ZooKeys 1297: 247–268 (2026)
DOI: 10.3897/zookeys.1297.209749

Research Article

# The firefly genus *Reductodrilus* Pic, 1943 (Coleoptera, Lampyridae) in the Philippines

Gabriela Packova[1], Oscar Vorst[2], Michael F. Geiser[3], Oliver Keller[4], Milada Bocakova[5], Robin Kundrata[1]

1 *Department of Zoology, Faculty of Science, Palacky University, 17. listopadu 50, 77900 Olomouc, Czech Republic*
2 *Naturalis Biodiversity Center, Darwinweg 2, 2333 CR, Leiden, Netherlands*
3 *Natural History Museum, London SW7 5BD, UK*
4 *Microbes, Parasites, and Biodiversity Initiative (MPABI), Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI 48108, USA*
5 *Department of Biology, Faculty of Education, Palacky University, Purkrabska 2, 77900 Olomouc, Czech Republic*

*Corresponding author: Robin Kundrata (robin.kundrata@upol.cz)*

## Abstract

The genus *Reductodrilus* Pic, 1943 has hitherto been considered monotypic, comprising a single described species from Borneo. Here, *Reductodrilus* from the Philippines is revised and three endemic species recognized. *Reductodrilus longelytratus* Packova & Kundrata, **sp. nov.** and *Reductodrilus maculatus* Packova, Vorst & Kundrata, **sp. nov.** are described. Furthermore, *Dodecatoma testaceiceps* Pic, 1924 (formerly placed in Rhagophthalmidae) is transferred to Lampyridae as *Reductodrilus testaceiceps* (Pic, 1924), **comb. nov.**, and *Ototretadrilus philippinus* Wittmer, 1941 established as its new junior synonym. In addition, a lectotype is designated for *Dodecatoma testaceiceps*. This revision improves our understanding of the poorly known Southeast Asian Ototretinae and demonstrates that the diversity of Philippine Ototretinae has been substantially underestimated.

**Key words:** Distribution, Elateroidea, Oriental Realm, paedomorphosis, Rhagophthalmidae, taxonomy

Academic editor: Vinicius S. Ferreira
Received: 29 July 2026
Accepted: 11 October 2026
Published: 11 November 2026

ZooBank: https://zoobank.org/C568B16D-4301-4CAD-9ADF-4D533278259F

Citation: Packova G, Vorst O, Geiser MF, Keller O, Bocakova M, Kundrata R (2026) The firefly genus *Reductodrilus* Pic, 1943 (Coleoptera, Lampyridae) in the Philippines. ZooKeys 1297: 247–268. https://doi.org/10.3897/zookeys.1297.209749

Copyright: © Gabriela Packova et al. This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0).

## Introduction

The diversity, biology, and evolution of bioluminescent elateroid beetles have received considerable attention in recent years (Li et al. 2021; Powell et al. 2022; Yang et al. 2023; Ferreira et al. 2024; Zhu et al. 2024; for a review, see Kundrata 2026). This is especially true for Lampyridae (fireflies), with numerous studies devoted to their phylogeny, fossil record, classification, and systematics during the past decade (e.g., Martin et al. 2017, 2019; Ballantyne et al. 2019; Chen et al. 2019; Ferreira et al. 2019, 2020; Ge et al. 2021, 2022; Silveira et al. 2021; Bocakova et al. 2022; Roza et al. 2022, 2024; Zaragoza-Caballero et al. 2023; Cai et al. 2024; Kazantsev 2024; Yang et al. 2024; Campello-Gonçalves et al. 2025; Fu and Ballantyne 2025; Yuan et al. 2026). However, some groups, such as Ototretinae, are less studied than others.

Ototretinae are a small subfamily of fireflies with approximately 200 species classified in 21 genera (Keller 2024; Yang et al. 2024; Kundrata 2026). They are most diverse in the Oriental realm (Keller 2024). The limits and classification

of Ototretinae have undergone dramatic changes since the establishment of the group (Crowson 1972; McDermott 1964; Branham and Wenzel 2003; Janisova and Bocakova 2013; Martin et al. 2019). The latest generic revision and classification was published by Janisova and Bocakova (2013) who recognized 18 genera in Ototretinae. Later, three more genera have been added (Jeng and Engel 2014; Bocakova and Bocak 2016; Kundrata et al. 2022). Little is known about the biology and ecology of this group, and larvae and females have been described only for a few genera. Among the genera for which females are known, female morphology varies considerably, ranging from fully winged forms resembling males to completely larviform females (e.g., Kawashima et al. 2005; Janisova and Bocakova 2013; Yiu and Jeng 2018). Bioluminescence has been documented in only a few genera and remains unreported in most members of the group (Janisova and Bocakova 2013).

*Reductodrilus* Pic, 1943 is one of the least-known genera of Ototretinae. It was established for a single species and one variety from northern Borneo (Pic 1943). The genus was originally placed in the broadly defined family Drilidae (Pic 1943; Wittmer 1948). After Crowson (1972) transferred most drilid genera to other families, including Lampyridae, Lycidae, Omethidae, and Rhagophthalmidae, the systematic position of *Reductodrilus* remained uncertain. In their revision of the Himalayan rhagophthalmid genus *Pseudothilmanus* Pic, 1918, Kundrata and Bocak (2011) listed *Reductodrilus* in Rhagophthalmidae without further comment. Finally, Kundrata et al. (2022) transferred the genus to Lampyridae: Ototretinae.

During the preparation of the annotated catalogue of Rhagophthalmidae (Kundrata et al. 2022), we recognized that *Dodecatoma testaceiceps* Pic, 1924 from the Philippines is not a rhagophthalmid but a member of Lampyridae: Ototretinae. Subsequent examination of lampyrid material deposited in the collection of the Naturalis Biodiversity Center in Leiden indicated that this species might be conspecific with *Ototretadrilus philippinus* Wittmer, 1941 and that these taxa should be accommodated in *Reductodrilus*. This finding prompted us to examine additional specimens of *Reductodrilus* from several museum collections and to conduct a taxonomic review of the genus in the Philippines.

## Materials and methods

Images of habitus and main diagnostic characters were photographed using a digital camera Canon EOS M6 Mark II attached to a stereoscopic microscope Olympus SZX12 (Figs 1–3, 7, 10) or a Zeiss Discovery V12 stereomicroscope equipped with an Axiocam digital camera (Figs 4–6, 8, 9). Stacks of photographs were combined using the software Helicon Focus Pro (version 7.6.4, Kharkiv, Ukraine). Extensive cleaning of the type specimens' surfaces was avoided to prevent any potential damage to the unique individuals. The genitalia were dissected after a short treatment in hot 10% KOH. The measurements were taken with a scale bar in an eyepiece (Figs 1–3, 7, 10) or directly in the AxioVision software (Figs 4–6, 8, 9). Body length was measured from the frons to both the apex of elytra (since abdomen is partially exposed and highly flexible) and the apex of abdomen, the body/elytral width at humeri, the head width including eyes, the antennomere length medially and without the serration/

ramus; the antennomere width at widest place across the serration/ramus; the pronotal length at midline, the pronotal width at the widest part, the scutellar shield length at midline, the scutellar shield width at the widest part, the aedeagus length medially from base to the apex of median lobe, and the aedeagus width at the widest part of phallobase. We follow the classification of Lampyridae used by Keller (2024) and subsequently adopted by Kundrata (2026). Label data were cited verbatim. The examined specimens are deposited in the following collections: Museum National d'Histoire Naturelle, Paris, France (**MNHN**), Naturalis Biodiversity Center, Leiden, The Netherlands (**RMNH**), Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Berlin, Germany (**MFNB**), and Naturhistorisches Museum Basel, Switzerland (**NHMB**). We follow Recommendation 73F of the Code (ICZN 1999) and provide lectotype designation to fix the species identity for *Dodecatoma testaceiceps* Pic, 1924.

## Systematics

### Genus *Reductodrilus* Pic, 1943

Figs 1–10

*Reductodrilus* Pic, 1943: 9.

**Type species.** *Reductodrilus nigroapicalis* Pic, 1943; by monotypy.

**Diagnosis.** *Reductodrilus* can be distinguished from all other genera of Ototretinae *sensu* Janisova and Bocakova (2013) by the following combination of characters: antennae strongly serrate to weakly pectinate; maxillary and labial palpi digitiform, simple, with terminal palpomeres not distinctly enlarged; posterior pronotal angles without a circular pit; elytra lack sutural coadaptation, each elytron dehiscent distally, abdomen partially exposed; median lobe and parameres distinctly elongate; and phallobase relatively short and transverse. For comparative information on the morphology of other ototretine genera, see Janisova and Bocakova (2013).

**Composition and distribution.** Four described species (one comprising two subspecies) are known from Borneo and the Philippines (see List of species below).

**Literature.** Pic (1943: 9): original description [in Drilidae]; Wittmer (1948: 116): catalogue [in Drilidae]; Kundrata and Bocak (2011: 57): remark [in Rhagophthalmidae]; Kundrata et al. (2022: 58): taxonomic remark, transfer from Rhagophthalmidae to Ototretinae.

### *Reductodrilus longelytratus* Packova & Kundrata, sp. nov.

https://zoobank.org/F1622696-0B0F-4021-96B1-E73847996C36

Figs 1–3

**Type material. *Holotype*:** male, "Philippinen Luzon M. Balbalasan // S Boettcher III. 1918" (MFNB).

**Type locality.** Philippines: Luzon, Balbalasang [Kalinga province, Balbalasang – Balbalan National Park, Cordillera Central mts., ~ 950 m, 17°29'N, 121°03'E; Bílý and Kubáň 2012].

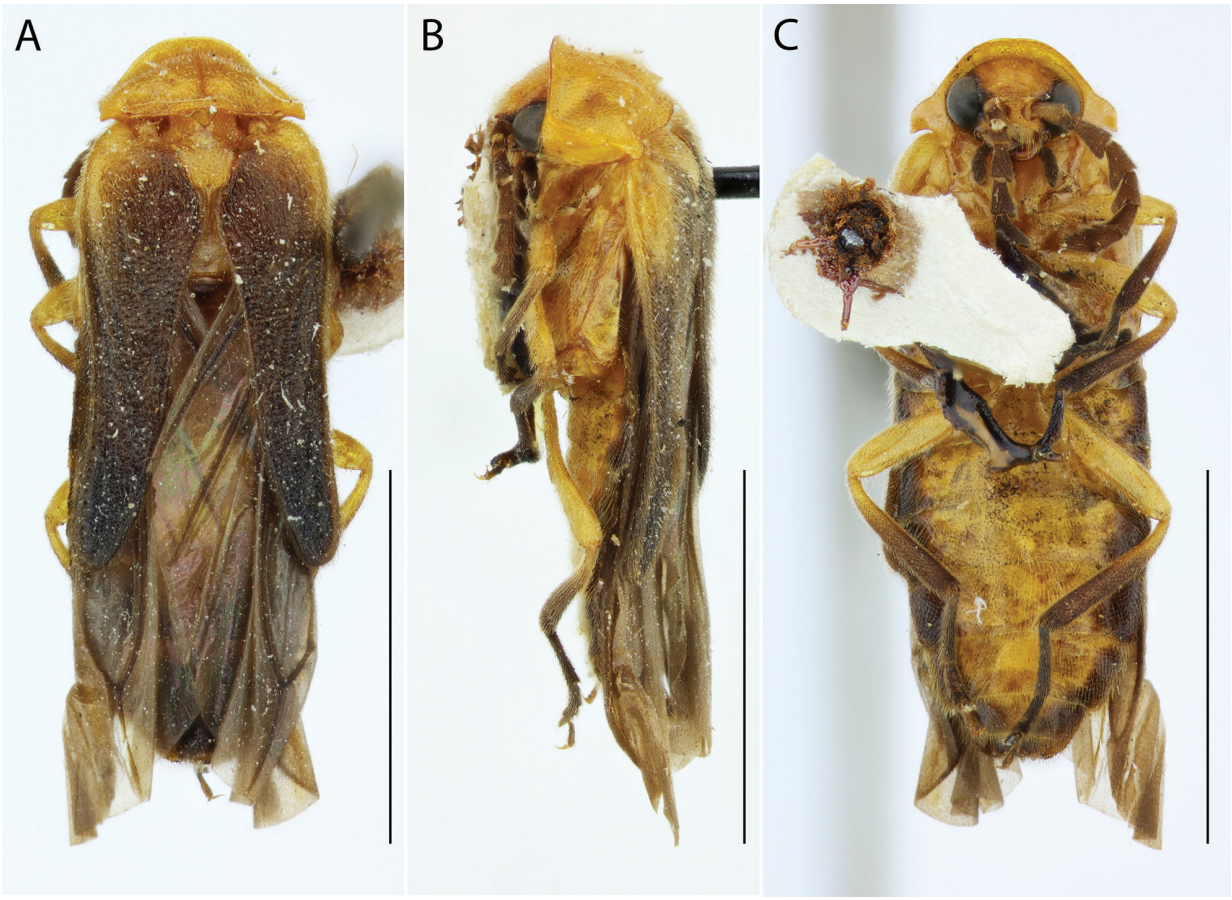



**Figure 1.** Habitus of *Reductodrilus longelytratus* Packova & Kundrata, sp. nov., male holotype. **A.** Dorsal view; **B.** Lateral view; **C.** Ventral view. Scale bars: 4.0 mm (**A–C**).

**Diagnosis and comparison.** This species can be unambiguously recognized by its relatively large body size (8.7 mm; up to 7.1 mm in all other congeners), antennomeres 4–10 approx. as long as wide (distinctly wider than long in all other congeners; Figs 5C, 9D), elytra being 1.7× as long as wide at humeri (up to 1.45× in all other congeners) and 3.2× as long as pronotum (up to 2.5× in other species; Figs 5E, 9E), and by the more or less uniformly lightly colored elytral pubescence (elytral pubescence bicolorous, with major portion of elytra having distinctly darker setae in all other congeners).

**Description. Male.** ***Body*** (Fig. 1A–C) 8.7 mm long from frons to apex of abdomen and 6.6 mm long from frons to apex of elytra, 2.8 mm wide at humeri; yellowish to pale brown, head slightly darker, antennae, palpi, major portions of elytra (except at humeri), major portions of tibiae (except basally), tarsomeres, and sides of abdominal ventrites dark brown; body surface covered with yellowish to pale brown setae.

***Head*** (Fig. 2A) including eyes 0.65× as wide as pronotum, dorsomedially very slightly convex, generally smooth, sparsely covered with fine punctures and short semi-erect setae mostly oriented anteriorly. Frontoclypeal region frontally abruptly declivous, antennal fossae separated by 0.7× longitudinal diameter of fossa; rim dorsally forming narrow supra-antennal carina. Eyes moderately large, basally slightly emarginate. Labrum beneath (i.e., not on the same plane with frontoclypeal region), weakly sclerotized, sparsely covered with long suberect to erected setae. Mandibles unidentate, moderately long and robust,

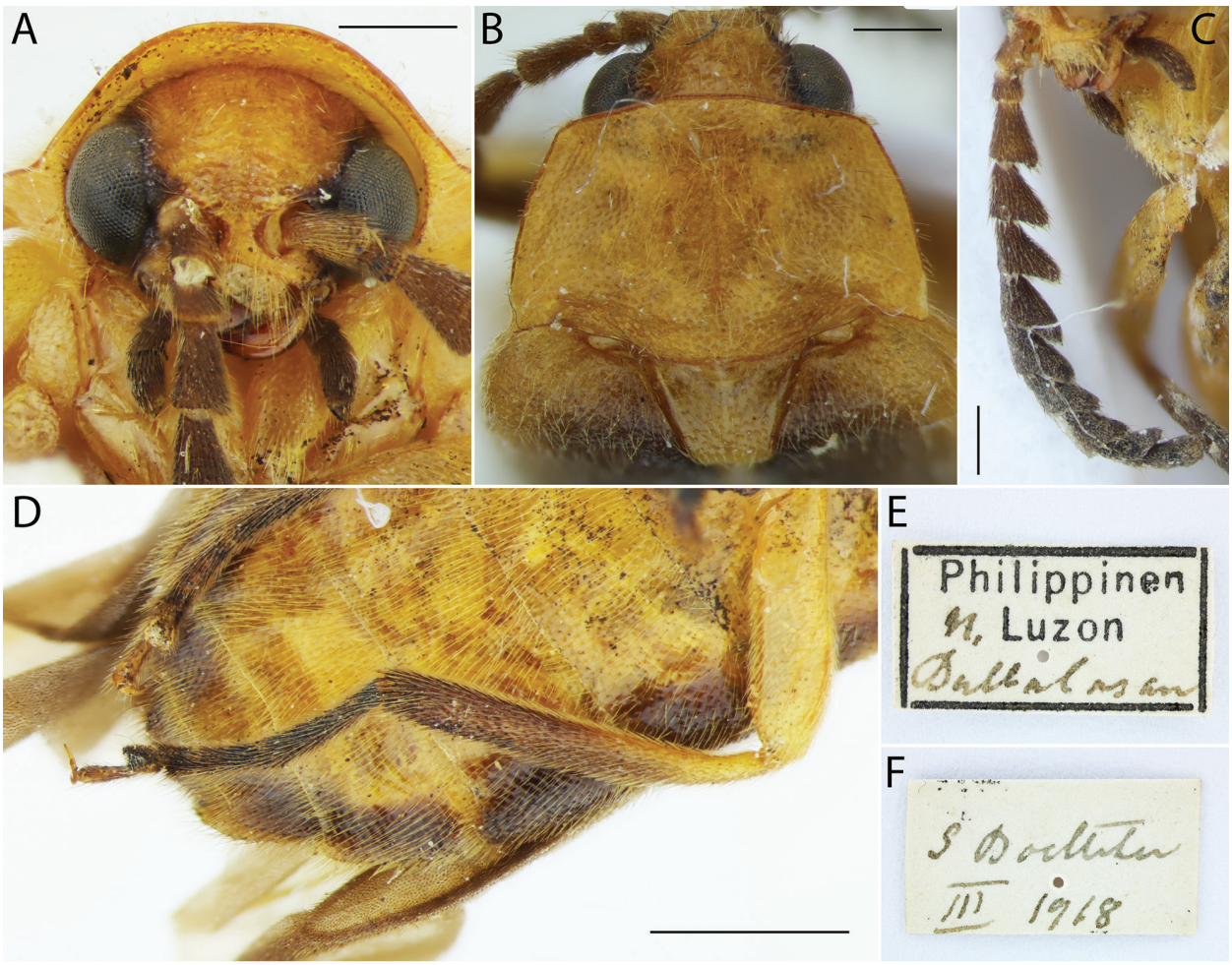



**Figure 2.** Morphology of *Reductodrilus longelytratus* Packova & Kundrata, sp. nov., male holotype. **A.** Head, frontal view; **B.** Pronotum; **C.** Left antenna; **D.** Left hind leg and abdomen; **E, F.** Labels. Scale bars: 0.5 mm (**A–C**); 1.0 mm (**D**).

sickle-shaped, strongly curved; basally covered with sparse long setae. Maxillary palpi relatively short, 4-segmented, basal palpomere shorter than wide, palpomere 2 slightly longer than wide; palpomere 3 shortest, wider than long; ultimate palpomere longest, ~ 2× as long as wide, apically dorsoventrally flattened and obliquely cut. Labial palpi minute, 3-segmented; palpomere 2 short, transverse; ultimate palpomere longer than wide, similar in shape to ultimate maxillary palpomere. Antenna (Fig. 2C) with 11 antennomeres, moderately long, almost reaching midlength of elytra (when positioned backwards), rather robust, scape longer than wide, antennomere 2 shortest, approximately as long as wide; antennomeres 3–10 strongly serrate, antennomere 3 ~ 2.2× as long as antennomere 2, ~ 1.25× as long as wide, antennomeres 4–10 subequal in shape and length, approx. as long as wide; antennomere 11 slightly longer than antennomere 10, elongate, widest behind midlength, apically rounded.

***Pronotum*** (Fig. 2B) ~ 1.5× wider than long, slightly convex, widest before posterior angles. Anterior margin slightly rounded, with the edge turned upwards; lateral margins slightly rounded, anteriorly also slightly turned upwards; posterior margin slightly bisinuate, medially slightly produced. Anterior angles inconspicuous; posterior angles very short, almost rectangular, apically narrowly rounded. Surface of disc uneven, with distinct median longitudinal groove, one smaller posteromedial depression, and two shallow anterolateral

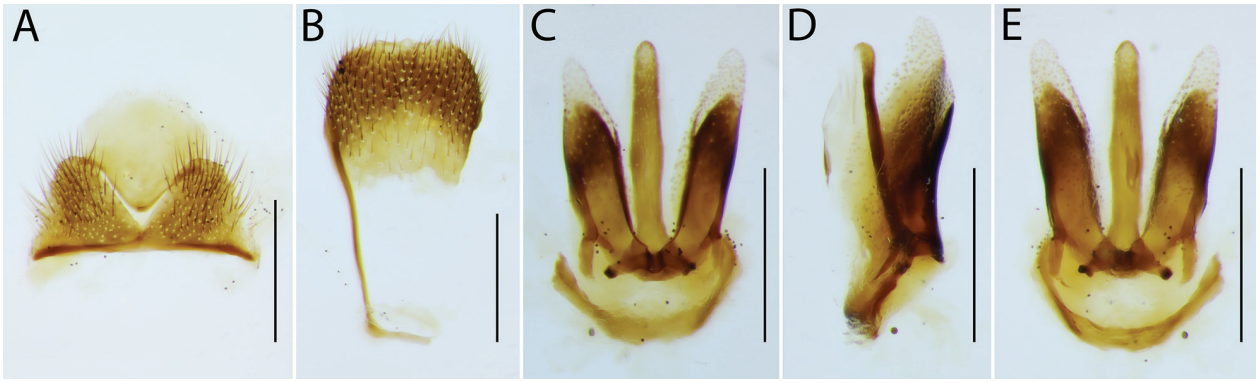



**Figure 3.** Pregenital segments and genitalia of *Reductodrilus longelytratus* Packova & Kundrata, sp. nov., male holotype. **A.** Abdominal tergites IX and X, dorsal view; **B.** Abdominal sternite IX, ventral view; **C.** Male genitalia, dorsal view; **D.** Male genitalia, lateral view; **E.** Male genitalia, ventral view. Scale bars: 0.5 mm (**A–E**).

depressions, moderately densely covered with punctures and setae; punctures moderately large, shallow, intervals between punctures usually 1–2 puncture diameters, interstices rather smooth; setae moderately long, semi-erect, mostly oriented posteriorly, those near posterior margin oriented anteriorly. Lateral pronotal carina complete, visible in dorsal view, anteriorly continuous with anterior margin of pronotum. Hypomeron with surface mostly smooth and shiny, with shallow punctures and semi-erect setae. Prosternum distinctly transverse, with prosternal process reduced to short median protrusion. Scutellar shield (Fig. 2B) tongue-shaped, large, almost as long as wide, widest anteriorly, gradually slightly narrowed toward apex, apex subtruncate; covered with relatively fine punctures which are approx. the same size as those on elytral bases, and with short semi-erect setae. Mesoventrite short, roughly triangular. Metaventrite with distinct long discrimen; metepisternum distinctly wider basally and gradually narrowed apicad. Elytra (Fig. 1A, B) elongate, both combined 1.7× as long as wide, 3.2× as long as pronotum, dehiscent, not meeting along suture, sides slightly sinuate, apically slightly divergent, apices separately rounded, surface rather uneven and covered with moderately large shallow punctures (smaller on elytral bases) which are subserial to irregularly distributed, and with short, semierect setae which are oriented posteriad. Leg (Fig. 2D) slender; coxa elongate; femur robust, elongate, flattened, obliquely attached to trochanter, distinctly wider than tibia, with short cavity for reception of tibia; tibia elongate, very slightly longer than femur, apically with two short spurs; tarsus slender, distinctly shorter than tibia in fore legs, less distinctly shorter in mid legs, and only slightly shorter in hind legs; tarsomeres 1–4 progressively shorter, tarsomere 1 longest, longer than combined lengths of tarsomeres 2 and 3, tarsomere 4 shortest, medially emarginate, ventrally with membrane, tarsomere 5 elongate, narrower than preceding tarsomeres; pretarsal claws simple, slightly curved.

***Abdomen*** (Figs 1C, 2D) with all ventrites densely covered with fine punctures and moderately long, semi-erect, posteriorly directed setae; tergites IX and X (Fig. 3A) tightly connected by membrane, tergite IX slightly more than twice as wide as long, anteromedially deeply emarginate to receive base of tergite X, densely covered with moderately long setae; tergite X weakly sclerotized, almost as long as wide, apically widely rounded; sternite IX (Fig. 3B) elongate, ~ 1.8× as long as wide, gradually slightly widened toward apex, widest subapically, apically subtruncate and medially slightly emarginate. Male genitalia

(Fig. 3C–E) ~ 1.9× as long as maximum phallobase width; median lobe ~ 2× as long as phallobase, not surpassing apices of parameres, elongate, slender, subparallel-sided but widest at mid-length, apically rounded, basal struts relatively short and distinctly divergent; parameres elongate, robust, narrowed from 3/5 of their length to apex, apically membranous and rounded; phallobase transverse, ~ 1.45× as wide as long, widely U-shaped.

**Females** and immature stages unknown.

**Etymology.** The species name refers to relatively long elytra of this species compared to its congeners.

**Distribution.** Philippines.

***Reductodrilus maculatus* Packova, Vorst & Kundrata, sp. nov.**

https://zoobank.org/E78B5837-C1E6-416A-8581-0E250B425AE7

Figs 4–6

*Ototretadrilus philippinus* ab. *maculata* Wittmer, 1941: 197 [unavailable name, ICZN 1999: Art. 45.6.2; see Keller and Hinson 2023].

**Type material. *Holotype*:** male, "Boettcher, Phil.: Socorro, [Bucas Grande] 19.X.1916 // HOLOTYPE: *Ototetradrilus* [sic!] *philippinus* 1939, W. Wittmer, ab. *maculatus* Wittm. // *O. philippinus* ab. *maculatus* Wittm., det. W. Wittmer // *Ototretadrilus philippinus maculatua* [sic!] Wittmer, 1941, ZMAN type COLE.1031.1 // RMNH.INS.1092883 [with a barcode]" (RMNH).

**Type locality.** Philippines: Socorro.

**Diagnosis and comparison.** This species can be recognized based on the following unique combination of characters: dorsum dark brown except for the lateral portions of pronotum and outer basal portions of elytra (Fig. 4A), antennomeres 4–10 ~ 1.7–1.8× as wide as long (Fig. 5C), pronotum ~ 1.45× wider than long (Fig. 5E), elytra ~ 1.4× as long as wide at humeri and 2.2× as long as pronotum (Fig. 4A), elytral pubescence bicolorous, with major portions of elytra having distinctly darker setae, and the aedeagal median lobe ~ 1.5× as long as phallobase, not surpassing apices of parameres, widest basally, subparallel-sided for most of its length and then narrowed at apical 3/5 of their length (Fig. 6D, F). While *R. maculatus* sp. nov. shares many external morphological characters with *R. testaceiceps*, it differs in much darker coloration of dorsum (Figs 7A, 8A), more strongly pectinate antennomeres 4–10 (1.7–1.8× as wide as long versus 1.5–1.6× in *R. testaceiceps*; Fig. 9D), less transverse pronotum (~ 1.45× wider than long versus 1.55–1.60× in *R. testaceiceps*; Fig. 9E), and different shape of male genitalia, with having relatively shorter median lobe and parameres compared to the phallobase, the median lobe widest basally (versus medially in *R. testaceiceps*; Fig. 10D, F) and not surpassing apices of parameres.

**Redescription. Male. *Body*** (Fig. 4A, B) 7.1 mm long from frons to apex of abdomen and 5.0 mm long from frons to apex of elytra, 2.4 mm wide at humeri; pale to dark brown, head (except frontal part), antennae, palpi, pronotum medially from anterior to posterior margin, scutellum, elytra (except outer basal portions), major portions of tibiae (except basally), tarsomeres, and several last abdominal segments distinctly darker, dark brown; body surface covered with yellowish to dark brown setae (coloration of setae roughly corresponding to coloration of cuticle).

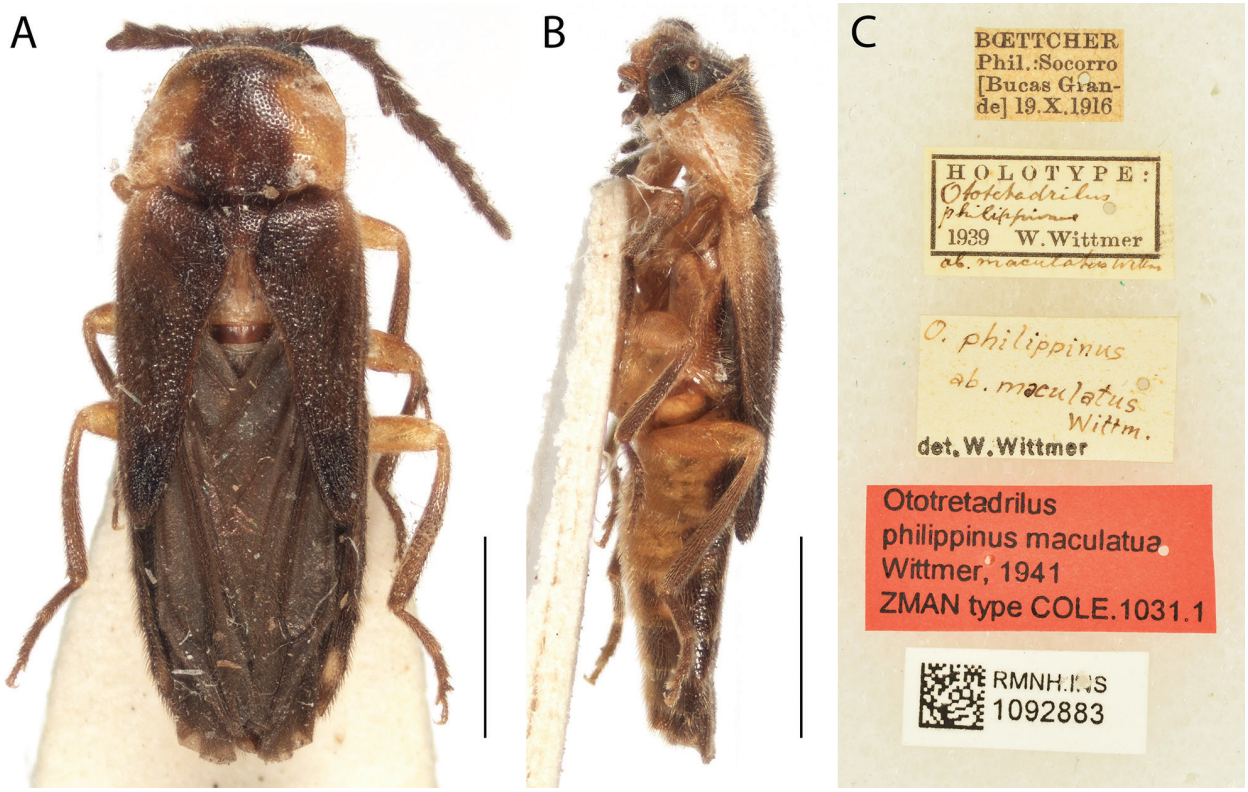



**Figure 4.** Habitus of *Reductodrilus maculatus* Packova, Vorst & Kundrata, sp. nov., male holotype. **A.** Dorsal view; **B.** Lateral view; **C.** Labels. Scale bars: 2.0 mm (**A, B**).

***Head*** (Fig. 5A, B, D) including eyes ~ 0.7× as wide as pronotum, dorsomedially very slightly convex, generally smooth, sparsely covered with fine punctures and short semi-erect setae mostly oriented anteriorly. Frontoclypeal region frontally abruptly declivous, antennal fossae separated by 0.8× longitudinal diameter of fossa; rim dorsally forming narrow supra-antennal carina. Eyes moderately large, basally slightly emarginate. Labrum beneath (i.e., not on the same plane with frontoclypeal region), weakly sclerotized, sparsely covered with long suberect to erected setae. Mandibles unidentate, moderately long and robust, sickle-shaped, strongly curved; basally covered with sparse long setae. Maxillary palpi relatively short, 4-segmented, basal palpomere shorter than wide, palpomere 2 slightly longer than wide; palpomere 3 shortest, wider than long; ultimate palpomere longest, apically dorsoventrally flattened and obliquely cut. Labial palpi minute, 3-segmented; palpomere 2 short, transverse; ultimate palpomere longer than wide, similar in shape to ultimate maxillary palpomere. Antenna (Fig. 5C) with 11 antennomeres, moderately long, slightly surpassing midlength of elytra (when positioned backwards), rather robust, scape longer than wide, antennomere 2 shortest, slightly wider than long; antennomeres 3–10 pectinate, antennomere 3 ~ 2.3× as long as antennomere 2, ~ 1.5× as long as wide, antennomeres 4–10 subequal in shape and length, ~ 1.7–1.8× as wide as long; antennomere 11 ~ 2× as long as antennomere 10, elongate, widest after half, apically rounded.

***Pronotum*** (Fig. 5E) ~ 1.45× wider than long, slightly convex, widest medially. Anterior margin widely rounded, with the edge slightly turned upwards; lateral margins slightly rounded; posterior margin slightly bisinuate, medially very slightly produced and shallowly emarginate. Anterior angles inconspicuous; posterior angles very short, almost rectangular, apically rounded. Surface of

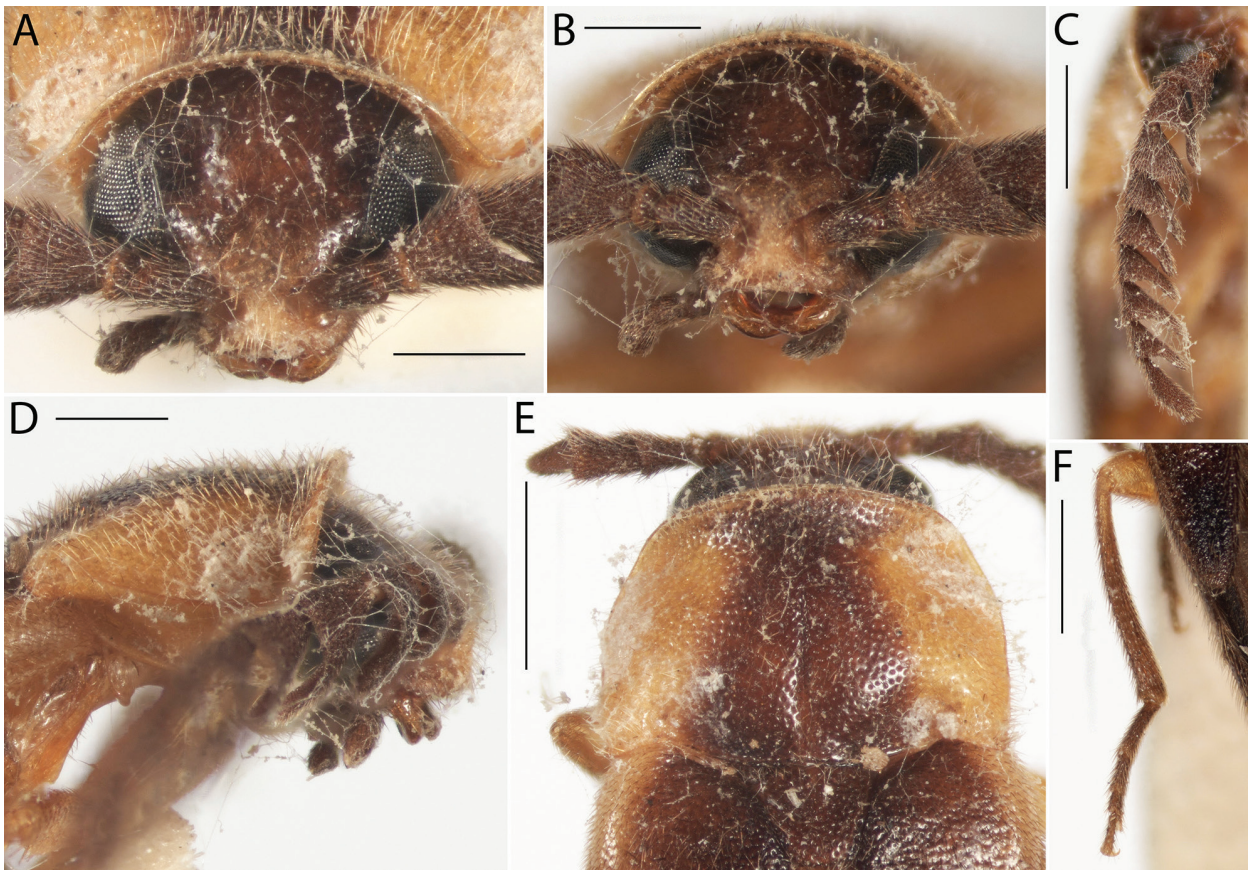



**Figure 5.** Morphology of *Reductodrilus maculatus* Packova, Vorst & Kundrata, sp. nov., male holotype. **A.** Head, dorsofrontal view; **B.** Head, frontal view; **C.** Right antenna; **D.** Head and prothorax, lateral view; **E.** Pronotum; **F.** Left hind leg. Scale bars: 0.5 mm (**A, B, D**); 1.0 mm (**C, E, F**).

disc uneven, with distinct median longitudinal groove, one small posteromedial depression, and two large shallow anterolateral depressions, rather densely covered with punctures and setae; punctures moderately large, shallow, intervals between punctures usually ~ 1 puncture diameter, interstices rather smooth; setae moderately long, semi-erect, mostly oriented posteriorly, those near posterior margin oriented anteriorly. Lateral pronotal carina complete, visible in dorsal view, anteriorly continuous with anterior margin of pronotum. Hypomeron with surface mostly smooth and shiny, with shallow punctures and semi-erect setae. Prosternum distinctly transverse, with prosternal process reduced to short median protrusion. Scutellar shield (Fig. 5E) tongue-shaped, rather large, almost as long as wide, widest anteriorly, gradually slightly narrowed toward apex, apex subtruncate; surface densely and coarsely punctate, punctures approx. the same size as those on elytra, and with short semi-erect setae. Mesoventrite short, roughly triangular. Metaventrite with distinct long discrimen; metepisternum distinctly wider basally and gradually narrowed apicad. Elytra (Fig. 4A, B) both combined ~ 1.4× as long as wide, 2.2× as long as pronotum, strongly dehiscent, not meeting along suture, sides slightly sinuate, apices separately rounded, oriented posteriad; surface rather uneven and covered with moderately large shallow punctures which are mostly irregularly distributed, and with short, semierect setae which are oriented posteriad. Leg (Fig. 5F) slender; coxa elongate; femur robust, elongate, flattened, obliquely attached to trochanter, distinctly wider than tibia, with short cavity for reception of tibia; tibia elongate,




**Figure 6.** Pregenital segments and genitalia of *Reductodrilus maculatus* Packova, Vorst & Kundrata, sp. nov., male holotype. **A.** Abdominal tergite X, dorsal view; **B.** Abdominal tergite IX, dorsal view; **C.** Abdominal sternite IX, ventral view; **D.** Male genitalia, dorsal view; **E.** Male genitalia, lateral view; **F.** Male genitalia, ventral view. Scale bars: 0.5 mm (**A–F**).

very slightly longer than femur, apically with two short spurs; tarsus slender, distinctly shorter than tibia in fore legs, less distinctly shorter in mid legs, and only slightly shorter in hind legs; tarsomeres 1–4 progressively shorter, tarsomere 1 longest, longer than combined lengths of tarsomeres 2 and 3, tarsomere 4 shortest, medially emarginate, ventrally with membrane, tarsomere 5 elongate, narrower than preceding tarsomeres; pretarsal claws simple, slightly curved.

***Abdomen*** (Fig. 4B) with all ventrites densely covered with fine punctures and moderately long, semi-erect, posteriorly directed setae; tergites IX and X (Fig. 6A, B) tightly connected by membrane, tergite IX slightly more than twice as wide as long, anteromedially deeply and narrowly emarginate to receive base of tergite X, densely covered with moderately long setae; tergite X weakly sclerotized, ~ 1.4× as wide as long, apicomedially slightly produced; sternite IX (Fig. 6C) elongate, ~ 1.8× as long as wide, gradually slightly widened toward apex, widest subapically, apically subtruncate and medially slightly emarginate. Male genitalia (Fig. 6D–F) ~ 2× as long as maximum phallobase width; median lobe ~ 1.5× as long as phallobase, not surpassing apices of parameres, elongate, slender, widest basally, subparallel-sided for most of its length and then narrowed at apical 3/5 of their length, narrowest subapically, apically rounded, basal struts short and distinctly divergent; parameres elongate, robust, apically membranous and narrowly rounded; phallobase transverse, ~ 1.3× as wide as long, U-shaped.

**Females** and immature stages unknown.

**Distribution.** Philippines.

***Reductodrilus testaceiceps* (Pic, 1924), comb. nov.**

Figs 7–9

*Dodecatoma testaceiceps* Pic, 1924: 713.

*Ototretadrilus philippinus* Wittmer, 1941: 197, syn. nov.

*Dodecatoma testaceipes*: Wittmer 1944: 212 [unavailable name, incorrect subsequent spelling not in prevailing usage].

**Type material.** ***Lectotype*** of *Dodecatoma testaceiceps* [here designated], male, “Mt Makiling Luzon, Baker // type // TYPE // *Dodecatoma testaceiceps* n sp” (MNHN).

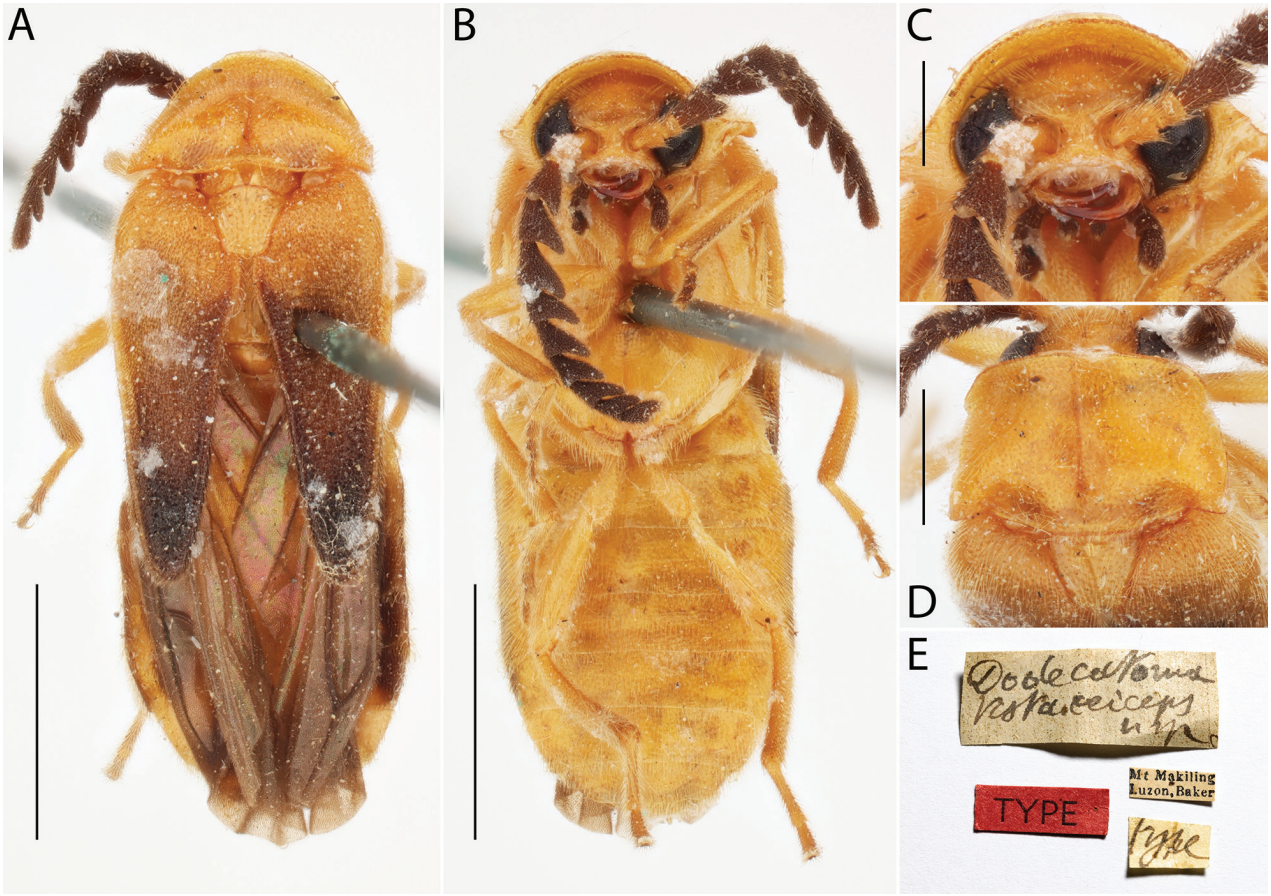



**Figure 7.** Habitus and morphology of *Reductodrilus testaceiceps* (Pic, 1924), comb. nov., male lectotype. **A.** Habitus, dorsal view; **B.** Habitus, ventral view; **C.** Head, frontal view; **D.** Pronotum; **E.** Labels. Scale bars: 2.0 mm (**A, B**); 0.5 mm (**C**); 1.0 mm (**D**).

**Other material examined (n = 3).** ***Holotype*** of *O. philippinus*, male, "Boettcher, Luzon. 2000', Mt. Banahao [Mt. Banahaw], 16.IV.1914 // Holotype: *Ototretadrilus philippinus*, 1939 W. Wittmer // *Ototretadrilus philippinus* Wittm., det. W. Wittmer // *Ototretadrilus philippinus* Wittmer, 1941, ZMAN type COLE.1030.1 // RMNH.INS 1092882 [with a barcode]" (RMNH); one male, "Philippinen, Luzon M Bulusan // S. Boettcher IX. 1917 (MFNB); one male, "Philippinen Siargao Dapa // S Boettcher 30.9.16" (MFNB).

**Type locality.** Philippines: Luzon, Mt. Makiling.

**Diagnosis and comparison.** This species can be recognized based on the following unique combination of characters: dorsum usually pale brown to brown except for the major portions of elytra (Figs 7A, 8A), antennomeres 4–10 ~ 1.5–1.6× as wide as long (Fig. 9D), pronotum 1.55–1.60× wider than long (Fig. 9E), elytra 1.30–1.45× as long as wide at humeri and 2.4–2.5× as long as pronotum (Figs 7A, 8A), elytral pubescence bicolorous, with major portions of elytra having distinctly darker setae, and the aedeagal median lobe ~ 1.8–2.0× as long as phallobase, slightly surpassing apices of parameres, subparallel-sided but apparently widened approximately at mid-length (Fig. 10D, F). This species is most similar to *R. maculatus* sp. nov., particularly in having relatively short elytra. For diagnostic differences between these species, see the Diagnosis and comparison section under *R. maculatus* sp. nov.

**Redescription. Male.** ***Body*** (Figs 7A, B, 8A, B) 6.5–7.0 mm long from frons to apex of abdomen and 4.1–5.4 mm long from frons to apex of elytra, 1.8–

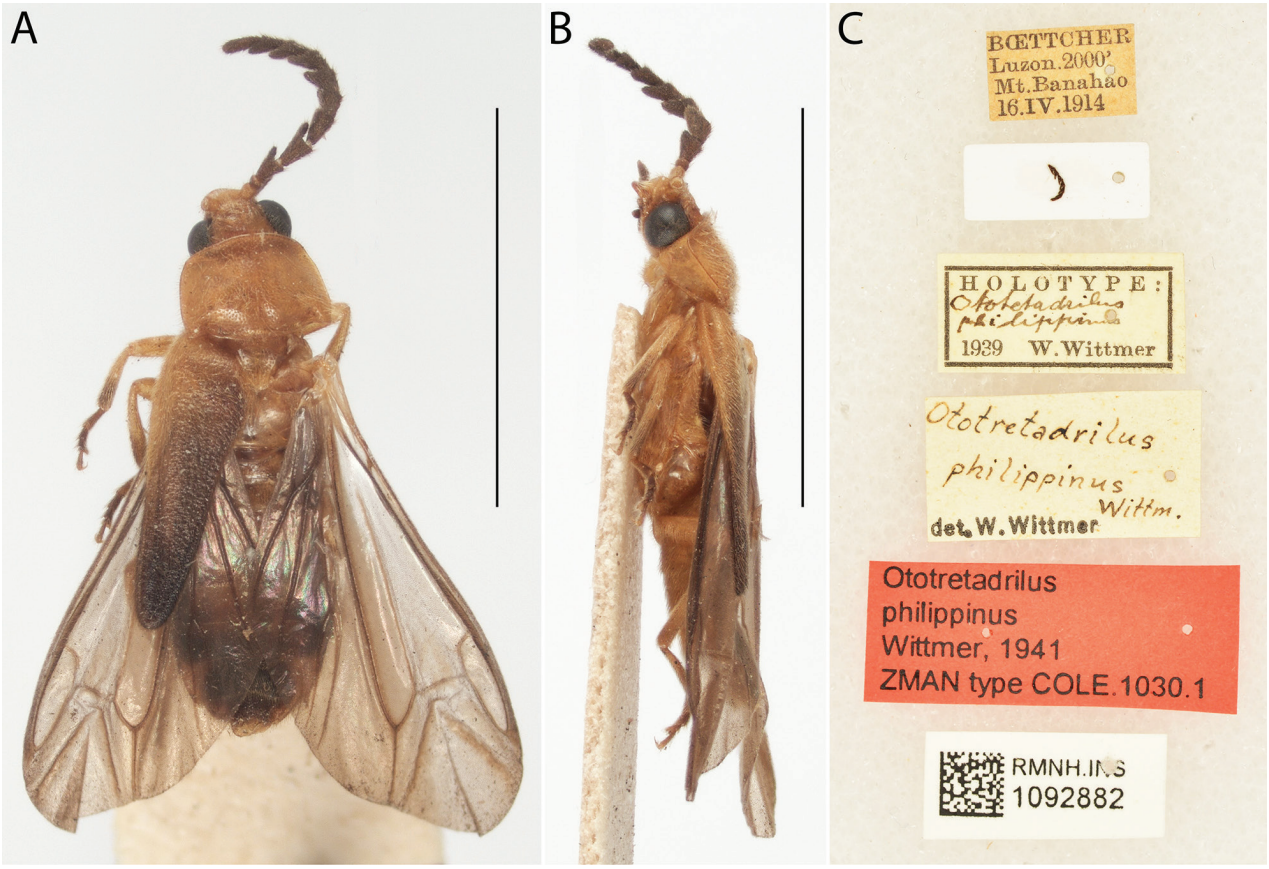



**Figure 8.** Habitus of *Reductodrilus testaceiceps* (Pic, 1924), comb. nov., male (holotype of *Ototretadrilus philippinus* Wittmer, 1941). **A.** Dorsal view; **B.** Lateral view; **C.** Labels. Scale bars: 5.0 mm (**A, B**).

2.4 mm wide at humeri (6.7 mm and 4.9 mm long, respectively, and 2.4 mm wide in the lectotype); yellowish to pale brown, head and anterior part of pronotum in some specimens slightly darker, antennomeres 3–11, palpi, major portions of elytra (except for humeri), major portions of tibiae (except basally), and tarsomeres dark brown; antennomere 2 variable, lighter to darker brown; body surface covered with yellowish setae, with elytra (except outer portions of humeri) being covered with dark brown to black setae.

***Head*** (Figs 7C, 9A–C) including eyes 0.65–0.70× as wide as pronotum, slightly convex, generally smooth, sparsely covered with fine punctures and short semi-erect setae mostly oriented anteriorly. Frontoclypeal region frontally abruptly declivous, antennal fossae separated by 0.7–0.8× longitudinal diameter of fossa; rim dorsally forming narrow supra-antennal carina. Eyes moderately large, basally slightly emarginate. Labrum beneath (i.e., not on the same plane with frontoclypeal region), weakly sclerotized, sparsely covered with long suberect to erect setae. Mandibles unidentate, moderately long and robust, sickle-shaped, strongly curved; basally covered with sparse long setae. Maxillary palpi relatively short, 4-segmented, basal palpomere shorter than wide, palpomere 2 slightly longer than wide; palpomere 3 shortest, wider than long; ultimate palpomere longest, ~ 2× as long as wide, apically dorsoventrally flattened and obliquely cut. Labial palpi minute, 3-segmented; palpomere 2 short, transverse; ultimate palpomere longer than wide, similar in shape to ultimate maxillary palpomere. Antenna (Fig. 9D) with 11 antennomeres, moderately long, almost reaching midlength of elytra (when positioned backwards), rather robust,

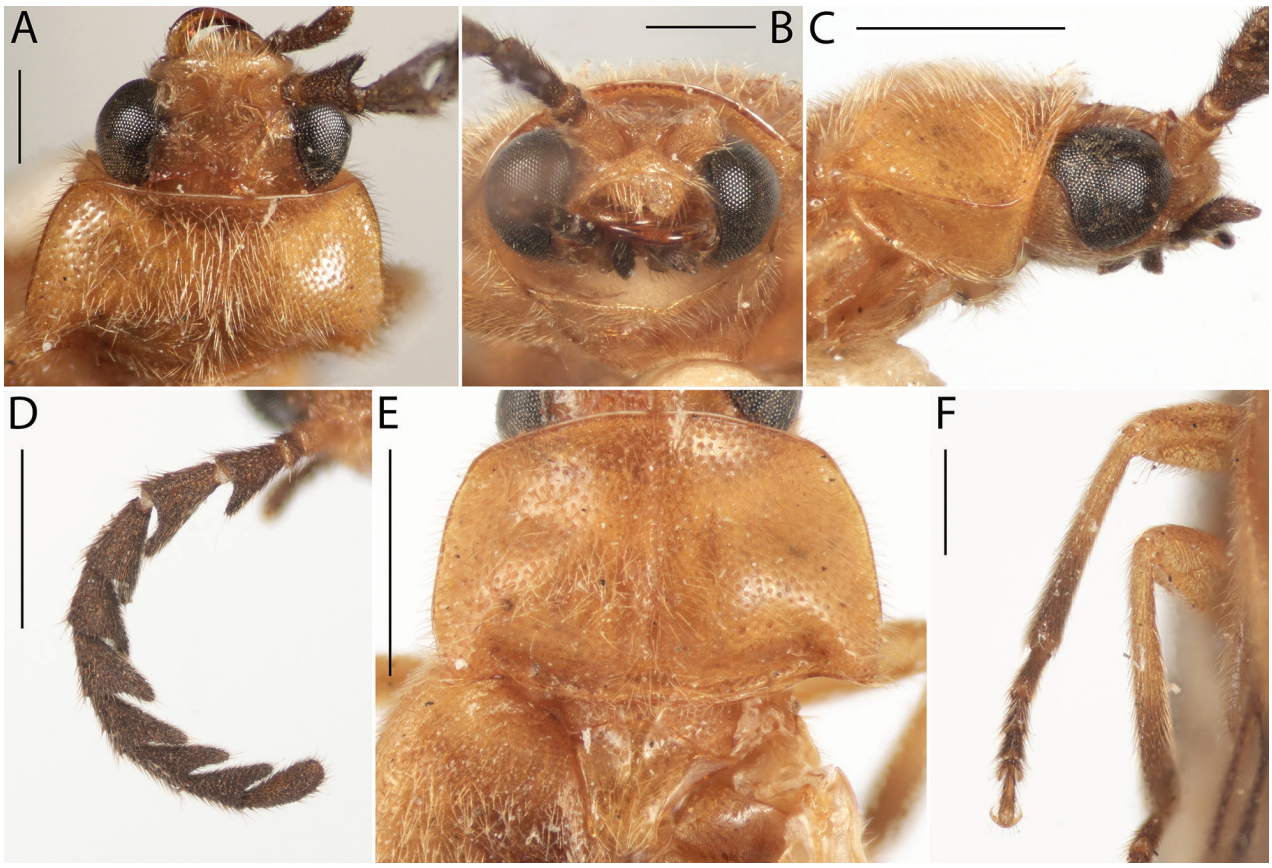



**Figure 9.** Morphology of *Reductodrilus testaceiceps* (Pic, 1924), comb. nov., male (holotype of *Ototretadrilus philippinus* Wittmer, 1941). **A.** Head, dorsal view; **B.** Head, frontal view; **C.** Head and prothorax, lateral view; **D.** Right antenna; **E.** Pronotum; **F.** Left hind leg. Scale bars: 0.5 mm (**A, B, F**); 1.0 mm (**C–E**).

serrate, scape longer than wide, antennomere 2 shortest, approximately as long as wide; antennomeres 3–10 serrate, antennomere 3 ~ 1.8–2.0× as long as antennomere 2, ~ 1.20–1.35× as wide as long, antennomeres 4–10 subequal in shape and length, ~ 1.5–1.6 as wide as long; antennomere 11 ~ 1.5–1.7× as long as antennomere 10, elongate, widest after half, apically rounded.

***Pronotum*** (Figs 7D, 9E) ~ 1.55–1.60× wider than long, slightly convex, widest before posterior angles. Anterior margin slightly rounded, with the edge turned upwards; lateral margins slightly rounded, anteriorly more or less also slightly turned upwards; posterior margin slightly bisinuate, medially slightly produced. Anterior angles inconspicuous; posterior angles very short, almost rectangular, apically rounded. Surface of disc uneven, with distinct median longitudinal groove, deep posteromedial depression, and two less distinct large shallow anterolateral depressions, moderately densely covered with punctures and setae; punctures moderately large, shallow, intervals between punctures usually 1–2 puncture diameters, interstices rather smooth; setae moderately long, semi-erect, mostly oriented posteriorly, those near posterior margin oriented anteriorly. Lateral pronotal carina complete, visible in dorsal view, anteriorly continuous with anterior margin of pronotum. Hypomeron with surface mostly smooth and shiny, with shallow punctures and semi-erect setae. Prosternum distinctly transverse, with prosternal process reduced to short median protrusion. Scutellar shield (Figs 7D, 9E) tongue-shaped, rather large, almost as long as wide, widest anteriorly, gradually slightly narrowed toward apex,

apex subtruncate; covered with relatively large and shallow punctures which are usually larger than those on elytral bases, and with short semi-erect setae. Mesoventrite short, roughly triangular. Metaventrite with distinct long discrimen; metepisternum distinctly wider basally and gradually narrowed apicad. Elytra (Figs 7A, 8A, B) both combined 1.30–1.45× as long as wide, 2.4–2.5× as long as pronotum, dehiscent, not meeting along suture, sides very slightly sinuate, towards apex with distinctly strengthened margins, apices separately rounded, surface rather uneven and covered with moderately large shallow punctures (smaller on elytral bases) which are subserial to irregularly distributed, and with moderately long, semierect setae which are oriented posteriad. Leg (Fig. 9F) slender; coxa elongate; femur robust, elongate, flattened, obliquely attached to trochanter, distinctly wider than tibia, with short cavity for reception of tibia; tibia elongate, apically with two short spurs; metatibia longer than femur; tarsus slender, distinctly shorter than tibia in fore legs, less distinctly shorter in mid legs, and only slightly shorter in hind legs; tarsomeres 1–4 progressively shorter, tarsomere 1 distinctly longest, longer than combined lengths of tarsomeres 2 and 3, tarsomere 4 shortest, minute, medially emarginate, ventrally with membrane, tarsomere 5 elongate, narrower than preceding tarsomeres; pretarsal claws simple, slightly curved.

***Abdomen*** (Figs 7B, 8B) with all ventrites densely covered with fine punctures and moderately long, semi-erect, posteriorly directed setae; tergites IX and X (Fig. 10A, B) tightly connected by membrane, tergite IX slightly more than twice as wide as long, anteromedially deeply emarginate to receive base of tergite X, densely covered with moderately long setae; tergite X weakly sclerotized, slightly wider than long, apically widely rounded; sternite IX (Fig. 10C) elongate, ~ 1.7–1.9× as long as wide, from ~ half gradually widened toward apex, widest subapically, apically subtruncate and medially emarginate. Male genitalia (Fig. 10D–F) ~ 1.85–2.10× as long as maximum phallobase width; median lobe ~ 1.8–2.0× as long as phallobase, slightly surpassing apices of parameres, elongate, slender, subparallel-sided but widest at approx. mid-length, apically rounded, basal struts relatively short and distinctly divergent; parameres elongate, robust, subparallel-sided, slightly curved, apically membranous and rounded; phallobase transverse, ~ 1.25–1.45× as wide as long, U-shaped.

**Females** and immature stages unknown.

**Variability.** The examined specimens show slight variation in coloration, particularly of antennomere 2 (yellowish brown to bicolored to dark brown), the head, the anterior portion of the pronotum, and the abdomen, as well as in the relative length of the elytra, which are 1.30–1.45× as long as wide. The specimen from Siargao differs from the Luzon specimens in the shape of the male genitalia (see Remarks below).

**Distribution.** Philippines.

**Literature.** Pic (1924: 713): original description of *Dodecatoma testaceiceps*; Wittmer (1941: 197): original description of *Ototretadrilus philippinus*, remark; Wittmer (1944: 212, 214): catalogue, both *Dodecatoma testaceiceps* (as *testaceipes*; sic!) and *Ototretadrilus philippinus*; Wittmer (1978: 61): comparison with another species; Kundrata et al. (2022: 74): taxonomic remark on *Ototretadrilus philippinus*.

**Remarks.** The lectotype of *Dodecatoma testaceiceps* Pic, 1924 (Fig. 7) and the holotype of *Ototretadrilus philippinus* Wittmer, 1941 (Fig. 8) both originate




**Figure 10.** Pregenital segments and genitalia of *Reductodrilus testaceiceps* (Pic, 1924), comb. nov., male lectotype. **A.** Abdominal tergite X, dorsal view; **B.** Abdominal tergite IX, dorsal view; **C.** Abdominal sternite IX, ventral view; **D.** Male genitalia, dorsal view; **E.** Male genitalia, lateral view; **F.** Male genitalia, ventral view. Scale bars: 0.2 mm (**A**); 0.5 mm (**B–F**).

from Luzon. They share the similar body size and coloration (differing only in the intensity of the brown coloration of antennomere 2 and abdominal tergites), highly similar external morphology (except for the slightly wider scutellar shield in *D. testaceiceps*), and male genitalia. We therefore consider *Ototretadrilus philippinus* Wittmer, 1941, syn. nov. to be a junior synonym of *Reductodrilus testaceiceps* (Pic, 1924). Further research including more specimens and molecular approach should test the limits of this species.

In the original description of *D. testaceiceps*, Pic (1924) cited "Luzon, Mount Maquiling, No. 17152" without explicitly stating the number of specimens examined. The specimen preserved in MNHN bears Pic's identification label and a locality label corresponding to the original description, but no label bearing the cited number is currently attached to it. Because the original number of specimens based on which Pic described the species cannot be established with certainty, we treat this specimen as a syntype (ICZN 1999) and designate it here as the lectotype to stabilize the nomenclature.

In the original description of *O. philippinus*, Wittmer reported the type locality as follows: "Luzon, Nueva Vizcaya, Imugan, 4000 Fuss Höhe, 8. Juli, 1917: Laguna, Mount Banahao, 2000 Fuss Höhe, 16. April, 1914 (Holotype)." (Wittmer 1941: 198). The holotype deposited in RMNH originates from Mt. Banahaw in Laguna Province (see above). The paratype deposited in NHMB (studied only based on the photograph kindly provided by T. Lackner) bears the following labels: "Boettcher, Luzon; Prov. Nueva Viscaya // Imugan, 4000 ft., 8.VI.1917 // *O. philippinus* Wittm., det. W. Wittmer // Holotypus [sic!] // Naturhistorisches Museum Basel, Coll. W. Wittmer".

The specimen from Siargao (ca 800 km southeast of Luzon) closely resembles the specimens from Luzon in external morphology but differs in the shape of the aedeagal median lobe, which is not distinctly widened at approx. mid-length, and in having relatively shorter parameres in relation to the phallobase. However, because the median lobe of the Siargao specimen was already damaged prior to dissection, with its apical portion missing, and because the specimen is otherwise externally almost indistinguishable from those from Luzon, we tentatively retain it in *R. testaceiceps* pending the availability of additional material.

### An identification key for the *Reductodrilus* species in the Philippines based on adult males

1 Body 8.7 mm long from frons to apex of abdomen and 6.6 mm long from frons to apex of elytra; antennomeres (Fig. 2C) 4–10 approx. as long as wide; elytra (Fig. 1A) relatively longer, 1.7× as long as wide at humeri, and 3.2× as long as pronotum; elytral pubescence more or less uniformly lightly colored..... ***R. longelytratus* Packova & Kundrata, sp. nov.**

– Body 6.5–7.1 mm long from frons to apex of abdomen and 4.1–5.4 mm long from frons to apex of elytra; antennomeres 4–10 (Figs 5C, 9D) ~ 1.5–1.8× wider than long; elytra (Figs 4A, 7A, 8A) relatively shorter, 1.30–1.45× as long as wide at humeri, and 2.2–2.5× as long as pronotum; bicolorous, with major portion of elytra having distinctly darker setae ..... **2**

2 Antennomeres 4–10 (Fig. 5C) ~ 1.7–1.8× wider than long; pronotum (Fig. 5E) dark brown except lateral portions, 1.45× as wide as long; aedeagal median lobe (Fig. 6D–F) 1.5× as long as phallobase, not surpassing apices of parameres, widest basally, subparallel-sided for most of its length and then narrowed at apical 3/5..... ..... ***R. maculatus* Packova, Vorst & Kundrata, sp. nov.**

– Antennomeres 4–10 (Fig. 9D) ~ 1.5–1.6× wider than long; pronotum (Fig. 9E) mostly yellowish to pale brown, 1.55–1.60× as wide as long; aedeagal median lobe (Fig. 10D–F) 1.8–2.0× as long as phallobase, slightly surpassing apices of parameres, subparallel-sided but apparently widened at approx. mid-length..... ***R. testaceiceps* (Pic, 1924)**

### Checklist and distribution of *Reductodrilus* species

1. *R. longelytratus* Packova & Kundrata, sp. nov. (Philippines: Luzon)
2. *R. maculatus* Packova, Vorst & Kundrata, sp. nov. (Philippines: Socorro)
3. *R. nigroapicalis nigroapicalis* Pic, 1943 (Malaysia: Borneo/Sabah)
   *R. nigroapicalis latetestaceus* Pic, 1943 (Malaysia: Borneo/Sabah)
4. *R. testaceiceps* (Pic, 1924), comb. nov. (Philippines: Luzon, Siargao)

## Discussion

The classification and relationships of Ototretinae are in urgent need of revision. The monophyly of the group likewise requires rigorous testing. Recent mitogenomic and multigene phylogenetic studies have consistently recovered Ototretinae as non-monophyletic, with *Drilaster* Kiesenwetter, 1879 forming a lineage separate from *Stenocladius* Fairmaire, 1878 (Chen et al. 2019; Ge et al. 2021, 2022; Yang et al. 2024). These findings are congruent with the conclusions of Jeng et al. (2007), who divided Ototretinae into two morphologically defined groups. *Reductodrilus* shares with *Stenocladius* the absence of dorsal circular pits on the posterior pronotal angles, as well as similar male pregenital segments and genitalia (Janisova and Bocakova 2013). In the identification key to the genera of Ototretinae (Janisova and Bocakova 2013; Bocakova and Bocak 2016), *Reductodrilus* (not included in the key as transferred to Ototretinae by Kundrata et al. 2022) keys out to the final couplet containing *Falsophaeopterus* Pic, 1911 and *Stenocladius*, where it would be identified as *Falsophaeopterus*.

The genus *Falsophaeopterus* is divided into two subgenera (Wittmer 1944; Janisova and Bocakova 2013). The nominotypical subgenus, restricted to northeastern India, is monotypic and characterized by filiform to subserrated antennae and aedeagal parameres apically cleft. In contrast, the subgenus *Mimophaeopterus* Pic, 1930, which comprises five species from Java, Sumatra and New Guinea, has serrate antennae and parameres with simply rounded apices (Pic 1911, 1930; Wittmer 1944, 1964; Janisova and Bocakova 2013). Given these morphological differences and the disjunct distribution of the two subgenera, *Mimophaeopterus* may in fact represent a distinct genus as already suggested by e.g., Wittmer (1964). In their generic revision, Janisova and Bocakova (2013) retained *Mimophaeopterus* within *Falsophaeopterus* which was followed by Martin et al. (2019) and Keller (2024).

The genus *Reductodrilus* shares with *Falsophaeopterus* sensu lato (i.e., both subgenera) several morphological characters, particularly the absence of a dorsal circular pit on each posterior pronotal angle, the general shape of the pregenital segments, and the distinctly elongate median lobe and parameres. However, based on its morphological characters and geographic distribution, *Reductodrilus* is here considered to be more closely related to *Mimophaeopterus*. These taxa also share the general morphology of the antennae and pronotum, an abdominal sternite IX distinctly narrower basally and wider apically, a short, distinctly transverse tergite IX with a deep anteromedian emargination, and aedeagal parameres partly membranous apically, lacking apical bifurcation (Janisova and Bocakova 2013). Despite these similarities, *Reductodrilus* differs from both *Falsophaeopterus* and *Mimophaeopterus* in having strongly serrate to pectinate antennae (Figs 2C, 5C, 9D), reduced, dehiscent elytra that do not meet along the suture and expose a substantial portion of hind wings and abdomen (Figs 1A, B, 4A, B, 7A, 8A, B), and a distinctly wider phallobase (Figs 3C, E, 6D, F, 10D, F). Future studies encompassing both the described and undescribed diversity of these taxa should clarify their phylogenetic relationships and test the limits of the currently recognized genera. Other morphologically similar ototretine genera lacking a distinct dorsal circular pit on each posterior pronotal angle, i.e., *Baolacus* Pic, 1915, *Brachypterodrilus* Pic, 1918, and *Stenocladius*, are readily distinguished from *Reductodrilus* by the morphology of the antennae, pronotum, and male genitalia (Janisova and Bocakova 2013).

The genus *Stenocladius*, as well as its related genus *Oculogryphus*, has highly paedomorphic females which are larva-like and wingless (Ohba et al. 1997; Kawashima 1999; Yiu and Jeng 2018). This condition, in which adult males are fully capable of flight whereas females remain larviform, has evolved repeatedly within Elateroidea and contributes to the limited dispersal ability of these lineages (e.g., Ferreira and Ivie 2022; Kundrata 2026). Because of their cryptic lifestyle on the forest floor, in the soil, or within the leaf litter, females of paedomorphic taxa are only rarely collected, and available material usually consists almost exclusively of males. The females of *Reductodrilus* remain unknown but, given that the morphologically similar *Stenocladius* has highly paedomorphic females and *Reductodrilus* is known only from adult males, we hypothesize that the females of *Reductodrilus* are likewise highly modified and flightless. The same may apply to *Baolacus*, *Brachypterodrilus*, and *Falsophaeopterus*, including the subgenus *Mimophaeopterus*. It should be noted that Janisova and Bocakova (2013) incorrectly reported the female of *Mimophaeopterus* as fully winged. However, it

was based on a misidentification, and the female of *Mimophaeopterus* remains unknown (MB, pers. obs.). Future collecting efforts focused on forest floor microhabitats may help to discover the unknown females and test this hypothesis.

The Philippine fauna of Ototretinae remains poorly known, and here we document the genus *Reductodrilus* from the Philippines for the first time. Before this study, only three species of *Drilaster* Kiesenwetter, 1879 (two belonging to the nominotypical subgenus and one to the subgenus *Apodrilus* Janisova & Bocakova, 2013) and *Ototretadrilus philippinus* had been described from the Philippines (Pic 1943; McDermott 1966; Janisova and Bocakova 2013; Keller 2024), and Janisova and Bocakova (2013) additionally reported some unidentified specimens of *Brachypterodrilus* from the country. In addition, each of the reported species is represented by very limited material. *Reductodrilus* appears to be endemic to northern Borneo and the Philippines. The Philippine species are readily distinguishable from the Bornean species, differing, for example, in body coloration and the shape of pronotum. At least one additional species may be discovered once more material from Siargao Island becomes available, as the only specimen currently known from the island, with a partly damaged aedeagus, is tentatively assigned here to *R. testaceiceps* (see Remarks above). In addition, the distribution of *Reductodrilus* across the central and southern Philippines remains virtually unknown. Future research should focus on the diversity, biology, and phylogenetic relationships of *Reductodrilus* to improve our understanding of this hitherto almost forgotten Southeast Asian firefly genus.

## Acknowledgements

We thank Antoine Mantilleri (MNHN) and Berndt Jaeger (MFNB) for providing access to the Lampyridae specimens in their care. We are grateful to Yvonne van Dam (RMNH) for her assistance with photographing the type specimens deposited in the RMNH, and to Tomáš Lackner (NHMB) for his help with locating *Ototretadrilus philippinus* paratype. We also sincerely thank the staff of the Naturalis Biodiversity Center, Leiden (RMNH) for their patience and continuous support during our studies on elateroid beetles. RK is especially grateful to Patrice Bouchard (CNCI, Canada) for his advice on the nomenclature of the *Reductodrilus* species from the Philippines. Additionally, we thank V. S. Ferreira (Subject Editor) and three anonymous reviewers for their helpful comments and suggestions.

## References

Ballantyne LA, Lambkin CL, Ho J-Z, Jusoh WFA, Nada B, Nak-eiam S, Thancharoen A, Wattanachaiyingcharoen W, Yiu V (2019) The Luciolinae of S. E. Asia and the Australopacific region: a revisionary checklist (Coleoptera: Lampyridae) including description of three new genera and 13 new species. Zootaxa 4687(1): 1–174. https://doi.org/10.11646/zootaxa.4687.1.1

Bílý S, Kubáň V (2012) A revison of the genus *Anthaxia* from the Philippines (Coleoptera: Buprestidae: Buprestinae: Anthaxiini). Acta Entomologica Musei Nationalis Pragae 52(2): 433–442.

Bocakova M, Bocak L (2016) A new genus of ototretine firefly endemic to Indian subcontinent (Coleoptera: Lampyridae). Annales Zoologici 66(3): 371–380. https://doi.org/10.3161/00034541ANZ2016.66.3.003

Bocakova M, Campello-Goncalves L, Silveira LFL (2022) Phylogeny of the new subfamily Cladodinae: neotenic fireflies from the Neotropics (Coleoptera: Lampyridae). Zoological Journal of the Linnean Society 195: 1181–1199. https://doi.org/10.1093/zoolinnean/zlab091

Branham MA, Wenzel JW (2003) The origin of photic behavior and the evolution of sexual communication in fireflies (Coleoptera: Lampyridae). Cladistics 19: 1–22. https://doi.org/10.1111/j.1096-0031.2003.tb00404.x

Cai C, Tihelka E, Ballantyne L, Li Y-D, Huang D, Engel MS, Kundrata R (2024) A light in the dark: a mid-Cretaceous bioluminescent firefly with specialized antennal sensory organs. Proceedings of the Royal Society B: Biological Sciences 291: 20241671. https://doi.org/10.1098/rspb.2024.1671

Campello-Gonçalves L, Roza AS, Rivera S, Miras Mermudes JR, Branham MA, Silveira LFL (2025) Systematics of Amydetinae (Coleoptera: Lampyridae). Systematics and Biodiversity 23(1): 2481663. https://doi.org/10.1080/14772000.2025.2481663

Chen X, Dong Z, Liu G, He J, Zhao R, Wang W, Peng Y, Li X (2019) Phylogenetic analysis provides insights into the evolution of Asian fireflies and adult bioluminescence. Molecular Phylogenetics and Evolution 140: 106600. https://doi.org/10.1016/j.ympev.2019.106600

Crowson RA (1972) A review of the classification of Cantharoidea (Coleoptera), with definition of two new families, Cneoglossidae and Omethidae. Revista de la Universidad de Madrid 21: 35–77.

Ferreira VS, Ivie MA (2022) Lessons from a museum's cabinet: DNA barcoding and collections-based life stage associations reveals a hidden diversity in the Puerto Rican bank paedomorphic Lycidae (Coleoptera: Elateroidea: Leptolycini). Insect Systematics and Diversity 6(3): 2. https://doi.org/10.1093/isd/ixac006

Ferreira VS, Keller O, Branham MA, Ivie MA (2019) Molecular data support the placement of the enigmatic *Cheguevaria* as a subfamily of Lampyridae (Insecta: Coleoptera). Zoological Journal of the Linnean Society 187: 1253–1258. https://doi.org/10.1093/zoolinnean/zlz073

Ferreira VS, Keller O, Branham MA (2020) Multilocus phylogeny support the nonbioluminescent firefly *Chespirito* as a new subfamily in the Lampyridae (Coleoptera: Elateroidea). Insect Systematics and Diversity 4(6): 2. https://doi.org/10.1093/isd/ixaa014

Ferreira VS, Roza AS, Barbosa FF, Vega-Badillo V, Zaragoza-Caballero S, Mermudes JRM, Ivie MA, Hansen AK, Brunke AJ, Douglas HB, Solodovnikov A, Kundrata R (2024) Phylogenomics of Phengodidae (Coleoptera: Elateroidea): towards a natural classification of a bioluminescent and paedomorphic beetle lineage, with recognition of a new subfamily. Zoological Journal of the Linnean Society 201(4): zlae093. https://doi.org/10.1093/zoolinnean/zlae093

Fu X, Ballantyne L (2025) An overview of the firefly genus *Pygoluciola* Wittmer, a phylogeny of the Luciolinae using mitochondrial genomes, a description of six new species, and an assessment of a copulation clamp in this genus (Coleoptera: Lampyridae: Luciolinae). Insects 16: 394. https://doi.org/10.3390/insects16040394

Ge X, Yuan L, Kang Y, Liu T, Liu H, Yang Y (2021) Characterization of the first complete mitochondrial genome of Cyphonocerinae (Coleoptera: Lampyridae) with implications for phylogeny and evolution of fireflies. Insects 12: 570. https://doi.org/10.3390/insects12070570

Ge X, Liu T, Kang Y, Liu H, Yang Y (2022) First complete mitochondrial genomes of Ototretinae (Coleoptera, Lampyridae) with evolutionary insights into the gene rearrangement. Genomics 114: 110305. https://doi.org/10.1016/j.ygeno.2022.110305

ICZN [International Commission on Zoological Nomenclature] (1999) International Code of Zoological Nomenclature. Fourth Edition. The International Trust for Zoological Nomenclature, London, 305 pp.

Janisova K, Bocakova M (2013) Revision of the subfamily Ototretinae (Coleoptera: Lampyridae). Zoologischer Anzeiger 252: 1–19. https://doi.org/10.1016/j.jcz.2012.01.001

Jeng M-L, Engel MS (2014) Description of *Oculogryphus shuensis* sp. n. (Coleoptera, Lampyridae), the first species of the genus in the Sino-Japanese realm, with a modified key to the subfamily Ototretinae. ZooKeys 378: 41–47. https://doi.org/10.3897/zookeys.378.6435

Jeng M-L, Engel MS, Yang P-S (2007) *Oculogryphus*, a remarkable new genus of fireflies from Asia (Coleoptera: Lampyridae). American Museum Novitates 3600: 1–19. https://doi.org/10.1206/0003-0082(2007)3600[1:OARNGO]2.0.CO;2

Kawashima I (1999) The lampyrid beetles of the genus *Stenocladius* (Coleoptera, Lampyridae) of the Ryukyu Islands, Southwest Japan with descriptions of two new species. Elytra (Tokyo) 27: 141–l58.

Kawashima I, Satou F, Satô M (2005) The lampyrid genus *Drilaster* (Coleoptera, Lampyridae, Ototretinae) of the Ryukyu Archipelago, Southwest Japan. Japanese Journal of Systematic Entomology 11(2): 225–262. https://doi.org/10.69343/jjsystent.11.2_225

Kazantsev SV (2024) *Eolamprohiza andrushchenkoi* gen. n., sp. n., a new firefly from Baltic amber, with a checklist of fossil Lampyridae (Insecta: Coleoptera). Russian Entomological Journal 33: 203–209. https://doi.org/10.15298/rusentj.33.2.05

Keller O (2024) The Lampyridae of the World. https://lampyridae.world [accessed June 15, 2026]

Keller O, Hinson KR (2023) Taxonomic notes on the Ototretinae, Photurinae, and Psilocladinae (Coleoptera: Lampyridae). Insecta Mundi 0987: 1–10.

Kundrata R (2026) Systematics, evolution, and diversity of elateroid beetles (Insecta: Coleoptera). Annual Review of Entomology 71: 107–127. https://doi.org/10.1146/annurev-ento-121423-013628

Kundrata R, Bocak L (2011) Redescription and relationships of *Pseudothilmanus* Pic (Coleoptera: Rhagophthalmidae) a long-term neglected glow-worm beetle genus from the Himalayas. Zootaxa 2794(1): 57–62. https://doi.org/10.11646/zootaxa.2794.1.4

Kundrata R, Hoffmannova J, Hinson KR, Keller O, Packova G (2022) Rhagophthalmidae Olivier, 1907 (Coleoptera, Elateroidea): described genera and species, current problems, and prospects for the bioluminescent and paedomorphic beetle lineage. ZooKeys 1126: 55–130. https://doi.org/10.3897/zookeys.1126.90233

Li Y-D, Kundrata R, Tihelka E, Liu Z, Huang D, Cai C (2021) Cretophengodidae, a new Cretaceous beetle family, sheds light on the evolution of bioluminescence. Proceedings of the Royal Society B 288(1943): 20202730. https://doi.org/10.1098/rspb.2020.2730

Martin GJ, Branham MA, Whiting MF, Bybee SM (2017) Total evidence phylogeny and the evolution of adult bioluminescence in fireflies (Coleoptera: Lampyridae). Molecular Phylogenetics and Evolution 107: 564–575. https://doi.org/10.1016/j.ympev.2016.12.017

Martin GJ, Stanger-Hall KF, Branham MA, Silveira LFL, Lower SE, Hall DW, Li X-Y, Lemmon AR, Lemmon EM, Bybee SM (2019) Higher-level phylogeny and reclassification of Lampyridae (Coleoptera: Elateroidea). Insect Systematics and Diversity 3(6): 11. https://doi.org/10.1093/isd/ixz024

McDermott FA (1964) The taxonomy of the Lampyridae (Coleoptera). Transactions of the American Entomological Society 90: 1–72.

McDermott FA (1966) Lampyridae. In: Steel WO (Ed.) Coleopterorum Catalogus Supplementa, Pars 9. Dr. W. Junk, 's-Gravenhage, 1–149.

Ohba N, Goto Y, Kawashima I (1997) Behavior and adult female morphology of firefly, genus *Stenocladius* (Coleoptera: Lampyridae) in Japan. Science Report of the Yokosuka City Museum 45: 23–37.

Pic M (1911) Quatre nouveaux genres de Malacodermes. L'Échange, Revue Linnéenne 27: 186–188.

Pic M (1924) Lampyrides et Telephorides des îles Philippines. Philippine Journal of Science 25: 711–731.

Pic M (1930) Contribution a l'étude des Coléoptères Malacodermes (2e article). Annales de la Société Entomologique de France 99: 311–324. https://doi.org/10.1080/21686351.1930.12280336

Pic M (1943) Coléoptères du globe (suite). L'Échange. Revue Linnéenne 59: 9–12.

Powell GS, Saxton NA, Pacheco YM, Stanger-Hall KF, Martin GJ, Kusy D, Silveira LFL, Bocak L, Branham MA, Bybee SM (2022) Beetle bioluminescence outshines extant aerial predators. Proceedings of the Royal Society B: Biological Sciences 289(1979): 20220821. https://doi.org/10.1098/rspb.2022.0821

Roza AS, Mermudes JRM, Silveira LFL (2022) A new genus and two new species of fireflies from South America (Lampyridae: Lampyrinae: Photinini). Diversity 14: 1005. https://doi.org/10.3390/d14111005

Roza AS, Kundrata R, Kusy D, Lian ZD, Silveira LFL (2024) The first firefly fossil (Coleoptera: Lampyridae) from Dominican amber. Palaeoentomology 7: 590–593. https://doi.org/10.11646/palaeoentomology.7.5.3

Silveira LFL, Roza AS, Vaz S, Mermudes JRM (2021) Description and phylogenetic analysis of a new firefly genus from the Atlantic Rainforest, with five new species and new combinations (Coleoptera: Lampyridae: Lampyrinae). Arthropod Systematics & Phylogeny 79: 115–150. https://doi.org/10.3897/asp.79.e67185

Wittmer W (1941) Malacodermata von den Philippinen aus der Sammlung des zoologischen Museums in Amsterdam. Philippine Journal of Science 74: 195–228.

Wittmer W (1944) Catalogue des Drilidae E. Oliv. (Coleoptera-Malacodermata). Revista de la Sociedad Entomológica Argentina XII: 203–221.

Wittmer W (1948) Supplement au catalogue des Drilidae E. Oliv. (Col. Malacodermata). Revista de la Sociedad Entomológica Argentina XIV: 115–116.

Wittmer W (1964) Neue Malacodermata aus Neu Guinea (24. Beitrag zur Kenntnis der indo-malayischen Malacodermata, Col.). Nova Guinea 30: 115–137.

Wittmer W (1978) Neue Coleoptera aus dem Orient, Neuguinea und Australien. Pacific Insects 18: 61–66.

Yang L, Borne F, Betz A, Aardema ML, Zhen Y, Peng J, Visconti R, Wu M, Roland BP, Talsma AD, Palladino MJ, Petschenka G, Andolfatto P (2023) Predatory fireflies and their toxic firefly prey have evolved distinct toxin resistance strategies. Current Biology 33: 5160–5168. https://doi.org/10.1016/j.cub.2023.10.063

Yang Y-X, Kang Y, Ge X-Y, Yuan S-L, Li X-Y, Liu H-Y (2024) A mysterious Asian firefly genus, *Oculogryphus* Jeng, Engel & Yang (Coleoptera, Lampyridae): the first complete mitochondrial genome and its phylogenetic implications. Insects 15: 464. https://doi.org/10.3390/insects15070464

Yiu V, Jeng M-L (2018) *Oculogryphus chenghoiyanae* sp. n. (Coleoptera, Lampyridae): a new ototretine firefly from Hong Kong with descriptions of its bioluminescent behavior and ultraviolet-induced fluorescence in females. ZooKeys 739: 65–78. https://doi.org/10.3897/zookeys.739.21502

Yuan S, Liu H, Lv S, Yang Y (2026) A true Luciolinae fossil from the mid-Cretaceous Burmese amber provides new insights into the early evolution of fireflies (Coleoptera: Lampyridae). Proceedings of the Royal Society B: Biological Sciences 293: 20253316. https://doi.org/10.1098/rspb.2025.3316

Zaragoza-Caballero S, López-Pérez S, González-Ramírez M, Rodríguez-Mirón GM, Vega-Badillo V, Domínguez-León DE, Cifuentes-Ruiz P (2023) Luciérnagas (Coleoptera: Lampyridae) del norte-occidente de México, con la descripción de 48 especies nuevas. Revista Mexicana de Biodiversidad 94: e945028. https://doi.org/10.22201/ib.20078706e.2023.94.5028

Zhu C, Lu X, Cai T, Zhu K, Shi L, Chen Y, Wang T, Yang Y, Tu D, Fu Q, Huang J, Zhen Y (2024) Firefly toxin lucibufagins evolved after the origin of bioluminescence. PNAS Nexus 3: pgae215. https://doi.org/10.1093/pnasnexus/pgae215

## Additional information

### Conflict of interest

The authors have declared that no competing interests exist.

### Ethical statement

No ethical statement was reported.

### Artificial Intelligence (AI) use

The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.
Regarding the use of AI in the preparation of this manuscript, the authors declare the following: GPT.
**Used for:** Language, style and writing.
AI-based tool ChatGPT (OpenAI), was used solely for language editing, text refinement, and spelling correction, without contributing to the study's scientific content, interpretation, or conclusions.

### Funding

This study was funded by the internal grant of the Faculty of Science, UP Olomouc (IGA_PrF_2026_032; to GP and RK).

### Author contributions

GP: Conceptualisation, Data curation, Investigation, Visualisation, Writing – original draft, Writing – review and editing. OV: Data curation, Investigation, Visualisation, Writing – review and editing. MFG: Investigation, Validation, Writing – review and editing. OK: Investigation, Writing – review and editing. MB: Investigation, Validation, Writing – review and editing. RK: Conceptualisation, Data curation, Funding acquisition, Investigation, Project administration, Supervision, Validation, Writing – original draft, Writing – review and editing.

### Author ORCIDs

G. Packova https://orcid.org/0000-0001-7949-619X
O. Vorst https://orcid.org/0000-0003-3508-8551
M.F. Geiser https://orcid.org/0000-0002-9278-2358
O. Keller https://orcid.org/0000-0001-5067-3316
M. Bocakova https://orcid.org/0000-0002-2507-0887
R. Kundrata https://orcid.org/0000-0001-9397-1030

### Data availability

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