D) prominently slender, PeL/PeW 12.62, shorter than tegmen; dorsal plate rod-shaped, with sides (not including sides of median struts) which are subparallel throughout, with rounded apex, basally with median struts about 1/3 length of penis; ventral membrane without sclerotized part, wider than dorsal plate.

Female terminalia (n = 1 for measurements). Ovipositor (Figs. 86E–G) short. Proctiger with a pair of short, straight baculi at base; coxites transversely subhexagonal, sparsely setiferous on each side of apical margin; styli short, rather slender, SlL/SlW 3.34, bearing several setae apically; ventral valve without setae; vagina sack-shaped (under incompletely inflated state); spermatheca slender tubular, long in length, widest in apical part.

Differential diagnosis. This species is very easily distinguished from Japanese other congeners by the large blue to purple marks on the elytra.

Specimens examined. Non-type material. **Japan**. Honshu — [Nagano] 1 ex., Karuizawa, Nagano Pref., 22.VI.1951, S. Hisamatsu leg. (NSMT; recorded by Kurosawa, 1976). [Kyoto] 3 exs., Mt. Daihizan, Kyoto-shi, 31.V.1958, T. Nakane leg. (SEHU); 1 ♂, 2exs., same locality, 1.VI.1958, T. Nakane leg. (SEHU); 1 ex., same locality, 29.V.1960, T. Nakane leg. (SEHU). [Osaka] 1 ex., Mino-o, 10.V.1936, H. Takenaka leg. (SEHU). [Okayama] 4 exs., Yoshiigawa River, Tsuyama-shi, 21–22.IV.2004, H. Takizawa leg. (SEHU). [Hiroshima] 2 exs., Onomichi, 19.V.1947, K. Ohbayashi leg. (SEHU); 1 ex., Mt. Haigamine, Kure-shi, 17.VII.1967, T. Kosaka leg. (SEHU). Shikoku — [Ehime] 1 ♀, Matsuyama, 18.V.1956, no collector name (YTJ); 1 ♂, Nomura Dam, Nomura-cho, 27.V.1994, M. Sakai leg. (YTJ); 1 ♀, same locality, 28.V.1994, M. Sakai leg. (YTJ); 1 ♂, 1 ♀, Shukugawa River, Kawanobori, Tobe-chô, Iyo-gun, 24.IV.2019, Y. Tamadera leg. (YTJ); 1 ex., Ushibuchi, Tô-on-shi, 14.VII.2021, Y. Tamadera leg., emerged from *Rosa multiflora*, 23.VII.2021, rearing no. 2021-160 (YTJ). Kyushu — [Fukuoka] 1 ♂, Mt. Fukuchi, 24.VI.1949, no collector name (YTJ). [Saga] 1ex., Kirigo-daichi, Yobuko, 30.IX.1952, no collector name (SEHU). [Kumamoto] 1 ex., Kumagawa River, Isshôchi, 18.VII.1983, T. & T. Nakane leg. (SEHU). Shimaurashima Is. (Miyazaki) — 1 ex., Shimaura-machi, Nobeoka-shi, 10.X.1968, A. Nagai leg. (SEHU). **China**. 2 exs., "Wôkô, Hunang, C.-China" (Wuchang, Hunan, Central China), IV.1946, K. Shirahata leg. (NSMT; recorded by Kurosawa, 1959); 2 exs., "Chokason, Busho Pref., Hunang, C.-China", II.1946, K. Shirahata leg. (NSMT; recorded by Kurosawa, 1959); 1 exs., "SiangIan, Hunang, C. China", IV.1945, K. Shirahata leg. (NSMT; recorded by Kurosawa, 1959); 1 ex., same locality, IV.1946, K, Shirahata leg., Host: Rubus sp. (NSMT; recorded by Kurosawa, 1959). **South Korea**. 1 ex., Bukkokuji, SE.-Korea, 2.VI.1940, S. Sato leg. (NSMT; recorded by Kurosawa, 1959); 1 ex., Mt. Sudosan, alt. 400 m, Kyongsangpuk-do, Korea, 17–18.VII.1971, K. Yamagishi leg. (NSMT); 1 ex., Karuizawa, Nagano Pref., 22.VI.1951, S. Hisamatsu leg. (NSMT; recorded by Kurosawa, 1976).

Distributions in Japan. Honshu, Shikoku, Kyushu, and Shimaurashima Is. (Miyazaki) — new record.

The northernmost locality of Japan is Shioya-machi in Tochigi Prefecture, Honshu (Maehara, 2014).

Other distributions. China and South Korea.

Adult food plant. Same as in the larvae mentioned below. Adult feeding scars are shown in Fig. 107A'.

Host plant. Rosaceae: *Rosa multiflora* Thunb. [Japanese name: Noibara] (Yano, 1952; confirmed by this study) in Japan.

Leaf-mining habit. Mines of *Habroloma* (*Parahabroloma*) *lewisii* were found on *Rosa multiflora* by this study (Figs. 104A, 107A): each mine was of the full-depth type and formed an elongate blotch occurring along leaf-margin; when full-grown, it occupied more than half of whole the leaf blade; eggs, which were black (remaining eggshell) and covered on powdery substances, were laid singly on near the leaf margin on the adaxial surface; hatched larvae ejected thread-like frass outside the mines from the abaxial surface as shown in Fig. 104B, but in the stage of final instar just before prepupa, they left the frass inside the mines around pupation sites; when the ejections of frass, larvae ejected frass just penetrating the epidermal layer of mines without holes or slits prepared; adults were usually emerged from the adaxial surface of the leaves with oval adult exit holes. See also Yano (1952) for descriptions of the leaf-mines and immature stages of this species.

Habroloma* (*Parahabroloma*) *nixilla insulicola Kurosawa, 1959

[Japanese name: Karakane-hirata-chibi-tamamushi]

(Figs. 74B, 87, 88, 104C, D, 107B)

Habroloma (*Parahabroloma*) *nixilla insulicola* Kurosawa, 1959: 261 (type locality: "Shimmura-Akatsuchiyama, Amami-Ôshima, Loo-Choo Is.", Japan); Kurosawa, 1976 a: 4 (note); Ohmomo & Fukutomi, 2013: 171, pl. 55 (pictorial book); Kubáň, 2016: 569 (Palaearctic catalog).

Habroloma (*Parahabroloma*) *nixillum insulicola*: Kurosawa, 1985: 37, pl.7 (pictorial book); Akiyama & Ohmomo, 1997: 52 (checklist); 2000: 287, pl. 120 (pictorial book); Kubáň, 2006: 417 (Palaearctic catalog).

Habroloma (*Habroloma*) *nixilla insulicola* [sic]: Bellamy, 2008 b: 2564 (*lapsus calami*; World catalog).

Description. Male and female. Body ovate, moderately convex dorsally (Figs. 87A, B). LB 3.51–3.80 mm (mean 3.60 mm); WB 2.00–2.11 mm (mean 2.04 mm); LB/WB 1.74–1.8 (mean 1.76) (n = 5 for all measurements except terminalia). Habitus as shown in Fig. 74B.

Integument above mainly bronzy to brassy black; underside, antennae, and legs black, with weak golden-bronze reflections, except for tarsal pads pale brown. Dorsal and ventral surfaces moderately shiny.

Vestiture mainly consisting of white, yellow to brown, and dark brown setae. Head clothed with short, recumbent, yellow setaePronotum clothed with short, semirecumbent yellow to brown setae becoming denser apicolaterally, sometimes mixing with more brownish setae in basal half, with an inconspicuous median stripe, occasionally with two small, inconspicuous white patches across middle. Elytra clothed with short, semirecumbent, white, yellow to brown, and dark brown setae which are arranged on each elytron as follows: 1) oblique band consisting of white and yellow to brown setae just before middle, sometimes being two separated patches; 2) first transvers band consisting of white and yellow to brown setae at apical 1/3, moderately wavy, zigzag-shaped; 3) second transvers band consisting of white and yellow to brown setae at subapical part, weakly wavy; 4) yellow to brown setae along basal margin, sutural margin, and lateral carina, on humeral callus and behind it, and at apex; and 5) dark brown setae in remaining space, occasionally being blackish-brown setae. Underside more sparsely setiferous, with fine, recumbent, whitish setae, except for prosternum and lateral parts of metacoxal plate with pale yellowish setae.

Head, when viewed from above, slightly narrow in width, shallowly concave on frons, with oculofrontal margins ridged and slightly weakly produced anteriorly. Eyes, when viewed from above, narrowly visible, weakly convex laterally. Vertex coarsely variolate-punctate; frons widely concave, weakly impressed along upper side of midline, with surface coarsely variolate-punctate except upper side around midline; suprantennal pores simply round; clypeus wide (Fig. 87D), with elevated basal margin, WC/LC 2.19–2.74 (mean 2.37), WC/LSC 1.63–1.78 (mean 1.71), faintly arcuately emarginate to nearly straight at apical margin.

Antennae (Fig. 87E) short, not reaching level of pronotal widest point when laid laterally; antennomere I stout claviform, longer than II; II ovate, longer than III; III subrectangular, longer than IV; IV–VI subrectangular, subequal each other in length; VII–X triangular, moderately enlarged; XI subtriangular to sublingulate.

Pronotum widest at base, WP/LP 2.63–2.97 (mean 2.79), BMP/AMP 1.91–2.7 (mean 2.12), slightly narrower than elytra; lateral margins moderately arcuately narrowed apicad; apicolateral angles nearly right (angle); basolateral angles broadly acute (angle); apical margin moderately deeply, arcuately emarginate, with inconspicuous, faint median lobe which is almost straight line at glance; basal margin trisinuate, with median lobe moderately produced; disk rather evenly convex, faintly depressed along basal median lobe, with apicolateral depressions bearing round pore on the middle of each; surface rather densely variolate-punctate, sculptures becoming sparse just before middle of median part. Scutellar shield small, triangular, shiny, faintly microsculptured laterally.

Elytra widest at base, LE/WE 1.29–1.34 (mean 1.32), LE/LP 3.53–4.14 (mean 3.82); humeral calluses weakly developed; lateral margins faintly narrowed posteriorly from base to middle and faintly constricted between them, then moderately arcuately convergent to conjointly rounded apices, serrated with one to three weak denticles at subapical part (Fig. 87C), but rarely without serrations on one side (n =3); marginal carinae distinct from base to subapical part; lateral carinae occurring from just behind humeri to subapical part, strongly sinuate behind basal parts; disk weakly depressed along lateral half of basal margin, constricted behind humeri; surface irregularly and sparsely sculptured with shortly, linearly incised punctures.

Underside. Prosternum (Fig. 87F) with arcuate prosternal lobe faintly emarginate at middle of apical margin which is weakly rimmed; prosternal process wide; trapezoidal plate longer than wide, WTP/LTP 0.89–0.97 (mean 0.94), WTP/BTP 1.34–1.46 (mean 1.38), with rounded apical corners, with sides which are weakly outwardly dilated from base to widest point around apical corners, with apex broadly, faintly arcuate; disk flattened on trapezoidal plate bearing marginal carinae along sides, evenly convex on prosternal lobe; surface on trapezoidal plate with setiferous pin-prick punctures and ocellate sculptures. Hypomera with large, transversely oval hypomeral markings consisting of linearly incised punctures (Fig. 87G). Metaventrite moderately variolate-punctate on inside of katepisternal suture and moderately variolate on outside of the suture. Legs stout in femora and tibiae; metacoxal plates without arcuate notches on medial posterior margins, weakly produced posteriorly at each lateral angle which is broadly acute (angle), with surface moderately variolate; metafemora obtusely angulate at about distal 1/3 of outer margins; metatibiae without a fringe of spines on each outer margin (Fig. 87H), but very sparsely bearing fine setae throughout; inner tooth of each claw large. Abdominal ventrites with sternal groove only on ventrite V, of which apex is rounded; surface variolate, in ventrite I with linearly confluent sculptures on median part.

Sexual dimorphism indistinct.

Male terminalia (n = 1 for measurements). Proctiger with a pair of short baculi at base. Sternite IX (Fig. 88A) rather slender, SL/SW 1.42, more or less emarginate at apical margin, without setae. Tegmen (Fig. 88B) elongate and slender; parameres long, PL/PW 4.63, bearing a pair of setae on apicolateral margins, with sides which are subparallel in basal 2/3, then weakly dilated to widest point at subapical part, and finally strongly convergent apicad; phallobase PbL/PbW 1.55, about 1/7 length of tegmen. Penis (Fig. 88C, D) prominently slender, PeL/PeW 12.79, slightly shorter than tegmen; dorsal plate rod-shaped, with sides (not including sides of median struts) which are subparallel throughout, with roundly truncate apex, basally with median struts about 1/3 length of penis; ventral membrane without sclerotized part, wider than dorsal plate.

Female terminalia (n = 1 for measurements). Ovipositor (Figs. 88E–G) short. Proctiger with a pair of short, straight baculi at base; coxites transversely subreniform, broadly, very weakly produced on median part of apical margin between styli, sparsely setiferous on each side of apical margin; styli short, slightly wide, SlL/SlW 3.22, bearing several setae apically; ventral valve without setae; vagina sack-shaped (under incompletely inflated state); spermatheca slender tubular, long in length, widest at near apical 1/3.

Differential diagnosis. This species is very easily distinguished from Japanese other congeners by the oval body and by the zigzag-shaped first transverse band on each elytron.

Specimens examined. Type material. Holotype of *Habroloma* (*Parahabroloma*) *nixilla inslicola* Kurosawa, 1959: ♂ (based on Kurosawa, 1959; no dissected terminalia), “SHINMURA – / AKATSUCHIYAMA / AMAMI-OSHIMA / 22.VII.1955 / T. SHIROZU” (NSMT).

Non-type material. **Japan**. The Ryukyus: Amami Islands — [Amami-Ôshima Is.] 2

exs., Ôdana, Yamato-son, Ôshima-gun, 23.V.2021, Y. Tamadera leg., emerged from *Lagerstroemia subcostata*, 25.V.2021, rearing no. 2021-011 & 2021-012 (YTJ); 2 ♂♂, Yuwan, Uken-son, Ôshima-gun, 27.V.2016, Y. Tamadera leg. (YTJ); 1 ex., same locality, 24.V.2021, Y. Tamadera leg., emerged from *L. subcostata*, VI.2021, rearing no. 2021-031 (YTJ); 1 ♂, 1 ♀, Nazeasado, Amami-shi, 25.V.2016, Y. Tamadera leg. (YTJ); 2 ♂♂, 2 ♀♀, Tsunagu, Yamato-son, Ôshima-gun, 18.IV.2017, Y. Tamadera leg. (YTJ); 2 ♂♂, 1 ♀, same locality, 19.IV.2017, Y. Tamadera leg. (YTJ).

Distributions in Japan. The Ryukyus: Amami Isls. (Amami-Ôshima Is.).

Other distribution. Unknown.

Adult food plant. Same as in the larvae mentioned below. Shirozu (1955) for the first time confirmed the adult food plant for “*Habroloma nixilla*” from Amami-Ôshima Is.

Host plant. Lythraceae: *Lagerstroemia subcostata* Koehne var. *subcostata* [Japanese name: Shima-sarusuberi] (confirmed by this study).

Leaf-mining habit. Mines of *Habroloma* (*Parahabroloma*) *nixilla inslicola* were found on *Lagerstroemia subcostata* var. *subcostata* by this study (Figs. 104C, 107B): each mine was of the full-depth type and formed a large, elongate blotch occurring usually along leaf-margin; when full-grown, it occupied about half of whole the leaf blade; eggs, which were black (remaining eggshell) and covered on powdery substances, were laid singly on usually near the leaf margin on the adaxial surface but rarely found on separate parts of the leaf margin; hatched larvae ejected thread-like frass outside the mines from the abaxial surface as shown in Fig. 104D, but in the stage of final instar just before prepupa, they left frass inside the mines around pupation sites (Fig. 104C); when the ejections of frass, larvae ejected frass just penetrating the epidermal layer of mines without holes or slits prepared; adults were usually emerged from the abaxial surface of the leaves with oval adult exit holes.

Habroloma* (*Parahabroloma*) *yuasai Kurosawa, 1976

[Japanese name: Naga-hirata-chibi-tamamushi]

(Figs. 74C, 89, 90, 104E, F, 107C)

Habroloma (*Parahabroloma*) sp.: Kurosawa, 1976 a: 4 (note).

Habroloma (*Parahabroloma*) *yuasai* Kurosawa, 1976 b: 130 (type locality: “Mimata, Shimane Pref., Honshû, Japan”); 1985 b: 37, pl. 7 (pictorial book); Akiyama & Ohmomo, 1997: 52 (checklist); 2000: 287, pl. 120 (pictorial book); Kubáň, 2006:

418 (Palaearctic catalog); Ohmomo & Fukutomi, 2013: 172, pl. 56 (pictorial book); Kubáň, 2016: 569 (Palaearctic catalog).

Habroloma (*Habroloma*) *yuasai* [sic]: Bellamy, 2008 b: 2567 (*lapsus calami*; Worlda catalog).

Habroloma ronino [non Obenberger, 1918a]: Chûjô & Kurosawa, 1950: 14 (Shikoku, Japan); Yano, 1952: 36 (immature stages).

Habroloma (*Parahabroloma*) *ronino* [non Obenberger, 1918a]: Kurosawa, 1959: 253 (description); 1963: 156 (noted in pictorial book).

Description. Male and female. Body wedge-shaped, moderately convex dorsally (Figs. 89A, B). LB 2.86–3.25 mm (mean 3.14 mm); WB 1.64–1.86 mm (mean 1.80 mm); LB/WB 1.73–1.75 (mean 1.74) (n = 5 for all measurements except terminalia). Habitus as shown in Fig.74C.

Integument above mainly black with weak golden-bronze tints; underside, antennae, and legs black, except for tarsal pads pale brown. Dorsal and ventral surfaces moderately shiny.

Vestiture mainly consisting of white, brownish-yellow, and black setae; brownish-yellow setae sometimes being yellow setae or paler ones. Head clothed with short, recumbent, brownish-yellow setae Pronotum clothed with short, semirecumbent brownish-yellow setae, becoming denser apicolaterally, with an inconspicuous median stripe, often with small white patches behind apicolateral angles and across middle. Elytra clothed with short, semirecumbent, white, brownish-yellow, and black setae which are arranged on each elytron as follows: 1) inconspicuous, undulated band consisting of white and brownish-yellow setae at basal 1/3; 2) first transverse band consisting of white and brownish-yellow setae at apical 1/3, moderately wavy; 3) second transverse band consisting of white and brownish-yellow setae at subapical part, weakly wavy; 4) brownish-yellow setae along basal margin, sutural margin, and lateral carina, on humeral callus and behind it, and at apex; and 5) black setae in remaining space. Underside more sparsely setiferous, with fine, recumbent, whitish setae.

Head, when viewed from above, shallowly concave on frons, with oculofrontal margins ridged and slightly weakly produced anteriorly. Eyes, when viewed from above, narrowly visible, weakly convex laterally. Vertex coarsely variolate-punctate; frons widely concave, weakly impressed along upper side of midline, with surface coarsely variolate-punctate except upper side around midline; suprantennal pores simply round; clypeus wide (Fig. 89D), with elevated basal margin, WC/LC 2.36–3.16 (mean 2.63), WC/LSC 1.59–1.96 (mean 1.82), faintly arcuately emarginate to nearly straight at apical margin.

Antennae (Figs. 89E, F) short, just reaching or slightly beyond level of pronotal widest point when laid laterally; antennomere I stout claviform, longer than II; II ovate, longer than III; III subrectangular, slightly longer than IV; IV–VI subrectangular, subequal each other in length; VII–X triangular, slightly more strongly enlarged in male than in female; XI subtriangular.

Pronotum widest at sub-basal part, WP/LP 2.83–2.92 (mean 2.87), BMP/AMP 1.93–2.04 (mean 1.98), faintly wider than elytra or almost same as elytral width; lateral margins evenly, strongly arcuately narrowed apicad; apicolateral angles nearly right (angle); basolateral angles sharply acute (angle); apical margin moderately deeply, arcuately emarginate, with inconspicuous, faint median lobe which is almost straight line at glance; basal margin trisinuate, with median lobe moderately produced; disk rather evenly convex, faintly depressed along basal median lobe, with ill-defined basolateral depressions, with apicolateral depressions bearing round pore on the middle of each; surface rather densely variolate-punctate, sculptures becoming sparse in apical half of median part except near apical margin. Scutellar shield small, triangular, shiny, faintly microsculptured laterally.

Elytra widest at base, LE/WE 1.28–1.31 (mean 1.30), LE/LP 3.6–3.82 (mean 3.72); humeral calluses weakly developed, weakly ridged; lateral margins gradually narrowed posteriorly from base to apical 1/3, then continuously, moderately arcuately convergent to conjointly rounded apices, serrated with one to three denticles at subapical part (Fig. 89C); marginal carinae distinct from base to subapical part; lateral carinae occurring from near bases of humeri to subapical part, strongly sinuate behind humeral parts; disk slightly weakly depressed along lateral half of basal margin, constricted behind humeri; surface irregularly and sparsely sculptured with shortly, linearly incised punctures.

Underside. Prosternum (Fig. 89G) with arcuate prosternal lobe faintly emarginate at middle of apical margin which is weakly rimmed; prosternal process wide; trapezoidal plate slightly longer than wide, WTP/LTP 1.02–1.13 (mean 1.08), WTP/BTP 1.34–1.49 (mean 1.40), with rounded apical corners, with sides which are dilated from base to widest point around apical corners and weakly constricted in basal part, with apex broadly, faintly arcuate; disk flattened on trapezoidal plate bearing marginal carinae along sides, evenly convex on prosternal lobe; surface on trapezoidal plate only with setiferous pin-prick punctures. Hypomera with large, transversely oval hypomeral markings consisting of linearly incised punctures (Fig. 89H). Metaventrite moderately variolate-punctate on inside of katepisternal suture and moderately variolate on outside of the suture. Legs slightly stout in femora and tibiae; metacoxal plates without arcuate notches on medial posterior margins, weakly produced posteriorly at each lateral angle which is broadly to slightly sharply acute (angle), with surface moderately variolate; metafemora obtusely angulate at about distal 1/4 of outer margins; metatibiae without a fringe of spines on each outer margin (Fig. 89I), but very sparsely bearing fine setae throughout; inner tooth of each claw large. Abdominal ventrites with sternal groove only on ventrite V, of which apex is faintly angulately rounded; surface variolate, in ventrite I with linearly confluent sculptures on median part.

Sexual dimorphism barely recognized on the relative size of serrate antennomeres (see above).

Male terminalia (n = 1 for measurements). Proctiger with a pair of short baculi at base. Sternite IX (Fig. 90A) rather slender, SL/SW 1.10, more or less emarginate at apical margin, usually without setae. Tegmen (Fig. 90B) elongate and slender; parameres long, PL/PW 6.22, bearing a pair of setae on apicolateral margins, with sides which are subparallel from base to subapical part, then arcuately convergent apicad; phallobase PbL/PbW 1.53, about 1/7 length of tegmen. Penis (Figs. 90C, D) prominently slender, PeL/PeW 18.00, slightly shorter than tegmen; dorsal plate rod-shaped, with sides (not including sides of median struts) which are subparallel throughout, with rounded apex, basally with median struts about 1/3 length of penis; ventral membrane without sclerotized part, wider than dorsal plate.

Female terminalia (n = 1 for measurements). Ovipositor (Figs. 90E–G) short. Proctiger with a pair of short, straight baculi at base; coxites transversely subhexagonal, sparsely setiferous on each side of apical margin; styli moderate in length, slightly wide, SlL/SlW 3.51, bearing several setae apically; ventral valve without setae; vagina sack-shaped (under incompletely inflated state); spermatheca slender tubular, long in length, widest in apical part.

Differential diagnosis. This species is extremely similar in general appearance to *Habroloma* (*Parahabroloma*) *subbicorne*, but easily distinguished from *H*. (*P*.) *subbicorne* by the elongated male aedeagus in parameres and penis and by the elongated female spermatheca. In addition, this species may be distinguishable from it by the combination of the following superficial character states: lateral carinae of elytra starting from near bases of humeri; prosternal trapezoidal plate often faintly narrower; black integument in dorsum with stronger golden-bronze tints (but *H*. (*P*.) *subbicorne* occasionally showing same colored individual).

Specimens examined. Type material. Holotype of *Habroloma* (*Parahabroloma*) *yuasai* Kurosawa, 1976: ♂ (based on Kurosawa, 1976; no dissected terminalia), “Mimata / Iwami / VIII.28.1924 / H. YUASA” (NSMT). Paratypes: 1 ex., Muya, Naruto C., Tokushima Pref., Shikoku, 20.V.1948, M. Chûjô leg. (NSMT); 1 ex., Hata, Yahata-City, Fukuoka Pref., 23.V.1965, M. Ueda leg. (NSMT); 1 ex., Wakasugiyama, nr. Fukuoka, 5.VI.1932, T. Shirozu leg. (NSMT).

Non-type material. Shikoku — [Kagawa] 1 ex., Mt. Kotohiza, 2.V.1980, S. Ohmomo leg. (NSMT). [Ehime] 2 ♂♂, Sue-machi, Matsuyama-shi, 23.IV.2019, Y. Tamadera leg. (YTJ); 1 ♀, Tamagawa-ko Lake, Ryûokashimo, Tamagawa-chô, Imabari-shi, 23.IV.2019, Y. Tamadera leg. (YTJ). Kyushu — [Fukuoka] 1 ex., Masubuchi Dam, Kagumeyoshi, Kokura-minami-ku, Kitakyushu-shi, 25.VII.2022., Y. Tamadera leg., emerged from *Platycarya strobilacea*, 29.VII.2022, rearing no. 2022-183 (YTJ); 2 exs., ditto, emerged from *P. strobilacea*, 1.VIII.2022, rearing no. 2022-184 (YTJ); 1 ♀, Ushikubi, Onojo-shi, 26.V.2018, Y. Hisasue leg. (YTJ); 1 ♂, same locality, 26.V.2019, Y. Hisasue leg. (YTJ). Tsushima Is. (Nagasaki) — 1 ex., Sugorokuzaka, Yoshida, Mine-machi, 16.VI.2005, Y. Komiya leg. (SEHU); 1 ex., Yamanoushiro-rindô, Mine-machi, 16.VI.2005, Y. Komiya leg. (SEHU); 1 ex., Uchiyama, Izuhara-chô, 9.VI.2005, Y. Komiya leg. (SEHU); 1 ♂, Kotsuki, Izuhara-machi, Tsushima-shi, 1.IX.2016, Y. Tamadera leg. (YTJ).

Distributions in Japan. Honshu, Shikoku, Kyushu, and Tsushima Is.

Other distribution. Unknown.

Adult food plant. Same as in the larvae mentioned below. Adult of this species probably prefers to the leaves of very lower branches of each tree.

Host plant. Juglandaceae: *Platycarya strobilacea* Siebold et Zucc. [Japanese name: Nogurumi] (Yano, 1952 for *Habroloma ronino*; confirmed by this study).

Leaf-mining habit. Mines of *Habroloma* (*Parahabroloma*) *yuasai* were found on *Platycarya strobilacea* by this study (Figs. 104E, 107C): mines were always found in the leaves of lower branches of each tree and very young small tree (shrub); each mine was of the full-depth type and formed a large, elongate blotch occurring usually along leaf-margin; when full-grown, it occupied less than half of whole the leaf blade in the typical size leaf; eggs, which were black (remaining eggshell) and covered on powdery substances, were laid singly on relatively near the base of leaf blade on the adaxial surface but occasionally found on the relatively distal parts of the blade on the same surface; hatched larvae ejected thread-like frass outside the mines from both surfaces as shown in Fig. 104F, but in the stage of final instar just before prepupa, they left the frass inside the mines around pupation sites; when the ejections of frass, larvae ejected frass just penetrating the epidermal layer of mines without holes or slits prepared; adults were usually emerged from the adaxial surface of the leaves with oval adult exit holes. See also Yano (1952) treated as "*Habroloma ronino*" for descriptions of the leaf-mines and immature stages of *H.* (*P.*) *yuasai*.

Notes. *Misidentifications*. Based on examinations of terminalia, it is revealed that the paratypes of *Habroloma* (*Parahabroloma*) *yuasai* Kurosawa (1976 b) includes several misidentifications of *H*. (*P*.) *subbicorne*. The following paratypes are misidentification of *H*. (*P*.) *subbicorne*: 1 ♀, "Onezawa, Hibara V., Yama D.", Fukushima Pref. 18.VIII.1948, Y. Kurosawa leg. (NSMT); 1 ♂, "Hatsu-shima, E-Izu, Shizuoka", 6.VI.1968, T. Maenami leg. (NSMT).

Nakane (1987) recorded *Habroloma* (*Parahabroloma*) *yuasai* from Tsushima Is. based on three specimens (3 ♂♂, Uchiyama, Izuhara-machi, 17.VII.1960, T. Nakane leg. (SEHU)), but I confirmed that theses specimens are *H*. (*P*.) *subbicorne* through examinations of terminalia.

Judging from these misidentifications of the coleopteran experts, *Habroloma* (*Parahabroloma*) *yuasai* is the most difficult species to determine species in the Japanese *Habroloma*. To prevent misidentifications, examinations of male or female terminalia are needed in doubtful specimens.

Group III (subbicorne)

Species included. *Habroloma* (*Parahabroloma*) *subbicorne* (Motschulsky, 1860), *H*. (*P*.) *marginicolle* (Fairmaire, 1888), 1959, *H*. (*P*.) *asahinai* Kurosawa, 1959, and *Habroloma* (*Parahabroloma*) sp. 1.

Diagnosis. Clypeus somewhat transverse; antennae without horn-shaped antennomere I; elytra without tufts of erect setae; metacoxal plates without arcuate notches at medial posterior margins; legs more or less slender in each femur and tibiae; male parameres moderate length; penis moderate length, with dorsal plate which is almost as wide as ventral membrane; female spermatheca moderate length.

Note. So many species are seemed to assigned to this species-groups based on the general appearance and male aedeagus (e.g. Peng, 2020, 2021a, b, 2022).

Habroloma* (*Parahabroloma*) *subbicorne (Motschulsky, 1860)

[Japanese name: Hirata-chibi-tamamushi; Kinke-chibi-tamamushi]

(Figs. 74D, 91–94, 105A, 108A, B)

Brachys subbicornis Motschulsky, 1860: 8 (type locality: Japan); Gemminger & Harold, 1869: 1451 (catalog).

Trachys subbicornis: Saunders, 1871: 132 (transferred from *Brachys*; listed in "*Species* *incertae sedis*" of *Trachys*); Lewis, 1879: 15 (catalog); Schönfeldt, 1887: 113 (catalog); Kerremans, 1892 a: 289 (catalog).

Trachys (*Habroloma*) *subbicornis*: Jakobson, 1913: 800 (catalog).

Habroloma (*Parahabroloma*) *subbicornis*: Kurosawa, 1959: 267 (as doubtful species transferred from *Trachys*); 1976 a: 5 (noted as unidentified species); Mühle, 2003: 47 (in checklist).

Habroloma (*Parahabroloma*) *subbicorne*: Akiyama & Ohmomo, 1995: 179, figs. 8, 9 (holotype examined; images of label); Seki & Kashizaki, 1996: 89 (Hokkaido, Japan); Akiyama & Ohmomo, 1997: 52 (checklist); 2000: 287, pl. 120 (pictorial book); Kubáň, 2006: 417 (Palaearctic catalog); Bellamy, 2008 b: 2564 (World catalog); Ohmomo & Fukutomi, 2013: 172, pl. 56 (pictorial book); Kubáň, 2016: 569 (Palaearctic catalog); Tamadera, 2021: 54 (Okinoshima Is., Kôchi); Peng, 2022 b: 307 (Fujian, China).

Trachys subbicornis [auct. non Motschulsky]: Kerremans, 1903: 310 (catalog); Obenberger, 1918 a: 19, 36, 64 (misidentification of *T. griseofasciatus*); 1929 a: 41, 93; Miwa & Chûjô, 1936: 25; Obenberger, 1937 a: 1379; 1958: 242.

Trachys elegantula Saunders, 1873: 520 (type locality: "Japan"); Lewis, 1879: 15 (catalog); Schönfeldt, 1887: 113 (catalog); Kerremans, 1892 a: 286 (catalog); Lewis, 1893: 338 (in list); Kerremans, 1903: 313 (catalog). Synonymized under *H.* (*P.*) *subbicorne* by Akiyama & Ohmomo, 1995: 179.

Trachys elongatula [sic]: Kerremans, 1885: 157 (misspelling; catalog).

Trachys (*Habroloma*) *elegantula*: Jakobson, 1913: 800 (catalog); Obenberger, 1918 a: 17, 29, 63 (in key; diagnosis; catalog); 1926 b: 661 (catalog); Obenberger, 1937 a: 1411 (World catalog).

Habroloma elegantula: Théry, 1935: 132 (in list); Chûjô & Matuda, 1940: 66 (Kyushu, Japan); Kurosawa, 1950 a: 14, fig. 24a (note); 1950 b: 1111, fig. 3184 (pictorial book); Chûjô & Kurosawa, 1950: 14 (Shikoku, Japan); Yano, 1952: 36 (immature stages); Iga, 1955 a: 11, pl.4 (pictorial book); 1955 b: 82, pl.24 (pictorial book); Obenberger, 1958: 240 (Yunnan, China); Kurosa, 1959: 459, fig. 3184 (pictorial book; larva).

Trachys (*Trachys*) *elegantula* [sic]: Miwa & Chûjô, 1936: 23 (*lapsus calami*; catalog; Japanese name: Kinke-chibi-tamamushi).

Habroloma (*Parahabroloma*) *elegantula*: Kurosawa, 1959: 251, fig. 15a (redescription); 1976 a: 2, fig. 16 (note; southern Korean Peninsula); 1963: 156, pl. 78 (pictorial book).

Habroloma (*Parahabroloma*) *elegantulum*: 1976 b: 130 (revised synonymy; noted on types in each European museum); Kurosawa, 1985 b: 37, pl. 7 (pictorial book; fig. 24 is a correct image).

Trachys (*Habroloma*) *ronino* Obenberger, 1918 a: 18, 30, 63, fig. 9 (in key; type locality: "Japan"; catalog); 1926 b: 661 (catalog); 1937 a: 1414 (World catalog). Synonymized under *H.* (*P.*) *elegantula* by Kurosawa, 1976 b: 130.

Habroloma ronino [auct. non Obenberger]: Chûjô & Kurosawa, 1950: 14 (misidentification of *H.* (*P.*) *yuasai* Kurosawa, 1976).

Habroloma (*Parahabroloma*) *ronino* [auct. non Obenberger]: Kurosawa, 1959: 253 (misidentification of *H.* (*P.*) *yuasai* Kurosawa, 1976).

Trachys (*Habroloma*) *suensoni* Gebhardt, 1929: 102 (type locality: "China: Soochow"); Obenberger, 1937 a: 1415 (World catalog). Synonymized under *H.* (*P.*) *elegantulum* by Kurosawa, 1976 b: 130.

Habroloma suensoni: Obenberger, 1958: 241 (Yunnan, China).

Trachys (*Habroloma*) *formaneki* Obenberger, 1930: 112 (type locality: "Ching-Kiang. (China.)"); 1937 a: 1411 (World catalog). Synonymized under *H.* (*P.*) *elegantulum* by Kurosawa, 1976 b: 130.

Habroloma formaneki: Obenberger, 1958: 241 ("Szecwan" [sic], China).

Description. Male and female. Body wedge-shaped to roundly wedge-shaped, moderately to slightly highly convex dorsally (Figs. 91A, B). LB 2.53–3.06 mm (mean 2.88 mm); WB 1.48–1.76 mm (mean 1.67 mm); LB/WB 1.68–1.77 (mean 1.72) (n = 5 for all measurements except terminalia). Habitus as shown in Figs.74D, 92.

Integument mainly black, with weak golden-bronze reflections, except for tarsal pads pale brown. Dorsal and ventral surfaces moderately shiny.

Vestiture mainly consisting of white, pale-yellow, and black setae. Head clothed with short, recumbent, pale-yellow setae. Pronotum clothed with short, semirecumbent pale yellow setae, becoming denser apicolaterally, with a median stripe between brownish-black patches. Elytra clothed with short, semirecumbent, white, pale yellow, and black setae which are arranged on each elytron as follows: 1) inconspicuous, undulated band consisting of white and pale yellow setae at basal 1/3; 2) first transverse band consisting of white and pale yellow setae at just before apical 1/3, moderately wavy; 3) second transverse band consisting of white and pale yellow setae at subapical part, rather straight; 4) pale yellow setae forming a longitudinal thin band mixing with whitish setae along sutural margin, sccatering at basal margin, humeri, and apex; and 5) black setae in remaining space. Underside more sparsely setiferous, with fine, recumbent, whitish to yellowish setae becoming slightly denser in lateral parts of metacoxal plates.

Head, when viewed from above, shallowly concave on frons, with oculofrontal margins ridged and slightly weakly to moderately produced anteriorly. Eyes, when viewed from above, narrowly visible, weakly convex laterally. Vertex coarsely variolate-punctate; frons widely concave, weakly impressed along upper side of midline, with surface coarsely variolate-punctate except upper side around midline; suprantennal pores simply round; clypeus wide (Fig. 91D), with elevated basal margin, WC/LC 2–2.32 (mean 2.18), WC/LSC 1.47–1.83 (mean 1.68), faintly arcuately emarginate to nearly straight at apical margin.

Antennae (Fig. 91E, F) short, just reaching or slightly beyond level of pronotal widest point when laid laterally; antennomere I stout claviform, longer than II; II ovate, longer than III; III subrectangular, slightly longer than IV; IV–VI subrectangular, subequal each other in length; VII–X triangular, slightly more strongly enlarged in male than in female; XI subtriangular to sublingulate.

Pronotum widest at sub-basal part, WP/LP 2.78–2.90 (mean 2.82), BMP/AMP 1.87–1.94 (mean 1.90), almost same as elytral width or faintly narrower than elytra; lateral margins showing continuous variations in shape as shown in Fig. 92: typically, evenly, strongly arcuately narrowed apicad; apicolateral angles nearly right (angle); basolateral angles sharply acute (angle); apical margin moderately deeply, arcuately emarginate, with inconspicuous, faint median lobe which is almost straight line at glance; basal margin trisinuate, with median lobe moderately produced; disk depressed laterally, faintly depressed along basal median lobe, with weak basaolateral depressions, with apicolateral depressions bearing round pore on the middle of each; surface rather densely variolate-punctate, sculptures becoming sparse in apical half of median part except near apical margin. Scutellar shield small, triangular, shiny, glabrous.

Elytra widest at base or just behind base, LE/WE 1.20–1.33 (mean 1.28), LE/LP 3.34–3.71 (mean 3.57); humeral calluses weakly developed; lateral margins gradually narrowed posteriorly from base to before apical 1/3, then usually, weakly arcuately narrowed to subapical part and finally arcuately convergent to conjointly rounded apices, or occasionally, continuously arcuately narrowed from before apical 1/3 to apices (Fig. 92D), serrated with one to three denticles at subapical part (Fig. 91C); marginal carinae distinct from base to subapical part; lateral carinae occurring from just behind humeri to subapical part, strongly sinuate behind basal parts; disk moderately to weakly depressed along lateral half of basal margin, constricted behind humeri; surface irregularly and sparsely sculptured with shortly, linearly incised punctures.

Underside. Prosternum (Fig. 91G) with arcuate prosternal lobe faintly emarginate at middle of apical margin which is weakly rimmed; prosternal process wide; trapezoidal plate slightly longer than wide or as wide as long, WTP/LTP 1.05–1.29 (mean 1.16), WTP/BTP 1.32–1.58 (mean 1.43), with rounded apical corners, with sides which are dilated from base to widest point around apical corners and weakly constricted in basal part, with apex broadly, faintly arcuate; disk flattened on trapezoidal plate bearing marginal carinae along sides, evenly convex on prosternal lobe; surface on trapezoidal plate only with setiferous pin-prick punctures. Hypomera with large, transversely oval hypomeral markings consisting of linearly incised punctures (Fig. 91H). Metaventrite moderately variolate-punctate on inside of katepisternal suture and moderately variolate on outside of the suture. Legs moderately slender in femora and tibiae; metacoxal plates without arcuate notches on medial posterior margins, weakly produced posteriorly at each lateral angle which is broadly acute (angle), with surface moderately variolate; metafemora obtusely angulate at about distal 1/4 of outer margins; metatibiae without a fringe of spines on each outer margin (Fig. 91I), but very sparsely bearing fine setae throughout; inner tooth of each claw large. Abdominal ventrites with sternal groove only on ventrite V, of which apex is rounded or faintly angulately rounded; surface variolate, in ventrite I with linearly confluent sculptures on median part.

Sexual dimorphism barely recognized on the relative size of serrate antennomeres (see above).

Male terminalia (n = 1 for measurements). Proctiger with a pair of short baculi at base. Sternite IX (Fig. 93A, E) rather slender, SL/SW 1.14, more or less emarginate at apical margin, usually bearing a pair of setae on each side of apical margin but rarely without setae. Tegmen (Fig. 93B, F) slender; parameres PL/PW 3.41, bearing a pair of setae on apicolateral margins, with sides which are gradually dilated from base to widest point at behind apical 1/3, then weakly arcuately narrowed to subapical part, and finally strongly convergent apicad; phallobase PbL/PbW 2.06, about 1/5 length of tegmen. Penis (Fig. 93C, D, G, H) wide, PeL/PeW 4.91, much shorter than tegmen; dorsal plate with sides (not including sides of median struts) which are subparallel in widest part of basal 1/3, and then slightly strongly convergent apicad, with apex slightly broadly, roundly truncate, basally with median struts about 1/2 length of penis, with an apically dilated, longitudinal, narrow depression in about apical 2/3 but not reaching apex (Fig. 93C, G); ventral membrane weakly sclerotized as a short liner patch at middle.

Female terminalia (n = 1 for measurements). Ovipositor (Figs. 94) short. Proctiger with a pair of short, straight baculi at base; coxites transversely subtrapezoidal with arcuate apical margin, sparsely setiferous on each side of apical margin; styli slightly long in length, slender, SlL/SlW 3.93, bearing several setae apically; ventral valve without setae; vagina sack-shaped (under incompletely inflated state); spermatheca slender tubular, moderate in length, widest in apical half.

Differential diagnosis. This species is very similar in general appearance to *Habroloma* (*Parahabroloma*) *yuasai*, but readily distinguished from *H*. (*P*.) *yuasai* by the non-elongated male aedeagus and by the non-elongated female spermatheca. In addition, this species may be distinguishable from it by the combination of the following superficial character states: elytral lateral carinae starting from near behind humeri; prosternal trapezoidal plate often faintly wider; and black integument in dorsum only with weak golden-bronze reflection (but occasionally with stronger golden-bronze tints as in *H*. (*P*.) *yuasai*).

Furthermore, this species is similar in general appearance to *Habroloma* (*Parahabroloma*) *marginicolle*, *H*. (*P*.) *asahinai*, and *H*. (*P*.) *hikosanense* of the species-group III, but is distinguished from them by the combination of the following character states: oculofrontal margins of head more weakly produced anteriorly; lateral carinae of elytra starting from just behind humeri (similar to *H*. (*P*.) *marginicolle* and *H*. (*P*.) *asahinai*); prosternal trapezoidal plate slightly narrower (similar to *H*. (*P*.) *hikosanense*), with rounded apical corners; surface of prosternal trapezoidal plate without ocellate sculptures; and gradually narrowed dorsal plate of penis in distal part.

Specimens examined. Non-type material. **Japan**. Hokkaido — 2 exs., Oyafune-chô, Ishikari-shi, 25.V.2022, Y. Tamadera leg., captured on *Rubus parvifolius* (YTJ); 2 exs., F1 of the above specimens, emerged from R. *parvifolius*, 6.VII.2022, rearing no. 2022-091 (YTJ). Honshu — [Fukushima] 1 ♀, "Onezawa, Hibara V., Yama D.", Fukushima Pref. 18.VIII.1948, Y. Kurosawa leg. (NSMT; paratype of *Habroloma* (*Parahabroloma*) *yuasai* Kurosawa, 1976 b). [Ibaraki] 1 ♂, Takyû-rindô, Suifu-mura, 23.VII.1995, S. Ohmomo leg. (SOCI; recorded as *H*. (*P*.) *atronitidum* by Ohmomo, 2018). [Tochigi] 1 ex., Itaga, Kanuma-shi, 9.VII.2000, H. Takizawa leg. (SEHU). [Gunma] 1 ex., Numata, 1.V.1968, T. Takei leg. (SEHU); 1 ex., Akagi-jinja Shrine – Miyagi-mura, 12.VI.2005, H. Takizawa leg. (SEHU). [Nagano] 1 ex., Minowa-machi, Kami-ina-gun, 15–16.VI.2013, N. Kikuchi leg. (SEHU); 3 ♂♂, 4 ♀♀, Shimauchi, Matsumoto-shi, 17.V.2015, W. Yamada leg. (YTJ). [Gifu] 5 exs., Ôgaki, 10.V.1946, Y. Moriya leg. (SEHU). [Shiga] 1 ex., Mt. Hira, 2.VI.1967, T. Shibata leg. (SEHU); 1 ex., same locality, 5.VIII.1955, T. Nakane leg. (SEHU); 1 ♂, Bô-mura, Ôtsu-shi, 15.VI.1957, T. Nakane leg. (SEHU). [Hyôgo] 1ex., Motoyama-mura (current: Higashi-nada-ku, Kôbe-shi), 16.VI.1938, K. Sakaguchi leg. (SEHU); 1 ex., same locality, 27.VIII.1940, K. Sakaguchi leg. (SEHU); 1 ex., Sasayama, 28.VI.1956, T. Nakane & T. Okutani leg. (SEHU). [Nara] 1 ex., Mt. Obako-dake, 27.VI.1976, T. Hatayama leg. (NSMT; identified as *H*. (*P*.) *atronitidum* by Y. Kurosawa); 1 ex., Tsubosaka, Takatori-chô, 30.X.1945, M. Azuma leg. (SEHU); 2 exs., Ikadaba, Mt. Ohdai, 21.VII.1953, T. Nakane leg. (SEHU). [Okayama] 1 ex., Yoshiigawa River, Kamagino, 21–22.IV.2002, H. Takizawa leg. (SEHU). [Hiroshima] 1 ex., Mt. Kammuri, 19.V.1968, T. Kosaka leg. (SEHU); 1 ♀, Ose River, Ohtake, 12.V.2001, A. Nishiyama leg. (SOCI; identified as *H.* (*P.*) *atronitidum* by S. Ohmomo). Hatsushima Is. (Shizuoka) — 1 ♂, "Hatsu-shima, E-Izu, Shizuoka", 6.VI.1968, T. Maenami leg. (NSMT; paratype of *Habroloma* (*Parahabroloma*) *yuasai* Kurosawa, 1976 b). Shikoku — [Ehime] 1 ex., Ishitegawa-kôen Park, Matsuyama-shi, 15.VII.2021, Y. Tamadera leg., emerged from *Rubus parvifolius*, rearing no. 2021-159 (YTJ). [Tokushima] 1 ♀, "Muya, Naruto C., Tokushima Pref., Shikoku, 5.V.1948, M. Chûjô" (NSMT; as *H.* (*P.*) *atronitidum* sensu Kurosawa, 1976 b (= *kagosimanum* sensu Kurosawa, 1959)) [Kagawa] 1 ex., Mt. Ryûô-san, 11.V.2000, H. Takizawa leg. (SEHU). [Ehime] 1 ♀, Omogo, 21.VIII.1969, T. Nakane leg. (SEHU). Okinoshima Is. (Kôchi) — 1 ex., 2–4.V.2019, Okinoshima Is., K. Kuroda & K. Yasuda leg. (YTJ; recorded by Tamadera, 2021); 1 ex., Shiroiwa-misaki, 2–4.V.2019, K. Kuroda leg., Yellow-pan Trap (YTJ; recorded by Tamadera, 2021). Kyushu — [Fukuoka] 1 ♂, 1 ♀, Fukakurakyo, Ochiai, Soeda-machi, Tagawa-gun, 28.IV.2017, Y. Tamadera leg. (YTJ). [Saga] 1 ex., Ogashirayama, 7.V1984, H. Yamaguchi leg. (SEHU); 2 exs., Kirigo-daichi, Yobuko, 30.IX.1952, H. Yamaguchi leg. (SEHU); 2 exs., Onoe-kôen Park, Yobuko, 12.V.1985, H. Yamaguchi leg. (SEHU); 1 ex., same locality, 16.IX.1983, H. Yamaguchi leg. (SEHU). [Kumamoto] 1 ex., Mt. Shiragadake, 4.VII.1982, M. Ôhara leg. (SEHU). [Miyazaki] 2 exs., Mt. Takahata-yama, Kushima-shi, 14.VI.2006, Y. Komiya leg. (SEHU). Kabejima Is. (Saga) — 1 ex., Yobuko, Karatsu-shi, 19.VI.1984, H. Yamaguchi leg. (SEHU). [Kagoshima] 1 ex., "Kagoshima, 11.V.1941, M. Tanaka" (NSMT; as *H.* (*P.*) *atronitidum* sensu Kurosawa, 1976 b (= *kagosimanum* sensu Kurosawa, 1959)). Tsushima Is. (Nagasaki) — 3 ♂♂, Uchiyama, Izuhara-machi, 17.VII.1960, T. Nakane leg. (SEHU; recorded by Nakane, 1987 as *Habroloma* (*Parahabroloma*) *yuasai*); 2 exs., Mogi, Kamitsushima-chô, 13.VI.2005, Y. Komiya leg. (SEHU); 2 exs., Tokue, Mine-machi, 17.VI.2005, Y. Komiya leg. (SEHU); 1 ♂, 1 ♀, near Baji-kôen Park, Seta, Kamiagata-machi, Tsushima-shi, 29.VIII.2016, Y. Tamadera leg. (YTJ). Danjo-guntô Isls. — [Meshima Is.] 1 ♂, Ôhama, Fukue-shi (current: Gotô-shi), Nagasaki-ken, 25.VIII.2001, K. Adachi leg. (YTJ; recorded by Adachi, 2004 as a *Habroloma* sp.).

Distributions in Japan. Hokkaido, Honshu, Shikoku, Kyushu, Hatsushima Is. (Shizuoka) — new record, Okinoshima Is (Kôchi), Kabejima Is. (Saga), and Danjo-guntô Isls. (Meshima Is.).

Other records based on literatures. Shôdoshima Is. (Fujimoto, 2007), Ugurujima Is. (Kôchi) (Doi & Fujita, 2012), Kashiwajima Is. (Saga) (Nishida, 2018), and the Koshikijima Isls. (Kamikoshikijima Is. (Imasaka *et al.*, 2020) and Shimokoshikijima Is.

(Kurosawa, 1978)).

Other distributions. China and Korea (probably, South Korea; Kurosawa, 1976a).

Adult food plant. Same as in the larvae mentioned below. Adult feeding scars are shown in Fig. 105A. Several adults were also captured on leaves of *Rubus corchorifolius* L.f. [Japanese name: Birôdo-ichigo] in Japan.

Host plant. Rosaceae: *Rubus parvifolius* L. [Japanese name: Nawashiro-ichigo] (Yano, 1952; confirmed by this study), *R. palmatus* Thunb. var. *palmatus* [Japanese name: Nagaba-momiji-ichigo] (Kurosawa, 1959 — adult record?; confirmed by this study), and *R. buergeri* Miq. [Japanese name: Fuyu-ichigo] (Kurosawa, 1959 — adult record?) in Japan.

Leaf-mining habit. Mines of *Habroloma* (*Parahabroloma*) *subbicorne* were found on *Rubus parvifolius* and *R. palmatus* var. *palmatus* by this study (Figs. 108AB): each mine was of the full-depth type and formed an elongate blotch occurring usually along leaf-margin; when full-grown, it occupied less than half of whole the leaf blade; eggs, which were black (remaining eggshell) and covered on powdery substances, were laid singly on near the leaf-margin on the adaxial surface; hatched larvae left short linear to granular frass inside the mines; adults were usually emerged from the adaxial surface of the leaves with oval adult exit holes. See also Yano (1952) treated as *Habroloma elegantulm* for descriptions of the leaf-mines and immature stages of *H.* (*P.*) *subbicorne*. That study mentioned that the frass are put either outside or inside of the mines in the younger stage of larva, but in my observation through all the immature stages under indoor rearing conditions (the populations of Ishikari-shi, Hokkaido), the larvae always left all the frass inside the mines.

Notes. *Intraspecific variations of pronotum*. *Habroloma* (*Parahabroloma*) *subbicorne* occasionally shows intraspecific variations in the shape and width of the pronotum. These characters are often used to determine species of the genus *Habroloma*, so that it is regarded as a very important one for taxonomy of this genus. However, the shape of pronotum in *H.* (*P.*) *subbicorne* occasionally become as in that of *H.* (*P.*) *hikosanense* and the width (basal) of pronotum sometimes become as in that of *H.* (*P.*) *atronitidum* (based on description of Kurosawa, 1959 as "*H.* (*P.*) *kagoshimana*") (Fig. 92). After carful examinations of male and female terminalia (except *H.* (*P.*) *hikosanense*), *H.* (*P.*) *atronitidum* from Japan is well recognized within the intraspecific variations of *H.* (*P.*) *subbicorne*. Therefore, the Japanese specimens identified with *H.* (*P.*) *atronitidum* by previous studies (e.g. Kurosawa, 1959, 1976 b) are regarded as *H.* (*P.*) *subbicorne* in this study and then *H.* (*P.*) *atronitidum* was removed from Japanese buprestid fauna (see the section of the removed species from the Japanese buprestid fauna).

Habroloma (Parahabroloma) marginicolle (Fairmaire, 1888)
[Japanese name: Shirôzu-hirata-chibi-tamamushi]
(Figs. 74E, 95, 96, 105B–D, 108C)

Trachys marginicollis Fairmaire, 1888: 24 (type locality: "Chine centrale"); Kerremans, 1892 a: 286 (catalog); 1903: 308 (catalog).

Trachys (*Habroloma*) *marginicollis*: Jakobson, 1913: 800 (catalog); Obenberger, 1918 a: 64 (catalog); 1926 b: 661 (catalog); 1937 a: 1412 (World catalog).

Habroloma (*Parahabroloma*) *marginicolle*: Kubáň, 2006: 43, 417 (new assignment; Palaearctic catalog); Bellamy, 2008 b: 2553 (World catalog); Ohmomo & Fukutomi, 2013: 171, pl. 55 (pictorial book); Kubáň, 2016: 569 (Palaearctic catalog); Tamadera & Yoshitake, 2017: 409 (Mie Pref, Honshu).

Trachys (*Habroloma*) *kagosimana* Obenberger, 1940: 39 (type locality: "Japan, Kiusiu, Kagosima"). Synonymized under *H.* (*P.*) *marginicolle* by Kubáň, 2006: 46.

Habroloma (*Parahabroloma*) *kagosimana*: Kurosawa, 1976 a: 3 fig. 18b (note).

Habroloma (*Parahabroloma*) *kagosimanum*: Kurosawa, 1976 b: 131 (noted on misidentification of Kurosawa, 1959): 1985 b: 37, pl. 7 (pictorial book; fig. 25 is a correct image); Akiyama & Ohmomo, 2000: 286, pl. 120 (pictorial book).

Habroloma (*Parahabroloma*) *kagoshimana* [sic] [auct. non Obenberger]: Kurosawa, 1959: 250 (misidentification of *H.* (*P.*) *atronitidum* auct. non Gebhardt, 1929).

Habroloma (*Parahabroloma*) *shirozui* Kurosawa, 1959: 256, fig. 16b (type locality: Ambô, Yakushima Is, Ryukyus, Japan); 1963: 156 (noted in pictorial book). Synonymized under *H.* (*P.*) *kagosimanum* by Kurosawa, 1976 b: 131.

Description. Male and female. Body roundly wedge-shaped, moderately convex dorsally (Figs. 95 A, B). LB 2.89–3.33 mm (mean 3.17 mm); WB 1.70–1.99 mm (mean 1.86 mm); LB/WB 1.66–1.78 (mean 1.70) (n = 5 for all measurements except terminalia). Habitus as shown in Fig. 74E.

Integument mainly black, with weak golden-bronze reflections, except for tarsal pads pale brown. Dorsal and ventral surfaces moderately shiny.

Vestiture mainly consisting of white, pale-yellow, and black setae; pale yellow setae occasionally replaced with white setae, as a result such individual bearing only two-colored setae. Head clothed with short, recumbent, pale-yellow or white setae. Pronotum clothed with short, semirecumbent, white to pale yellow and black setae which are arranged as follows: 1) inconspicuous, four black patches across middle, the two median patches reaching basal margin of pronotum; 2) white to pale yellow setae in remaining space, becoming denser apicolaterally, forming three stripes between black patches, the two lateral stripes often being inconspicuous. Elytra clothed with short, semirecumbent, white, pale yellow, and black setae which are arranged on each elytron as follows: 1) pale yellow longitudinal band consisting of three to two rows of setae occurred along medial half of basal margin to basal 2/3 of sutural margin, and then often continuing to a single row of pale yellow setae occurred along apical 1/3 of sutural margin; 2) roughly gridded band consisting of white to pale yellow setae in basal half; 3) first white transverse band at just before apical 1/3, moderately wavy; 4) second white transverse band at subapical part, rather straight; 5) white setae in apical part; and 6) black setae in remaining space, at least forming two oval patches in basal 1/4 and basal 2/4 at medial half. Underside more sparsely setiferous, with fine, recumbent, whitish to yellowish setae becoming slightly denser in lateral parts of metacoxal plates.

Head, when viewed from above, shallowly concave on frons, with oculofrontal margins strongly sharply ridged and strongly produced anteriorly. Eyes, when viewed from above, narrowly visible, weakly convex laterally. Vertex coarsely variolate-punctate; frons widely concave, weakly impressed along upper side of midline, with surface coarsely variolate-punctate except upper side around midline; suprantennal pores simply round; clypeus wide (Fig. 95D), with elevated basal margin, WC/LC 2.43–2.93 (mean 2.65), WC/LSC 1.76–2.09 (mean 1.97), faintly arcuately emarginate to nearly straight at apical margin.

Antennae (Fig. 95E, F) short, just reaching or slightly beyond level of pronotal widest point when laid laterally; antennomere I stout claviform, longer than II; II ovate, longer than III; III subrectangular, slightly longer than IV; IV–VI subrectangular, subequal each other in length; VII–X triangular, slightly more strongly enlarged in male than in female; XI subtriangular to sublingulate.

Pronotum widest at sub-basal part, WP/LP 2.81–3.11 (mean 2.98), BMP/AMP 1.74–1.91 (mean 1.84), slightly narrower than elytra; lateral margins evenly arcuately narrowed apicad, often being faintly angulate at behind middle and becoming more straight line in apical half than in basal half; apicolateral angles nearly right (angle); basolateral angles sharply acute (angle); apical margin moderately deeply, arcuately emarginate, with very small median lobe; basal margin trisinuate, with median lobe moderately produced; disk depressed laterally, weakly depressed along basal median lobe, with weak basaolateral depressions, with apicolateral depressions bearing small round pore on the middle of each; surface rather densely variolate-punctate, sculptures becoming slightly sparse in median part. Scutellar shield small, triangular, shiny, glabrous.

Elytra widest just behind base, LE/WE 1.21–1.26 (mean 1.25), LE/LP 3.45–3.99

(mean 3.77); humeral calluses weakly developed; lateral margins gradually narrowed posteriorly from base to middle and weakly constricted between them, then weakly arcuately, more strongly narrowed to subapical part, and finally strongly convergent to conjointly rounded apices after faintly angulated, serrated with one to three denticles at constricted part behind subapical part (Fig. 95A); marginal carinae distinct from base to subapical part; lateral carinae occurring from just behind humeri to subapical part, strongly sinuate behind basal parts; disk moderately depressed along lateral half of basal margin, slightly strongly constricted behind humeri; surface irregularly and sparsely sculptured with shortly, linearly incised punctures.

Underside. Prosternum (Fig. 95G) with arcuate prosternal lobe which is weakly rimmed; prosternal process wide; trapezoidal plate almost as wide as long, WTP/LTP 1.30–1.48 (mean 1.39), WTP/BTP 1.39–1.65 (mean 1.50), with obtusely angulate apical corners, with sides which are gradually dilated apicad in rather straight line, with apex broadly, faintly arcuate; disk flattened on trapezoidal plate bearing marginal carinae along sides, evenly convex on prosternal lobe; surface on trapezoidal plate with setiferous pin-prick punctures and ocellate sculptures. Hypomera with large, transversely oval hypomeral markings consisting of linearly incised punctures, the markings rarely divided in lateral parts (Fig. 95H). Metaventrite moderately variolate-punctate on inside of katepisternal suture and moderately variolate on outside of the suture. Legs moderately slender in femora and tibiae; metacoxal plates without arcuate notches on medial posterior margins, weakly produced posteriorly at each lateral angle which is broadly acute (angle), with surface moderately variolate; metafemora obtusely angulate at about distal 1/3 of outer margins; metatibiae without a fringe of spines on each outer margin (Fig. 95I), but very sparsely bearing fine setae throughout; inner tooth of each claw large. Abdominal ventrites with sternal groove only on ventrite V, of which apex is rounded or faintly angulately rounded; surface variolate, in ventrite I with linearly confluent sculptures on median part.

Sexual dimorphism barely recognized on the relative size of serrate antennomeres (see above).

Male terminalia (n = 1 for measurements). Proctiger with a pair of short baculi at base. Sternite IX (Fig. 96A) rather slender, SL/SW 1.00, more or less emarginate at apical margin, without setae. Tegmen (Fig. 96B) slender; parameres PL/PW 4.41, bearing a pair of setae on apicolateral margins, almost parallel-sided, but with sides which are subparallel in about basal half, then weakly arcuately, faintly dilated to widest point at apical 1/3, and finally continuously arcuately, weakly convergent apicad; phallobase PbL/PbW 1.60, about 1/5 length of tegmen. Penis (Fig. 96C, D) wide, PeL/PeW 4.54, shorter than tegmen; dorsal plate with sides (not including sides of median struts) which are subparallel in widest part of basal 1/3, then slightly strongly narrowed to apical 1/3, and finally subparallel but faintly narrowed apicad, with distinctly broad apex which is roundly truncate, basally with median struts about 1/2 length of penis, with an longitudinal, narrow depression in about apical 2/3, this depression reaching apex of penis and strongly dilated in its apical part (Fig. 96C); ventral membrane without sclerotized part.

Female terminalia (n = 1 for measurements). Ovipositor (Figs. 96E–G) short. Proctiger with a pair of short, straight baculi at base; coxites transversely subhexagonal to subtrapezoidal with arcuate apical margin, sparsely setiferous on each side of apical margin; styli slightly long in length, slender, SlL/SlW 4.09, bearing several setae apically; ventral valve without setae; vagina sack-shaped (under incompletely inflated state); spermatheca slender tubular, moderate in length, widest in apical half.

Differential diagnosis. This species is similar in general appearance to *Habroloma* (*Parahabroloma*) *subbicorne*, *H*. (*P*.) *asahinai*, and *H*. (*P*.) *hikosanense* of the species-group III, but is distinguished from them by the combination of the following character states: oculofrontal margins of head in dorsal view strongly produced anteriorly (slightly more weakly produced than those of *H*. (*P*.) *hikosanense*); lateral margins of pronotum rather evenly arcuate, often being faintly angulate at behind middle; lateral margins of elytra constricted between base and middle (similar to *H*. (*P*.) *asahinai*), sometimes emarginate at subapical part; lateral carinae of elytra starting from just behind humeri (similar to *H*. (*P*.) *subbicorne* and *H*. (*P*.) *asahinai*); prosternal trapezoidal plate slightly wider (similar to *H*. (*P*.) *asahinai*), with obtusely angulate apical corners and with sides which are dilated apicad in rather straight line; surface of prosternal trapezoidal plate with ocellate sculptures (similar to *H*. (*P*.) *asahinai*); male penis (dorsal plate) subparallel-sided in apical 1/3; apex of penis broad and roundly truncate; ventral membrane of penis without a sclerotized patch (similar to *H*. (*P*.) *asahinai*).

Specimens examined. Type material. Holotype of *Habroloma* (*Parahabroloma*) *shirozui* Kurosawa, 1959: ♂ (based on Kurosawa, 1959; no dissected terminalia), “KURIO / YAKUSHIMA Is. / KYUSHU / 8.V.1954 / Y. Kurosawa leg.” (NSMT). Paratypes (part) of *H*. (*P*.) *shirozui*: 2 exs., Nishino-omote, Tanegashima Is., 4.VII.1952, Y. Kurosawa leg. (NSMT).

Non-type material. **Japan**. Honshu — [Mie] 1 ex., Tategasaki-enchi, Hobo-chô, Kumano-shi, 30.IV.2011, H. Yoshitake leg. (NIAES; recorded by Tamadera & Yoshitake, 2017). Itsukushima Is. (Miyajima Is.; Hiroshima) — 1 ex., Miyajima-chô, 11.VI.1967, T. Kosaka leg. (SEHU). Kyushu — [Fukuoka] 1 ♂, Sajibarai, Ukiha G., Fukuoka Pref., 27.VIII.1965, N. Gyotoku leg. (NSMT); [Ôita] 8 ♂♂, 5 ♀♀, Kamaeura, Kamae, Saiki-shi, 25.IV.2017, Y. Tamadera leg. (YTJ). [Miyazaki] 3 exs., Udo, Nichinan-shi, 7.X.1973, A. Nagai leg. (SEHU); 1 ex., Inohae, Nichinan-shi, 24.V.1987, T. & T. Nakane leg. (SEHU); [Kagoshima] 2 exs., Sata, Ôsumi Peninsula, 23.V.1952, T. Nakane leg. (SEHU); 3 exs., same locality, 24.V.1952, T. Nakane leg. (SEHU); 4 exs., same locality, 9.III.1964, Y. Kishi leg. (SEHU); 4 exs., same locality, 8.III.1964, no collector name (SEHU). Otojima Is. (Miyazaki) — 2 exs., Kadokawa-chô, 28.V.1970, A. Nagai leg. (SEHU). The Ryukyus: Ôsumi Isls. — [Yakushima Is.] 1 ♂, 1♀, Nakasegawa-rindô, Hirano, 28.V.2006, Y. Komiya leg. (SEHU); 1 ex., Onoaida, Yaku-chô, 28.V.2006, Y. Komiya leg. (SEHU).

Distributions in Japan. Honshu, Shikoku, Kyushu, Itsukushima Is. (Hiroshima) — new record, Otojima Is. (Miyazaki) — new record, and the Ryukyus: Ôsumi Isls. (Tanegashima Is. and Yakushima Is.).

Other records based on literatures. The Koshikijima Isls. (Kurosawa, 1985 b) and Kashiwajima Is. (Saga) (Mizokami, 2014).

Other distributions. China and Korea.

Adult food plant. Same as in the larvae mentioned below.

Host plant. Rosaceae: *Rubus sieboldii* Blume [Japanese name: Hôroku-ichigo] (Kurosawa, 1959 — adult record?; confirmed by this study), *R. buergeri* Miq. [Japanese name: Fuyu-ichigo] (Kurosawa, 1976 a — adult record?; confirmed by this study), and *R. pseudosieboldii* Makino [Japanese name: Ôfuyu-ichigo] (confirmed by this study) in Japan.

Leaf-mining habit. Mines of *Habroloma* (*Parahabroloma*) *marginicolle* were found on *Rubus sieboldii*, *R. buergeri*, and *R. pseudosieboldii* by this study (Figs. 105B, 108C): each mine was of the full-depth type and formed an irregular blotch; when full-grown, it usually occupied much less than one quarter of whole the leaf blade due to the relatively large-sized host leaves; eggs, which were black (remaining eggshell) and covered on powdery substances, were laid singly on the side relatively close to the leaf-margin on the adaxial surface; hatched larvae left granular to thread-like frass inside the mines; adults were usually emerged from the adaxial surface of the leaves with oval adult exit holes.

Notes. *Powdery substances on body*. In this study, it is revealed that *Habroloma* (*Parahabroloma*) *marginicolle* secrets powdery substances. White powders are sometimes secreted from the elytral humeral parts and occasionally from the pronotal apicolateral depressions and the elytral first and second white transverse bands (Figs. 105C, D). The powders were not found on *H.* (*P.*) *marginicolle* when emerging new adults under the rearing condition.

In the Buprestidae, some genera and species in a living state have colored powdery substances in specific body parts, for example elytral concaved parts and/or underside of body in the genera *Chrysodema*, *Nipponobuprestis*, and *Chalcophora* and parts of elytral patterns of setae, abdominal ventrites, and/or laterosternites in the genera *Aglirus*, *Coraebus* (Ohmomo and Fukutomi, 2013; Hespenheide and Westcott, 2018; Fukutomi, *et al*., 2022). The function and secretory mechanism of the powdery substances of Buprestidae is not studied. At least, in *Nipponobuprestis* (*Nipponobuprestis*) *amabilis* it is known that these powders are secreted after feeding on plant leaves and never found when emerging new adults (Ichihara, 2020, 2022).

Habroloma* (*Parahabroloma*) *asahinai asahinai Kurosawa, 1959
[Japanese name: Asahina-hirata-chibi-tamamushi Meigi-taipu-ashu]
(Figs. 74F, 97, 98, 105E, F, 108D)

Habroloma (*Parahabroloma*) *asahinai* Kurosawa, 1959: 257, fig. 16a (type locality: "Isakawa-yama, Okinawa I., Loo-Choo Is.", Japan); 1976 a: 2, fig. 18a (note); 1976b: 129 (part; Ishigakijima Is. Ryukus, Japan); 1985: 37, pl. 7 (part; pictorial book); Akiyama & Ohmomo, 1997: 50 (part; checklist); 2000: 286, pl. 120 (part; pictorial book); Kubáň, 2006: 417 (part; Palaearctic catalog); Bellamy, 2008 b: 2538 (part; World catalog); Inada & Fukutomi, 2008 (distribution); Ohmomo & Fukutomi, 2013: 172, pl. 55 (part; pictorial book); Kubáň, 2016: 568 (part; Palaearctic catalog).

Description. Male and female. Body wedge-shaped, moderately convex dorsally (Figs. 97A, B). LB 2.91–3.09 mm (mean 3.05 mm); WB 1.81–1.92 mm (mean 1.88 mm); LB/WB 1.60–1.63 (mean 1.62) (n = 5 for all measurements except terminalia). Habitus as shown in Fig. 74F.

Integument mainly black, with weak golden-bronze reflections, except for tarsal pads pale brown. Dorsal and ventral surfaces moderately shiny.

Vestiture mainly consisting of white, yellow, and black setae; white setae occasionally with weak yellowish tints; yellow setae showing various shade from paler yellow to brownish-yellow. Head clothed with short, recumbent, yellow setae. Pronotum clothed with short, semirecumbent, yellow setae, becoming denser apicolaterally, with a median stripe occasionally mixing with a few white setae, with four small brownish-black patches across middle, the two median patches barely reaching basal margin. Elytra clothed with short, semirecumbent, white, yellow, and black setae which are arranged on each elytron as follows: 1) yellow setae in basal half at lateral half, along basal margin, sutural margin, and lateral carina, and in apical part; 2) white circular band in basal 1/4 at medial half, mixing with yellow setae; 3) first white transverse band at just before apical 1/3, moderately wavy; 4) second white transverse band at subapical part, rather straight; 5) a few white setae along lateral margin of apex; and 5) black setae in remaining space. Underside more sparsely setiferous, with fine, recumbent, whitish to yellowish setae becoming slightly denser in lateral parts of metacoxal plates.

Head, when viewed from above, shallowly concave on frons, with oculofrontal margins sharply ridged and slightly strongly produced anteriorly. Eyes, when viewed from above, narrowly visible, weakly convex laterally. Vertex coarsely variolate-punctate; frons widely concave, weakly impressed along upper side of midline, with surface coarsely variolate-punctate except upper side around midline; suprantennal pores simply round; clypeus wide (Fig. 97D), with elevated basal margin, WC/LC 2.44–2.98 (mean 2.72), WC/LSC 1.83–2.00 (mean 1.92), faintly arcuately emarginate to nearly straight at apical margin.

Antennae (Fig. 97E, F) short, not reaching level of pronotal widest point when laid laterally; antennomere I stout claviform, longer than II; II ovate, longer than III; III subrectangular, longer than IV; IV–VI subrectangular, subequal each other in length; VII–X triangular, slightly more strongly enlarged in male than in female; XI subtriangular to sublingulate.

Pronotum widest at sub-basal part to basal 1/3, WP/LP 2.88–3.15 (mean 3.05), BMP/AMP 1.93–2.01 (mean 1.97), slightly wider than elytra; lateral margins rather subparallel or slightly dilated anteriorly in basal 1/3, where are somewhat rounded, and then relatively straightly, strongly narrowed apicad; apicolateral angles nearly right (angle); basolateral angles sharply acute (angle); apical margin moderately deeply, arcuately emarginate, with very small median lobe; basal margin trisinuate, with median lobe moderately produced; disk rather evenly convex, faintly depressed along basal median lobe, with weak basaolateral depressions, with apicolateral depressions bearing round pore on the middle of each; surface rather densely variolate-punctate. Scutellar shield small, triangular, shiny, glabrous.

Elytra widest at base, LE/WE 1.17–1.23 (mean 1.21), LE/LP 3.36–3.76 (mean 3.63); humeral calluses weakly developed; lateral margins gradually narrowed posteriorly from base to middle and slightly strongly constricted between them, then slightly straightly, more strongly narrowed to subapical part, and finally strongly arcuately convergent to conjointly rounded apices, serrated with one to two denticles at subapical part (Fig. 97C), but rarely without serrations on one side (n =1); marginal carinae distinct from base to subapical part; lateral carinae occurring from posterior parts of humeri to subapical part, strongly sinuate behind humeral parts; disk moderately depressed along lateral half of basal margin, strongly constricted behind humeri; surface irregularly and sparsely sculptured with shortly, linearly incised punctures.

Underside. Prosternum (Fig. 97G) with arcuate prosternal lobe which is weakly rimmed; prosternal process wide; trapezoidal plate wider than long or almost as wide as long, WTP/LTP 1.34–1.44 (mean 1.39), WTP/BTP 1.45–1.62 (mean 1.52), with obtusely angulate apical corners, with sides which are slightly strongly dilated from base to widest point around apical corners, with apex broadly, faintly arcuate; disk flattened on trapezoidal plate bearing marginal carinae along sides, evenly convex on prosternal lobe; surface on trapezoidal plate with setiferous pin-prick punctures and ocellate sculptures. Hypomera with large, transversely oval hypomeral markings consisting of linearly incised punctures (Fig. 97H). Metaventrite moderately variolate-punctate on inside of katepisternal suture and moderately variolate on outside of the suture. Legs moderately slender in femora and tibiae; metacoxal plates without arcuate notches on medial posterior margins, weakly produced posteriorly at each lateral angle which is broadly acute (angle), with surface moderately variolate; metafemora obtusely angulate at about distal 1/3 of outer margins; metatibiae without a fringe of spines on each outer margin (Fig. 97I), but very sparsely bearing fine setae throughout; inner tooth of each claw large. Abdominal ventrites with sternal groove only on ventrite V, of which apex is rounded or faintly angulately rounded; surface variolate, in ventrite I with linearly confluent sculptures on median part.

Sexual dimorphism barely recognized on the relative size of serrate antennomeres (see above).

Male terminalia (n = 1 for measurements). Proctiger with a pair of short baculi at base. Sternite IX (Fig. 98A) rather slender, SL/SW 1.16, more or less emarginate at apical margin, without setae. Tegmen (Fig. 98B) slender; parameres PL/PW 4.06, bearing a pair of setae on apicolateral margins, almost parallel-sided, but with sides which are subparallel in about basal half, then weakly arcuately, faintly dilated to widest point at apical 1/3, and finally continuously arcuately, weakly convergent apicad; phallobase PbL/PbW 1.75, about 1/5 length of tegmen. Penis (Figs. 98C, D) wide, PeL/PeW 6.79, shorter than tegmen; dorsal plate with sides (not including sides of median struts) which are subparallel in widest part of basal 1/3, then slightly strongly narrowed to middle, and finally subparallel but faintly dilated apicad, with distinctly broad apex truncately rounded then faintly emarginate at middle, basally with median struts nearly 1/2 length of penis, with an longitudinal depression in about apical 3/4, this depression reaching apex of penis and strongly dilated in its apical 2/3 (Fig. 98C); ventral membrane without sclerotized part.

Female terminalia (n = 1 for measurements). Ovipositor (Figs. 98–E–G) short. Proctiger with a pair of short, straight baculi at base; coxites transversely subhexagonal to subtrapezoidal with arcuate apical margin, sparsely setiferous on each side of apical margin; styli slightly long in length, slender, SlL/SlW 5.00, bearing several setae apically; ventral valve without setae; vagina sack-shaped (under completely inflated state); spermatheca slightly wide tubular, moderate in length, widest in apical part.

Differential diagnosis. This species (subspecies) is similar in general appearance to *Habroloma* (*Parahabroloma*) *subbicorne*, *H*. (*P*.) *marginicolle*, and *H*. (*P*.) *hikosanense* of the species-group III, but is distinguished from them by the combination of the following character states: oculofrontal margins of head in more weakly produced anteriorly than those of *H*. (*P*.) *asahinai* and *H*. (*P*.) *hikosanense*; lateral margins of pronotum rather subparallel and somewhat rounded in basal 1/3 then strongly narrowed apicad; lateral margins of elytra constricted between base and middle (similar to *H*. (*P*.) *marginicolle*); lateral carinae of elytra starting from just behind humeri (similar to *H*. (*P*.) *subbicorne* and *H*. (*P*.) *marginicolle*); prosternal trapezoidal plate with obtusely angulate apical corners; surface of prosternal trapezoidal plate with ocellate sculptures (similar to *H*. (*P*.) *marginicolle*); male penis (dorsal plate) subparallel-sided in apical half; apex of penis broad and roundly truncate; ventral membrane of penis without a sclerotized patch (similar to *H*. (*P*.) *marginicolle*).

Specimens examined. Type material. Holotype of *Habroloma* (*Parahabroloma*) *asahinai* Kurosawa, 1959: ♂ (based on Kurosawa, 1959; no dissected terminalia), “14.V.1931 / Isakawa / yama / Okinawa” (no collector name) (NSMT).

Non-type material. **Japan**. The Ryukyus: Okinawa Islands — [Okinawajima Is.] 1 ♀, Ôkuni-rindô, Shashiki, Kunigami-son, Kunigami-gun, 21.IV.2017, Y. Tamadera leg. (YTJ). [Yagachijima Is.] 2 exs., Sumuide, Nago-shi, 30.V.2022, Y. Tamadera leg., emerged from *Rubus sieboldii*, 5.VI.2022, rearing no. 2022-035 & 2022-039 (YTJ).

Distributions in Japan. The Ryukyus: Okinawa Isls. (Okinawajima Is. and Yagachijima Is. — new record).

Other distribution. Taiwan.

Adult food plant. Same as in the larvae mentioned below.

Host plants. Rosaceae: *Rubus sieboldii* Blume [Japanese name: Hôroku-ichigo] (Kurosawa, 1976 b — adult record?; confirmed by this study), *R*. *nesiotes* Focke [Japanese name: Kuwanoha-ichigo] (confirmed by this study), and *Rubus* x *utchinensis* Koidz. [Japanese name: Hozaki-ichigo] (confirmed by this study) in Okinawajima Is.

The latter two *Rubus* plants are regarded as hosts of *Habroloma* (*Parahabroloma*) *asahinai* based on only observation in my field survey for the adults, larvae, and leaf-mines at Mt. Fuenchijidake, Kunigami, Okinawajima Is., Japan on May 31th, 2022 (this area is needed permissions to collect insects).

Leaf-mining habit. Mines of *Habroloma* (*Parahabroloma*) *asahinai* were found on *Rubus sieboldii*, *R*. *nesiotes* (eggs, mature larvae, and pupae), and *Rubus* x *utchinensis* (only one egg) by this study (Figs. 105E,F, 108D), but the recognitions of the latter two hosts are only based on the field observation on May 2022 (Mt. Fuenchijidake, Okinawajima Is, Ryukyus) due to no permission for collecting them: each mine was of the full-depth type and formed an irregular blotch occurring usually along leaf-margin; when full-grown, it occupied much less than one quarter half of whole the leaf blade in the *R*. *sieboldii* leaf and much more than half of whole the leaf blade in *R*. *nesiotes* leaf; eggs, which were black (remaining eggshell) and covered on powdery substances, were laid singly on near the leaf-margin on the adaxial surface of the *R*. *sieboldii* leaf and on near the apex of the leaf blade on the adaxial surface of the *R*. *nesiotes* leaf and *Rubus* x *utchinensis* leaf; hatched larvae left granular to thread-like frass inside the mines; adults were usually emerged from the abaxial surface of the *R*. *sieboldii* leaf with oval adult exit holes.

***Habroloma* (*Parahabroloma*) *asahinai* subsp. 1**

[Japanese name: Asahina-hirata-chibi-tamamushi Ishigakijima-ashu]

(Figs. 74G, 99)

Habroloma (*Parahabroloma*) *asahinai* [part]: Kurosawa, 1976 b: 129 (Ishigakijima Is. Ryukus, Japan); 1985 b: 37, pl. 7 (pictorial book); Akiyama & Ohmomo, 1997: 50 (checklist); 2000: 286, pl. 120 (pictorial book); Kubáň, 2006: 417 (Palaearctic catalog); Bellamy, 2008: 2538 (World catalog); Inada & Fukutomi, 2008 (adult food); Ohmomo & Fukutomi, 2013: 172, pl. 55 (pictorial book); Kubáň, 2016: 568 (Palaearctic catalog).

Description. Male and female. Body wedge-shaped, slightly weakly convex dorsally. LB 2.83–2.93 mm (mean 2.87 mm); WB 1.66–1.76 mm (mean 1.70 mm); LB/WB 1.67–1.72 (mean 1.69) (n = 6 for all measurements except terminalia). Habitus as shown in Fig. 74G.

Differs from nominotypical subspecies as follows: body relatively slender, as a result head wider at glance. Ratios of body parts as follows: WC/LC 2.16–3.05 (mean 2.58), WC/LSC 1.74–2.13 (mean 1.97), WP/LP 2.88–3.21 (mean 3.05), BMP/AMP 1.79–1.91 (mean 1.86); LE/WE 1.24–1.33 (mean 1.27), LE/LP 3.51–3.99 (mean 3.80), WTP/LTP 1.28–1.44 (mean 1.37), WTP/BTP 1.41–1.58 (mean 1.46).

Terminala as shown in Fig. 99. Ratios as follows (n = 1 ♂, 1 ♀ for all measurements): SL/SW 1.21, PL/PW 3.85, PbL/PbW 2.07, PeL/PeW 6.75, SlL/SlW 3.50.

Specimens examined. **Japan**. The Ryukyus: Yaeyama Islands — [Ishigakijima Is.] 4 ♂♂, 2 ♀♀, 2 exs., Mt. Omoto-dake, 9.IV.1975, H. Irie leg. (NSMT); 1 ex., same locality, 14.VII.1973, H. Takizawa leg. (SEHU); 1 ♀, Mt. Omotodake, Ishigaki-shi, 23.III.2001, H. Fukutomi leg. (YTJ).

Distributions in Japan. The Ryukyus: Yaeyama Isls. (Ishigakijima Is.).

Other distributions. Unknown.

Adult food plant. Inada & Fukutomi (2008) was recorded *Rubus nesiotes* Focke (as *R*. *swinhoei* Hance) [Japanese-name: Kuwanoha-ichigo] based on the adult feeding behavior. In this study, plant's taxonomic identification of *R*. *nesiotes* from Ishigakijima Is. was followed Ohashi *et al*. (2016).

Host plant. Unknown.

Leaf-mining habit. Unknown.

Habroloma* (*Parahabroloma*) *hikosanense Kurosawa, 1959
[Japanese name: Hikosan-hirata-chibi-tamamushi]
(Figs. 74H, 100)

Habroloma (*Parahabroloma*) *hikosanensis* Kurosawa, 1959: 255 (type locality: "Mt. Hikosan, Fukuoka Pref.", Kyushu, Japan); 1976 a: 3 (note).

Habroloma (*Parahabroloma*) *hikosanense*: Kurosawa, 1985: 37 (noted in pictorial book); Akiyama & Ohmomo, 1997: 51 (checklist); 2000: 286, pl. 120 (pictorial book); Kubáň, 2006: 417 (Palaearctic catalog); Bellamy, 2008 b: 2549 (World catalog); Ohmomo & Fukutomi, 2013: 172, pl. 56 (pictorial book; fig. 216-1 — holotype; fig. 216-2, misidentification); Kubáň, 2016: 569 (Palaearctic catalog).

Description of Holotype. Male (sex determination based on the original description). Body wedge-shaped, moderately convex dorsally (Figs.100A, B). LB 3.40 mm (original description: 3.1 mm); WB 1.96 mm (original description: 1.8 mm); LB/WB 1.73. Habitus as shown in Fig. 74H.

Integument above mainly black, with weak brassy tints, basal half of pronotal lateral margin and elytral basal margin tinged with slightly stronger brass. Underside, antennae, and legs black, except for tarsal pads pale brown. Dorsal and ventral surfaces moderately shiny.

Vestiture mainly consisting of white and brownish-black setae. Head clothed with short, semirecumbent, white setae. Pronotum clothed with short, semirecumbent, white setae, becoming denser apicolaterally, with a few brownish-black setae in median part, pronotal setae more or less missing in median part. Elytra clothed with short, semirecumbent, white and brownish-black setae, elytral setae more or less missing partly, but arranged on each elytron as follows: 1) white setae appearing to occur irregularly in basal half, mixing with brownish-black setae; 2) first white transverse band at just before apical 1/3, moderately wavy; 3) second white transvers band at apical 1/5, rather straight; 4) white setae in apical part; and 5) brownish-black setae in remaining space of apical half. Underside more sparsely setiferous, with fine, recumbent, whitish setae becoming slightly denser in lateral parts of metacoxal plates, prosternal setae more or less lost.

Head, when viewed from above, shallowly concave on frons, with oculofrontal margins strongly sharply ridged and strongly produced anteriorly. Eyes, when viewed from above, narrowly visible, weakly convex laterally, posteiror part hidden beneath pronotum. Vertex coarsely variolate-punctate; frons widely concave, weakly impressed along upper side of midline, with surface coarsely variolate-punctate except upper side around midline; suprantennal pores simply round; clypeus wide (Fig. 100C), with elevated basal margin, WC/LC 2.37 (original description: WC/LC ca. 2.5), WC/LSC 1.97, almost straight at apical margin but faintly arcuately emarginate.

Antennae at rest position, short, right antennae in frontal view missing antenomeres X and XI; antennomere I stout claviform, longer than II; II ovate, longer than III; III subrectangular, slightly longer than IV; IV–VI subrectangular, subequal each other in length; VII–X triangular, moderately enlarged; XI subtriangular.

Pronotum widest at sub-basal part, WP/LP 3.1 (original description: WP/LP ca. 3), BMP/AMP 1.99, slightly narrower than elytra; lateral margins rather subparallel and faintly rounded in basal 1/3, and then straightly, strongly narrowed apicad; apicolateral angles nearly right (angle); basolateral angles sharply acute (angle); apical margin moderately deeply, arcuately emarginate, with faint median lobe; basal margin trisinuate, with median lobe moderately produced; disk depressed laterally, faintly depressed along basal median lobe, with weak basaolateral depressions, with apicolateral depressions bearing round pore on the middle of each; surface rather densely variolate-punctate, sculptures becoming faintly sparse in median part. Scutellar shield small, triangular, slightly irregularly emarginate at apical margin and faintly depressed along midline, shiny, glabrous.

Elytra widest at base, LE/WE 1.31 (original description: LE/WE ca. 1.28), LE/LP 4.07 (original description LE/maximum length of pronotum ca. 3.6); humeral calluses weakly developed, weakly ridged; lateral margins gradually narrowed posteriorly from base to before middle (left elytron) or to middle (right elytron) and faintly constricted between them, then rather straightly, more strongly narrowed to subapical part, and finally strongly arcuately convergent to conjointly rounded apices, serrated with three denticles at subapical part (Fig. 100A); marginal carinae distinct from base to subapical part; sutural margin faintly elevated in about apical 2/3; lateral carinae occurring from near bases of humeri to subapical part, strongly sinuate behind humeral parts; disk moderately depressed along lateral half of basal margin, slightly strongly constricted behind humeri; surface irregularly and sparsely sculptured with shortly, linearly incised punctures.

Underside. Prosternum (Fig. 100D) with arcuate prosternal lobe faintly emarginate at middle of apical margin which is weakly rimmed; prosternal process wide; trapezoidal plate slightly longer than wide, WTP/LTP 1.18 (original description: as long as wide), WTP/BTP 1.50, with rounded apical corners, with sides which are dilated from base to widest point around apical corners and weakly constricted in basal part, with apex broadly, faintly arcuate; disk flattened on trapezoidal plate bearing marginal carinae along sides, evenly convex on prosternal lobe; surface on trapezoidal plate with setiferous pin-prick punctures and obscure ocellate sculptures. Hypomera with large, transversely oval hypomeral markings consisting of linearly incised punctures (Fig. 100E). Metaventrite moderately variolate-punctate on inside of katepisternal suture and moderately variolate on outside of the suture. Legs moderately slender in femora and tibiae, missing the following leg parts in ventral view: in protarsi, right tarsomeres VI and V; in mesotarsi, right tarsomeres unknown and left tarsomeres IV and V; and in metatarsi, right tarsomeres I-V and left tarsomoeres IV and V; metacoxal plates without arcuate notches on medial posterior margins, weakly produced posteriorly at each lateral angle which is broadly acute (angle), with surface moderately variolate; metafemora obtusely angulate at about distal 1/3 of outer margins; metatibiae without a fringe of spines on each outer margin, but very sparsely bearing fine setae throughout; inner tooth of claws on left proleg large. Abdominal ventrites with sternal groove only on ventrite V, of which apex is rounded; surface variolate, in ventrite I with linearly confluent sculptures on median part.

Male terminalia not examined.

Female unknown (Sexual dimorphism unknown).

Differential diagnosis. This species (subspecies) is similar in general appearance to *Habroloma* (*Parahabroloma*) *asahinai*, *H*. (*P*.) *marginicolle*, and *H*. (*P*.) *asahinai* of the species-group III, but is distinguished from them by the combination of the following character states: oculofrontal margins of head in dorsal view distinctly strongly produced anteriorly (slightly similar to *H*. (*P*.) *marginicolle*); lateral margins of pronotum rather subparallel and faintly rounded in basal 1/3, and then straightly, strongly narrowed apicad; lateral margins of elytra faintly constricted between base and middle; lateral carinae of elytra starting from near bases of humeri; prosternal trapezoidal plate with rounded apical corners and with sides which are weakly constricted in basal part (similar to *H*. (*P*.) *subbicorne*); surface of prosternal trapezoidal plate with obscure ocellate sculptures.

Specimens examined. Type material. Holotype of Habroloma (Parahabroloma) hikosanense Kurosawa, 1959: ♂ (based on Kurosawa, 1959; no dissected terminalia), "[Kyushu / Hikosan / (Buzen) / V.23.1950 / A. Habu" (NSMT).

Distributions in Japan. Kyushu.

Other distribution. Unknown.

Adult food plant. Unknown.

Host plant. Unknown.

Leaf-mining habit. Unknown.

***Habroloma* (*Parahabroloma*) sp. 1**

[Japanese name: Kobammochi-hirata-chibi-tamamushi]

(Figs. 75, 101, 102, 105G, 109)

Description. Male and female. Body wedge-shaped, slightly weakly convex dorsally (Figs. 101A, B). LB 3.22–3.41 mm (mean 3.29 mm); WB 1.87–2.02 mm (mean 1.93 mm); LB/WB 1.69–1.72 (mean 1.71) (n = 3 for all measurements except terminalia). Habitus as shown in Fig. 75.

Integument above black, with weak golden-bronze reflections; head sometimes with strong brassy tints from lower side of frons to clypeus; underside, antennae, and legs black, sometimes with weak golden-bronze reflections, except for tarsal pads pale brown. Dorsal and ventral surfaces moderately shiny.

Vestiture mainly consisting of white, pale yellow, brown, and black setae. Head clothed with short, recumbent, pale yellow setae, but upper side of frons medially naked, with inconspicuous brown spots on vertex. Pronotum predominantly clothed with short, semirecumbent, pale yellow setae, forming a median stripe, with black patches across middle, with a few brown setae occurring around black bands. Elytra clothed with short, semirecumbent, pale yellow to white, pale brown, and black setae which are arranged on each elytron as follows: 1) pale yellow to white setae occurring along basal margin, sutural margin, and lateral carina throughout and in apical part, mixing with a few pale brown setae, each of white setae zone becoming denser; 2) inconspicuous undulated pale yellow to white band just before middle, obscurely connected with pale yellow pattern on basal margin, each of white setae zone becoming denser; 3) first pale yellow to white transverse band at near apical 1/3, strongly wavy from just behind middle to apical 1/3, each of white setae zone becoming denser; 4) second pale yellow to white transverse band at subapical part, rather straight, thicker than the first transverse band, each of white setae zone becoming denser; 5) pale brown setae occurring just behind second transverse band; 6) black setae in remaining space. Underside more sparsely setiferous, with fine, recumbent, yellowish setae.

Head, when viewed from above, shallowly concave on frons with a small incision at middle, with oculofrontal margins ridged and very weakly produced anteriorly. Eyes, when viewed from above, slightly broadly visible, moderately convex laterally. Vertex coarsely variolate-punctate; frons widely concave, weakly impressed along upper side of midline, with surface coarsely variolate-punctate except upper side around midline; suprantennal pores transvesely oval; clypeus distinctly wide (Fig. 101D), with elevated basal margin, WC/LC 2.78–2.99 (mean 2.91), WC/LSC 2.40–2.60 (mean 2.48), weakly arcuately emarginate at apical margin, of which middle becoming almost straight.

Antennae (Fig. 101E, F) slightly long or moderately short, in male distinctly beyond level of pronotal widest point when laid laterally, while in female just reaching or slightly beyond; antennomere I stout claviform, longer than II; II ovate, longer than III; III subrectangular, slightly longer than IV; IV–VI subrectangular, subequal each other in length; VII–X triangular, more strongly enlarged in male than in female, VII largest in triangular antennomeres; XI weakly elongate triangular.

Pronotum widest at sub-basal part, WP/LP 3.16–3.32 (mean 3.22), BMP/AMP 1.66–1.75 (mean 1.71), usually slightly wider than elytra, but occasionally almost same as elytral width; lateral margins arcuately, weakly narrowed anteriorly from widest point to apical 1/3 and then more strongly narrowed apicad; apicolateral angles broadly acute to nearly right (angle); basolateral angles sharply acute (angle); apical margin moderately deeply, arcuately emarginate, with inconspicuous, faint median lobe which is almost straight line at glance; basal margin trisinuate, with median lobe moderately produced; disk depressed laterally, weakly depressed along basal median lobe, with ill-defined basaolateral and apicolateral depressions, without pores in the apicolateral depressions; surface rather densely variolate-punctate throughout. Scutellar shield small, triangular, glabrous.

Elytra widest at base, LE/WE 1.26–1.28 (mean 1.27), LE/LP 3.98–4.17 (mean 4.04); humeral calluses weakly developed; lateral margins gradually narrowed posteriorly from base to middle, then more strongly, faintly arcuately narrowed to subapical part, and finally arcuately convergent to conjointly rounded apices, serrated with three to four denticles at subapical part (Fig. 101C); marginal carinae distinct from base to subapical part lateral carinae occurring from just behind humeri to subapical part, strongly sinuate behind basal parts; disk moderately depressed along lateral half of basal margin, weakly constricted behind humeri; surface irregularly and sparsely sculptured with shortly, linearly incised punctures.

Underside. Prosternum (Fig. 101G) with arcuate prosternal lobe sometimes weakly emarginate at apical margin which is faintly rimmed; prosternal process wide; trapezoidal plate wider than long, WTP/LTP 1.34–1.36 (mean 1.35), WTP/BTP 1.33–1.72 (mean 1.53), with obtusely angulate apical corners, with sides which are dilated apicad in rather straight line, with apex broadly, faintly arcuate; disk flattened on trapezoidal plate bearing marginal carinae along sides, evenly convex on prosternal lobe; surface on trapezoidal plate with setiferous pin-prick punctures and ocellate sculptures. Hypomera with large, rather round hypomeral markings consisting of linearly incised punctures (Fig. 101H), sparsely setiferous only in anterior side of hypromeral markings. Metaventrite moderately variolate-punctate on inside of katepisternal suture and more densely variolate on outside of the suture. Legs stout in femora and tibiae; metacoxal plates without arcuate notches on medial posterior margins, weakly produced posteriorly at each lateral angle which is broadly acute (angle), with surface moderately variolate; metafemora obtusely angulate at about distal 1/3 of outer margins; metatibiae without a fringe of spines on each outer margin (Fig. 101I), but very sparsely bearing fine setae throughout; inner tooth of each claw large. Abdominal ventrites with sternal groove only on ventrite V, of which apex is rounded; surface variolate, in ventrite I with linearly confluent sculptures on median part.

Sexual dimorphism distinctly recognized in the relative size of antennae.

Male terminalia (n = 1 for all measurements). Proctiger with a pair of short baculi at base. Sternite IX (Fig. 102A) wide, SL/SW 0.73, weakly emarginate at apical margin, without setae. Tegmen (Fig. 102B) slightly wide; parameres PL/PW 2.78, bearing a pair of short setae on apicolateral margins, with sides which are gently dilated from base to beyond middle, then subparallel to subapical part, and finally weakly arcuately, strongly convergent apicad; phallobase PbL/PbW 1.49, about 1/4 length of tegmen. Penis (Fig. 102C) wide, PeL/PeW 4.26, shorter than tegmen; dorsal plate with sides (not including sides of median struts) which are subparallel but faintly narrowed from base to middle, and then slightly arcuately, weakly convergent to broadly rounded apex, basally with median struts about 1/2 length of penis; ventral membrane without sclerotized part, with finely tuberculate part in apical half.

Female terminalia (n = 1 for all measurements). Ovipositor (Figs. 102D, E) short. Proctiger with a pair of short, straight baculi at base; coxites transversely subtrapezoidal, sparsely setiferous on each side of apical margin; styli short, slightly wide, SlL/SlW 3.25, bearing several setae apically; ventral valve without setae; vagina sack-shaped (under incompletely inflated state); spermatheca wide tubular, slightly short in length, widest in apical part.

Differential diagnosis. This species is slightly similar to other congeners of the species-group III in the patterns of setae on dorsum, but is readily distinguished from them by the following character states: oculofrontal margins of head very weakly produced anteriorly; head distinctly wide; lateral margins of pronotum arcuately, weakly narrowed anteriorly from widest point to apical 1/3 and then more strongly narrowed apicad; lateral margins of elytra not constricted between base and middle (similar to *H.* (*P.*) *subbicorne*); lateral carinae of elytra starting from just behind humeri (similar to *H.* (*P.*) *subbicorne*, *H.* (*P.*) *marginicolle*, and *H.* (*P.*) *asahinai*); prosternal trapezoidal plate with obtusely angulate apical corners and with sides which are dilated apicad in rather straight line (similar to *H.* (*P.*) *marginicolle*); surface of prosternal trapezoidal plate with ocellate sculptures; male penis (dorsal plate) rather subparallel-sided; apex of penis broadly rounded; ventral membrane of penis with finely tuberculate part in apical half; and female spermatheca wide tubular.

Specimens examined. [Saga] 10 ♂♂, 11 ♀♀, Arita Dam, Mt. Kurokami-yama, Arita-chô, Nishi-matsuura-gun, 20.VIII.2020, M. Nishida leg. (YTJ). [Ôita] 2 ♂♂, Ume, Saiki-shi, 4.X.2020, Y. Tsutsumiuchi leg. (YTJ); 1 ex., Aoyama, Saiki-shi, 6.VII.2021, Y. Tamadera leg., emerged from *Elaeocarpus japonicus*, 15.VII.2021, rearing no. 2021-099 (YTJ); 1 ex., same locality, 8.VII.2021, Y. Tamadera leg., emerged from *E. japonicus*, 17.VII.2021, rearing no. 2021-103 (YTJ). The Ryukyus: Ôsumi Islands — [Yakushima Is.] 1 ♀, Nagata-issô-rindô, Yakushima-chô, 4.VIII.2019, T. Saeki leg. (YTJ); 1 ♀, Koseda-rindô, Koseda, Yakushima-chô, 11.VII.2020, T. Saeki leg. (YTJ); 2 exs., ditto, emerged from *E. japonicus*, 23.VII.2020, rearing no. 2020-084 (YTJ); 1 ex., ditto, emerged from *E. japonicus*, 25.VII.2020, rearing no. 2020-085 (YTJ); 1 ex., Yudomari, Yakushima-chô, 25.X.2019, W. Yamada leg. (WYCA).

Distributions in Japan. Kyushu and the Ryukyus: Ôsumi Isls. (Yakushima Is.).

Other distribution. Unknown.

Adult food plant. Same as in the larvae mentioned below.

Host plant. Elaeocarpaceae: *Elaeocarpus japonicus* Siebold et Zucc. [Japanese name: Kobammochi] (confirmed by this study).

Leaf-mining habit. Mines of *Habroloma* (*Parahabroloma*) sp. 1 were found on *Elaeocarpus japonicus* by this study (Figs. 105G, 109): each mine was of the upper surface type and formed a broadly linear blotch occurring one side of the leaf blade divided by the midrib; when full-grown, it occupied less than half of whole the leaf blade and its leaf usually found on the ground (Fig. 105G); eggs, which were black (remaining eggshell) and covered on powdery substances, were laid singly on the base of leaf blade on the adaxial surface; hatched larvae mined toward the leaf apex, and then usually make an U-turn after becoming the three instar (final), left zigzag-shaped to coiled frass smeared on inner side of the adaxial surface; the side of the leaf blade mined by the larva was somewhat kept green color in longer time, whereas the other side more early became red color, especially prominent in the abaxial surface — it may suggest that the larvae secrete something chemical substances to prevent the deterioration of leaf tissues, for example cytokinin in saliva and in frass reported in leaf-mining moths (Engelbrecht, 1971) ; adults were usually emerged from the adaxial surface of the leaves with oval adult exit holes.

Removed species from the Japanese buprestid fauna

Habroloma* (*Parahabroloma*) *atronitidum (Gebhardt, 1929)
[Japanese name: Hime-hirata-chibi-tamamushi]

Trachys (*Habroloma*) *atronitida* Gebhardt, 1929: 98 (type locality: "China: Chekiang"); Obenberger, 1937 a: 1410 (World catalog).
Habroloma atronitida: Obenberger, 1958: 241 (Yunnan, China).
Habroloma (*Parahabroloma*) *atronitidum*: Kurosawa, 1976 b: 131 (designated lectotype, preserved in National Museum, Prague); Kubáň, 2006: 417 (Palaearctic catalog); Kubáň, 2016: 568 (Palaearctic catalog).
Habroloma (*Habroloma* [sic]) *atronitidum*: Bellamy, 2008 b: 2538 (*lapsus calami*; World catalog).

The identifications of the following references are regarded as *Habroloma* (*Parahabroloma*) *subbicorne* in this study:
Habroloma (*Parahabroloma*) *kagoshimana* [sic] [non Obenberger, 1940]: Kurosawa,

1959: 250 (misidentification; misspelling of *kagosimana*, corrected by Kurosawa, 1976 b: 131).

Habroloma (*Parahabroloma*) sp.: Kurosawa, 1976 a: 5 (note; Japan).

Habroloma (*Parahabroloma*) *atronitidum* [non Gebhardt]: Kurosawa, 1985 b: 37 (misidentificatiron of *H.* (*P.*) *subbicorne*; noted in pictorial book); Akiyama & Ohmomo, 1997: 50; 2000: 286, pl. 120; Ohmomo & Fukutomi, 2013: 172, pl. 56.

Distributions. China.

Adult food plant. Unknown.

Host plant. Unknown.

Leaf-mining habit. Unknown.

Note. Records of this species from Japan (e.g. Kurosawa, 1959, 1976b; Ohmomo, 1981, 2018; Yoshitake *et al*., 2018) are removed in this study because the adult morphological states of *H.* (*P.*) *atronitidum* from Japan is well recognized within the intraspecific variations of *H.* (*P.*) *subbicorne*. Thus, this study at least regards Japanese *H.* (*P.*) *atronitidum*, identified by previously studies, as *H.* (*P.*) *subbicorne*.

Key to the Japanese subgenera, species, and subspecies of the genus *Habroloma*

1. Pronotum distinctly depressed in apicolateral part, with a large fovea on each the depression. When viewed from above, oculofrontal margins of head not produced anteriorly. … Subgenus ***Habroloma*** Thomson — ***H.* (*H.*) *bifrons*** Kiesenwetter, 1879

–. Pronotum more or less depressed in apicolateral part, with or without round pore on each the depression. When viewed from above, oculofrontal margins of head more or less ridged and produced anteriorly. … 2. Subgenus ***Parahabroloma*** Kurosawa.

2. Using genital morphology for determination of species-groups. … 3 (2-A)

–. Not using genital morphology (no determination of species-groups). … 15 (2-B)

2-A. Using genital morphology for determination of species-groups

3. Metacoxal plates with arcuate notches at medial posterior margins. [Group I] …5

–. Metacoxal plates without arcuate notches at medial posterior margins. … 4

4. Male penis prominently slender and elongate in dorsal plate, distinctly wider in ventral membrane than in dorsal plate. Female spermatheca distinctly long. [Group II] … 8

–. Male penis moderate width in dorsal plate, in ventral membrane almost as wide as in dorsal plate. Female spermatheca moderate length. [Group III] … 10

Group I

5. Post-scutellar part of elytra with a large, reddish-brown or orange to yellow triangular mark (e.g. Fig. 73B). Body well convex dorsally (e.g. Fig. 78B). Clypeus subparallel-sided (e.g. Fig. 78D). Pronotum without round pores on apicolateral depressions (Fig. 78A). … 6

–. Post-scutellar part of elytra without a large triangular mark (Fig. 73E). Body weakly convex dorsally (Fig. 83B). Clypeus divergent apicad (Fig. 83D). Pronotum with round pores on apicolateral depressions (Fig. 83A). Terminalia as shown in Fig. 84.
… ***H.* (*P.*) *griseonigrum*** (Saunders, 1873)

6. Oculofrontal margins of head moderately produced anteriorly (Fig. 73B). Terminalia as shown in Fig. 80. … ***H.* (*P.*) *eximium eximium*** (Lewis, 1893)

–. Oculofrontal margins of head weakly produced anteriorly (Figs. 73C, D). … 7

7. Relative size of body slightly larger. Post-scutellar triangular mark of elytra distinct (Fig. 79C–G). (Distribution: Yaeyama Isls. in the Ryukyus and Taiwan.)
… ***H.* (*P.*) *eximium eupoetum*** (Obenberger, 1929)

–. Relative size of body slightly smaller. Post-scutellar triangular mark of elytra usually indistinct (Fig. 79H–I). (Distribution: Amami Isls. and Okinawa Isls. in the Ryukyus.)
… ***H.* (*P.*) *eximium* subsp. 1** (= *liukiuense* sensu Kurosawa, 1976 b)

Group II

8. Elytral integument with two large, blue to purple marks in about basal 2/3 (Fig. 74A). Terminalia as shown in Fig. 86. … ***H.* (*P.*) *lewisii*** (Saunders, 1873).

–. Elytral integument without them, dark brass to dark bronze throughout (Fig. X). … 9

9. Body oval (Fig. 74B). Prosternal trapezoidal plate distinctly longer than wide (Fig. 87F). Terminalia as shown in Fig. 88. … ***H.* (*P.*) *nixilla inslicola*** Kurosawa, 1959

–. Body wedge-shaped (Fig. 74C). Prosternal trapezoidal plate almost as wide as long at glance (Fig. 89G). Terminalia as shown in Fig. 90. … ***H.* (*P.*) *yuasai*** Kurosawa, 1976

Group III

10. Oculofrontal margins of head moderately to strongly produced anteriorly (Fig. 74D–H). Clypeus moderately wider than long. Prosternal trapezoidal plate with or without ocellate sculptures on surface. … 11

–. Oculofrontal margins of head prominently weakly produced anteriorly (Fig. 75A). Clypeus distinctly much wider than long (Fig. 101D). Prosternal trapezoidal plate with ocellate sculptures on surface. Terminalia as shown in Fig. 102.
… ***Habroloma* (*Parahabroloma*) sp. 1**

11. Prosternal trapezoidal plate without ocellate sculptures on surface, nearly as wide as

long at glance. … 12

–. Prosternal trapezoidal plate with ocellate sculptures on surface, wider than long. … 13

12. Oculofrontal margins of head sharply, strongly produced anteriorly (Fig. 74H). Lateral margins of pronotum subparallel in basal 1/3. Lateral carinae of elytra starting from near bases of humeri (Fig. 100A). … ***H.* (*P.*) *hikosanense*** Kurosawa, 1959

–. Oculofrontal margins of head slightly weakly to moderately produced anteriorly (Figs. 74D, 92). Lateral margins of pronotum usually evenly arcuate. Lateral carinae of elytra starting from just behind humeri. Terminalia as shown in Figs. 93, 94.
… ***H.* (*P.*) *subbicorne*** (Motschulsky, 1860)

13. Body roundly wedge-shaped (Fig. 74E). Oculofrontal margins of head sharply, strongly produced anteriorly (Fig. 95A). Pronotum slightly narrower than elytra. Lateral margins of pronotum rather evenly arcuately narrowed apicad. Terminalia as shown in Fig. 96. … ***H.* (*P.*) *marginicolle*** (Fairmire, 1888)

–. Body wedge-shaped (Fig. 74F, G). Oculofrontal margins of head moderately produced anteriorly. Pronotum slightly wider than elytra. Lateral margins of pronotum rather subparallel and somewhat rounded in basal 1/3 then strongly narrowed apicad. … 14

–. Body narrower in width (head narrower at a glance). (Distribution: Okinawajima Is. and Yagachijima Is. in the Ryukyus.) … ***H.* (*P.*) *asahinai asahinai*** Kurosawa, 1959

–. Body wider in width (head wider at a glance). (Distribution: Ishigakijima Is. in the Ryukyus.) … ***H.* (*P.*) *asahinai* subsp. 1**

2-B. Not using genital morphology (no determination of species-groups)

15. Metacoxal plates with arcuate notches at medial posterior margins. … 16

–. Metacoxal plates without arcuate notches at medial posterior margins. … 19

16. Post-scutellar part of elytra with a large, reddish-brown or orange to yellow triangular mark (e.g. Fig. 73B). Body well convex dorsally (e.g. Fig. 78B). Clypeus subparallel-sided (e.g. Fig. 78D). Pronotum without round pores on apicolateral depressions. … 17

–. Post-scutellar part of elytra without a large triangular mark (Fig. 73E). Body weakly convex dorsally (Fig. 83B). Clypeus divergent apicad (Fig. 83D). Pronotum with round pores on apicolateral depressions (Fig. 83A).
… ***H.* (*P.*) *griseonigrum*** (Saunders, 1873)

17. Oculofrontal margins of head moderately produced anteriorly (Fig. 73B).
… ***H.* (*P.*) *eximium eximium*** (Lewis, 1893)

–. Oculofrontal margins of head weakly produced anteriorly (Fig. 73C, D). … 18

18. Relative size of body slightly larger. Post-scutellar triangular mark of elytra distinct (Fig. 79C–G). (Distribution: Yaeyama Isls. in the Ryukyus and Taiwan.)

… ***H.* (*P.*) *eximium eupoetum*** (Obenberger, 1929)

–. Relative size of body slightly smaller. Post-scutellar triangular mark of elytra usually indistinct (Fig. 79H–J). (Distribution: Amami Isls. and Okinawa Isls. in the Ryukyus.) … ***H.* (*P.*) *eximium* subsp. 1** (= *liukiuense* sensu Kurosawa, 1976 b)

19. Elytral integument with two large, blue to purple marks in about basal 2/3(Fig. 74A). … ***H.* (*P.*) *lewisii*** (Saunders, 1873).

–. Elytral integument black, dark brass, or dark bronze, without two large, blue to purple marks in about basal 2/3. … 20

20. Body oval (Fig. 74B). Prosternal trapezoidal plate distinctly longer than wide (Fig. 87F). … ***H.* (*P.*) *nixilla inslicola*** Kurosawa, 1959

–. Body wedge-shaped to roundly wedge-shaped. Prosternal trapezoidal plate wider than long or almost as wide as long at glance. … 21

21. Prosternal trapezoidal plate without ocellate sculptures on surface, nearly as wide as long at glance. … 22

–. Prosternal trapezoidal plate with ocellate sculptures on surface, wider than long. … 24

22. Oculofrontal margins of head sharply, strongly produced anteriorly (Fig. 74H). Lateral margins of pronotum subparallel in basal 1/3. Lateral carinae of elytra starting from near bases of humeri (Fig. 100A). … ***H.* (*P.*) *hikosanense*** Kurosawa, 1959

–. Oculofrontal margins of head slightly weakly to moderately produced anteriorly. Lateral margins of pronotum usually, evenly arcuately narrowed apicad. Lateral carinae of elytra starting from behind bases of humeri or from just behind humeri. … 23

23. Lateral carinae of elytra starting from near bases of humeri (Fig. 89A). Prosternal trapezoidal plate faintly narrower (Fig. 89G). Integument above black, but tend to be tinged with slightly stronger golden-bronze. Terminalia as shown in Fig. 90 (most reliable character). … ***H.* (*P.*) *yuasai*** Kurosawa, 1976

–. Lateral carinae of elytra starting from just behind humeri (Fig. 91A). Prosternal trapezoidal plate faintly wider (Fig. 91G). Integument above black, usually with weaker golden-bronze reflections. Terminalia as shown in Figs. 93, 94 (most reliable character). … ***H.* (*P.*) *subbicorne*** (Motschulsky, 1860)

24. Oculofrontal margins of head prominently weakly produced anteriorly (Fig. 75A). Clypeus distinctly much wider than long (Fig. 101D).
… ***Habroloma* (*Parahabroloma*) sp. 1**

–. Oculofrontal margins of head moderately to strongly produced anteriorly. Clypeus moderately wider than long. … 25

25. Body roundly wedge-shaped (Fig. 74E). Oculofrontal margins of head sharply, strongly produced anteriorly. Pronotum slightly narrower than elytra (Fig. 95A).

Lateral margins of pronotum rather evenly arcuately narrowed apicad. … ***H.* (*P.*) *marginicolle*** (Fairmire, 1888)

–. Body wedge-shaped (Fig. 74F). Oculofrontal margins of head moderately produced anteriorly. Pronotum slightly wider than elytra (Fig. 97A). Lateral margins of pronotum rather subparallel and somewhat rounded in basal 1/3 then strongly narrowed apicad. … 26

26. Body narrower in width (head narrower at a glance). (Distribution: Okinawajima Is. in the Ryukyus.) … ***H.* (*P.*) *asahinai asahinai*** Kurosawa, 1959

–. Body wider in width (head wider at a glance). (Distribution: Ishigakijima Is. in the Ryukyus.) … ***H.* (*P.*) *asahinai* subsp. 1**

Host associations of Japanese *Habroloma*

Eleven species of Japanese *Habroloma* is associated with various eudicot plants including six families in five orders (see below the host list). All of Japanese species show the monophagous diet breadth (defined as using a single plant genus) except two host unknown species. Among them, the specialist (defined as using a single plant species) is recognized in four species. Although host information of *Habroloma* is extremely poor, other diet breadth, oligophagy and polyphagy, are rarely found in other regions (Bílý, 2003; Niehuis, 2004; Verdugo, 2005). For example, *H.* (*H.*) *triangulare* (Lacordire, 1835) is polyphagous (Geraniaceae, Rosaceae, and Lamiaceae). Japanese *Habroloma* at least shows stronger preferences in host associations than those of Japanese *Trachys* (see the correspondence section).

Host list for Japanese *Habroloma*

Host plant — Japanese *Habroloma* [diet breadth; species-groups]

Elaeocarpaceae (Malvales)

Elaeocarpus …………… *H.* (*Parahabroloma*) sp. 1 [monophagy (specialist); III]

Fagaceae (Fagales)

Quercus …………… *H.* (*P.*) *griseonigrum* [monophagy; I]

Juglandaceae (Fagales)

Platycarya …………… *H.* (*P.*) *yuasai* [monophagy (specialist); II]

Lythraceae (Myrtales)

Lagerstroemia …………… *H.* (*P.*) *nixilla inslicola* [monophagy (specialist); II]

Rosaceae (Rosales)

Rubus	…………… *H.* (*P.*) *asahinai asahinai* [monophagy; III]
	…………… *H.* (*P.*) *asahinai* subsp. 1 [monophagy; III] (adult food)
	…………… *H.* (*P.*) *marginicolle* [monophagy; III]
	…………… *H.* (*P.*) *subbicorne* [monophagy; III]
Rosa	…………… *H.* (*P.*) *lewisii* [monophagy (specialist); II]

Symplocaceae (Ericales)

Symplocos	…………… *H.* (*P.*) *eximium eupoetum* [monophagy; I] (adult food)
	…………… *H.* (*P.*) *eximium eximum* [monophagy; I]
	…………… *H.* (*P.*) *eximium* subsp. 1 [monophagy; I]

Unknown	…………… *H.* (*H.*) *bifrons*
	…………… *H.* (*P.*) *hikosanense* [III]

Chapter 4.

Phylogenetic relationships and host associations

In this chapter, cladistic analyses for the generic relationships of the tribe Tracheini and species relationships of Japanese and Taiwanese *Trachys* and *Habroloma* were conducted, respectively.

Exemplars and characters

Each cladistic analysis used the following exemplars and characters:

Exemplars for generic relationships of Tracheini. The tribe Tracheini consists of twelve genera in four subtribes (Bellamy, 2008 b; Hespenheide, 2014; Migliore *et al*., 2020 a). Among them, nine genera are only distributed in the Nearctic and Neotropical Regions. Unfortunately, it was very difficult to prepare specimens of all the genera of Tracheini. In this study, exemplars for the analysis were selected at least one taxon from each subtribe. This analysis is to reveal and assess diagnostic character states for the genera *Trachys* and *Habroloma* mentioned in the chapter 3 of this study and is a preliminary one to reveal phylogenetic relationships in future studies based on comprehensive taxa including other tribes of subfamily Agrilinae. In some exemplars, character information was also selected from descriptions and illustrations in literatures. Outgroups were selected from the subfamily Buprestinae, regarded as a sister group of Agrilinae based on a molecular study (Evans *et al*., 2015), and from other tribes of Agrilinae (Agrilini — genus *Agrilus*; Coraebini — genus *Coraebus*; and Aphanisticini — genera *Aphanisticus* and *Endelus* in subtribe Aphanisticina and genus *Paracylindromorphus* in subtribe Paracylindromorphina). The tribe Aphanisticini is regarded as a sister group of Tracheini (Hołyński, 1993; Bellamy, 2003, 2008 b) or the same group (subfamily Trachyinae *sensu* Cobos, 1979), so that multiple exemplars were selected. Among the outgroup exemplars, *Buprestis* (*Ancylocheira*) *haemorrhoidalis arakii* was used to root the tree. Examined specimen data for this analysis are shown in Appendix 1 (except Japanese *Trachys* and *Habroloma*).

Characters for generic relationships of Tracheini. The analysis used fifty-two adult morphological characters mentioned below, nine of which were multistate and the remainders were binary. Generally, uninformative characters should be excluded from the matrix, but the analysis used the matrix included 14 uninformative ones because one of the aims of this analysis is to show the potentially useful morphological information for future studies. Character length (L), consistency index (CI), and retention index (RI) calculated using WinClada version 1.00.08 (Nixon, 2002) are also indicated below.

Head

1. Condyle-shaped part of postocciput (attaching with cervical sclerites): [0] absent; [1] present. L = 1; CI = 1; RI = 1.
2. Ocular grooves: [0] absent; [1] present, along inner margins of eyes throughout; [2] present, only along upper side of inner margins of eyes; [3] present, only along lower side of inner margins of eyes. L = 11; CI = 0.27; RI = 0.55.
3. Suprantennal pores: [0] absent; [1] present, simple; [2] present, into grooves. L = 3; CI = 0.66; RI = 0.50.
4. Frontoclypeal median pore: [0] absent; [1] present. L = 2; CI = 0.50; RI = 0.50.
5. Inner ocular pores (Migliore *et al*., 2020 a): [0] absent; [1] present. L = 3; CI = 0.33; RI = 0.33.
6. Outer ocular pores (Migliore *et al*., 2020 a): [0] absent; [1] present. L = 2; CI = 0.50; RI = 0.
7. Pores at near proximal end of subantennal grooves: [0] absent; [1] present. L = 2; CI = 0.50; RI = 0.50.
8. Gulamentum (submentum in a strict sense): [0] longer than mentum; [1] almost as long as mentum; [2] much shorter than mentum. L = 3; CI = 0.66; RI = 0.
9. Corpotentorium (tentorial bridge): [0] present; [1] absent. L = 1; uninformative.
10. Antennae: [0] dilated from antennomere IV (with sensorial fovea or field); [1] dilated from antennomere V; [2] dilated from antennomere VI (with sensorial fovea or field); [3] dilated from antennomere VII (with sensorial fovea or field); [4] dilated from antennomere VIII (with sensorial fovea or field). L = 5; CI = 0.80; RI = 0.90.
11. Mandibular hole: [0] absent; [1] present. L = 3; CI = 0.33; RI = 0.50.
12. Delimitation of basistipes and palpifer: [0] distinct; [1] reduced. L = 1; CI = 1; RI = 1.
13. Laciniae: [0] developed; [1] reduced. L = 1; uninformative.

Thorax

14. Submarginal carinae on hypomera: [0] absent; [1] present. L = 1; uninformative. (For *Agrilus*.)
15. Antennal grooves on hypomera: [0] absent; [1] present. L = 3; CI = 0.33; RI = 0.50.
16. Hypomeral marking: [0] absent: [1] present. L = 1; CI = 1; RI = 1.

17. Prosternal lobe: [0] absent; [1] present. L = 3; CI = 0.33; RI = 0.33.
18. Marginal carinae of prosternum: [0] absent; [1] present. L = 1; CI = 1; RI = 1.
19. Disk of prosternum: [0] without transverse grooves above procoxal cavities; [1] with transverse grooves above procoxal cavities. L = 1; CI = 1; RI = 1.
20. Median depression on prosternum: [0] absent; [1] present. L = 1; uninformative. (For *Brachys*.)
21. Scutellar shield: [0] small to moderate in size, much narrower to slightly wider than half width of mesonotum; [1] large in size, far wider than half width of mesonotum. L = 1; uninformative.
22. Boundary suture between mesanepisternum and mesepimeron: [0] present; [1] absent. L = 3; CI = 0.33; RI = 0.66.
23. Separation of mesoventrite from mesanepisternum and mesepimeron: [0] present; [1] absent. L = 1; CI = 1; RI = 1.
24. Depressions on thorax for receiving legs: [0] absent; [1] present. L = 1; uninformative.
25. Metepimeron: [0] partly exposed; [1] completely concealed. L = 1; CI = 1; RI = 1.

Elytra

26. Lateral carinae on elytra: [0] absent; [1] present. L = 2; CI = 0.50; RI = 0.50.
27. Epipleura: [0] distinct from humeral angles to near apices; [1] distinct only in thoracic region. L = 2; CI = 0.50; RI = 0.66.
28. Marginal carina on elytra: [0] distinct from humeral angles to near apices; [1] distinct only in thoracic region. L = 2; CI = 0.50; RI = 0.66.

Hind wing

29. 3rd axillary sclerite: [0] not elongated in distal process; [1] elongated in distal process. L = 1; uninformative.
30. Anal field: [0] present; [1] absent. L = 2; CI = 0.50; RI = 0.66.
31. Radial cell: [0] present, closed; [1] present, proximally opened; [2] present, distally opened; [3] absent. L = 7; CI = 0.42; RI = 0.60.
32. Wedge cell: [0] present; [1] absent. L = 1; CI = 1; RI = 1.
33. First cubito-anal cell: [0] present; [1] absent. L = 2; CI = 0.50; RI = 0.75.

Leg

34. Inner margin of each femur: [0] not expanded to conceal tibia beneath at rest; [1] expanded to conceal tibia beneath at rest. L = 2; CI = 0.50; RI = 0.50.
35. Tibia: [0] simple; [1] laterally expanded and dorsally flattened to receive tarsi on dorsal side. L = 1; uninformative.
36. Tibial spurs on metaleg: [0] present; [1] absent. L = 1; CI = 1; RI = 1.
37. A pair of claws on each leg: [0] symmetrical; [1] asymmetrical. L = 1; uninformative.

38. Claws: [0] without inner tooth; [1] with inner tooth. L = 2; CI = 0.50; RI = 0.50.
39. A fringe of spines on outer margin of each metatibia: [0] absent; [1] present. L = 2; CI = 0.50; RI = 0.50.

Abdomen

40. Lateral sternal process: [0] concealed by elytral epipleura (invisible); [1] more or less exposed (visible). L = 4; CI = 0.25; RI = 0.25.
41. Sub-grooves between abdominal intercoxal process and metacoxal plates for receiving metatarsi at rest: [0] absent; [1] present. L = 1; CI = 1; RI = 1.
42. Sternal grooves: [0] absent; [1] present, on ventrites I–V; [2] present, on ventrites II–V; [3] present, only on ventrite V. L = 10; CI = 0.30; RI = 0.36.
43. Sternal grooves: [0] simple grooves; [1] partly modified as "ostia" (Jendek, 2001). L = 1; uninformative.
44. Outside area of sternal groove on ventrite V: [0] not enlarged; [1] enlarged posteriorly. L = 1; uninformative.
45. Sternal cuticuralia: [0] on sternites IV–VI (ventrite II–IV); [1] on sternite IV and V (ventrites II and III); [2] on sternite IV (ventrite II). L = 5; CI = 0.40; RI = 0.40.
46. Delimitation of laterosternites: [0] absent; [1] present. L = 1; uninformative.
47. Laterosternal sulci: [0] absent; [1] present on laterosternite I–IV; [2] present on laterosternites I–V; [3] present on laterosternite I–VI; [4] present on laterosternite I–VII. L = 9; CI = 0.44; RI = 0.54.

Male terminalia

48. Paraproct (tergite IX) and epiproct (tergite X): [0] more or less separated; [1] fused with each other (forming proctiger). L = 2; CI = 0.50; RI = 0.
49. Penis: [0] movable; [1] unmovable (completely fixed with parameres). L = 1; uninformative.

Female terminalia

50. Paraproct and epiproct: [0] more or less separated; [1] fused with each other (forming proctiger) L = 1; uninformative.
51. Valvifers: [0] present (independent); [1] fused with paraproct (proctiger) baculi (formed ventrally curved baculi); [2] unpigmented (almost membranous). L = 3; CI = 0.66; RI = 0.50.
52. Dorsal projections of coxite baculi: [0] absent; [1] present. L = 1; CI = 1; RI = 1.

***Exemplars for species relationships of Japanese* Trachys.** Nineteen *Trachys* species recognized in the chapter 3 of this study were included in the analysis. In addition, nine Taiwanese species are added to investigate true sister species for each Japanese species. Several outgroup exemplars (genera *Habaroloma*, *Ahanisticus*, and *Endelus*) were selected. Among the outgroup exemplars, *Endelus collaris kerremansi* was used to root the tree. Examined specimen data for this analysis are shown in Appendix 2 (except Japanese species).

***Characters for species relationships of Japanese* Trachys**. The analysis used fifty adult morphological characters listed below, ten of which were multistate and the remainders were binary. Character length (L), consistency index (CI), and retention index (RI) calculated using WinClada version 1.00.08 (Nixon, 2002) are also indicated below.

Body

1. Body shape in dorsal view: [0] narrowly to broadly ovate; [1] wedge-shaped. L = 3; CI = 0.33; RI = 0.
2. Body shape in lateral view: [0] highly to moderately convex dorsally; [1] lowly convex dorsally; [2] depressed dorsally. L = 6; CI = 0.33; RI = 0.55.

Head

3. Frons outline of head in dorsal view: [0] faintly concave; [1] arcuately, well concave; [2] triangularly, well concave; [3] well concave like an upward opening curly brace ({). L = 9; CI = 0.33; RI = 0.45.
4. Oculofrontal margin in dorsal view: [0] rounded (not ridged); [1] ridged. L =4; CI = ;0.25 RI = 0.75.
5. Eyes in dorsal view: [0] broadly visible; [1] narrowly visible. L = 7; CI = 0.14; RI = 0.57.
6. Frons: [0] smoothly convex from just above each antennal insertion to inner margin of each eye; [1] transversely ridged from just above each antennal insertion to inner margin of each eye. L = 1; CI = 1; RI = 1.
7. Proportion of clypeus (WC/LSC ratio): [0] WC/LSC < 1.0; [1] $1.0 \leq$ WC/LSC ≤ 2.0; [2] $2.0 <$ WC/LSC. L = 5; CI = 0.40; RI = 0.25.
8. Coloration of maxillary palps: [0] brownish-black to black; [1] light to dark brown. L = 3; CI = 0.33; RI = 0.80.
9. Palpomere IV of maxillary palps: [0] oval, somewhat longer than wide; [1] round, nearly as long as wide. L = 3; CI = 0.33; RI = 0.33.

Thorax

10. Anterior margin of pronotum: [0] with median lobe; [1] without median lobe. L = 2; CI = 0.50; RI = 0.92.
11. Apicolateral depressions of pronotum: [0] absent; [1] present, with pores; [2] present, with fovea. L = 2; CI = 1; RI = 1.

12. Hypomeral marking: [0] absent: [1] present. L = 2; CI = 0.50; RI = 0.50.
13. Well-defined prosternal lobe: [0] absent; [1] present. L = 1; CI = 1; RI = 1.
14. Prosternal apical margin: [0] rimed; [1] not rimed, but weakly lobed anteriorly. L = 1; CI = 1; RI = 1.
15. Prosternal process: [0] subparallel; [1] constricted between procoxa. L = 4; CI = 0.25; RI = 0.40.
16. Marginal carinae of prosternal process: [0] subparallel; [1] diverging posteriad; [2] absent. L = 4; CI = 0.50; RI = 0.60.
17. Elevated portions of prosternum along procoxal cavities: [0] absent; [1] present. L = 2; CI = 0.50; RI = 0.80.
18. Disk of prosternum: [0] without transverse grooves above procoxal cavities: [1] with transverse grooves. L = 1; CI = 1; RI = 1.

Elytra

19. Lateral carinae on elytra: [0] absent; [1] present. L = 1; CI = 1; RI = 1.
20. Lateral margins on elytra: [0] without serrations; [1] with serrations. L = 2; CI = 0.50; RI = 0.90.
21. Epipleura: [0] distinct only in thoracic region; [1] distinct from humeral angles to near apices. L = 1; CI = 1; RI = 1.
22. Marginal carina on elytra: [0] distinct from humeral angles to near apices; [1] distinct only in thoracic region. L = 1; CI = 1; RI = 1.
23. Disk of elytron: [0] not swollen in subapical part; [1] swollen in subapical part. L = 3; CI = 0.33; RI = 0.86.
24. Surface of elytra: [0] without linearly incised short punctures; [1] with linearly incised short punctures. L = 2; CI = 0.50; RI = 0.50.
25. First and second transverse bands on apical half of elytra: [0] absent; [1] consisting of unicolor setae; [2] consisting of multicolor setae. L = 4; CI = 0.50; RI = 0.66.
26. Elytral tufts of erect setae: [0] absent; [1] present. L = 1; CI = 1; RI = 1.

Hind wing

27. Anal field: [0] present; [1] absent. L = 2; CI = 0.50; RI = 0.50.

Leg

28. Inner margin of each femur: [0] not expanded; [1] expanded to conceal tibia at rest. L = 1; CI = 1; RI = 1.
29. Coloration of basal four tarsomeres on each leg except tarsal pads: [0] brownish-black to black; [1] light to dark brown. L = 8; CI = 0.12; RI = 0.50.
30. Claws: [0] with large inner tooth; [1] with small inner tooth. L = 2; CI = 0.50; RI = 0.50.

31. A fringe of spines on outer margin of each metatibia: [0] present; [1] absent. L = 2; CI = 0.50; RI = 0.50.
32. One long spine in base of the fringe of spines on each metatibia: [0] absent; [1] present. L = 3; CI = 0.33; RI = 0.75.

Abdomen

33. Laterosternal sulci: [0] on laterosternites I–IV; [1] on laterosternite I–VI. L = 1; CI = 1; RI = 1.
34. Sternal grooves on ventrite I: [0] present; [1] present, but prominently reduced; [2] absent. L = 5; CI = 0.40; RI = 0.85.
35. Sternal grooves on ventrite II–IV: [0] present; [1] absent. L = 2; CI = 0.50; RI = 0.50.

Male terminalia

36. Apical margin of male sternite IX: [0] (truncately) rounded; [1] truncate; [2] clearly emarginate. L = 9; CI = 0.22; RI = 0.41.
37. Apical angles of male sternite IX: [0] not produced; [1] clearly produced. L = 3; CI = 0.33; RI = 0.50.
38. Sides of parameres: [0] continuously dilated from base to widest point; [1] expanded in distal part. L = 8; CI = 0.12; RI = 0.46.
39. Apico-lateral margins of parameres: [0] bearing with multiple setae; [1] bearing with a pair of setae; [2] not bearing but rarely with setae. L = 10; CI = 0.20; RI = 0.33.
40. Shape of penis (not including median struts): [0] subparallel at least from widest point of base to middle; [1] narrowed from widest point of base to apex. L = 2; CI = 0.50; RI = 0.90.
41. Apex of penis: [0] produced; [1] not produced. L = 6; CI = 0.16; RI = 0.54.
42. Apex of penis: [0] rounded; [1] pointed. L = 4; CI = 0.25; RI = 0.
43. Sclerotized area on ventral membrane of penis: [0] absent; [1] present. L = 3; CI = 0.33; RI = 0.50.

Female terminalia

44. Baculi on female proctiger in lateral view: [0] curved ventrally; [1] straight (curved parts are membranous and transplant, as a result the baculi look as if they are not curving ventrally). L = 2; CI = 0.50; RI = 0.50.
45. Transverse depression on apical part of coxites in ventral side: [0] absent; [1] present. L = 1; CI = 1; RI = 1.
46. Dorsal projections of coxite baculi: [0] absent; [1] present. L = 1; CI =1; RI = 1.
47. Shape of stylus: [0] subtrapezoidal to lingulate; [1] fan-shaped. L = 5; CI = 0.20; RI = 0.50.

48. Length of spermatheca: [0] normal length; [1] extremely long. L = 2; CI = 0.50; RI = 0.
49. Shape of spermatheca: [0] slender tubular; [1] moderately wide tubular; [2] prominently wide tubular. L = 10; CI = 0.20; RI = 0.42.
50. Spermathecal gland: [0] absent; [1] present. L = 1; CI = 1; RI = 1.

***Exemplars for species relationships of Japanese* Habroloma**. Eleven *Habroloma* species recognized in the chapter 3 of this study were included in the analysis. In addition, five Taiwanese species are added to investigate true sister species for each Japanese species. Several outgroup exemplars (genera *Trachys*, *Ahanisticus*, and *Endelus*) were selected. Among the outgroup exemplars, *Endelus collaris kerremansi* was used to root the tree. Examined specimen data for this analysis are shown in Appendix 3 (except Japanese species).

***Characters for species relationships of Japanese* Habroloma**. The analysis used forty-six adult morphological characters listed below, seven of which were multistate and the remainders were binary. Character length (L), consistency index (CI), and retention index (RI) calculated using WinClada version 1.00.08 (Nixon, 2002) are also indicated below.

Body

1. Body shape in dorsal view: [0] ovate; [1] wedge-shaped. L = 3; CI = 0.33; RI = 0.
2. Body shape in lateral view: [0] highly to moderately convex dorsally; [1] lowly convex dorsally; [2] depressed dorsally. L = 3; CI = 0.66; RI = 0.66.

Head

3. Oculofrontal margins in dorsal view: [0] not produced anteriorly; [1] produced anteriorly. L = 1; CI = 1; RI = 1.
4. Produced oculofrontal margins: [0] very weakly produced; [1] moderately to strongly produced. L = 2; CI = 0.50; RI = 0.
5. Proportion of clypeus (WC/LSC ratio): [0] WC/LSC < 1.0; [1] 1.0 ≤ WC/LSC ≤ 2.0; [2] 2.0 < WC/LSC. L = 5; CI = 0.40; RI = 0.40.
6. Sides of clypeus: [0] subparallel (simply constricted by antennal insertions); [1] dilated apicad. L = 1; CI = 1; RI = 1.

Thorax

7. Anterior margin of pronotum: [0] with median lobe; [1] without median lobe. L = 5; CI = 0.20; RI = 0.42.

8. Apicolateral depressions of pronotum: [0] absent; [1] present, without pores; [2] present, with simple pores; [3] present, with large fossae. L = 4; CI = 0.75; RI = 0.83.
9. Hypomera: [0] without pores; [1] with pores. L = 1; uninformative.
10. Hypomeral marking: [0] absent: [1] present. L = 1; CI = 1; RI = 1.
11. Prosternal lobe: [0] absent; [1] present. L = 1; CI = 1; RI = 1.
12. Prosternal trapezoidal plate: [0] wider than long; [1] longer than wide. L = 2; CI = 0.50; RI = 0.
13. Surface of prosternal trapezoidal plate: [0] only with setiferous pin-prick punctures; [1] with setiferous pin-prick punctures and ocellate sculptures. L = 3; CI = 0.33; RI = 0.50.
14. Disk of prosternum: [0] without transverse grooves above procoxal cavities: [1] with transverse grooves above procoxal cavities. L = 1; CI = 1; RI = 1.

Elytra

15. Lateral carinae on elytra: [0] absent; [1] present, starting from near behind humeri; [2] present, starting from near bases of humeri. L = 3; CI = 0.66; RI = 0.80.
16. Lateral margins of elytra: [0] constricted between base and middle; [1] not constricted between base and middle. L = 3; CI = 0.33; RI = 0.77.
17. Lateral margins on elytra: [0] without serrations; [1] with serrations. L = 2; CI = 0.50; RI = 0.66.
18. Epipleura: [0] distinct from humeral angles to near apices; [1] distinct only in thoracic region. L = 1; CI = 1; RI = 1.
19. Marginal carina on elytra: [0] distinct from humeral angles to near apices; [1] distinct only in thoracic region. L = 1; CI = 1; RI = 1.
20. Surface of elytra: [0] without linearly incised short punctures; [1] with linearly incised short punctures. L = 2; CI = 0.50; RI = 0.50.
21. Elytral integument: [0] without colored marks (patches); [1] with colored large marks. L = 3; CI = 0.33; RI = 0.
22. First and second transverse bands on apical half of elytra: [0] present; [1] absent. L = 2; CI = 0.50; RI = 0.50.

Hind wing

23. Anal field: [0] present; [1] absent. L = 2; CI = 050.; RI = 0.50.

Leg

24. Legs: [0] with slender femora and tibia; [1] with stout femora and tibia. L = 3; CI = 0.33; RI = 0.75.
25. Metacoxal plates: [0] without arcuate notches at medial posterior margins; [1] with arcuate notches at medial posterior margins. L = 1; CI = 1; RI = 1.

26. Outer margins of metafemora: [0] not angulate in distal part; [1] angulate in distal part. L = 1; CI = 1; RI = 1.
27. Inner margin of each femur: [0] not expanded; [1] expanded to conceal tibia at rest. L = 1; CI = 1; RI = 1.
28. Claws: [0] with large inner tooth; [1] with small inner tooth. L = 2; CI = 0.50; RI = 0.
29. A fringe of spines on outer margin of each metatibia: [0] present; [1] absent. L = 1; CI = 1; RI = 1.

Abdomen

30. Laterosternal sulci: [0] on laterosternites I–IV; [1] on laterosternite I–VI. L = 1; CI = 1; RI = 1.
31. Sternal grooves on ventrite I: [0] present; [1] present, but prominently reduced; [2] absent. L = 2; uninformative.
32. Sternal grooves on ventrite II–IV: [0] present; [1] absent. L = 2; CI = 0.50; RI = 0.50.

Male terminalia

33. Aedeagus (in broad sense): [0] without elongated parameres and penis; [1] with elongated parameres and penis. L = 1; CI = 1; RI = 1.
34. Sides of parameres: [0] subparallel; [1] continuously dilated from base to widest point; [1] expanded in distal part. L = 2; CI = 0.50; RI = 0.
35. Apico-lateral margins of parameres: [0] bearing with multiple setae; [1] bearing with a pair of setae. L = 4; CI = 0.25; RI = 0.57.
36. Width of dorsal plate of penis: [0] wide; [1] slender; [2] prominently slender (rod-shaped). L = 3; CI = 0.66; RI = 0.66.
37. Distal part (non-covered ventral membrane) of dorsal plate of penis; [0] not narrowed; [1] gradually narrowed; [2] narrowed then becoming subparallel-sided; [3] narrowed then becoming subparallel-sided, elongated. L = 3; CI = 1; RI = 1.
38. Apex of penis: [0] produced; [1] not produced. L = 3; CI = 0.33; RI = 0.60.
39. Apex of penis: [0] rounded; [1] truncated. L = 5; CI = 0.20; RI = 0.50.
40. Dorsal plate of penis: [0] without a longitudinal depression; [1] with a longitudinal depression. L =1; CI = 1; RI = 1.
41. Ventral membrane of penis: [0] without finely tuberculate part; [1] with finely tuberculate part. L = 1; CI = 1; RI = 1.
42. Sclerotized area on ventral membrane of penis: [0] absent; [1] present. L = 4; CI = 0.25; RI = 0.62.

Female terminalia

43. Baculi on female proctiger in lateral view: [0] curved ventrally; [1] straight (curved parts are membranous and transplant, as a result the baculi look as if they are not curving ventrally). L = 2; CI = 0.50; RI = 0.50.
44. Dorsal projections of coxite baculi: [0] absent; [1] present. L = 1; CI = 1; RI = 1.
45. Median part of apical margin of coxites: [0] not protruded; [1] protruded. L = 1; CI = 1; RI = 1.
46. Length of spermatheca: [0] normal length; [1] distinctly elongated. L = 1; CI = 1; RI = 1.
47. Shape of spermatheca: [0] slender tubular; [1] wide tubular. L =1; uninformative.

Cladistic analyses

The three data matrixes (Tables 3–5) were assembled in Nexus format using Mesquite version 3.61 (Maddison & Maddison, 2019), respectively. Each parsimony analysis was conducted in TNT version 1.5 (Goloboff & Catalano, 2016) under traditional search running with 1000 replicates of random addition sequence, followed by tree-bisection-reconnection (TBR) swapping, and saving 10 trees per replication. All characters treated as unordered and as equally weighted (*a priori*), but as needed, implied weighting (*a posteriori*) was applied. Character distributions were mapped on a strict consensus tree using WinClada version 1.00.08 (Nixon, 2002).

Result and discussion for generic relationships of Tracheini

The cladistic analysis resulted in five equally most parsimonious trees of the length of 119 steps, CI = 0.57, and RI of 0.64. The strict consensus tree of these five trees was constructed as the length of 124 steps, CI = 0.54, and RI = 0.61. The obtained five trees are shown in Fig. 108. These five trees are different in the relationships among the subtribe Tracheina, Brachyina, Leiopleurina, Pachyschelina, and genera of the tribe Aphanisticini. To estimate better trees, the implied weighting technique was performed with $k = 2$ to 10. Those analyses resulted in one tree (same topology in each analysis). The cladogram is identical with one of the five trees in the first analysis (Fig. 108A). Based on the weighting analyses, one trees (Fig. 109; L = 119, CI = 0.57, RI = 0.64) was selected from the five trees as the better estimation of phylogenetic relationships of the genera of Tracheini.

Relationships of tribes. The analysis shows that Tracheini is polyphyletic in all of reconstructed trees (Fig. 108). In the estimated better tree (Fig. 109), members of Tracheini are recognized in the clade B together with members of Aphanisticini. Hołyński (1993) divided the subfamily Trachyinae *sensu* Cobos (1979) into Tracheini and Aphanisticini based on the character of the antennal grooves on the hypomere and the ambiguous additional characters (see the note of subgenus Tracheina in the chapter 3). These characters, however, are not support separation of Tracheini and Aphanisticini in the analysis, although the presence of the antennal grooves (character 15: state 1) supports the monophyly of the Tracheini excluded the members of the subtribe Tracheina. Thus, the recent higher classification of them is probably artificial. In addition, members of Tracheini and Aphanisticini used in the analysis are recovered in the clade A supported by three unique character states — character 1: state 1, condyle-shaped part of postocciput present; character 10: state 1, antennae dilated from antennomere V; and character 33: state 1, first cubito-anal cell absent, but the reductions of antennal dilated segments and the absence of the first cubito-anal cell are also recognized in some genera of Agrilini and Coraebini (Kubáň *et al*., 2001). The condyle-shaped postocciput, therefore, is regarded as autapomorphy for the clade A consisted of Tracheini and Aphanisticini. Morphological information of the postocciput is, unfortunately, unknown in most of members of Buprestidae. At the present time, the taxonomic importance of the condyle-shaped postocciput is ambiguous. The support of the single autapomorphic character state for the two tribes may be suggested unstableness in the tribe concepts of the subfamily Agrilinae. The recent molecular phylogeny of Buprestoidea based on 6756 bp of mitochondrial (COI and CAD) and nuclear (28S and 18S) DNA (Evans *et al*., 2015) showed that each tribe of Agrilinae were recognized as polyphyletic, although there were no support bootstrap values for most of generic relationships. The result of this study based on morphology also seems to be implied doubtful monophyly of each agriline tribe. To reclassify the Tracheini, future studies should treat all the tribes of the subfamily Agrilinae for phylogenetic analyses as ingroup exemplars.

Relationships of subtribes and genera. The four subtribes of Tracheini are well recognized as monophyletic within the clade B (exemplars in two out of four subtribes were only one examined representative genus, respectively), although positions of each subtribe are unstable in the analysis based on *a priori* assumption (Fig. 108). The clade C is consisted of members of the subtribe Tracheina (*Neotrachys* was not examined) and is supported by three unique character states — character 10: state 3, antennae dilated from antennomere VII; character 16: state 1, hypomeral markings present; and character 18: state 1, marginal carinae of prosternum present.

In the clade B, the genus *Pachyschelus* belonging to the subtribe Pachyschelina (the remaining three genera, *Hylaeogena*, *Hedwigiella*, and *Euhylaeogena* were not included in the analysis) is supported by seven character states, of which four are unique — character 13: state 1, laciniae reduced; character 21: state 1, scutellar shield large in size, far wider than half width of mesonotum; character 24: state 1, depressions on thorax for receiving legs present; and character 35: state 1, tibia laterally expanded and dorsally flattened to receive tarsi on dorsal side. At least, each state of characters 21, 24, and 35 are shared with the other genera of Pachyschelina based on literatures (Hespenheide, 2014; Hornburg, 2014). Therefore, the reduced laciniae is regarded as autapomorphic for the genus *Pachyschelus* (it also confirmed in other congeners by Kogan, 1963, 1964b), although the mouth parts of the other congeners of Pachyschelina have never been described and illustrated in previous studies. In addition, the unmovable penis (fixed by parameres; character 49: state 1) may be an autapomorphic character state for *Pachyschelus*, although it is not recognized as autapomorphic due to the unknown character scores of four exemplars within the clade D. Based on illustrations for the male aedeagi of the Pachyschelina (Kogan, 1963, 1964 b; Hornburg, 2014), this character state is found only in *Pachyschelus*.

With regard to other subtribes of Tracheini, Brachyina (*Brachy*s, *Lius*, and *Taphrocerus*, the latter is not included exemplars) and Leiopuleurina (*Leiopleura* and *Callimicra*, the latter is not included exemplars) are recovered as monophyletic within the clade D, although taxon sampling is very poor. The monophyly of Brachyina is supported by four character states, of which one is unique — character 41: state 1, the presence of sub-grooves between abdominal intercoxal process and metacoxal plate for receiving metatarsi at rest. The clade of two *Leiopleura* species (subtribe Leiopleurina) is supported by only one homoplastic character states — character 4: state 1, frontoclypeal median pore present. This character state is also found on *Paracylindromorphus japanensis* (tribe Aphanisticini) in a sister clade of clade D. At least, more exemplars and well scored character states in each selected character of this study are needed to resolve phylogenetic relationships of the subtribe Leiopleurina among Tracheini.

Judging from these results on the subtribes of Tracheini, the genus composition of each subtribe seems to be mostly stable, while the morphological concept of each subtribe may have potential for improvement. The stableness of subtribes of Tracheini are also indicated by molecular studies (Evans *et al*., 2015), except for the subtribe Pachyschelina recovered as polyphyletic (*Pachyschelus* and *Hylaeogena* are separated).

Relationships between Trachys *and* Habroloma. In the subtribe Tracheina, the genera *Trachys* and *Habroloma* has been discussed about their taxonomic concepts (e.g.

Obenberger, 1929 a; Théry, 1938; Cobos, 1979; Hołyński, 2003), especially on the independence of *Habroloma* from *Trachys*. Within the clade C, *Trachys* and *Habroloma* are well recovered as an independent genus, respectively. The clade of *Trachys* is supported by six character states, of which two are unique — character 12: state 1, delimitation of basistipes and palpifer reduced; character 52: state 1, dorsal projections of coxite baculi present. In contrast, the clade of *Habroloma* is done by six character states, of which one is unique — character 19: state 1, disk of prosternum with transverse grooves above procoxal cavities. These character states for *Trachys* and *Habroloma* are expected as autapomorphic ones.

As a result of this study, it is revealed that *Trachys* and *Habroloma* are distinguishable each other by sixteen character including autapomorphic character states shown in Table 6. Among those characters, three characters (denoted by darker shade in Table 6) were not included in the cladistic analysis due to their continuous differences between other exemplars. In addition, the difference in the number of sternal grooves (character 42), which show a sufficient difference for identifying *Trachys* and *Habroloma* (Table 6), does not support each clade of the two genera. In this study, high homoplasy of this character is indicated. Although there is no discussion based on cladistic analyses, Jendek (2001) implies the high homoplasy of the sternal grooves between closely related genera in Tracheini and Aphanisticini.

A comparison with *Malobroha* species is required to verify the reliability of the estimated morphological differences between *Trachys* and *Habroloma* (Table 6) in future studies, because of the intermediate species between the two genera that are generally classified into the subgenus *Malobroha* Cobos, 1979 in *Habroloma* were not included in the cladistic analysis. At least, the pronotal apicolateral depressions of *Habroloma*, the elytral lateral carinae of *Habroloma*, and the metatarsal fringe of spines of *Trachy* are doubtful as synapomorphic character states, since there are exceptional species against typical character states of each genus (the pronotal apicolateral depressions and/or the elytral lateral carinae of *Malobroha* species, *H. bicarinatus* (Kerremans, 1892), and *H. glyphicum* Hołyński, 2003; the metatarsal fringe of spines of *T. problematicus*).

Result and discussion for species relationships of Japanese *Trachys*

The cladistic analysis resulted in four equally most parsimonious trees of the length of 167 steps, CI = 0.36, and RI = 0.65. The strict consensus tree of these four trees was constructed as the length of 169 steps, CI = 0.36, and RI = 0.64. The topology is shown in Fig. 110. The obtained four trees are different in the relationships among *Trachys toringoi*, *T. elvira*, and *T.* sp. 4 and among *T. pecirkai* and *T.* sp. 2. To estimate better trees, additional analysis using the implied weighting technique was performed with k = 2 to 10. Those analyses resulted in one tree (same topology obtained in each analysis of different k values). The cladogram is identical with one of the four trees in the first analysis. Based on the weighting analyses, one trees (Fig. 111; L = 167, CI = 0.36, RI = 0.65) was selected from the four trees as the better estimation of phylogenetic relationships of Japanese *Trachys* species.

Japanese and Taiwanese *Trachys* is divided into two clades, of which one is a very small clade A consisted of three species. The remining 25 species are recognized within a large clade B supported by one unique character state — character 33: state 0, the laterosternal sulci on laterosternite I–IV. This character state is also regarded as a unique one in the analysis for the generic relationships of Tracheini (Fig X).

Tentative species-groups. Within the tentative species-groups defined in the chapter 3 of this study, the groups III, IV, V, and VII are recovered in the clade B as monophyletic, whereas the groups II and VI are in the clade B as paraphyletic and the group I is in the clade A and in the basal branches of the clade B as paraphyletic.

The members of the group I, readily distinguished from other species-groups of *Trachys* by the unserrated elytral lateral margins, are divided into four clades. The subgroup I-1 is recovered as monophyletic and supported by three character states, of which one is unique — character 6: state 0, frons of head smoothly convex from just above each antennal insertion to inner margin of each eye. In contrast, the subgroup I-2 is recovered as polyphyletic. The three species (*Trachys tsushimae*, *T. ineditus*, and *T.* sp. 1) are recognized in the clade A supported by six homoplastic character states. In addition, one symplesiomorphic character state is distinguished them from other *Trachys* species — character 33: state 1, laterosternal sulci occurring on laterosternite I–VI. The remaining two species of the subgroup I-2 are recovered in basal branches of the clade C supported by one unique character state — character 40: state 1, side of dorsal plate of penis narrowed from widest point of base to apex. As a result, the paraphyly of the group I and the polyphyly of the subgroup I-2 seem to indicate the possibility that the group I can be additionally divided into some groups.

The group II, III, VI, and VII are recovered in the clade D supported by two character states, of which one is unique but reversed at two Taiwanese species, *Trachys* sp. 4 and *T. hornianus* — character 23: state 1, disk of elytra swollen in subapical part. The group II distinguished from other species-groups of *Trachys* by the wedge-shaped body are recovered as paraphyletic. Within the members of the group II, *Trachys toringoi* is recovered in the clade of an estimated group which is characterized by one unique character state — character 14: state 1, prosternal apical margin not rimed but weakly lobed anteriorly. This result probably indicates the group II is artificial and the unique character state in prosternum is regarded as an important state for grouping of *Trachys* species. Thus, *T. toringoi* should be assigned to the estimated group recovered in the sister clade of *T. auricollis* (group II).

Two characteristic Taiwanese species *Tarchys kurosawai* and *T. ohbayashii* which are characterized by the presence of the elytral tufts of erect setae, are recovered as an estimated group in the sister of clade E. In the Oriental Region, more than species show this character state (Obenberger, 1929 a; Descarpentries & Villiers, 1965) and more divers states seem to occur in this character, so that exemplars of such species may be needed to reassess the monophyly of this clade.

The group VI and VII are recovered in the clade E supported by two character states, of which one is unique — character 45: state 1, transverse depression on apical part of coxites in ventral side present. Within the clade E, the group VI is recognized as paraphyletic, whereas the group VII is as monophyletic and is supported by two character states, of which one is unique — character 25: state 2, first and second transverse bands on apical half of elytra consisting of multicolor setae. Judging from these results, it may be appropriate to treat the two species-groups as a single group in the clade E characterized by the state of the female coxites.

Evolutions of host associations. Japanese and Taiwanese *Trachys* are associated with 53 plant species belonging to 13 families in seven orders (Taiwanese species are based on adult foods after Ong & Hattori, 2019 and personal communication with U. Ong). The result of mapping of host information (family level) onto the strict consensus tree is shown in Fig. X.

In herbivorous insects, it is generally known that related species tend to be associated with plants in the same group such as family level (e.g. Leppänen et al., 2012; Doorenweerd et al., 2015). However, most Japanese and Taiwanese *Trachys* species are associated with distant plants between related species, except for relationships between species of the group VII, *T. robustus*, *T. variolaris*, and T. *dilaticeps* (associated with Fagaceae plants). The host associations shown by them suggest that host shifts toward phylogenetically distant plants may be contributed to the speciation of *Trachys* and to its species diversity. On the other hand, these host associations may imply that the phylogenetic relationships shown by this study are wrong due to the lack of exemplars such as true sister species distributed only in adjacent regions. The addition of more species is necessary to well understand evolutions of host associations of *Trachys*.

Because of poor knowledge of hosts for most of *Trachys* species except Japanese and European ones, future studies should accumulate ecological information of *Trachys*.

With regard to host utilizations based on Japanese species, significant differences are not recognized between the tentative species-groups. However, each species shows unique leaf-mining habits. For example, the oviposition site of *Trachys minutus* is always the apex of leaf on the adaxial surface and of *T. pseudoscrobiculatus* is always the abaxial surface of leaf (detailed position is not determined), the mines of *T. robustus* and *T. dilaticeps* are of the upper surface type (only feed on the upper epidermis and palisade layer). Such habits may be related to host plant characteristics and natural enemies rather than phylogenetic relationships.

Result and discussion for species relationships of *Habroloma*

The cladistic analysis including all the exemplars resulted in two equally most parsimonious trees of the length of 99 steps, CI = 0.56, and RI = 0.70. These two trees are only different in the positions of *Habroloma* (*Parahabrolma*) *eximium* and *H.* (*P.*) *praxilla* (Taiwan) (Figs. 114 & 115). The strict consensus tree of these two trees was constructed as the length of 100 steps. To estimate better trees, the implied weighting technique was performed with $k = 2$ to 10. Those analyses resulted in one tree (same topology in each analysis). The cladogram is identical with one of the two trees in the first analysis. Based on the weighting analyses, one trees (Fig. 114; L = 99, CI = 0.56, RI = 0.70) was selected from the two trees as the better estimation of phylogenetic relationships of Japanese *Habroloma* species.

Relationships of subgenera. Japanese (and Taiwanese) *Habroloma* are divided into two clades. The subgenera *Habroloma* and *Parahabroloma* are recovered as monophyletic, although the former is examined only one representative for this analysis. The subgenus *Habroloma* is recognized as a sister of the subgenus *Parahabroloma* in the clade A. In the supported character states for *Habroloma* (*Habroloma*) *bifrons*, the state 1 of character 9 was unique for this species. This character state, however, possibly does not characterize the subgenus *Habroloma* because at least the type species of this genus, *H.* (s. str.) *nanum*, show no same character state based on external examination of specimens (see Appendix 1). The state 3 of character 8, apicaolateral depressions of pronotum with large fovea, has been well known as the diagnostic character state of this subgenus (Kurosawa, 1959). In the cladogram, this character state is only found in *H.* (*H.*)

bifrons, but the polarity of the character 8 is recognized as ambiguous and the state 3 is not regarded as unique for this species.

The clade A for the subgenus *Parahabroloma* is supported with four character states, of which two are unique — character 3: state 1, oculofrontal margins in dorsal view produced anteriorly; and character 25: state 1, outer margins of metafemora angulated in distal part. The former unique character state, however, is also recognized in the type species of this genus, *H.* (*H.*) *nanum* (1 ex., Bisamberg, Wien, Austria, 13.IX.1992, T. Zabransky leg. (SOCI); 1 ex., Kreuznach, Germany, 7.VII.1971, M. Niehuis leg. (SOCI)). Thus, it is not regarded as autapomorphy for *Parahabroloma*.

Tentative species-groups for Parahabroloma. Within the clade A, the subgenus *Parahabroloma* is divided into two major clades B and C, although the latter clade supported only with two homoplastic character states. The three tentative species-groups of this subgenus, established in the chapter 3 of this study, are recognized as monophyletic in the group I and II. In contrast, the polyphyletic group III is recovered in the clade B and in the sister clade of the group I within the clade E, namely, this group is an artificial one. Members of the group III in the clade B are distinctly characterized by three character states, of which two are unique — character 37: state 2, distal part of dorsal plate of penis narrowed then subparallel-sided (state 2); and character 40: state 1, dorsal plate of penis with a longitudinal depression. In addition, these species are associated with *Rubus* plants discussed below. The remaining species, *Habroloma* (*Parahabroloma*) sp. 1, is regarded as a sister of the members of the group I within the clade E supported by two unique character states — character 8: state 1, apicolateral depressions of pronotum without pores (but reversed at *H.* (*P.*) *griseonigrum*); and character 41: state 1, ventral membrane of penis with finely tuberculate part. The clade of group I is supported by three character states, of which one is unique — character 25: state 1, metacoxal plates with arcuate notches at medial posterior margins. Based on the distinct unique character states of the clade B and E, *Habroloma* (*Parahabroloma*) sp. 1 should be assigned to the group I. Thus, the characters 41 and 8 (but the state of the latter is occasionally reversed) has to be added in the contents of diagnoses for the tentative species-groups to revise them. In addition, the revised group I may be divided into two subgroups, of which one is consisted of three species (original members of the group I) characterized by the arcuate notches of metacoxal plates (character 25: state 1). The remaining one subgroup (*H.* (*P.*) sp. 1) is characterized by the wide tubular spermatheca (character 47: state 1).

Within the clade of the original members of group I, the positions of *Habroloma* (*Parahabroloma*) *eximium* and *H.* (*P.*) *praxilla* (Taiwan) is different in the non-selected tree (Fig. 115). In the estimated better tree (Fig. 114), *H.* (*P.*) *praxilla* is recovered as a sister of the terminal clade for *H.* (*P.*) *griseonigrum* and *H.* (*P.*) *miwai* (Taiwan) and the apically dilated clypeus (character 6: state 1) supports the clade of these three species as a unique character state. If *H.* (*P.*) *eximium* is recovered as a sister of the terminal clade (Fig. 115), the absence of the first and second transverse bands on apical half of elytra (character 21: state 1) supports the clade of these three species.

Within the clade C, the members of the monophyletic group II are recovered in the clade D supported by three unique character states — character 33: state 1, aedeagus with elongated parameres and penis; character 36: state 2, width of dorsal plate of penis prominently slender (rod-shaped); and character 46: state 1, length of spermatheca distinctly elongated.

Evolutions of host associations. Japanese and Taiwanese *Habroloma* are associated with 21 plant species belonging to seven families in six orders (Taiwanese species are based on adult foods after Ong & Hattori, 2019 and personal communication with U. Ong). The result of mapping of host information (family level) onto the better estimation tree (Fig. 114) is shown in Fig. 116.

Japanese and Taiwanese *Habroloma* species shows two tendencies in their host associations. The members of clade B are consisted of the species associated with Rosaceae, especially in *Rubus* plants. In contrast, species of the clade C are associated with various family plants.

The exclusive host associations with *Rubus* plant (Rosaceae) in the species of the clade B (group III) suggest that a host shift to *Rubus* is considered to be occurred once in the basal node of the clade A or B and then speciation occurred due to factors other than the host shift to other plant groups (e.g. geographical isolation). Each species, however, shows host preferences to some extent. For example, *Habroloma* (*Parahabroloma*) *subbicorne* is exclusively associated with deciduous *Rubus* species, whereas *H.* (*P.*) *marginicolle* is exclusively with evergreen *Rubus* species.

In the members of the clade C, prominently distant plants at order level are used as hosts between *Habroloma* species, except for *H.* (*Parahabroloma*) *griseonigrum* and *H.* (*P.*) *miwai* (Taiwan) are shared with host plant family, Fagaceae, especially in *Quercus* plants. This result indicates host shifts to phylogenetically distant family plants are attributed to speciation of the members of group I and II, although it is also considered the same reason of *Trachys* discussed above section (lacking of true sister species).

With regard to host utilizations based on Japanese species, significant differences are recognized in the discharge behavior of frass. All the species of group II eject frass outside mines (Fig. X). This behavior is only confirmed in species of this group, whereas other species left frass inside mines. When parsimoniously mapped this behavior onto the cladogram as a character, the frass ejection behavior evolved only in the clade D. Thus, it is regarded as autapomorphic for group II. As in *Trachys* species discussed above, each species of *Habroloma* also shows unique leaf-mining habits. For example, *Habroloma* (*Parahabroloma*) sp. 1 left characteristic mining traces and frass and *H*. (*P*.) *eximium* (subspecies *eximium* and subsp. 1) left linear mine in the first instar then left blotch one in the second and third instar larvae.

Brief conclusions

The tribe Tracheini are recognized as a polyphyletic group, but the genus components of each subtribe are generally appropriate. Comprehensive exemplars of subfamily Agrilinae may be needed to revise the concept of Tracheini due to the possibility of polyphyly of each agriline tribe. The genera *Trachys* and *Habroloma* are recognized as monophyletic independent genus, respectively, based on a single autapomorphic state in *Habroloma* and two autapomorphic ones in *Trachys*. Two autapomorphic states for the genus *Pachyschelus* are predicted.

In Japanese (and Taiwanese) *Trachys*, the tentative species-groups III, IV, V, and VII are recognized as monophyletic groups, but the groups I, II, and VI are as paraphyletic groups. The potential of additional grouping in group I is indicated. The assignment of *Trachys toringoi* should be changed into an estimated additional group consisted of two Taiwanese species. The group VI and VII should be combined each other due to the paraphyly of group VI. With regard to host associations, *Trachys* species shows that phylogenetically distant family plant are used as hosts between related species as a major tendency.

In Japanese (and Taiwanese) *Habroloma*, the tentative species-groups I and II are recognized as monophyletic groups, but the group III is as a polyphyletic group. As a result, it is indicated that the assignment of *Habroloma* (*Parahabroloma*) sp. 1 (group III) should be changed into group I. With regard to host associations, two major tendencies are indicated: 1) the species exclusively associated with Rosaceae plants (*Rubus* spp.) are recognized in one major clade; and 2) the species associated with various plant families are in the remining major clade. The frass ejection behavior is recognized only in the species of group II. This behavior is regarded as autapomorphy for group II.

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Figures and Tables

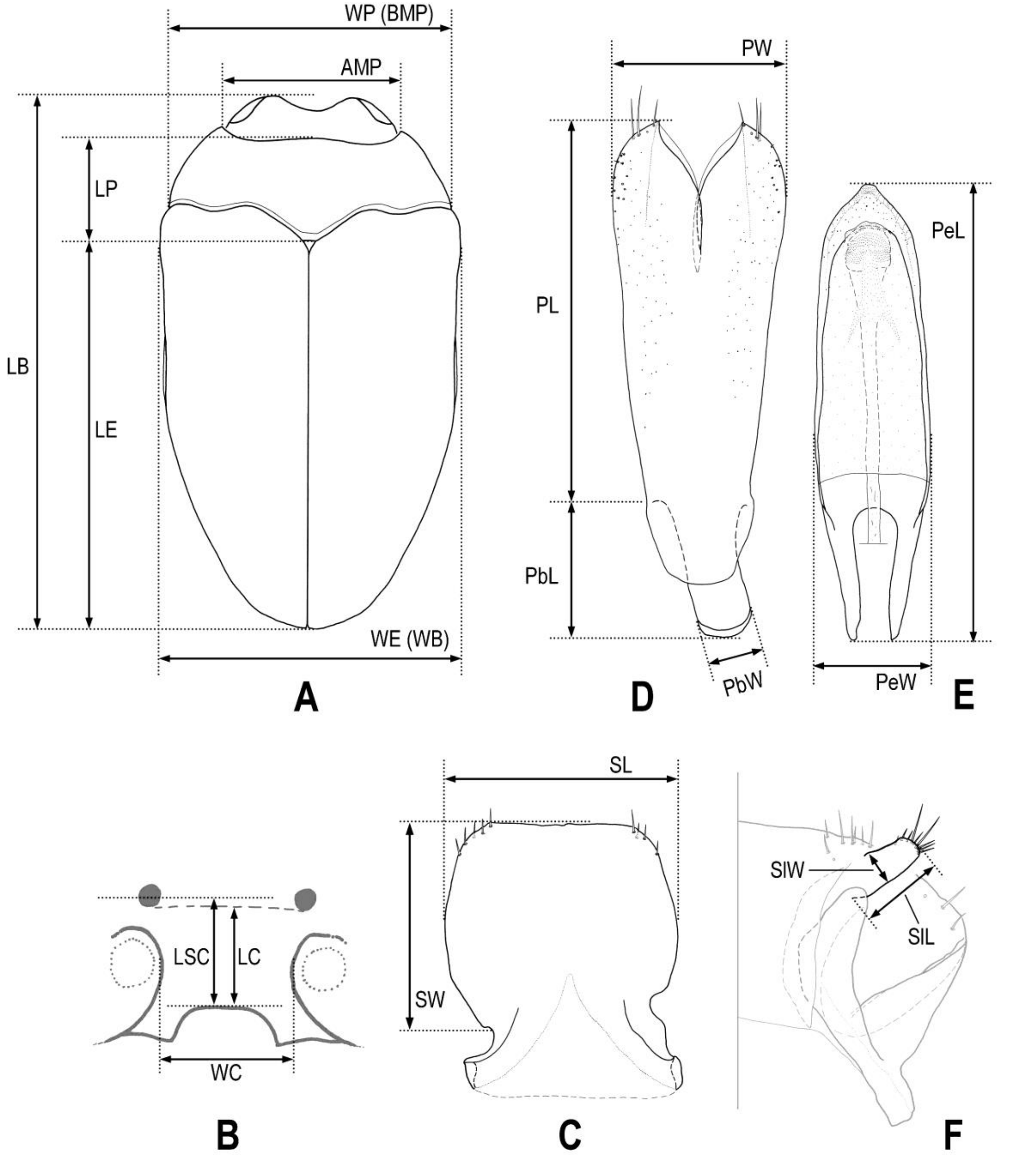


FIGURE 1. Used measurements for Japanese Tracheini. —— A) Dorsal habitus; B) clypeus; C) male sternite IX; D) tegmen; E) penis; F) stylus.

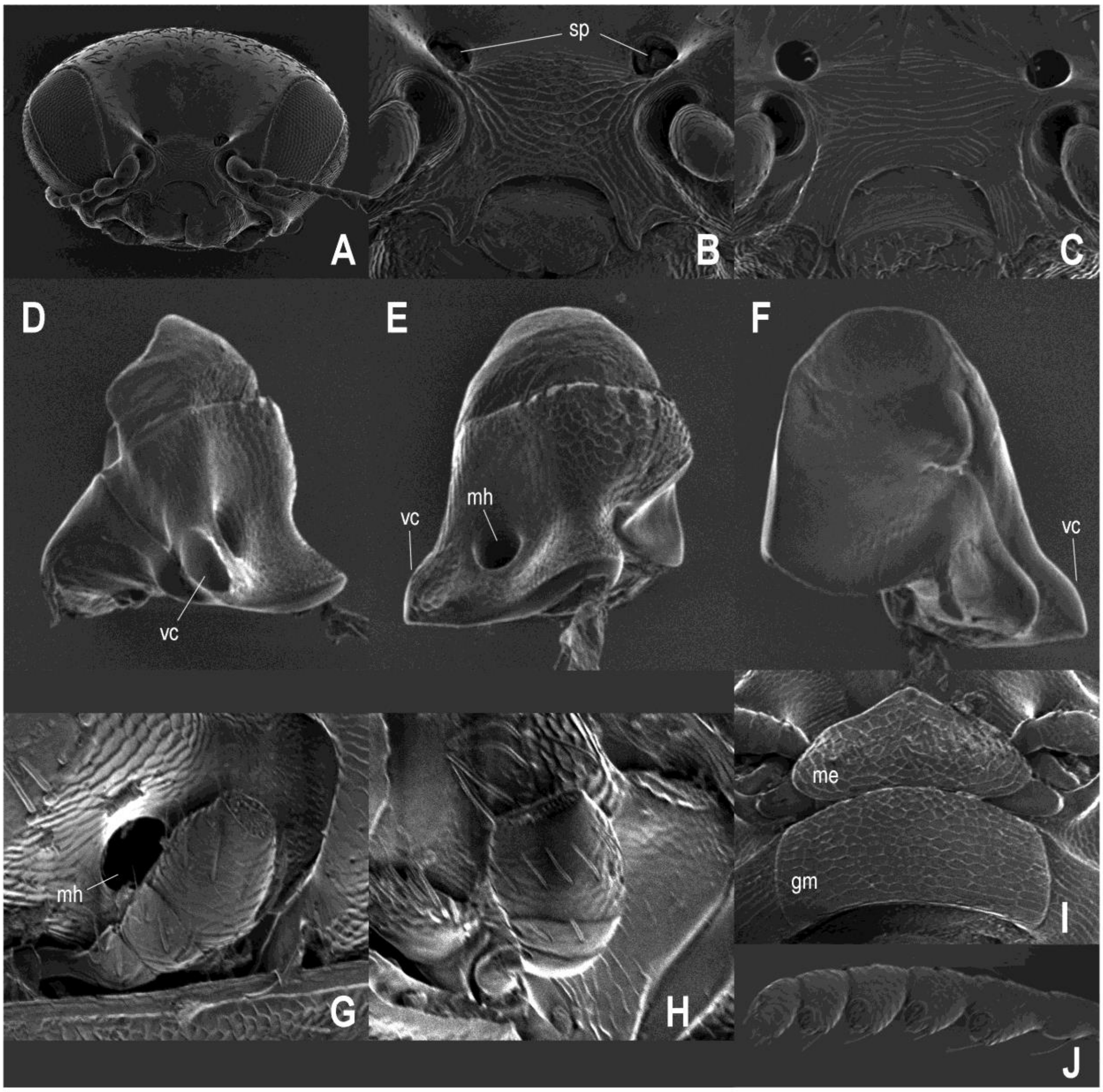


FIGURE 2. Head and its appendages of *Trachys* spp. SEM —— A, B, D–G, I, J) *Trachys minutus* (Linnaeus); C) *T. dilaticeps* Gebhardt; H) *T. pseudoscrobiculatus* Obenberger. —— A) Head, frontal view; B, C) clypeus; D–F) mandible, ventral view (D), lateral view (E), inner side (F); G, H) maxillary palps; I) mentum and submentum; J) antenomeres VII–XI, inner side. Abbreviations: me — mentum; mh — mandibular hole; sm — submentum; sp — suprantennal pore; vc — ventral condyle.

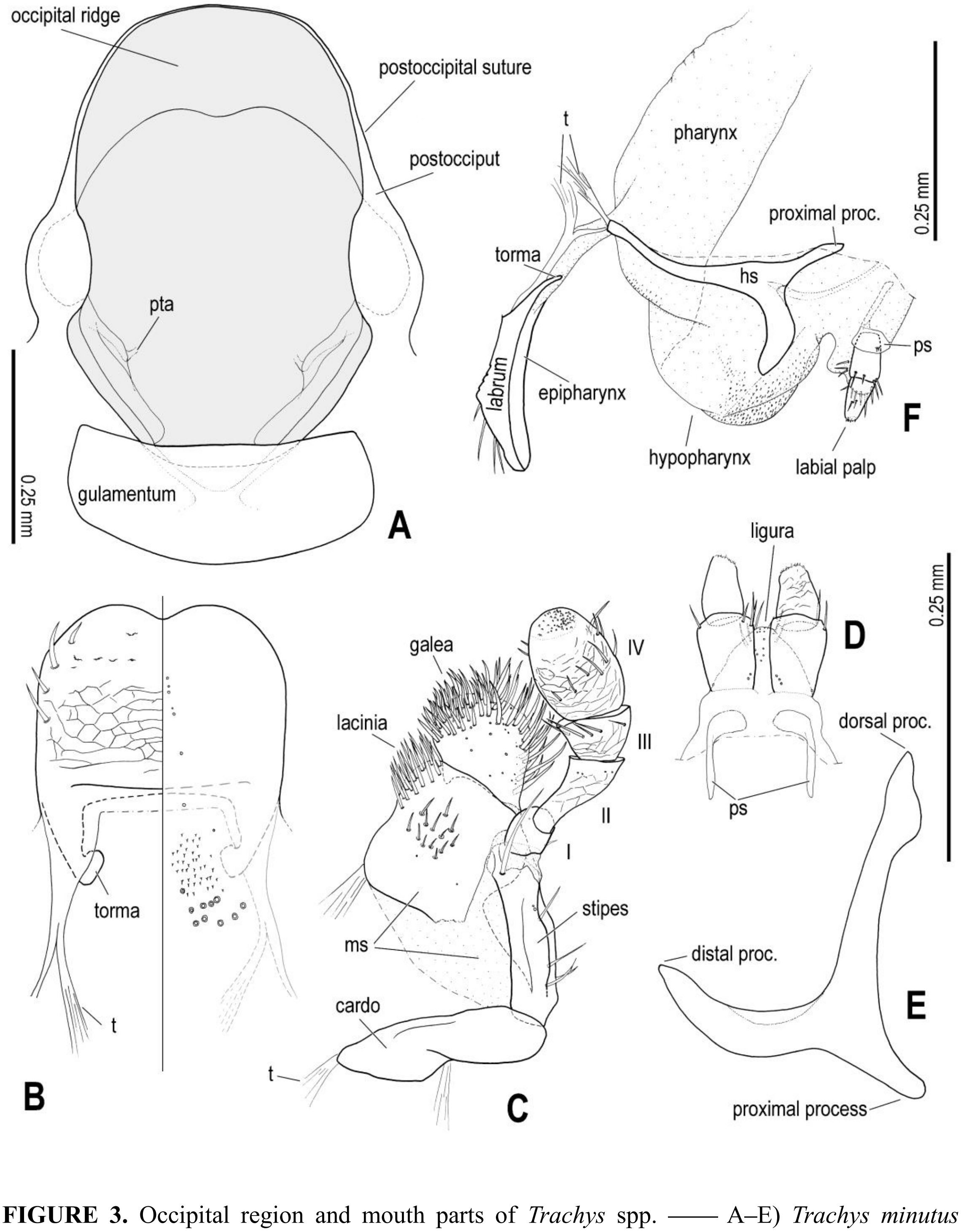


FIGURE 3. Occipital region and mouth parts of *Trachys* spp. —— A–E) *Trachys minutus* (Linnaeus); F) *T. yanoi* Kurosawa. —— A) Occipital region, ventro-caudal view (darker shade area indicates occipital foramen); B) labrum (left) and epipharynx (right); C) maxilla; D) labium, except mentum; E) hypopharyngeal sclerite, lateral view (forward face); F) preoral cavity and hypopharynx, lateral view (ventrally oriented). Abbreviations: hs — hypopharyngeal sclerite; ltp — lateral tormal process; ms — medio stipes; ps — premental sclerite; pta — posterior tentrial arm; t — tendon.

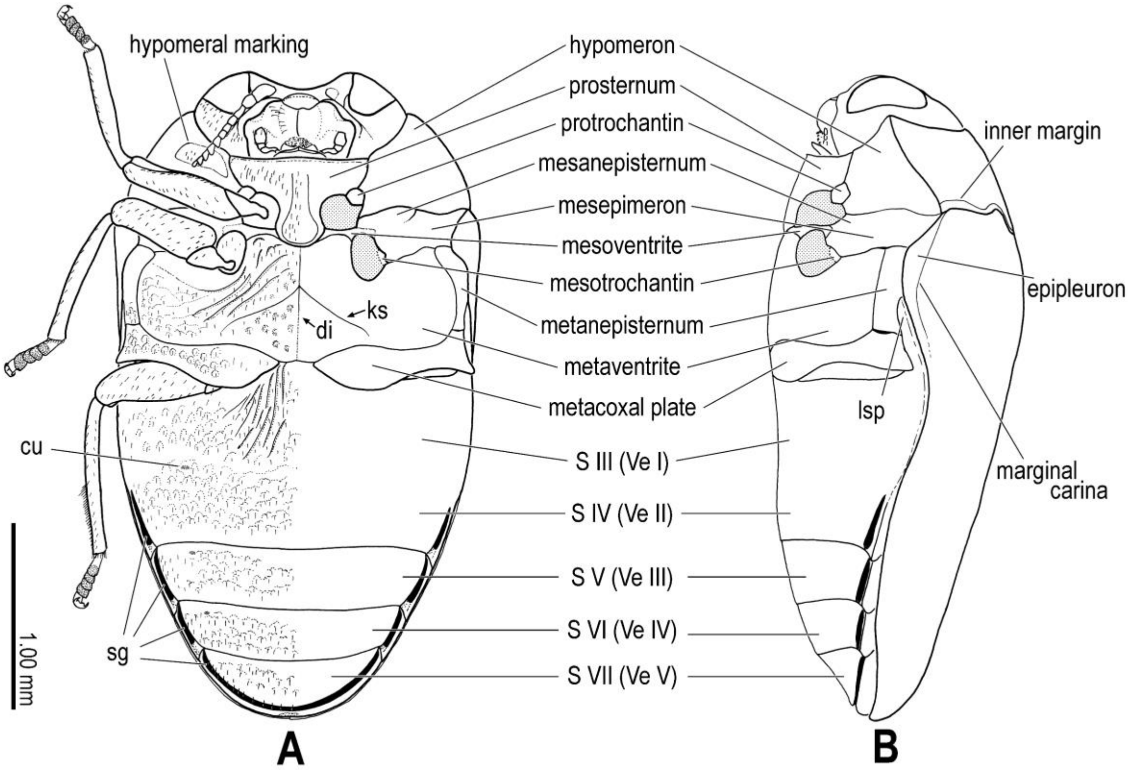


FIGURE 4. General appearance, *Trachys minutus* (Linnaeus). —— A) Body, ventral view; B) ditto, lateral view. Abbreviations: cu — cuticularium; di — discrimen; ks — katepisternal suture; lsp — lateral sternal projection; sg — sternal groove.

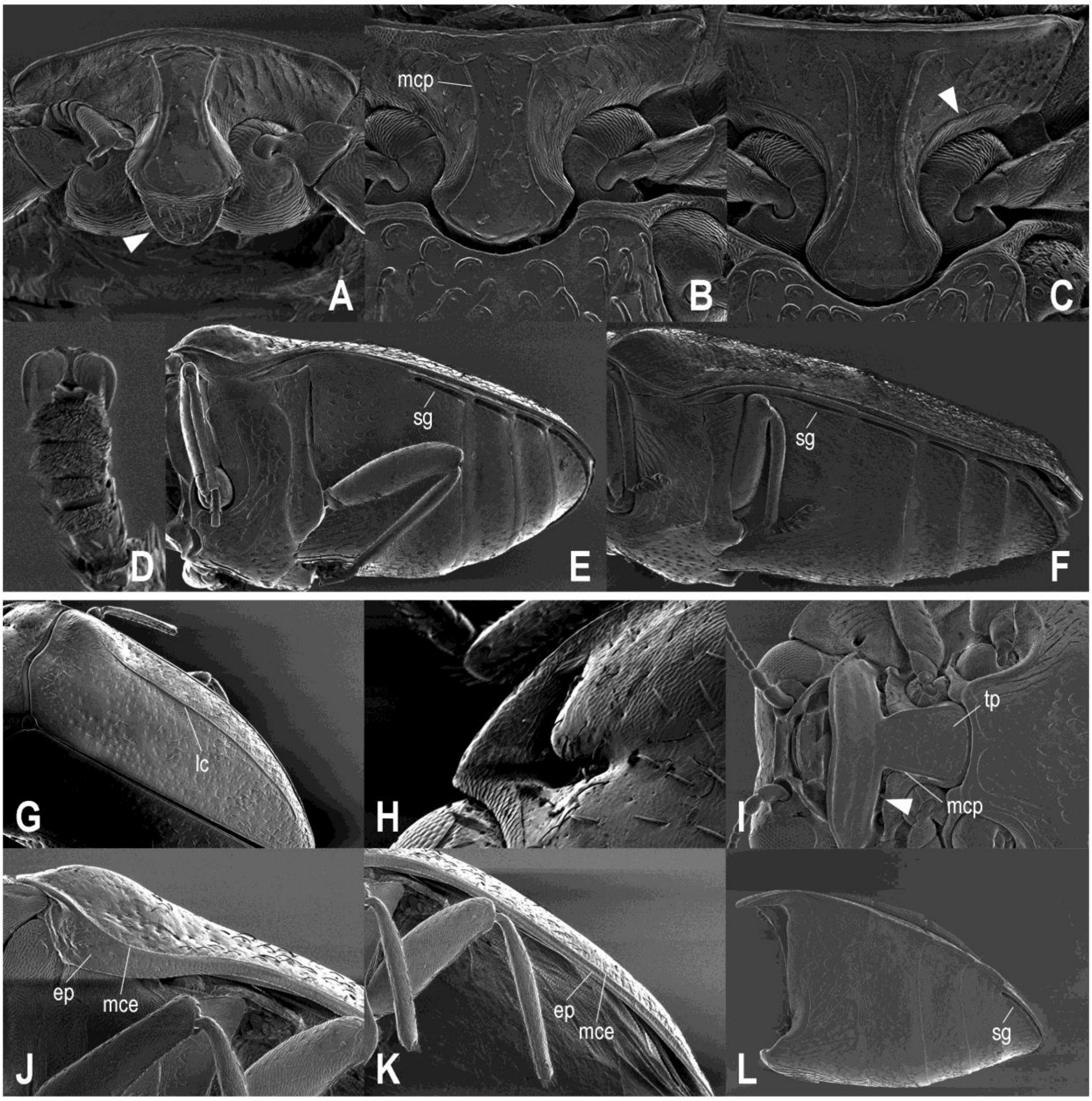


FIGURE 5. Thorax and abdomen of *Trachys* spp. and *Habroloma* sp., SEM. —— A, B, D, E) *Trachys minutus* (Linnaeus); C) *T. saundersi* Lewis; F) *T. dilaticeps* Gebhardt; G–L *Habroloma* (*Habroloma*) *bifrons* (Kiesenwetter). —— A–C, I) Prosternum, ventro-caudal view (A; a white triangular mark indicates a true apex of prosternal process), ventral view (B, C; a white triangular mark indicates an elevated portion), and oblique ventral view (I; a white triangular mark indicates a transverse groove); D) claws on protarsus; E, F, L) abdominal ventrites, oblique view; G) elytral lateral carina; H) pronotal impression; J, K) lateral part of elytron, thoracic region (J) and abdominal region (K), oblique view. Abbreviations: ep — epipleuron; lc — lateral carina; mce — marginal carina of elytron; mcp — marginal carina of prosternal process; sg — sternal groove; tp — trapezoidal plate.

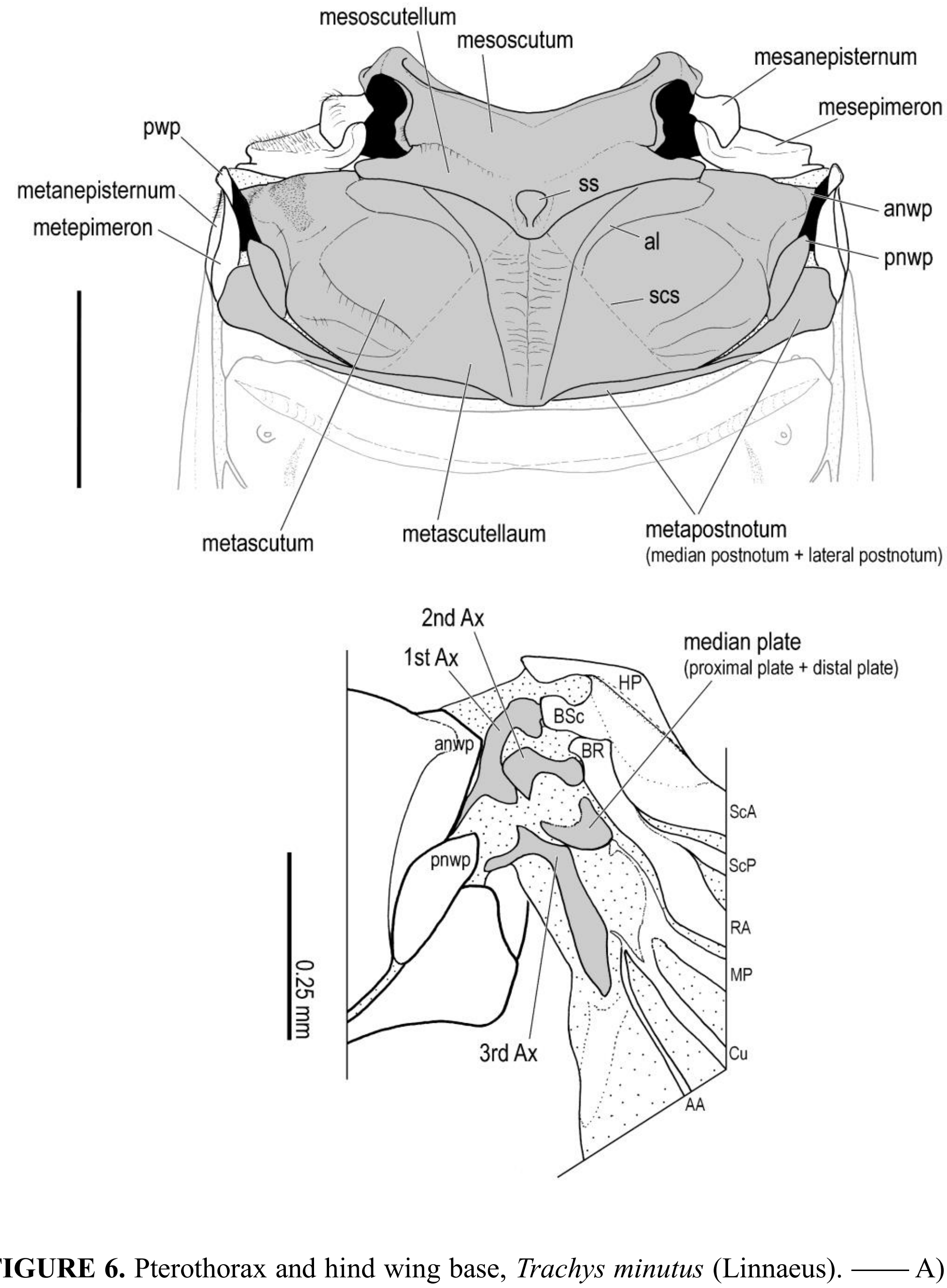


FIGURE 6. Pterothorax and hind wing base, *Trachys minutus* (Linnaeus). —— A) Pterothorax removed winges, lateral view (darker shade area indicates terga); B) hind wing base. Abbreviations: al — alacrista; anwp — anterior notal wing process; HP — humeral plate; pnwp — posterior notal wing process; pwp — pleural wing process; scs — scutoscutellar suture; ss — scutellar shield.

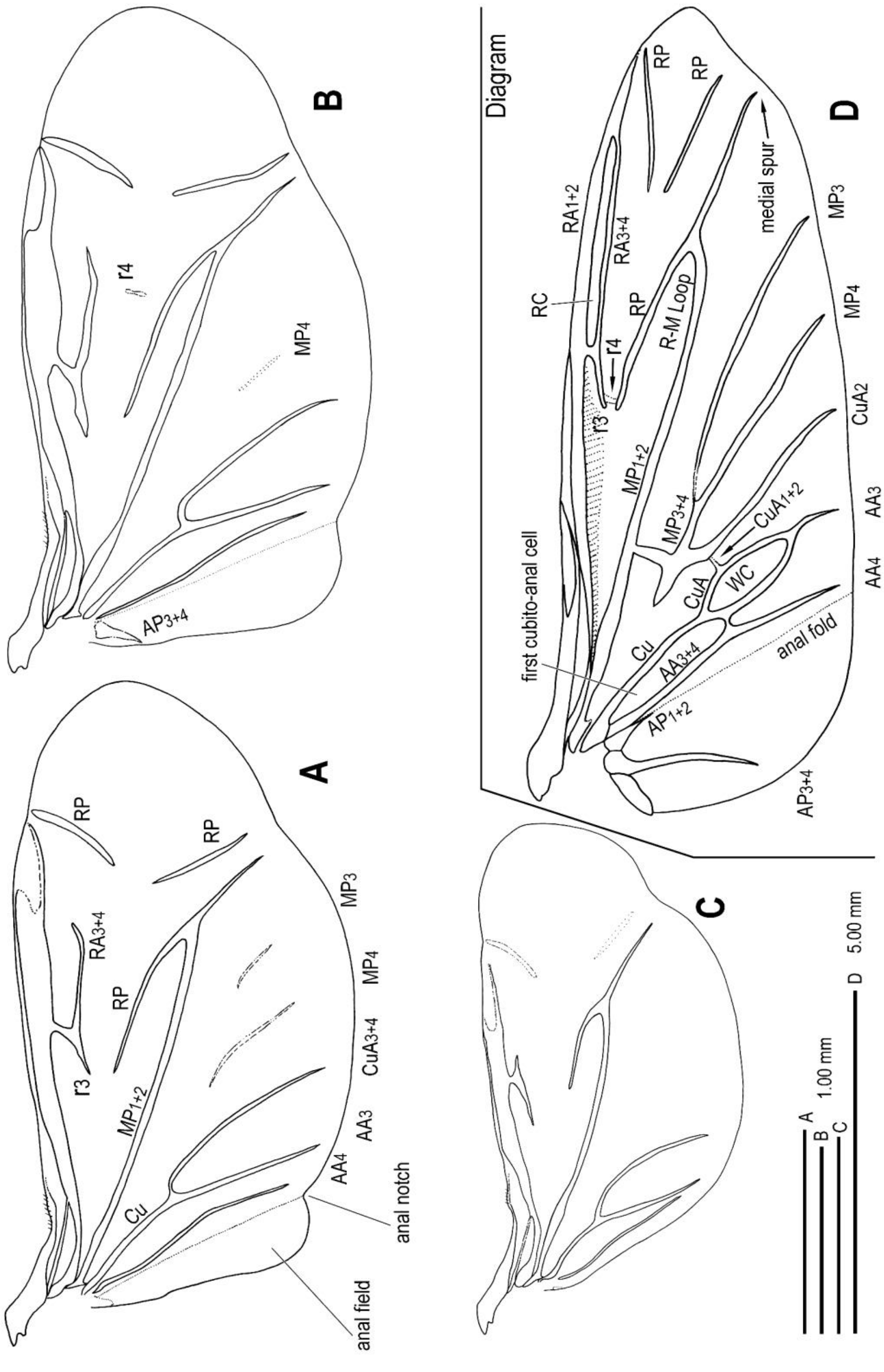


FIGURE 7. Hind wings and their venations. ——A) *Trachys minutus* (Linnaeus); B) *T. auricollis* Saunders; C) *Habroloma* (*Habroloma*) *bifrons* (Kiesenwetter); D) *Buprestis* (Ancylocheira) *haemorrhoidalis arakii* Kurosawa for the diagram of the hind wing venation.

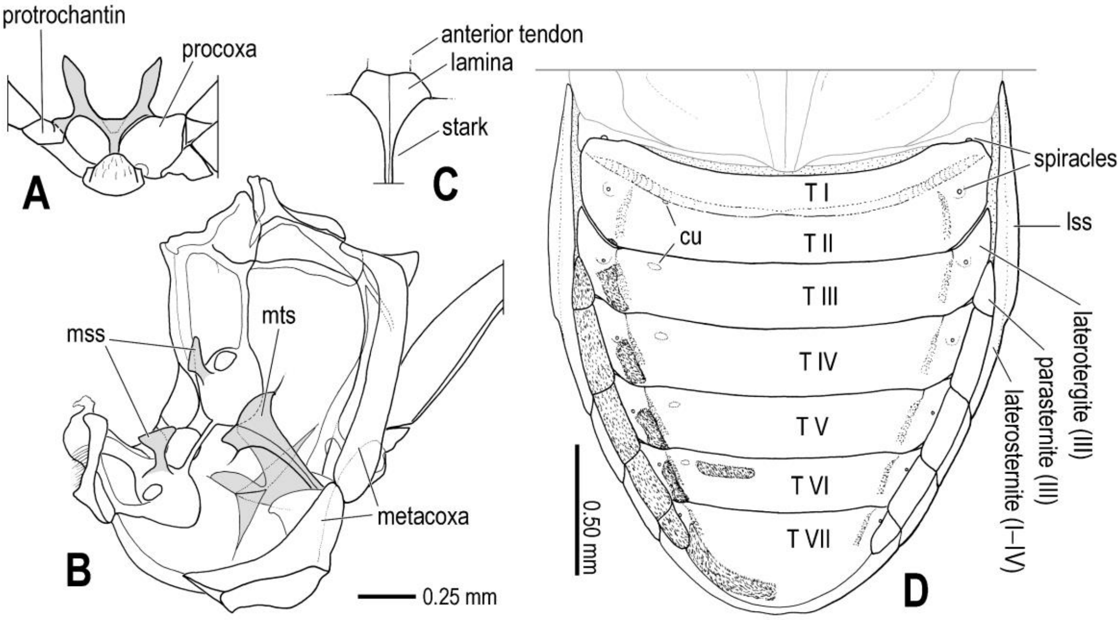


FIGURE 8. Thoracic endoskeleton and abdominal segments, *Trachys minutus* (Linnaeus). —— A) profurca (shown as darker shade area), caudal view; B) ventrites and pleura in meso and metathoraces (except right side metapleuron) and metacoxae, internally oblique view (darker shade area indicates endoskeltal structures of ventrites); C) metendosternite, dorsal view; D) abdomen, dorsal view. Abbreviations: cu — cuticularium; lsp — lateral sternal projection; lss — laterosternal sulcus; mss — mesendosternite; mst — metendosternite.

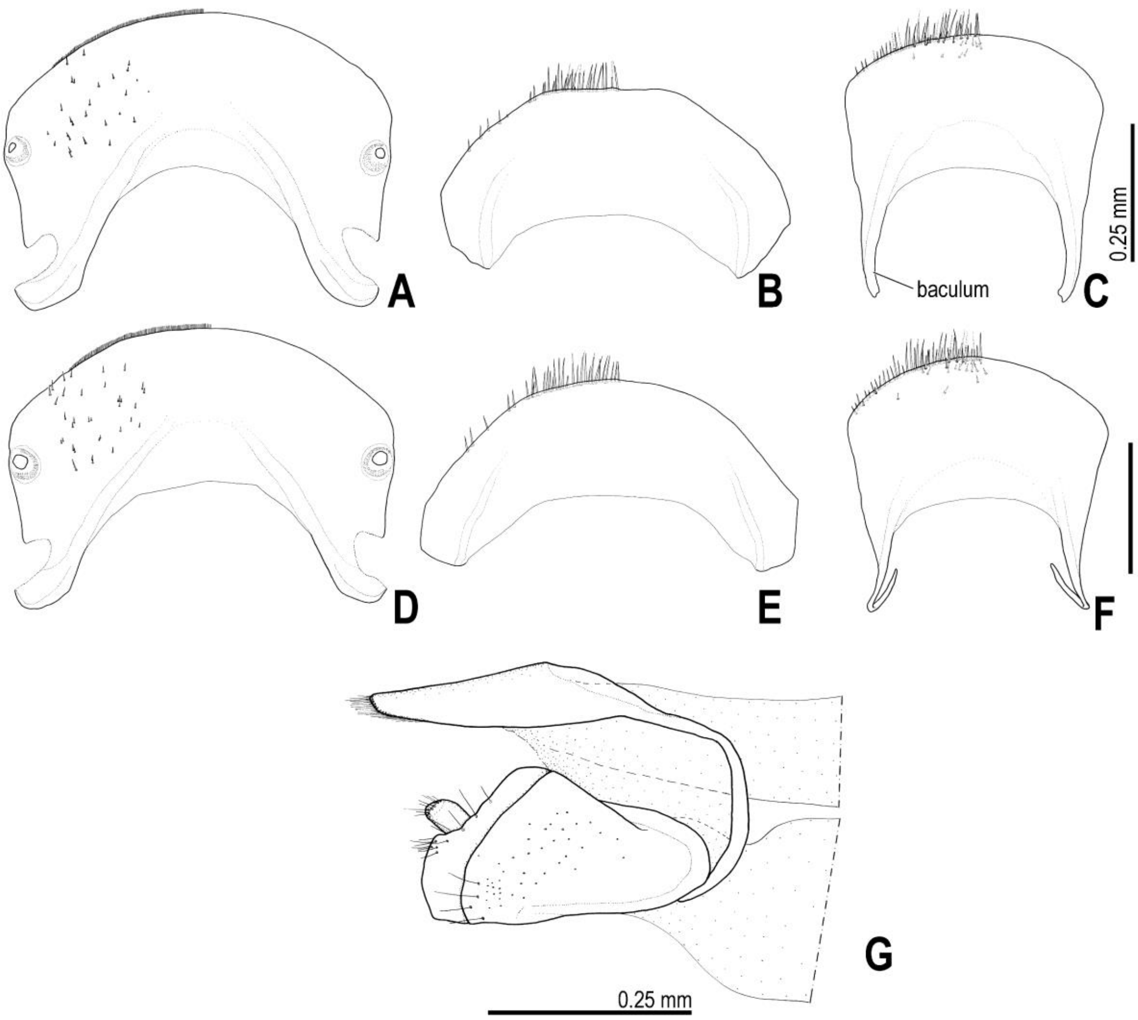


FIGURE 9. Male and female terminalia (part) of *Trachys*., *T. minutus* (Linnaeus). —— A, D) Tergite VIII, male (A) and female (D); B, E) sternite VIII, male (B) and female (E); C, F) proctiger, male (C) and female (F); G) female ovipositors (external part), lateral view.

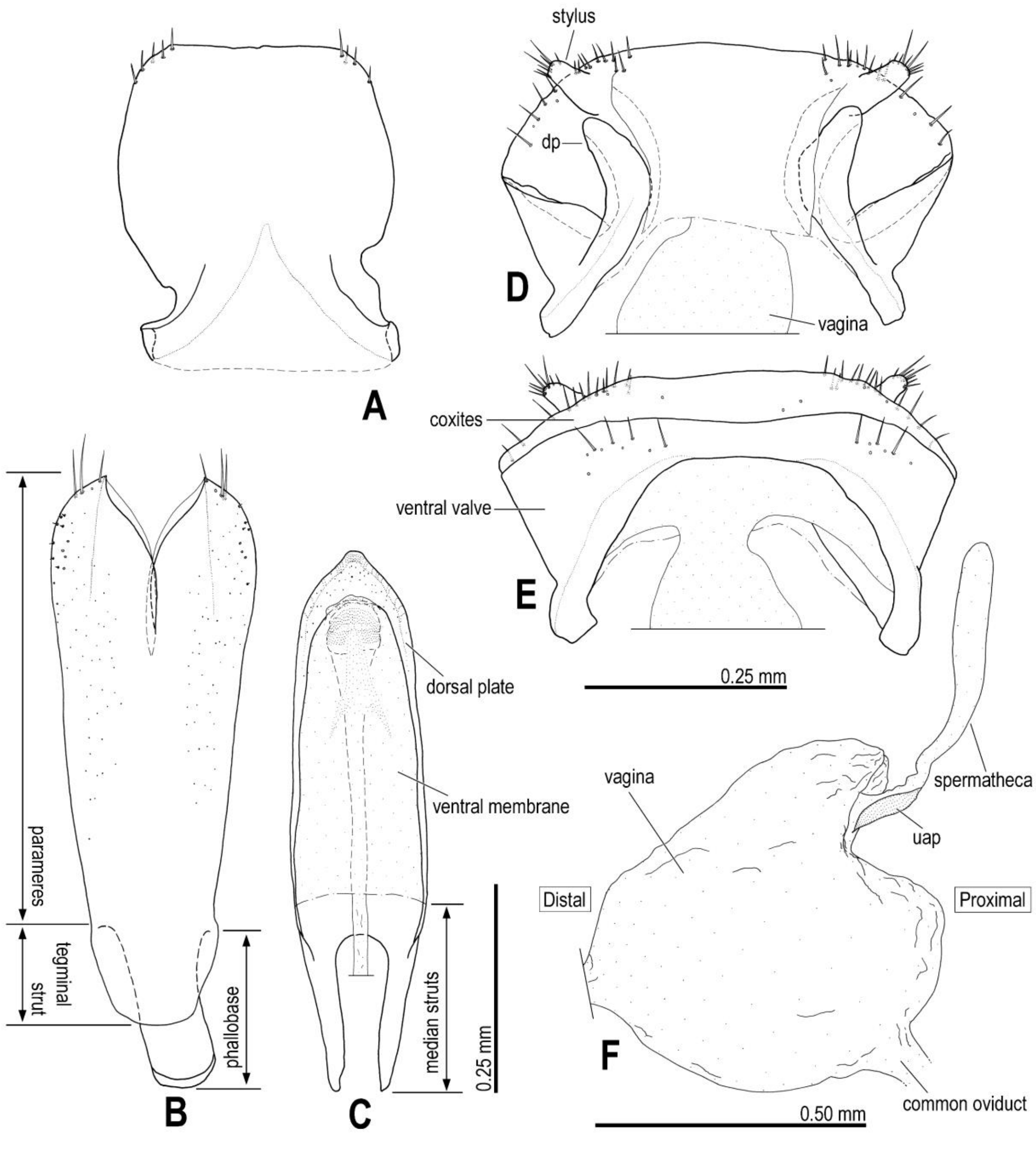


FIGURE 10. Male and female terminalia (part), *Trachys minutus* (Linnaeus). —— A) Sternite IX, male; B) tegmen; C) penis; D, E) external part of ovipositor (except proctiger), dorsal view (D) and ventral view (E); F) internal part of ovipositor, lateral view. Abbreviations: dp — dorsal projection of baculum; uap — unpigmented accessary portion.

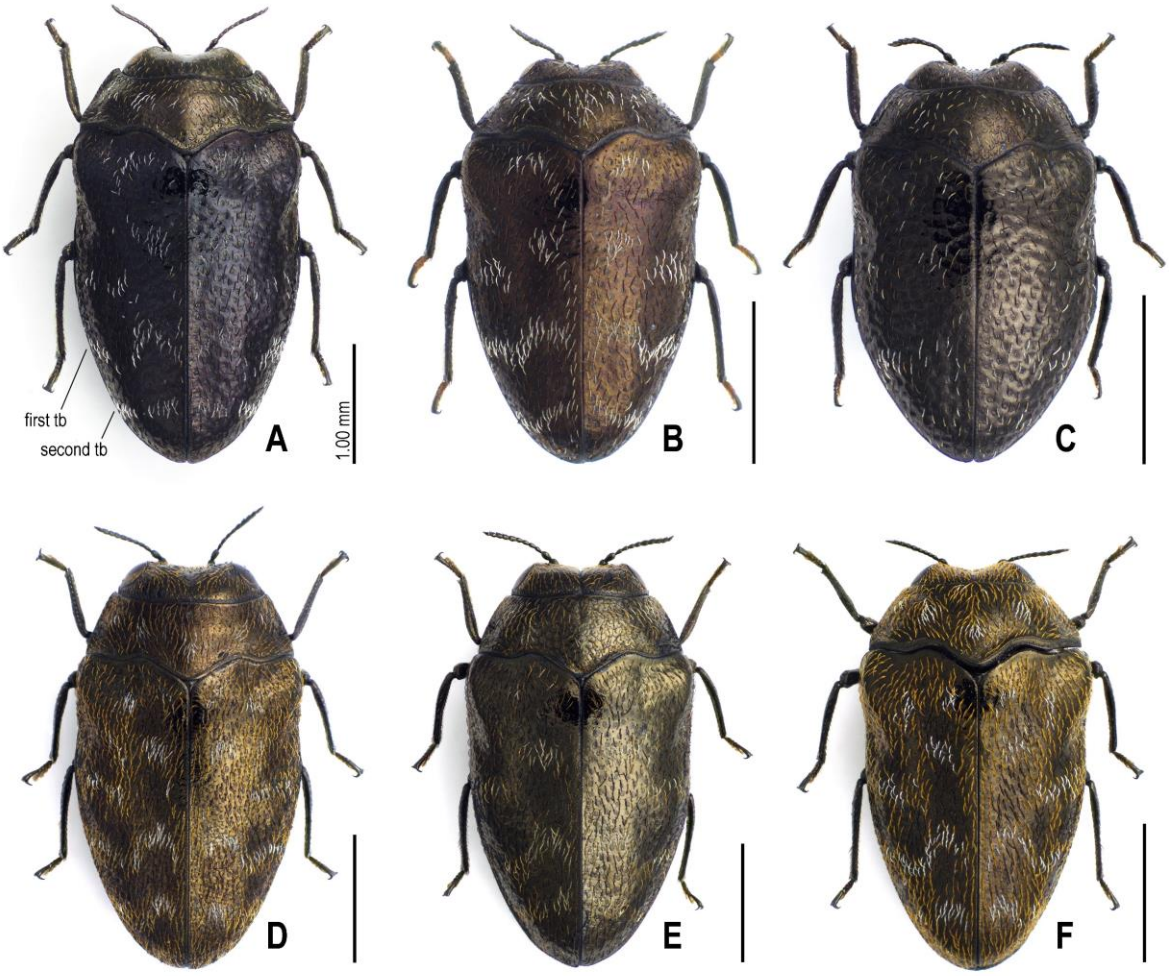


FIGURE 11. Dorsal habitus of Japanese *Trachys* spp. in the tentative species-group I. —— A) *Trachys minutus* (Linnaeus); B) *T. inconspicuus* Saunders; C) *T. pseudoscrobiculatus* Obenberger; D) *T. ineditus* Saunders; E) *T. tsushimae* Obenberger; F) *T. broussonetiae* Kurosawa. Abbreviation: tb — transverse band.

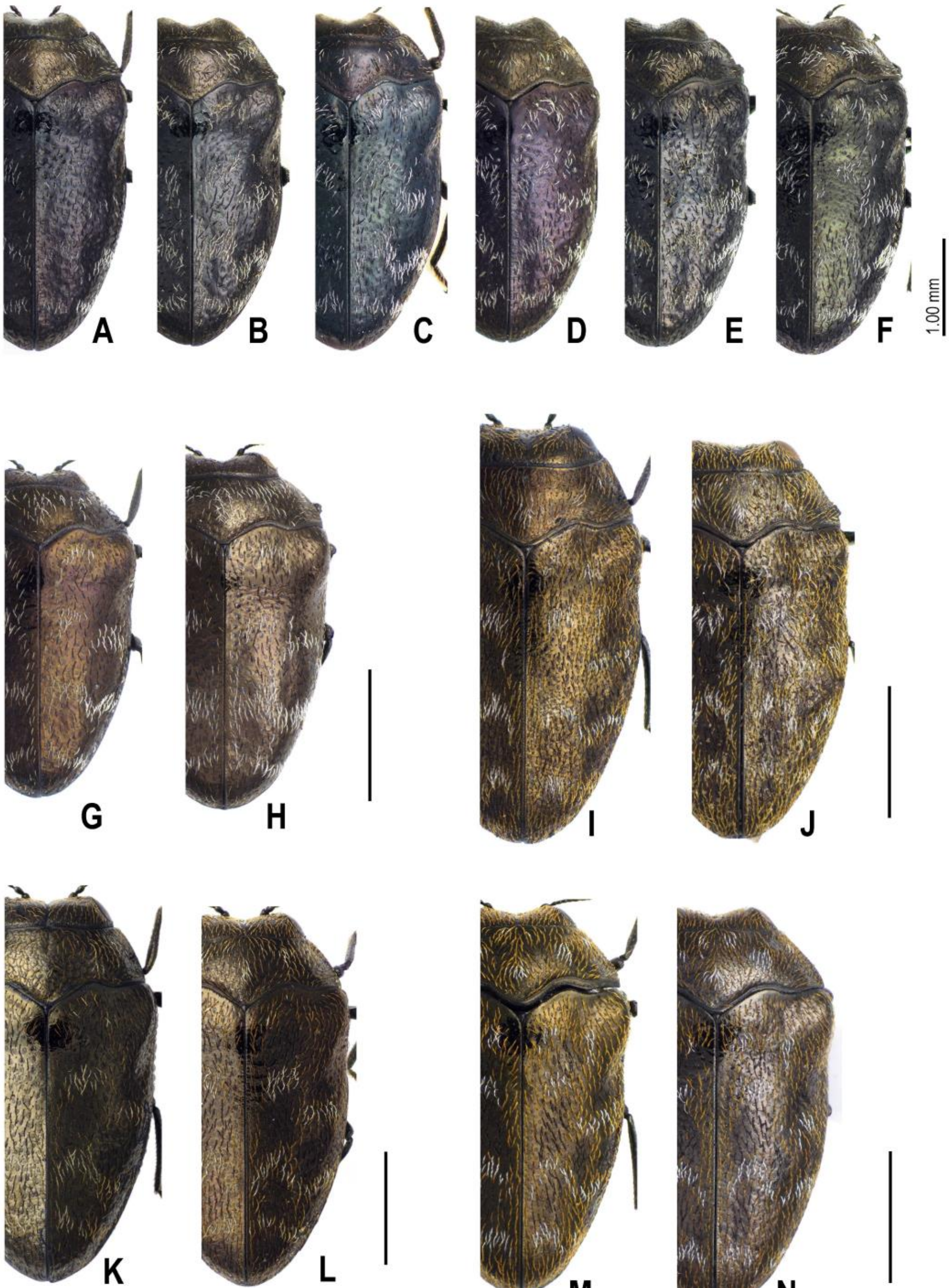


FIGURE 12. Variations in dorsal habitus (part) of Japanese *Trachys* spp. in the tentative species-group I. —— A–F) *Trachys minutus* (Linnaeus) from Japan (A–C), South Korea (D), France (E), and Italy (F); G, H) *T. inconspicuus* Saunders; I, J) *T. ineditus* Saunders; K, L) *T. tsushimae* Obenberger; M, N) *T. broussonetiae* Kurosawa.

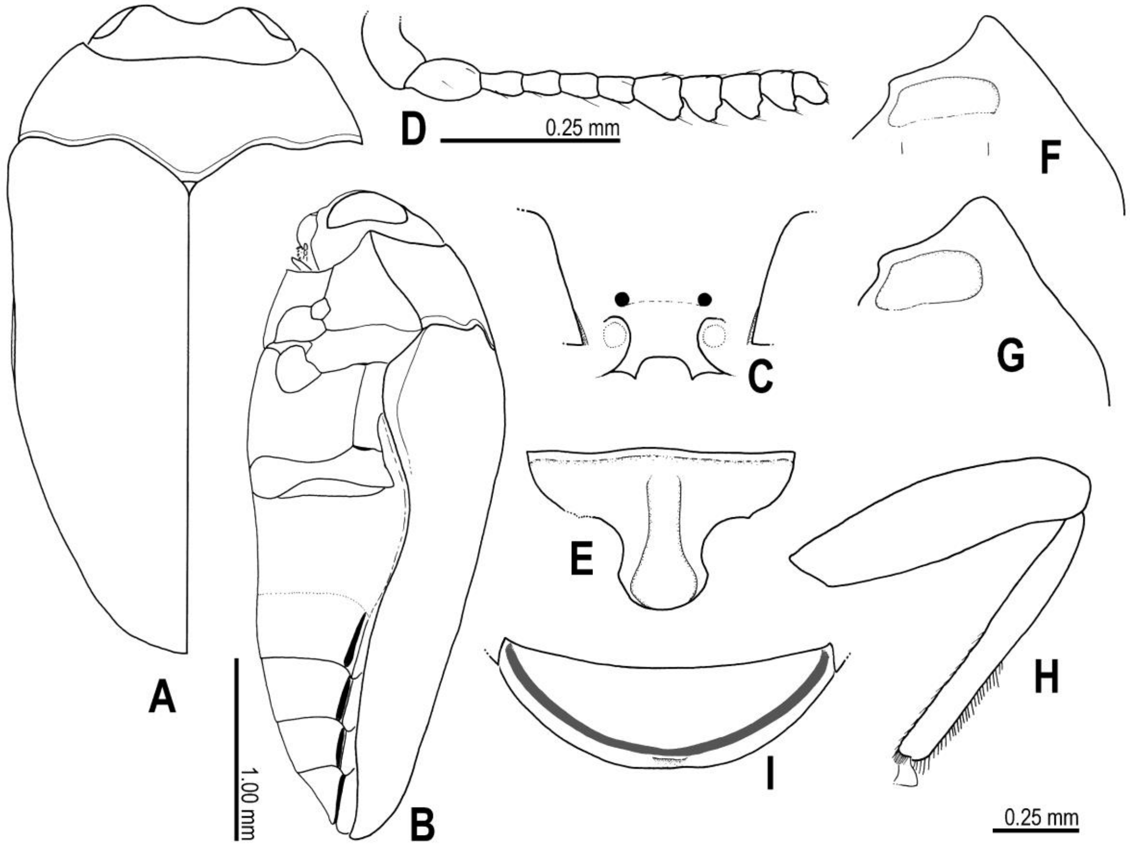


FIGURE 13. *Trachys minutus* (Linnaeus). —— A) Head, pronotum, and left elytron; B) body, lateral view; C) clypeus; D) antenna, outer side; E) prosternum; F, G) hypomeral markings, oblique view; H) metaleg (femur and tibia), ventral view; I) abdominal ventrite V.

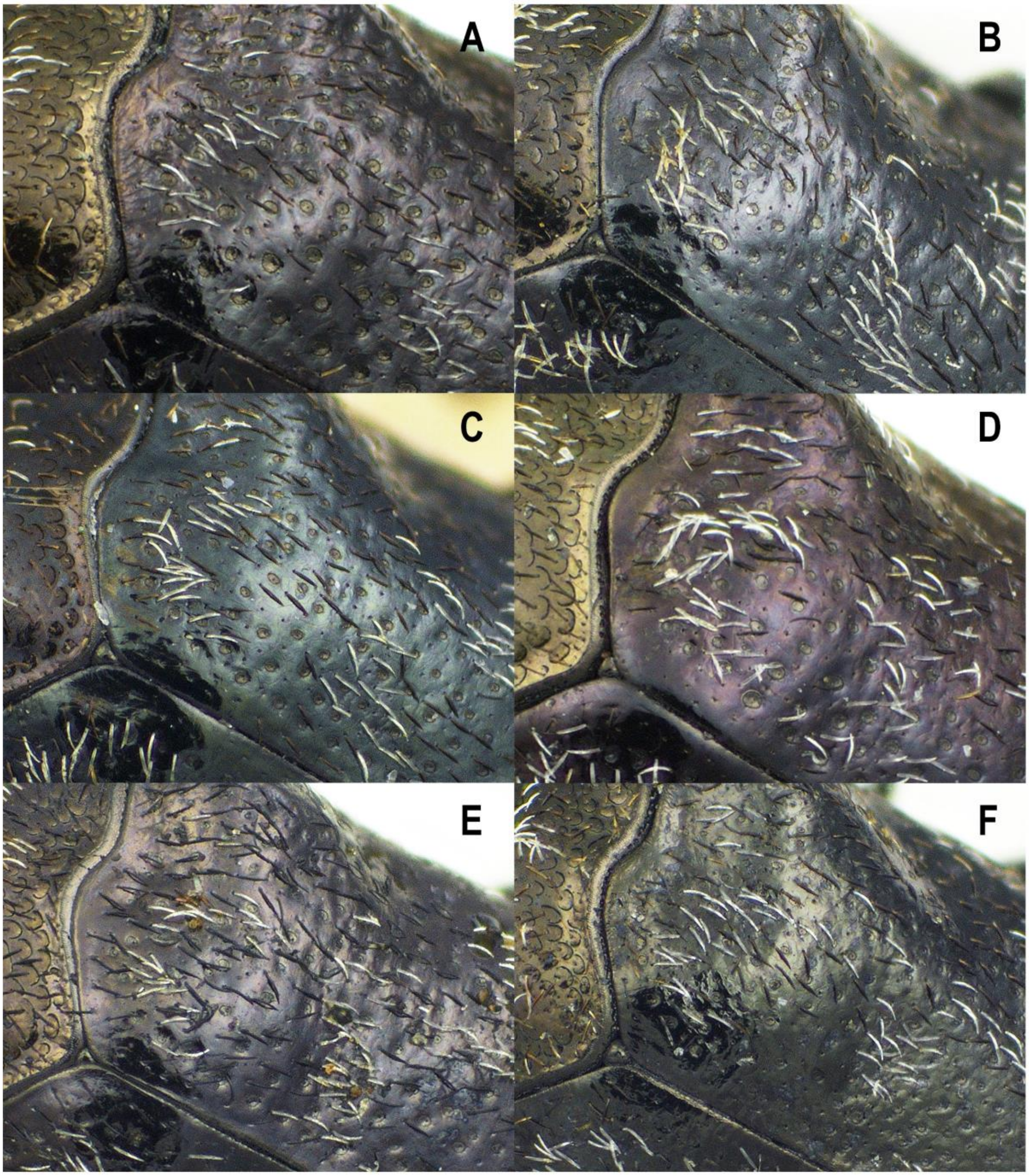


FIGURE 14. Basal elytral surfaces of *Trachys minutus* (Linnaeus), oblique view. —— A–C) Japan; D) South Korea; E) France; F) Italy.

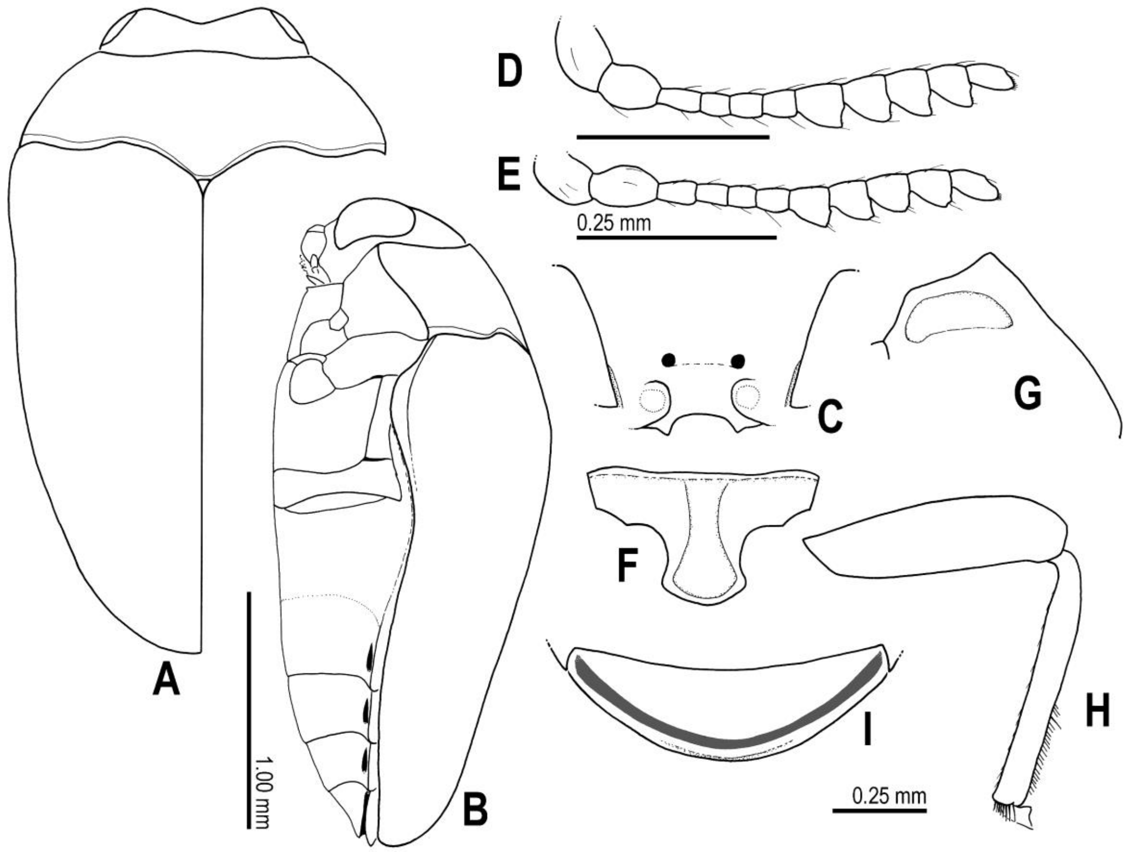


FIGURE 15. *Trachys inconspicuus* Saunders. —— A) Head, pronotum, and left elytron; B) body, lateral view; C) clypeus; D, E) antennae, outer side, male (D) and female (E); F) prosternum; G) hypomeral marking, oblique view; H) metaleg (femur and tibia), ventral view; I) abdominal ventrite V.

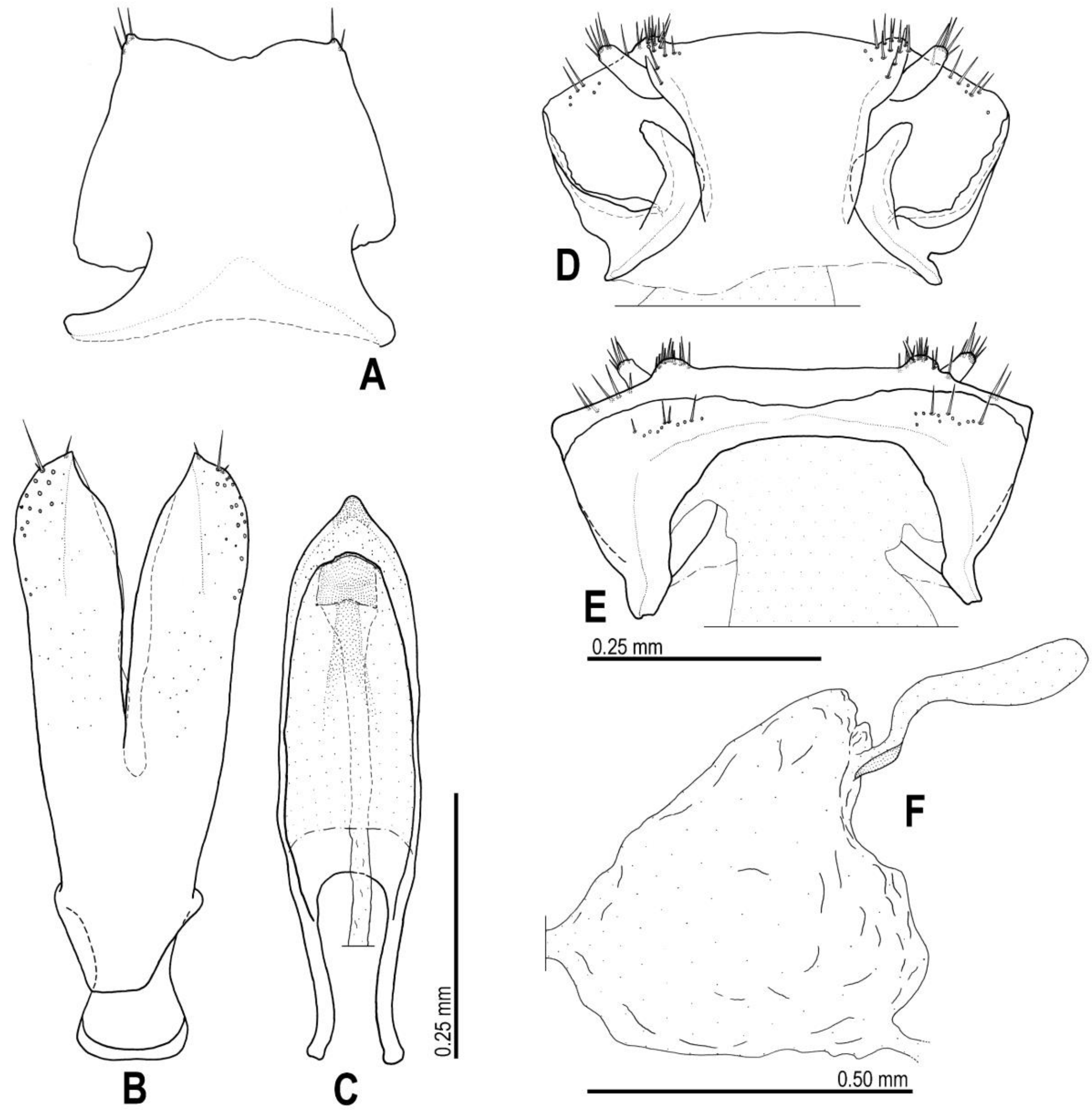


FIGURE 16. Male and female terminalia (part), *Trachys inconspicuus* Saunders. —— A) Sternite IX, male; B) tegmen; C) penis; D, E) external part of ovipositor (except proctiger), dorsal view (D) and ventral view (E); F) internal part of ovipositor, lateral view.

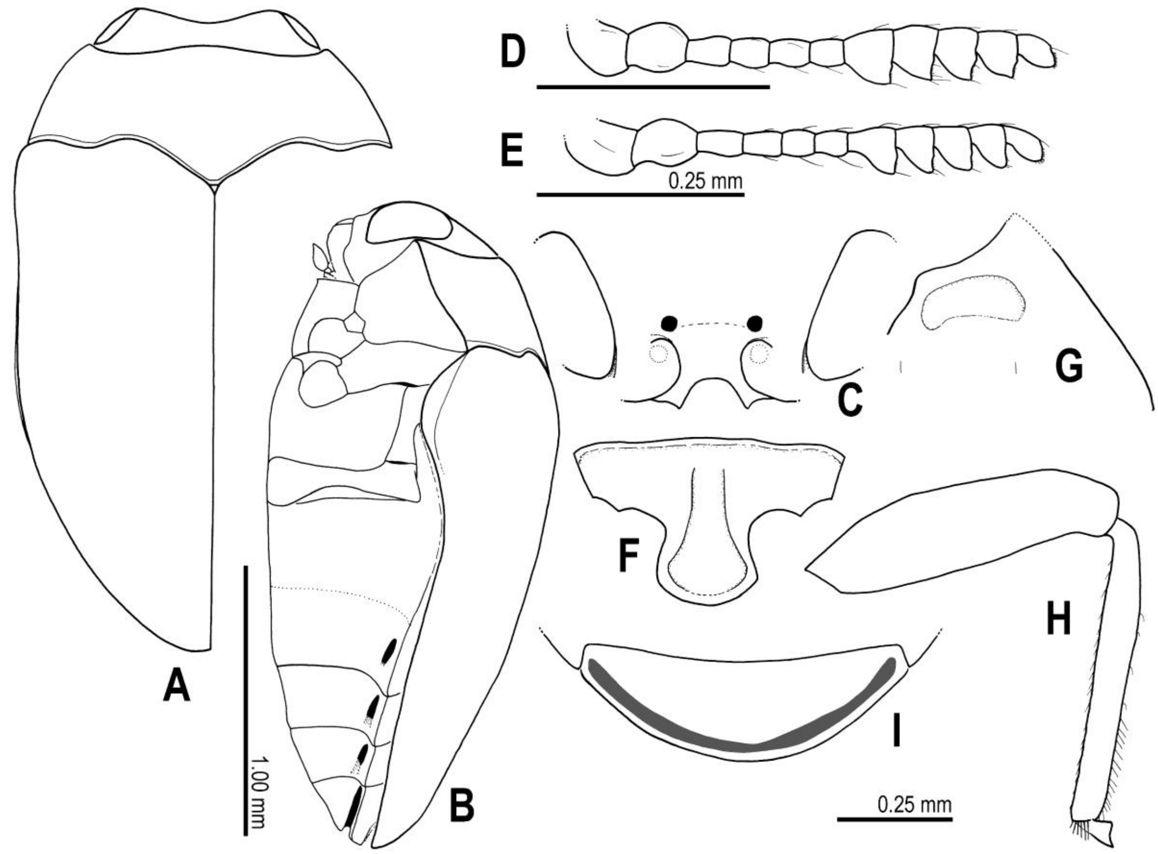


FIGURE 17. *Trachys pseudoscrobiculatus* Obenberger. —— A) Head, pronotum, and left elytron; B) body, lateral view; C) clypeus; D, E) antennae, outer side, male (D) and female (E); F) prosternum; G) hypomeral marking, oblique view; H) metaleg (femur and tibia), ventral view; I) abdominal ventrite V.

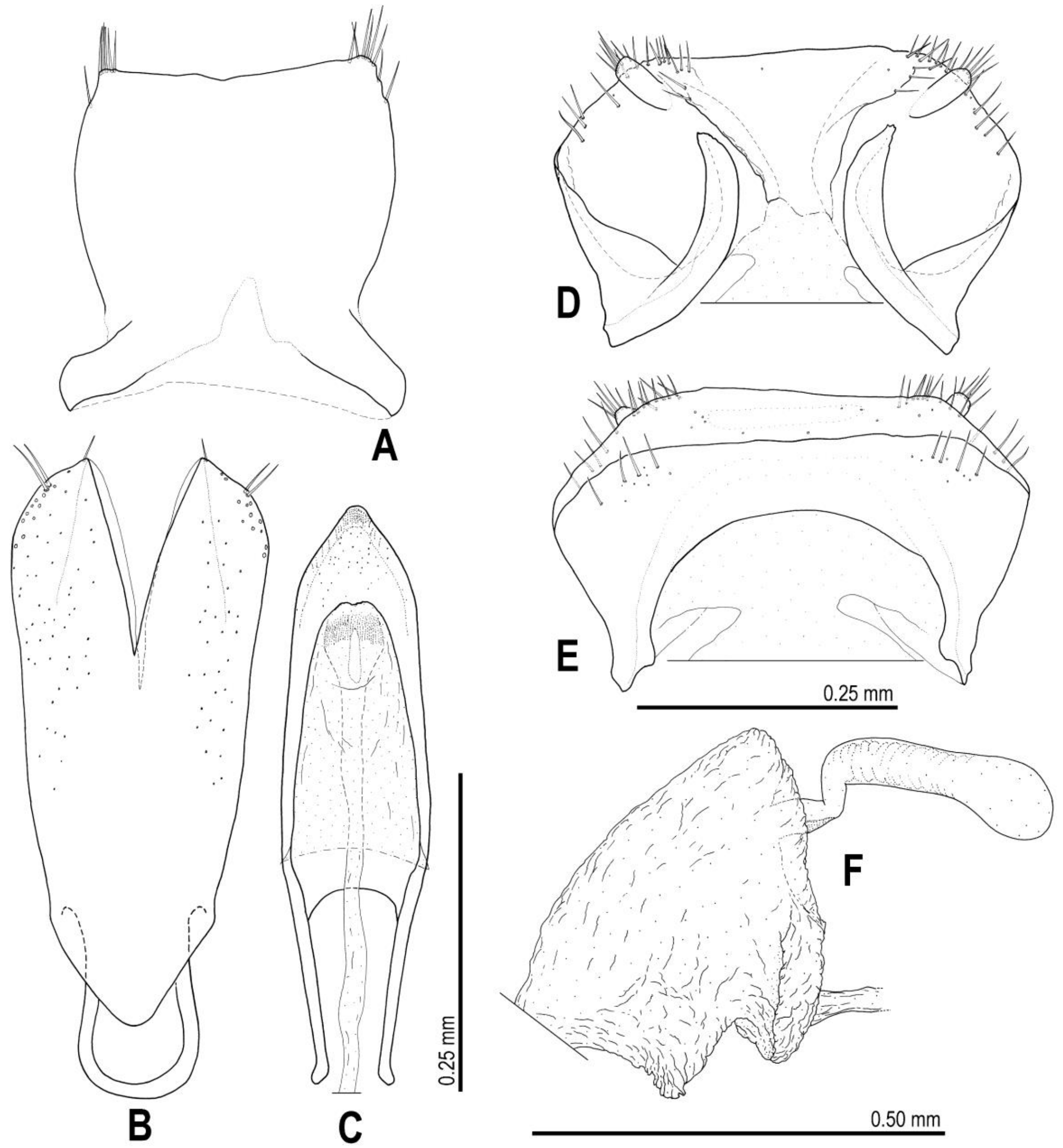


FIGURE 18. Male and female terminalia (part), *Trachys pseudoscrobiculatus* Obenberger. —— A) Sternite IX, male; B) tegmen; C) penis; D, E) external part of ovipositor (except proctiger), dorsal view (D) and ventral view (E); F) internal part of ovipositor, lateral view.

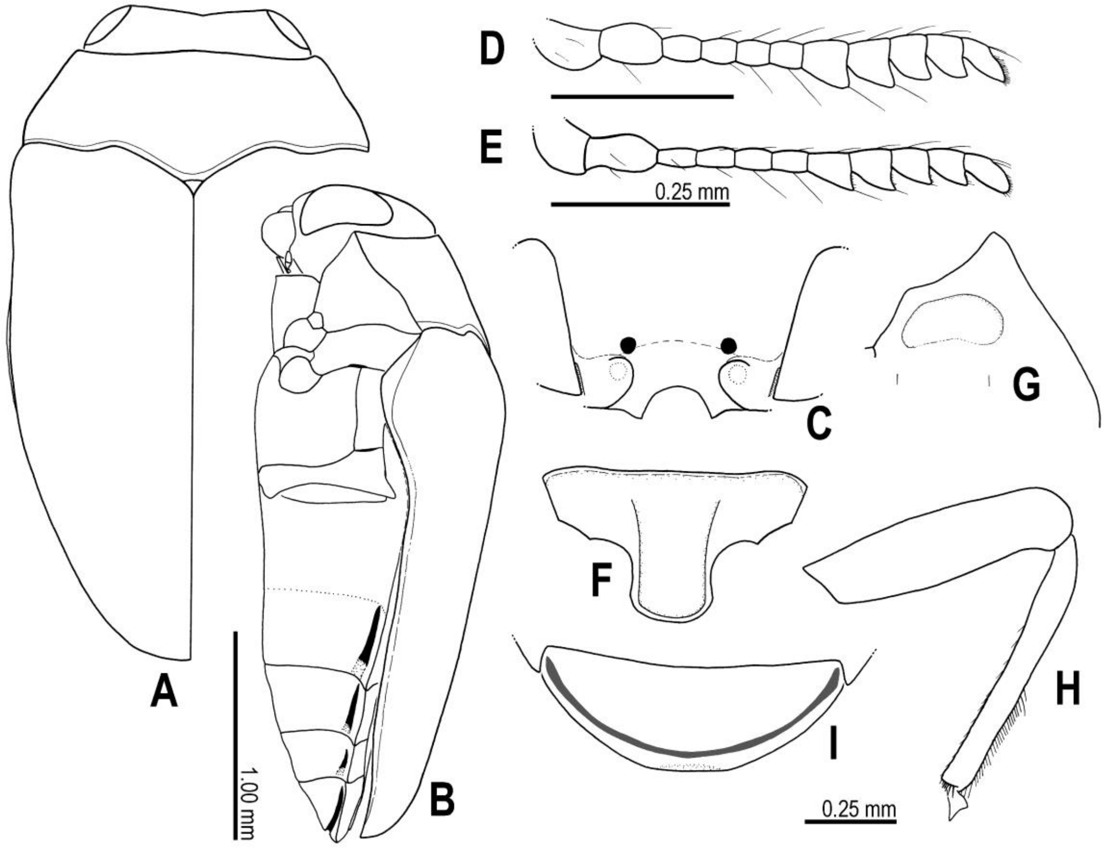


FIGURE 19. *Trachys ineditus* Saunders. —— A) Head, pronotum, and left elytron; B) body, lateral view; C) clypeus; D, E) antennae, outer side, male (D) and female (E); F) hypomeral marking, oblique view; G) prosternum; H) metaleg (femur and tibia), ventral view; I) abdominal ventrite V.

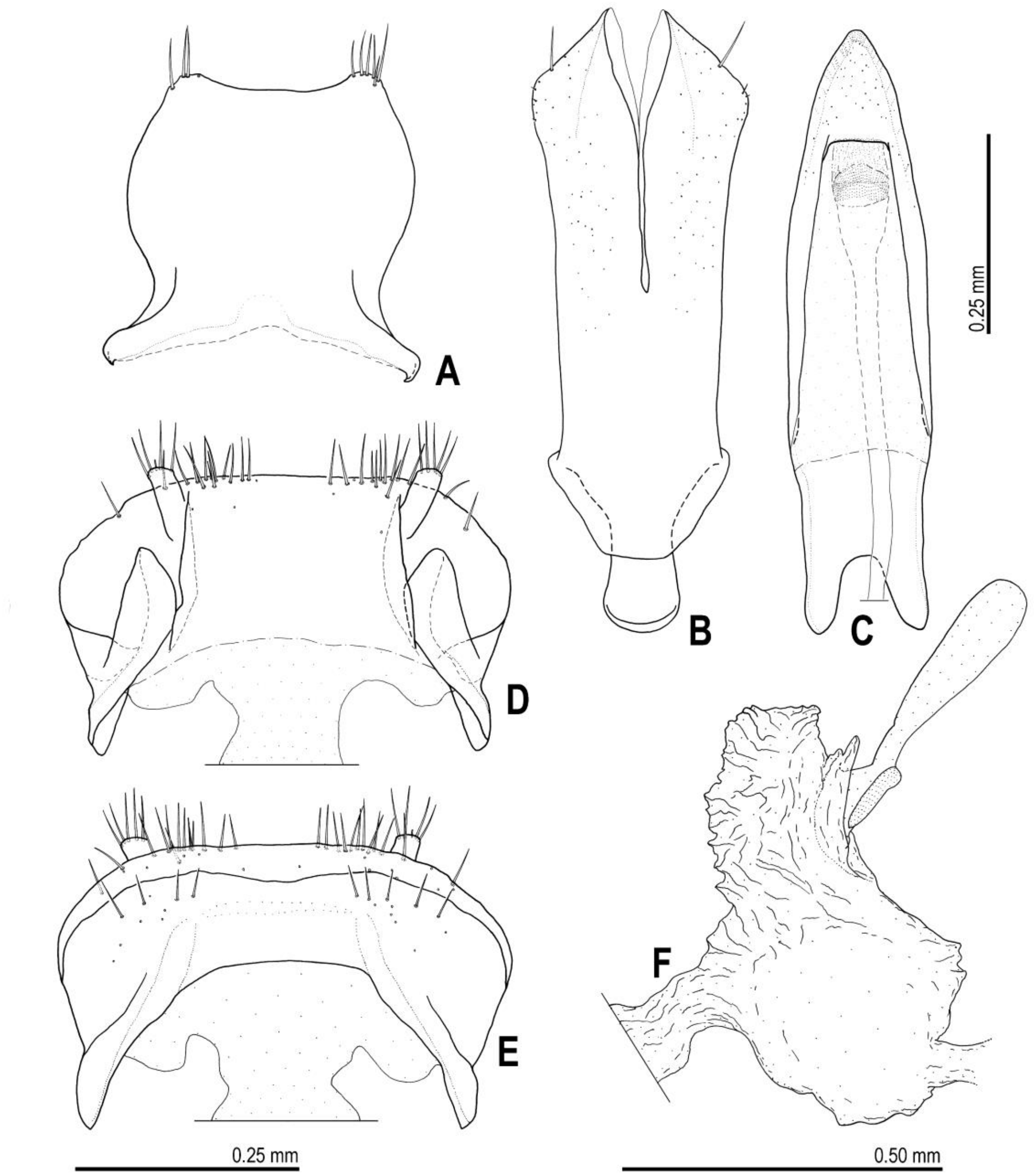


FIGURE 20. Male and female terminalia (part), *Trachys ineditus* Saunders. —— A) Sternite IX, male; B) tegmen; C) penis; D, E) external part of ovipositor (except proctiger), dorsal view (D) and ventral view (E); F) internal part of ovipositor, lateral view.

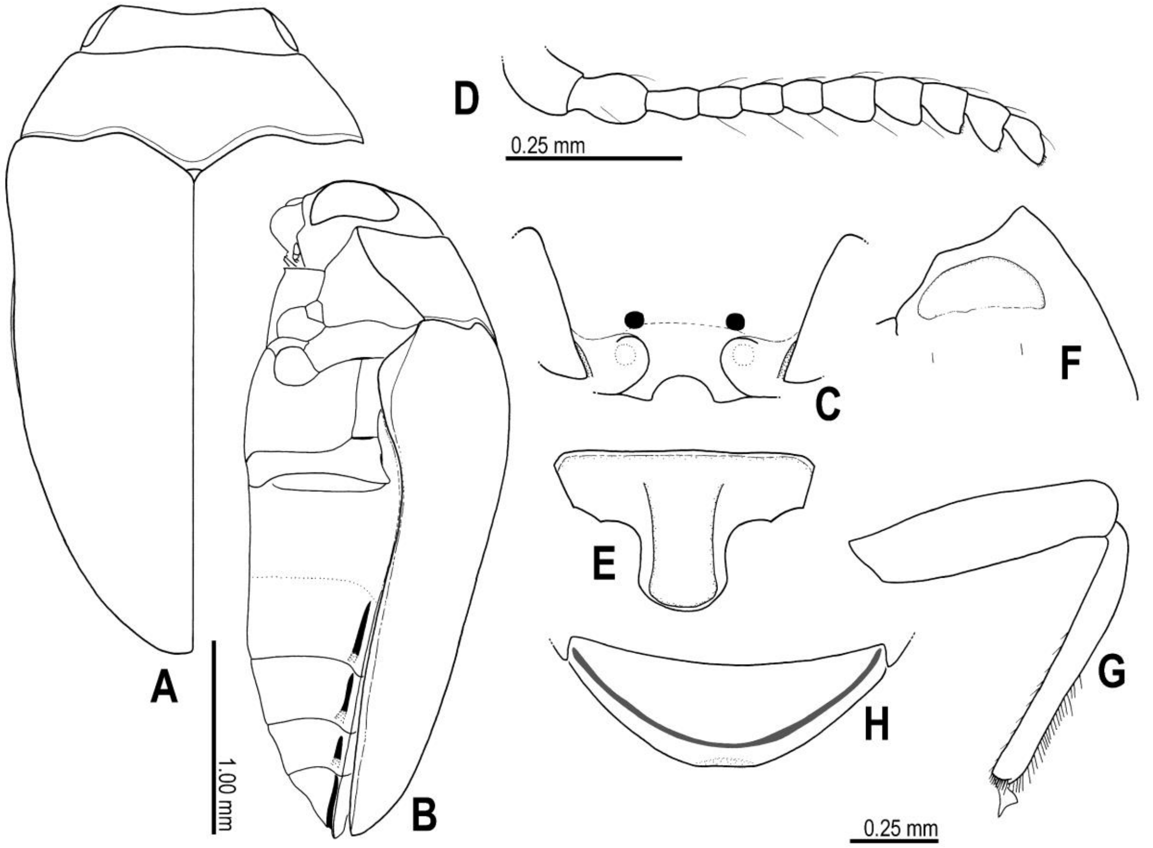


FIGURE 21. *Trachys tsushimae* Obenberger. —— A) Head, pronotum, and left elytron; B) body, lateral view; C) clypeus; D) antenna, outer side; E) prosternum; F) hypomeral marking, oblique view; G) metaleg (femur and tibia), ventral view; H) abdominal ventrite V.

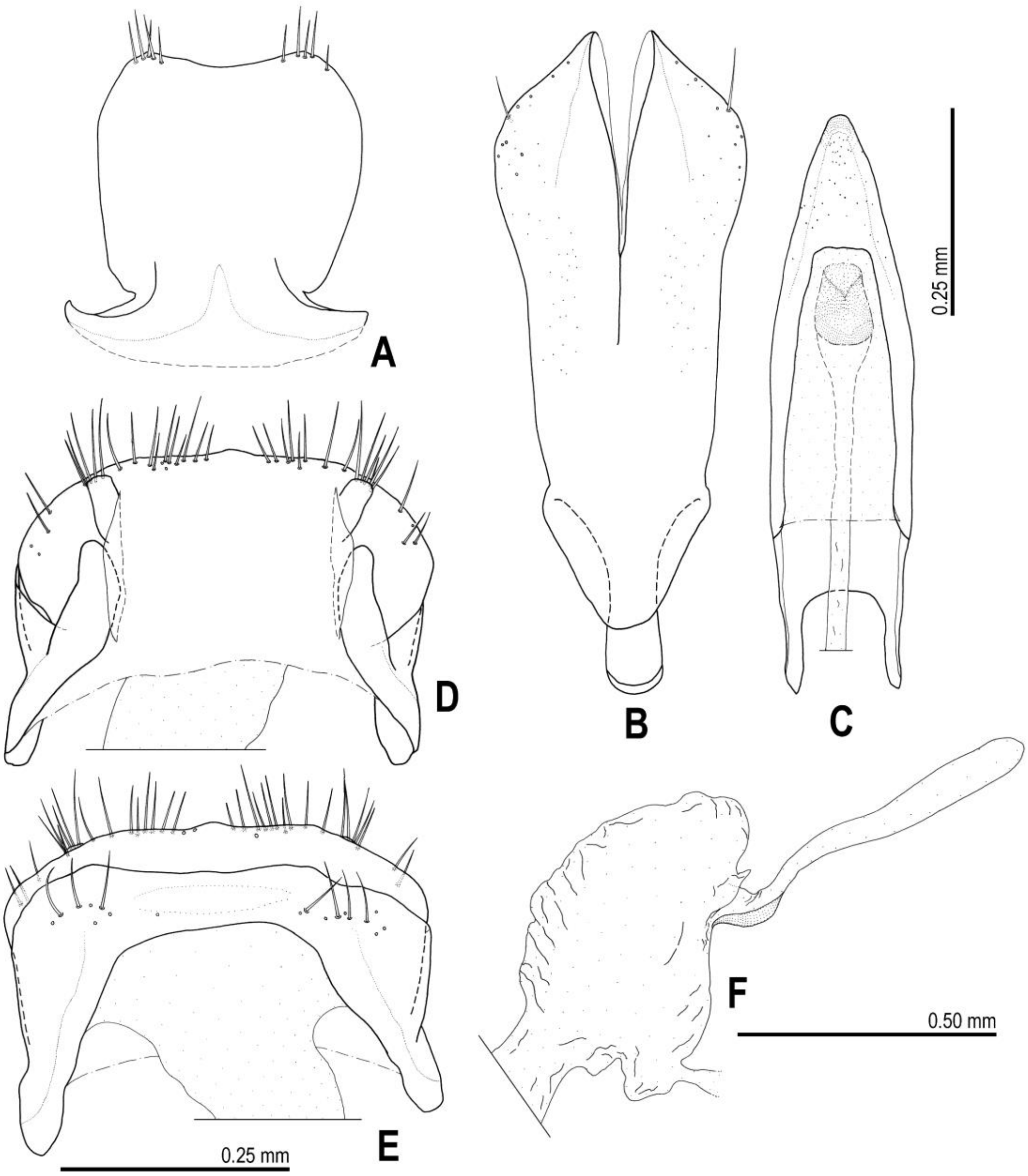


FIGURE 22. Male and female terminalia (part), *Trachys tsushimae* Obenberger. —— A) Sternite IX, male; B) tegmen; C) penis; D, E) external part of ovipositor (except proctiger), dorsal view (D) and ventral view (E); F) internal part of ovipositor, lateral view.

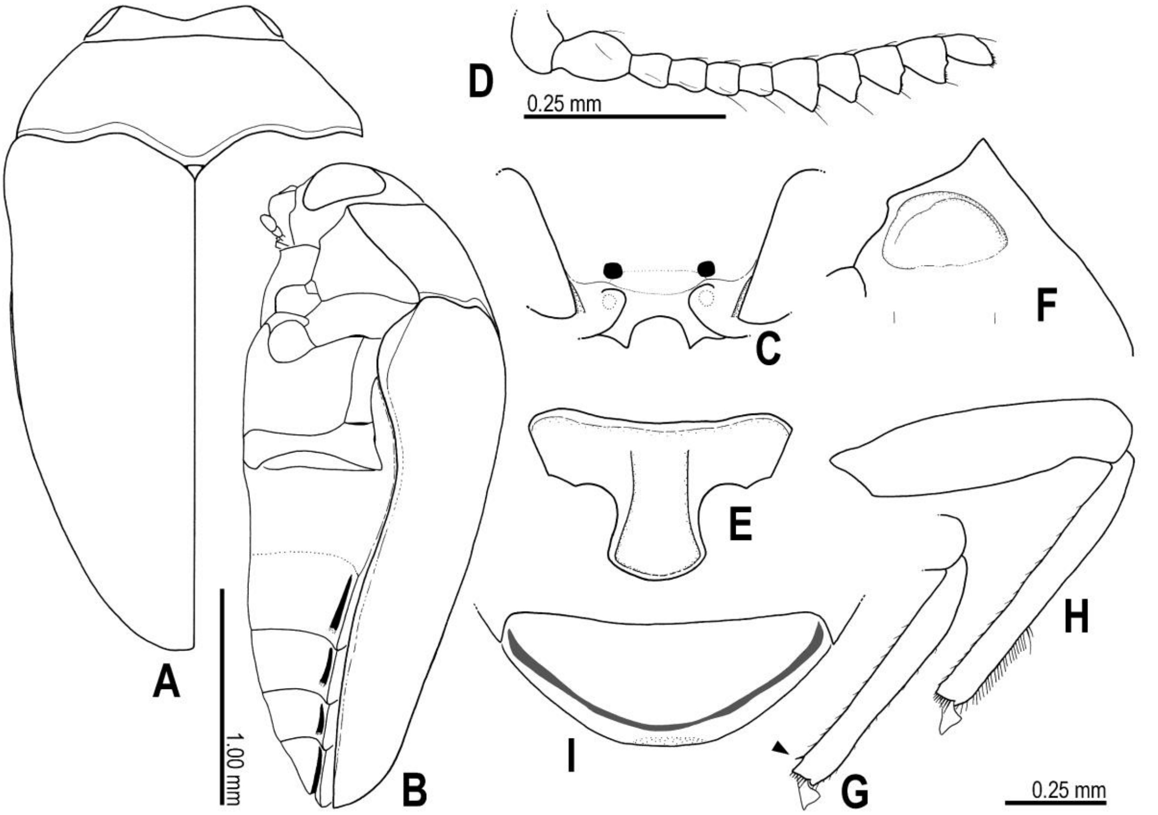


FIGURE 23. *Trachys broussonetiae* Kurosawa. —— A) Head, pronotum, and left elytron; B) body, lateral view; C) clypeus; D) antenna, outer side; E) prosternum; F) hypomeral marking, oblique view; G) mesotibia, ventral view (a black triangular mark indicates erect robust spines); H) metaleg (femur and tibia), ventral view; I) abdominal ventrite V.

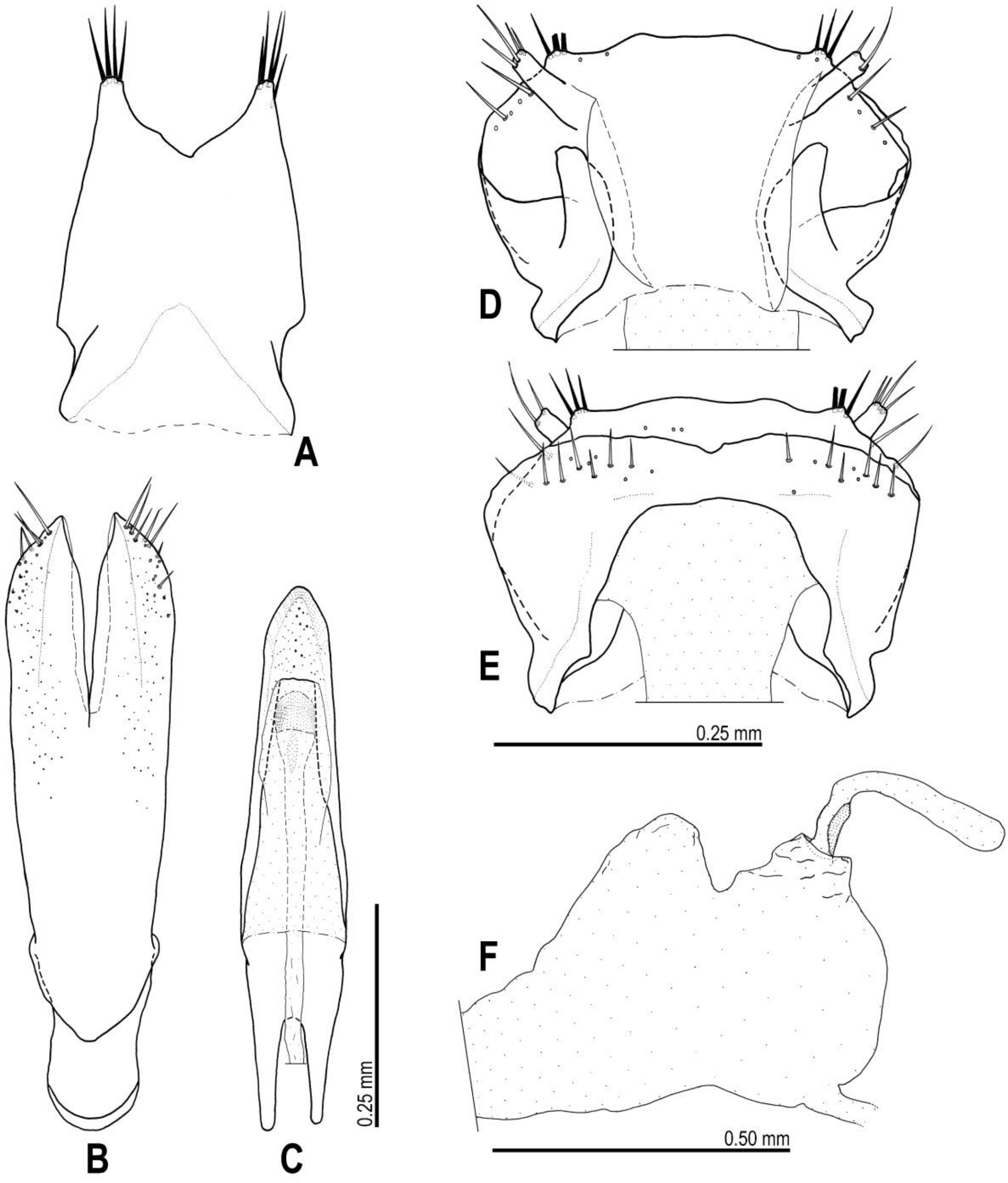


FIGURE 24. Male and female terminalia (part), *Trachys broussonetiae* Kurosawa. —— A) Sternite IX, male; B) tegmen; C) penis; D, E) external part of ovipositor (except proctiger), dorsal view (D) and ventral view (E); F) internal part of ovipositor, lateral view.

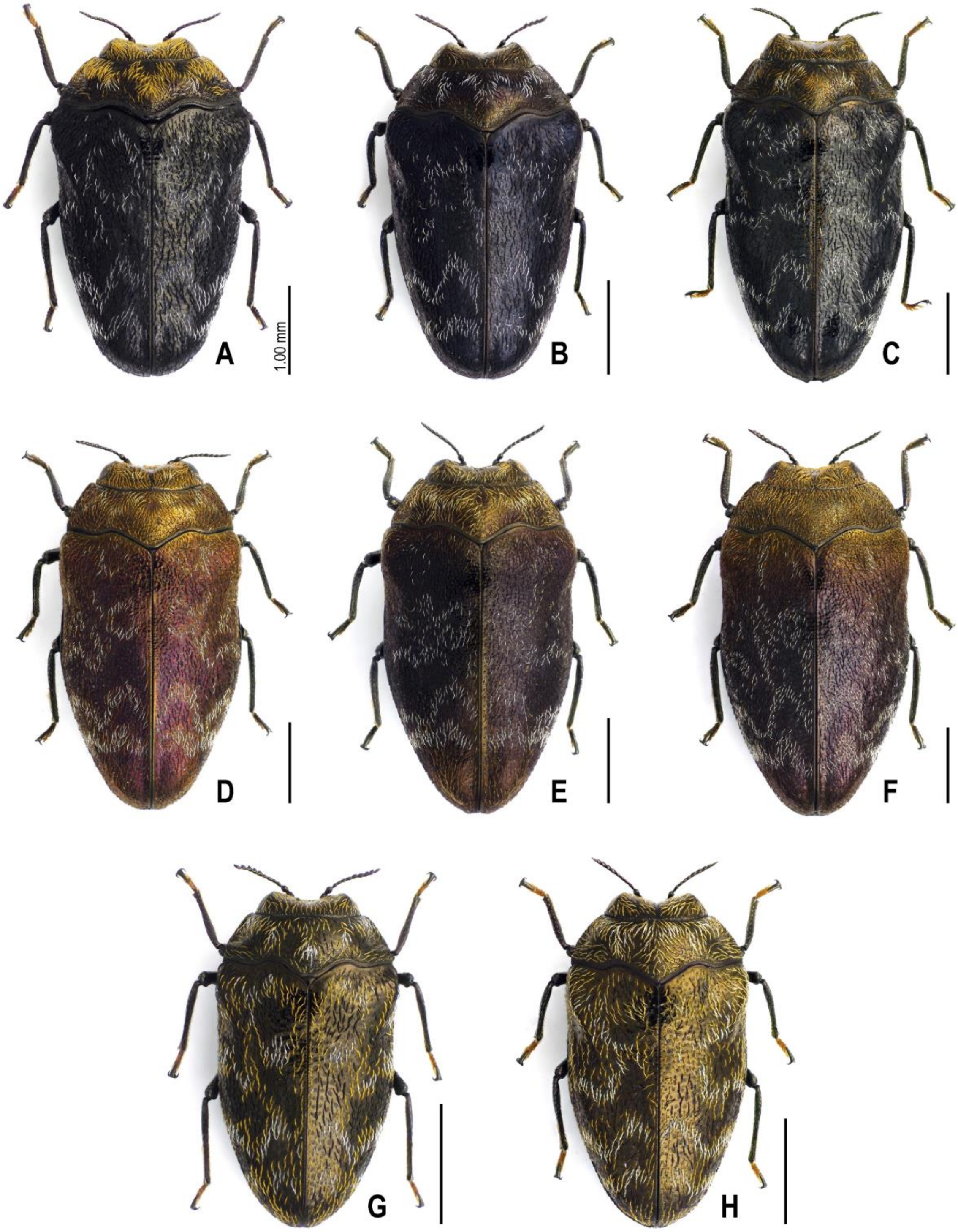


FIGURE 25. Dorsal habitus of Japanese *Trachys* spp. in the tentative species-groups II–V. —— A, B) Group II; C–F) group III; G) group IV; H) group V. —— A) *Trachys auricollis* Saunders; B) *T. toringoi* Kurosawa; C) *T. saundersi* Lewis; D) *T. cupricolor* Saunders; E) *T. pecirkai* Obenberger; F) *T. aurifluus* Solsky; G) *T. reitteri* Obenberger; H) *T. tokyoensis* Obenberger.

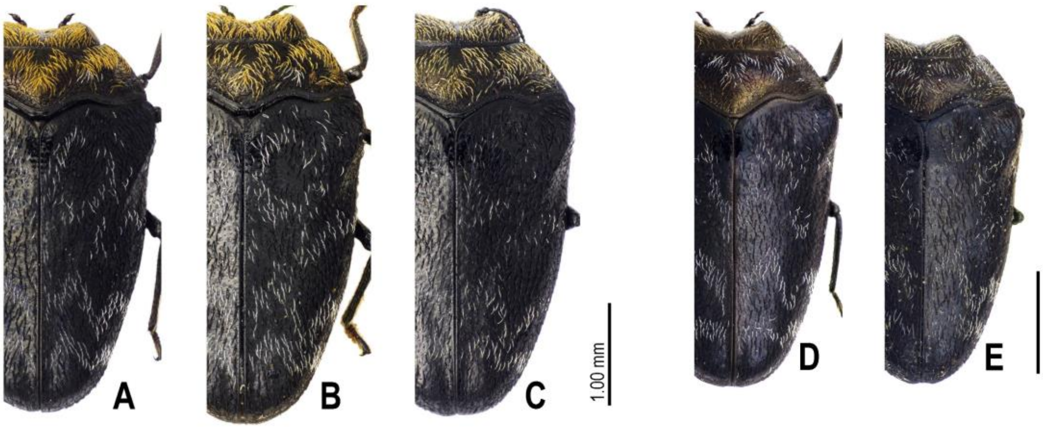


FIGURE 26. Variations in dorsal habitus (part) of Japanese *Trachys* spp. in the tentative species-group II. —— A–C) *Trachys auricollis* Saunders; D, E) *T. toringoi* Kurosawa.

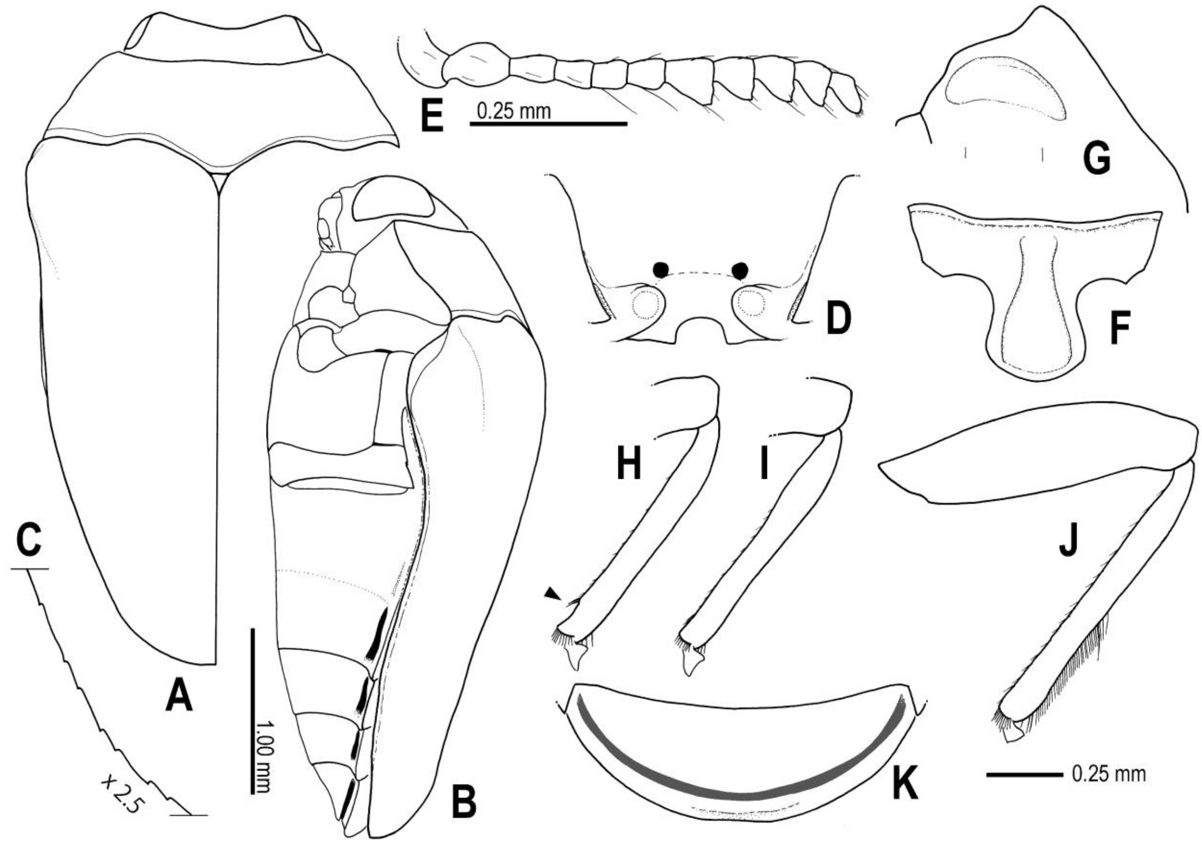


FIGURE 27. *Trachys auricollis* Saunders. —— A) Head, pronotum, and left elytron; B) body, lateral view; C) serration of elytral lateral margin, obliquely ventral view; D) clypeus; E) antenna, outer side; F) prosternum; G) hypomeral markings, oblique view; H, I) mesotibiae, ventral view, male (H) and female (I) (a black triangular mark indicates erect robust spines); J) metaleg (femur and tibia), ventral view; K) abdominal ventrite V.

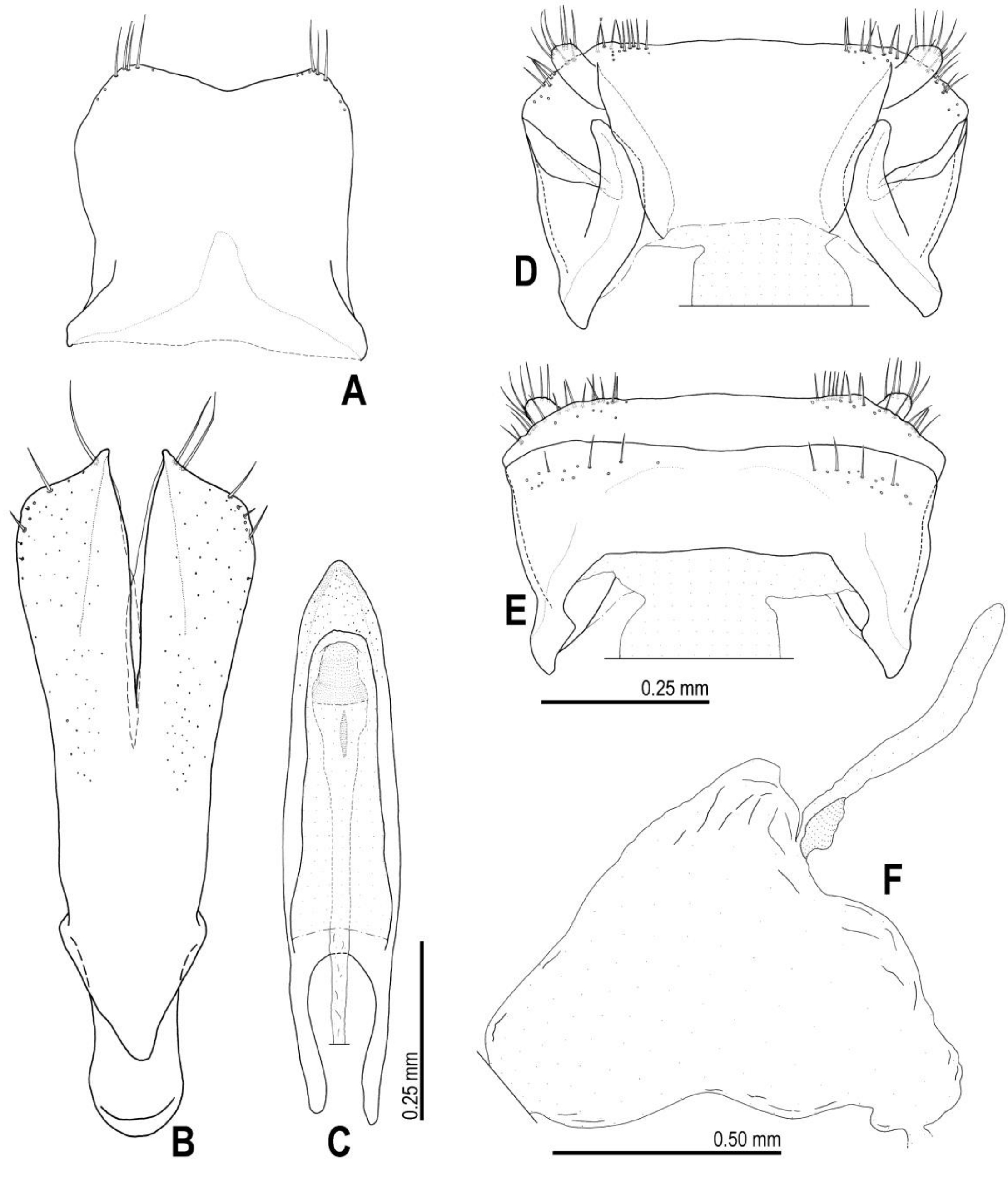


FIGURE 28. Male and female terminalia (part), *Trachys auricollis* Saunders. —— A) Sternite IX, male; B) tegmen; C) penis; D, E) external part of ovipositor (except proctiger), dorsal view (D) and ventral view (E); F) internal part of ovipositor, lateral view.

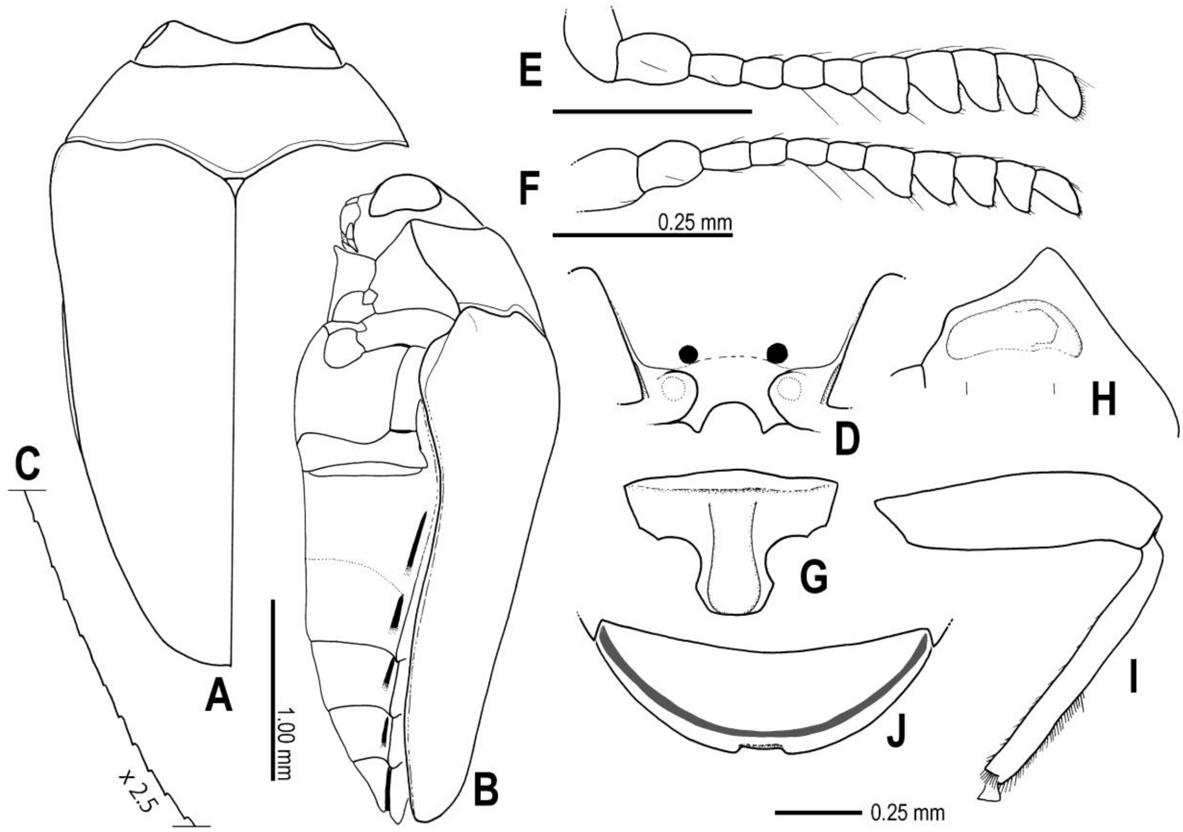


FIGURE 29. *Trachys toringoi* Kurosawa. —— A) Head, pronotum, and left elytron; B) body, lateral view; C) serration of elytral lateral margin, obliquely ventral view; D) clypeus; E, F) antennae, outer side, male (E) and female (F); G) prosternum; H) hypomeral markings, oblique view; I) metaleg (femur and tibia), ventral view; J) abdominal ventrite V.

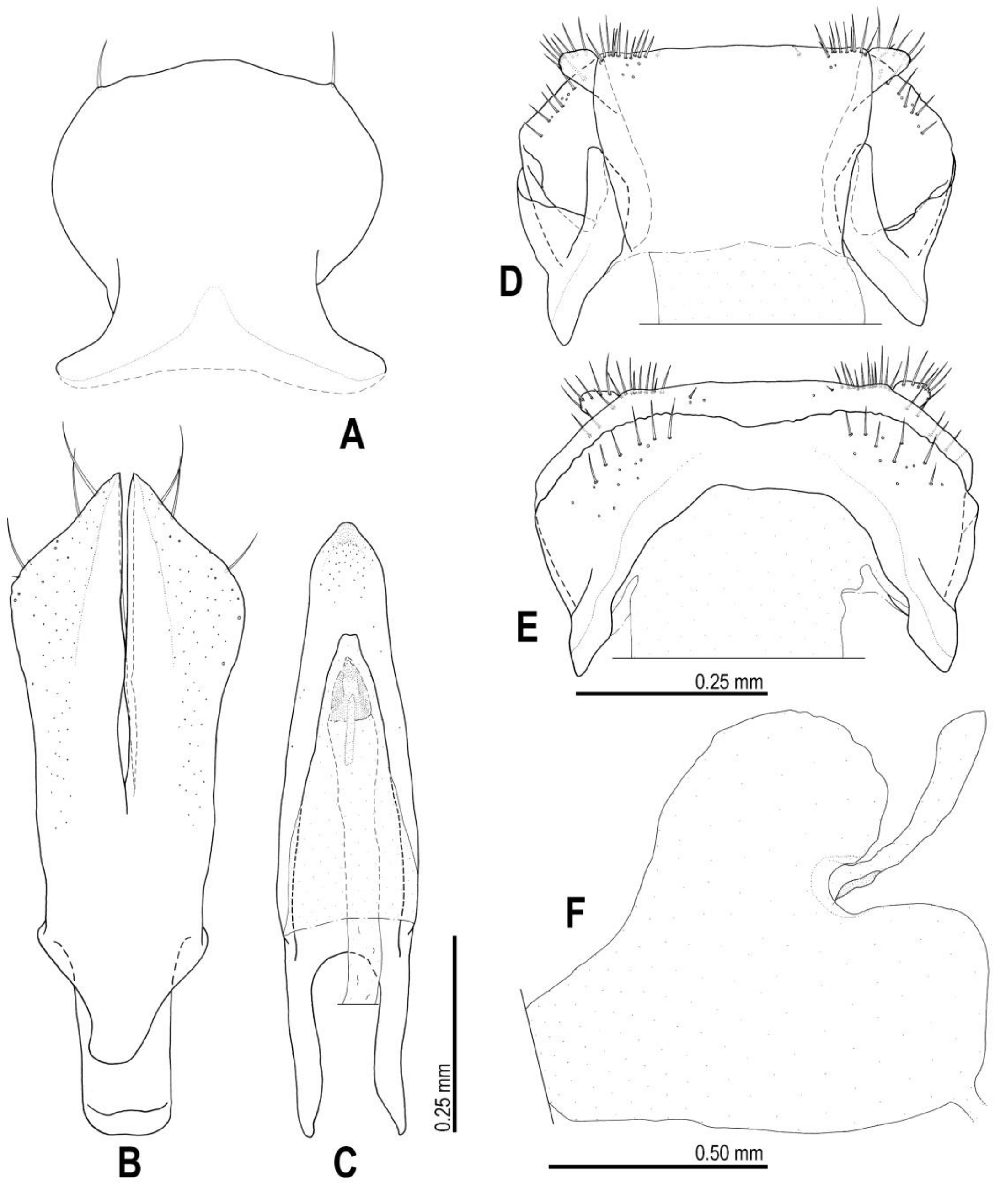


FIGURE 30. Male and female terminalia (part), *Trachys toringoi* Kurosawa. —— A) Sternite IX, male; B) tegmen; C) penis; D, E) external part of ovipositor (except proctiger), dorsal view (D) and ventral view (E); F) internal part of ovipositor, lateral view.

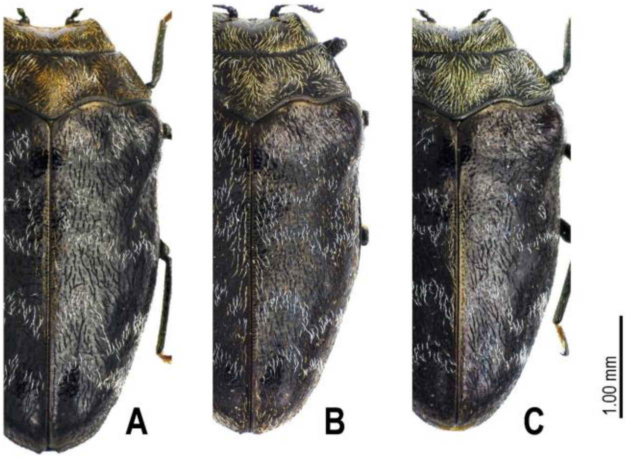


FIGURE 31. Variations in dorsal habitus (part) of *Trachys saundersi* Lewis.

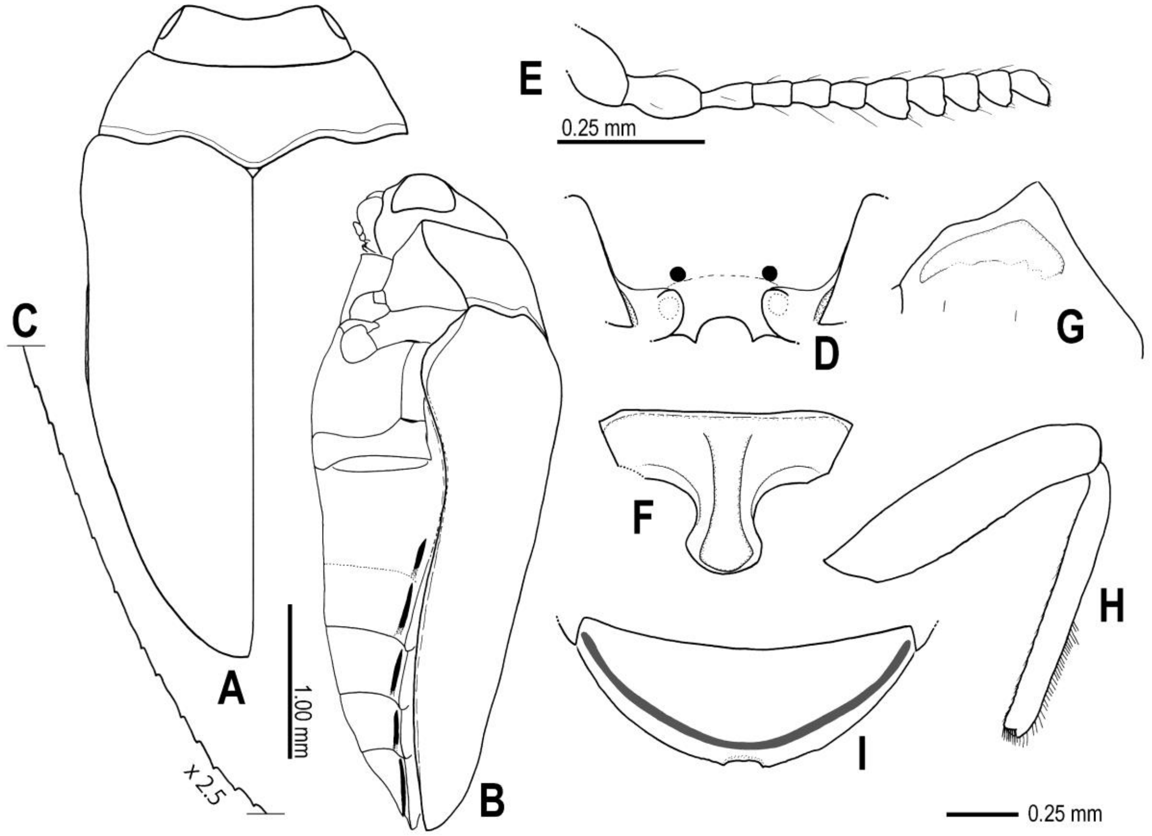


FIGURE 32. *Trachys saundersi* Lewis. ——A) Head, pronotum, and left elytron; B) body, lateral view; C) serration of elytral lateral margin, obliquely ventral view; D) clypeus; E) antenna, outer side; F) prosternum; G) hypomeral markings, oblique view; H) metaleg (femur and tibia), ventral view; I) abdominal ventrite V.

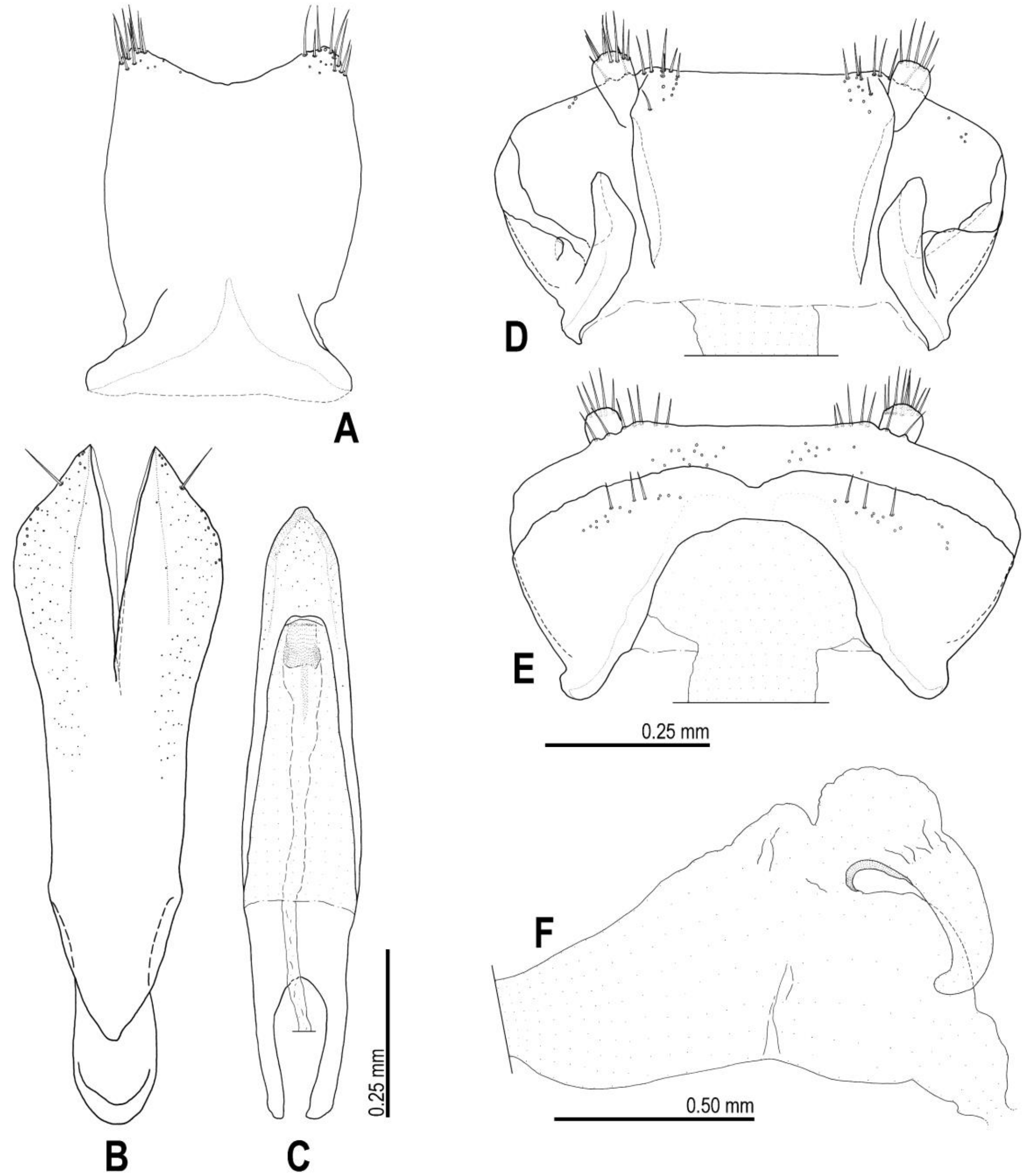


FIGURE 33. Male and female terminalia (part), *Trachys saundersi* Lewis. —— A) Sternite IX, male; B) tegmen; C) penis; D, E) external part of ovipositor (except proctiger), dorsal view (D) and ventral view (E); F) internal part of ovipositor, lateral view.

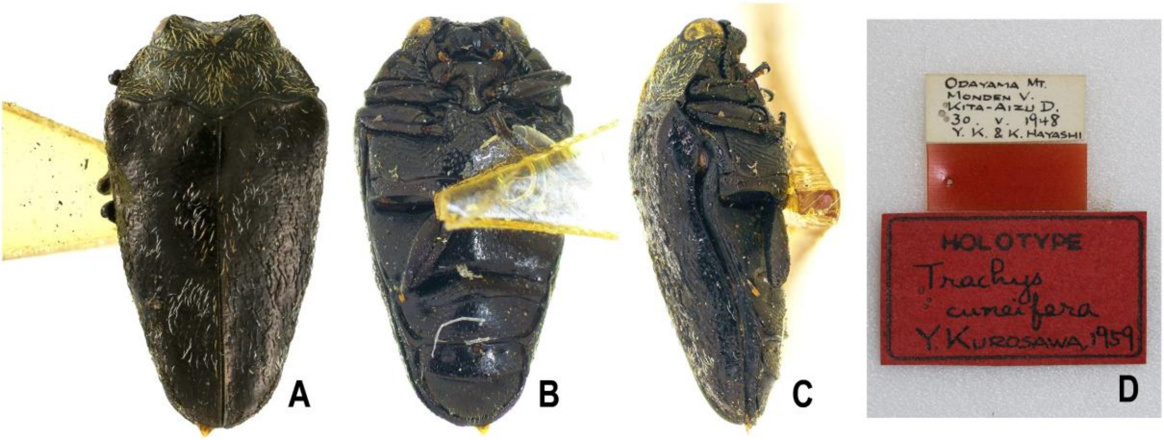


FIGURE 34. Holotype of *Trachys cuneiferus* Kurosawa. —— A) Dorsal habitus; B) ventral habitus; C) lateral habitus; D) pined labels under the specimen.

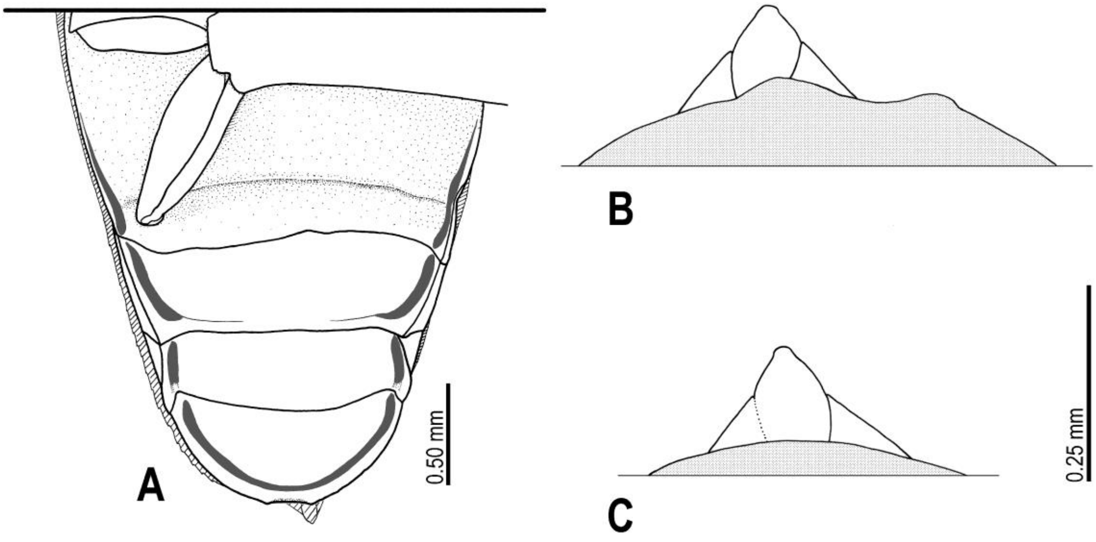


FIGURE 35. Abdominal ventrite and aedeagus of holotype of *Trachys cuneiferus* Kurosawa. —— A) Abdominal ventrite; B, C) apical part of aedeagus, ventral view (B) and dorsal view (C).

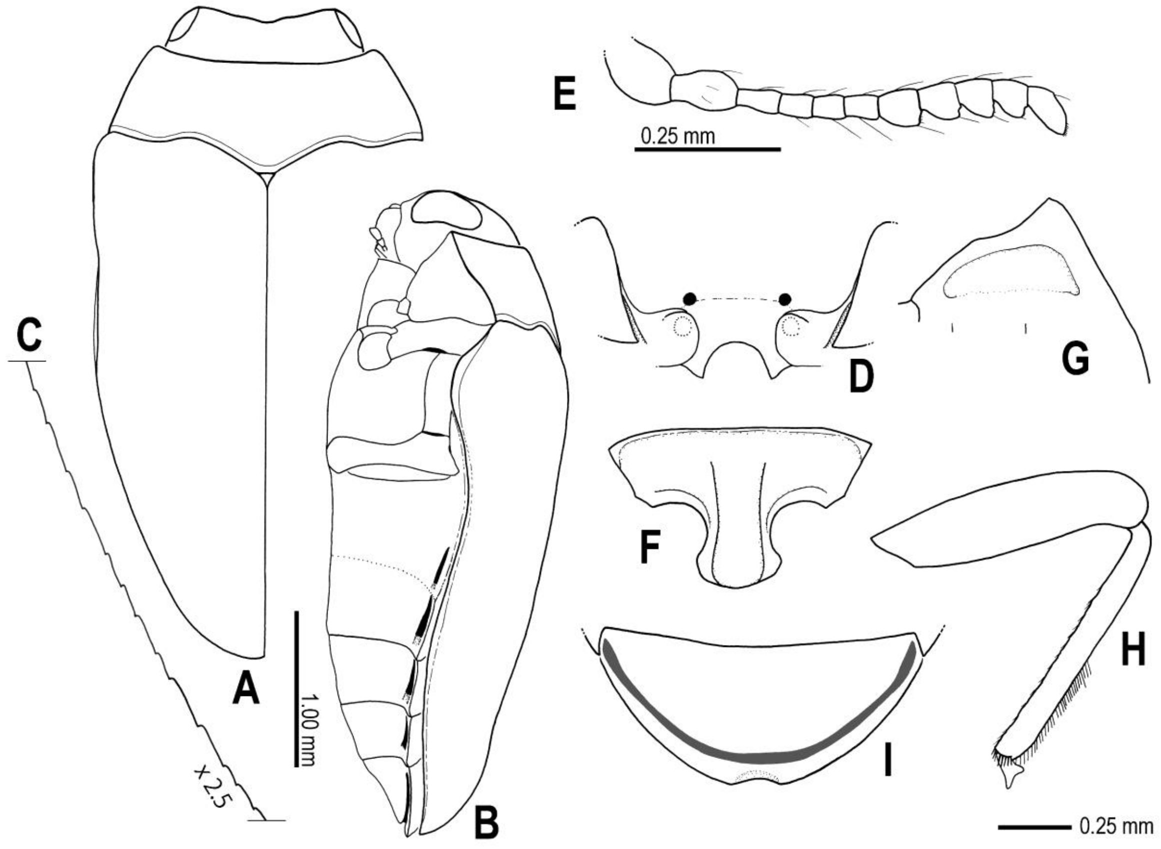


FIGURE 36. *Trachys cupricolor* Saunders. —— A) Head, pronotum, and left elytron; B) body, lateral view; C) serration of elytral lateral margin, obliquely ventral view; D) clypeus; E) antenna, outer side; F) prosternum; G) hypomeral markings, oblique view; H) metaleg (femur and tibia), ventral view; I) abdominal ventrite V.

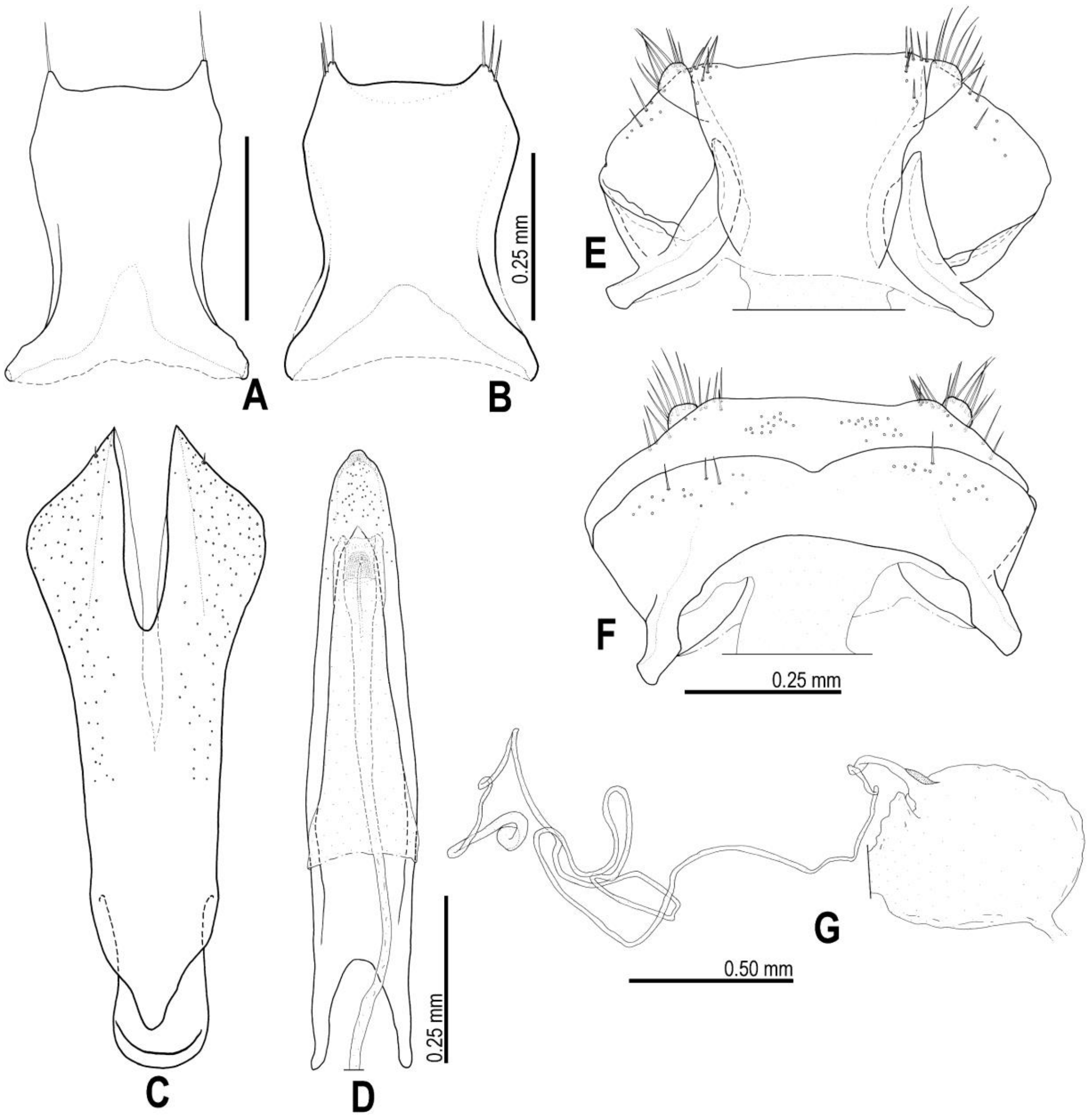


FIGURE 37. Male and female terminalia (part), *Trachys cupricolor* Saunders. —— A, B) Sternites IX, male; C) tegmen; D) penis; E, F) external part of ovipositor (except proctiger), dorsal view (E) and ventral view (F); G) internal part of ovipositor, lateral view.

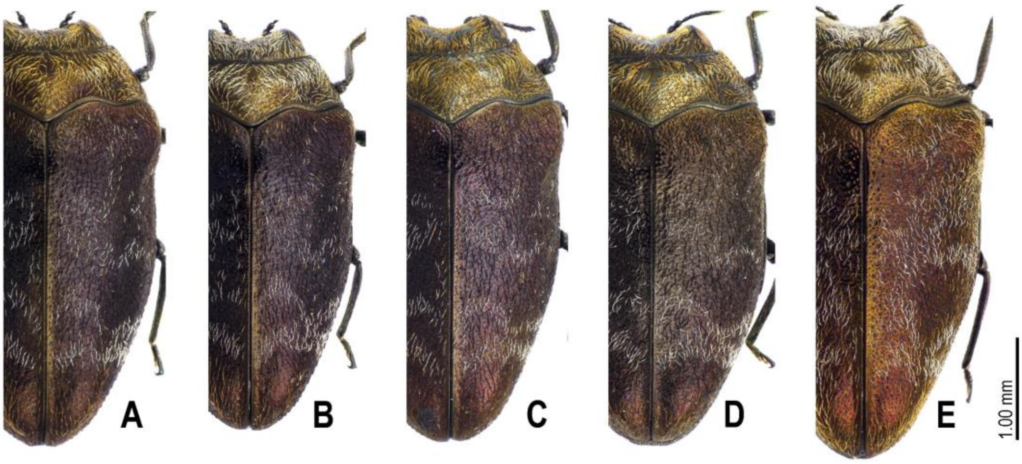


FIGURE 38. Variations in dorsal habitus (part) of *Trachys pecirkai* Obenberger.

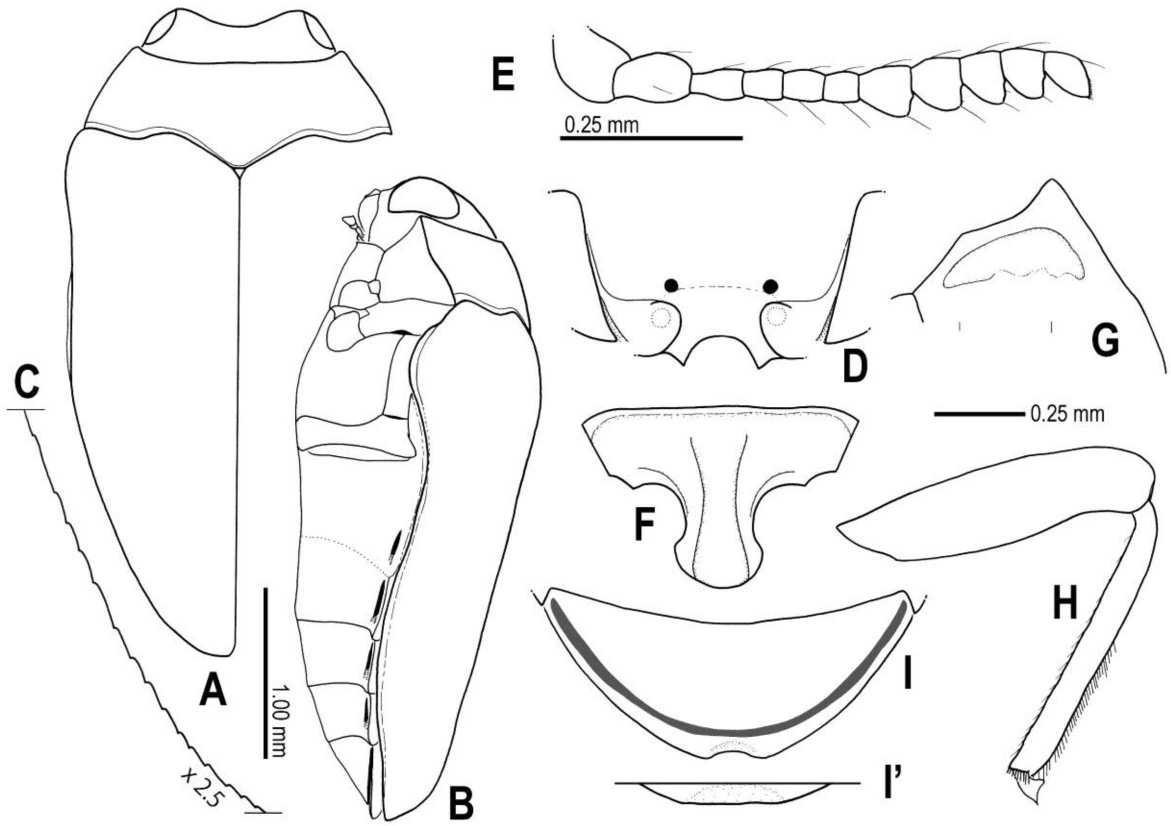


FIGURE 39. *Trachys pecirkai* Obenberger. —— A) Head, pronotum, and left elytron; B) body, lateral view; C) serration of elytral lateral margin, obliquely ventral view; D) clypeus; E) antenna, outer side; F) prosternum; G) hypomeral markings, oblique view; H) metaleg (femur and tibia), ventral view; I) abdominal ventrite V (I’ shows only the apex).

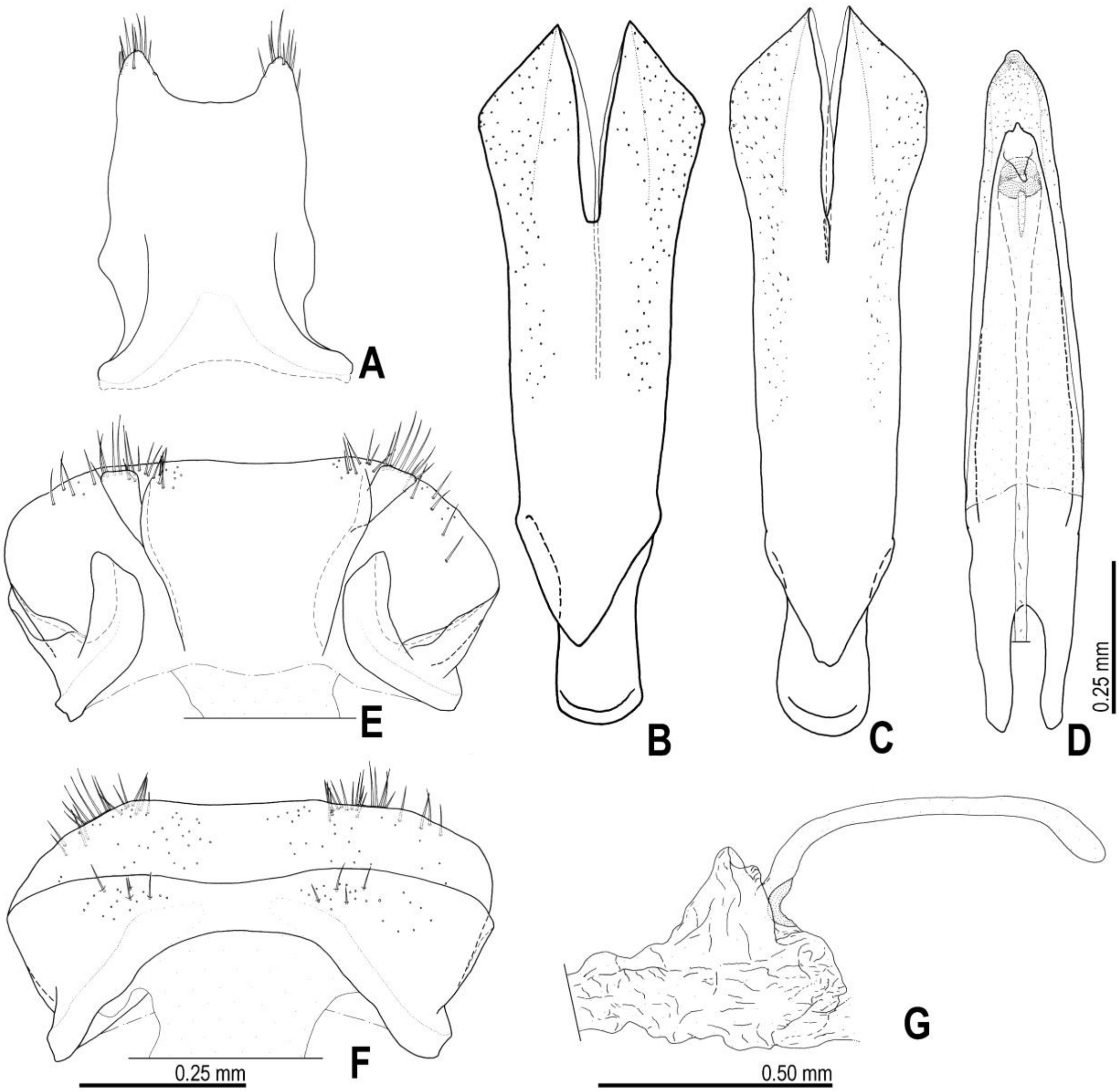


FIGURE 40. Male and female terminalia (part), *Trachys pecirkai* Obenberger. —— A) Sternite IX, male; B, C) tegmen; D) penis; E, F) external part of ovipositor (except proctiger), dorsal view (E) and ventral view (F); G) internal part of ovipositor, lateral view.

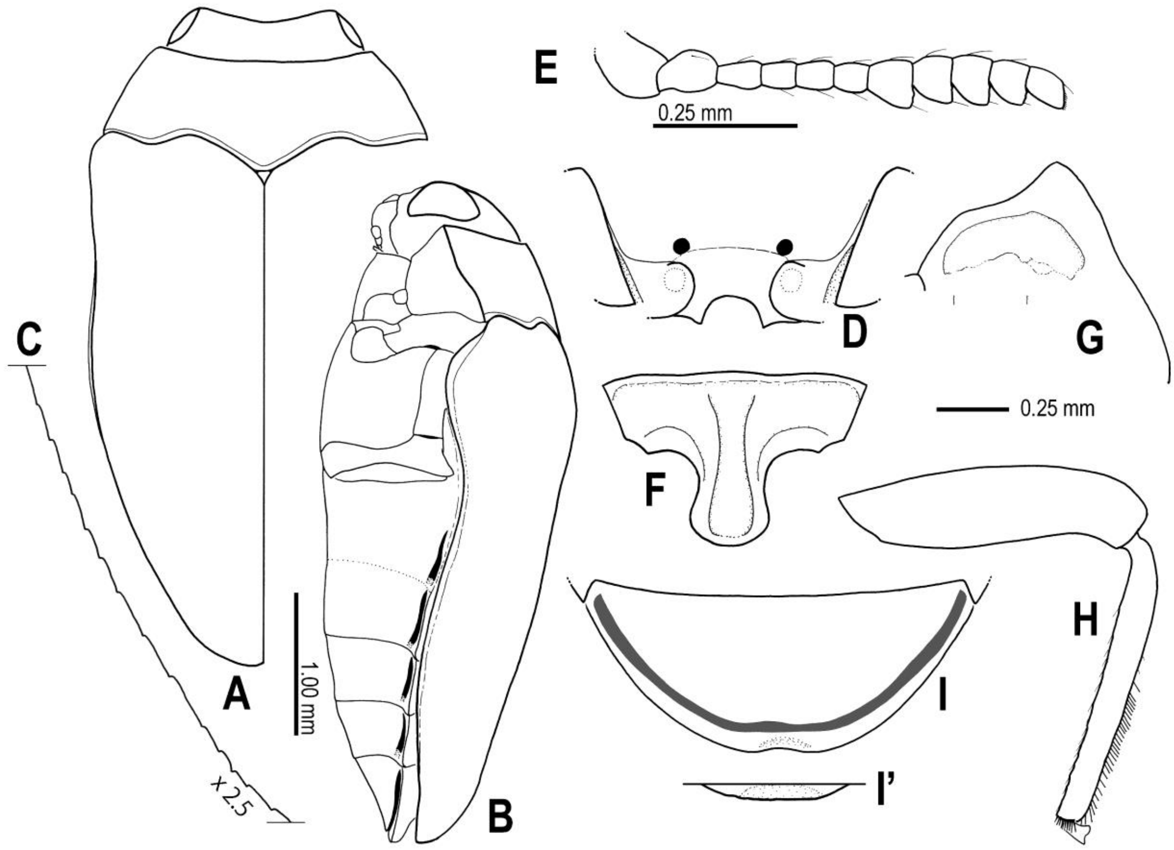


FIGURE 41. *Trachys aurifluus* Solsky. —— A) Head, pronotum, and left elytron; B) body, lateral view; C) serration of elytral lateral margin, obliquely ventral view; D) clypeus; E) antenna, outer side; F) prosternum; G) hypomeral markings, oblique view; H) metaleg (femur and tibia), ventral view; I) abdominal ventrite V (I’ shows only the apex).

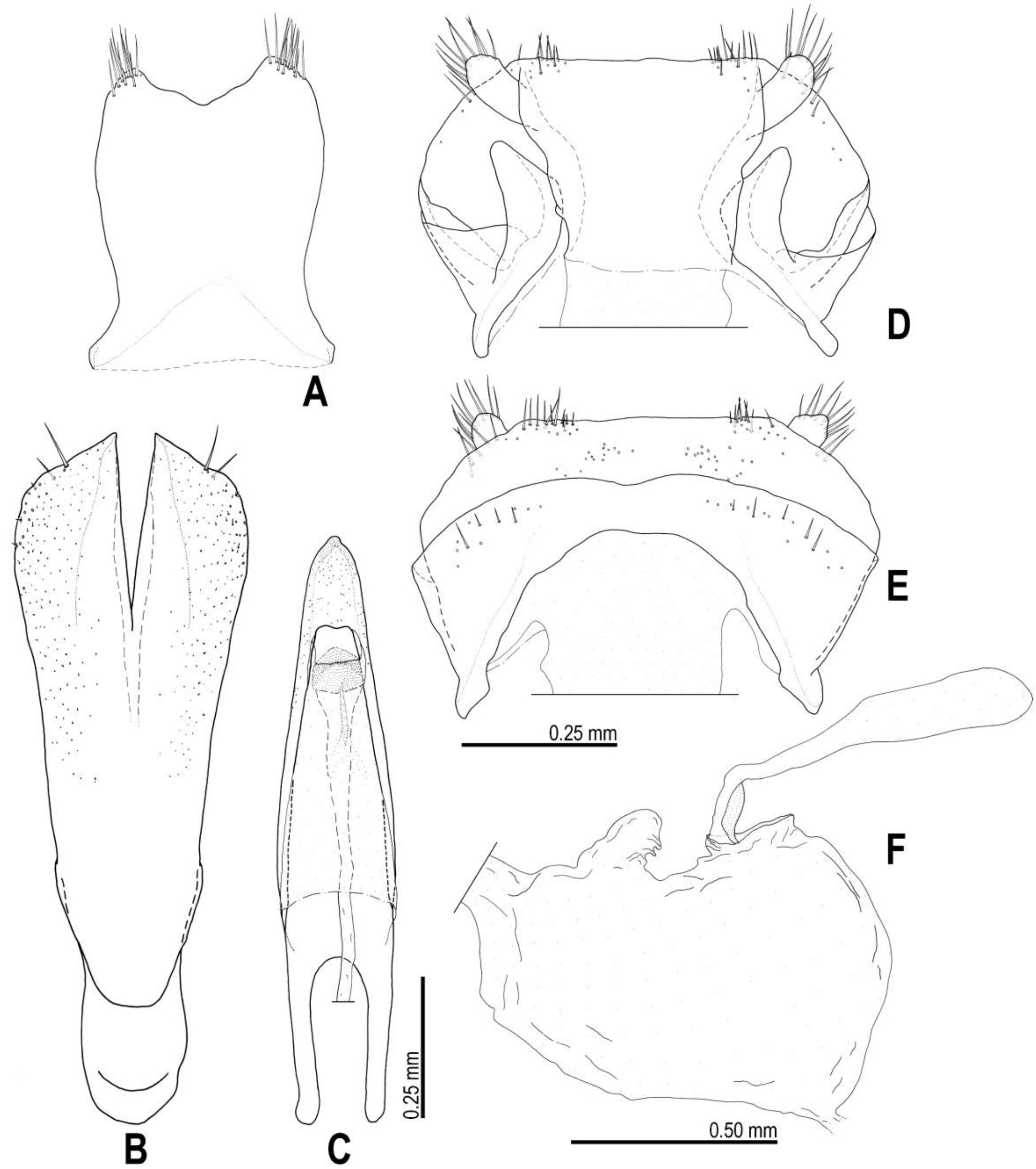


FIGURE 42. Male and female terminalia (part), *Trachys aurifluus* Solsky. —— A) Sternite IX, male; B) tegmen; C) penis; D, E) external part of ovipositor (except proctiger), dorsal view (D) and ventral view (E); F) internal part of ovipositor, lateral view.

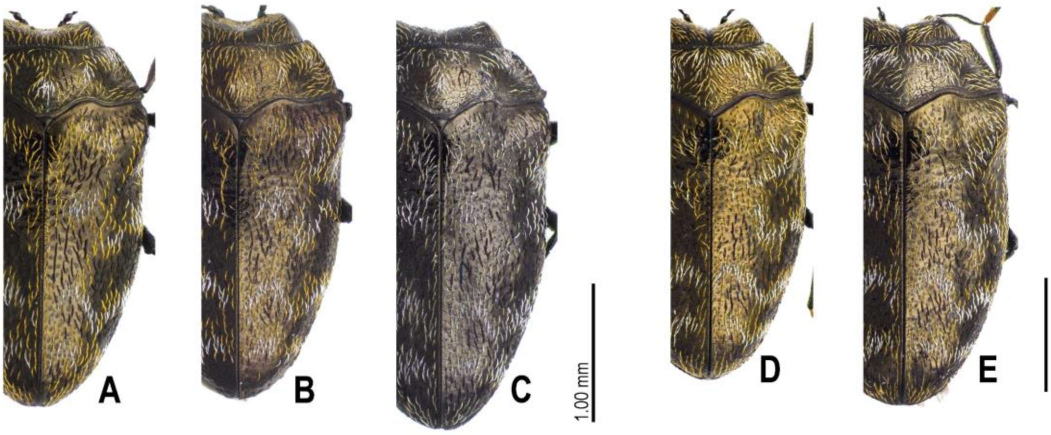


FIGURE 43. Variations in dorsal habitus (part) of Japanese *Trachys* spp. in the tentative species-groups IV and V. —— A–C) *Trachys reitteri* Obenberger; D, E) *T. tokyoensis* Obenberger.

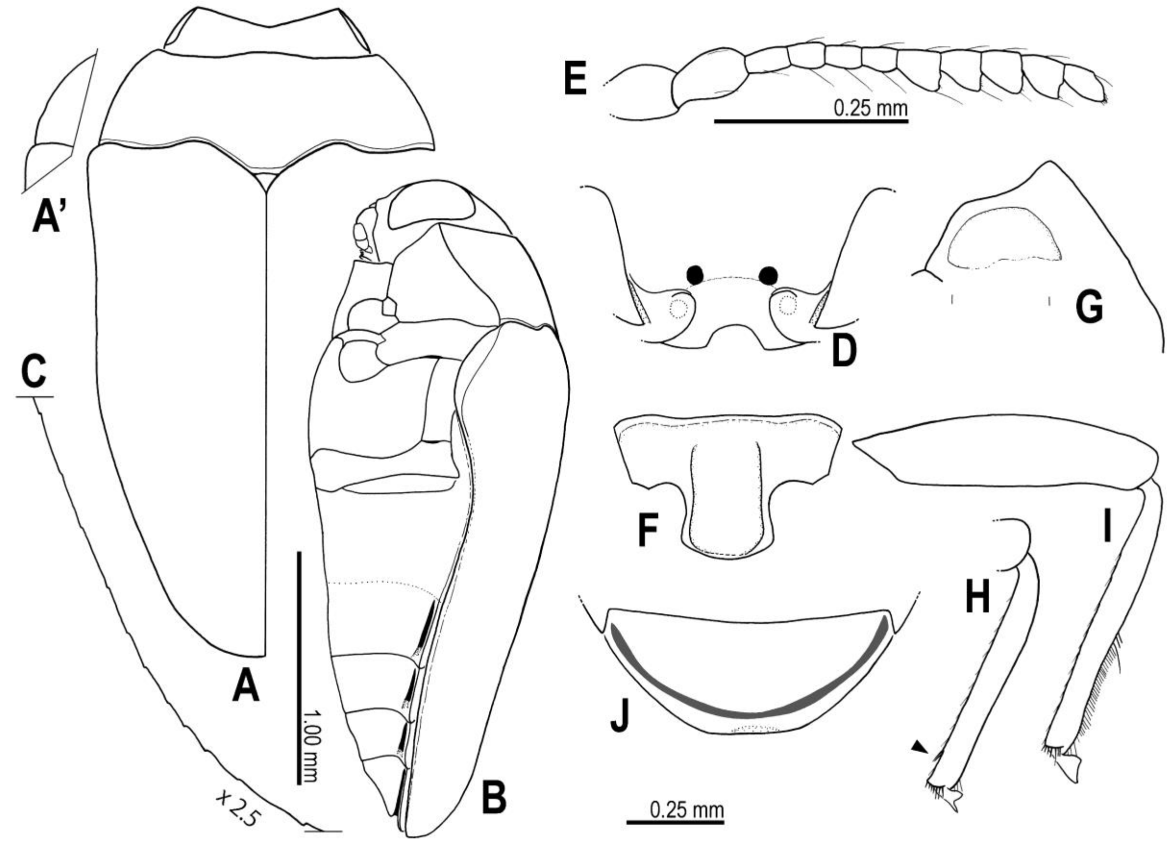


FIGURE 44. *Trachys reitteri* Obenberger. —— A) Head, pronotum, and left elytron (A' indicates outline of pronotal and elytral bases in a different individual); B) body, lateral view; C) serration of elytral lateral margin, obliquely ventral view; D) clypeus; E) antenna, outer side; F) prosternum; G) hypomeral markings, oblique view; H) mesotibia, ventral view (a black triangular mark indicates erect robust spines); I) metaleg (femur and tibia), ventral view; J) abdominal ventrite V.

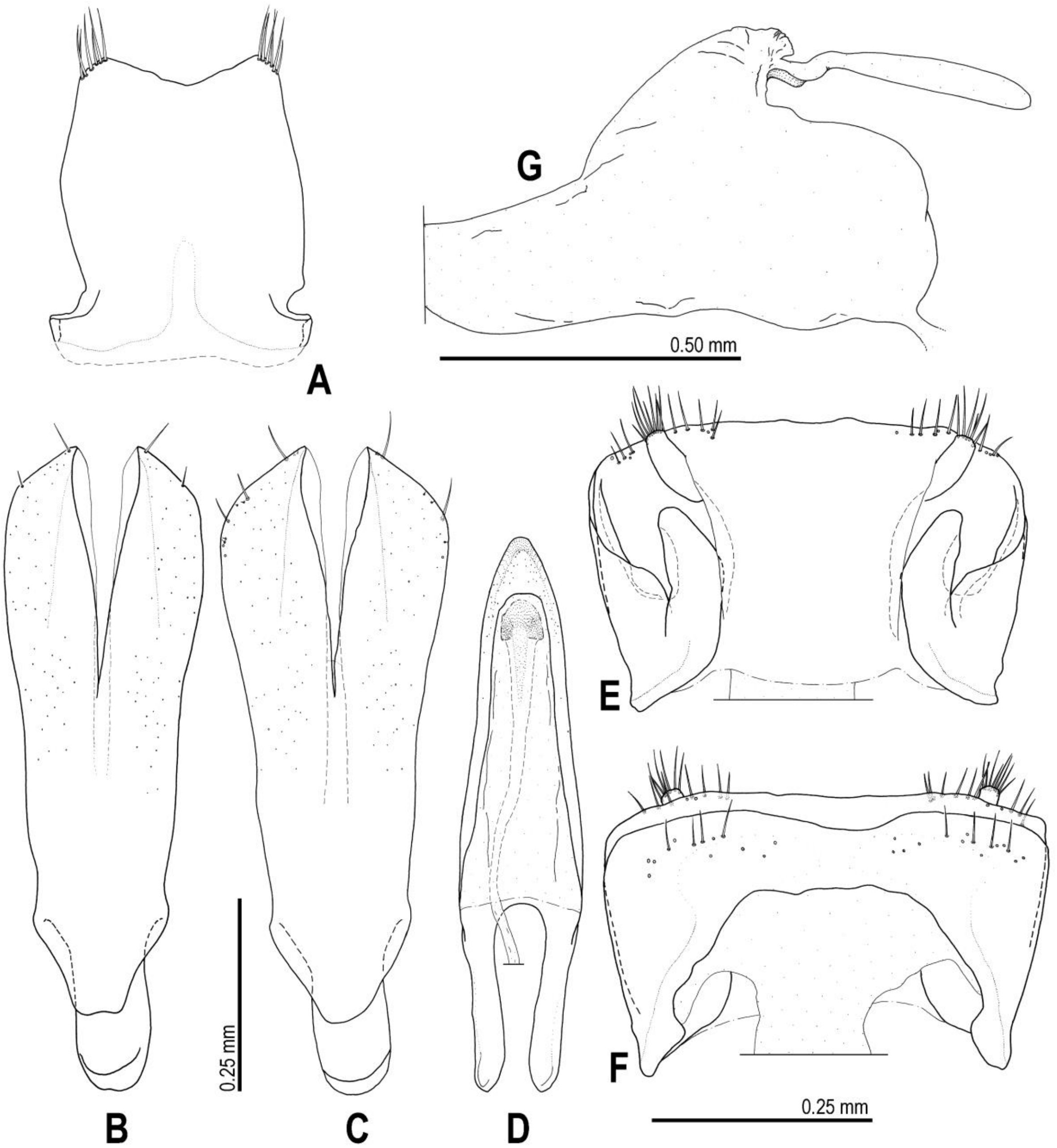


FIGURE 45. Male and female terminalia (part), *Trachys reitteri* Obenberger. —— A) Sternite IX, male; B, C) tegmen; D) penis; E, F) external part of ovipositor (except proctiger), dorsal view (E) and ventral view (F); G) internal part of ovipositor, lateral view.

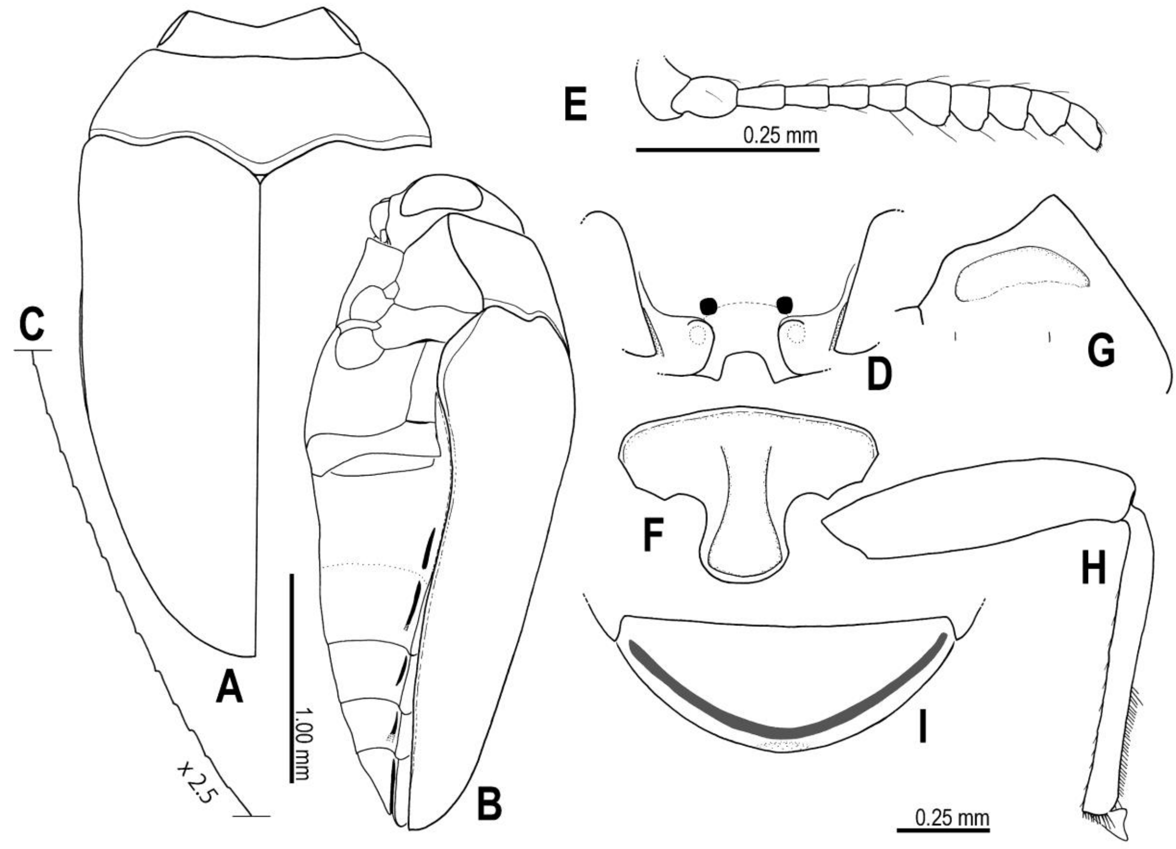


FIGURE 46. *Trachys tokyoensis* Obenberger. —— A) Head, pronotum, and left elytron; B) body, lateral view; C) serration of elytral lateral margin, obliquely ventral view; D) clypeus; E) antenna, outer side; F) prosternum; G) hypomeral markings, oblique view; H) metaleg (femur and tibia), ventral view; I) abdominal ventrite V.

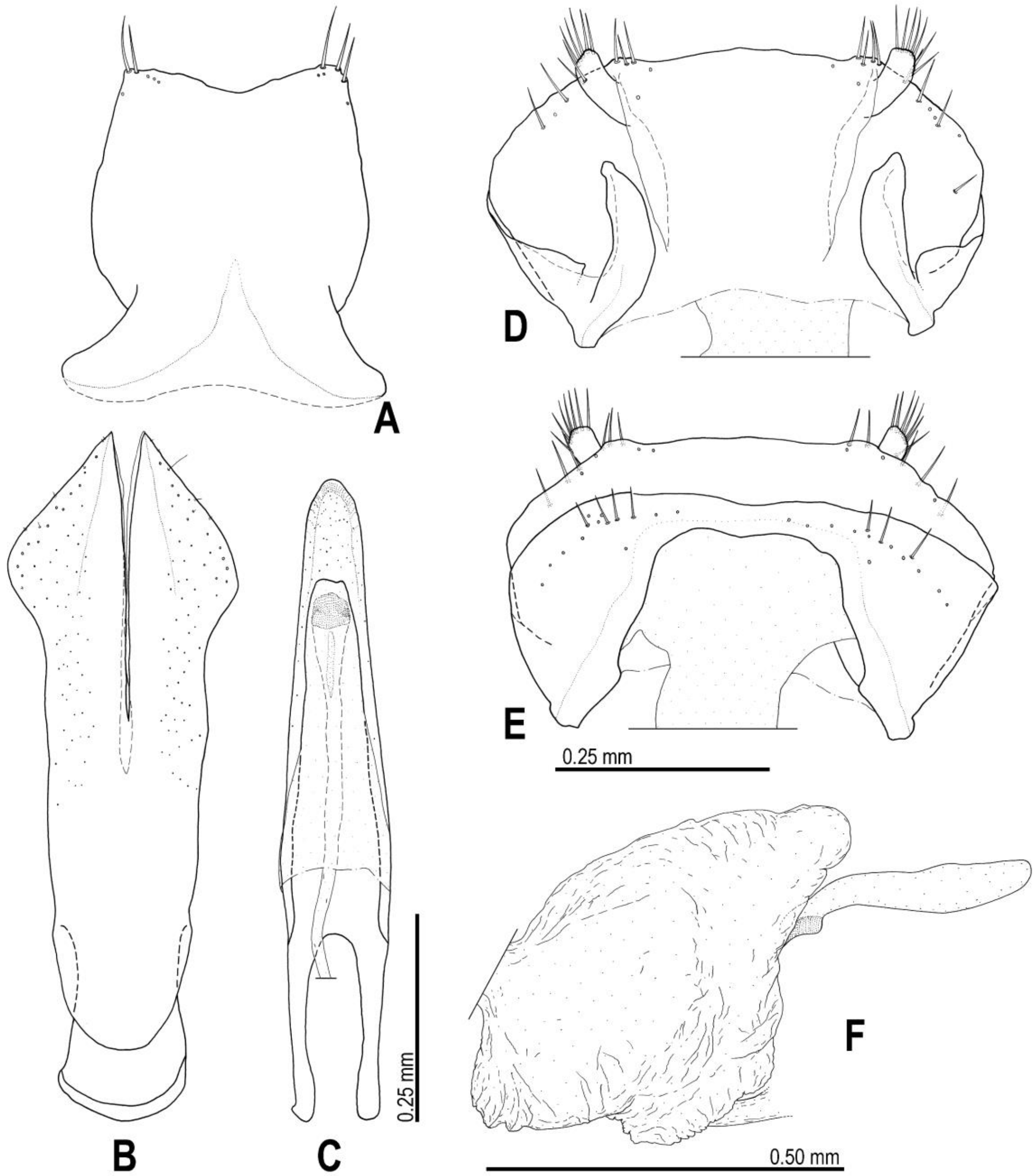


FIGURE 47. Male and female terminalia (part), *Trachys tokyoensis* Obenberger. —— A) Sternite IX, male; B) tegmen; C) penis; D, E) external part of ovipositor (except proctiger), dorsal view (D) and ventral view (E); F) internal part of ovipositor, lateral view.

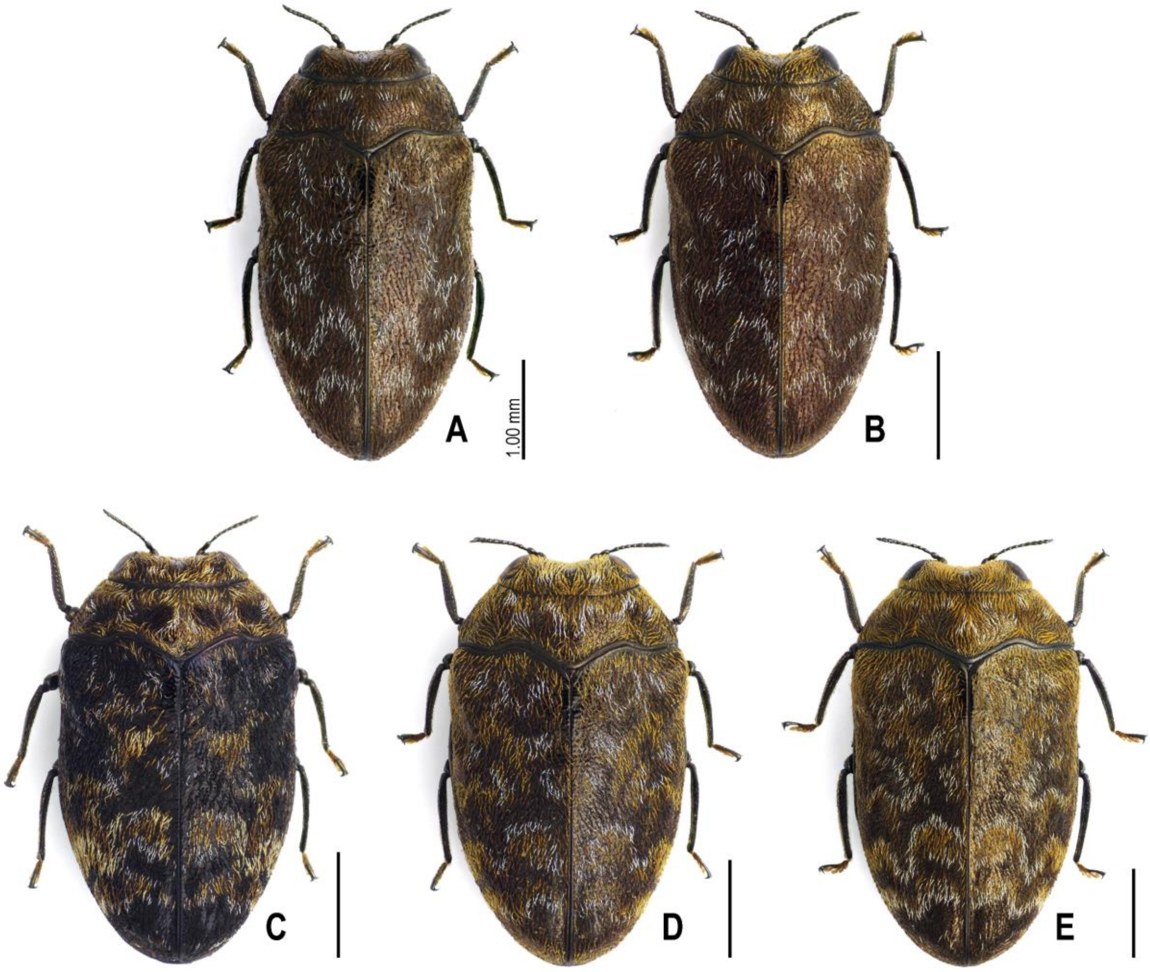


FIGURE 48. Dorsal habitus of Japanese *Trachys* spp. in the tentative species-groups VI–VII. —— A, B) Group VI; C–E) group VII. —— A) *Trachys griseofasciatus* Saunders; B) *T. yanoi* Kurosawa; C) *T. variolaris* Saunders; D) *T. robustus* Saunders; E) *T. dilaticeps* Gebhardt.

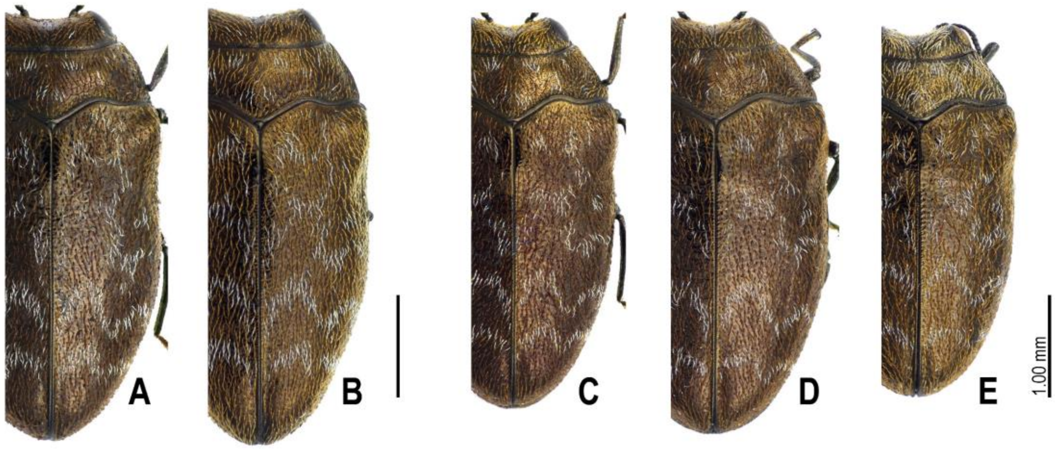


FIGURE 49. Variations in dorsal habitus (part) of Japanese *Trachys* spp. in the tentative species-group VI. —— A, B) *Trachys griseofasciatus* Saunders; C–E) *T. yanoi* Kurosawa.

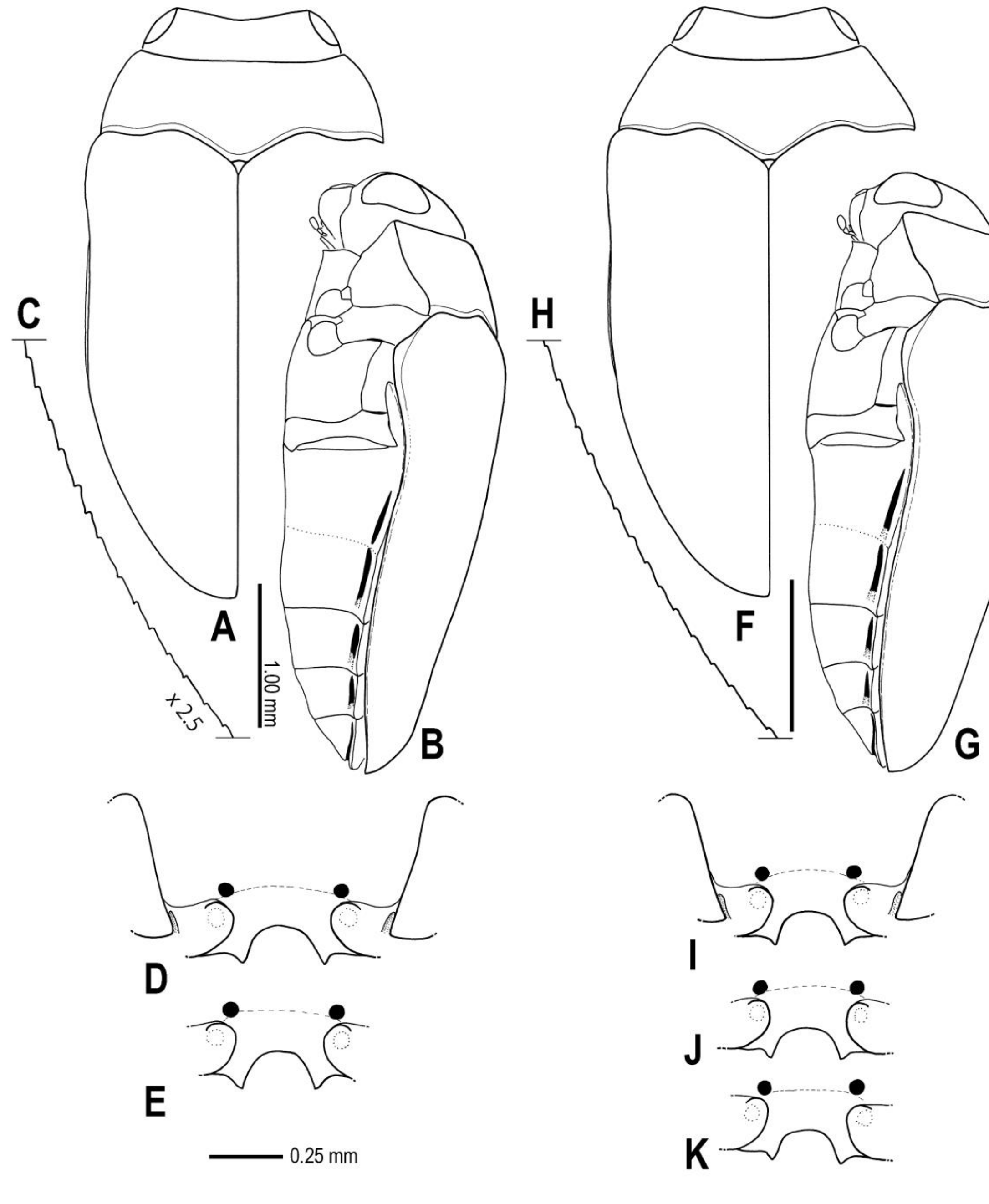


FIGURE 50. *Trachys griseofasciatus* Saunders and *T. yanoi* Kurosawa. —— A–E) *T. griseofasciatus*; F–K) *T. yanoi*. —— A, F) Head, pronotum, and left elytron; B, G) body, lateral view; C, H) serration of elytral lateral margin, obliquely ventral view; D, E, I–K) clypeus.

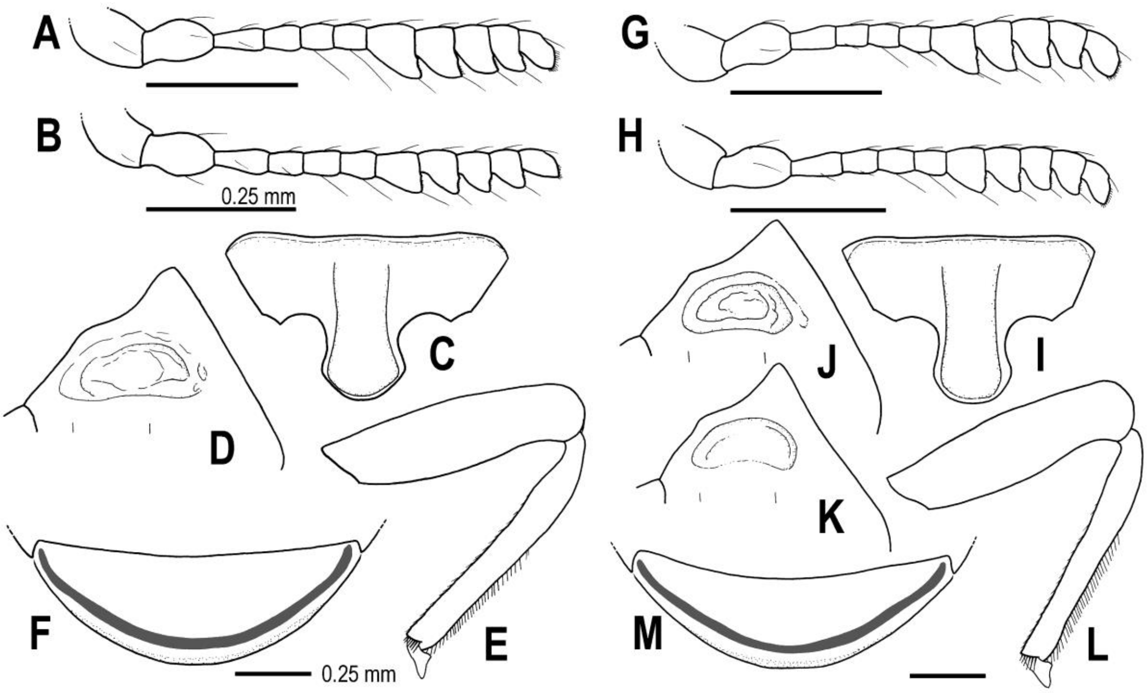


FIGURE 51. *Trachys griseofasciatus* Saunders and *T. yanoi* Kurosawa. —— A–F) *T. griseofasciatus*; G–M) *T. yanoi*. —— A, G) male antennae, inner side; B, H) female antennae, inner side; D, J, K) hypomeral markings, oblique view; C, I) pronotum; E, L) metaleg (femur and tibia), ventral view; F, M) abdominal ventrite V.

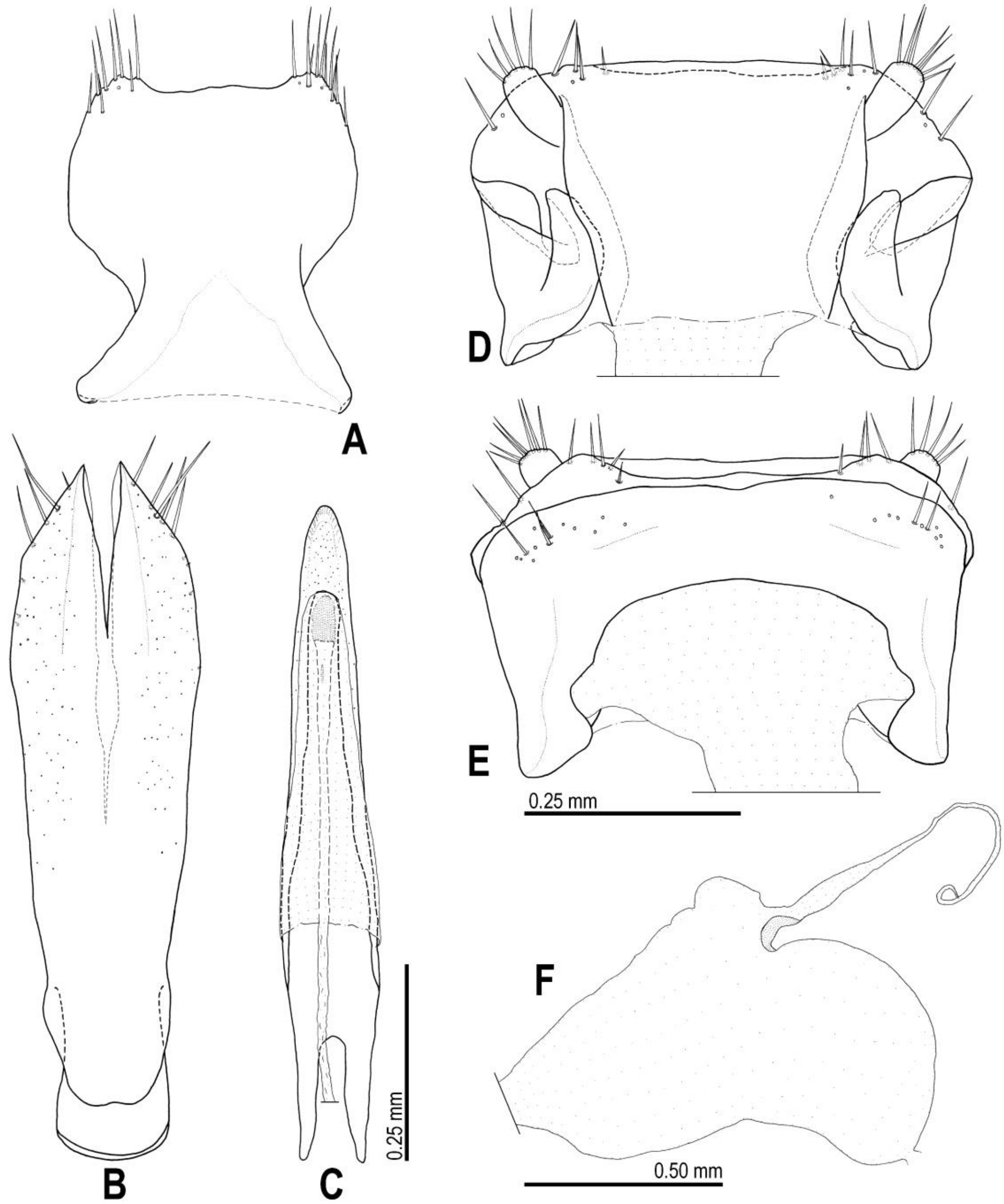


FIGURE 52. Male and female terminalia (part), *Trachys griseofasciatus* Saunders. —— A) Sternite IX, male; B) tegmen; C) penis; D, E) external part of ovipositor (except proctiger), dorsal view (D) and ventral view (E); F) internal part of ovipositor, lateral view.

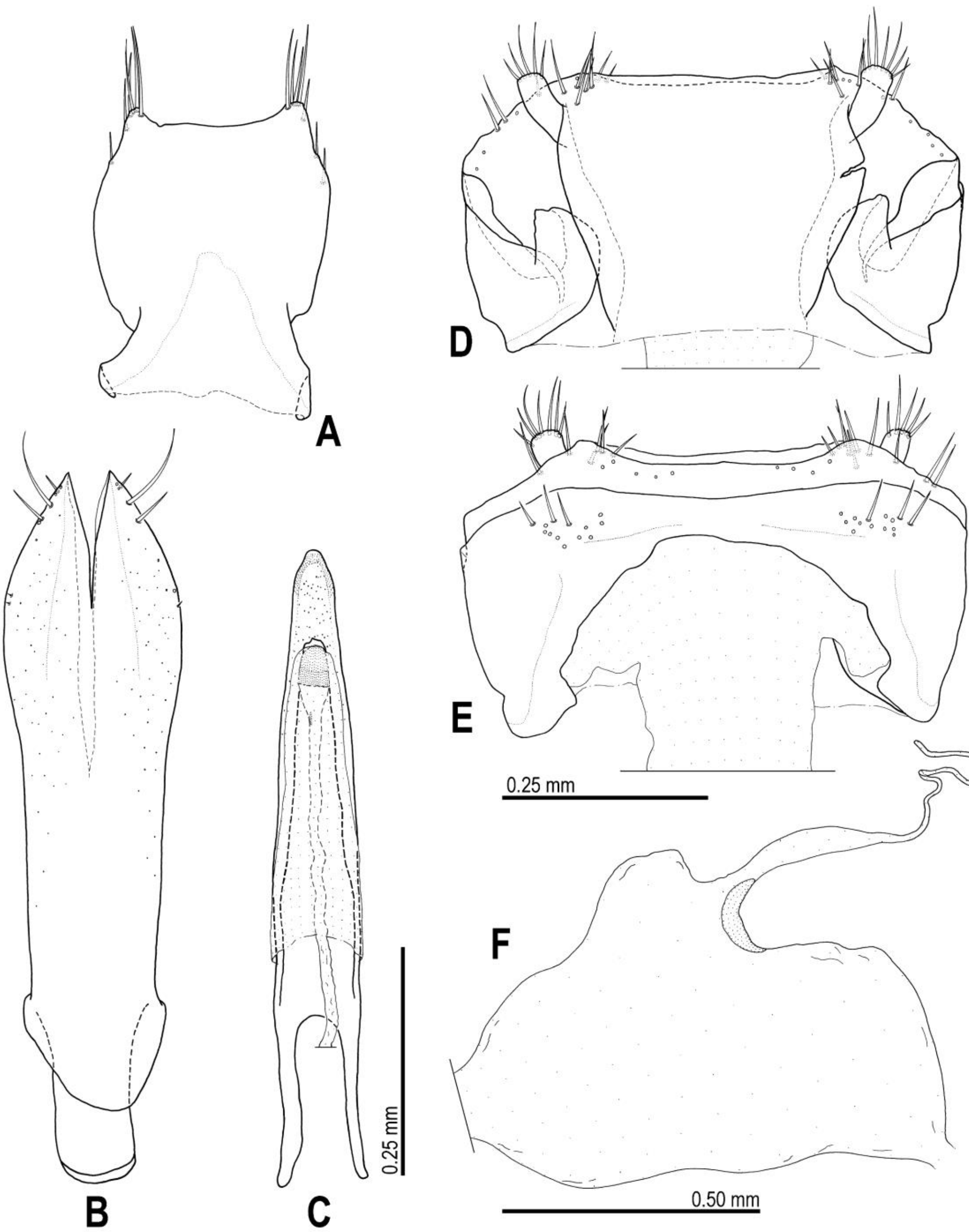


FIGURE 53. Male and female terminalia (part), *Trachys yanoi* Kurosawa. —— A) Sternite IX, male; B) tegmen; C) penis; D, E) external part of ovipositor (except proctiger), dorsal view (D) and ventral view (E); F) internal part of ovipositor, lateral view.

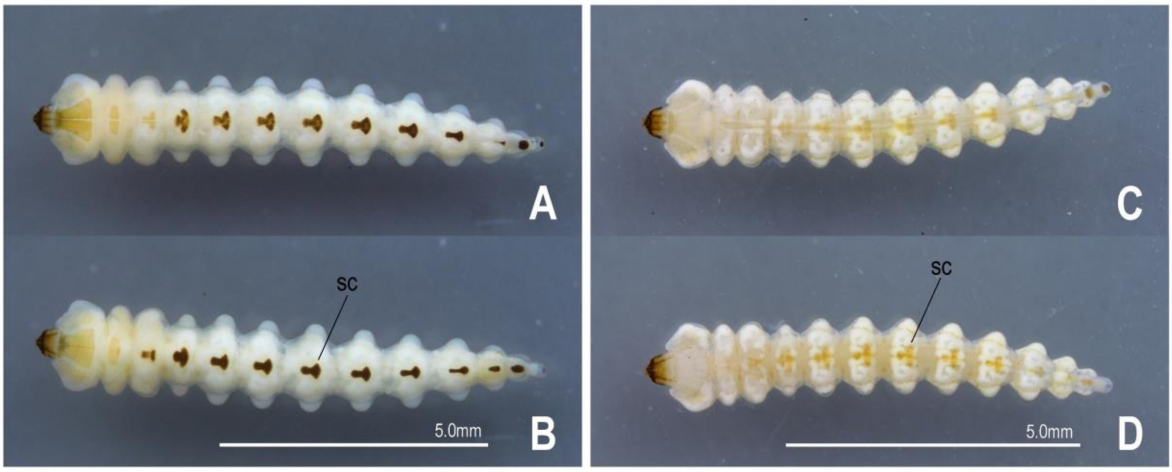


FIGURE 54. Third instar larvae of *Trachys griseofasciatus* Saunders and *T. yanoi* Kurosawa. — — A, B) *T. griseofasciatus*, dorsal habitus (A) and ventral habitus (B); C, D) *T. yanoi*, dorsal habitus (C) and ventral habitus (D). Abbreviation: sc — sclerotized plate.

FIGURE 55. Variations in dorsal habitus (part) of Japanese *Trachys* spp. in the tentative species-group VII. —— A–E) *Trachys vaiolaris* Saunders (B, D, male; A, C, E, female); F–J) *T. robustus* Saunders (F, I, male; G, H, J, female); K–O) *T. dilaticeps* Gebhardt, (K, M, O, male; L, N, female).

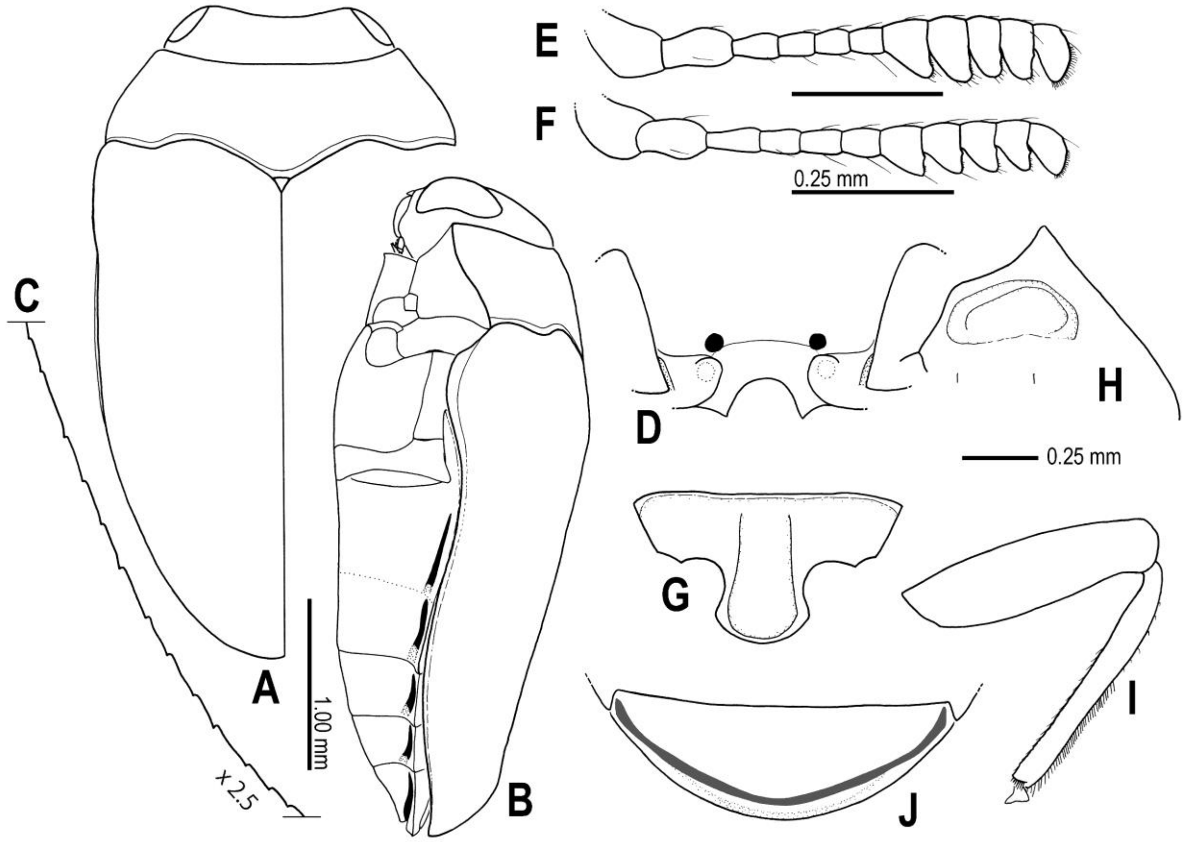


FIGURE 56. *Trachys vaiolaris* Saunders. —— A) Head, pronotum, and left elytron; B) body, lateral view; C) serration of elytral lateral margin, obliquely ventral view; D) clypeus; E, F) antennae, outer side, male (E) and female (F); G) prosternum; H) hypomeral marking, oblique view; I) metaleg (femur and tibia), ventral view; J) abdominal ventrite V.

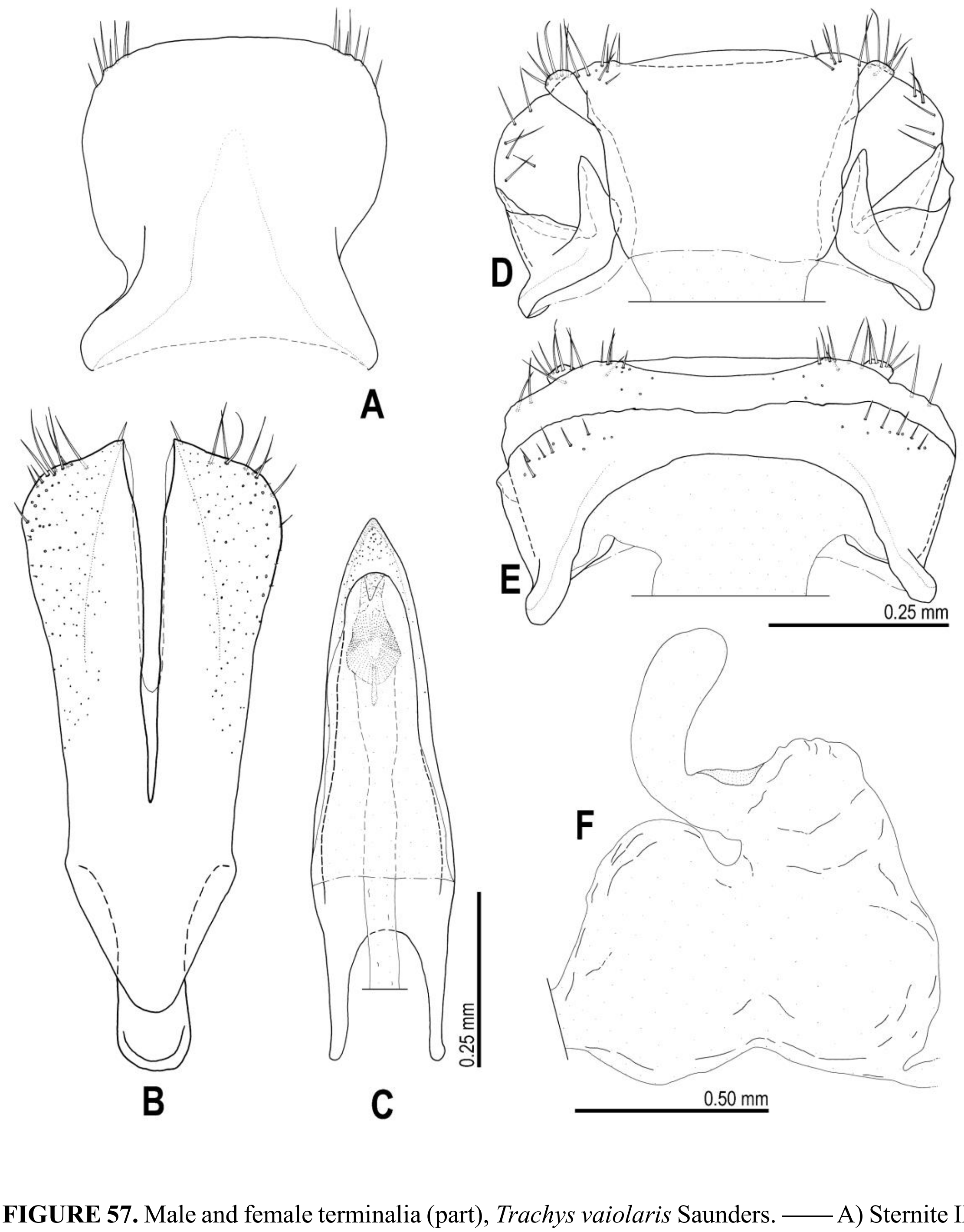


FIGURE 57. Male and female terminalia (part), *Trachys vaiolaris* Saunders. —— A) Sternite IX, male; B) tegmen; C) penis; D, E) external part of ovipositor (except proctiger), dorsal view (D) and ventral view (E); F) internal part of ovipositor, lateral view.

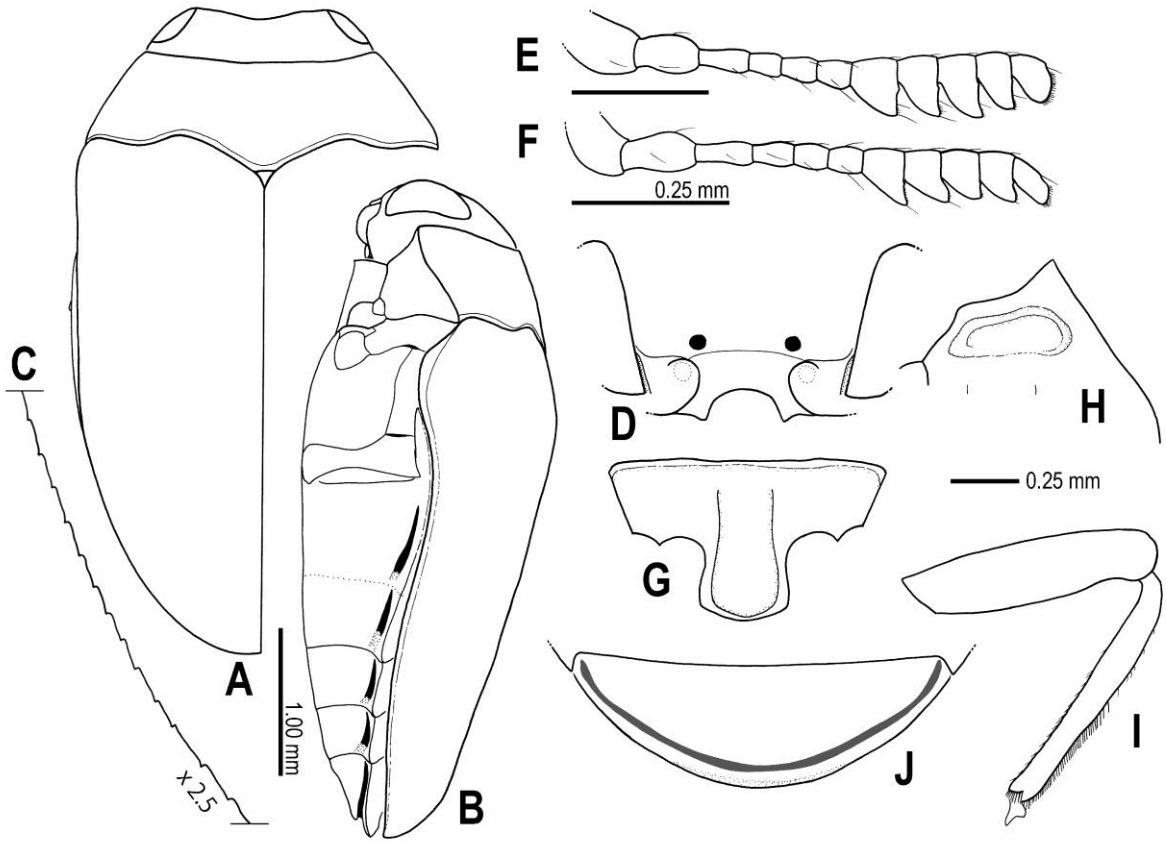


FIGURE 58. *Trachys robustus* Saunders. —— A) Head, pronotum, and left elytron; B) body, lateral view; C) serration of elytral lateral margin, obliquely ventral view; D) clypeus; E, F) antennae, outer side, male (E) and female (F); G) prosternum; H) hypomeral marking, oblique view; I) metaleg (femur and tibia), ventral view; J) abdominal ventrite V.

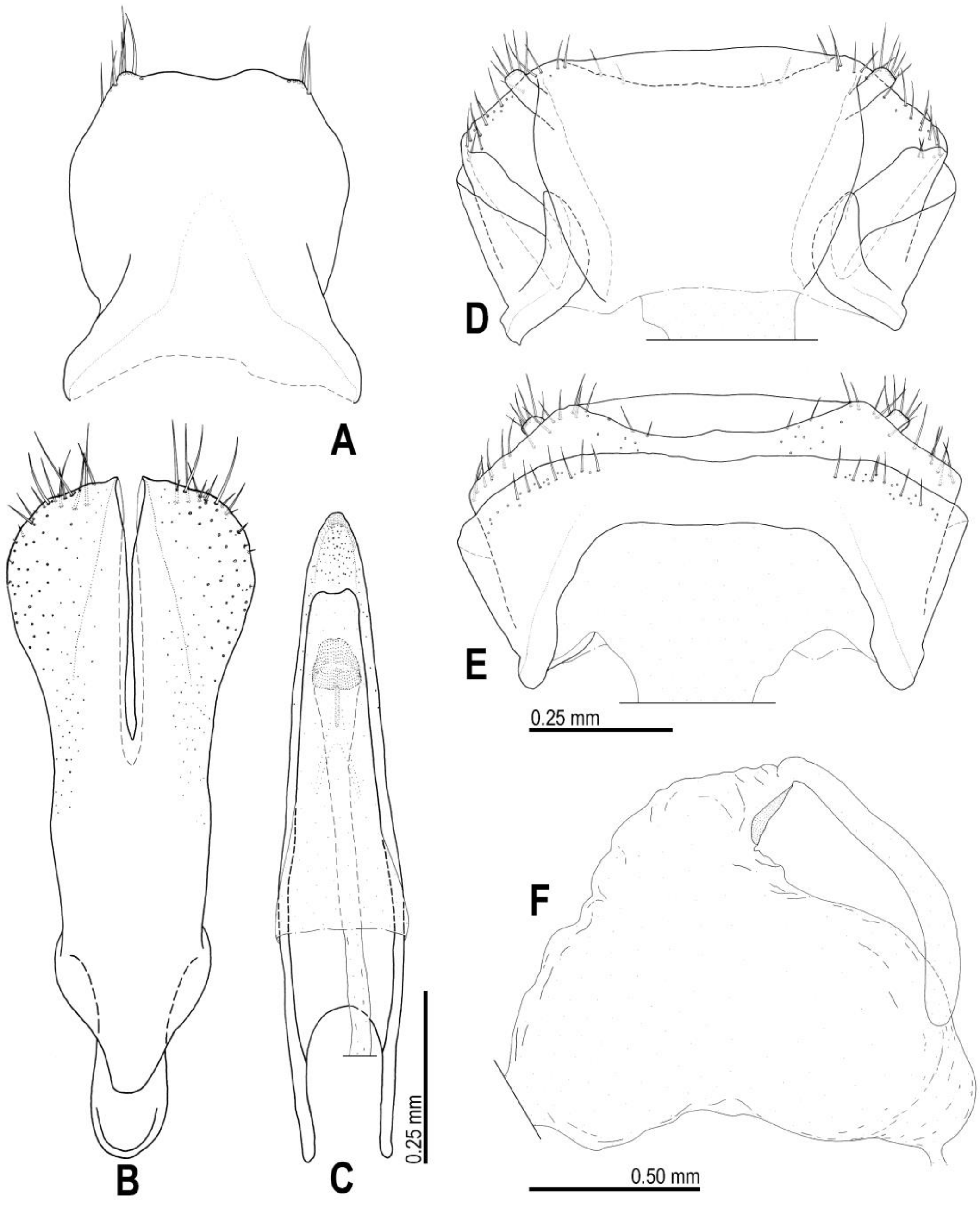


FIGURE 59. Male and female terminalia (part), *Trachys robustus* Saunders. —— A) Sternite IX, male; B) tegmen; C) penis; D, E) external part of ovipositor (except proctiger), dorsal view (D) and ventral view (E); F) internal part of ovipositor, lateral view.

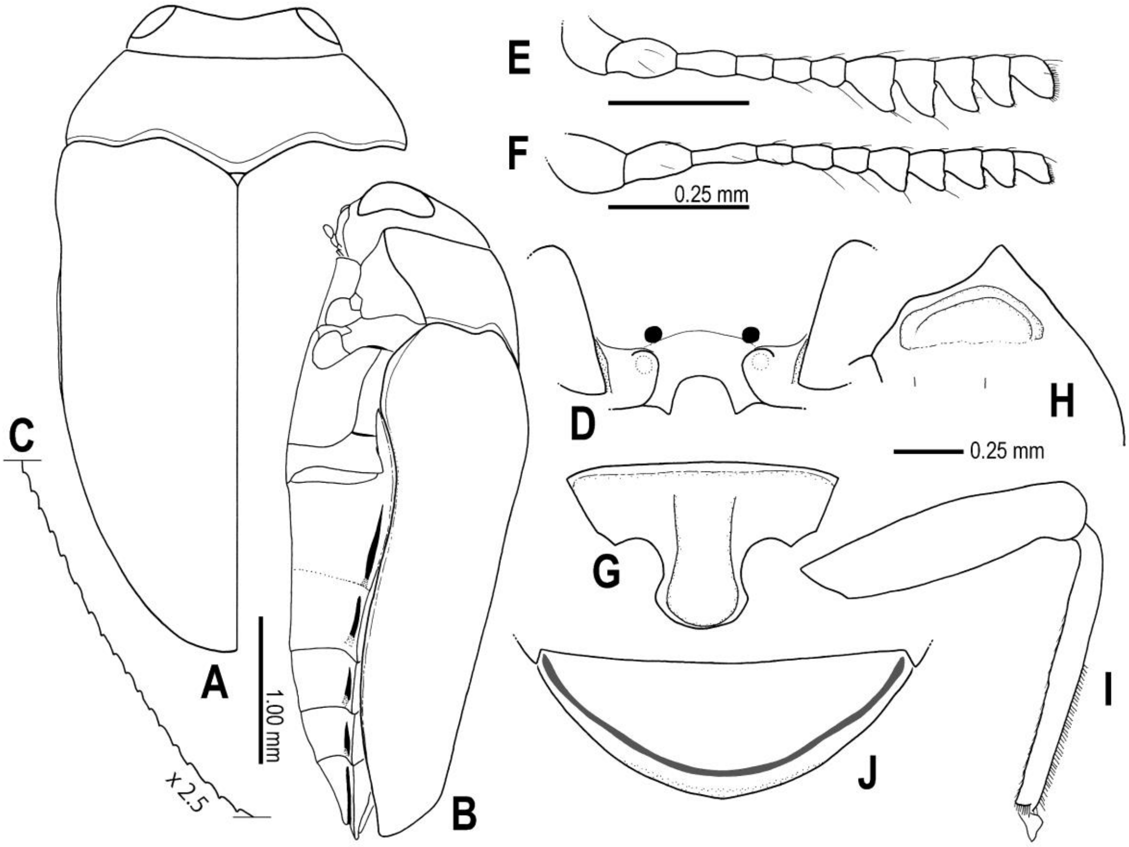


FIGURE 60. *Trachys dilaticeps* Gebhardt. —— A) Head, pronotum, and left elytron; B) body, lateral view; C) serration of elytral lateral margin, obliquely ventral view; D) clypeus; E, F) antennae, outer side, male (E) and female (F); G) prosternum; H) hypomeral marking, oblique view; I) metaleg (femur and tibia), ventral view; J) abdominal ventrite V.

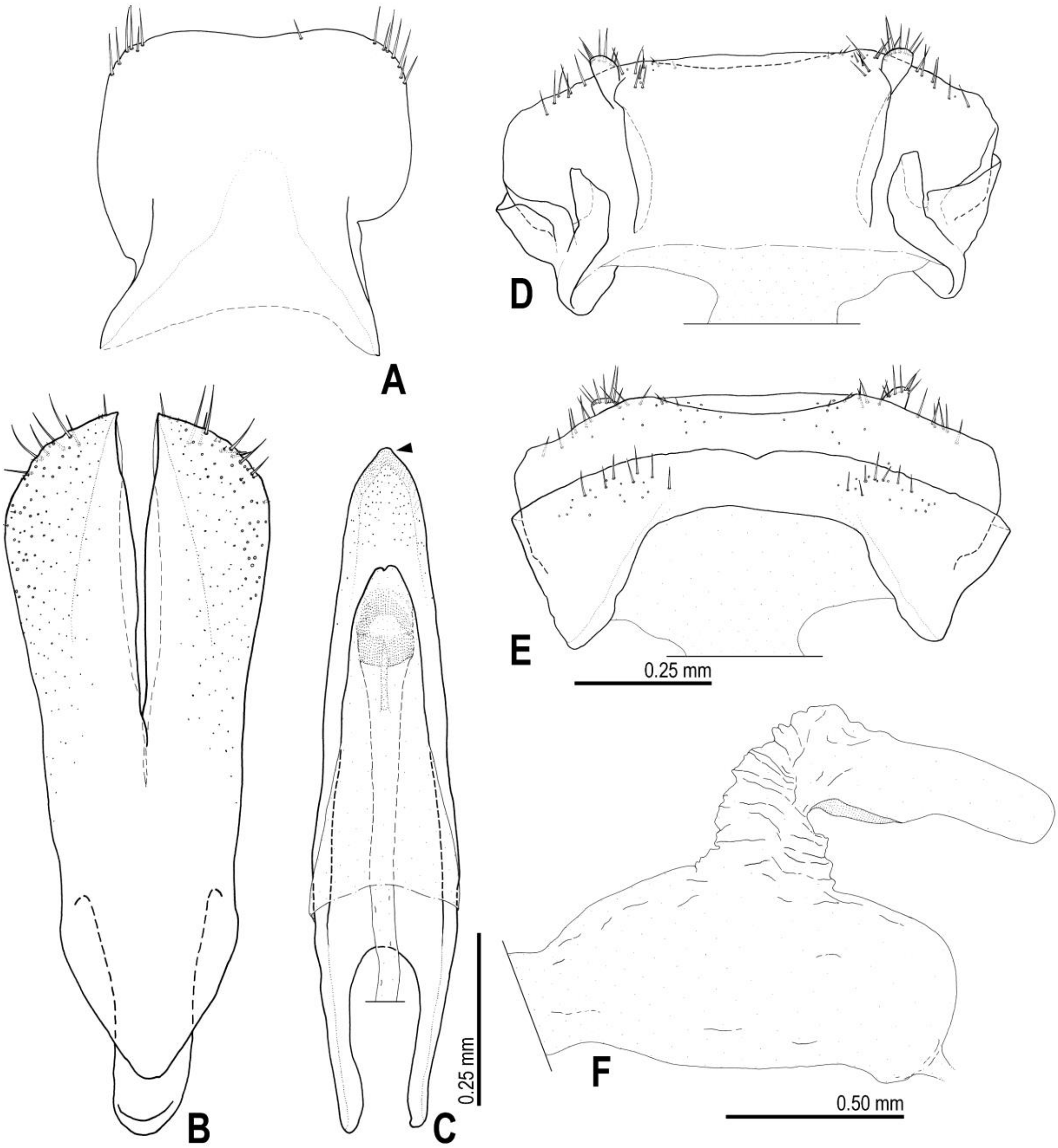


FIGURE 61. Male and female terminalia (part), *Trachys dilaticeps* Gebhardt. —— A) Sternite IX, male; B) tegmen; C) penis (a black triangular mark indicates a produced apex); D, E) external part of ovipositor (except proctiger), dorsal view (D) and ventral view (E); F) internal part of ovipositor, lateral view.

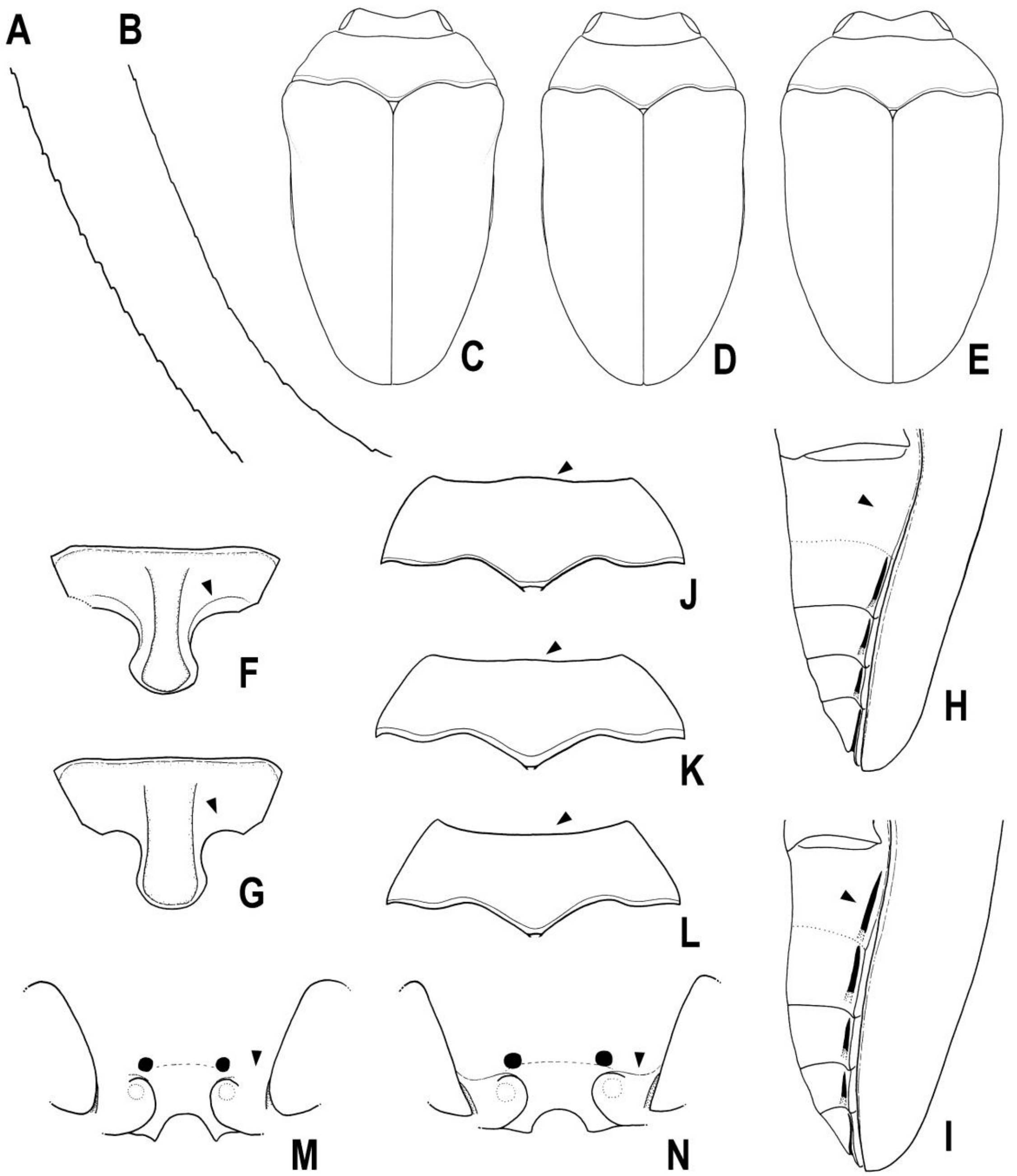


FIGURE 62. Some supplementary illustrations for the key to *Trachys* species. —— A, B) Serrations of elytral lateral margins; C) dorsal counter, wedge-shaped type; D, E) ditto, ovate type (D, ovate; E, subovate); F, G) precoxal lines on prosterna (F, present; G, absent); H, I) sternal grooves on abdominal ventrites, lateral view (H, absent on ventrite I; I, present on ventrite I); J–K) median lobes of anterior margins on pronota (J, K, present; L, absent); M, N) transverse ridges from just above antennal insertions to inner margins of eyes (M, absent; N, present). Black triangular marks indicate differential points in each structure.

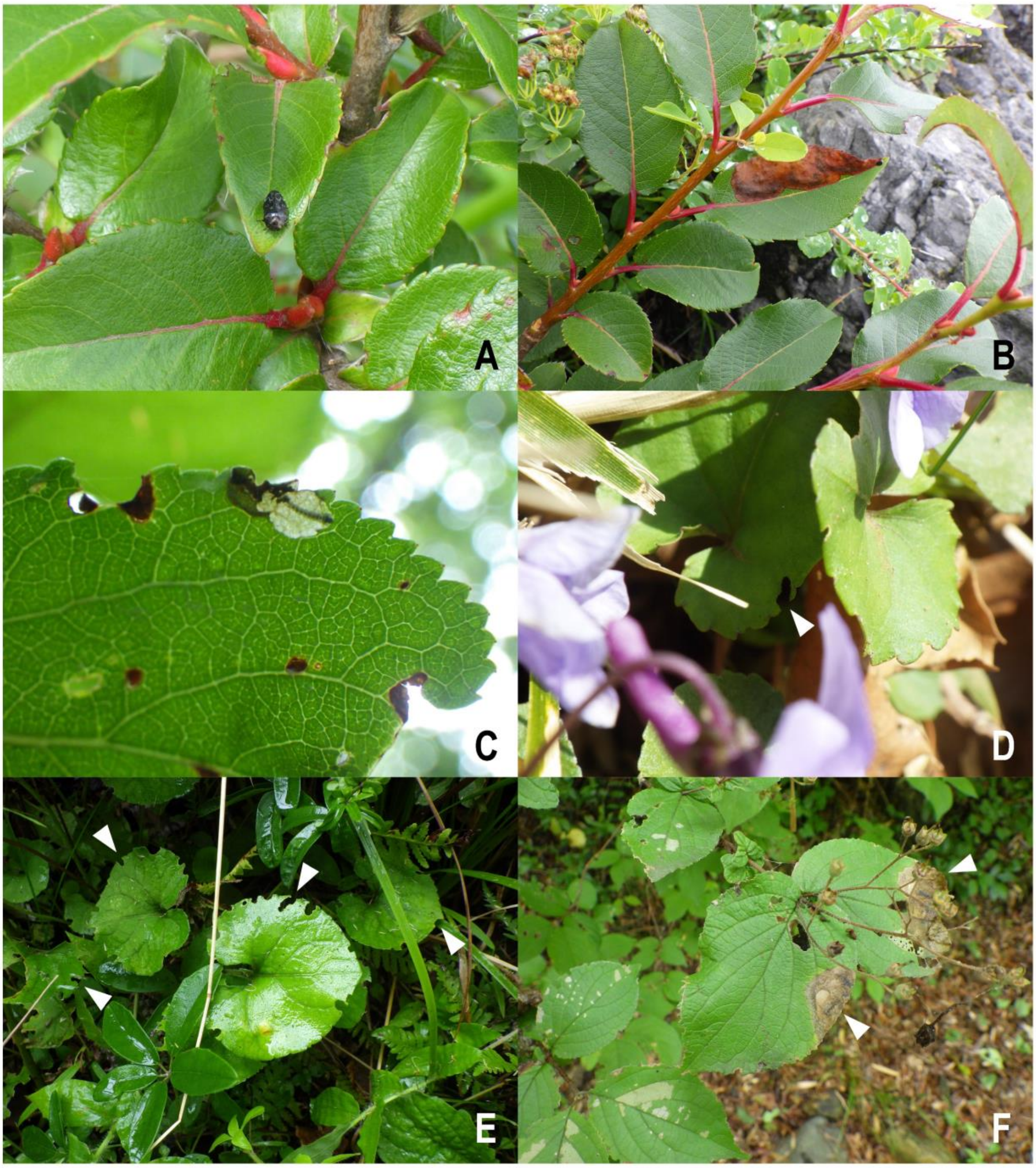


FIGURE 63. Adult, adult feeding scars, and leaf-mines of Japanese *Trachys* spp. in the field. —— A) An adult of *Trachys minutus* (Linnaeus) on *Salix shiraii* var. *shiraii* (Saitama-ken, Honshu); B) a mine (full-grown) of *T. minutus* on *S. shiraii* var. *shiraii* (Saitama-ken, Honshu); C) a mine of *T. inconspicuus* Saunders on *Prunus mume* (Kanagawa-ken, Honshu); D) an adult feeding scar of *T. pseudoscrobiculatus* Obenberger on *Viola grypoceras* var. *grypoceras* (indicated by a white triangular mark) (Tokyo, Honshu); E) adult feeding scars of *T. pseudoscrobiculatus* on *V. hondoensis* (indicated by white triangular marks) (Tokyo, Honshu); F) mines of *T. tsushimae* Obenberger on *Deutzia scabra* (indicated by white triangular marks) (Tokyo, Honshu).

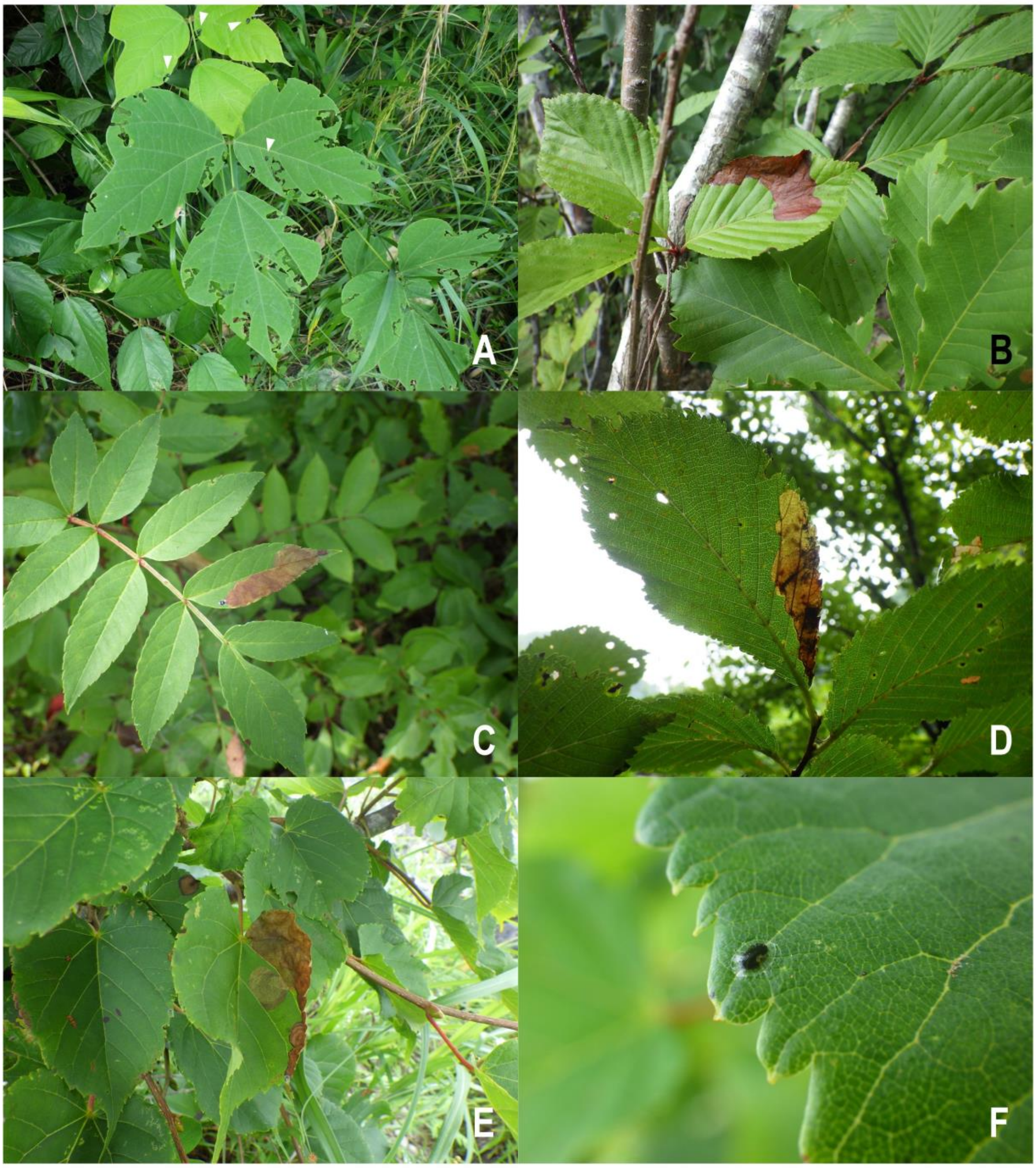


FIGURE 64. Adults, adult feeding scars, leaf-mines, and egg of Japanese *Trachys* spp. in the field. —— A) Adults and their feeding scars of *Trachys auricollis* Saunders on *Pueraria lobata* (white triangular marks indicate adults) (Ehime-ken, Shikoku); B) a mine of *T. toringoi* Kurosawa on *Aria alnifolia* (Fukushima-ken, Honshu); C) a mine of *T. toringoi* on *Sorbus commixta* (Fukushima-ken, Honshu); D) a mine of *T. pecirkai* Obenberger on *Ulmus davidiana* var. *japonica*; E) a mine of *T. aurifluus* Solsky on *Tilia japonica*; F) an egg of *T. aurifluus* on *Ti. japonica*.

FIGURE 65. Adult feeding scars and leaf-mines of Japanese *Trachys* spp. in the field. —— A) Leaf-mines of *Trachys reitteri* Obenberger on *Amphicarpaea edgeworthii*; B) a mine of *T. tokyoensis* Obenberger on *Hylodesmum podocarpum*; C) adult feeding scars and a mine of *T. yanoi* Kurosawa on *Zelkova serrata*; D) a mine of *T. variolaris* Saunders on *Quercus salicina*; E) a fallen mine of *T. robustus* Saunders on *Castanopsis sieboldii* subsp. *sieboldii* (indicated by a white triangular mark); F) a mine of *T. dilaticeps* Gebhardt on *C. sieboldii* subsp. *lutchuensis*.

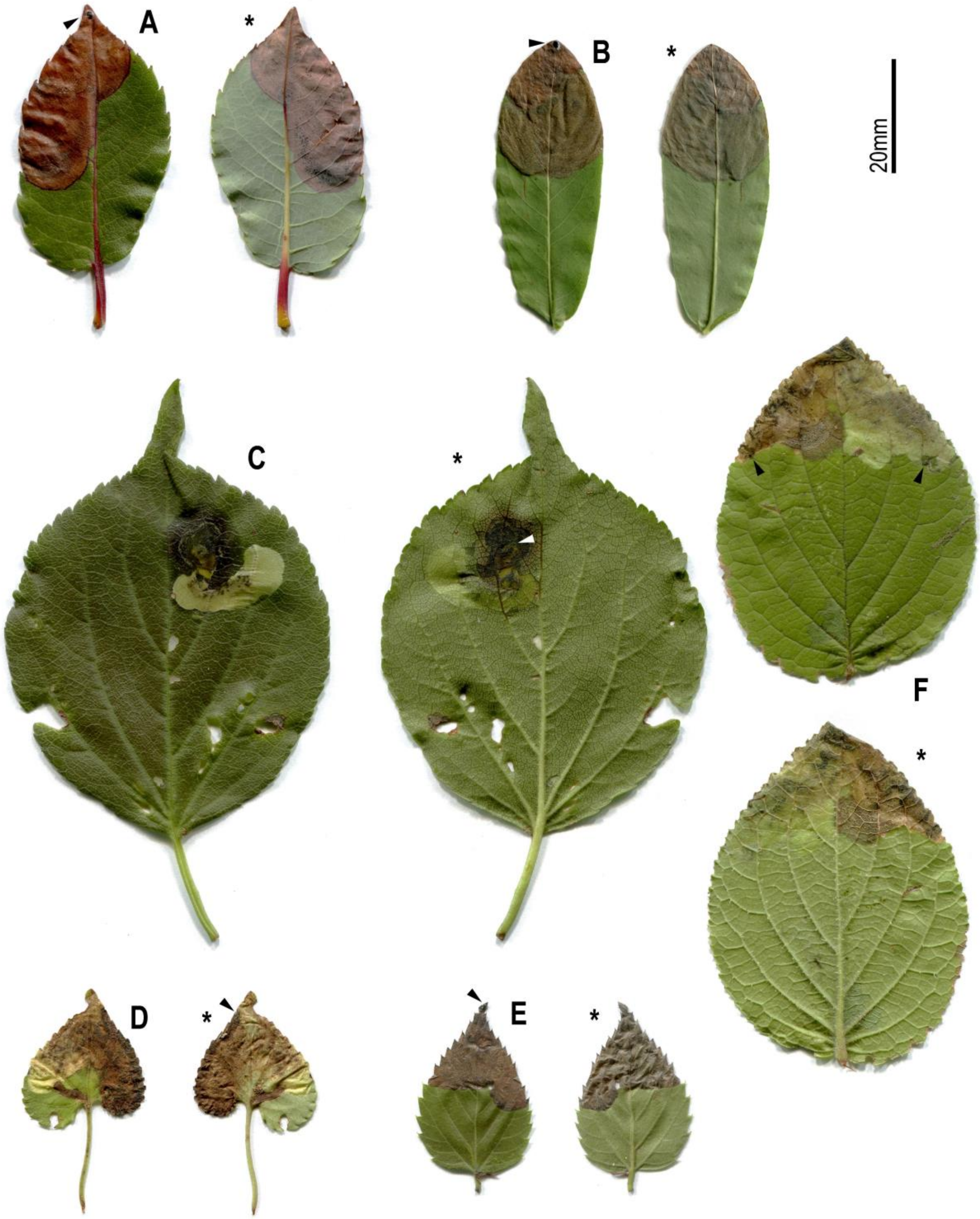


FIGURE 66. Leaf-mines of Japanese *Trachys* spp. —— A) A mine (full-grown) of *Trachys minutus* (Linnaeus) on *Salix shiraii* var. *shiraii*; B) a mine (full-grown) of *T. minutus* on *S. integra*; C) a mine of *T. inconspicuus* Saunders on *Prunus mume*; D) a mine of *T. pseudoscrobiculatus* Obenberger on *Viola grypoceras* var. *grypoceras*; E) a mine (full-grown) of *T. ineditus* Saunders on *Aphananthe aspera*; F) two mines of *T. tsushimae* Obenberger on *Deutzia scabra*. Asterisks (*) indicate leaves in the abaxial side. Black or white triangular marks indicate the oviposition sites.

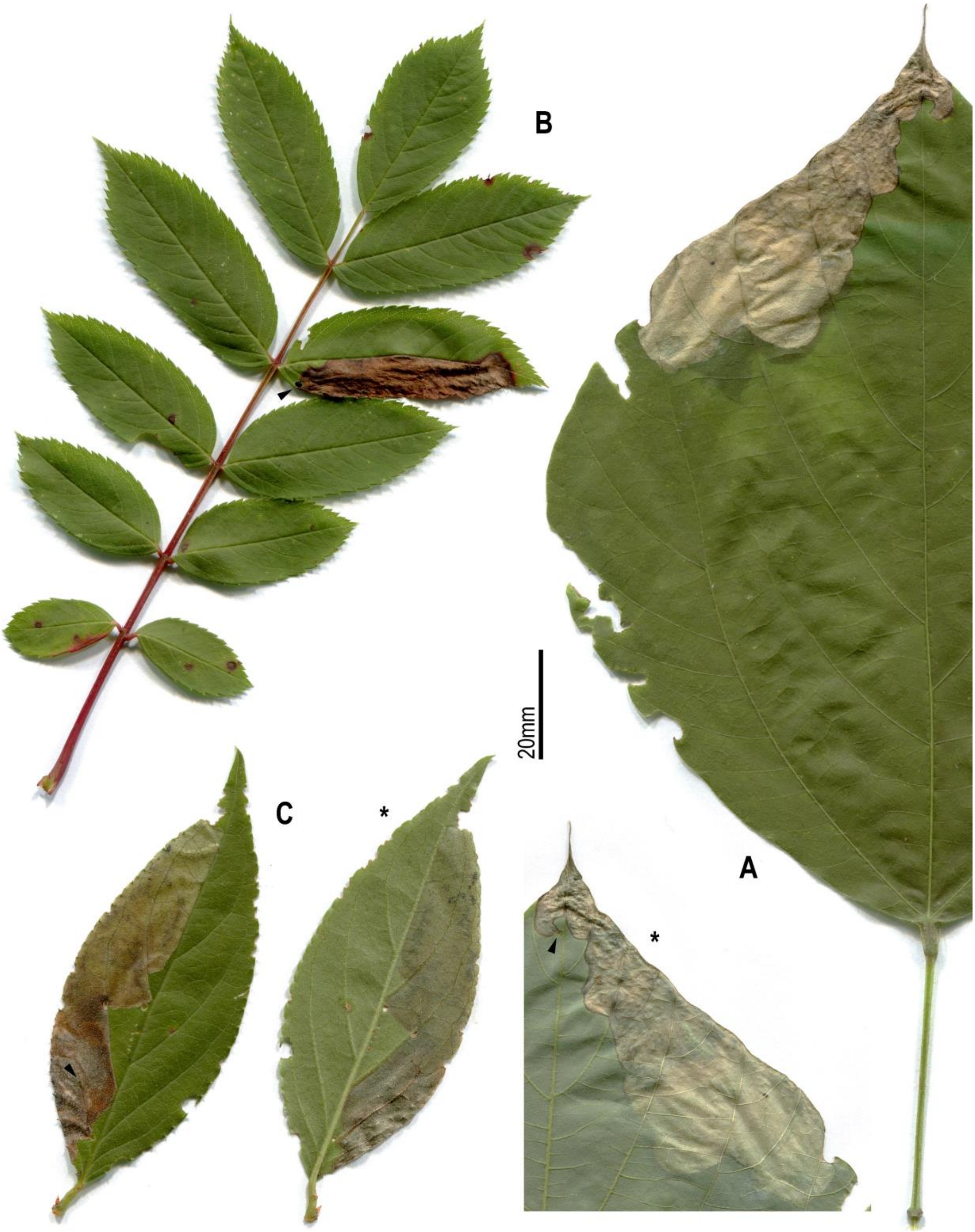


FIGURE 67. Leaf-mines of Japanese *Trachys* spp. ——A) A mine of *Trachys auricollis* Saunders on *Pueraria lobata*; B) a mine of *T. toringoi* Kurosawa on *Aria alnifolia*; C) a mine of *T. saundersi* Lewis on *Deutzia crenata*. Asterisks (*) indicate leaves in the abaxial side. Black triangular marks indicate the oviposition sites.

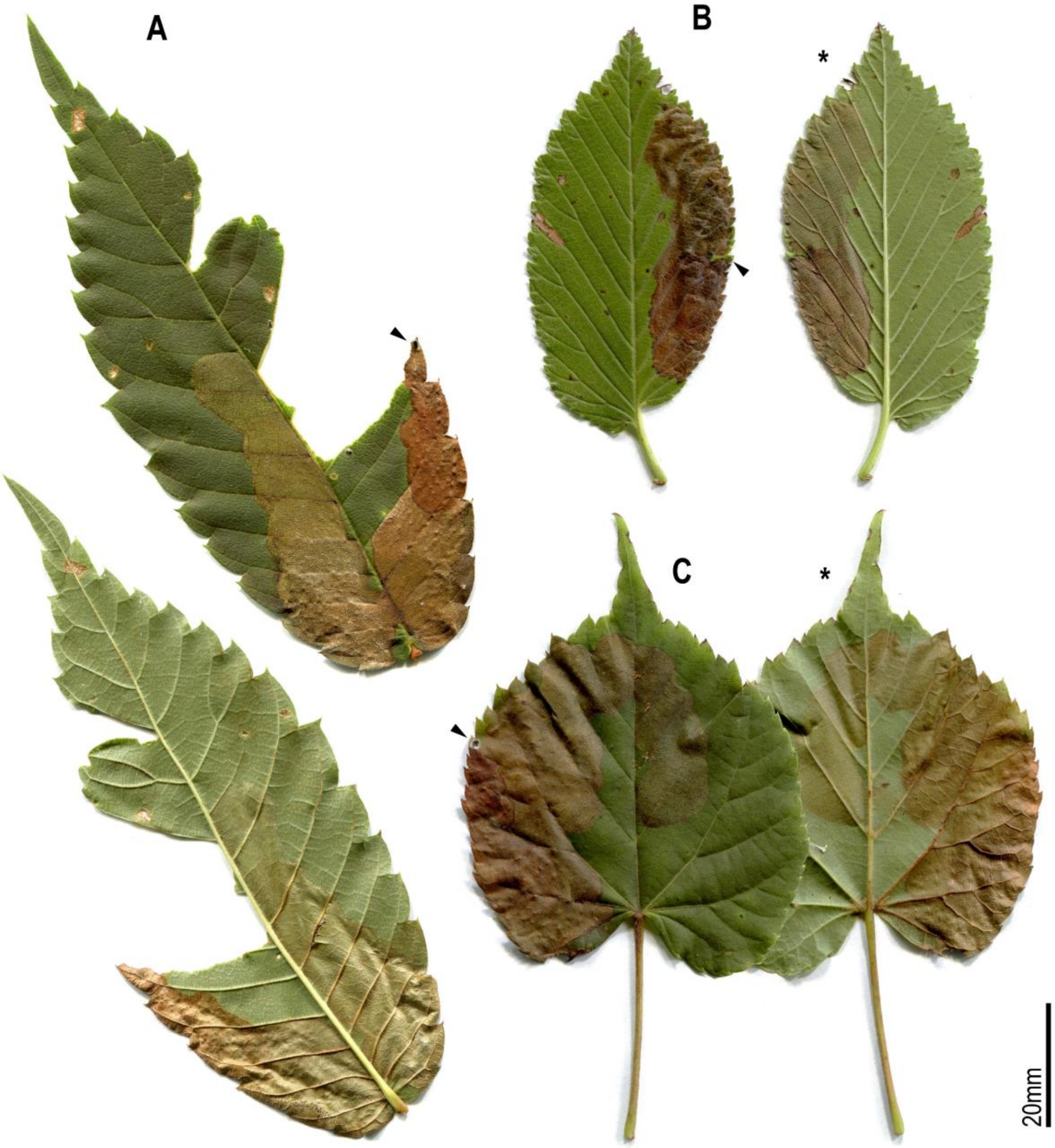


FIGURE 68. Leaf-mines of Japanese *Trachys* spp. —— A) A mine of *Trachys cupricolor* Saunders on *Zelkova serrata*; B) a mine of *T. pecirkai* Obenberger on *Ulmus davidiana* var. *japonica*; C) a mine of *T. auriflluus* Solsky on *Tilia japonica*. Asterisks (*) indicate leaves in the abaxial side. Black triangular marks indicate the oviposition sites.

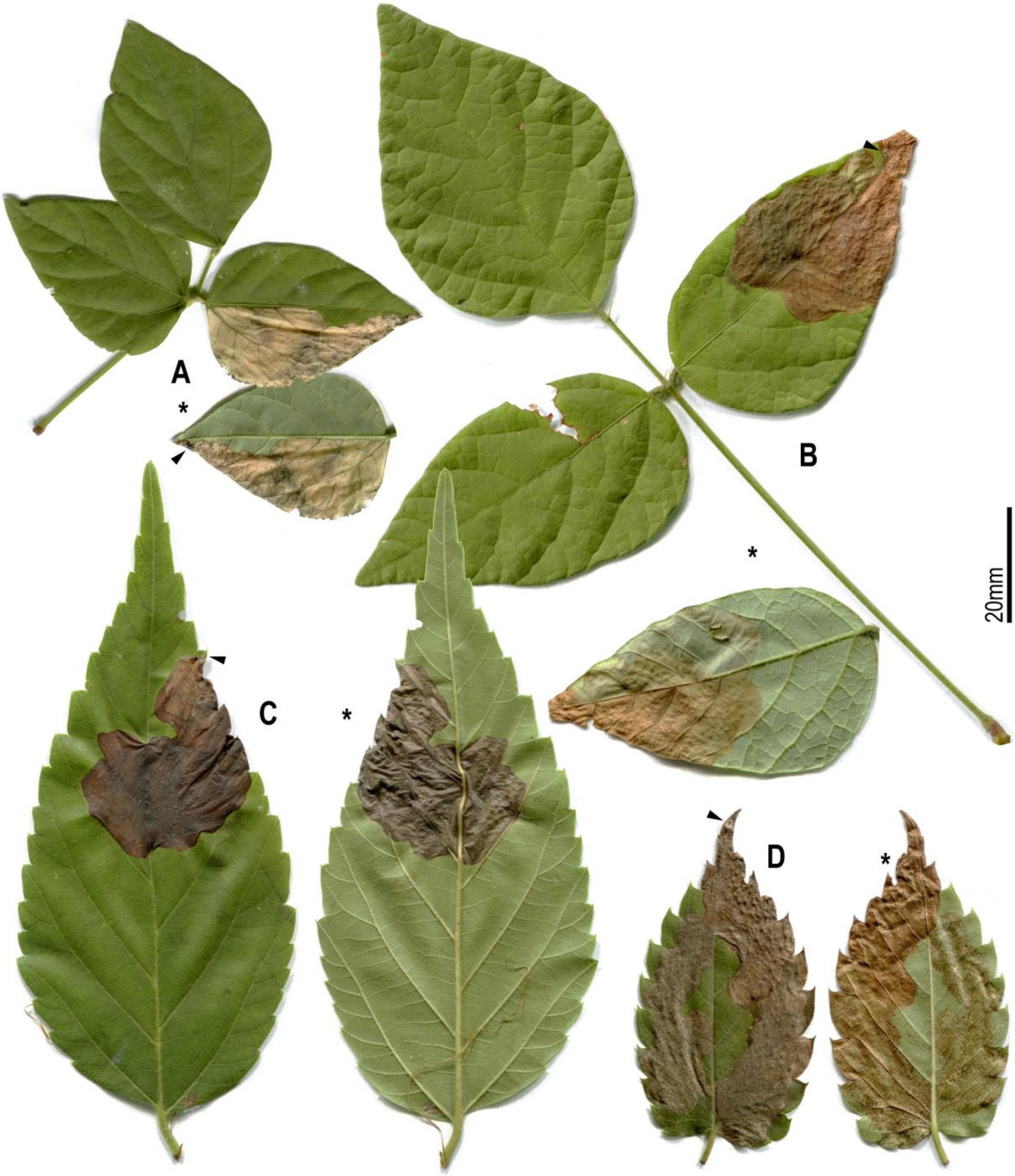


FIGURE 69. Leaf-mines of Japanese *Trachys* spp. —— A) A mine (full-grown) of *Trachys reitteri* Obenberger on *Amphicarpaea edgeworthii*; B) a mine of *T. tokyoensis* Obenberger on *Hylodesmum podocarpum*; C) a mine of *T. griseofasciatus* Saunders on *Aphananthe aspera*; D) a mine of *T. yanoi* Kurosawa on *Zelkova serrata*. Asterisks (*) indicate leaves in the abaxial side. Black or white triangular marks indicate the oviposition sites.

FIGURE 70. Leaf-mines of Japanese *Trachys* spp. —— A) A mine of *Trachys variolaris* Saunders on *Quercus dentata*; B) a mine of *T. robustus* Saunders on *Castanopsis sieboldii* subsp. *sieboldii*; C, D) mines of *T. dilaticeps* Gebhardt on *C. sieboldii* subsp. *lutchuensis*. Asterisks (*) indicate leaves in the abaxial side. Black or white triangular marks indicate the oviposition sites.

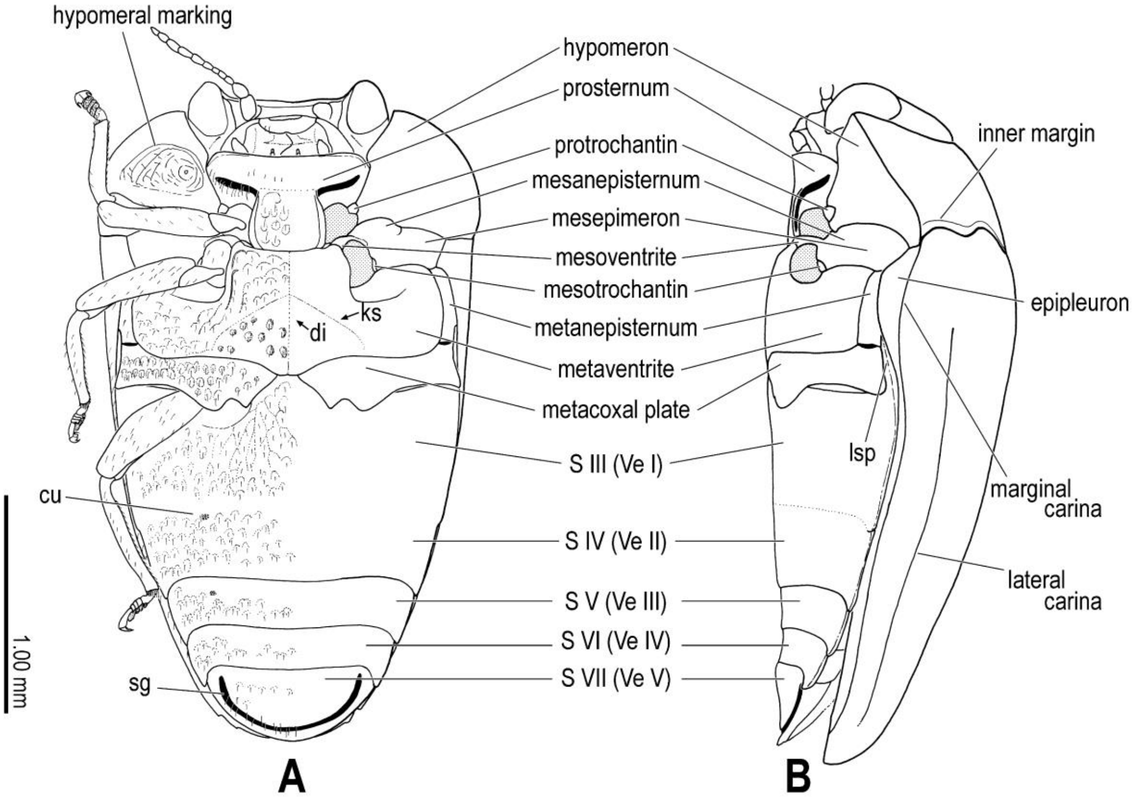


FIGURE 71. General appearance, *Habroloma* (*Parahabroloma*) *eximium eximium* (Lewis). — — A) Body, ventral view; B) ditto, lateral view. Abbreviations: cu — cuticularium; di — discrimen; ks — katepisternal suture; lsp — lateral sternal projection; sg — sternal groove.

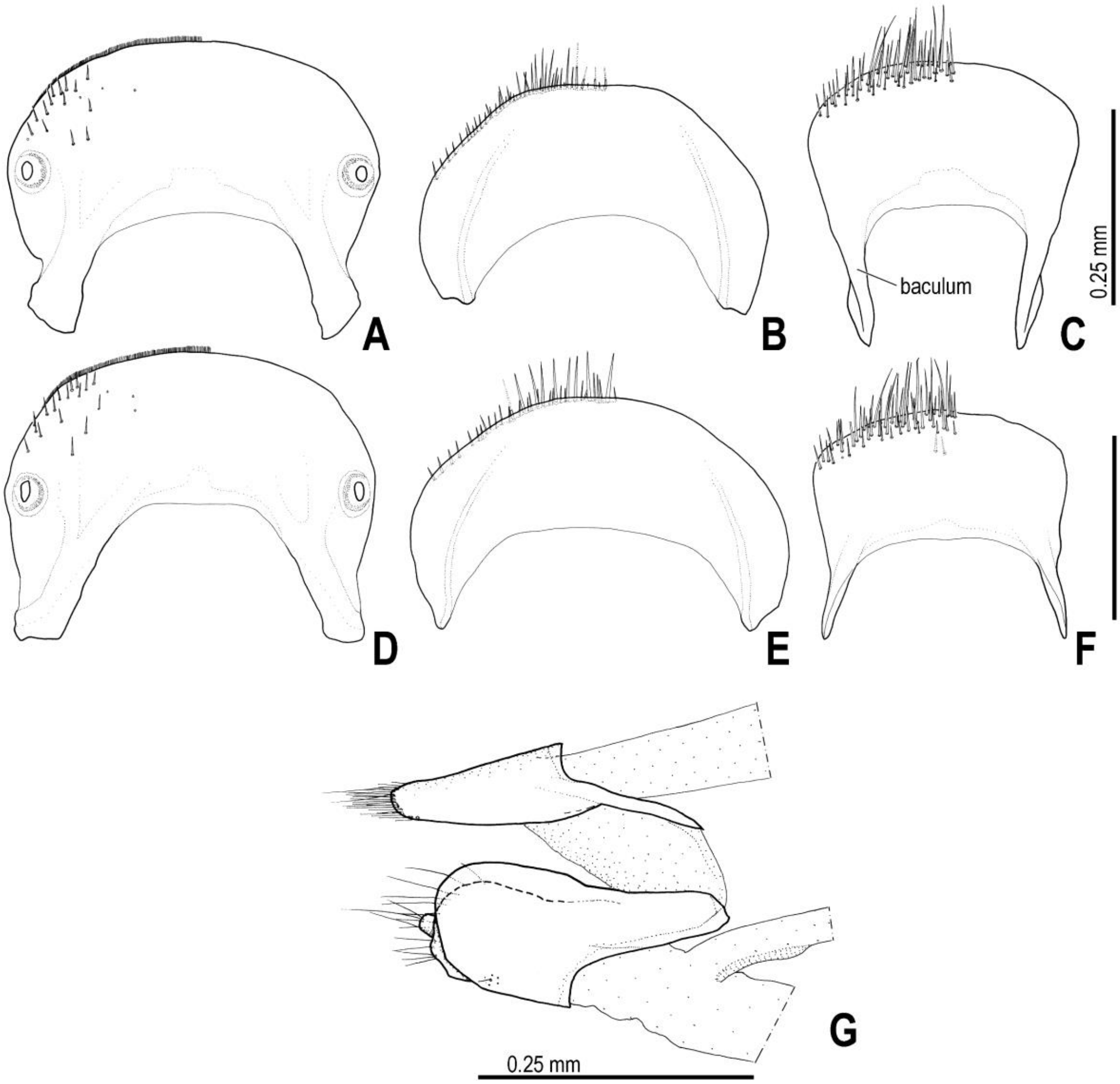


FIGURE 72. Male and female terminalia (part) of *Habroloma*., *H*. (*H*.) *bifrons* (Kiesenwetter). —— A, D) Tergite VIII, male (A) and female (D); B, E) sternite VIII, male (B) and female (E); C, F) proctiger, male (C) and female (F); G) female ovipositors (external part), lateral view.

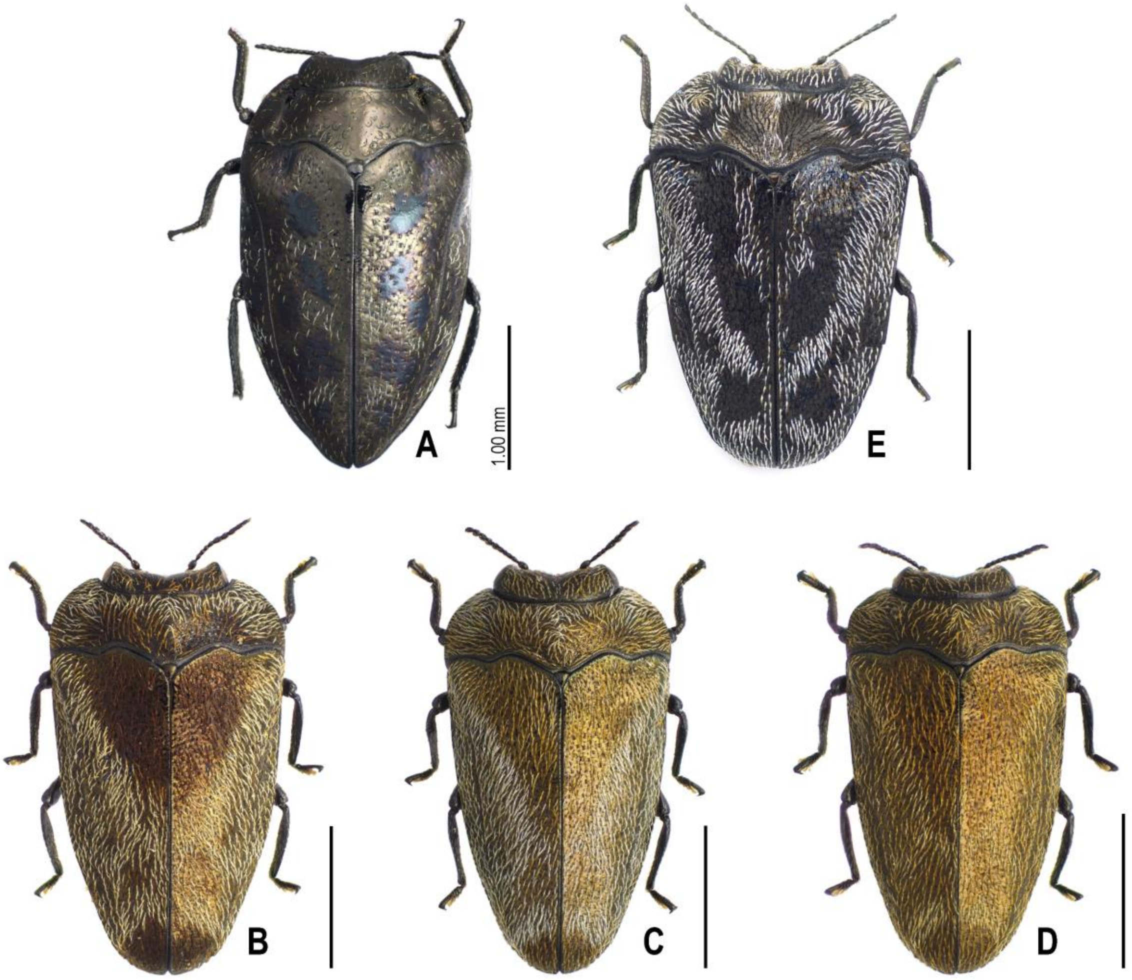


FIGURE 73. Dorsal habitus of Japanese *Habroloma* spp. —— A) *Habroloma* (*Habroloma*) *bifrons* (Kiesenwetter); B) *H*. (*Parahabroloma*) *eximium eximium* (Lewis); C) *H*. (*P*.) *eximium eupoetum* (Obenberger); D) *H*. (*P*.) *eximium* subsp. 1; E) *H*. (*P*.) *griseonigrum* (Saunders).

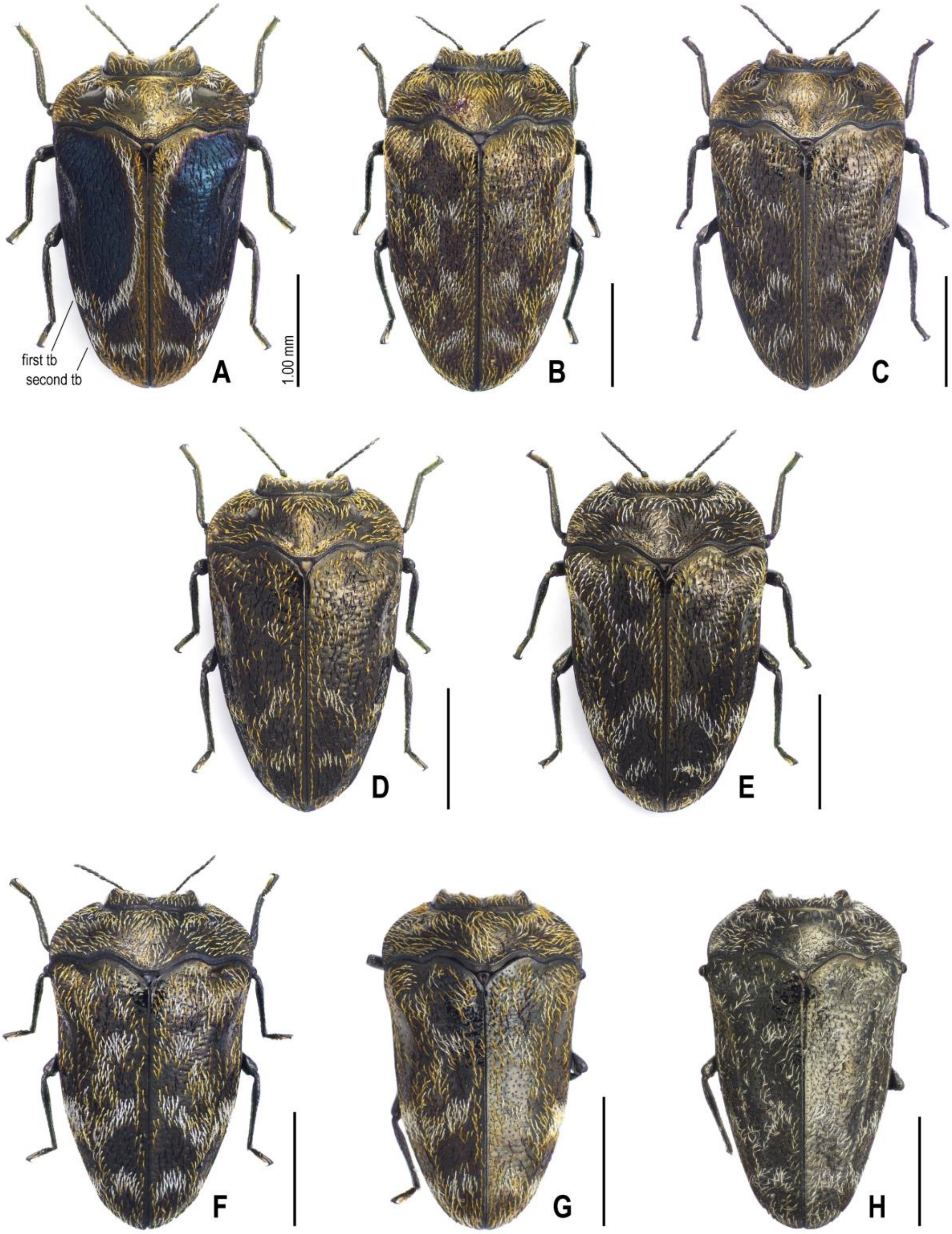


FIGURE 74. Dorsal habitus of Japanese *Habroloma* (*Parahabroloma*) spp. in the species group II and III —— A) *Habroloma* (*Parahabroloma*) *lewisii* (Saunders); B) *H*. (*P*.) *nixilla inslicola* Kurosawa; C) *H*. (*P*.) *yuasai* Kurosawa; D) *H*. (*P*.) *subbicorne* (Motschulsky); E) *H*. (*P*.) *marginicolle* (Fairmaire); F) *H*. (*P*.) *asahinai asahinai* Kurosawa; G) *H*. (*P*.) *asahinai* subsp. 1; H) *H*. (*P*.) *hikosanense* Kurosawa. Abbreviation: tb — transverse band.

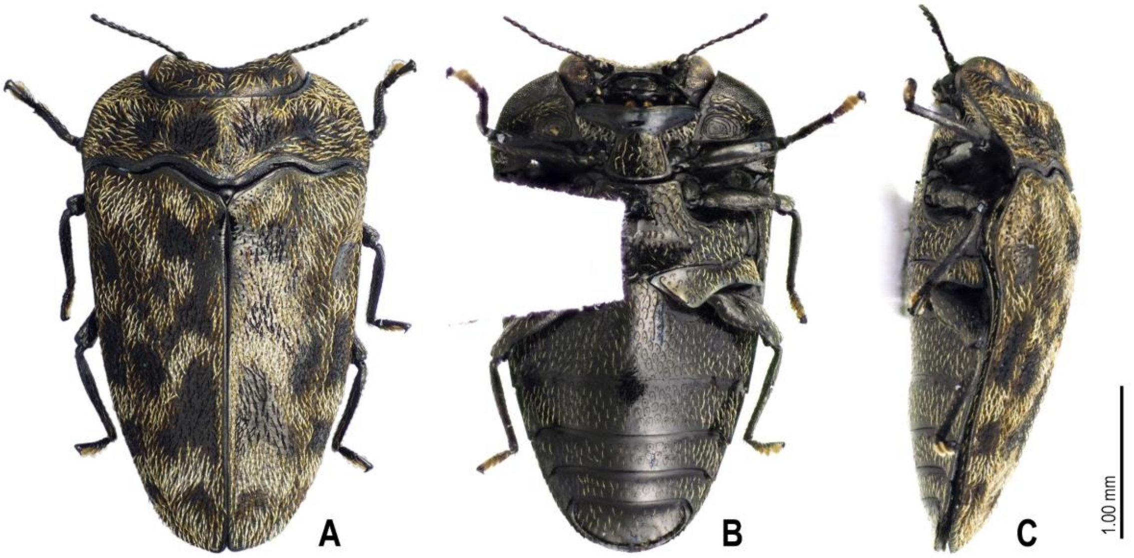


FIGURE 75. Habitus of *Habroloma* (*Parahabroloma*) sp. 1. —— A) Dorsal view; B) ventral view; C) lateral view.

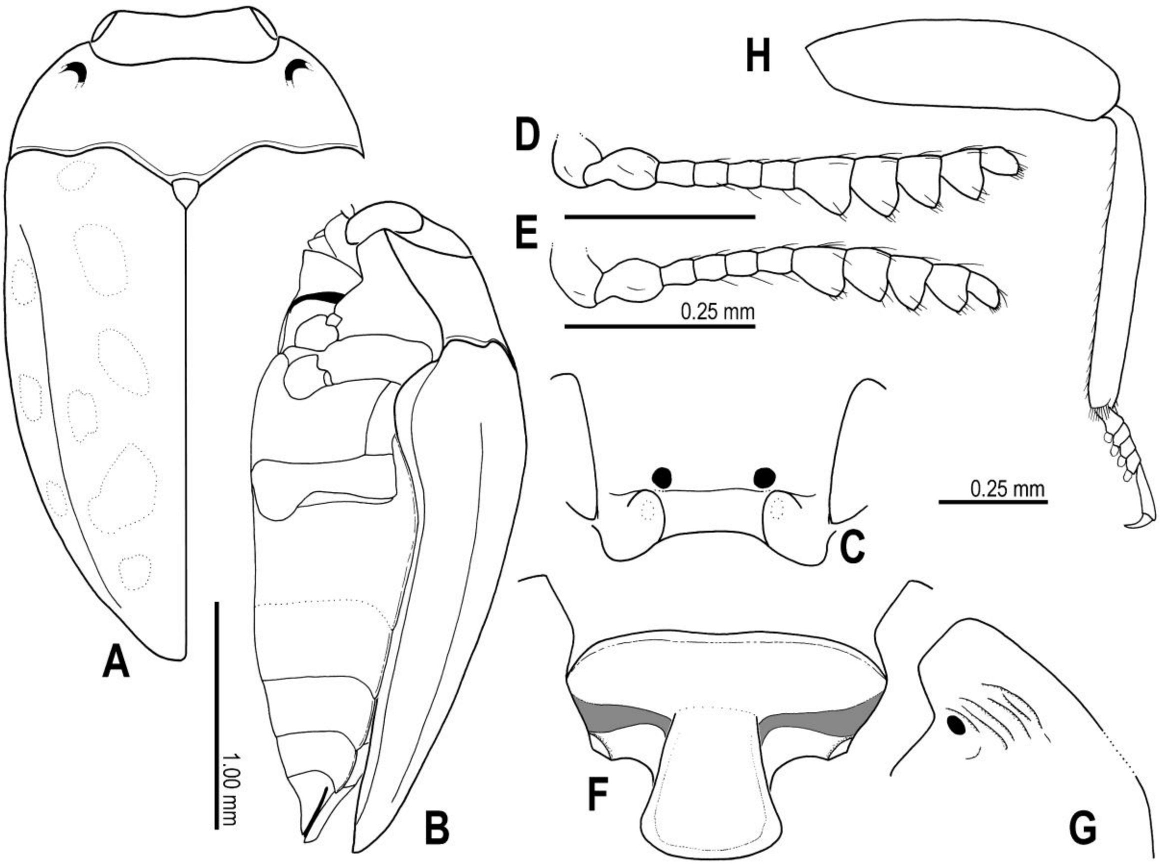


FIGURE 76. *Habroloma* (*Habroloma*) *bifrons* (Kiesenwetter). —— A) Head, pronotum, and left elytron; B) body, lateral view; C) clypeus; D, E) antennae, outer side, male (D) and female (E); F) prosternum; G) hypomeral marking, oblique view; H) metaleg (femur and tibia), ventral view.

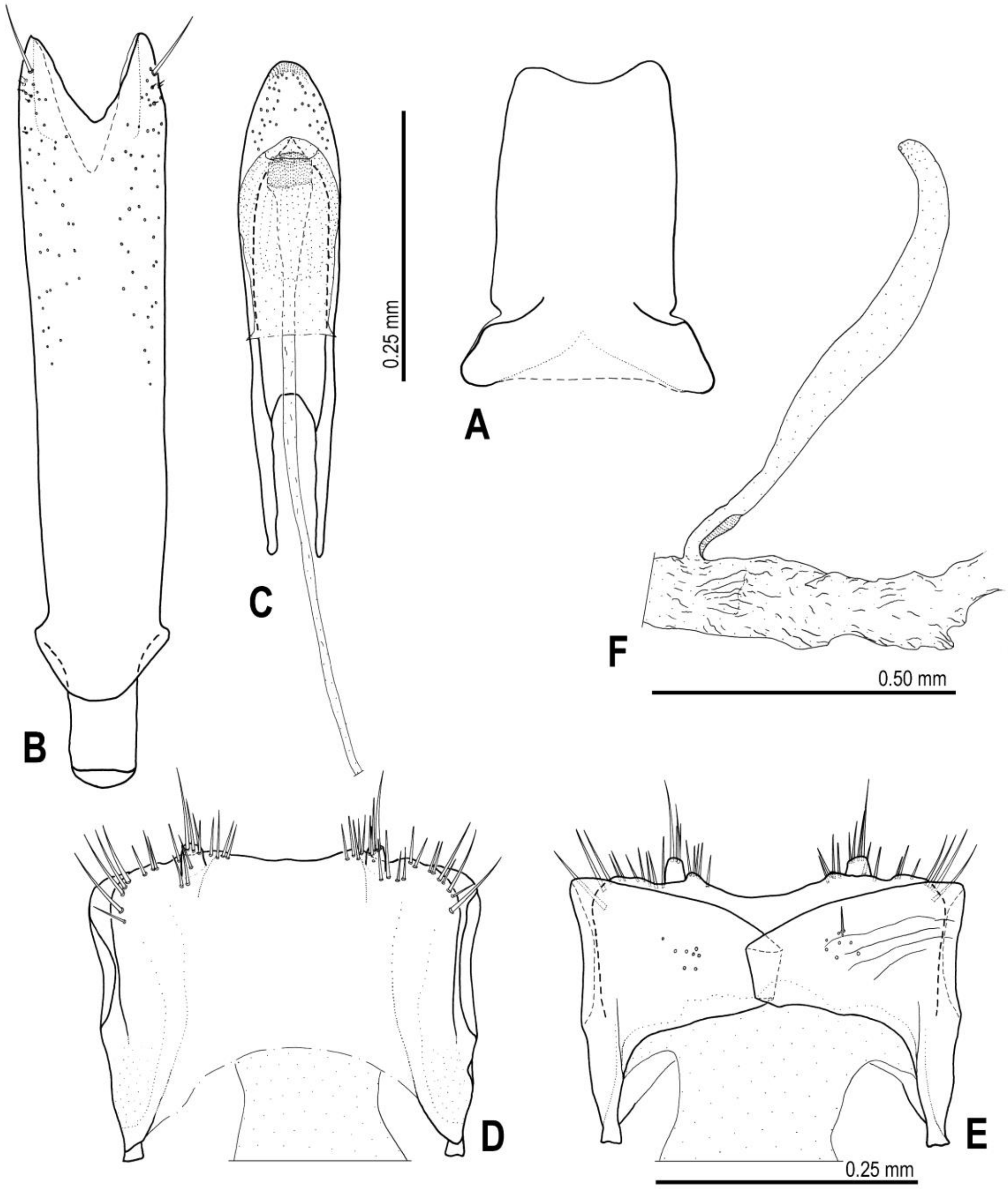


FIGURE 77. Male and female terminalia (part), *Habroloma* (*Habroloma*) *bifrons* (Kiesenwetter). —— A) Sternite IX, male; B) tegmen; C) penis; D, E) external part of ovipositor (except proctiger), dorsal view (D) and ventral view (E); F) internal part of ovipositor, lateral view.

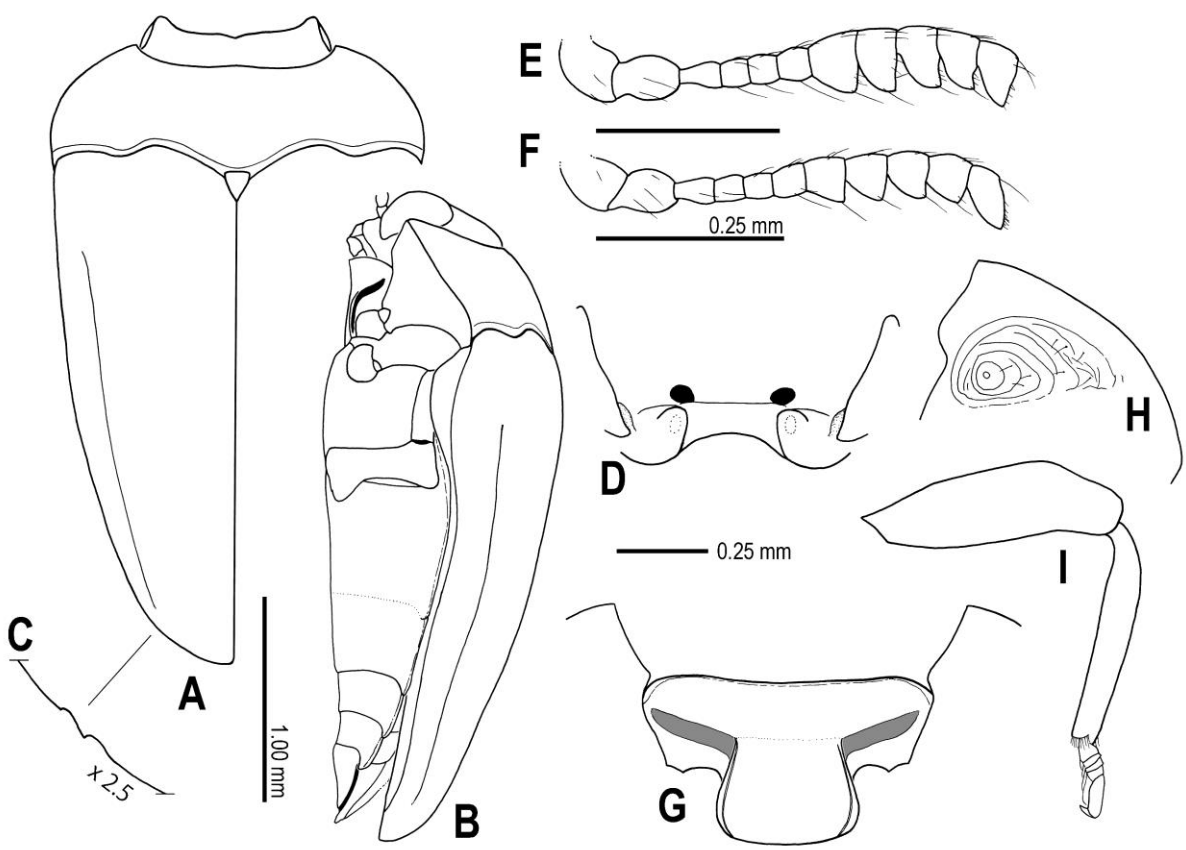


FIGURE 78. *Habroloma* (*Parahabroloma*) *eximium eximium* (Lewis). —— A) Head, pronotum, and left elytron; B) body, lateral view; C) serration of elytral lateral margin, obliquely ventral view; D) clypeus; E, F) antennae, outer side, male (E) and female (F); G) prosternum; H) hypomeral marking, oblique view; I) metaleg (femur and tibia), ventral view.

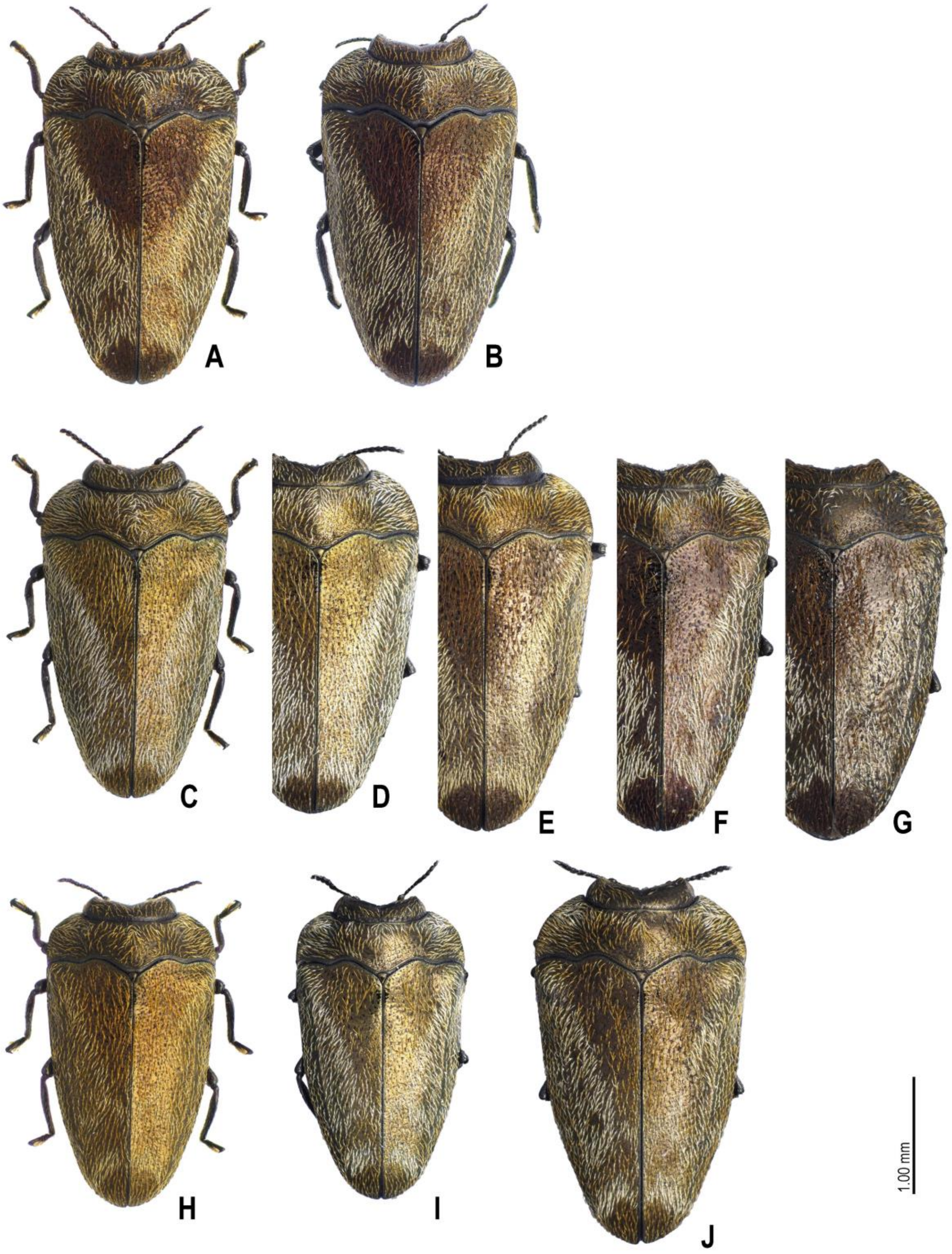


FIGURE 79. Variations in dorsal habitus between three subspecies and intraspecific variations, *Habroloma* (*Parahabroloma*) *eximium*. —— A, B) *H*. (*P*.) *eximium eximium* (Lewis) from Kyushu; C–G) *H*. (*P*.) *eximium eupoetum* (Obenberger) from Iriomotejima Is. (C), Ishigakijima Is. (D, E), and Taiwan (F, G); H–J) *H*. (*P*.) *eximium* subsp. 1 from Amami-Ôshima Is. (H) and Okinoerabujima Is. (I, J).

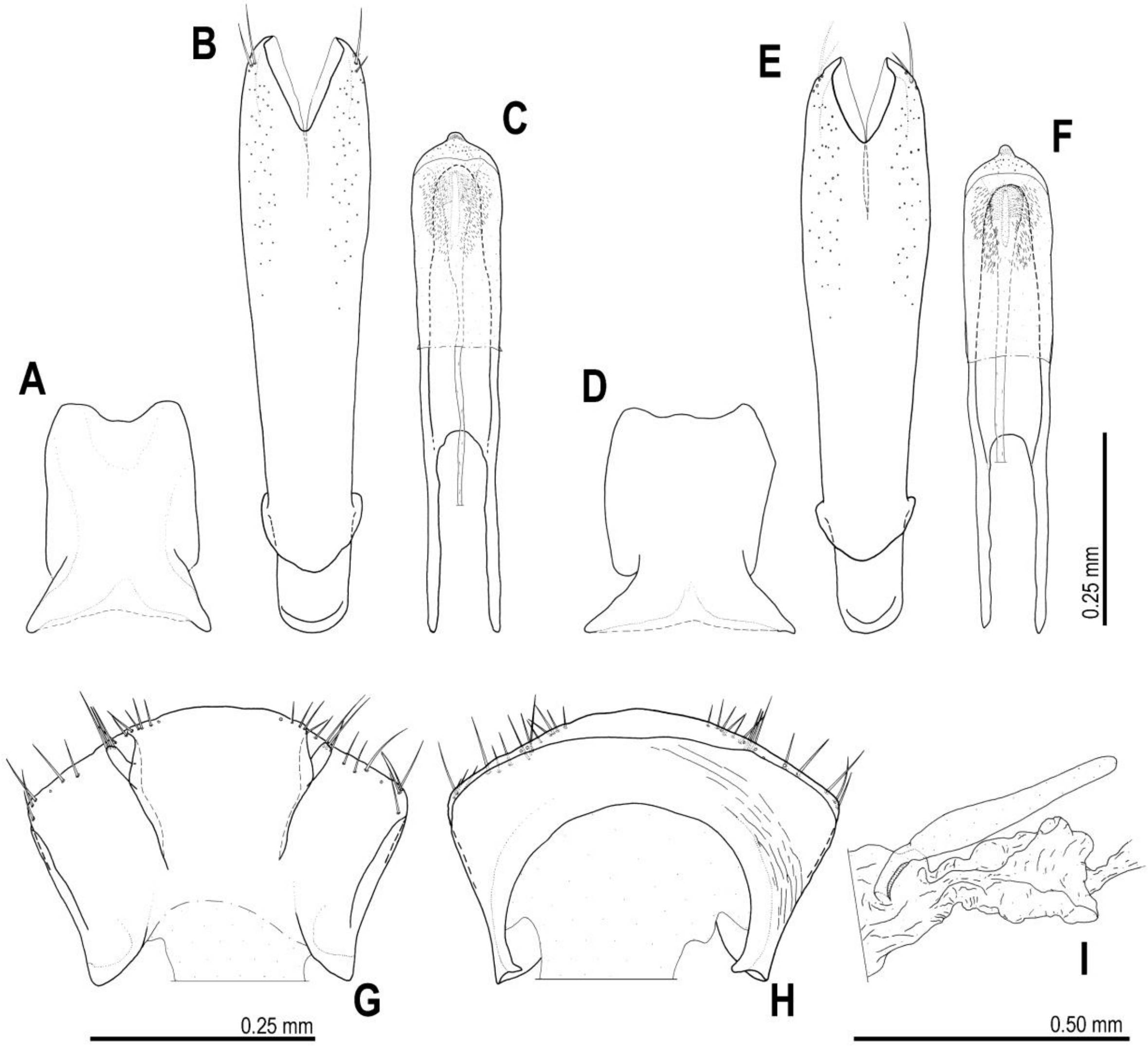


FIGURE 80. Male and female terminalia (part), *Habroloma* (*Parahabroloma*) *eximium eximium* (Lewis). —— A, D) Sternite IX, male; B, E) tegmen; C, F) penis; G, H) external part of ovipositor (except proctiger), dorsal view (G) and ventral view (H); I) internal part of ovipositor, lateral view.

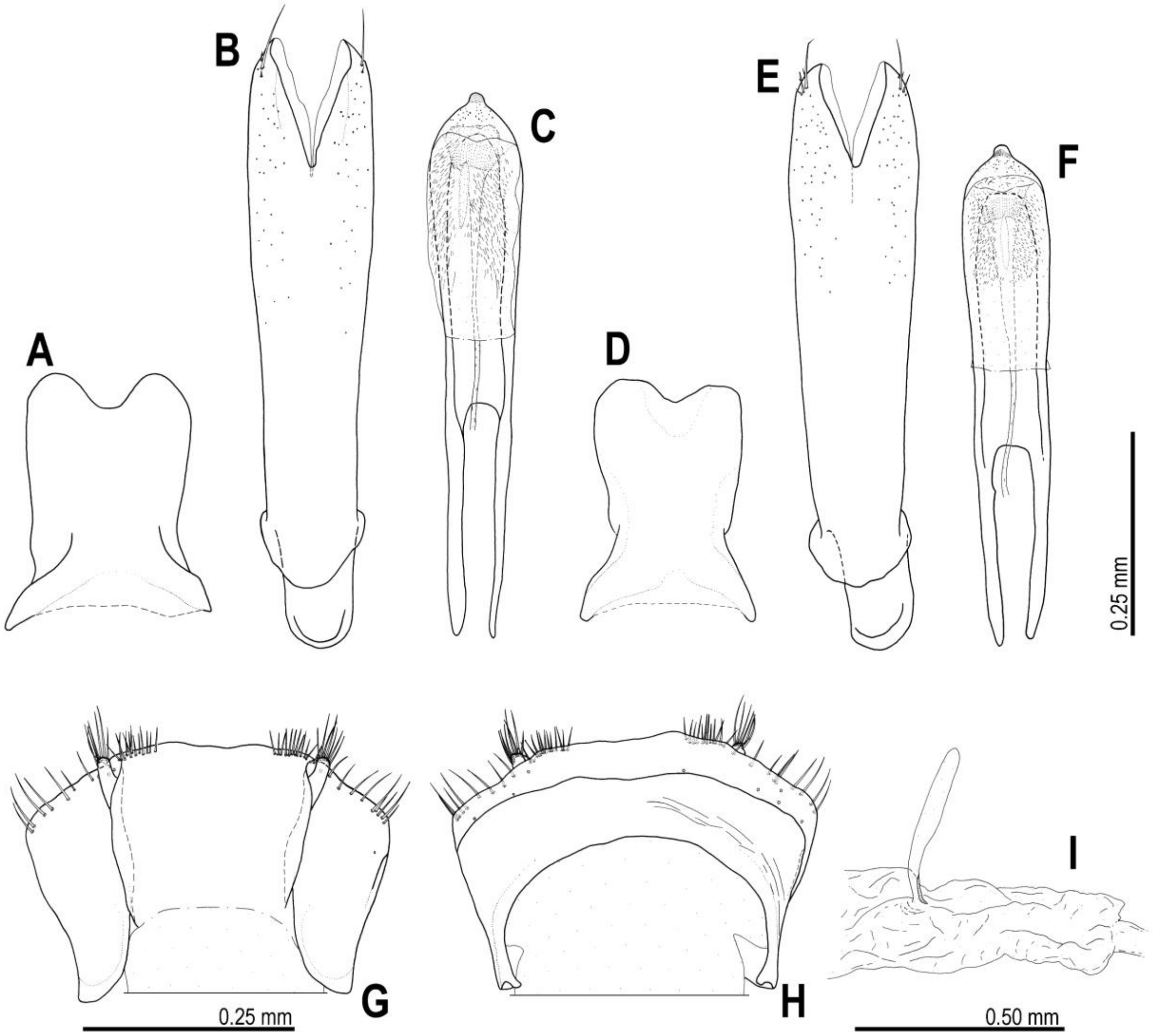


FIGURE 81. Male and female terminalia (part), *Habroloma* (*Parahabroloma*) *eximium eupoetum* (Obenberger). —— A, D) Sternite IX, male; B, E) tegmen; C, F) penis; G, H) external part of ovipositor (except proctiger), dorsal view (G) and ventral view (H); I) internal part of ovipositor, lateral view.

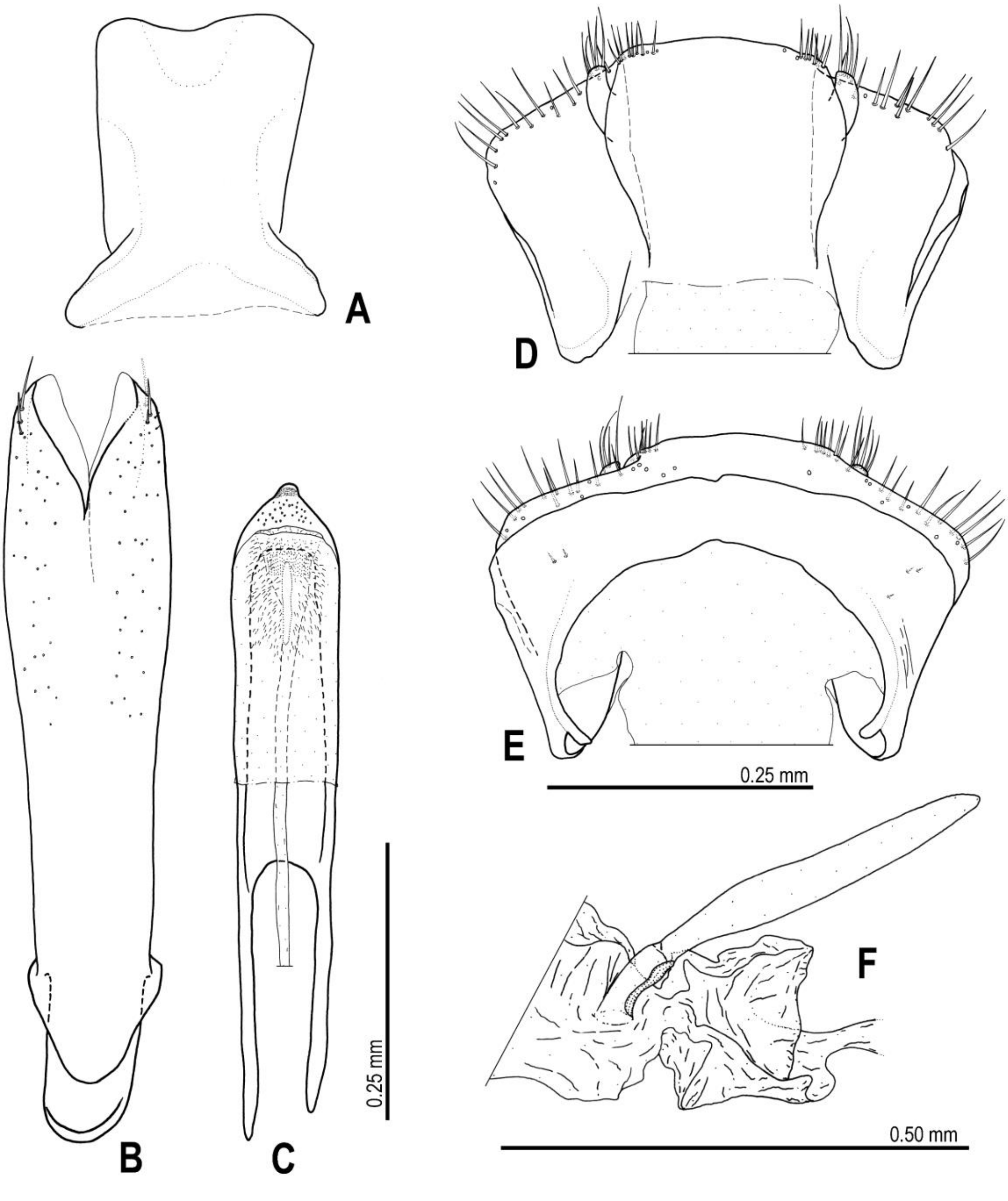


FIGURE 82. Male and female terminalia (part), *Habroloma* (*Parahabroloma*) *eximium* subsp. 1. —— A) Sternite IX, male; B) tegmen; C) penis; D, E) external part of ovipositor (except proctiger), dorsal view (D) and ventral view (E); F) internal part of ovipositor, lateral view.

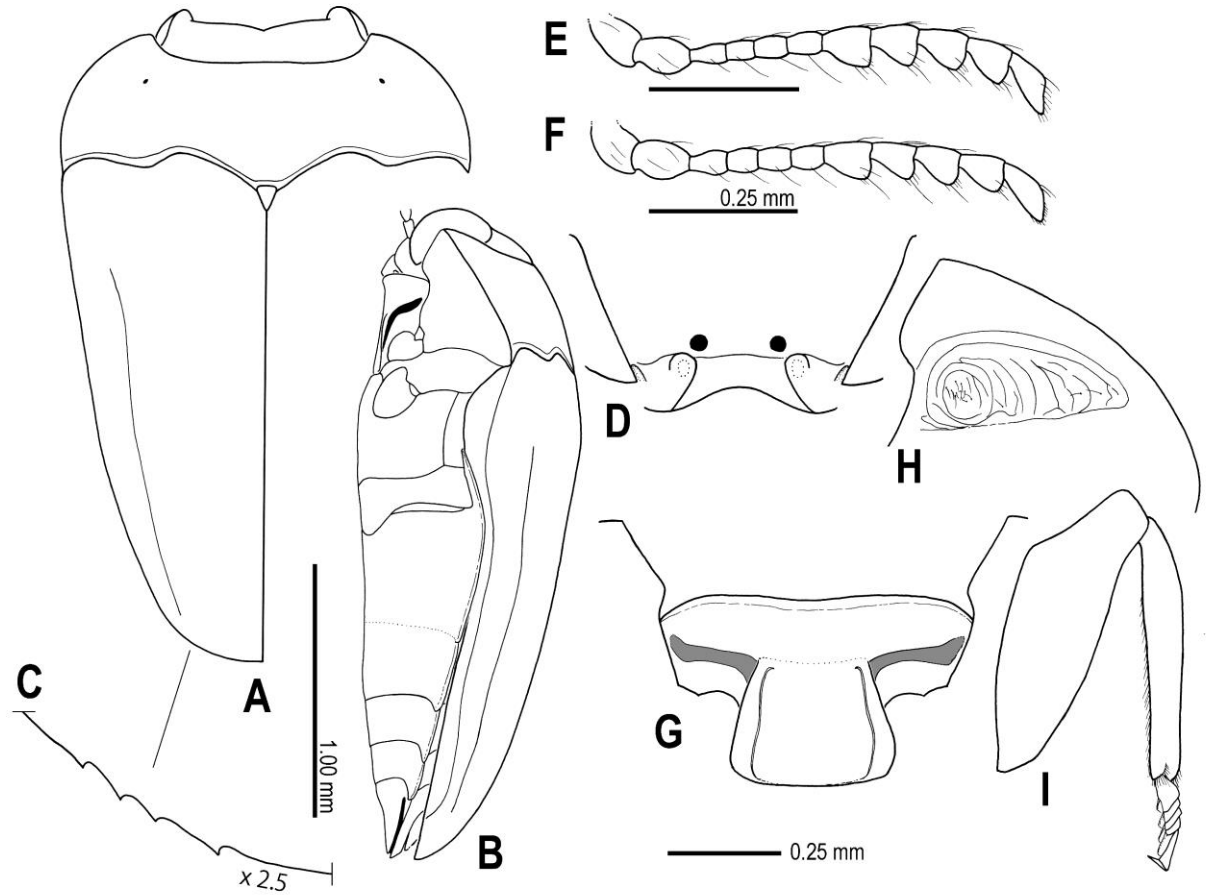


FIGURE 83. *Habroloma* (*Parahabroloma*) *griseonigrum* (Saunders). —— A) Head, pronotum, and left elytron; B) body, lateral view; C) serration of elytral lateral margin, obliquely ventral view; D) clypeus; E, F) antennae, outer side, male (E) and female (F); G) prosternum; H) hypomeral marking, oblique view; I) metaleg (femur and tibia), ventral view.

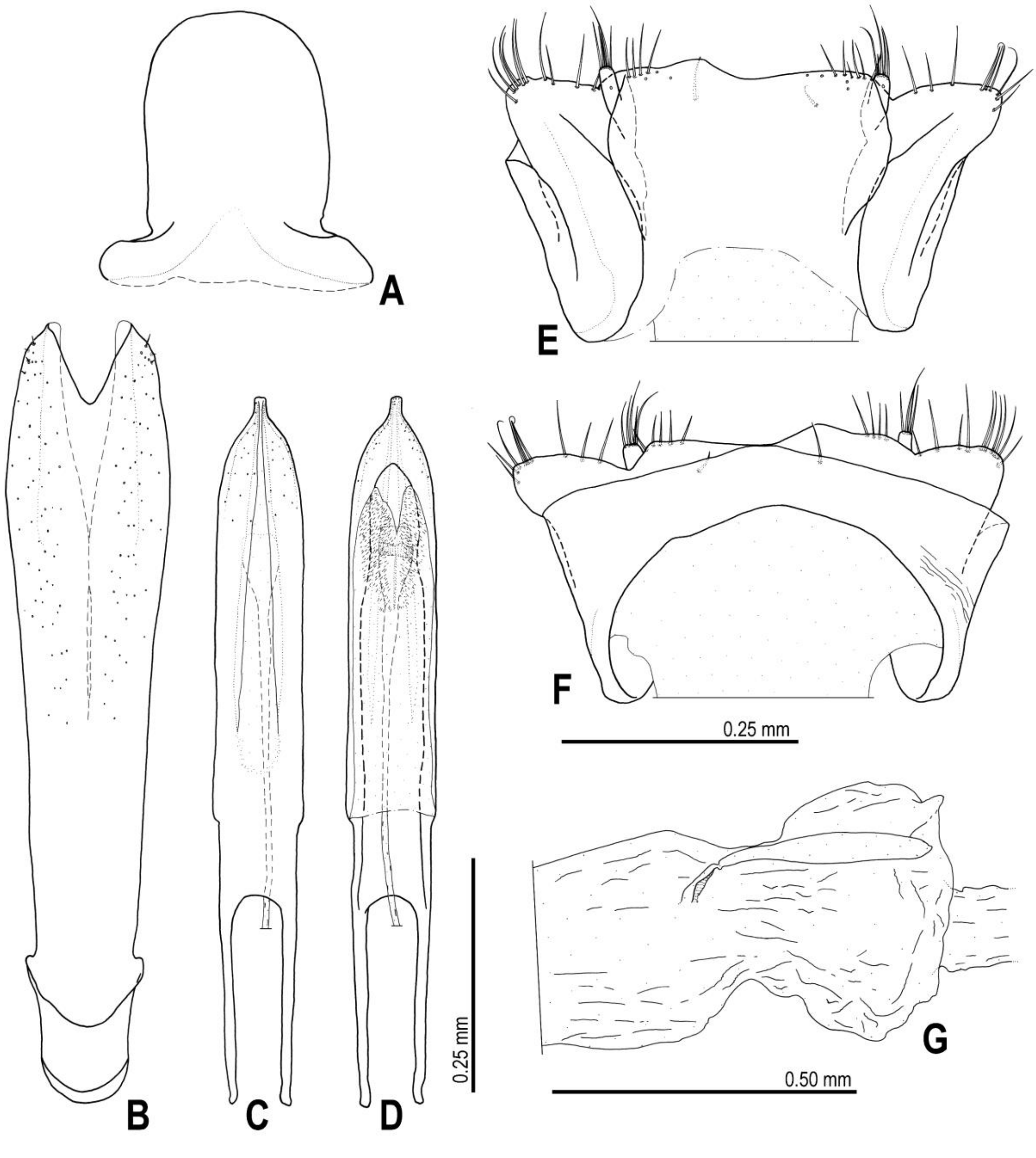


FIGURE 84. Male and female terminalia (part), *Habroloma* (*Parahabroloma*) *griseonigrum* (Saunders). —— A) Sternite IX, male; B) tegmen; C, D) penis, dorsal view (C), ventral view (D); E, F) external part of ovipositor (except proctiger), dorsal view (E) and ventral view (F); G) internal part of ovipositor, lateral view.

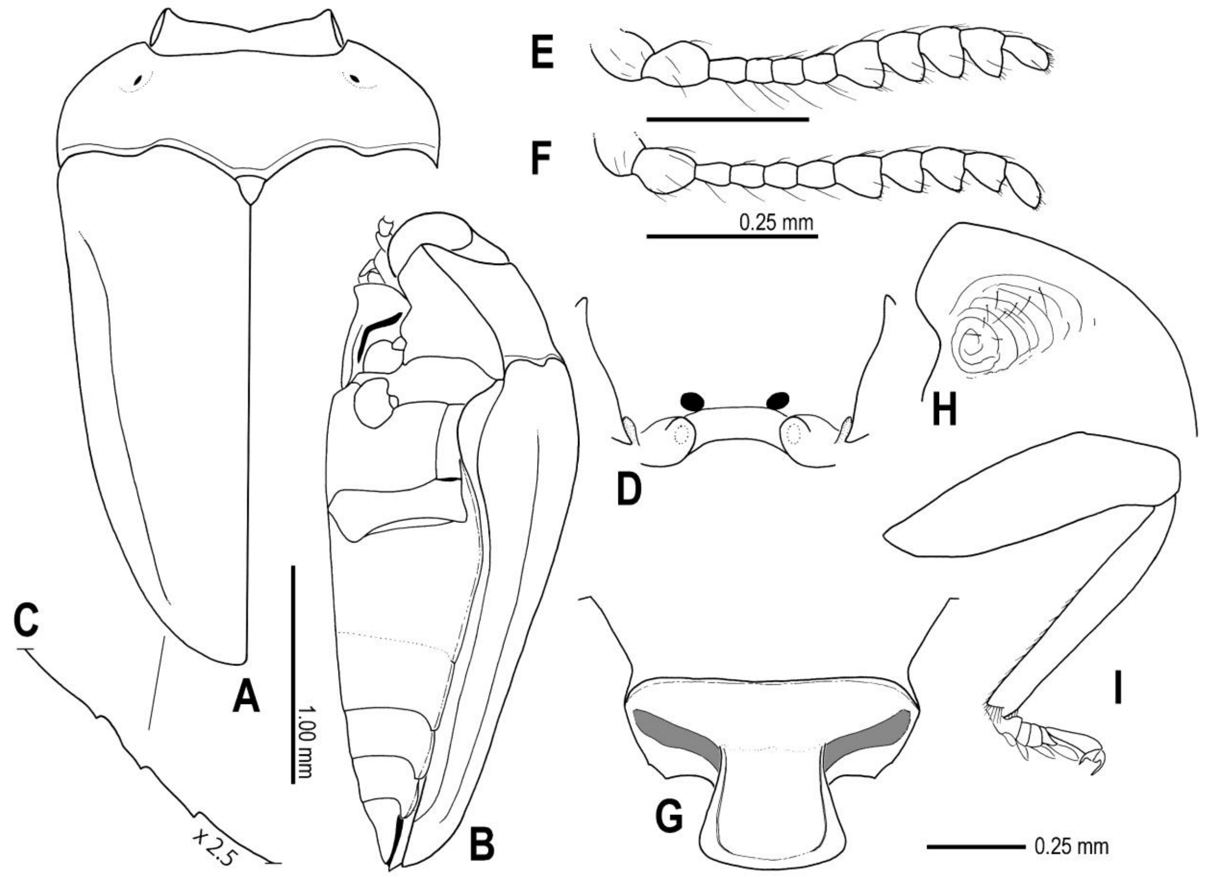


FIGURE 85. *Habroloma* (*Parahabroloma*) *lewisii* (Saunders). —— A) Head, pronotum, and left elytron; B) body, lateral view; C) serration of elytral lateral margin, obliquely ventral view; D) clypeus; E, F) antennae, outer side, male (E) and female (F); G) prosternum; H) hypomeral marking, oblique view; I) metaleg (femur and tibia), ventral view.

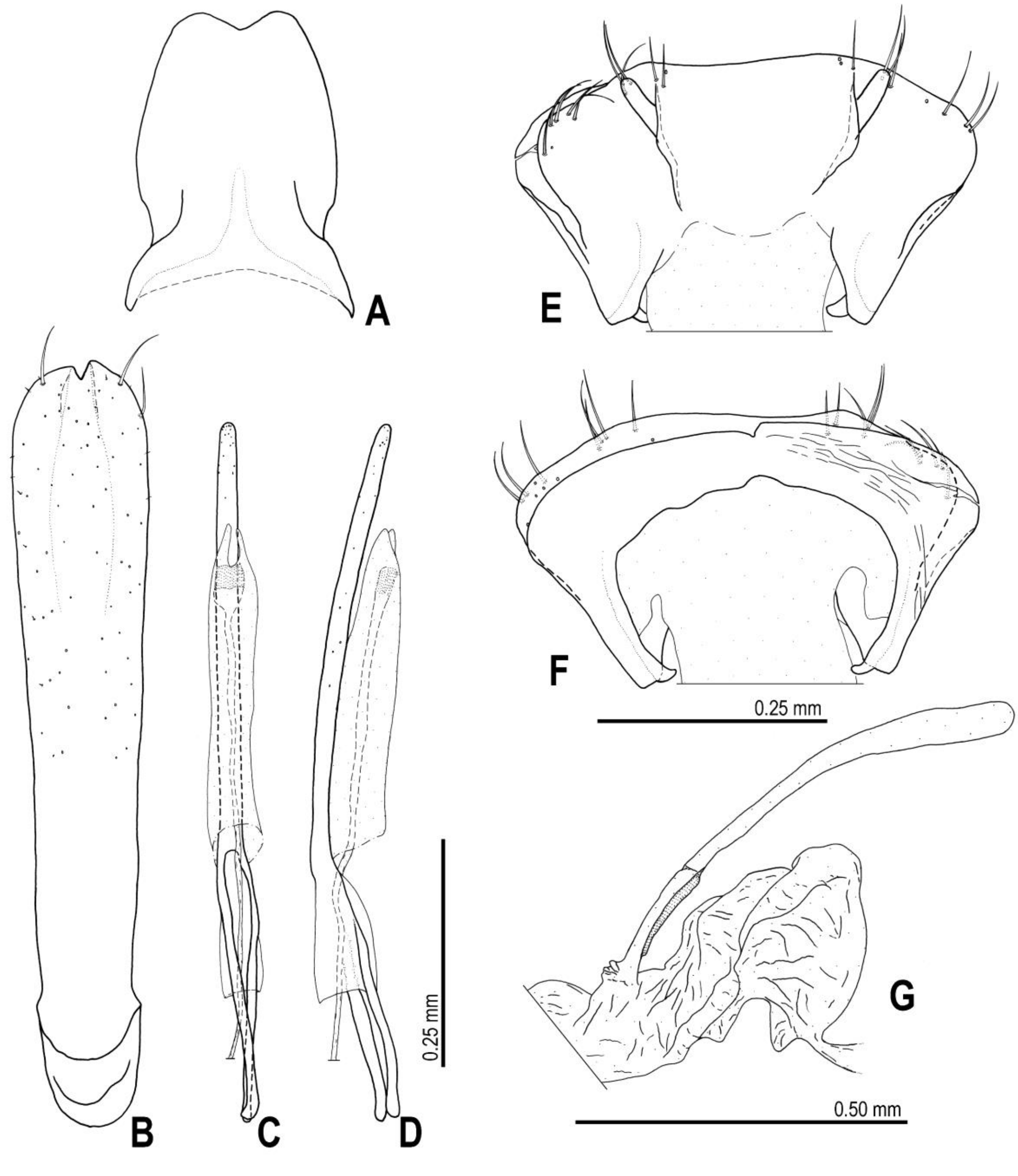


FIGURE 86. Male and female terminalia (part), *Habroloma* (*Parahabroloma*) *lewisii* (Saunders). —— A) Sternite IX, male; B) tegmen; C, D) penis, ventral view (C), lateral view (D); E, F) external part of ovipositor (except proctiger), dorsal view (E) and ventral view (F); G) internal part of ovipositor, lateral view.

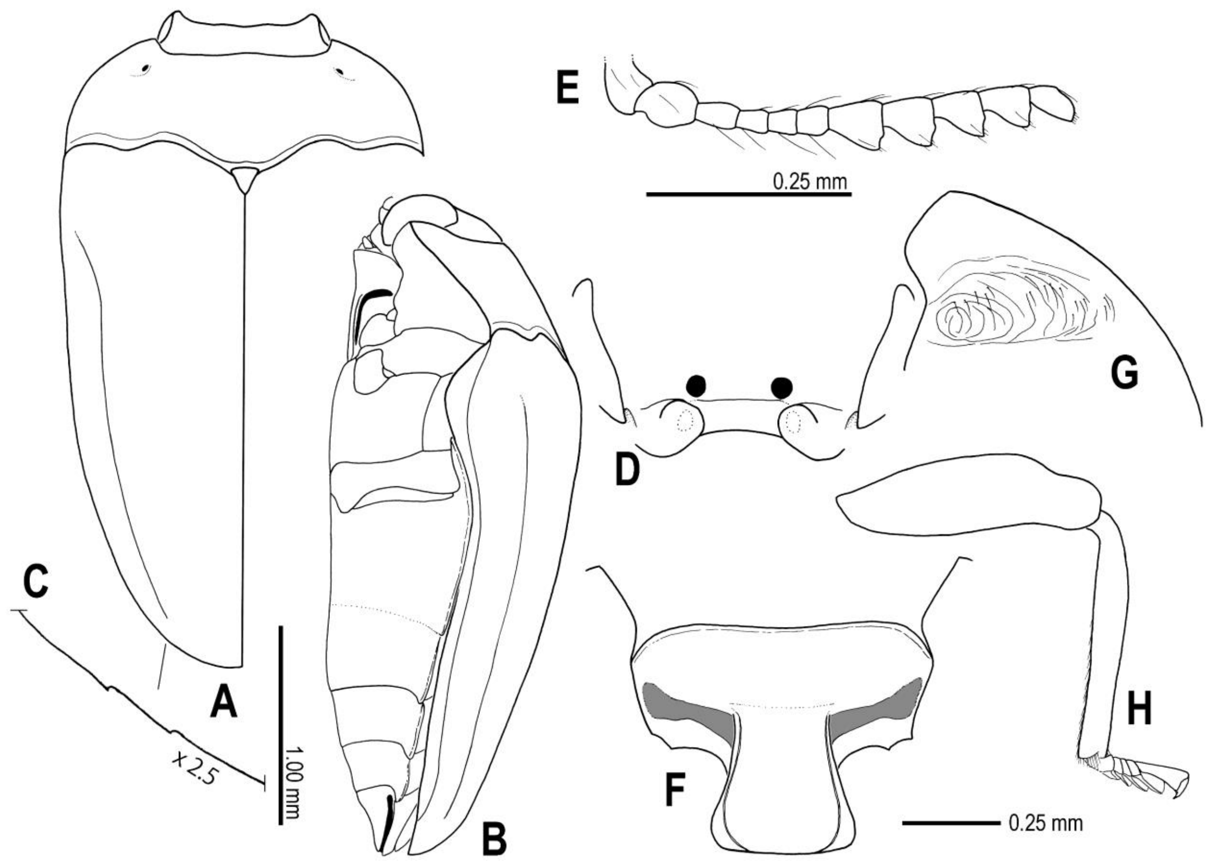


FIGURE 87. *Habroloma* (*Parahabroloma*) *nixilla inslicola* Kurosawa. —— A) Head, pronotum, and left elytron; B) body, lateral view; C) serration of elytral lateral margin, obliquely ventral view; D) clypeus; E, F) antennae, outer side, male (E) and female (F); G) prosternum; H) hypomeral marking, oblique view; I) metaleg (femur and tibia), ventral view.

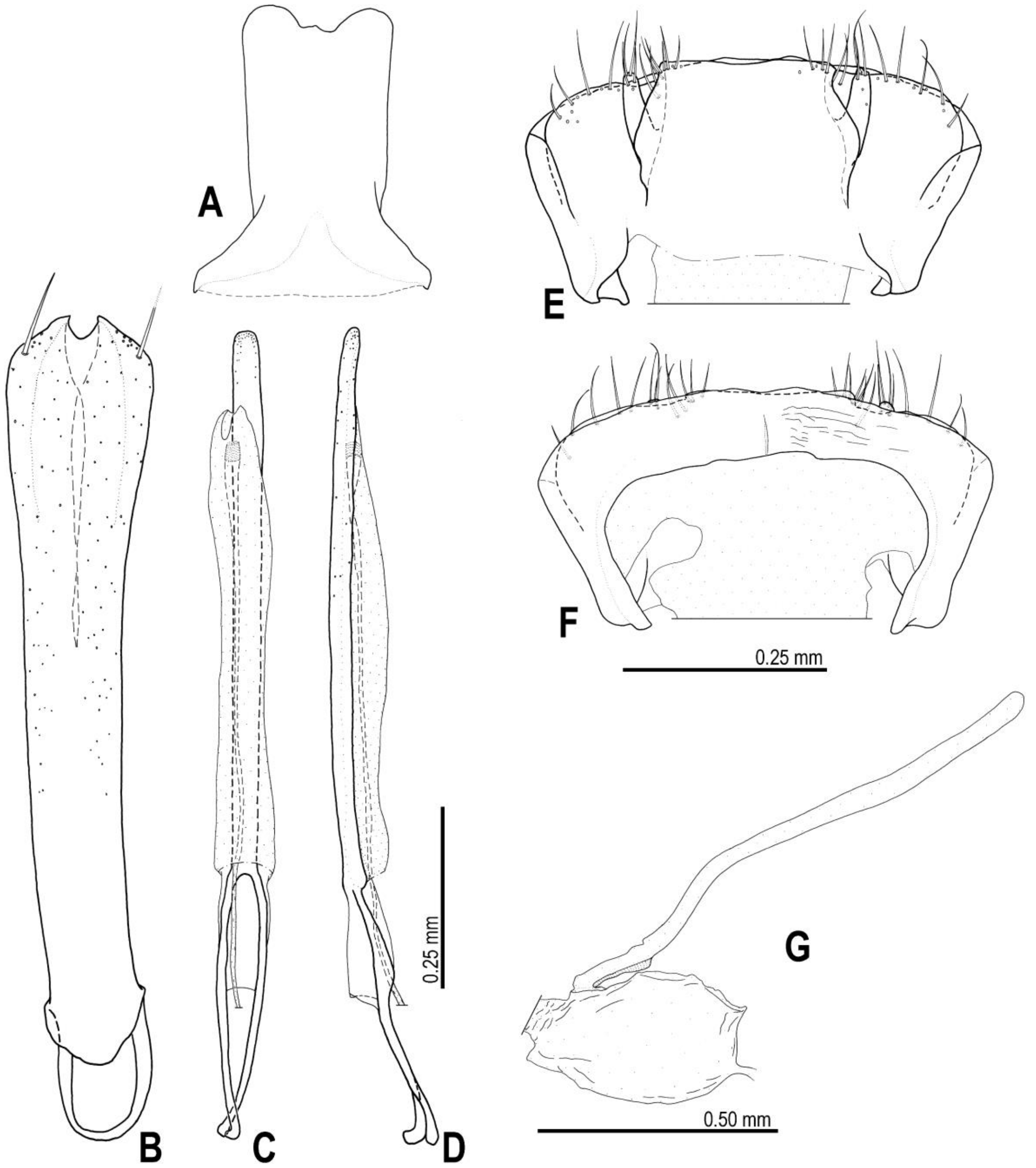


FIGURE 88. Male and female terminalia (part), *Habroloma* (*Parahabroloma*) *nixilla inslicola* Kurosawa. —— A) Sternite IX, male; B) tegmen; C, D) penis, ventral view (C), lateral view (D); E, F) external part of ovipositor (except proctiger), dorsal view (E) and ventral view (F); G) internal part of ovipositor, lateral view.

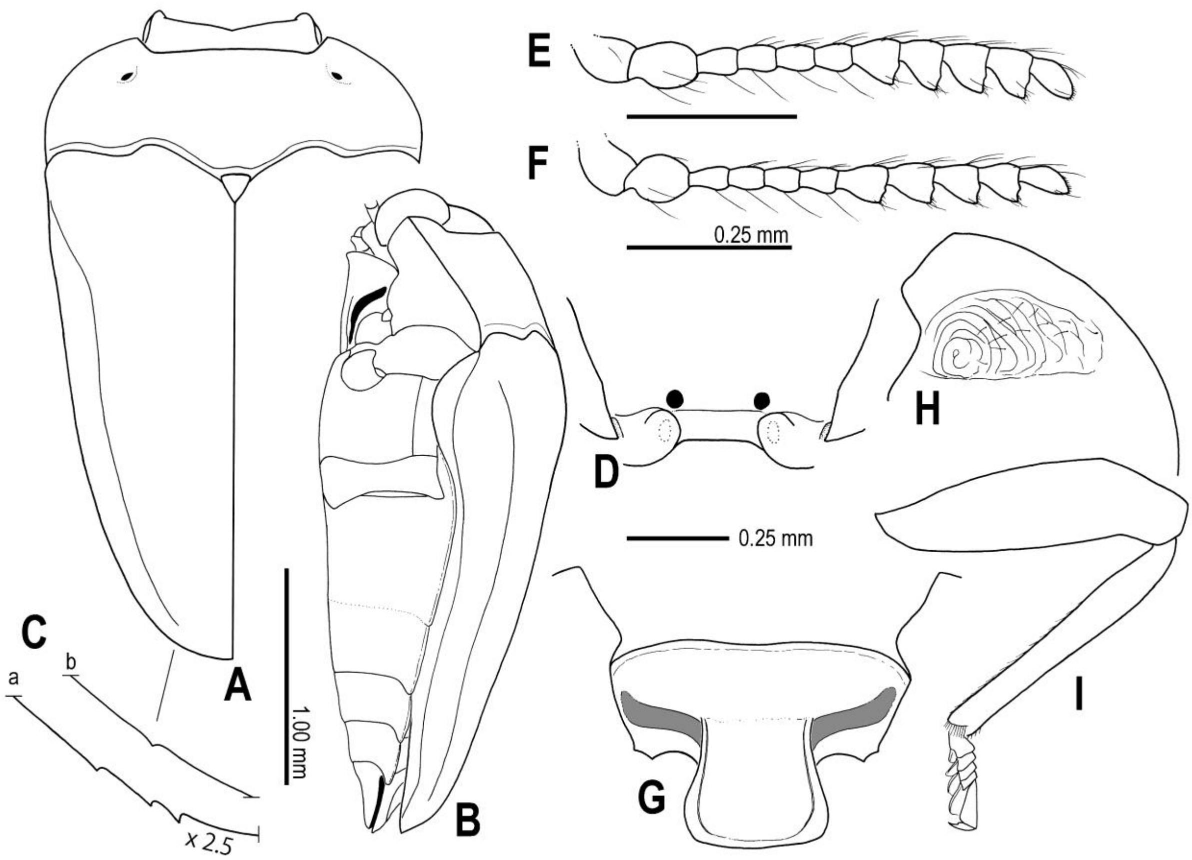


FIGURE 89. *Habroloma* (*Parahabroloma*) *yuasai* Kurosawa. —— A) Head, pronotum, and left elytron; B) body, lateral view; C) serration of elytral lateral margin, obliquely ventral view; D) clypeus; E, F) antennae, outer side, male (E) and female (F); G) prosternum; H) hypomeral marking, oblique view; I) metaleg (femur and tibia), ventral view.

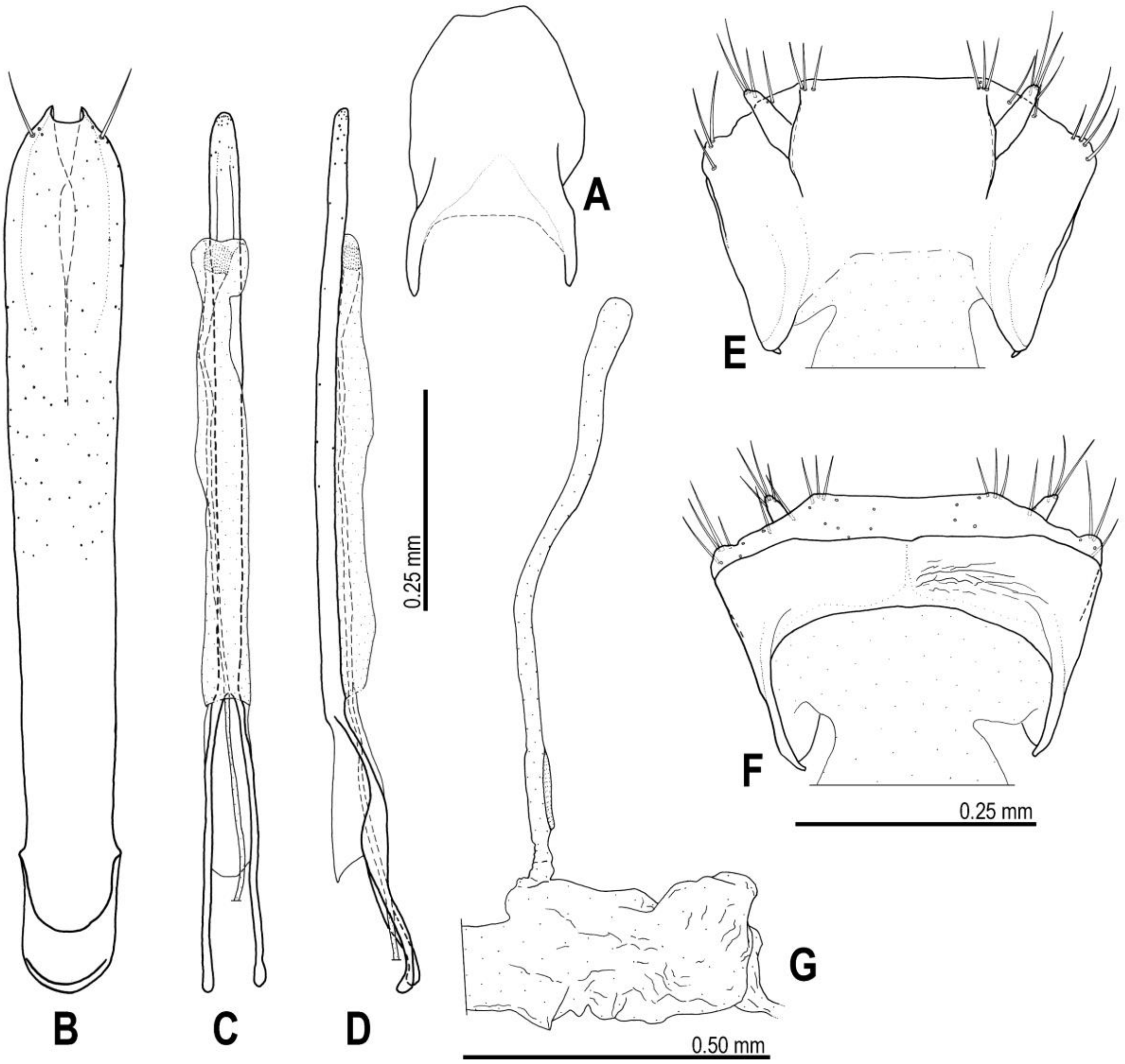


FIGURE 90. Male and female terminalia (part), *Habroloma* (*Parahabroloma*) *yuasai* Kurosawa. —— A) Sternite IX, male; B) tegmen; C, D) penis, ventral view (C), lateral view (D); E, F) external part of ovipositor (except proctiger), dorsal view (E) and ventral view (F); G) internal part of ovipositor, lateral view.

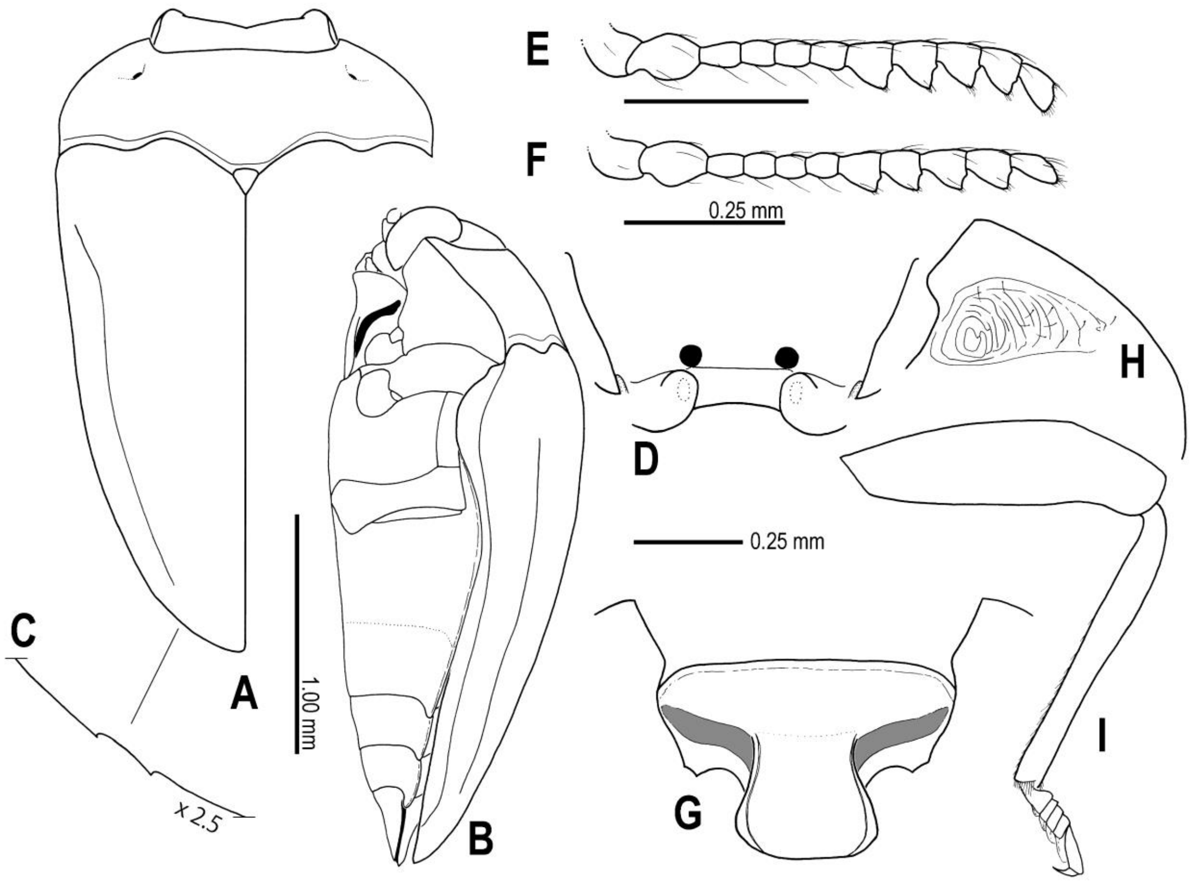


FIGURE 91. *Habroloma* (*Parahabroloma*) *subbicorne* (Motschulsky). —— A) Head, pronotum, and left elytron; B) body, lateral view; C) serration of elytral lateral margin, obliquely ventral view; D) clypeus; E, F) antennae, outer side, male (E) and female (F); G) prosternum; H) hypomeral marking, oblique view; I) metaleg (femur and tibia), ventral view.

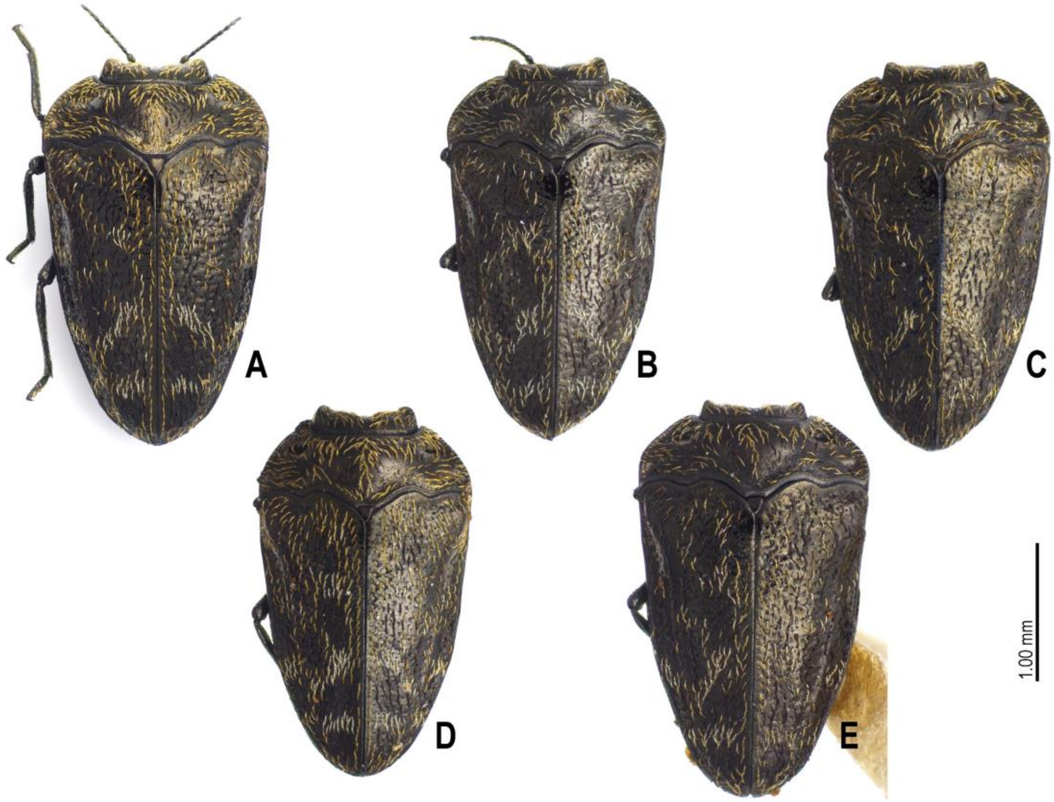


FIGURE 92. Variations in dorsal habitus of *Habroloma* (*Parahabroloma*) *subbicorne* (Motschulsky).

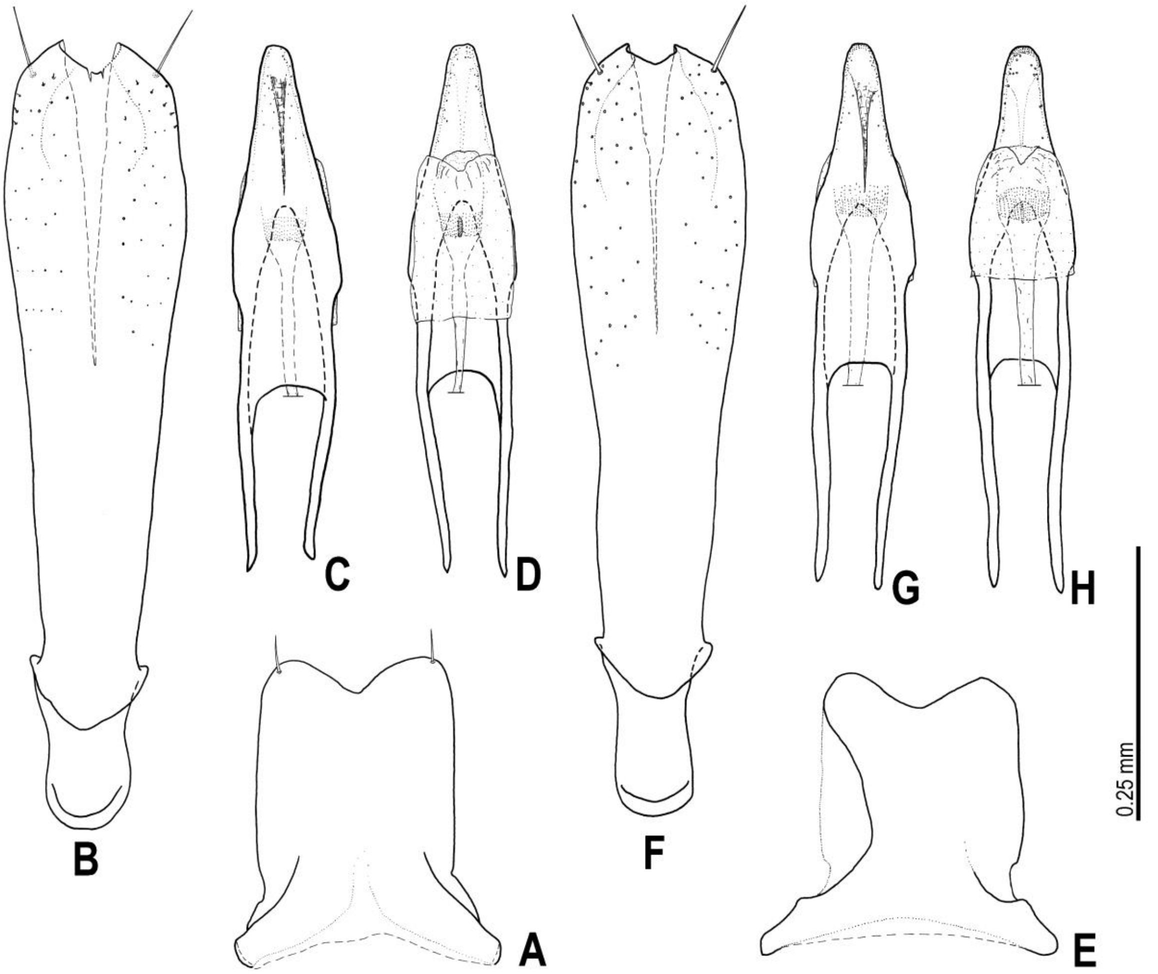


FIGURE 93. Male terminalia (part), *Habroloma* (*Parahabroloma*) *subbicorne* (Motschulsky). —
— A, E) Sternite IX, male; B, F) tegmen; C, G) penis, dorsal view; D, H) penis, ventral view.

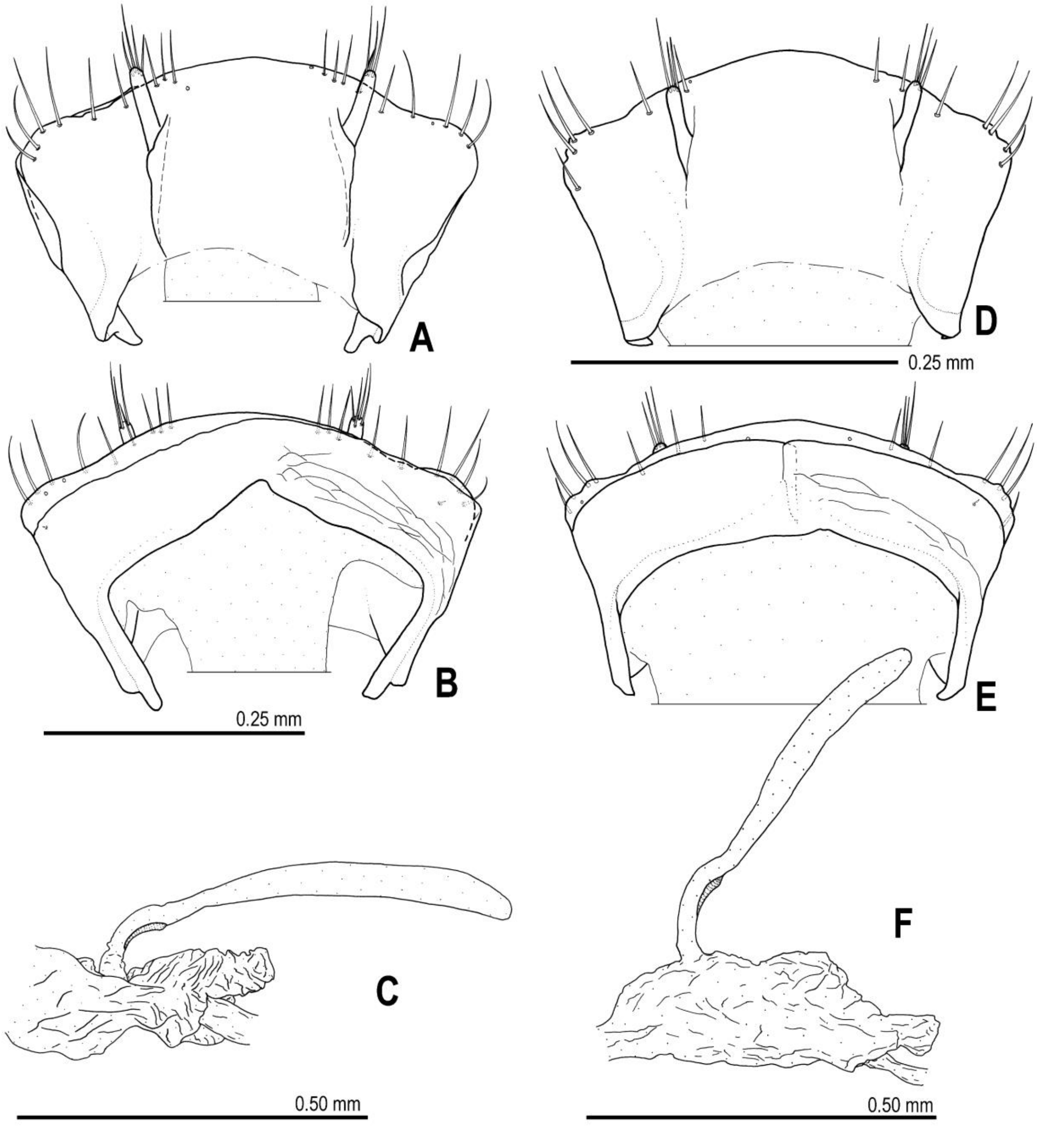


FIGURE 94. Female terminalia (part), *Habroloma* (*Parahabroloma*) *subbicorne* (Motschulsky). —— A, D) external part of ovipositor (except proctiger), dorsal view; B, E) external part of ovipositor (except proctiger), dorsal view; C, F) internal part of ovipositor, lateral view.

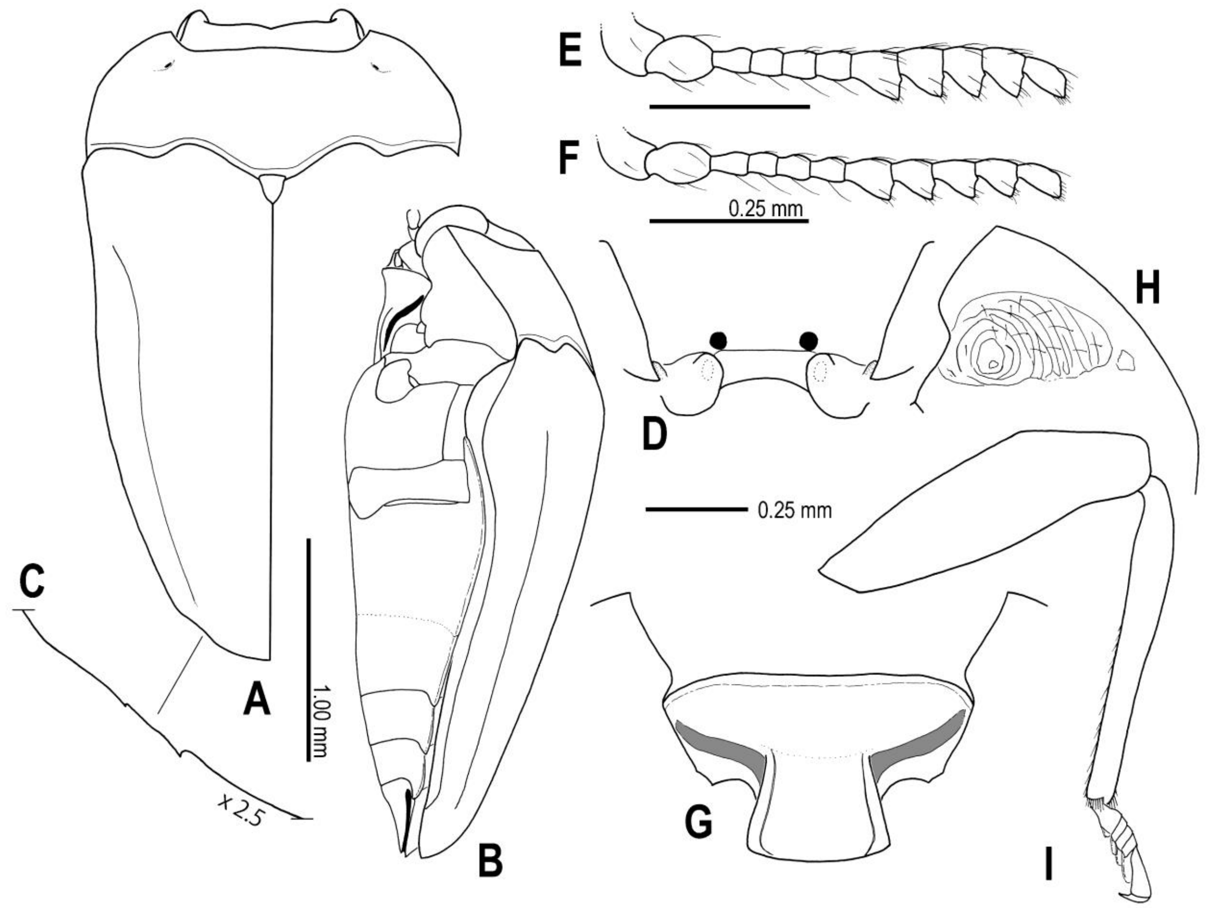


FIGURE 95. *Habroloma* (*Parahabroloma*) *marginicolle* (Fairmire). —— A) Head, pronotum, and left elytron; B) body, lateral view; C) serration of elytral lateral margin, obliquely ventral view; D) clypeus; E, F) antennae, outer side, male (E) and female (F); G) prosternum; H) hypomeral marking, oblique view; I) metaleg (femur and tibia), ventral view.

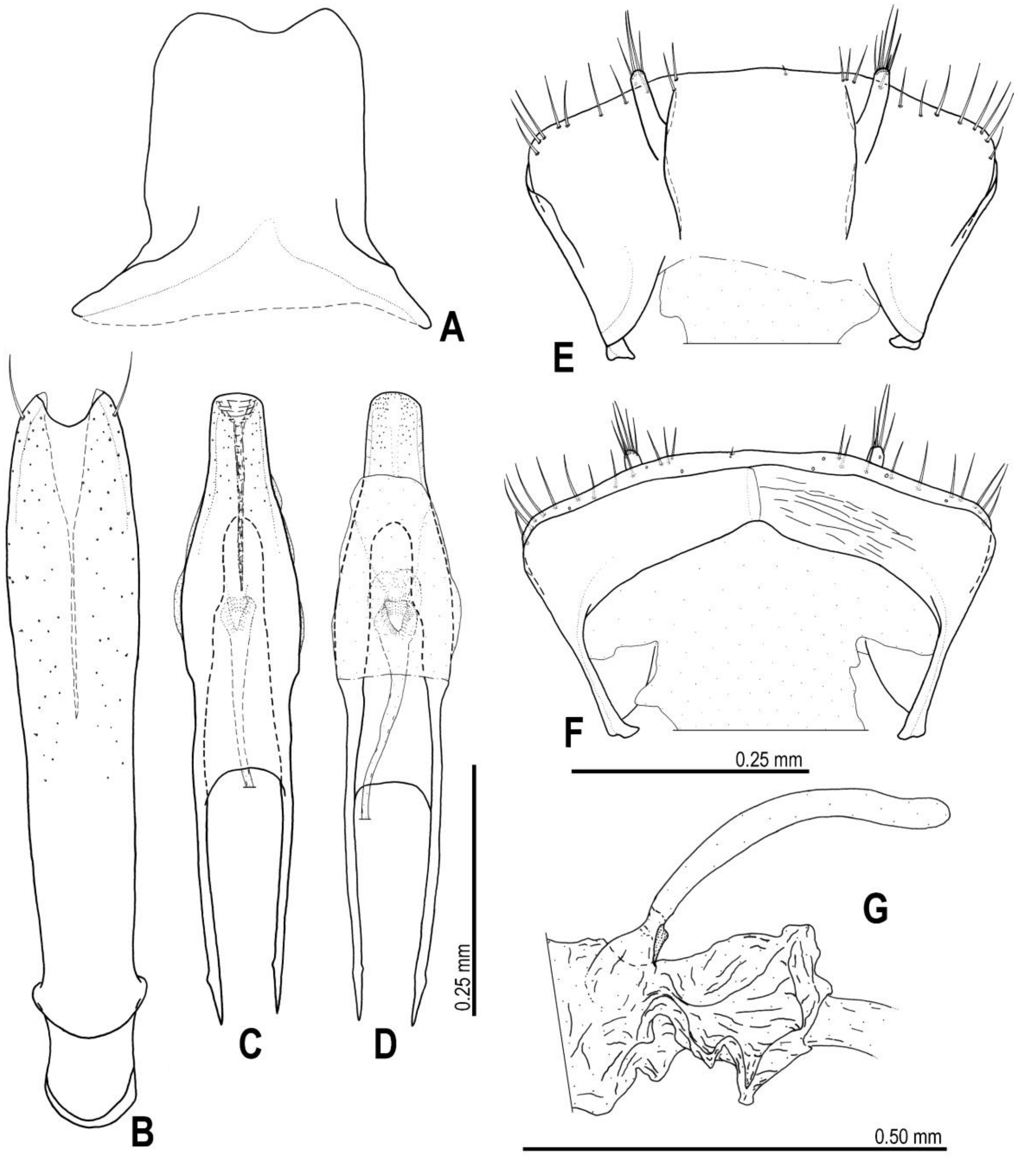


FIGURE 96. Male and female terminalia (part), *Habroloma* (*Parahabroloma*) *marginicolle* (Fairmire). —— A) Sternite IX, male; B) tegmen; C, D) penis, dorsal view (C), ventral view (D); E, F) external part of ovipositor (except proctiger), dorsal view (E) and ventral view (F); G) internal part of ovipositor, lateral view.

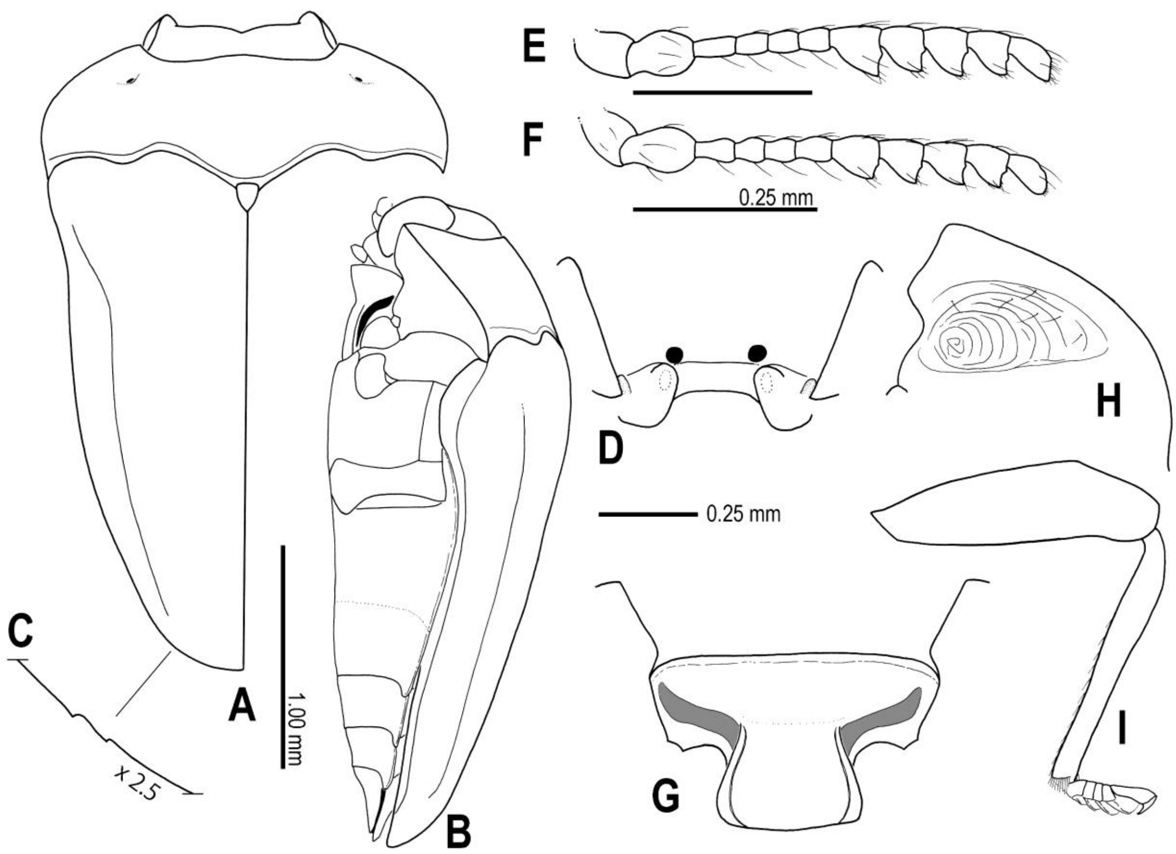


FIGURE 97. *Habroloma* (*Parahabroloma*) *asahinai asahinai* Kurosawa. —— A) Head, pronotum, and left elytron; B) body, lateral view; C) serration of elytral lateral margin, obliquely ventral view; D) clypeus; E, F) antennae, outer side, male (E) and female (F); G) prosternum; H) hypomeral marking, oblique view; I) metaleg (femur and tibia), ventral view.

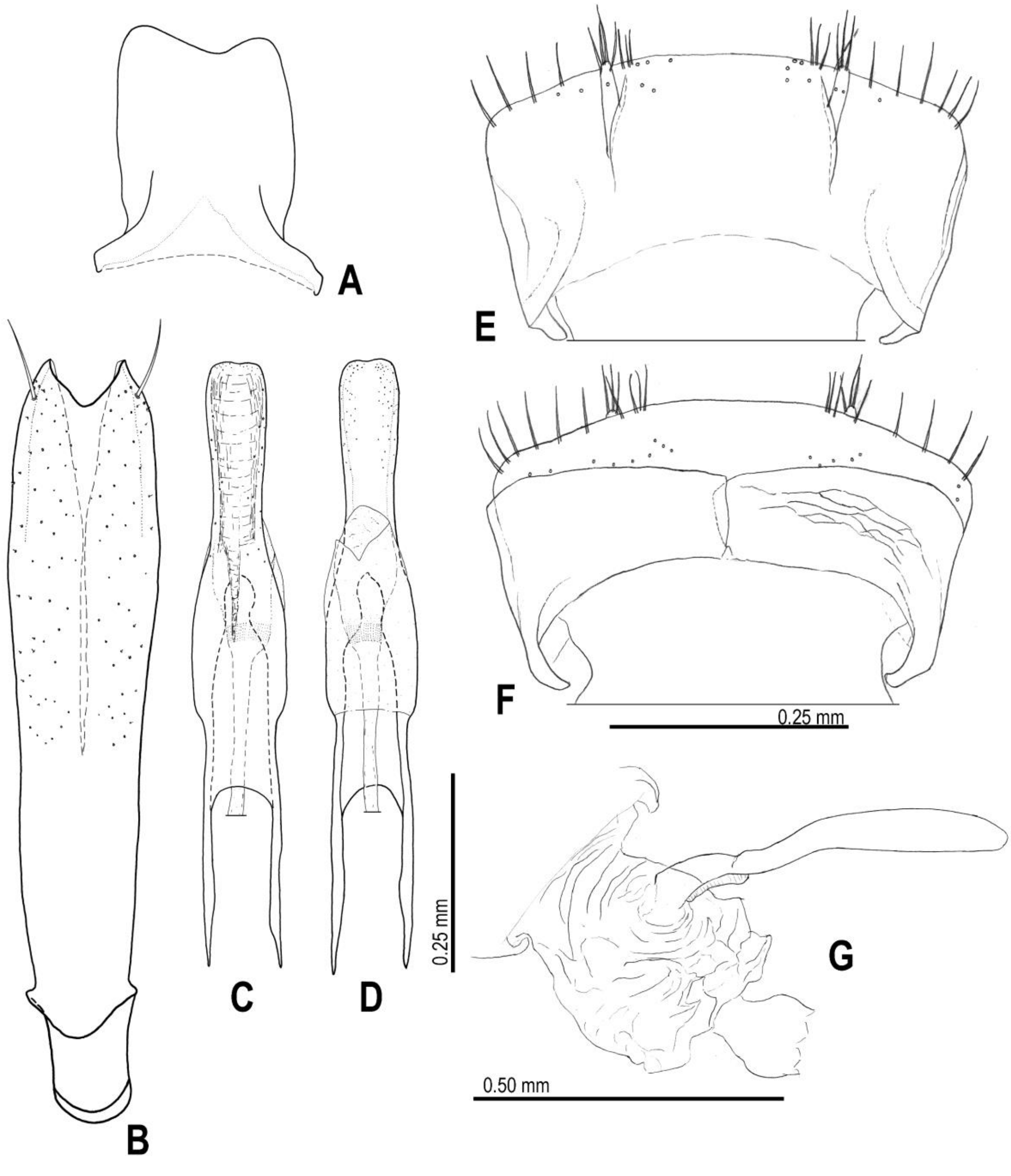


FIGURE 98. Male and female terminalia (part), *Habroloma* (*Parahabroloma*) *asahinai asahinai* Kurosawa. —— A) Sternite IX, male; B) tegmen; C, D) penis, dorsal view (C), ventral view (D); E, F) external part of ovipositor (except proctiger), dorsal view (E) and ventral view (F); G) internal part of ovipositor, lateral view.

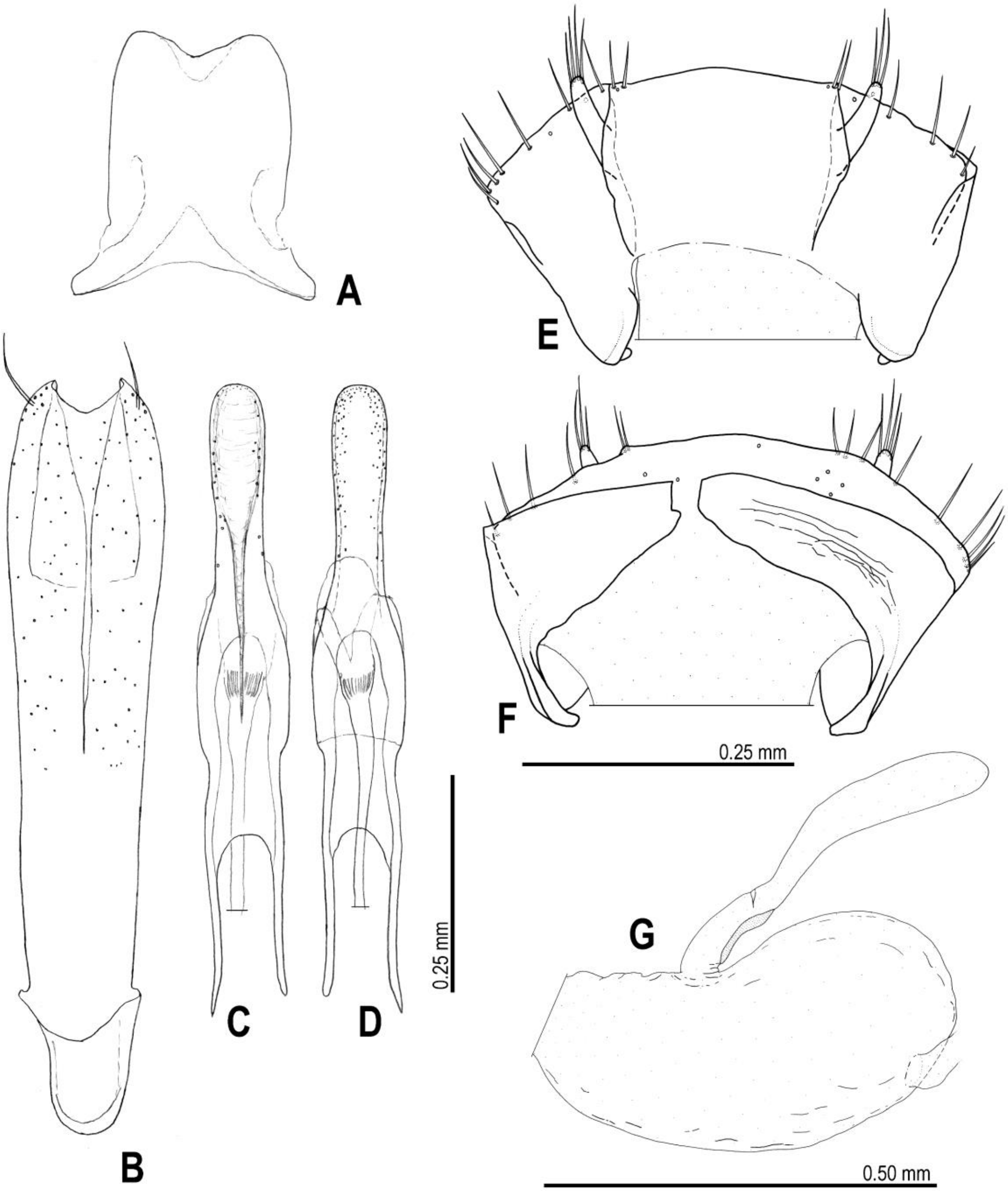


FIGURE 99. Male and female terminalia (part), *Habroloma* (*Parahabroloma*) *asahinai* subsp. 1 (Ishigakijima Is.). —— A) Sternite IX, male; B) tegmen; C, D) penis, dorsal view (C), ventral view (D); E, F) external part of ovipositor (except proctiger), dorsal view (E) and ventral view (F); G) internal part of ovipositor, lateral view.

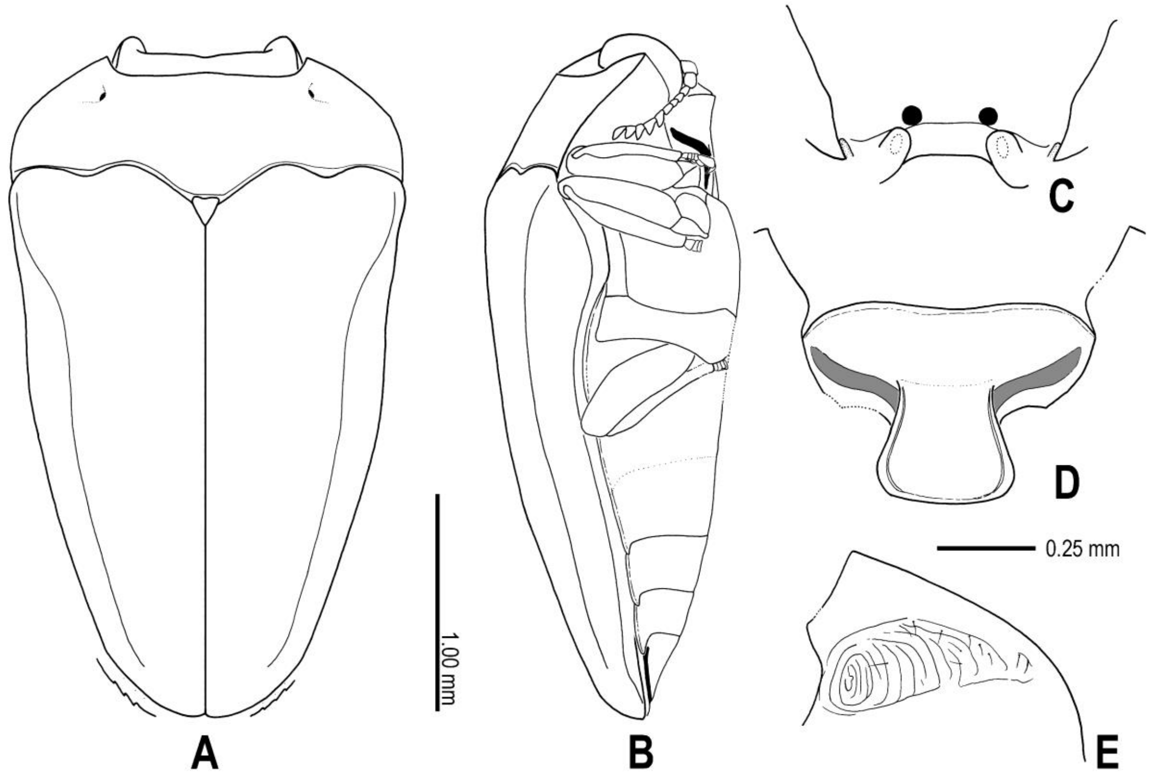


FIGURE 100. Holotype of *Habroloma* (*Parahabroloma*) *hikosanense* Kurosawa. —— A) Head, pronotum, and left elytron; B) body, lateral view; C) clypeus; D) prosternum; E) hypomeral marking, oblique view.

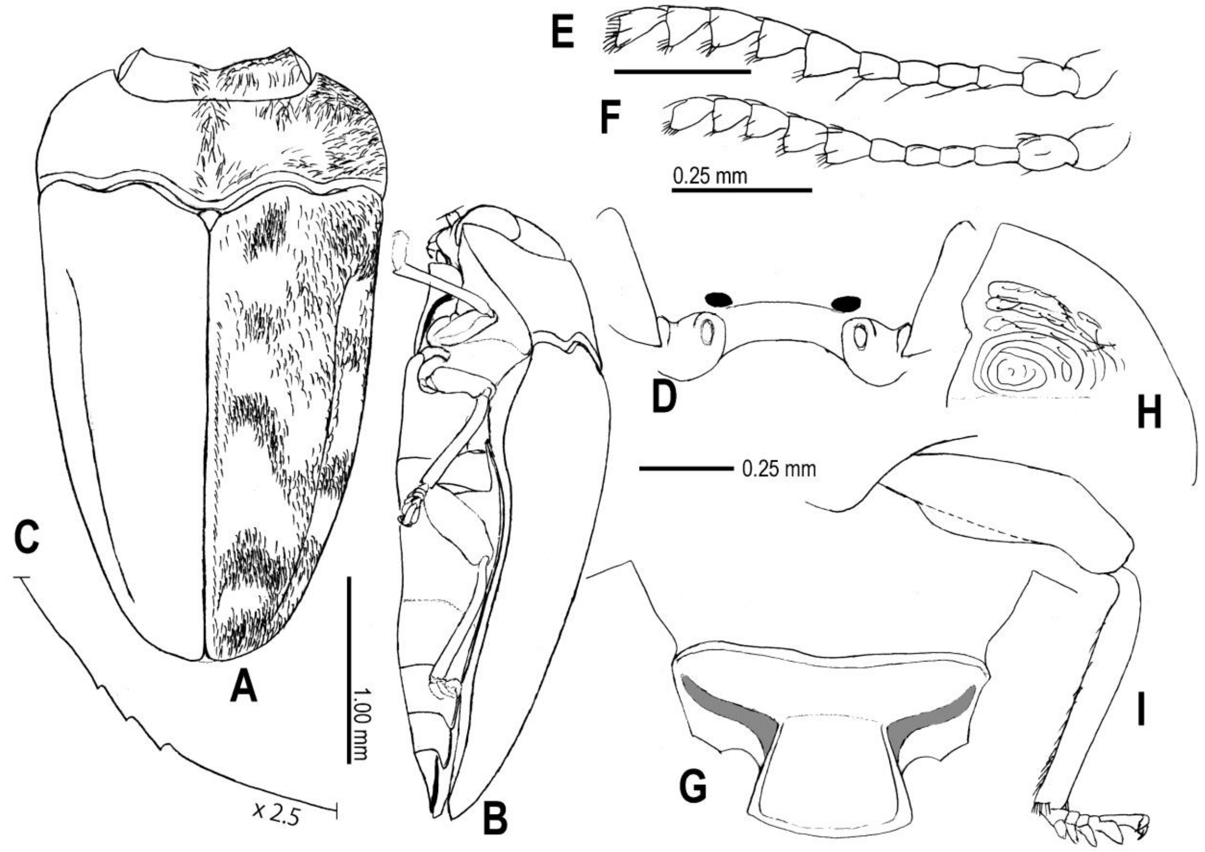


FIGURE 101. *Habroloma* (*Parahabroloma*) sp. 1. —— A) Head, pronotum, and left elytron; B) body, lateral view; C) serration of elytral lateral margin, obliquely ventral view; D) clypeus; E, F) antennae, outer side, male (E) and female (F); G) prosternum; H) hypomeral marking, oblique view; I) metaleg (femur and tibia), ventral view.

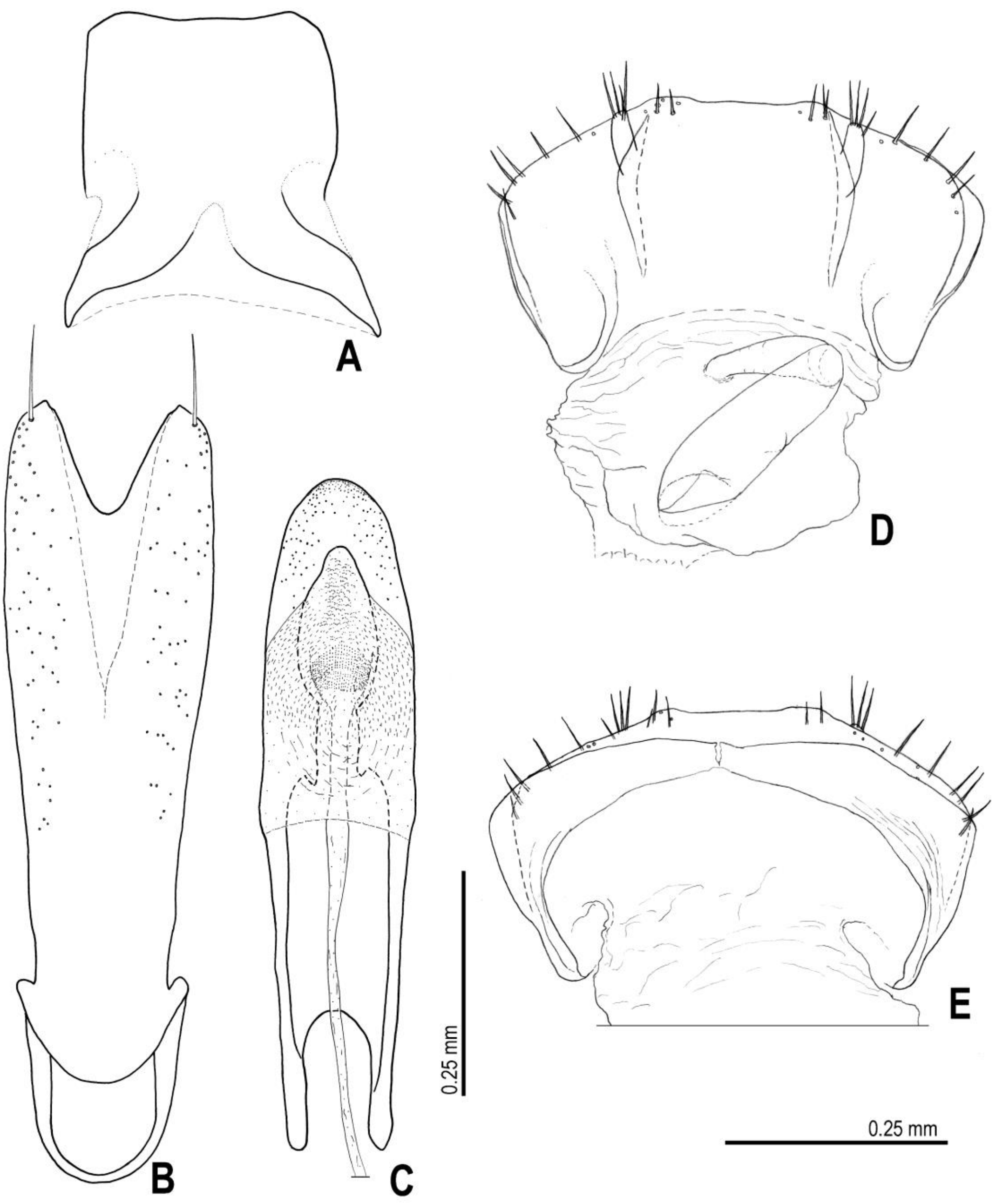


FIGURE 102. Male and female terminalia (part), *Habroloma* (*Parahabroloma*) sp. 1. —— A) Sternite IX, male; B) tegmen; C) penis; D, E) ovipositor (except proctiger), dorsal view (D) and ventral view (E).

FIGURE 103. Habitat**,** adult, and leaf-mines of Japanese *Habroloma* spp. —— A) Habitat of *Habroloma* (*Parahabroloma*) *eximium eximium* (Lewis), Ôita Prefecture, Honshu; B) a mine of *H*. (*P*.) *eximium eximium* (second instar larva) on a fallen leaf of *Symplocos lancifolia*; C) fallen leaves of *Symplocos myrtacea* infested by *H*. (*P*.) *eximium eximium* larvae (indicated by white triangular marks); D) a mine of *H*. (*P*.) *eximium eximium* (first instar larva) on a fallen leaf of *S*. *myrtacea* (indicated by a white triangular mark); E) an adult of *H*. (*P*.) *eximium* subsp. 1 on *Symplocos formosana*; F) a mine of *H*. (*P*.) *eximium* subsp. 1 on *S*. *formosana*: a black triangular mark indicates a remaining egg shell; a white triangular mark indicates a linear part of mine and frass of the first instar larva.

FIGURE 104. Leaf-mines and ejected frass of Japanese *Habroloma* spp. —— A) A mine of *Habroloma* (*Parahabroloma*) *lewisii* (Saunders) on *Rosa multiflora* (a white triangular mark indicates a remaining egg shell); B) ejected frass of *H.* (*P.*) *lewisii* from the abaxial surface of mine; C) a mine of *H.* (*P.*) *nixilla inslicola* Kurosawa on *Lagerstroemia subcostata* var. *subcostata* (a black triangular mark indicates the pupation site); D) ejected frass of *H.* (*P.*) *nixilla inslicola* from the abaxial surface of mine; E) mines of *H.* (*P.*) *yuasai* Kurosawa on *Platycarya strobilacea* (indicated by white triangular marks); F) ejected frass of *H.* (*P.*) *yuasai* from both surfaces of mine.

FIGURE 105. Adults, adult feeding scars, and leaf-mines of Japanese *Habroloma* spp. —— A) Adult feeding scars of *Habroloma* (*Parahabroloma*) *subbicorne* (Motschulsky, 1860) on *Rubus parvifolius* (indicated by white triangular marks); B) a mine of *H*. (*P*.) *marginicolle* (Fairmaire, 1888) on *Rubus buergeri* (indicated by a white triangular mark); C, D) adults and secreted white powders of *H*. (*P*.) *marginicolle* (the powders are indicated by white triangular marks); E) a mine of *H*. (*P*.) *asahinai asahina* Kurosawa on *Rubus sieboldii*; F) a mine of *H*. (*P*.) *asahinai asahina* on *Rubus nesiotes* (indicated by a white triangular mark); G) a fallen mine of *H*. (*P*.) sp. 1 on *Elaeocarpus japonicus*.

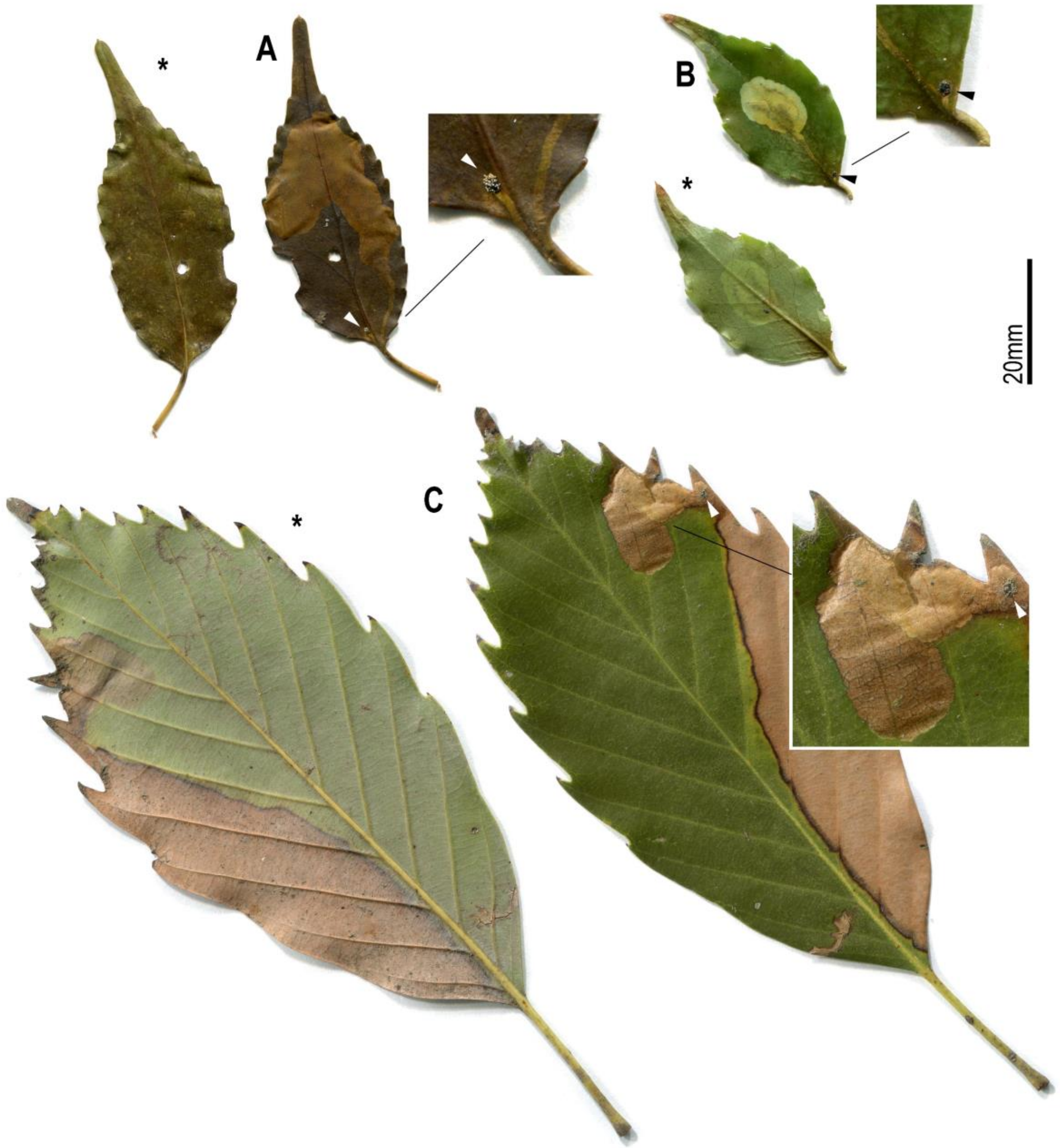


FIGURE 106. Leaf-mines of Japanese *Habroloma* spp. —— A) A mine of *Habroloma* (*Parahabroloma*) *eximium eximium* (Lewis) on *Symplocos myrtacea*; B) a mine of *H*. (*P*.) *eximium* subsp. 1 on *Symplocos formosana*; C) a mine of *H*. (*P*.) *griseonigrum* (Saunders) on *Quercus glauca*. Asterisks (*) indicate leaves in the abaxial side. Black or white triangular marks indicate the oviposition sites.

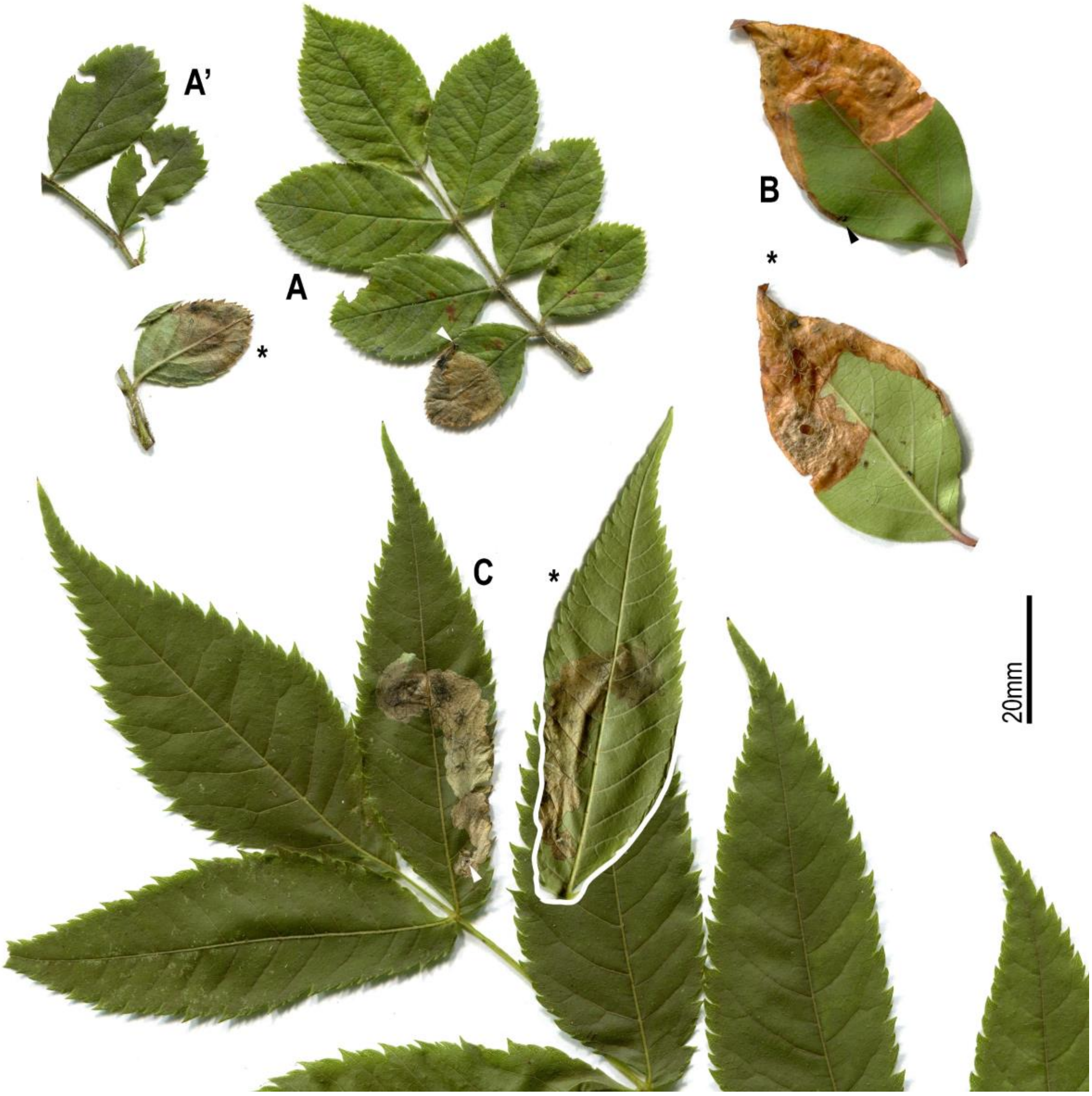


FIGURE 107. Leaf-mines of Japanese *Habroloma* spp. —— A) A mine of *Habroloma* (*Parahabroloma*) *lewisii* (Saunders) on *Rosa multiflora*; A') adult feeding scars; B) *H*. (*P*.) *nixilla inslicola* Kurosawa on *Lagerstroemia subcostata* var. *subcostata*; C) a mine of *H*. (*P*.) *yuasai* Kurosawa on *Platycarya strobilacea*. Asterisks (*) indicate leaves in the abaxial side. Black or white triangular marks indicate the oviposition sites.

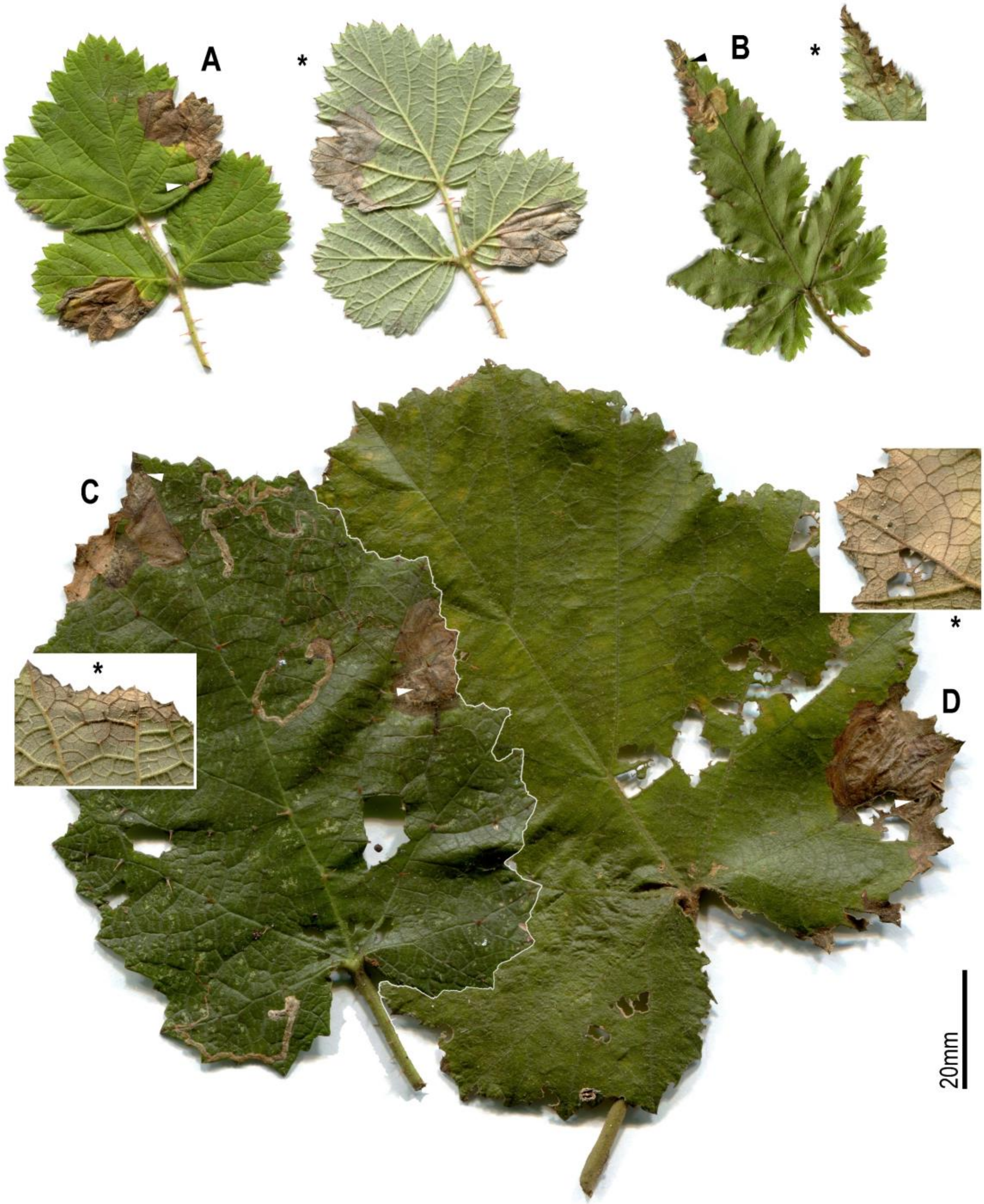


FIGURE 108. Leaf-mines of Japanese *Habroloma* spp. —— A) mines of *Habroloma* (*Parahabroloma*) *subbicorne* (Motschulsky, 1860) on *Rubus parvifolius*; B) a mine of *H*. (*P*.) *subbicorne* on *Rubus palmatus* var. *palmatus*; C) mines of *H*. (*P*.) *marginicolle* (Fairmaire, 1888) on *Rubus sieboldii*; D) a mine of *H*. (*P*.) *H*. (*P*.) *asahinai asahina* Kurosawa on *R*. *sieboldii*. Asterisks (*) indicate leaves in the abaxial side. Black or white triangular marks indicate the oviposition sites.

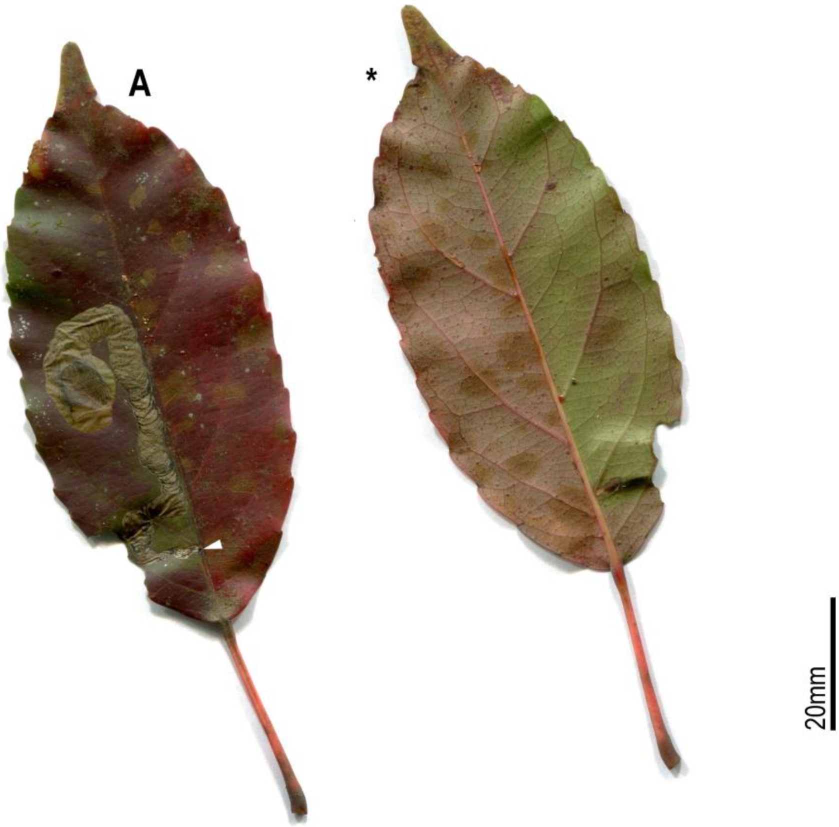


FIGURE 109. A leaf-mine of *Habroloma* (*Parahabroloma*) sp. 1. on *Elaeocarpus japonicus*. Asterisk (*) indicates the leaf in the abaxial side. White triangular marks indicate the oviposition site.

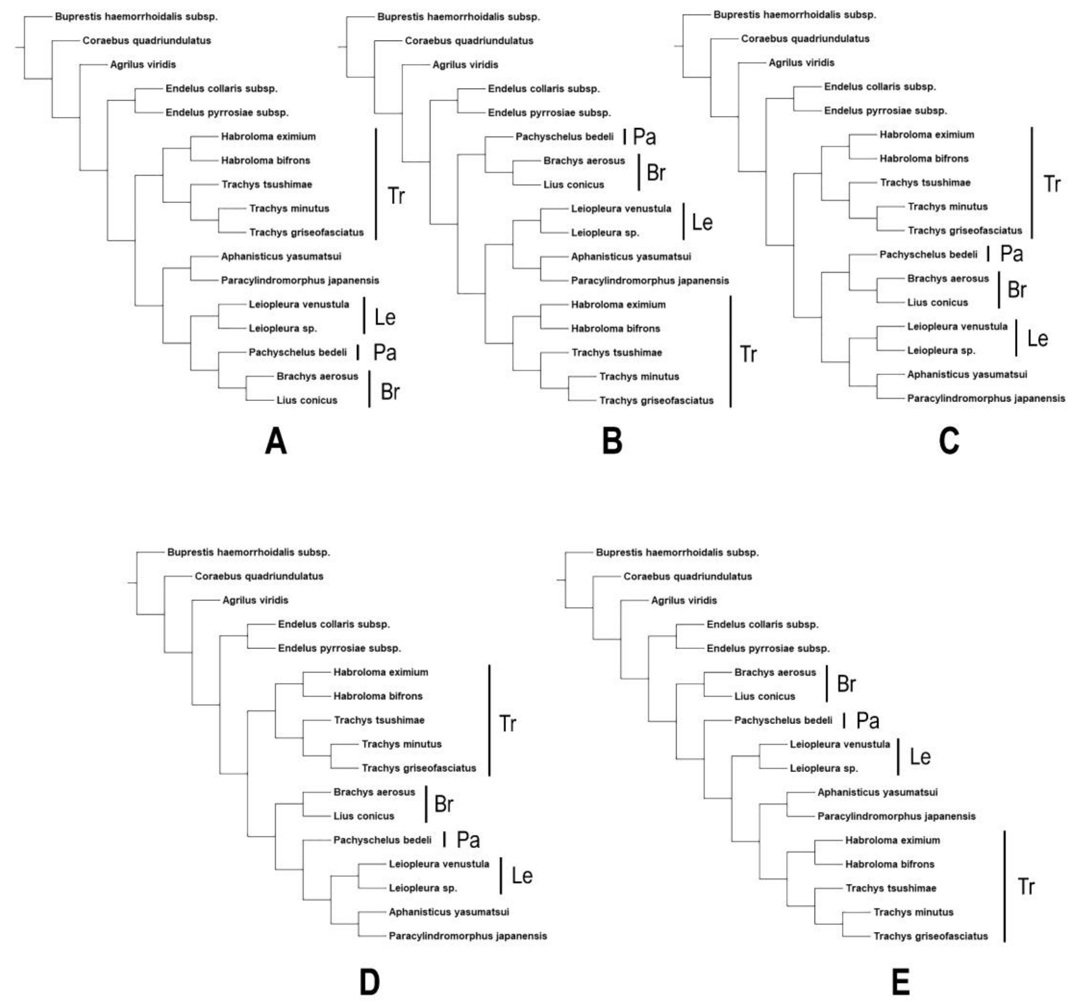


FIGURE 110. Five trees obtained from the cladistic analysis for generic relationships of Tracheini. Abbreviations: Br — Brachyina; Le — Leiopleurina; Pa — Pachyschelina; Tr — Tracheina.

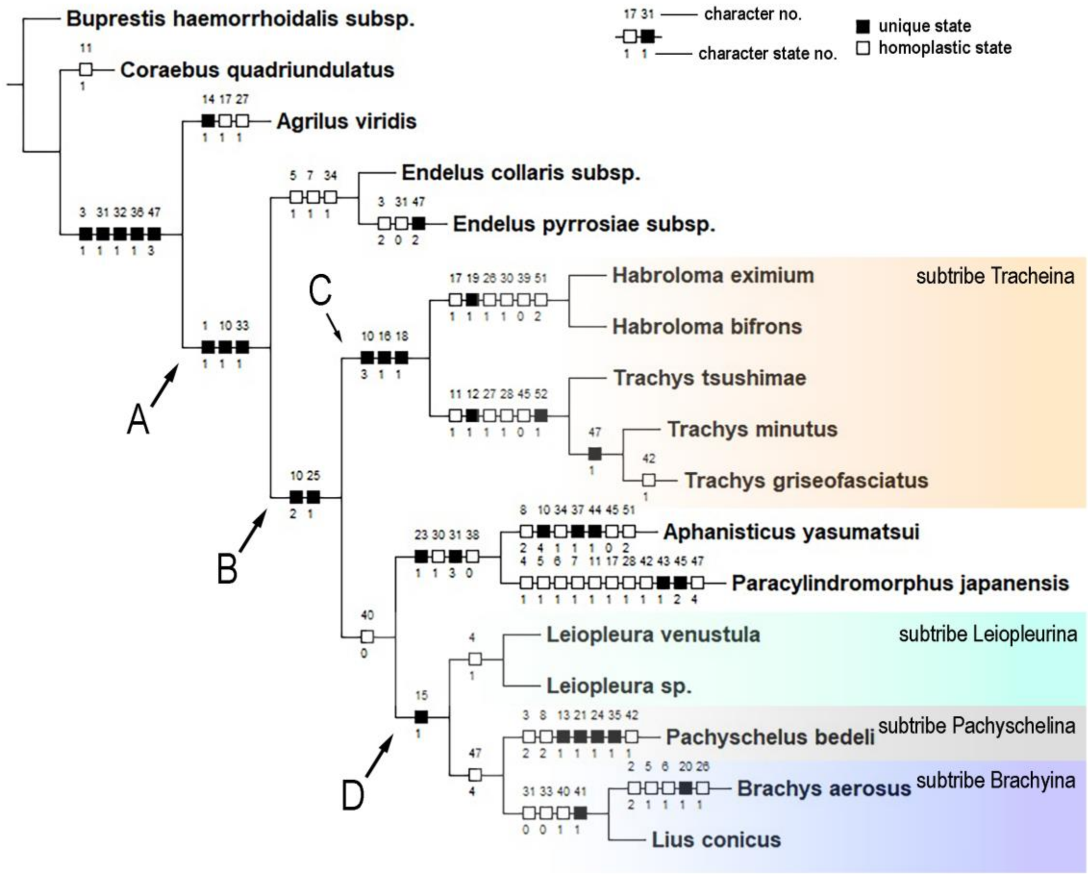
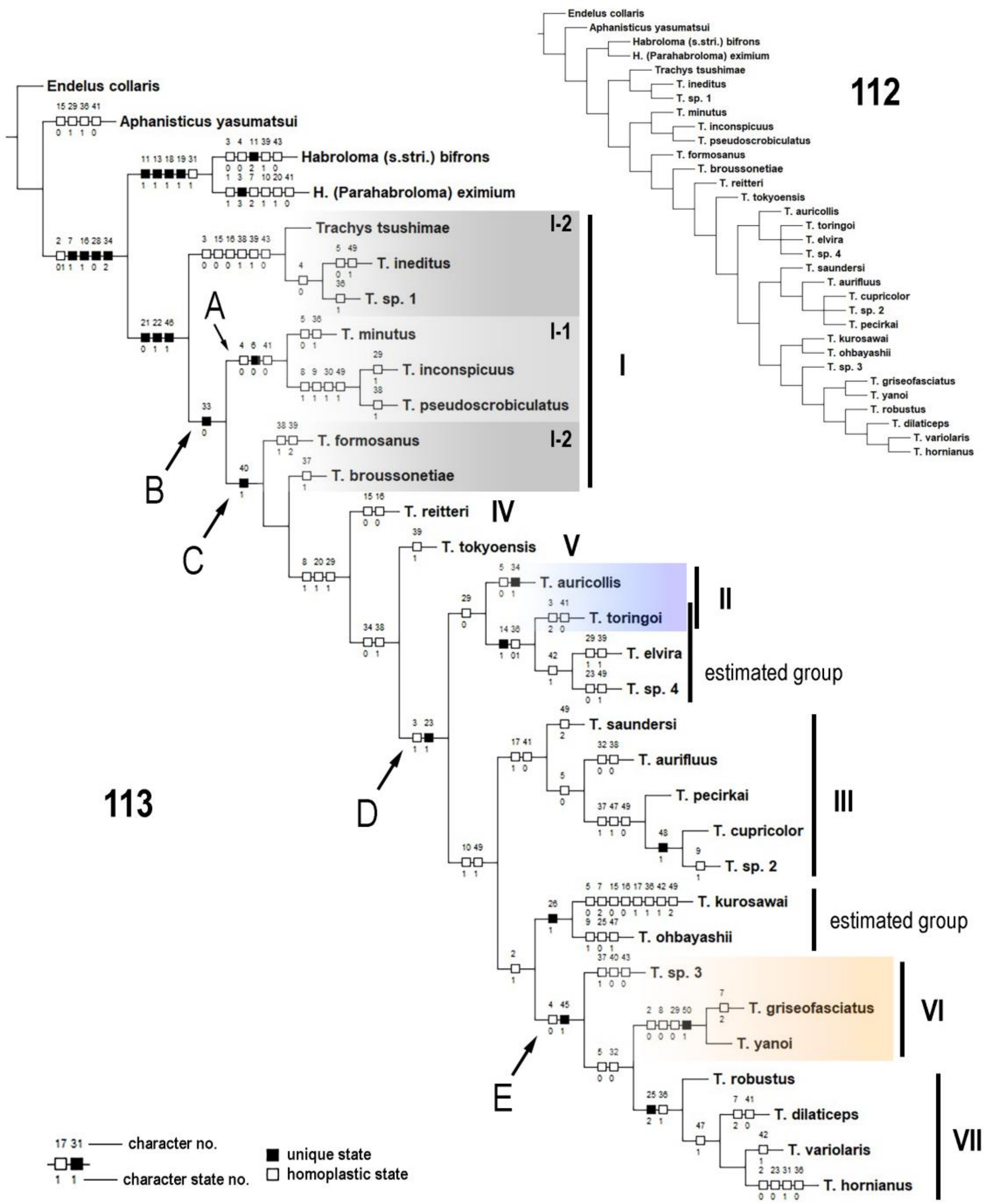


FIGURE 111. Preferred cladogram of Tracheini. A series of clades (A–D) are used in the main text.



FIGURES 112 & 113. 112 —— Strict consensus of four trees of Japanese *Trachys* (incl. Taiwanese species). 113 —— Preferred cladogram of Japanese *Trachys* (incl. Taiwanese species). A series of clades (A–E) are used in the main text. Paraphyletic or polyphyletic groups are indicated as different colored area.

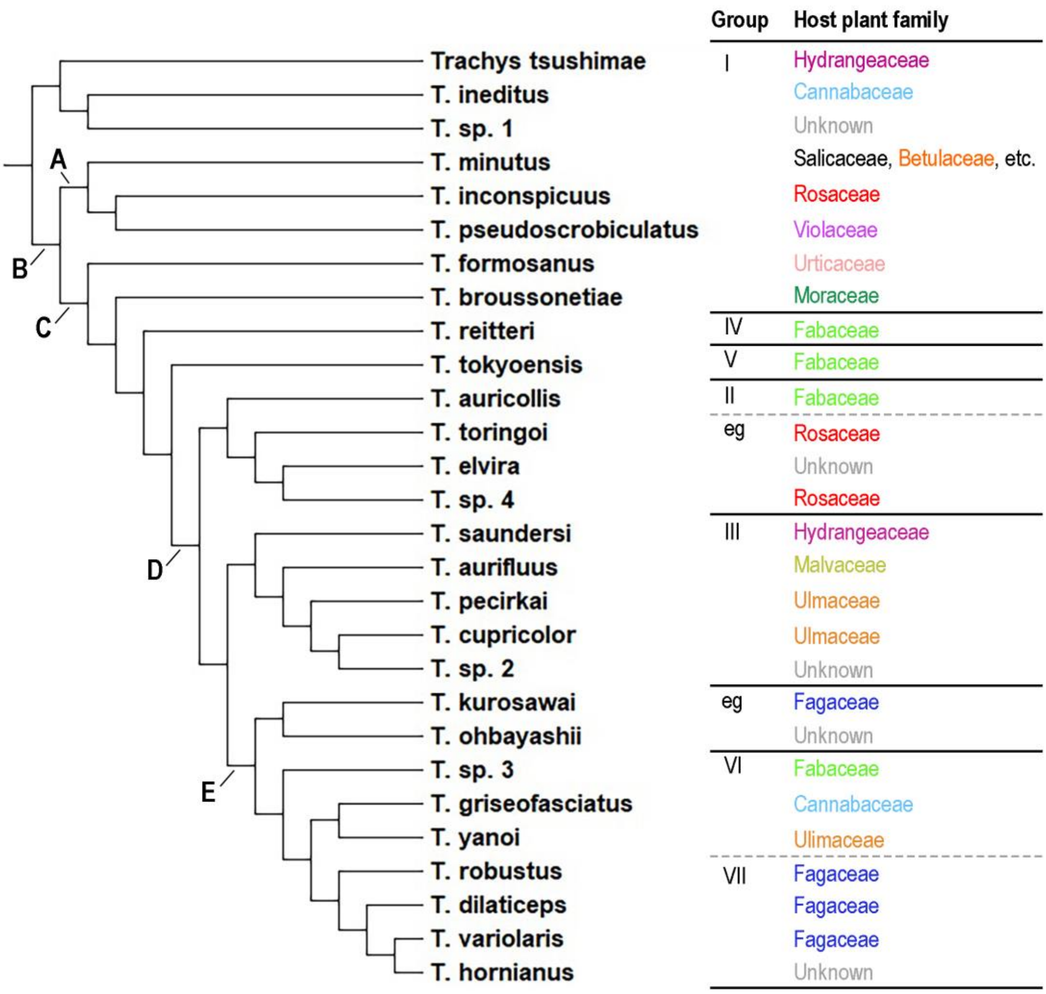
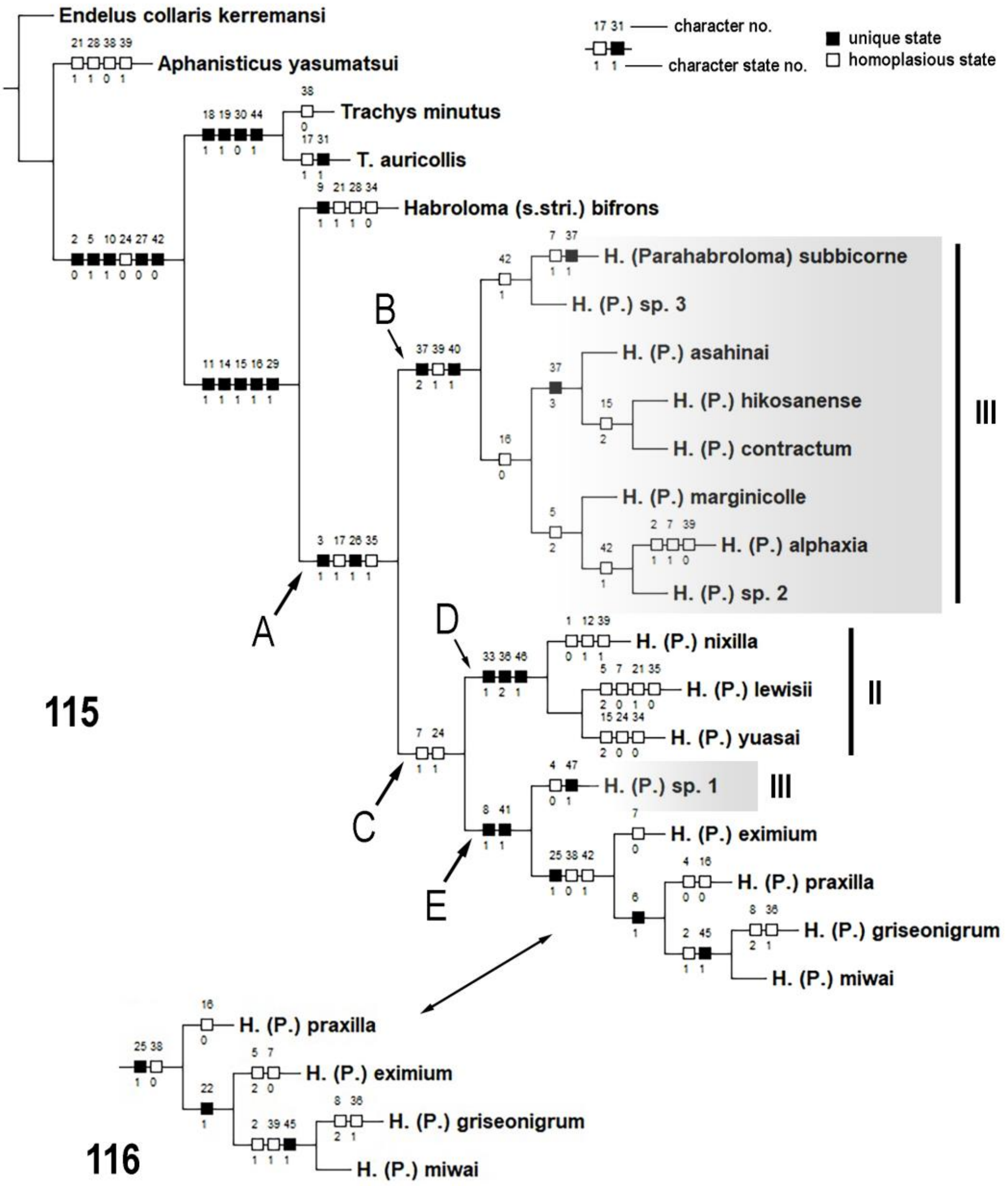


FIGURE 114. Host associations and phylogenetic relationships of Japanese *Trachys* (incl. Taiwanese species), mapping host information onto the preferred cladogram. Outgroups are omitted. A series of clades (A–E) are same as Fig. 113. Abbreviation: eg — estimated group.



FIGURES 115 & 116. 115 —— Preferred cladogram of Japanese *Habroloma* (incl. Taiwanese species). 116 —— different part in one out of two equally most parsimonious trees. A series of clades (A–E) are used in the main text. Polyphyletic group is indicated as colored area.

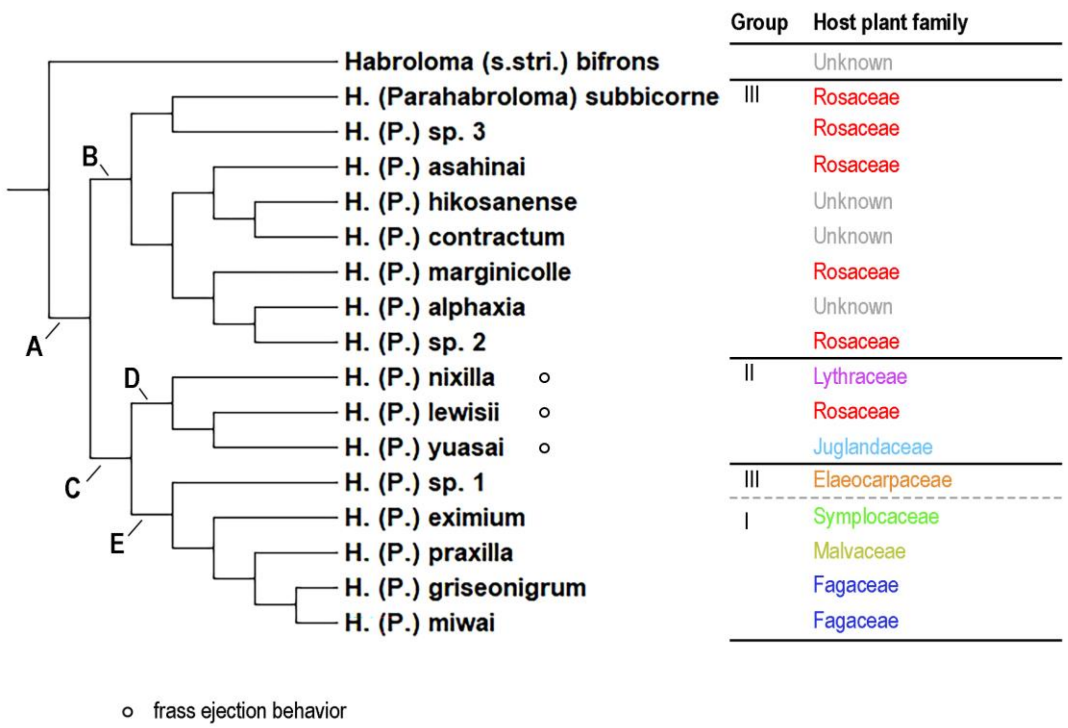


FIGURE 117. Host associations and phylogenetic relationships of Japanese *Habroloma* (incl. Taiwanese species), mapping information of hosts and larval frass ejection behavior onto the preferred cladogram. Outgroups are omitted. A series of clades (A–E) are same as Fig. 114.

TABLE 1.

TABLE 1. Comparison of the measurement value for the proportion of the clypeus in Kurosawa (1959) and this study.

Japanese species		*Trachys minutus*	*T. inconspicuus*	*T. pseudoscrobiculatus*	*T. ineditus*	*T. tushimae*
Kurosawa	**WC/LC**	ca. 1.3	ca. 1.5	ca. 1.3	ca. 1.5	ca. 1.3
This study	**WC/LC**	1.25–1.57 (mean 1.39)	1.23–1.60 (mean 1.37)	1.15–1.78 (mean 1.53)	1.48–1.88 (mean 1.67)	1.25–1.67 (mean 1.47)
	WC/LSC	1.22–1.39 (mean 1.30)	1.13–1.33 (mean 1.18)	1.01–1.35 (mean 1.15)	1.56–1.88 (mean 1.75)	1.24–1.67 (mean 1.44)
Japanese species		***T. broussonetiae***	***T. auricollis***	***T. toringoi***	***T. saundersi***	***T. cupricolor***
Kurosawa	**WC/LC**	ca. 1.7	ca. 1.3	no data	ca. 1.8	ca. 1.7 *
This study	**WC/LC**	2.00–3.00 (mean 2.52)	1.33–1.9 (mean 1.51)	1.31–1.77 (mean 1.58)	1.50–2.00 (mean 1.75)	1.69–2.42 (mean 2.00)
	WC/LSC	1.29–1.76 (mean 1.57)	1.2–1.77 (mean 1.34)	1.21–1.50 (mean 1.36)	1.33–1.65 (mean 1.54)	1.69–2.07 (mean 1.86)
Japanese species		***T. pecirkai***	***T. aurifluus***	***T. reitteri***	***T. tokyoensis***	***T. variolaris***
Kurosawa	**WC/LC**	ca. 1.7 *	ca. 1.8	ca. 1.0	around 1.0	ca. 2.0
This study	**WC/LC**	1.49–2.04 (mean 1.71)	1.47–2.17 (mean 1.74)	1.35–1.86 (mean 1.53)	1.17–1.73 (mean 1.46)	1.76–2.25 (mean 2.02)
	WC/LSC	1.44–2.00 (mean 1.67)	1.47–1.90 (mean 1.69)	1.29–1.60 (mean 1.42)	1.17–1.55 (mean 1.38)	1.74–2.64 (mean 2.00)
Japanese species		***T. robustus***	***T. dilaticeps***	***T. griseofasciatus***	***T. yanoi***	
Kurosawa	**WC/LC**	ca. 2.0	ca. 2.0	ca. 2.0	ca. 1.5	
This study	**WC/LC**	1.71–2.44 (mean 2.19)	1.75–2.73 (mean 2.20)	2.00–2.88 (mean 2.49)	1.64–2.30 (mean 1.82)	
	WC/LSC	1.71–2.10 (mean 1.96)	1.75–2.33 (mean 2.09)	2.00–2.71 (mean 2.41)	1.64–1.97 (mean 1.74)	

*) In Kurosawa (1959), *Trachys* pecirkai is included in *T. cupricolor* since the former species had not been recognized in Japan at that time.

TABLE 2.

TABLE 2. Historical transition of misidentifications between four *Trachys* species in Japanese researchers.

Original description	Main works (*sensu* Japanese researchers)					
	Matsumura 1931 →	Chujo & Kurosawa 1950 →	Yano 1952 →	Yano 1954 →	Kurosawa 1959 →	Kurosawa 1976c,d & 1985a → Thsi study
ineditus Saunders, 1873	—	—	—	—	*oviformis* sp. nov.	*ineditus* (= *ovifrmis*)
tsushimae Obenberger, 1922	*ineditus* ("*medita* ")	*ineditus*	—	*ineditus*	*ineditus*	*tsushimae* (= *japonicus*)
broussonetiae Kurosawa, 1985	—	*tsushimae*	*tsushimae*	—	*tsushimae*	*broussonetiae*
tokyoensis Obenberger, 1940	—	*japonicus* Obenerger,1923	*japonicus*	—	*japonicus* (= *tokyoensis*)	*tokyoensis*

TABLE 3.

TABLE 3. Data matrix for cladistic analysis of generic relationships of Tracheini.

Taxa	Characters 1	1 1 1 1 1 1 1 1 1 2	2 2 2 2 2 2 2 2 2 3	3 3 3 3 3 3 3 3 3 4	4 4 4 4 4 4 4 4 4 5	5 5
	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2
Buprestis_haemorrhoidalis_arakii	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 - - 0 0 0 0 0 0	0 0
Agrilus_viridis	0 1 1 0 0 0 0 1 1 0	0 0 0 1 0 0 1 0 0 0	0 0 0 0 0 0 1 0 1 0	1 1 0 0 0 1 0 1 1 1	0 2 0 0 1 1 3 0 0 1	1 0
Coraebus_quadriundulatus	0 1 0 0 0 0 0 1 1 0	1 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 1 0	0 0 0 0 0 0 0 1 1 1	0 1 0 0 1 1 0 1 0 1	1 0
Aphanisticus_yasumatsui	1 0 1 0 0 0 0 2 1 4	0 0 0 0 0 0 0 0 0 0	0 1 1 0 1 0 0 0 1 1	3 1 1 1 0 1 1 0 1 0	0 3 0 1 0 1 3 1 0 1	2 0
Endelus_collaris_kerremansi	1 3 1 0 1 0 1 1 1 1	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 1 0	2 1 1 1 0 1 0 1 1 1	0 1 0 0 1 1 3 1 0 1	1 0
Endelus_pyrrosiae_pyrrosiae	1 3 2 0 1 0 1 1 1 1	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 1 0	0 1 1 1 0 1 0 1 1 1	0 1 0 0 1 1 2 1 0 1	1 0
Paracylindromorphus_japanensis	1 2 1 1 1 1 1 1 1 2	1 0 0 0 0 0 1 0 0 0	0 1 1 0 1 0 0 1 1 1	3 1 1 0 0 1 0 0 1 0	0 1 1 0 2 1 4 1 0 1	1 0
Trachys_minutus	1 3 1 0 0 0 0 1 1 3	1 1 0 0 0 1 0 1 0 0	0 1 0 0 1 0 1 1 1 0	2 1 1 0 0 1 0 1 1 1	0 2 0 0 0 1 1 1 0 1	1 1
Trachys_tsushimae	1 3 1 0 0 0 0 1 1 3	1 1 0 0 0 1 0 1 0 0	0 1 0 0 1 0 1 1 1 0	2 1 1 0 0 1 0 1 1 1	0 2 0 0 0 1 3 1 0 1	1 1
Trachys_griseofasciatus	1 3 1 0 0 0 0 1 1 3	1 1 0 0 0 1 0 1 0 0	0 1 0 0 1 0 1 1 1 0	2 1 1 0 0 1 0 1 1 1	0 1 0 0 0 1 1 1 0 1	1 1
Habroloma_eximium	1 3 1 0 0 0 0 1 1 3	0 0 0 0 0 1 1 1 1 0	0 1 0 0 1 1 0 0 1 1	2 1 1 0 0 1 0 1 0 1	0 3 0 0 1 1 3 1 0 1	2 0
Habroloma_bifrons	1 3 1 0 0 0 0 1 ? 3	0 ? 0 0 0 1 1 1 1 0	0 1 0 0 1 1 0 0 1 1	2 1 1 0 0 1 0 1 0 1	0 3 0 0 1 1 3 1 0 1	2 0
Pachyschelus_bedeli	1 0 2 0 0 0 0 2 1 2	0 0 1 0 1 0 0 0 0 0	1 0 0 1 1 0 0 0 1 0	2 1 1 0 1 1 0 1 1 0	0 1 0 0 1 1 4 1 1 1	1 0
Brachys_aerosus	1 2 1 0 1 1 0 1 1 2	0 0 0 0 1 0 0 0 0 1	0 0 0 0 1 1 0 0 1 0	0 1 0 0 0 1 0 1 1 1	1 3 0 0 1 1 4 ? ? 1	1 0
Lius_conicus	? 0 1 0 0 0 ? ? ? 2	? ? 0 0 1 0 0 0 0 0	? 1 ? 0 1 0 0 0 ? 0	0 1 0 0 0 1 0 1 1 1	1 3 0 0 1 ? 4 ? ? ?	? ?
Leiopleura_venustula	? 0 1 1 0 0 ? ? ? 2	? ? ? 0 1 0 0 0 0 0	? ? ? 0 ? 0 0 0 ? ?	? ? ? 0 0 ? ? 1 1 ?	? ? ? ? ? ? ? ? ? 1	? ?
*Leiopleura_* sp.	? 0 1 1 0 0 ? ? ? 2	? ? ? 0 1 0 0 0 0 0	? ? 0 0 1 0 0 0 ? ?	? ? ? 0 0 1 0 1 1 0	0 3 0 0 0 ? 3 ? ? ?	? ?

TABLE 4. Data matrix for cladistic analysis of species relationships of Japanese *Trachys*.

Taxa	Characters 1	1 1 1 1 1 1 1 1 1 2	2 2 2 2 2 2 2 2 2 3	3 3 3 3 3 3 3 3 3 4	4 4 4 4 4 4 4 4 4 5
	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0
Endelus_collaris_kerremansi	- 2 2 1 0 1 0 0 0 0	0 0 0 0 1 2 0 0 0 0	1 0 0 1 0 0 0 1 0 1	0 0 1 0 0 2 0 0 0 0	1 0 1 0 0 0 0 0 0 0
Aphanisticus_yasumatsui	- 2 2 1 1 1 0 0 0 0	0 0 0 - 0 2 0 0 0 0	1 0 0 0 0 0 1 1 1 -	0 0 1 0 1 1 0 0 0 0	0 0 1 1 0 0 0 0 0 0
*Habroloma_* (s.stri.)*_bifrons*	0 1 0 0 1 1 1 ? ? 0	2 0 1 0 1 1 0 1 1 0	1 0 0 1 1 0 1 0 0 0	1 - 1 2 1 2 0 0 1 0	1 0 0 1 0 0 0 0 0 0
H._(Parahabroloma)_eximium	1 0 3 1 1 1 2 0 0 1	1 1 1 0 1 1 0 1 1 1	1 0 0 1 0 0 1 0 0 0	1 - 1 2 1 2 0 0 0 0	0 0 1 1 0 0 0 0 0 0
T._minutus	0 0 1 0 0 0 1 0 0 0	0 1 0 0 1 1 0 0 0 0	0 1 0 0 1 0 0 0 0 0	0 1 0 2 0 1 0 0 0 0	0 0 1 0 0 1 0 0 0 0
T._inconspicuus	0 0 2 0 1 0 1 1 1 0	0 1 0 0 1 1 0 0 0 0	0 1 0 0 1 0 0 0 1 1	0 1 0 2 0 2 0 0 0 0	0 0 1 0 0 1 0 0 1 0
T._pseudoscrobiculatus	0 0 1 0 1 0 1 1 1 0	0 1 0 0 1 1 0 0 0 0	0 1 0 0 1 0 0 0 0 1	0 1 0 2 0 2 0 1 0 0	0 0 1 0 0 1 0 0 1 0
T._ineditus	0 0 0 0 0 1 1 0 0 0	0 1 0 0 0 0 0 0 0 0	0 1 0 0 1 0 0 0 0 0	0 1 1 2 0 2 0 1 1 0	1 0 0 0 0 1 0 0 1 0
Trachys tsushimae	0 0 0 1 1 1 1 0 0 0	0 1 0 0 0 0 0 0 0 0	0 1 0 0 1 0 0 0 0 0	0 1 1 2 0 2 0 1 1 0	1 0 0 0 0 1 0 0 0 0
*T._*sp. 1 [Taiwan]	0 0 0 0 1 1 1 0 0 0	0 1 0 0 0 0 0 0 0 0	0 1 0 0 1 0 0 0 0 0	0 1 1 2 0 1 0 1 1 0	1 0 0 0 0 1 0 0 0 0
T._koshunensis	0 0 2 1 1 1 1 0 0 0	0 1 0 0 1 1 0 0 0 0	0 1 0 0 1 0 0 0 0 0	0 1 0 2 0 2 1 0 0 1	1 0 1 0 0 1 0 0 0 0
T._formosanus [Taiwan]	0 0 2 1 1 1 1 0 0 0	0 1 0 0 1 1 0 0 0 0	0 1 0 0 1 0 0 0 0 0	0 1 0 2 0 2 0 1 2 1	1 0 1 0 0 1 0 0 0 0
T._auricollis	1 0 1 1 0 1 1 1 0 0	0 1 0 0 1 1 0 0 0 1	0 1 1 0 1 0 0 0 0 0	0 1 0 1 0 2 0 1 0 1	1 0 1 0 0 1 0 0 0 0
T._toringoi	1 0 2 1 1 1 1 1 0 0	0 1 0 1 1 1 0 0 0 1	0 1 1 0 1 0 0 0 0 0	0 1 0 0 0 0 0 1 0 1	0 0 1 0 0 1 1 0 0 0
T._saundersi	0 0 1 1 1 1 1 1 0 1	0 1 0 0 1 1 1 0 0 1	0 1 1 0 1 0 0 0 1 0	0 1 0 0 0 2 0 1 1 1	0 0 1 0 0 1 0 0 2 0
T._cupricolor	0 0 1 1 0 1 1 1 0 1	0 1 0 0 1 1 1 0 0 1	0 1 1 0 1 0 0 0 0 0	0 1 0 0 0 2 1 1 1 1	0 0 1 0 0 1 1 1 0 0
*T._*sp. 2 [Taiwan]	0 0 1 1 0 1 1 1 1 1	0 1 0 0 1 1 1 0 0 1	0 1 1 0 1 0 0 0 1 0	0 1 0 0 0 2 1 1 2 1	0 0 1 0 0 1 1 1 0 0
T._pecirkai	0 0 1 1 0 1 1 1 0 1	0 1 0 0 1 1 1 0 0 1	0 1 1 0 1 0 0 0 0 0	0 1 0 0 0 2 1 1 2 1	0 0 1 0 0 1 1 0 0 0
T._aurifluus	0 0 1 1 0 1 1 1 0 1	0 1 0 0 1 1 1 0 0 1	0 1 1 0 1 0 0 0 1 0	0 0 0 0 0 2 0 0 0 1	0 0 1 0 0 1 0 0 1 0
T._reitteri	0 0 2 1 1 1 1 1 0 0	0 1 0 0 0 0 0 0 0 1	0 1 0 0 1 0 0 0 1 0	0 1 0 2 0 2 0 0 0 1	1 0 1 0 0 1 0 0 0 0
T._tokyoensis	0 0 2 1 1 1 1 1 0 0	0 1 0 0 1 1 0 0 0 1	0 1 0 0 1 0 0 0 1 0	0 1 0 0 0 2 0 1 1 1	1 0 1 0 0 1 0 0 0 0
T._griseofasciatus	0 0 1 0 0 1 2 0 0 1	0 1 0 0 1 1 0 0 0 1	0 1 1 0 1 0 0 0 0 0	0 0 0 0 0 2 0 0 0 1	1 0 1 0 1 1 0 0 0 1
T._yanoi	0 0 1 0 0 1 1 0 0 1	0 1 0 0 1 1 0 0 0 1	0 1 1 0 1 0 0 0 0 0	0 0 0 0 0 2 0 1 0 1	1 0 1 0 1 1 0 0 0 1
T. sp. 3 [Taiwan]	0 1 1 0 1 1 1 1 0 1	0 1 0 0 1 1 0 0 0 1	0 1 1 0 1 0 0 0 1 0	0 1 0 0 0 2 1 0 0 0	1 0 0 0 1 1 0 0 1 0
T._variolaris	0 1 1 0 0 1 1 1 0 1	0 1 0 0 1 1 0 0 0 1	0 1 1 0 2 0 0 0 1 0	0 0 0 0 0 1 0 0 0 1	1 1 1 0 1 1 1 0 2 0
T._robustus	0 1 1 0 0 1 1 1 0 1	0 1 0 0 1 1 0 0 0 1	0 1 1 0 2 0 0 0 1 0	0 0 0 0 0 1 0 1 0 1	1 0 1 0 1 1 0 0 0 0
T._dilaticeps	0 1 1 0 0 1 2 1 0 1	0 1 0 0 1 1 0 0 0 1	0 1 1 0 2 0 0 0 1 0	0 0 0 0 0 1 0 0 0 1	0 0 1 0 1 1 1 0 2 0
T._hornianus [Taiwan]	0 0 1 0 0 1 1 1 0 1	0 1 0 0 1 1 0 0 0 1	0 1 0 0 2 0 0 0 1 0	1 0 0 0 0 0 0 0 0 1	1 0 1 0 1 1 1 0 1 0
T._elvira [Taiwan]	0 0 1 1 1 1 1 1 0 0	0 1 0 1 1 1 0 0 0 1	0 1 1 0 1 0 0 0 1 0	0 1 0 0 0 1 0 1 1 1	1 1 1 0 0 1 1 0 0 0
*T._*sp. 4 [Taiwan]	0 0 1 1 1 1 1 1 0 0	0 1 0 1 1 1 0 0 0 1	0 1 0 0 1 0 0 0 0 0	0 1 0 0 0 0 0 1 0 1	1 1 1 0 0 1 0 0 1 0
T._kurosawai [Taiwan]	0 1 1 1 0 1 2 1 0 1	0 1 0 0 0 0 1 0 0 1	0 1 1 0 1 1 0 0 1 0	0 1 0 0 0 1 0 1 0 1	1 1 1 0 0 1 0 0 2 0
T._ohbayashii [Taiwan]	0 1 1 1 1 1 1 1 1 1	0 1 0 0 1 1 0 0 0 1	0 1 1 0 0 1 0 0 1 0	0 1 0 0 0 2 0 1 0 1	1 0 1 0 0 1 1 0 1 0

TABLE 5. Data matrix for cladistic analysis of species relationships of Japanese *Habroloma*.

Taxa	Characters 1	1 1 1 1 1 1 1 1 1 2	2 2 2 2 2 2 2 2 2 3	3 3 3 3 3 3 3 3 3 4	4 4 4 4 4 4 4
	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7
Endelus_collaris_kerremansi	- 2 0 - 0 0 0 0 0 0	0 - - 0 0 0 0 0 0 1	0 0 0 1 0 0 1 0 0 1	0 0 0 1 0 1 0 1 0 0	0 1 0 0 0 0 0
Aphanisticus_yasumatsui	- 2 0 - 0 0 0 0 0 0	0 - - 0 0 0 0 0 0 0	1 0 1 1 0 0 1 1 0 1	2 1 0 1 0 0 0 0 1 0	0 1 1 0 0 0 0
Trachys_minutus	0 0 0 - 1 0 0 0 0 1	0 - - 0 0 0 0 1 1 0	0 0 0 0 0 0 0 0 0 0	2 0 0 1 0 0 0 0 0 0	0 0 0 1 0 0 0
T._auricollis	1 0 0 - 1 0 0 0 0 1	0 - - 0 0 0 1 1 1 0	0 0 0 0 0 0 0 0 0 0	1 0 0 1 0 0 0 1 0 0	0 0 0 1 0 0 0
*Habroloma_* (s.stri.)*_bifrons*	0 0 0 - 1 0 0 3 1 1	1 1 0 1 1 1 0 0 0 1	1 0 1 0 0 0 0 1 1 1	2 1 0 0 0 0 0 1 0 0	0 0 1 0 0 0 0
H._ (*Parahabroloma*)*_eximium*	1 0 1 1 2 0 0 1 0 1	1 0 1 1 1 1 1 0 0 1	0 1 1 1 1 1 0 0 1 1	2 1 0 1 0 0 0 0 0 0	1 1 1 0 0 0 0
H._ (*P.*)*_griseonigrum*	1 1 1 1 1 1 1 2 0 1	1 0 1 1 1 1 1 0 0 1	0 1 1 1 1 1 0 0 1 1	2 1 0 1 0 1 0 0 1 0	1 1 1 0 1 0 0
H._ (*P.*)*_miwai* [Taiwan]	1 1 1 1 1 1 1 1 0 1	1 0 1 1 1 1 1 0 0 1	0 1 1 1 1 1 0 0 1 1	2 1 0 1 1 0 0 0 1 0	1 1 1 0 1 0 0
H._ (*P.*)*_praxilla* [Taiwan]	1 0 1 0 1 1 1 1 0 1	1 0 1 1 1 0 1 0 0 1	0 0 1 1 1 1 0 0 1 1	2 1 0 1 ? 0 0 0 ? ?	? ? 1 0 0 0 0
H._ (*P.*)*_lewisii*	1 0 1 1 2 0 0 2 0 1	1 0 0 1 1 1 1 0 0 1	1 0 1 1 0 1 0 0 1 1	2 1 1 1 0 2 0 1 0 0	0 0 1 0 0 1 0
H._ (*P.*)*_nixilla*	0 0 1 1 1 0 1 2 0 1	1 1 1 1 1 1 1 0 0 1	0 0 1 1 0 1 0 0 1 1	2 1 1 1 1 2 0 1 1 0	0 0 1 0 0 1 0
H._ (*P.*)*_yuasai*	1 0 1 1 1 0 1 2 0 1	1 0 0 1 2 1 1 0 0 1	0 0 1 0 0 1 0 0 1 1	2 1 1 0 1 2 0 1 0 0	0 0 1 0 0 1 0
H._ (*P.*)*_subbicorne*	1 0 1 1 1 0 1 2 0 1	1 0 0 1 1 1 1 0 0 1	0 0 1 0 0 1 0 0 1 1	2 1 0 1 1 0 1 1 1 1	0 1 1 0 0 0 0
H._ (*P.*)*_marginicolle*	1 0 1 1 2 0 0 2 0 1	1 0 1 1 1 0 1 0 0 1	0 0 1 0 0 1 0 0 1 1	2 1 0 1 1 0 2 1 1 1	0 0 1 0 0 0 0
H._ (*P.*)*_asahinai*	1 0 1 1 1 0 0 2 0 1	1 0 1 1 1 0 1 0 0 1	0 0 1 0 0 1 0 0 1 1	2 1 0 1 1 0 3 1 1 1	0 0 1 0 0 0 0
H._ (*P.*)*_hikosanense*	1 0 1 1 1 0 0 2 0 1	1 0 1 1 2 0 1 0 0 1	0 0 1 0 0 1 0 0 1 1	2 1 ? ? ? ? ? ? ? ?	? ? ? ? ? ? ?
H._ (*P.*)*_contractum* [Taiwan]	1 0 1 1 1 0 0 2 0 1	1 0 1 1 2 0 1 0 0 1	0 0 1 0 0 1 0 0 1 1	2 1 0 1 1 0 3 1 1 1	0 0 1 0 0 0 0
H._ (*P.*)*_alphaxia* [Taiwan]	1 1 1 1 2 0 1 2 0 1	1 0 1 1 1 0 1 0 0 1	0 0 1 0 0 1 0 0 1 1	2 1 0 1 1 0 2 1 0 1	0 1 ? ? ? ? ?
H._ (*P.*)*_sp. 1*	1 0 1 0 2 0 1 1 0 1	1 0 1 1 1 1 1 0 0 1	0 0 1 1 0 1 0 0 1 1	2 1 0 1 1 0 0 1 0 0	1 0 1 0 0 0 1
H._ (*P.*)*_sp. 2* [Taiwan]	1 0 1 1 2 0 0 2 0 1	1 0 1 1 1 0 1 0 0 1	0 0 1 0 0 1 0 0 1 1	2 1 0 1 1 0 2 1 1 1	0 1 1 0 0 0 0
H._ (*P.*)*_sp. 3* [Taiwan]	1 0 1 1 1 0 0 2 0 1	1 0 0 1 1 1 1 0 0 1	0 0 1 0 0 1 0 0 1 1	2 1 0 1 1 0 2 1 1 1	0 1 1 0 0 0 0

TABLE 6. Morphological differences between *Trachys* and *Habroloma*, with studies that proposed them (black squares indicate autapomorphic character states estimated in the cladistic analysis; darker shade characters are not used in the cladistic analysis).

Trachys Fabricius, 1801	***Habroloma*** Thomson, 1864	Proposed by
1. the mandibles **with** the mandibular holes [character 11: 1]	1. the mandibles **without** the mandibular holes [character 11: 0]	this study
2. the delimitation of the basistipes and parpifers **reduced** [character 12: state 1]	2. the delimitation of the basistipes and parpifers **distinct** [character 12: state 0]	this study
3. the pronotum **without** the apicolateral depressions	3. the pronotum **with** the apicolateral depressions	● Thomson (1864)
4. the prosternum **without** the prosternal lobe [character 17: state 0]	4. the prosternum **with** the prosternal lobe [character 17: state 1]	Thomson (1864)
5. the prosternum **without** transverse grooves above procoxal cavities [character 19: state 0]	5. the prosternum **with** transverse grooves above procoxal cavities [character 19: state 1]	Schaefer (1950) *
6. the prosternal process is **narrow** and **does not form** trapezoidal plate	6. the prosternal process is **wide** and **forms** trapezoidal plate	Thomson (1864)
7. the elytra **without** the lateral carinae [character 26: state 0]	7. the elytra **with** the lateral carinae [character 26: state 1]	● Thomson (1864)
8. the elytral surface with **shallow circular punctures**	8. the elytral surface with **linearly incised short punctures**	this study
9. the epipleura of the elytra are distinctly recognized **only in thoracic region** [character 27: state 1]	9. the epipleura of the elytra are distinctly recognized **from the bases to subapical parts of elytra** [character 27: state 0]	Théry (1938)
10. the marginal carinae of the elytra distinctly recognized **only in thoracic region** [character 28: state 1]	10. the marginal carinae of the elytra distinctly recognized **from the bases to subapical parts of elytra** [character 28: state 0]	Hespenheide (1982) **
11. the hind wing **with** the anal field [character 30: state 0]	11. the hind wing **without** the anal field [character 30: state 1]	this study
12. the metatarsi **with** a fringe of spines [character 39: state 1]	12. the metatarsi **without** a fringe of spines [character 39: state 0]	● this study
13 ***. the abdominal ventrites **I–V or II–V** with the sternal grooves [character 42: states 1 or 2]	13 ***. **only** the abdominal ventrite **V** with the sternal groove [character 42: states 3]	Théry (1938)
14. the abdominal ventrite **II–IV** with the sternal cuticularia [character 45: state 0]	14. the abdominal ventrite **II and III** with the sternal cuticularia [character 45: state 1]	Jendek (2001)
15. the female proctiger with a pair of **ventrally curved** baculi [character 51: state 0]	15. the female proctiger with a pair of **straight, short** baculi [character 51: state 1]	this study
16. the female coxites **with** the dorsal projections of baculi [character 52: state 1]	16. the female coxites **without** the dorsal projections of baculi [character 52: state 0]	this study

*) Schaefer (1950) may be recognized this character state in *Habroloma*: "Un sillon transversal entre le sommet de la plaque et l'épisterne".

**) Hespenheide (1982) discussed this character for morphological differences between Trachys and *Neotrachys*.

***) This character does not support each clade of *Trachys* and *Habroloma* in the cladogram of Fig. 111.

● Black dots indicate doubtful characters for distinguishing *Trachys* and *Habroloma*.

Appendix

Appendix 1. Examined species and specimen data or literatures for the cladistic analyses of the generic relationships of Tracheini.

Subfamily Buprestinae
Tribe Buprestini
Subtribe Buprestina

Buprestis (*Ancylocheira*) *haemorrhoidalis arakii* Kurosawa, 1942: 1♂, 1 ♀, Naze-Chinase, Amami-shi, Amami-Ôshima Is., Ryukyus, Japan, 26.V.2016, Y. Tamadera leg. (YTJ).

Subfamily Agrilinae
Tribe Agrilinae
Subtribe Agirilina

Agrilus viridis (Linnaeus, 1758): 1♂, 1 ♀, Jôzankei, Minami-ku, Sapporo-shi, Hokkaido, Japan, 25.VII.2021, Y. Tamadera leg. (YTJ).

Tribe Coraebini
Subtribe Coraebina

Coraebus quadriundulatus (Motschulsky, 1860): 1♂, Nanasawa, Atsugi-shi, Kanagawa-ken, Hnoshu, Japan, 1.V.2016, Y. Tamadera (YTJ); 1 ♀, Daibo, Hakushu-machi, Hokuto-shi, Yamanashi-ken, Honshu, Japan, 5.V.2011, M. Miyao leg. (YTJ).

Tribe Aphanisticini
Subtribe Aphanisticina

Aphanisticus yasumatsui Kurosawa, 1954: 1♂, 1 ♀, Kamagase-rindô, Ono, Hita-shi, Ôita-ken, Kyushu, Japan, 26.IV.2017, Y. Tamadera leg. (YTJ).

Endelus (*Endelus*) *collaris kerremansi* Théry, 1927: 1♂, 1 ♀, Yona-rindô, Yona, Kunigami-son, Kunigami-gun, Okinawajima Is., 22.IV.2016, Y. Tamadera leg. (YTJ).

Endelus (*Endelus*) *pyrrosiae pyrrosiae* Kurosawa, 1985: 1♂, 1 ♀, Mt. Mikuma-yama, Sumoto-shi, Awajishima Is., Japan, 19.VIII.2021, Y. Tamadera leg. (YTJ).

Subtribe Paracylindromorphina

Paracylindromorphus japanensis (Saunders, 1873): 1♂, 1 ♀, Arahata, Tokorozawa-shi, Saitama-ken, Honshu, Japan, 4.VI.2016, Y. Tamadera leg. (YTJ).

Tribe Tracheini

Subtribe Brachyina

Brachys aerosus Melsheimer, 1845: 1 ♀, Lively Grove, Illinois, USA, R. J. Barkey leg. (YTJ); 1 ♀, E. Tawas, MICH, Iosco Co., 28.VI.1980, S. G. Wellso leg. (YTJ).

Lius conicus (Gory & Laporte, 1840): 3 exs., Brasilia, 6.XII.1982, A. Tanaka leg. (SEHU); illustrations of Migliore *et al*. (2020 a).

Subtribe Leiopleurina

Leiopleura venustula (Gory, 1841): description and illustrations of Kogan (1964 b).

Leiopleura sp.: 1 ex., Yurimaguas, Peru, 28.IX.1984, A. Tanaka leg. (SEHU).

Subtribe Pachyschelina

Pachyschelus bedeli Obenberger, 1921: 1 ♂, Ren’ai Township, Nantou County, Taiwan, 16.V.2016, Y. Tamadera leg. (YTJ); 1 ♀, Puli Township, Nantou County, Taiwan, 18.V.2016, Y. Tamadera leg. (YTJ); 1 ♂, Mudan Township, Pingtung County, Taiwan, 25.X.2017, H. Shigetoh leg. (YTJ); 1 ♂, Daren, Taitung County, Taiwan, S. Ohmomo leg. (YTJ).

Appendix 2. Examined Taiwanese *Trachys* species for the cladistic analysis for species relationships of Japanese *Trachys*.

Group I (minutus)

Trachys sp. 1 (similar to tsushimae): 1 ♂, Pilu, Hualien Hsien, Taiwan, 26.VI.1989, M. Satô leg. (EUM): 1 ♀, 1 ex., Mt. Dahanshan, Pingtung County, 29.VI.2019, Sinyan Shih leg. (YTJ).

Trachys formosanus Kerremans, 1912 [= *taiwanensis* Obenberger, 1929]: 3 ♂♂, Duona, Kaohsiung City, Taiwan, 22.III.2017, Uitsiann Ong leg. (YTJ); 2 ♀♀, Baolai, Kaohsiung City, Taiwan, 22.III.2018, Uitsiann Ong leg. (YTJ); images of one syntype of *Trachys formosanus* (National Museum of Natural Science, Taichung, 2017 *).

Group III (saundersi)

Trachys sp. 2 (similar to cupricolor): 1 ♂, Baolai, Kaohsiung City, Taiwan, 22.III.2018, Uitsiann Ong leg. (YTJ); 1 ♂, Meiling, Tainan City, Taiwan, 15.VII.2017, Uika Ong leg. (YTJ); 1 ♂, 2♀♀, 2 exs., near Mt. Jianfushan, Taoyuan district, Kaohsiung City, Taiwan, 3.IV.2018, Y. Fukuda leg. (YTJ).

Group VI (griseofasciatus)

Trachys sp. 3 (strongly serrated elytra): 2 ♂♂, 3 ♀♀, Baolai, Kaohsiung City, Taiwan, 19.IV.2018, Uitsiann Ong leg. (YTJ); 1 ex., (SEHU).

Group VII (variolaris)

Trachys hornianus Obenberger, 1918: 1 ♂, Baolai, Kaohsiung City, Taiwan, 29.V.2018, Uitsiann Ong leg. (YTJ); 1 ♀, same locality, 7.VI, 2018, Uitsiann Ong leg. (YTJ); 1 ♀, same locality, 19.IV, 2018, Uitsiann Ong leg. (YTJ).

Estimated groups

Trachys elvira Obenberger, 1929: 1 ♂, 1 ♀, Ren'ai Township, Nantou County, 24.III.2018, Y. Fukuda leg. (YTJ).

Trachys sp. 4 (similar to toringoi): 2 ♂♂, 1 ♀, 6 exs., Mudan Township, Pingtung County, Taiwan, 21.X.2017, Y. Tamadera leg. (YTJ).

Trachys ohbayashii Kurosawa, 1954: 1 ♀, 1 ex., Shizi Township, Pingtung County, Taiwan, 24.X.2017, Y. Tamadera leg. (YTJ); 1 ♀, Mudan Park, Mudan, Pintung County, 27.X.2017, J. Okayasu leg. (YTJ); 1 ♂, Kenting Park, Pingtung Hsien, Taiwan, 28–30.IV.1972, M. Sakai leg. (EUM). Holotype: "KURARU / S. -FORMOSA / 21.III.1941 / K. OHBAYASHI" (NSMT).

Trachys kurosawai Bellamy, 2004: 2 ♂♂, 2♀♀, Tapurun, Keeling City, Taiwan, 9.VII.2017, Uitsiann Ong leg. (YTJ). Holotype: ♀, "BARON / N.-FORMOSA / 10.VIII.1941, H. HASEGAWA" (NSMT).

Outgroup taxa (*Endelus* (*Endelus*) *collaris kerremansi* Théry, 1927 and *Aphanisticus yasumatsui* Kurosawa, 1954) are same specimens shown in Appendix 1.

*) National Museum of Natural Science, Taichung, 2017. Integrated insect types database of Taiwanese species. Available from: http://twinsecttype.nmns.edu.tw (15 February 2017).

Appendix 3. Examined Taiwanese *Habroloma* species for the cladistic analysis for species relationships of Japanese *Habroloma*.

Group I (eximium)

Habroloma (*Parahabroloma*) *miwai* (Obenberger, 1929): 1 ♂, Mt. Jianfushan, Baoshan Village, Taoyuan district, Kaohsiung City, Taiwan, 26.IV.2019, T. Saeki leg. (YTJ); 1♀, same locality, 30.IV.2019, T. Saeki leg. (YTJ).

Habroloma (*Parahabroloma*) *praxilla* (Obenberger, 1929): 1 ♂ (terminalia missing), Duona, Kaohsiung City, Taiwan, 22.VII.2018, Uitsiann Ong leg. (YTJ); 1 ♀, Kueishan, Taipei, Taiwan, 22.IV.1972, M. Sakia leg. (EUM); 1 ♀, Mudan Township, Pingtung County, Taiwan, 25.X.2017, Y. Tamadera leg. (YTJ).

Group III (subbicorne)

Habroloma (*Parahabroloma*) *alphaxia* (Obenberger, 1929): 1 ♂, Mudan Township, Pingtung County, Taiwan, 23.X.2017, Y. Tamadera leg. (YTJ); 1 ♂, same locality, 4.III.2016, Y. Fukuda leg. (YTJ); 1 ♂, Caopu Village, Shizi Township, Pingtung County, 27.X.2017, K. Yoshida leg. (YTJ); 1 ex., Shizi Township, Pingtung County, 24.X.2017, Y. Tamadera leg. (YTJ); 1 ♂, Mt. Jianfushan, Baoshan Village, Taoyuan district, Kaohsiung City, Taiwan, 26.IV.2019, T. Saeki leg. (YTJ).

Habroloma (*Parahabroloma*) *contractum* Peng, 2021: 1♂, 1♀, near Mt. Jianfushan, Taoyuan district, Kaohsiung City, Taiwan, 3.IV.2018, Y. Fukuda leg. (YTJ).

Habroloma (*Parahabroloma*) sp. 2 (alphaxia sensu U. Ong; on Rubus sp.): 3 ♂♂, 1 ♀, 2 exs., Alishan, Chiayi County, Taiwan, 15.I.2019, Uitsiann Ong leg. (YTJ).

Habroloma (*Parahabroloma*) sp. 3 (on Rubus sp.): 1 ♂, 1 ♀, Ren'ai Township, Nantou County, Taiwan, 16.V.2016, Y. Tamadera leg. (YTJ); 1 ♀, same locality, 19.V.2016, Y. Tamadera leg. (YTJ); 1 ♂, Puli Township, Nantou County, Taiwan, 18.V.2016, Y. Tamadera leg., 1 ♂, Shikeng Road, Puli Township, Nantou County, Taiwan, 23.III.2018, Y. Tamadera leg. (YTJ).

Outgroup taxa (*Endelus* (*Endelus*) *collaris kerremansi* Théry, 1927 and *Aphanisticus yasumatsui* Kurosawa, 1954) are same specimens shown in Appendix 1.