

Research on Chrysomelidae 9

edited by
Caroline S. Chaboo, Michael Schmitt



ZooKEYS 1177 (SPECIAL ISSUE)

RESEARCH ON CHRYSOMELIDAE 9

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Cover photo: Adult of *Stolas cucullata* (Boheman, 1862) (Cassidini: Mesomphaliini) in Costa Rica (photograph: Kenji Nishida).

First published 2023

ISBN 978-619-248-119-3 (e-book)

Pensoft Publishers

12 Prof. Georgi Zlatarski Street, 1700 Sofia, Bulgaria

Fax: +359-2-870-42-82

info@pensoft.net

www.pensoft.net

Printed in Bulgaria, September 2023

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Editorial

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This is volume 9 in the series ‘Research on Chrysomelidae (RoC-9)’. This started from RoC-1 in 2008, named as a series to reflect the dream of Pierre Jolivet for a long tradition into the future. This dream was built on previous special volumes of Chrysomelidae research that emerged largely through Jolivet’s efforts since 1988 (‘Biology of Chrysomelidae’) and from various international symposia. For example, ‘Special Topics in Leaf Beetle Biology’, edited by David Furth, emerged from the International Congress of Entomology held in Iguassu, Brazil in 2000.

We hope that Chrysomelidae-focused symposia will continue to be organised in the future and that the RoC series will continue to assemble diverse research and researchers into these valuable volumes that accelerate and enrich research on Chrysomelidae. This family of beetles is one of the most speciose on Earth, is ancient, and their herbivorous nature altogether make it an enormously significant group. These special issues also reflect the cooperation and collaboration within the Chrysomelidae community. Today, we have a valuable partnership with the ZooKeys production team that helps manage the process and prepare the high-quality layouts and publications.

RoC-9 assembles nine articles, four from the 10th International Symposium on the Chrysomelidae (26th International Congress of Entomology in Helsinki, Finland, July 2022) and five from independent submissions. This range of topics, questions, and problems reflects the dynamic and diverse research being conducted today on leaf beetles.

Since RoC-8 was published in 2019, we lost several figures central to recent decades of leaf beetle research: Andrzej Warchałowski (17 September 1927 – 20 September 2019), Dieter Siede (14 November 1955 – 10 August 2020), and Pierre Hippolyte Auguste Jolivet (12 October 1922 – 30 September 2020). We also commemorate Terry Lee Erwin (1 December 1940 – 11 May 2020) whose seminal 1982 paper ‘Tropical forests: Their richness in Coleoptera and other arthropod species’ was based largely on leaf beetle data. We dedicate this volume to the memory of these deceased colleagues, whose scientific legacy forms the foundation of future research and whose tireless zeal remains both an incentive and obligation for us. We are confident that the leaf beetle workers’ community will continue to widen knowledge on Chrysomelidae and will also maintain future ‘Research on Chrysomelidae’ issues.



Academic editor: Editorial Secretary

Received: 23 August 2023

Accepted: 23 August 2023

Published: 30 August 2023

ZooBank: <https://zoobank.org/1F92B7AB-8735-4DCC-A54B-0AB2A7350905>

Citation: Chaboo CS, Schmitt M (2023) Editorial. In: Chaboo CS, Schmitt M (Eds) Research on Chrysomelidae 9. ZooKeys 1177: 1–2. <https://doi.org/10.3897/zookeys.1177.111533>

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We thank all authors and reviewers for their share in the production of RoC-9, and also the ZooKeys team at Pensoft Publishers, especially Yordanka Banalieva and Nathalie Yonow. They made our work as editors a joy and a reward.



Caroline S. Chaboo



Michael Schmitt

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

No funding was reported.

Author contributions

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Data availability

All of the data that support the findings of this study are available in the main text.

Demarchus hsui (Coleoptera, Chrysomelidae, Galerucinae, Alticini), a new species from Taiwan, with notes on immatures and biology

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Abstract

A new species of the little-known genus *Demarchus* Jacoby was discovered at Pilu, East Taiwan, and is here described as *Demarchus hsui* **sp. nov.** The larvae and adults utilise showy mistletoes as food plants. Their remarkable biology is described in detail, including egg deposition and leaf mining behaviour. Their biology is compared with that of other members of the genus.

Key words: Host plant, leaf beetles, leaf miner, Loranthaceae, new species, *Taxillus rhododendricolus*, taxonomy



Academic editor: Michael Schmitt

Received: 22 November 2022

Accepted: 3 March 2023

Published: 30 August 2023

ZooBank: <https://zoobank.org/E867FD68-1EF1-49FC-8DE7-ACC73F837CA8>

Citation: Lee C-F, Chen J-C (2023) *Demarchus hsui* (Coleoptera, Chrysomelidae, Galerucinae, Alticini), a new species from Taiwan, with notes on immatures and biology. In: Chaboo CS, Schmitt M (Eds) Research on Chrysomelidae 9. ZooKeys 1177: 3–21. <https://doi.org/10.3897/zookeys.1177.97854>

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Introduction

Demarchus Jacoby, 1887 is a little-known flea beetle (Coleoptera, Chrysomelidae, Galerucinae, Alticini) with only three species described. The genus was proposed for *D. pubipennis* Jacoby, 1887 from Sri Lanka. A second species, *D. javanus* Bryant, 1941, was described from Indonesia. The third species, *D. nigriceps* Chen & Wang, 1988, was described from China. Odak et al. (1969) reported that *D. pubipennis* caused considerable damage to pigeon pea, *Cajanus cajan* (Linnaeus) (Fabaceae), in India. However, Mushtaque and Baloch (1979) observed that larval and adult *D. pubipennis* fed on leaves of *Loranthus longiflorus* Desr. (Loranthaceae) in Pakistan, but not pigeon pea, based on testing. *Loranthus longiflorus* is a species of showy mistletoes, a common name for members of the plant families Loranthaceae. Many members of both families are hemiparasites (Wikipedia 2023). Jolivet and Hawkeswood (1995) reported that *Demarchus* is the only chrysomelid genus whose members utilise Loranthaceae as a food source. Recently, Reid (2017) recorded that species of *Cadmus* (Cryptocephalinae) fed on a narrow range of families, Fabaceae, Myrtaceae, Loranthaceae, and Sapindaceae. Staines (2011) reported that members of *Sceloenopla multistriata* Uhmann (Cassidinae, Hispines) feed on *Phoradendron* sp. (Loranthaceae). Note that The Angiosperm Phylogeny Group (2016) placed *Phoradendron* within the Santalaceae.

Although the genus *Demarchus* had been redescribed by Maulik (1926), many diagnostic characters for genera proposed by Konstantinov and

Vandenberg (1996) are still missing. Results of the current study include re-description of the genus, description of the new species, its immatures, and their remarkable biology.

Materials and methods

Dr. Yu-Feng Hsu, a butterfly taxonomist, discovered numerous chrysomelid leaf-miners on *Taxillus rhododendricolus* (Hayata) S.T. Chiu (Loranthaceae), at Pilushenmu (碧綠神木), east Taiwan, during late August 2020. However, rearing success in the laboratory was minimal, with only one adult reared from larvae. During the following year, many more larvae (~ 50) were brought into the laboratory for rearing. Eight adults were successfully reared from larvae but a further 18 adults were collected during late June 2022. This material was sufficient for a detailed taxonomic study.

For rearing studies, more than 50 larvae (see above) were placed in small glass containers (diameter 142 mm × height 50 mm) with cuttings from their host plants. When mature larvae began searching for pupation sites, they were transferred to smaller plastic containers (diameter 90 mm × height 57 mm) filled with moist soil (~ 80% of container volume).

For taxonomic study, five larvae collected from the type locality (see above), and the abdomens of four adults (two collected from the type locality, see above; two reared from larvae) were soaked in hot 10% KOH solution, followed by washing in distilled water to prepare genitalia for illustrations. Head and legs of larvae, and aedeagus, abdominal ventrites, spermatheca, and gonocoxae of adults were dissected from the abdomens, mounted on slides in glycerine, and studied and drawn using a Leica M165 stereomicroscope. For detailed examinations a Nikon ECLIPSE 50i microscope was used. Length of adults was measured from the anterior margin of the eye to the elytral apex, and width at the greatest width of the elytra.

The terminology for larval stages followed Ruan et al. (2020), and for the adult stage Konstantinov and Vandenberg (1996) and Furth (1988).

Exact label data are cited for all type specimens of described species; a double slash (//) separates different labels and a single slash (/) divides the different rows of data on a label. Other comments and remarks are in square brackets: [p] – preceding data are printed, [h] – preceding data are handwritten, [b] – blue label, [w] – white label, and [r] – red label.

Type and non-type specimens or images of both known species of *Demarchus* were studied for comparison, as follows:

Demarchus pubipennis. Holotype ♂ (by monotype, The Natural History Museum, London, UK [BMNH]): "Type / H.T [p, w] (circle label with red border) // 4 12/81 [h, w] // Ceylon. / G. Lewis. / 1910–320. [p, w] // Right [h] Hind leg / mounted / in balsam. / S. Maulik, 1929. [p, w] // Galle. / On coast level. / 27.XI.-4.XII.81 [p, w] // *Demarchus* / *pubipennis* Jac [h] / S. Maulik det. [p, w] // *Demarchus* / *pubipennis* / Jac. [h, b] // Examined [h] / K. Prathanan / 2005 [p, w]; 1 ♀ (BMNH): "Larva feeding on leaves / *Loranthus longiflorus* [h, w] // Kahuta (in Punjab, Pakistan) / 25.VII.74 [h, w] // C.I.B.C / Lor- 7/74- 11 [h, w] // 2022 [h, w] // C.I.E. COLL. / A. [p] 7351 [h, r] // Pres by / Com Inst Ent / B M. 1973-1 [p, w] // Nr. *pubipennis* ? [h] / det E.A.J. Duffy, 197[p]4 [h, w] // W.

PAKISTAN [h, w]"; 1♂ (BMNH): "On Loranthus / Aug. 1929 / Peechi (in Kerala, South India) / Nair. K. S. S. [h, w] // Sebae the Baly ? / pubipennis Baly [h, y] // Demarchus / pubipennis Jac. [h] / det. M.L. Cox, 198[p]1 [h, w] // Ch. 1(a) [h, w] // C.I.E. COLL. / A. [p] 13361 [h, y] // Pres By / Com Inst Ent / B.M. 1981-1 [p, w]" 1♀ (BMNH): "On Loranthus / Aug. 1929 / Peechi (in Kerala, South India) / Nair. K. S. S. [h, w] // Ch. 1(b) [h, w] // C.I.E. COLL. / A. [p] 13361 [h, y] // Pres By / Comm Inst Ent / B.M. 1981-1 [p, w]" 1♂ (BMNH): "Mus. / Collr. / Calcutta [p] (in West Bengal, India) / 31-X-[h]07 [p, w] // Pres By / Com Inst Ent / B M 195[p]3-597 [h, w]"; 1 (glued on the card, sex undetermined) (BMNH): "Fraserpet, / Corrg. (in India) / F.R.I. Sandal / Insect Survey / 16[p]IV[h]30 [p, w] // 1041 [h, w] // Demarchus [h, w]"; 1♂ (BMNH): "Colombo / Ceylon, Sept. 1923 [h, w] // Feeding on / *Loranthus* sp. [h, w] // Pres By / Com Inst Ent / B M 195[p]3-597 [h, w]".

Demarchus javanus. 1 (sex undetermined, abdomen lost) (BMNH): "Java. [p, w] // Bowring. / 6347* [p, w] // ? Demarchus sp. [h] / det. M.L. Cox[p], 2000 [h, w]".

Demarchus nigriceps (based on images). Holotype ♂ (by original designation, Institute of Zoology, Chinese Academy of Sciences, Beijing, China [IZAS]): "西藏 [p] (Xizang) 墨脫 (Medog) / 800 – 1000 m [h] / 中國科學院 [p, w] (Chinese Academy of Sciences) // 1983.V.15 [h] / 采集者 (collector): 韓寅恒 (Heng-Yin Han) [p, w] // HOLOTYPE [p, r] // *Demarchus nigriceps* [h] // 鑑定者 (determiner): 陳世驥 (Sicien Chen) [p, w].

***Demarchus hsui* sp. nov.**

<https://zoobank.org/6F1961AF-38D3-4C8D-AE84-B2E5127098AB>

Figs 1–7

Type material. *Holotype* ♂ (TARI, The Insect Collection, Applied Zoology Division, Taiwan Agricultural Research Institute, Taichung, Taiwan): TAIWAN. Hualien: Pilu (碧綠), 20.VI.2022, leg. Y.-F. Hsu. Paratypes: 7♂, 10♀ (3♂, 3♀: BMNH; 4♂, 7♀: TARI), data same as holotype; 4♂, 4♀ (TARI) same locality as holotype, 13.VII.2022, leg. Z.-I. Chen.

Additional material examined. Five mature larvae (TARI), same locality as holotype, 20.IX.2022, leg. Y.-F. Hsu.

Description. Adults. Colour (Fig. 1A–C) reddish brown, head black, but antenna dark brown or black, prothorax pale yellow, legs yellow with outer margins blackish brown. Pronotum transverse, 2.0× wider than long, disc convex and with lateral fovea, disc with sparse, coarse punctures, lacking antebasal transverse groove; lateral margin rounded, anterior margin slightly concave, posterior margin slightly convex. Elytra slightly wider posteriorly, with shallow transverse impression, widest at apical 1/3, apex convergently rounded, 1.5–1.7× longer than wide, disc with dense, fine punctures and dense pubescence.

Male. Length 4.8–5.5 mm, width 2.2–2.5 mm. Antenna filiform (Fig. 2A), ratio of length of antennomeres I to XI 1.0: 0.5: 0.6: 0.8: 0.8: 0.9: 0.9: 0.8: 0.7: 0.7: 0.9; ratio of length to width of antennomeres I to XI 3.0: 2.4: 3.1: 3.0: 3.2: 3.3: 3.4: 3.6: 3.2: 3.2: 3.9. Aedeagus (Fig. 2C–E) with apical 1/2 lanceolate, apex narrowly rounded, basally narrowed; strongly curved in lateral view, slightly recurved near base; tectum slightly sclerotised, with median, longitudinal, strongly sclerotised area from basal margin; endophallic sclerites absent. Apex

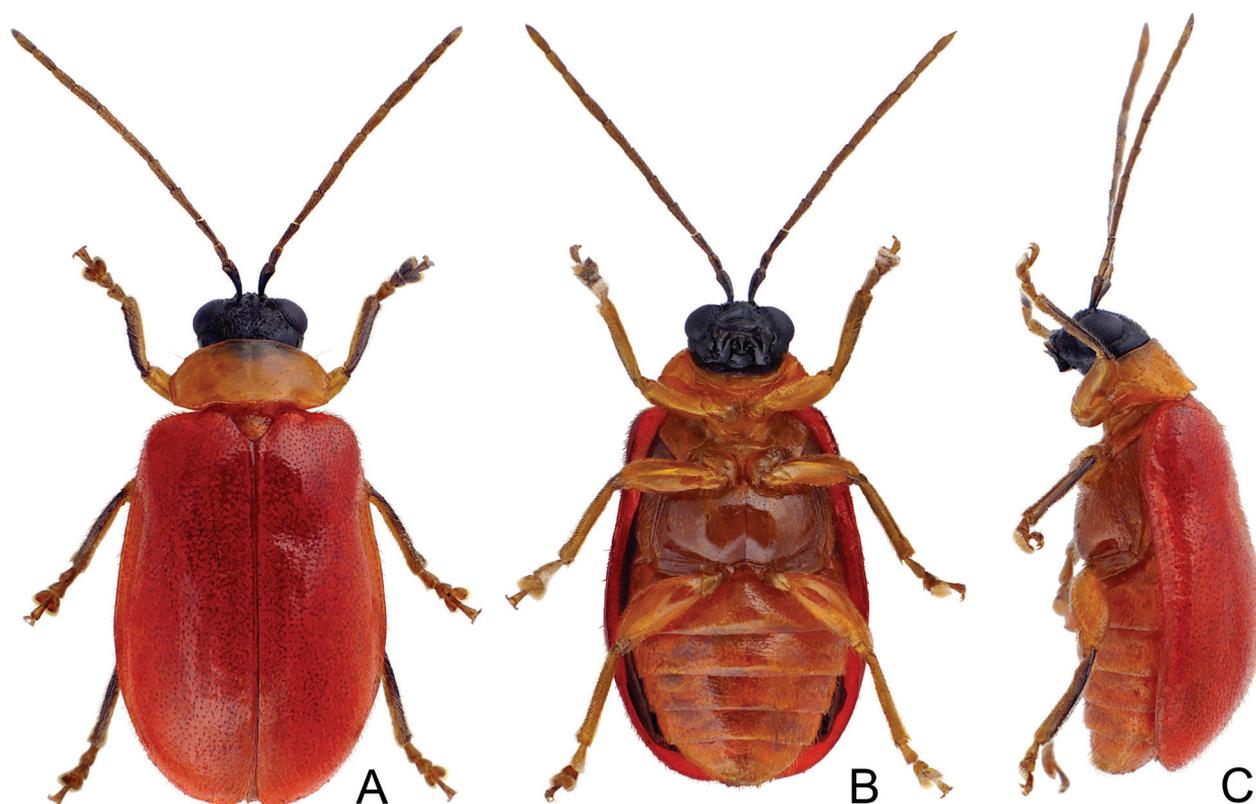


Figure 1. *Demarchus hsui* sp. nov. female **A** dorsal view **B** lateral view **C** ventral view.

of abdominal ventrite V (Fig. 2I) with median, angular notch, internally covered by flattened sclerite.

Female. Length 5.1–6.0 mm, width 2.4–3.0 mm. Antenna (Fig. 2B) similar to males, ratio of length of antennomeres I to XI 1.0: 0.5: 0.6: 0.9: 0.9: 0.8: 0.8: 0.7: 0.7: 0.6: 0.9; ratio of length to width of antennomeres III to XI 3.6: 2.6: 2.7: 3.7: 3.6: 3.5: 3.7: 3.4: 3.5: 3.0: 4.5. Ventrite VIII (Fig. 2F) weakly sclerotised, T-shaped, with dense, short setae along apical margin, apical margin irregular, spiculum short. Spermathecal receptaculum (Fig. 2G) slightly swollen; pump long and strongly curved, apex widely rounded; spermathecal duct short, shallowly projecting into receptaculum. Gonocoxae (Fig. 2H) short and widely conjoined at base, each gonocoxa widest at apical 1/3, with dense setae along apical areas.

Diagnosis. Adults of this new species are similar to those of *D. nigriceps* in colour pattern, but differ in possessing black antennae and outer margins of tibiae (Fig. 1A–C) (yellow antennae and tibiae in *D. nigriceps* (Fig. 11C, F)), pronotum without antebasal transverse groove (Fig. 1A) (pronotum with antebasal transverse groove in *D. nigriceps* (Fig. 11C)), elytra with transverse impression (Fig. 1A) (elytra without transverse impression in *D. nigriceps* (Fig. 11C)), antennomeres IV–VII subequal in length and longer than antennomere III (IV–VII subequal in length and shorter than antennomere III in *D. nigriceps*), antennomeres VIII–X subequal in length and shorter than antennomere XI (antennomere VIII–XI subequal in length in *D. nigriceps*).

Mature larvae. Length 9.5–9.6 mm, width 2.5–2.6 mm. Live specimens (Fig. 7E): body form elongate, flattened; pale yellow, head and legs blackish brown; prothoracic and abdominal tergite IX with large sclerotised patches; thoracic tergites with small, longitudinal, curved sclerotised patches at sides;

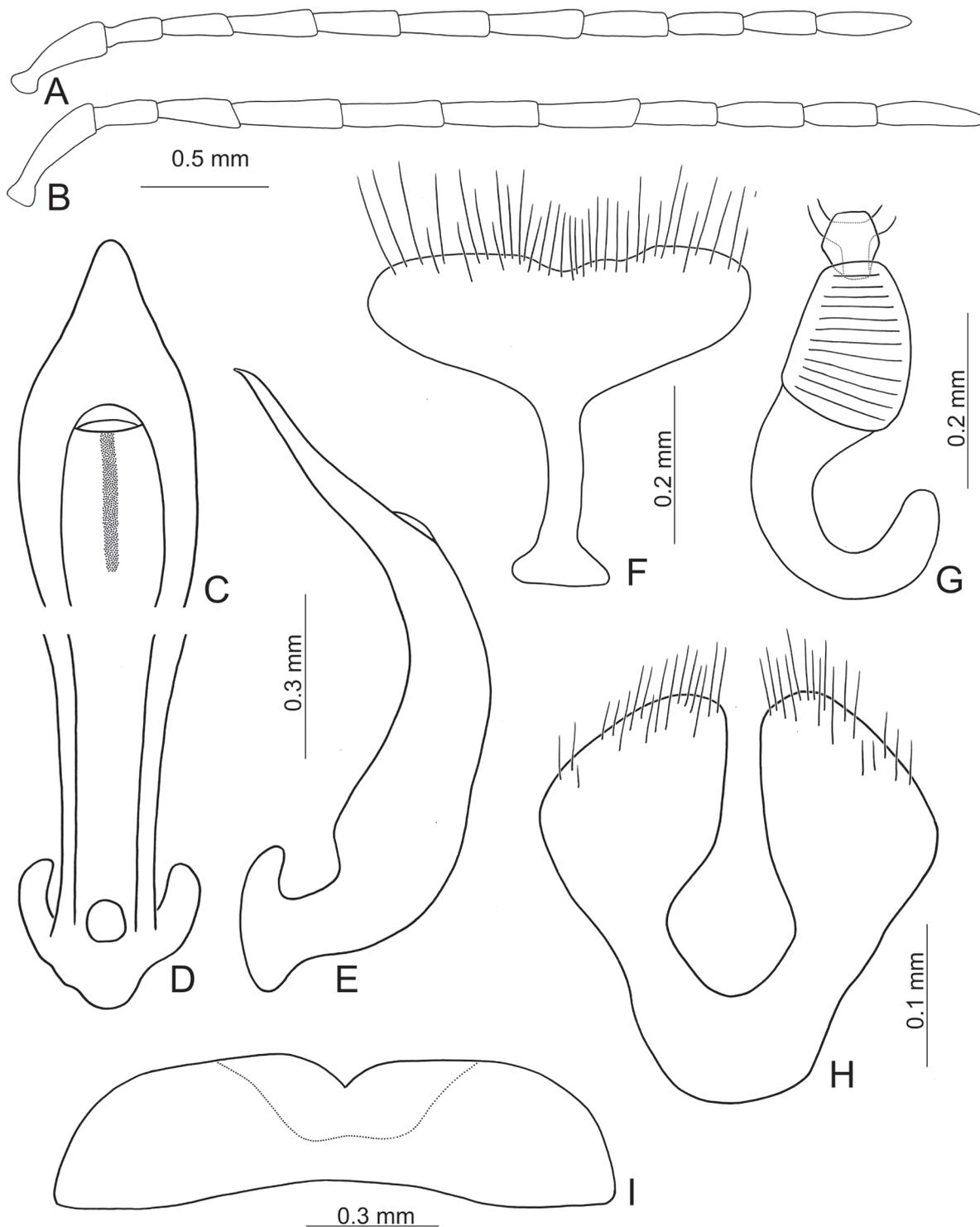


Figure 2. *Demarchus hsui* sp. nov. adult **A** antenna, male **B** antenna, female **C** apex of aedeagus, front view **D** base of aedeagus, dorsal view **E** aedeagus, lateral view **F** abdominal ventrite VIII, female **G** spermatheca **H** gonocoxae **I** abdominal ventrite V, male.

thoracic ventrites with small rounded sclerotised patches medially; lateral margins of meso- and metathoracic, and abdominal segments I–VIII expanding outwards, abdominal segments I–VIII each bearing one small process at lateral margins. body bearing tiny setae, the latter sometimes reduced to pores. Spiracles present on mesothorax and abdominal segments I–VIII (Fig. 3A).

Head (Fig. 4A). Flattened, narrower than prothorax, partly retracted into prothorax; frontal sutures (Frs) V-shaped, epicranial suture (Eps) short; endocarina (En) wide. Stemmata absent. Epicranium (Ep): with six pairs of short setae (e1–7) and nine pairs of pores (p1–9); e4–6 situated at posterolateral part of epicranial halves. Frons (Fr): with three pairs of short setae (f1–3) and one pair of pores. Clypeus (Cly): transverse, with three pairs of tiny setae near base. Clypeus and frons divided by apistomal sulcus. Labrum (Lbr): transverse, with one pair of short setae near midline; apical edge rounded. Epipharynx (Fig. 4E): densely setose anteriorly; with four or five large setae on each side; sensilla arranged in one pair of transverse rows. Mandibles (Fig. 4D): symmetrical, palmate, each mandible with four sharp teeth, without penicillus. Antennae (Fig. 4C): weakly sclerotised, two segmented, attached to membranous area at end of frontal suture; first antennomere partly membranous, bearing one small conical sensory papilla and several sensilla; second antennomere small, without sensilla. Maxilla (Fig. 4B): Stipes (St) elongate, bearing one pair of long setae and two pairs of short setae near lateral margin; with a long, curved sclerotisation (Scl). Mala with galea (Gal) and lacinia (Lac) not fused; galea wide, bearing six stout setae and numerous hair-like setae at apex; apical part of lacinia with dense hair-like setae; maxillary palpus (Mxp) three-segmented, second palpomere bearing two setae, one and third palpomeres each bearing one sensilla. Labium (Fig. 4B): submentum (Smen) trapezoid, bearing two pairs of long setae at sides; mentum not well defined; prementum short and transparent, with horseshoe-shaped mental sclerite (Mens), bearing one pair of setae at base; ligula (Lig) membranous, not separated from prementum, anterior edge broadly concave, bearing numerous hair-like setae; labial palpi (Lbip) small, two segmented; with three pairs of sensilla near labial palpi.

Thorax. Prothorax: dorsum (Fig. 3B) with one pair of pores and two pairs of short setae at basal areas of sclerotised patches; two pairs of short setae near base halfway between sclerotised patches and bases of lateral process; three pairs of short setae at sides. Sternal region (Fig. 3D) with one small, sclerotised patch medially, two pairs of short setae at anterior and posterior parts of sclerotised patch respectively. Mesothorax: dorsal region (Fig. 3B) with pores and short setae arranged into two transverse rows, anterior row with two pairs of pores and one pair of setae, posterior row with four setae; lateral longitudinal, sclerotised patches bearing three short setae. Sternal region (Fig. 3D) with one very small, sclerotised patch, one pair of short setae and one pair of pores at anterior and posterior parts outside sclerotised patch. Metathorax: same pattern as mesothorax, except for absence of spiracle. Legs (Fig. 4F): five segments; trochantin (Tn) triangular, without setae or pores; coxa (Co) transverse, bearing several pores at basal half, and two short setae near apical margin; trochanter (Tr) triangular, lacking setae but with several pores; femur (Fe) small, with one long seta on mesal margin, and one small setae at inner face; tibia (Ti) enlarged at base decreasing toward apex, bearing seven short setae at apical 1/2; tarsungulus sclerotised, falciform, bearing one basal setae; pulvillus (Pu) bladder-like, as long as tarsungulus.

Abdomen. Segments I–VIII: dorsal region (Fig. 3C) lacking setae, pores arranged into two transverse rows, bearing three pairs of pores at anterior and posterior row respectively, and three pairs of pores on lateral process; sternal region (Fig. 3E) with pores arranged into three transverse rows, one pair of pores in anterior row, four pairs of pores in middle row, and two pairs of pores

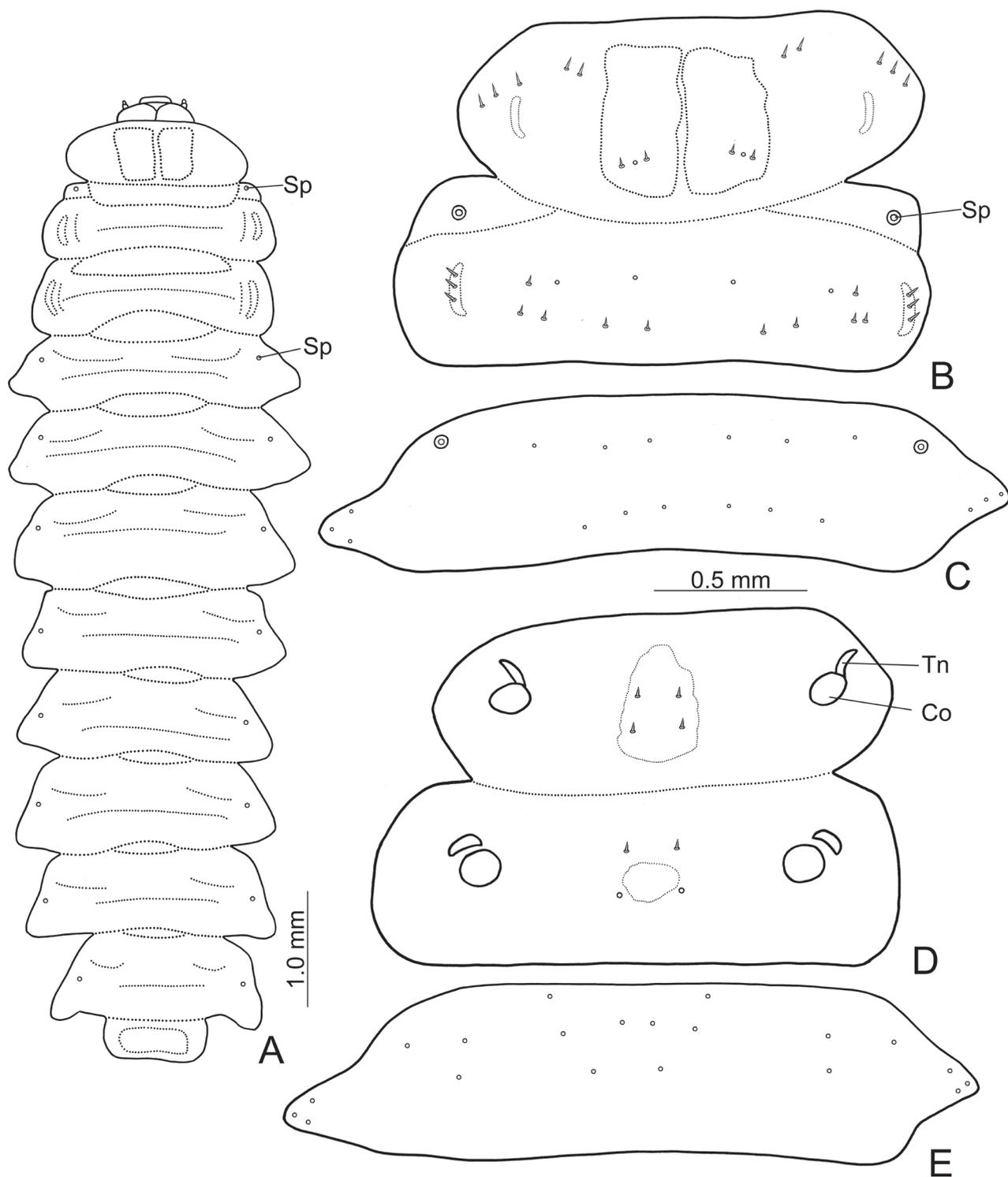


Figure 3. *Demarchus hsui* sp. nov. mature larva. **A** dorsal view. **B** pro-mesothorax, dorsal view **C** abdominal segment I, dorsal view **D** pro-mesothorax, ventral view **E** abdominal segment I, ventral view. Abbreviations: Co-Coxa; Sp-spiracle; Tn-Trochantin.

in posterior row, three pairs of pores on lateral process. Segment IX (Fig. 4G): pygidium moderately sclerotised; disc with pores arranged into two transverse rows, three pairs of pores in anterior and posterior rows respectively; three pairs of short setae along lateral margin.

Host plant. Loranthaceae: *Taxillus rhododendricolus* (Hayata) S.T. Chiu.

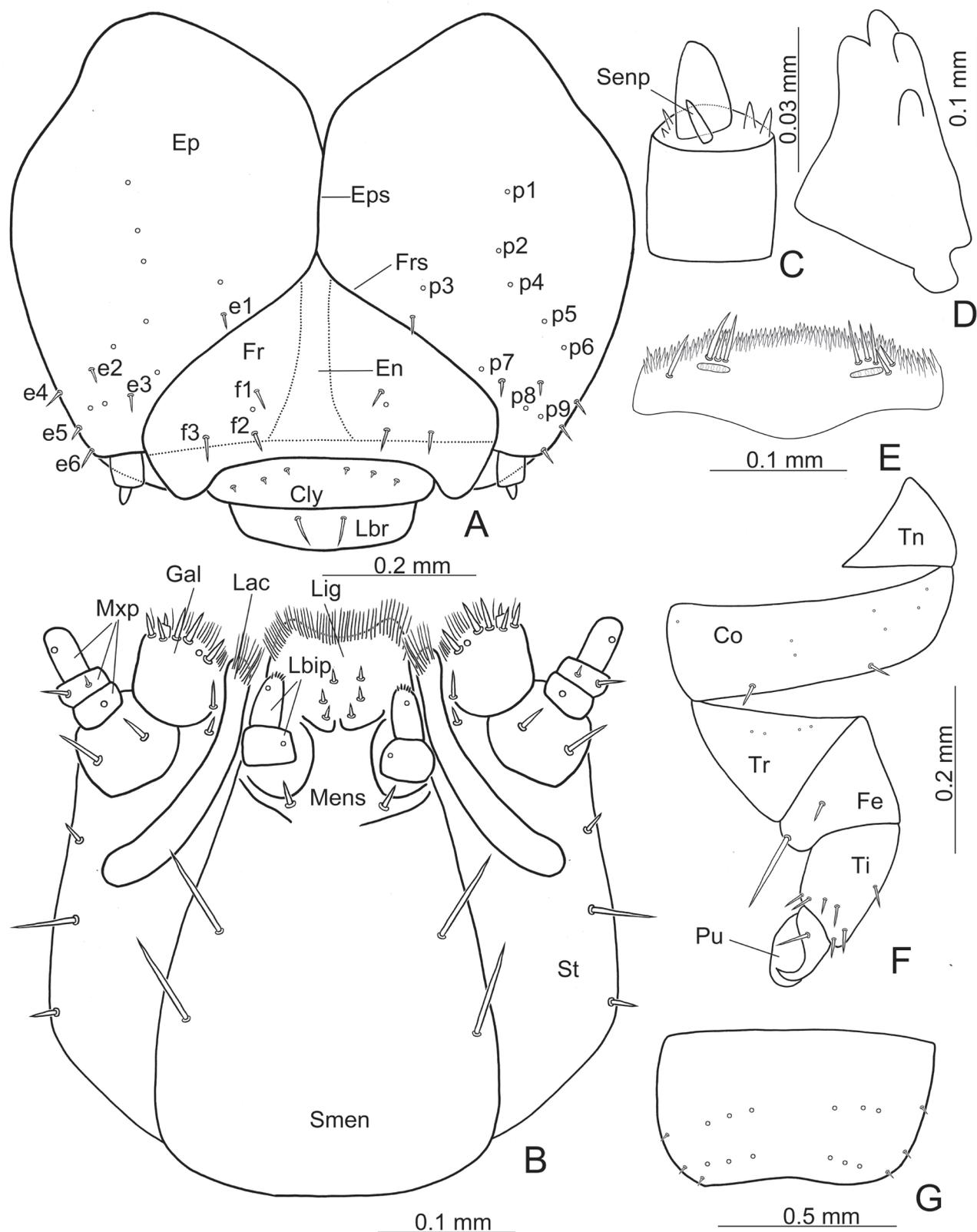


Figure 4. *Demarchus hsui* sp. nov. mature larva **A** head **B** maxilla and labium **C** antenna **D** mandible **E** epipharynx **F** middle leg **G** abdominal segment IX, dorsal view. Abbreviations: Cly-clypeus; Co-coxa; e1-e6-epicranial setae; En-endocarina; Ep-epicranium; Eps-epicranial suture; f1-f3-frontal setae; Fe-femur; Fr-frons; Frs-frontal suture; Gal-galea; Lac-lacinia; Lbip- labial palpus; Lig-ligula; Mens-mental sclerite; Mxp-maxillary palpus; p1-p9-epicranial pores; Pu-pulvillus; Scl-sclerotisation; Senp-sensory papilla; St-stipes; Ti-tibia; Tn-trochantin; Tr-trochanter.



Figure 5. Field photographs taken from the type locality, Pilu (碧綠) **A** host plant, *Taxillus rhododendricolus* (indicated by arrows) **B** close-up and another angle of *T. rhododendricolus* **C** branch of *T. rhododendricolus* with egg masses (indicated by black arrows) and larvae (indicated by red arrows) **D** branch of *T. rhododendricolus* with young larvae (indicated by arrows) mining leaves **E** branch of *T. rhododendricolus* with older and younger larvae (indicated by red arrows) mining leaves **F** branch of *T. rhododendricolus* with egg masses (indicated by black arrows).

Biology. Larvae are leaf miners of *Taxillus rhododendricolus*, which is a hemiparasite. More than 20 larvae (Fig. 5C–E) were collected from branches (Fig. 5A, B) cut from the host tree, *Salix fulvopubescens* Hayata var. *fulvopubescens* Hayata (褐毛柳) at a height of approximately six meters during late

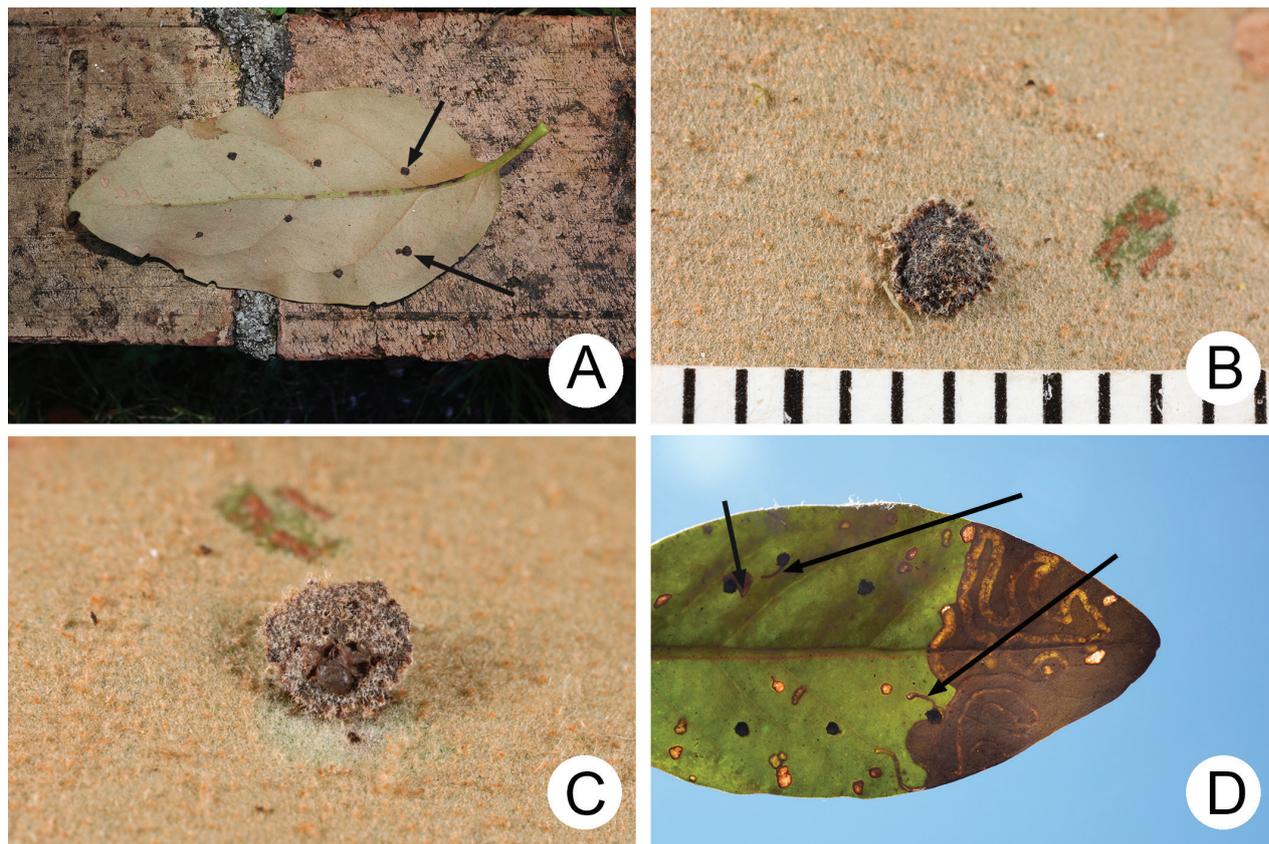


Figure 6. Egg masses of *Demarchus hsui* sp. nov. **A** typical distribution of egg masses of *Demarchus hsui* sp. nov. on underside of leaf **B** egg mass removed from point where it was deposited, scratch marks indicated by arrows **C** egg mass from a different angle with eggs exposed (indicated by arrow) **D** backlit image with tunnels constructed by the new hatched larvae indicated by arrows.

August 2020. Forest type is mixed coniferous, including *Picea asperata* Mast., *Tsuga chinensis* (Franch.) Pritzel ex Diels., and *Cunninghamia konishii* Hayata, with some evergreen broad-leaved and deciduous trees. During 2022, 18 adults were collected using sweep nets from the same plant on June 20 by Dr. Hsu (see types). Eight additional adults were collected from the host plant on trees of *Carpinus rankanensis* Hayata on July 13. Some other collecting trips were carried out during different months. These collecting events indicated that adults appear during June and July, egg masses during early August, and larvae only during late August and September, no life stages were found after October, and it is clear that *D. hsui* sp. nov. is an univoltine species. By contrast, populations of *D. pubipennis* in Pakistan are multivoltine, with up to four generations a year (Mushtaque and Baloch 1979).

Egg masses were deposited at some distance from each other on undersides of leaves (Fig. 6A). Females scratched the leaf surface several times (Fig. 6B) so that neonate larvae could burrow into the leaves easily. Then four or five eggs (Fig. 6C) were laid and covered by faeces. Usually only one larva hatched successfully from each egg mass (Fig. 6D) and began mining leaves.

Leaves of *T. rhododendricolus* decayed as soon as larvae constructed tunnels (Fig. 7A). Tunnels made by larvae were always transverse and turned towards the leaf apex (Fig. 7B, C). Larvae turned tunnels basally when conditions were not suitable to maintain the apical direction. Such a feeding pattern

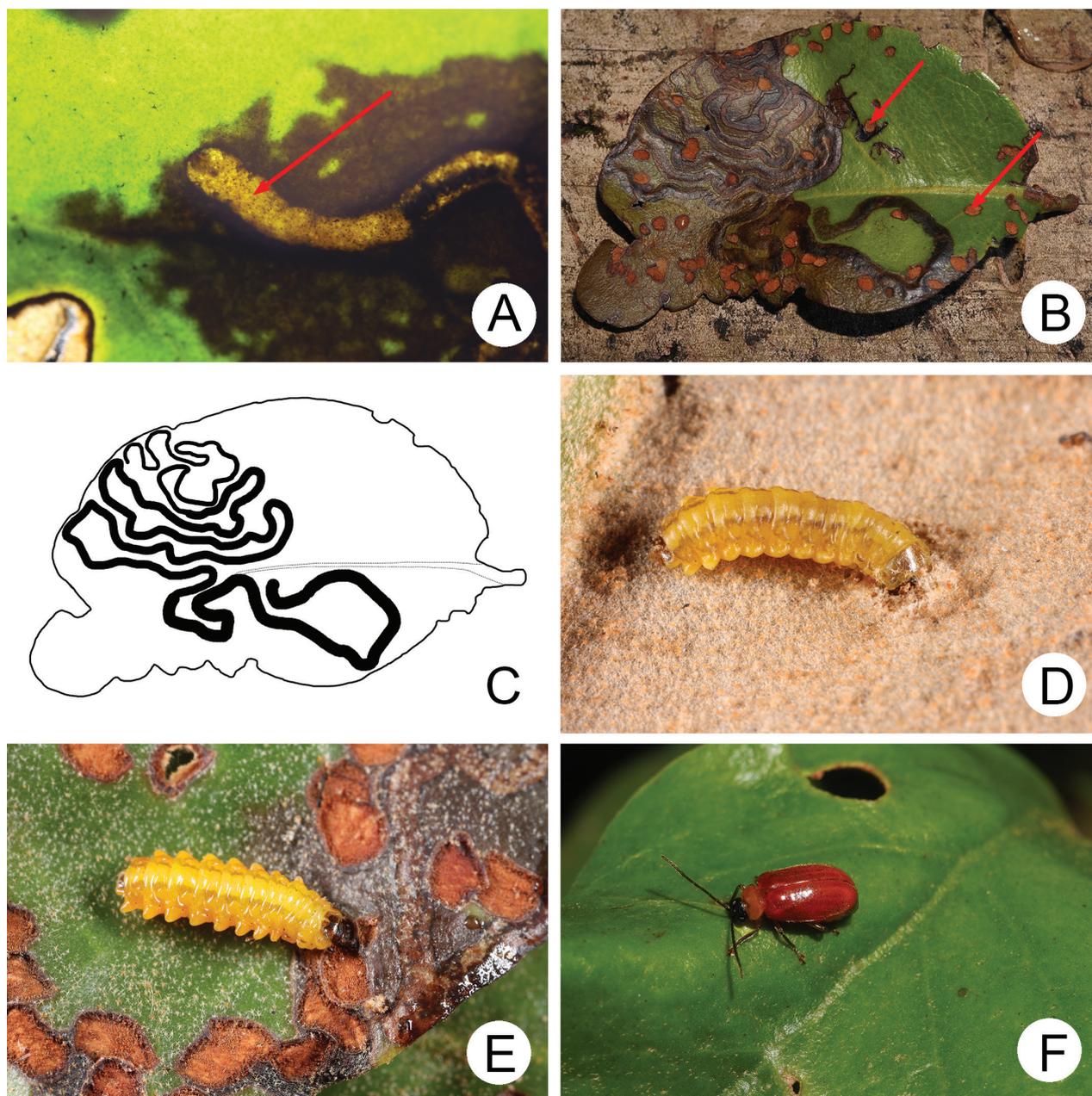


Figure 7. Larvae and adult of *Demarchus hsui* sp. nov. **A** young larva (indicated by arrow) mining leaf **B** larval tunnels and feeding marks made by adults on leaf (indicated by arrows) **C** diagrammatic illustration of larval tunnels for Fig. 9B **D** older larva starting to mine leaf **E** mature larva that emerged from larval tunnel **F** adult feeding on leaf.

caused the entire leaf to decay from apex to base (Figs 5D, E, 6D, 7B). Larvae exited tunnels when conditions deteriorated and searched for more suitable leaves. They were able to tunnel into newly selected leaves and continue development (Fig. 7D). Mature larvae (Fig. 7E) emerged from tunnels and walked or fell to the ground, mainly falling when disturbed. They burrowed into soil and built underground chambers for pupation.

Adults on leaves of *T. rhododendricolus* were active during the day (Fig. 7F). They fed on the upper surface of leaves, leaving round feeding scars (Fig. 7B, E).

Remarks. Larvae of *D. hsui* sp. nov. exhibit unusual characters that are typical for leaf miners (Takizawa 2005), including flattened body and head, head with vertex incised in a U- or V-shape posteriorly, and body surface without setae or tubercles.

Etymology. This new species is named for Dr. Yu-Feng Hsu (徐堉峰), who is a well-known butterfly expert and the first person to collect specimens.

Distribution. The new species is only recorded from the type locality – Pilu (碧綠), in Hualien County, East Taiwan. It is located at 24°10'51.3"N, 121°24'11.6"E, 2150 m MSL, and protected by the Taroko National Park (太魯閣國家公園). This locality seems to be the biodiversity hotspot. The rarely collected chrysome-line *Ambrostoma chinkinyui* Kimoto & Osawa, 1995 is also only known from this locality (Kimoto and Osawa 1995), as well as multiple undescribed species (unpublished data).

***Demarchus* Jacoby, 1887**

Demarchus Jacoby, 1887: 101 (type species: *Demarchus pubipennis* Jacoby, 1887, by original designation); Maulik 1926: 135 (redescription); Scherer 1969: 196 (catalogue).

Included species. *Demarchus pubipennis* Jacoby, 1887, *D. javanus* Bryant, 1941, *D. nigriceps* Chen & Wang, 1988, *D. hsui* sp. nov.

Redescription. Body elongate rounded, head visible from above. Head (Fig. 8A) drawn into prothorax, hypognathous, broadly oval in frontal view; vertex large, covered with dense, coarse punctures and short setae; antennal calli rectangular, well separated from vertex by deep furrow, not separated from antennal sockets; antennal sockets large, distance between sockets smaller than diameter of socket, sockets separated by frontal ridge, not separated from eyes; frontal ridge triangular, anterior surface of frons convex, bearing short setae at the sides of frontal ridge; frontal area, including mouth region, not separated from genae; eyes small, convex, the longest diameter of eye smaller than the distance between eyes, not delineated by sulci from vertex and frons. Antenna (Fig. 2A, B) 11-segmented, filiform, long, extending beyond middle of body; antennomere I shorter than two following antennomeres combined. Labrum with two pairs of setae.

Prothorax. Pronotum distinctly wider than long, disc glabrous, with antebasal transverse impression, limited laterally by short longitudinal furrows; hypomera (hyp) (Fig. 8B) large, hypomerical sutures reduced; prosternum above procoxal cavities narrow, narrower than width of procoxal cavities, intercoxal prosternal process (ipp) narrow, its anterior edge straight; procoxal cavities (prc) closed, transversely elongate.

Mesothorax. Mesonotum (Fig. 8C) of typical shape, lightly sclerotised, prealar projection (pp) well developed, elongate; postmedial projections (pmp) reduced; scutum (scm) widely rounded. Mesoventrite short, mesanepimera and mesaepesterna narrow.

Metathorax. Metanotum (Fig. 8D) well sclerotised, well developed, and typical for alticines; prescutum (psc) and postnotum (pn) wide. Metaventrite as wide as first abdominal segment, metaventral process reduced, posterior edge of metaventrite medially with deep incision, metaepisterna of typical shape, narrow. Metendosternite (Fig. 8E) with branches of anterior part of ventral process (avp) well developed, short; furcal arm (fa) narrow and well sclerotised; stalk (s) wide and short.

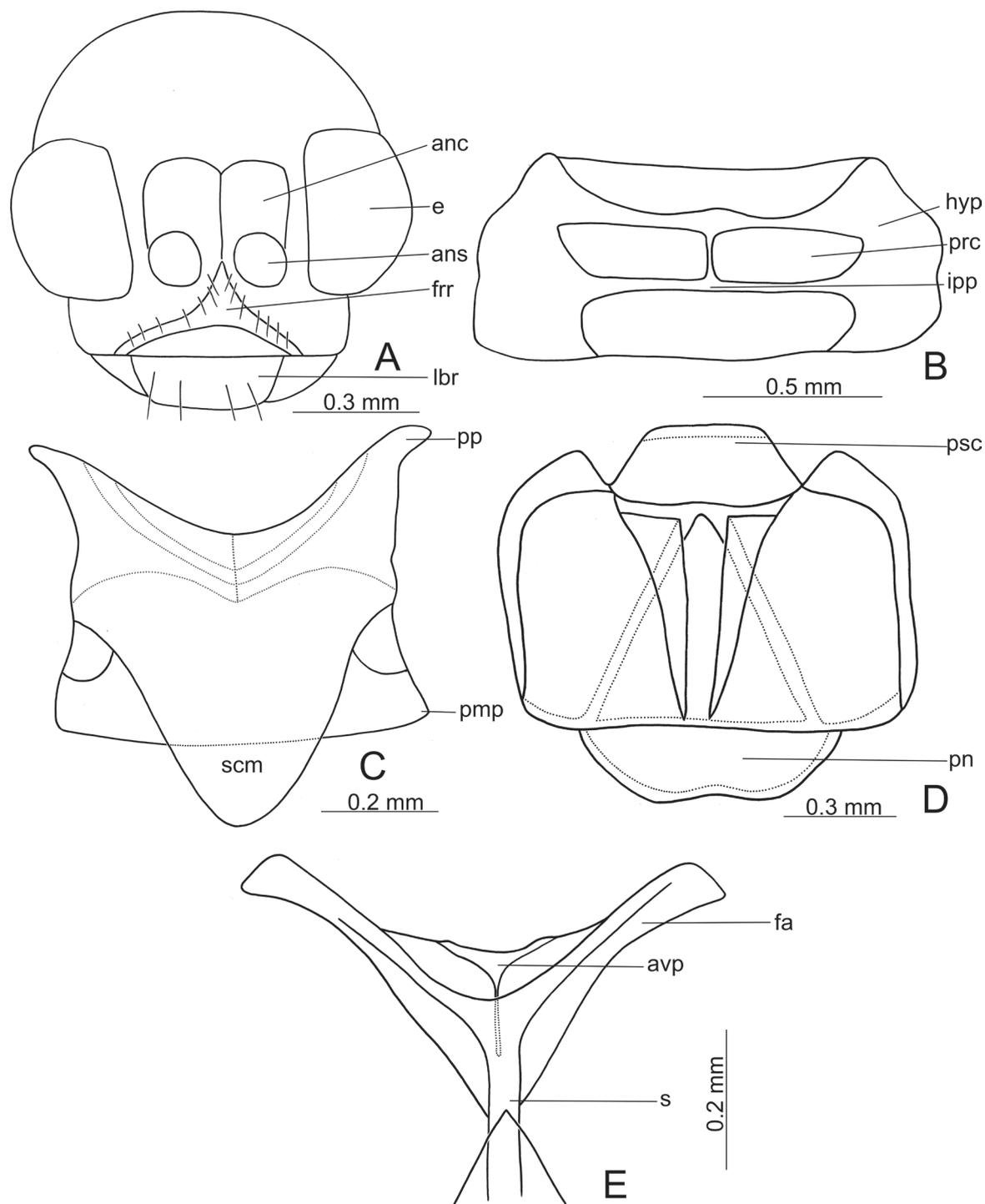


Figure 8. Diagnostic features of adults of *Demarchus hsui* sp. nov. **A** head **B** ventral view of prothorax **C** mesonotum **D** metanotum **E** metendosternite. Abbreviations: anc-antennal calli; ans-antennal socket; avp-anterior part of ventral projection; e-eye; fa-furcal arm; frr-frontal ridge; hyp-hypomera; ipp-intercoxal prosternal process; lbr-labrum; pmp-post-medial projection; pn-postnotum; pp-prealar projection; prc-procoxal cavity; psc-prescutum; s-stalk; scm-scutum.

Elytra elongate oval. Humeral callus well developed. Elytral punctures and pubescence dense and confused. Epipleuron (Fig. 9A, B) wide, horizontal, and recurved at apical 1/3, and then vertical, almost reaching elytral apex. Elytral binding patch covered with numerous teeth that are rounded in shape, ventral surface of elytra glabrous.

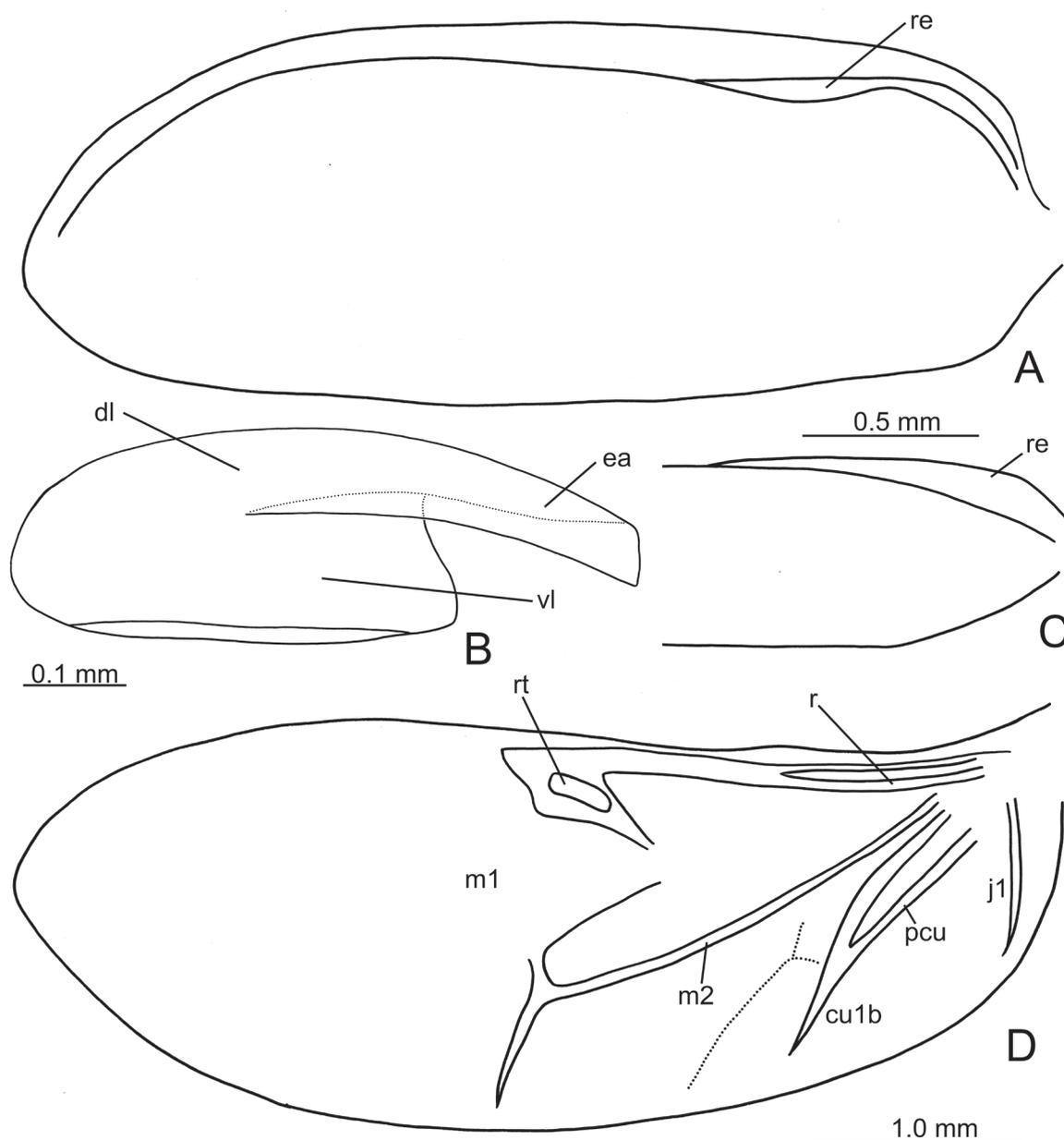


Figure 9. Diagnostic features of adults of *Demarchus hsui* sp. nov. **A** elytron, ventral view **B** metafemora spring **C** base of elytra, lateral view **D** hind wing. Abbreviations: cu-cubital vein; dl-dorsal lobe; ea-extended arm; j-jugal vein; m-medial vein; r-radial vein; re-recurved part of epipleuron; rt-sector of radial vein; vl-ventral lobe.

Hind wings. Wing venation (Fig. 9C) typical for alticines (Konstantinov and Vanderberg 1996), with completely developed wings and no tendency to reduction. Typical set of veins is present; radius (r), sector of radial vein (rt), medial veins 1 (m1) and 2 (m2), cubital vein 1b (cu1b), and precubital vein (pcu). In addition, first jugal vein (j1) is also visible.

Abdomen. Ventrites short, wide, without projections or convexities, ventrite I shorter than metasternum; sexual dimorphism present in the shape of ventrite V (apical margin with median notch in males but absent in females); pygidium without medial longitudinal groove; tergite VIII well-developed.

Male genitalia (Figs 2C–E, 10A, B) consisting of median lobe of aedeagus, and Y-shaped tegmen. Aedeagus lacking endophallic spiculae.

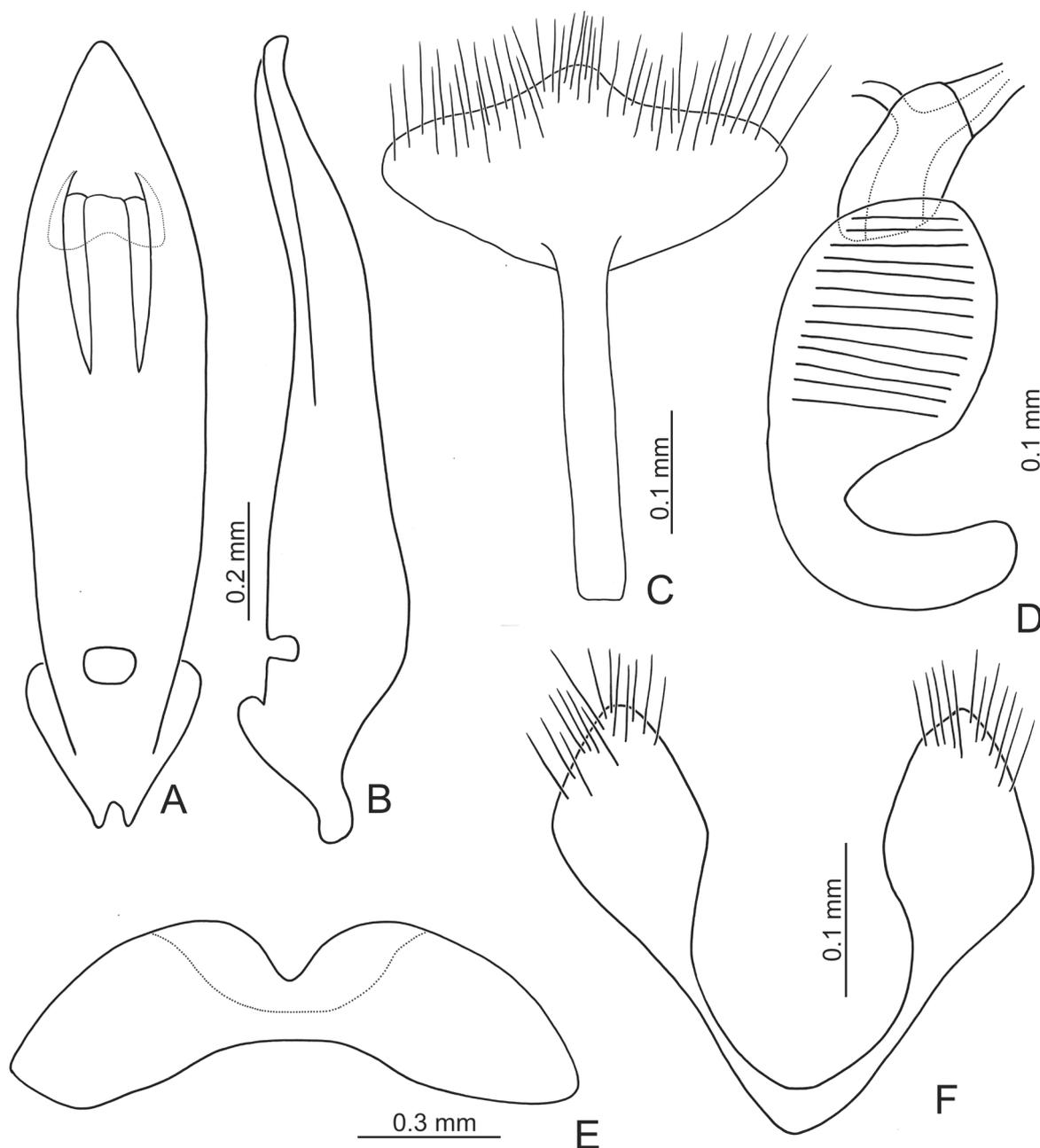


Figure 10. *Demarchus pubipennis* Jacoby, adult **A** aedeagus, dorsal view **B** aedeagus, lateral view **C** abdominal ventrite VIII, female **D** spermatheca **E** abdominal ventrite V, male **F** gonocoxae.

Female genitalia consisting of ventrite VIII, gonocoxae, and spermatheca. Ventrite VIII (Figs 2F, 10C) T-shaped, base well-sclerotised, speculum short, slightly longer than wide, its apical margin with dense setae. Spermathecal receptacle (Figs 2G, 10D) slightly swollen, sclerotised spermathecal duct very short, pump long, and strongly curved. Gonocoxae (Figs 2H, 10F) short and wide, basally joined, with dense setae at apical areas.

Legs. Anterior and middle legs of typical shape, without modifications; tibiae without apical spurs, furrows, grooves, ridges, or excavations. Posterior femora slightly swollen; posterior tibiae comparatively short, not longer than length of femora; metafemoral spring simplified (Fig. 9C), lightly sclerotised, dorsal edge of dorsal lobe (dl) flat, extended arm (ea) of dorsal lobe relative long, ventral

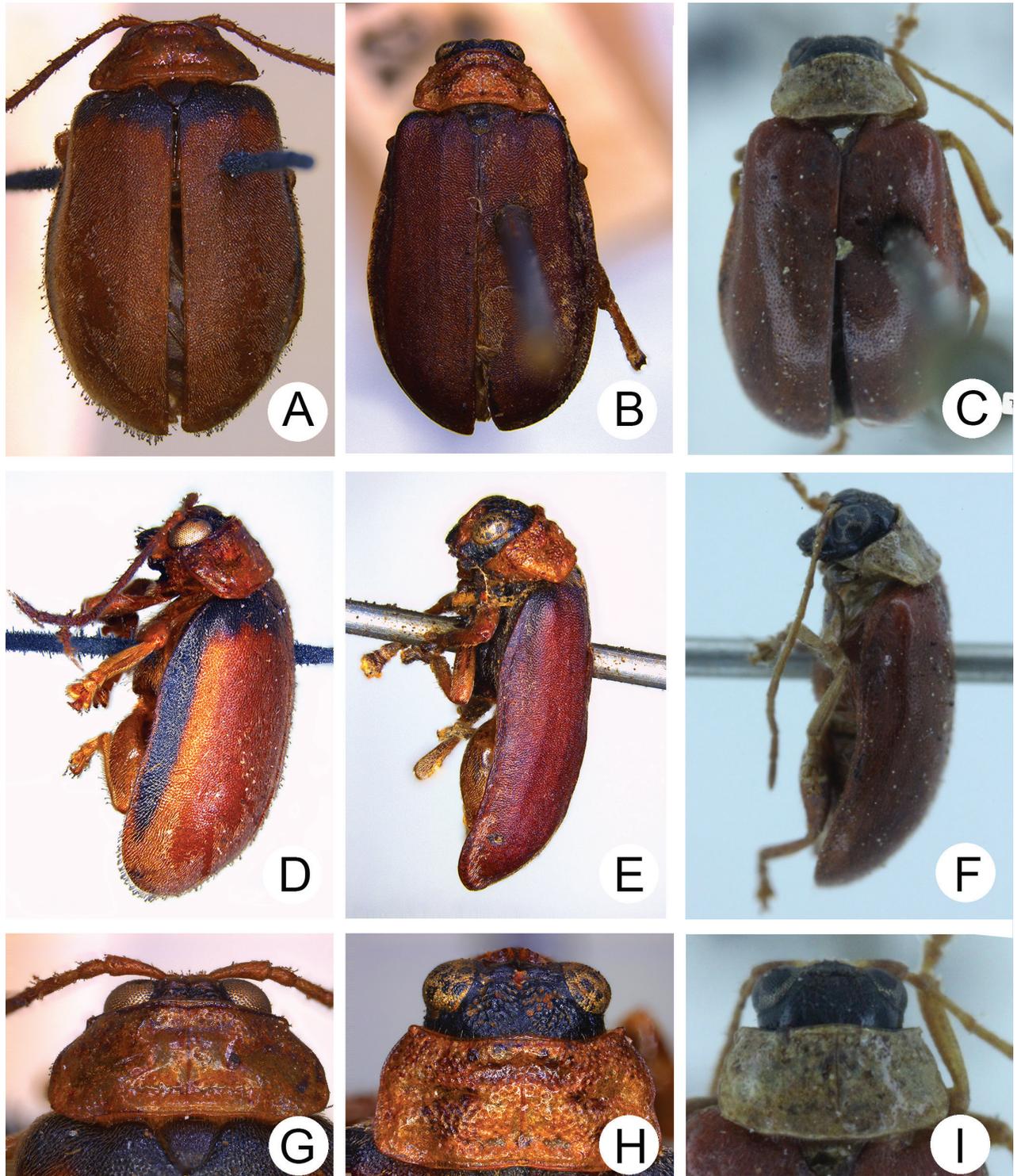


Figure 11. Diagnostic characters of *Demarchus pubipennis* Jacoby, non-type male from Sri Lanka; *D. javanus* Bryant, non-type adult from Java; *D. nigriceps* Chen & Wang, holotype. Dorsal view: **A** *D. pubipennis* **B** *D. javanus* **C** *D. nigriceps*; lateral view: **D** *D. pubipennis* **E** *D. javanus* **F** *D. nigriceps*; head and pronotum: **G** *D. pubipennis* **H** *D. javanus* **I** *D. nigriceps*.

lobe (vi) cylindrical, apically rounded, without lower part curving dorsally, and no basal angle, ventral edge of ventral lobe recurved; posterior tarsus attached to tibia apically; tarsus slightly longer than half of tibia; metatarsomere I shorter than three following tarsomeres combined, ventrally with short, dense setae. Tarsomeres III bilobed; tarsal claws bifid.

Remarks. One character misjudged by Jacoby (1887) and Maulik (1926) is the closed procoxal cavities. Since the posterior margins of the procoxal cavities are so slender, both authors regarded it as the open. In fact, the posterior margins of the procoxal cavities are not reduced in the type specimens of *D. hsui* sp. nov. and the holotype of *D. pubipennis*.

Demarchus is easily recognised by the following combination of characters: pubescent elytra, glabrous pronotum, closed procoxal cavities, and unique shape of elytral epipleura, typical form of the Pyrrhalta-like Morpho-Group which, was defined by Furth and Suzuki (1998) based on the metafemoral spring.

Biology. Immature stages and biology for *Demarchus pubipennis*, reported by Mushtaque and Baloch (1979), occur on Loranthaceae and larvae are leaf miners. Assertions by Odak et al. (1969) are not supported because the host plant, *Cajanus cajan* L., belongs to the Fabaceae. Larvae and adults of *D. pubipennis* did not feed on this plant when tested by Mushtaque and Baloch (1979). Moreover, Odak et al. (1969) indicated that the larvae were root feeders, which is incorrect since they possess morphological characters that are typical of leaf miners, and this lifestyle has been confirmed through field and laboratory observations. The current study confirms that adults of *D. hsui* sp. nov. feed on leaves of another species of Loranthaceae, *Taxillus rhododendricolus*, and their larvae are also leaf miners.

Distribution. Sri Lanka, India, Pakistan, China (Xizang), Indonesia (Java), Taiwan.

Key to adults of *Demarchus* species of the world

- 1 Elytra yellowish brown or dark brown, with basal areas darker (Fig. 11A, B); discs of elytra with extremely dense punctures and pubescence (Fig. 11A, B, D, E) **2**
- Elytra entirely reddish brown (Figs 1A, 11C); discs of elytra with dense punctures and pubescence (Figs 1A, C; 11C, E)..... **3**
- 2 Elytra widely rounded (Fig. 11A), dark areas on basal margin extending into middle of lateral margins (Fig. 11D); punctures on pronotum medially absent (Fig. 11G)..... ***D. pubipennis* Jacoby**
- Elytra parallel-sided (Fig. 11B), dark areas on basal margin not extending into lateral margins (Fig. 11E); punctures on pronotum entirely dense (Fig. 11H) ***D. javanus* Bryant**
- 3 Antennae yellowish brown, tibiae entirely yellow-brown (Fig. 11C, F); pronotum with antebasal transverse groove (Fig. 11 I); elytra without transverse impression (Fig. 11C) ***D. nigriceps* Chen & Wang**
- Antennae dark brown or blackish brown, outer margins of tibiae yellow (Fig. 1A–C); pronotum without antebasal transverse groove (Fig. 1A); elytra with transverse impression (Fig. 1A) ***D. hsui* sp. nov.**

Acknowledgements

We thank Mei-Hua Tsou (曹美華) for field photography, and Chih-Kai Yang (楊智凱) for identification of host plants. In addition, we thank Yongying Ruan (阮用穎) for identification and taking photos of the holotype of *D. nigriceps*, and Michael Geiser for loan of the holotype and non-type specimens of *D. pubipennis*. I especially thank Chris Carlton for reading the draft and editing for English.

Additional information

Conflict of interest

No conflict of interest was declared.

Ethical statement

No ethical statement was reported.

Funding

No funding was reported.

Author contributions

Investigation: JCC. Writing - original draft: CFL. Writing manuscript, conducting experiment.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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The morphology and spectral characteristics of the compound eye of *Agasicles hygrophila* (Selman & Vogt, 1971) (Coleoptera, Chrysomelidae, Galerucinae, Alticini)

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Academic editor: Caroline Chaboo

Received: 9 January 2023

Accepted: 6 April 2023

Published: 30 August 2023

ZooBank: <https://zoobank.org/8B1DAC1E-B03D-465E-AE7A-2EBC5F47A9C8>

Citation: Fan W-L, Liu X-K, Zhang T-H, Liang Z-L, Jiang L, Zong L, Li C-Q, Du Z, Liu H-Y, Yang Y-X, Wu F-M, Ge S-Q (2023) The morphology and spectral characteristics of the compound eye of *Agasicles hygrophila* (Selman & Vogt, 1971) (Coleoptera, Chrysomelidae, Galerucinae, Alticini). In: Chaboo CS, Schmitt M (Eds) Research on Chrysomelidae 9. ZooKeys 1177: 23–40. <https://doi.org/10.3897/zookeys.1177.100084>

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Abstract

The first exploratory study was conducted on the compound eye morphology and spectral characteristics of *Agasicles hygrophila* (Selman & Vogt, 1971) to clarify its eye structure and its spectral sensitivity. Scanning electron microscopy, paraffin sectioning, and transmission electron microscopy revealed that *A. hygrophila* has apposition compound eyes with both eucones and open rhabdom. The micro-computed tomography (CT) results after 3D reconstruction demonstrated the precise position of the compound eyes in the insect's head and suggested that the visual range was mainly concentrated in the front and on both sides of the head. The electroretinogram (ERG) experiment showed that red, yellow, green, blue, and ultraviolet light could stimulate the compound eyes of *A. hygrophila* to produce electrical signals. The behavioural experiment results showed that both males and females had the strongest phototaxis to yellow light and positive phototaxis to red, green, and blue light but negative phototaxis to UV light. This study of the compound eyes of *A. hygrophila* will be helpful for decoding its visual mechanism in future studies.

Key words: Electroretinogram, insect vision, phototaxis, rhabdomere, 3D reconstruction

Introduction

Compound eyes are the most prominent visual organ of most insects (Buschbeck and Friedrich 2008) and play a significant role in feeding, nesting, rhythm regulation, navigation, and other behaviours (Duelli and Wehner 1973; Helfrich-Förster et al. 2001; Cronin et al. 2003; Jia and Liang 2015; Ogueta et al. 2018). Compound eyes consist of ommatidia, whose number varies with insect species (Fischer et al. 2014). Ommatidia comprise five basic structures: the cornea, crystalline cone, rhabdom, basement membrane, and a number of pigment cells between the ommatidia. Generally, a positive correlation is reported between the ommatidial number, the radius curvature, and better vision. In addi-

* These authors contributed equally to this work.

tion, the arrangement and size of the ommatidia can also affect the visual field and resolution of the compound eye (Schwarz et al. 2011). The compound eyes consist of the apposition eye and the superposition eye, most diurnal insects, such as bees (Hymenoptera) and dragonflies (Odonata: Anisoptera), have apposition eyes that possess a high visual resolution and low photosensitivity (Land 1997), nocturnal insects, such as most moths (Lepidoptera), often have superposition eyes that are sensitive to light but have a low visual resolution (Fischer et al. 2014). The structure of compound eyes has an intricate relationship with insect behaviour and is also considered the best model for studying biological visual physiology and behavioural responses (Evangelin et al. 2015).

Compound eyes have a high regulating ability and can adapt to optical conditions ranging from 0 to 150000 lux (Meyer-Rochow and Nilsson 1999). Previous studies have shown that most insects can detect three primary light wavelengths and are mostly sensitive to blue (400–500 nm), long-wavelengths (480–600 nm), and UV light (300–400 nm). *Papilio xuthus* (Linnaeus, 1767) (Lepidoptera, Papilionidae) has six categories of photoreceptors (Briscoe and Chittka 2001; Koshitaka et al. 2008; Sharkey et al. 2017; van der Kooi et al. 2021; Xu et al. 2021), which can interact with different spectra to identify colours (Warrant and Nilsson 2006; Buschbeck and Friedrich 2008), inducing phototactic insect behaviour. For example, blue colour can induce the feeding behaviour of *Hycleus apicornis* (Guérin, 1847) (Coleoptera, Meloidae), yellow colour can induce the phototaxis of *Meligethes aeneus* (Fabricius, 1775) (Coleoptera, Nitidulidae), and red colour can cause *Megalagrion xanthomelas* (Selys-Longchamps, 1876) (Odonata, Coenagrionidae) to be aggressive (Lebesa et al. 2011; Doering et al. 2012; Schröder et al. 2018).

Agasicles hygrophila (Selman & Vogt, 1971) (Coleoptera: Chrysomelidae, Galerucinae) is a leaf beetle that feeds exclusively on *Alternanthera philoxeroides* ((Mart.) Griseb, 1879); Caryophyllales, Amaranthaceae). We selected this beetle as our research model because this is diurnal insect and exhibits monophagous habit. *Alternanthera philoxeroides* is an invasive species in China (Li 2016), and *Agasicles hygrophila* was introduced to control this weed. It has since become economically significant and maintains an ecological balance in China.

Herbivorous insects locate host plants mainly by their vision and olfactory sensory organs. Li (2017) observed olfactory receptors using electron microscopy, but vision has not been widely studied. The aim of this study is to use vision and olfactory senses to find a more effective way to control *Agasicles hygrophila* (Fig. 1). We studied the visual system of this species in multiple dimensions by scanning electron microscopy, transmission electron microscopy, micro-computed tomography (CT), 3D reconstruction, and electroretinogram.

Materials and methods

Specimen collection

Live specimens of *A. hygrophila* were gifted from the Institute of Plant Protection, Chinese Academy of Agricultural Sciences and Shanxi Agricultural University. In the laboratory, adult male and female *A. hygrophila* were raised in an incubator with a controlled temperature of 25 ± 0.2 °C, relative humidity of $70 \pm 5\%$, and photoperiod of 12:12 h. Leafy branches of the host plant,



Figure 1. Adult male of *Agasicles hygrophila*.

Alternanthera philoxeroides, gifted from the Institute of Plant Protection, Chinese Academy of Agricultural Sciences, were provided. The females of *A. hygrophila* could lay eggs on the leaves, then these leaves with eggs were moved to a cleaned Petri dish underlaid with wet filter paper. Both larvae and adults of *A. hygrophila* were fed with *A. philoxeroides* leaves. Old leaves were replaced with fresh leaves, and the Petri dishes were cleaned daily to provide a more comfortable environment. Adult males and females were collected immediately after eclosion and moved to clean Petri dishes underlaid with wet filter paper, and the experiment was conducted three days later.

Morphological terminology

The naming of compound eye structures and the method of continuous section follow Wen et al. (2022).

Scanning electron microscopy (SEM)

To observe the compound eye external structure, nine male and female adult heads and prothoraxes were separated from the body and kept in water with 2.5% Tween 20 in a cryogenic vial, which was placed in a 40 kHz ultrasonic bath (KQ-50DE) for three cycles of 100 s of cleaning. After each cleaning, the sample was rinsed with distilled water for 20 s. After three cycles, a cleaned sample was obtained and then dehydrated with graded ethanol (once in 75%, 80%, 85%,

90%, and 95%, and 100% (3 × 30 min)). Then, the head and prethorax samples were dried using a critical-point dryer (Leica EM CPD 300), and later, with an electrically conductive adhesive were mounted on a rotatable specimen holder in a certain order and set with the desired spatial angle.

After sputter-coating with gold for 120 s (Leica EM SCD 050) from two different directions, the samples were examined with a scanning electron microscope (Leica FEI Quanta 450), and micrographs were captured at an accelerating speed of 5–15 kV.

Light microscopy (LM)

The adult head was dehydrated in a series of ethanol (70%, 80%, 95%, and 100%) for 30 min at each concentration. After vitrification by xylene (2 × 20 min), the samples were embedded in paraffin twice for 30 min each. The series tissue sections (2 µm) were cut by microtome, dried in an oven, and then deparaffinised by xylene (2 × 10 min) each. Next, the stepwise staining of the sections was carried out as follows: 100% ethanol for 5 min, 95% ethanol for 5 min, 80% ethanol for 5 min, water for 5 min, haematoxylin staining solution for 5 min, water for 5 min, 1% ethanol hydrochloride for 3–5 s, water for 30 s, 1% ammonia for 10 s, water for 3 min, water for 1 min, 0.5% eosin staining solution (G1100-100, Beijing Solarbio Science & Technology Co., Ltd) for 1 min, water for 5 min, 95% ethanol (2 × 10 s), 100% ethanol (2 × 5 min), and xylene (2 × 5 min). After staining, the excess xylene was wiped off, environmentally friendly neutral gum was dropped on the tissue section, which was covered with a coverslip, and the order was marked. The images were observed and captured by an upright light microscope (Nikon Eclipse Ni-E) at a magnification of 20×.

Transmission electron microscopy (TEM)

The adult head was fixed in fixation solution (2.5% (vol/vol) glutaraldehyde and 4% paraformaldehyde with phosphate buffer (PB)). Then, the tissues were fixed with 2.5% (vol/vol) glutaraldehyde and 1% tannic acid with phosphate buffer (0.1 M, pH 7.4), washed twice in PB and twice in double-distilled water (ddH₂O). Then, the tissues were immersed in 1% (wt/vol) OsO₄ and 1.5% (wt/vol) potassium ferricyanide aqueous solution at 4 °C for 2 h. After washing, tissues were dehydrated by washing with graded ethanol (30%, 50%, 70%, 80%, 90%, 100%, 100%, 10 min each) and pure acetone (2 × 10 min). Samples were infiltrated in graded mixtures (8:1, 5:1, 3:1, 1:1, 1:3, 1:5) of acetone and Spurr's resin (10 g ERL 4221, 8 g DER 736, 25 g NSA, and 0.7% DMAE), and then pure resin. Finally, tissues were embedded in pure resin and polymerised for 12 h at 45 °C and 48 h at 70 °C. The ultrathin sections (70 nm thick) were sectioned with a microtome (Leica EM UC6), double-stained with uranyl acetate and lead citrate, and examined with a transmission electron microscope (FEI Tencai Spirit 120 kV). Micrographs were captured at an accelerating speed of 100 kV.

Micro-computed tomography and 3D reconstruction

Decapitated samples were dehydrated in a series of graded ethanol 75%, 80%, 85%, 90%, 95%, and 3 × 100% (30 min in each concentration). After dehydration,

the samples were dried in a freeze-dryer (Marin Christ) for 12 h, mounted on an Eppendorf tube and scanned using an X-radia scanner (Leica Micro XCT-400) at a magnification of 4×. A series image data set was captured at an interval of 9.0 s. 2D image stacks obtained through micro-CT scanning were reconstructed, and different compound eye structures were segmented by Amira software version 6.0.1. The segmented materials were imported into VG Studio Max 3.1 for rendering, polishing, colouring, and visualisation.

Electroretinogram (ERG)

Three days after emergence, 12 male and female adults of *A. hygrophila* were selected for the ERG test. Appendages of samples were cut after 5 min of cryo-anaesthesia. A pair of glass electrodes fabricated using a micropipette puller were primed with conductive fluid (128.34 mM NaCl, 4.69 mM KCl, and 1.89 mM CaCl₂·2H₂O in water). A reference electrode was inserted into the abdomen intersegmental membrane, while the recording electrode was in contact with the compound eye surface. When the potential signal stabilised, five different light sources (red, yellow, green, blue, ultraviolet) were used for compound eye stimulation with three cycles of 10:10 s light:dark. After enlarging, the potential signal was recorded by a computer through WinWCP: Strathclyde Electrophysiology Software v. 5.1.1.1.

Phototaxis test

For each light source set, three repeat tests were performed, with 20 samples for each test. The test chamber was improved from Kim et al.'s (2018) design (Fig. 9A), We designed a behaviour chamber with the different wavelength of light source on one side and *A. hygrophila* under free walking conditions in the middle of the box. Before light stimulation, samples were dark-adapted in the starting area for 20 min. Then, the light was turned on, and the visor was extracted for 5 min. Then, the number of individuals in the light area and dark area was counted. Ninety-five percent ethanol was used to clean the inner side of the chamber between each test. Red (620–625 nm), yellow (588–590 nm), green (515–525 nm), blue (460–465 nm), and ultraviolet (365–400 nm) light were used.

Data analyses

ERG data were examined by Clampex software v. 10.6. The phototactic response was calculated by the following formula:

$$\begin{aligned}\text{Positive phototaxis} &= (\text{number of individuals in the} \\ &\quad \text{light area/total individuals}) \times 100\% \\ \text{Negative phototaxis} &= (\text{number of individuals in the} \\ &\quad \text{dark area/total individuals}) \times 100\% \\ \text{Nonphototaxis} &= (\text{number of individuals in the starting} \\ &\quad \text{area/total individuals}) \times 100\%\end{aligned}$$

Analyses of the phototaxis data were performed with Origin 2021 and IBM SPSS Statistics 26 software. ANOVA and Tukey honestly significant difference (HSD) multiple comparisons were used to determine the significant differences

between multiple groups. The significant difference between two treatments was determined using the independent-sample T test (Student's t-test). Figures were produced with GraphPad Prism 8 software.

Vouchers

The images of the SEM and microscope slides of serial sections are stored in the Institute of Zoology, Chinese Academy of Sciences.

Results

External morphology

Both male and female adults of *A. hygrophila* showed similar external morphological compound eye structures. The eyes are ellipsoid, located on both sides of the head, have a smooth surface, and exhibit no structural disparity (Figs 1, 2A, B). The number of ommatidia (341.00 ± 3.35 and 345.22 ± 4.48) was not significantly different between male and female compound eyes. The compound eyes lacked interommatidial hair between facets (Fig. 2C, D). Several facet shapes were observed: ommatidia in the central area of the compound eyes showed regular hexagonal facets, while ommatidia in the periphery of the compound eyes showed irregular shapes, mainly quadrilateral and pentagon (Fig. 2E, F).

Internal morphology

We observed the internal morphological structure of adults of *A. hygrophila* compound eyes through a light microscope (Fig. 3) and transmission electron microscope. The ommatidium structures from the distal end to the proximal end are the corneal lens, crystalline cone, retinular cells with rhabdom, and basement membrane. The crystalline cone is surrounded by primary pigment cells, while secondary pigment cells spread around the entire ommatidium. We observed the corneal lens are directly in contact with the crystalline cone, with no clear zone. Therefore, we confirmed that *A. hygrophila* possesses apposition compound eyes (Fig. 4A, B).

The corneal lens is the outermost structure of the ommatidium, with both outer and inner sides raised. It has a laminated structure composed of dense layers at the distal end and looser layers at the proximal end, ~ 60 layers with a total thickness of 25 μm (Fig. 4C). The cornea has a spiral shape in the cross-section, and the proximal end is surrounded by cone cells (Fig. 5A, B). Four wedge-shaped cone cells located just beneath the cornea are involved in forming the eucones. Each cone cell has a large, edge-located nucleus, which constitutes a quarter of the cone (Fig. 5C). The corneal lens and crystalline cone together form the dioptric apparatus.

Cell membranes near the longitudinal axis of the ommatidium are specialised to form rhabdomeres. Each ommatidium contains eight retinular cells, which means that each rhabdom is composed of eight rhabdomeres. Among them, six of all eight rhabdomeres form a wheel-shaped peripheral rhabdom, while the remaining two form a circular-shaped centred rhabdom. Thus, we confirm that

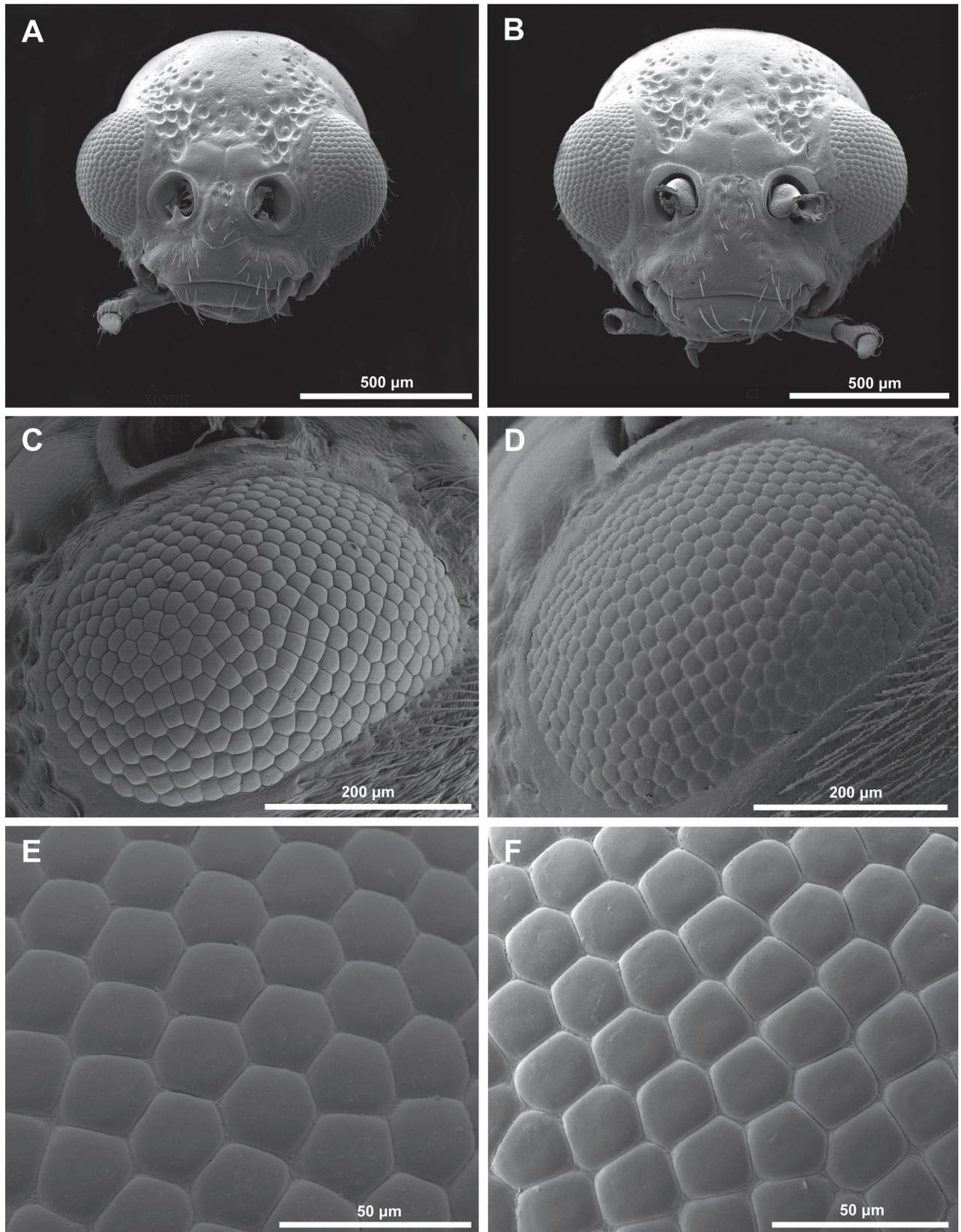


Figure 2. Scanning electron microscopy (SEM) of *Agasicles hygrophila* **A** head of male **B** head of female **C** compound eye of male **D** compound eye of female **E** hexagonal facet **F** pentagonal facet. Scale bars: 50 μm (**E**, **F**); 200 μm (**C**, **D**); 500 μm (**A**, **B**).

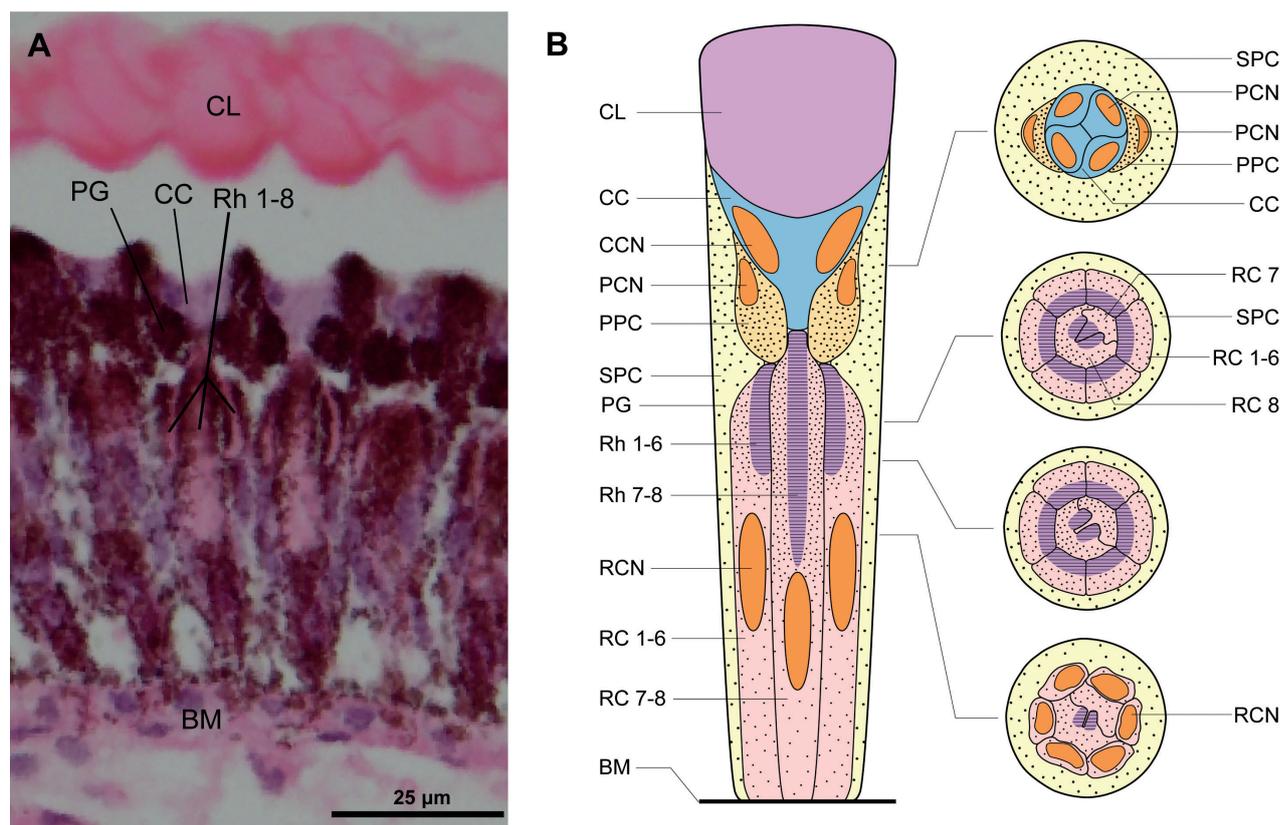


Figure 3. Diagram of one ommatidium of *Agasicles hygrophila* **A** light micrographs (LM) of the compound eye of *Agasicles hygrophila* **B** semi-schematic drawing of one ommatidium of *Agasicles hygrophila*. Abbreviations: CL: Corneal Lens; CC: Crystalline Cone; PG: Pigment Granule; Rh: Rhabdomere; BM: Basement Membrane; CCN: Cone Cell Nucleus; PPC: Primary Pigment Cell; PCN: Primary Pigment Cell Nucleus; SPC: Secondary Pigment Cell; RC: Retinular Cell; RCN: Retinular Cell Nucleus.

A. hygrophila has an open rhabdom (Fig. 5D). We observed that two members of the centred rhabdom are not uniform in size but possess a strong rhabdom (Rh8) and a weak rhabdom (Rh7). The distal end containing Rh8 has a complete section, while the proximal end is divided into two parts by Rh7 (Fig. 5D, E). Rh7 is shorter than Rh8, and the distally centred rhabdom contains only Rh8 (Fig. 5F). However, the lengths of retinular cells 7 and 8 are the same.

Three-dimensional reconstruction of the compound eye of *A. hygrophila*

In the reconstructed 3D image, the integral structure of the compound eyes and their location in the head are observed. Three distinguishable structures are shown (Fig. 6). The corneal lens in the outermost layer covered the crystalline cone, and the photoreceptive layer is beneath the cone layer. The retinular cells and pigment cells appeared to merge, the rhabdom tapers spanned from the distal to the proximal ends and finally connects with the brain (Fig. 6).

The distances from the compound eye to the front, top, bottom, and rear of the head were measured with the software Amira 6.0.1, with a distance ratio of 1:1.23:1.43:1.90. As a result, we determined that the compound eyes and vision range of *A. hygrophila* are located primarily on the front and sides of the head (Fig. 6C–J).

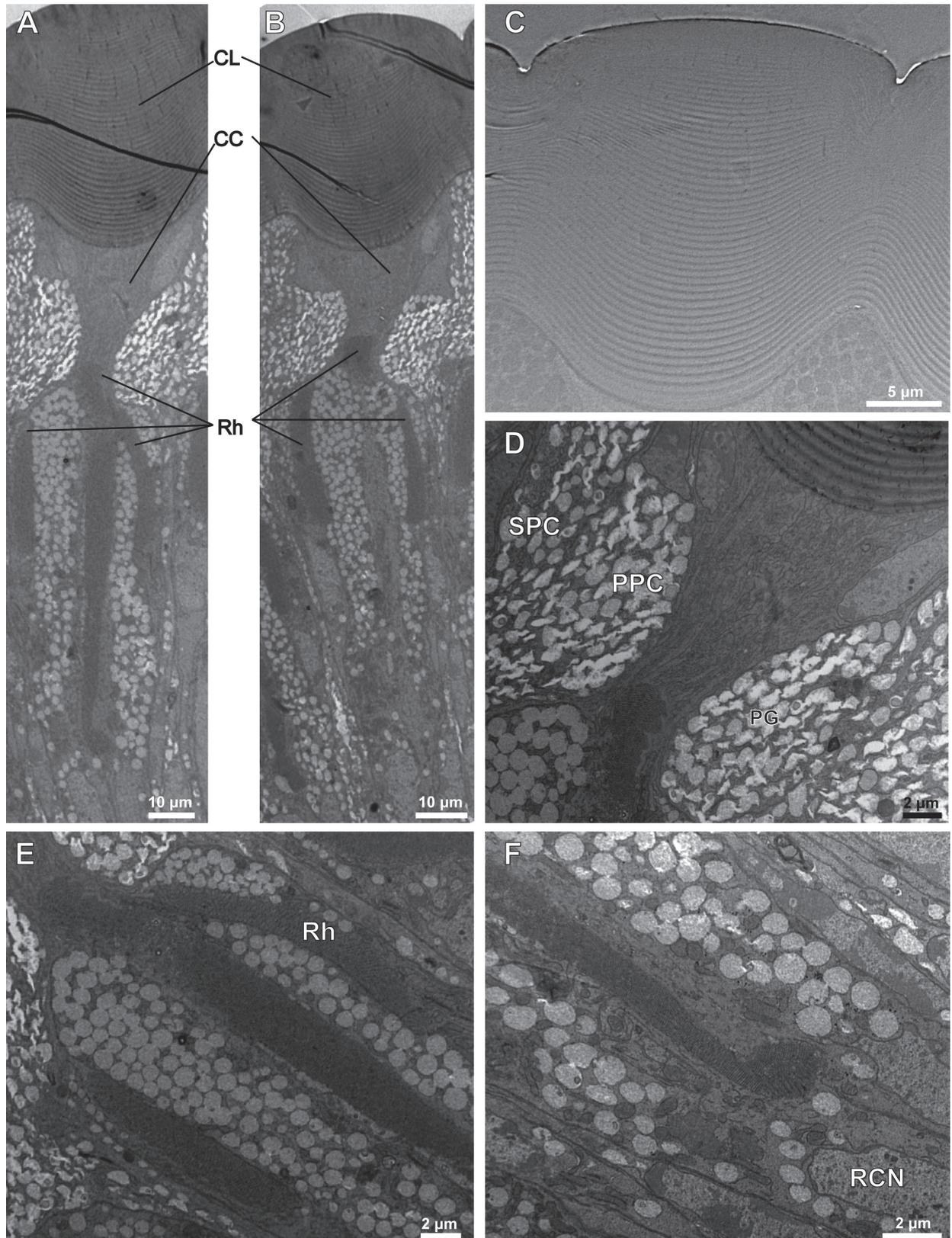


Figure 4. Transmission electron microscopy (TEM) of *Agasicles hygrophila* **A, B** longitudinal section at different levels of the compound eye of *Agasicles hygrophila* **C** corneal lens of one ommatidium of *Agasicles hygrophila* **D** crystalline cone of one ommatidium of *Agasicles hygrophila* **E, F** part of rhabdom of the compound eye of *Agasicles hygrophila*. Abbreviations: CL: Corneal Lens; CC: Crystalline Cone; Rh: Rhabdomere; BM: Basement Membrane; PPC: Primary Pigment Cell; SPC: Secondary Pigment Cell; RCN: Reticular Cell Nucleus.

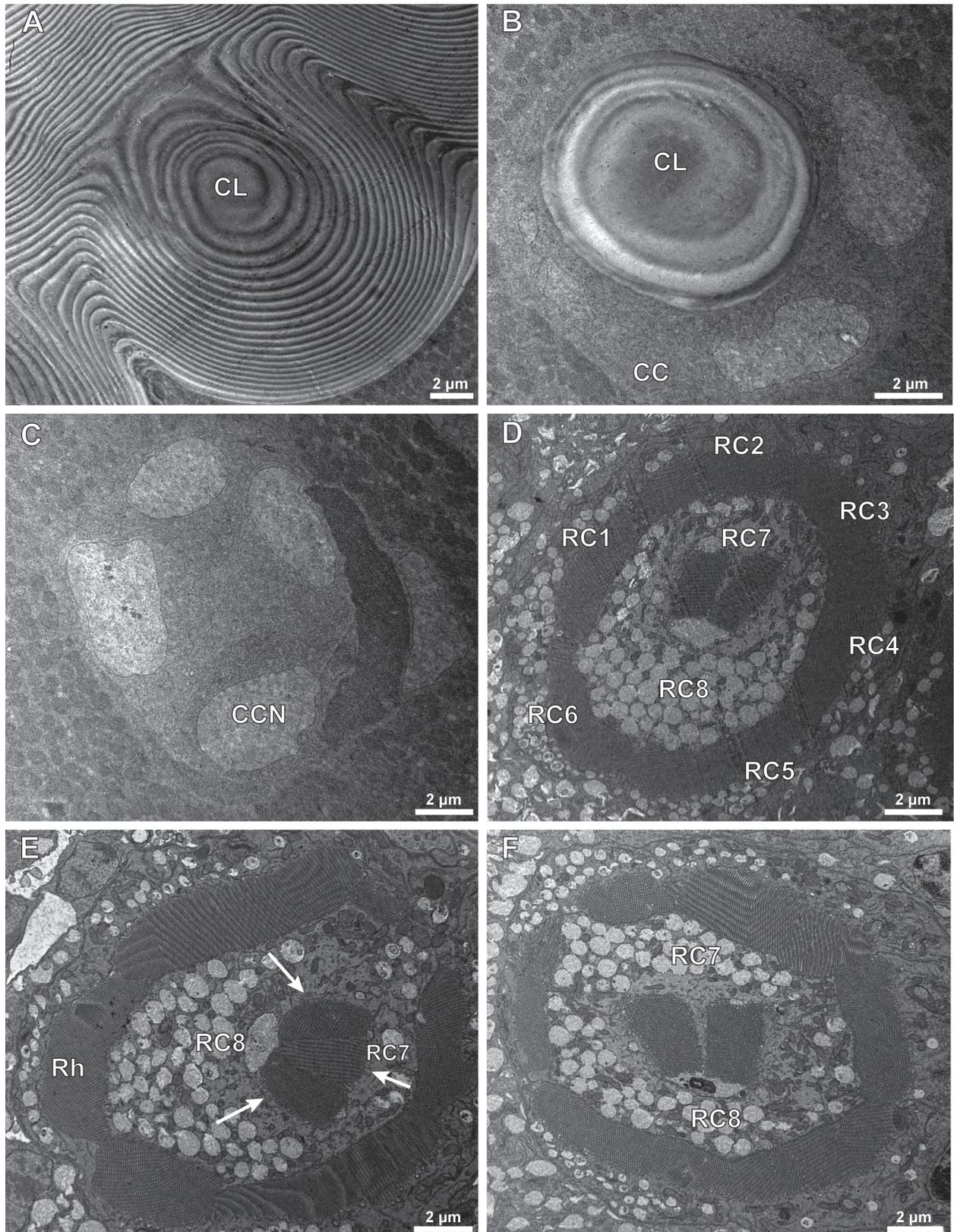


Figure 5. Transmission electron microscopy (TEM) of *Agasicles hygrophila* **A** corneal lens of one ommatidium of *Agasicles hygrophila* **B** corneal lens and crystalline cone of *Agasicles hygrophila* **C** crystalline cone of *Agasicles hygrophila* **D–F** transmission electron microscopy at different levels of the compound eye of *Agasicles hygrophila*. Abbreviations: CL: Corneal Lens; CC: Crystalline Cone; CCN: Cone Cell Nucleus; RC: Reticular Cell; Rh: Rhabdomere.

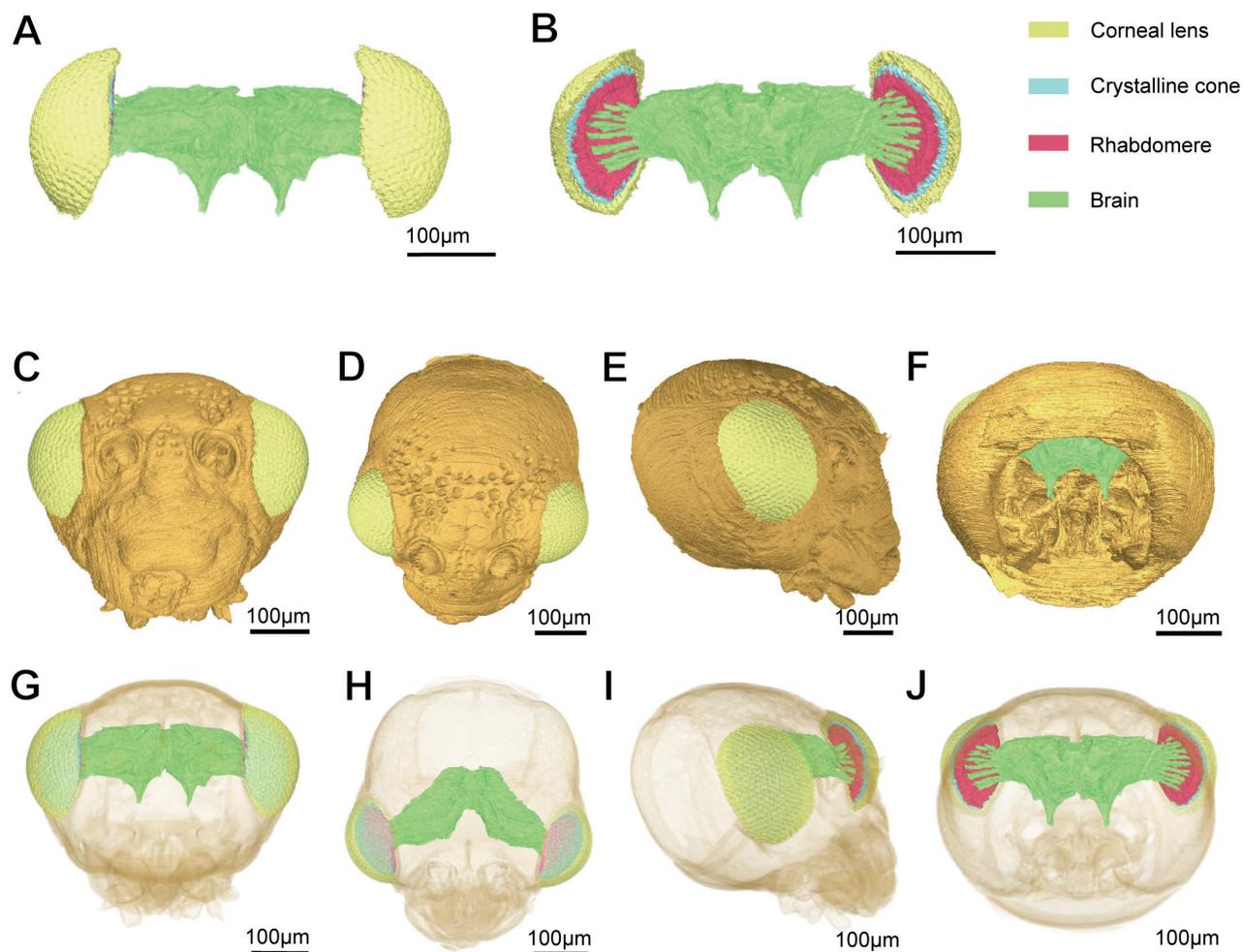


Figure 6. 3D reconstruction of the head of *Agasicles hygrophila* **A** front view of compound eye **B** rear view of compound eye **C** front view of head **D** top view of head **E** side view of head **F** rear view of head **G** perspective drawing of front view of head **H** perspective drawing of top view of head **I** perspective drawing of side view of head **J** perspective drawing of rear view of head.

Electroretinogram and phototaxis

In the ERG experiments, the compound eyes of *A. hygrophila* emit signals after stimulation by five light colours (red, yellow, green, blue, and UV) (Fig. 7), but there are differences in the potentiometric responses between different light colours (Fig. 8). In this study, the signal intensity of the male *A. hygrophila* compound eyes generated by UV light stimulation is significantly higher than that generated by the other light colours, followed by that generated by yellow light. The responses of the male *A. hygrophila* compound eyes to blue light and green light are lower and not significantly different (Fig. 8A). In contrast, the signal intensity of female *A. hygrophila* compound eyes generated by yellow light is significantly higher than that generated by certain other light colours (red, green, blue, and UV), while that generated by the other light colours showed no significant difference. However, female *A. hygrophila* compound eyes are the least sensitive to blue light (Fig. 8B).

This study showed differences in the responses of the compound eyes of male and female *A. hygrophila* to five light colours (red, yellow, green, blue, and

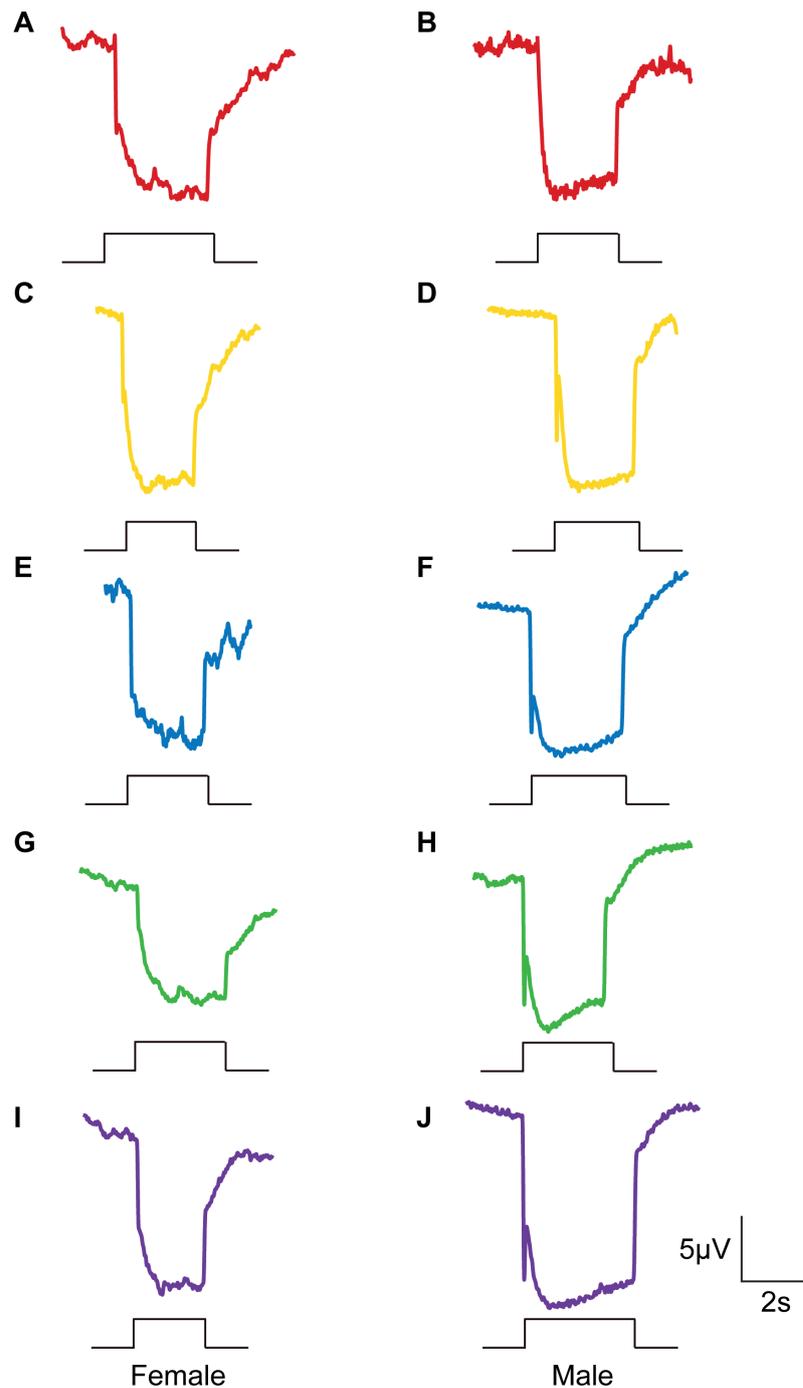


Figure 7. Electrophysiological waveforms of *Agasicles hygrophila* compound eyes at different wavelengths of light for females and males **A, B** red (620–630 nm) **C, D** yellow (588–590 nm) **E, F** blue (460–470 nm) **G, H** green (520–530 nm) **I, J** ultraviolet (365 nm).

UV) via ERG experiments. However, we did not define here any differences in the phototaxis of males and females to the five lights. The male and female *A. hygrophila* showed significant phototaxis when exposed to red, yellow, green, and blue light, and the highest phototaxis was observed in yellow light, while avoidance was observed when UV light was used as the light source. Interestingly, the red colour also caused higher phototaxis in male and female *A. hygrophila* (Fig. 9).

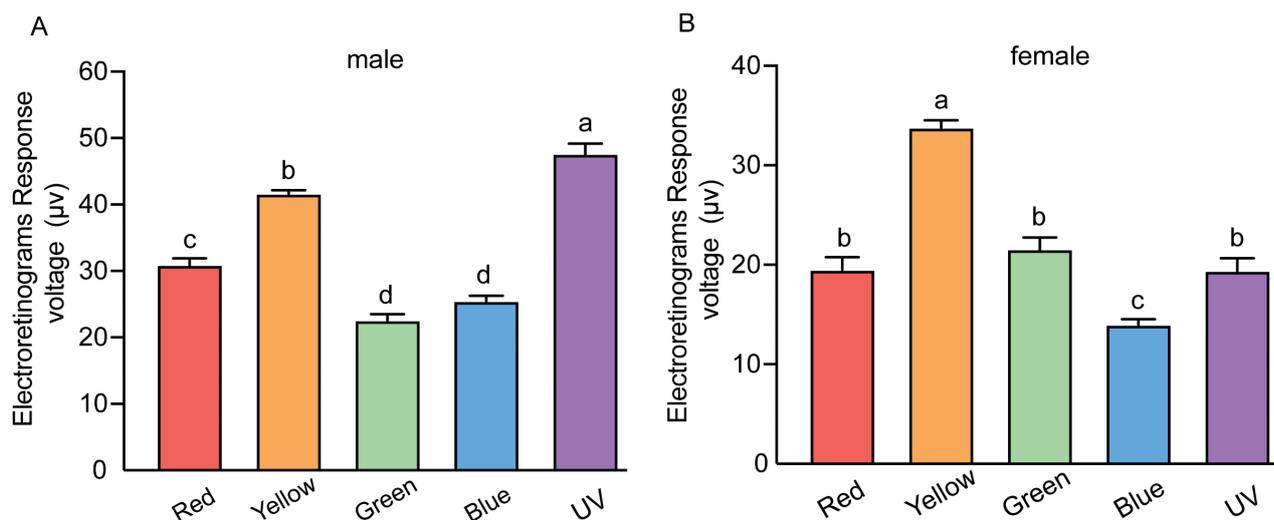


Figure 8. Quantification of Electroretinogram (ERG) voltage responses of *Agasicles hygrophila* that were exposed to a different light stimulus **A** responses of male **B** responses of female. Difference analysis was performed at the $P < 0.05$ level, and different letters indicate significant differences between ERG responses.

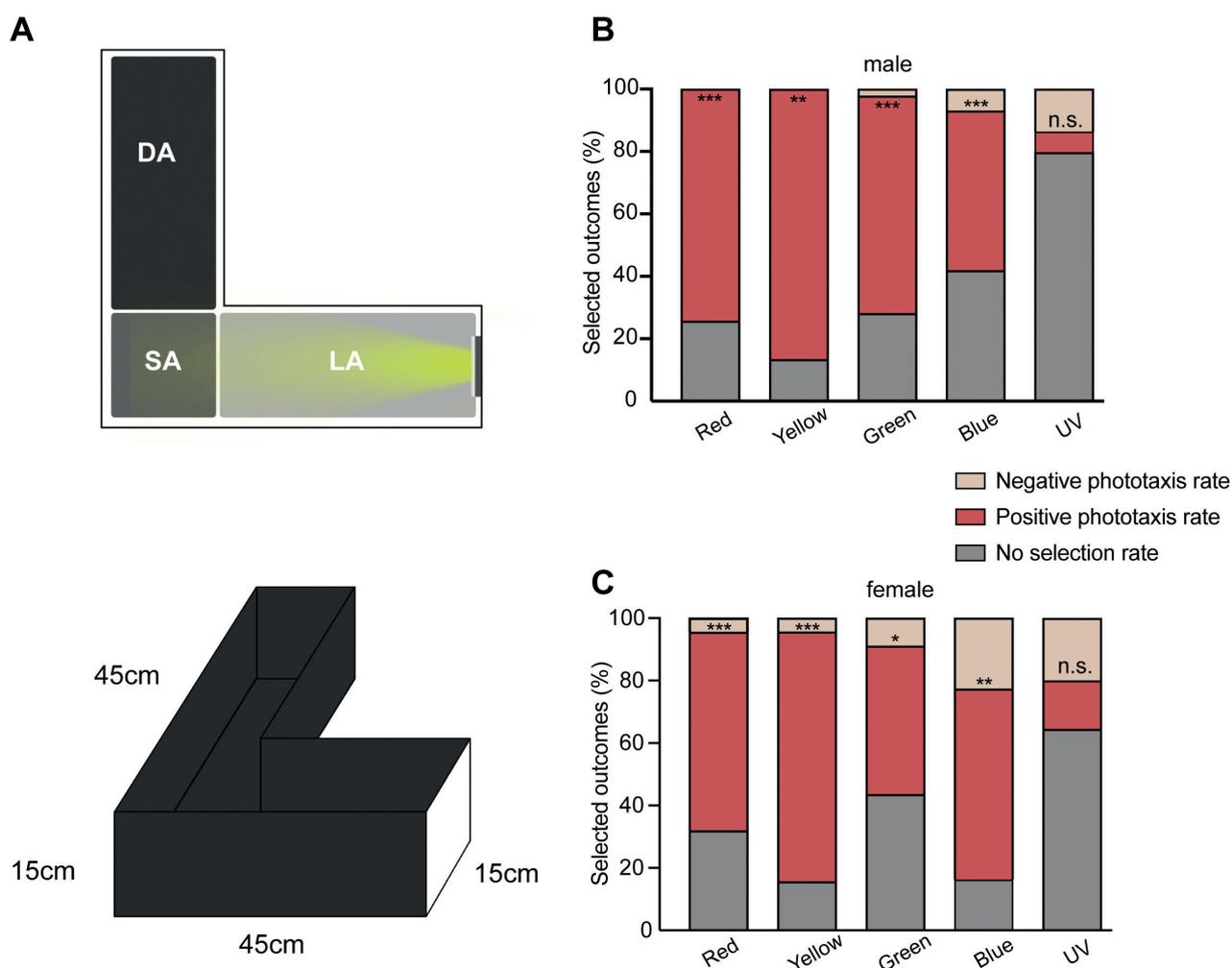


Figure 9. Results of behavioural experiments **A**, **B** behavioural experimental equipment **C** the phototaxis of male **D** the phototaxis of female. Data is presented as mean \pm standard error of the mean (SEM). Abbreviations: DA: Dark Area, LA: Light Area, SA: Standing Area.

Discussion

In this study, SEM and TEM experiments revealed that the compound eyes of *A. hygrophila* contains few ommatidia whose shape is irregular. There are without clear zone of compound eyes, this structure is a typical feature of apposition eyes. Through the ERG experiment, we found that there are a variety of photoreceptors in this species. The behaviour experiment showed that *A. hygrophila* has positive phototaxis to red, yellow, green, and blue light and has negative phototaxis to UV light.

The arrangement of microvilli affects the light perception of compound eyes. When the microvilli in the cross-section of the rhabdomere are arranged perpendicular to each other, there is a good possibility that the ommatidium could perceive polarised light. The rhabdomere abnormality leads to a decrease in light sensitivity (Labhart 1999). Our results from *A. hygrophila* compound eyes show that it has typical apposition compound eyes without clear zone and the microvillus of the rhabdomere are arranged irregularly. Therefore, we speculate that compound eyes of this species may be less sensitive to light.

There are significant differences in the surface structure and density of the ommatidium of different insects. Adult *A. hygrophila* feed and mate both during the day and night, and have a slightly convex ommatidium surface, which may increase the light contact area of the individual ommatidium and improve compound eye sensitivity. Numerous species of Coleoptera have six peripheral rhabdomeres and two central rhabdomeres, an arrangement pattern referred to as open rhabdom (Wachmann, 1979). The central rhabdomere and the peripheral rhabdomere are obviously separated from each other in *A. hygrophila*, resulting in an open rhabdom. The two central rhabdomeres in this ommatidium are arranged in a semi-enveloped structure, and the microvilli of the two rhabdomeres are not aligned in the same direction. Understanding the specific role of this structure in compound eye vision requires further investigation.

Most insects have at least two visual pigments, one detecting yellow–green light at ~ 550 nm wavelengths and the other detecting blue–violet light at wavelengths less than 480 nm (Briscoe and Chittka 2001). Previous studies found that the compound eyes of *Anomala corpulenta* (Motschulsky, 1854) (Coleoptera, Scarabaeidae) are sensitive to near-UV, green–yellow, and blue light (Jiang et al. 2015). In our study, the ERG experiments showed that the compound eyes of *A. hygrophila* are sensitive to five light colours, red, yellow, green, blue, and UV, and they may have multiple visual pigments. Previous studies have found that beetles, such as *Thermonectus marmoratus* (Gray, 1831) (Coleoptera, Dytiscidae) and *Tribolium castaneum* (Herbst, 1797) (Coleoptera, Tenebrionidae), lack blue opsins, but there is evidence that the effects caused by the loss of blue opsins can be compensated by alternative mechanisms that restore sensitivity to blue light (Sharkey et al. 2017), such as in *Agrilus planipennis* (Fairmaire, 1888) (Coleoptera, Buprestidae), which achieves sensitivity to blue light through the replication of other opsin genes. The compound eyes of *A. hygrophila* are sensitive to blue light, but this sensitivity may comprise abilities resulting from other opsin genes. Therefore, further molecular experiments are needed to verify this hypothesis.

Phytophagous insects, such as *M. aeneus*, *Diaphorina citri* (Kuwayama, 1907) (Hemiptera, Liviidae), *Bactrocera dorsalis* (Hendel, 1912) (Diptera, Tephritidae),

and *Liriomyza huidobrensis* (Blanchard, 1926) (Diptera, Agromyzidae), use yellow colour as a cue to find host plants (Bernays and Chapman 2007; Doering et al. 2012; Sétamou et al. 2014; Said et al. 2017). *Phyllotreta striolata* (Fabricius, 1801) (Coleoptera, Chrysomelidae) has strong phototaxis to UV and blue light (Yang et al. 2003); *Leptinotarsa decemlineata* (Say, 1824) (Coleoptera, Chrysomelidae) shows a strong response to green and yellow light (Otálora-Luna and Dickens 2011). We found that both male and female *A. hygrophila* show strong phototaxis to yellow light, and yellow light may be an important cue for *A. hygrophila* to find host plants. In addition, blue light can stimulate phototaxis in some insects, such as *Frankliniella bispinosa* (Morgan, 1913) (Thysanoptera, Thripidae) (Childers and Brecht 1996). *Agasicles hygrophila* also showed significant phototaxis to blue light.

The wavelength of green colour is one of the common perceptive areas for most insects (van der Kooi et al. 2021). While insects can perceive green light, phototaxis to green light is low (Lebesa et al. 2011). Similarly, in this study, the phototaxis of *A. hygrophila* to green light is also relatively low among multiple green light colours, which may be related to the low green reflectance (43%) (Lebesa et al. 2011). Adult *A. hygrophila* prefer humidity and light avoidance (Wu et al. 2000), while sunlight contains a large amount of UV light, which may account for its low phototaxis to UV light (Fig. 9). Most beetles are insensitive to red light (van der Kooi et al. 2021); however, in this study we found that red light not only arouses the signal response of *A. hygrophila* compound eyes but also led to its phototaxis to red light. This characteristic may be related to the living environment of *A. hygrophila*: the adults mostly stay on leaves (Chen et al. 2009), and sunlight can appear as red light when shining through small gaps, while sunlight scattered in the sky at dusk also has a red spectrum (Endler 1993). Our hypothesis about the mechanisms of the perception of red light by *A. hygrophila* deserves further exploration.

Acknowledgements

We thank Zhichuang Lv and Jisu Jin, Institute of Plant Protection (IPP), Chinese Academy of Agricultural Sciences (CAAS), for providing the initial insect source. We are grateful to Xueke Tan for helping with electron microscopy sample preparation and taking TEM images at the Center for Biological Imaging (CBI), Institute of Biophysics, Chinese Academy of Science. We thank Wenjie Li, Kuiyan Zhang and Caixia Gao for taking SEM and Micro-CT images at Key Laboratory of Zoological Systematics and Evolution, Institute of Zoology (IOZ). We thank the reviewers for their positive comments. This work was supported by the National Natural Science Foundation of China (No. 32270460).

Additional information

Conflict of interest

No conflict of interest was declared.

Ethical statement

No ethical statement was reported.

Funding

This work was supported by the National Natural Science Foundation of China (No. 32270460).

Author contributions

S.G. and F.W. Y.Y. methodology; S.G. and T.Z. W.F. sample collection; W.F. and L.Z. sample identification and sorting; H.L., Z.D., Z.L., X.L., L.J. and T.Z. data analysis and processing; W.F. writing—original draft; F.W., S.G. and C.L. writing—review and editing.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Current knowledge on the diversity of Eumolpinae (Coleoptera, Chrysomelidae) in New Caledonia*

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Abstract

The Eumolpinae leaf beetles of New Caledonia are very diverse, but our knowledge about their diversity is still incomplete. Following a renewed interest in the group in the last two decades, there has been an exponential increase in the number of species described, with species descriptions and taxonomic reassessment ongoing. In this work, the catalogue of New Caledonian Eumolpinae is updated, incorporating all these recent changes, and also indicating the collection where type specimens are currently available. The updated catalogue includes 120 species in 13 genera, and more additions and taxonomic changes, including new combinations, are expected in forthcoming years. Here two new synonymies are reported, namely *Dumbea striata* Jolivet, Verma & Mille, 2007 = *Taophila cancellata* Samuelson, 2010, **syn. nov.**; and *Dematochroma theryi* Jolivet, Verma & Mille, 2010 = *Dematochroma poyensis* Jolivet, Verma & Mille, 2010, **syn. nov.** Moreover, two species still retaining their original adscription to the genus *Colaspis* Fabricius, 1801, are treated as incertae sedis. This catalogue represents a useful tool for future taxonomic studies of New Caledonian Chrysomelidae and can assist biodiversity surveys and conservation studies within the archipelago.

Key words: Catalogue, conservation, leaf beetles, Linnean shortfall, South Pacific, synonymies, taxonomy



Academic editor: Michael Schmitt

Received: 31 January 2023

Accepted: 27 February 2023

Published: 30 August 2023

ZooBank: <https://zoobank.org/C6159E84-D44B-42BC-A3A1-DAD90B4637C1>

Citation: Platania L, Gómez-Zurita J (2023) Current knowledge on the diversity of Eumolpinae (Coleoptera, Chrysomelidae) in New Caledonia. In: Chaboo CS, Schmitt M (Eds) Research on Chrysomelidae 9. ZooKeys 1177: 41–55. <https://doi.org/10.3897/zookeys.1177.101293>

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Introduction

Within the Chrysomelidae, a highly diverse insect family accounting some 40,000 species (Leschen and Beutel 2014), Eumolpinae is an important subfamily representing approximately 7,000 species and 500 genera, mainly distributed in tropical areas (Jolivet and Verma 2010; Jolivet et al. 2014). Large part of the diversity of Eumolpinae is still unknown (Jolivet and Verma 2010) and their supraspecific systematics is unsatisfactory (Gómez-Zurita et al. 2005; Jolivet et al. 2014, Reid 2017). All issues related to the so-called Linnaean shortfall are relevant for this group, as the limited taxonomic knowledge makes it difficult to advance in many other fields (Lomolino 2004). An important taxonomic gap affects the group across the tropics, including South Pacific islands, where the last relatively comprehensive works on Eumolpinae had been published ~ 50

* Extended version of a talk presented to the 10th International Symposium on the Chrysomelidae, Helsinki, Finland, 21 July 2022.

years ago and were restricted to the archipelagos of Fiji and Samoa, and partially for New Zealand (Gressitt 1956; Bryant and Gressitt 1957; Shaw 1957). This insular region is interesting for this group, because it is disharmonious for the distribution of Chrysomelidae, with several subfamilies missing or poorly represented in native faunas, whereas Eumolpinae are disproportionately diverse, particularly in New Caledonia (Jolivet and Verma 2008; Papadopoulou et al. 2013). The Eumolpinae of New Caledonia, briefly illustrated in Fig. 1, belong to two tribes, the Typophorini, represented by a single species, *Rhyparida foaensis* (Jolivet et al. 2007a), probably the result of a recent introduction (Gómez-Zurita 2011a), and the Eumolpini, highly diverse, estimated to have more than 200 species, most of them still to be described, and possibly the result of a large radiation in situ (Gómez-Zurita 2011b; Papadopoulou et al. 2013). Apart from the high species richness of Eumolpinae, the geological, geographical, and ecological features of New Caledonia make it particularly interesting to invest on a good knowledge about the diversity and ecology of this group. New Caledonia is an archipelago of relatively small size and with a long history of isolation from the mainland, and it hosts an enormous and nearly entirely endemic diversity across several groups of organisms, having been recognised as a biodiversity hotspot, central for conservation concerns and for the study of island evolution and biogeography (Myers et al. 2000; Grandcolas 2008).

The past fifteen years have seen an increased interest on the diversity of New Caledonian Eumolpinae. The previous knowledge on these beetles was made available in the early works by Xavier Montrouzier (Montrouzier 1861; Perroud and Montrouzier 1864), Albert Fauvel (Fauvel 1862), and Karl M. Heller (Heller 1916). After the passionate rediscovery of this important group of beetles in the fauna of New Caledonia by Pierre Jolivet, Krishna Verma, and Christian Mille, a real renaissance in the taxonomic research of the subfamily took place. In the first years of the new Century, these entomologists started surveying the diversity of New Caledonian Eumolpinae and described numerous species (Jolivet et al. 2005, 2007a, b, c, 2009a, b, 2010, 2013). Allan Samuelson contributed relevant revisionary studies on the genus *Taophila* Heller, 1916 (Samuelson 2010) and described a new genus, *Acronymolpus* Samuelson, 2015, and Lev Medvedev also described a single species of Eumolpinae from New Caledonia together with several other tropical Eumolpinae (Medvedev 2007). More recently, in the past 12 years, our group took on the task to contribute towards the taxonomic knowledge of New Caledonian Eumolpinae, reassessing the data from previous studies and also describing new genera and species (Gómez-Zurita 2011a, b, 2017a, b, 2018, 2020, 2022; Gómez-Zurita and Cardoso 2014; Platania et al. 2020; Gómez-Zurita et al. 2020; Platania and Gómez-Zurita 2022; Gómez-Zurita and Pàmies-Harder 2022). Finally, Mille and Jolivet (2021) published the illustrated catalogue of New Caledonian Chrysomelidae, including the available knowledge on Eumolpinae, although new species and taxonomic rearrangements affected the group while this catalogue was still in production. Here, we report an updated list of Eumolpinae, including 120 species, keeping track of taxonomic and nomenclatural changes, and proposing two new synonymies, to facilitate access to taxonomic knowledge on the New Caledonian fauna of Eumolpinae. We hope that this can become a useful tool to guide forthcoming work on this group, a fundamental task to tackle the Linnaean shortfall, and to deal with the pressing matter of conservation in New Caledonia and elsewhere.

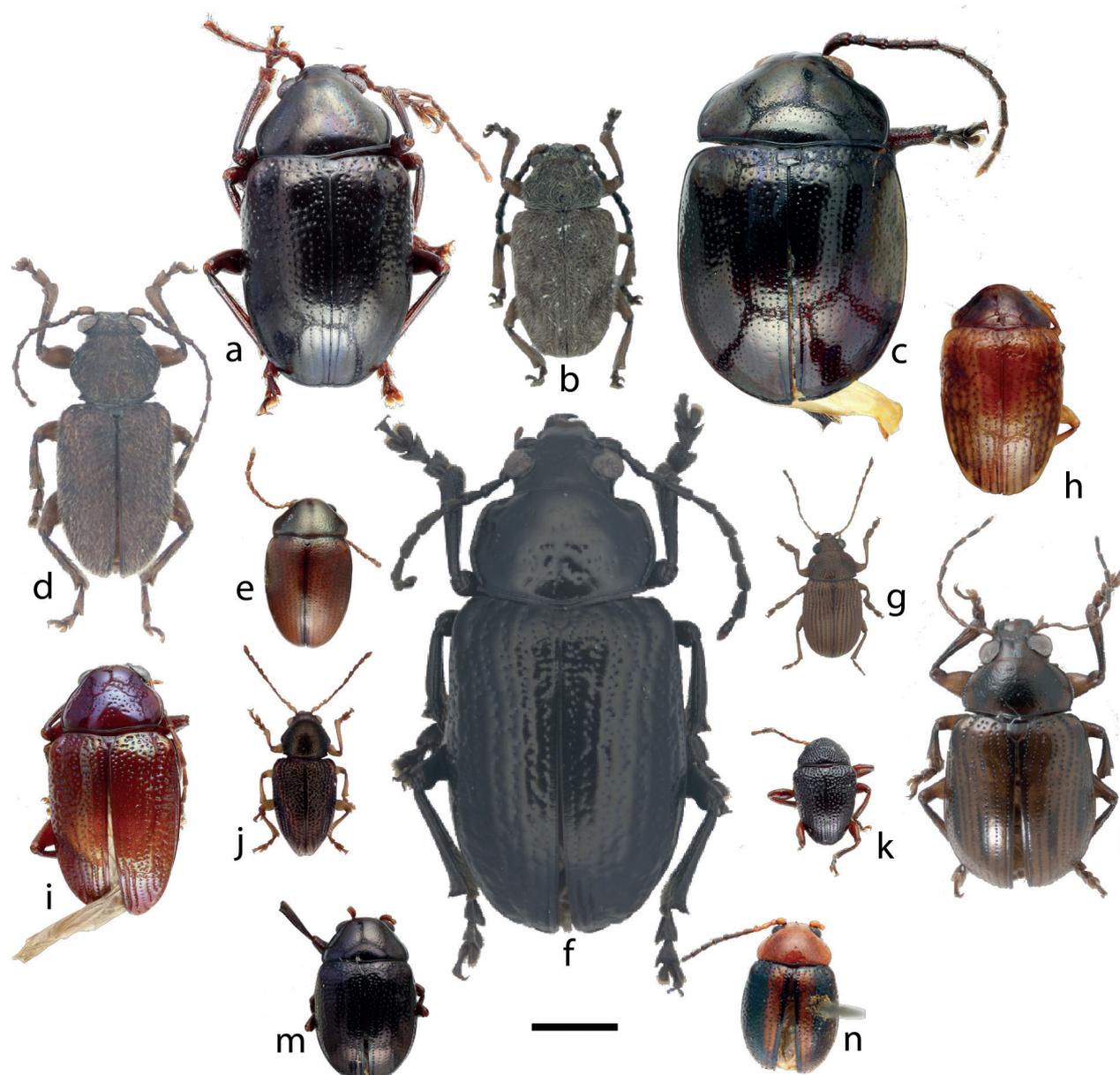


Figure 1. Dorsal views of the holotypes of Eumolpinae of New Caledonia **a** *Cazeresia montana* Jolivet, Verma & Mille, 2005 **b** *Tricholapita olympica* (Platania & Gómez-Zurita, 2020) **c** *Colaspoides fontis* Jolivet, Verma & Mille, 2008 **d** *Dematotrichus villosus* Gómez-Zurita, 2022 **e** *Montrouzierella brinoni* Jolivet, Verma & Mille, 2007 **f** *Thasycles magnus* Gómez-Zurita, 2022 **g** *Kumatoeides megale* Gómez-Zurita, 2018 **h** *Dumbea montana* Jolivet, Verma & Mille, 2011 **i** *Dematochroma theryi* Jolivet, Verma & Mille, 2010 **j** *Taophila draco* Platania & Gómez-Zurita, 2022 **k** *Acronymolpus bertiae* (Jolivet, Verma & Mille, 2007) **l** *Rhyparida foensis* (Jolivet, Verma & Mille, 2007) **m** *Samuelsonia melas* Jolivet, Verma & Mille, 2007 **n** *Colaspis solani* Perroud & Montrouzier, 1864. Scale bar: 2.00 mm.

Materials and methods

The catalogue is based on all the published information on New Caledonian Eumolpinae, including data on the confirmed availability of the typical series or types, whereby the institution holding the primary type is highlighted in bold in the list below, and paratypes or other material in regular font (an asterisk denotes lack of information about the primary type, although paratypes may be available). The type species of each genus is underlined.

Acronyms of entomological collections and museums reported in the catalogue:

AMS	Australian Museum, Sydney;
BPBM	Pauahi Bishop Museum of Polynesian Ethnology and Natural History, Honolulu;
CXMNC	Collection Xavier Montrouzier, Institut Agronomique néo-Calédonien, La Foa;
HNHM	Hungarian Natural History Museum, Budapest;
JGZC	Jesús Gómez-Zurita Collection, CSIC, Barcelona;
MNHN	Muséum National d'Histoire Naturelle, Paris;
MNHW	Museum of Natural History, Wrocław University, Wrocław;
NHM	Natural History Museum, London;
NRM	Swedish Museum of Natural History, Stockholm;
RBINS	Royal Belgian Institute of Natural Sciences, Bruxelles;
SMTD	Staatliches Museum für Tierkunde, Dresden;
ZISP	Zoological Institute of Russian Academy of Sciences.

Species catalogue

Eumolpini

1. *Acronymolpus bertiae* (Jolivet, Verma & Mille, 2007) (Fig. 1k) – Rev. fr. Entomol. 29: 81. **(MNHN)**
= *Acronymolpus meteorus* Samuelson, 2015 – ZooKeys 547: 100. **(BPBM)**
= *Acronymolpus turbo* Samuelson, 2015 – ZooKeys 547: 97. **(CXMNC/MNHN)**
2. *Acronymolpus jourdani* (Jolivet, Verma & Mille, 2013) – Nouv. Revue Ent. (N.S.) 29: 145. **(MNHN)***
= *Acronymolpus gressitti* Samuelson, 2015 – ZooKeys 547: 99. **(BPBM)**
= *Acronymolpus joliveti* Samuelson, 2015 – ZooKeys 547: 95. **(BPBM)**
3. *Cazeresia montana* Jolivet, Verma & Mille, 2005 (Fig. 1a) – Rev. fr. Entomol. 27: 70. **(MNHN)**
4. *Colaspoides caledonica* Medvedev, 2007 – Euroasian Ent. J. 6(4): 434. **(ZISP)**
5. *Colaspoides fontis* Jolivet, Verma & Mille, 2008 (Fig. 1c) – Nouv. Revue Ent. (N.S.) 24: 198. **(MNHN)**
6. *Colaspoides kanalensis* (Perroud & Montrouzier, 1864) – Annls. Soc. linn. Lyon 11: 207. **(MNHN)**
7. *Colaspoides sarrameae* Jolivet, Verma & Mille, 2008 – Nouv. Revue Ent. (N.S.) 24: 198. **(MNHN)**
8. *Dematochroma antipodum* (Fauvel, 1862) – Bull. Soc. Linn. Normandie 7: 167. **(MNHN)**
9. *Dematochroma culminicola* (Heller, 1916) – Sarasin and Roux, Nova Caled., Zool. 2: 304. **(SMTD)**
10. *Dematochroma difficilis* (Heller, 1916) – Sarasin and Roux, Nova Caled., Zool. 2: 305. **(SMTD)**
11. *Dematochroma doiana* Jolivet, Verma & Mille, 2007 – Rev. fr. Entomol. 29: 38. **(MNHN)***
12. *Dematochroma helleri* Jolivet, Verma & Mille, 2007 – Rev. fr. Entomol. 29: 42. **(MNHN)**

13. *Dematochroma humboldtiana* (Heller, 1916) – Sarasin and Roux, Nova Caled., Zool. 2: 301. **(SMTD)**
14. *Dematochroma lepros* (Heller, 1916) – Sarasin and Roux, Nova Caled., Zool. 2: 301. **(SMTD)**
15. *Dematochroma maculifrons* (Heller, 1916) – Sarasin and Roux, Nova Caled., Zool. 2: 302. **(SMTD)**
16. *Dematochroma samuelsoni* Jolivet, Verma & Mille, 2011 – Nouv. Revue Ent. (N.S.) 26: 334. **(MNHN)**
17. *Dematochroma sylviae* Jolivet, Verma & Mille, 2010 – Nouv. Revue Ent. (N.S.) 26: 10. **(MNHN)**
18. *Dematochroma terastiomerus* (Heller, 1916) – Sarasin and Roux, Nova Caled., Zool. 2: 303. **(SMTD)**
19. *Dematochroma terminaliae* Jolivet, Verma & Mille, 2010 – Nouv. Revue Ent. (N.S.) 26: 10. **(MNHN)**
20. *Dematochroma theryi* Jolivet, Verma & Mille, 2010 (Fig. 1i) – Nouv. Revue Ent. (N.S.) 26: 12. **(MNHN)**
= *Dematochroma poyensis* Jolivet, Verma & Mille, 2010, syn. nov. – Nouv. Revue Ent. (N.S.) 26: 12 **(MNHN)**
21. *Dematochroma thyiana* Jolivet, Verma & Mille, 2008 – Nouv. Revue Ent. (N.S.) 24: 196. **(MNHN)**
22. *Dematotrichus capillaris* Gómez-Zurita, 2022 – System. Biodivers. 20: 8. **(JGZC)**
23. *Dematotrichus capillosus* Gómez-Zurita, 2022 – System. Biodivers. 20: 12. **(MNHW)**
24. *Dematotrichus comans* Gómez-Zurita, 2022 – System. Biodivers. 20: 13. **(MNHW)**
25. *Dematotrichus comatulus* Gómez-Zurita, 2022 – System. Biodivers. 20: 15. **(JGZC, MNHW, MNHN)**
26. *Dematotrichus crinitus* Gómez-Zurita, 2022 – System. Biodivers. 20: 16. **(MNHW, JGZC)**
27. *Dematotrichus hirsutus* Gómez-Zurita, 2022 – System. Biodivers. 20: 17. **(JGZC, MNHW, MNHN)**
28. *Dematotrichus hirtus* Gómez-Zurita, 2022 – System. Biodivers. 20: 18. **(JGZC, MNHW, MNHN)**
29. *Dematotrichus hispidus* (Jolivet, Verma & Mille, 2013) – Nouv. Revue Ent. (N.S.) 29: 152. **(MNHN)***
30. *Dematotrichus horridus* Gómez-Zurita, 2022 – System. Biodivers. 20: 21. **(MNHW)**
31. *Dematotrichus pilosus* (Jolivet, Verma & Mille, 2007) – Rev. fr. Entomol. 29: 38. **(MNHN)**
32. *Dematotrichus pubescens* Gómez-Zurita, 2022 – System. Biodivers. 20: 23. **(JGZC, MNHW)**
33. *Dematotrichus setosus* Gómez-Zurita, 2022 – System. Biodivers. 20: 24. **(MNHW)**
34. *Dematotrichus villosus* Gómez-Zurita, 2022 (Fig. 1d) – System. Biodivers. 20: 25. **(MNHW, JGZC)**
35. *Dumbea gigas* Jolivet, Verma & Mille, 2007 – Rev. fr. Entomol. 29: 81. **(MNHN)**
36. *Dumbea montana* Jolivet, Verma & Mille, 2011 (Fig. 1h) – Nouv. Revue Ent. (N.S.) 26: 337. **(MNHN)**

37. *Dumbea paulaudi* Jolivet, Verma & Mille, 2007 — Rev. fr. Entomol. 29: 80. **(MNHN)**
38. *Dumbea striata* Jolivet, Verma & Mille, 2007 — Rev. fr. Entomol. 29: 80. **(MNHN)**
= *Taophila cancellata* Samuelson, 2010, syn. nov. — Zootaxa 2621: p. 49. **(MNHN, BPBM)**
39. *Edusella flaveola* (Montrouzier, 1861) — Anns. Soc. ent. Fr. 4: 396*.
40. *Kumatoides anomala* Gómez-Zurita, 2018 — Zootaxa 4521: 5. **(MNHN, MNHW)**
41. *Kumatoides aulacia* Gómez-Zurita, 2018 — Zootaxa 4521: 6. **(HNHM)**
42. *Kumatoides costata* (Jolivet, Verma & Mille, 2007) — Rev. fr. Entomol. 29: 88. **(MNHN)**
43. *Kumatoides leptalei* Gómez-Zurita, 2018 — Zootaxa 4521: 11. **(MNHN, MNHW)**
44. *Kumatoides megale* Gómez-Zurita, 2018 (Fig. 1g) — Zootaxa 4521: 12. **(MNHN, MNHW)**
45. *Kumatoides metallica* Gómez-Zurita, 2018 — Zootaxa 4521: 16. **(MNHN, MNHW)**
46. *Kumatoides millei* Gómez-Zurita, 2018 — Zootaxa 4521: 17. **(MNHN, MNHW)**
47. *Kumatoides tarsalis* Gómez-Zurita, 2018 — Zootaxa 4521: 19. **(MNHN, MNHW, JGZC)**
48. *Kumatoides wanati* Gómez-Zurita, 2018 — Zootaxa 4521: 22. **(MNHN, MNHW)**
49. *Montrouzierella brinoni* Jolivet, Verma & Mille, 2007 (Fig. 1e) — Rev. fr. Entomol. 29: 89. **(MNHN)**
50. *Montrouzierella flava* Jolivet, Verma & Mille, 2007 — Rev. fr. Entomol. 29: 89. **(MNHN)**
51. *Montrouzierella metrosiderosi* Jolivet, Verma & Mille, 2011 — Nouv. Revue Ent. (N.S.) 26: 338. **(MNHN)**
52. *Montrouzierella nana* Jolivet, Verma & Mille, 2007 — Rev. fr. Entomol. 29: 87. **(MNHN)**
53. *Montrouzierella subtuberculata* Jolivet, Verma & Mille, 2010 — Nouv. Revue Ent. (N.S.) 26: 14. **(MNHN)**
54. *Montrouzierella tuberculata* Jolivet, Verma & Mille, 2007 — Rev. fr. Entomol. 29: 88. **(MNHN)**
55. *Samuelsonia bicolor* Jolivet, Verma & Mille, 2007 — Rev. fr. Entomol. 29: 85. **(MNHN)**
56. *Samuelsonia dunali* (Montrouzier, 1861) — Anns. Soc. ent. Fr. 4: 396. **(RBINS)**
57. *Samuelsonia fauveli* Jolivet, Verma & Mille, 2007 — Rev. fr. Entomol. 29: 87. **(MNHN)**
58. *Samuelsonia fusca* Jolivet, Verma & Mille, 2007 — Rev. fr. Entomol. 29: 84. **(MNHN)**
59. *Samuelsonia gomyi* Jolivet, Verma & Mille, 2013 — Nouv. Revue Ent. (N.S.) 29: 147. **(MNHN)***
60. *Samuelsonia histrio* (Perroud & Montrouzier, 1864) — Anns. Soc. linn. Lyon 11: 205. **(MNHN)**
61. *Samuelsonia lemerrei* Jolivet, Verma & Mille, 2013 — Nouv. Revue Ent. (N.S.) 29: 148. **(MNHN)***

62. *Samuelsonia mayonae* Jolivet, Verma & Mille, 2010 – *Nouv. Revue Ent. (N.S.)* 26: 14. **(MNHN)**
63. *Samuelsonia melas* Jolivet, Verma & Mille, 2007 (Fig. 1m) – *Rev. fr. Entomol.* 29: 83. **(MNHN)**
64. *Samuelsonia minima* Jolivet, Verma & Mille, 2013 – *Nouv. Revue Ent. (N.S.)* 29: 150. **(MNHN)***
65. *Samuelsonia nitida* Jolivet, Verma & Mille, 2013 – *Nouv. Revue Ent. (N.S.)* 29: 149. **(MNHN)***
66. *Samuelsonia panieensis* Jolivet, Verma & Mille, 2011 – *Nouv. Revue Ent. (N.S.)* 26: 336. **(MNHN)**
67. *Samuelsonia pardalis* Jolivet, Verma & Mille, 2007 – *Rev. fr. Entomol.* 29: 86. **(MNHN)**
68. *Samuelsonia pilosa* Jolivet, Verma & Mille, 2007 – *Rev. fr. Entomol.* 29: 85. **(MNHN)**
69. *Samuelsonia pygmaea* Jolivet, Verma & Mille, 2010 – *Nouv. Revue Ent. (N.S.)* 26: 15. **(MNHN)**
70. *Samuelsonia rubiacearum* (Perroud & Montrouzier, 1864) – *Annl. Soc. linn. Lyon* 11: 203. **(MNHN)**
71. *Samuelsonia rugosa* Jolivet, Verma & Mille, 2013 – *Nouv. Revue Ent. (N.S.)* 29: 150. **(MNHN)***
72. *Samuelsonia turgida* Jolivet, Verma & Mille, 2007 – *Rev. fr. Entomol.* 29: 86. **(MNHN)**
73. *Samuelsonia viridescens* Jolivet, Verma & Mille, 2013 – *Nouv. Revue Ent. (N.S.)* 29: 151. **(MNHN)***
74. *Taophila (Jolivetiana) mantillerii* Jolivet, Verma & Mille, 2007 – *Rev. fr. Entomol.* 29: 44. **(MNHN)***
75. *Taophila (Taophila) bituberculata* Platania & Gómez-Zurita, 2022 – *Insect Syst. Evol.* 53: 13. **(JGZC)**
76. *Taophila (Taophila) carinata* Platania & Gómez-Zurita, 2022 – *Insect Syst. Evol.* 53: 17. **(MNHN, MNHW, JGZC)**
77. *Taophila (Taophila) corvi* Samuelson, 2010 – *Zootaxa* 2621: 51. **(BPBM)**
78. *Taophila (Taophila) dapporoi* Platania & Gómez-Zurita, 2022 – *Insect Syst. Evol.* 53: 25. **(MNHN, MNHW)**
79. *Taophila (Taophila) davincii* Platania & Gómez-Zurita, 2022 – *Insect Syst. Evol.* 53: 29. **(MNHN, MNHW, JGZC)**
80. *Taophila (Taophila) deimos* Samuelson, 2010 – *Zootaxa* 2621: 53. **(BPBM)**
81. *Taophila (Taophila) draco* Platania & Gómez-Zurita, 2022 (Fig. 1j) – *Insect Syst. Evol.* 53: 33. **(MNHN, MNHW)**
82. *Taophila (Taophila) goa* Platania & Gómez-Zurita, 2022 – *Insect Syst. Evol.* 53: 38. **(MNHN, MNHW, JGZC)**
83. *Taophila (Taophila) hackae* Platania & Gómez-Zurita, 2022 – *Insect Syst. Evol.* 53: 42. **(JGZC)**
84. *Taophila (Taophila) hydrae* Samuelson, 2010 – *Zootaxa* 2621: 53. **(BPBM)**
85. *Taophila (Taophila) joliveti* Samuelson, 2010 – *Zootaxa* 2621: 54. **(BPBM)**
86. *Taophila (Taophila) millei* Samuelson, 2010 – *Zootaxa* 2621: 58. **(BPBM)**
87. *Taophila (Taophila) nigrans* Jolivet, Verma & Mille, 2007 – *Rev. fr. Entomol.* 29: 44. **(MNHN)**
88. *Taophila (Taophila) sagittarii* Samuelson, 2010 – *Zootaxa* 2621: 58. **(BPBM)**

89. *Taophila (Taophila) samuelsoni* Platania & Gómez-Zurita, 2022 – Insect Syst. Evol. 53: 50. **(MNHN, MNHW)**
90. *Taophila (Taophila) scorpis* Samuelson, 2010 – Zootaxa 2621: 59. **(BPBM, MNHN)**
91. *Taophila (Taophila) sideralis* Platania & Gómez-Zurita, 2022 – Insect Syst. Evol. 53: 53. **(MNHN, MNHW, JGZC)**
92. *Taophila (Taophila) subsericea* Heller, 1916 – Sarasin and Roux, Nova Caled., Zool., 2: 306. **(SMTD)**
= *Stethotes mandjeliae* Jolivet, Verma & Mille, 2010 – Rev. fr. Entomol. 32: 143. **(MNHN)**
93. *Taophila (Taophila) taaluny* Platania & Gómez-Zurita, 2022 – Insect Syst. Evol. 53: 59. **(MNHN)**
94. *Taophila (Taophila) wanati* Platania & Gómez-Zurita, 2022 – Insect Syst. Evol. 53: 61. **(MNHN, MNHW, JGZC)**
95. *Thasycles castaneus* Gómez-Zurita, 2022 – Zool. Anz. 297: 24. **(MNHW)**
96. *Thasycles compactus* Gómez-Zurita, 2022 – Zool. Anz. 297: 25. **(JGZC, MNHW)**
97. *Thasycles cordiformis* Chapuis, 1874 – Hist. nat. Ins., Gen. Col. X: p. 255. **(RBINS)**
98. *Thasycles fuscus* (Jolivet, Verma & Mille, 2007) – Rev. fr. Entomol. 29: 36. **(MNHN)**
99. *Thasycles grandis* Gómez-Zurita, 2022 – Zool. Anz. 297: 31. **(MNHW)**
100. *Thasycles laboulbenei* (Montrouzier, 1861) – Anns. Soc. ent. Fr. 4: 396. **(RBINS)**
101. *Thasycles magnus* Gómez-Zurita, 2022 (Fig. 1f) – Zool. Anz. 297: 34. **(MNHW)**
102. *Thasycles panieensis* (Jolivet, Verma & Mille, 2007) – Rev. fr. Entomol. 29: 79. **(NHM)**
103. *Thasycles puncticollis* Gómez-Zurita, 2022 – Zool. Anz. 297: 35. **(MNHW)**
104. *Thasycles tenuis* Gómez-Zurita, 2022 – Zool. Anz. 297: 36. **(MNHW, MNHW, JGZC)**
105. *Thasycles variegatus* Gómez-Zurita, 2022 – Zool. Anz. 297: 37. **(MNHW, MNHW, JGZC)**
106. *Tricholapita aphrodita* (Gómez-Zurita, 2014) – Syst. Entomol. 39: 115. **(MNHN, BPBM, JGZC)**
107. *Tricholapita atlantis* (Platania & Gómez-Zurita, 2020) – Zool. J. Linn. Soc. 189: 15. **(MNHN)**
108. *Tricholapita gaea* (Gómez-Zurita, 2014) – Syst. Entomol. 39: 119. **(MNHN, BPBM, JGZC, AMS, NRM)**
109. *Tricholapita hermes* (Platania & Gómez-Zurita, 2020) – Zool. J. Linn. Soc. 189: 10. **(MNHN, MNHW)**
110. *Tricholapita kronos* (Platania & Gómez-Zurita, 2020) – Zool. J. Linn. Soc. 189: 12. **(MNHN, MNHW)**
111. *Tricholapita mars* (Samuelson, 2010) – Zootaxa 2621: 56. **(BPBM)**
112. *Tricholapita oceanica* (Platania & Gómez-Zurita, 2020) – Zool. J. Linn. Soc. 189: 23. **(MNHN, MNHW)**
113. *Tricholapita olympica* (Platania & Gómez-Zurita, 2020) (Fig. 1b) – Zool. J. Linn. Soc. 189: 6. **(MNHN, MNHW, JGZC)**
114. *Tricholapita ouranos* (Platania & Gómez-Zurita, 2020) – Zool. J. Linn. Soc. 189: 24. **(MNHN, MNHW)**

115. *Tricholapita reidi* Gómez-Zurita, Platania & Cardoso, 2020 – Zootaxa 4857: 89. (MHNW)
116. *Tricholapita riberai* (Platania & Gómez-Zurita, 2020) – Zool. J. Linn. Soc. 189: 17. (MNHN, MNHW)
117. *Tricholapita tridentata* (Platania & Gómez-Zurita, 2020) – Zool. J. Linn. Soc. 189: 4. (MNHN, MNHW)
118. Incertae sedis: *Colaspis metallica* Montrouzier, 1861 – Annls. Soc. ent. Fr. 4: 396*.
119. Incertae sedis: *Colaspis solani* Perroud & Montrouzier, 1864 (Fig. 1n) – Annls. Soc. linn. Lyon 11: 208. (MNHN)

Typophorini

120. *Rhyparida foensis* (Jolivet, Verma & Mille, 2007) (Fig. 1l) – Rev. Fr. Entomol. 29: 43. (MNHN)

Discussion

In this work, we updated the fragmented knowledge on species numbers and taxonomic changes over the past decades on the Eumolpinae of New Caledonia, whereby 120 species in 13 genera should be currently considered, although this figure will be notably increased in the future and many generic attributions changed. This exercise was required, since the Eumolpinae of New Caledonia have seen a rapid increase in the number of taxa proposed recently and in a relatively short amount of time, and also because a relatively important fraction of the global diversity of the subfamily (~ 1.7%) is found in this small archipelago.

The potential magnitude of this diversity was already suggested by Papadopoulou et al (2013), and it is still far from being completely known. Despite the increased rate of species descriptions in the last decade, several clades still need a revision (Papadopoulou et al. 2013) and the archipelago has not been exhaustively explored, which possibly results in a major underestimation of the diversity of New Caledonian Eumolpinae. This is exemplified by the high number of species that are discovered whenever a putative natural group is revised (Gómez-Zurita 2018, 2022; Platania et al. 2020; Platania and Gómez-Zurita 2022; Gómez-Zurita and Pàmies-Harder 2022), and the numbers of species described in the past few years in these revisions is indicative of this trend.

The Eumolpinae of New Caledonia are currently arranged in 13 genera. The assignment to genera is a problem for the group, since notions of diagnostic characters for monophyletic groups only started to be incorporated recently (Gómez-Zurita and Cardoso 2014; Gómez-Zurita 2018; Platania et al. 2020; Gómez-Zurita 2022; Gómez-Zurita and Pàmies-Harder 2022; Platania and Gómez-Zurita 2022). So far, only a handful of genera of New Caledonian Eumolpinae have been assessed based on these principles, including *Acronymolpus*, *Dematotrichus* Gómez-Zurita, 2022, *Kumatoeides* Gómez-Zurita, 2018, *Taophila*, *Thasycles* Chapuis, 1874, and *Tricholapita* Gómez-Zurita & Cardoso, 2020 (Gómez-Zurita and Cardoso 2014; Samuelson 2015; Gómez-Zurita 2018; Platania et al. 2020; Gómez-Zurita 2022; Gómez-Zurita and Pàmies-Harder 2022; Platania and Gómez-Zurita 2022). Most others will require profound

reassessment of their boundaries, but not only, since nomenclatural changes are also expected. Some ‘container’ genera, rich in species, usually showing marked differences between them, were proposed based on the general appearance of some species, but their monophyly will be probably challenged when they are studied in greater detail. This would be the case of *Samuelsonia* Jolivet, Verma & Mille, 2007, *Montrouzierella* Jolivet, Verma & Mille, 2007, *Dumbea* Jolivet, Verma & Mille, 2007, and *Dematochroma* Baly, 1864. We have already provided some objective data about the last genus, demonstrating with molecular phylogenetic data and principles that New Caledonian species in this genus must be transferred to other existing or new genera, since they are not monophyletic with the type species of *Dematochroma*, from Lord Howe Island (Gómez-Zurita and Pàmies-Harder 2022). Recent revisions began to address this issue, transferring some of the species to the genera *Dematotrichus* and *Thasycles* (Gómez-Zurita 2022; Gómez-Zurita & Pàmies-Harder 2022). Others, like *Colaspoides* Laporte, 1833, where some current taxa may require synonymization (Jolivet et al. 2013), must be removed from the catalogue, since none of the species of this possibly polyphyletic genus present in the eastern Palaearctic, Oriental, and Neotropical regions, are related to the New Caledonian species, deeply nested within the island radiation (Papadopoulos et al. 2013).

In this work, we also advocate two taxonomic changes that involve species in two of those problematic genera, based on the study of their types. The first one involves the species *Taophila cancellata*, which had been tentatively transferred to *Dematochroma* by Gómez-Zurita and Cardoso (2014), and it can be confirmed as a junior synonym of *Dumbea striata*. The second illustrates a common problem in previous taxonomic works of New Caledonian Eumolpinae whereby strong sexual dimorphism in some species resulted in the description of males and females as different species or difficulties to recognise males and females as conspecific (Gómez-Zurita 2017a, b). Specifically, *Dematochroma poyensis* is recognised here as the female and *D. theryi* as the male of the same species, and consequently synonymised. Thus, the new synonymies proposed in this work are *Dumbea striata* Jolivet, Verma & Mille, 2007 = *Taophila cancellata* Samuelson, 2010, syn. nov.; and *Dematochroma theryi* Jolivet, Verma & Mille, 2010 = *Dematochroma poyensis* Jolivet, Verma & Mille, 2010, syn. nov.

The high rate of species descriptions and the expected increase in the number of species, together with expected nomenclatural changes, highlight the importance of this catalogue, which provides data on the current knowledge of Eumolpinae diversity in New Caledonia and the basis for future taxonomic studies, grounded on the study of types, most of them available in just a handful of institutions, as well as phylogenetic information. Thus, the main stimulus of this work is taxonomic in scope, to update and condense in a single place the current taxonomic knowledge on New Caledonian Eumolpinae to aid future biodiversity research in this group. However, species catalogues are also a fundamental tool for conservation biology, since it is obvious that to know what to protect and to design efficient conservation strategies, it is essential to know what species are present in a particular area. This is especially relevant in the case of New Caledonian Eumolpinae, since they represent a highly vulnerable group of New Caledonian biota for several reasons. Beyond the recognised vulnerability of island biotas, among the most threatened in the world, with a

third of all terrestrial species at high risk of extinction (Ricketts et al. 2005), all the species and most genera of New Caledonian Eumolpinae are endemic. Moreover, most species studied to date have confined distributions, known from a single locality or group of nearby localities, a condition that can be referred to as micro-endemicity. Indeed, micro-endemicity is a characteristic feature of New Caledonian biodiversity, shared by many different organisms (Caesar et al. 2017) and indicative of their high vulnerability, which together with the extraordinary species richness and the reduced area, led to classify the archipelago as a biodiversity hotspot of high conservation priority (Mittermeier et al. 1999; Myers et al. 2000). Leaf beetles show strong associations with plants with different degrees of ecological specialization. Thus, their vulnerability is also potentially influenced by cascade effects derived from conservation issues of their hosts. The microendemic distributions of many species of both plants and beetles increase exponentially their risk of extinction. Their survival is jeopardized by several factors with global or regional effects, such as climate change (Mora et al. 2013; Wulff et al. 2013; Bellard et al. 2014). However, it is also susceptible to threats resulting from local changes in the environment, which can typically result from human activities, such as mining, timber extraction, or cattle raising, leading to habitat degradation (Pascal et al. 2008; Wulff et al. 2013), but also the introduction of alien species (Gargominy et al. 1996) or other stochastic natural or human-induced events, such as fires (McCoy et al. 1999).

Raising awareness about the high species diversity of Eumolpinae, uncovered thanks to the taxonomic work that is ongoing, building upon the knowledge generated by previous authors, as well as their compromised situation owing to their reduced ranges, would be a first argument to include them in future conservation plans.

Acknowledgements

This work benefited from funds from the Spanish Agencia Estatal de Investigación (Grants No. CGL2017-83324-P and PID2021-123668NB-I00) to JGZ, the predoctoral scholarship associated to the first grant to LP (PRE2018-083172) and the European Union Synthesys+ Translational access programme (Grant No. FR-TAF-011). All grants except for the last received support from the European Regional Development Fund. The Unit of Information Resources for Research (URICI) kindly supported the Open Access publication fee thanks to the CSIC Open Access Publication Support Initiative. Finally, we are indebted to Stefano Zoia (Milano, Italy) and Christian Mille (IAC, Institut Agronomique néo-Calédonien, La Foa, Pocquereux, New Caledonia) for the time devoted to study our manuscript and for their suggestions to improve it.

Additional information

Conflict of interest

No conflict of interest was declared.

Ethical statement

No ethical statement was reported.

Funding

- Grants No. CGL2017-83324-P and PID2021-123668NB-I00 and predoctoral scholarship (PRE2018-083172) from the Spanish Agencia Estatal de Investigación, all supported from the European Regional Development Fund.
- Grant No. FR-TAF-011 from European Union Synthesys+ Translational access programme.
- Open Access publication fee supported by the Unit of Information Resources for Research (URICI) through the CSIC Open Access Publication Support Initiative.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Rediscovery of a lost semi-aquatic Leaf Beetle in the Hula Valley, Israel (Coleoptera, Chrysomelidae, Donaciinae)*

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Abstract

Between 1951–1958, most of the Hula Lake and its surrounding swamps in the Upper Jordan River (Rift) Valley of Israel were drained with the supposed purposes to eliminate malaria and to reclaim land for agriculture; both reasons later proved to be unnecessary decisions. With the paucity of biological knowledge of the Hula region, especially its aquatic invertebrates, accurate assessment of the environmental damage from this drainage is still being realized. Based on natural history museum collection specimen records, the pre-drainage presence of some aquatic insect species has been verified. Among these was *Donacia bicolora*, a member of a semi-aquatic subfamily (Donaciinae) of Leaf Beetles (Chrysomelidae) and whose Israeli populations were thought to have gone extinct because of the drainage of the Hula and other locations. Recently this species was rediscovered in two populations. However, the molecular identification of two of these recently collected specimens from one population revealed that the identity of this species is actually *Donacia simplex*. In this work, the re-discovery of this species is detailed, and its conservation importance discussed.

Key words: conservation, DNA taxonomy, Hula Lake and Swamps, land reclamation/restoration, morphology, reed beetles, wetland drainage



Academic editor: Michael Schmitt

Received: 4 February 2023

Accepted: 24 March 2023

Published: 30 August 2023

ZooBank: <https://zoobank.org/5E6BE887-543D-4518-A10B-A14F5468FB94>

Citation: Furth DG, Montagna M, Magoga G (2023) Rediscovery of a lost semi-aquatic Leaf Beetle in the Hula Valley, Israel (Coleoptera, Chrysomelidae, Donaciinae). In: Chaboo CS, Schmitt M (Eds) Research on Chrysomelidae 9. ZooKeys 1177: 57–74. <https://doi.org/10.3897/zookeys.1177.101498>

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Introduction

The Hula (sometimes spelled Huleh) Lake and Swamps (Figs 1, 2) are considered as the “limnological lungs” of the Jordan River, i.e., the sources of this important river (FD Por, in Dimentman et al. 1992). The area has a long history of thousands of years in the ancient literature such as those by Pharaoh Amenhotep IV (14th Century BC), Josephus Flavius (1st Century AD) and others (Dimentman et al. 1992). Even in the Talmud (1st Century AD) it is referred to as the Merom; in limnological studies in the Hula Valley by G. Evelyn Hutchinson and colleagues as the “Waters of the Merom” (Dimentman et al. 1992). The first true natural history studies of the Hula were done by Tristram between 1864 and

* Extended version of a talk presented to the 10th International Symposium on the Chrysomelidae, Helsinki, Finland, 21 July 2022



Figure 1. Map of Middle East (partial) with the Hula Lake Preserve indicated.

1884 (Tristram 1884), mostly a survey of vertebrates and a few other groups like molluscs, a few water beetles, dragonflies, and other invertebrates, as well as the flora (Dimentman et al. 1992). When the idea of draining the Hula was first proposed in the early 20th Century, the 1935 Percy Sladen Expedition to the Hula was initiated and surveyed mostly plants, some vertebrates, and a few invertebrate groups (Paz 1976). Other pre-drainage floral information can be found in Jones (1940). Part of the reason for this paucity of knowledge of the fauna and flora was because the Hula area was considered too dense for explorers to penetrate, as well as the presence of Malaria (Dimentman et al. 1992).

Previously the senior author (1977) reported that Israeli populations of *Donacia bicolora* Zschach, 1788 (Coleoptera, Chrysomelidae, Donaciinae) and *Galerucella nymphaeae* (Linnaeus, 1758) (Chrysomelidae: Galerucinae) were apparently extinct there due to the drainage of the Hula Lake and Swamps between 1951 and 1958. This drainage apparently caused the local extinction of various plants and animals (Furth 1977, 1993), including the known food plant of *D. bicolora*. Also mentioned in these publications was the previously reported *D. thalassina* Germar, 1811 (= *Donacia marginata* Hoppe, 1795) and that both these species were known to feed on the same or congeneric food plants, *Sparganium erectum* Linnaeus 1753 [Typhaceae].

This study is an update of the long history of awareness of fauna and flora that were devastated or even extirpated from the Hula Lake and Swamps effected by the drainage of these areas between 1951–1958. This drainage was conducted because of ideas that this would allow arable land reclamation and would eradicate a significant malaria epidemic there or, as has been said, to “sanitize the malaria infested and evil marshes and to turn them over to healthy agriculture” (Dimentman et al. 1992). But after this drainage it was discovered that the reasons were mistaken. Subsequently the government attempted to restore the Hula Lake and Swamps by re-inundating these areas with new water



Figure 2. Map of current Hula Lake Preserve surrounded by agricultural fields.

sources. The Hula Lake and Swamps became the first national park in Israel in 1964 and now is both a World Heritage site and a RAMSAR site, rich in wetland habitats and therefore a special place to view migrating birds (Fig. 2).

The biogeography of the Hula is rather unique because it is the northern limit of many Afrotropical species and the southern limit for Palearctic species. For example, Tristram (1884) stated that ~ 30% of the mammal species of the Hula were Afrotropical species and Kugler and Wool (1968) thought ~ 50% of the midge (Diptera: Chironomidae) species were Afrotropical. Other more recent examples can be found in Dumont (1991) for Odonata and Yanai et al. (2020) for Ephemeroptera. One of the dominant plants in the Hula is Papyrus (*Cyperus papyrus* Linnaeus, Cyperaceae), an Afrotropical species; the Hula is the only place outside Africa where this plant is found naturally. Similarly, several species of *Tilapia* (Cichlidae) are found in the Hula, the only place they are known outside Africa.

In addition to *D. bicolora*, several animal species were thought to have been extirpated by the drainage of the Hula, such as the endemic Hula Painted Frog (*Latonia nigriventris* (Mendelssohn & Steinitz, 1943) (Alytidae, Discoglossinae)), that has been recently rediscovered (Biton et al. 2013). However, there are still some species not recorded since the Hula drainage, for example, the beetle *Galerucella nymphaeae* (Furth 1993) and species of water beetles, mosquitoes, midges, dragonflies, giant water bugs, etc. (Dimentman et al. 1992). Before the drainage of the Hula, *Sparganium erectum*, the food plant of *D. bicolora*, was found commonly along the western and eastern edges of the Hula Lake and Swamps but virtually disappeared after the drainage and is currently considered a protected plant in Israel. Historical information about the flora of the Hula can be found in Zohary and Orshansky (1947) and Zohary (1966).

Much of the history of this project was provided in two previous publications by the senior author (Furth 1977, 1993) and will not be repeated here. Many other historical aspects of the Hula region can be found in Paz (1976) and Diment-

man et al. (1992). In Furth (1977, 1993) this species of *Donacia* was referred to as *D. bicolor* Zschach in error. *Donacia bicolora* has been recorded from most of eastern and western Europe, Iran, and Turkey (Löbl and Smetana 2010), making the Hula the most southern limit of distribution for this species, also true for many other taxa. It has been recorded in much of Europe as feeding on *Sparganium erectum* (Mohr 1966). In Furth (1977) this host plant was mistakenly referred to as *S. neglectum*, but the error was corrected (Furth 1993).

The distributions of *Donacia* species recorded nearest to Israel are from Löbl and Smetana (2010), while the records confirmed by Geiser and Jäch (2021) are indicated by an asterisk (*). *Donacia bicolora* was also recorded from Israel by Furth (1977, 1993):

D. bicolora: Iran; Israel; Turkey; Albania*; Serbia*; Bosnia-Herzegovina*; Montenegro*

D. marginata: Iran; Israel; Greece: Turkey; Morocco; Bosnia-Herzegovina*; Serbia*

D. simplex Fabricius, 1775: Turkey; Algeria; Morocco; Croatia; Bulgaria; Serbia*; Iran*; Syria (Anti-Lebanon mountains)*

D. tomentosa Ahrens, 1810: Croatia*; Greece*; Iran; Israel*

Historically, specimens identified as *Donacia bicolora* documented in the entomology collection at the Steinhardt Museum of Natural History (SMNH TAU) (except as noted) are as follows (exact label data): Palestine, Hulata, 29 March 1940, Bytinski-Salz; Palestine, July 1940, Bytinski-Salz; Palestine, Binyamina, Kabarah, July 1940 Bytinski-Salz; Hula, 20 April 1941, leg. Steinitz et al. [larva, ex Hebrew University collections]; Hulatah, Palestine, 29 March 1942, Bytinski-Salz; Palestine, Hula 29 March 1942, Bytinski-Salz; Hula, 1 April 1942; Palestine, Hula 8 April 1945; Palestine, Huleh 25 April 1945, leg. Bytinski-Salz, on *Sparganium*. Haifa District 9 April 1945 [this record is from the Natural History Museum, London [NHM]], E. Geiser, pers. comm. 2022].

Because of the more recent records in SMNH TAU collection, the senior author began to investigate the potential that *D. bicolora* survived the drainage of the Hula Lake and Swamps.

Material and methods

For this study Israeli historical specimens of *Donacia* were examined from Steinhardt Museum of Natural History, Tel Aviv University, Israel (**SMNH TAU**). Between 2011 and 2022 the first author and Ariel “Laibale” Leonid Friedman collected regularly at the Dan River tributary behind the Bet Ussishkin Nature Museum belonging to Kibbutz Dan. This site was chosen because of indications in relatively recent history of the rediscovery of this *Donacia* based on specimens at SMNH TAU from 1993 and 2009 (see Results). Other collecting sites visited were Hula Lake Park, Kibbutz Dan, Ein Afeq, Binyamina swamps (Fig. 3), as well as some other potential sites such as Ein Nymphit, Baniass, and Granot Hadera canal (see Results for exact dates of visits).

Based on the 2018 information about the flora in the Israel Nature Protection and National Parks Authority databases (Y. Malihi, pers. comm. 2018) the senior author visited the following national parks in search of populations of *Sparganium erectum* and *Donacia bicolora*: Hula Lake Preserve, Ahu Binyamina, Ein Nymphit, Ein Afeq, and Baniass.

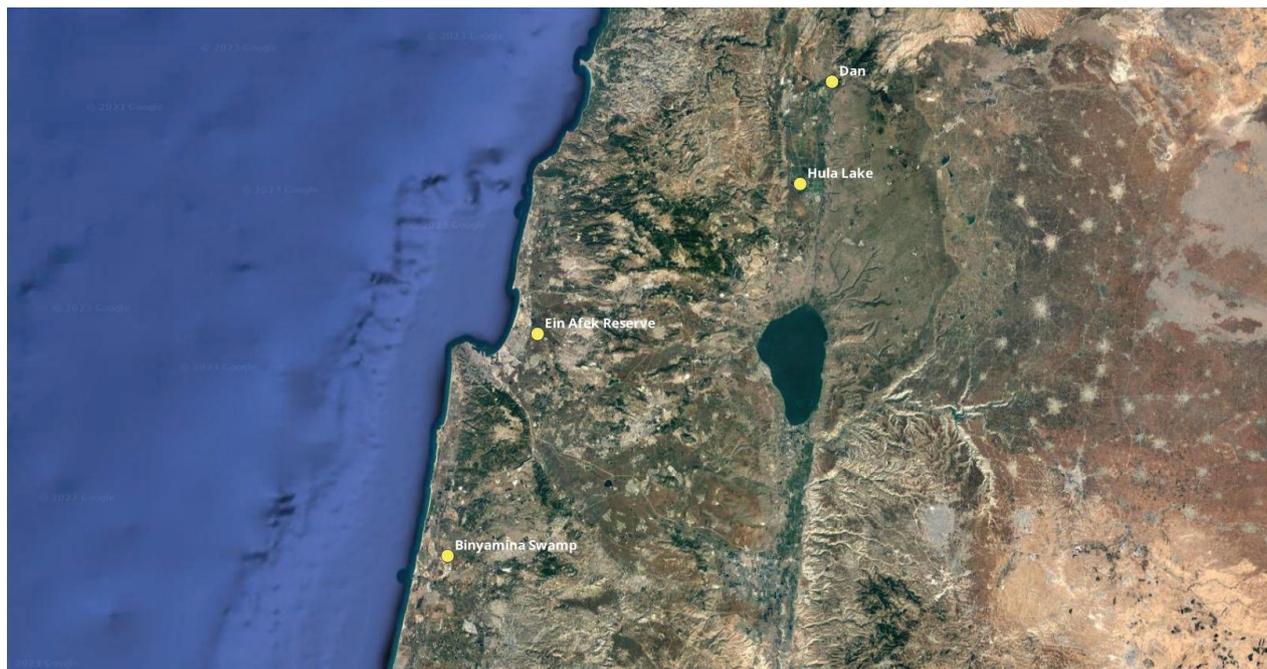


Figure 3. Map of Israel showing locations of Hula Lake, Kibbutz Dan, Ahu Binyamina (as Binyamina swamp), and Ein Afek.

Recently *Donacia* specimens were collected at Kibbutz Dan by sweep netting and then either placed directly into 95% ethanol or put into 95% ethanol shortly after collecting to preserve them for molecular analyses. Specimens used for molecular analyses were collected on 11/12 March 2013. Moreover, three *D. bicolora* specimens from the entomology collections of NHM collected in Ukraine were also included in this study as reference of precise identity for the molecular identification of Israel specimens. Some specimens were also pinned as vouchers for the museum collections at SMNH TAU. A photo of the lateral view in copula of this species dated 11/12 March 2013 was also sent to an expert on *Donacia* (Dr. Elisabeth Geiser, Salzburg).

DNA was extracted from three specimens of *D. bicolora* collected in Ukraine (collecting information: Ukraine - Volynska Oblast', Shatsky District, Pischa vill., fishing ponds, 161 m, 51°35'53.8"N, 23°46'13.3"E 26.V.2019, K. Matsumoto leg., NHM(E) 2019-91) and from two *Donacia* sp. specimens from Israel (Israel - Upper Galilee, Kibbutz Dan, 12.III.2013, leg. D.G. Furth). Specimens processing took place at the laboratories of University of Milan, Italy. Non-destructive DNA extraction was performed from the whole insect body using Qiagen DNeasy Blood and Tissue Kit (Qiagen, Hilden, Germany) following the method described in Magoga et al. (2016). After DNA extraction, the voucher specimens were dry mounted on pins.

A 658 bp region of the mitochondrial cytochrome oxidase subunit 1 (COI) was amplified by PCR using the barcode primers LC01490/HCO219821 (Folmer et al 1994). PCRs were performed in a volume of 25 μ L reaction mix containing 1 \times GoTaq reaction Buffer (10 mM Tris-HCl at pH 8.3, 50 mM KCl and 1.5 mM MgCl₂), 0.2 mM of each deoxynucleoside triphosphate, 0.5 pmol of each primer, 0.3 U of GoTaq DNA Polymerase, and 10/20 ng of template DNA. The adopted thermal protocol was that described in Montagna et al. (2013). Positive amplicons were directly sequenced on both strands using Sanger sequencing

(Microsynth, Balgach, Switzerland). Consensus sequences were obtained by editing electropherograms using Geneious R8 (Biomatters Ltd., Auckland, New Zealand). The presence of an open reading frame was verified using the on-line tool EMBOSS Transeq (http://www.ebi.ac.uk/Tools/st/emboss_transeq/).

The obtained COI sequences were matched with those available in GenBank and in BOLD (Ratnasingham and Hebert 2007) databases through a Basic Local Alignment Search Tool analysis (BLAST, default parameters; BLAST: <http://www.ncbi.nlm.nih.gov/BLAST/>; Altschul et al. 1990) and BOLD identification engine, respectively. Newly developed sequences were registered in BOLD system (BOLD IDs: MEDLB961-23 to MEDLB65-23).

All sequences of *Donacia* publicly available in BOLD were retrieved (March 2022; Suppl. material 1). Sequences derived from contamination were discarded. The remaining sequences were aligned at codon level using MUSCLE (Edgar 2004) together with the sequences developed in this study. Sequences with length < 400 bp were removed and haplotypes were reduced using R software (R v. 3.5.2; R Core Team 2020). The obtained dataset (91 sequences belonging to 26 species) was used for estimating K2P pairwise nucleotide distances between sequences using the R package ape (Popescu et al. 2012) and for the COI dendrogram inference. Prior to the dendrogram inference, the best nucleotide substitution model was estimated using jModelTest 2 (Darriba et al. 2012) and selected according to Akaike Information Criterion (AIC) (Akaike 1974). Maximum likelihood phylogenetic inferences were performed using PhyML version 3.0 (Guindon et al. 2010) with the following options: evolutionary nucleotide substitution model as obtained by model selection procedure (GTR + I + G); the best of NNI and SPR tree searching operation; approximate likelihood ratio test as node support (aLRT; Anisimova et al. 2011). A COI sequence of *Plateumaris braccata* (Scopoli) was used as outgroup. A subset of the sequences retrieved from BOLD (15 species) aligned with the sequences generated in this study was used to infer a minimum-spanning haplotype network (Bandelt et al. 1999) with PopART software (Leigh and Bryant 2015).

Results

Museum specimens

Relatively recent specimens collected in Israel and identified as *Donacia bicolora* were found within the entomology collections of SMNH TAU. These few specimens were as follows: Hula Lake Preserve, 1 July 1993, collected by V. Chikatunov (2 specimens); and Dan, 33°14'N, 35°39'E, 19 May 2009, collected by L. Goren (1 specimen). Because of these records, multiple field trips were made to the Kibbutz Dan (Dan River tributary = Bet Ussishkin) and to the Hula Preserve as well as other sites with either historical records of *D. bicolora* or those suspected of having populations of its food plant *Sparganium erectum*, as follows (see Figs 4, 5).

Collected material (in chronological order)

13 July 2011, the Hula Lake Preserve and Kibbutz Dan (Dan River tributary = Bet Ussishkin), *Sparganium erectum* was swept by D. Furth (DF), L. Friedman (LF), Z. Yanai (ZY), but no *Donacia* were found.



Figure 4. D. Furth searching for *Sparganium erectum* and *Donacia simplex* in the Hula Preserve in 2011 (photograph by Z. Yanai).



Figure 5. D. Furth searching for *Sparganium erectum* and *Donacia simplex* at Kibbutz Dan (Bet Ussishkin) in 2011 (photograph by Z. Yanai)

11–12 March 2013 DF collected many *Donacia* at the Bet Ussishkin location, including mating pairs (see Figs 6–8).

1 April 2014 DF and ZY visited Ahu Binyamina (32.501465°N, 34.946319°E), no *Sparganium* were found, no *Donacia* collected.

1 April 2014 DF and ZY visited the Hadera Granot canal (32.449819°N, 34.939678°E), a large population of *Sparganium* was found, but no *Donacia* collected.

26 March 2015 DF checked Bet Ussishkin, *Donacia* leaf damage, no *Donacia*.

28 April 2015 DF collected at Dan, no *Donacia*.

3 March 2016, 1 May 2016, and 20 February 2018 a few *Donacia* were collected by LF at Dan stream (Bet Ussishkin).

8 March 2017 DF checked Ahu Binyamina, no *Donacia* found.

14 March 2017 DF checked Granot Canal, Hadera (32.26.979N, 34.56.384E, 12 m), no *Donacia* found.

15 March 2017 Bet Ussishkin, DF and LF checked, no *Donacia* found or plant damage.

20 February 2018 LF collected 3 *Donacia* at Bet Ussishkin.

13 March 2018 DF collected *Donacia* at Bet Ussishkin but none at Hula Park or Baniass Park.

15 March 2018 DF and LF collected at Ein Afek (no *Sparganium* found) and at Ein Nymphit (one *Sparganium* found), but neither location produced *Donacia*.

27 February 2020 LF collected a few *Donacia* at Bet Ussishkin.

16 March 2020 LF collected a few *Donacia* at Bet Ussishkin.

18 March 2022 DF checked *Sparganium* at Bet Ussishkin, no *Donacia* found.



Figure 6. *Donacia simplex* adults in copula (photograph by D. Furth).



Figure 7. *Donacia simplex* adult damage on leaf of *Sparganium erectum* (photograph by D. Furth).



Figure 8. *Sparganium erectum* flowers (photograph by D. Furth).

Molecular identification

The COI sequences obtained from the three specimens collected in Ukraine belong to two different haplotypes, while both specimens from Israel shared the same haplotype.

The individuals of *D. bicolora* collected in Ukraine showed an identity between 99.7% and 100% (e-value $< 1 \times 10^{-20}$) with sequences of *D. bicolora* collected in Finland (BLAST analysis) and a similarity between 99.5% and 100% with sequences of *D. bicolora* collected in Finland and Norway (BOLD identification engine analysis). For the specimens collected in Israel, an identity between 96.5% and 96.8% (e-value $< 1 \times 10^{-20}$) was observed with sequences of *D. simplex* collected in Finland and Germany using BLAST; using BOLD, a similarity between 97.3% and 97.7% was observed with the same sequences. A nucleotide distance of $\sim 13\%$ was estimated between the sequences of *D. bicolora* from Ukraine and those of *Donacia* from Israel generated in this study. In the maximum likelihood tree inferred from the alignment of *Donacia* COI sequences, *Donacia* from Ukraine clustered in a monophyletic group with other *D. bicolora* (aLRT = 1) (Fig. 9), whereas the individuals from Israel grouped with *D. simplex* from Germany, Finland, and United Kingdom (aLRT of 0.89) (Fig. 9). In the haplotype network, the same clusters were observed (Fig. 10).

Note

After examination of the photograph (lateral view) of a copulating pair of this species (see Fig. 6) from the Kibbutz Dan population collected on 11/12 March 2013, Dr. E. Geiser was not able to definitively identify it as *D. bicolora* or *D. simplex* based on its morphology (E. Geiser, pers. comm. 2023). Dr. Geiser confirmed that the photograph in Furth (1977: fig. 3) was indeed *D. bicolora* but the specimen in that photograph was not from Israel, but from the entomology collections at the Museum of Comparative Zoology, Harvard University, only as a representative of *D. bicolora*.

Discussion

The nucleotide distance comparison between the sequences of *D. bicolora* (whose identity was further confirmed through the molecular analyses) from Ukraine with those of the *Donacia* specimens from Israel, as well as the *Donacia* dendrogram and the haplotype network analyses, suggest that the *Donacia* specimens collected in Israel do not belong to *D. bicolora*. The Israeli *Donacia* is closer to *D. simplex*, having a sequence identity/similarity of $\sim 97\%$ with *D. simplex* sequences publicly available in the reference databases. The $\sim 3\%$ nucleotide distance value estimated between *D. simplex* public COI sequences and those of *Donacia* from Israel generated in this study is higher than the optimal threshold for the molecular identification of Donaciinae identified in Magoga et al. (2018). However, from the haplotype network, we can observe that the number of nucleotide substitutions elapsing between Israeli *Donacia* and *D. simplex* from Finland and Germany is comparable to the one observed between the different haplotypes of other species (e.g., *D. marginata* Hoppe and *D. impressa* Paykull) (Fig. 10). This evidence suggests that this species of *Donacia* from Israel is *D. simplex*, and that the nucleotide distance observed is likely related to the geographic distance between

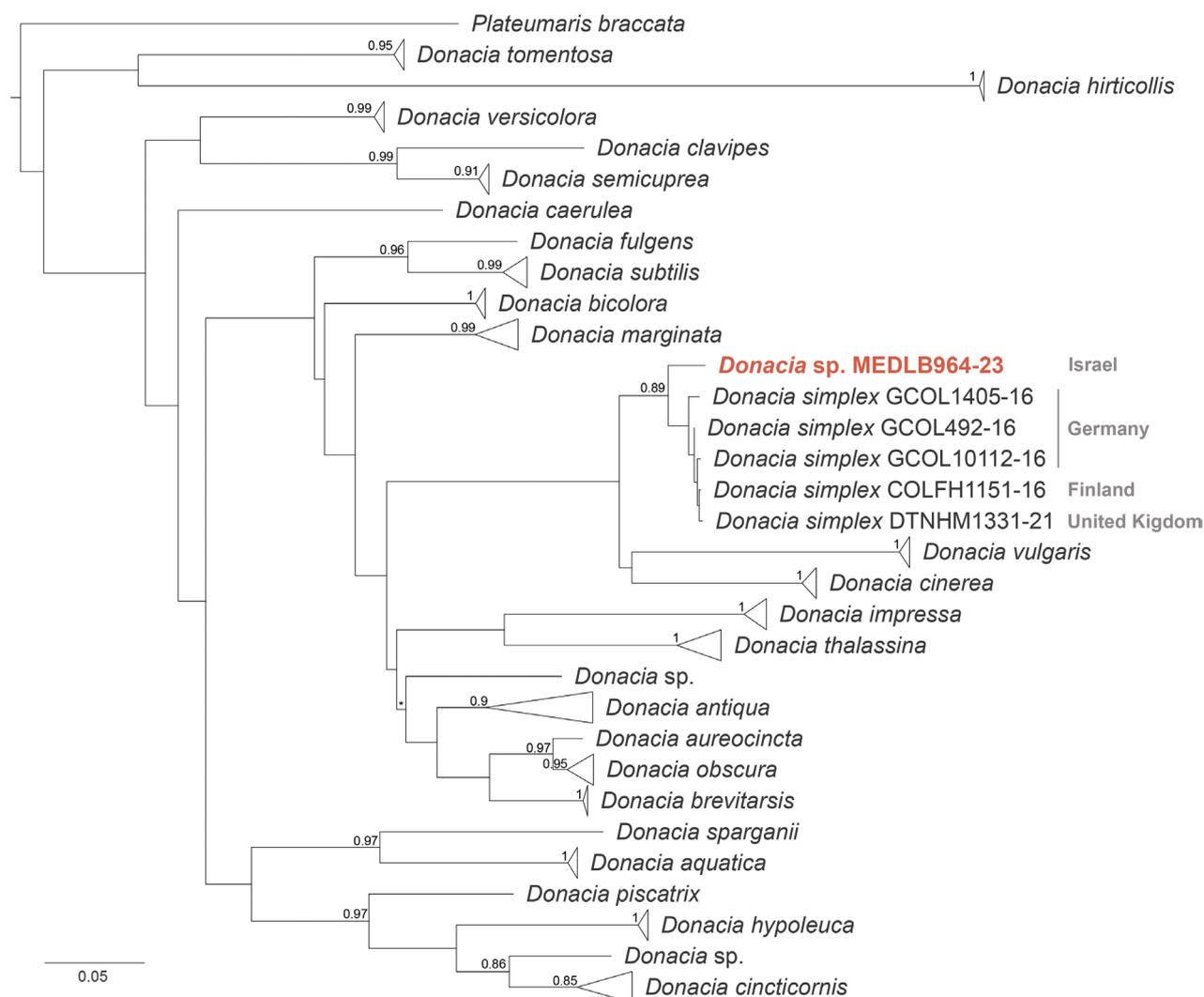


Figure 9. Maximum likelihood dendrogram of the genus *Donacia* inferred using COI gene nucleotide sequences. Terminal nodes are visually collapsed to species level, except in the case of *D. simplex* clade. *Donacia* sp. collected in Israel is indicated in red. Collection countries of the specimens falling in the *D. simplex* clade are indicated in grey. The tree scale bar indicates the distance in nucleotide substitutions per site. The aLRT values are reported on nodes; * represents aLRT values < 0.70 (created by M. Montagna and G. Magoga).

the considered populations. The clusters found on the *Donacia* COI dendrogram further confirmed these molecular identifications (Fig. 9).

The results obtained in this study by integrating various sources of evidence (analyses of historical collections, faunal surveys, the morphological and molecular analyses) have revealed that the species present in Israel that has been historically referred to as *D. bicolora* (in SMNH TAU collections; Furth (1977, 1993)) is actually *D. simplex*. Previous identifications of this species, especially within the collections in Israel, were not verified by *Donacia* experts thus creating a misunderstanding that protracted over time.

Based on morphological observations, especially the photograph in Furth (1977: fig. 3, as a representative of *D. bicolora* and not from Israel), and the fact that the species in Fig. 6 cannot definitively be identified by morphology, Dr. E. Geiser still has concerns as to the identity of this single species from the Hula Valley and she feels there may be some discrepancy between the molec-

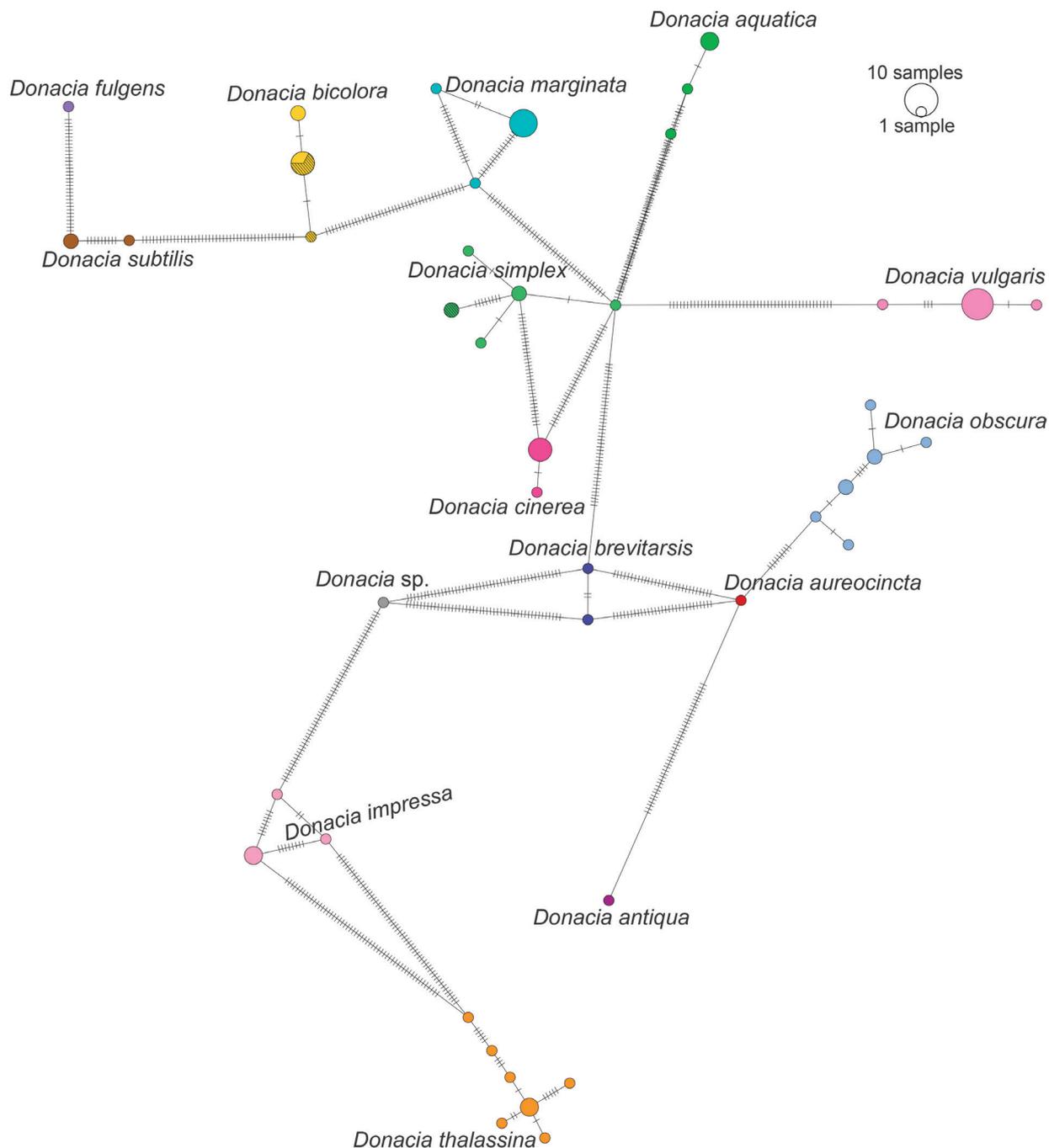


Figure 10. Minimum Spanning Haplotype Network of *Donacia* inferred from COI gene nucleotide sequences. Each color represents a species. The diameter of the circle is proportional to the abundance of the haplotypes, vertical lines on edges represent the nucleotide substitutions between haplotypes. Diagonal lines on yellow and green circles identify haplotypes of Ukrainian and Israeli specimens (created by M. Montagna and G. Magoga).

ular and morphological identity of this single species of *Donacia* (*D. simplex* or *D. bicolora*, respectively). Therefore, subsequent molecular and morphological research about this will be conducted. Nevertheless, it is a single species from the Hula Valley and the principles of its rediscovery and conservation will not change no matter what the taxonomic nomenclature finally reveals.

Even though Donaciinae species are globally primarily Holarctic, it is probable that other species of *Donacia* that are possibly cryptic may be discovered or re-

discovered in the biogeographically diverse biotopes of Israel in the future, such as *D. marginata* (Furth, 1993) or *Donacia tomentosa* (Geiser and Jäch 2021).

Based on the results of this study, the most viable re-discovered population of *D. simplex* is present at Kibbutz Dan. It may also be present in much smaller numbers in the Hula Lake Preserve/National Park based on the 1993 record mentioned above in the Results. This establishes the Israeli populations of *D. simplex* as the southernmost population of this species. However, the Kibbutz Dan population is endangered because the primary population of the food plant (*S. erectum*) is at risk because the water is directed via this canal to the Kibbutz fishponds (Fig. 11): in order to allow the water to flow more easily, Kibbutz workers have been clearing all plants from this canal each year (Fig. 12). The late Yossi Levari (a long-time Kibbutz member, botanist, and former director of the Kibbutz Dan Bet Ussishkin Museum) arranged an informal agreement with the Kibbutz fisheries to allow *S. erectum* plants to remain and grow on the south side of the canal behind the Museum, thus allowing the population of *D. simplex* to flourish. However, Mr. Levari passed away in 2020 and the informal agreement with the Kibbutz fisheries could change at any time without a more formal written agreement. This publication is dedicated to Mr. Levari (Fig. 13).

This study has revealed the necessity to try to conserve any populations of *D. simplex* as well as its food plant *S. erectum*. Although there is currently no endangered and threatened list for insects in Israel, there is a plan to create something similar via a website (Z. Yanai, pers. comm. 2023). When such a list is compiled in the future, this species (*D. simplex*) should be included. Fortunately, its food plant, *S. erectum*, is on the Red List of Endangered Plants of Israel (Y. Malihi, pers. comm. 2018). A future goal is to try to re-introduce *Donacia simplex* to locations where it was historically recorded, e.g., Binyamina (Ahu Binyamina) as well as other parks or locations that support its food plant (*S. erectum*), e.g., Ein Afek. Another such potential re-introduction location is the Granot Canal near Hadera (Fig. 14) where there is a large population of *S. erectum*; however, such locations that are not protected as in a park could

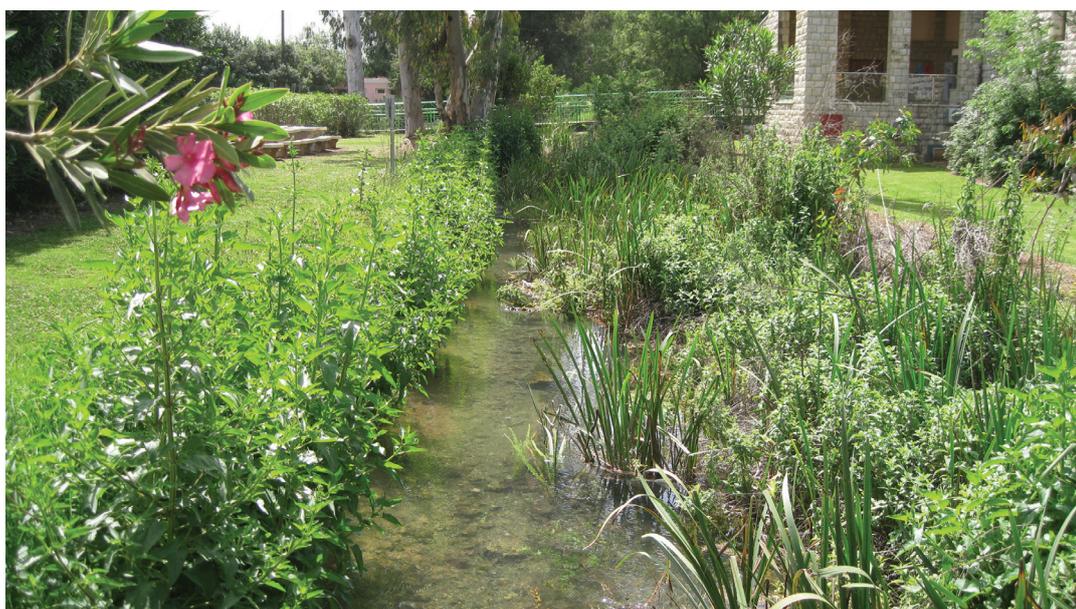


Figure 11. Kibbutz Dan, Bet Ussishkin canal with *Sparganium erectum* (photograph by D. Furth).



Figure 12. Kibbutz Dan, Bet Ussishkin canal cleaned on one side (photograph by D. Furth).

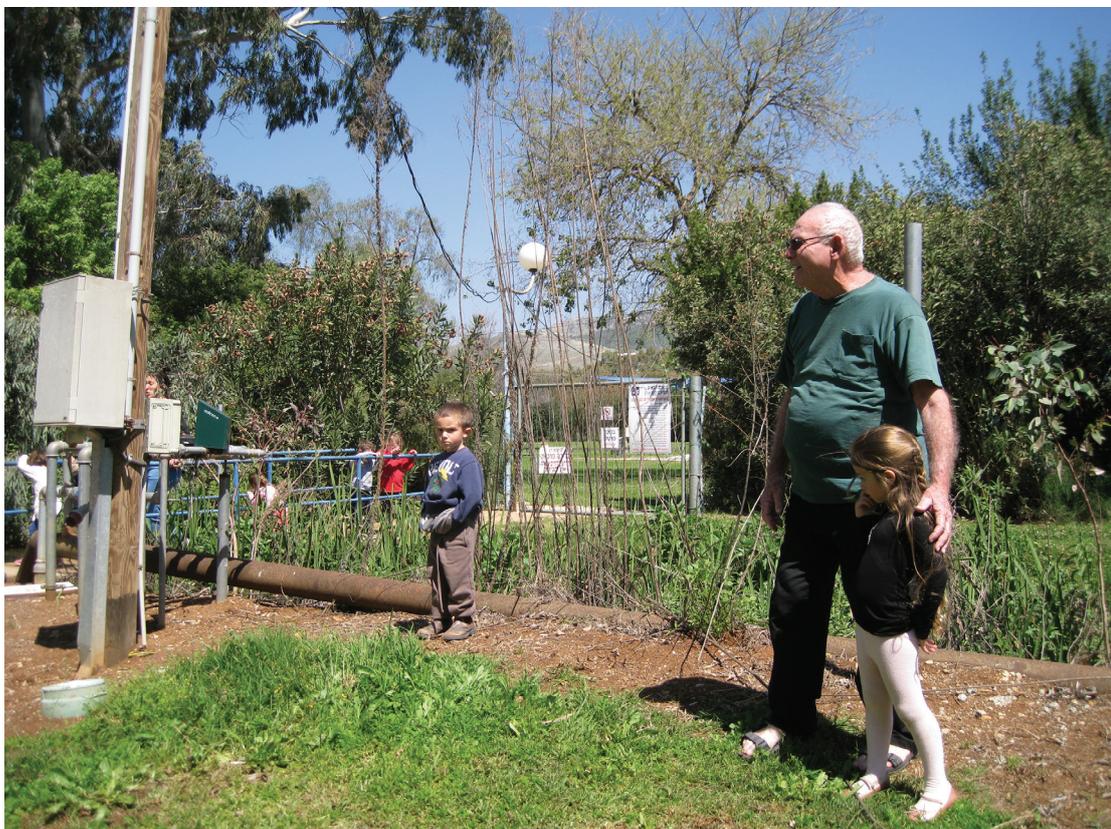


Figure 13. Yossi Levari with two of his grandchildren, near the Bet Ussishkin canal, Kibbutz Dan (photograph by D. Furth with permission from Rachel Levari).



Figure 14. Hadera Granot canal, full of *Sparganium erectum* (photograph by D. Furth).

be decimated by local authorities for road enhancement, construction of housing, and in Granot Canal, agriculture is a threat due to pollution from pesticide run off from adjacent fields. Therefore, the optimum reintroduction locations should be in protected areas.

Conclusion

The Israeli populations of this semi-aquatic Leaf Beetle have been historically referred to as *D. bicolora*, but the molecular analysis presented here demonstrates that it belongs to *D. simplex*. The historical records from museum specimens, primarily in SMNH TAU, indicated that this species may have been extirpated from the region because of the drainage of the Hula Lake and Swamps in the 1950s, because its food plant *S. erectum* was also severely restricted due the drainage. However, the evidence presented in this study demonstrates that *D. simplex* has survived in very limited populations and should be preserved to enable it to flourish once again.

Acknowledgements

We are grateful to Prof. Netta Dorchin and Ariel “Laibale” Leonid Friedman (Steinhardt Museum of Natural History, Tel Aviv University), the former for help with collecting permits, and the latter for valuable assistance collecting specimens, especially at Kibbutz Dan. A special thanks to the late Yossi Levari (Kibbutz Dan) for the conservation of and access to the part of the Dan stream behind Bet Ussishkin Nature Museum of the Kibbutz, and to his widow (Rachel Levari) for permission to use the photograph in Fig. 14. We also thank Dr. Elizabeth

Geiser (Salzburg, Austria) for various museum records of *D. simplex* and *D. bicolora* and for valuable comments on this manuscript. Special thanks are due to Dr. Zohar Yanai (SMNH TAU) for help with collecting in 2011, for valuable suggestions for this manuscript, and for help improving the maps for Figs 1, 2, and 3. A special gratitude goes to Prof. Chanan Dimentman (Hebrew University of Jerusalem, Israel) for discussions about the Hula Lake and Swamp history.

We are grateful to the Israel Nature Protection and National Parks Authority for access to Hula Lake Preserve, especially Yifat Artzi, and to Dr. Yariv Malihi (Israel Nature Protection and National Parks Authority, Central region, Afek National Park) for assistance with *Sparganium* population locations. A special debt goes to the late Prof. Hanan Bytinski-Salz (Tel Aviv University) who not only collected most of the historical (pre-Hula drainage) specimens of *Donacia simplex* but was also an important mentor to the senior author. We are also indebted to Symposium co-organisers Prof. Dr. Michael Schmitt (Universität Greifswald, Germany) and Dr. Caroline Chaboo (University of Nebraska State Museum, Lincoln, USA).

Additional information

Conflict of interest

No conflict of interest was declared.

Ethical statement

No ethical statement was reported.

Funding

No funding was reported.

Author contributions

DGF performed the fieldwork and wrote most of the text except the molecular biology and bioinformatic analyses. MM and GM performed the molecular biology lab work and bioinformatic analyses and wrote the parts of the text relevant to those analyses.

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Data availability

All of the data that support the findings of this study are available in the main text or Suppl. material 1.

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Supplementary material 1

Sequences retrieved from BOLD system for performing the analyses of this study

Authors: David G. Furth, Matteo Montagna, Giulia Magoga

Data type: table (Excel spreadsheet)

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Anatomy of male and female genitalia of *Acanthoscelides obtectus* (Say, 1831) (Coleoptera, Chrysomelidae, Bruchinae) in interaction*

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Abstract

Armatures of the male intromittent copulatory structures have been surmised to increase male fitness by imposing physiological costs on female re-mating. Female kicking could, consequently, be a counterstrategy to avoid wounding or to prevent males from mating. The membranous endophallus of male *Acanthoscelides obtectus* (Say, 1831) is armed with denticles. Checking if these denticles penetrate the wall of the female genital tract during copulation revealed that only the tip of the median lobe of the aedeagus is intromitted into the female genital opening during copulation. The everted endophallus extends over the full length of the ovipositor, and the spermatophore is placed in the bursa. Identification by means of light microscopy and Micro-CT of the exact relative position of male and female copulatory organs while mated confirmed that the denticles do not cause wounds in the vagina wall. Parts of the inner wall of the bursa copulatrix are covered with inward pointing denticles. Already mated females kick mounting males by vehement movements of their hind legs, thereby preventing mating. In contrast, virgin females usually accept the first male they encounter and terminate copulation by slower movements of their hind legs. The same applied to females who accepted re-mating the second day after the first copulation. *Acanthoscelides obtectus* females kick males off to prevent rather than to terminate copulation. Copulatory structures as well as behaviour may have different functional roles in different beetle species, even within the Bruchinae.

Key words: Bursa copulatrix, endophallus, female kicking, morphology



Academic editor: Caroline Chaboo

Received: 7 February 2023

Accepted: 3 April 2023

Published: 30 August 2023

ZooBank: <https://zoobank.org/37266E41-17B5-4A8B-81E8-70E1BCAF0A99>

Citation: Schmitt M, Neumann A, Lin S-W (2023) Anatomy of male and female genitalia of *Acanthoscelides obtectus* (Say, 1831) (Coleoptera, Chrysomelidae, Bruchinae) in interaction. In: Chaboo CS, Schmitt M (Eds) Research on Chrysomelidae 9. ZooKeys 1177: 75–85. <https://doi.org/10.3897/zookeys.1177.101621>

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Introduction

The evolutionary interests of males and females regularly differ due to the different amounts of resources invested in reproduction. There is also a high differential in certainty of parentage between males and females. This leads to sexual conflict, and this conflict resulted in evolutionarily frequent morphological and behavioural adaptations in males to induce wounds in females during copulation and respective counteradaptations in females (Parker 1979; Arnqvist and Rowe 2005). In many insect taxa the male intromittent organ is armed with hooks, spines or denticles (Rönn and Hotzy 2012). This fact had been observed in seed beetles (Bruchinae) long before a possible functional explanation was hypothesised, see, e.g., the drawings of aedeagi in Borowiec (1987), Johnson (1990), or

* Extended version of a talk presented to the 10th International Symposium on the Chrysomelidae, Helsinki, Finland, 21 July 2022.

Schmitt (1985: fig. 40). When Crudgington and Siva-Jothy (2000) found that the spines of the everted endophallus of male cowpea weevils, *Callosobruchus maculatus* (Fabricius, 1775) (Chrysomelidae: Bruchinae), perforated the wall of the bursa copulatrix in the female, they conjectured that this kind of genital damage prevents females from re-mating thereby increasing the fitness of the male by helping the male to control copulation duration or by decreasing the probability of subsequent matings of the female with other males. However, Edvardsson and Tregenza (2005) found no reluctance to re-mate in female *C. maculatus*, and Rönn and Hotzy (2012) showed that the male spines probably do not function as an anchor that prevents the male being kicked off, a possible alternative functional role suggested, e.g., by Edvardsson and Tregenza (2005). Female *C. maculatus* regularly kick off males during mating and by doing so terminate copulation and presumably reduce the probability of wounding (van Lieshout et al. 2014). Dougherty and Simmons (2017) studied *C. maculatus* pairs in copula by means of X-ray micro-CT scanning and found a temporal separation between the onset of wounding and the onset of female kicking.

Female bean weevils, *Acanthoscelides obtectus* (Say, 1831), have an ovipositor consisting of an internal and an external sclerotised tube through which the membranous vagina extends (Fig. 1). The vagina is proximally enlarged and forms a blind ending, the bursa copulatrix. There the spermatophore is placed during copulation. The spermathecal duct reaches the genital tract at the transition between bursa and vagina near the opening of the oviduct (Huignard 1968).

The male copulatory organ, the aedeagus, consists of a sclerotised median lobe, essentially a tube through which the ejaculatory duct runs from the bas-

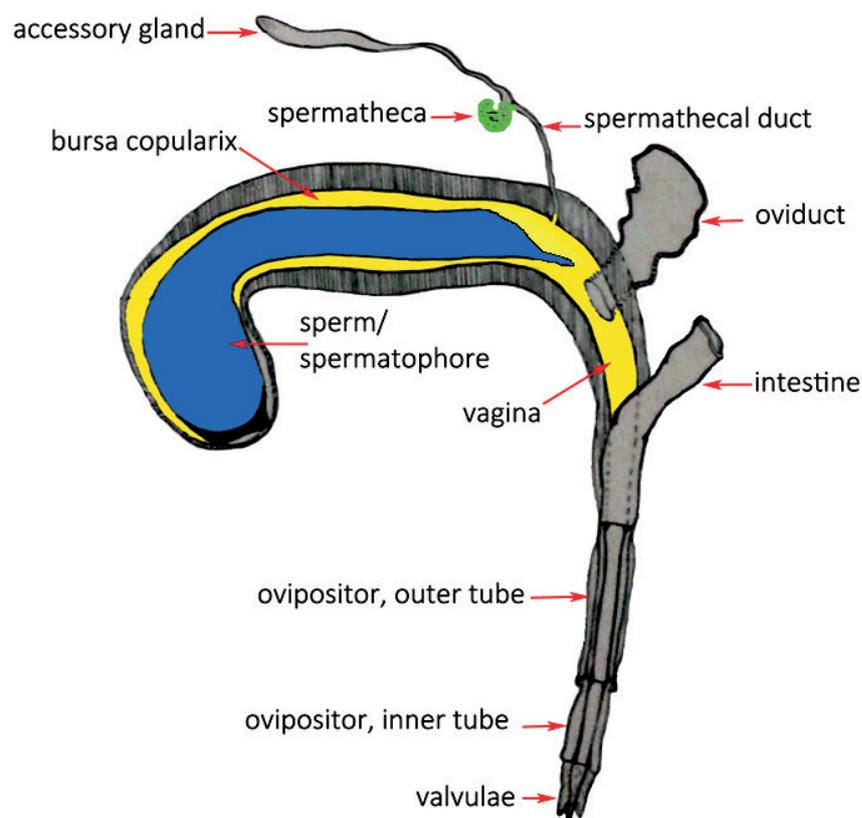


Figure 1. The female genital tract of *A. obtectus*. Schematic drawing after Huignard (1968).

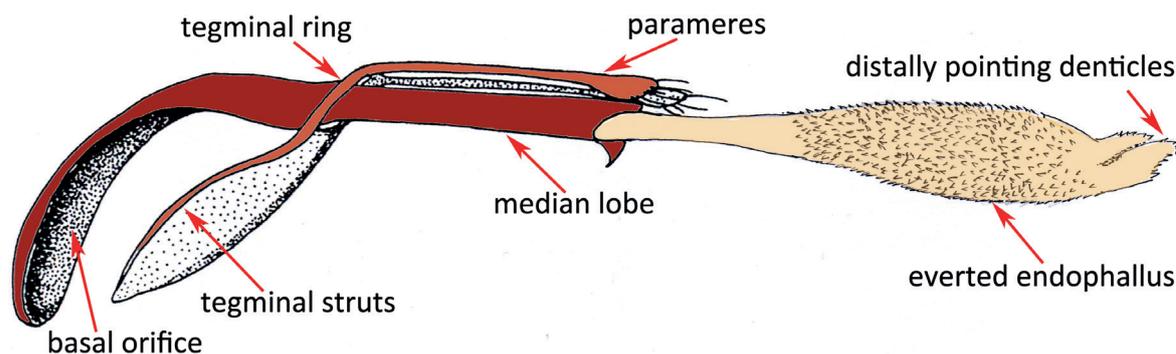


Figure 2. The male copulatory organ of *A. obtectus*. Schematic drawing after Schmitt (1985) and Dungelhoef and Schmitt (2006).

al orifice to the distal opening, and the tegmen that forms a ring around the median lobe and extends basically into paired struts and distally into paired parameres. The ejaculatory duct is distally enlarged and forms a membranous inflatable enlargement, the endophallus (Fig. 2).

Since the endophallus of male bean weevils is equipped with denticles or spicules (Dungelhoef and Schmitt 2006), we wanted to know if these denticles could also perforate the wall of the bursa copulatrix like the spines in *C. maculatus*. To this aim, we studied the anatomy of mated pairs with light microscopy and micro-CT. We also conducted mating experiments to explore female mating behaviour depending on their reproductive status.

Cowpea weevils and bean weevils are cosmopolitan pests on stored products. Therefore, the life history of these two species has been studied for a long time and is well known (e.g., Zacher 1933; Devi and Devi 2014). Since their larvae develop in dry legume seeds, these beetles can easily be kept in the laboratory.

Materials and methods

Animal keeping

A live population of *Acanthoscelides obtectus* beetles (bean weevils) that we obtained from Dr. Thomas Degenkolb, Justus-Liebig-Universitat Gieen, Germany, was kept at room temperature in the lab building of the Zoological Institute of the University of Greifswald, Germany, in a transparent plastic container of 23 × 14 × 15 cm (L × W × H) with a close-mesh fabric covered airing opening at room temperature of ca. 21 °C. They fed on and developed in organic bean seeds of ca. 1 cm length.

Light microscopy

Ten females and males were randomly taken from the breeding container and set in a block bowl of 4 × 4 cm. When they copulated they were fixed by liquid nitrogen and dissected in distilled water or 96% ethanol under an Olympus Stereomicroscope SZ4045. The isolated genitalia were studied using an Olympus CX40RF200 or an Olympus BX60 equipped with a Zeiss AxioVision 4.8 digital camera. We used a manually sharpened minuten pin to dissect the isolated coupled male and female genitalia that were glued onto a surface with

a viscose Polyvinylpyrrolidone solution. To trace the progress of sperm ingestion into the bursa copulatrix we fixed five pairs 3, 5, 6, 7, and 8 minutes after the start of the copulation.

Micro-CT

Two copulating pairs were fixed with liquid nitrogen, transferred into 99% methylated spirit, and stored at -41 °C. The probes were contrasted in 99% ethanol and 1% Iodine. They were critical-point-dried in a Leica EM CPD300 and mounted on a metal pole of 40 × 1.8 mm. Using an Xradia MicroXCT-200 (Carl Zeiss X-ray Microscopy Inc.) one pair was scanned at 10× magnification at 40 kV and 8 W and a pixel size of 1.15 µm, the other at 40 kV at 6 W and a pixel size of 2.22 µm, yielding 980 virtual sections for each pair. We analysed the data and reconstructed the 3D picture by means of Amira 5.6.0 (FEI Visualization Science Group, Burlington, USA).

Mating tests

Virgin beetles hatched from singly kept bean seeds were sexed and set into a block bowl of 4 × 4 cm together with a randomly chosen male. Thirty-three tests were performed. Re-mating trials were done with 14 females of these on day 1 after the first copulation and with 23 females on day 2. In the re-mating trials, the females were offered up to three different males for 10 min each.

Results

Light microscopy

Dissecting the genitalia of mated bean weevil pairs revealed the position of the endophallus inside the female genital tract. Fig. 3 shows the proximal section of the ovipositor with the inner tube in repose. The endophallus spines can clearly be seen, however no traces of perforations of the vagina wall were apparent. The denticles on the tip of the endophallus are longer than those on the main part and point distally.

The tip of the endophallus reaches the transition of the vagina into the bursa (arrowhead in Fig. 4a). We found that parts of the inner wall of the bursa are covered with fine denticles (Fig. 4b). These denticles point towards the proximal end of the bursa.

Micro-CT

Analysis of the micro-CT virtual sections revealed that the inner and the outer tube of the ovipositor are made up of two half-tubes each, a dorsal and a ventral one. Outer and inner tube of the ovipositor are connected by membranes and muscles that allow for extension and retraction of the tubes (Fig. 5).

The endophallus carrying the spermatophore lies inside the vagina that stretches through the inner tube of the ovipositor. Only the tip of the median lobe of the aedeagus is inserted into the female genital opening during copulation, while the parameres remain outside the female abdomen (Fig. 6). The everted endophallus

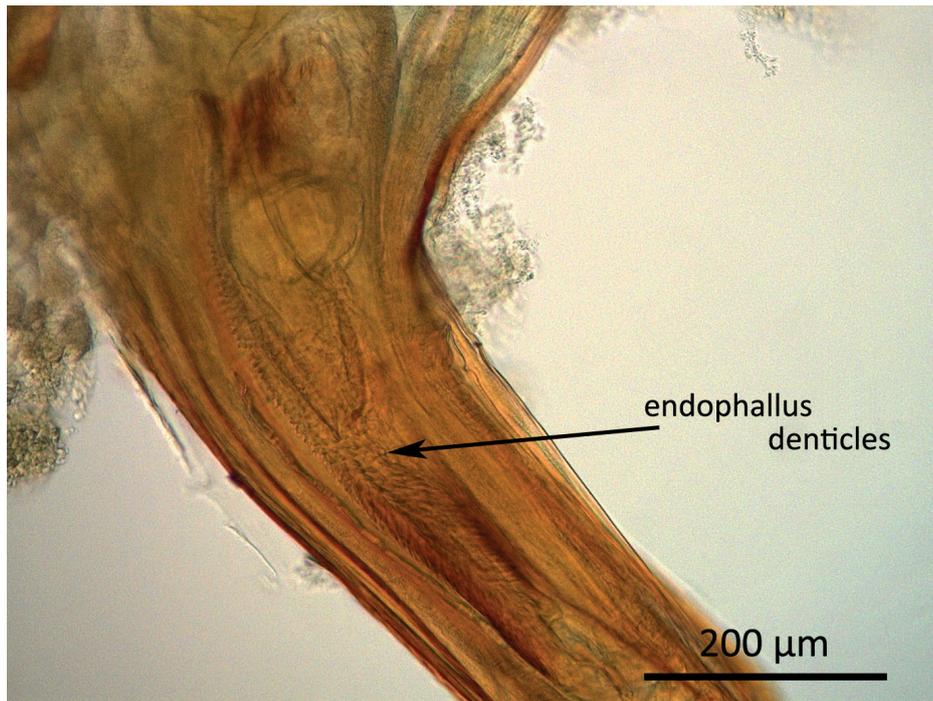


Figure 3. Light microscopic image of a dissected *A. obtectus* specimen. Proximal section of the genital tract of a mated female with endophallus inside.

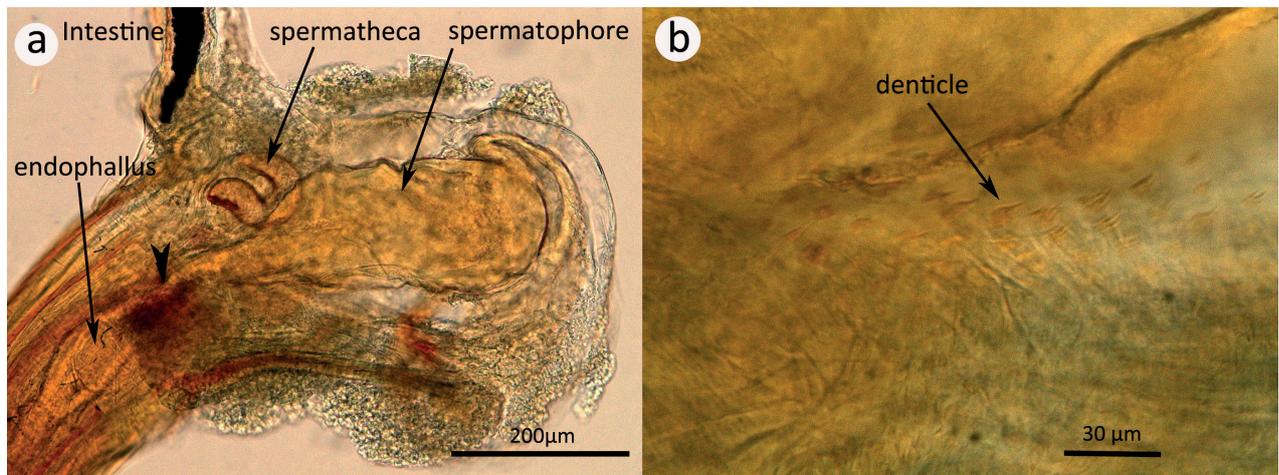


Figure 4. Dissected bursa copulatrix of a mated *A. obtectus* female **a** relative position of endophallus and spermatophore inside the bursa. The arrowhead points to the tip of the endophallus **b** detail showing the inwards pointing denticles on the inner wall of the bursa.

extends through the vagina over the whole length of the retracted ovipositor to the entrance of the bursa copulatrix (Fig. 6b). The female genital tract lies, at least during copulation, immediately under the last visible tergite, the so-called pygidium.

Mating tests

Of the 33 virgin females, 22 (73%) accepted copulations without kicking or wriggling, and two after initial kicking. Copulations of these 24 females ended not by the females kicking off the males but either the females pushed the males

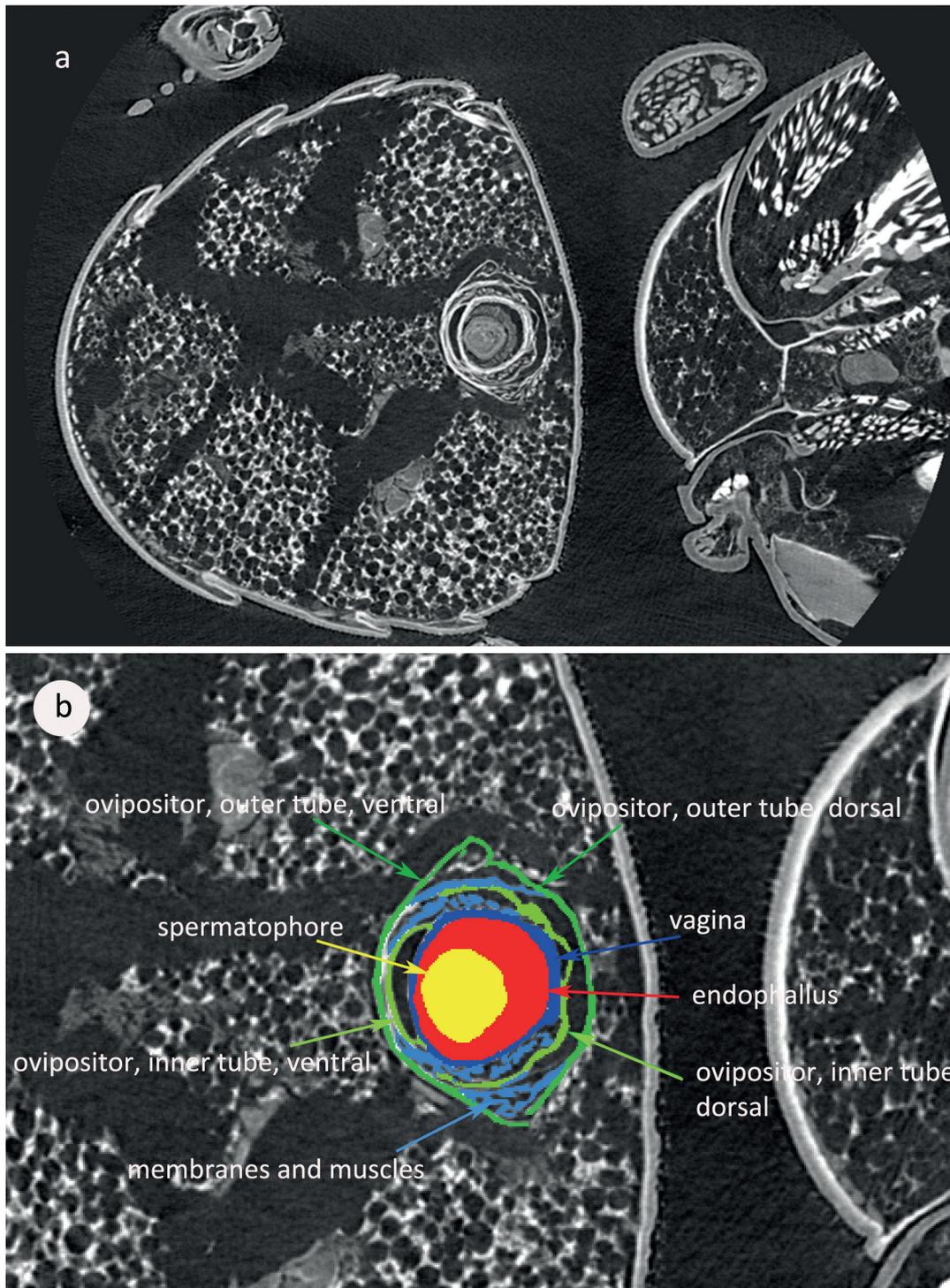


Figure 5. A virtual section through the abdomens of male (right) and female (left) *A. obtectus* fixed in copula. Micro-CT photograph **a** unaltered virtual slice, pixel size 1.15 μm **b** elements of the copulatory organs and the spermatophore labelled (“segmented”) in different colours. Red and yellow: male structures, green and blue: female structures.

away by slow hind leg movements, wriggled their body, or simply ran away after the male had dismounted. Copulation lasted between 6:00 and 11:35 minutes, on average 9:24 minutes. Of the nine females who did not mate, five prevented mating by kicking the males away and three moved away. In one case the female seemed to accept a male but the male did not successfully mate.

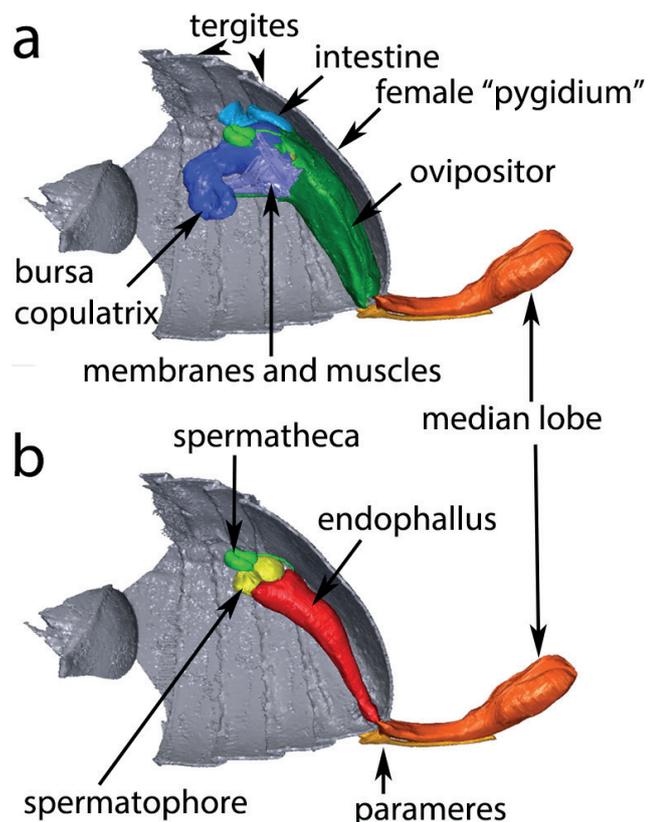


Figure 6. Micro-CT photograph of the 3D reconstruction of the coupled male and female *A. obtectus* genitalia, fixed during copulation. The spermatophore had not yet completely filled the bursa copulatrix at the time of fixation **a** the outer tube of the ovipositor covers the inner tube and the vagina **b** all components of the female genital tract except the spermatheca removed to show the shape and the extension of the everted endophallus.

All females that were tested for re-mating on day 1 after the first copulation ($n = 14$) prevented a second copulation by kicking off a male that aimed at mounting. Eight of the 23 females that were tested on the second day after their first copulation, accepted re-mating. Copulations lasted between 5:35 and 11:37 minutes. The 15 that did not mate kicked the male or ran away.

Discussion

The central question of our study could be answered: in *Acanthoscelides obtectus*, the denticles on the surface of the endophallus do not perforate the wall of the vagina during copulation. The function of the denticles on the endophallus might be to enhance the friction between male and female copulatory organs when the endophallus is inflated inside the female genital tube. Kingsolver (1970) surmised that in seed beetles these armatures provide a certain foothold of the male during copulation, but it is unclear if they have an impact on the copulation duration. Since the spikes on the tip of the endophallus point distally (Fig. 2), they might also push the spermatophore into the bursa copulatrix. These distally pointing denticles could as well pierce the spermatophore and by doing so aid sperm release, as it was suggested for *Callosobruchus maculatus* by Dougherty and Simmons (2017).

An alternative functional role could be the mechanical stimulation of the female during copulation (see Eberhard 1985: 157–166). Simmons (2014) sum-

marises that “non-intromittent genitalia are subject to sexual selection through their effects on mating success, while intromittent genitalia are subject to selection through their effects on fertilisation success”. This underlines the idea that the endophallus ornaments enhance male fitness by stimulating the female and so possibly signalling male quality, i.e., prospective fitness.

The male inserts only the tip of the median lobe into the female genital opening (Düngelhoef and Schmitt 2006) and the parameres remain outside of the female body and function most probably as “genital feelers” (Düngelhoef and Schmitt 2010). The sclerotised parts of the copulatory organs of both sexes do not couple mechanically, i.e., there is no sign of a “lock-and-key” mechanism. Thus, our observations are in accordance with the general hypothesis of Eberhard (1985) that the copulatory organs are shaped during evolution by sexual selection. Other than many Coccinellidae (Yadav and Pervez 2022), males of *Acanthoscelides obtectus* do not perform vigorous shaking during copulation. Consequently, there is no external sign of movements of the male genitalia inside the female genital tract. The males, however, move the tips of the parameres softly over the last sternite of the females during mating (Düngelhoef and Schmitt 2006). These movements are governed by muscles that are in direct connection to the muscles everting the endophallus. This suggests a coupling of movements of the parameres and of the endophallus so that a stimulatory function is easily possible.

The inner tube of the ovipositor is in repose slipped into the outer one “like a telescope” (Lindroth and Palmén 1970), similarly to the Eumolpinae (Flowers and Eberhard 2006). The virtual cross-section through the abdomen of a female in copula (see Fig. 5) shows that the ovipositor tubes are each composed of two half-tubes. These half-tubes are most probably phylogenetically and ontogenetically derivatives of the tergites and sternites of the female 8th and 9th abdominal segments (Verhoeff 1893). The denticles on some areas of the wall of the bursa copulatrix can possibly keep a spermatophore in place and prevent it from sliding out.

While *Callosobruchus maculatus* virgin and mated females regularly terminated copulation by kicking off the mating male (van Lieshout et al. 2014), we found that *A. obtectus* mated females prevented subsequent mating by kicking off males. When the males did not terminate the copulation by dismounting, the females terminated the copulation by wriggling their body and/or pushing the males with their hind legs. It seems that female kicking plays a different role in the two species. Seemingly, *C. maculatus* females kick to terminate copulation while *A. obtectus* females kick to prevent copulation. However, Mbata et al. (1997) observed that mated females of *Callosobruchus subinnotatus* (Pic, 1914) in some cases prevented males from mating by kicking them off. Thus, female kicking to prevent mating is either a species-specific behaviour or *A. obtectus* females can also terminate mating by kicking males off but did not so in our trials, for whatever reasons.

Earlier authors have found cuticular spicules (small needle-like processes) or denticles (small tooth-like sclerotised structures) on the endophallus (or “internal sac”) in all investigated seed beetle species (e.g., Hoffmann 1945; Borowiec 1987). Düngelhoef and Schmitt (2010) found endophallus denticles in *Mecynodera coxalgica* (Boisduval, 1835) of the chrysomelid subfamily Sagrinae (the putative sister group of the Bruchinae, Reid 2014). We hypothesise that these structures were present in the ancestor of Bruchinae and Sagrinae. No such armatures were found in a reed beetle (Donaciinae) and a shining leaf beetle (Criocerinae) (Schmitt and Uhl 2015). Flowers and Eberhard (2006) described microspicules,

hooks, spines, and needles on the endophalli of Neotropical Eumolpinae and Galerucinae. Most probably such structures are phylogenetically as old as the earliest Coleoptera and were reduced and/or modified many times independently.

In the groups in which spines or denticles occur on the endophallus, they are of different length, shape, and position in the different species where they were observed. This suggests that these structures fulfil different functional roles in different groups, e.g., terminating copulation in *Callosobruchus* species or preventing copulation in *A. obtectus*. Van Haren et al. (2017) found that ablating genital armatures in *Callosobruchus subinnotatus* (Pic, 1914) males resulted in a reduction in female egg production. This means that post-mating sexual selection might play a crucial part in the evolution of the equipment of male genitalia with denticles, hooks, or spines. As Flowers and Eberhard (2006) have stated, the morphological diversity of leaf beetle genitalia certainly also represents a diversity of functional roles.

Acknowledgements

We thank Dr. Thomas Degenkolb (Justus-Liebig-Universität Gießen, Germany) for a breeding set of bean weevils, Gabriele Uhl (University of Greifswald, Germany) for reading the manuscript, and the Uhl lab group at the University of Greifswald for inspiring discussions. We are also grateful for valuable reviews of our manuscript by R. Wills Flowers (Tallahassee, FL, USA), Geoffrey Morse (San Diego, CA, USA), an anonymous reviewer, and the subject editor, Caroline S. Chaboo (Lincoln, NE, USA).

Additional information

Conflict of interest

No conflict of interest was declared.

Ethical statement

No ethical statement was reported.

Funding

No funding was reported.

Author contributions

Conceptualization: acquisition of morphological and behavioural data: AN, 3D reconstruction: SL. MS. Data curation: MS. Formal analysis: MS.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Architecture, construction, retention, and repair of faecal shields in three tribes of tortoise beetles (Coleoptera, Chrysomelidae, Cassidinae: Cassidini, Mesomphaliini, Spilophorini)

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Academic editor: Michael Schmitt

Received: 24 February 2023

Accepted: 10 May 2023

Published: 30 August 2023

ZooBank: <https://zoobank.org/C4092EE1-1D66-447F-8419-6AE3839B7756>

Citation: Chaboo CS, Adam S, Nishida K, Schletzbaum L (2023) Architecture, construction, retention, and repair of faecal shields in three tribes of tortoise beetles (Coleoptera, Chrysomelidae, Cassidinae: Cassidini, Mesomphaliini, Spilophorini). In: Chaboo CS, Schmitt M (Eds) Research on Chrysomelidae 9. ZooKeys 1177: 87–146. <https://doi.org/10.3897/zookeys.1177.102600>

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Abstract

Animal constructions are the outcomes of complex evolutionary, behavioural, and ecological forces. A brief review of diverse animal builders, the materials used, and the functions they provide their builders is provided to develop approaches to studying faecal-based constructions and faecal-carrying in leaf beetles (Coleoptera: Chrysomelidae). Field studies, rearing, dissections, photography, and films document shields constructed by larvae in two species in two tribes of the subfamily Cassidinae, *Calyptocephala attenuata* (Spaeth, 1919) (Spilophorini), and *Cassida sphaerula* Boheman, 1853 (Cassidini). Natural history notes on an undetermined Cassidini species and *Stolas cucullata* (Boheman, 1862) (Tribe Mesomphaliini) outline the life cycle of tortoise beetles and explain terms. Commonly, the cassidine shield comprises exuviae onto which faeces are daubed, producing a pyramidal-shaped shield that can cover most of the body (up to the pronotum). In *Cal. attenuata* the larval shield comprises only exuviae, while in *Cass. sphaerula*, instar 1 initiates the shield by extending its telescopic anus to apply its own faeces onto its paired caudal processes; at each moult the exuvia is pushed to the caudal process base but remains attached, then more faeces are applied over it. The larva's telescopic anus is the only tool used to build and repair the shield, not mouthparts or legs, and it also applies chemicals to the shield. Pupae in *Cal. attenuata* retain part of the exuviae-only shield of instar VI, while pupae in *Cass. sphaerula* retain either the entire 5th instar larval shield (faeces + all exuviae) or only the 5th larval exuvia. The caudal processes are crucial to shield construction, shield retention on the body, and as materials of the central scaffold of the structure. They also move the shield, though the muscular mechanism is not known. Altogether the faecal + exuviae shields may represent a unique morpho-behavioural synapomorphy for the crown-clade Cassidinae (10 tribes, ~ 2669 species) and may have been a key innovation in subsequent radiation. Defensive shields and domiciles may help explain the uneven radiation of chrysomelid subfamilial and tribal clades.

Key words: Behaviour, *Calyptocephala*, camouflage, *Cassida*, debris-carrying, exuviae, faeces, pupae

Introduction

Animal constructions have fascinated humans for centuries (Smeathman 1781), perhaps as building is one hallmark for our own genus, *Homo* L. (Hominidae). Coral reefs, beaver dams, bird nests, and spider webs are familiar structures, long attracting research attention (von Frisch 1974). The size of animal constructions ranges from microscopic diatoms to coral reef formations visible from space; between their dams and lodges, beavers (Rodentia: *Castor* L.) construct the largest mammalian constructions (Larsen et al. 2021). Animals build with many endogenous and/or exogenous materials secreted or excreted by the maker, taken from other animals, or gathered from the environment. For example, silk is the most renowned animal fibre and is produced only by arthropods; it is very versatile, in cocoons, webs, and for knitting other materials together. Silk is even secondarily co-opted by other animals, including by humans. A bird's nest may be constructed from exogenous materials (e.g., plants, spider webs), lined with feathers (endogenous), or comprise salivary secretions (endogenous) as in nests of swifts (Aves: Apodidae) which humans eat as the birds' nest soup delicacy (Hobbs 2004; Marcone 2005). Constructions may be fashioned by an individual or a community to serve diverse purposes—nurseries and homes, traps, pantry, defences, dispersal devices, to mark territory, to aid communication (e.g., sexual and courtship displays), as physical and chemical barriers to deter predation and parasitism, or as camouflage to sneak up on prey (Hansell 2005). Constructions may be built to withstand wind, tide, and rain and some provide thermoregulation with air-conditioning. In the marine environment, decorator crabs (Hultgren and Stachowicz 2009), sea urchins (Ziegenhorn 2017) and sand mason worms (Carey 1987) build structures for camouflage, defence, and dwelling. A few books offer a primer into the diversity, roles, and engineering skills of animal architects (e.g., McCook 1907; von Frisch 1974; Hansell 1984, 2005, 2007; Turner 2000; Gould and Gould 2007; Arndt 2013). There are also children's book on this topic (Hutchins 1959; Dewey 1991; Nicholson 2003; Nassar and Blasco 2015; Butterfield and Hutchinson 2017). Building behaviours overlap with self-decoration behaviours where animals accumulate diverse debris on their body (see review of Ruxton and Stevens 2015).

This paper concerns building behaviours and structures of certain beetles (Coleoptera: Chrysomelidae). As context for our study, we briefly review animal builders to understand the range of study, research approaches, and implications of materials and architecture. Constructions are the outcomes of complex evolutionary, behavioural, and ecological forces. In his chapter on "Instinct", Darwin (1859: 247–256) discussed these elements in his experiments and analyses of "cell-making insect in the Hive-bee". His approach remains valid today: observe building repertoires, design elements, materials, and purposes. Comparative multi-level analyses of physiology, ecology, ontogeny, and history are required to understand these remarkable morpho-behavioural complexes. Constructions are rich opportunities to investigate the "extended phenotypes" of their builders (Dawkins 1982).

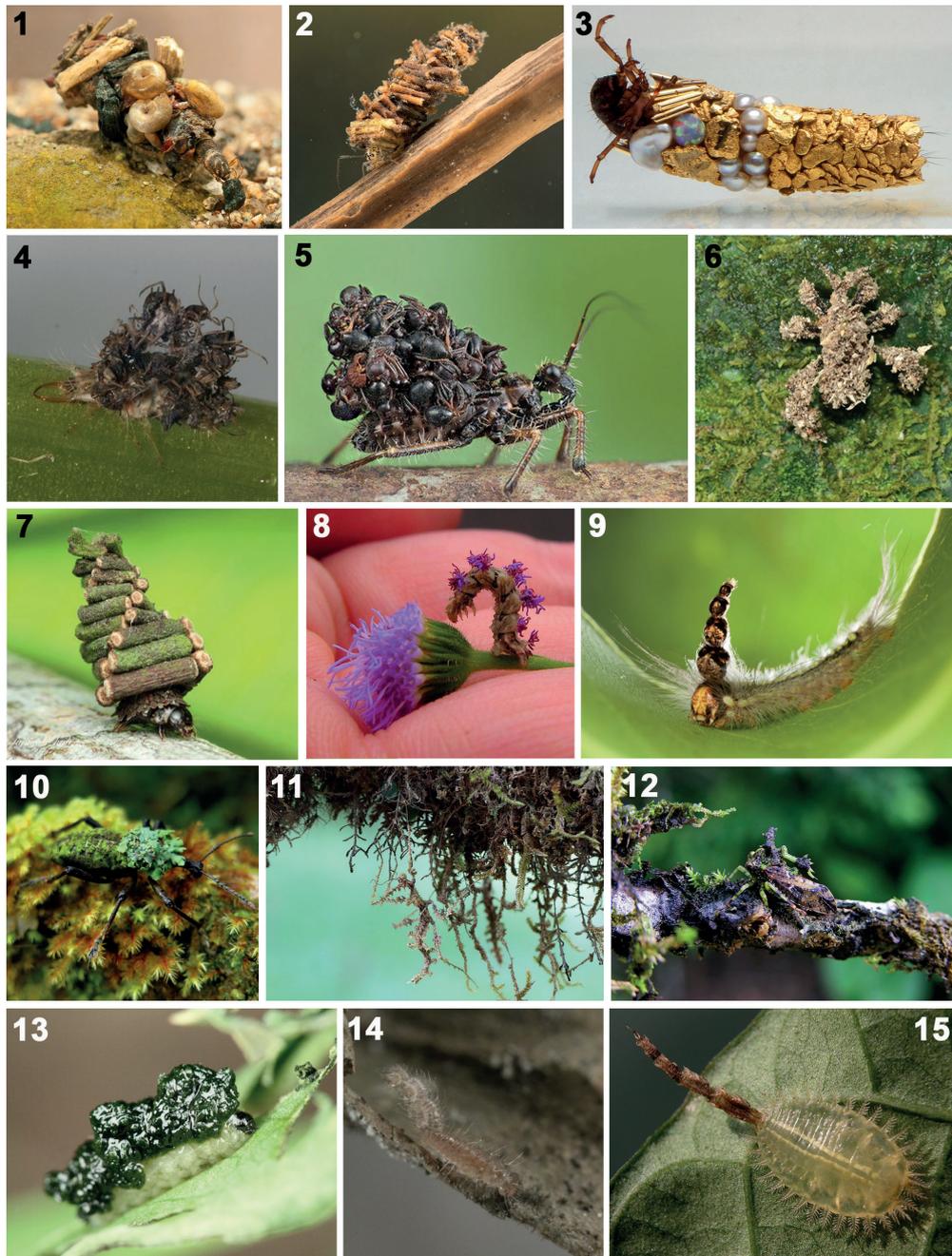
The study of constructions is well-developed in birds, mammals, spiders, and Hymenoptera, as evidenced by documentation of specimens (i.e., in museum collections), construction behaviours, materials, terminology, and functions.

The best-known insect architects are those social insects where the entire colony builds a communal “city”, Hymenoptera (ants, bees, wasps; Fabre 1915; Wheeler 1928; Sakagami and Michener 1962; Wilson 1971) and Isoptera (termites; Lüscher 1961; Krishna and Weesner 1969; Jeanne 1975; Mathews and Mathews 1978). Constructions can be prominent surface features or extend over a wide expanse and deep underground, where specialised chambers and corridors support different activities of members and enable precise control of ventilation, heat, humidity, and responses to invasions.

Many insects are solitary architects (Figs 1–15), but they are far less known, likely due to few collections of these builders, their constructions, scant study of building repertoires, and limited evolutionary analyses. Their constructions serve most commonly to protect the vulnerable egg, larval, and pupal stages that cannot easily escape an attack. These insect mothers invest in protective devices around eggs, including elaborate oothecae (e.g., Dictyoptera: Legendre et al. 2015) and nests (e.g., mud and clay cells of some Carabidae beetles: Claassen 1919; Brandmayr and Brandmayr Zetto 1974). In Scolytidae beetles, females oviposit on or under the bark and the larvae tunnel through the wood by eating the wood and creating galleries under bark. Many insects build protections for their sedentary pupae (e.g., golden cages in Curculionidae: Hyperinae: Hoffman 1954; Scherf 1964; Janzen 1979, 1983; Aiello and Stockwell 1996). Constructions may serve as nutritional shelters, protecting the individual and providing a food source; for example, in “cigar” weevils (Curculionidae: Rhynchitinae), females roll leaves into a dual-purpose nest that serves later as a paedotrophic chamber where larvae feed on the inner walls (Brandmayr 1992).

Building materials are as diverse as the builders. Materials may be secreted by the body (endogenous), extracted from the environment (exogenous), or a combination. Endogenous secretions can create colonial structures (e.g., a coral reef) or be carried by a single individual (e.g., molluscs in their secreted shells; McDougal and Degan 2018). Integumental secretions of slime and wax occur in sawfly larvae (Hymenoptera; Eisner 1994). Homoptera species exhibit diverse constructions: wax tail filaments (Smith 2010), sugary ‘lerp’ domiciles of scale insects (Gilby et al. 1976), and liquid marbles in aphids (Kasahara et al. 2019). Salivary secretions can serve as a glue or a building material (e.g., salivary foam moulded into pupation chambers for Criocerinae leaf beetles (Tishechkin et al. 2011). Anal secretions form the elaborate oothecae in Dictyoptera (Legendre et al. 2015).

Exogenous building materials of insects are difficult to catalogue, being so diverse, and include both organic and inorganic materials. Soil is a readily available building resource; tiger beetle larvae (Coleoptera: Cicindelidae) build burrows in the ground from where they can grab prey; some add a mud turret to raise the entrance above possible flooding (Kinsley and Pearson 1981; Shivashankar et al. 1988). Mobile residences include ornate cases by Trichoptera larvae with small pebbles or leaves (Figs 1, 2), a behaviour even co-opted for insect-built jewellery (Fig. 3; Duprat 2020). Leaves are an abundant resource; simple leaf constructions can be achieved by targeted cutting to bend over the leaf (e.g., some Lepidoptera, Loeffler 1996; some cassidine beetles, Prathapan et al. 2009). Complex leaf constructions require more time (e.g., rolled leaves of Attelabidae weevils, Vanin and Bená 2020; glued leaves of some Thysanoptera (thrips), Mound and Morris 1999). Many Lepidoptera caterpillars use their



Figures 1–15. Insects with backpacks. **1** Trichoptera: Caddisfly larvae in case (photograph: S. Marshall) **2** Trichoptera: Caddisfly larvae in case (photograph: S. Marshall) **3** Trichoptera: larva with its case, 1980–1994, gold, opal, pearls (case length = 1 inch; photograph: H. Del Olmo (from Hubert Duprat exhibition, ADAGP)) **4** Neuroptera: Chrysopidae: larva with exuvial debris (photograph: Masayuki Hayashi) **5** Hemiptera: Reduviidae: assassin bug, Singapore (photograph: Nicky Bay) **6** Hemiptera: Reduviidae, assassin bug, Costa Rica (photograph: Dieter Mahsberg) **7** Lepidoptera: Psychidae: caterpillar with its bag **8** Lepidoptera: Geometridae: Wavy Emerald Moth caterpillar, *Synchlora aerata* (Fabricius, 1798), covering itself with petals of its host, *Liatrix Gaertn. ex Schreb. sp.* (Asteraceae) (photograph: Hope Abrams) **9** Lepidoptera: Nolidae: caterpillar of *Uraba lugens* Walker, 1866 with stack of their exuvial head capsules, Australia (photograph: Alan Henderson) **10** Coleoptera: Curculionidae, *Gymnopholus* Heller, 1901 weevil carrying lichen garden, Papua New Guinea (photograph: Adrian Tejedor) **11** Phasmida: stick insect, *Trychopeplus laciniatus* (Westwood, 1874), with exoskeleton modified to appear like moss, Costa Rica (photograph: Kenji Nishida) **12** Hemiptera: Membracidae with exoskeleton modified to appear like moss, Costa Rica (photograph: Kenji Nishida) **13** Coleoptera: Curculionidae: weevil larva retains moist faecal coat (photograph: Filip Trnka) **14** Coleoptera: Erotylidae: larva of *Toramus Grouvelle, 1916* with shield of exuviae held on setae (photograph: Takahiro Yoshida) **15** Coleoptera: Cassidinae: Cassidini: larva of *Microctenochira* Spaeth, 1926 undetermined species with shield of exuviae only (photograph: Kenji Nishida).

silk to sew twigs (Fig. 7) or leaves into tunnels, tubes, and portable cases (e.g., Psychidae bagworms, Sharp 1899; Frowhawk 1913; Bucheli 2002). Embioptera make silken galleries where they live (Büsse et al. 2015). Exogenous materials may be harvested from the droppings of other animals; for example, mollusc shells adopted or robbed by hermit crabs (Rodrigues and Rodrigo 2009) or homopteran wax stolen by Neuroptera (Eisner and Silberglied 1988). Some constructions are compound combinations of exogenous and endogenous materials (e.g., a bird's nest of twigs and spider silk, Hansell 2005).

Many solitary insect builders carry a 'backpack' with simple or compound 'debris' (endogenous, exogenous, environmentally acquired, organic or inorganic). Debris backpacks provide the builder with a mobile cloak that is usually assumed as a camouflage to avoid predators or a disguise for hunting (Cardé and Bell 1995; Tauber et al. 2014; Wang et al. 2016). Inorganic 'debris cloaks' of soil dust and small sand grains are found in insects (Odihambo 1958; McMahan 1982, 1983a, b; Cardé and Bell 1995; Eisner 2003). In Trichoptera (caddisflies) constructed cases of silk may be decorated with sand, stones or shells and are used as retreats, homes, and to seine water for food (Wallace 1975; Wallace and Sherberger 1975; Otto and Svenson 1980; Ferry et al. 2013). The plaster bagworm (Lepidoptera: Tineidae) similarly makes a silken case that traps soil, lint, and even paint chip (Aiello 1979; Villanueva-Jimenez and Fasulo 1996). Organic debris cloaks can comprise small plant fragments such as twigs, leaves, trichomes, and wood fibres (Eisner et al. 2001). Nymphs of *Reduvius personatus* (L.) (Hemiptera: Reduviidae) are called "masked hunters" because of their debris of dust and soil (Fig. 6; Harz 1952; Dispons 1955; Cardé and Bell 1995; Cai et al. 2002; Weirauch 2006; Ramírez et al. 2013). Some Chrysopidae (Neuroptera) retain trichome debris covers (Smith 1922, 1923; Stitz 1931; Eisner et al. 1978, 2001; Eisner and Eisner 2000b; Anderson et al. 2003; Nakahira and Arakawa 2006; Haruyama et al. 2012). Remarkably, some insects grow a living backpack, a garden of lichens, algae, mosses, and fungi (Fig. 10; Gressitt et al. 1965, 1968). Gressitt (1977) used the term "epizoic symbiosis"; this camouflage resembles those insects that truly are morphologically adapted with a moss-like appearance that matches their lichen + moss covered habitat (e.g., Figs 11, 12).

Organic debris backpacks comprising insect exoskeletons (exuviae, cast skins) appear in diverse insects (Figs 4, 5, 9, 14, 15). These exuviae can be the builder's own castoffs or, more macabre, from their prey. Examples of the first type, retaining their own exuviae, are exhibited in some Lepidoptera and Coleoptera larvae. An Australian caterpillar retains a stack of its previous head capsules, giving it the nickname "mad hatterpillar" (Fig. 9; Lepidoptera: Nolidae; McFarland 1980; Pearson 2013). In Coleoptera, exuvial retention by larvae is known in some Erotylidae (Figs 14; Leschen 2003; Yoshida and Leschen 2020) and in Cassidinae (Fig. 15; Chaboo 2007). The second type of exuvial retention uses those of prey and has been described as a "corpse cover" (Brandt and Mahsberg 2002), a "corpse camouflage" (Stromberg 2012), and a "wolf in sheep's clothing" strategy (Eisner et al. 1978, after ancient rhetorical Greek and Italian fables, e.g., Basilakis in the 12th century; Beneker and Gibson 2016; Absternius 14th century; the Bible (King James Bible Online 2023)). Some Chrysopidae larvae (Fig. 4; Neuroptera) carry the exuviae of their aphid prey, to fool aphid-tending ants (Hayashi and Nomura 2011). Many Hemiptera adults and nymphs retain corpse backpacks (Fig. 5; Odihambo 1958; McMahan

1982, 1983a, b; Zeledón et al. 1973; Weirauch 2006), some adding dust and soil, for a mix of organic and inorganic debris. Corpse covers and debris cloaks may provide mechanical protection, from weather or predators (e.g., spiders, lizards), or permit aggressive mimicry towards their prey (e.g., ants, termites). Olfactory cues can mask the predator (Odihambo 1958; Brandt and Mahsberg 2002; Jackson and Pollard 2007; Stromberg 2012) or may become a secondary signal that attracts enemies (Agelopoulus et al. 1995; Benelli et al. 2013; Huang et al. 2022).

Dung (faeces, frass, fecula) is an unconventional organic debris as faeces are typically considered unappetising and unhygienic waste products, vectors of pathogens, and an offensive by-product of animal metabolism. Most animals simply eliminate and avoid their waste, even finding creative ways to dispose of their faeces (e.g., mining insects, Frost 1942). Yet, faeces are a cost-free and readily available benefit of regular feeding. In Mammals, faecal piles function as territory markers (e.g., Stewart et al. 2001) and latrine sites (e.g., meerkats, Jordan et al. 2007). Counter-intuitively, faeces are a resource; indeed, humans have been using dung (Henry et al. 2016; Arranz-Otaegui et al. 2017; Smith et al. 2022) as a fertiliser since early agriculture, to burn as fuel, for plastering adobe walls and floors (faeces mixed with mud and twigs), in beauty facials ("Uguisu no fun", Moore 2001) and even in ancient (Ge 2000 [4th century]) and contemporary medical faecal transplants and enemas (e.g., Fecal Microbiota Transplantation or FMT; Eiseman et al. 1958; Zhang et al. 2012).

Dung beetles (Scarabaeidae) may be the most famous insects associated with faeces. Both dung beetles and burying beetles (Silphidae) use vertebrate dung for brood balls (Waterhouse 1974; Scholtz and Grebennikov 2004). Many fly groups are also renowned to use faecal habitats.

Many terms for insect faeces appear in the literature. Frost (1942) used 'faeces, fecula and frass' which have become widely used. Other terms are excrement (Hislop 1872; Scudder 1891; Muir and Sharp 1904; Blatchley 1924; Flinte and Valverde de Macédo 2004), excreta (Wood 1966; LeSage 1982; Jolivet and Verma 2002), and scat (Lécaillon 1896; Hinton 1981). Faeces are produced mainly by immature insects since most adult insects produce little wastes. Insect faeces can serve various purposes, such as adult aggregation, finding mates, brooding, or oviposition deterrent; they can signal pest issues. They can also recycle faeces in multiple ways; the process is sophisticated in social insects where faeces are used as a structural component of the nest and hive walls and as a substrate for growing fungi (Hansell 2005; Weiss 2006). In Coleoptera, faeces can serve for adult aggregation (Tenebrionidae: flour beetles; Suzuki 1985), to find mates (e.g., Cerambycidae: *Hylotrupes bajulus* (L.); Fettköther et al. 2000), brooding, or as an oviposition deterrent (e.g., weevils and cerambycids; Anbutsu and Togashi 2002; Adesso et al. 2007).

Insects in Coleoptera, Diptera, and Lepidoptera have evolved dung-carrying behaviours. Some Lepidoptera caterpillars retain a dry crust of their excreta (e.g., Noctuidae; Preston-Mafham and Preston-Mafham 2003: 406); others use their silk to knit their faeces into "frass chains" (resembling sticks) to build a retreat (e.g., Nymphalidae; Freitas and Oliveira 1992; Caldas 1994; Machado and Freitas 2001). Excremental cases are known in Diptera (e.g., Mycetophilidae; Holmgren 1907; Knab and van Zwaluwenburg 1918) and in Lepidoptera (e.g., Hesperidae; Sharp 1899). Weevils (Curculionidae) exhibit diverse

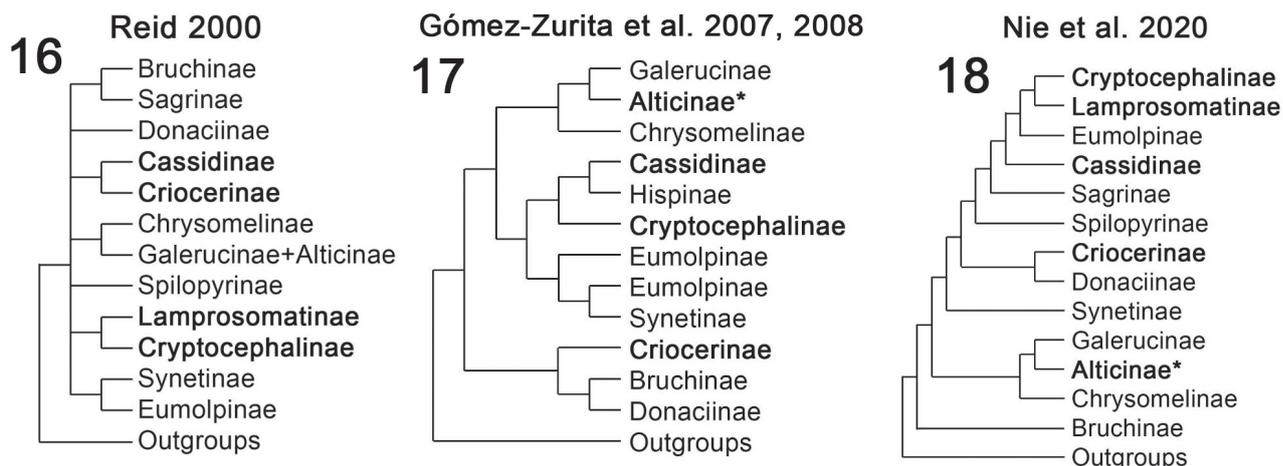
constructions: leaf-rollers (e.g., Attelabidae, Daanje 1975; Mathews and Mathews 1978), lichen-carriers (e.g., Fig. 13, Gressitt et al. 1965; Gressitt 1977; Jolivet 1988a), solid dung (e.g., Ceutorhynchini, Knab 1915), and liquid excremental covers (e.g., Cionini, Gonipterini; Knab 1915; Arzone and Meotto 1978; Janzen 1979, 1983; Crowson 1981; Aiello and Stockwell 1996). Other beetles may construct a faecal or faecal-fungal canopy or retreat (Leschen and Carlton 1993; Leschen 1994; Hanley 1996). It is important to note that faecal retention is most often exhibited by insect larvae and the behaviour has been interpreted mostly as armour, camouflage, or physical barrier to enemies (Weiss 2006).

Debris-carrying, including dung-carrying, is not simply just 'carrying' since individuals often exhibit specialised morphology associated with handling faeces (e.g., anal comb in some Lepidoptera, Frost 1919) or with retaining materials (special setation; Weirauch 2006; Skuhrovec et al. 2017) to build, carry, wear and even repair structures. Enhanced survivorship is often assumed, and in cases where tested, the adaptive value of debris such as frass and faeces has been demonstrated.

In this paper, we focus on faecal-recycling behaviours in Chrysomelidae (leaf beetles), one of the largest clades of beetles with > 40,000 species (Leschen and Beutel 2014). Chrysomelids use their faeces as a biomaterial for constructions and self-decoration behaviours that serve as defensive coats, mobile debris shields, and protective domiciles. Such faecal-based constructions appear as a striking pattern within Chrysomelidae, diagnosing some large subfamilies and appearing also in some small clades.

In general, leaf beetles exhibit diverse building behaviours, including oothecae with multi-layered colleterial secretions (e.g., some Cassidinae), faecal covers (Kalaichelvan and Verma 2000), or with stomach regurgitate (Jolivet and Verma 2002), larval galls (e.g., Sagrinae, Reid and Beatson 2019), and pupation chambers of soil, sand (e.g., some Galerucinae, Prathapan and Chaboo 2011), faeces (Cryptocephalinae; Brown and Funk 2005), or salivary 'foam' (e.g., some Criocerinae, Tishechkin et al. 2011). Bruchine adults build walls within seeds to inhibit fighting (Mano and Toquenaga 2008). Simple leaf shelters are made by larvae and adults of *Leptispa* Baly, 1858 (Cassidinae: Leptispini; Prathapan et al. 2009). Many chrysomelid mothers coat eggs with glandular and excremental applications, often mixed with anal and buccal secretions, and then may cover eggs further with plant pieces or oothecal membranes or faecal cases (Muir and Sharp 1904; Fiebrig 1910; Prevett 1966; Hinton 1981; Jolivet and Verma 2002; Müller and Hilker 2004).

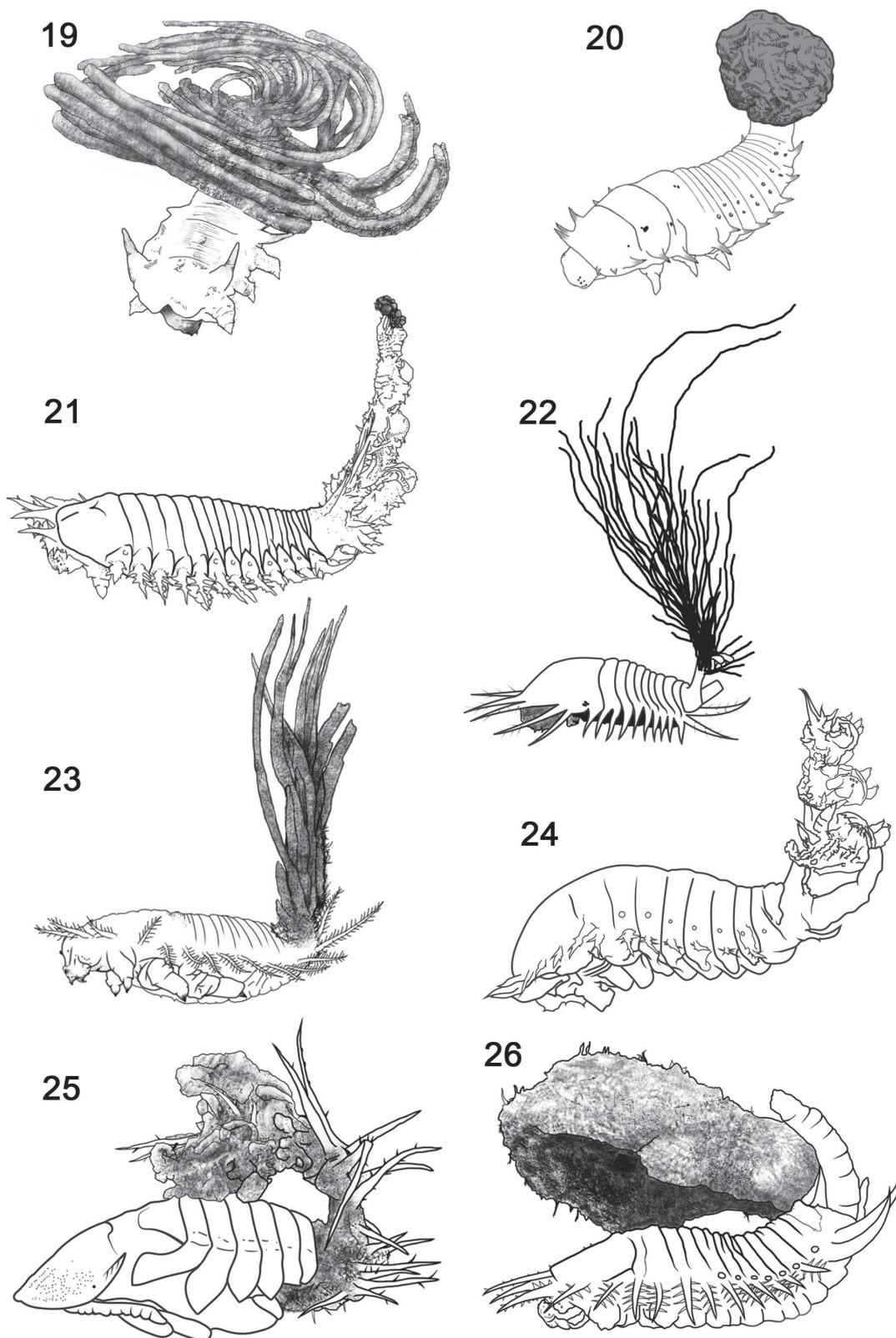
The faecal-based constructions of Chrysomelidae are not a diffuse pattern but are taxonomically focused, are ancient, dated at least 45 million years ago (Chaboo and Engel 2008; Chaboo et al. 2009), and may have three or four independent origins given simple mapping on recent phylogenetic hypotheses of the family (Figs 16–18): within the subfamily Cassidinae; the *Blepharida*-group within the subfamily Galerucinae; Criocerinae; and in the sister subfamilies Cryptocephalinae + Lamprosomatinae. Within Cassidinae (6,320 species in 37 tribes), faecal constructions diagnose a derived monophyletic clade of ten tribes (= the tortoise beetle tribes) where most larvae use their exuviae and/or faeces to build shields over the body (Figs 15, 19–26; Chaboo 2007); these shields may be retained in pupae of some species (Fig. 25). Cryptocephalinae + Lamprosomatinae (~ 6000 species) form a well-accepted clade, called Camptosomata,



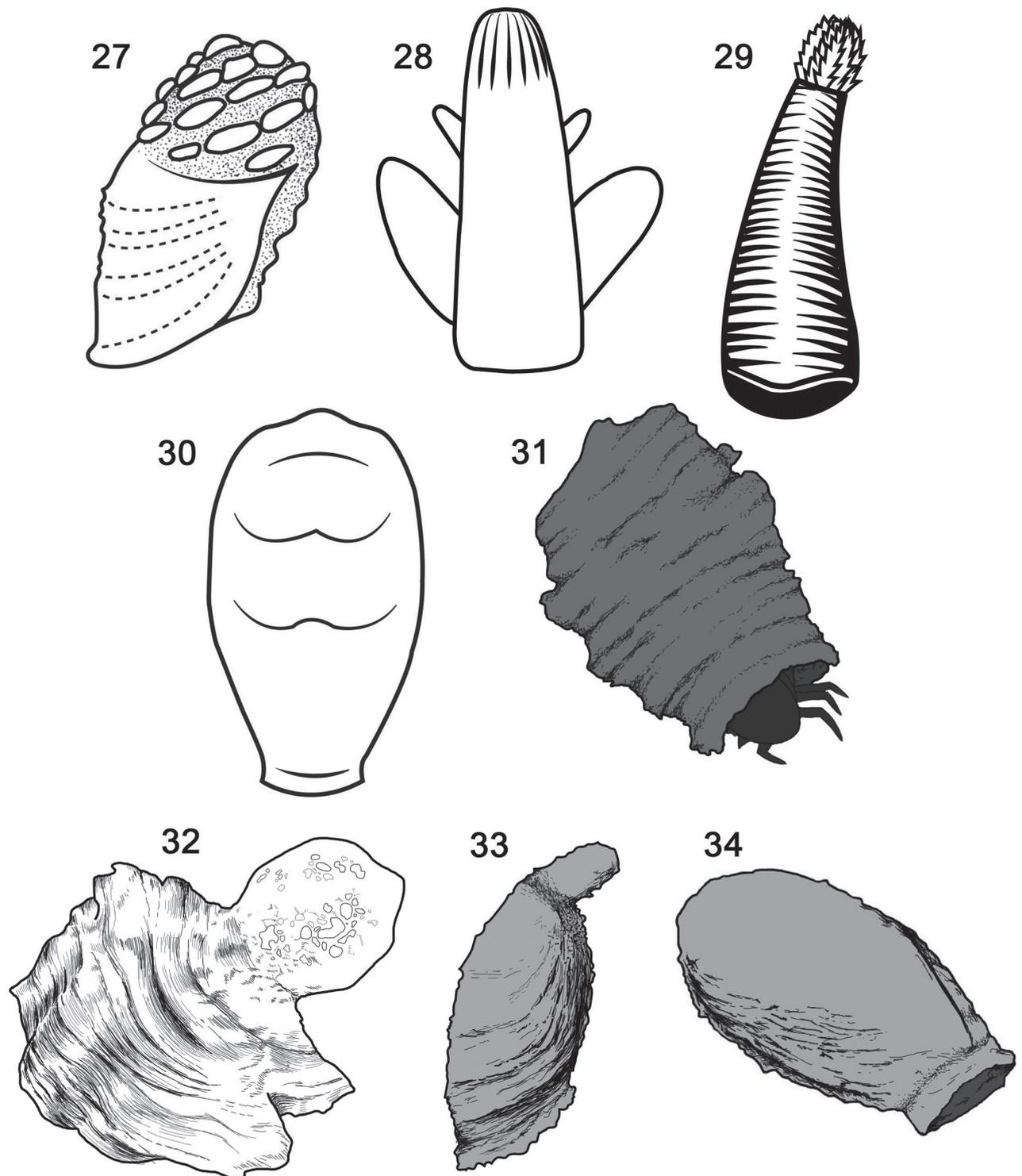
Figures 16–18. Recent phylogenetic hypotheses of Chrysomelidae subfamily relationships, redrawn by L. Schletzbaum from original sources **16** Reid (2000) (morphology-based) **17** Gómez-Zurita et al. (2007, 2008) (sequence-based) **18** Nie et al. (2020) (sequence-based). Other chrysomelid hypotheses to compare are Farrell (1998), Hunt et al. (2007), and Zhang et al. (2018, 2022). These available hypotheses are based on less than 1% taxon sampling of clade diversity. Subfamilies in bold font exhibit major patterns of faecal-based constructions. Alticinae (flea-beetles) is now regarded as the tribe Alticini within Galerucinae, so the faecal-retaining *Blepharida*-group is recognized now within Galerucinae. Only a single species in *Phola* Weise, 1890 (Chrysomelinae) has been reported to retain faeces (Chen 1964, 1985) so it is not a major pattern.

that is distinguished by a complex behaviour where females construct a faecal case around the single eggs and the natal larva keeps that egg case as a rigid portable home (Figs 27–34; Lawson 1976). This faecal case (= faecal bag, scatoshell) becomes the nucleus that the larva continues expanding with their own faeces; eventually the pupa inherits this construction as their pupation chamber (Brown and Funk 2005; Chaboo et al. 2016). Criocerinae is a smaller subfamily of ~ 1400 species whose larvae maintain a wet or semi-solid mass of their faeces directly on their back (Figs 35–37; Vencl et al. 2004). The *Blepharida*-group comprises ~ 21 genera (D’Alessandro and Biondi 2023) within the hyperdiverse Galerucinae (7145 species: Lingafelter and Konstantinov 2000; Nie et al. 2017); this group is distinguished by larvae that keep a single faecal strand held over the body (Fig. 38; Furth 1982, 2004; Furth and Lee 2000) or many faecal pellets directly on the dorsum (Figs 39, 40; Prathapan and Chaboo 2011; Calcetas et al. 2023). In Chrysomelinae (~ 3000 species), larval faecal tubes have been reported only in *Phola octodecimguttata* (Fabricius, 1775) (Chen 1964, 1985) and is a minor building pattern within this large subfamily. It is unclear at present what could be trends in innovations and maternal investments in oviposition site selection, and oothecal and egg-case construction. These chrysomelid constructions and body coats appear to be composites of endogenous and exogenous materials (Table 1), with their own faeces, exuviae, plant materials (trichomes, bark, twigs, decomposing fragments), chemical (plant or animal made), and even fungi. The endogenous materials can include faeces, anal, buccal, and other glandular products, and exuviae. The roles of each material are unknown.

Comparative surveys of the architectures of leaf-beetle constructions, detailed study of morphology associated with construction, retention and repair, and study of constructing behaviours are all needed to elucidate the apparent multiple origins and diversification of these structures. Experimental studies

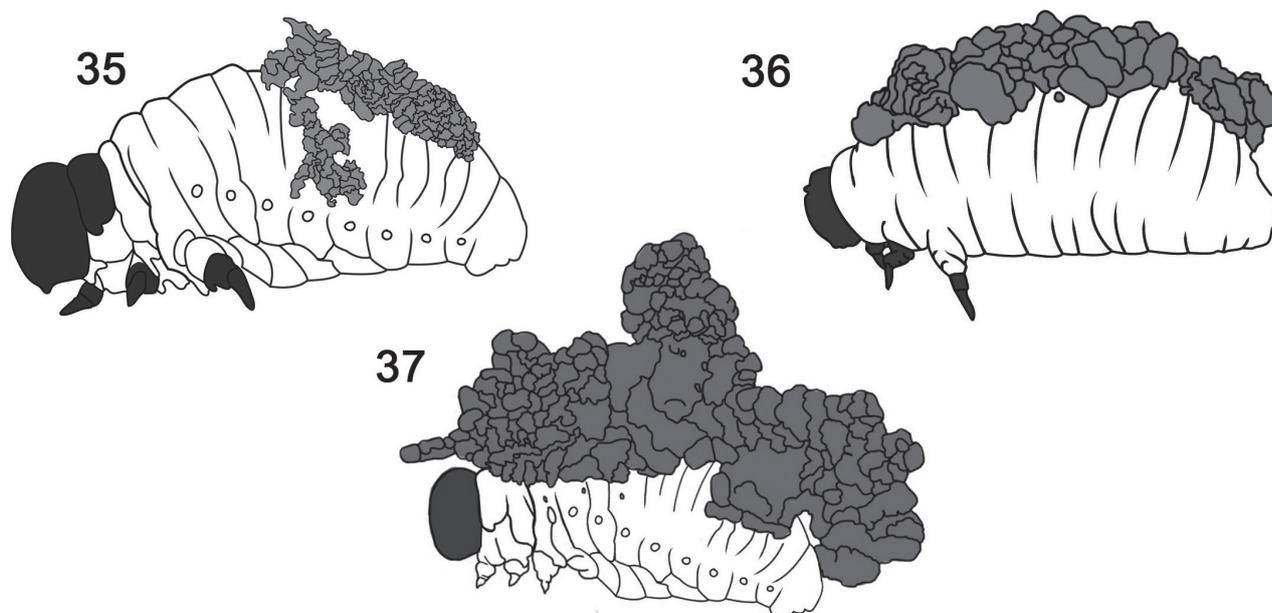


Figures 19–26. Shields of larvae and pupae in four tribes of Cassidinae (Coleoptera: Chrysomelidae) **19** Hemisphaerotini: *Hemisphaerota* Chevrolat, 1836 **20** Ischyrosonychini: *Physonota* Boheman, 1854 **21** Cassidini: *Agroiconota bivittata* (Say, 1827) **22** *Aspidimorpha sanctaerucis* (Fabricius, 1792) **23** Cassidini: undetermined sp. 1 **24** Cassidini: undetermined sp. 2 from Africa, collected by C.S. Chaboo **25** Cassidini: undetermined sp. 3 pupa from Brazil, collected by D. Yanega **26** Cassidinae: Undetermined sp. 4 Costa Rica, collected by K. Nishida. Darkened sections = faeces. Redrawn by L. Schletzbaum from original sources or from specimens.

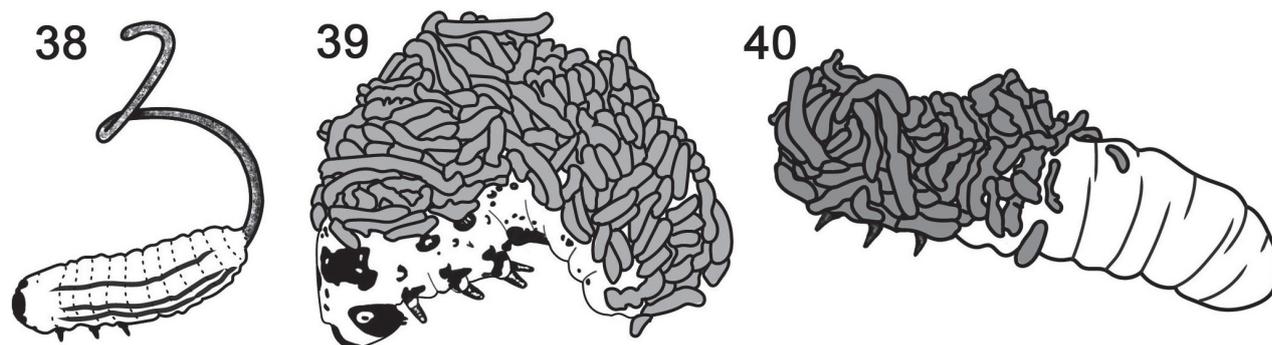


Figures 27–34. Faecal structures of larvae and pupae in Cryptocephalinae (Coleoptera: Chrysomelidae) **27** *Adiscus taiwanus* **28** *Chlamisus* sp. 1 **29** *Chlamisus* sp. **30** *Coenobius taiwanus* **31** *Cryptocephalus trifasciatus* **32** *Fulcidax* **33** *Neochlamisus* **34** Lamprosomatinae. Redrawn by L. Schletzbaum from original sources.

are needed to test proposed hypotheses about the adaptive significance of faecal-based constructions. Such data can explain if and how these unusual faecal constructions could have influenced chrysomelid diversification, producing such uneven subfamilial species diversities.



Figures 35–37. Faecal-based coats of larvae in Criocerinae (shining leafbeetles). **35** Criocerinae sp. 1 **36** Criocerinae sp. 2 **37** *Lema hexastigma*. Redrawn by L. Schletzbaum from original sources.



Figures 38–40. Faecal-based structures and coats maintained by larvae in the *Blepharida*-group (Galerucinae: Alticini; flea beetles). **38** *Blepharida sacra* **39** *Diamphidia* sp. **40** *Podontia* sp. Redrawn by L. Schletzbaum from original sources.

In Cassidinae (~ 6000 species), faecal-based construction behaviour is a significant macroevolutionary event with a radiation of ~ 2700 species after its origin (Chaboo 2007), assuming a single evolutionary origin of faecal shield construction. This crown-clade is called “tortoise beetles” and is distinguished by a unique combination of morphology and behaviours: the larvae are exophagous (or ectophagous) and have paired caudal processes (= urogomphi) onto which they build and carry a debris shield (Figs 15, 19–26) moulded from their own exuviae and faeces. These larvae use a telescopic anus to apply faeces to the shield. The shield can be moved over the body like an umbrella or parasol (Fiebrig 1910; Takizawa 1980; Chaboo 2007; Flinte et al. 2009; Świętojańska 2009). Some exceptions, absence of shield retention, are also known but these appear to be secondary losses given the current phylogenetic views. Tortoise beetles comprise ~ 2700 species classified into ten tribes: Basipriotonini Hincks, 1952; Cassidini Gyllenhal, 1813 (now includes Aspidimorphini and Charidotini); Dorynotini Monrós & Viana, 1949; Eugenysini Hincks, 1952;

Table 1. Architects and materials used for faecal-based shields in subfamilies of Chrysomelidae: Cassidinae (Chaboo 2007; Świętojańska 2009), Criocerinae (Vencl et al. 2004), Cryptocephalinae and Lamprosomatinae (Chaboo et al. 2016), and Galerucinae (Prathapan and Chaboo 2011). Comparison of life stages, materials of larval/pupal faecal-based cases and shields, and larval body parts for construction. Key: + = present; – = absent; ? = unknown.

Feature		Cassidinae: 10 tribes, tortoise beetles	Chrysomelinae: <i>Phola</i> sp. ⁸	Criocerinae	Galerucinae: Alticini: <i>Blepharida</i> -group	"Camptosomata"		
						Cryptocephalinae	Lamprosomatinae	
Stage	Mother	–	?	–	+	+	+	
	Egg	+/-	?	–	+/-	+	+	
	Larvae	+/-	+	+	+	+	+	
	Pupae	+/-	?	–	?	+	+	
Endogenous								
Larval/pupal material	Faeces	+/-	+	+	+	+	+	
	Exuviae	+/-	?	+ ¹ /-	–	–	–	
	Chemicals	+/-	?	+/-	+/-	?	?	
	Waxes	?	?	?	?	?	?	
	Saliva	?	?	?	?	?	?	
	Regurgitates	?	?	?	?	?	?	
	Exogenous							
	Soil	–	?	–	–	+/-	+/-	
	Debris	–	?	+	–	+/-	+/-	
	Trichomes	–	?	–	–	+/-	+ ⁹ /-	
	Leaf fragments, fresh	–	–	–	–	+/-	?	
	Leaf fragments, decomposed	–	–	–	–	+/-	?	
	Bark, twigs	–	–	–	–	+ ⁵ /-	?	
	Chemicals	+/-	?	+/-	+/-	?	?	
Fungi	+ ⁷ /-	?	–	–	+/-	?		
Micro-organisms	?	?	?	?	?	?		
Morphology	Abdomen	+	?	–	–	+	+	
	Caudal Process	+	?	–	–	–	–	
	Setation	?	?	?	?	?	?	
	Anus	+	?	+	+	+	+	

¹*Lema jacobiana* Linell includes exuviae in faecal coat (Kaufmann 1967). ²Waxes were reported in *Saxinis saucia* LeConte, 1857 (Spruyt 1925) and in *Fulcidax bacca* (Bokerman 1964). ^{3,4}*Neochlamisus* use saliva mixed with faeces in cases (Briggs 1905; Brown and Funk 2005). ⁵*Fulcidax cuprea* (Klug, 1824) females integrate bark in egg-cases (Bokerman 1964). ⁶*Podontia lutea* (Olivier, 1790) include exuviae in faecal coat (Takizawa 1978). ⁷Fungi was found in larval shields of *Lacoptera (Sindia) sulcata* (Olivier, 1808) (Rane and Ghate 2005) and *Cyrtanota sericinus* (Erichson, 1847) (Cedeño-Loja and Chaboo 2020); mycelia can be seen in other shields (e.g., *Canistra*, Flinte et al. 2009). ⁸*Phola* Weise, 1890 (Chrysomelinae) reported by Chen (1964, 1985). ⁹Described in Chaboo et al. (2008). Questions about Lamprosomatine cases arise due to their close relationship to Cryptocephaline cases that suggests possibly similar materials and constructions.

Goniocheniini Spaeth, 1942; Hemisphaerotini Monrós & Viana, 1951; Ischyrosomychini Chapuis, 1875; Omocerini Hincks, 1952; Mesomphaliini Chapuis, 1875; and Spilophorini Chapuis, 1875. The systematics of Cassidinae has been dynamic in the last 15 years and there are some disagreements on classification; we briefly discuss some issues relevant to our taxon focus in 'Materials and methods' below.

An obvious question is "How do tortoise beetles build their shields?" We address this specifically in three tribes Cassidini, Mesomphaliini, and Spilophorini. We aim to understand how the architecture is achieved and what morphological equipment is involved. We examine the materials, building processes,

retention and repair of faecal constructions, and their inheritance from one instar to the next. Still images and short films document building behaviours and dissections help puzzle out how the materials are fitted together. We briefly review explanatory hypotheses for possible functions of cassidine shields. To date, the only study of chrysomelid faecal-constructing behaviour has been in *Neochlamisus* Karren, 1972 in the hyperdiverse subfamily Cryptocephalinae (~ 6000 spp.) by Brown and Funk (2005). Our study complements that work. Finally, we discuss the evolutionary-phylogenetic context to frame future research on chrysomelid faecal-based constructions.

Materials and methods

We compare architectures and study construction behaviours in four species in three tortoise beetle tribes (derived Cassidinae, *sensu* Chaboo 2007) based on fieldwork in Costa Rica (2011–2021) and South Africa (2021–2022). To minimise confusion of species, we use these genus-name abbreviations: *S. cucullata* for *Stolas cucullata* (Boheman, 1862) (tribe Mesomphaliini), *Cassidini* undet. sp. 4 for an unidentified species (tribe Cassidini), *Cal. attenuata* for *Calyptocephala attenuata* (Spaeth, 1919) (tribe Spilophorini), *Cass. sphaerula* for *Cassida sphaerula* Boheman, 1854 (tribe Cassidini).

Research approach

First, we introduce concepts of life stages, structures and morphology involved in Cassidinae construction by reporting the natural history of *S. cucullata* and *Cassidini* undet. sp. 4 (three undet. species of Cassidini are illustrated in Figs 23–25). Second, we report on shield construction in two focal species, *Cal. attenuata* (Spilophorini) and *Cass. sphaerula* (Cassidini). Third, we compare and contrast the construction behaviours and resultant architectures, contextualising our findings within Cassidinae and Chrysomelidae. Our focal taxa here are:

1. **Tribe Mesomphaliini:** *Stolas cucullata* (Boheman, 1862) (Figs 41–44). Observations, photographs, and specimen collection were made at COSTA RICA: Cartago Province, Orosi, Tapantí National Park, 9°45'38.63"N, 83°47'3.98"W, 1280 m ele., 24-vii-2011, coll. Kenji Nishida. Oviposition was observed and photographs were taken also on 31-vii-2011 by KN. The live beetles were observed in a cloud forest habitat, along an open trail. The host plant was not determined initially as the female was flying then and landed on vegetation. Later, oviposition was observed, the host plant could be identified, and the hatched larvae were followed in the field on that host plant. Identifications: there are only five or six *Stolas* Billberg, 1820 species in Costa Rica. The red marginal spot on the black elytra is found in adults of three species: one spot in *Stolas cucullata* (Boheman, 1862), two spots in *Stolas costaricensis* (Champion, 1893), and two spots in *Stolas lebasii* (Boheman, 1850). Świętojańska (2009) indicated that juvenile stages are known for just five of the 187 recognised species of *Stolas*: *Stolas chalybea* (Germar, 1824), *Stolas festiva* (Klug, 1829), *Stolas implexa* (Boheman, 1850), *Stolas lacardairei* (Boheman, 1850), and

Stolas lineaticollis (Boheman, 1850). Vouchers are deposited in the Museo de Zoología (MZUCR), Universidad de Costa Rica, San Pedro de Montes de Oca, Costa Rica. *Stolas cucullata* was identified by CSC using the online catalogue of Borowiec and Świętojańska (2002–present). The latter indicates that the type specimen was collected by Warszewicz in Panama: Veraguas, and that Bolivia is an inaccurate locality; the type is supposed to be in the J. Weise collection, Zoologisches Museum, Humboldt Universität, Berlin, Germany, but it cannot be located (Bernd Jaeger, pers commun.). This species is distributed in Costa Rica and Panama (Chaboo 2003). Plant: this was identified as *Neomirandea angularis* (B.L.Rob.) (Asteraceae) by B. Haber, Monteverde. This is a new host record; Windsor et al. (1992) previously recorded *Neomirandea homogama* (Hieron.) Rob & Brett. as a host of *S. cucullata* in Panama.

2. **Tribe Cassidini:** Cassidini undet. sp. 4 (Figs 45–50). All life stages have been documented on the host plant by KN in COSTA RICA: Puntarenas Province, Monteverde, 2016. Identifications: We await further study for more conclusive species determination. Plant: *Chione sylvicola* (Standl.) W. C. Burger (Rubiaceae) was identified by B. Haber, Monteverde. This is a new host record for Cassidinae; only six species of Cassidinae (4 Cassidini, 2 Notosacanthini) have been reported on Rubiaceae hosts (Borowiec and Świętojańska 2002–present; Monteith et al. 2021).
3. **Tribe Spilophorini:** *Calyptocephala attenuata* (Spaeth, 1919 (Figs 51–58). Live populations were studied on four *Smilax* spp. (Smilacaceae) at COSTA RICA: Puntarenas Province, Monteverde, 1530m, 10°19'08.5"N, 84°48'32.0"W, periodically over 2014–2020, Author KN led field studies and published some natural history reports (Nishida 2014, 2015; Nishida et al. 2020). Beetles were identified by CSC. Vouchers are deposited in the Museo de Zoología (MZUCR), Universidad de Costa Rica, San Pedro de Montes de Oca, Costa Rica. The four species of *Smilax* host plants were identified by L. Ferrufino-Acosta. The life cycle of *Cal. attenuata* includes six larval instars and the pupa; all carry exuvio-faecal shields on paired caudal processes (Figs 54–57; = urogomphi). The shield is composed solely of exuviae of previous instars and no faeces. Adults exit the pupal exuvia by splitting the anterior margin of the pupa (Figs 57, 58). Interestingly, adults eclose partly but stay in situ for 2-3 days, hardening up, before exiting completely from the pupal exuvia. Photographs of juveniles (Figs 59, 60) of an unidentified third species from Ecuador were sent by photographer Eerika Schulz to author CSC in 2018 who identified the species as belonging to Spilophorini. Pedro Ríos Guayasamín and students, Universidad Estatal Amazónica, are studying this population on an Orchidaceae host, and will send specimens to CSC for identification.
4. **Tribe Cassidini:** *Cassida sphaerula* (Figs 65–89). Author SA conducted fieldwork in 2021–2022, observing populations of an endemic beetle on its host, *Arctotheca prostrata* (Salisb.) Britten (Asteraceae) in various locations around Mossel Bay, South Africa, 33°57'58"S, 22°5'24"E. Adam et al. (2022) reported on natural history. The life cycle has five larval stages, all with exuvio-faecal shields, and the pupa that may carry shields of exuviae only or shields of exuviae and faeces. **Identifications.** Beetles were identified by CSC and confirmed by E. Grobbelaar. **Vouchers.** These are deposited at South Africa National Insects Collection (SANBI) and loaned to CSC.

Permits

Resolutions # 039-2013-SINAC; # 080-2013-SINAC; SINAC-SE-GASP-PI-R-058-2014 (3 total) were issued by Ministerio de Ambiente y Energía (MINAE), Costa Rica. These allowed research/collecting and specimen export. Permits were issued by Sistema Nacional de Áreas de Conservación, Ministerio de Ambiente y Energía (MINAE), San José, Costa Rica, with assistance of Lourdes Vargas-Fallas and Javier Guevara-Sequeira.

Photography and film

Various digital cameras were used for photography and filming KN used Nikon Coolpix E4500, Canon EOS 7D, Olympus STYLUS TG-4 Tough, and Sony α7S. The movie of *Calyptocephala* moulting was filmed with at 4K movie resolution using Sony's digital camera "α7S" with Canon MP-E65mm F2.8 1–5× Macro Photo lens. SA used a Panasonic DMC-FZ200 camera plus a Raynox macroscopic lens M-150 and live individuals were observed with a Zeiss stereoscopic microscope plus a Dino-Lite eyepiece digital microscope/camera. CSC used a Basler camera attachment on a Nikon SMZ800 microscope. Photo editing was done in Paint.net or Photoshop. LS did the illustrations in Adobe Photoshop and Adobe Illustrator.

Taxonomic names, morphological terms, phylogenetic characters

We follow the Cassidinae classification and taxonomic names of Staines (2015) and Borowiec and Świętojańska (2002–present). We follow Chaboo (2007) for morphological terms and phylogenetic character numbers discussed herein (see more discussion under Phylogeny below). Other group-taxon names for beetles follow Bouchard et al. (2011).

Terminology

This section provides definitions of entomology and cassidine larvae terms that are used to describe the shield construction process. In addition to our illustrative plates, shields can be found in these other synthetic sources: Takizawa (1980), Chaboo (2007), Flinte et al. (2009), and Świętojańska (2009).

In holometabolous insects, larvae instars are demarcated by ecdysis events. Since the process of ecdysis lasts a few seconds (Hemimetabola juveniles are called nymphs), in practice, entomologists recognise the new instar starting when the previous instar's exuvia separates from the epidermal cells of the new instar's exoskeleton (a process called "apolyosis"). The section aims to help readers understand the interactions between processes and parts involved in shield formation, described in the 'Results' section.

Exuviae

We use "exuvia" (singular) and "exuviae" (plural) for the exoskeletons ("skins") shed at ecdysis following Snodgrass (1935) and Chapman (1982: 519). Entomologists have co-opted the Latin terms that translates as "things stripped off"

(Latin is Simple 2023). Schuh (1989) recognises “exuviae” only. Exuvium is linguistically incorrect and hardly used. “Pharate” is used to describe when the exuvia is retained and encloses the teneral insect (Chapman 1982: 518); in tortoise beetles, the exuvia is retained without enclosing the emerging larvae, so the latter is not pharate. In *Aproida* Pascoe (tribe Aproidini), the pupa is suspended from the larval exuvia (Monteith 1970), probably by everted foregut cuticle lining as in some other beetles (Francia 2011); this is unlike the exuvial retention of tortoise beetles. We describe some shields below as exuvia-only (single exoskeleton of Instar II larvae and pupae?) or exuviae-only (with more than one exoskeleton).

Caudal process

‘Urogomphus’ (singular) and ‘urogomphi’ (plural) are used widely in insects, referring to the paired spine-like dorsal projections originating from the 9th abdominal tergite of many larvae (Duporte 1977; Schuh 1989). They are not homologues of cerci, projections of the 11th abdominal segment, nor are they universally homologous across Insecta. Within Chrysomelidae, the ten tribes of tortoise beetles (= the crown clade) in the Cassidinae share a character of larvae having paired projections (a few species secondarily exhibit a single process, Chaboo 2007: char. 11). Plesiomorphic ‘hispine’ larvae lack these dorso-caudal processes but some mining and cryptic feeders have their 9th abdominal tergite modified, heavily sclerotised and concave, into a “urogomphal plate” (Maulik 1931; Chaboo 2007). The tortoise beetle processes are also not morphologically homologous with such processes in juveniles of other chrysomelid subfamilies (e.g., urogomphi in Chrysomelinae larvae *sensu* Reid 1992a, b), other beetle families, or other insects. In the chrysomelid literature, the cassidine caudal processes have been called many terms: posterior spikes (Kershaw and Muir 1907), anal furca (Buzzi and Miyazaki 1992), supra-anal furca (Heron 2007), and supra-anal processes (Borowiec and Świętojańska 2014). Some labelled figures of Cassidine structures are in Chaboo (2007: fig. 18F of larva and 19C of pupa) and Adam et al. (2022: figs 21–25). We use the term caudal processes here for Cassidinae but indicate “(= urogomphi)” in discussions below to remind readers who may be more familiar with that term.

Scolus, scoli

We follow the Torre-Bueno Glossary of Entomology (Schuh 1989) using both singular and plural terms for lateral projections from the thorax and abdomen of the larval and pupal body. Scoli are not homologous with tergal-originating caudal processes (= urogomphi). Cassidinae larvae and pupae may have scoli on the pronotum, metathorax and abdomen; these are unbranched and can be simple, spinose or have short setae.

Anus (Figs 45–50). Tortoise beetle larvae have a unique anus, sub-terminally-opening, muscular, extensible, and highly manoeuvrable unlike other chrysomelid larvae, which have a simple pore-like anus. The telescopic anus of Cassidinae likely represents the plesiomorphic abdominal segments X–XI. The anus is moved by peristaltic movements (Gómez et al. 1999).

Shield (Figs 19–26). This is attached to the caudal processes and held over the cassidine larval and pupal body, sometimes reaching over the pronotum.

Annex, parasol, shield, and umbrella (Jolivet and Verma 2002) have been used to describe the structure. Tortoise beetle shields have been called other names: larval clothing (Muir and Sharp 1904), 'kotanhang'" (= faecal appendage; Fiebrig 1910), faecal mask (Engel 1935), faecal shield (Eisner et al. 1967), faecal pad (Hawkeswood 1982), and exuvio-faecal annex (Buzzi 1988). Buzzi's (1988) term is precise about materials (i.e., exuvio-faecal) and does not imply function (i.e., annex is neutral compared to shield). "Annex" is probably the best term, however at this time, shield has become so widely used in the literature and concurs with the experimental work demonstrating its functions, thus we will retain this term.

Faeces, frass, fecula

Many terms for insect excrement appear in the literature: excrement (Hislop 1872; Scudder 1891; Blatchley 1924; Muir and Sharp 1904; Flinte and Valverde de Macédo 2004), faeces (Snodgrass 1935), 'faeces, fecula and frass' (Frost 1942), excreta (Wood 1966; LeSage 1982; Jolivet and Verma 2002), scat (Lécaillon 1896; Hinton 1981), and fecula (Gómez et al. 1999). In this context, the term "faeces" is used to refer to waste substances emerging at the anus (Snodgrass 1935; Chapman 1982; Schuh 1989), which should not be confused with other exudations (honey dew, spittle froth, glandular and salivary secretions, etc.). Terms like merdigery (Jones 1994) and psammophory (Bameul 1989) refer to faeces and sand, respectively.

Experiments to unravel shield architecture

Chaboo's (2007) subfamily phylogenetic study of Cassidinae determined that the exuvio-faecal shield represents a unique morpho-behavioural complex supporting monophyly of tortoise beetles (10 tribes, ~ 2700 species). The majority of these species has exophagous larvae that retain the cast exuviae and apply their own faeces to build the distinct globular or pyramidal structure. This is held on their caudal processes and can be moved about. Within this crown clade, a few species do not retain a shield and we will discuss this pattern in our evolutionary discussion below.

Typically, a tortoise beetle female may deposit faecal pellets onto eggs or oothecae, but it is the instar 1 that initiates the shield with its faecal material. Instar II retains the exuvia of instar I on its own caudal processes and attaches its own faeces. For *Cass. sphaerula*, we dissected shields to understand how it is fitted and held together.

Calyptocephala attenuata (Spaeth, 1919) (Figs 51–58). Observations and imaging were made over a 2-yr period by KN; specimens collected by KN were studied by CSC by dissection and imaging to determine how the shields are held together. The moulting process was filmed in Costa Rica for some Japanese television nature documentaries (Yamamoto 2018, 2020), assisted by KN; KN also photographed published nature notes (Nishida 2014, 2015; Nishida et al. 2020). We describe the moulting process and shield architecture under 'Results'. The moulting process exhibits active and quieter periods; to ease description, we use 'phases' and timing to describe the sequence filmed.

Cassida sphaerula (Figs 65–89). Given access to a large population, we were able to access many live specimens for various manipulations indoor to document

the construction, enlargement, and transfer of the exuvio-faecal shield from one instar to the next, then to the pupa. We observed multiple larvae of various instars indoors, maintained in plastic containers at ambient temperatures and light and supplied daily with fresh host leaves. We followed these larvae until the emergence of adults. We studied the effects of shield removal in three experiments as follows:

Experiments 1–2: remove the shield entirely, sliding the structure off the caudal processes and leaving the live larva naked.

Experiment 3: abrade only the faecal part of the shield, leaving the exuviae *in situ* on the caudal processes.

We photographed and filmed these individuals at 2-hr time (T) intervals to capture the initiation, expansion, and maintenance of the exuvio-faecal shield. We paid attention to larval movements and pupation. Based on these observations, dissections, and imagery, we describe the shield architecture, shield construction and reconstruction, and the moulting process under ‘Results’ below.

Phylogeny relations

Faecal constructions are considered here at two levels, first in Chrysomelidae and second in Cassidinae. For Chrysomelidae (Figs 16–18), we only present the broad pattern of faecal constructions and their possible role in sub-familial diversification, so we simplify the original sampled taxa to subfamily names to show the overall topology of recent major analyses (Reid 1995, 2000; Gómez-Zurita et al. 2007, 2008; Nie et al. 2020). We do not discuss the underlying evidence and premises supporting these topologies.

For Cassidinae, subfamilial monophyly is well-supported in hypotheses of chrysomelid evolutionary relationships (Farrell 1998; Reid 1995, 2000; Gómez-Zurita et al. 2007, 2008; Hunt et al. 2007; Haddad and McKenna 2016; Song et al. 2017; Nie et al. 2020). The internal relations are not fully settled. Cassidinae were historically treated as two subfamilies, Hispinae (“hispines”) and Cassidinae (“tortoise beetles”), but are now recognised as a single subfamily, Cassidinae *sensu lato*, based on life history, morphological, and molecular evidence (Borowiec 1995; Hsiao and Windsor 1999; Chaboo 2007); other phylogenetic studies target subsets of tribes. Two online catalogues are available for “hispines” (plesiomorphic Cassidinae, 3,371 species in 24 tribes; Staines 2015) and for “tortoise beetles” (2,948 species in 12 tribes; Borowiec and Świętojańska 2002–present). Opinions differ about the status of certain tribes, arising largely from lack of natural history data, and are reflected in the catalogues (Staines 2015; Borowiec and Świętojańska 2002–present) and in higher-level phylogenies. For example, the catalogues overlap regarding Imatidiini and Spiophorini. These catalogues are still valuable and allow us to extract information on faecal-building behaviours from the documented life cycles. Chaboo and Engel (2009) examined the phylogenetic positions of two crucial fossils, *Denaesapis chelonopsis* Chaboo and Engel 2008 (tribe Imatidiini) and *Eosacantha delocranioides* Chaboo and Engel 2008 (tribe Notosacanthini) at the transition zone between basal Cassidinae (“hispiforms”) and tortoise beetles (derived Cassidinae or Cassidinae *sensu stricto*) so these topologies are also pertinent to discussing the origins and timing of the shield-constructing behaviour.

Results

We report on four tortoise beetle species from three tribes: Cassidini, Mesomphaliini, and Spilophorini. We outline the basic life cycle of tortoise beetles with two models, *S. cucullata* and Cassidini undet. sp. 4, and introduce special terminology and morphology used for tortoise beetle shields. Then we describe shield architecture, shield retention, and shield construction and reconstruction in *Cal. attenuata* and *Cass. sphaerula*, based on field observations and laboratory manipulations and dissections. We pay particular attention to the caudal processes and the telescopic anus in the two latter species to understand their roles.

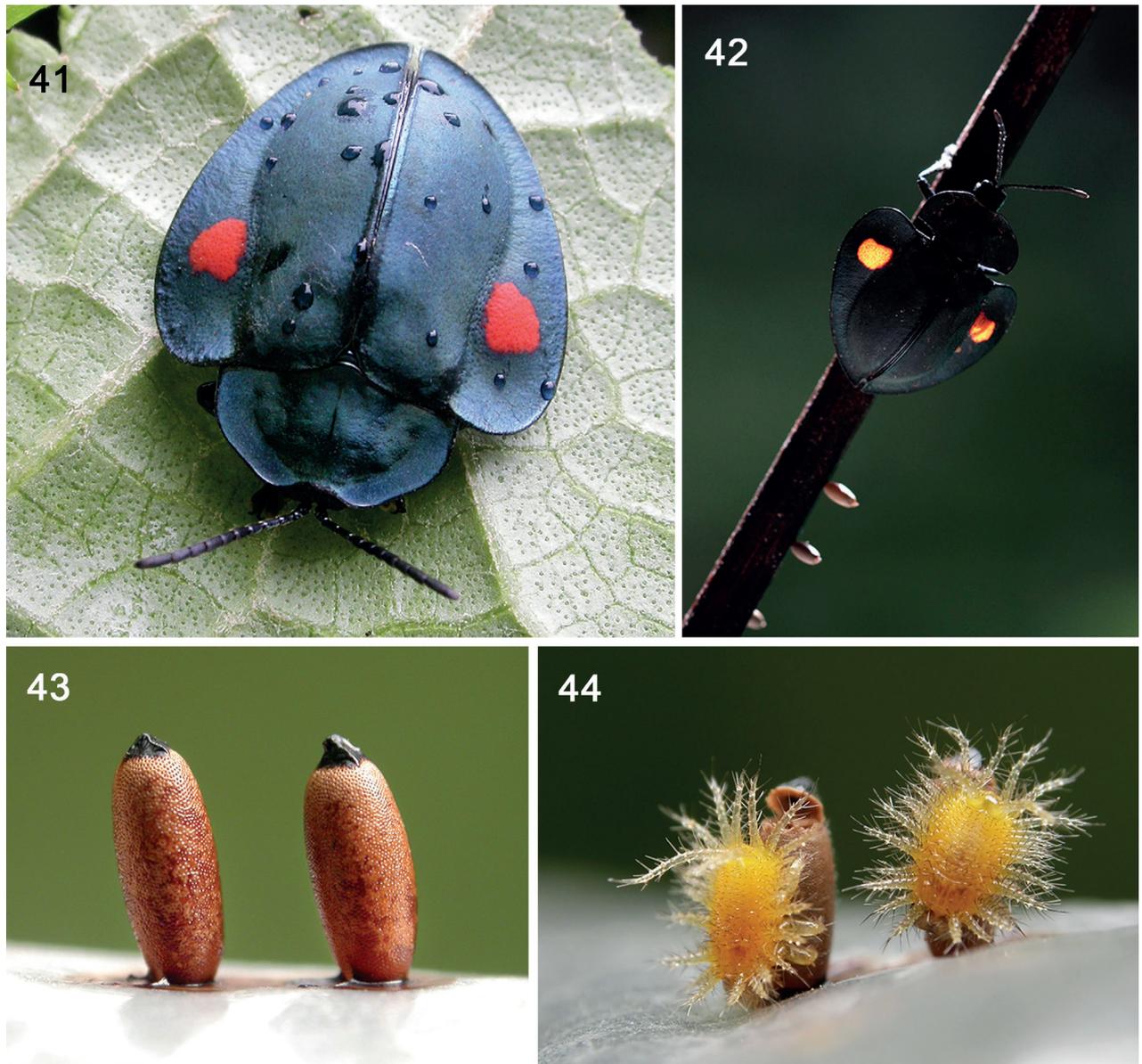
Natural history of *Stolas cucullata* (Tribe Mesomphaliini) (Figs 41–44)

This species serves to outline the general life cycle of tortoise beetles and to explain special terms and definitions in Cassidinae. The female (Fig. 41) was captured and provided with a dry twig on which she deposited three eggs (Fig. 42). **Egg.** Cassidinae eggs may be solitary or grouped, and some are even guarded by mothers (i.e., subsocial); in *S. cucullata*, the female oviposits a group but each egg is separated. Cassidine eggs may be covered with plant debris, oothecal membranes, or faecal depositions; in *S. cucullata*, the eggs are naked. They are initially white, then turn grey within a few minutes, then reddish brown with a black apical disc (Fig. 42). Egg size (n = 2: 2.4 mm long; 1.0 mm wide). **Larvae** (Fig. 44). The neonate larvae have a yellow body with yellowish cream scoli and are densely setose. They wandered away after hours/days, living a solitary life which contrasts with many tortoise beetles that maintain a gregarious group that can additionally be guarded by the mother (subsociality; Chaboo et al. 2014). **Comments.** The host plant, *Neomirandia*, has 56 known species and may host other *Stolas* species; its interesting chemistry (Tamayo-Castillo et al. 1989) is suggestive of a possible role in the beetle's biology and its exuvio-faecal shield.

Shield construction behaviour. The natal larva (Fig. 44) has many scoli and paired caudal processes, all with long setation. As the larva feeds, faeces accumulate on these paired caudal processes and, it appears, are held additionally by the long hairs. We have not yet observed the other life stages of this species, but we note how the shield is initiated in Instar I.

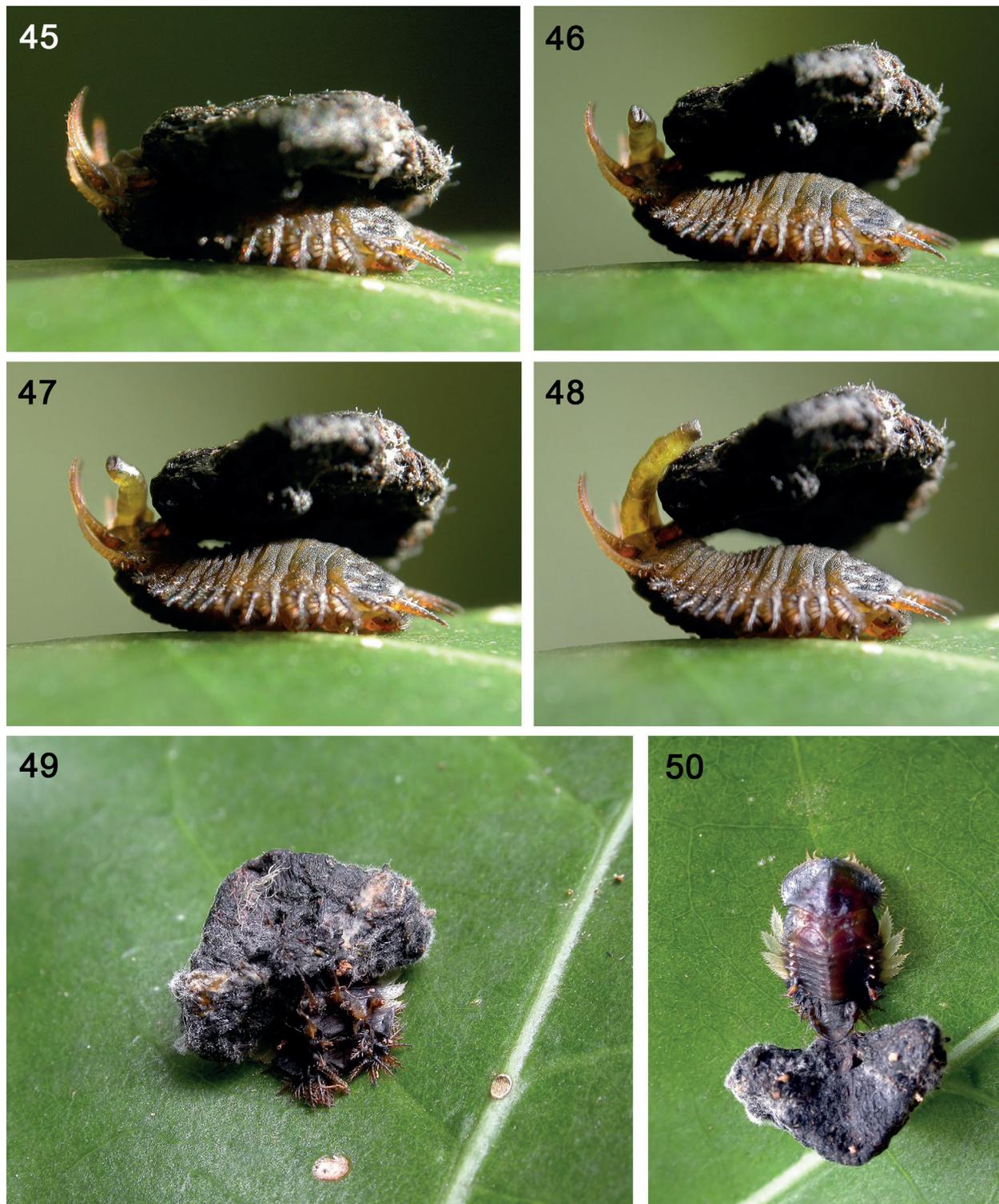
Natural history of Cassidini undet. sp. 4 (Tribe Cassidini) (Figs 45–50)

These larvae build a wide fan-like shield. **Shield construction behaviour** (Figs 45–50). At each moult, the exuvia is shed, from the head to the hind end, but is not cast off. Instead, the exuvia remains attached to the caudal processes. Faeces are added all over, enlarging the shield structure which becomes dry and black-brown in colour. We observed the long, telescopic anus extend and deposit faeces; the anus is highly manoeuvrable and can extend nearly $\frac{2}{3}$ of the body length (note different positions of the anus in Figs 45–50). The shield becomes a large triangular structure with the exuviae stacked internally but not apparent externally, being so daubed over with thick faeces. **Materials.** The instar I initiates the faeces-only shield but later instars have a shield of all larval exuviae and faeces. This is inherited by the pupa (Figs 49, 50); note the fungal



Figures 41–44. Life history in *Stolas cucullata* (Boheman, 1862) (tribe Mesomphaliini) in Costa Rica **41** adult **42** female laying eggs **43** eggs, grouped but not in contact **44** neonate larvae resting on egg shell (photographs: K. Nishida).

hyphae growing upon the shield. **Associated morphology.** The extensible anus builds the shield, placing wet faeces on the caudal process (instar 1) or on the exuviae + faeces of older instars. In older instars, the chaetotaxy is much smaller, raising a question if long chaetotaxy on the instar I caudal processes help hold on to moist faeces, until a hardened structure forms; older instars do not have such long chaetotaxy. The caudal processes in both larva and pupa provide the scaffold of construction (internally, the exuviae become inter-nested at their caudal processes, giving stability). In the larva, caudal processes also rotate the shield vertically, forward and lowered onto the dorsum, backward and extending flat behind the body, and side to side. This raises a question of stability of the larva's body while moving such a relatively large structure; certainly, the feet must be firmly anchored, temporarily glued perhaps, on the leaf and stem substrate. The two caudal processes move but we do not know if each



Figures 45–50. Telescopic anus and shield of larva, Cassidini undetermined sp. 4 on *Chione sylvicola* (Standl.) W. C. Burger (Rubiaceae) in Costa Rica 45–48 anus at different positions 49 pupa, postero-dorsal view 50 pupa, dorsal view (photographs: K. Nishida).

process can move independently of the other. In the solitary pupa (Figs 49, 50), we noted shields held in different positions, directly on the dorsum (Fig. 49) or backwards (Fig. 50). The pupa's abdomen is firmly glued and anchored to the leaf substrate.

Natural history of *Calyptocephala attenuata* (Spaeth, 1919) (Spilophorini) (Figs 51–56)

Illustrated natural history notes have been reported (Nishida 2014, 2015; Yamamoto 2018, 2020; Nishida et al. 2020). Shield construction behaviour: The larvae retain a shield comprised solely of exuviae of previous instars on the paired caudal processes (“urogomphi”) (Figs 51–54). The mature larva carries five exuviae (Figs 51, 52), thus indicating that larva as Instar VI and this is an atypical life cycle for Cassidinae (Chaboo 2007).

The process of shield-building in *Cal. attenuata* begins at the end of Instar I. We describe this process, based on field data and photographs of KN (Nishida 2014, 2015; Nishida et al. 2020), including his assistance on staging the beetle to film the behaviour for two nature documentaries (Yamamoto 2018, 2020; we indicate time (T) in minutes and seconds below based on the film, but readers must access film).

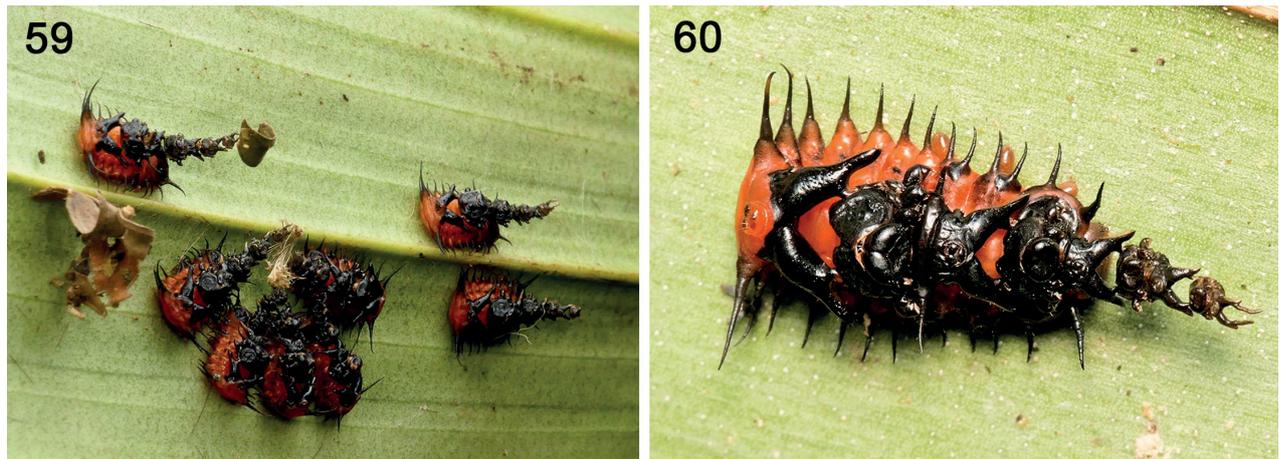
Phase 1 (Fig. 61). Larva, instar I (~ 4.1 mm long), naked, lacking a shield. The larva becomes quiescent as it prepares to moult (T 0–1 min). The six legs are firmly anchored on the leaf and the claw tips appear to be a little embedded on the leaf surface. With a few large inspirations, air fills the gap between the old instar I exuvia and the new instar II; the former seems to lift away. Then the old thoracic nota split medially (T 1 min 35 secs). The abdomen and caudal process move slowly and gently forward and back. The larva inspires air again, inflates a little, and the new prothorax pushes out of the old skin (T 2 mins 5 secs), further widening the breach along the notum. The head capsule splits along the epicranial suture (T 2 mins 28 secs); the new prothorax pushes out further (T 2 mins 40 secs), freeing the lateral scoli (T 2 mins 38 secs), and pulling the head out (Time 3 mins 5 secs). The head and thorax are lifted and freed of the exuvia I, then the new legs are lifted free of their old exoskeleton (T 3 mins 16 secs - 3 mins 25 secs); the instar II abdomen is still encased in instar I abdominal exoskeleton that has not yet split open (Fig. 62).

There is a pause as the head, thorax and legs are lifted vertically, with only slight movements of new legs. The instar II integument is white; yellow haemolymph is apparent internally at the coxal bases. The six pairs of stemmata are black.

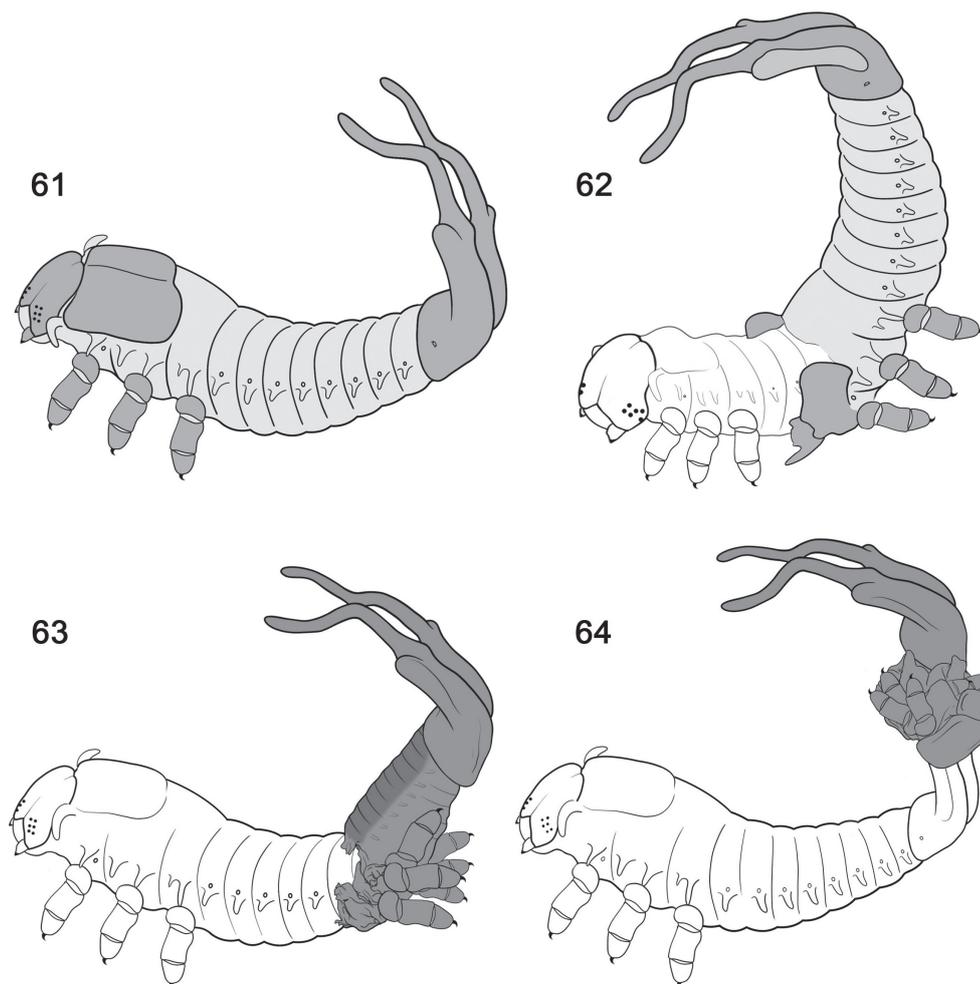
Phase 2 (T 6 mins 30 secs - 6 mins 44 secs). Exuvia II legs drop to the surface, then position on the leaf rib and surface, perhaps anchoring claws into the substrate. The entire body heaves a little, gently, then faster, pulling the instar II abdomen free of the Instar I exuvia. The instar I legs lift free of the substrate. Instar II does not walk forward, but pro- and meso-legs stay fixed on the vein as at the start of Phase II. The body is now lifted and rotated, in 360°, extending the abdomen which pushes the anterior section of the old exoskeleton further posteriad (T 7 mins 10 secs). The larva heaves the body anterior and posteriad, pushing the instar I exuvia backwards (T 6 mins 53 secs). The metaleg positions and re-positions during this phase. The abdomen is held close to the substrate allowing the old head capsule to be dragged against the substrate and pushed further posteriad. At T 7 mins 36 secs, abdominal segments I–II become liberated of the old exoskeleton;



Figures 51–58. *Calyptocephala attenuata* on the host, *Smilax domingensis* Willd. (Smilacaceae), Monteverde, Costa Rica **51** larva with shield of five exuviae, dating this as instar VI **52** dorsal view **53** showing exuviae folded to expose head capsule and caudal processes **54** teneral instar II larva has just exited exuvia I and is retaining it on elaborate paired caudal processes (photographs: K. Nishida) **55** instar I (~ 42 mm long), showing caudal processes **56** instar I caudal processes (photographs: CS Chaboo) **57** adult partially exiting pupal exuvia, fronto-lateral view **58** adult partially exiting pupal exuvia, frontal view (photographs: K. Nishida).



Figures 59, 60. Unidentified genus, 5th instar larvae of Spilophorini on orchid host in Ecuador **59** mature larvae feeding in a group; note color contrast which may be aposematic and the leaf fragment on shield of one larva **60** single larva, dorsal view, with shield of four exuviae. Note exuvial folding exposes the anus and head capsule. Bases of caudal processes are also exposed (photographs: E. Schulz).



Figures 61–64. Timing of moulting process and exuviae retention in *Calyptocephala attentuata*. **61** at 17 seconds. Instar I larva lacks the shield **62** at 7 mins, instar II exiting from instar I exuvia **63** at 8 mins, the old head capsule is folded caudad, the instar II pulls forward, pushing the exuvia posteriad **64** at 13 mins, instar II larva with exuvia of instar I on urogomphi. Other instars with additional exuviae (drawn by L. Schletzbaum; timing follows films (Yamamoto 2018, 2020)).

shortly after, most of the larval abdomen is extracted from the old exuvia (Fig. 63). By T 9 mins 31 secs (Fig. 64), the old exuvia has been pushed to the posterior half of the new caudal processes (In the sped-up film, the process looks violent). The entire process takes about 17 mins in real time.

Phase 3. T 11 mins, it appears that abdominal sternites I and II may anchor to the substrate. The anus appears protuberant. The larva sits for another 6 mins before it slightly repositions all its legs. The exuvia of instar I is now positioned on the posterior half of the new caudal processes, with the body folded over and its caudal processes free. The abdominal section of the exuvia is oriented anteriorly; the legs, thorax and head sections are folded over and oriented posteriorly. Only the posterior half of instar II's caudal processes are inserted into exuvia I, holding it together.

Phase 4. T 14 mins 3 secs, the instar II larvae changes position and we gain a posterior view of its abdomen and caudal processes. The curvature and width of the new caudal processes retains the exuvia I firmly, with some tension.

Instars II–V. These instars were not observed, but ecdysis at the end of each instar probably follows a similar process as above, with the preceding shield retained on the posterior section of the caudal processes.

Pupa. The mature larva attaches the abdomen to the leaf and undergoes pupation. Of the pupae collected, all retained a shield; some shields comprised of two or three older exuviae, but not the younger exuviae that would be most apical in the stacked structure. These shields extended only up to the pronotum, so it is possible that the younger exuviae fell off during ecdysis or were subsequently abraded. Figs 57 and 58 show a pupa with five exuviae, suggesting that exuvia I is detached (these pupae could have six larval exuviae); thus, the pupa inherits shields with varying numbers of exuviae. Figs. 57–58 also show the teneral adult partly exiting this pupal exoskeleton.

Materials

The larval shield of *Cal. attenuata* is comprised only of exuviae; there are no faecal deposits, secretions, nor plant materials.

Morphology

Roles of caudal processes in larva and in pupa. These are critical to retaining the shield on the body and to connecting all the previous exuviae together in a single structure. The posterior sections of each caudal process are entirely enclosed within the previous exuvia. **Repair.** It seems obvious that the larvae have no way to repair these exuvia-only shields; if one or more exuviae are removed, the larva must wait until the next moult to add a new exuvia. The movements of the abdomen and caudal processes are responsible for moving the shield in various directions, forwards, laterally and backwards, including above the head. The pupae lack the processes; instead, the final larval exuvia is wrapped around the pupa's caudal region and retains the larval exuvial shield. Some shields (Fig. 59) in our unidentified Ecuadorean Spilophorini have leaf fragments attached; these are possibly accidental.

Natural history of *Cassida sphaerula* (Cassidini) (Figs 65–89)

Cassida Linnaeus, 1758 comprises 484 species (Borowiec and Świętojańska 2002–present). Immatures have been described for 64 species and exuvio-faecal shields have been noted in most documented larvae to date (Świętojańska and Borowiec 2007: Table 1; Świętojańska et al. 2013). Natural history of *Cass. sphaerula* was reported by Adam et al. (2022) and we summarise in Figs 65–70. Females oviposit small clusters of eggs with oothecal membranes, there are five larval instars (Figs 65, 67), all solitary, and pupae are solitary (Figs 68, 69).

Shield construction behavior

Soon after the natal larva (Fig. 65) begins feeding, it begins accumulating its faeces on its paired caudal processes (Fig. 66). At each moult, the cast exuvia is pushed to the base of the caudal processes. The shield becomes a rough triangular-shape, with dark brown-black faeces obscuring the lighter-brown exuviae slightly visible at the base (Fig. 68). The pupa retains the entire larval shield of exuviae + faeces (Fig. 68) or retains only the 5th larval exuvia (Fig. 69). The faeces are dense, at different times appearing wet, moist, or desiccated.

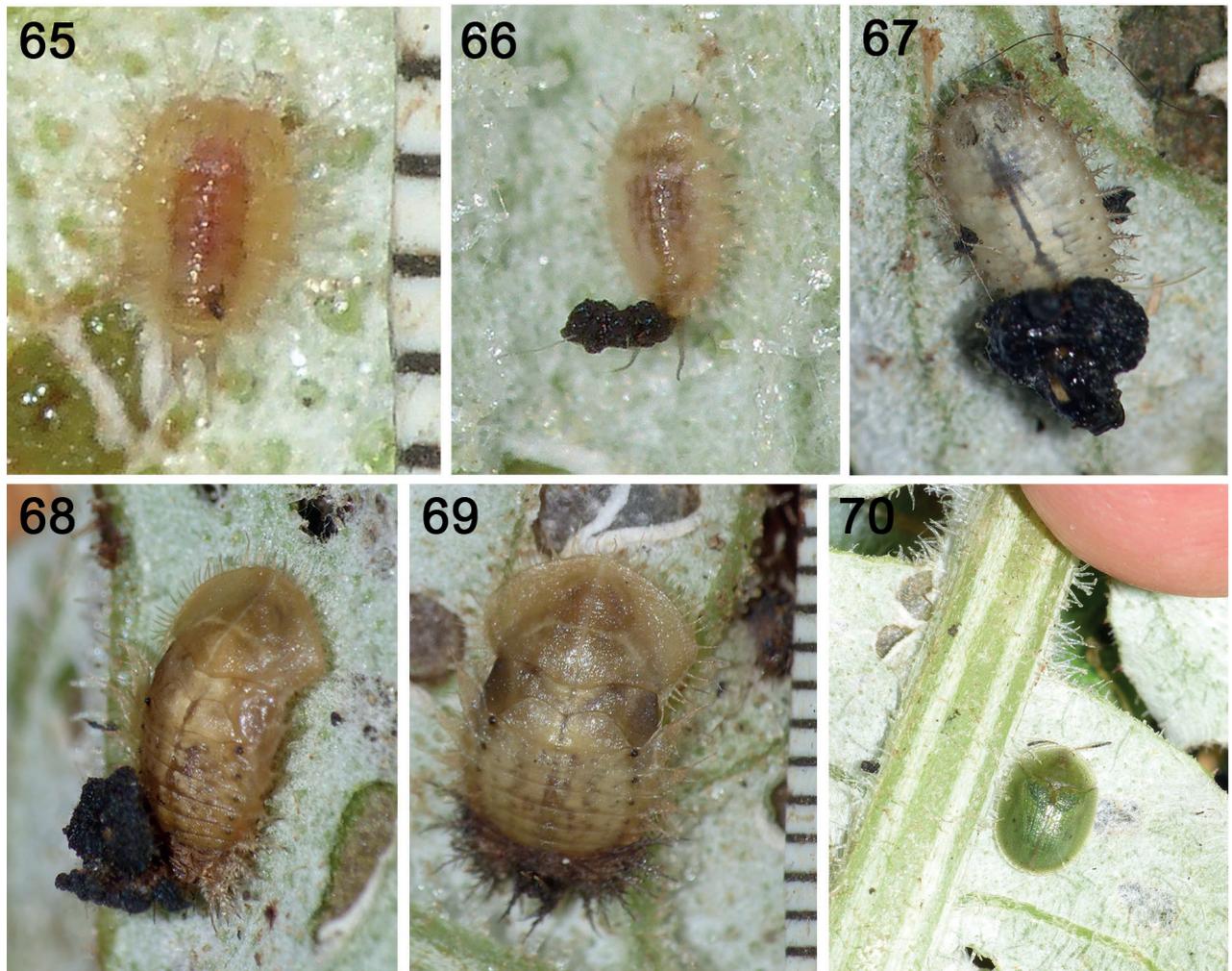
Incorporation of exuviae into shield

At ecdysis, the old exuvia splits along the ecdysial line of the head and is peeled and pushed backwards, as the teneral instar pulls forward to free its legs. It fixes the legs to the leaf surface, then wriggles its abdomen forward to free itself of the old exuvia. In this way, the previous exuvia becomes positioned at the base of the caudal processes of the teneral larva, beneath the existing exuvio-shield structure. Since all the caudal processes are nested (all previous exuviae atop the living caudal processes of the current instar), the former exuvia becomes crumpled at the base of the existing shield. Soon this recently added exuvia becomes daubed with faeces, and so becomes indistinguishable within the entire shield structure (unless the latter is dissected). No exuviae are omitted from the central scaffold. Apart from the shield structure, excess faeces may be left on the leaf.

We address the question “Will larvae rebuild the shield” with several shield-removal experiments to observe responses of larvae. We present results of three experiments below.

Experiment 1, instar I (Figs 71–76)

T 0 mins, (Fig. 71): Shield removed completely, exposing the living paired caudal processes. T 2 hours, (Fig. 72): a small quantity of faeces accumulates on the anus. T 4 hours (Fig. 73): moist faecal material has accumulated on the urogomphi, covering it up to the apices. T 6 hours (Fig. 74): faecal material almost the same as at T 4 hours. T 23 hours (Fig. 75): The faecal shield is almost twice as large. T 48 hours (Fig. 76): The faecal shield is about three times larger than it was at T 2 hours.



Figures 65–70. Life stages of *Cassida sphaerula* Boheman, 1853 (Cassidini) **65** instar I, neonate **66** instar II, with faeces on caudal processes **67** mature larva with faeces + exuvia shield **68** pupa with entire larval shield (faeces + exuvia) **69** pupa with shield comprised of only 5th instar exuvia **70** adult (photographs: S. Adam, September 2021).

Experiment 2, instar I (Figs 77–82)

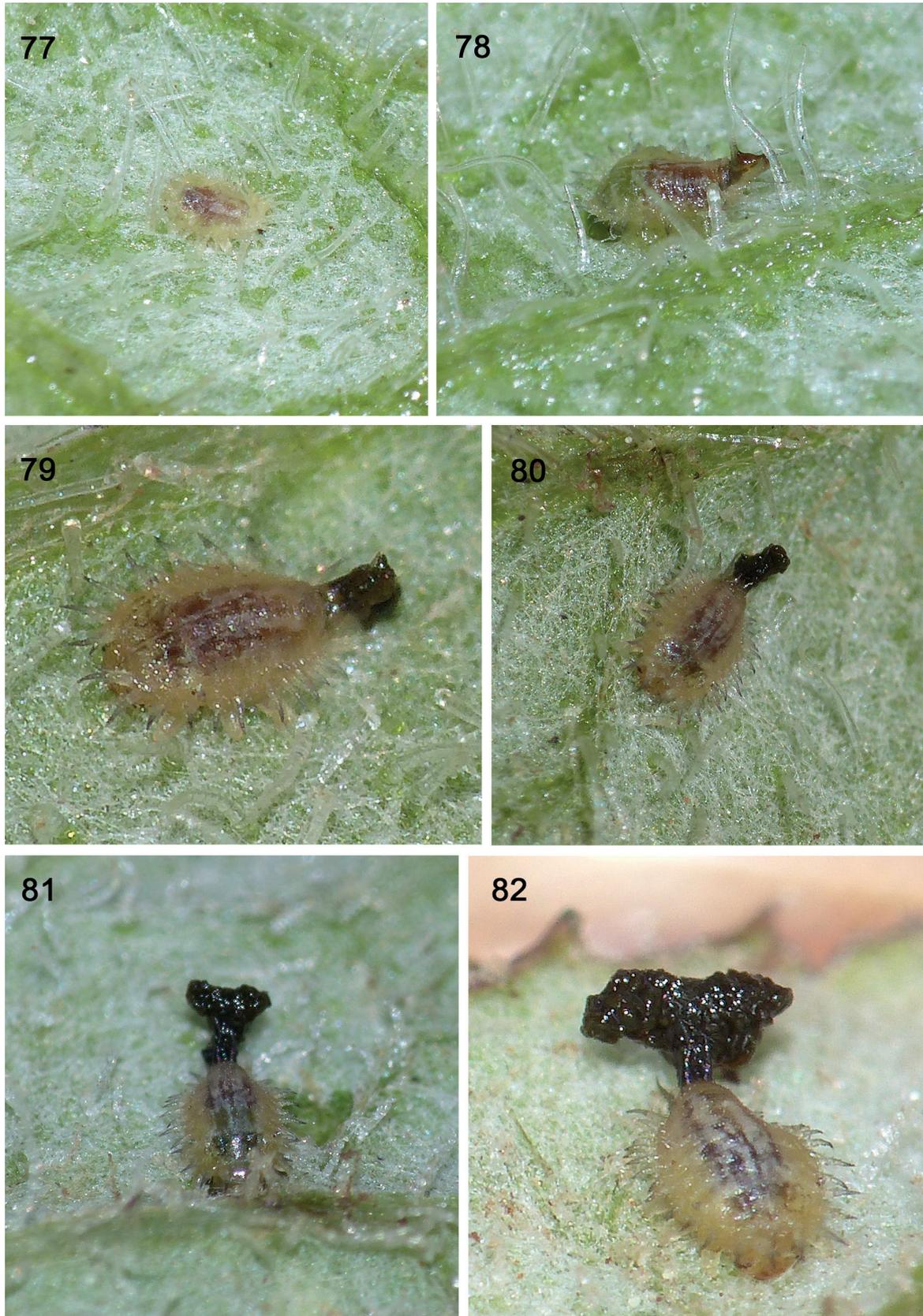
Time 0 (Fig. 77): We removed the shield entirely, both exuvia I and faeces. T 2 hours (Fig. 78): a small amount of fresh faeces accrue on the caudal processes. T 4 hours (Fig. 79): more new faeces accumulate, obscuring the caudal processes. T 6 hours (Fig. 80): more new faeces accumulate. T 23 hours (Fig. 81): the faeces have grown into a small, dimensional inverted pyramid. T 48 hours (Fig. 82): the inverted pyramidal shield is larger, held together on the caudal processes. This shape seems unstable, that lateral sections should break off yet hold together.

Experiment 3, instar II (Figs 83–86)

T 0 mins (Fig. 83): we scraped away only the faeces to expose the Instar I exuvia still attached to the caudal processes. T 23 hours (Fig. 85): faeces have been applied to the sides of the old exuvia, so the overall shield width is almost as wide as the larva. T 48 hours (Fig. 86): More faeces have been applied to the



Figures 71–76. Re-construction of faeces on exuvio-faecal shield in Experiment 1, starting with instar I larva (so no prior exuvia), *Cassida sphaerula* Boheman, 1853 (Cassidini; photos: S. Adam, September 2021) **71** instar 1 (~ 2 mm long) at time 0 when faecal shield is removed, exposing urogomphi **72** larva at two hours, small faecal blob at anus **73** larva at four hours, urogomphi encased in faeces **74** larva at six hours, urogomphi encased in faeces **75** larva at 23 hours, lateral view. **76** larva at 48 hours, dorso-ventral view (photographs: S. Adam, September 2021).



Figures 77–82. Re-construction of faeces on exuvio-faecal shield in Experiment 2 with *Cassida sphaerula* Boheman, 1853 (Cassidini) **77** instar I (~ 2 mm long) before shield construction **78** instar II at time 0 with faeces removed (scraped off) **79** after 2 hours, dorsal view **80** after four hours, dorsal view **81** after 23 hours **82** after 48 hours (photographs: S. Adam, September 2021).

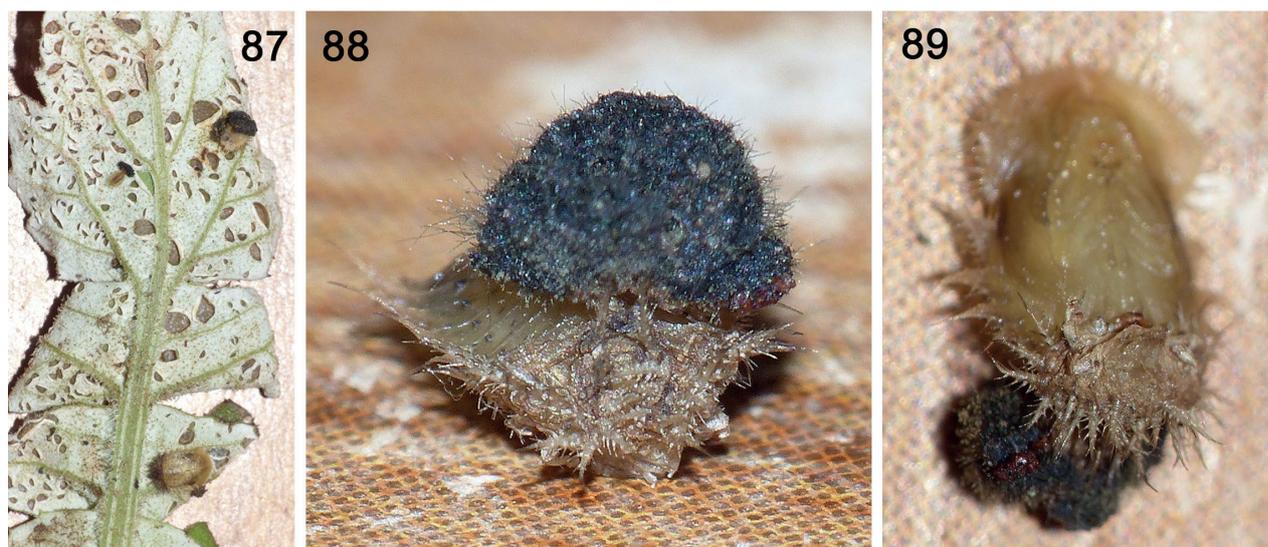


Figures 83–86. Faecal re-construction in experiment 3 with instar II larva, *Cassida sphaerula* Boheman, 1853 (Cassidini) **83** time 0 when faecal shield is removed, exposing instar I exuvia **84** larva at two hours, exuvia I still exposed **85** larva at four hours, faeces attached to lateral projections (scoli) of exuvia I **86** larva at six hours, exuvia I with a lot of faeces (photographs: S. Adam, September 2021).

lateral margins, so the shield is now a little wider than the larva. The old exuvia is in the centre, exposed, and the moist black faeces hang on to the sides.

The entire exuvio-faecal structure was gently eased off the living caudal processes using forceps and these intact larvae continued feeding. In each case, the larva soon produced a faeces-only shield, small at 2 hours after removal, then bigger and bigger at hours 4 and hours 6 after removal. By hours 23 and 48, 1–2 days after the earlier removal, the new shield was larger and club-shaped. In the three experiments of shield manipulation, the timing, and responses to reconstruct a new shield were similar. The experimental larvae of *Cass. sphaerula* moulted normally and retained the exuvia into the inherited shield.

The larva can rotate the shield in a circular plane over the body, forward up to the mesothorax, and backward almost 180°, and in a horizontal plane with the body (Suppl. material 1). Films of the acrobatic movements of the larva's



Figures 87–89. Shield of pupa of *Cassida sphaerula* Boheman, 1853 (Cassidini) **87** host leaf chewed by beetles, with one larva and two pupae (dorsal views; upper one with exuvio-faecal shield; lower one with exuviae-only shield) **88** posterior view showing exuvial-faecal shield (of instars I–IV) attached to caudal processes of instar V exuviae **89** ventral view showing complete instar V exuvia and exuvio-faecal shield (photographs: S. Adam, September 2021).

extensible anus reveal that it applies faeces to the existing shield and, also periodically exudes large, mostly clear, droplets that are applied to and absorbed into the shield (Suppl. material 2). We found no trichomes in dissected shields even though we observed consumption of trichomes in *Cass. sphaerula* (Adam et al. 2022).

Shield retention in pupae (Figs 87–89)

In *Cass. sphaerula*, we observed pupae can have either an exuvia-only shield (Figs 69, 87) or the entire inherited exuvio-faecal shield structure of the earlier larvae (Figs 68, 88, 89). The faeces of the latter are dry since new faeces are not being applied. We found several discarded exuvio-faecal shields next to pupae. Given the observation of the moulting process (from 6th instar to pupa) in *Calyptocephala* (described above), we infer that pupation is similar, with splitting of the ecdysial sutures on the cranium and thorax of the 5th instar split and the pupa pulls forward and out. In the larval moults, the new legs and the old legs serve to anchor the emerging larva at different times in the process.

Discussion

Faecal-based constructions and faecal debris-carrying are widespread behaviours in Chrysomelidae. Chrysomelid faecal-based constructions have been studied in terms of ecological function (Olmstead and Denno 1992; Gómez 1997, 2004; Morton 1997; Vencel and Morton 1998a, b, 1999; Morton and Vencel 1998; Gómez et al. 1999; Müller and Hilker 1999, 2001a, b, 2003, 2004; Vencel et al. 1999, 2005, 2011; Nogueira-de-Sá and Trigo 2002, 2005; Bacher and Luder 2005; Bottcher et al. 2009; Huang et al. 2022). Until now, this faecal building behaviour has been studied in only one chrysomelid, *Neochlamisus* by Brown and Funk (2005).

Materials in cassidine shields

The macro-materials in shields of our observed species comprised exuviae only or faeces + exuviae. These two materials are side effects of metabolism and moulting respectively. Additional analyses may identify other possible components (Table 1) and their functions. The construction processes we documented allow us to now analyse how the two primary materials originate, are manipulated into the construction, and are held to the body. We briefly discuss evolutionary insights as we compare these aspects with other Cassidinae and other Chrysomelidae.

Building stages in Cassidinae?

Larvae are the builders in our four studied species and building begins in two possible ways: 1) during instar I when faeces are deposited and held on the caudal processes as the larva feeds (in *S. cucullata*, Cassidini undet. sp. 4, *Cass. sphaerula*) or, 2) in the transition moult from instar I to instar II when the cast exoskeleton is retained on the caudal processes (*Cal. attenuata*). Cassidinae pupae in tortoise beetle tribes are not active builders; they receive their shields as an inheritance from the final larval instar and their shield is either the entire exuvio-faecal shield or only the final instar exuvia. Given the life cycle of Spilophorini, the final instar could be the 5th or 6th for tortoise beetles. For pupation, the pre-pupa anchors itself by gluing the abdomen to the host surface. Then the larval exoskeleton splits along the head and thoracic midlines and the pupa pushes out as the larval exuvia is propelled caudad. The shield is retained passively, attached on the pupa's own caudal processes. This pupal inheritance recalls that of camptosomate chrysomelids where the final instar seals the larval faecal case to the substrate and so provides a pupation chamber (Chaboo et al. 2008).

Cassidinae shield architectures

The common pattern is the exuvio-faecal shield built by larvae, retained in all instars, and which may be inherited by pupae. The faeces are variable in moisture, from desiccated (Figs 19, 22, 23, 25, 26) to wet (e.g., *Plagiometriona flavescens* (Boheman, 1855): Flinte et al. 2009); this is certainly tied to the excretion of water, retention by Malpighian tubules, and rectal resorption. Dried faeces can be in long strands; these strands are arranged in a circular heap in Hemisphaerotini (Fig. 19; Chaboo and Nguyen 2004) or are held as vertical strands (Figs 22, 23). Within the tribe Ischyrosonychini, larval shields are varied: desiccated stacked exuvio-faecal shields (e.g., *Cistudinella obducta* (Boheman, 1894) (Fiebrig 1910; Buzzzi 1988), wet faeces (e.g., *Physonota unipunctata* (Say, 1823); Keefover-Ring 2013, 2015), or older larvae that lack shields altogether (e.g., some *Physonota* Boheman, 1854). Larvae of *Eurypepla* Boheman, 1854 have a unique tapered body that is curved verticad, allowing wet faeces to slide down and coat the body (Chaboo 2004).

Architectural elements of cassidine faecal structures may be diagnostic for species-, genus- or tribal-level diagnoses. Shield architecture is determined by how exuviae are compressed and how faeces are arranged (long vertical strands, a dense clump, or a fan). Basket-like shields are diagnostic of

Hemisphaerotini (Fig. 19; Eisner et al. 1967; Beshear 1969; Chaboo and Nguyen 2004) and appear to have some limited mobility, particularly in younger stages (note its position in Fig. 19). As the larval shield enlarges, it becomes less mobile, suggesting that this shield is relatively heavy and/or the caudal processes may not be as freely mobile. Although exuviae are retained in Hemisphaerotini, these are so compressed that only torn remnants remain at the base of the caudal processes, and it seems impossible to determine how many distinct exuviae are held. This shield architecture has been demonstrated to be protective (Eisner and Eisner 2000a).

We propose here that the particular exuviae-only shield architecture described herein is diagnostic for Spilophorini (Figs 51–54, 57, 59, 60). Life cycles of two species of *Calyptocephala* Chevrolat, 1836 (Buzzi and Miyazaki 1992; Córdova-Ballona and Sánchez-Soto 2008) on palm hosts reveal larvae with paired caudal processes and exuviae-only shields. Maulik (1932) described the larva of an *Oediopalpa* Baly, 1858 species with paired caudal processes and an exuvial shield; Chaboo (2007: 184) examined larvae in this genus and noted the unique pattern of exuviae compression. Hsiao and Windsor (1999) determined *Oediopalpa* as most closely related to *Calyptocephala* and *Spilophora* Boheman 1850 and Staines (2002) re-classified it in Spilophorini. Sekerka et al. (2014) reported an Orchidaceae host, the larval form, and exuviae-only shields for one species of *Cladispa* Baly, 1858 (Spilophorini). Monophyly of Spilophorini has been supported by adult characters (Chaboo 2007) and molecular data (Sekerka et al. 2014). The documented larvae exhibit exuviae-only materials arranged in a similar architecture, with a stable exuvial stack, a distinct spatial arrangement, and large partly exposed caudal processes. The exuviae are compressed and curved so the head capsule and the anus are exposed in posterior view. The shape of the caudal processes, like the yoke of a lyre, is unique in Cassidinae; the exposure (Fig. 57) of the large basal section of each process is also unique. These features altogether support monophyly of Spilophorini.

Other tortoise beetles exhibit exuviae-only shields (Figs 15, 21, 24) but the spatial arrangement of those exuviae and the underlying caudal process morphologies are unlike those in Spilophorini. In other documented species, exuviae are compressed differently, more closely at caudal processes, and head capsules are exposed in distinct ways (see examples: *Stolas implexa* (Boheman, 1850), Flinte et al. 2009: pl. 18K; *Chiridopsis undecimnotata* (Boheman, 1855), Świętojańska 2009: fig. 128). As species and their constructions are documented, it may be possible to diagnose more groups based on more shield and process features.

Shields may be present or absent in pupae of tortoise beetles. We found that pupae of *Cass. sphaerula* retain different shields (the entire structure or only the final exuvia). Some pupae retain only the 5th instar exuvia and their caudal processes are a dominant exposed feature (e.g., *Anacassis* Spaeth, 1913, Buzzi 1975; *Discomorpha* Chevrolat, 1836; Flowers and Chaboo 2015). In the Cassidini, pupal shields are known in species of *Charidotis* Boheman, 1854, *Drepanocassis* Spaeth, 1936, *Metriona* Weise, 1896, and *Syngambria* Spaeth, 1911 (Buzzi 1988). In some cassidines, the 5th exuvia is retained by the pupa, encircling the terminal abdominal segments, e.g., *Anacassis* Spaeth, 1913 (Buzzi 1975, 1996). In *Eugenysa columbiana* (Boheman, 1850) (Chaboo 2002), *Dorynota pugionota* (Germar, 1824) (Buzzi 1976), and *Chelymorpha* Chevrolat,

1836 (Buzzi 1998) this exuvia becomes part of the pupal attachment to the substrate. Shield removal is required to determine if this exuvia is wrapped around the base of the abdomen only or if it is attached to a pupal caudal process.

What is the building equipment in Cassidinae?

We documented the anus moving freely over the posterior surface of the shield (Figs 45–48). We observed anal droplets excreted and quickly absorbed into the shield (Suppl. material 2). We also documented the application of fresh moist faecal deposits to the intact shield and, in our experiments, application to the exposed exuviae to rebuild the shield (Figs 71–86). Gómez (1997) reported the repair of damaged shields with precise deposits of faeces. Thus, the anus is the applicator for constructing and repairing the shield and appears to replenish the shield with moist droplets. Certainly, the cassidine anus has manipulative skill for these distinct roles (applying, building, repair, replenishment). Such replenishment may involve chemicals that sustain the shield's chemo-barrier functioning. If pupal shields are not being replenished, this raises a question about their chemistry and functional effectiveness versus larval shields.

The muscled extensible anus of larvae is a second synapomorphy of the ten tortoise beetle tribes. Plesiomorphic Cassidinae larvae which do not exhibit shield-retaining behaviours have the typical posterior or ventrally opening simple anus pore and also lack caudal processes. As far as we know currently, no other chrysomelid larvae have an extensible anus. One question we have is the status of the anus in those Cassidinae with exuviae-only shields; we were unable to determine this in *Cal. attenuata*. Pinpointing the first appearance of the telescopic anus on phylogenetic topologies is one crucial element in the assembly of shield building traits.

Cassidinae larvae do not use their legs or mouthparts as building tools. Females may defecate on their eggs, but their genitalia lack rectal plates (as in Camptosomata: Erber 1968, 1969, 1988). In Camptosomata, the larva's arrangement within its case positions the anus near the mouthparts and legs. Brown and Funk (2005) reported that faeces are mixed with a regurgitated yellow fluid and then applied to the margin of the case to continue building it or to repair holes, so the larva's position with the mouth, anus and legs in proximity allows the faecal mixing and manipulation. Camptosomate larvae use their mouthparts to cut a longitudinal section which is then filled with faeces; this expands the girth of the case to accommodate the growing larva (Brown and Funk 2005; Chaboo et al. 2008). Calcetas et al. (2023) reports that *Podontia* larvae use legs and mouthparts to manipulate soil and faeces to build the pupation chamber.

Building routines in Cassidinae

Cassidinae larvae use simple materials in simple building routines. Each shield has a distinct appearance due to the compression pattern of individual exuviae (Figs 15, 21, 24, 51, 52, 57, 59, 60) and due to the arrangements of faeces (strands, blobs, fan, bird nests, etc.). The shield enlarges at each transformation to the next instar as another exuvia is added basally to the mass. The extensible anus deposits faeces precisely on various parts of the exuviae to give the distinct appearance of shields. Faeces are extruded moist or wet, allowing

attachment to the existing structure, before drying. Our simple experiments allowed us to understand the repair of the shields. If a portion of faeces is removed or broken off on one side of the structure, the anus can repair the faecal part to apply fresh faeces to recover a more balanced shield. Our study demonstrates that the shield-constructing behaviour is intrinsic and is probably not requiring any external activator to elicit the building response.

Role of caudal processes (= urogomphi)

Many animals that retain debris covers possess fastening structures, frequently specialised chaetotaxy (e.g., Weirauch 2006). We determined here several roles of the paired caudal processes— the anchorage or fastener for cast exuviae and faeces to the body, part of the shield materials, the crucial central scaffold by their inter-nesting, and movement of the shield. During instar I, faeces are applied directly to the caudal processes; in *S. cucullata* dense chaetotaxy around the anal area may enhance faecal retention.

The exuvia is added to the shield with each moult, expanding the area for faecal attachment. In some species, exuviae alone make up the shield. The caudal processes become inter-nested from instar to instar, further strengthening the central scaffold of the exuvio-faecal shield and provide mobility, allowing it to be moved as needed to startle or hit an attacker or be the distasteful barrier. The caudal processes move the shield for a more active defence.

In pupae, we have no reports of cassidine pupae moving their shields, although there are reports of pupa jerking reflexively when disturbed (even in unison in gregarious pupae). It appears the entire pupal body jerks so pupal caudal processes may not be mobile.

Role of chaetotaxy

In one unidentified species and in *Cass. sphaerula* we observed that dense chaetotaxy in the caudal area of the neonate larva appears to aid initial faecal build-up. Specialised chaetotaxy may aid faecal retention in the faecal retaining chrysomelid clades. Specialised setae to hold on to debris have been described in unrelated beetles (Leschen and Carlton 1993; Leschen 1994; Yoshida and Leschen 2020), in other insects (e.g., Reduviidae, Weirauch 2006), and in other animals (e.g., spiders, Duncan et al. 2007; Gawryszewski 2014). In *Uraba* caterpillars (Fig. 9), it is a question how the old head capsules become stacked on the living caterpillar's head, since the head capsule typically splits first during the moulting process, then becomes distorted as it is pushed posteriad, and the larva propels forward to exit its old exoskeleton. We suspect that specialised chaetotaxy on the caudal processes of tortoise beetle larvae and on the dorsum of larvae in Criocerinae and in the *Blepharida*-group may hold onto the faecal debris. Each debris-retaining animal has different strategies for attaching and retaining debris.

Materials of coats, cases, and shields across Chrysomelidae (Table 1)

Chrysomelid constructions are composed mainly of endogenous faeces and, in Cassidinae, of exuviae. Documented exogenous materials are soil, fungi,

leaf fragments (fresh, undigested, decayed), plant extracts, and trichomes (Table 1). We will not review here how exactly these materials may be mixed or intermingled with the other structural materials. In Cassidinae, fungal elements have been noted but not identified taxonomically (Figs 49, 50; Rane and Ghate 2005; Flinte et al. 2009; Cedeño-Loja and Chaboo 2020). Fig. 59 shows a larva with plant fragment on the exuvial shield but this may be accidental. It has been well-established that animal guts are rich with microbiota that can be passed to the next generation via the egg surface; Stammer (1935) established such transmission in Cassidinae. Faeces are also rich with microbiota (thus, Faecal Transplant technique); we can presume that the cassidine shield is harbouring microbiota that await discovery and study. The exuviae are a low-cost material that add substantial structural value to the shield (like straw added to dung) but we do not know yet their chemical contributions. All debris materials have pros and cons, depending on how they originate (time to produce or assemble) and their consequences (e.g., weight, odour, chemistry) so every chrysomelid material likely has a functional role simply because of the cost in carrying the weight and bulk of a structure; it is unlikely that unnecessary materials are selected. Most of these chrysomelid materials are actively manipulated, although it is possible that some (e.g., blown soil) may be passively integrated.

Chrysomelid construction behaviours: ecological implications

Chrysomelid larval and pupal shields are hypothesised to serve multiple functions, including protection from extreme temperature (Réaumur 1737), humidity, precipitation and desiccation (Weise 1893), camouflage or mimicry (e.g., bird or caterpillar droppings: Briggs 1905; Blatchley 1910; Jenks 1940; Balsbaugh 1988; plant detritus: Lee and Morimoto 1991a, b), as a distasteful physical barrier deterring predators and parasitoids (Réaumur 1737; Eisner et al. 1967; Olmstead and Denno 1992; Olmstead 1994, 1996; Eisner and Eisner 2000a; Bacher and Luder 2005), or as chemical deterrents from exocrine glands of retained exuviae (Olmstead 1994). They can also be used as a mobile club to hit intruders or as a protective umbrella (CSC, pers. obs.). The term 'shield' implies passive protection, which may lower the body temperature or decrease wind shear (Olmstead and Denno 1992). The material and consistency (including cementing and chemistry) must ease accumulation and attachment. It appears that chrysomelid shields are generally resistant to rain as they do not absorb water and fall apart.

Testing of function hypotheses

The hypothesis of a mechanical defence against predators has been tested experimentally and found to be supported (Eisner et al. 1967; Wallace 1970; Olmstead and Denno 1992; Eisner and Eisner 2000a; Schaffner and Müller 2001; Müller 2002). Blum's (1994) hypothesis of defensive chemicals in shields has led to some analytical studies, usually of single chrysomelid species, aimed at comparing compounds in the faecal shields and the host plants (Mummery and Valadon 1974; Morton and Vencl 1998; Gómez et al. 1999; Vencl et al. 1999; Aregullín and Rodríguez 2003; Bacher and Luder 2005; Nagasawa and Matsuda 2005; Nogueira-de-Sá and Trigo 2005; Vencl et al. 2005, 2009, 2011;

Bottcher et al. 2009; Keefover-Ring 2013, 2015; Vencl and Srygley 2013). Maybe a chemical barrier is achieved by integrating plant tissues and trichomes or by applying secretions (plant-sequestered or de novo chemicals) that volatilise around the animal, maybe creating a small chemosphere. Exuvial glands may have residual chemicals that may disguise the wearer or deter enemies.

In testing Ehrlich and Raven's (1964) "escape and radiate" hypothesis, Vencl et al. (2011) compared differential functioning in defence of shields with/without faeces, larval solitary/gregarious living, and maternal care and deduced a sequence of trait accumulation correlated with enhanced defences and, likely, species diversification. Such creative experiments can assess the contribution of each trait within the defense array.

Others have determined the shields to have mixed effects, deterring some predators yet attracting others (Müller and Hilker 1999; Bacher and Luder 2005; Huang et al. 2022). Certainly, faeces can have chemical signatures that attract enemies (Van Leerdam et al. 1985; Agelopoulus et al. 1995).

Chemical deterrents in exocrine glands of retained exuviae (Hinton 1951; Olmstead 1994) have not been investigated. Furthermore, the traits accumulated in the defence arsenal must now include the morphological features that accompany the structures; for example, caudal processes enhance shield mobility in tortoise beetles and may enhance defence success. Our research here highlights the morphological features used by tortoise beetle larvae within their arsenal of weapons.

Construction behaviours: evolutionary implications

The primary hypotheses proposed to explain chrysomelid hyperdiversity have been their ancient age (Farrell et al. 1992), herbivory and the rise of angiosperms (Farrell 1998), adaptive radiation with plants (Gómez-Zurita et al. 2007), and chemical adaptation to plants (Farrell et al. 1992). However, the great unevenness in subfamilial diversity begs for additional explanations. Transitions to new habitats within Chrysomelidae (e.g., aquatic, seeds, subterranean, mosses) and to the jumping escape mechanism (in ~8000 flea-beetle species, Begossi and Benson 1988; Furth 1988) await finer-scale study of correlated adaptations in morphology, physiology, and behaviour. Behaviours such as cycloaexy (larval defence formations; Jolivet 1988b), sound production (Schmitt 1994), myrmecophily (Agrain et al. 2015), and subsociality with maternal care (Chaboo et al. 2014) probably impact speciation in more restricted clades of Chrysomelidae. On the available phylogenetic hypotheses of Chrysomelidae (Figs 16–18), faecal armours appear as independent macroevolutionary events in speciose clades (part of Cassidinae; Cryptocephalinae; Lamprosomatinae) and in minor lineages (*Blepharida*-group within Galerucinae; Criocerinae; *Phola* within Chrysomelinae). Systematic analyses of these nodes of transitions, from no faecal recycling to faecal recycling, are needed to understand possible speciation impacts after the origin of constructions. We can surmise a shared genetic history for faecal constructions, that they have value in the survival of their builders, and they could be considered adaptive. To understand evolutionary relevance and even possible character information for phylogeny reconstruction, many more species-level studies are needed to document the life stages and to compare roles of different building materials and building repertoires.

Chrysomelid faecal-based constructions are not homologous, being formed in different ways and are held to the body by different structural modifications. Interesting points emerge when subfamily comparisons are made (Table 1). The common material of faeces points to its cheapness and ready availability. Some architectures may be convergent. Dorsal coats of faecal pellets and similar anus position in Criocerinae and in the *Blepharida*-group suggest similar neuro-physiological mechanisms (a “conveyor belt”) to move faecal pellets from anus towards the head and similar purposes. The cassidine *Eurypepla* Boheman, 1854 (Chaboo 2004) also has a wet shield, but this is built differently – the upwardly held abdomen permits the flow of viscous faeces (not pellets) down the body to coat it. It is highly likely, given findings in other non-chrysomelid debris-carriers, that specialised chaetotaxy hold the pellets onto the dorsum. The case architecture of Camptosomata—similar architecture, similar construction behaviours, and similar correlated morphologies (i.e., maternal abdominal fovea and genital ‘kotpresse’; larval flattened head, swollen abdomen, long legs, and curved claws)—support the close relationship of Cryptoccephalinae and Lamprosomatinae. Comparing these aspects in the arboreal, terrestrial, and myrmecophilous species of this clade might reveal additional informative characters for taxonomy and phylogeny.

Cassidinae (e.g., Chaboo 2007) and Criocerinae (Vencl et al. 2004) both exhibit mining, cryptic and exposed larval feeders but faecal shields are made only in exposed forms; this pattern suggests these larvae use shields to protect themselves against a range of abiotic and biotic dangers that are different from those faced by their mining relatives. A bulky structure like a shield is unlikely in the constrained space of a mine.

A question in Cassidinae now is “Which tribe is the sister for the ten tortoise beetle tribes?” Borowiec (1995: fig. 2) proposed two major lineages of tortoise beetles, without identifying a particular basal tribe. Hsiao and Windsor’s topology (1995: fig. 1) resolved Spilophorini + *Oediopalpa* as phylogenetically distant from other tortoise beetles; their topology suggests either two origins of shield construction or a single origin with some losses. Chaboo (2007) found *Oediopalpa* among “hispinines” and Spilophorini and Hemisphaerotini at the base of the tortoise beetle clade; this also suggests a minimum of two origins of the shield construction, yet the shields and caudal processes in these two tribes are very different. A few tortoise beetle species lack a shield, but our current phylogenetic hypotheses suggest these are secondary losses. We also know now that exuviae-only shields appear scattered over the tortoise beetle clade, suggesting multiple origins.

Two Cassidinae fossils (Chaboo and Engel 2008) support a close relationship between Notosacanthini which have mining larvae (Monteith et al. 2021) and Delocraniini which have cryptic exophagous larvae but no shield (CSC, pers. obs.). These fossils suggest that the typical tortoise beetle larval shields probably originated once and during the latest Paleocene or earliest Eocene (Chaboo and Engel 2008).

Recent field observations of *Aproidea* (Aproidini) in Australia reveal that the larvae have a single caudal process and that faeces can pile up from time to time but falls off quickly: there is no fixed stable faecal shield and exuviae are not retained by larvae except at the pre-pupation stage (Chaboo, Sandoval, Campos, and Monteith unpubl. data). Leptispini have exophagous larvae that live in a cryptic leaf shelter they construct; these larvae also exhibit a single

caudal process, but no shield (Prathapan et al. 2009). Species of *Eurispia* Baly, 1858 (Eurispini) have exophagous sheath-feeding larvae but the illustrations of Hawkeswood and Takizawa (1997) are unclear if they have typical caudal processes (tergal) or marginal extensions of an urogomphal plate (not homologous with caudal processes). The single caudal process appears as multiple independent origins within Cassidinae. *Discomorpha* (Omocerini) larvae exhibit a functionally single process but this appears to be a fusion of two and it retains the exuvio-faecal shield (Flowers and Chaboo 2015).

Conclusions

We demonstrate general and widespread models of shield construction in tortoise beetles. We indicate variations in shields over the tortoise beetle clade that raise new challenges to study odd species. Many characters of shields can be defined to benefit phylogeny reconstruction, including construction repertoire, architecture, materials, and associated morphology. Natural history studies and specimen collections can integrate more species to achieve finer-scaled phylogenies of Cassidinae, particularly around nodes of transitions (e.g., mining to exophagy; presence/absence of caudal processes; presence/absence of shields). Clarifying these nodes will help us understand how life history and shields affected diversification within Cassidinae.

Defecation ecology is an important yet under-researched area that is intertwined with the building behaviours and morphology of chrysomelid beetles. Their constructions are crucial for their survival and represent adaptive macro-evolutionary events. Comparative and inter-disciplinary studies of construction behaviours are needed to better understand the evolution of chrysomelids. Until now, explanations of chrysomelid hyperdiversity have relied on the association and radiation with plants. Yet, constructions are a pervasive feature that may help explain the great subfamilial unevenness in Chrysomelidae. The major challenge is fieldwork and specimen assembly of juvenile stages and their constructions, as they are poorly represented in museum collections.

Acknowledgements

In Costa Rica fieldwork, we thank Mauricio Fernandez, Bill Haber, Paul Hanson, Alan Pounds, and Angel Solís for help and Sistema Nacional de Áreas de Conservación, Ministerio de Ambiente y Energía (MINAE) for the research permits. We thank Michael Thomas and Paul Skelley for specimen loans of *S. cucullata*. In South Africa fieldwork, we thank Beth Grobbelaar (SANBI), Hugh Heron, and Maureen Coetzee, University of Witwatersrand, for help and discussion. This paper had a long gestation with valuable discussions, citations, and specific examples from: John Wenzel; colleagues at Cornell University—Thomas Eisner (deceased), Maurice (deceased) and Catherine Tauber, Karen Sime, Nico Franz, Kelly Miller, and Quentin Wheeler; many beetle colleagues—Cheryl Barr, Mary Liz Jameson, Elizabeth Grobbelaar, Hugh Heron, Alfred Newton, Karen Olmstead, Margaret Thayer, William Shepard, and Martha Weiss; and many chrysomelid specialists—Federico Agrain, Christopher Brown, Lourdes Chamorro, Cibele Rebeiro Costa, Vivian Flinte, R. Wills Flowers, Daniel Funk, David Furth, Ken Keefover-Ring, Karen Olmstead, Divarkaran Prathapan, Chris Reid, Paula Alex Trillo, Fred Ven-

cl, and Rob Westerduijn. We thank the following for sending photographs and permission to use: Hope Abrams, Nicky Bay, H. Del Olmo, Hubert Duprat, Dimitri Forero, Jan Hamryski, Masayuki Hayashi, Alan Henderson, Steve Marshall, Dieter Mahsberg, Nick Porch, Filip Trnka, Eerika Schulz, Adrian Tejedor, Gil Wizen, and Takahiro Yoshida. We also thank Ichiro Yamamoto (Director), KAZE Co., Japan for allowing us to view his film of *Cal. attenuata*. We thank Federico Agrain, Jesús Gómez-Zurita, Divakaran Prathapan, and Michael Schmitt for discussing chrysomelid phylogenies, and particularly thank Sara López-Pérez for collaborating on phylogenetic characters. During this long study some results were presented at scientific meetings: Coleopterists Society, Entomological Collections Network, Entomological Society of America, European Congress of Entomology, Kansas Entomological Society, and International Congress in Entomology. We are very grateful to our manuscript readers, Orly Calcetas, Charles Staines, and Nick Upton, to our two valued reviewers, and to Editor Michael Schmitt for all comments and suggestions that improved the final text. Finally, CSC dedicates this paper to her husband, Fernando Merino, and their daughter Teresa Merino.

Additional information

Conflict of interest

No conflict of interest was declared.

Ethical statement

No ethical statement was reported.

Funding

This work was supported by the U.S.A. National Science Foundation grant EAGER 1663680 (PI: CS Chaboo).

Author contributions

Conceptualization: CSC. Data curation: CSC, SA, KN. Formal analysis: CSC. Investigation: CSC, SA, KN. Methodology: CSC, SA, KN. Project administration: CSC. Visualization: CSC, SA, KN, LS. Writing – original draft: CSC, SA, LS. Writing – review and editing: CSC, SA, KN, LS.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Film 1: *Cassida sphaerula* (Chrysomelidae, Cassidinae, Cassidinae)

Authors: Caroline Simmrita Chaboo, Sally Adam, Kenji Nishida, Luke Schletzbaum

Data type: Video (wmv file)

Explanation note: Larva moving shield over dorsum (1.21 mins; real-time speed; Sally Adam). YouTube link: <https://youtu.be/bDyqjys6M-0>.

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Link: <https://doi.org/10.3897/zookeys.1177.102600.suppl1>

Supplementary material 2

Film 2: *Cassida sphaerula* (Chrysomelidae, Cassidinae, Cassidinae)

Authors: Caroline Simmrita Chaboo, Sally Adam, Kenji Nishida, Luke Schletzbaum

Data type: Video (wmv file)

Explanation note: Telescopic anus of larva excreting wet droplet (3.08 mins; real-time speed; Sally Adam). YouTube link: <https://youtu.be/3vNZN60IRM8>.

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Link: <https://doi.org/10.3897/zookeys.1177.102600.suppl2>

Description of three new species of *Benedictus* (Coleoptera, Chrysomelidae, Galerucinae, Alticini) from China, with comments on their biology and modified ethanol traps for collecting flea beetles

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Academic editor: Caroline Chaboo

Received: 3 March 2023

Accepted: 24 April 2023

Published: 30 August 2023

ZooBank: <https://zoobank.org/72997BC7-B301-4EAB-95FB-3B6FD839B1F4>

Citation: Ruan Y, Konstantinov AS, Damaška AF, Zheng L, Chen J, Meng Z (2023) Description of three new species of *Benedictus* (Coleoptera, Chrysomelidae, Galerucinae, Alticini) from China, with comments on their biology and modified ethanol traps for collecting flea beetles. In: Chaboo CS, Schmitt M (Eds) Research on Chrysomelidae 9. ZooKeys 1177: 147–165. <https://doi.org/10.3897/zookeys.1177.102811>

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Abstract

The diversity and biology of the moss and leaf litter-inhabiting flea beetles are still poorly known. In this study, three new species of *Benedictus* are described from China: *Benedictus fuanensis* Ruan & Konstantinov, **sp. nov.**, *Benedictus quadrimaculatus* Ruan & Konstantinov, **sp. nov.**, and *Benedictus wangi* Ruan & Konstantinov, **sp. nov.** Comments on their biology are given. *Benedictus quadrimaculatus* has a highly unusual morphological feature not reported before in flea beetles: black spots on the abdominal tergites that are visible through the elytra. Traditional and modified ethanol traps were tested and proven useful for collecting leaf litter- and moss-inhabiting flea beetles. Based on our tests, eight traps could collect one specimen each day in the testing sites in Fujian Province; three traps could collect one specimen each day in the testing sites in Guangdong Province.

Key words: Diversity, flea beetles, leaf litter, pan trap, pitfall trap, taxonomy

Introduction

Benedictus Scherer, 1969 consists of 26 species prior to this study, of which eight species are known from China. *Benedictus* species occur in Oriental Region and Papua New Guinea, and the adults are usually wingless and inhabit moss cushions and leaf litter (Sprecher-Uebersax et al. 2009). The most recent studies on *Benedictus* include the taxonomic revisional work by Sprecher-Uebersax et al. (2009) which reported 25 species of the genus, and the description of a new species by Damaška and Aston (2019). *Benedictus* is morphologically allied to *Microcrepis* Chen and *Loeblaltica* Scherer (Sprecher-Uebersax et al. 2009). Recent molecular phylogenetic studies (Damaška et al. 2022; Douglas et al. 2023) revealed that flea beetles from multiple and often distant lineages adapted to moss and leaf litter habitats. Damaška et al. (2022) revealed that *Benedictus* belongs to the *Manobia* generic group, which contains the moss-inhabiting genus *Benedictoides* and leaf surface-living genera *Aphthonoides* Jacoby, *Manobia*

Jacoby, and *Phyllotreta* Chevrolat. Despite the studies mentioned above, the true diversity and the biology of the moss-inhabiting species of *Benedictus* are still poorly known. In this work, we describe three new species from China and provide insights into their biology. We also provide a key to the 11 species occurring in China. The feeding habit and living environment of *Benedictus fuanensis* sp. nov. are found to be very similar to that of *Cangshanaltica fuanensis* Ruan et al. (2022). In Fujian province, they were found in the same location and share the same host plant *Hypnum plumaeforme* Wilson (Hypnaceae). When reared in the laboratory, they both feed on the distal ends of moss branches of the host plant.

Moss and leaf litter-inhabiting flea beetles are usually collected by the traditional Berlese funnel (e.g., Konstantinov et al. 2013; Linzmeier and Konstantinov 2020; Konstantinov and Linzmeier 2020) and the fan-driven Berlese funnel (Ruan et al. 2020). In Damaška and Konstantinov (2016), specimens were collected by simply beating semi-dry moss surfaces and cushions on standing and fallen trees. Moss and leaf litter sifting technique was used to concentrate the samples and thus speed up the extraction process. However, Berlese funnels usually require electricity and a suitable room to accommodate them. In this study, we test the ethanol trap for collecting moss and leaf litter inhabiting flea beetles. This method may enhance our abilities to collect these groups of flea beetles and contribute to revealing their diversity and biology.

Materials and methods

Morphological and taxonomic methods

Observations of the habitus and diagnostic characters of flea beetles were made using the Nikon SMZ645 stereomicroscope and Nikon OPTIPHOT microscope. Genitalia with the last few abdominal tergites were separated using sharp insect pins attached to plastic sticks. The tissues surrounding the aedeagus were cleared. Female genitalia and accompanying structures (the last tergites) were immersed in a hot 10% NaOH solution for 30 s (or the appropriate time required to soften irrelevant tissue). The extra tissues surrounding the genitalia were carefully removed using insect pins. For photography, the female genitalia were mounted on slides with glycerine; male genitalia were glued to paper card points. Digital images were taken with a Canon D800 camera attached to Canon MP-E 65-mm lens or microscope lens.

Morphological terminology follows Ruan et al. (2019). Specimen labels are cited verbatim. Ninety-two specimens were assembled for this study based on museum collections and our fieldwork. Abbreviations for insect collections. **IZCAS**: Institute of Zoology, Chinese Academy of Sciences, Beijing, China. **SZPT**: Plant Protection Research Center, Shenzhen Polytechnic, Shenzhen, Guangdong, China. Field-collected and lab-reared specimens are deposited in SZPT and IZCAS.

Rearing methods

Benedictus fuanensis sp. nov. were reared and observed in the laboratory environment. Rearing methods mainly follow those used for *Cangshanaltica fuanensis* Ruan, Konstantinov & Damaška, 2022 (see Ruan et al. 2020). Transparent plastic rearing containers (15 cm × 7 cm × 5 cm) were selected and

placed in a north-facing room to avoid direct sunlight. Two small openings were carved and sealed with non-woven fabrics, allowing for air to circulate and preventing other organisms from coming into the container. A thick layer of moist paper towel was placed at the bottom of the container to maintain proper humidity and avoid larvae from drowning in water drops; a thin layer of soil was placed above the paper towel to provide nutrition for the host plant; fresh host plant moss was collected and placed loosely above the soil layer. Distilled water was sprayed on the moss once a day to maintain humidity using a small spraying device.

Ethanol traps

Two types of ethanol pan traps (as ethanol traps hereinafter) were used: a regular one to collect dead specimens (Fig. 8A–C) and a modified one for collecting live specimens (Fig. 8D, E). The modified trap consists of the following components: 1) a plastic container such as a plate or a bowl; 2) ethanol dipped sponge (or paper towel) placed on the bottom of the container; 3) the upper opening of the bowl is sealed by plastic film leaving a narrow opening in the middle for beetles to crawl in.

The plastic film forms a slope with a central opening at the bottom. Usually, the flea beetles would either stay close to the ethanol-dipped sponge or be trapped at the higher part of the plastic film.

Ethanol traps were usually placed close to concentrations of moss, leaf litter, or liverworts. Sometimes moss or leaf litter on the ground was slightly excavated to accommodate the ethanol traps.

Test 1. In this test, 35 modified ethanol traps (Fig. 8D, E) were placed in three moist and moss-abundant sites in a village near Fuan City, Fujian Province. Each site is approximately 100 m². The experiment lasted 26 days (including five rainy days) in January and February 2021. The ethanol traps were refreshed, and the specimens were collected each day. The number of flea beetles collected was counted each day.

Test 2. In this test, 37 traditional ethanol traps (Fig. 8A–C) were used. They were placed in three sites in the Che-ba-ling nature reserve, Guangdong Province, in June 2021. The ethanol traps were refreshed, and the specimens were collected each day. The experiment lasted for three days (including one rainy day).

Results

Taxonomy

Genus *Benedictus* Scherer, 1969

Benedictus Scherer, 1969: 99. Type species: *Benedictus elisabethae* Scherer, 1969, by original designation.

Himalalta Medvedev, 1990: 42. Type species: *Himalalta brevicornis* Medvedev, 1990 (= *Benedictus leoi* Scherer, 1989). Synonymised by Sprecher-Uebersax et al. 2009: 476.

Distribution. China (Fujian, Guangdong, Hongkong, Sichuan, Yunnan, Tibet), India, Nepal, Thailand, Philippines, Papua New Guinea.

Key to Chinese *Benedictus* species

- 1 Elytral punctures shallow and tiny, arranged in barely perceptible striae....
.....***B. sichuanensis* Sprecher-Uebersax et al., 2009**
- Elytral punctures deep and large, arranged in well-developed striae.....**2**
- 2 Transverse antebasal groove of pronotum poorly defined, shallow, barely visible, and without large punctures.....**3**
- Transverse antebasal groove of pronotum well defined and deep; if shallow, then marked by a row of much deeper and larger punctures**5**
- 3 Pronotum and elytra dark chestnut-brown, apex of aedeagus broadly rounded***B. kurbatovi* Sprecher-Uebersax et al., 2009**
- Pronotum pale brown or yellowish; elytra usually as pale as pronotum, but sometimes slightly darker; apex of aedeagus narrow, not broadly rounded.....**4**
- 4 Ventral surface of aedeagus with relatively sharp ridge stretching from basal opening to apical 2/3
.....***B. belousovi* Sprecher-Uebersax et al., 2009**
- Ventral surface of aedeagus without ridge stretching from basal opening to apical 2/3.....***B. cangshanicus* Sprecher-Uebersax et al., 2009**
- 5 Transverse antebasal groove of pronotum shallow, marked by a row of much deeper and larger punctures***B. wangi* sp. nov.**
- Transverse antebasal groove of pronotum deep, well defined**6**
- 6 Body bicoloured, pronotum yellowish to pale brown, head and elytra dark brown***B. kabaki* Sprecher-Uebersax et al., 2009**
- Body unicolorous.....**7**
- 7 In ventral or dorsal view, apex of aedeagus wide and emarginate at middle; four dark maculations present on the abdominal tergites (Figs 4G, 5A, B), which are visible through elytra when the beetle is alive.....
.....***B. quadrimaculatus* sp. nov.**
- In ventral or dorsal view, apex of aedeagus not wide or emarginate at middle; abdominal tergites without dark maculations**8**
- 8 Apex of aedeagus sagittalis ***B. sagittalis* Damaška & Aston, 2019**
- Apex of aedeagus not sagittalis..... **9**
- 9 In ventral view, sides of aedeagus parallel from base to apical fourth; in lateral view, aedeagus straight at middle part, curved ventrad at basal and apical fourth, apex very slightly bent dorsad
.....***B. tibetanus* Sprecher-Uebersax et al., 2009**
- In ventral view, sides of aedeagus slightly convex, widest at middle; in lateral view, aedeagus not straight at middle part.....**10**
- 10 Head without longitudinal impression above supracallinal sulci. In ventral view, sides of aedeagus slightly and evenly convex from base to near apex, middle part not prominently wider than base; in lateral view, aedeagus evenly curved ventrad, apex not bending ventrad
.....***B. nigrinus* Sprecher-Uebersax et al., 2009**
- Head with two short longitudinal impressions above supracallinal sulci. In ventral view, sides of aedeagus not evenly convex, with middle part prominently wider than base; in lateral view; aedeagus strongly curved ventrad at basal half, nearly straight at apical half, apex very slightly bent ventrad..... ***B. fuanensis* sp. nov.**

***Benedictus fuanensis* Ruan & Konstantinov, sp. nov.**

<https://zoobank.org/6F2A1FBE-6CCC-42C0-B2A8-37196C16A07D>

Figs 1–3

Type material. Holotype: ♂ (SZPT), labels: 1) China, Fujian Prov., Fuan (福安), Shuyang (柘洋), 290 m, 27.1578°N, 119.6809°E, site1, 25.I–21.II.2021, Leg. Ruan, Ethanol-traps nr. moss; 2) HOLOTYPE *Benedictus fuanensis* sp. nov. Des. Ruan et al. 2022.

Paratypes (72 specimens): 21♂16♀ (SZPT; some would be transferred to IZCAS), labels: 1) China, Fujian Prov., Fuan (福安), Shuyang (柘洋), 290 m, 27.1578°N, 119.6809°E, site1, 25.I–21.II.2021, Leg. Ruan, Ethanol-traps nr. moss; 2) PARATYPE *Benedictus fuanensis* sp. nov. Des. Ruan et al. 2022. • 10♂7♀ (SZPT), labels: 1) China, Fujian Prov., Fuan (福安), Shuyang (柘洋), 300 m, 27.1573°N, 119.6812°E, site2, 25.I–21.II.2021, Leg. Ruan, Ethanol-traps nr. moss; 2) PARATYPE *Benedictus fuanensis* sp. nov. Des. Ruan et al. 2022. • 3♂2♀ (SZPT), labels: 1) China, Fujian Prov., Fuan (福安), Shuyang (柘洋), 320 m, 27.1599°N, 119.6774°E site3, 25.I–21.II.2021, Leg. Ruan, Ethanol-traps nr. moss; 2) PARATYPE *Benedictus fuanensis* sp. nov. Des. Ruan et al. 2022. • 2♂5♀ (SZPT), labels: China, Fujian Prov., Fuan (福安), Shuyang (柘洋), 290 m, 27.1611°N, 119.6763°E, 13-II-2020, Extracted from moss, Leg. Y. Ruan; 2) PARATYPE *Benedictus fuanensis* sp. nov. Des. Ruan et al. 2022. • 1♂ (SZPT), labels: China, Fujian Prov., Fuan, Shuyang, 16-VIII-2019, unknown moss, Leg. Y. Ruan; 2) PARATYPE *Benedictus fuanensis* sp. nov. Des. Ruan et al. 2022. • 4♂1♀ (SZPT), labels: Guangdong, Shaoguan, Chebaling nature reserve, Luzidong, V.30-VI.4.2021, 24.6979°N, 114.1758°E, 600 m, Leg. Yongying Ruan; 2) PARATYPE *Benedictus fuanensis* sp. nov. Des. Ruan et al. 2022.

Diagnosis. This new species may be distinguished from other known species of *Benedictus* by the following combination of characters: pronotum strongly convex; aedeagus widest at middle in ventral view; two longitudinal impressions present above supracallinal sulci; the facial part of the head strongly elongated; tormae of labrum (Fig. 2C) extremely long, ~ 3.5× as long as visible part of labrum.

Description. Male body length 1.30–1.60 mm, width 0.80–0.90 mm; female body length 1.40–1.70 mm, width 0.90–1.00 mm (measured for all type specimens). Ratio of body length to body width: 1.55–1.78 (measured in one male and one female). Dorsum yellow-brown to chestnut-brown. Venter slightly paler than dorsum. Antennae and legs uniformly pale yellow-brown to yellow-brown. Legs and antennae covered with yellow setae.

Head. Head hypognathous. Vertex smooth, with very shallow reticulation; a few punctures bearing setae present above supraorbital sulci on each side; two short longitudinal impressions present at mesal side of punctures above supra-callinal sulci. Antennal calli well delimited, triangular, with flattened surface. Supracallinal and supraorbital sulci deep, forming oblique straight line. Supra-antennal sulcus poorly developed. Facial part of head strongly elongated. Frontal ridge widest between antennal sockets, much narrowed and ridged towards clypeus; each side of frontal ridge concave and looks coarse being covered with minute longitudinal ridges. Fronto-genal ridge present. Labrum with two pairs of setae, deeply emarginate on anterior margin. Mandibles symmetrical,

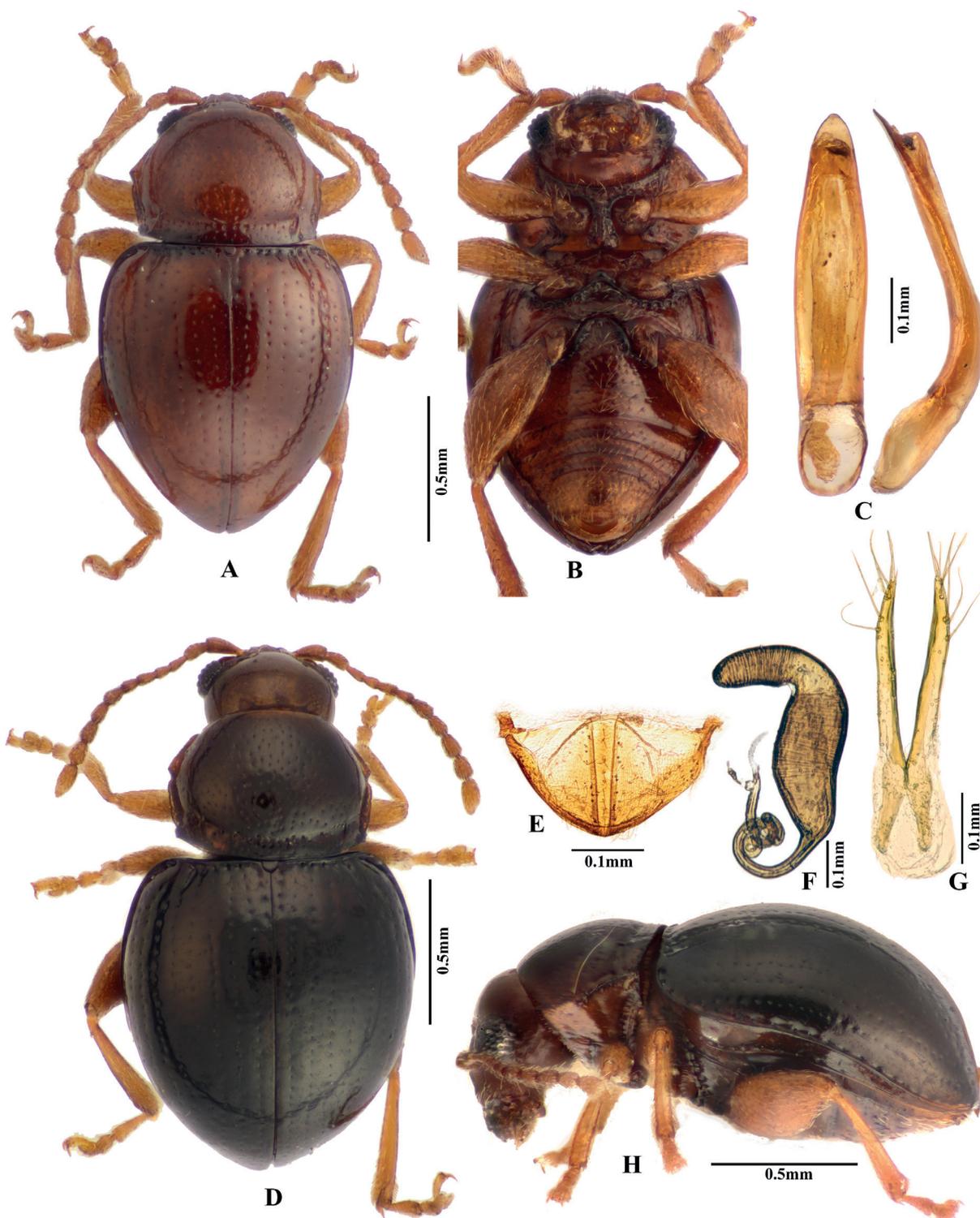


Figure 1. Adult morphology of *Benedictus fuanensis* sp. nov. **A** holotype, male, dorsal view **B** holotype, male, ventral view **C** median lobe of aedeagus (holotype), ventral and lateral views **D** female (paratype), dorsal view **E** last visible abdominal tergite of female **F** spermatheca **G** vaginal palpi **H** female (paratype), lateral view.

palmate; each mandible with five sharp teeth, mesal side with a membranous lobe bearing dense microtrichia. Tormae of labrum extremely long, ~ 3.5× as long as visible part of labrum. Proportions of antennomere lengths: 100: 56: 45: 33: 47: 42: 54: 53: 56: 58: 87 (measured in one individual).

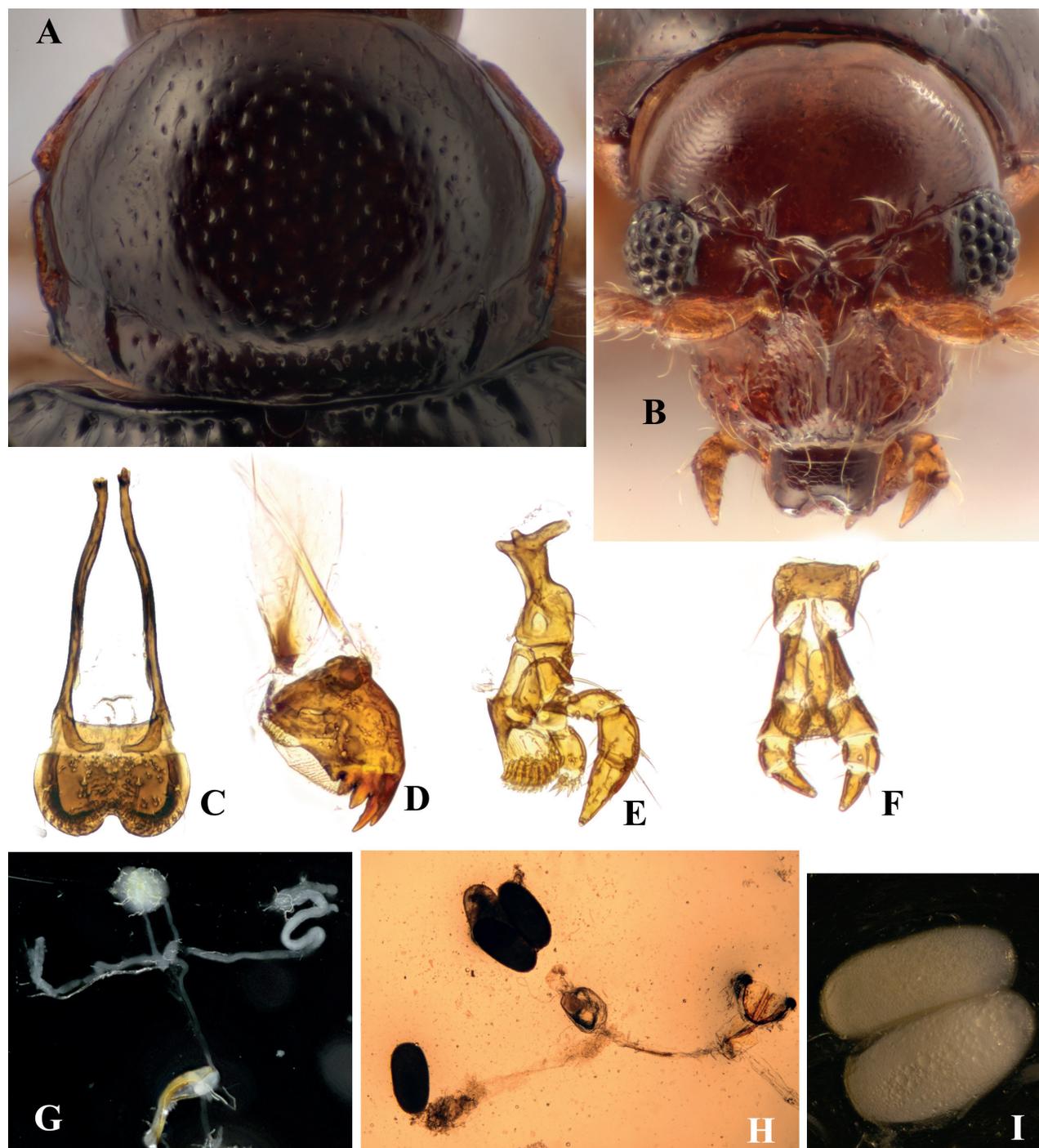


Figure 2. Adult morphology of *Benedictus fuanensis* sp. nov. **A** pronotum, female **B** head, female **C** labrum, showing the extremely long tormae **D** mandible **E** maxilla **F** labium **G** male reproductive system **H** female reproductive system, four eggs are visible **I** immature eggs in the ovary.

Thorax. Pronotum strongly convex, ratio of pronotum width (measured at posterior edge) to length: 1.37–1.42 (measured in two males and two females). Pronotum widest at posterior part of anterolateral callosity. Anterolateral callosity well-developed, elongate, and straight, with an anterolateral setiferous pore situated at posterior end. Procoxal cavities open posteriorly. Base of pronotum with deep and transverse antebasal groove, delimited by well-developed longitudinal grooves on each side.

Elytra strongly convex, humeral calli absent. Elytra with punctures arranged in regular lines. Hind wings absent.

Legs. First male protarsomere larger than that of female. Length of metatibia to first metatarsomere in male: 100: 31.

Male genitalia. Median lobe of aedeagus in ventral view: widest at middle, ventral surface smooth, sides narrowing from middle to apex; apex narrowly rounded, without denticle. Median lobe of aedeagus in lateral view: widest at base, strongly curved ventrad at basal half, apical half nearly straight, with apex very slightly bent ventrad.

Female genitalia. Spermathecal pump cylindrical, very slightly curved, apex broad and rounded; without clear border with receptacle; more or less perpendicular to receptacle. Receptacle of spermatheca cylindrical, gradually narrowed towards spermathecal duct, with sides slightly curved near middle. Spermathecal duct has coils.

Variation. In the specimens collected from Fujian province, males have a paler colour than females; males vary slightly in body size; females have more or less invariable body size. In the specimens from Guangdong province, males have a deeper colour than females.

Etymology. This species is named after the type locality, Fuan city; the name also indicates that the species is sympatric with *Cangshanaltica fuanensis* Ruan et al. (2022). The specific epithet is a noun in apposition.

Type locality. Shuyang, Fuan, Fujian Prov., China.

Distribution. China (Fujian, Guangdong).

Host plant. *Benedictus fuanensis* sp. nov. primarily fed on *Hypnum plumaeforme* Wilson (Hypnaceae) in the laboratory environment. They were spotted on *H. plumaeforme* at night in the type locality. We found they also feed on *Racopilum* cf. *aristatum* when there is no *H. plumaeforme* present in the rearing container.

Biology. Forty live individuals were collected by modified ethanol traps (Fig. 8D, E) and reared in a plastic container in the laboratory. Rearing methods are the same as those used for *Cangshanaltica fuanensis*, follows Ruan et al. (2020). Copulation was observed frequently in the lab-reared individuals of *B. fuanensis*; in some cases, a single copulation could last for more than 24 hours, with the male constantly staying on the back of the female. The rearing lasted for 46 days; however, no eggs or larvae were found. This means the biological habits of *B. fuanensis* may be slightly different from those of *Cangshanaltica fuanensis*.

Benedictus fuanensis sp. nov. and *Cangshanaltica fuanensis* were found on the same host plant in the same moss cushion in Fuan, Fujian Province. They are also quite similar in some biological characteristics. For instance, adults of both species were usually discovered on the surface of *Hypnum plumaeforme* Wilson at night with high humidity; they both like to feed on the top of the young shoots of the host plant, so that the ends of young shoots are usually chopped off by beetle feeding, which is destructive to the host plant; the faeces of their larvae and adults mainly consist of undigested fragments of host plant leaf (see Fig. 3G). The interaction of the two species in nature is still unknown.

Benedictus fuanensis sp. nov. also has large eggs, small egg numbers, and fewer ovarioles. These features are similar to those of *Cangshanaltica fuanensis*.

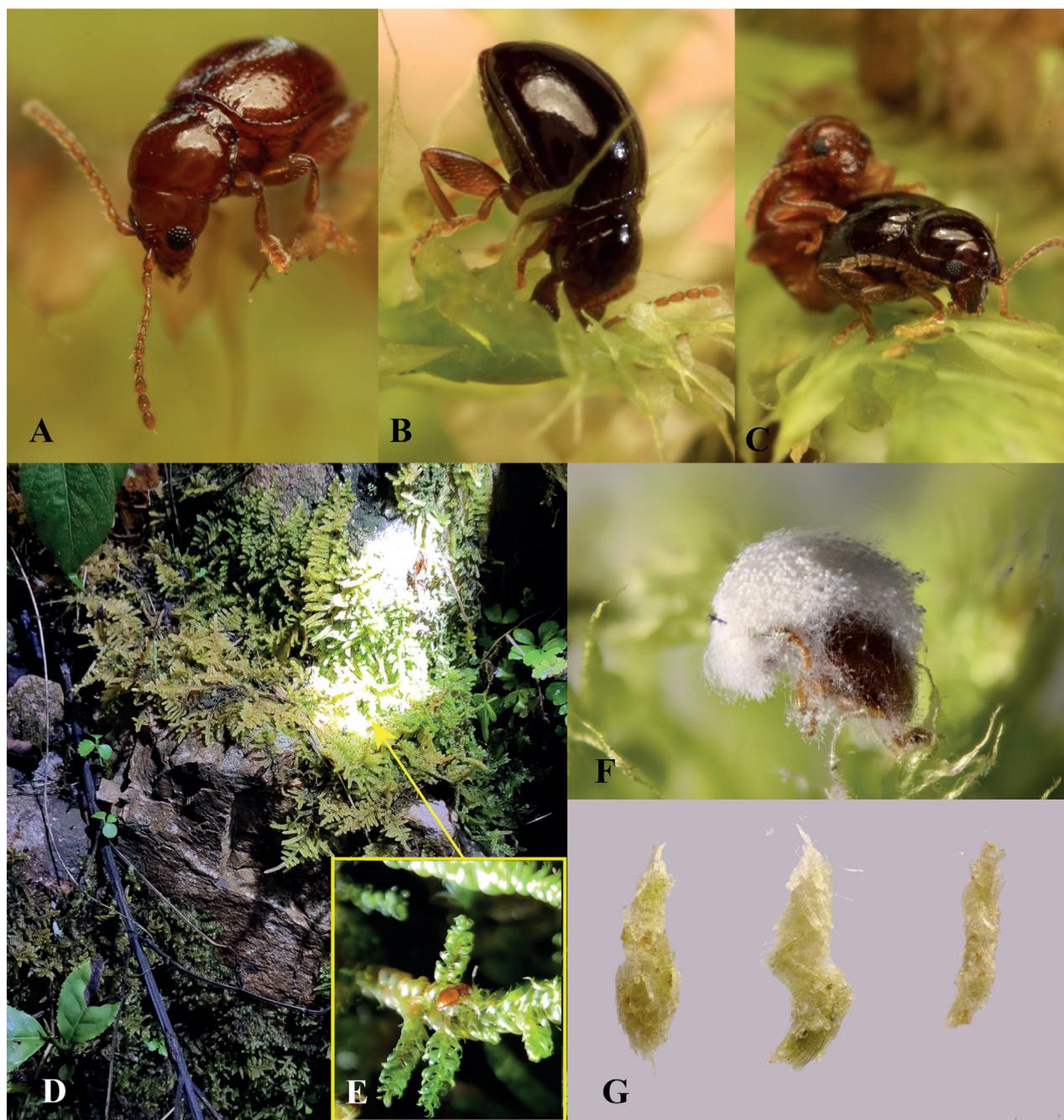


Figure 3. Biology of *Benedictus fuanensis* sp. nov. **A** male **B** female adult feeding on the top of a young shoot of the *Hypnum plumaforme* Wilson **C** male and female *in copula* **D** habitat at the type locality, photographed at night **E** an individual discovered on the host plant at night at the type locality **F** an individual reared in the lab infected by fungi **G** faeces of individuals reared in the lab.

Based on the dissection of three female specimens, four to six eggs could be found inside a female abdomen. Egg length 0.60–0.62 mm; width 0.25–0.31 mm (measured on two eggs); egg length equals ~ 40% of female body length.

The jumping ability of two individuals was tested. The horizontal jumping distance ranged from 3.5 cm to 11.7 cm. *Benedictus fuanensis* sp. nov. has far less explosive jumps compared to *Gangshanaltica fuanensis*.

***Benedictus quadrimaculatus* Ruan & Konstantinov, sp. nov.**

<https://zoobank.org/86DA5B90-EA05-4008-B22F-6DC74CF9C8CF>

Figs 4, 5

Type material. Holotype: ♂ (SZPT), labels: 1) China, Yunnan, Yuanyang County, Xinjie, 23.1163°N, 102.7690°E, 1900 m. Leg. Y. Ruan & M. Zhang 2019.VII.28, Extracted from moss; 2) HOLOTYPE *Benedictus quadrimaculatus* sp. nov. Des. Ruan et al. 2022.

Paratypes: 6♂6♀ (SZPT; some would be transferred to IZCAS), labels: 1) China, Yunnan, Yuanyang County, Xinjie, 23.1163°N, 102.7690°E, 1900 m. Leg. Y. Ruan & M. Zhang 2019.VII.28, Extracted from moss; 2) PARATYPE *Benedictus quadrimaculatus* sp. nov. Des. Ruan et al. 2022.

Diagnosis. This new species may be distinguished from other known species of *Benedictus* by the following combination of characters: in ventral or dorsal view, apex of median lobe of aedeagus wide and emarginate at middle; four dark maculations present on the abdominal tergites (Figs 4G, 5A, B), which are more prominent when the beetle is alive; antennal calli subquadrate with a fovea present between them. Black spots on the abdominal tergites that are visible through elytra is a highly unusual feature that we have not observed in flea beetles before.

Description. Male body length 1.35–1.45 mm, width 0.80–0.85 mm; female body length 1.45–1.50 mm, width 0.80–0.85 mm (based on all type specimens). Ratio of body length to body width: 1.70–1.77 (one male and one female measured). Entire body evenly yellow-brown to chestnut-brown, including antennae and legs.

Head. Head hypognathous. Vertex smooth, without reticulation; a few punctures bearing setae situated above supraorbital sulci on each side. Antennal calli well delimited, subquadrate, and slightly convex; fovea present between antennal calli. Supracallinal and supraorbital sulci deep, forming oblique straight line. Supra-antennal sulcus poorly developed. Facial part of head relatively short. Frontal ridge widest between antennal sockets, strongly narrowed and ridged towards clypeus; frons concave and smooth on each side of frontal ridge, surface without minute longitudinal ridges. Proportions of antennomere lengths: 100: 64: 45: 45: 66: 53: 72: 78: 73: 78: 110 (measured in one individual).

Thorax. Pronotum moderately convex, ratio of pronotum width (measured at middle) to length: 1.30–1.42 (measured in one male and one female). Pronotum widest at middle part. Anterolateral callosity strongly developed, elongate, and somewhat straight, with anterolateral setiferous pore situated at posterior end. Procoxal cavities open posteriorly. Base of pronotum with deep and transverse antebasal groove bearing coarse and large punctures; transverse antebasal groove delimited by a well-developed longitudinal groove on each side.

Elytra convex, humeral calli absent. Elytra with punctures arranged in regular lines. Hind wings absent.

Legs. First male protarsomere larger than that of female. Length of metatibia to first metatarsomere in male: 100: 30.

Male genitalia. Median lobe of aedeagus in ventral view: widest at middle; ventral surface smooth; sides parallel from base to apical fourth, abruptly narrowed with a step at apical fourth; apex wide, emarginated in middle, without

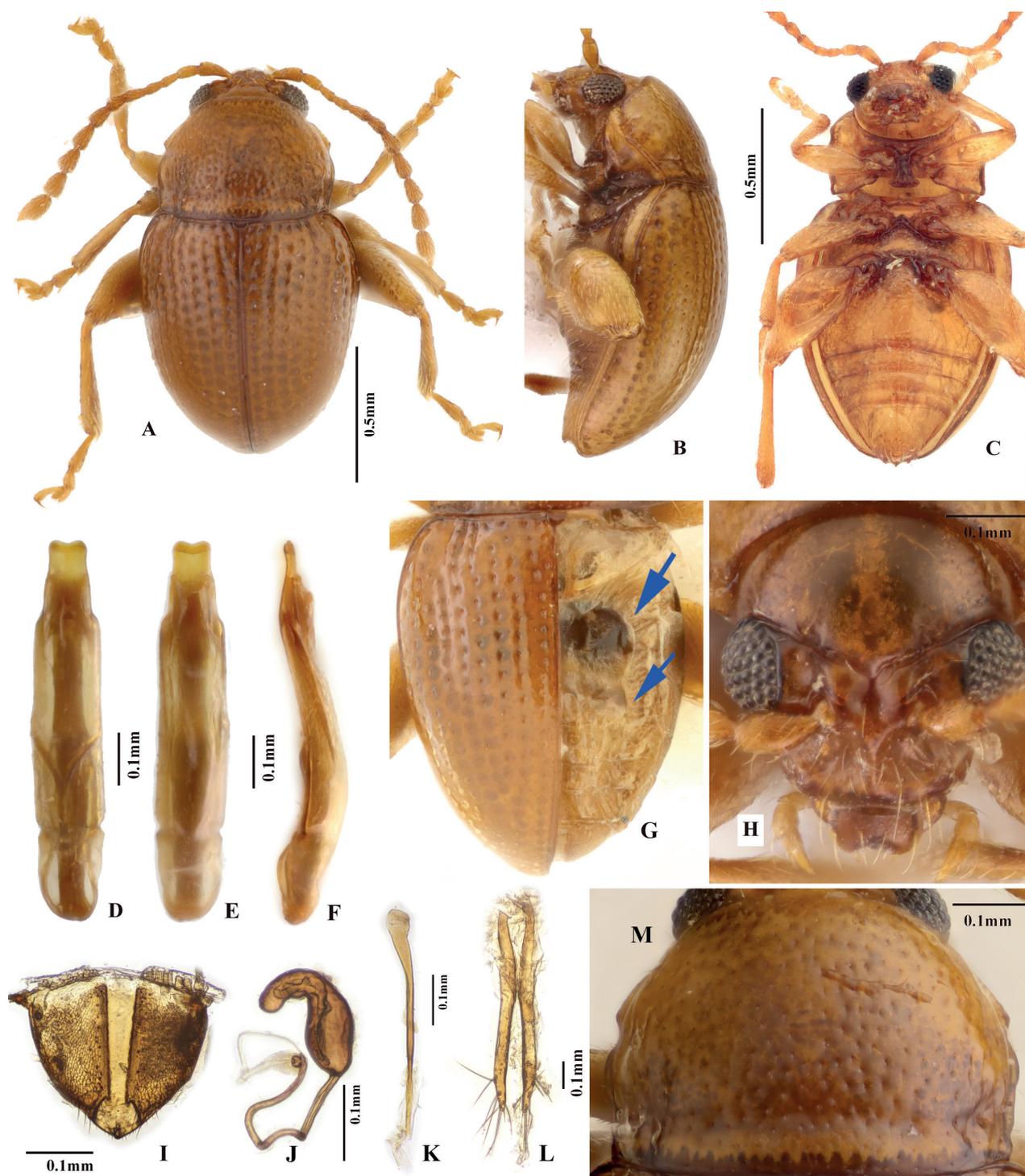


Figure 4. Adult morphology of *Benedictus quadrimaculatus* sp. nov. **A–C** holotype, dorsal, lateral, and ventral views **D–F** median lobe of aedeagus (holotype), ventral, dorsal, and lateral views **G** sclerotised and darkened area on the abdominal tergites (arrowed), which are visible through elytra as black spots when the beetle is alive **H** head **I** last visible abdominal tergite of female **J** spermatheca **K** tignum **L** vaginal palpi **M** pronotum.

denticle. Median lobe of aedeagus in lateral view: slightly sinuate, curved ventrad at basal 3/4, bent dorsad at apical 1/4, apex straight.

Female genitalia. Spermathecal pump cylindrical, very slightly curved, apex broad and rounded; without clear border with receptacle; more or less perpen-

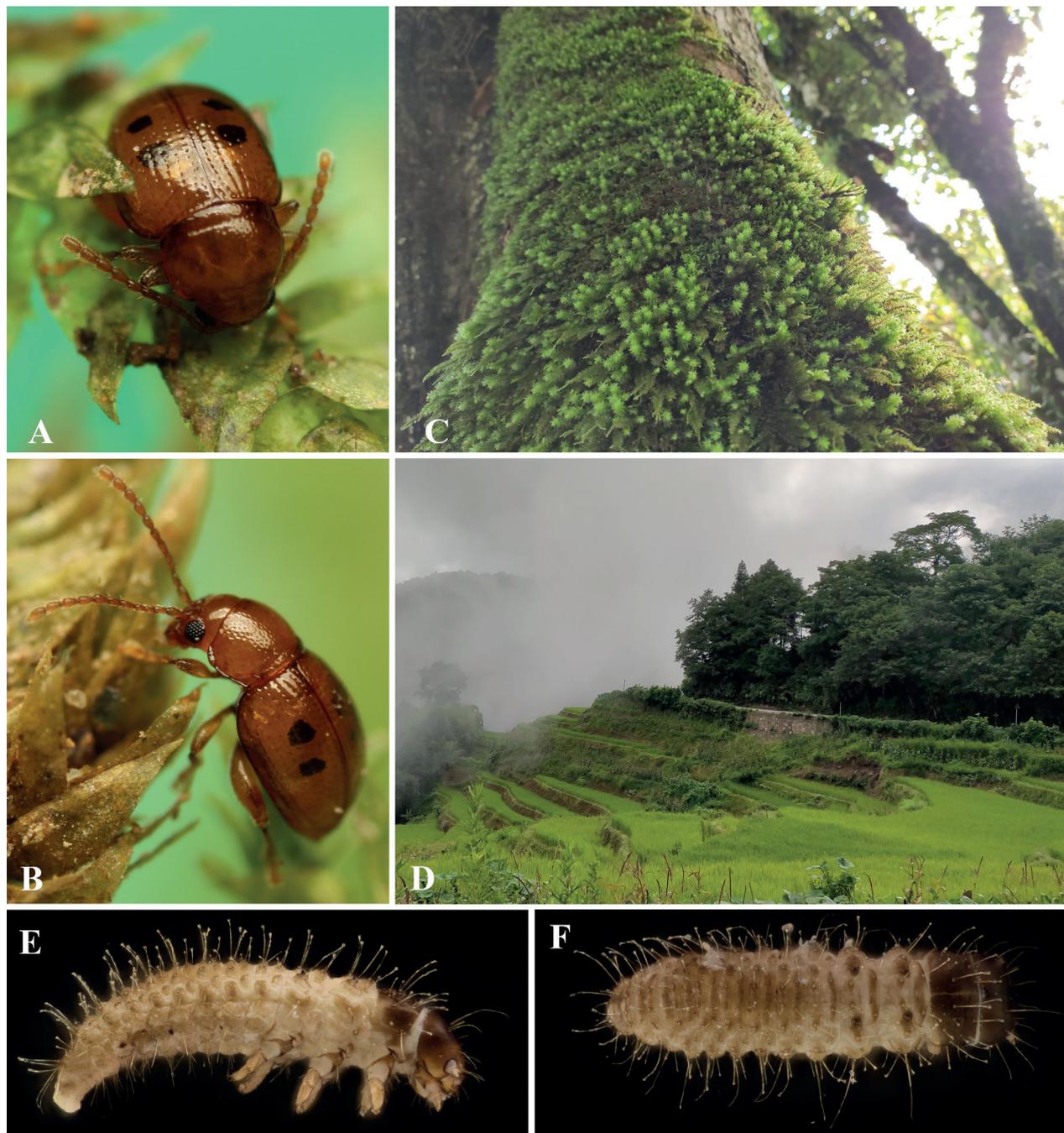


Figure 5. Biology of *Benedictus quadrimaculatus* sp. nov. **A, B** photography of living individuals in lab environment **C** photography of the moss cushion at the type locality **D** habitat environment near the type locality **E, F** habitus of two unknown larvae extracted along with the adults of *B. quadrimaculatus* from moss.

dicular to receptacle. Receptacle of spermatheca pear-shaped, with sides convex. Spermathecal duct without coils.

Variation. The shape of the pronotum varied slightly by having slightly lesser widths and straighter lateral sides in some individuals.

Etymology. This species is named after the four dark maculations on its abdominal tergites (Fig. 4G), which are prominent when the beetle is alive (Fig. 5A, B).

Type locality. Yuanyang County, Yunnan Prov., China.

Distribution. China (Yunnan).

Host plant. Unknown.

Biology. This species is extracted from moss cushions containing multiple moss species using a modified fan-driven Berlese funnel (see Ruan et al. 2020). Live individuals were reared in the laboratory environment; however, no feeding behaviour was observed.

Although two larvae (Fig. 5E, F) were extracted along with the adults from moss, it is unknown if they are conspecific.

***Benedictus wangi* Ruan & Konstantinov, sp. nov.**

<https://zoobank.org/0019D11C-D497-4805-A567-4382902120DA>

Fig. 6

Type material. Holotype: ♂ (IZCAS), labels: 1) Tibet, Linzhi, Milin county, Sejilashan, 318 km, 4174 km, 29°38'15.37"N, 94°42'52.89"E, 4106 m, from the soil under rhododendron, 2016-VI-13, Leg. Yi Wei; 2) HOLOTYPE *Benedictus wangi* sp. nov. Des. Ruan et al. 2022.

Paratypes: 2♂3♀ (SZPT), labels: 1) Tibet, Linzhi, Milin county, Sejilashan, 318 km, 4174 km, 29°38'15.37"N, 94°42'52.89"E, 4106 m, from the soil under rhododendron, 2016-VI-13, Leg. Yi Wei; 2) PARATYPE *Benedictus wangi* sp. nov. Des. Ruan et al. 2022. [Part of the paratype materials will be transferred to IZCAS]

Diagnosis. This new species may be distinguished from other known *Benedictus* species by the following combination of characters: a line of deep and large punctures present on the antebasal groove of pronotum; spermathecal pump has a bulge at base; in lateral view, median lobe of aedeagus almost straight, only slightly curved ventrad near apex.

This new species is close to those *Benedictus* species that have a broad pronotum without a constriction near the base, such as *B. nobding* Sprecher-Uebersax, Konstantinov, Prathapan & Döberl, 2009; *B. thumsila* Sprecher-Uebersax, Konstantinov, Prathapan & Döberl, 2009; *B. yatongla* Sprecher-Uebersax, Konstantinov, Prathapan & Döberl, 2009; *B. lauribina* Sprecher-Uebersax, Konstantinov, Prathapan & Döberl, 2009, and *B. kurbatovi* Sprecher-Uebersax, Konstantinov, Prathapan & Döberl, 2009. This species could be distinguished from all these by having a line of deep and large punctures on the transverse antebasal groove of the pronotum.

This new species is especially close to *Benedictus lauribina* in the general shape of the body and spermatheca. However, it can be differentiated from *B. lauribina* by the following characters: the body colour is chestnut-brown to dark brown, the apex of aedeagus is broadly rounded, and a line of deep and large punctures present on the transverse antebasal groove of the pronotum. While in *B. lauribina*, the body colour is yellow-brown, the apex of aedeagus is acute, and there are no deep and large punctures on the transverse antebasal groove of the pronotum.

Description. Male body length 1.55–1.65 mm, width 0.95–1.05 mm; female body length 1.75–1.80 mm, width 1.09–1.11 mm (based on all type specimens). Ratio of body length to width: 1.59–1.63 (measured in one male and one female). Entire body evenly chestnut-brown to deep brown; antennae and legs yellow-brown to chestnut-brown.



Figure 6. Adult morphology of *Benedictus wangi* sp. nov. **A–C** holotype; dorsal, ventral, and lateral views **D, E** median lobe of aedeagus (holotype), ventral, and lateral views **F** tignum **G** last visible abdominal tergite of female **H** vaginal palpi **I** spermatheca **J** head **K** pronotum.

Head. Head hypognathous. Vertex smooth, without reticulation, a few punctures bearing setae present above supraorbital sulci on each side. Antennal calli well delimited, triangular, slightly convex; fovea present between antennal calli. Supracallinal and supraorbital sulci deep, forming nearly straight line. Supra-antennal sulcus poorly developed. Facial part of head slightly elongated.

Frontal ridge widest between antennal socket, strongly narrowed and ridged towards clypeus; frons concave on each side of frontal ridge, surface without minute longitudinal ridges. Proportions of antennomere lengths: 100: 64: 58: 58: 66: 62: 75: 64: 65: 70: 107 (measured in one individual).

Thorax. Pronotum moderately convex, ratio of pronotum width (measured at middle) to length: 1.36–1.39 (measured in one male and one female). Pronotum widest at middle. Anterolateral callosity poorly developed. Procoxal cavities open posteriorly. Base of pronotum with deep and transverse antebasal groove bearing coarse and large punctures, delimited by well-developed longitudinal grooves on each side.

Elytra convex, humeral calli absent. Elytra with punctures arranged in regular lines. Hind wings absent.

Legs. First male protarsomere only slightly larger than that of female. Length of metatibia to first metatarsomere in male: 100: 28.

Male genitalia. Median lobe of aedeagus in ventral view: widest at basal third; ventral surface smooth; sides parallel from basal half, gradually narrowed apically; apex widely rounded, without denticle. Median lobe of aedeagus only slightly curved in lateral view: straight at basal 2/3, slightly curved ventrad at apical 2/3, apical end bent dorsad.

Female genitalia. Spermathecal pump cylindrical, apex broad and rounded; without clear border with receptacle; make acute angle with receptacle. Receptacle of spermatheca more or less cylindrical, with sides slightly convex.

Variation. No prominent variation was observed.

Etymology. The specific name is after the Chinese entomologist and flea beetle specialist Mr. Shuyong Wang.

Type locality. Linzhi, Tibet, China.

Distribution. China (Tibet).

Host plant. Unknown.

Testing of the ethanol traps for collecting leaf litter and moss-inhabiting flea beetles

Test 1 (Figs 7, 8D, E; see Materials and methods section for more information)

The number of specimens collected presents a positive correlation with the temperature. The efficiency of the ethanol traps was highly affected by the lower air temperature and the rain in winter, which may reduce the activity of the flea beetles. In total, 122 individuals of moss or liverwort-feeding flea beetles were collected: 82 individuals of *Benedictus fuanensis* sp. nov., 19 individuals of *Cangshanaltica fuanensis*, and 21 individuals of *Minota* sp. The data show that four or five individuals of moss or liverwort-feeding flea beetles were collected each day; on average, every eight ethanol traps yield one individual each day.

Except for those flea beetle species mentioned above, four individuals of *Chaetocnema constricta* Ruan et al. 2014, and one individual of *Longitarsus* sp. were also discovered in the traps. Many other insects were also found in the trap, and this method may also be useful to collect other moss and leaf litter inhabiting beetles.

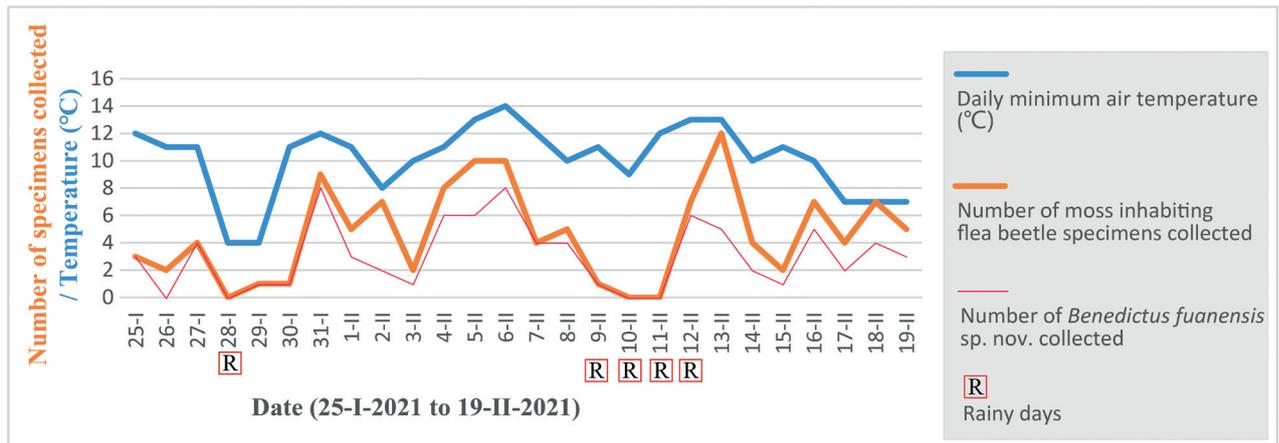


Figure 7. Number of moss-inhabiting flea beetles collected by ethanol traps influenced by the weather. The lowest air temperature of each day (provided by the local weather bureau) is marked in the blue line; the number of all moss-inhabiting flea beetle specimens collected each day is marked in the orange line; the number of *Benedictus fuanensis* sp. nov. is marked by the red line. The letter R in a red box indicates rainy days. The figure shows that lower temperatures and rainy weather highly reduce the efficiency of the ethanol traps.

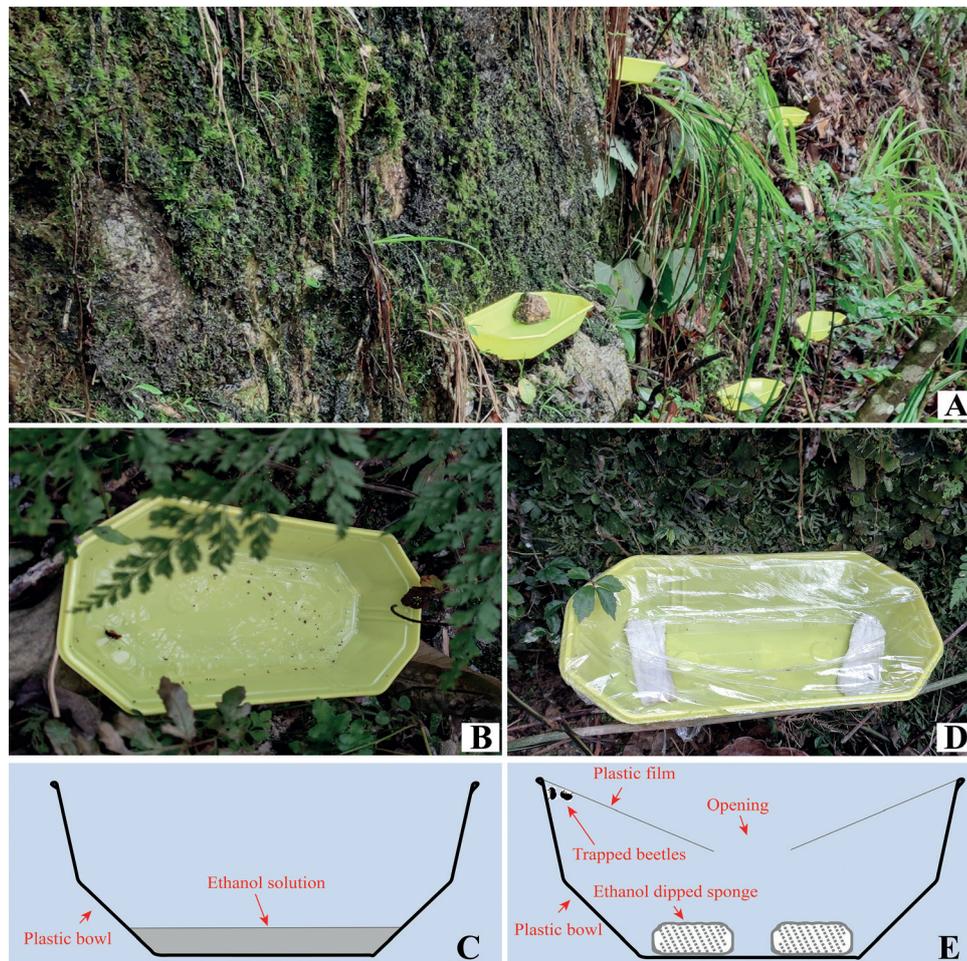


Figure 8. Ethanol traps used for collecting leaf litter and moss-inhabiting flea beetles **A–C** regular ethanol traps were placed close to moist moss, liverwort, or leaf litter to collect flea beetles **D, E** modified ethanol trap for collecting living individuals; diagram in inset **E** shows that ethanol-dipped sponge is used as bait, the upper opening of the bowl is sealed by plastic film leaving a narrowing opening for beetles to crawl in, the plastic film forms a slope; when the flea beetles try to escape, they usually crawl upwards and could be trapped by the slope.

Test 2 (Fig. 8A–C; see Material and methods section for more information)

In total, 39 individuals of moss-, liverwort-, or leaf litter-inhabiting flea beetles were collected. They belong to three flea beetle genera: *Benedictus*, *Minota* Kutschera, and *Clavicornaltica* Scherer. The data show that 13 specimens could be collected each day; on average, approximately every three ethanol traps yield one flea beetle each day.

Discussion

Counting three new species described in this work, there are now 11 *Benedictus* species known from China and 29 species from the world. The previously reported *Benedictus* species all inhabit middle to high altitudes (based on published works). However, the discovery of *Benedictus fuanensis* sp. nov. shows that they also adapt to low-elevation (290–320 m) environments.

It is rather intriguing that *Benedictus fuanensis* sp. nov. and *Cangshanaltica fuanensis* are not only sympatric but also share the same host plant. They are also similar in feeding on the top of the young shoots of the host plant and having small number of large eggs and fewer ovarioles. These may be related to the miniaturisation of their body size. The rearing environment of *Benedictus fuanensis* sp. nov. was maintained similarly to that in the rearing of *C. fuanensis* (Ruan et al. 2020). The failure to produce the second generation implies that the microenvironment they adapt to may differ slightly from that of *C. fuanensis*. The high humidity maintained in the rearing process of *C. fuanensis* may not be optimal for *Benedictus fuanensis* sp. nov.

The ethanol traps were tested and proven quite efficient in collecting moss- and leaf litter-inhabiting flea beetles. However, it is uncertain if ethanol works as bait for the beetles, which needs to be tested in future field works.

Acknowledgments

This research was supported by the following grants: the National Natural Science Foundation of China (Grant No. 32270483), the Guangdong Basic and Applied Basic Research Foundation (Grant No. 2023A1515030133, Grant No. 2021A1515110368), the Post-doctoral Later-stage Foundation Project of Shenzhen Polytechnic (Grant No. 6020271010K), the GDAS Special Project of Science and Technology Development (Grant No. 2020GDASYL-20200102021), the Second Tibetan Plateau Scientific Expedition and Research Program (STEP) (Grant No. 2019QZKK05010600), and the grant SVV 260686/2023.

We would like to express our heartfelt thanks to Drs. Elisabeth Geiser, Viswajyothi Keezhpattillam, Chi-feng Lee, and Caroline Chaboo for reviewing and improving the manuscript. We thank Dr. Zulong Liang for his companionship in the Nanling Mountains collecting trips and for help collecting specimens of *Benedictus fuanensis* sp. nov.

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Additional information

Conflict of interest

No conflict of interest was declared.

Ethical statement

No ethical statement was reported.

Funding

Funding information is listed in the Acknowledgments section.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Revision of the Palaearctic species of the genus *Plateumaris* C. G. Thomson, 1859 (Coleoptera, Chrysomelidae, Donaciinae)*

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Abstract

Ten of the 27 species of *Plateumaris* Thomson (Chrysomelidae: Donaciinae) occur in the Palaearctic. Due to the intraspecific variation and the large distributions of some species, descriptions exist for at least 80 taxa plus five nomina nuda. The status of each valid species is clarified and the remaining 70 names are allocated as synonyms. New synonymies are *P. tenuicornis* Balthasar, considered a synonym of *P. consimilis* (Schrank), *P. sulcifrons* Weise as a synonym of *P. rustica* (Kunze), and *P. caucasica* Zaitzev as a synonym of *P. sericea* (Linnaeus). Two controversial synonyms are confirmed: *P. discolor* (Panzer) and *P. sericea sibirica* (Solsky) are both synonyms of *P. sericea*. Finally, *P. obsoleta* Jacobson is a synonym but at present it is not possible to decide whether it belongs to *P. shirahatai* Kimoto or to *P. sericea*. Forty-one new country records are added, compared with the Catalogue of Palaearctic Coleoptera published in 2010; 28 records are based on recently published records and 13 are first records for a specific country.

Key words: Identification key, leaf beetles, new country records, new synonymies, reed beetles, revision, Systematics, taxonomy



Academic editor: Caroline Chaboo

Received: 8 March 2023

Accepted: 26 June 2023

Published: 30 August 2023

ZooBank: <https://zoobank.org/DF38DD37-843C-467B-9DD5-98CC7A6290E7>

Citation: Geiser E (2023) Revision of the Palaearctic species of the genus *Plateumaris* C. G. Thomson, 1859 (Coleoptera, Chrysomelidae, Donaciinae). In: Chaboo CS, Schmitt M (Eds) Research on Chrysomelidae 9. ZooKeys 1177: 167–233. <https://doi.org/10.3897/zookeys.1177.103214>

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* Extended version of a talk presented to the 10th International Symposium on the Chrysomelidae, Helsinki, Finland, 21 July 2022.

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Introduction

The genus *Plateumaris* Thomson, 1859 belongs to the subfamily Donaciinae (reed beetles) which is part of the beetle family Chrysomelidae (leaf beetles). This family includes more than 37,000 (probably at least 50,000) species in more than 2,500 genera, making up one of the largest beetle families (Jolivet et al. 1988). The Donaciinae comprise approximately 180 species belonging to six genera (Geiser 2015). Seventeen species of *Plateumaris* occur in the Nearctic region (Askevold 1991) and ten species in the Palaearctic region. Their distribution area extends from 30° north latitude to the Arctic Circle (pers. obs.).

Most life stages in Chrysomelidae (larvae and imagines) are terrestrial; however, the larvae of the Donaciinae develop submerged on roots of aquatic plants. These larvae breathe by tapping the aerenchyma of the plant with two hollow abdominal hooks which are connected to their tracheal system. Therefore, they can stay permanently under water. Monophyly of Donaciinae is supported by these special morphological and physiological adaptations as well as by molecular data (Kölsch and Pedersen 2008; Sota et al. 2008). These molecular analyses also revealed that the genus *Plateumaris* is a monophylum within the Donaciinae.

This number of ten species in the Palaearctic is not without controversy; in fact, different authors recognise nine to 19 species in the region (Table 1). This problem became virulent when I was editing the Donaciinae for the update of the catalogue of Palaearctic Chrysomelidae (Löbl and Smetana 2010; Silfverberg 2010), where the *Plateumaris* species are listed. To decide how many species occur in the Palaearctic region and what are their valid names, it became clear that a major revision was necessary. Simultaneously, several comprehensive works were published on Palaearctic Donaciinae, e.g., the 'Identification Key on Palaearctic Chrysomelidae' by Warchałowski (2010) and the book by Bieńkowski (2014) on the Russian Donaciinae, where almost all the Palaearctic *Plateumaris* species were treated. Hayashi (2020) dealt only with the Japanese Donaciinae that include half the Palaearctic *Plateumaris* species; his text complements Bieńkowski's book. Finally, the molecular analyses of Hayashi and Sota (2014) are an invaluable help with systematic revisions.

A revision of the Palaearctic species of *Plateumaris* was needed, not only for the Palaearctic catalogue (Bezděk and Sekerka in press; Geiser in press). Colleagues working in physiology or ecology, especially in applied limnology, or those who are trying to reconstruct the dynamics of postglacial resettlement and similar topics which are important to understand climate changes and threat to biodiversity, all rely on solid species delimitations.

Knowledge of species distributions is necessary for systematic revisions. Therefore, I evaluated records from museum specimens and the literature. For the catalogue (Geiser in press) I provided this information only in a very concise manner. A revision is a good place to publish the detailed data and also provides an opportunity to explain the significance of a new record. For systematic revisions it is mandatory to study the first description of the taxa concerned. Many of these descriptions are in Latin or at least begin with Latin text. To make my arguments more understandable a companion article in this issue (Geiser and Geiser 2023) is published, where translations are provided of many original descriptions into English.

Materials and methods

For this revision, approximately 1500 adult specimens including six type specimens from 16 museum collections were examined. These museums are indicated below, together with other museums which are cited as depositories.

Museum acronyms

BMNH	The Natural History Museum [formerly British Museum (Natural History)], London, UK (Michael Geiser, Maxwell V.L. Barclay, Keita Matsumoto, Dmitry Telnov)
HNHM	Hungarian Natural History Museum, Budapest, Hungary (Ottó Merkl †, Tamás Németh)
HNSA	Haus der Natur, Salzburg, Austria (Patrick Gros)
KUEC	Entomological Laboratory, Faculty of Agriculture, Kyushu University, Fukuoka, Japan
LUOMUS	Finnish Museum of Natural History, Helsinki, Finland (Jaakko Mattila)
MNHN	Muséum national d'Histoire naturelle, Paris, France
MSNV	Museo Civico di Storia Naturale, Verona, Italy (Mauro Daccordi, Roberta Salmaso, Leonardo Latella)
NHMB	Natural History Museum, Basel, Switzerland (Matthias Borer, Christoph Germann, Eva Sprecher, Isabelle Zuercher)
NHMW	Natural History Museum, Vienna, Austria (Manfred A. Jäch, Helena Shaverdo, Michaela Brojer, Harald Schillhammer, Matthias Seidel, Wolfgang Schönleithner †, Wolfgang Brunnbauer)
NHRS	Swedish Museum of Natural History, Stockholm (Johannes Bergsten)
NMEG	Natural History Museum, Erfurt, Germany (Matthias Hartmann)
NMPC	National Museum (Natural History), Prague, Czech Republic (Lukáš Sekerka, Jiří Hájek)
OMNH	Osaka Museum of Natural History, Japan
RBINS	Royal Belgian Institute of Natural Sciences, Brussels, Belgium
SDEI	Senckenberg German Entomological Institute, Müncheberg, Germany (Thomas Schmitt, Stephan Blank, Mandy Schröter)
SMF	Senckenberg Museum Frankfurt, Germany (Andrea Hastenpflug-Vesmanis, Damir Kovac)
SNMC	Slovak National Museum, Bratislava, Slovakia (Vladimir Janský, Martin Sečanský)
ZFMK	Zoological Research Museum Alexander Koenig, Bonn, Germany (Dirk Ahrens, Karin Ulmen)
ZIN	Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia (Alexey Moseyko)
ZMHB	Natural History Museum, Berlin, Germany (Johannes Frisch, Bernd Jaeger)
ZSM	Bavarian State Collection of Zoology, Munich, Germany (Michael and Ditta Balke, Katja Neven, Martin Baehr †)

Other abbreviations

A1, A2, ... Number of an antennomere.

ab.	aberratio.
coll.	collection: the location where the specimen is stored.
det.	determinavit: name of the person who identified this specimen.
ex.	specimen(s).
ex coll.	previous collection where the specimen was stored.
f.	forma.
ICZN	International Code of Zoological Nomenclature.
leg.	legit: name of the person who collected this specimen.
T1, T2, ...	number of a tarsomere.
var.	variatio.
vid.	vidit: name of the person who confirmed the identification.
[]	Text in square brackets [] are additions or comments by the author; in records data they do not form part of the label text tagged to the specimen.
[leg.]	name of the person who probably collected this specimen.
[det.]	name of the person who probably identified this specimen.
[new in PalCat]	This indicates that the country mentioned was not listed in Silfverberg (2010) but is now listed in the update of the Palaearctic Catalogue (Geiser in press). This refers to already published records, and the data source is listed below.
[first record]	If a country record was not published in detail until now, it is indicated as “first country record”. The same applies for a part of a country if it is treated as separate unit within a country, according to Bezděk and Sekerka (in press). These records were published in Geiser (in press) but only with the country or province abbreviation in most cases so the record details are given here.
//	If original text is cited from different labels tagged to the pin of one specimen, the double slash indicates the text separation between these labels.

Data sources

Museum specimens

Except for *Plateumaris sericea*, it is very difficult to deliberately catch *Plateumaris* specimens in their habitat. Many voucher specimens were gained as by-catch in field studies motivated by other goals. The study of the variation of characters from many different sites of the whole distribution area is important for systematic revisions. Therefore, museum collections that have existed for a long time and where specimens from many different locations are stored are essential for such studies, but even smaller collections could provide a pleasant surprise to find some voucher specimens of a rare species from an interesting site.

The specimens in the museum collections were sorted in boxes with a species label. The compilation was usually done by non-specialists, who sorted the various collections donated to the museum into the overall collection, regardless of whether they were correctly identified or not. The vouchers of *P. braccata*, *P. consimilis*, *P. rustica*, and *P. sericea* were usually correctly identified. Specimens of other *Plateumaris* species are rare, and these were all examined in detail. Some of them

already had identifier labels. If not, I tagged my label on the needle with the information “genus species Author det. E. Geiser Year”. I also did that when a specimen was misidentified, leaving the original identifier label on the needle. When a species was difficult to identify I used a similar label, with “vid. E. Geiser Year” to state that I have confirmed the identification. Specimens of the four species mentioned above were also studied carefully for the purpose of this revision. Here I did not tag my label to all of them, but mainly on vouchers that showed some variation of the typical characters or were collected in an interesting location.

The importance of museum collections has increased in recent years. Some areas of the Palaearctic region are inaccessible today for political or security reasons like Xinjiang in western China, or Syria, or Afghanistan. Fortunately, some natural history field studies dating more than 100 years ago enabled vouchers to be deposited in European museums. These historic specimens are an invaluable source for further studies. Additionally, it is more difficult today to collect Donaciinae and therefore *Plateumaris* species because man-made changes of limnic and wetland environments are contributing to the decline of habitats and, therefore, of species. Many previous habitats no longer exist and the only chance to study specimens from these districts is to examine the museum vouchers.

Main literature sources

In addition to the museum specimens studied, the author relied on certain important publications for additional data, mainly Hayashi (2020), Askevold (1991), and Bieńkowski (2014). Hayashi (2020) is a comprehensive recent study on Japanese Donaciinae which comprises five of the ten Palaearctic *Plateumaris* species occurring. Two species (*P. akiensis* and *P. constricticollis* with its three subspecies) are endemic in Japan, *P. shirahatai* is restricted to the East Palaearctic, and *P. sericea* and *P. weisei* occur across the Palaearctic region. Some figures and texts parts from Hayashi (2020) are cited here. The extensive study of Askevold (1991) on the Nearctic *Plateumaris* species is also important because it contains significant information about the Palaearctic *Plateumaris* species, and much information about the taxonomic aberrations affecting the genus. The comprehensive book of Bieńkowski (2014) on the Donaciinae of Russia was also helpful because this country covers a large part of the Palaearctic region and most of the Palaearctic *Plateumaris* species occur here. It also contains information about biology, ecology, food plants, and larvae of *Plateumaris*.

Original descriptions and type specimens

The study of original taxonomic descriptions is essential for any systematic revision. Many of the species or subspecies were first described in Latin with very specific phrases used in scientific entomological scripts in the 18th and 19th centuries. Some original descriptions are in German, French, or Russian; some are multilingual, starting with Latin for the main characters of a presumed new species, and then more details were added in the native language of the author. Therefore, to overcome these challenges, Geiser and Geiser (2023) present the original descriptions and their translations of all Palaearctic *Plateumaris* species including many synonyms. That comprises seven species, because three were originally described in English, and 19 taxa are now synonyms.

The study of type specimens is also essential in revisions, and I was able to examine six type specimens. Many types from the 18th and 19th centuries could not be located or no longer exist. Another problem is that specimens in collections may be labelled as “type” or indicated as types by red or red-bordered labels but are not actually type specimens.

Synonyms

For each species, in “Taxonomic history and synonymies” most synonymies are explained, where changes were made (Geiser in press) compared to Silfverberg (2010). Also, I attempted to provide the reference for the synonymisation. Although the literature was studied thoroughly, I could not track down this information in most cases. Some publications that are repeatedly cited in the literature in fact did not contain this information at all. Some synonyms listed here are confirmations of synonyms elaborated by previous authors but not accepted by some authors. In most cases new arguments are presented to validate these synonymisations.

Distribution data

For each species, the countries, or the part of a country, with reliable records are listed. Detailed information on the data source is given for the countries or part of a country which are new in Geiser (in press) compared to Silfverberg (2010). The subdivisions of some large countries (e.g., Russia, China) are the same in this work as in Bezděk and Sekerka (in press).

Results

Identification keys

Many previous researchers have published keys to the Palaearctic species of *Plateumaris*, but these keys often use characters that are difficult to see from the beginning. Although only ten species occur in the Palaearctic region, some specimens are not easy to identify even for experienced coleopterologists. The new key reduces the species designation available for a particular specimen. The detailed characters and the pictures provided in the species sections should allow definitive identification. Because only two species occur in the whole Palaearctic region, the separation of the West and East Palaearctic in different keys leads to more reliable identifications. If the information on the specimen location label is very imprecise (e.g., “Siberia” or “Russia”) then both keys need to be applied.

Plateumaris species which occur in the West Palaearctic

- 1 Antennae and legs entirely metallic, same colour as pronotum and elytra. Sometimes the antennomeres can be reddish near the joints. At the legs small reddish parts may be occur near the joints or, exceptionally, on the tibiae or tarsomeres. Pronotum and elytra in various metallic colours (Fig. 11). Size: 6.5–10.5 mm. Occurs throughout the Palaearctic region..... ***P. sericea***
- Antennae and legs yellow reddish brown, some parts more or less darkened..... **2**

- 2 Pronotum and elytra black or with dark metallic lustre, elytra elongate, their length twice as long as wide, side contour of elytra parallel, not convex, the largest of all species (Fig. 4). Size: 8.0–12.0 mm. Occurs in most parts of the West Palaearctic except north Fennoscandia and southern Europe ***P. braccata***
- Elytra not twice as long as wide **3**
- 3 Pronotum cordate, upper side with metallic lustre in different colours or entirely black, elytra 1.5–1.8× longer than wide, never 2× longer than wide, side contour of elytra not parallel but slightly convex (Figs 4d, 5). Size: 6.0–9.2 mm. Occurs in most parts of the West Palaearctic, mainly in continental Europe including south Sweden, very rare in south and eastern Europe and west Siberia ***P. consimilis***
- Pronotum not cordate **4**
- 4 Pronotum distinctly flattened, almost quadrate, only slightly constricted at the basis, with flat disc and indistinct anterior tubercles, upper side bronze or black with greenish, bluish, or purplish metallic lustre, colour of pronotum and elytra mostly the same but can also differ significantly (Fig. 10). Size: 7.0–9.0 mm. Occurs in most parts of the West Palaearctic ***P. rustica***
- Pronotum neither distinctly cordate nor flattened, outline subquadrate, slightly longer than wide, basal part narrowed, slightly cone-shaped, anterior tubercles distinctly visible or almost entirely smooth, upper side cupreous or bronze, sometimes metallic green, blue, purple, or non-metallic brown (Fig. 17; Table 3). Size: 6.2–8.0 mm. Trans-Palaearctic species, from northern Fennoscandia through Siberia to the Far East, northern China, the Korean peninsula, and Japan ***P. weisei***

Remarks: Some specimens of *P. weisei* are difficult to distinguish from *P. consimilis* and *P. rustica*. The variation of several characters is sometimes within the same range. It occurs also within the distribution area of *P. consimilis* and *P. rustica* in southeast Finland and some parts of Russia, though these three species are very rare here. To avoid misidentification, use all the details and figures provided in the species sections.

***Plateumaris* species which occur in the East Palaearctic**

- 1 Femora and tibia entirely metallic in colour **2**
- Femora and tibia partly metallic or dark, femoral base usually rufous **3**
- 2 Median line of pronotum deep, male pygidial apex usually emarginate; apex of median lobe of male genitalia without subapical corner; apex of median ejaculatory guide of endophallus rounded (Figs 11, 12a). Size: 6.5–10.5 mm. Occurs in the whole Palaearctic region ***P. sericea***
- Median line of pronotum indistinct, male pygidial apex usually truncate; apex of median lobe of male genitalia with subapical corner; apex of median ejaculatory guide of endophallus notched (Figs 12b, 13). Size: 6.5–8.2 mm. Occurs in the East Palaearctic region ***P. shirahatai***
- 3 Metafemoral tooth present but blunt, pronotum neither distinctly cordate nor flattened, outline subquadrate, slightly longer than wide, basal part narrowed, slightly cone-shaped, anterior tubercles distinctly visible or almost entirely smooth, upper side cupreous or bronze, sometimes

- metallic green, blue, purple, or non-metallic brown (Fig. 17; Table 3). Size: 6.2–8.0 mm. Trans-Palaearctic species, from northern Fennoscandia through Siberia to Far East, northern China, the Korean Peninsula, and Japan***P. weisei***
- Metafemoral tooth well developed.....**4**
 - 4 Body robust in shape, with conspicuously short elytra and legs, elytra length is only 1.6× longer than width, at least always less than 1.7, pronotum finely and densely punctate; colour black or bronze-metallic, also with a bluish or greenish lustre, elytra shiny (Fig. 2; Table 3). Size: 6.4–7.6 mm. Endemic species of Honshu, Japan..... ***P. akiensis***
 - Elytra and legs not conspicuously short, normal, ratio of elytral length to width > 1.7**5**
 - 5 Pronotum cordate, surface shiny as if varnished, most parts without wrinkles or punctures, anterior tubercles protruding but smooth, gently narrowed with a shallow, transverse groove behind them, dorsal colouration variable (Fig. 7). Size: 6.6–11.9 mm. Occurs only in the Japanese Archipelago (Distinguishing characters of the three subspecies: 5a *P. constricticollis constricticollis* – Colouration of pronotum and elytra differs between specimens. Femora and tibia entirely rufous, sometimes partly dark rufous, apex of cap of tegmen deeply and sharply notched in most specimens. 5b *P. constricticollis babai* – Same colouration of pronotum and elytra, apical half of femora black metallic, tibia usually rufous, sometimes partly dark rufous, apex of cap of tegmen not deeply notched. 5c *P. constricticollis toyamensis* – Pronotum and elytra entirely metallic, apical half of femur black, sometimes darkly rufous, tibia usually rufous, sometimes partly dark rufous, apex of cap of tegmen slightly notched or rounded, subapical angle of ovipositor nearly right, apex slightly prominent, finely serrated subapically).....***P. constricticollis***
 - Pronotum not cordate, covered with rugae and punctures**6**
 - 6 Antennae and legs mostly rufous, sometimes apically darkened, femora reddish on the basal half and metallic-dark on the apical half (Fig. 9). Size: 6.7–9.7 mm. East of Lake Baikal to Far East, Sakha (Yakutia) Republic, Amur region in Russia, and northeast China***P. roscida***
 - Legs usually rufous, sometimes apical area of femora dark (Fig. 3). Size: 7.1–7.7 mm. In Russia east of Lake Baikal, Sakhalin, and Kurile Islands ...
.....***P. amurensis***

Remarks: The three species found in the east of Russia and northeast China, *P. amurensis*, *P. roscida*, and *P. weisei*, are not easy to distinguish because their external characters sometimes overlap. To distinguish *P. amurensis* from *P. weisei* see also Table 3. The best distinguishing character of *P. roscida* is the dark colour on the apical half of the femora; especially on the metafemur where it appears that the femur had been dipped to the half-way point in a pot with brown paint. Unfortunately, there are some *P. roscida* specimens with entirely rufous legs. The best differential character is then the aedeagus, which is very different from those of all the other Palaearctic *Plateumaris* species: the apex of the median lobe shows a conspicuous elongated peak and the cap of the tegmen has a deep, narrow apical notch (Fig. 9).

Opinions on species delimitation in the literature

Although only a few Palaearctic *Plateumaris* species exist (compared with other beetle genera), there are many differing opinions between authors. Almost every comprehensive publication about Palaearctic *Plateumaris* shows a different number of species (Table 1).

Table 1. Comparison of major publications: names of Palaearctic species of the genus *Plateumaris* Thomson including the different opinions about valid species and synonyms.

<i>Plateumaris</i> species names	Palaearctic Region					Parts of Palaearctic Region		
	Silfverberg 2010	Warchalowski 2010	Askevold 1991	Borowiec 1984	Goecke 1960	Japan: Hayashi 2020	Russia: Bienkowski 2014	China & Korea: Gressitt and Kimoto 1961
<i>P. affinis</i>	*	syn of <i>P. rustica</i>	syn of <i>P. rustica</i>	*	*	—	syn: <i>P. rustica</i>	—
<i>P. akiensis</i>	*	*	*	o: described in 1984	o: described in 1984	*	—	—
<i>P. amurensis</i>	*	*	"syn of <i>weisei</i> by Goecke which is probably correct"	o: clarified 2001 to be different from <i>P. weisei</i>	syn of <i>P. weisei</i>	—	*	*
<i>P. bradata</i>	*	*	*	*	*	—	*	o: first record 2023
<i>P. caucasica</i>	*	o	possible syn of <i>P. roscida</i>	*	o	—	ssp of <i>P. sericea</i>	—
<i>P. consimilis</i>	*	*	*	*	*	—	*	—
<i>P. constricticollis</i>	* including 3 ssp	*	*	*	*	* including 3 ssp.	—	—
<i>P. discolor</i>	*	syn of <i>P. sericea</i>	syn of <i>P. sericea</i>	*	*	syn of <i>P. sericea</i>	*	—
<i>P. mongolica</i>	syn of <i>P. weisei</i>	syn of <i>P. weisei</i>	probable syn of <i>P. weisei</i>	*	*	syn of <i>P. weisei</i>	—	*
<i>P. obsoleta</i>	*	*	probable syn of <i>P. sericea</i>	*	*	—	*	—
<i>P. roscida</i>	*	*	*	*	*	—	*	as <i>P. annularis</i>
<i>P. rustica</i>	*	*	*	*	*	—	*	—
<i>P. sachalinensis</i>	syn of <i>P. weisei</i>	*	probable syn of <i>P. weisei</i>	*	o: described in 1973	syn of <i>P. weisei</i>	*	—
<i>P. sericea</i>	*	*	*	*	*	*	*	as <i>P. socia</i>
<i>P. shirahatai</i>	*	as syn of <i>P. obsoleta</i>	*	*	o: described in 1971	*	*	o: described in 1971
<i>P. sibirica</i>	ssp of <i>P. sericea</i>	ssp of <i>P. sericea</i>	o	o	syn of <i>P. sericea</i>	ssp of <i>P. sericea</i>	ssp of <i>P. sericea</i>	—
<i>P. socia</i>	syn of <i>P. sericea</i> <i>sibirica</i>	syn of <i>P. sericea</i> <i>sibirica</i>	probable syn of <i>P. sericea</i>	*	o	syn of <i>P. sericea</i>	—	*
<i>P. sulcifrons</i>	*	*	probable syn of <i>P. rustica</i>	*	*	—	—	—
<i>P. tenuicornis</i>	*	o	probable syn of <i>P. consimilis</i>	*	*	—	—	—
<i>P. weisei</i>	*	*	*	*	*	*	*	o
Number of valid species	16	12	9	17 (+2)	13 (+4)			

* = valid species; o = not mentioned although it occurs in the studied area; — = does not occur in the studied area; ssp = subspecies; syn = synonym.

The highest number of species is recorded by Borowiec (1984): he regarded 17 species as valid. At that time *P. akiensis* was not described and *P. amurensis* was regarded as a synonym of *P. weisei*. Therefore, two more species can be added. Goecke (1960) mentioned 13 *Plateumaris* species for the Palaearctic region in his world checklist; three were not described then and he regarded *P. amurensis* as a synonym. Therefore, four more species must be added. In his major work about the Nearctic *Plateumaris* species, Askevold (1991) also treated the Palaearctic species. He established several synonyms, some of them as probable new synonyms. He regarded nine names as valid for Palaearctic *Plateumaris* species. I agree with his assessment except concerning *P. amurensis*, which he regarded to be synonymous with *P. weisei*. Hayashi (2001) showed that *P. amurensis* is a separate species, bringing the total to ten species.

Two major books were published in 2010: Warchalowski treated 12 species in his identification key and Silfverberg listed 16 species (and some more subspecies) in Löbl and Smetana (2010). Some large works which cover only a part of the Palaearctic region also contain invaluable information such as Bienkowski (2014) on the Russian Donaciinae, which covers a large part of the Palaearctic region and almost all the Palaearctic *Plateumaris* species. The recent publication by Hayashi (2020) deals with the five Japanese *Plateumaris* species, which includes half of all the Palaearctic species; the paper contains the species that do not occur in Russia, so the Palaearctic region is completely covered with these two publications. Gressitt and Kimoto (1961) named four *Plateumaris* species in their comprehensive study on the Chrysomelidae of China and Korea; except for *P. amurensis* the other three names are synonyms.

Taxonomic accounts

Genus *Plateumaris* C. G. Thomson, 1859

Plateumaris C. G. Thomson, 1859: 154.

Euplateumaris lablokoff-Khnzorian, 1966: 121.

Juliusina Reitter, 1920: 41.

Type species and localities. *Plateumaris* C. G. Thomson, 1859: *Donacia nigra* Fabricius, 1792: Germania.

= *Prionus bracatus* Scopoli, 1772: Carniola [now Slovenia].

Euplateumaris lablokoff-Khnzorian, 1966: *Leptura sericea* Linnaeus, 1758: Europe.

Juliusina Reitter, 1920: *Prionus bracatus* Scopoli, 1772: Carniola [now Slovenia].

Timeline of taxonomic history and synonymies. 1758: Linnaeus described the genus *Leptura* with 22 species. Two of these species belong to the (later established) Donaciinae: *Donacia aquatica* and *Plateumaris sericea* (Geiser and Geiser 2023). Linnaeus established only the taxonomic categories: classis – ordo – genus – species, e.g.: Insecta – Coleoptera – *Leptura* – *sericea*.

1760: Linnaeus mentioned *Leptura sericea* in his 'Fauna Suecica' with the same diagnosis as in Linnaeus (1758) but with more details. Therefore, the species is sometimes cited as *Leptura sericea* Linnaeus, 1760 (e.g., in Silfverberg 2010), but the first description date is clearly Linnaeus, 1758 (see Geiser and Geiser 2023 for original Latin text of Linnaeus and translation).

1762: Geoffroy erected the genus *Prionus* for the species *Cerambyx coriarius* Linnaeus, 1758. It now belongs to the Cerambycidae as does the genus *Leptura*.

1772: Scopoli described *Prionus bracata*.

1775: The genus name *Donacia* was erected by Fabricius. He described *Donacia crassipes* and *Donacia simplex* and assigned *Leptura aquatica* L., 1758 to the genus *Donacia*, but he did not change the genus name of *Leptura sericea* L., 1758. Other *Plateumaris* species were described as *Leptura*, e.g., *Leptura consimilis* Schrank, 1781. It is remarkable that these early entomologists had already assigned them to a genus other than *Donacia*.

1796: The category “familia” was established between order and genus for insects by Latreille.

1802: Latreille established the coleopteran family Chrysomelidae.

1837: Kirby established the subfamily Donaciinae.

1859: The genus name *Plateumaris* was erected by C. G. Thomson (translation in Geiser and Geiser 2023), but some authors, especially Americans, preferred *Donacia* as the genus name in their new descriptions. Even Marx (1957) regarded *Plateumaris* as a subgenus of *Donacia*. The Palaearctic *Plateumaris weisei* (Duvivier, 1885) and *P. constricticollis* (Jacoby, 1885) were also originally described as *Donacia*.

1920: Reitter split the Palaearctic *Plateumaris* into two subgenera: *Plateumaris* sensu stricto and *Juliusina*. He assigned *P. sericea* and *P. discolor* to *Plateumaris* s. str. and he described *P. annularis* in a footnote to *P. sericea*. In the same footnote he assigned *P. obsoleta* to *P. annularis*, but not as a synonym, and he placed *P. amurensis* near to *P. discolor*. The subgenus *Juliusina* contained *P. bracata*, *P. consimilis*, *P. rustica*, and *P. affinis*. To the latter species he assigned *P. sulcifrons* and *P. mongolica*. Moreover, Reitter made no designation of type specimens to either of the new subgenera.

Type species designations. Thomson (1859) stated “Typus *P. nigra* (FAB.) [= Fabricius]” in the original description of the genus *Plateumaris*, but most authors cited “Thomson, 1866” as the year of the original description. Thomson (1866) is an extensive book but contains no type designation because this had been done previously in 1859. Therefore, the prevailing opinion was that there existed no type designation for the genus *Plateumaris* (which was wrong) and nor for the subgenera *Juliusina* and *Plateumaris* s. str. (which is true). Subsequently, Chen (1941) designated *Donacia affinis* Kunze as the type species for *Plateumaris*, but this was overlooked by Monrós (1959) who designated *Donacia geniculata* Thomson (= *Donacia discolor* Panzer) as the type species for *Plateumaris* s. str. and *Prionus bracatus* Scopoli for *Juliusina* Reitter.

Iablokoff-Khuzorian (1966) suggested the name *Euplateumaris* for the subgenus *Plateumaris* s. str. established by Reitter, with *Donacia sericea* (L.) as type species. He also re-established *D. nigra* F. (= *bracata*) as type species of the genus *Plateumaris*, apparently unaware of both designations by Monrós (1959) and Chen (1941), and therefore placed *Juliusina* as a junior synonym of *Plateumaris* because both were named based on the same nominal taxon. Jolivet (1970) followed the designation of Iablokoff-Khuzorian (1966) but Mann and Crowson (1983) accepted Monrós’ designations and advocated acceptance of *Plateumaris* s. str. (= *Euplateumaris*) and *Plateumaris (Juliusina)* as the correct subgeneric classifications of *Plateumaris*. Lopatin (1984) correctly cited *P. bracata* as type species of *Plateumaris* but he assigned this species to *Plateumaris (Juliusina)*.

The same, clearly incorrect, arrangement was used by Lopatin and Kulenova (1986) when assigning *P. sericea* to *Plateumaris* (*Plateumaris*).

The names *Plateumaris* Thomson, 1859 and *Juliusina* Reitter, 1920 are based on the same type species (*Prionus braccatus*) which makes the subgenus *Juliusina* a synonym of *Plateumaris* in the sense of the whole genus, which was endorsed by Warchałowski (2010). This synopsis of the type species designations and the use of the names as described was elaborated in detail by Askevold (1991). Also, he was the first who attempted to assess the validity of *Plateumaris* as a genus and the validity of the two subgenera.

Taxonomic status of *Plateumaris*. Most European authors accepted the genus *Plateumaris*, but North American authors were reluctant and oscillated between the use of this name at generic and subgeneric ranks within the genus *Donacia*. This ambiguity led to confusion about the genus name *Plateumaris*, worsening the existing confusion over the name *Plateumaris* of the Palaearctic species (see above).

Askevold (1990) understood that *Plateumaris* was monophyletic, defined by the synapomorphy of the ovipositor structure, and that *Plateumaris* was the sister group to all other Donaciinae, and his morphologically based conclusions were confirmed by several independent molecular analyses (Sota and Hayashi 2007; Kölsch and Pedersen 2008; Sota et al. 2008; Hayashi and Sota 2014; Reis et al. 2020).

Previous subgeneric classifications. Askevold (1990, 1991) concluded that the division into two subgenera by Reitter (1920) did not reflect the phylogenetic reality. The two subgenera were erected based on characters that do not occur in all members assigned to them or they were based on plesiomorphic characters. Notably, neither subgenus can be characterised by a synapomorphy. His conclusion that *Euplateumaris* and *Juliusina* cannot be regarded as subgenera has also been confirmed by molecular studies (Kölsch and Pedersen 2008; Sota et al. 2008). Therefore, this paper does not deal with the confusion over subgeneric names and various designated type species.

In central Europe, the widely used key of Mohr (1966a) separated *Plateumaris* into two subgenera. The short note in the updated key by Kippenberg (1994: 22), "The separation into the subgenera *Juliusina* Rtt. and *Plateumaris* s. str. is not tenable," did not prevent coleopterologists from using the subgeneric names in their collections or publications, and even on a Palaearctic scale, the subgeneric names *Euplateumaris* and *Juliusina* were still used by Silfverberg (2010) and Bieńkowski (2014). Possibly the title 'Classification, Reconstructed Phylogeny, and Geographic History of the New World Members of *Plateumaris* Thomson, 1859' of Askevold (1991) suggested that this publication dealt only with new world *Plateumaris* species and did not contain relevant information on Palaearctic *Plateumaris* species or their subgeneric statuses.

Diagnosis of the genus *Plateumaris* Thomson, 1959. Askevold (1991) detailed the diagnosis so only the most necessary characters needed to distinguish the *Plateumaris* species from all other Donaciinae are listed below:

- Sutural margin of elytron explanate apically, sutural interval sinuates distinctly before apex, lower sutural margin broadly exposed (Fig. 1A);
- Elytral apex rounded, inner angle sharp, no outer angle protruding;
- First abdominal segment as long as the others combined;

- Host plants are typically Cyperaceae, but also a few other wetland plants.

The aedeagus of *Plateumaris* species and some other representatives of the Donaciinae consists of a median lobe which contains the endophallus and the lateral parameres (Fig. 1B). The parameres are fused basally and distally, forming a ring around the median lobe. This parameric structure is the tegmen, composed of a ventral strut and a dorsal cap (for more details and functional descriptions see Askevold 1991 and Hayashi 2020). The frontal view towards the apex of the median lobe and of the cap of tegmen are usually very characteristic of each *Plateumaris* species and therefore suitable to distinguish them in most cases. Some species can be distinguished only by subtle morphological characters of their endophallus.

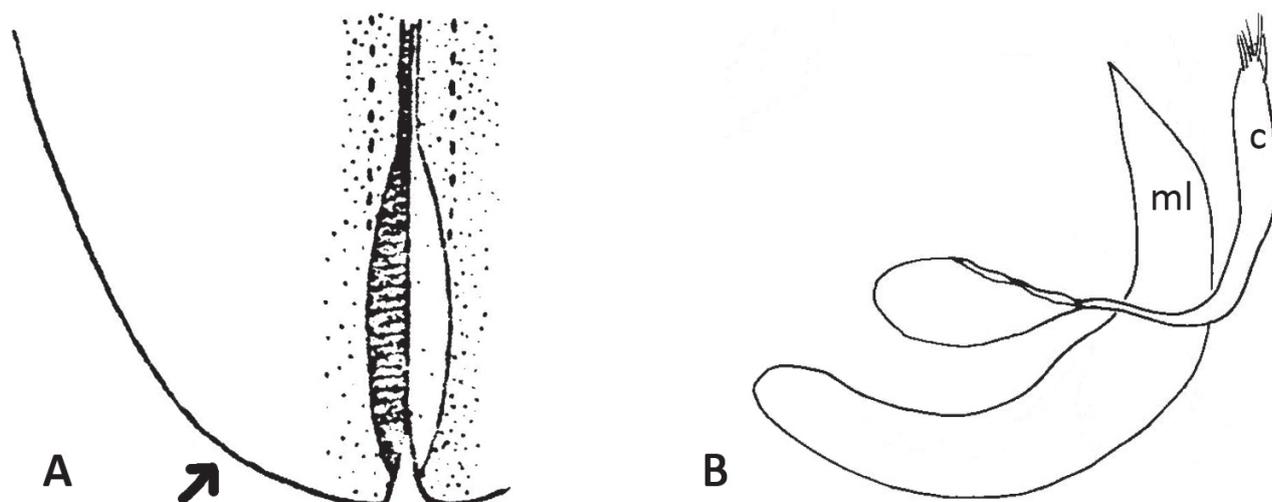


Figure 1. Diagnostic characteristics of *Plateumaris* sp. **A** elytral apex with sutural margin broadly exposed, no outer angle protruding (arrowed; from Kaszab 1962) **B** typical structure of aedeagus in lateral view (from Askevold 1991). Abbreviations: **ml** median lobe, **c** cap of tegmen.

Biology. Reed beetles live on plants in wetlands. The larvae develop attached to the roots in the sediment and live as sap suckers gnawing a hole into the root. They breathe by tapping the aerenchyma of the plant using two hollow abdominal hooks, which are connected to their tracheal system; therefore, they can live even in anoxic mud (Böving 1910). Adults remain mostly above the surface sitting on aquatic plants but are able to hide under water while the ventral hairs serve as plastron respiration (Rheinheimer and Hassler 2018). The larvae pupate at the end of their second summer in a cocoon, attached to the root of the food plant. The beetle overwinters in an air-filled cocoon and emerges the following spring. In warmer climates the larvae may pupate after their first summer (Böving 1910; Kleinschmidt and Kölsch 2011).

The larval host plants are mostly members of Cyperaceae, but include some Juncaceae and Poaceae (e.g., *Phragmites australis* (Cav.) Trin. ex Steud.). *Acorus calamus* L. (Araceae), *Caltha palustris* L. (Ranunculaceae), and *Iris versicolor* L. (Iridaceae) are also mentioned as food plants (Borowiec 1984; Bieńkowski 2014). Most species are mono- or oligophagous, especially the larvae. Adult beetles feed on the leaves, although some species are pollen feeders, and some may also feed on petals. If a larva is attached to the root of a plant and gnawing traces are found, we can be sure that this is a host plant for this species. Adults

may use a slightly broader range of plants. Several species feeding on pollen use the plants of their habitat. Therefore, adults can be observed on wetland plants that are mostly not larval food plants. The adults are active mainly in spring and early summer, sometimes also in autumn. No specific phenology data are provided here for the species because many have a wide distribution range and the time of "spring" differs between the populations within the Palearctic region.

Plateumaris species prefer habitats of wet sedge meadows, peat bogs, and fens, in contrast to *Donacia* species which live on aquatic plants with emerging parts and in contrast to *Macrolea* species which live on totally submerged aquatic plants.

Historical biogeography. *Plateumaris* species are found only in the Holarctic region with ten species in the Palaearctic and 17 species in the Nearctic (Askevold 1991); the latter occur mainly in Canada and the northern states of the USA. These two subregions have neither a *Plateumaris* species nor any other Donaciinae species in common, although molecular analysis shows that many Palaearctic *Plateumaris* species are more closely related to Nearctic species than to other Palaearctic species (Askevold 1991; Hayashi 2020). Dispersal vicariance analysis and divergence time estimation revealed that the European and North American-Asian lineages diverged during the Eocene. Moreover, subsequent differentiation occurred repeatedly between North American and Asian species, which was facilitated by three dispersal events from North America to Asia and one in the opposite direction during the late Eocene through the late Miocene (Kölsch and Pedersen 2008; Sota et al. 2008; Hayashi and Sota 2014).

Checklist and distribution. A summary of the distribution of the *Plateumaris* species in the Palaearctic region is shown in Table 2.

Palaearctic region: *Plateumaris sericea* has the largest distribution area of any Donaciinae species: it is recorded from Ireland and Great Britain to the whole of continental Europe, North Africa, and almost all Asian countries which belong to the Palaearctic region. *Plateumaris weisei* occurs from northern Europe to east Asia, from Siberia to northern China, Japan (Hokkaido), and South Korea.

Western Palaearctic region: Three species occur only in Europe and in Asia west of Lake Baikal: *P. braccata*, *P. consimilis*, and *P. rustica*.

Eastern Palaearctic region: Five species occur only in Asia east of Lake Baikal: *P. amurensis*, *P. roscida*, and *P. shirahatai*, and two species are endemic to the Japanese archipelago, *P. akiensis* and *P. constricticollis*.

Table 2. Checklist and distribution of the *Plateumaris* species in the Palaearctic region.

	<i>Plateumaris</i> species	Distribution
1	<i>P. akiensis</i> Tominaga & Katsura, 1984	Japanese endemic: records only from Hiroshima prefecture so far
2	<i>P. amurensis</i> Weise, 1898	Russia: East Siberia and Far East
3	<i>P. braccata</i> (Scopoli, 1772)	West Palaearctic except of south Mediterranean including Kazakhstan and west Siberia
4	<i>P. consimilis</i> (Schrank, 1781)	Europa and west Siberia
5	<i>P. constricticollis</i> (Jacoby, 1885)	Endemic of the Japanese archipelago
6	<i>P. roscida</i> Weise, 1912	East Siberia and Far East, from northern China to Amur River region, Lake Baikal, and the Sakha (Yakutia) Republic
7	<i>P. rustica</i> (Kunze, 1818)	West Palaearctic
8	<i>P. sericea</i> (Linnaeus, 1758)	Palaearctic
9	<i>P. shirahatai</i> Kimoto, 1971	East Palaearctic: Russian Far East, Japan, and South Korea
10	<i>P. weisei</i> (Duvivier, 1885)	Northern Europe and northern Asia, Japan, and South Korea

Palaearctic species of the genus *Plateumaris*

***Plateumaris akiensis* Tominaga & Katsura, 1984**

Fig. 2

Plateumaris akiensis Tominaga & Katsura, 1984: 25.

Type locality. Japan, Honshu, Shinkawa-tameike, altitude 770 m, Nishi-yawata-hara, Geihoku-cho, Yamagata-gun, Hiroshima Prefecture.

Type material. Holotype: JAPAN • ♂; Honshu, Hiroshima Prefecture, Yamagata-gun, Geihoku-cho, Nishi-yawata-hara, Shinkawa-tameike; 770 m a.s.l.; 13 Jun 1982; I. Hiura leg.; OMNH-TI-16. The holotype was not examined.

Taxonomic history. Because this species was not described until 1984 it is possible that some small *Plateumaris* specimens from Japan are misidentified as another species in old collections.

Diagnosis. Habitus (Fig. 2A) like a typical *Plateumaris*, but with conspicuously short elytra and legs, elytra length is at the most 1.6× longer than wide, colour black or bronze-metallic, also with a bluish or greenish lustre, elytra shiny, antennomeres thicker than in most *Plateumaris* species, legs reddish but femora dark.

Description. There are comprehensive descriptions in Tominaga and Katsura (1984) and in Hayashi (2020) with many detailed figures so the description below is confined to the essentials.

Size: 6.4–7.6 mm.

Colour: Colour of pronotum and elytra entirely metallic black or reddish coppery, some specimens with a bluish or greenish lustre.

Head: Supraocular furrow indistinct, frontal tubercle weakly convex.

Antennae: Antennae short and robust, slightly shorter than half as long as the body, A1 dark, A2–A11 entirely reddish brown or apical antennomeres with darker parts. A1 is longest, A2 is shortest, A3–A11 are only slightly longer than A2, $A3 \geq A4 \leq A5$.

Pronotum: Slightly longer than wide, outline more or less cordate, gradually narrowed backwards with anterior margin strongly produced forward; dorsal surface with feebly raised anterior and posterior tubercles, disc densely but finely punctate, median line shallow, with a conspicuous broad collar along the posterior margin.

Elytra: Robust and short, 1.6× as long as wide, with arched outer margin, rows of punctures regular, their interstices smooth, usually sparsely but sometimes densely punctate.

Legs: Legs short, reddish brown, partly dark rufous or black, especially the apical half of the femora, metafemur robust in shape, with a tooth; T2 shorter than its width, $T1 > T2 < T3$.

Pygidium: Entirely rufous, but apical part black, apex pubescent, shallowly emarginate in both sexes.

Aedeagus: See Fig. 2B, C.

Similar species. *Plateumaris akiensis* looks similar to *P. constricticollis* but can be identified by its shorter elytra. In *P. constricticollis* the elytral length is distinctly $> 1.6\times$ longer than wide.

Biology. The adults feed on pollen of *Carex* sp. and *Scirpus juncooides* (Hayashi 2020). Narita (2003) described the larvae from *Carex otaruensis* Franch. *Scirpus* sp. is also thought to be a larval host plant (Hayashi 2020).

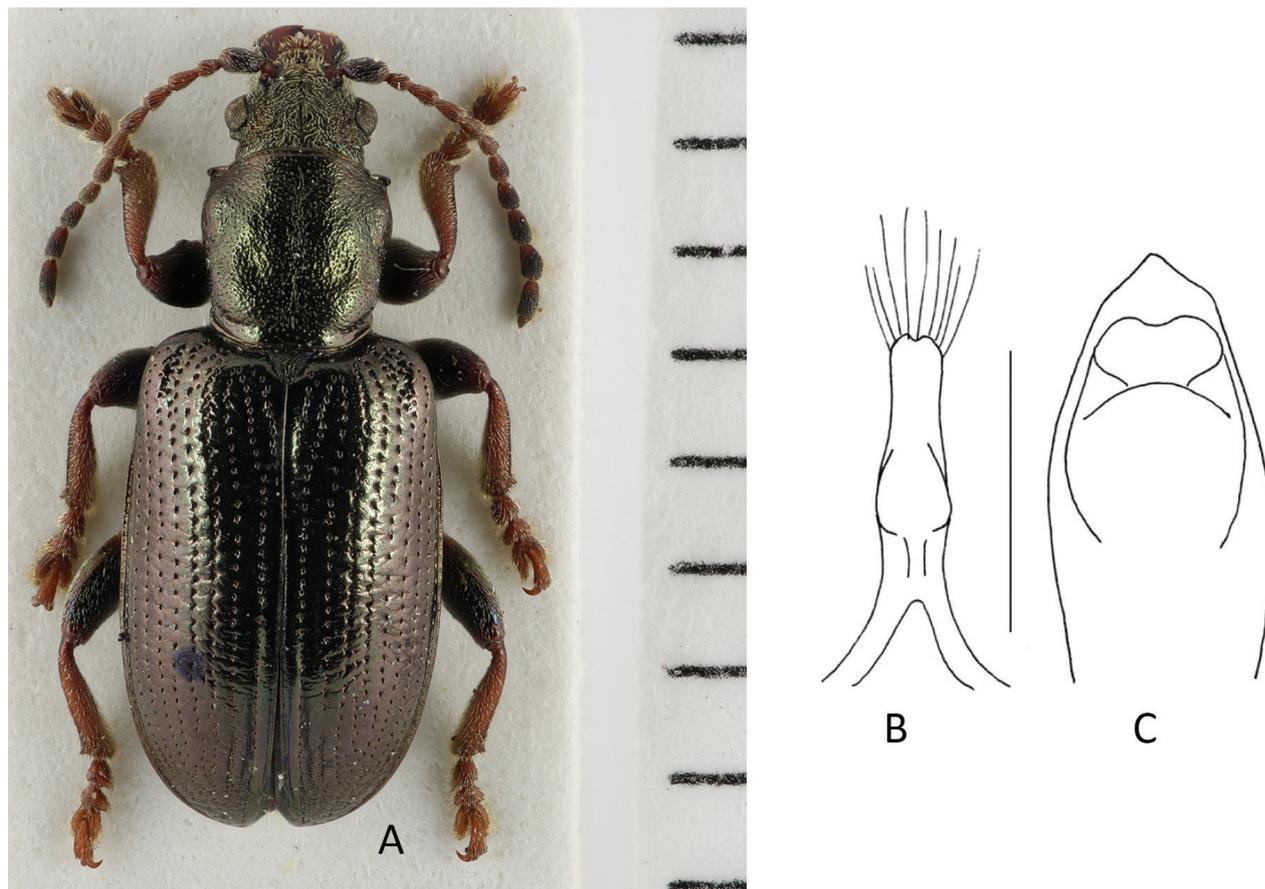


Figure 2. *Plateumaris akiensis* A habitus (photograph by K. Matsumoto) B cap of tegmen C median lobe (B, C from Hayashi 2020). Scale bars: one unit – 1 mm (A); 0.5 mm (B, C).

Distribution. Endemic species found in Honshu, Japan. The only records so far are from Hiroshima and Shimane prefectures in south-west Honshu.

Material examined. Five specimens from Hiroshima prefecture, stored in BMNH, HHM, and NMPC.

Plateumaris amurensis Weise, 1898

Fig. 3

Plateumaris amurensis Weise, 1898: 179.

Type locality. Amur [assumed Russia, further details unknown].

Type material. Types could not be located so far. In his original description (translation in Geiser and Geiser 2023), Weise gave no indication from whom he received the material, where the type is stored, nor the number of specimens he studied.

Taxonomic history and synonymies. Weise (1898) assumed a relationship to *P. discolor* and further compared it with *P. weisei* that is similar in colour. Reitter (1920) mentioned both *P. amurensis* and *P. weisei* in a footnote with some characters from their original descriptions but not in his identification key. He also noted no distinguishing characters. Both species are also mentioned in the catalogue of Winkler (1930). Goecke (1937) regarded *P. amurensis*

as synonymous with *P. weisei* in his modification to Reitter's (1920) identification key, but he provided no reason or reference for this synonymy and subsequently, *P. amurensis* was considered a synonym (Goecke 1960; Jolivet 1970). Askevold (1991) agreed with Goecke's view. Only in the key of Gressitt and Kimoto (1961) is *P. amurensis* regarded as a species propria with different characters to *P. mongolica* (which is now a synonym of *P. weisei*) but those characters are not adequate to distinguish these two species. Medvedev (1992) regarded *P. amurensis* a valid species; Hayashi (2001) then confirmed that *P. amurensis* was a species propria. Many external characters are highly variable and sometimes overlap with the characters of *P. weisei*. Due to the situation described above, specimens of *P. amurensis* are sometimes hidden in collections because they were identified as *P. weisei*.

Diagnosis. Metafemur with a prominent, blade-like tooth, apical part of median lobe of aedeagus gradually narrowed towards the apex.

Description. Size: 7.1–7.7 mm.

Colour: Pronotum and elytra bronze, cupreous, also which greenish reflex.

Head: Supraocular furrow indistinct, vertex pubescent with deep median line. Antennae entirely rufous, sometimes apex darkly rufous; A4 = 1.6× A2, A5 longest and ~ 2.5× as long as wide.

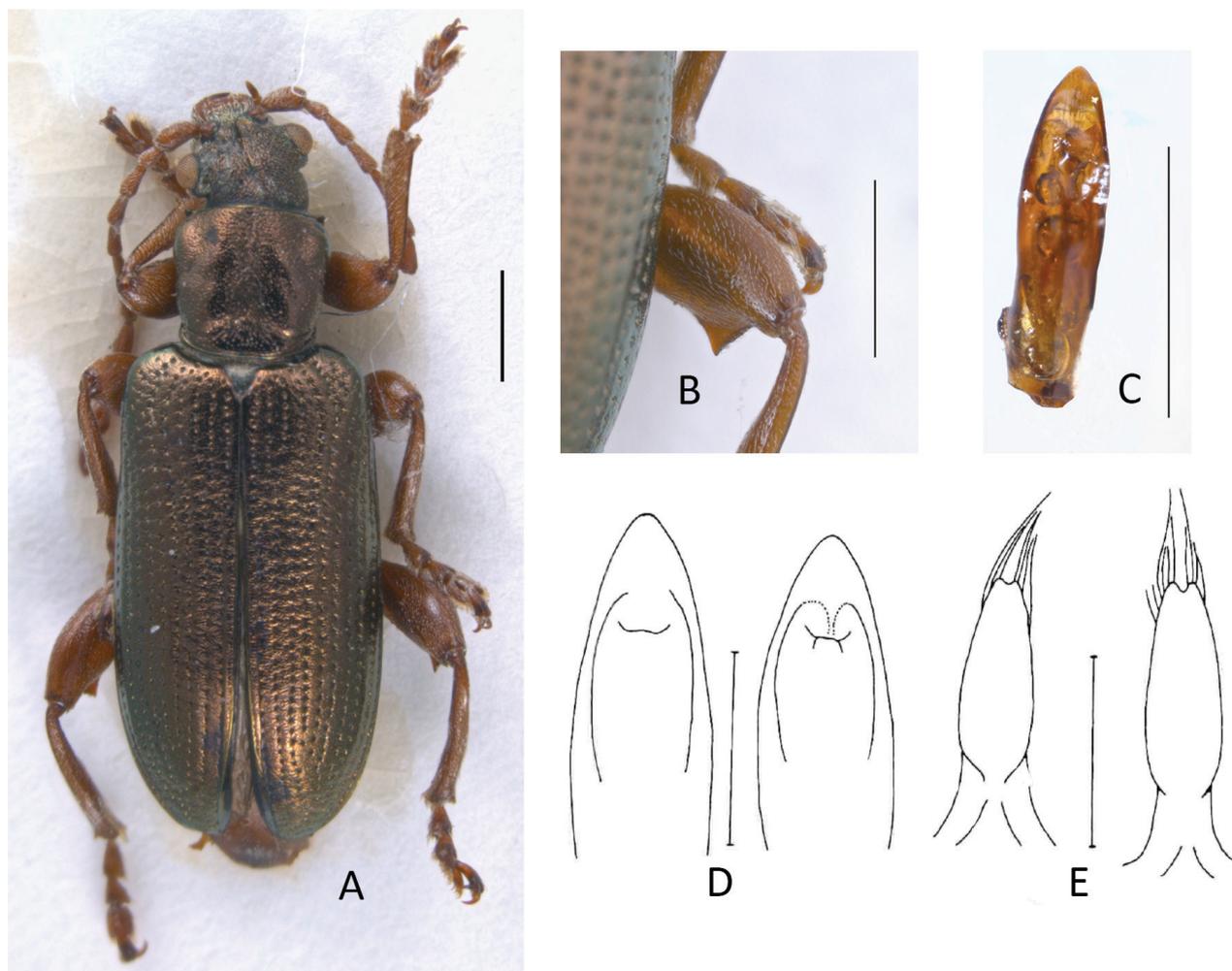


Figure 3. *Plateumaris amurensis* **A** habitus **B** metafemur with prominent tooth **C** aedeagus (**A–C** photographs by E. Geiser) **D** median lobe **E** cap of tegmen (**D, E** from Hayashi 2001). Scale bars: 1 mm (**A–C**); 0.5 mm (**D, E**).

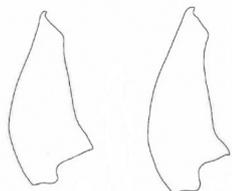
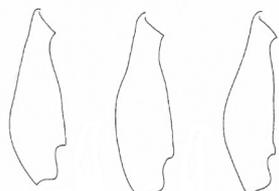
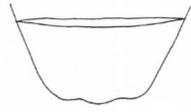
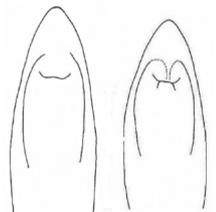
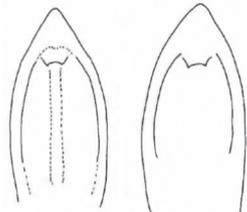
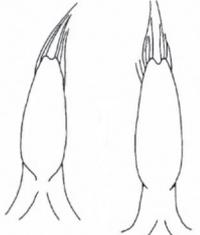
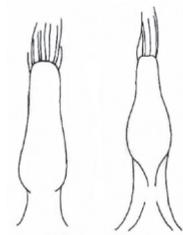
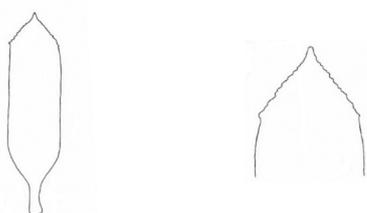
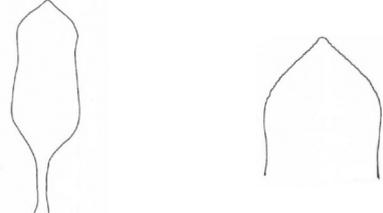
Pronotum: More or less quadrate, anterior part slightly widened by shallow anterior tubercles, disc shiny, coarsely punctate, rugose, sometimes with microsculpture in major part of the disc, basal sulcus prominent with rugae and dense punctures, median groove indistinct.

Elytra: Sparsely rugose, shiny, densely punctate on disc.

Legs: In most specimens rufous, sometimes apical area of femora dark, metafemur with a prominent, blade-like tooth (Fig. 3B; Table 3).

Pygidium: Apex pubescent, shallowly emarginate or sometimes truncate in male and rounded in female. Last sternite entirely coppery but apex at middle part rufous, apical shape variable in male, acute in female (Table 3).

Table 3. Distinguishing characters of *Plateumaris amurensis* und *P. weisei* (drawings from Hayashi 2001).

	<i>P. amurensis</i>	<i>P. weisei</i>
Metafemur		
Last sternite male		
Last sternite female		
Aedeagus: apex of median lobe		
Cap of tegmen		
Ovipositor: ventral view and apex contour		

Ovipositor: Elongate, both sides paralleled, apical angle acute, subapical corner with teeth, apex remarkably prominent (Table 3).

Aedeagus: With median lobe, acute but slightly rounded at the apex; cap of tegmen gradually narrowed distally, notched, or sometimes rounded at apex (Fig. 3C–E).

Similar species. The most similar species is *Plateumaris weisei* and the main distinguishing characters are shown in Table 3. Otherwise, the East Palaearctic *Plateumaris* species are not easy to distinguish. I found specimens of *P. amurensis* in museums also identified as *P. roscida*, *P. sericea*, or as their synonyms.

Biology. Host plant and larvae are unknown.

Distribution. East Palaearctic only. Records exist for Asia: Russia: Transbaikalia, Republic of Sakha (Yakutia): southern part of river Lena; Amur Oblast, Khabarovsk Krai, Primorsky Krai, Sakhalin, Kurile Islands. Sometimes *P. amurensis* is mentioned from Japan (e.g., Bieńkowski 2014) but these are erroneous records caused by confusion with *P. weisei* (Hayashi 2001, 2020).

Material examined. 15 specimens from different localities in East Siberia and Far East.

***Plateumaris bracata* (Scopoli, 1772)**

Fig. 4

Prionus bracatus Scopoli, 1772: 100.

Donacia abdominalis Olivier, 1800: 9.

Plateumaris bracatus var. *fairmairi* LeGrand, 1861a: 265.

Donacia nigra Fabricius, 1792: 117.

Donacia palustris Herbst, 1784: 100.

Leptura violacea Pallas, 1773: 724.

Type locality. *Plateumaris bracatus*: Carniola, a historical region which comprised parts of present-day Slovenia.

Type material. Type specimens of *P. bracatus* do not exist anymore. Sadly, Scopoli's collection of insects from Carniola decayed during his life time. He committed this collection to a printer in Vienna who apparently did not store it adequately. Before all the pictures were printed, Scopoli complained in his 1773 letter to Linnaeus (Brelvič et al. 2006) that the insects "had either decayed or fallen apart".

Taxonomic history and synonymies. In nearly all publications the species name has been misspelled "braccata". The spelling in the original description by Scopoli (1772) is "Prionus Bracatus" with a single "c" (Geiser and Geiser 2023). Scopoli used this epithet presumably because "bracae" means "trousers" or "pants" referring to the clubbed shape of the metafemora. A variant of this word exists in later medieval Latin and was spelled "braccae", which Schenkling (1917) used in his explanation of the scientific names of beetles. Because the spelling of the original description is linguistically correct it must be preserved unaltered (ICZN, Art. 32.2.1). Because the original description by Scopoli is very short, Weise (1893) published a more detailed redescription (see Geiser and Geiser 2023).

Donacia abdominalis (Olivier, 1800): Silfverberg (2010) cited this synonym as *abdominalis* (Olivier, 1795). Despite the title page dated 1795, the fourth

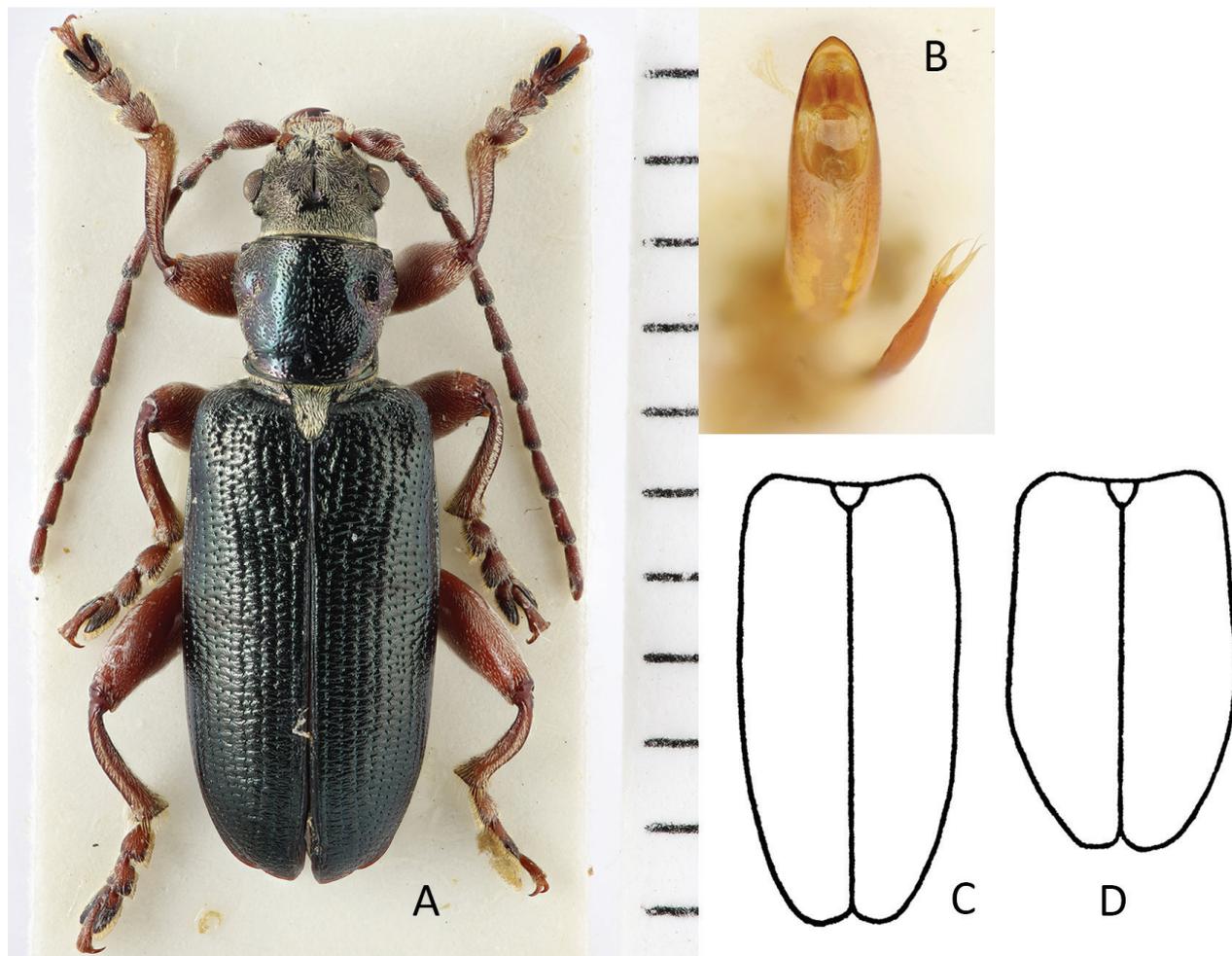


Figure 4. *Plateumaris bracata* **A** habitus **B** aedeagus (photographs by K. Matsumoto) **C** elytra **D** elytra of *Plateumaris consimilis* (drawings from Mohr 1966a). Scale bar: one unit – 1 mm.

volume of Olivier's 'Entomologie, ou histoire naturelle des insectes' was issued in two parts, one probably in 1795 and the second one in 1800. All new taxa made available in this work have previously been dated 1795 in the literature (Bousquet 2018). In any case, Olivier's volume does not contain the original description. He also listed another name of this species, *Leptura violacea* Pallas, and then described the typical characters of *P. bracata*. Later, *P. abdominalis* was regarded synonymous with *P. rustica* because it was mixed up with *P. abdominalis* Bedel, 1891, who intentionally did not describe it as a new species (see section on *P. rustica* for details).

Plateumaris fairmairi was first described by LeGrand (1861a) on page 265 as variation of *Donacia nigra* (see Geiser and Geiser 2023) from a specimen with complete black antennae and legs. The often-mentioned page 89 derives from the reprint (LeGrand 1861b).

Fabricius described *Donacia nigra* by 1792 (see Geiser and Geiser 2023). He allocated it close to *D. festucae* which is now synonymous with *P. sericea*. The name *Plateumaris* was not established then, but Fabricius (1792) noticed some differences from other *Donacia* species.

Diagnosis. This is the largest *Plateumaris* species, body length: 8.0–12.0 mm (Fig. 4A).

Head, pronotum and elytra entirely black or with a weak blue, purple or green metallic lustre, antennae and legs reddish brown in most specimens, elytra elongate, ~ 2× as long as wide, side contour of the elytra very straight, almost parallel.

Description. Size: 8.0–12.0 mm.

Colour: Dark, entirely black or at the most with weak blue, purple or green metallic lustre.

Head: Entirely black or with weak metallic lustre. Fine punctures and very fine wrinkles. Antennae minimum as long as the half length of the beetle, basal part of the antennomere always reddish (with rare exceptions), apical part dark; $\frac{1}{2} A1 \geq A2$, $\frac{1}{2} A3 \geq A2$, $A4 \geq A3$, $A1 \approx A4$, $A5 \dots A11 \approx A4$.

Pronotum: Cordate, ahead distinctly wider than behind, anterior tubercles only slightly convex, slightly pubescent. Disc with fine punctures, median line well developed, sometimes shortened, but also very shallow and almost invisible in some specimens.

Elytra: Base of elytra with short, distinct setae in most specimens, elytral disc rugose, punctures delicate, not deep, interstices strongly transversely wrinkled; contour of the margin very straight, almost parallel; elytra elongate, ~ 2× as long as wide, ratio of length to width = (1.8–2.1): 1.

Legs: Colour variation from complete reddish brown to dark apical parts and completely dark legs, femora basally very broad, metafemur with broad tooth, robust in male, in female feeble or indistinct.

Aedeagus: see Fig. 4B.

Similar species. The most similar species is *Plateumaris consimilis*, which is smaller (6.0–9.2 mm) on average, its elytra are shorter with a ratio of length to width ≤ 1.8 , and the outer contour of the elytra are slightly rounded, not parallel.

Biology. *Plateumaris bracata* is monophagous on *Phragmites australis* (Cav.) Trin. ex Steud., the common reed, Poaceae (Bieńkowski 2014). The beetle can be found concealed in the *Phragmites* leaf-folds. When feeding, it penetrates the young leaf shoots which later unfold to present a characteristic transverse series of round holes. *Donacia clavipes* feeds on the same plant species in a similar fashion but, in this case, the series of holes produced are irregularly elongated (Menzies and Cox 1996; Rheinheimer and Hassler 2018). For identification of the larvae see Steinhausen (1994) and Bieńkowski and Orlova-Bieńkowskaja (2004). Despite its large distribution area and its common food plant, its number of specimens stored in museum collections is always remarkably fewer than the number of *P. consimilis* or *P. sericea*. Compared with *Donacia clavipes*, which occurs on the same food plant, the numbers of *P. bracata* specimens are also much fewer. Recent records are extremely rare.

Distribution. All parts of Europe except southern Europe and north Scandinavia, continuing to central Asia, including southern parts of Russia and western Siberia. Records exist for Europe: Austria, Belgium, Bosnia-Herzegovina [new in PalCat], Belarus, Bulgaria, Croatia [first record], Czech Republic, Denmark, Estonia, Finland, France, Germany, Great Britain, Hungary, Ireland, Italy, Latvia, Lithuania, Luxembourg, Moldavia, Montenegro [first record], The Netherlands, Norway, Poland, Romania, Russia (central and south parts of European Russia), Serbia [new in PalCat], Slovakia, Slovenia, Sweden, Switzerland, Ukraine.

Asia: Azerbaijan, China (Xinjiang [first record]), Georgia, Iran [new in PalCat], Kazakhstan, Kyrgyzstan [new in PalCat], Russia (south Siberia [new in PalCat], west Siberia).

New country records additional to Silfverberg (2010). BOSNIA-HERZEGOVINA: Mohr (1966b).

CROATIA • 3 ex.; Dalmatia; E. Geiser 2019 det.; coll. Frey in NHMB.

MONTENEGRO • 2 ex.; Montenegro; E. Geiser 2019 det.; coll. Frey in NHMB.

SERBIA: Gavrilović and Ćurčić (2011) and Mohr (1966b).

CHINA • 2 ex.; Xinjiang, “Ost-Turkestan, Bagratsch-Kul” [Bosten-Lake], Kurla; May 1902; Hauser leg.; E. Geiser 2019 det.; HNHM • 1 ex.; Xinjiang, Kuldscha province, Upper Ili valley [“Ober Jli-Thal”]; 1897; F. Hauser leg.; “*Pl. braccata*” H. Goecke 1956 det., E. Geiser 2019 vid.; coll. Frey in NHMB. Note: Bosten-Lake lies east of Kurla; Kuldscha is now called Yining (in Chinese). Both Bosten-Lake and Kuldscha are located in north-western Xinjiang, on the northern side of the Ili River in the Dzungarian basin, ~ 70 km east of the border with Kazakhstan.

IRAN • 2 ex.; Khorasan-e Razavi province, Sabzevar; 36°12'N, 57°35'E; 1024 m a.s.l.; 23. Aug 2012 (Samin 2018).

KYRGYZSTAN: Bieńkowski (2014).

RUSSIA: South Siberia (Gus'kova et al. 2018).

Material examined. More than 100 specimens from different localities throughout the distribution area.

***Plateumaris consimilis* (Schrank, 1781)**

Fig. 5

Leptura consimilis Schrank, 1781: 155.

Plateumaris consimilis f. *aerea* Bechyné, 1942: 234, 236 [infrasubspecific name].

Leptura assimilis Schrank, 1781: 156.

Plateumaris consimilis f. *coerulea* Bechyné, 1942: 234, 236 [infrasubspecific name].

Donacia discolor Hoppe, 1795: 45 [homonym].

Plateumaris consimilis f. *flavipes* Bechyné, 1942: 234, 236 [infrasubspecific name].

Plateumaris consimilis f. *nigripes* Bechyné, 1942: 234, 236 [infrasubspecific name].

Donacia rufipes Olivier, 1791: 292.

Plateumaris tenuicornis Balthasar, 1934: 128 [syn. nov.].

Donacia variabilis Kunze, 1818: 39.

Plateumaris consimilis f. *violacea* Bechyné, 1942: 234, 236 [infrasubspecific name].

Plateumaris consimilis f. *viridis* Bechyné, 1942: 234, 236 [infrasubspecific name].

Type locality. *Plateumaris consimilis*: unknown, but possibly in Austria (the country in 1781 was much larger than today) because the original description is in a book titled ‘Enumeratio insectorum Austriae indigenorum’.

Type material. Holotype or type series of *P. consimilis* unknown.

Taxonomic history and synonymies. Bechyné (1942) detailed statistics about the different colours and subtle structures on the pronotum of *P. consimilis*, but without convincing results. He named colour variations as “forma” but conceded that there also existed combinations of colours in between. These names are indicated above for the sake of completeness, but they are irrelevant to systematics.

Schrank de Paula (1781: 155) described *Leptura consimilis* with bronze and black-golden colouration. On the next page of this publication, he described a new species *Leptura assimilis*. The difference from the former species is indicated as “black” and the elytra with nine rows of punctures in contrast to those

of *P. consimilis* which he described with ten rows of punctures [both species have elytra with 11 rows of punctures]. In that pioneer period, this species common in central Europe was also described as *Donacia rufipes* by Olivier (1791), *Donacia discolor* by Hoppe (1795), and *Donacia variabilis* by Kunze (1818), who already mentioned the great variability of this species by its specific name.

Donacia discolor was described by Hoppe (1795). According to Bousquet (2016) this was published on [30] April 1795, but a description of a *Donacia discolor* had been already published by Panzer on 14 February 1795 (Bousquet 2016). Therefore, *Donacia discolor* Hoppe was immediately a homonym. Later, both species were assigned to *Plateumaris*, therefore *D. discolor* Hoppe remained a homonym.

Plateumaris consimilis orientalis was described by Shavrov (1948) (see Geiser and Geiser 2023), which he thought to represent a subspecies of *P. consimilis*, but it resulted in being synonymous with *P. weisei* (see at *P. weisei* below for further explanation).

Diagnosis. Pronotum cordate, anterior tubercles slightly convex. Upper side with metallic lustre in varying colours, antennae, and legs at least partly reddish brown. Elytra 1.5–1.8× longer than wide.

Description. Size: 6.0–9.2 mm.

Colour: Very variable, upper side greenish, bluish, cupreous, bronze, or black with metallic lustre, some black specimens almost without metallic lustre (Fig. 5A, B).

Head: Same colour as pronotum. Antennae approximately half the body length or slightly longer, Antennomeres reddish brown at least at the basal part, the apical part can be darkened. $\frac{1}{2} A1 \geq A2$, $\frac{1}{2} A3 \geq A2$, $A4 \geq A3$, $A1 \approx A4$, $A5 \dots A11 \approx A4$.

Pronotum: cordate, ahead wider than behind, anterior tubercles only slightly convex, disc uniformly punctate, median line obsolete to fine but distinct.

Elytra: 1.5–1.8× longer than wide, never twice as long as wide, side contours slightly convex, not parallel, elytra rugose and punctulate.

Legs: Colour variation from completely reddish brown to only reddish at the joints, femora basally very broad, metafemora with sharp or broad tooth.

Aedeagus: The shape varies between the short, more rounded form in *P. braccata* and the elongated acute form of *P. rustica* (Fig. 5C, D).

The most similar species are *Plateumaris braccata* and *P. rustica*: *P. braccata* has longer elytra, ~ 2× as long as wide and the side contour of the elytra is parallel, not convex (Fig. 4C). *Plateumaris rustica* has the pronotum not cordate, and disk and tubercles flattened (Fig. 10A). *Plateumaris weisei* could be mistaken for *P. consimilis* but their distribution areas hardly overlap.

Biology. Although *P. consimilis* is one of the common *Plateumaris* species, its larva was not described until 2014 by Medvedev and Muravitsky. The larvae and adults feed on *Carex* sp. (Cyperaceae). Also, *Juncus articulatus* (Juncaceae) and *Caltha* sp. (Ranunculaceae) are mentioned as food plants of adults, on which they feed on the pollen (Rheinheimer and Hassler 2018). *Plateumaris consimilis* lives in wetlands, fens, near springs, and moor grass meadows. It is more frequent on low calcareous soils, where it is usually the only species of Donaciinae. It is site-loyal and cannot be caught in pitfall traps (with rare exceptions) (Krause 1982; pers. obs.).

Distribution. Western Palaearctic: mainly continental Europe up to southern Sweden, very rare in south and east Europe and west Siberia. Records exist for: Europe: Albania [first record], Austria, Belarus, Belgium, Bosnia-Herzegovina, Bulgaria, Croatia, Czech Republic, Denmark, France, Germany, Hungary, Italy, Latvia,

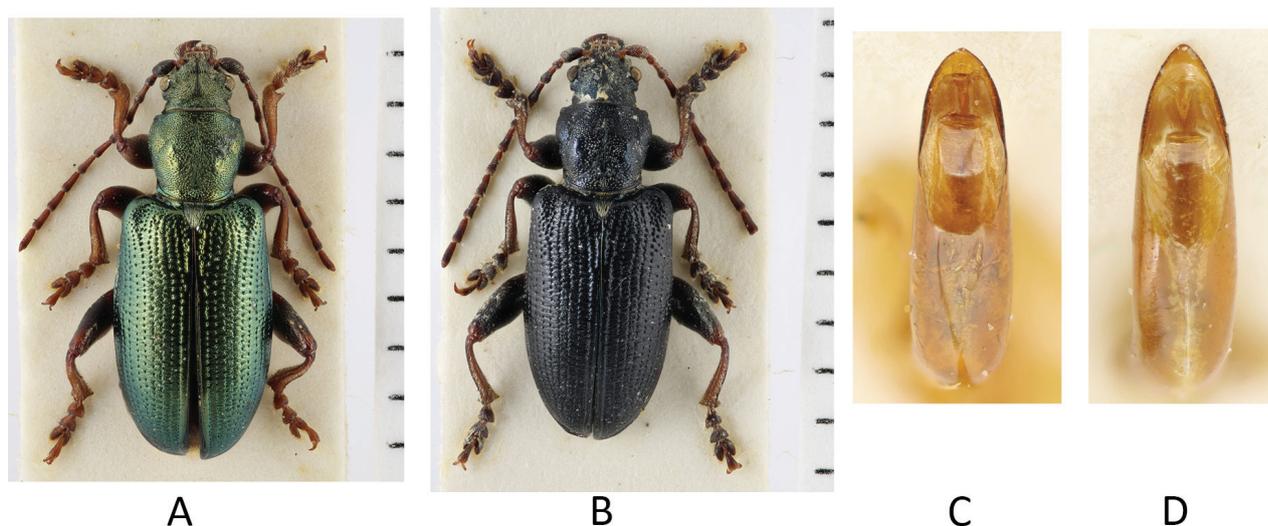


Figure 5. *Plateumaris consimilis*: Variability of colours and of the shape of the median lobe **A, B** habitus **C, D** median lobe (photographs by K. Matsumoto). Scale bars: one unit – 1 mm.

Liechtenstein [new in PalCat], Lithuania, Luxembourg, The Netherlands, North Macedonia [new in PalCat], Poland, Romania, Russia (central part of European Russia), Serbia [new in PalCat], Slovakia, Slovenia, Spain, Sweden, Switzerland, Ukraine.

Asia: Georgia [first record], Russia (west Siberia), Turkey [new in PalCat].

New country records additional to Silfverberg (2010). ALBANIA [first records] • 3 ex.; Qarku i Kukësit, Kula e Lumës, “Albanien Expedition, Kula Ljums”; 18–28 May 1918; H. Goecke 1956 det., E. Geiser 2019 vid.; NHMB [ex coll. Frey] • 1 ex.; Qarku i Kukësit, Gjallica e Lumës, “Albanien Expedition, Gjallica Ljums”; 17–26 Jun 1918; H. Goecke 1956 det., E. Geiser 2019 vid.; NHMB [ex coll. Frey].

LIECHTENSTEIN: Walter (1990).

NORTH MACEDONIA: Gruev and Tomov (1984).

SERBIA: Gavrilovic and Curcic (2011).

GEORGIA [first record] • 2 ex.; Mtskheta, “Transcaucasia, Mazcheta, pr. Tiblisi”; 4–23 Jun 1987; Wrase and Schülke leg.; E. Geiser 2019 det.; NHMB.

TURKEY: Ekiz et al. (2020).

Remarks. *Plateumaris consimilis* does not occur in the East Palaearctic which has also been confirmed recently by Hayashi (2020). Records from Far East and Japan, e.g., in Goecke (1960) or Warchalowski (2010), are due to records of “*Plateumaris consimilis orientalis* Shavrov, 1948” which is synonymous with *P. weisei* (see below). Note that specimens of *P. weisei* misidentified as *P. consimilis* were found in collections (pers. obs.).

Material examined. More than 200 specimens from different localities throughout the distribution area.

***Plateumaris tenuicornis* Balthasar, 1934, syn. nov.**

Fig. 6

Type locality. Bosnia-Herzegovina: Dol. Tuzla, Bosnia.

Type material. Holotype of *Plateumaris tenuicornis*. BOSNIA-HERZEGOVINA • 1 ex.; Bosnia, Dol. [Dolina?] Tuzla; Em. Fritsch leg.; SNMC. Fig. 6A, B. I examined the holotype in 2020 and it is the only specimen known.

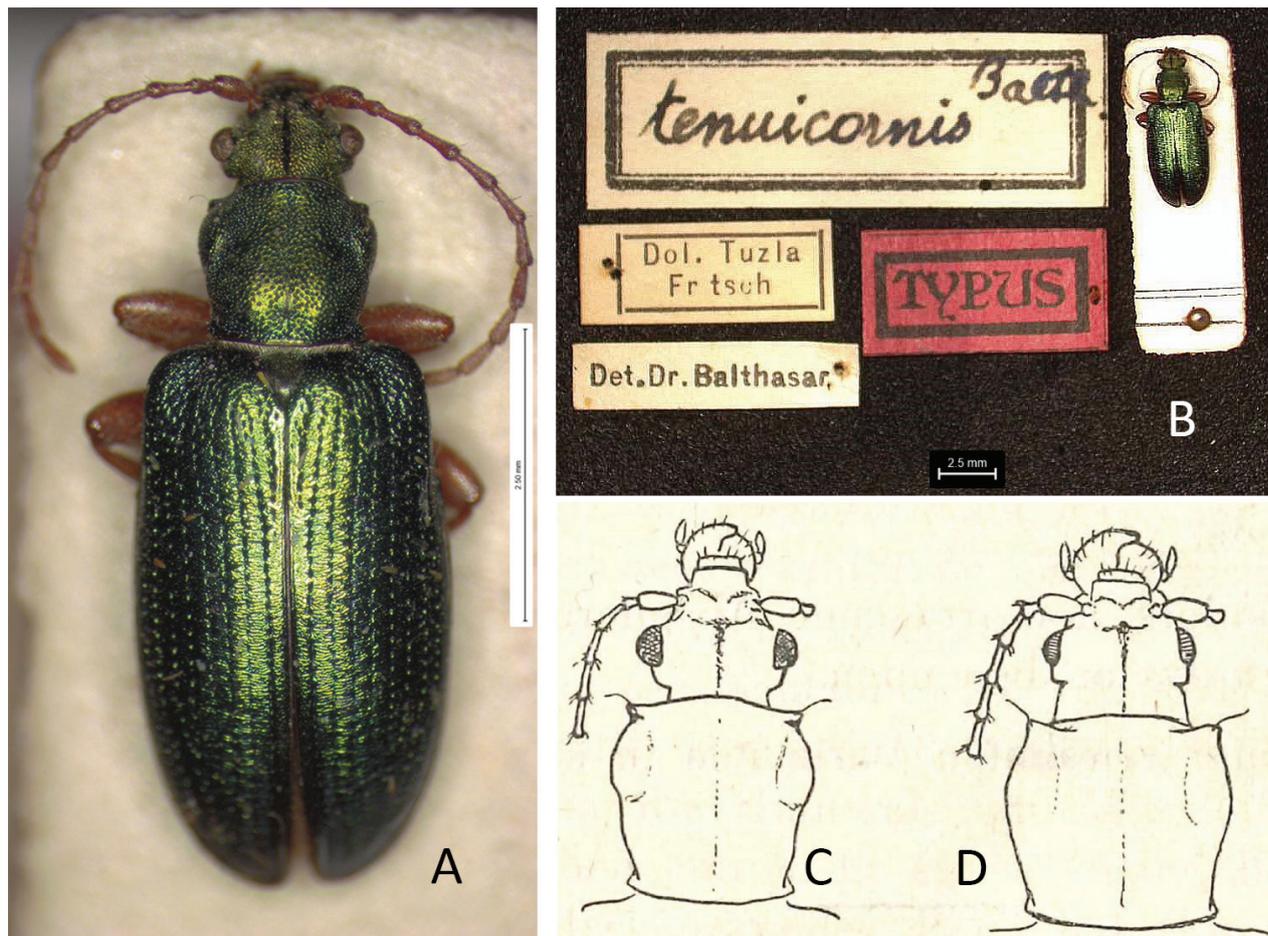


Figure 6. *Plateumaris tenuicornis* Holotype **A** habitus **B** labels of Holotype (photographs by M. Sečanský), comparison of the pronotum of **C** *P. tenuicornis* with **D** *P. consimilis* (from the original description of *P. tenuicornis* by Balthasar 1934: 128). Scale bars: 2.5 mm.

Remarks. Balthasar (1934) described a species *Plateumaris tenuicornis* from one *P. consimilis* specimen collected in Bosnia, which he studied in the collection of the Slovak National Museum, Bratislava. The sketches where he compared the pronotum of both species are provided in Fig. 6C, D. Bechyné (1942) published an article about this description. He studied 335 specimens of *P. consimilis*, mostly from the area which belongs now to the Czech Republic, but also from central France and Podolia, a historic region in Eastern Europe located in the west-central and south-western parts of Ukraine and north-eastern Moldova, but he did not study the holotype of *P. tenuicornis* (possibly due to the political situation in Europe at that time). He meticulously worked out that all described characters of *P. tenuicornis* were within the variation range of the characters of *P. consimilis*. Bechyné published this article in Czech and Latin in a Czech journal, which has been ignored by most Donaciinae specialists. The English translation of the Latin text is now available in Geiser and Geiser (2023).

Askevold (1991) knew neither of the article of Bechyné (1942) nor of the holotype of *P. tenuicornis*, but he studied the description of Balthasar (1934) and concluded “All character states used by Balthasar are ones that I have also found among *P. consimilis*” and then declared *P. tenuicornis* as a probable new synonym. I studied the holotype of *P. tenuicornis* still stored in the Slovak

National Museum in Bratislava (Fig. 6A, B) and I can confirm that Bechyné and Askevold were correct in every detail.

Because Bechyné only indirectly treated *P. tenuicornis* as a synonym, and because Askevold only suggested that *P. tenuicornis* should be considered as a probable new synonym, I determined that *P. tenuicornis* Balthasar, 1934 is a new synonym of *P. consimilis* (Schrank, 1781) according to Bechyné (1942), supposed by Askevold (1991), and now confirmed based on a study of the type material and original descriptions.

***Plateumaris constricticollis* (Jacoby, 1885)**

Fig. 7

Donacia constricticollis Jacoby, 1885: 192.

Plateumaris constricticollis babai Chûjô, 1959: 2.

Donacia constricticollis constricticollis Jacoby, 1885: 192 (= *Plateumaris constricticollis kurilensis* L. N. Medvedev, 1978b: 83).

Plateumaris constricticollis toyamensis Tominaga & Katsura, 1984: 27 (= *Plateumaris constricticollis chugokuensis* Tominaga & Katsura, 1984: 28).

Type localities. *Plateumaris constricticollis*: Japan; *P. constricticollis babai*: Honshu: Niigata Prefecture, Yoshigahira, Shitada-mura; *P. constricticollis toyamensis*: Tsubura-ike, alt. 690 m, Kamiichi-machi, Naka-niikawa-gun, Toyama prefecture; *P. constricticollis chugokuensis*: Koiga-kubo, alt. 570 m, Tessei-cho, Atetsu-gun, Okayama prefecture.

Type material. Holotype of *P. constricticollis*: JAPAN • 1 ♂; Hokkaido, Lake Junsai, N of Hakodate; 43°7'N, 145°6'E; 28–30 Jul 1880; G. Lewis leg.; BMNH 1910-320. The holotype was examined in 2019.

Holotype of *P. constricticollis babai*: JAPAN • 1 ♀; Honshu, Niigata Prefecture, Yoshigahira in Mt. Sumon; 25 Jun 1955; K. Baba [leg.]; "*P. constricticollis babai* Chûjô" M. Chûjô 1959 det.; KUEC.

Holotype of *P. constricticollis toyamensis*: JAPAN • 1 ♂; Honshu, Toyama Prefecture, Kamiichi-machi, Naka-niikawa-gun, Nakanomata, Tsubura-ike; 690 m a.s.l.; 20 Jun 1983; K. Katsura leg.; OMNH TI-17.

Holotype of *P. constricticollis chugokuensis*: JAPAN • 1 ♂; Honshu, Okayama prefecture, Tessei-cho, Atetsu-gun, Koiga-kubo; 570 m a.s.l.; 13 Jun 1982; O. Tominaga leg.; OMNH TI-18.

Taxonomic history and synonymies. Jacoby (1885) described this *Plateumaris* species as *Donacia constricticollis*. The details of the location and the date are not tagged to the holotype, and the label contains only "Japan G. Lewis, BMNH 1910-320". Bates (1883) published the itinerary of G. Lewis' journey through Japan from February 1880 to September 1881 that contains the exact data. The type specimen was collected at Lake Junsai near Hakodate in south Hokkaido where Lewis sojourned 28–30 July 1880.

Lays (2002) refers to a female type specimen: 1 ♀, "Type", "*Donacia constricticollis* Jac." [no further label data, origin unknown], stored in RBINS. It is unlikely that this "type" specimen could be a paratype or allotype of the series collected in Hokkaido at the same site as the holotype. According to Lays (2002) this specimen belongs to the subspecies *P. constricticollis babai*, which



Figure 7. *Plateumaris constricticollis* Habitus (photograph by K. Matsumoto). Scale bar: one unit – 1 mm.

occurs only in central Honshu. One must keep in mind that some decades ago “type” labels were sometimes added later to specimens in several museum collections without thorough studies.

Specimens of *P. constricticollis* reveal a remarkable variation in body size and colouration, pronotal disc, and even genital structures. This resulted in the description of four subspecies. Further studies concluded that there were two subspecies in addition to the nominate species, and therefore the other two subspecies names are synonyms (Hayashi and Shiyake 2004). This is also confirmed by several molecular studies (Sota and Hayashi 2007; Sota et al. 2007; Sota et al. 2008; Hayashi and Sota 2014). However, the morphological discrimination of these subspecies is very difficult because of the variations in some key characters.

Chûjô (1959) was the first to describe a subspecies, *P. c. babai* from Niigata Prefecture. In 1978, Medvedev described *P. c. kurilensis* from Kunashiri, the southernmost Kurile Island, near Hokkaido. This subspecies was synonymised with *P. c. constricticollis* by Hayashi and Shiyake (2004: 114). Tominaga and Katsura (1984) described the two subspecies *P. c. toyamensis* and

P. c. chugokuensis, and the latter was synonymised with the former by Hayashi and Shiyake (2004: 116).

Diagnosis. The characters common to all subspecies are the following: surface very shiny (Fig. 7), dorsal colouration variable, bronze brown or dark cupreous, black, blue, or green, pronotum cordate, slightly longer than broad, anterior tubercles prominent, elytra regularly and strongly punctate, metafemora with blade-like tooth. It looks similar to a glossy *P. consimilis* that does not occur in the East Palaearctic region.

Description. Size: 6.6–11.9 mm.

Plateumaris constricticollis and its subspecies have been thoroughly studied by Japanese colleagues, with detailed descriptions of their morphological characters and their variations, as well as phylogeny, biogeographical history, biology, and molecular analyses (Tominaga and Katsura 1984; Hayashi 2002, 2020; Hayashi and Shiyake 2004; Hayashi and Sota 2014). The three subspecies and their distinguishing characters are described in the section “Identification Key”.

The similar species *Plateumaris weisei* is not shiny or glossy, its pronotum not cordate, and the legs are longer and slenderer.

Biology. Sota et al. (2007) analysed the geographic variation in body size and ovipositor dimensions in three subspecies in different climatic conditions and on different host plants, and reported a significant correlation of the body size and ovipositor size with snow depth. The larvae feed on *Carex* sp. (Cyperaceae) (Narita 2003). Cocoons of *P. c. babai* were also found on roots of *Phragmites australis* (Poaceae), *Carex thunbergia*, and *Carex ampliata*. *Eleocharis* sp. is recorded as a larval host plant for *P. c. toyamensis* (Sota et al. 2007).

Distribution. *Plateumaris constricticollis* is endemic to the Japanese Archipelago (Hokkaido, Honshu, and Kunashiri).

Plateumaris constricticollis constricticollis: southernmost Kurile Island Kunashiri, Hokkaido and northern part of Honshu until prefecture of Yamagata (Medvedev 1978; Tominaga and Katsura 1984).

Plateumaris constricticollis babai: Honshu: prefectures Fukushima, Niigata, Nagano, Gunma, Tochigi, Ibaraki, and Chiba.

Plateumaris constricticollis toyamensis: Honshu: prefectures Toyama, Gifu, Ishikawa, Aichi, Hyogo, and Okayama.

Material examined. Approximately 60 specimens from Japan.

***Plateumaris roscida* Weise, 1912**

Figs 8, 9

Plateumaris roscida Weise, 1912: 77.

Plateumaris annularis Reitter, 1920: 41.

Type localities. *Plateumaris roscida*: Russia, Transbaikalia (Zabaykalsky Krai): Tschita; *Plateumaris annularis*: Russia, Far East, Khabarovsk Krai, Nikolaevsk-on-Amur.

Type material. Holotype of *P. roscida*: RUSSIA • 1 ♂; East Siberia, Transbaikalia, Tschita; ZMHB. Label text: “Typus [red]// roscida m. //coll. J. Weise //Zool. Mus. Berlin //Holotype ♂ *Plateumaris roscida* Weise [red]//*Plateumaris roscida* Weise det. I.S. Askevold 1989”.

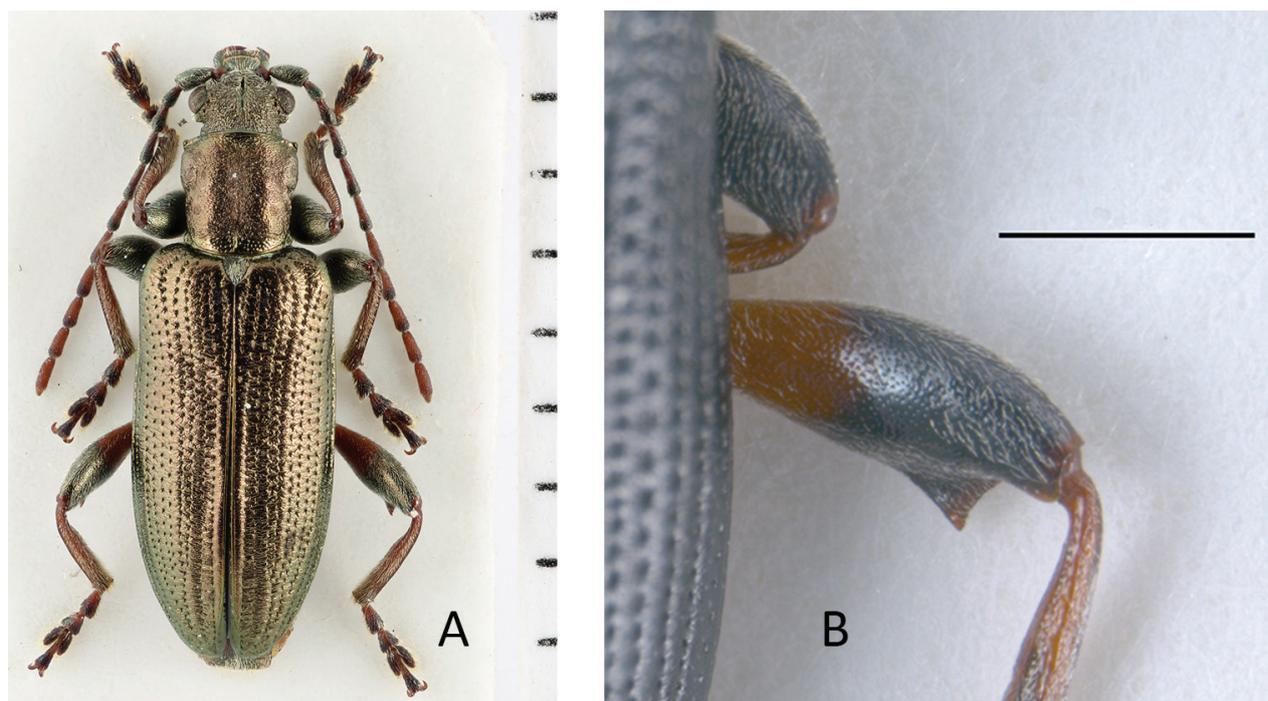


Figure 8. *Plateumaris roscida* **A** habitus (photograph by K. Matsumoto) **B** metafemur with typical double colouring and prominent tooth (photograph by E. Geiser). Scale bars: one unit – 1 mm (**A**, **B**).

No location label is tagged to the holotype, but the type locality “Tschita” is indicated in the original description by Weise (1912). The holotype was examined in May 2023.

Holotype of *Plateumaris annularis*: RUSSIA • 1 ex.; Far East, Khabarovsk Krai, Nikolayevsk-on-Amur, “Amur region, Chabarowsk, Nikolajewsk”; L. Graeser leg.; depository unknown. At first stored in coll. W. Koltze, current depository presumably SDEI, but needs confirmation.

Taxonomic history and synonymies. Weise (1912) described *Plateumaris roscida* (see Geiser and Geiser 2023) based on a specimen from Tschita. He obtained it from Johann Nepomuk Ertl (1860–1925, Munich, Germany), a dedicated beetle collector who had connections to missionaries. This specimen was presumably collected during a journey to China.

Reitter (1920) published an identification key for Palaearctic Donaciinae. In a footnote to *P. sericea* he described *P. annularis* from Russia, Far East, Amur region, Chabarowsk (krai), Nikolajewsk, coll. Koltze (see Geiser and Geiser 2023). Reitter did not mention in the description that this *P. annularis* is armed with a prominent metafemoral tooth, but he provided this information indirectly two paragraphs later when he contemplated if *P. obsoleta* could be the same species as *P. annularis*. He also described that, in contrast, *P. obsoleta* has completely dark legs and the posterior femora are practically unarmed, or only bluntly angled. This description and further notes in Reitter (1920) match completely with the characters of *P. roscida*.

Kolossow (1930: 29) synonymised *P. annularis* with *P. roscida* with the laconic line “*Plateumaris annularis* Reitt. (1920) = *Pl. roscida* Weise (1912)”. Goecke (1957a) studied a specimen from ZSM, labelled “Samml. Ertl” [= collection of Ertl] and “*Pl. roscida* n. sp. Wse” in the handwriting of Weise. He also examined four specimens from the then “Deutsches Entomologisches Institut Berlin” (now

SDEI) labelled "*Pl. annularis* Reitter", one of them labelled "Nikolajewsk, Graeser" and "*Pl. annularis* Rtr., Chabaroska, Weise" and another two specimens labelled "*Pl. annularis*" without location labels. All four specimens were labelled as "Type". He then compared the *P. roscida* specimen with the *P. annularis* specimens and confirmed the statement of Kolossow (1930) that they all belong to *P. roscida*.

Askevold (1991) studied other specimens from Russia and north China identified as *P. annularis* and confirmed that they belonged unambiguously to *P. roscida*. He also suggested that *P. caucasica* may be synonym of *P. roscida* because of the description of Zaitzev (1930), but he conceded that the geographic distance between the Caucasus and Transbaikalia caused a problem.

Diagnosis. Upper side bronze, bluish, or purplish, flat-lustrous, habitus similar to *P. sericea*, antennomeres reddish basally and darkened apically, pronotum with flattened anterior tubercles, femora reddish on basal half and dark on apical half. Aedeagus with a conspicuous elongated peak.

Description. Size: 6.7–9.7 mm.

Colour: Bronze or dark with bluish or purplish lustre.

Antennae: Slender, annulated, antennomeres basally rufous, apical dark or metallic, $A_2 < A_3 < A_4$.

Pronotum: Almost quadratic or slightly longer than wide, anterior tubercles flattened, disc coarsely and closely punctate with fine wrinkles, median groove narrow or indistinct, in posterior part short and slightly deeper, then forked into two horizontal grooves near the bottom line.

Elytra: Oblong, with shallow impressions, coarsely and densely rugose on most of surface, punctures regular, strong, and deep, interstices wrinkled, interstices ~ 2–4× puncture diameter.

Legs: In most specimens the femora are reddish on basal half and dark metallic on apical half, tibia reddish with dark parts, tarsomeres dark or with reddish basal part. Some specimens with entirely reddish legs. Metafemora with prominent, thorn-shaped tooth in most specimens.

Pygidium of females with an apical notch, males broadly emarginate.

Aedeagus: Median lobe with a conspicuous elongated peak, cap of tegmen with a deep apical notch (Fig. 9).

Two similar species are *Plateumaris sericea* and *P. shirahatai* which differ: in *P. roscida* the pronotum and its tubercles are flattened, legs with large reddish parts, and the aedeagus has a conspicuous elongated peak.

Biology. Bierńkowski 2014 mentions: *Carex* sp. (Cyperaceae) as host plants. The larva has not yet been described.

Distribution. East Palaearctic: East of Lake Baikal to Far East, the Sakha (Yakutia) Republic, Amur region in Russia and north-east China (Harbin, Heilongjiang). Records exist for Asia: northern China (Heilongjiang, Inner Mongolia) [new in PalCat], Russia (East Siberia, Far East).

New country records additional to Silfverberg (2010). CHINA – Heilongjiang • 1 ex.; Harbin; 3 Jul 1952; E. Geiser 2021 det.; BM1953-715, (BMNH). • 2 ex.; Xinkai (Khanka) Lake, Bathing beach area; 45°21'52"N, 132°18'55"E; 11 Jun 2018; among strandline detritus; R.B. Angus, F.L. Jia, Z.L. Liang leg., E. Geiser 2021 det.; BMNH.

CHINA: Heilongjiang and Inner Mongolia: Askevold (1991).

Material examined. More than 30 specimens from different localities throughout the distribution area.

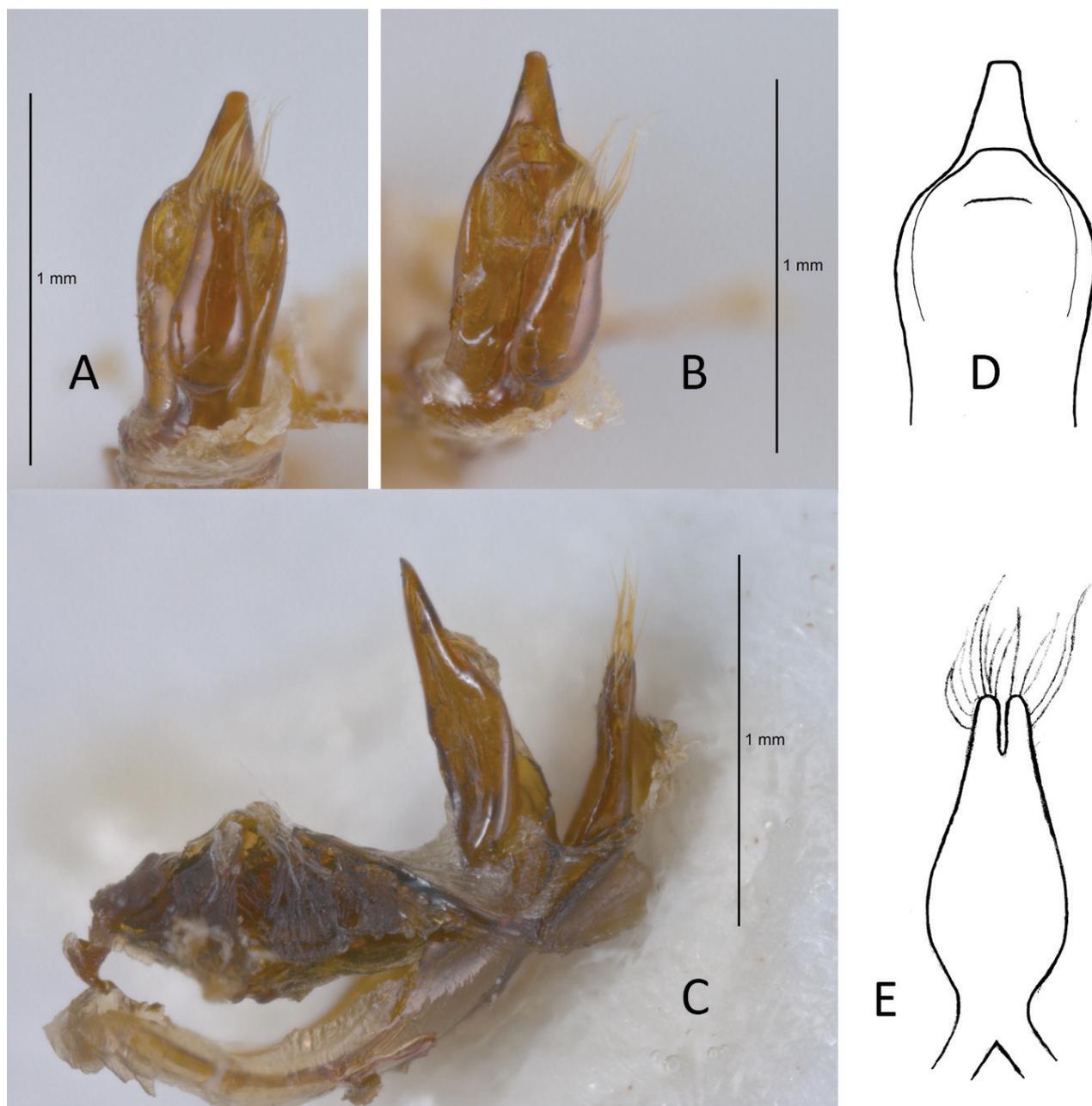


Figure 9. *Plateumaris roscida* aedeagus, photographed from different angles and drawings in frontal view **A, B** specimen from Primorsky Krai (ZMS) **C** specimen from Amur Oblast (NHMB) **D** median lobe **E** cap of tegmen (**A–C** photographs by E. Geiser, **D, E** drawings by G. Geiser). Scale bars: 1 mm.

***Plateumaris rustica* (Kunze, 1818)**

Fig. 10

Donacia rustica Kunze, 1818: 31.

Donacia abdominalis Bedel, 1891: 218 [nomen nudum].

Donacia affinis Kunze, 1818: 37.

Plateumaris rustica ab. *forojulensis* Gortani, 1906: 20 [infrasubspecific name].

Donacia fusca Zschach, 1788: 27 [nomen oblitum].

Donacia pallipes Kunze, 1818: 35.

Plateumaris rustica var. *picipes* Weise, 1898: 180.

Donacia planicollis Kunze, 1818: 34.
Donacia rustica Schüppel, 1818: 31 [nomen nudum].
Plateumaris sulcifrons Weise, 1900: 267 [syn. nov.].

Type locality. Germany, surroundings of Berlin [Kunze, 1818: 31: “in der Gegend von Berlin”].

Type material. Type specimens missing.

Taxonomic history and synonymies. Kunze (1818) described four new *Donacia* species (see original text and translation in Geiser and Geiser 2023) which in fact belong to one single *Plateumaris* species (Askevold 1991 in part). The name *Donacia rustica* was described first in this publication, so *planicollis*, *pallipes*, and *affinis* are now synonyms.

Some authors, like Jolivet (1970) and Borowiec (1984), cited the authority of *P. rustica* as Schüppel (1818, in Kunze 1818) but this is inaccurate since Kunze (1818) wrote after the description: “*D. rustica* Schüppel in litt.” Therefore, the suggestion is there that the name is derived from J. Schüppel (Berlin), but Kunze actually described this species and published it. The unambiguous authority of *P. rustica* is Kunze; therefore, *D. rustica* (Schüppel, 1818) is a nomen nudum. Note that there is no publication of “Schüppel (1818)”.

The names *P. abdominalis* Bedel, 1891 and *P. (Donacia) abdominalis* Olivier, 1795 [1800 is correct, see above for *P. braccata*] were erroneously attributed to *P. rustica*. The name *P. abdominalis* is frequently mentioned as a synonym for *P. rustica* or *P. affinis* as occurs in the key by Jacobson (1892): “*abdominalis* Oliv.” with *P. affinis* as its synonym. Clavareau (1913) defined “*abdominalis* Bedel” as synonymous with *P. affinis* and this was followed by Reitter (1920), Winkler (1930), Goecke (1960), and Jolivet (1970); the latter also mentioned “*abdominalis* Olivier” as synonymous with *P. braccata*, but Olivier did not describe it [see above for *P. braccata*]. Also, Bedel (1891) did not describe *P. abdominalis*; in his list of the Coleoptera of the Seine basin he mentioned *P. abdominalis* Olivier, together with the synonyms *affinis* Kunze, 1818 and [sic!] *fusca* Zschach, 1788 (synonymous with *P. braccata*). Therefore, *P. abdominalis* Bedel is a nomen nudum, a misidentification or misinterpretation by Bedel, but not a synonym of *P. affinis*.

Donacia affinis was also described in Kunze (1818) (see Geiser and Geiser 2023). Goecke (1943) suggested that *P. affinis* should be considered synonymous with *P. rustica*. Askevold (1991: 37) synonymised it after examination of ~ 250 specimens from various locations in Europe. These beetles are typically separated in keys by the colour of the antennae, legs, and ventral side, and by the metafemoral tooth size, but these are highly variable characters among many Donaciinae (pers. obs.). In fact, the aedeagi of these two “species” are indistinguishable.

Plateumaris forojulensis was described by Gortani (1906) as aberration.

Donacia fusca was regarded as synonymous with *P. affinis*, but it is a nomen oblitum (Jolivet 1970).

Plateumaris pallipes was assigned as a synonym of *P. affinis* and *P. planicollis* as a synonym of *P. rustica*. As the original descriptions of Kunze (1818) show, all characters are within the variation range of the typical characters of *P. rustica* (Geiser and Geiser 2023).

Plateumaris picipes was described by Weise (1898) as a variation (Geiser and Geiser 2023). It refers to specimens with at least very dark femora up to very dark legs. Albeit the basal joints of the femora are always reddish.

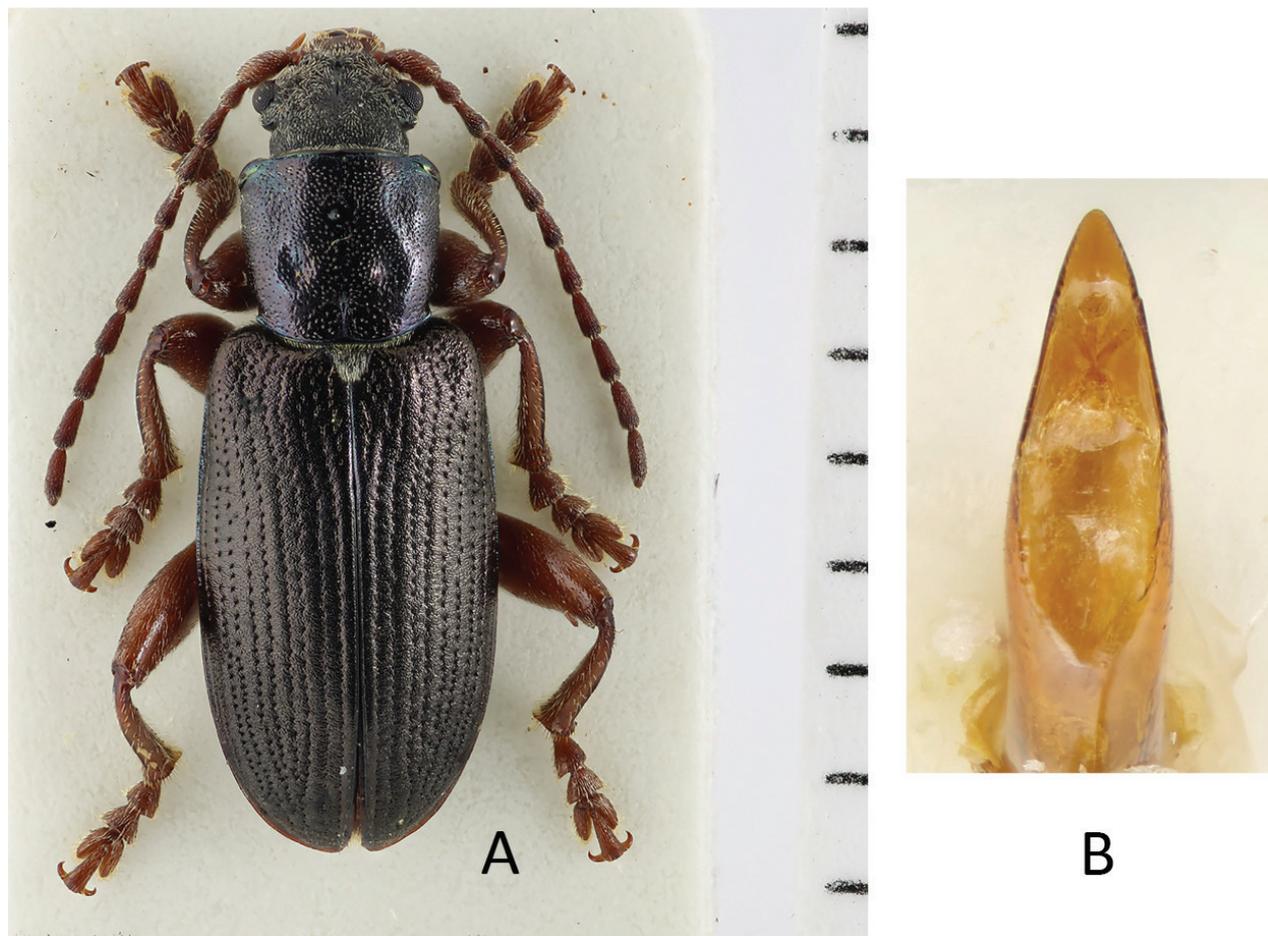


Figure 10. *Plateumaris rustica* A habitus B median lobe (photographs by K. Matsumoto). Scale bar: one unit – 1 mm.

Diagnosis. Upper side mostly metallic, antennae and legs entirely or partly reddish brown. It has a very smooth and the most flattened pronotum of all Palaearctic *Plateumaris* species (Fig. 10A).

Description. Size: 6.5–9.0 mm.

Colour: Upper side bronze or black with greenish, bluish, or purplish metallic lustre, colour of pronotum and elytra mostly the same but can also differ significantly. Antennae and legs entirely or partly reddish brown.

Head: Frons with deep or shallow groove, longitudinal calli distinctive or flattened.

Antennae: Filiform, each antennomere yellow or reddish at the basis, darkened at the apex, extent of darkened zone very variable, 2nd antennomere 2–3× smaller than other antennomeres which are approximately equal in length, only the 3rd antennomere is sometimes slightly smaller than the others: $(2-3) \times A_2 = A_1 = A_4 \dots A_{11}$; $A_3 \leq A_4$.

Pronotum: Almost quadratic, only at the basis slightly constricted, with flat disc and indistinct anterior tubercles; surface shiny or alutaceous, disc smooth with small shallow dots, more or less densely dotted, median line varies from imperceptible to distinctive.

Elytra: Punctures very delicate, interstices with slight transversal rugae, interstices 2–4× puncture diameter. Ratio of elytral length to width: 1.7–2.0.

Legs: Yellow reddish, sometimes partly or almost entirely darkened, piceous, but always with reddish joints (var. *picipes* Weise, 1898). Femora basally broad, metafemoral tooth very variable, mostly prominent, in some (mostly female)

specimens very small or imperceptible. There is no geographic correlation concerning the size of the tooth.

Aedeagus: Median lobe distinctly elongated, apex acute (Fig. 10B).

There are two similar species. *Plateumaris consimilis* has the pronotum distinctly cordate and the disc is not flattened. The pronotum of *P. weisei* is trapeziform and slightly longer than wide. In the territories where their distribution areas are overlapping (European part of Russia) it can be distinguished from *P. weisei* by the quadratic shape of the pronotum.

Also, the aedeagi of these species are clearly different (compare Fig. 10B with Fig. 17B, C, E).

Biology. The larvae are oligophagous on *Carex* sp. and other Cyperaceae. Adults feed on leaves and stems, not on pollen (Rheinheimer and Hassler 2018). For identification of the larvae see Steinhausen (1994) and Bieńkowski and Orlova-Bieńkowskaja (2004). Although *P. rustica* is widespread in the West Palaearctic region and there are many of its food plants available, it is rather rare suggesting that it needs not only wetland with Cyperaceae but also additional ecological conditions.

Distribution. West Palaearctic region: throughout Europe, further in Algeria, Turkey, Iran, and west Siberia. Records exist for Europe: Austria, Belarus, Belgium, Bosnia-Herzegovina [new in PalCat], Bulgaria, Croatia, Czech Republic, Denmark, Estonia, Finland, France, Germany, Great Britain, Hungary, Ireland, Italy, Crimea [new in PalCat], Latvia, Liechtenstein, Lithuania, Luxembourg, Montenegro [first record], The Netherlands, Norway, Poland, Romania, Russia: northern, central, and southern parts [new in PalCat] of European Russia), Serbia [new in PalCat], Slovakia, Slovenia, Spain, Sweden, Switzerland, Ukraine.

North Africa: Algeria.

Asia: Iran [first record], Russia (west Siberia), Turkey [new in PalCat].

New country records additional to Silfverberg (2010). BOSNIA-HERZEGOVINA: Mohr (1966b).

CRIMEA: Listed in Catalogue: Beetles of the Krym (pers. comm. S. Mosiakin 2019).

MONTENEGRO • 11 ex.; Poljane north-west of Podgorica “PoJane”; *P. rustica* E. Geiser 2019 det.; NHMB [ex coll. Breit in coll. Frey]. Remark: Some specimens were previously identified as *P. forojulensis* (1 ex.) and *P. picipes* (4 ex.).

RUSSIA • 1 ex.; Southern European territory, town Samara Nikolayevsky Uyezd; May 1916; Bostanzhoglo leg.; Zoological Museum of Moscow State University, Russia. Remark: private record by Bieńkowski 2016.

SERBIA: Gavrilović and Ćurčić (2011), Mohr (1966b).

IRAN • 1 ex.; “Persien, Elbrus Gebirge” [Elbrus mountains]; *Donacia affinis* H. Goecke det., *Donacia rustica* E. Geiser 2019 det.; NHMB [ex coll. Reitter in coll. Frey].

TURKEY • 25 ex.; Bolu Province, Abant Dağı [mountain], Abant Gölü [lake]; 1298 m a.s.l.; 31 May 1999; J. Voříšek and J. Kodada leg.; *P. rustica* E. Geiser 2021 det.; BMNH [ex coll. J. Voříšek]. Bolu province and Kahramanmaraş province (Ekiz et al. 2020). Remarks: *Plateumaris rustica* was unknown from Turkey. There was no record in the “Checklist of leaf beetles of Turkey” (Ekiz et al. 2013). In 2019 I identified 12 specimens from Bolu province stored in Verona (MSNV) and their detailed data are published in Ekiz et al. (2020), including the type location of *P. sulcifrons* in Kahramanmaraş province. In 2021 I found 25 specimens in the coll. Voříšek which is now stored in BMNH. These specimens

were labelled as "*P. sulcifrons* Weise J. Voříšek det." but are now relabelled as *P. rustica*. Also, the aedeagi of these "*P. sulcifrons*" were identical with the aedeagus of *P. rustica*.

Material studied. More than 200 specimens throughout the West Palaearctic region.

***Plateumaris sulcifrons* Weise, 1900, syn. nov.**

Type locality. TURKEY, Kahramanmaraş province: Süleymanlı "Zeytun" [old name].

Type material. Holotype: TURKEY • 1 ♀; Kahramanmaraş province, Süleymanlı "Zeytun" [old name]; 37°53'N, 36°50'E; O. Staudinger leg. Probably collected in 1872 (see below for details). Depository unknown.

Remarks. Askevold (1991) declared *P. sulcifrons* as a "probable new synonymy" for *P. rustica*. The holotype (♀) is missing but the analysis of the elaborate original description (see Geiser and Geiser 2023) indicates that the characters of *P. sulcifrons* are within the variation range of *P. rustica* characters (Table 4). Weise indicates a range of [body] length: 8–9 mm and colour variation in the antennae and legs. This suggests that he had examined more than one (female) specimen. Since 1900 the name *P. sulcifrons* is mentioned in almost all catalogues and identification keys for the (West) Palaearctic, but no new records were published.

Besides, there was a confusion about the locus typicus. Weise (1900) published only: "Zeitun (Staudinger)". This sparse note of the collection site led to misinterpretations: "Zeitun" is correctly assigned to Asia Minor (Reitter 1920; Winkler 1930), but it was misinterpreted by Goecke (1960) as "Zejtun", a town in the east of Malta. Henceforward it was mentioned as a species from Malta (Jolivet 1970; Borowiec 1984; Askevold 1991; Silfverberg 2010; Warchałowski 2010). This location error confirmed the opinion that *P. sulcifrons* is probably endemic to Malta, therefore missing further records were less suspect.

Otto Staudinger (1830–1900) was a German entomologist who went on numerous collecting trips or promoted them, but insects were not collected in Malta, neither on his own journeys nor on his commissioned trips. In 1872 he visited the Cilician Taurus (Anonymous 1901; Wikipedia [05.10.2022]). Therefore, "Zeitun" mentioned in Weise (1900) is actually "Zeytun" district (now Süleymanlı) of today's Kahramanmaraş province of Turkey (Ekiz et al. 2020). Different spellings and change of geographical names also did not help to clarify this case.

Unfortunately, the first description does not indicate where these specimens are stored. It is unlikely that Weise returned the type(s) to Staudinger, who was then working on his Lepidoptera Catalogues in his last years. Weise's private collection and especially the Chrysomelidae part are stored in the Museum für Naturkunde in Berlin (ZMHB), but no *Plateumaris* specimen labelled "*sulfifrons*" could be found there, despite the search by J. Frisch in 2019. I screened the *Plateumaris* collection in 2023 but found no specimen that could be considered the type.

Like other species, where only the type specimen is known, *P. sulcifrons* was suspected to be a synonym of a well-known species. Weise wrote that it is similar to *P. rustica* and *P. affinis*. Askevold (1991) synonymised *P. affinis* with *P. rustica*. He noticed that the characters Weise mentioned are typical for *P. rustica* and suggested that *P. sulcifrons* may be conspecific. Warchałowski (2003) treated *P. sulcifrons* also as synonym to *P. rustica* in his key of the Chrysomelidae of

the Europe and the Mediterranean area. However, he treated it as valid species, although doubtful, in his key of the Chrysomelidae of the Palaearctic region (Warchałowski 2010). In Silfverberg (2010) it was listed as valid species from Malta. The locus typicus was corrected to Turkey in Löbl and Smetana (2013).

Unfortunately, I could not examine the type specimen. To confirm the arguments of Askevold (1991) with more details, the characters mentioned by Weise (1900) are compared with the characters of *P. rustica* in Table 4.

Table 4. Comparison of the characters of *Plateumaris sulcifrons* (as described by Weise 1900) and the corresponding characters of *P. rustica* (by EG).

Characters of <i>P. sulcifrons</i>	Characters of <i>P. rustica</i> with comments
Length: 8–9 mm	Length of <i>P. rustica</i> : 6.5–9.0
Description based on female specimens	Females are usually larger than males in <i>Plateumaris</i> species, therefore 8–9 mm matches very well
Slightly convex	Same as <i>P. rustica</i>
Upper side bronze-coloured, below jet-black, silky grey	The same colours occur in some specimens of <i>P. rustica</i>
Antennae, tibiae and tarsomeres dark reddish	Same as <i>P. rustica</i>
Frons with a wide and deep groove	In <i>P. rustica</i> frons with deep or shallow groove, narrow or broad, longitudinal calli of every side of the groove distinctive or flattened
Prothorax square, very finely pubescent, very slightly constricted before the base, disc almost flat, shiny, rather densely punctured, middle groove anterior and posterior deepened impressed, the tubercles on both sides almost imperceptible, slightly smooth	These are typical characters of a pronotum of <i>P. rustica</i> , the median groove varies from imperceptible to distinctive
Elytra with dotted stripes, interstices narrow	Same as <i>P. rustica</i>
Femora unarmed	Tooth of metafemur mostly prominent, in some female [sic!] specimens very small or imperceptible
Similar to <i>P. rustica</i> and <i>P. affinis</i> but more elongated	Without type specimens it is impossible to estimate what means “more elongated” as the ratio length to width varies in specimens of <i>P. rustica</i>

The characters which should distinguish *P. sulcifrons* from *P. rustica* are either the same or within the variation range of *P. rustica*. Therefore *P. sulcifrons* is a synonym of *P. rustica*. This was also mentioned in Ekiz et al. (2020) and in Geiser and Bezděk (in press), but without the reason provided here.

***Plateumaris sericea* (Linnaeus, 1758)**

Figs 11, 12

Leptura sericea Linnaeus, 1758: 397.

Donacia aenea Olivier, 1791: 292.

Donacia armata Paykull, 1799: 194.

Donacia asiatica Faldermann, 1837: 322.

Donacia sericea var. *atropurpurea* Westhoff, 1882: 256.

Plateumaris caucasica Zaitzev, 1930: 111 [syn. nov.].

Plateumaris discolor discolor f. *coelicolor* Bechyné, 1945: 89 [infrasubspecific name].

Donacia comari Suffrian, 1846: 84.

Plateumaris discolor discolor f. *cupraria* Bechyné, 1945: 89 [infrasubspecific name].

- Donacia discolor* Panzer, 1795: 216.
Donacia festucae Fabricius, 1792: 116.
Donacia geniculata C. G. Thomson, 1866: 123.
Plateumaris imitatrix Apfelbeck [nomen nudum].
Plateumaris intermedia Apfelbeck, 1912: 239.
Plateumaris discolor kratochvili f. *isocoelicolor* Bechyné, 1945: 89 [infrasubspecific name].
Plateumaris discolor kratochvili f. *isocupraria* Bechyné, 1945: 89 [infrasubspecific name].
Plateumaris discolor kratochvili f. *isolacordairei* Bechyné, 1945: 89 [infrasubspecific name].
Plateumaris discolor kratochvili f. *isopurpuricena* Bechyné, 1945: 89 [infrasubspecific name].
Plateumaris discolor kratochvili f. *isoviolacea* Bechyné, 1945: 89 [infrasubspecific name].
Plateumaris discolor kratochvili Bechyné, 1945: 89.
Donacia lacordairii Perris, 1864: 300.
Donacia laevicollis C. G. Thomson, 1866: 125.
Plateumaris sericea ab. *levigata* Csiki, 1953: 120 [infrasubspecific name].
Donacia sericea var. *luctuosa* Westhoff, 1882: 256.
Donacia micans Panzer, 1795: 9.
Plateumaris discolor var. *nigrita* Schilsky, 1908: 603.
Plateumaris nipponensis Nakane, 1963: 18.
Donacia nymphaeae Fabricius, 1792: 116.
? *Plateumaris obsoleta* Jacobson, 1894: 243.
Donacia palustris Schilling, 1838: 99 [homonym].
Donacia proteus Kunze, 1818: 23.
Plateumaris discolor discolor f. *pseudoviolacea* Bechyné, 1945: 89 [infrasubspecific name].
Plateumaris discolor discolor f. *purpuricena* Bechyné, 1945: 89 [infrasubspecific name].
Donacia sibirica Solsky, 1871: 245.
Plateumaris socia S.-H. Chen, 1941: 9.
Plateumaris slovacica Balthasar [nomen nudum].
Plateumaris discolor ab. *tatrica* Balthasar, 1934: 130 [infrasubspecific name].
Donacia sericea var. *tenebricosa* Westhoff, 1882: 256.
Donacia violacea Hoppe, 1795: 44 [homonym].
Plateumaris sericea ab. *viridis* Csiki, 1953: 120 [infrasubspecific name].

Type locality and type material. Because Linnaeus described *sericea* (*Leptura*) in 1758 no type specimen was designated. He stated that it “occurs in Europe” which is correct.

Remarks. *Plateumaris sericea* exhibits the highest variability in colour among Donaciinae. The upper side colour is metallic and can be green, golden green, blue, purple, red, violet, bronze, black and all shades in between. This is one of the causes so many “variations” were described which were often used like subspecies names. Additionally, throughout the whole distribution area, some specimens show a reddish base at the antennomeres. Also, few specimens exist with a reddish part near the joints of the femora, tibiae or tarsomeres. In

(most) identification keys *P. sericea* is characterised by “antennae and legs entirely metallic”, which is usually correct. Only in recent keys it is mentioned that there can also be reddish parts at some joints. Therefore, these “not entirely metallic” specimens supported the idea that specimens with a reddish spot belong to a different species or at least subspecies. I examined many specimens from the whole distribution area and determined their morphologic characters inclusive of the aedeagus shape are within the variety range of *P. sericea*.

In large European collections, where Asian specimens are stored, many of these Asian specimens show a red base of their antennomeres. Perhaps, these specimens were preferentially collected and stored whereas “entirely metallic” specimens were considered as common and not worth keeping.

Taxonomic history and synonymies. The correct data of the first description is *Leptura sericea* (Linnaeus, 1758): 397, and not “Linnaeus, 1760: 196” as it was printed in Silfverberg (2010: 358). See explanation in section “Genus *Plateumaris* C. G. Thomson, 1859, Taxonomic history and synonymies” and in Geiser and Geiser (2023).

The genus name *Donacia* was erected later in 1775 by Fabricius. There he described *Donacia crassipes* and *Donacia simplex* and assigned *Leptura aquatica* L., 1758 to the genus *Donacia*, but, significantly, he did not change the genus name of *Leptura sericea*.

Plateumaris asiatica was described as *Donacia asiatica* by Faldermann (1837) from “Persien” (today’s Iran) and never found again. It was synonymised with *P. sericea* by Kolossow (1929).

Plateumaris caucasica Zaitzev, 1930: syn. nov., see below.

Plateumaris discolor kratochvili f. *coelicolor* was described by Bechyně (1945) based on a series of specimens he collected from Přebyslav (central Bohemia). Therefore, *coelicolor* is a published but infrasubspecific name.

Plateumaris discolor discolor f. *cupraria* was described by Bechyně (1945) in contrast to *P. discolor kratochvili* f. *isocupraria* (see below) but both are infrasubspecific names.

Plateumaris discolor (Panzer, 1795): confirmed synonym, see below.

Plateumaris imitatrix: This name with the author “Apfelbeck” can be found on several museum specimens from Bosnia-Herzegovina (HNHM, coll. Frey in NHMB, SDEI), but a description was never published, therefore *P. imitatrix* is a nomen nudum. Viktor Apfelbeck (1859–1934) was a former curator of entomology at the National Museum of Bosnia and Herzegovina, Sarajevo. He labelled several specimens from the Balkans with new names which he regarded as new species. Some of them he described later, some of them not. Nevertheless, some of these specimens were also stored in other museums and can be found nowadays. Goecke (1942a) examined one specimen stored in those days in “Deutsches Entomologisches Institut” in Berlin-Dahlem (now SDEI) and identified it as *P. sericea* unambiguously. I examined three specimens of “*P. imitatrix*” in HNHM and one in NHMB which are also clearly *P. sericea*. Presumably, the reddish base of the antennomeres tempted Apfelbeck to regard it as a new species.

Plateumaris intermedia was described by Apfelbeck (1912) on page 239 and not on page 238 in Latin and Serbian (Geiser and Geiser 2023). It was synonymised with *P. sericea* by Goecke (1942b) who examined a specimen labelled “cotype” from Livanskopolje near Livno (Bosnia) stored in those days in “Deutsches Entomologisches Institut” in Berlin-Dahlem (now SDEI).

Plateumaris discolor kratochvili was described by Bechyné (1945) as a new subspecies in contrast to *P. discolor discolor*. Both subspecies live in the same habitat. Therefore, they could not be subspecies by definition. The characters to distinguish these two “subspecies” are completely within the variation range of *P. sericea*. I examined a specimen from Drholec (southern Moravia Czech Republic) leg. et det. Bechyné as *P. discolor kratochvili* Bechyné, 1945, ex coll. Roubal (SNMC) which is unambiguously *P. sericea*.

Plateumaris discolor kratochvili forma *isocoelicolor*, also the forma *isocupraria*, forma *isolacordairei*, forma *isopurpuricena*, and forma *isoviolacea* were described by Bechyné (1945) based on a series of specimens from Přebyslav (central Bohemia) collected by Bechyné. All these form names are infrasubspecific.

Perris (1864) described *Donacia lacordairii* based on a specimen from Spain (Geiser and Geiser 2023). He allocated it to the same group (“dans la même division”) as *Donacia sericea*. It was later regarded as an aberration of *P. discolor* (Winkler 1930; Balthasar 1934) or as a variation or subspecies *P. discolor lacordairii* (Silfverberg 2010). Askevold (1991) examined the endophallus of specimens from Spain which are assignable to *P. lacordairii*. He found it typical for *P. sericea* from other regions and therefore synonymised it with this species. I examined 31 specimens from BMNH and I agree.

Plateumaris levigata was described by Csiki in 1953 as an aberration of *P. sericea*.

He wrote: “*Plateumaris sericea* ab[erratio]. *levigata*[sic!] nom[en]. nov[um]. pro *violacea* Gyll. (nec Pall., nec Hoppe)”. *Plateumaris “levigata”* is not a spelling error although “*laevigata*” is more common, but both spellings were used in classical Latin for the word “smoothed”, so “*levigata*” is correct. Anyway, this is an infrasubspecific name.

Plateumaris micans was described as *Donacia micans* by Panzer in 1795 and not in 1796 according to Alonso-Zarazaga and Evenhuis (2017).

Plateumaris nipponensis was described by Nakane (1963) from Kamikochi, Nagano (Japan). He assigned it closely to *P. sericea* but listed several relative characters (“more shining”, “relatively shorter”) which fit easily in the variability of *P. sericea*. It is regarded as subspecies in Warchałowski (2010) and as a synonym in Hayashi (2020) to *P. sericea*.

Plateumaris nymphaeae: Fabricius (1792) spelled *Donacia nymphaeae* in his original description, but this original spelling was an inadvertent error. According to ICZN 1999 (Art. 32.5.1) it has to be spelled *nymphaeae* as it was applied in Silfverberg (2010).

Plateumaris obsoleta Jacobson, 1894: questionable synonym, see below in *P. shirahatai*.

Plateumaris palustris was described as *Donacia palustris* by Schilling in 1838 on page 99 and not in 1837 on page 104. It is a homonym because Herbst (1784) described a *Donacia palustris* which is now synonymous with *P. braccata*.

Plateumaris discolor kratochvili forma *pseudoviolacea* and forma *purpuricena* were described by Bechyné (1945) based on a series of specimens from Přebyslav (central Bohemia) collected by Bechyné. All these form names are infrasubspecific.

Plateumaris sibirica (Solsky, 1871), confirmed synonym, see below.

Plateumaris socia was described by Chen (1941) based on three specimens from Chekiang (Zhejiang). In Silfverberg (2010) it is stated as a synonym to

P. sericea sibirica. Askevold (1991) considered it a probable new synonym and Hayashi (2020) a synonym of *P. sericea*. The description of Chen (1941) mentions only characters which are clearly within the variation range of *P. sericea*, to which this species “is very closely allied”. It is also interesting that Gressitt and Kimoto (1961) mentioned in their key of the Chinese species not *P. sericea* (which occurs in China) but *P. socia*, separated from the other Chinese *Plateumaris* species by typical characters of *P. sericea*.

Plateumaris sericea slovacica Balthasar: In the coll. generalis in SNMC two specimens are stored which are labelled “Čeklís, Slovensko, *Plateumaris sericea slovacica* det. V. Balthasar, Typus n[ova]. ssp.” which I identified as *P. sericea*. I assume that Vladimir Balthasar (1897–1978), who described other species and subspecies of *Plateumaris* (Balthasar 1934) intended to describe these specimens as a new subspecies but never did. Therefore, *P. sericea slovacica* is a nomen nudum.

Plateumaris discolor ab. *tatrica* was described by Balthasar (1934) based on one or several specimens (the number is unclear) characterised by a dark purple pronotum and dark violet-blue elytra, collected by Al. Procházka, from Štrbské pleso, High Tatras, Slovakia. Anyway, this is an infrasubspecific name.

Plateumaris violacea was described by Hoppe (1795) as *Donacia violacea*, but this is a homonym to *Plateumaris violacea* (Pallas, 1773), originally described as *Leptura violacea*, which is synonym with *P. braccata*.

Csiki described 1953 “*Plateumaris sericea* ab[erratio]. *viridis* nom[en]. nov[um]. pro *micans* Panz. (nec Hoppe)”, but that does not matter because this is an infrasubspecific name.

General remarks on the morphology and distribution of *Plateumaris sericea*. *Plateumaris sericea* has the largest distribution area of all *Plateumaris* species. It is no surprise that it is also genetically very variable (Hendrich et al. 2015), which is shown also in the variability of the morphological characters. Additionally, to the colour variations mentioned above, *P. sericea* also varies in the shape and microstructure of the pronotum. While many Donaciinae species can be characterised by a typical shape of the tooth on the metafemur, *P. sericea* can show no tooth at all, or a very prominent sharp tooth and all shapes in between. Even the aedeagus varies in shape.

Diagnosis. Legs and antennae usually entirely metallic, some specimens with reddish parts near the joints; pygidium of females rounded, in some specimens slightly emarginate, that of males emarginate; apex of median ejaculatory guide rounded.

Description. Size: 6.5–10.5 mm.

Colour: *Plateumaris sericea* shows the greatest colour variety among all Donaciinae species: The whole beetle can be bronze, green, blue, black, cupreous, purple, red, yellow, and all shades in between. Antennae and legs are mostly completely metallic, but there are some specimens with red base of the antennomeres and even with red parts of the legs, usually at the tibiae or tarsomeres.

Head: Same colour as pronotum, supraocular furrow indistinct; vertex with a median line, antennomeres always apically darkened, either completely dark metallic or the basal part reddish to varying degrees, A3 slightly longer than A2, A4 2× as long as A2 in most specimens. $A3 \geq A2$, $A4 = 2 \times A2$.

Pronotum: Outline more or less quadrate, in some specimens longer than wide; anterolateral tubercles prominent but sometimes flattened, the disc varies from

alutaceous and impunctate to finely or coarsely punctate with deep transverse wrinkles, the median line can be clear and deep or only a very shallow furrow.

Elytra: Disc rugose, rows of punctures, shape, and apex typical like in other *Plateumaris* species.

Legs: Entirely metallic and same colour as upper side. Rarely, some specimens show reddish parts near the joints, mostly on the tibiae or tarsomeres, metafemora of most specimens with a prominent, blade-like tooth, but some specimens with an indistinct or without any tooth.

Pygidium: Emarginate in males, usually rounded but sometimes shallowly emarginate in females.

Aedeagus: Examples of its variability are shown in Fig. 11D, E.

There are no reliable external characters to distinguish *P. sericea* from *P. shirahatai*. The only reliable feature can be found at the endophallus. The apex of the median ejaculatory guide of the endophallus is notched in *P. shirahatai* (Fig. 12B) whereas it is rounded (Fig. 12A) in *P. sericea*. The habitus of *P. sericea* also looks very similar to *P. roscida*, but the latter always has large red parts on the legs and antennae, and their aedeagi are strikingly different (Figs 9, 11D, E).

Biology. *Plateumaris sericea* feeds on *Carex* sp., *Juncus* sp., *Eriophorum* sp., *Scirpus* sp. and related plant species. For details and identification of the larvae see Steinhausen (1994), Narita (2003) and Bieńkowski and Orlova-Bieńkowskaja

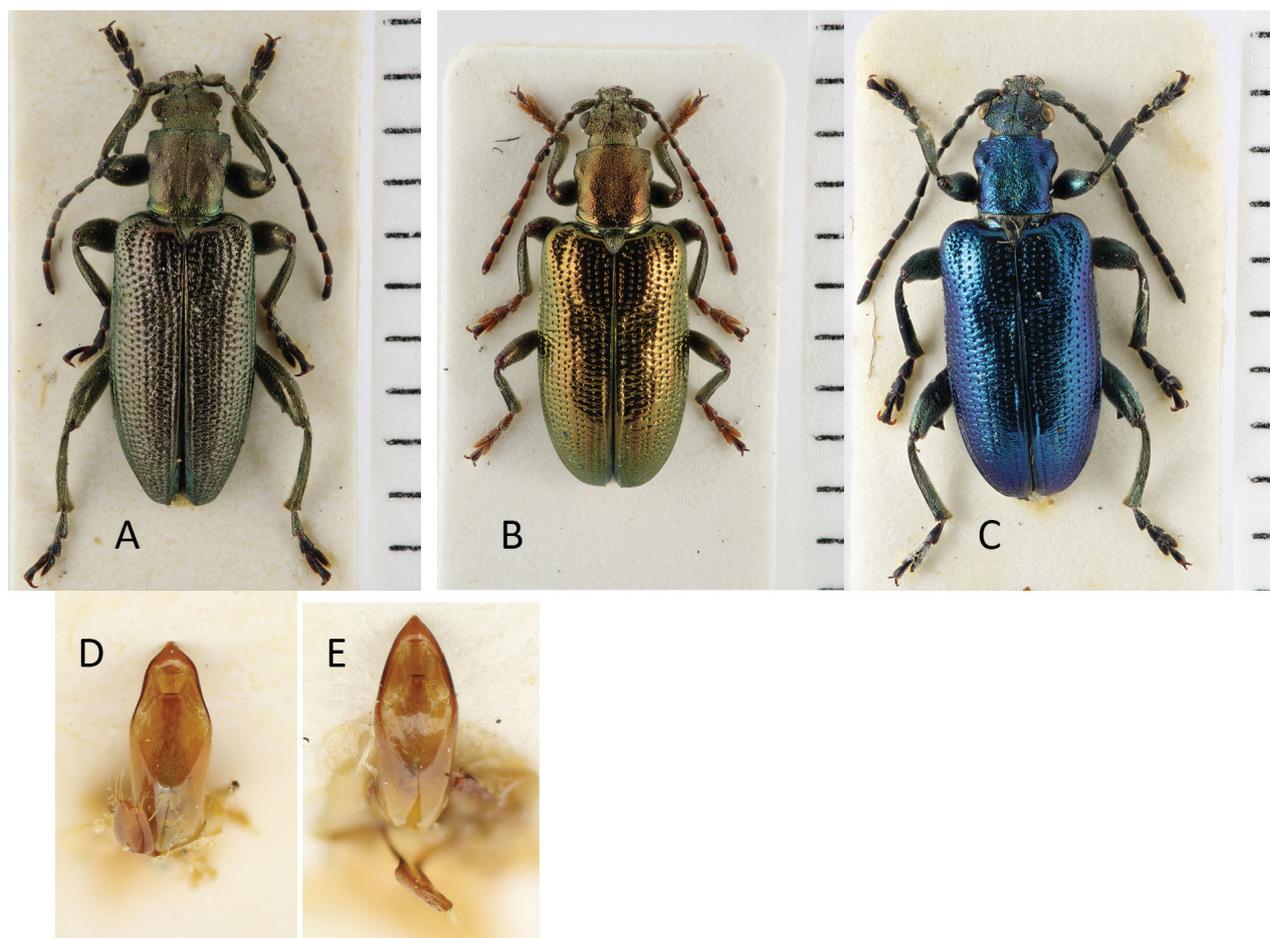


Figure 11. *Plateumaris sericea* A–C habitus illustrating variability in colours, but there are more D, E aedeagus: two examples of the variability of the shape of the median lobe (photographs by K. Matsumoto). Scale bars: one unit – 1 mm.

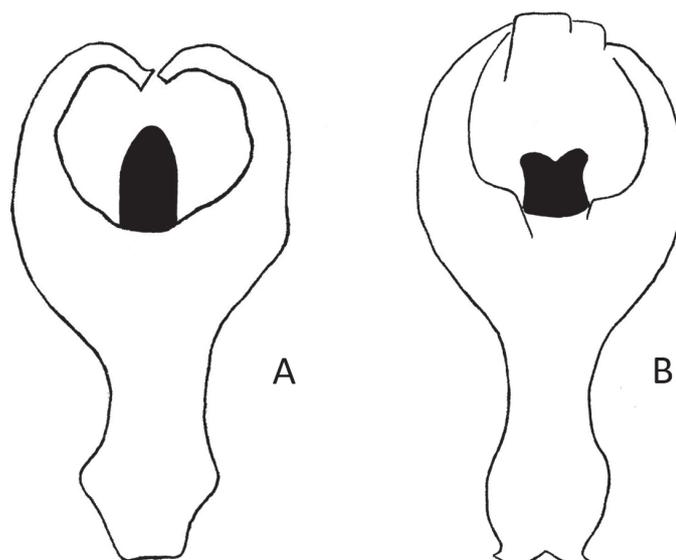


Figure 12. Schematic sketch of the endophallus. Median ejaculatory guide blackened **A** *Plateumaris sericea* (and specimens identified as *P. discolor*) with apex of median ejaculatory guide rounded. The endophalli of specimens from Poland, Italy and Japan all look the same as in this sketch **B** *Plateumaris shirahatai* with apex of median ejaculatory guide notched (drawings by G. Geiser based on photographs from Askevold 1991 and Hayashi 2020).

(2004). *Plateumaris sericea* is the most common *Plateumaris* species and can be found in many wetland habitats throughout the Palearctic region. It tolerates a broad range of ecological conditions if it is only wet enough.

Distribution. *Plateumaris sericea* has not only the largest distribution area of all *Plateumaris* species but also of all Donaciinae species. It occurs in the whole Palearctic region. Any lack of records in some parts of its area is most probably due to a lack of collection trips there. Records exist for Europe: Austria, Belgium, Bosnia-Herzegovina [new in PalCat], Belarus, Bulgaria, Croatia [first record], Czech Republic, Denmark, Estonia, Finland, France, Germany, Great Britain, Greece [first record], Hungary, Ireland, Italy, Latvia, Liechtenstein, Lithuania, Luxembourg, Crimea [first record], Montenegro [first records], The Netherlands, North Macedonia [first record], Norway, Poland, Romania, Russia (north, central, and south parts of European territory), Serbia [new in PalCat], Slovakia, Slovenia, Spain, Sweden, Switzerland, Turkey [new in PalCat], Ukraine.

North Africa: Algeria [new in PalCat].

Asia: Armenia, Azerbaijan, China (Beijing, Hebei, Zhejiang), Georgia, Iran, Japan, Kazakhstan, Mongolia, North Korea [new in PalCat], Russia (west, east, and south Siberia [new in PalCat], Far East), South Korea [new in PalCat], Turkey [new in PalCat].

New country records additional to Silfverberg (2010). BOSNIA-HERZEGOVINA: Mohr (1966b) and further new records:

BOSNIA • 1 ex.; Livno [north of Buško Jezero]; collected from *Cladium mariscus*; *Donacia imitatrix* Apfelbeck [V. Apfelbeck det.], *Plateumaris sericea* E. Geiser 2019 det.; HNHM • 2 ex.; Jezero near Jaice; on *Cladium mariscus*; *Donacia imitatrix* Apfelbeck [V. Apfelbeck det.], *Plateumaris sericea* E. Geiser 2019 det.; HNHM • 1 ♀; Jezero; 1902; Apfelbeck leg.; *Plateumaris intermedia* V. Apfelbeck det., *Plateumaris sericea* E. Geiser 2019 det.; NHMB [ex coll. L. Weber in coll. Frey] • 1 ex.; Alps [Dinaric Alps]; Tomov det., E. Geiser 2019 vid.; HNHM • 1 ex.; Vrelo Bosne [spring of the Bosna river, in Ilidža, west of Sarajevo];

Plateumaris discolor Apfelbeck [det.], *Plateumaris sericea* I.K. Lopatin det.; HNHM • 1 ex.; Sarajevo, Igman Planina [Igman mountain west of Sarajevo]; 9 May 1930; Dr. J. Fodor leg., J. Bezděk 2017 det.; HNHM.

CROATIA • 1 ex.; Pakrac [town in western Slavonia]; *Plateumaris discolor* ab. *lacordairii* Z. Kaszab det., *Plateumaris sericea* E. Geiser 2020 det., HNHM [ex coll. Apfelbeck] • 5 ex.; Plitvice [Plitvice Lakes National Park]; May 1970; [each with a different colour]; E. Geiser 2021 det.; ZFMK [coll. Prof. H. Bick].

CRIMEA • 1 ex.; Sebastopol; W. Pliginsky [leg.?]; *Plateumaris discolor* ab. *lacordairii* W. Balthasar [det.?], *Plateumaris sericea* E. Geiser 2020 det.; SMNC. Remark: Balthasar (1934) published a small key where he described *P. discolor* ab. *tatica* to distinguish it from *P. discolor* ab. *lacordairii*. This is most likely the specimen he examined for this key because it shows exactly the same characters that he mentioned there.

GREECE • 1 ex.; Thessalia, Pindos mountains, Dessi, Kalambaka, Pertouli, 1110 m; 23. May 2001; A. & F. Riedel leg.; E. Geiser 2023 det.; SMNS.

MONTENEGRO • 1 ex.; Crna Gora, Žabljak; 18. Jul 1934; Dr. J. Fodor leg.; J. Bezděk 2017 det.; HNHM • 7 ex.; Žabljak; 4 Jul. 1983; W. Grosser leg.; E. Geiser 2021 det.; BMNH [ex coll. Voříšek].

NORTH MAKEDONIA • 6 ex.; Delčevo; 3 Jun. 1982; I. Rozner leg.; J. Bezděk 2017 det.; HNHM.

SERBIA: Gavrilovic and Curcic (2011).

TURKEY: Many records from European and Asian territory in Ekiz et al. (2020).

ALGERIA: Goecke 1957b.

NORTH KOREA: Cho and An (2020).

SOUTH KOREA: Cho and An (2020).

RUSSIA (South Siberia): Gus'kova et al. (2018).

Material examined. More than 500 specimens from different localities, labelled as various species or subspecies throughout the distribution area.

***Plateumaris caucasica* Zaitzev, 1930, syn. nov.**

Type locality. RUSSIA: Stavropol and Dagestan.

Type material. Type series: RUSSIA • 4 ex; Ciscaucasia, Stavropol; Apr 1905; DM Maljuzhenko leg.; RUSSIA • 5 ex; Daghestan, Chasav-jurt; E. Koenig leg.

Remarks. According to Zaitzev (1930) these specimens were stored in the "Collection of the Georgian Museum". The currently depository is unknown.

Geiser (in press) and Geiser and Bezděk (in press) treated *P. caucasica* as a synonym of *P. sericea* "based on study of comparative material, descriptions, and of biogeographical research". Zaitzev (1930) described a new species *Plateumaris caucasica* (see Geiser and Geiser 2023) based on reddish parts of the antennomeres and legs. Additionally, he stated as different characters: "a more rugose pronotum (almost like *P. discolor*)" and "compared with *P. discolor* more slender antennae, the fourth antennomere which is twice as large as the second". Also, he stated, it is a "intermediate species between *sericea* L. and *discolor* Panz."

As I explained in "General remarks on synonyms of *Plateumaris sericea*" above, this is a typical example of establishing a new "species" on colour characters. The other mentioned "different" characters are completely within the variation range of *P. sericea* or characteristic of this species. The morphology of the aedeagus is

also completely within the variation range of *P. sericea*. In the same area also typical *P. sericea* (that is: with completely metallic antennae and legs) could be found, the colour variation form "*P. sericea caucasica*" could not even be a subspecies.

Zaitzev assumed that *Plateumaris caucasica* is also "very close" to *P. annularis*, because both have a red base at their antennomeres and legs which are partly reddish brown. To the credit of Zaitzev it is necessary to mention that he had doubts if *P. caucasica* is really a new species or a synonym to *P. annularis*. He suggested to treat it as a new species until further knowledge is available about the East Siberian *Plateumaris* species.

Plateumaris annularis was synonymised by Kolossow (1930) with *P. roscida* (see there for details). Askevold (1991) suggested that "*Donacia caucasica* (Zaitzev) (1930: 11)" [sic! it was described it as *Plateumaris* and not as *Donacia*] is a "possible new synonym" to *P. roscida*. He argued that both have the red base of the antennomeres and the description of Zaitzev agrees well with specimens of *P. roscida*, but he had doubts because *P. roscida* is known only from Asia east of lake Baikal whereas *P. caucasica* only occurs in the Caucasus region.

First, it is actually biogeographically implausible that these two species should be synonyms. Second, the pygidium is emarginate in *P. roscida* and not emarginate in *P. caucasica* in both sexes. Third, the aedeagi of *P. roscida* and *P. caucasica* are strikingly different. For the median lobe of *P. roscida* see Fig. 9. The median lobe of *P. caucasica* fits well into the variation range of *P. sericea* (Fig. 11D, E). Therefore *P. caucasica* is a synonym of *P. sericea*.

Bieńkowski (2014) stated in his identification key at *P. sericea*: The taxonomic status of the subspecies *caucasica* and *sibirica* needs further studies. This has been done here for *caucasica* and *sibirica* (see below).

Material examined. More than 30 specimens from the Caucasus region (north and south) labelled as "*P. caucasica*", "*P. sericea caucasica*" or "*P. roscida*" which were all clearly *P. sericea*.

***Plateumaris discolor* (Panzer, 1795)**

Type location. Germany.

Type material. The holotype is unknown.

Remarks. *Plateumaris discolor* was described by Panzer (1795) as *Donacia discolor* (Geiser and Geiser 2023), but the morphological variability of *P. discolor* is within the range of the variability of *P. sericea*. It was finally synonymised with *P. sericea* by Askevold (1991) by examination of the endophalli from *P. discolor* and *P. sericea* specimens which showed constant characters throughout their distribution area (Fig. 12a), but some authors continue to regard *P. discolor* as a species propria (Silfverberg 2010; Bieńkowski 2014; Rheinheimer and Hassler 2018); therefore, further arguments are discussed below.

Several characters are used to distinguish *P. discolor* from *P. sericea*. The first are the antennomeres: in *P. discolor* A3 and A4 are a little bit longer than A2, whereas in *P. sericea* A3 is 1.5× as long as A2 and A4 is twice as long as A2. In fact, the length of the antennomeres is very variable, therefore the difference between "a little bit" and "one and a half" is not clear.

The second is the pronotum disc: in *P. discolor* it is more punctured and transversely wrinkled whereas in *P. sericea* it is very finely sculptured. However,

the structure of the pronotum disc varies in both “species” in its sculpture and shows an intermediary form in many cases.

The third is the median lobe of the aedeagus, which is also very variable (Fig. 11D, E). This is shown also in the drawings and pictures in identification keys. Sometimes the aedeagus picture of *P. discolor* in one key looks most similar to the picture of the aedeagus of *P. sericea* in another key. When a drawing or photograph was made from different angles of view, the same aedeagus can look different in shape and contour. There exist specimens with “*discolor*” antennomeres and “*sericea*” pronotum and vice versa. Also, each shape of the aedeagus can occur with any combination of the antennomere or pronotum characters.

Due to these variations, there are no reliable morphological characters to distinguish *P. discolor* from *P. sericea*. Other evidence suggests that they may be separate species: *P. discolor* is reported to be assigned to acid soil and peat bogs where the larvae develop on *Carex*, *Juncus* and related plants, whereas *P. sericea* prefers various wetland habitats with alkaline soil (Rheinheimer and Hassler 2018). Their larvae feeds on *Sparganium* sp. and *Iris pseudacorus* (Bienkowsky, 2014). However, *P. sericea* has such a large distribution area and is very abundant even nowadays in contradiction to almost all other Donaciinae species, therefore, it is more likely that the food plant is also widespread and abundant. This is the case with *Carex* or *Juncus* but not with *Sparganium* and *Iris*. In the key to Donaciinae larvae in Japan Narita (2003) mentions *Carex dispalata* Boott. and *Scirpus fluviatilis* (Torr.) A. Gray as food plants for the larvae of *P. sericea*. This is definitely not a confusion with *P. discolor* because the latter does not occur in Japan. Therefore, the assignment to the food plants in Bienkowsky (2014) contradicts the study of Narita (2003) and is in general not a suitable argument that *P. discolor* is a separate species.

Molecular studies by Hendrich et al. (2015) and J. Bergsten (pers. comm. NHRS, 23 Jan 2023) indicate that *P. sericea* is genetically very variable. In molecular phylogenetic trees, specimens identified as *P. discolor* are resolved in between *P. sericea* specimens, sometimes in groups and separated from *P. sericea* groups, sometimes not. It is likely that some of these specimens identified as *P. sericea* are “some kind of” *P. discolor* and vice versa, because morphological characters are not reliable to distinguish them. There is another problem: it is possible that *P. sericea* consists of several cryptic species but *P. discolor* may not be one of them.

Material examined. More than 100 specimens labelled “*P. discolor*” from different localities in Europe.

***Plateumaris sibirica* (Solsky, 1871)**

Type locality. Russia, Irkutsk.

Type material. Solsky (1871) did not indicate the depository. It is unknown if the holotype still exists.

Remarks. *Plateumaris sibirica* was described as *Donacia sibirica* by Solsky (1871) as a new species from Irkutsk which resembles *P. sericea* (Geiser and Geiser 2023). It was not described as a “variation” as is sometimes cited in the literature. Jacoby (1885: 193) doubted it: “*Donacia sericea* var. *sibirica*? Solsky: The dozen specimens obtained at Nikko show scarcely any difference from our European form ... Structural differences I can see none.”

Eventually, the original description only mentions characters which are typical for *P. sericea*. It has been regarded as a synonym to *P. sericea* by Goecke (1960) and Hayashi (2020), but it is treated as a subspecies in Silfverberg (2010), in Warchałowski (2010), and in Bieńkowski (2014). The latter mentioned that “the taxonomic status of the subspecies *P. sericea sibirica* needs further studies”.

I examined more than 60 specimens identified as *P. sericea sibirica*, mainly from the BMNH, NHMB, NMPC and SDEI, and I agree with Jacoby, Goecke and Hayashi that all characters are clearly within the variation range of *P. sericea*. I could not find any differences compared with European or other Siberian specimens. Therefore, I confirm the decision of Goecke (1960) and Hayashi (2020) that *P. sibirica* is neither a valid species nor a subspecies, but synonym of *P. sericea*.

The original description was mostly cited as Solsky (1872). It was described in “*Horae Societatis Entomologicae Rossiae*” volume 8 comprising the years 1871 and 1872. There it was described in the part of 1871 according to Standfuss and Kerzhner (2004).

***Plateumaris shirahatai* Kimoto, 1971**

Fig. 13

Plateumaris shirahatai Kimoto, 1971: 1.

Plateumaris macropenis Nakane, 1999: 45.

? *Plateumaris obsoleta* Jacobson, 1894.

Type localities. *Plateumaris shirahatai*: Japan, Honshu, Yamagata Prefecture, Shizu, Gassan; *Plateumaris macropenis*: Japan, Honshu, Oze.

Type material. Holotype of *P. shirahatai*: JAPAN • 1♂, Yamagata Prefecture, Shizu, Gassan; 17 Jun 1960; K. Shirahata leg.; Entomological Laboratory, Faculty of Agriculture, Kyushu University, Fukuoka. The holotype was not examined.

Paratype. JAPAN • 3 ♀; same data as for the holotype; Japanese Insect Collection No. 21963, OMNH.

Holotype of *P. macropenis*. JAPAN • 1 ♀; Honshū, Oze; 15 Jul. 1950; H. Hasegawa leg.; *Plateumaris macropenis* T. Nakane det.; Laboratory of Systematic Entomology, Faculty of Agriculture, Hokkaido University, Sapporo, Japan.

Taxonomic history and synonymies. *Plateumaris macropenis* Nakane, 1999 was synonymized by Hayashi and Shiyake (2004) on page 117. The holotype of *P. macropenis* is a female specimen of *P. shirahatai*.

? *Plateumaris obsoleta* Jacobson, 1894: see below.

Diagnosis. Pronotal disc rugose, antennae, and legs entirely metallic, although in some specimens the basis of the antennomeres is reddish, A3 = 1.5–2× A2, tooth on metafemur sharp blade-like or obtuse, pygidium of females rounded, in some specimens slightly emarginate, pygidium of males emarginate or truncate, median process of endophallus notched.

Description. Size: Males 6.5–7.3 mm, females 7.8–8.2 mm.

Colour: Upper side colour very variable: blackish, blue, green, bronze, cupreous, purple, same colours as *P. sericea*. Antennae and legs same colour as upper side, in some specimens with reddish parts near the joints.

Head: Rugulose punctate and pubescent, frontal calli convex, interocular area with a longitudinal median furrow.

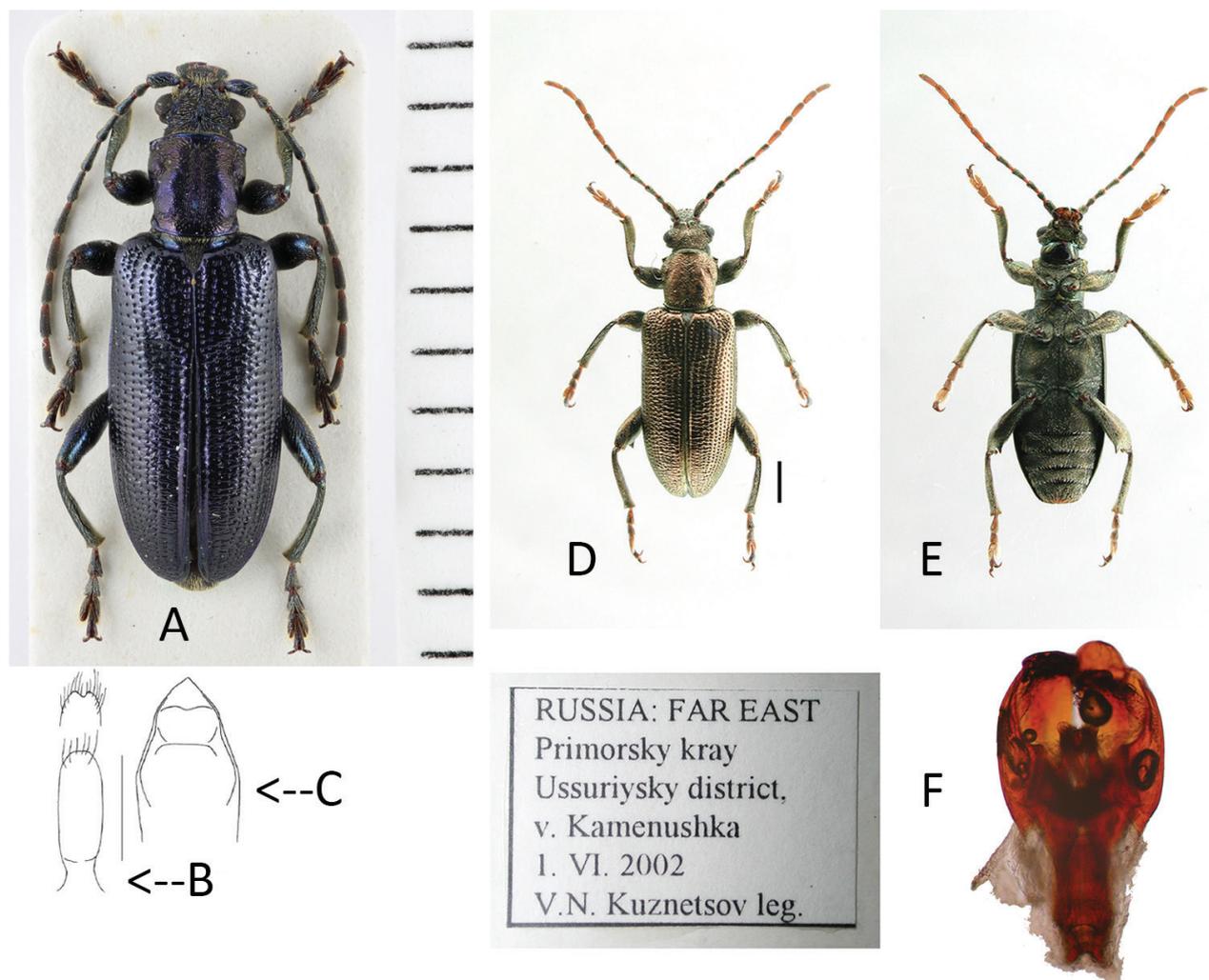


Figure 13. *Plateumaris shirahatai* **A** habitus (photograph by K. Matsumoto) **B** cap of tegmen, shape slightly variable **C** median lobe (**B, C** from Hayashi 2020) **D, E** habitus from dorsal and ventral **F** endophallus (**D–F** photographs by M Hayashi). Scale bars: one unit – 1 mm (**A**); 0.5 mm (**B–E**).

Antennae: Entirely metallic with same colour as dorsum, antennomeres in some specimens basically reddish, filiform, A1 robust, club-shaped, $A1 = 2 \times A2$, $A3 \cong 2 \times A2$, $A3 < A4 \leq A5$.

Pronotum: Slightly longer than broad, gradually narrowed posteriorly, dorsal surface with a pair of distinctly raised antero-lateral tubercles, and with a triangular depression medio-basally, disc punctate with transverse rugae, median line indistinct, shallowly furrowed.

Elytra: Interstices of the rows of punctures with close oblique or transverse corrugations and showing a rugged appearance.

Legs: Entirely metallic, same colour as dorsum, in some specimens small reddish parts at the base of the joints, tooth of metafemur prominent and blade-like but also in some specimens obtuse.

Pygidium: Apex pubescent, apical shape in females rounded, in some specimens slightly emarginate, in males emarginate or truncate.

Male genitalia: Median lobe of aedeagus (Fig. 13C) very similar to *P. sericea* (Fig. 11D). Cap of tegmen rounded or slightly notched (Fig. 13B). Apex of median ejaculatory guide of the endophallus notched (Figs 12B, 13F).

Remarks. The only reliable feature to distinguish *P. shirahatai* from *P. sericea* is the notched apex at the median ejaculatory guide of the endophallus. The habitus of *P. shirahatai* looks also very similar to *P. roscida*, but the latter always has large red parts on the legs and antennae, and their aedeagi are remarkably different (Figs 9, 13B, C).

Biology. The larvae feed on *Carex* sp. (Narita, 2003). Adults were collected on the florescence of *Carex* sp. (Hayashi and Tominaga 2005).

Distribution. East Palaearctic species. The distribution area of *P. shirahatai* is situated completely within the eastern area of *P. sericea*. Unfortunately, it is almost impossible to distinguish *P. shirahatai* from *P. sericea* without male genitalia. Both species share the same colour spectrum and same variation of the other external characters.

Records exist for Asia: China (Jilin) [new in PalCat], Japan (Hokkaido and Honshu), Mongolia [new in PalCat], Russia (Far East: Primorsky Krai, Sakhalin), South Korea, South Kuril (Etorofu).

New country records additional to Silfverberg (2010). CHINA (Jilin): Hayashi (2020); Jilin Province, det. M. Hayashi (Zoological Institute, Chinese Academy of Science, Beijing).

MONGOLIA: • 2 ♂♂, 1 ♀; central Mongolia, Terelj; 47°59'24"N, 107°27'E; 28 Jun 2004; M. Hayashi leg.; M. Hayashi det.; Hoshizaki Institute for Wildlife Protection, Izumo, Japan. Remark: Some parts of this data are published in Hayashi (2020). The details were obtained from M. Hayashi (pers. comm. 27 May 2020).

This recent record from central Mongolia shows clearly that the distribution area is not known until now. As *P. shirahatai* was described only in 1971 it is likely that some specimens from the East Palaearctic stored in collections may be identified as *P. sericea*.

Material examined. 20 specimens from Hokkaido and Honshu.

? *Plateumaris obsoleta* Jacobson, 1894

Figs 14, 15, 16

Type locality. Russia, Far East, Primorsky Krai, Bay of Posyet.

Type material. Holotype: RUSSIA • 1 ♀; Far East; Primorsky Krai; Bay of Posyet; ZIN. Only the holotype exists. It was examined from photographs only (Figs 14, 15).

Remarks. At first, I intended to synonymise *P. obsoleta* with *P. sericea* based on studies of the type material and description, but doubts remained that it is more likely that *P. obsoleta* is a synonym with *P. shirahatai*. I am sure that *P. obsoleta*, described based on one female specimen and never recorded again in more than 100 years, is a synonym. However, I cannot prove if it belongs to *P. sericea* or to *P. shirahatai* because it is impossible to distinguish these two species by external morphological characters. These two species differ only by subtle morphological differences in the apical part of the endophallus (Fig. 12).

Plateumaris obsoleta was described by Jacobson (1894) (see Geiser and Geiser 2023) based on a single specimen collected in Russia, Far East: Posyet in Primorsky Krai. No other specimen of *P. obsoleta* has been recorded in the last 130 years; it only appears regularly in identification keys. Jacobson found

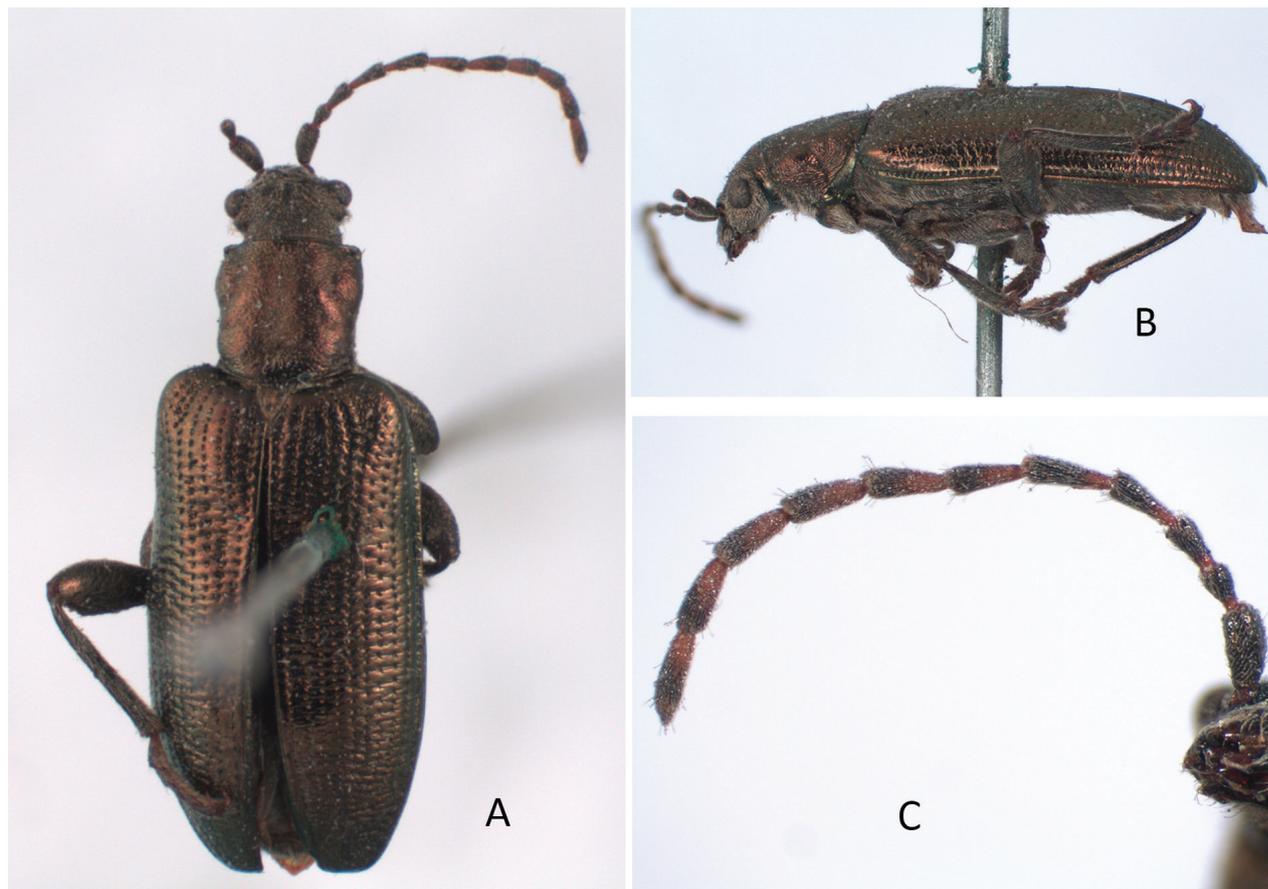


Figure 14. *Plateumaris obsoleta* holotype **A** habitus **B** lateral view **C** right antennae with red base of the antennomeres (photographs by A. Moseyko).

it most similar to *P. discolor* and *P. sericea*. All characters he described are also typical characters of *P. sericea*. Whereas many specimens of *P. sericea* have a sharp and prominent tooth at the metafemur, in some specimens this tooth can be blunt or is lacking completely. According to Jacobson (1894) this holotype is a male specimen. However, Bieńkowski (2014) wrote in his key: only one single female specimen is known. He also published four drawings of some details of this specimen. In fact, the holotype is stored in ZIN, from which I obtained some detailed photographs (Figs 14, 15, 16).

The controversy about the sex of this specimen can now be solved: the apical part of the ovipositor protrudes, which Jacobson misinterpreted as a part of the aedeagus. Although Askevold (1991) had not seen the holotype, but he suspected that the specimen described by Jacobson was female. According to the original description, "Pygidium apice rotundatum" is a description of a female specimen because no known males of species of *Plateumaris* have a rounded pygidium. All the characters described by Jacobson and the characters which could be examined on the photographs of the holotype fit easily within the variation range of *P. sericea*. However, *P. shirahatai* also occurs in southern Primorsky Krai (Hayashi and Tominaga 2005). Photographs (Figs 14C, 15A) show that many features of *P. obsoleta* are consistent with those of *Plateumaris shirahatai* identified in Primorsky (Fig. 13D, E) including metallic legs and an indistinct median line on the pronotum. In addition, the antennae of *P. shirahatai* are variable in colouration, with some individuals having

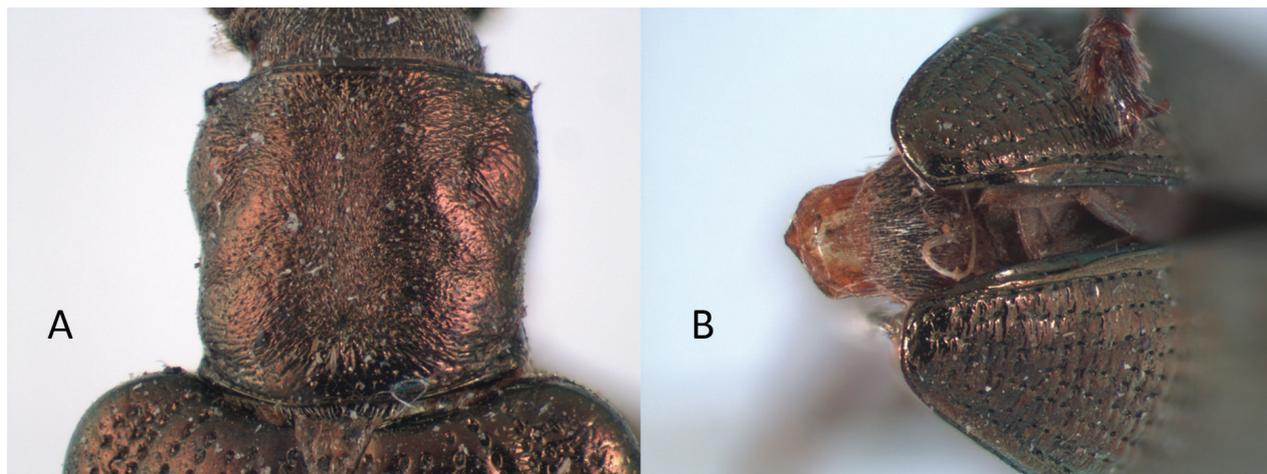


Figure 15. *Plateumaris obsoleta* holotype A pronotum B ovipositor protruding from abdomen (photographs by A. Moseyko).



Figure 16. *Plateumaris obsoleta*: All labels tagged to the holotype (photographs by A. Moseyko).

the same colouration as the type of *P. obsoleta*. This strongly supports the possibility that *P. shirahatai* is a synonym of *P. obsoleta*. On the other hand, *P. obsoleta* has a small metafemoral tooth, but it is suspected that the shape of this tooth may be malformed. This is a recurrent problem with species described on single specimen (pers. comm. M. Hayashi, 04 Apr 2023). Therefore, it seems more likely that *P. obsoleta* is synonym with *P. shirahatai* than with *P. sericea*,

that was also suspected by Askevold (1991), Hayashi and Tominaga (2005), and Warchałowski (2010). The pronotum of the type specimen of *P. obsoleta* (Fig. 15A) looks similar to the pronotum of *P. shirahatai* (Fig. 13A, D). All in all, the decision of the synonymisation cannot be made now.

Perhaps it will be possible in the near future to solve this problem without destroying this single specimen with more elaborate methods than historical DNA analysis. The solutions used to extract the DNA may be destroy the connecting membranes between the chitinous parts. Nowadays, nobody can guarantee that this specimen would NOT be damaged! Additionally, it is very questionable whether the results will be clear enough. Usually, the DNA in old, stored insects is fragmented and cannot be sufficiently reconstructed to make the decision to which species the specimens belong. *Plateumaris sericea* and *P. shirahatai* are closely related, which was proofed by DNA analysis (Hayashi and Sota 2014). There are only few sections of the DNA where the differences are shown. It is unlikely that exact these few sections could be tracked down by the current methods. Therefore, according to the current state of knowledge, I cite it as a “probable new synonymy”. If it once can be proved that *P. shirahatai* and *P. obsoleta* are synonyms, the name *P. obsoleta* has priority because it was described in 1894 and *P. shirahatai* in 1971.

***Plateumaris weisei* (Duvivier, 1885)**

Fig. 17

Donacia weisei Duvivier, 1885: cxvi.

Donacia borealis Mannerheim [nomen nudum].

Plateumaris hirashimai Kimoto, 1963: 13.

Donacia (Plateumaris) mongolica Semenov, 1895: 267.

Plateumaris morimotoi Kimoto, 1963: 13.

Plateumaris consimilis orientalis Shavrov, 1948: 49.

Plateumaris sachalinensis L. N. Medvedev, 1973: 876.

Type localities. *Plateumaris weisei*: Siberia. Original label text: “Sibérie coll. Duvivier”; *Plateumaris consimilis orientalis*: Far East, Vladivostok, Sedanka, Russia; *Plateumaris hirashimai*: Hokkaido, Ashoro in Tokachi, Japan; *Plateumaris mongolica*: North Mongolia, Borchá-Urga, Mongolia; *Plateumaris morimotoi*: Hokkaido, Tenninkyo Mt. Daisetsu, Japan; *Plateumaris sachalinensis*: Far East, Sakhalin, Yuzhno-Sakhalinsk, Russia.

Type material. Type of *Plateumaris weisei*: 1 syntype, Siberie coll. Duvivier; Museum Paris coll. H. Clavareau 1932, vid. I.S. Askevold 1984 (MNHN-EC-EC2129). Image of type specimen: <https://science.mnhn.fr/institution/mnhn/collection/ec/item/ec2129?listIndex=2&listCount=6>.

Type series of *P. consimilis orientalis*: RUSSIA • 3 ♀; Far East, Vladivostok, Sedanka; 19 Jun. 1937 [present depository unknown].

Type of *P. hirashimai*: JAPAN • 1 ♀; Hokkaido, Ashoronuma in Tokachi; 28 Jul. 1949; R. Matsuda leg.; collection Entomological Laboratory, Faculty of Agriculture, Kyushu University, Fukuoka, Japan.

Type of *P. mongolica*: MONGOLIA • 1 ♂; valley of the river Borchá, from Urga to the East; 6 Jul. 1894, B. Kaschkarow leg.; collection Semenov [present depository unknown].

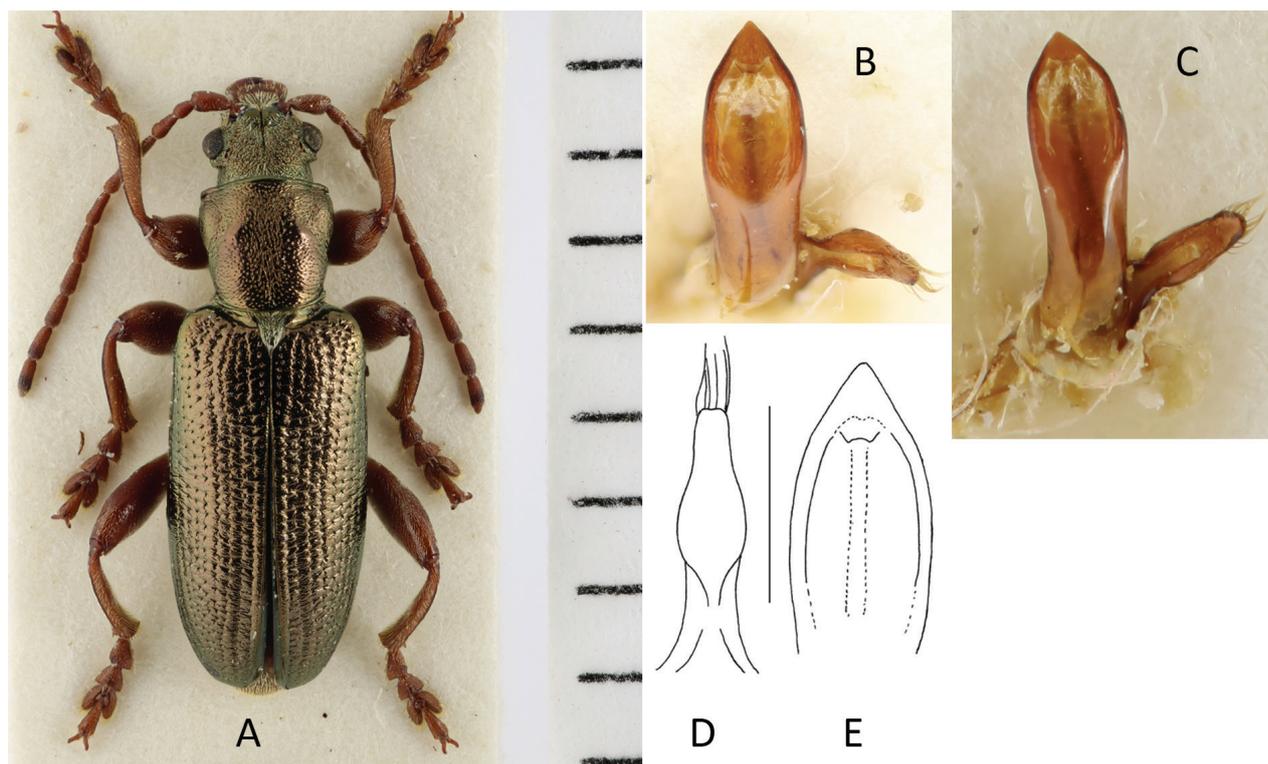


Figure 17. *Plateumaris weisei* **A** habitus **B, C** aedeagus: Median lobe and cap of tegmen (photographs by K. Matsumoto) **D** cap of tegmen **E** median lobe (from Hayashi 2020). Scale bars: one unit – 1 mm (**A**); 0.5 mm (**D, E**).

Type of *P. morimotoi*: JAPAN • 1 ♂; Hokkaido, Tenninkyo Mt. Daisetsu; 27 Jul. 1955; K. Morimoto leg.; collection Entomological Laboratory, Faculty of Agriculture, Kyushu University, Fukuoka, Japan.

Type of *P. sachalinensis*: RUSSIA • 1 ♂; Far East, Sakhalin, Yuzhno-Sakhalinsk; 12 Jul. 1955; collection of N.N. Filippov [present depository unknown]. Paratype: RUSSIA • 1 ♂; Far East, Sakhalin, Yuzhno-Sakhalinsk; 10 Jul. 1955; [red label:] Paratype *Plateumaris sachalinensis* Medvedev, *Plateumaris weisei* Duv. E. Geiser 2021 det.; NMEG.

The photographs of the syntype of *P. weisei* and the paratype of *P. sachalinensis* were examined.

Taxonomic history and synonymies. This list of synonyms and their shifting positions (see below) indicate the main systematic problems with *P. weisei*. First, it is difficult to distinguish it from other *Plateumaris* species. The variety of conspicuous morphological characters (colour, relative length of antennomeres, shape and structure of pronotum, shape of metafemoral tooth, etc.) overlap with other species. Second, the locality name in the first description “Siberie” is anything but precise. Third, *P. weisei* has a particularly wide distribution range, from northern Fennoscandia through European Russia and Siberia to Far East, Mongolia, Northern China, the Korean peninsula, and Japan. Altogether this resulted in the new descriptions of *Plateumaris* species when a specimen was found outside Siberia with slightly different characters.

Donacia borealis (Mannerheim), nomen nudum: the first who recognised that a specimen of still undescribed *Plateumaris weisei* belonged to a new species was Carl Gustav Mannerheim, a Finnish entomologist (1797–1854). He labelled a specimen (possibly more than one specimen, but I only found this one) from

“Laponica” with “*Donacia borealis*”, which clearly is *P. weisei* (vid. E. Geiser 20 Jul. 2022). This specimen is stored in the coll. Mannerheim (LUOMUS). Mannerheim had the intention to describe it, but he died before he could publish a description.

Plateumaris hirashimai was first described by Kimoto (1963) from Japan, Hokkaido. Askevold (1991: 58) synonymised it with the statement “The endophallus of specimens of *P. hirashimai* is indistinguishable from that of specimens of *P. weisei* from Finland in any significant way nor do they differ significantly in external structure”.

Donacia mongolica was described by Semenov (1895) based on a single male specimen from Mongolia, east of Ulaanbaatar. He also regarded *Plateumaris* as a subgenus to *Donacia* where this new species should be allocated. The description is very detailed (Geiser and Geiser 2023). Additionally, Semenov listed many characters to distinguish the new species from *P. consimilis*, *P. rustica* and *P. weisei*. Nevertheless, he suspected that this new species could be an aberration of *P. weisei*, which he had never seen then. Askevold (1991: 58) checked the description and suggested that *P. mongolica* is probably a synonym of *P. weisei*. It is regarded as a genuine synonym by Hayashi (2001, 2020), Warchałowski (2010) and Silfverberg (2010). I examined 9 specimens from northern and central Mongolia identified as *P. mongolica* (stored in coll. Frey in NHMB, in NMEG, and in ZFMK). They show completely yellow legs and almost completely yellow antennomere (only some distal antennomeres are darkened at the apex). Their metafemoral tooth is clearly visible but well within the variation of *P. weisei* and not so prominent as in *P. amurensis*. They all are typical *P. weisei* and *P. mongolica* is a synonym of *P. weisei*.

Plateumaris morimotoi was first described by Kimoto (1963) from a single male specimen from Japan Hokkaido. After studying additional material Kimoto (1981: 25) concluded that *P. morimotoi* is only an infraspecific variation of *P. hirashimai* and therefore synonymised it with the latter. Then Askevold (1991: 58) synonymised *P. hirashimai* with *P. weisei* (see above). Subsequently, *P. morimotoi* became a synonym to *P. weisei*, too.

Plateumaris consimilis orientalis was described by Shavrov (1948) as a new subspecies of *P. consimilis* from Vladivostok, based on three female specimens. His detailed description (Geiser and Geiser 2023) fits to *P. consimilis* as well as *P. weisei*. He also discussed the contraverted opinion of Kolossow (1930) that *P. consimilis* is distributed only in the western Palaearctic, whereas Reitter indicated “Europa, Sibirien, Japan”. For Shavrov this new subspecies was a proof or a very strong likelihood that *P. consimilis* occurred in the whole Palaearctic region. He also recognised that some features are different from the European specimens, but he deduced that such differences are due to the huge distance. Therefore, separate subspecies of European species are common in beetles of the Far East.

Askevold (1991: 58) assessed *P. consimilis orientalis* as a “probable new synonymy” by studying the original description. However, he also considered *P. amurensis* as synonym to *P. weisei*. Therefore, it is not clear, to which of these two species it is synonym because *P. amurensis* also occurs in the same area. Hayashi (2001) studied *P. weisei* and *P. amurensis* thoroughly and worked out that these are unambiguously two different species. *Plateumaris amurensis* has (mostly!) a prominent, blade like metafemoral tooth whereas *P. consimilis orientalis* has no metafemoral tooth or only a slight protrusion. He also listed *P. consimilis orientalis* as synonym with *P. weisei*.

In the coll. Frey (NHMB) I found two specimens from Japan, Honshu, Fukushima, labelled "*Plateumaris consimilis* Schrank det. M. Chūjō", both collected in 1948. These two specimens refer not to *P. consimilis orientalis* Shavrov but were only misidentifications of *P. constricticollis*. At this time, the distribution area of *P. consimilis* was regarded to reach as far as Japan. I never saw a specimen from East of Ural which had some similarity with *P. consimilis*.

Plateumaris sachalinensis was described by Medvedev (1973) as a new *Plateumaris* species from the Sakhalin Island (Geiser and Geiser 2023). He compared it with *P. weisei* in some characters (long antennae, metaformal tooth very weak) but put it close to *P. obsoleta* (which is synonymous with *P. sericea* or *P. shirahatai*). He regarded it as an intermediate form between the *P. weisei* and *P. amurensis* group and the *P. sericea* group. Later, Medvedev (1978) even regarded *P. sachalinensis* as a synonym of *P. obsoleta*. I studied the paratype specimen from NMEG: In contrast to many *P. weisei* specimens which have reddish antennae and legs, in this specimen large parts of the legs are metallic darkened. Probably, this colouration of the legs prompted Medvedev (1973) to place this species close to *P. obsoleta*. Also, the apical part of each antennomere is darkened. This and the other characters fit easily into the range of variability shown by *P. weisei* (for more morphological details see Hayashi 2001).

After the study of the original description Askevold (1991: 58) suggested that *P. sachalinensis* should be regarded as a "probable new synonymy" to *P. weisei*. Hayashi (2001, 2020) and Silfverberg (2010) regarded it as a synonym, Bieńkowski (2014) considered it as a valid species. Warchałowski (2010) separated it in his key from other *Plateumaris* species because of the dark metallic legs but also mentioned that it is regarded as synonym to *P. weisei* by some authors. Although Askevold (1991) regarded *P. amurensis* as synonym to *P. weisei*, the weak metafemoral tooth of *P. sachalinensis* is a typical character of *P. weisei* and excludes *P. amurensis* here. Hayashi (2001), who finally separated *P. weisei* and *P. amurensis*, confirmed the synonymy of *P. sachalinensis* with *P. weisei*.

Diagnosis. Pronotal disc finely rugose and punctured, sometimes with microsculpture, median line obsolete, sometimes shallowly furrowed (similar to *P. shirahatai*), metafemur with a small, not blade-like tooth, usually rufous at the base; aedeagus with apex of median lobe arced on both sides, gradually narrowed apically, without a median lip.

Description. Size: Males 6.2–7.0 mm, females 6.8–8.0 mm.

Colour: Most specimens dorsally cupreous or bronze, sometimes metallic green, blue, purple, or non-metallic brown.

Head: Eyes small, supraocular furrow indistinct, vertex pubescent with deep median line, antenna entirely rufous in most specimens but in some specimens darkly rufous or apically metallic, antennomeres: A5 longest in second to A6 and ca 3.5× as long as wide, A4 ca 2.2× as long as A2.

Pronotum: Outline subquadrate, slightly longer than wide, basal part narrowed, slightly cone-shaped, anterior tubercles distinctly visible or almost entirely smooth, disc more or less punctate, rugulose, median groove indistinct or shallowly furrowed.

Elytra: Transverse rugae between the rows of punctures, especially on interstices 1–4.

Legs: Yellow-reddish, in some specimens more or less darkened, femur, tibia, and tarsomere pubescent, outer apical angles of pro- and mesotibiae with a

spine, outer apical angles of metatibiae with a small spine, metafemoral tooth mostly blunt or moderate.

Aedeagus: Apex of median lobe arced on both sides, gradually narrowed apically, without a median lip, cap of tegmen rounded at apex (Fig. 17).

The main different features between *P. amurensis* and *P. weisei* are shown in Table 3. The east Palaearctic *Plateumaris* species are not easy to distinguish which was also explained in the comments to the synonyms. Misidentifications are common. Oddly enough, in several collections I found the label "*Plateumaris* [or *Donacia*] *weisei* Duvivier" attached to blue specimens from central Asia, collected circa 1900, which in fact were *Donacia bactriana* Weise, 1887. Somehow the author's name has been shifted and was then regarded as the species name.

Biology. Larvae were found at the roots on *Carex* sp. (Bieńkowski and Orlova-Bieńkowskaja 2004; An 2019). Narita (2003) described the last instar of the larvae which he gained from the host plant *Carex middendorffii*.

Distribution. *Plateumaris weisei* is a Trans Palaearctic species, it occurs from northern Fennoscandia through Siberia to the Far East, northern China, the Korean peninsula, and Japan. Also, it occurs in a broad span of latitudes, from the arctic polar circle (67°N) to 35°N in Korea. Records exist for Europe: Sweden, Finland, Russia (north and central part of European Russia).

Asia: China (Heilongjiang [new in PalCat], Inner Mongolia), Japan (Hokkaido), Mongolia, Russia (west, east, and south Siberia [new in PalCat], Far East), South Korea [new in PalCat].

In Japan records exist only from Hokkaido so far (Hayashi 2020), whereas fossil and subfossil records are known from Honshu and Kyushu, too (Hayashi and Shiyake 2011).

New country records additional to Silfverberg (2010). CHINA • 1 ex.; Heilongjiang, "Manchuria" Harbin; *Plateumaris weisei* E. Geiser 2020 det.; SDEI [coll. K.-H. Mohr]. Remarks: Silfverberg (2010) recorded *P. weisei* for China with "NE" because the specimens are labelled only with the locality "Manchuria", a historical region in northeast China. NE China today comprises the provinces of Heilongjiang and Jilin, and Harbin belongs to Heilongjiang. I examined 8 of these specimens stored in BMNH, in coll. Frey in NHMB, and in SDEI.

RUSSIA • 5 ex.; South Siberia, Angara (near Baikal); I. Askevold 1985 det., E. Geiser 2019 vid.; Sharp-coll. 1905 – 313, BMNH; Bieńkowski (2014).

SOUTH KOREA: Hayashi and Cho (2017); An (2019).

Material examined. More than 80 specimens from Europe and Asia.

Discussion

The changes in Geiser (in press) compared with the statuses in Silfverberg (2010) concerned mostly synonymies and country records for Palaearctic *Plateumaris* species. Forty-one countries or parts of countries could be added to the lists. These records are due mostly to faunistic publications since 2010. Many faunistic studies of small areas have been published in respective local languages and can be easily overlooked. Thanks to colleagues who provided me with such papers, many of these records could now be evaluated. Museum studies and personal communications from colleagues also provided many unpublished records. Thirteen of them were first country records and many others were confirmations of the occurrence of a specific species in these countries.

A primary objective was to declutter doubtful species and ambiguous synonymisations to answer these questions: how many species of *Plateumaris* exist in the Palaearctic region, what are their names, and how should the remaining 70 names used in a description for a *Plateumaris* taxon be allocated to the valid species? This was successful in most cases. Additionally, some holotypes could be tracked down, e.g., of *P. tenuicornis*, which could be identified unambiguously as synonymous with *P. consimilis*. This also confirmed Bechyné's (1942) opinion that had been ignored. *Plateumaris sulcifrons*, often allocated to the wrong country, could now be identified as *P. rustica* by the detailed and clear first description.

In general, this study largely confirmed the systematic status published by Askevold (1991). He stated nine valid species of Palaearctic *Plateumaris* and I agree with eight of them: his ninth species is *P. weisei*, which he thought to be synonymous with *P. amurensis*. Later Hayashi (2001) concluded that *P. amurensis* is in fact a valid species, so there are ten species in the genus. I also agree with the opinions of Hayashi and Sota (2014) and Hayashi (2020) about the valid species and their synonyms for *Plateumaris*.

Many problems could be solved unambiguously, but not all *P. obsoleta* may be a synonym of *P. shirahatai*: it could in fact be a synonym of *P. sericea*, which also occurs at the same locality and cannot be distinguished from *P. shirahatai* by external characters alone.

A problem does remain concerning the synonymisation of *P. discolor* with *P. sericea*. They are not distinguishable morphologically, even if some identification keys suggest that they are. The allocations to their ecological requirements and food plants are contradictory: because *P. sericea* shows very high genetic variability and has a very large distribution area, it may consist of cryptic species, possibly indicating evolution in progress.

I am reluctant to designate neotypes at this point. Before choosing specimens as neotypes one should be certain that the holotype or type series do not exist. Some museum collections, where I expect to find a missing holotype, could not be visited in the last years due to Covid 19, but this should be rectified in the near future. Additionally, the specimens for neotypes should be from the same location or as near as possible to where the original type or type series were collected, and this require visits to museums in which such specimens are stored.

Finally, I do not want to sweep the most severe problem in researching Palaearctic *Plateumaris* species under the carpet: the majority of specimens for systematic studies is stored in museums. It is not very hopeful to try to catch specimens in the field. Most museum specimens are by-catches acquired by luck: there exists specimens from expeditions which took place 100 and more years ago from large areas of Asia. From areas like Syria, Afghanistan, and large parts of China such Xinjiang Province, the only information we can access now is from museum specimens. The application of historical DNA methods seems to be helpful but is problematic: its success is questionable, mostly due to the severe fragmentation of the DNA in old specimens. Also, damaging these few very precious specimens by the extraction solution is likely. Perhaps, in the future, there will be gentler methods developed for such studies.

Even without restrictions for field studies caused by politics, in Europe, too, it is difficult to obtain new samples. Many colleagues who know that I am working on Donaciinae have tried to catch specimens during their own field trips in the last years. Besides *P. sericea*, all other species are rare because of many changes of

the limnic environment during the last 100 years. Water pollution is not such an issue as it was 40 years ago, but man-made changes to diverse limnic habitats, especially bank straightening and drainage, has probably led to the extinction of *Plateumaris* populations that need specific ecological conditions to survive and thrive.

Acknowledgements

This generic revision was possible only with the help of many colleagues, particularly important in the last years with travel and entry restrictions. The colleagues responsible for the museum collections I visited are indicated in the list of museum abbreviations. Many thanks for their support during my on-site studies and their useful suggestions. Further essential help was obtained from the following colleagues: Jan Bezděk (Brno, Czechia) provided me with rare literature and his huge knowledge of tricky systematic and nomenclatorial details. I received answers from Horst Kippenberg (Herzogenaurach, Germany) and from Ron Beenen (Nieuwegein, Netherlands) whenever I asked them questions. Johannes Bengsten (Stockholm, Sweden) provided me with unpublished phylogenetic trees of *P. sericea* and *P. discolor*. I thank Klaas Reißmann (Kamp-Lintfort, Germany) for interesting discussions about *P. discolor*.

I also thank the following for support with images: Keita Matsumoto (London, United Kingdom), who provided me with excellent photos from specimens of the coll. Voříšek (BMNH); Alexey Moseyko (St. Petersburg, Russia), who tracked down the holotype of *P. obsoleta* and sent to me essential pictures and other helpful information; Peter Vdáčný, Vladimír Janský, and Martin Sečanský (all in Bratislava, Slovakia) helped to find the holotype of *P. tenuicornis*. From Masakazu Hayashi (Izumo, Japan) I received pictures of *P. shirahatai* from Primorsky Krai and other useful information, including permission to use drawings from his publications.

Gloria Geiser (Salzburg, Austria) made several drawings. Irmgard Geiser (Salzburg, Austria) helped with cryptic locality label texts written in Albanian. Helena Shaverdo (Vienna, Austria) deciphered many handwritten labels in Russian. Remigius Geiser senior (Salzburg, Austria) made meticulous corrections and improved the manuscript with tough discussions. Finally, I would like to thank the editorial team, especially Caroline Chaboo (Lincoln, Nebraska, USA) who also significantly improved the language, Yuri Mikhailov (Yekaterinburg, Russia) and two anonymous reviewers for their useful advice, and Nathalie Yonow (Swansea, United Kingdom) for the linguistic proof.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

The research in the SNMC was funded by the Operational Program of Research and Development and co-financed with the European Fund for Regional Development (EFRD)

ITMS 26230120004: Building of Research and Development Infrastructure for Investigation of Genetic Biodiversity of Organisms and joining the IBOL initiative.

Author contributions

The author solely contributed to this work.

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Data availability

All of the data that support the findings of this study are available in the main text.

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Original descriptions of Palaearctic species of the genus *Plateumaris* C. G. Thomson, 1859 (Coleoptera, Chrysomelidae, Donaciinae) and their translations*

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Abstract

Many original descriptions of beetles were published in Latin with specific idioms and technical terms, which are sometimes difficult to understand. The exact meaning of these descriptions is necessary for taxonomic and systematic research. Of the ten Palaearctic *Plateumaris* species regarded as valid three were described in English, the remaining seven in Latin, French, or German: *P. amurensis* Weise, 1898, *P. bracata* (Scopoli, 1772), *P. consimilis* (Schrank, 1781), *P. roscida* Weise, 1912, *P. rustica* (Kunze, 1818), *P. sericea* (Linnaeus, 1758), and *P. weisei* (Duvivier, 1885). These seven non-English original descriptions and their translations into English are presented here. Additionally, the translations of the first descriptions of the genus *Plateumaris* and of its 19 synonyms (some were described in Russian, also) are given.

Key words: French descriptions, German descriptions, Latin descriptions, leaf-beetles, Palaearctic Region, reed-beetles, Russian descriptions, taxonomy



Academic editor: Caroline Chaboo

Received: 8 March 2023

Accepted: 25 May 2023

Published: 30 August 2023

ZooBank: <https://zoobank.org/01DB6CEB-0287-43DE-B05C-85832DDDF84F>

Citation: Geiser E, Geiser R (2023) Original descriptions of Palaearctic species of the genus *Plateumaris* C. G. Thomson, 1859 (Coleoptera, Chrysomelidae, Donaciinae) and their translations. In: Chaboo CS, Schmitt M (Eds) Research on Chrysomelidae 9. ZooKeys 1177: 235–258. <https://doi.org/10.3897/zookeys.1177.103212>

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* Extended version of a talk presented to the 10th International Symposium on the Chrysomelidae, Helsinki, Finland, 21 July 2022.

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Introduction

Since Linnaeus (1758) many animal taxa have been described in Latin with very specific phrases used in scientific entomological scripts in the 18th and 19th centuries, which are not easily understandable for classicists who are not also entomologists. Furthermore, knowledge of the Latin language is in rapid decline. It is no longer part of the education curriculum of grammar schools, but was mandatory in Europe for centuries. Nowadays, English is the worldwide communication language used in science. The second author is a classicist and an entomologist with profound knowledge in systematics who translated numerous original Latin descriptions of Donaciinae taxa in the last years for systematic studies by the first author, such as *Donacia clavareau* Jacobson, 1906 (Geiser 2019). Many translations are yet unpublished, but were used in Geiser and Jäch (2021).

First descriptions were also given in German, French, or Russian. These languages can be translated by electronic tools into understandable, but not always into directly printable English. However, these means do not offer the possibility to translate Latin into English. The Latin language was used for texts for more than 2000 years, for different purposes: in theology, law, medicine, philosophy, and scientific texts up to the 20th century, and in all these topics with different grammar and vocabulary rules. Even the Latin descriptions of beetles vary between beetle families. Also, they depended upon the specific education and on the preference of the authors. Therefore, “hand-made” or better “brain-made” translations by a knowledgeable specialist will provide the most adequate results.

In the update of the Catalogue of Palaearctic Chrysomelidae – Donaciinae (Geiser and Bezděk in press; Geiser in press) the first author made many changes concerning the taxonomy and systematics of the *Plateu-*

maris species compared with the first edition of the catalogue (Silfverberg 2010). These changes are explained in Geiser (2023). For such systematic revisions it was essential to study not only many specimens, but also the original descriptions.

In the genus *Plateumaris* 80 taxa were described for the Palaearctic region. Ten species names are regarded as valid, the other 70 are synonyms. We provide here the translations of the original descriptions of seven valid species (the other three were described in English) of the genus *Plateumaris*, and, additionally, of 19 taxa which are regarded as synonyms. These taxa are discussed in detail in Geiser (2023). Some original descriptions in other languages than Latin or English were also translated here into English. All these texts were essential for arguments why some systematic changes, especially synonymisations, were made in Palaearctic *Plateumaris* species.

Material and method

All original descriptions published in Latin were translated into German by the second author. Then the first author translated them into English. There also exist some original descriptions in German, which were translated into English by the first author. Some original descriptions were published in French, Russian, and Serbian. They were first translated into English by Google translate. Then the translations of French texts were revised together with Gloria Geiser. Translations of texts in a Slavic language were checked with Irmgard Geiser. Some original descriptions are multilingual. They begin in Latin, but often more details are explained in the author's native language. The original orthography of the description is printed here, even though it is now outdated; the translation into English is as accurate and faithful as possible to the original text. The names of the *Plateumaris* taxa are arranged alphabetically, regardless of whether they are now synonyms or names of a valid species. The Palaearctic species *P. akiensis* Tominaga & Katsura, 1984, *P. constricticollis* Jacoby, 1885, and *P. shirahatai* Kimoto, 1971 are not included here because they were originally described in English.

Text in square brackets contains additions by the authors and is not part of the original description.

Results

Plateumaris Thomson, 1859

Described on page 154.

Latin	English
Familia Donaciidæ	Family Donaciidae
Antennæ ante oculos insertæ. Caput exsertum, paullo pone oculos constrictum. Elytra striata, striola suturali abbreviata. Coxæ posticæ late distantes. Tibiæ calcarî obsolete. Abdomen segmento 1:o ceteris simul sumtis longitudine æquali.	Antennae inserted in front of the eyes. Head prominent, slightly constricted behind the eyes. Elytra striated, sutural stripe shortened. Posterior coxae far apart. Tibiæ with an inconspicuous spur. 1 st abdominal segment as long as the others put together.

<i>Donacia</i> Fab. Gyll. Typus <i>D. crassipes</i> (Fab.): Gyll. III. 646. 1. Tibiae margine postico subcarinato. Oculi magni, prominuli. Mandibulae breves.	<i>Donacia</i> Fab. Gyll. Typus <i>D. crassipes</i> (Fab.): Gyll. III. 646. 1. Hind margin of the tibiae to some extent carinate. Eyes large, slightly protruding. Mandibles short.
<i>Plateumaris</i> . <i>Donacia</i> Gyll. Typus <i>P. nigra</i> (Fab.): Gyll. IV. 678. 10–11. Tibiae multi-angulatae. Femora breviora, crassa. Mandibulae validae, labrum longe superantes. Antennae inter se non magis quam ab oculis parvulis distantes.	<i>Plateumaris</i> . <i>Donacia</i> Gyll. Typus <i>P. nigra</i> (Fab.): Gyll. IV. 678. 10–11. Tibiae polygonal. Femora shorter, thick. Strong mandibles, well overlapping the labrum. Antennae not further distant from each other than from the small eyes.
<i>Haemonia</i> Latr. <i>Donacia</i> Gyll. Typus <i>H. Zosteræ</i> (Fab.): Gyll. IV. 683. 17. Tarsi articulo ultimo ceteris simul sumtis longiore. Elytra apice spinoso-producta. Antennae basi subcontiguæ.	<i>Haemonia</i> Latr. <i>Donacia</i> Gyll. Typus <i>H. Zosteræ</i> (Fab.): Gyll. IV. 683. 17. Last [sic!] segment of the tarsi longer than the others put together. Elytra extended thorn-like at the apex. Antennae to some extent close together at base.

***Plateumaris affinis* (Kunze, 1818)**

Described as *Donacia affinis* on page 37. Synonym of *P. rustica*.

Latin	English
<i>Donacia affinis</i>	<i>Donacia affinis</i>
<i>D. affinis</i> ; thorace elongato subquadrato, depresso, subimpresso, punctato, angulis anticis rotundatis, lateribus subsinuatis; elytris convexiusculis, subtilissime punctulato-rugulosis, apice rotundatis, punctis striarum levibus, discretis, striis remotiusculis, pedibus pallescentibus. <i>D. nigra</i> Payk. Fn. Suec. II. p. 196. 10. <i>D. discolor</i> Gyll. Ins. Suec. III. 660. 10. (teste Zetterstedt.) <i>D. fusca</i> Mus. Lesk. nr. 591 ? <i>D. simplex</i> Thunberg. N. Act. Ups. V. p. 118. 55. <i>L. fusca</i> Gmel. L. Syst. Nat. 18. 67. 86. 2. ?	<i>D. affinis</i> ; the elongated pronotum almost square, flat, slightly depressed, punctured, front corners rounded, sides slightly convex; elytra slightly arched, extremely finely punctate and wrinkled, rounded at the end, the points of the stripes are faint, separated, the stripes are a little bit distant, legs slightly paler. <i>D. nigra</i> Payk. Fn. Suec. II. p. 196. 10. <i>D. discolor</i> Gyll. Ins. Suec. III. 660. 10. (teste Zetterstedt.) <i>D. fusca</i> Mus. Lesk. nr. 591 ? <i>D. simplex</i> Thunberg. N. Act. Ups. V. p. 118. 55. <i>L. fusca</i> Gmel. L. Syst. Nat. 18. 67. 86. 2. ?

***Plateumaris amurensis* Weise, 1898**

Described on page 179. The German part of the text is shown in the original but the now-outdated orthography.

Latin	English
<i>Plateumaris amurensis</i>	<i>Plateumaris amurensis</i>
Oblonga, convexiuscula, obscure aenea, subtus cinereo-sericea, abdominis segmentis postice, ano, pedibus, ore antennisque dilute ferrugineis, his brevibus, articulo 3: o: 2: o longiore,	Long, slightly convex, dark ore-coloured, underside silky grey, the abdominal segments from behind, anus, legs, mouth, and antennae are pale reddish brown, these [the antennae] are short, the third antennomere is longer than the second one, [3: o: 2: o is surely an error of the typesetter, presumably caused by misunderstanding of the [handwritten?] manuscript; the correct Latin description is: "articulo tertio secundo longiore" or "articulo 3° 2° longiore" or "articulo 3o: 2o longiore"]
prothorace brevi subcordato, disco dense ruguloso-punctato, subopaco, basi profunde arcuatim impresso, canalicula media sat profunda, angulis anticis minimis, acutis, elytris apice rotundato-truncatis, striato-punctatis, interstitiis nitidis, transversim strigosis, femoribus posticis dente valido armatis.	the short prothorax subcordate, the disc is rugose and densely dotted, almost dark, at the basis a deep arcuate impression, the middle groove rather deep, anterior angles very small and acute, elytra at apex rounded truncate, with rows of punctures, intervals shiny, lean in transverse direction, hind femora armed with a stout tooth.
Long 7,5 mm.	Length 7.5 mm
Amur	Amur [location of the type specimen]

German	English
Mit <i>Pl. discolor</i> verwandt, Fühler und Halsschild kürzer, letzteres viel unebener, erstere nebst den Mundtheilen, dem Hinterrande der Bauchringe und dem Aftersegmente hell rostroth.	Related to <i>Pl. discolor</i> , antennae and pronotum shorter, the latter much more uneven, the former together with the mouth parts, the posterior margin of the abdominal segments and the anal segment pale rusty red.
Halsschild etwas breiter als lang, die Vorderecken bilden einen kleinen, aber scharfen Borstenkegel, die Seiten sind dahinter gerundet-erweitert, von $\frac{1}{4}$ der Länge ab allmählich nach hinten verengt, in der Mitte sanft ausgeschweift. Die Oberfläche ist uneben, dicht runzelig punktiert und mehr glänzend; sie fällt nach innen sanft zur scharfen Mittelrinne ab, die vor der Basis in einem tiefen, bogenförmigen Quereindrucke endet. So entstehen auf jeder Seite 2 niedrige Beulen, die vordere derselben ist kleiner als die hinter der Mitte.	Pronotum slightly wider than long, the anterior angles form a small but sharp conical edge with bristles, behind it the sides are rounded-expanded, gradually narrowing backwards from $\frac{1}{4}$ of length, gently flared in the middle. The surface is uneven, densely rugose dotted and more lustrous; it slopes gently inwards to the sharp median groove, which ends with a deep, arched transverse impression before the basis. This creates 2 low tubercles on each side, of which the anterior one is smaller than the one behind the middle.
Die Flügeldecken sind wie bei den schwach sculptirten Exemplaren von <i>discolor</i> punktiert, die Punkte scharf eingestochen, die Zwischenstreifen glänzend, fein quer gerunzelt. Halsschild und Flügeldecken sind schwarzbraun, mit einem starken Messingschimmer.	The elytra are punctured like the weakly sculptured specimens of <i>discolor</i> , the points are sharply engraved, the intervals are shiny and finely wrinkled transversely. The pronotum and elytra are blackish brown with a strong brassy lustre.
¹⁾ Aehnlich gefärbt ist die nahestehende <i>Plateumaris Weisei</i> Duviv. von Irkutsk (Jakowlew), welche Jacobsohn, Horae 26 p. 435 irrthümlich zu den Arten mit behaartem Halsschild zählt. Das zweite Fühlerglied ist bei ihr stets halb so lang als das dritte, das Halsschild ähnelt dem von <i>consimilis</i> ist aber bedeutend schmäler und flacher, die Punktirung der Flügeldecken ist ziemlich dieselbe wie bei <i>Donacia cuprea</i> .	¹⁾ The nearby <i>Plateumaris Weisei</i> Duviv. from Irkutsk ([leg.] Jakowlew) is similarly coloured, which Jacobsohn, Horae 26 p. 435 [= reference to Jakobson [= Jacobson, Jacobsohn] G. G. 1892a: Analytische Übersicht der bekannten Donacia- und Plateumaris-Arten der Alten Welt. Horae Societatis Entomologicae Rossicae 26: 412–437] erroneously aligned with the species with a hairy pronotum. The second antennal segment is here [concerning <i>P. weisei</i>] always half as long as the third one, the pronotum resembles that of [<i>Plateumaris</i>] <i>consimilis</i> but is significantly narrower and flatter, the puncturing of the elytra is rather the same as in <i>Donacia cuprea</i> [= <i>Donacia semicuprea</i> , Panzer, 1796].

***Plateumaris annularis* Reitter, 1920**

Described on page 41. Synonym of *P. roscida*.

German	English
<i>Plateumaris annularis</i>	<i>Plateumaris annularis</i>
Eine Art, die in der Mitte zwischen <i>discolor</i> und <i>sericea</i> steht, da sie zum Teil Eigenschaften der beiden vereinigt. Die Fühler sind auffallend dünn, von der Form, wie bei <i>sericea</i> , aber die Glieder breit gelbrot geringelt. Halsschild ebenso wie bei <i>sericea</i> , aber ohne längs der Mitte eingerissene Mittellinie und die Lateralbeulen ganz flach und nicht glänzend, die metallischen Schenkel und Schienen an der Basis fast bis zur Mitte gelbbraun, Pygidium und Apikalsaum des Analsternites rot ; kupferig, erzfarben.	A species that stands in the middle between <i>discolor</i> and <i>sericea</i> , since it partly combines characteristics of both. The antennae are remarkably thin, the same form as in <i>sericea</i> , but the segments are broadly annulated in yellow-red. Pronotum as in <i>sericea</i> , but without median line engraved along the centre, and the lateral tubercles quite flat and not shiny, the metallic femora and tibiae from the base almost to the middle yellow-brown, pygidium and apical margin of anal sternite red; coppery, bronze.
L. 8–9 mm.	L[ength] 8 – 9 mm.
Ost Sibirien: Amurgebiet. (Chabarowka, Nikolajewsk, in Col. Koltze.)	East Siberia: Amur region. (Chabarowsk, Nikolajewsk, in col[lection] Koltze.)

***Plateumaris assimilis* (Schrank, 1781)**

Described as *Leptura assimilis* on page 156. Synonym of *P. consimilis*.

Latin	English
<i>Leptura assimilis</i>	<i>Leptura assimilis</i>
Vergleichbarer Holzkäfer [translation into in German]	Comparable xylobiontic beetle
<i>Leptura nigra</i> ; pedibus testaceis ; posticis dentatis; elytris simplicibus.	Black xylobiontic beetle; legs testaceous, hind ones with a tooth; elytra simple.
Mensurae. Longit. a cap. ad an. 3 ½ lin. elytri 2 1/5 – Latitudo insecti 1 1/3 –	Measurements: *) Length from head to anus 7.7 mm of an elytron 4.8 mm Width of the insect 2.9 mm
Descr. Nigra; elytro singulo striis novem punctatis. Pedes testacei, femora postica dentata.	Descr[ption] Black; the single elytron with nine rows of punctures. Legs testaceous, hind femora with a tooth.

*) Calculated from the unit “Vienna line”: 1 lin. = 2.195 mm. This unit would most likely be used by Schrank, especially in a book about Austrian insects.

***Plateumaris bracata* (Scopoli, 1772)**

Described as *Prionus bracatus* on page 100.

Latin	English
<i>PRIONUS Bracatus</i>	<i>PRIONUS Bracatus</i>
Diagn. Niger; antennis pedibusque rufis. Femoribus posticis crassis, spina armatis.	Diagn[osis:] Black; antennae and legs red. Hind femora thick, armed with a spine.
In Carniolia.	In Carniola [historical region in West Slovenia].
Elytra lin. 3–4. longa, non truncata, punctata: punctis in lineas ordinatis. Antennae breves.	Elytra *) 6.8 – 9 mm long [calculated from Parisian line], not truncated, punctured: dots arranged in rows. Antennae short.

*) Calculated from the unit “Parisian line”: 1 lin. = 2.2558 mm. This unit would most likely be used by Scopoli.

Because this original description was very short, Weise (1893) published a more detailed redescription on page 49.

Latin	English
<i>Pl. braccata</i>	<i>Pl. braccata</i>
Elongata, convexuscula, supra violaceo-nigra, subtus griseo-vel aureo-sericea; abdomine basi exeptha, pedibus antennisque rufo-ferrugineis; prothorace subcordato, viridescens, canalicula media obsoleta, angulis anticis vix prominulis; elytris apice conjunctim-rotundatis, striato-punctatis, interstitiis transversim rugosis. Long. 9–11 mm.	Elongated, slightly convex, purplish black above, below grey or silky golden; abdomen except base, legs and antennae light reddish-rusty brown; the prothorax subcordate, greenish, the central groove inconspicuous, the front angles hardly protruding; the elytra rounded together at the apex, with dotted stripes, the intervals transversely wrinkled. Length 9 – 11 mm.
Mas[culus]: prothoraces parce punctato, nitido, metasterno et segmento primo medio late impresso, 5: o apice emarginato; femoribus posticis dente valido armatis.	Male: prothorax sparsely punctured, shiny, metasternum and the first abdominal segment in the middle broadly impressed, the 5 th one at the tip emarginated; the hind femora armed with a strong tooth.

Fem[inae]: prothorace crebre punctato, segmento 5: o apice subtruncato, femoribus posticis obsolete dentatis vel muticis.	Female: prothorax densely punctured, the 5 th segment somewhat truncated at the apex, the hind femora with an inconspicuous tooth or blunted.
Var. a. Antennis, pedibus abdomineque nigris.	Var[iation] a. Antennae, legs, and abdomen black.
Var. b. (femina). Supra aenea, thorace chalybaeo-micans. Suffr. Stett. Zeit. 1846. 56.	Var[iation] b. (female). Upper side bronze-coloured, pronotum shiny like steel. [reference:] Suffr[ian] Stett[iner entomologische] Zeit[ung] 1846: 56.
[Reference first description:] Scopoli Annus V. Hist. nat. [p.]100.	
[Synonyms:] <i>Donacia nigra</i> Fabr[icius]. Ent. Syst. I. 2. 117. – Germ[ar] Neue Schrift. Ges. Halle VI. 31. – Lac[ordaire] Mon. 171. 46. – Redtb [Redtenbacher] Faun[a] A[ustriaca] II. 441. – Seidl[itiz] F[auna] balt[ica] 508.	
<i>D. palustris</i> Herbst. Füessl. Arch. V. 100. – Panz[er] Ent. Germ. 217. 13; Faun. Germ. 29. 10.	

***Plateumaris caucasica* Zaytsev, 1930**

Described on page 111. Synonym of *P. sericea*.

Latin	English
<i>Plateumaris caucasica</i>	<i>Plateumaris caucasica</i>
♂♀. Species inter <i>sericea</i> L. et <i>discolor</i> Panz. intermedia, sed illius manifeste affiniior.	♂♀. Intermediate species between <i>sericea</i> L. and <i>discolor</i> Panz., but clearly closer to the former.
Ab ambobus differt pedum colore: femoribus in triente basali, tibiaram parte $\frac{3}{4}$ longitudinis (nonnunquam usque ad apicem), tarsorum articulis omnibus (ultimo saepe excepto), segmentorum abdominalium summo margine, pygidio rufo-ferrugineis.	It differs from both by the colour of the legs: the femora at the basal third, the tibiae at 3/4 of the length (sometimes up to the apex), all tarsomeres (often except the last one), the very margin of the abdominal segments and the pygidium are reddish-rubiginous.
Praeterea a <i>P. sericea</i> discrepat corporis forma robustiore, subtus brevius pubescente, antennis gracilioribus atque longioribus, rubro-castaneis, articulis solum apice vel nihilo obscuratis, pronoto fortius ruguloso (fere ut in <i>P. discolor</i> [sic!]) angulis anticis haud prominulis; ceterum cum <i>P. sericea</i> congruens.	Further it differs from <i>P. sericea</i> by a more sturdy, ventrally shorter and densely pubescent physique, more slender and longer testaceous antennae with antennomeres darkened only at the apex or nowhere, a more rugose pronotum (almost like <i>P. discolor</i> [sic!]) with not protruding anterior angles; otherwise consistent with <i>P. sericea</i> .
A. <i>P. discolor</i> magis adeo distat antennis gracilibus, articulo quarto quam secundo duplo longiore etc. Superficie colore variat viride vel aurichalceo.	Many more differences exist compared with <i>P. discolor</i> by more slender antennae, the fourth antennomere which is twice as long as the second one etc. The surface colour varies between green and brassy.
Long. 7–8,5 mm.	Length 7–8.5 mm.
Hab. 'Ciscaucasia: Stavropol (IV. 1905, Maljuzhenko, 4 specimina), Daghestan: Chasav-jurt (E. Koenig, 5 sp.). – Coll. Musei Georgici.	Dis[tribution] 'Ciscaucasia: Stavropol (IV. 1905, Maljuzhenko, 4 specimens), Daghestan: Chasav-jurt (E. Koenig, 5 sp.). [stored in the] Coll[ection] of the Georgian Museum.
<i>P. annularis</i> Reitt. (e prov. Amurensis) verisimiliter maxime affinis, species nostra tamen secundum auctoris descriptionem corpore minore, tibiis amplius rufo-coloratis diversa esse videtur.	Probably very close to <i>P. annularis</i> Reitt[er] (from the Amur Prov[ince]), but it seems that our species differs according to the author's description by a smaller body and more extensively red-coloured tibiae.
Russian	English
Хотя указанных сейчас отличий от восточно-сибирского вида и недостаточно для признания видовой самостоятельности за нашей формой, но разорванность ареалов обитания, лаконичность описания у Reitter'a и отсутствие для сравнения амурских представителей этого вида дают основания пока считать их различными видами.	Although the differences now indicated from the East Siberian species are not enough to regard this form as an independent species, the fragmentation of the habitats, the brevity of Reitter's description and the lack of comparison with specimens from the Amur give reasons to consider it as a different species for the time being.

***Plateumaris consimilis* (Schrank, 1781)**

Described as *Leptura consimilis* on page 155.

Latin	English
<i>Leptura consimilis</i>	<i>Leptura consimilis</i>
Aehnlicher Holzkäfer [German vernacular name]	Similar xylobiontic beetle
<i>Leptura aenea</i> ; antennis pedibusque testaceis, femoribus posticis dentatis; elytris simplicibus.	Bronze-coloured xylobiontic beetle; antennae and legs testaceous, hind femora with a tooth; elytra simple.
Mensurae. Longit. a cap. ad an. 4 lin. elytri 2 ½ – Latitudo elytri 2/3 –	Measurements: *) Length from head to anus 8.78 mm of an elytron 5.48 mm Width of an elytron 1.46 mm
Descr. Nigro-aurea, subtus obscurior. Antennae fusco – testaceae, pedes rubro – testacei, postici femoribus dentatis.	Description: black-golden, underside darker. Antennae brown-testaceous, legs red-testaceous, hind ones with toothed femora.
Elytra non lacunosa, striis singular decem punctatis exarata.	Elytra without impressions, each one furrowed with ten rows of punctures.

*) Calculated from the unit “Vienna line”: 1 lin. = 2.195 mm. This measure would most likely be used by Schrank, especially in a book about Austrian insects.

***Plateumaris discolor* (Panzer, 1795)**

Described as *Donacia discolor* on page 216. Synonym of *P. sericea*.

Latin	English
<i>Donacia discolor</i>	<i>Donacia discolor</i>
obscure aenea, elytris cupreis crenato striatis, femoribus posticis dentatis. Habitat in <i>Caltha palustri</i> primo vere. (Variat elytris aeneo nitidulis et obscure cupreis. Elytra linearia, obtusa nec apice attenuata. Femora postica in utroque sexu dentata.)	dark bronze, the copper-coloured elytra with notched grooves, the hind femora dentate. Dwells in the marsh marigold in early spring. (Varies with shiny bronze and dark copper-coloured elytra. The elytra straight, blunt and not narrowed towards the tip. The posterior femora in both sexes dentate.)

***fairmairi*: *Plateumaris bracata* var. *fairmairi* (LeGrand, 1861)**

Described as variation of *Donacia nigra* (synonym of *Plateumaris bracata*) on page 265.

French	English
<i>Donacia nigra</i> var. <i>fairmairi</i>	<i>Donacia nigra</i> var. <i>fairmairi</i>
D[onacia] nigra Fab[ricius]	D[onacia] nigra Fab[ricius]
Dans les fossés du château de Regnault. R.R. [Département de l'Aube]	In the moats of the castle of Regnault. R.R. [Department Aube]
– Var. A. Lacordaire. D. Fairmairi Nobis.	Var. A. Lacordaire. D. Fairmairi Nobis.
Avec le précédent, trouvée une seule fois.	With the previous one [= <i>Donacia nigra</i> , synonymous with <i>Plateumaris bracata</i>], found only once.
Cette variété, mentionnée par M. Lacordaire, comme ayant été trouvée par Dejean, en Dalmatie, se distingue par son abdomen, ses pieds et ses antennes entièrement noirs.	This variety, which was mentioned by M. Lacordaire as having been found by Dejean in Dalmatia, is distinguished by its entirely black abdomen, legs and antennae.

***Plateumaris intermedia* Apfelbeck, 1912**

Described on page 239. Synonym of *P. sericea*.

Latin	English
<i>Plateumaris intermedia</i>	<i>Plateumaris intermedia</i>
<i>D. sericeae</i> L. simillima, antennis crassioribus, earum articulis rubro-variegatis; prothorace longiore, angulis anticis rotundatis, tuberculis lateralibus obtusis; elytris longioribus, planioribus, antrorsum densius punctatis; a <i>D. discolorae</i> Panz. antennarum articulo secundo et tertio longiore (ut in <i>D. sericea</i> L.); prothorace longiore et planiore, supra magis depresso, antrorsum dilatato, ad marginem apicalem latissimo, sericeo, haud vel vix rugoso, subtiliter, aequaliter et confertissime punctato; elytris longioribus et planioribus, subnitidis, confertim punctatis distinguenda.	Very similar to <i>D[onacia] sericea</i> L., antennae thicker, antennomeres red-variegated; pronotum more elongated, anterior corners rounded, lateral tubercles blunt; elytra more elongated, more flattened, in basal part more densely punctate; it can be distinguished from <i>D[onacia] discolorae</i> Panz. by a longer second and third antennal segment (as in <i>D. sericea</i> L.); the pronotum is longer and flatter, upper side more depressed, widening forward, at the apical margin very broad, silky, not or hardly wrinkled, punctured faintly, evenly and densely; elytra longer and more flattened, rather shiny, densely punctured.
Bosnia c. (Jezero) et occ. (Livno).	In central (Jezero) and western Bosnia (Livno).
[Then the very same description is printed in Serbian language in Cyrillic letters. Only the location data are slightly more detailed]:	
Serbian	English
Средња и западна Босна: Језеро код Јајца, Басташи код Ливна (Reiser) на <i>Cladium mariscus</i> -у.	Central and western Bosnia: Jezero near Jajca, Bastaši near Livno ([leg.?] Reiser) on <i>Cladium mariscus</i> .

***Plateumaris lacordairii* (Perris, 1864)**

Described as *Donacia lacordairii* on page 300. Synonym of *P. sericea*.

Latin	English
<i>Donacia Lacordairii</i>	<i>Donacia Lacordairii</i>
Supra viridi-ænea, nitida, juxta suturam subviolacea; subtus plumbeo-ænea, opaca, argenteo-sericea;	Green-bronze coloured above, shiny, somewhat violet near the seam; below lead-grey-bronze, dull, silvery-silky;
capite fortiter, densissime et rugose punctato; antennis nigris, articulis quinque ultimis basi rubris;	the head with strong, very dense and wrinkled punctures; the antennae black, the last five segments red at the base;
prothorace subdeplanato, tenuiter, densissime et fere reticulatim ruguloso, canaliculato, basi angustiore et transversim foveolato; angulis anticis prominentibus;	the prothorax somewhat flattened, delicately, very densely wrinkled, almost like a net, furrowed, narrower at the base and with dimples across; the front corners protruding;
elytris sat convexis præsertim postice, apice truncato-rotundatis, fortiter striato-punctatis; interstitiis striarum transversim strigosis;	the elytra are conspicuously arched, especially at the back, truncated-rounded at the apex, with strong dotted striae; the spaces between the striae striped across;
pedibus crassis, brevibus, femoribus inflatis; posticis fortiter et acute unidentatis.	legs thick, short, femora swollen; the rear ones with a strong and sharp tooth.
Long. 7 mill.	Length 7 mill[imeters]
French	English
Antennes noires, leurs cinq derniers articles rouges à la base; 3 ^e article une fois et demie aussi long que le 2 ^e , plus court que le 4 ^e .	Antennae black, their last five segments red at the base; 3 rd antennomere one and a half times as long as 2 nd , shorter than 4 th .
Tête presque plane, recouverte d'une pubescence soyeuse, argentée; très densément et comme rugueusement ponctuée; front un peu convexe, longitudinalement sillonné.	Head almost flat, covered with silky, silvery pubescence; very densely and roughly punctate; slightly convex forehead, furrowed longitudinally.

Prothorax plus long que large, plus étroit à la base qu'au sommet, peu convexe, canaliculé au milieu, marqué à la base d'une fossette transversale et triangulaire; dilaté sur le côtés au-dessous des angles antérieurs qui sont saillants en forme de dent obtuse et un peu rejetée en arrière; tout couvert de petites rides ou d'une sorte de réticulation très confuse et très serrée. Écusson subtriangulaire, très finement soyeux.	Prothorax longer than wide, narrower at the base than at the top, not very convex, channelled in the middle, marked at the base with a transverse and triangular dimple; dilated on the sides below the anterior angles which are projecting in the form of an obtuse tooth and a bit reflected; all covered with little wrinkles or some sort of very confused, very tight reticulation. Subtriangular dorsal disk, very finely silky.
Élytres à vagues reflets violacés le long de la suture et principalement autour de l'écusson; marquées d'une dépression transversale au tiers antérieur et d'une autre peu visible un peu au-delà du milieu; assez convexes, surtout postérieurement; subtronquées à l'extrémité; fortement striées-punctuées; points der stries très rapprochés; intervalles transversalement ridés.	Elytra with vague purplish reflections along the suture and mainly around the dorsal disk; marked with a transverse depression in the anterior third and another inconspicuous one a little behind the middle; quite convex, especially posteriorly; truncated at the apex; strongly striate-punctate; stitches of very close striae; transversely wrinkled interstices.
Dessous du corps d'un noirâtre un peu bronzé, revêtu d'une pubescence soyeuse, argentée, très serrée.	Underside of the body a little tanned blackish, covered with a silky, silvery, very dense pubescence.
Pattes de la même couleur, courtes épaisses, cuisses très renflées, les postérieures munies d'une forte dent triangulaire.	Legs of the same colour, short thick, very swollen thighs, the posterior ones provided with a strong triangular tooth.
Elle se place dans la même division que la <i>D. sericea</i> L. et elle a de grands rapports avec elle. Elle en diffère néanmoins par de caractères bien tranchés. Les tubercules placés derrière les angles antérieurs du prothorax sont moins saillants; à partir de ces tubercules les côtes sont un peu arqués en dedans dans la <i>sericea</i> et la base finit par avoir la même largeur que le sommet; dans la <i>Lacordairii</i> le prothorax se rétrécit au contraire insensiblement jusqu'à la base en s'arrondissant très légèrement; il est en outre plus court. Les ponts des stries des élytres sont plus rapprochés, et par-dessous tout les pattes sont plus courtes, plus épaisses et les cuisses sensiblement plus renflées.	It is placed in the same division as <i>D. sericea</i> L. to which it is closely related. However, it differs from it by well-defined characters. The tubercles placed behind the anterior angles of the prothorax are less protruding; from these tubercles the ridges are arched inwards in <i>sericea</i> , and the base ends up with the same width as the anterior part; in <i>Lacordairii</i> the prothorax narrows, on the contrary, imperceptibly to the base, rounding out very slightly; it is also shorter. The bridges of the elytral striae are closer together, and below all the legs are shorter and thicker, and the thighs noticeably more swollen.
J'ai pris cette espèce en Espagne, aux bords d'un ruisseau sur la route de la Granja à San Rafaël. Je la dédie à mon illustre ami M. Lacordaire, comme témoignage d'affectueuse admiration pour son caractère et ses travaux.	I caught this species in Spain, on the banks of a stream at the road from La Granja to San Rafaël. I dedicate it to my illustrious friend M. Lacordaire, as a testimony of affectionate admiration for his character and his work.

***Plateumaris mongolica* (Semenov, 1895)**

Described as *Donacia* (subgenus *Plateumaris*) *mongolica* on page 267. Synonym of *P. weisei*.

Latin	English
<i>Donacia (Plateumaris) mongolica</i>	<i>Donacia (Plateumaris) mongolica</i>
♂. Minor, sat debilis, modice convexa, capite, prothorace corporeque subtus obscure viridi-aeneis, nitidis, elytris obscure cupreis, opacis, suturae margine infero postice late patente aeneo-nigro, nitido, pedibus, ore antennisque dilute testaceis, his ad apicem leviter infuscatis, segmentorum abdominalium margine postico plus minusve rufescenti.	♂. Smaller, rather weak, medium convex, head, prothorax and underside of the body dark green-ore-coloured, shiny, elytra dark cupreous, elytra dark copper-coloured, gloomy, the lower margin of the suture, which is wide open at the back, is ore-black, shiny, legs, mouth and antennae are wanly clay-coloured, these are slightly browned towards the apex, the posterior margin of the abdominal segments is more or less reddish.
Antennis dimidium corpus saltem sesqui superantibus, articulo 2° tertio plus quam sesqui brevior, 4° tertium fere 1 ¹ / ₃ superante. Capite confertim punctulato, tenuiter pubescenti, vertice utrinque oculos versus praeterea tenuissime ruguloso, sulco longitudinali medio profunde impresso postice abrupte abbreviato, sulcis juxtaorbitalibus nullis; oculis parvis extrorsum valde prominentibus; temporibus pone oculos breviter inflatis, hos nonnihil amplectentibus, deinde fortiter constrictis: genis diametro oculorum fere aequilongis. Mandibulis validiusculis labrum multo superantibus.	Antennae at least half longer than half the body [antennae $\frac{3}{4}$ total body length], the 2 nd segment more than half shorter than the third one, the 4 th one ca. 1 ¹ / ₃ times longer than the third one. The head is densely punctured, finely hairy, the vertex in addition very finely wrinkled on both sides towards the eyes, the deeply depressed central longitudinal furrow abruptly shortened behind, without furrows next to the eye sockets; the small eyes protruding distinctly outwards; the temples shortly inflated behind the eyes, enclosing them a little, then strongly contracted: the cheeks about the same length as the diameter of the eyes. Mandibles somewhat strong, much longer than the labrum.

<p>Prothorace subquadrato latitudine distincte longiore, lateribus mox pone angulos anticos denticuliformes breviterque extrorsum prominulos leviter tumido et ibi summam latitudinem attingente, dein basin versus sensim vix distincte subangustato, ante angulos posticos non sinuato, his (aspectu desuper) extrorsum paulo prominulis, puncto setigero notatis; apice recte truncato, basi utrinque ad angulos posticos sat fortiter obliquata; disco parum convexo, nitidulo, haud crebre (medio fere disperse) subtiliter punctato, minutissime parce pubescenti, utrinque ad angulum anticum subimpresso subtilissimeque vix distincte ruguloso, paulo ante medium trinque tuberculo indeterminato nitido signato, linea media obsoleta vel omnino oblitterata solum ante basin profunde foveatim impressa.</p>	<p>The almost square pronotum is distinctly longer than wide, slightly swollen on the sides just behind the tooth-shaped and slightly outwards protruding anterior corners, and reaches its greatest width there, then noticeably and vaguely slightly narrower towards the base, not sinuated in front of the posterior corners, these (viewed from above) slightly protruding outwards, marked by a bristle-bearing point; the end truncated straight across, the base on both sides very sharply bevelled towards the rear corners; the disc is slightly convex, slightly shiny, not densely (almost scattered in the middle) finely punctured, with extremely tiny and sparse hairs, slightly dented on both sides towards the front angle with extremely fine and rather indistinct wrinkles, slightly in front of the middle on both sides marked with an indistinct shiny tubercle, the inconspicuous or completely obliterated median line deeply depressed and excavated only in front of the base.</p>
<p>Elytris prothoracis basi duplo latioribus, summa latitudine circiter $1\frac{2}{3}$ longioribus, pone medium levissime ampliatis, deinde ad apicem sat abrupte angustatis, apice singulatim simpliciter angustato-rotundatis, dorso convexiusculis, impressionibus prorsus destitutis, tenuius striato-punctatis, interstitiis fere planis vel vix convexiusculis, confertim alutaceis, subopacis, 1° (juxtaturali) inde ab apice striae juxtascutellaris elongatae valde convexo, calloso-elevato, nitidiusculo, 9° pone humerum plicam crassiusculam efficiente; sutura posteriori fortiter replicata, margine infero laevi, nitido; humeris rectis modice obtusis.</p>	<p>The elytra twice as wide as the base of the pronotum, ca. $1\frac{1}{3}$ times as long as the maximum width, very slightly widened behind the middle, then narrowed rather abruptly towards the end, at the end each one individually simply narrowed-rounded, slightly arched on the back, completely without impressions, with rather narrow punctured stripes, the intervals almost flat or hardly slightly arched, densely leather-like, rather dark, the 1^{st} one (next to the seam) very arched from the end of the extended stripe next to the scutellum, bulging-raised, slightly shiny, the 9^{th} one forming a podgy fold behind the shoulder; the seam is well folded back at the rear, the lower edge is smooth and shiny; the straight shoulders moderately blunted.</p>
<p>Subtus corpore toto nec non pygidio haud dense longiusque subsericeo-cano-pubescentibus. Abdomine confertissime punctulato; segmento basali duobus sequentibus unitis vix longiore, simplici: neque impresso neque tuberculato; segmento anali apice late et fere recte truncato, haud impresso.</p>	<p>Below, the whole body and also the pygidium are not densely covered with quite long, silky grey hairs. The abdomen very densely punctured; the basal segment scarcely longer than the following two together, simple: neither indented nor bulging; at the end the anal segment is truncated broadly and almost straight, not indented.</p>
<p>Pedibus haud longis, validiusculis; femoribus crassis omnibus ad apicem valde inflatis, posticis marginem apicalem segmenti penultimi abdominalis haud vel vix superantibus, infra ante apicem dente valido late triangulari, nonnihil retrorsum directo munitis; tibiis omnibus simplicibus, integris, ad apicem leniter sensimque dilatatis, anticis apice extus breviter subproductis; tarsis articulo penultimo lobis modice elongatis.</p>	<p>Legs not long, quite strong; the thick femora all very expanded towards the end, the rear ones not or hardly exceeding the rear edge of the penultimate abdominal segment, reinforced below before the end with a strong, broad, triangular tooth that points a little backwards; all tibiae simple, complete, slightly and noticeably widened towards the end, the anterior ones shortly and slightly protruding outwards at the end; the tarsi on the penultimate segment moderately lengthened by lobes.</p>
<p>Long. $6\frac{1}{2}$, lat. ad humer. $2\frac{3}{5}$ mm.</p>	<p>Leng[th] $6\frac{1}{2}$, wid[th] at the shoul[ders] $2\frac{3}{5}$ mm.</p>
<p>Mongolia septentr.: vallis fluvii Borchia, orientem versus ab Urga (B. Kaschkarow. 6. VII. 1894). – Specimen unicum ♂ (coll. P. a Semenow). Mera subgeneris <i>Plateumaris</i> C. G. Thoms. ¹⁶⁾ species.</p>	<p>North[ern] Mongolia: valley of the river Borchia, from Urga towards the east (B. Kaschkarow. 6. VII. 1894). – A single specimen ♂ (in) coll. P. of Semenov). A real species of the subgenus <i>Plateumaris</i> C. G. Thoms. ¹⁶⁾.</p>
<p>A <i>Don. abdominalis</i> Oliv. (<i>affinis</i> Kunze) cui proxima, differt imprimis statura debiliore, antennis gracilioribus articulis omnibus magis elongatis, 4° praecedente distincte longiore, prothorace angustiore lateribus pone angulos anticos extrorsum fere denticulatim prominulos fortius inflato, disco parcius punctato, magis lucido, elytris ad apicem magis abrupte angustatis, dorso paulo tenuius striato-punctatis, interstitio primo inde ab apice striae juxtascutellaris calloso-elevato, 9° pone humerum plicam abbreviatam formante, suturae margine infero posteriori magis patente, abdominis segmento basali in ♂ simplici brevique, metasterno haud impresso quoque, femoribus posticis in eodem sexu dente validiore et obtusiore armatis, tibiis gracilioribus, etc.</p>	<p>From <i>Don. abdominalis</i> Oliv. (<i>affinis</i> Kunze) [*]), to which it is closest, it differs above all by the weaker stature, by the more delicate antennae with consistently longer antennomeres, the 4^{th} one clearly longer than the previous one, by the narrower pronotum with sides more swollen behind the anterior corners, almost dentiformly protruding outwards, by the more sparsely dotted, lighter disc, by the elytra more abruptly narrowed towards the end, with a little narrower dot-stripes on the back, by the bulging-raised first interval from the end of the stripe next to the scutellum, by the 9^{th} one forming a shortened fold behind the shoulder, by the lower edge of the seam more gaping further back, by the simple and short basal abdominal segment in the ♂, by the metasternum, which is also not impressed, by the hind femora armed with a stronger and more blunted tooth in the same sex, by the more delicate tibiae, etc. [*]): <i>Donacia abdominalis</i> Olivier is now synonym with <i>Plateumaris bracata</i> and not with <i>P. affinis</i> Kunze.</p>

A <i>Don. consimili</i> Schrank, cui affinis quoque, discedit praesertim iisdem notis atque a <i>D. abdominali</i> . A <i>Don. rustica</i> Kunze praeterea colore antennarum pedumque discrepat.	Above all, from <i>Don. consimilis</i> Schrank, to which it is also closely related, it differs by the same characters as from <i>D. abdominalis</i> . Furthermore, it also differs in the colour of the antennae and legs from <i>Don. rustica</i> Kunze.
A <i>Don. Weisei</i> Duviv. ¹⁷⁾ differt imprimis prothorace disco nitido haud confertim punctato, angulis anticis extrorsum denticulatim prominulis, elytris opacis interstitio primo pone striam juxtascutellarem fortiter callosaelevato, 9° pone humerum breviter plicato. –Facile tamen fieri potest, ut <i>D. mongolica</i> m. nil nisi maris <i>Donaciae Weisei</i> (mihi prorsus ignotae) mera sit aberratio.	From <i>Don. Weisei</i> Duviv. ¹⁷⁾ it differs above all by the shiny and not densely dotted pronotal disc, with tooth-shaped and outwards protruding front corners, by dark elytra with the first interval behind the stripe next to the scutellum, which is very bulging and raised, and the 9 th one behind the shoulder that is briefly folded up. –Nevertheless, it is easily possible that m[y] <i>D. mongolica</i> is just a simple aberration of the male of <i>Donacia Weisei</i> (which is totally unknown to me).
¹⁶⁾ Genus <i>Plateumaris</i> (C. G. Thoms.) Weise, Jacobs. ad gradum subgeneris reducendum esse censeo; nam nonnullae species orientali-asiaticae, imprimis <i>Plateumaris excisipennis</i> Jacobs. (Horae Soc. Ent. Ross., XXVIII, 1894, p. 241), cujus in descriptione auctor sexum speciminis originalis unci indicare verisimiliter invitus neglexit, transitum nimis manifestum ad genus <i>Donacia</i> F. praebere videntur. Ceterum praesumo <i>Donaciam excisipennem</i> (Jacobs.) subgenus proprium constituere.	¹⁶⁾ I think that the genus <i>Plateumaris</i> (C. G. Thoms.) Weise, Jacobs. should be relegated to the category of a subgenus; because a number of East Asian species, above all <i>Plateumaris excisipennis</i> Jacobs. (Horae Soc. Ent. Ross., XXVIII, 1894, p. 241), where the author probably reluctantly failed to indicate the sex of the only original specimen in its description, seems to provide a very clear transition to the genus <i>Donacia</i> F. Incidentally, I suspect that <i>Donacia excisipennis</i> (Jacobs.) establishes its own subspecies.
¹⁷⁾ Duvivier: Ann. Soc. Ent. Belg., XXIX, 1885, Bull., p. CXVI. – Jacobson: Horae Soc. Ent. Ross., XXVI, 1892, p. 435.	¹⁷⁾ Duvivier: Ann. Soc. Ent. Belg., XXIX, 1885, Bull., p. CXVI. – Jacobson: Horae Soc. Ent. Ross., XXVI, 1892, p. 435.

***Plateumaris nigra* (Fabricius, 1792)**

Described as *Donacia nigra* on page 117. Synonym of *P. braccata*.

Latin	English
<i>Donacia nigra</i>	<i>Donacia nigra</i>
6. <i>D. nigra</i> elytris substriatis, abdomine pedibusque rufis.	6. Black <i>D[onacia]</i> with somewhat striped elytra, abdomen, and legs red.
Habitat in Germaniae aquis Dom. Smidt.	Inhabits waters of Germany [according to] Mr. Smidt.
Statura & summa affinitas <i>D. Festucae</i> . Antennae nigrae: primo articulo rufo. Caput & thorax nigra, immaculata, nitidula. Elytra minus striata minusque depressa. Adomen rufum. Pedes rufi femoribus posticis in altero sexu simplicibus in altero dentatis.	Stature and next of kin to <i>D. Festucae</i> *). Antennae black: first segment red. Head & chest black, spotless, shiny. Elytra less striped and less depressed. Abdomen red. Legs red, hind femora simple in one sex, dentate in the other.
*) <i>D. festucae</i> (Fabricius, 1792): 116: synonym of <i>P. sericea</i>	

***Plateumaris obsoleta* Jacobson, 1894**

Described on page 243. Probable synonym of *P. shirahatai*.

Latin	English
<i>Plateumaris obsoleta</i>	<i>Plateumaris obsoleta</i>
E divisione prima opusculi mei (Horae Soc. Ent. Ross. XXVI, p. 433), cujus inter species <i>discolorem</i> Pz. et <i>sericeam</i> L. ponenda.	From the first section of my work (Horae Soc. Ent. Ross. XXVI, p. 433), to be placed between its species <i>discolor</i> Pz. and <i>sericea</i> L.
Convexiuscula, aurichalcea; corpore subtus, capite, scutello, pedibus antennisque argenteo-tomentosis. Cuput [sic! a typing error, it should be: Caput] densissime punctatum, linea media impressa frontis tenui, profunda.	Slightly convex, brass coloured; underside of the body, the head, the scutellum, legs and antennae silvery tomentose. The head extremely densely punctured, the impressed narrow median line in the head deep.
Antennae dimidio corpori longitudine aequales, sed multo magis tenues quam in <i>Pl. discolore</i> , articulo primo crasso, ceteris subtilibus, articulo 2° sesqui brevior quam tertius, 4° hoc sesqui longior, ceteris subaequali; articulorum 2 ⁱ –11 ⁱ basibus rufo-ferrugineis.	Antennae in length equal to half the body, but much thinner than in <i>Pl. discolor</i> , the first segment thick, the others fine, the 2 nd segment is half as short as the third one, the 4 th one by half longer than this one, the rest almost the same; the basis of the 2 nd –11 th segment is reddish-rusty brown.

Prothorax latitudine multo longior, disco subplano, lateribus subparallelis; tuberculo laterali minime convexo, parum determinato; angulis omnino non prominulis, rectis; linea longitudinali disci vix distincta; disco subtilissime remote punctato, inordinate subtiliter et dense ruguloso, nudo, sericeo-opaco (basi nitida excepta).	Prothorax much longer than wide, the disc nearly flat, the sides nearly parallel; lateral tubercles minimally convex, not very pronounced; the angles not a bit protruding, straight; the longitudinal line of the disc scarcely pronounced; the disk very finely widely punctured, irregularly, finely and densely wrinkled, hairless, silky dusky (except the shiny base).
Elytra lateribus subparallelis, a triente ultimo ad apicem rotundato-truncatum angustata, dorso juxta suturam leviter biimpressa, haud fortiter striato-punctata, inter puncta rugulis transversis haud altis ornata, nitida.	The elytra with almost parallel lateral sides, narrowed from the last third to the rounded, truncated apex, slightly impressed twice on the back next to the suture, not strongly striped-punctured, decorated with non-raised transverse wrinkles between the dots, shiny.
Abdomen segmento primo medio plano; segmento anali apice rotundato. Pygidium apice rotundatum.	First segment of abdomen flat in the centre; anal segment apically rounded. The pygidium apically rounded.
Pedes corpori concolores, articulationibus omnibus unguiculisque rufo-ferrugineis; femoribus posterioribus omnino inermibus, subtus solum obtuse angulatis.	The legs with the same colour as the body, all joints and the claws reddish-rusty brown; the hind femora completely unarmed, only bluntly angled below.
Long. 7 mm.	Length 7 mm.
Siberia orientalis: sinus Possiet. Specimen unicum (♂).	East Siberia: Bay of Posyet. Single specimen (♂). [In fact, this is a female specimen. The protruding ovipositor was mistaken for the aedeagus (Geiser 2023: figs 14b, 15b).]

***orientalis: Plateumaris consimilis orientalis* Shavrov, 1948**

Described as subspecies on page 49. Synonym of *P. weisei*.

Latin	English
<i>Plateumaris consimilis orientalis</i>	<i>Plateumaris consimilis orientalis</i>
Corpore supra splendidiore, rugulis striarum interstitiorum elytrarum humilioribus, dente femorum posticorum minore vel obsoleto.	Body shinier above, the wrinkles between the grooves of the elytra lower, tooth on the hind femora smaller or extinct.
Russian	English
Размеры тел и соотношение длин и ширин всех частей те же, что и у типичной формы, но тело значительно более блестящее, благодаря менее грубой скульптуре надкрылий.	The dimensions of the body and the ratio of the lengths and widths of all parts are the same as in the typical form, but the body is much more lustrous due to the less coarse sculpture of the elytra.
Точечные ряды надкрылий менее углублены, поперечные морщины промежутков, как основные так и мельчайшие, выражены менее резко и более сглажены. Пунктировка в основаниях надкрылий более тонкая и менее спутанная. Переднеспица с более резким перехватом за боковыми бугорками.	The dotted grooves of the elytra are less deepened, the transverse wrinkles of the intervals, both the basal and the tiny ones, are less pronounced and smoother. The punctuation at the basis of the elytra finer and less confused. The pronotum with a sharper recess behind the lateral tubercles.
Задние бедра ♀ без зубца или с незначительным бугорком на его месте. Верхняя сторона бронзово – медная с зеленоватым оттенком. Четыре последних брюшных стернита, усики и ноги – краснобурые. Волоски нижней стороны и конечностей золотистые или желтоватые.	Hind femora of ♀ without tooth or with a slight tubercle in its place. The upper side is bronze-copper with a greenish tint. The last four ventral sternites, antennae, and legs are reddish brown. Underside the hairs and limbs are golden or yellowish.
Длина 8 мм, такая же как у типичной формы.	Length 8 mm, like that of the typical form.
Владивосток, Седанка 19.VI.37 3 ♀, Н. Н. Филиппов.	Vladivostok, Sedanka 19.VI.37 3 ♀, N. N. Filippov.
<i>Plateumaris consimilis</i> Schrank в прошлом столетии считался видом, распространенным по всей средней и южной Европе и, кроме того, в Сибири (Якобсон, 1892) и в Японии (Jacoby, 1885) поскольку в литературе были указания для Иркутска (Сольский, около 1870 г.) Урала (Редикорцев, 1908) и Японии (Jacoby, 1885) [originally written: Jacoby], относящиеся к виду <i>Plateumaris discolor</i> Hoppe (= <i>P. consimilis</i> Schrank). Других указаний не были, в промежуточных местностях вид тоже нигде найден не был. Clavareau (1913) и Reitter (1920) давали без изменений те же сведения, что и Якобсон.	In the last century <i>Plateumaris consimilis</i> Schrank was considered as a species distributed throughout central and southern Europe and furthermore in Siberia (Jakobson, 1892) and Japan (Jacoby, 1885), since there were indications in the literature for Irkutsk (Solsky, about 1870), Ural (Redikortsev, 1908) and Japan (Jacoby, 1885) belonging to the species <i>Plateumaris discolor</i> Hoppe (= <i>P. consimilis</i> Schrank). There were no other indications, and the species was not found anywhere in localities in between either. Clavareau (1913) and Reitter (1920) give the same unmodified information as Jacobson.

По категорическому утверждению Колосова (1930)', <i>P. consimilis</i> Schrank есть чисто западноевропейский вид, восточная граница которого (по материалам его коллекции) проходит по территории Польши, а указания на более восточные местонахождения не верны и относятся к другим видам.	According to the categorical assertion of Kolossow (1930), <i>P. consimilis</i> Schrank is a purely Western European species, whose eastern boundary passes through the territory of Poland (according to the materials of his collection), while records from more eastern localities are not correct and refer to other species.
Теперь же нахождение данного вида под Владивостоком вносит полную ясность и подтверждает правильность старых указаний для Иркутска и Японии или во всяком случае очень большую вероятность их.	But now the occurrence of this species near Vladivostok brings complete clarity and confirms the correctness of the old records from Irkutsk and Japan, or at least a very high probability.
Вместе с тем мы имеем теперь сборы <i>P. consimilis</i> Schrank из Черниговской и Полтавской областей и можем считать его видом не только западно-европейским. Указание для Урала (Редикорцев), сделанное по литературным источникам середины прошлого столетия, можно считать лишь вероятным.	At the same time, we now have collections of <i>P. consimilis</i> Schrank from the Chernigov and Poltava regions [both sites are in the Ukraine], so we can consider it as a species not only of Western Europe. The indication for the Ural (Redikortsy), made according to the literary sources from the middle of the last century, can only be considered as probable.
Наличие <i>P. consimilis</i> Schrank на Дальнем Востоке именно в форме особой расы при условии такого большого территориального разрыва представляется вполне естественным. Структурные различия от западно формы в виде большего блеска и меньшей морщинистости надкрылий, дерехвата переднеспинки и более светлого цвета ноги усиков совершенно аналогичны таким же признакам у дальневосточных подвигов других видов донаций, как, например, <i>D. clavipes glabrata</i> Solsky, <i>D. obscura splendens</i> Jacobs. и <i>D. thalassina rufovariegata</i> Jacobs.	The presence of <i>P. consimilis</i> Schrank as a separate race in the Far East seems quite natural given such a large territorial distance. Structural differences from the western form by stronger shine and less wrinkling of the elytra, the more straight-lined pronotum, and a lighter coloration of the antennae are completely analogous to the same characters in the Far Eastern subspecies of other <i>Donacia</i> species, like, for example, <i>D. clavipes glabrata</i> Solsky, <i>D. obscura splendens</i> Jacobs. and <i>D. thalassina rufovariegata</i> Jacobs.
Пробел между ареалами западной и восточной форм, возможно, будет выполнен при более подробном изучении фауны СССР, и мы, быть может, получим довольно непрерывное распространение вида с запада на восток, но это только подтвердит наличие довольно типичного восточного подвида <i>Plateumaris consimilis orientalis</i> .	The gap between the distribution areas of the western and eastern form will probably be filled by a more detailed study of the fauna of the USSR, and we may have a fairly continuous distribution of the species from west to east, but this will only confirm the presence of a rather typical eastern subspecies <i>Plateumaris consimilis orientalis</i> .

***Plateumaris pallipes* (Kunze, 1818)**

Described as *Donacia pallipes* on page 35. Synonym of *P. rustica*.

Latin	English
<i>Donacia pallipes</i>	<i>Donacia pallipes</i>
<i>D. pallipes</i> : thorace subquadrato, planiusculo, subtiliter impresso, punctulato, angulis anticis truncatis, lateribus subsinuato; elytris depressiusculis, rugulosis, punctis striarum profundis, striisque approximatis, apice rotundatis, pedibus pallescentibus.	<i>D. pallipes</i> : the breast somewhat quadrangular, fairly flat, slightly impressed, finely punctured, with truncated front corners, lightly sinuate on the sides; the elytra a little flattened, wrinkled, with deep points in neatly lines, rounded at the apex, the legs paler.

***picipes*: *Plateumaris rustica* var. *picipes* Weise, 1898**

Described as variation of *Plateumaris rustica* on page 180. Synonym of *P. rustica*.

Latin	English
<i>Plateumaris rustica</i> var. <i>picipes</i>	<i>Plateumaris rustica</i> var. <i>picipes</i>
Pedibus piceis vel nigris, geniculis interdum obscure ferrugineis.	Legs pitch-brown or black, knees sometimes dark rubiginous.

German	English
Von rustica habe ich bis jetzt nur ein Stück aus Krain von Stussiner erhalten, welches auf dem Rücken angedunkelte Schenke besitzt, bei den übrigen sind die Beine einfarbig rostroth. Zwischen normal gefärbten Exemplaren fing Herr A. Fiori in der Umgegend von Modena (Emilia: Jala, März 1894) nun auch abweichende Stücke, von denen er mir ein oberseits schwarzes, auf dem Halsschilde bläulich schimmerndes M und 2 W schickte. Bei ihnen sind die Beine pechschwarz', in den Gelenken dunkel rostroth, oder einfarbig schwarz. Es ist möglich, dass diese Varietät auch noch in Deutschland aufgefunden wird.	Until now I have received only one specimen of rustica from Stussiner from Carniola, with femora darkened on their upper side, all others have legs which are uniformly rufous. In the vicinity of Modena (Emilia: Jala, March 1894) Mr. A. Fiori now also caught differing specimens between normally coloured specimens, from which he sent me a ♂ which is black on the upper side and shimmering bluish on the pronotum, and 2 ♀. Their legs are pitch-black, darkly rufous in the joints, or plain black. It is possible that this variety will also be found in Germany.

***Plateumaris planicollis* (Kunze, 1818)**

Described as *Donacia planicollis* on page 34. Synonym of *P. rustica*.

Latin	English
<i>Donacia planicollis</i>	<i>Donacia planicollis</i>
D. planicollis: thorace elongato, subquadrato, planiusculo, leviter impresso et punctato, postice angustato, margine nonnihil producto, lateribus subintegris, linea postica; elytris convexis, rugulosis, distincte punctato-striatis, apice rotundato, pedibus rufescentibus.	D. planicollis: the pronotum elongated, nearly quadrangular, rather flat, slightly impressed and punctured, narrowed posteriorly, the margin slightly convex, the sides reasonably complete, with a posterior line; the elytra arched, wrinkled, with distinct dotted stripes, rounded at the apex, the legs reddish.

***Plateumaris roscida* Weise, 1912**

Described on page 77.

Latin	English
<i>Plateumaris roscida</i>	<i>Plateumaris roscida</i>
Elongata, subdepressa, supra obscuro-aenea, leviter aurichalceocupreo induta, subopaca, sericeo-micans, subtus argenteo-sericea, antennis pedibusque testaceo-variegatis;	Elongate, slightly flattened, upper side dark bronze-coloured, with thin brass-cupreous hairs, slightly dull, silky-lustrous, underside silvery-silky, antennae and legs patterned testaceous;
prothorace subquadrato, basin versus angustato, subtiliter ruguloso-punctato, elytris apice rotundato-truncatis, punctato-striatis, interstitiis dense subtilissime rugulosis, femoribus posticis dente valido armatis.	the prothorax almost square, narrowed towards the base, punctured finely and wrinkly, elytra at the apex roundly truncated, with dotted stripes, intervals densely and very finely wrinkled, hind femora armoured with a stout tooth.
Long. 7,5 mm.	Leng[th] 7.5 mm.
Transbaikalien: Dschitah (Ertl).	Transbaikalia: Chita ([donated by] Ertl).
German	English
Einer <i>Don. thalassina</i> Germ. ähnlich, aber neben <i>Plat. discolor</i> Panz. gehörig, von dieser und <i>sericea</i> L. durch gestreckten, viel flacheren Körper und die ziemlich matte Oberseite sofort zu unterscheiden.	Similar to <i>Don[acia] thalassina</i> Germ., but next to <i>Plat[eumaris] discolor</i> Panz., to be immediately distinguished from this one and <i>sericea</i> L. by the elongated, much flatter body and the rather dull upper side.
Dunkel metallisch braun, mit gelblichem Kupferschimmer, matt seidenartig glänzend, unterseits äußerst fein und dicht weißlich behaart,	Dark metallic brown, with a yellowish cupreous shimmer, matt silky shine, ventrally with extremely fine and dense whitish hairs,
Fühler und Beine dunkel rötlich gelbbraun, das erste Fühlerglied und die Spitze der folgenden Glieder mehr oder weniger weit schwärzlich, die obere Hälfte der Schenkel metallisch grünlich schwarz, die Spitze der Schienen und die Tarsen angedunkelt. Fühler schlank, Glied 3 länger als 2, 4 länger als 3.	antennae and legs dark reddish yellow-brown, the first antennal segment and the tip of the following segments more or less widely blackish, the upper half of the femora metallic greenish black, the apex of the tibiae and of the tarsi darkened. Antennae slender, segment 3 longer than 2, 4 longer than 3.

Thorax länger als breit, hinter dem heraustretenden vorderen Borstenkegel durch einen schwachen, schlecht begrenzten Seitenhöcker etwas erweitert, sodann eine Spur eingeschnürt, endlich bis zur Basis schwach verengt, auf der Scheibe sehr fein und dicht runzelig punktiert, mit einer feinen, verloschenen Mittelrinne. Diese erweitert und vertieft sich hinten und geht hier in einen Quereindruck über.	Thorax longer than wide, slightly widened behind the protruding anterior bristle cone by a weak, poorly defined lateral tubercle, then feebly constricted, finally weakly narrowed till to the base, very finely and densely wrinkled and punctate on the disc, with a fine, obliterated median groove, which widens and deepens towards the base and turns into a transverse impression there.
Flügeldecken äußerst dicht und fein querrunzelig, regelmäßig in Reihen punktiert, mit zwei verloschenen Eindrücken jederseits an der Naht.	Elytra wrinkled extremely densely and finely transversely, regularly punctured in rows, with two obliterated impressions on each side of the suture.

***Plateumaris rustica* (Kunze, 1818)**

Described as *Donacia rustica* on page 31.

Latin	English
<i>Donacia rustica</i>	<i>Donacia rustica</i>
<i>D. rustica</i> : thorace subquadrato, depresso, subimpresso, vage et subtiliter punctato, angulis anticis rotundatis, lateribus integro, linea postica; elytris depressiusculis, subtiliter et obsolete punctato-striatis, interstitiis rugosis, coleopterorum apice rotundato; pedibus rufescentibus. a) Femoribus apice obscurioribus. mas. <i>D. rustica</i> Schüppel in litt. Leptura discolor Marsh. Ent. brit. I. 346; 14. fem. - fusca Marsh. I. c. 349. 20. mas. (secundum specimina a cel. Leachio missa.)	<i>D. rustica</i> : pronotum approximately square, flattened, slightly depressed, punctured sparsely and finely, front corners rounded, sides entire, with a posterior line; the elytra slightly flattened, finely and faintly streaked with dots, the interstices wrinkled, the apex of the elytra rounded; legs reddish. a) The femora darker at the posterior end. Male. <i>D. rustica</i> Schüppel in litt. Leptura discolor Marsh[am] Ent. brit. I. 346; 14. fem[ale] - fusca Marsh[m] I[oco] c[itato] 349. 20. Male. (according to the specimens sent by the known Leach.) [William Elford Leach (1790–1836), a then famous zoologist.]

***Plateumaris sachalinensis* Medvedev, 1973**

Described on page 876. Synonym of *P. weisei*.

Russian	English
<i>Plateumaris sachalinensis</i>	<i>Plateumaris sachalinensis</i>
Бронзово-зеленый или медный, переднеспинка красновато-медая, основания всех члеников усиков, а также основания бедер и голеней рыжле, задние края стернитов брюшка с желто-рыжей окантовкой.	Bronze-green or cupreous, pronotum medium-reddish, bases of all antennal segments, as well as bases of femora and tibiae rufous, posterior margins of abdominal sternites with a yellow-rufous fringe.
Верх слабо блестящий, лобные бугры очень слабые, усики тонкие, длинные, как у <i>P. weisei</i> Duv., задние бедра с очень слабым, едва выступающим зубцом. Вершина пигидия и последний стернит брюшка притупленно округленные. Длина тела 6.6–7.1 мм. Эдеагус с экозаостренной вершиной, снизу блестящий, в сглаженной продольной морщинистости, парамеры значительно не достигают вершины эдеагуса, с перетяжкой у основания.	Upper side slightly shining, frontal tubercles very weak, antennae thin, long, like in <i>P. weisei</i> Duv., hind femora with a very weak, barely protruding tooth. The apex of the pygidium and the last sternite of the abdomen are obtusely rounded. Body length 6.6–7.1 mm. Aedeagus with sharply pointed apex, shining ventrally, with smoothed longitudinal rugosity, parameres do not significantly reach the apex of the aedeagus and are constricted at the base.
Описываемый вид относится к номинативному подроду и наиболее близок к <i>P. obsoleta</i> Jacobs., от которого отличается двупветной окраской ног. От <i>P. weisei</i> Duv. и <i>P. amurensis</i> Wse. отличается окраской ног и слабым зубцом на задних бедрах. Очевидно, вид занимает промежуточное положение между группой <i>P. sericea</i> и группой <i>P. weisei</i> . Надо сказать, что сравнение нового вида с <i>P. obsoleta</i> Jacobs., известного по единственной самке, затруднено тем, что в нашем распоряжении имелись только самцы.	The described species belongs to the nominative subgenus [<i>Plateumaris</i> was regarded as subgenus of <i>Donacia</i> by some authors] and is closest to <i>P. obsoleta</i> Jacobs. From <i>P. weisei</i> Duv. and <i>P. amurensis</i> Wse. it differs in the coloration of the legs and a weak tooth on the hind femora. Obviously, the species occupies an intermediate position between the <i>P. sericea</i> group and the <i>P. weisei</i> group. It must be said that the comparison of the new species with <i>P. obsoleta</i> Jacobs., known from a single female, is difficult, because we had only males at our disposal.
Сахалин: Южно-Сахалинск, 12 VII 1955 (голотип) и 10 VII 1955 (2 паратипа); сбор Н.Н. Филиппова.	Sakhalin: Yuzhno-Sakhalinsk, 12 VII 1955 (holotype) = and 10 VII 1955 (2 paratypes); collection H.H. Filippova.

***Plateumaris sericea* (Linnaeus, 1758)**

Described as *Leptura sericea* on page 397. First description in Linnaeus (1758); description of additional characters in Linnaeus (1760) below.

Latin	English
<i>Leptura sericea</i>	<i>Plateumaris sericea</i>
INSECTA COLEOPTERA. Leptura.	INSECTA COLEOPTERA. Leptura.
180. LEPTURA. <i>Antennæ setaceæ.</i> <i>Elytra apicem versus attenuata.</i> <i>Thorax teretiusculus.</i>	180. LEPTURA. Antennæ setaceous. Elytra narrowed toward the apex. Thorax terete [elongated and rounded].
<i>Thorace ovato s. antrorsum oblongiusculo angustiore. Elytris apice truncatis.</i>	Thorax egg-shaped or toward anterior part elongated-narrowed. Apex of the elytra truncated.
sericea. 5. L. viridi-cærulea, elytris subfastigiatis.	sericea. 5. green-blue L[eptura], with rather bevelled elytra.
<i>Habitat in Europa.</i>	Lives in Europe.

Description of additional characters on page 196.

683. LEPTURA <i>sericea</i> Habitat apud nos rarius.	683. LEPTURA <i>sericea</i> [starts with the same text as in Linnaeus (1758) and additional:] Lives with us rarer. [with us = in Sweden]
<i>DESCR. Corpus</i> magnitudine Lept. aquaticæ, sed cæruleum, nitens totum. <i>Antennæ</i> nigræ vix corporis longitudine. <i>Thorax</i> quasi medius inter Lepturas & Cincindelas. <i>Elytra</i> punctato-striata.	<i>DESCR[PTION]</i> Same size of the <i>body</i> as Lept[ura] aquatica, but blue, totally shiny. The black <i>antennæ</i> scarcely as long as the body. The <i>thorax</i> more or less median between Leptura and Cincindela [species]. <i>Elytra</i> with dotted stripes.

***Plateumaris sibirica* (Solsky, 1871)**

Remark: "Solsky, 1872" is wrong. For details see Geiser (2023).

Described as *Donacia sibirica* on page 245. Synonym of *P. sericea*.

Latin	English
<i>Donacia sibirica</i>	<i>Donacia sibirica</i>
Oblongo-ovata, supra varicolor, viridi vel cupreo-metallica, subtus aureo-holosericæ; prothorace elongato, angulis anterioribus acute extrorsum prominulis, utrinque antice tuberculato, supra planiusculo, basi leviter impresso, subtiliter coriaceo, obsolete canaliculato; elytris convexis, apice conjunctim rotundatis, vix impressis, punctato-striatis, interstitiis transversim rugosis; femoribus posterioribus subtus dente valido armatis. Long. 7–8 mlm.	Elongated-ovate, with varying colours above, green- or copper-metallic, golden-silky below; Prothorax elongated, the front angles pointed outwards, bulging on both sides ahead, almost flat at the top, slightly impressed at the base, finely leathery, with a faint groove; elytra convex, rounded together at apex, scarcely impressed, with dotted stripes, the interstices wrinkled across; hind femora reinforced with a strong tooth below. L[ength] 7–8 mm.
French	English
Voisine de la <i>D. sericea</i> L. à côté de laquelle elle doit aussi prendre place; elle lui ressemble par son habitus général, la forme et la sculpture des élytres, mais elle est plus petite, moins obèse, à antennes plus grêles et plus allongées; les mandibules, sauf la base et l'extrémité sont ainsi que le palpes, moins l'extrémité des articles, d'un rouge ferrugineux. La tête, l'écusson et tout le dessous sont couverts d'une fine pubescence soyeuse dorée, le corselet et les élytres en dessus tantôt cuivreux tantôt d'un vert bronzé.	Closely related to <i>D. sericea</i> L., next to which it must also take place; it resembles it by its general habitus, the shape and the sculpture of the elytra, but it is smaller, less obese, with more green and more elongated antennae; the mandibles except the base and the apex, as well as the palps except the apex of the joints, are ferruginous red. The head, the scutellum and all the underside are covered with fine golden silky hairs, the pronotum and the elytra above sometimes coppery, sometimes brown-green.

La tête plus finement chagrinée que chez <i>D. sericea</i> avec sillon frontal plus faible; les yeux plus globuleux et plus saillants, l'étranglement postoculaire plus fort. Les articles des antennes allongés, 3 plus long que 2, mais plus court que les suivants.	The head more finely shagreened than in <i>D. sericea</i> with a weaker frontal groove; eyes more protruding and more prominent, with a stronger postocular constriction. The antennomeres are elongated, the 3 rd one longer than the 2 nd one, but shorter than the following ones.
Le corselet comme chez <i>D. sericea</i> L., mais avec les angles antérieurs très pointus et saillants en dehors; sa surface est plus densément et plus finement rugueuse, subopaque, avec un très faible sillon au milieu et faiblement impressionnée près de la base. Les points des tries des élytres sont plus serrés, les stries elles mêmes plus profondes, les intervalles plus convexes et beaucoup plus fortement transversalement rides.	The pronotum as in <i>D. sericea</i> L., but with the very pointed anterior angles protruding outside; its surface is more densely and more finely rough, subopaque, with a very weak groove in the middle and weakly impressed near the base. The punctures of the rows on the elytra are more densely packed, the stripes themselves deeper, the interstices more convex and much more strongly wrinkled transversely.
Irktsk, VII.	Irkutsk, VII. [July? The meaning of "VII." is unclear; no date or even year of collection given in the first description.]

***Plateumaris sulcifrons* Weise, 1900**

Described on page 267. Synonym of *P. rustica*.

Latin	English
<i>Plateumaris sulcifrons</i> ♀:	<i>Plateumaris sulcifrons</i> ♀:
Oblonga, convexiuscula, supra aenea, subtus piceo-nigra, griseo-sericea, antennis, tibiis tarsisque obscure rufescentibus, fronte late et profunde sulcata, prothorace quadrato, subtilissime pubescente, ante basin obsolete constricto, disco planiusculo, nitido, sat crebre punctato, canalicula media antice posticeque profundiore impresso, tuberculo obsolete utrinque, subpolito, elytris punctato-striatis, interstitiis transversim strigosis, femoribus inermibus.	Long, slightly convex, bronze coloured above, below jet-black, silky-grey, the antennae, tibiae and tarsi dark reddish, the frons with a wide and deep groove, the prothorax square, very finely pubescent, very slightly constricted before the base, disc almost flat, shiny, rather densely punctured, the impressed middle groove deepened ahead and behind, the tubercles on both sides hardly perceptible, slightly smoothed, the elytra with dotted stripes, intervals narrow in width, the femora unarmed.
Long. 8–9 mm.	Leng[th] 8–9 mm
Zeitun (Staudinger).	Zeitun ([leg.] Staudinger).
Var. a. Antennis pedibusque testaceis.	Var[iation] a. Antennae and legs testaceous.
German	English
Der <i>Plat. rustica</i> und <i>affinis</i> ähnlich, neben letztere zu stellen, gestreckter als beide, durch die tiefe und breite Stirnfurche, deren Seiten hohe Längswülste bilden, das glänzende Halsschild, dessen beiderseits abgekürzte Mittelrinne am Anfange und Ende tief und scharf, in der Mitte flach ist und neben der sich jederseits ein sehr flacher, spiegelglatter Höcker befindet, sowie die völlig ungezähnten Hinterschenkel sicher verschieden.	Similar to <i>Plat. rustica</i> and <i>affinis</i> , to be placed next to the latter, more elongated than both, certainly different due to the deep and broad frontal furrow, whose sides form high longitudinal ridges, the shiny pronotum, whose median groove, which is shortened on both sides, is deep and sharp at the beginning and the end, flat in the middle, and next to which there is a very flat, mirror-smooth tubercle on each side, as well as the completely unarmed hind femora.

***Plateumaris tenuicornis* Balthasar, 1934**

Described as *Plateumaris (Juliusina) tenuicornis* on page 128. Synonym of *P. consimilis*.

German	English
<i>Plateumaris tenuicornis</i>	<i>Plateumaris tenuicornis</i>
Der <i>Pl. consimilis</i> Schrank äußerst nahestehende Art, mit ihr auch wahrscheinlich bisher vermengt.	A species very closely related to <i>Pl. consimilis</i> Schrank, with which it has also probably been confused till now.
Kopf sehr dicht und fein punktiert, mit einer scharfen, länglichen Rinne, die Erhabenheiten an der Wurzel der Fühler nur mäßig, die Augen sehr stark vorgequollen, die Schläfen stark entwickelt, mächtig hervorragend, nach hinten deutlich konvergierend. Die Halspartie stark eingeschnürt, daher auffällig akzentiert. Fühler sehr schlank, die einzelnen Glieder zur Spitze nur mäßig verstärkt.	Head punctured very densely and finely, with a sharp, elongated groove, the elevations at the base of the antennae are only moderate, the eyes are very protruding, the temples are well developed, powerfully prominent, clearly converging towards the base. The neck area is severely constricted, therefore conspicuously accentuated. Antennae very slender, the individual segments only moderately widened towards the tip.

Halsschild mit einer ziemlich deutlich angedeuteten Mittelfurche, auf der Scheibe nicht besonders dicht, aber ziemlich fein punktiert, dazwischen äußerst fein chagriniert, nur an den Seiten mit kaum wahrnehmbaren anliegenden Härchen (erst bei der Vergrößerung, 40×, Zeiß, binokulares Mikroskop) besetzt. Die Seitenbeulen ziemlich stark entwickelt, die Seiten nach hinten stärker zusammenlaufend, die Vorderwinkel spitzig vorragend.	Pronotum with a fairly clearly indicated central furrow, punctured on the disc not particularly densely, but quite finely, extremely finely shagreened in between, only on the sides overgrown with barely perceptible flat small hairs (only by magnification, 40×, Zeiss, binocular microscope). The side tubercles fairly well developed, the sides tapering more towards the end, the front angles pointedly prominent.
Flügeldecken ziemlich fein in Längsreihen punktiert, die Zwischenräume sehr fein und sehr dicht quengerunzelt, zur Basis vollkommen flach, gegen die Spitze mäßig gewölbt. Unterseite seidenglänzend, dicht, kurz, anliegend behaart.	Elytra rather finely punctured in longitudinal rows, the intervals very finely and very densely wrinkled transversely, completely flat at the base, moderately convex towards the apex. Underside silky shiny, dense, short, hairy.
Hinterschenkel nur mit kleinem Zähnen (beim ♀), die Schienen verhältnismäßig schlank.	Hind femora only with small teeth (♀), the tibiae relatively slender.
L. 6.5 mm	L[ength] 6.5 mm
Oberseite grün, ziemlich matt erscheinend, Beine und Fühler hell gelbrot.	Upper surface green, appearing rather dull, legs and antennae pale yellow-red.
Bosnien, Dol. Tuzla, Em. Fritsch leg.	Bosnien, Dol[na] Tuzla, Em[merich] Fritsch leg.
Von der sehr verwandten Art <i>Pl. consimilis</i> Schrank durch folgende Merkmale ziemlich schwer, aber sicher zu unterscheiden: Fühler auffallend schlanker, Augen sehr stark vorgequollen, die Schläfen nach hinten konvergierend, nicht parallel und viel mehr akzentiert, Hals sehr deutlich stärker eingeschnürt, schmaler, die Lateralbeulen des Halsschildes deutlicher, oben tiefer abgegrenzt, der Halsschild schmaler, nach hinten stärker zusammenlaufend. Außerdem sind die Vorderwinkel mehr seitlich gerichtet und spitziger. Die Flügeldecken bei der neuen Art (im Falle, daß die Skulptur vollkommen konstant ist) scheinen viel feiner und dichter skulptiert zu sein. Im ganzen subtiler gebaut und kleiner.	Rather difficult to distinguish but surely from the very related species <i>Pl. consimilis</i> Schrank by the following characters: antennae noticeably slimmer, eyes very much bulging, temples converging backwards, not parallel and much more accentuated, neck much more constricted, narrower, the lateral bulges of the pronotum more distinct, more deeply demarcated above, the pronotum narrower, converging more towards the end. In addition, the front angles are more laterally directed and more pointed. The elytra in the new species (in case the sculpture is perfectly constant) appear to be much finer and more densely sculptured. On the whole built more subtly and smaller.

Bechyné (1942) wrote in a paragraph that *Plateumaris tenuicornis* Balthasar looks the same as *P. consimilis*. This article was ignored for decades, perhaps because it was printed in Czech and Latin. Here the part of that article that deals with *P. tenuicornis* in Latin is copied and translated into English.

Latin	English
De variatione <i>Plateumaris consimilis</i> Schrank. (Col. Donaciidae.)	About the variability of <i>Plateumaris consimilis</i> Schrank. (Col. Donaciidae.)
In opusculo hoc recensionem <i>Plateumaris tenuicornis</i> Balthasar, Entom. Nachrichtenbl. VIII, 1934, pp. 128–129 affero. Secundum exempl. quae ante oculos habeo, <i>Pl. consimilis</i> et <i>Pl. tenuicornis</i> haud specificè differunt. Variat enim <i>Pl. consimilis</i> in characteribus sequentibus: in longitudine corporis, in convexione oculorum, in forma temporum, in forma singulorum articulorum antennarum, in punctatione capitis, prothoracis elytrorumque nec non in forma angulorum anticorum pronoti, in dentibus femorum posteriorum etiamque in colore species haec maximam variationem demonstrat.	In this work I provide a review of <i>Plateumaris tenuicornis</i> Balthasar, Entom. Newsletter VIII, 1934, pp. 128–129. According to the specimens on hand, there are no typical differences between <i>Pl. consimilis</i> and <i>Pl. tenuicornis</i> . That is to say <i>Pl. consimilis</i> varies in the following characters: In the length of the body, in the curvature of the eyes, in the shape of the temples, in the shape of the individual antennal segments, in the dotting of the head, the prothorax and the elytra and also in the shape the front angles of the pronotum, in the teeth of the hind femora and also in the colouring this species shows a very large variability.

Plateumaris weisei (Duvivier, 1885)

Described as *Donacia* (*Plateumaris*) *weisei* on page cxvi [116].

French	English
<i>Donacia weisei</i>	<i>Donacia weisei</i>
Corps oblong, rétréci en arrière, d'un bronzé verdâtre ou d'un violet foncé, couvert en dessous d'une pubescence d'un gris argenté assez dense, avec les pattes, les antennes et la bouche ferrugineuses; corselet allongé, presque plan en dessus, très-rétréci en arrière, sillonné à la base, densément ponctué; élytres allongées, ponctuées-striées, à intervalles ridés transversalement, peu convexes, rétrécies en arrière.	Body elongated, back narrowed, greenish-brown or dark purple, ventrally covered with a fairly dense silvery-grey pubescence, legs, antennae and mouth rufous; pronotum elongated, almost flat above, very narrow behind, furrowed at the base, densely punctured; elytra elongated, with punctured stripes, at the intervals transversely wrinkled, not very convex, narrowed behind.
♂ Plus petit, étroit, allongé; antennes des $\frac{2}{3}$ de la longueur du corps. ♀ Plus grande, large, robuste; antennes de la $\frac{1}{2}$ de la longueur du corps. Long. 7 to 7 $\frac{3}{4}$ mill. – Sibérie (H. Deyrolle).	♂ Smaller, narrow, elongated; antennae $\frac{2}{3}$ the length of the body. ♀ larger, broad, sturdy; antennae $\frac{1}{2}$ the length of the body. L[ength] 7 to 7 $\frac{3}{4}$ mm – Siberia (H. Deyrolle).
♂ Corps allongé, étroit, rétréci en arrière, d'un beau vert bronzé ou d'un violet foncé en dessus. Bouche ferrugineuse. Tête marquée d'un profond sillon longitudinal plus ou moins prolongé en arrière, finement rugueuse, profondément ponctuée. Yeux noirs, assez saillants.	♂ Body elongated, narrow, back narrowed, of a beautiful bronze-green or dark purple above. Mouth rufous. Head marked with a deep longitudinal groove more or less long, finely rugose, deeply punctured. Black eyes, rather prominent.
Antennes des $\frac{2}{5}$ de la longueur du corps, ferrugineuses, à art. 3–4 subégales, le 3 ^e (= third) cependant un peu plus court et plus robuste que le suivant. Prothorax un peu plus long que son plus grand diamètre transversal et assez fortement rétréci en arrière; coupé carrément en avant, légèrement arrondi et subsinué à la base, à angles peu distincts; angles antérieurs suivis en arrière d'un renflement arrondi, occupant les $\frac{2}{5}$ des côtés, nettement limité en dessous par une dépression assez marquée provoquant en cet endroit un rétrécissement du corselet; disque presque plan, couvert de points, enfoncés, très-serrés et confluent, sans sillon dorsal, ayant, près de la base, un sillon transversal anguleux n'atteignant pas les côtés.	Antennae $\frac{2}{5}$ of body length, rufous, with antennomeres 3–4 nearly equal, the 3 rd one however a little shorter and more robust than the next one. Prothorax slightly longer than its greatest transversal diameter and quite fiercely narrowed posteriorly; cut squarely in front, slightly rounded and emarginate at the base, with slightly distinct angles; anterior angles followed behind by a rounded swelling, occupying $\frac{2}{5}$ of the sides, clearly limited below by a fairly marked depression causing in this spot a narrowing of the pronotum; disc almost flat, covered with dots, sunken, very close and confluent, without a dorsal groove, near the base with an angular transverse groove not reaching the sides.
Ecusson en triangle curviligne, ponctué. Elytres oblongues, très-rétrécies en arrière, finement ponctuées-striées, à points très rapprochés; intervalles entre les stries à peine relevés, couverts de fines rugosités transversales. Dessous coloré comme le dessus, avec l'extrémité abdominale ferrugineuse, couvert d'une pubescence d'un gris argenté assez dense. Pattes ferrugineuses, cuisses postérieures légèrement renflées, munies près de leur extrémité d'une dent triangulaire de dimension variable.	Scutellum punctured. Elytra elongated, distinctly narrowed behind, finely punctured-striated, with very close dots; intervals between the stripes barely raised, covered with fine transverse wrinkles. Underside coloured like above, with a rufous abdominal apex, covered with a fairly dense silvery grey pubescence. Legs rufous, hind femora slightly bulging, provided near to their end with a triangular tooth of variable size.
♀ Forme plus robuste, corselet relativement plus large, antennes n'atteignant que la moitié de la longueur du corps.	♀ Shape more robust, pronotum relatively wider, antennae reaching only half the length of the body.
Cette espèce est très-voisine de <i>D. discolor</i> Hoppe; elle en diffère par sa forme plus svelte, plus étroite, sa taille plus petite, son corselet plus allongé, plus rétréci en arrière, avec ses côtés non régulièrement arrondis mais renflés légèrement sur le premier tiers, par l'absence de sillon longitudinal sur le prothorax, par ses élytres plus étroites et la dent triangulaire des fémurs postérieurs moins saillante.	This species is closely related to <i>D. discolor</i> Hoppe [= synonymous with <i>Plateumaris consimilis</i> Schrank]; it differs from it by its more slender, narrower shape, its smaller size, its more elongated pronotum which is more narrowed behind, with its sides not regularly rounded but slightly swollen on the first third, by the absence of a longitudinal groove on the prothorax, by its narrower elytra and the less prominent triangular tooth of the hind femora.
Je dédie cette espèce à notre collègue, M. Julius Weise de Berlin, à qui la science entomologique est redevable de sérieux travaux sur les Phytophages.	I dedicate this species to our colleague, Mr. Julius Weise from Berlin, to whom entomological science is indebted for serious work on Phytophages.

Discussion

There are ten Palaearctic *Plateumaris* species regarded as valid: three of them were described in English (*P. akiensis*, *P. constricticollis*, *P. shirahatai*), six in

Latin (*P. amurensis*, *P. bracata*, *P. consimilis*, *P. roscida*, *P. rustica*, *P. sericea*), and one (*P. weisei*) was originally described in French. In general, most of the original descriptions of *Plateumaris* taxa are in Latin or began with a Latin diagnosis at least, and further explanations were then added in German, Russian, or French in most cases.

In addition to the first descriptions of the valid species in the Palaearctic, another 19 original descriptions are presented here with their translations and the species names published therein are now regarded as synonyms. Mostly, these are names which were synonymized or their synonymisation was confirmed in Geiser (2023). This list is not complete, because more than 70 names are now known to be allocated to one of the ten valid *Plateumaris* species. We intend to continue publishing translations of original descriptions of Donaciinae taxa. Furthermore, we encourage other colleagues to do the same in their areas of expertise.

The Latin first description of the genus *Plateumaris* established by Thomson (1859) and its translation are also given here. At first, Donaciinae species were assigned to the genus *Leptura* by Linnaeus (1758). Later, Fabricius (1775) established the genus *Donacia*, but did not change the genus name of *Leptura sericea*. Later, some authors described *Plateumaris* species with *Donacia* as the genus name, even after Thomson had established the name *Plateumaris*. Some authors regarded *Plateumaris* only as a subgenus of *Donacia*, and these opinions are reflected in the first descriptions. For more details see Geiser (2023).

Acknowledgements

Although many original descriptions printed in the 18th or 19th centuries are available online today, we benefitted from the huge literature collection about Chrysomelidae of Jan Bezděk (Brno, Czechia). Wolfgang Brunnbauer (Vienna, Austria), the former librarian of the Natural History Museum Vienna, tracked down literature that seemed to be unavailable. We also had additional linguistic help from Gloria Geiser (Salzburg, Austria) with French and from Irmgard Geiser (Salzburg, Austria) with Slavic languages. Many thanks to all of them. We would also like to thank the editorial team, especially Caroline Chaboo (Lincoln, Nebraska, USA), the reviewer Michael Schmitt (Greifswald, Germany) and an anonymous reviewer for their advice to improve our manuscript, and Nathalie Yonow (Swansea, United Kingdom) for the linguistic corrections.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

No funding was reported.

Author contributions

Elisabeth Geiser: translation of all original descriptions (some of them in German) to English language. Remigius Geiser: translation of all original descriptions from Latin to German language.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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