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Rhytomus Génier & Saxton: A new dung beetle genus from New Guinea with five new species and phylogenetic insights (Coleoptera: Scarabaeidae: Scarabaeinae)

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Abstract

In this study, we utilize both morphological and molecular data of Australasian dung beetles to establish *Rhytomus* Génier & Saxton, **new genus**. Using ultra-conserved element (UCE) data, we reconstruct the relationships between *Rhytomus* and related genera within the Australasian endemic clade. We provide a comprehensive revision for all mainland New Guinea species including the description of five new species: *R. fervidus* Saxton & Génier, **new species**, *R. larseni* Saxton & Génier, **new species**, *R. latidentatus* Saxton & Génier, **new species**, *R. sodalis* Saxton & Génier, **new species**, and *R. vanus* Saxton & Génier, **new species**. We transfer seven species originally described within the genus *Tesserodon* Hope, 1837; *Rhytomus heurni* (Paulian, 1937), **new combination**, *Rhytomus howdeni* (Paulian, 1985), **new combination**, *Rhytomus papuanus* (Paulian, 1985), **new combination**, *Rhytomus seramicus* (Krikken & Huijbregts, 2009), **new combination**, *Rhytomus setulosus* (Balthasar, 1965), **new combination**, *Rhytomus waigeoensis* (Ochi, Kon & Hartini, 2017), **new combination.** Furthermore, we designate a lectotype for *Tesserodon elongatum* van Lansberge, 1885, correct name bearing type data for *Tesserodon howdeni* Paulian, 1985 and provide both a traditional dichotomous and an online illustrated interactive identification key for mainland New Guinea species.

Key words: Australasia, dung beetles, Indonesia, New Guinea, phylogeny, taxonomy

Introduction

Molecular studies have repeatedly recovered an "Australasian endemic clade" (Tarasov & Dimitrov 2016; Gunter *et al.* 2019b; Lopes *et al.* 2024) comprised of the majority of dung beetle genera found in Australia and New Guinea in addition to those from New Zealand and New Caledonia (Gunter *et al.* 2019a). This clade is currently treated as *incertae sedis* and includes genera formerly classified in the Deltochilini and Coprini (Tarasov & Dimitrov 2016). Revisionary work within this clade has largely been grounded on the works completed by Matthews (1974, 1976). Prior to this study, there were eight native Scarabaeinae genera known from New Guinea including *Amphistomus* van Lansberge, 1875 (7 species; Gunter *et al.* 2019a), *Coptodactyla* Burmeister, 1846 (4 species; Reid 2000), *Lepanus* Balthasar, 1966 (6 species; Gunter *et al.* 2019a, 2022), *Onthophagus* Latreille, 1802 (123 species; Krikken & Huijbregts 2012a, 2012b, 2012c 2013), *Paraphacosomoides* Balthasar, 1968 (1 species), *Penalus* Paulian, 1985 (1 species), *Temnoplectron* Westwood, 1842 (5 species; Reid & Storey 2000), and *Tesserodon* Hope, 1837 (5 species; Paulian 1985).

The genus *Tesserodon* was originally erected for the species *Scarabaeus novaehollandiae* Fabricius, 1775 collected in Australia during the 1770 Banks expedition, and probably collected at Endeavour River, Queensland. Interestingly, the only diagnostic character given by Hope to distinguish this new genus from other "Scarabaeidae" was the quadridentate clypeus, implied from the genus name. Reiche (1842) in his treatment of the genera is uncertain about many characters in his diagnosis of the genus. He states that the clypeus is bidentate "épistome avec une large

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et profonde échancrure antérieure, à deux lobes avancés dans son milieu", indicating confusion about the number of clypeal teeth. In fact, the clypeal edge of *Tesserodon* appears quadridentate, but only has two true medial teeth, as Matthews (1974) accurately describes it. The quadridentate appearance is due to the medial teeth being flanked by deep V-shape indentations, giving the impression of four teeth.

Thirteen species of *Tesserodon*, including the type species *T. novaehollandiae* are endemic to Australia. Work focused almost exclusively on Australian species includes Matthews (1974), Storey (1991), and Gunter *et al.* (2019a). In Storey (1991), four groups for the Australian species were proposed based on the aedeagi shape. An additional seven species of *Tesserodon* are found outside Australia in both Papua New Guinea and Indonesia. The first described was *Tesserodon elongatum* van Lansberge, 1885 from New Guinea, followed by three additional species described by Paulian (1937, 1985) and a fifth species described by Balthasar (1965). Krikken & Huijbregts (2009) expanded the geographic range of the genus to include the Indonesian Moluccas with the description of *T. seramicum* Krikken & Huijbregts, 2009. Most recently, *Tesserodon waigeoensis* Ochi, Kon & Hartini, 2017 was described from Waigeo Island, West Papua. Specimens of these species key out to *Tesserodon* in the key to Australian Scarabaeinae in Gunter *et al.* (2019). However, they lack the typical "quadridentate" clypeus found in Australian *Tesserodon*, have only 9 elytral striae as opposed to 10, and have a different configuration of the fore tibia.

Generic limits within the Australasian endemic clade have historically been difficult to elucidate due to many species in different genera sharing similar characters (Matthews 1974). As such, here we use both morphological and molecular evidence to establish the new genus *Rhytomus* Génier & Saxton, **new genus,** which is found on mainland New Guinea, Seram Island (Maluku), and Waigeo Island (West Papua). The few specimens with collecting data indicate that the genus is attracted to carrion and unspecified dung. However, the dung used as bait is most likely of human origin. With the transfer of seven *Tesserodon* species and the description of the five new species, *Rhytomus* becomes the second most speciose genus in New Guinea. In total *Rhytomus* has ten known species found on mainland New Guinea and two additional species found on neighboring islands. With the establishment of the new genus and transfer of species, the genus *Tesserodon* is now considered endemic to Australia.

Material and Methods

Study material and morphology. Most of the 438 specimens studied here came from recent collecting (2013) by Trond Larsen. This was part of a Conservation International (CI) Rapid Assessment program (RAP) in the Western Province of Papua New Guinea (PNG). It also includes material previously deposited in the collection of the Canadian Museum of Nature, most of which was studied by Renaud Paulian.

Morphological terminology follows that used by Matthews (1974) and Lawrence & Slipinski (2013). In the case of *Rhytomus*, we consider the two elytral striae along the epipleural carina to be homologous with striae 9 and 10, with stria 8 presumed to be completely lost/reduced.

Our study of the morphology of *Rhytomus* suggests that we should clarify the definition of some key elytral characters for generic delimitation. In Scarabaeinae, the lateral edges of the elytra may be evenly convex or deflexed, either partially or along the entire length of the elytra, with variability in the dorsal edge of this deflection. This variability is key in whether this deflection forms the pseudepipleuron. When the deflection lies in the same plane as the epipleuron, and its dorsal edge is clearly demarcated, at least in part, by a sharp ridge, carina, rounded fold, or row of tubercles, this portion of the elytral surface is classified as the pseudepipleuron (Fig. 1A). In most Australasian genera, this distinct dorsal edge (if present) is located just outside the seventh stria; however, in *Diorygopyx* Matthews, 1974 it is short and occurs along the eighth stria (Gunter *et al.* 2019a). In some genera, such as *Matthewsius* Gunter & Weir, 2017, not all species have evenly rounded elytra; some species show a poorly defined elytral deflection outside the seventh stria. This slight deflection, however, is not in the same plane as the epipleuron and lacks a clearly defined dorsal edge, so it is not considered a pseudepipleuron (Gunter & Weir 2017), though it may represent an intermediate state.

The epipleuron is the distinct elevated lateral portion of the elytra delimited dorsally by a sharp carina (epipleural carina) which usually extends from the elytral external anterior angle to the elytral suture dorsally on apical declivity (Fig. 1B). This carina is usually well-defined and connected to the fine carina usually present along the elytral suture at the internal posterior elytral angle; however, the epipleural carina may be completely absent in rare cases like *Sisyphus* (*Neosisyphus*) Müller, 1942. Typically, there is an additional carina running along the lateral elytral edge,

the external epipleural carina (Fig. 1A), which is usually absent or ill-defined along the posterior elytral declivity. In *Sisyphus* (*Neosisyphus*), the external epipleural carina is the only visible carina and can be mistaken for the epipleural carina. In other cases, as in *Ontherus* Erichson, 1847, the epipleural carina is complete but the external epipleural carina is effaced on the anterior half of the elytra.

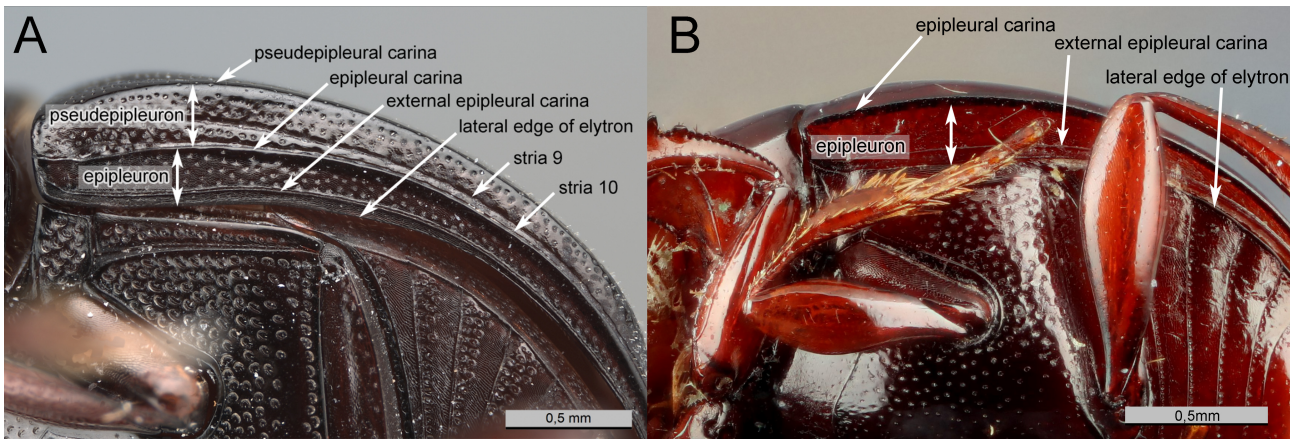

FIGURE 1. Elytral characters used in generic delimitation. A, *Rhytomus larseni*, note presence of pseudepipleural carina; B, *Lepanus topend*, note absence of pseudepipleural carina.

Examined material data and chresonomy were compiled and generated with the Mantis database (Naskrecki & Génier 2024, A Manager of Taxonomic Information and Specimens, version 2.9.2). Name-bearing type data are cited verbatim with "||" encompassing labels and "|" separating text line. Unless otherwise stated, labels are printed on white paper. Missing or additional information in the name-bearing type data and material examined list is presented between square brackets "[]". The specimens examined are deposited in the following institutions:

ANIC	Australian National Insect Collection (Canberra, ACT, Australia)
CMNC	Canadian Museum of Nature (Gatineau, QC, Canada)
MSNG	Museo Civico di Storia Naturale "Giacomo Doria" (Genova, Italy)
MNHN	Muséum national d'Histoire Naturelle (Paris, France)
NHMUK	The Natural History Museum (London, United Kingdom)
NMPC	National Museum (Prague, Czech Republic)
QM	Queensland Museum (Brisbane, QLD, Australia)
SDEI	Senckenberg Deutsches Entomologisches Institut (Müncheberg, Germany)
USNM	National Museum of Natural History (Washington, D.C., United States)

We have chosen to offer users both an online interactive illustrated identification key, created using Lucid software version 4 (http://www.lucidcentral.org), in addition to a traditional dichotomous identification key. This online tool (https://keys.lucidcentral.org/keys/v4/rhytomus/) presents high-resolution images of the habitus of each species as well as key species characteristics, facilitating easy discrimination between species. It employs a minimum of six distinguishing features to separate closely related species. The base for each species description has been generated using the same software.

Molecular phylogenetics. DNA work was completed on both pinned and recently collected specimens with an emphasis on genera morphologically similar to *Rhytomus* (i.e., *Matthewsius* Gunter & Weir, 2017, *Aptenocanthon* Matthews, 1974) (Table 1). Taxon sampling is limited to genera within the well-established Australasian endemic clade (Tarasov & Dimitrov 2016; Gunter *et al.* 2019b; Lopes *et al.* 2024). In total, we included representatives from nine additional genera. Extractions were completed using Qiagen's DNeasy blood and tissue kits following a standard protocol with the exception that the last elution step was repeated 2x, with a 10-minute incubation period between each elution, resulting in a total volume of 180ul. Extractions were quantified using Qubit dsDNA HS Assay Kit with a Qubit 4 Fluorometer (Thermo Fisher Scientific). DNA samples were selected based on total DNA concentration and final extracts were concentrated or diluted to have ~200ng per 40 ul. Final extractions containing

40ul were sent to RAPiD Genomics LLC (Gainesville, Florida) for library preparation and enrichment. DNA was sheared to a mean fragment length of 500 bp followed by adenine litigation to the 3'-end. Next, unique dual-indexed adapters were introduced, and fragments were PCR-amplified. Samples were then pooled and enriched using a Scarabaeinae specific probe set Scarab_3kv1 (Gustafson *et al.* 2023). Samples were sequenced after enrichment on an Illumina HiSeq 2500. RAPiD then performed demultiplexing.

We used the software package Phyluce 1.7.1 (Faircloth 2016) to clean, assemble, and align our UCE data. Reads were first cleaned using illumiprocessor (Faircloth 2013) and then assembled using SPAdes (Prjibelski *et al.* 2020) using default settings. UCE loci were extracted from clean reads (min_coverage = 80, min_identity=80), and aligned using Mafft (Katoh & Standley 2013), in which all sequences with ambiguous bases were removed. Gblocks (Talavera & Castresana 2007), as implemented within Phyluce, was then used to trim our alignments (settings b1=0.5, b2=0.85, b3=8, b4=10). A final matrix was concatenated and exported for phylogenetic analysis incorporating all alignments containing at least 75% of taxa. Our final UCE alignment can be accessed at Open Science Framework (https://osf.io/9zsr5/) (DOI 10.17605/OSF.IO/9ZSR5). We used IQ-Tree (Nguyen *et al.* 2015) in the CIPRES portal (Miller *et al.* 2015) to reconstruct a maximum likelihood phylogeny utilizing both ModelFinder (Kalyaanamoorthy *et al.* 2017) and 1000 ultrafast bootstraps (Hoang *et al.* 2017).

TABLE 1. Taxon sampling used in phylogenetic analysis.

Voucher Code	Genus	Species	Locality
COL2474	*Matthewsius*	*vanleeuweni*	WA: 16 km E of Mt Meharry
COL3011	*Matthewsius*	*speewah*	QLD: Mt Williams
COL3013	*Aptenocanthon*	*monteithi*	QLD: Lambs Head summit
COL3114	*Tesserodon*	*intricatum*	QLD: W. of Adelaide River
COL3182	*Lepanus*	*mirabilis*	PNG: Western Prov. P'nvana
COL3190	*Rhytomus*	*papuanum*	PNG
COL3191	*Rhytomus*	*vanus*	PNG: Madang Province, Baitabag
COL3207	*Temnoplectron*	*lewisense*	QLD: Mt Lewis National Park
COL3870	*Aptenocanthon*	*hopsoni*	NSW: Chinchester State Forest
COL3893	*Rhytomus*	*latidentatus*	PNG: Prov., P'nvana
COL3934	*Lepanus*	*ustulatus*	NSW: Wilson's Park
COL3946	*Matthewsius*	*illlawarensis*	NSW: Mt Keira
COL3948	*Sauvagesinella*	*becki*	WA: Waychinnucup National Park
COL3964	*Canthonosoma*	*castelnaui*	QLD: Bulburin National Park
COL3976	*Tesserodon*	*granulatum*	WA: Beagle Bay
COL3995	*Tesserodon*	*novaehollandiae*	WA: Beagle Bay
COL4067	*Monteithocanthon*	*arator*	QLD: Mt Lewis National Park
COL4590	*Rhytomus*	*larseni*	PNG: Western Prov. P'nvana
COL769	*Matthewsius*	*rossi*	NSW: Newnes State Forest

Results and Discussion

In total 19 specimens were included in the analysis (Table 1) with an alignment length of 466,607bp composing 844 loci. ModelFinder found GTR+F+I+R5 as the best-fit model for the dataset with a BIC score of 4818102.896. Most nodes were recovered with 100% bootstrap (BS) except for outgroup generic relationships. Due to the limited taxon sampling among those genera this lower support is not unexpected.

Our results based on UCE data builds upon previous analyses within the Australasian endemic clade using sanger data (i.e., Gunter & Weir 2017; Gunter *et al.* 2019) but includes for the first time "*Tesserodon*" specimens from mainland New Guinea. Molecular evidence supports the establishment of the new genus *Rhytomus* distinct from *Tesserodon.* In fact, *Rhytomus* is recovered as more closely related to genera *Matthewsius* and *Aptenocanthon* than *Tesserodon* species (Fig. 2). The transfer of five species from *Tesserodon* to *Rhytomus* leaves the former

with thirteen species all of which are restricted to Australia. *Tesserodon* is recovered as monophyletic (100 BS), but only includes three of its thirteen species representing only two of the species groups proposed by Storey (1991). This tree includes the type species for the genus (i.e., *T. novaehollandiae*). The *Rhytomus* are recovered as a monophyletic clade with high support (100 BS) with *Matthewsius speewah* (Storey & Monteith 2000) sister to it, rendering *Matthewsius* paraphyletic (Fig. 2).

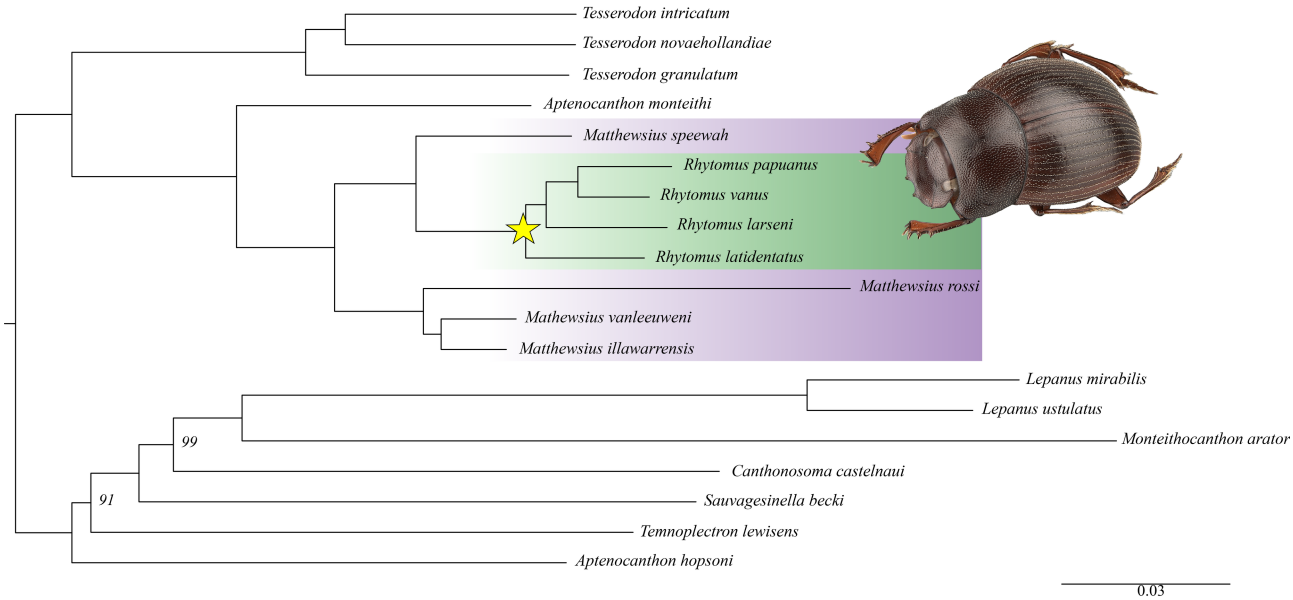

FIGURE 2. Phylogeny of *Rhytomus* showing its placement among closely related genera. Nodes recovered with 100% BS unless otherwise indicated. Star represents most recent common ancestor of *Rhytomus.*

Matthewsius currently contains six species, of which four are included our phylogeny here. While the type of the genus, *M. stricklandensis* Gunter & Weir, 2017 is not included in this phylogeny, we infer its position in the clade containing *M. rossi* (Matthews, 1974), *M. illawarensis* (Matthews, 1974), and *M. vanleuweni* Gunter & Weir, 2017 on the basis of relationships established in the multigene phylogenies that include sanger sequencing data for all six *Matthewsius* species and also recover *M. speewah* as the earliest branching taxon (Gunter & Weir 2017; Gunter *et al.* 2019). Although *Matthewsius* shares many characters with *Rhytomus*, there are several important characters that indicate a need for a distinct genus. Both genera share a combination of characters including a trochanterofemoral pit, protibial brush and comb, equal metatarsomeres 5 and 2, simple claws, a basal groove on the pygidium, and asymmetrical aedeagi with the right paramere bend downwards and expanded. *Rhytomus* differ from *Matthewsius*, however, in having 9 elytral striae, the presence of pseudepipleura with a defined dorsal edge, wide eyes (10–15 facets across), and an interocular space of 3–6 times eye width. *Matthewsius* specimens have only 8 elytral striae, no pseudepipleuron, narrow eyes (3–7 facets across), and an interocular space of 15–18 times eye width (Table 2).

We also recovered *Aptenocanthon* as paraphyletic, a result that has been noted in past studies (Gunter & Weir 2017; Gunter *et al.* 2019). *Aptenocanthon monteithi* Storey, 1984 is recovered sister to *Matthewsius* + *Rhytomus*. In previous phylogenetic analyses *A. monteithi* has been recovered with *A. winyar* (Gunter & Weir, 2017), although the latter is missing from our analysis. These two species were not transferred to *Matthewsius* due to their pseudepipleura having a carinate dorsal edge, the presence of 10 elytral striae, and no pygidial groove (Gunter & Weir 2017). *Aptenocanthon hopsoni* (Carter, 1936) is distantly related to *A. monteithi* in having a pseudepipleuron, 9 elytral striae, and both a basal and apical groove. As noted in previous studies, we suggest a full revision of *Aptenocanthon* is needed to define generic boundaries here.

Two species in *Matthewsius* were formerly classified as *Aptenocanthon*, *M. speewah* and *M. rossi* both included in our phylogeny here. These species were noted to differ from other *Aptenocanthon* species in that they lacked a carinate pseudepipleuron (Storey & Monteith 2000; Gunter & Weir 2017). In our UCE phylogeny, *M. rossi* is recovered within the main *Matthewsius* clade of our phylogeny while *M. speewah* is recovered sister to *Rhytomus* rendering *Matthewsius* paraphyletic. The close relationship of *M. speewah* with *Rhytomus* prompted further examination of this species, particularly the configuration of the elytra striae. Under normal light microscopy

conditions, it is very difficult to determine the number of elytral striae due to their faintness, proximity to the epipleural edge and apparent variability between specimens. Examination of teneral specimens, in which the striae are more easily visible, suggest that there are 9 elytral striae as opposed to the 8 reported in the original description (Fig. 3A) (Storey & Monteith 2000) and by Gunter & Weir (2017). Stria 9 appears very short, connecting with and barely separated from stria 10 that runs along the elytral edge (and stria 8 being lost). Stria 9 is difficult to see in specimens with full dark-black coloration, and is visible on one elytron of the holotype (Fig. 3B), or if legs obscure the view. The possible presence of stria 9, along with other differences such as the unique pygidial configuration with the transverse groove narrowed medially and terminating with a pit in each end may warrant further revisionary changes. More work is needed to fully understand this relationship, but we refrain from changing the current classification of *M. speewah* at this time.

TABLE 2. Morphological characters used to diagnose closely related genera in the Australasian endemic clade. Modified from Gunter & Weir (2017). Interocular space given in number of eye widths. S: simple; SD: subdentate. *Note that in *M. speewah* elytral striae often appear as 8.

Taxon	Claws	Setae groups on protibial teeth	Pygidium	number of facets across dorsal part of eyes	Interocular space
Matthewsius	S or SD	2	basal groove	3–7	15–18
M. speewah	S	2	basal groove	7	14
Rhytomus	S or SD	2	basal groove	10–15	3–6
Aptenocanthon winyar + *monteithi*	S	variable 2-2-2/1	smooth, no groove	8–10	9.5–10.0

.....continued below

TABLE 2. (Continued)

Taxon	Elytral striae	Pseudepipleura	Trochanterofemoral pit	Protibial brush and comb	Metatarsomere 5 versus 2
Matthewsius	8	absent	present	present	equal length
M. speewah	9*	absent	present	present	equal length
Rhytomus	9	present	present	present	equal length
Aptenocanthon winyar + *monteithi*	10	present	present	present	equal length

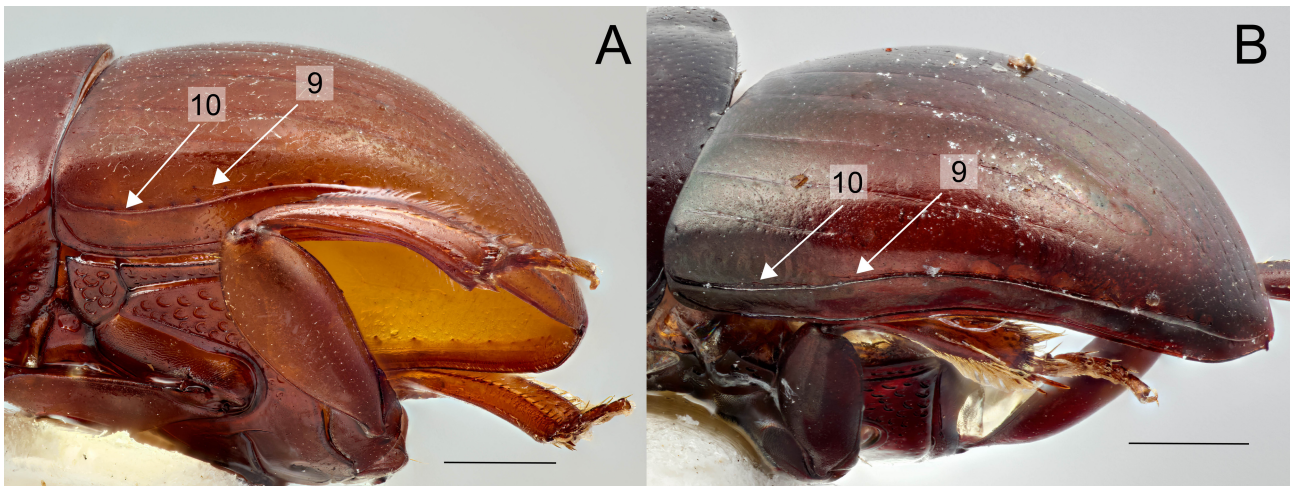

FIGURE 3. *Matthewsius speewah* lateral view showing elytral striae. A, Paratype T54712 (QM), B, Holotype T54713 (QM). Imaged by Lily Kumpe. Scale bar = 0.5 mm.

***Rhytomus* Génier & Saxton, new genus**
urn:lsid:zoobank.org:act:3800DB4F-9D65-4AD7-9A13-8809F0F0C3F0

Types species. *Tesserodon elongatum* van Lansberge, 1885.

Diagnosis. The presence of a trochanterofemoral pit combined with a pseudepipleuron, the presence of a posterior hypomeral carina and well-defined elytral striae 9 and 10 will separate *Rhytomus* from all the other genera in New Guinea. Within the Australasian endemic clade, *Rhytomus* can be distinguished from other genera by those previous characters listed in conjunction with having 9 elytral striae, and wide eyes with an interocular space 3–6 times the eye width.

Description. Body. Total length 3.0–6.3 mm. Tegument hard, brittle. Color dark reddish brown to black (teneral specimens lighter in color), ventral surface and legs usually lighter in color, lacking metallic sheen. **Head.** Anterior edge of clypeus with two clypeal teeth, with or without emargination on external side of each tooth. Dorsal part of eyes wide (Fig. 4A,B), inner edge straight basally, outer edge arcuate, with at least 12 facets along its widest portion. Ocular canthus incomplete. Occiput of head simply rounded (Fig. 4C,D). Antennae nine segmented, with 3-antennomere club, club antennomeres approximately equal width. Antennomeres 7 and 8 lacking median cavity. **Pronotum.** Basal edge of pronotum broadly arcuate. Posterior hypomeral carina present, almost as long as half lateral pronotal edge. Anterior edge lacking membranous imbrication, anterior marginal bead very narrow. **Elytra.** Elytra with 9 striae, 7 on disc and 2 on the pseudepipleuron adjacent to the epipleural edge (Fig. 4D). Stria 8 missing. Stria 9 effaced anteriorly, fused or very closely set with tenth stria past basal third to posterior declivity where it is distinct again. With a well-defined pseudepipleural fold from base to apical declivity outside stria 7. Laterobasal elytral pit present or absent (Fig. 4A). **Hind wings.** Present, fully developed. **Pygidium.** Deeply and narrowly sulcate across the base, sulcus usually wider and deeper laterally (Fig. 8). **Pterothoracic ventrite.** Mesepimera with coarse semicircular ocellate punctures. **Abdominal ventrite**. Ventrite 6 approximately as long as 1–5 combined along midline. **Legs.** Protibiae (Fig. 4E) of male abruptly internally expanded apically, distal edge of internal angle with a row of contiguous spiniform setae flanked posteriorly by a row of long squamiform setae, with more or less elongated triangular spur. Protibiae distally straight with 3 teeth on outer edge, each tooth with two groups of setae dorsally. Prothoracic legs with trochanterofemoral anterior pit (Fig. 4C), trochanter excavated dorsally for reception of inner apical edge of protibia. Protarsi with 5 tarsomeres, tarsomere 1 and 5 longer. Long, setae on all tarsomeres or tarsomere 1 lacking setae. Male mesotibiae with dense setae on ventral edge. Metatibiae of males with well-developed tooth on inner apical angle. Mesotarsi with 5 tarsomeres, tarsomere 2 about same length as tarsomere 5. Metatarsomere 1 widest, metatarsomere 2 equal to metatarsomere 5 in length, all tarsomeres with long setae ventrally. Claws simple or slightly angulate at base. Metacoxal connecting membrane apodeme present, oval (internal). **Genitalia.** Aedeagus with parameres asymmetrical, right paramere apically bent downwards and expanded, left paramere more or less bent downward apically or simply rounded (Figs. 9, 10). Spermatheca V-shaped, with or without apodeme distally and basally.

Etymology. Based on the combination of two Greek words. The feminine noun ῥυτίς (rhytís) meaning wrinkle, crease and the masculine noun ὦμος (omos) meaning shoulder, the terminal component transliterated in Latin with the masculine ending -us (ICZN art. 30.1.2). The name refers to the presence of a crease on the humeral surface of the elytron.

Distribution. Papua New Guinea and Indonesia (Seram Island, Waigeo Island and Papua). Specimens collected at elevations from 3 m to 2050 m (Fig. 5).

Remarks. *Tesserodon seramicum* Krikken & Huijbregts, 2009 (described from Seram Island, Indonesia) and *Tesserodon waigeoensis* Ochi, Kon & Hartini, 2017 (described from Waigeo Island, West Papua) are from outside the study area. However, examination of the illustrations provided in the original descriptions and images of a specimen (RMNH.INS.1488474) substantiate their transfer to the genus *Rhytomus* and should be combined as follows: *Rhytomus seramicus* (Krikken & Huijbregts, 2009), **new combination** and *Rhytomus waigeoensis* (Ochi, Kon & Hartini, 2017), **new combination**. Spermathecal morphology was studied only for species where enough material was available. Males of *R. heurni* Paulian, 1937 **new combination** and *R. setulosus* (Balthasar, 1965) **new combination** are unknown; the online identification key will be updated when additional material becomes available.

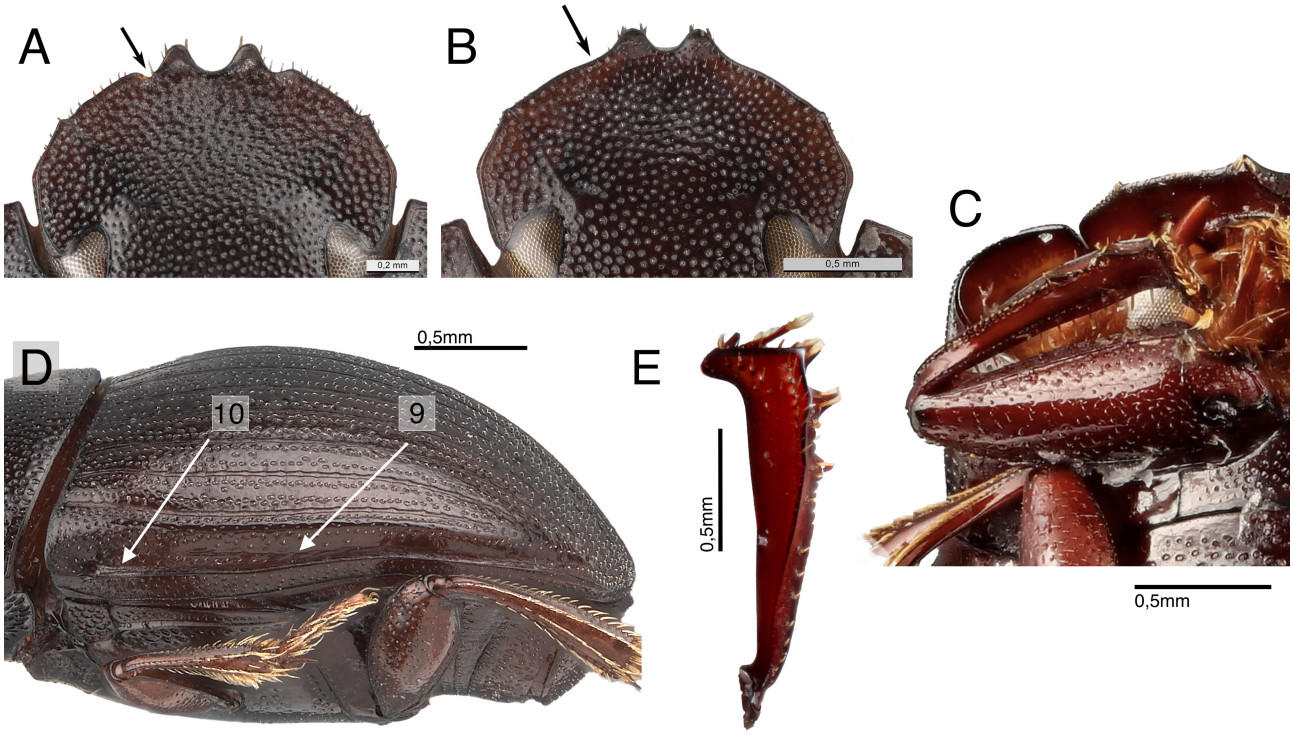

FIGURE 4. Diagnostic characters of *Rhytomus*. A, dorsal head showing emargination and interocular space (*R. howdeni*); B, dorsal head showing lack of emargination and interocular space (*R. fervidus*) C, ventral view of male foreleg (*R. latidentatus*); D, lateral view of elytra (*R. vanus*); E, dorsal view of male protibia (*R. latidentatus*).

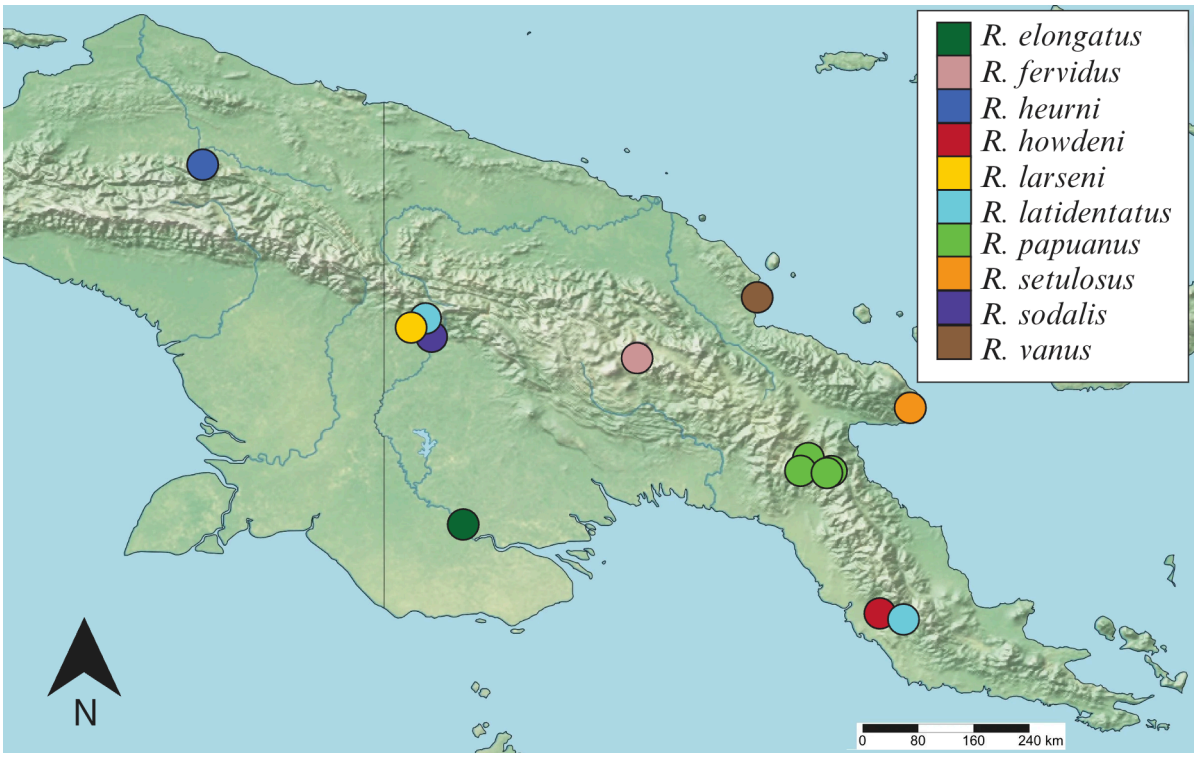

FIGURE 5. Distribution of *Rhytomus* in mainland New Guinea. Note that some distribution points are extrapolated based on best available data, view treatment of each species for more detail.

Species checklist

Rhytomus elongatus (van Lansberge, 1885), new combination (type species)
Rhytomus fervidus Saxton & Génier, new species
Rhytomus heurni (Paulian, 1937), new combination
Rhytomus howdeni (Paulian, 1985), new combination
Rhytomus larseni Saxton & Génier, new species
Rhytomus latidentatus Saxton & Génier, new species
Rhytomus papuanus (Paulian, 1985), new combination
Rhytomus seramicus (Krikken & Huijbregts, 2009), new combination
Rhytomus setulosus (Balthasar, 1965), new combination
Rhytomus sodalis Saxton & Génier, new species
Rhytomus vanus Saxton & Génier, new species
Rhytomus waigeoensis (Ochi, Kon & Hartini, 2017), new combination

Rhytomus elongatus (van Lansberge, 1885), new combination

Figs 6, 9A

***Tesserodon elongatum* van Lansberge, 1885: 376 (original description)**—Paulian 1934: 287 (identification key, distribution); Paulian 1985: 221 (identification key, distribution)
Tesserodon elongatus—Gillet 1911: 40 (catalogue); Gunter *et al*. 2019: 453 (distribution)

Name-bearing type data. Lectotype ♂ (MSNG) by present designation: || Nuova Guinea | Fly River | L.M.D Albertis 1876-77 ||; || TYPUS || [bordered and printed in red]; || Tesserodon | elongatum | Lansberge Type || [handwritten]; ||

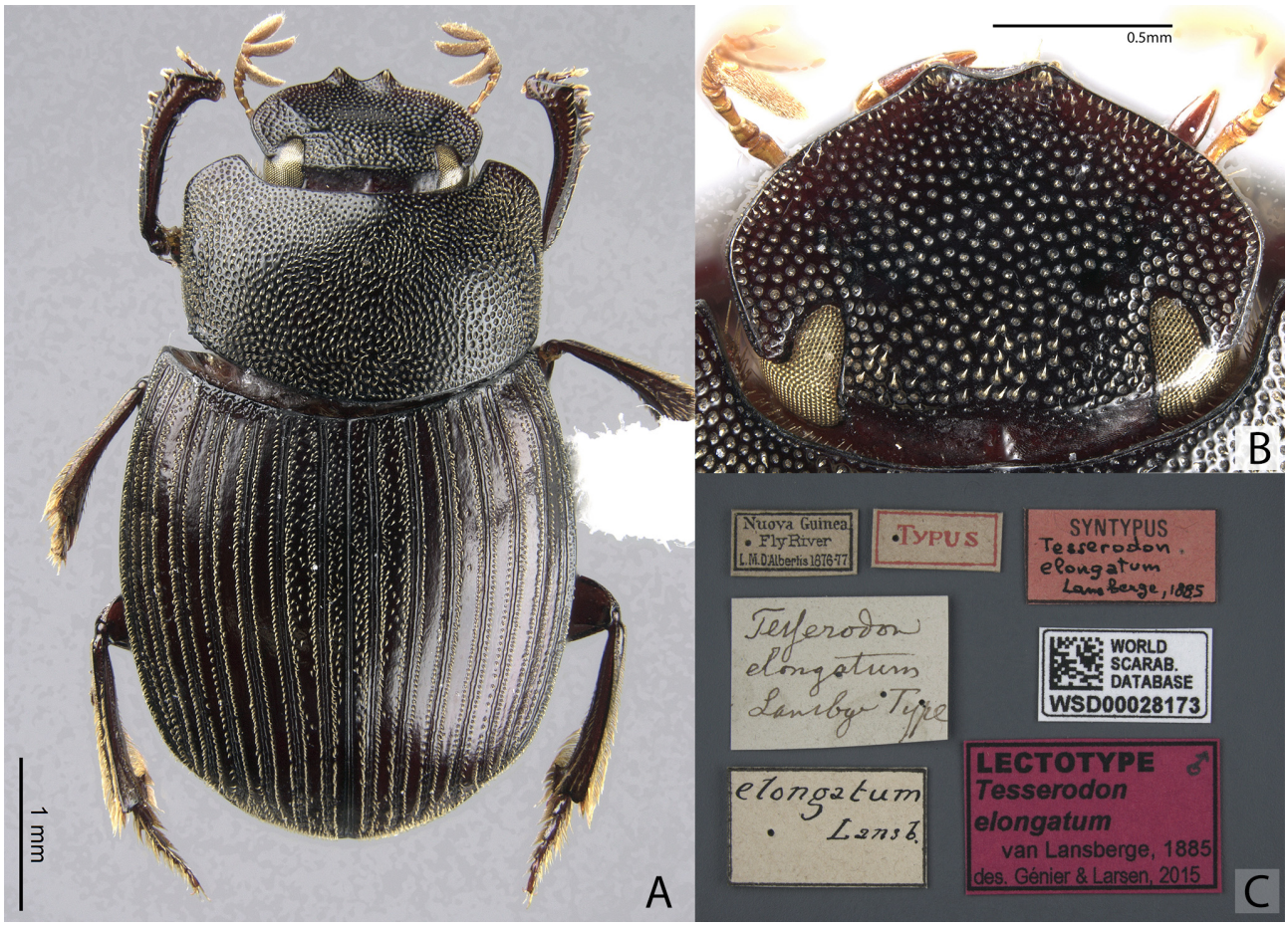

FIGURE 6. Lectotype of *Rhytomus elongatus*. A, dorsal habitus; B, dorsal head; C, label data.

elongatum | Lansb. || [handwritten with a border]; || SYNTYPUS | Tesserodon | elongatum | Lansberge, 1885 || [partly handwritten]; || WORLD SCARAB. | DATABASE | WSD00028173 || [QR code label]; || LECTOTYPE ♂ | *Tesserodon* | *elongatum* | van Lansberge, 1885 | des. Génier & Larsen, 2015 || [red card]. **Studied**.

Material examined (1♂, 1♀)**. PAPUA NEW GUINEA**: WESTERN PROVINCE, Fly River, [08°00'S, 142°00'E], 1876–1877, L.M. D'Albertis—♂ lectotype, 1 ♀ paralectotype (MHNG).

Redescription. Measurements. Body length 6.0 mm, maximum body width 2.9 mm. **Body.** Overall body shape in dorsal view elongate-oval, elytral edge slightly subangular at apical third. **Head.** Clypeal edge lateral to clypeal teeth lacking emargination (Fig. 6B), head margin at clypeogenal suture of females slightly protruding. Dorsal parts of eyes semi-ovoid, separated by an interocular space of about 5.3 times eye width. **Pronotum.** Pronotal width to length along midline ratio 1.7, lateral pronotal edge sharply defined throughout, pronotal pubescence long and conspicuous, pronotal basal portion along midline lacking fine longitudinal depression. **Elytra.** Elytral maximum width to length along suture ratio 1.1, elytral outline moderately convex in lateral view, elytral pubescence long and conspicuous, elytral surface between punctures appearing glossy, at most with ill-defined microsculptures (Fig. 6A), basal elytral pit wide and deep, basal surface of pseudepipleuron with sharply defined simple punctures, interstriae 3–5 on basal fifth with two rows of punctures along striae, with at most a few scattered punctures. **Legs.** Profemoral anterior surface deeply furrowed, male metatibial apicointernal tooth set anteriorly to posterior tibial edge (e.g. Fig. 12D). **Pygidium.** Pygidial surface along midline with punctures similar in density to rest of discs, pygidial surface along basal groove smooth between punctures, pygidium of female evenly convex. **Aedeagus.** Left paramere apex produced into a rounded oblique projection (Fig. 9A).

Remarks. This species was described based on two syntypes. In 2015, Génier and Larsen labeled one male from this series as the lectotype.

Rhytomus fervidus Saxton & Génier, new species

urn:lsid:zoobank.org:act:27C09598-572B-4AF0-904F-59067A688C08
Figs. 4B, 7A, 8A, 9B, 11A, 11D, 11E, 12B

Name-bearing type data. Holotype ♂ (CMNC): || PAPUA NEW GUINEA | Western highlands, Mt. | Hagen, 6000' | 5-8.VII.1974, S.Peck | oak forest dung tps. 24-25 ||; || Canadian Museum of | Musée canadien de la | NATURE | CMNEN 00049283 || [QR code label]; || HOLOTYPE ♂ | *Rhytomus* | *fervidus* | Des. N. Saxton & F. Génier, 2024 || [red card].

Material examined (20 ♂♂, 9 ♀♀)**. PAPUA NEW GUINEA**: WESTERN HIGHLANDS PROVINCE, Mount Hagen, 1829 m, [05°52'S, 144°14'E], 5–8.vii.1974, oak forest, dung traps, S. Peck, (dung traps 24-25)—♂ holotype, ♀ allotype, 12 ♂♂, 6 ♀♀ paratypes (CMNC), 6 ♂♂, 1 ♀ paratypes (MNHN), 1 ♂, 1 ♀ paratypes (QM).

Description. Measurements. Body length 4.2–5.0 mm, maximum body width 2.6–3.1 mm. Holotype: body length 4.7 mm, maximum body width 3.0 mm. **Body.** Overall shape in dorsal view oval, elytral edge evenly rounded from base to apex. **Head.** Clypeal edge lateral to clypeal teeth lacking emargination (Fig. 4C), head margin at clypeogenal suture of females slightly protruding. Dorsal parts of eyes semi-ovoid, separated by an interocular space of about 3.9 times eye width. **Pronotum.** Pronotal width to length along midline ratio 1.9, lateral pronotal edge sharply defined throughout, pronotal pubescence short and fine, pronotal basal portion along midline lacking fine longitudinal depression. **Elytra.** Elytral maximum width to length along suture ratio 1.0, elytral outline moderately convex in lateral view, elytral pubescence short and fine, elytral surface between punctures appearing glossy, at most with ill-defined microsculptures (Fig. 12B), basal elytral pit slightly wider than stria 10 and shallow (Fig. 11D), basal surface of pseudepipleuron with irregularly distributed more or less defined punctures (Fig. 11E), interstriae 3–5 on basal fifth with scattered unaligned punctures. **Legs.** Profemoral anterior surface flat, male metatibial apicointernal tooth approximately in line with posterior tibial edge. **Pygidium.** Pygidial surface along midline with punctures absent or distinctly more scattered than rest of discs, at least basally, pygidial surface along basal groove smooth between punctures (Fig. 8A), pygidium of female depressed apically. **Aedeagus.** Left paramere apex truncated apically, distinctly angular externally (Fig. 9B). **Female genitalia.** Spermatheca with two apodemes basally.

Etymology. The specific epithet for this species is the masculine nominative Latin adjective meaning "boiling hot" or "fiery" in reference to the type locality, which is near an old composite volcano.

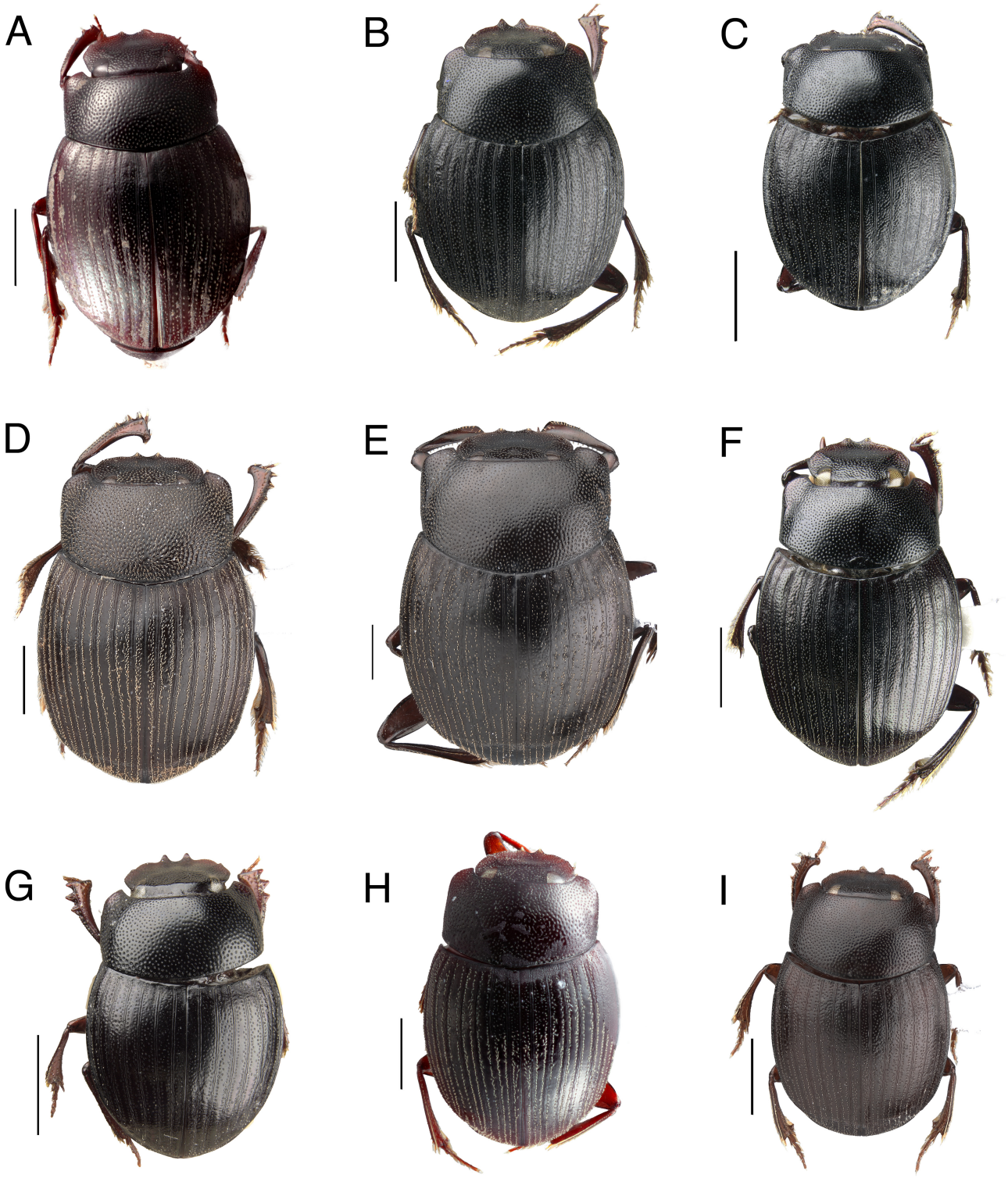

FIGURE 7. Habitus of *Rhytomus* species in mainland New Guinea. A, *R. fervidus;* B, *R. heurni;* C, *R. howdeni;* D, *R. larseni;* E, *R. latidentatus;* F, *R. papuanus;* G, *R. setulosum;* H, *R. sodalis*; I, *R. vanus*; Scale bar = 1 mm.

Rhytomus heurni (Paulian, 1937) new combination

Fig. 7B, 8B, 11F

***Tesserodon heurni* Paulian, 1937: 122 (original description)**—Paulian 1985: 221 (diagnosis, distribution, comment); Gunter *et al*. 2019: 453 (distribution)

Name-bearing type data. Holotype ♀ (SDEI): || N. Guinea Exped. | W.C. van Heurn | 1410 m. Okt. 1920 | Dormanpadbivak ||; || Holotypus || [red card]; || DEI Müncheberg | Col-05059 || [blue card]; || WORLD SCARAB. | DATABASE | WSD00028176 || [QR code label]; || Tesserodon | Heurni n. sp. Type | det. R. Paulian 1937 || [partly handwritten]. **Studied**.

Redescription. **Measurements.** Body length 4.3 mm, maximum body width 3.1 mm. **Body.** Overall body shape in dorsal view oval, elytral edge evenly rounded from base to apex. **Head.** Clypeal edge lateral to clypeal teeth lacking emargination, head margin at clypeogenal suture of females slightly protruding. Dorsal parts of eyes semi-ovoid, separated by an interocular space of about 4.1 times eye width. **Pronotum.** Pronotal width to length along midline ratio 1.8, lateral pronotal edge sharply defined throughout, pronotal pubescence short and fine, pronotal basal portion along midline lacking fine longitudinal depression. **Elytra.** Elytral maximum width to length along suture ratio 1.1, elytral outline moderately convex in lateral view, elytral pubescence short and fine, elytral surface between punctures appearing glossy, at most with ill-defined microsculptures, basal elytral pit slightly wider than stria 10 and shallow, basal surface of pseudepipleuron with sharply defined ocellate punctures (Fig. 11F), interstriae 3–5 on basal fifth with scattered unaligned punctures. **Legs.** Profemoral anterior surface flat. **Pygidium.** Pygidial surface along midline with punctures similar in density to rest of discs, pygidial surface along basal groove smooth between punctures, pygidium of female evenly convex (Fig. 8B).

Remarks. The original description of this species is based on a single female specimen collected during W. C. van Heurn New Guinea expedition in October 1920. The type locality "Dormanpadbivak" roughly translates to "Doorman path bivouac." According to Holthuis and Husson (1973) this locality was approximating 3º24'S 138º38'E at 1410-1450m, which is about 25km S. of Prauwenbivak.

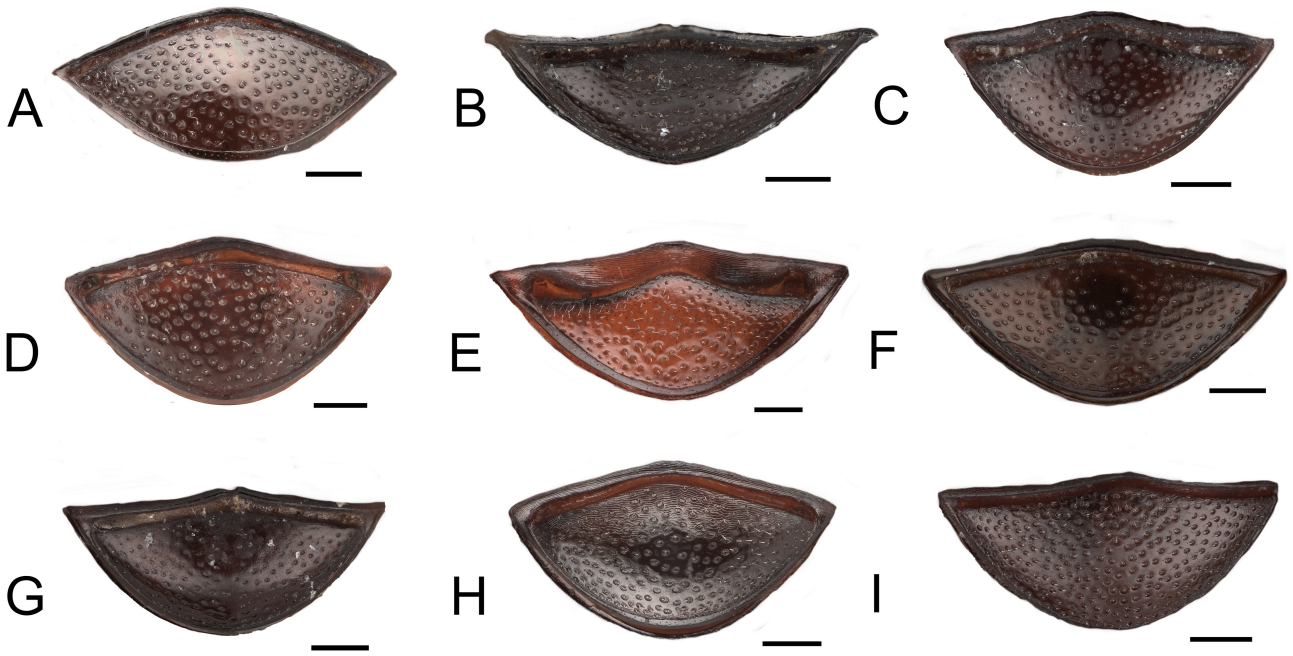

FIGURE 8. Pygidium of *Rhytomus* species. A, male *R. fervidus;* B. female *R. heurni*; C, male *R. howdeni*; D, male *R. larseni;* E, male *R. latidentatus;* F, male *R. papuanus;* G, female *R. setulosus*; H, male *R. sodalis*; I, male *R. vanus*. Scale bar = 0.2 mm.

Rhytomus howdeni (Paulian, 1985), new combination

Fig. 7C, 4A, 8C, 9C

***Tesserodon howdeni* Paulian, 1985: 222 (original description)**

Name-bearing type data. Holotype ♂ (CMNC): || Papua N.Guinea | Brown R.30mi.N | Fort Moresby | 15-16.VII.1974 ||; || S. Peck | collector ||; || H. & A. Howden | collection ||; || HOLOTYPE || [red card]; || Canadian Museum of | Musée canadien de la | NATURE | CMNEN 00011854 ||; || Tesserodon | howdeni | n. sp. | R. Paulian

det. || [partly handwritten]. **Note**. Previously stated as: “Nouvelle-Guinée (Papouasie) : Brown River, 20 miles N. Port Moresby, 14/16-VII-1974 (S. Peck), piège à excréments, en forêt” by Paulian. **Studied**.

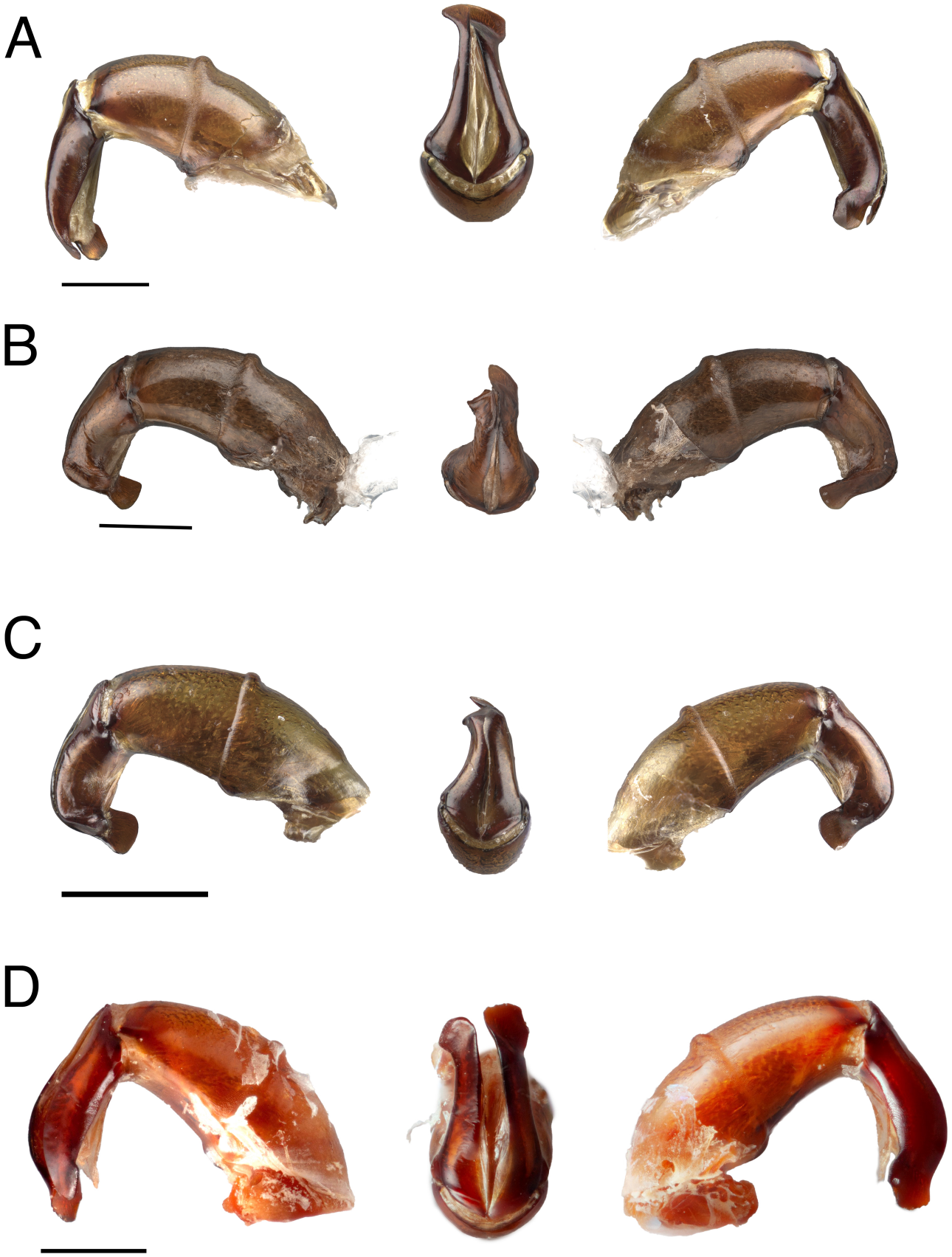

FIGURE 9. Male aedeagus of *Rhytomus* species, left lateral, dorsal, right lateral. A, *R. elongatus*; B, *R. fervidus*; C, *R. howdeni;* D, *R. larseni.* Scale bar = 0.5 mm.

Material examined (5 ♂♂, 2 ♀♀)**. PAPUA NEW GUINEA**: CENTRAL PROVINCE, 18 mi. N port Moresby, Brown River, 3 m, [09°12’15’’S, 147°17’15’’E], 14–18.vii.1974, forest, dung traps, S. Peck, (dung traps 39-42)—1 ♂, 1 ♀ (CMNC); 20 mi. N Port Moresby, Brown River, 3 m, [09°11’30’’S, 147°19’00’’E], 16–18.vii.1974, dung traps, S. Peck, (dung traps 39-41)—1 ♀ (CMNC); same locality, 16–18.vii.1974, dung trap, S. Peck, (dung traps 39-41)—2 ♂♂ paratypes (MNHN); 30 mi. N Port Moresby, Brown River, [09°11’S, 147°20’30’’E], 15–16.vii.1974, S. Peck—♂ holotype, 1 ♂ paratype (CMNC).

Redescription. Measurements. Body length 3.6–4.1 mm, maximum body width 2.3–2.7 mm. **Body.** Overall body shape in dorsal view oval, elytral edge evenly rounded from base to apex. **Head.** Clypeal edge lateral to clypeal teeth emarginate (Fig. 4D), head margin at clypeogenal suture of females moderately protruding. Dorsal parts of eyes semi-ovoid, separated by an interocular space of about 5.6 times eye width. **Pronotum.** Pronotal width to length along midline ratio 1.9, lateral pronotal edge sharply defined throughout, pronotal pubescence short and fine, pronotal basal portion along midline lacking fine longitudinal depression. **Elytra.** Elytral maximum width to length along suture ratio 1.1, elytral outline moderately convex in lateral view, elytral pubescence short and fine, elytral surface between punctures appearing glossy, at most with ill-defined microsculptures, basal elytral pit slightly wider than stria 10 and shallow, basal surface of pseudepipleuron with sharply defined simple punctures, interstriae 3–5 on basal fifth with scattered unaligned punctures. **Legs.** Profemoral anterior surface flat or might appear furrowed in some individuals, male metatibial apicointernal tooth approximately in line with posterior tibial edge. **Pygidium.** Pygidial groove transverse, narrowed medially, and terminating in a pit at each end (Fig. 8C), pygidial surface along midline with punctures similar in density to rest of discs, pygidial surface along basal groove smooth between punctures, pygidium of female evenly convex. **Aedeagus.** Left paramere apex truncated apically, distinctly angular externally (Fig. 9C).

Remarks. Examination of the allotype revealed that the specimen labeled by Paulian is actually a male and is here considered a male paratype in the material examined. Additionally, the date ranges provided by Paulian (1985) in the original description do not match any label data from the specimens studied. Recent examination of the specimens at the MNHN (by FG) confirmed that both are males, indicating that the female specimen described by Paulian is either missing or that Paulian misidentified the gender of the allotype. Two female specimens in the CMNC are not labeled as paratypes. While one of these could theoretically be the allotype, it is unclear if Henry Howden ever sent them to Paulian for study, as he often retained some specimens as a precaution against parcels being lost in the mail. Consequently, these specimens cannot be definitively considered part of the type series.

Rhytomus larseni Saxton & Génier, new species

urn:lsid:zoobank.org:act:277D719A-381F-4447-8665-B42E8617FA3A
Fig. 7D, 8D, 9D, 11B, 11C, 12D

Name-bearing type data. Holotype ♂ (CMNC): || PAPUA NEW GUINEA: Western | Prov., P’nvang, CI RAP Survey | Camp 1. 05º29.5S 141º32.6E | 573 m. May 2013. T. Larsen ||; || Canadian Museum of | Musée canadien de la | NATURE | CMNEN 00049307 || [QR code label]; || HOLOTYPE ♂ | *Rhytomus* | *larseni* | Des. N. Saxton & F. Génier, 2024 || [red card].

Material examined (163 ♂♂, 90 ♀♀)**. PAPUA NEW GUINEA**: WESTERN PROVINCE, CI RAP Survey Camp 1, P’nvang, 575 m, 05°29’S, 141°32’E, v.2013, T. Larsen—2 ♂♂, 2 ♀♀ paratypes (ANIC), 2 ♂♂, 2 ♀♀ paratypes (NHMUK), ♂ holotype, ♀ allotype, 101 ♂♂, 54 ♀♀ paratypes (CMNC), 2 ♂♂, 2 ♀♀ paratypes (MNHN), 2 ♂♂, 2 ♀♀ paratypes (NMPC), 2 ♂♂, 2 ♀♀ paratypes (USNM); CI RAP Survey Camp 2, P’nvang, 800 m, 05°30’S, 141°34’E, v.2013, T. Larsen—49 ♂♂, 23 ♀♀ paratypes (CMNC), 2 ♂♂, 2 ♀♀ paratypes (QM).

Description. Measurements. Body length 4.1–5.4 mm, maximum body width 2.7–3.1 mm. Holotype: body length 4.7 mm, maximum body width 3.0 mm. **Body.** Overall body shape in dorsal view elongate-oval, elytral edge slightly subangular at apical third. **Head.** Clypeal edge lateral to clypeal teeth lacking emargination, head margin at clypeogenal suture of females slightly protruding. Dorsal parts of eyes semi-ovoid, separated by an interocular space of about 5.5 times eye width. **Pronotum.** Pronotal width to length along midline ratio 1.8, lateral pronotal edge sharply defined throughout, pronotal pubescence long and conspicuous, pronotal basal portion along midline lacking fine longitudinal depression. **Elytra.** Elytral maximum width to length along suture ratio 1.0, elytral outline moderately convex in lateral view, elytral pubescence long and conspicuous, elytral surface between punctures with distinct microsculptures (Fig. 11B), basal elytral pit wide and deep (Fig. 11C), basal surface of pseudepipleuron with

sharply defined simple punctures, interstriae 3–5 on basal fifth with two rows of punctures along striae, with at most a few scattered punctures in some individuals. **Legs.** Profemoral anterior surface deeply furrowed, male metatibial apicointernal tooth set anteriorly to posterior tibial edge (Fig. 12D). **Pygidium.** Pygidial groove terminating in a pit at each end, pygidial surface along midline with punctures similar in density to rest of discs, pygidial surface along basal groove smooth between punctures (Fig. 8D), pygidium of female evenly convex. **Aedeagus.** Left paramere apex produced into a rounded oblique projection (Fig. 9D). **Female genitalia.** Spermatheca lacking apodemes.

Etymology. This specific epithet of this species is the Latinized genitive form of "Larsen", in honor of Trond H. Larsen who collected all the specimens in the type series and contributed greatly to the number of *Rhytomus* specimens available for study from PNG.

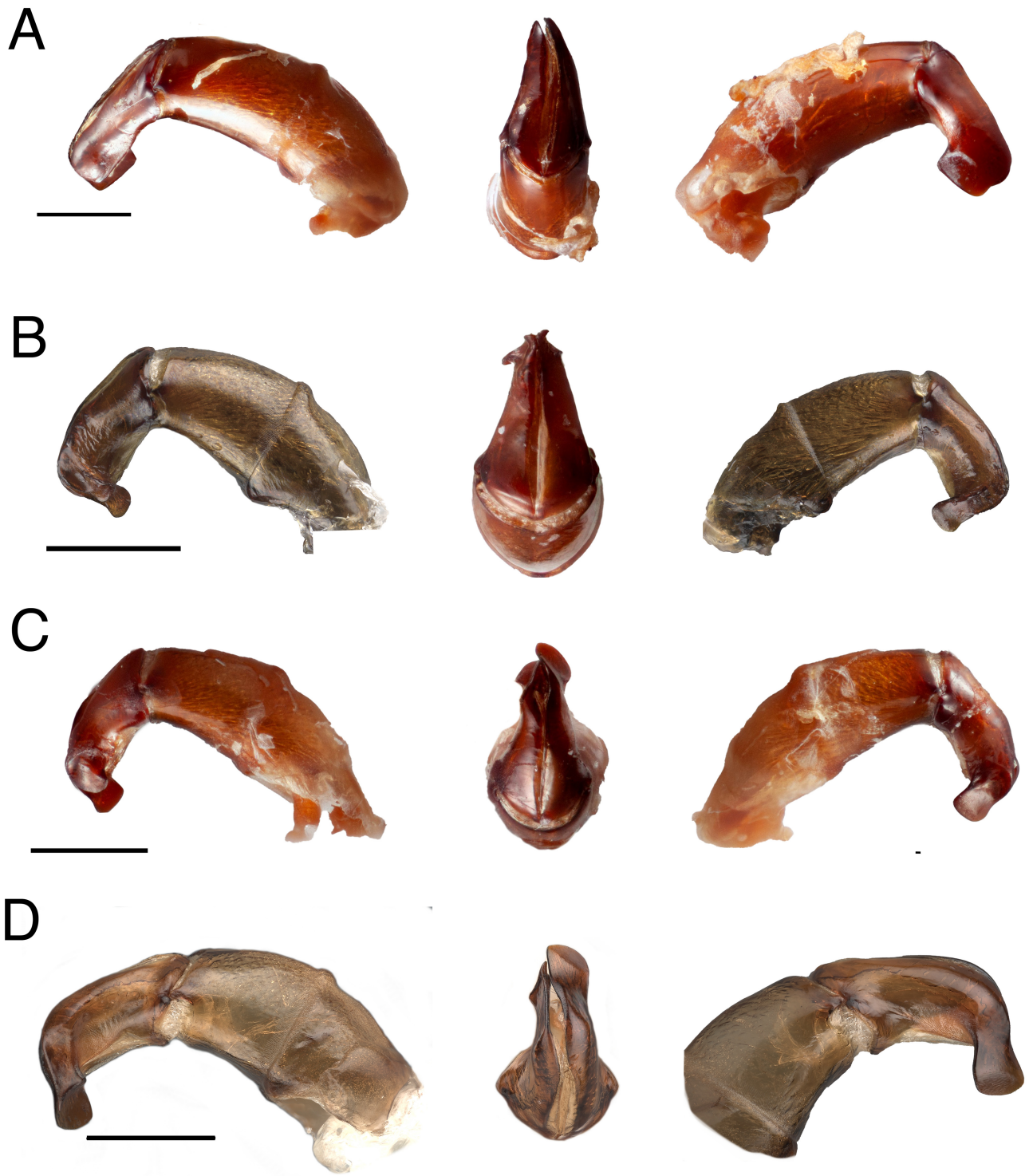

FIGURE 10. Male aedeagus of *Rhytomus* species, left lateral, dorsal, right lateral. A, *R. latidentatus*; B, *R. papuanus*; C, *R. sodalis*; D, *R. vanus*. Scale bar = 0.5 mm.

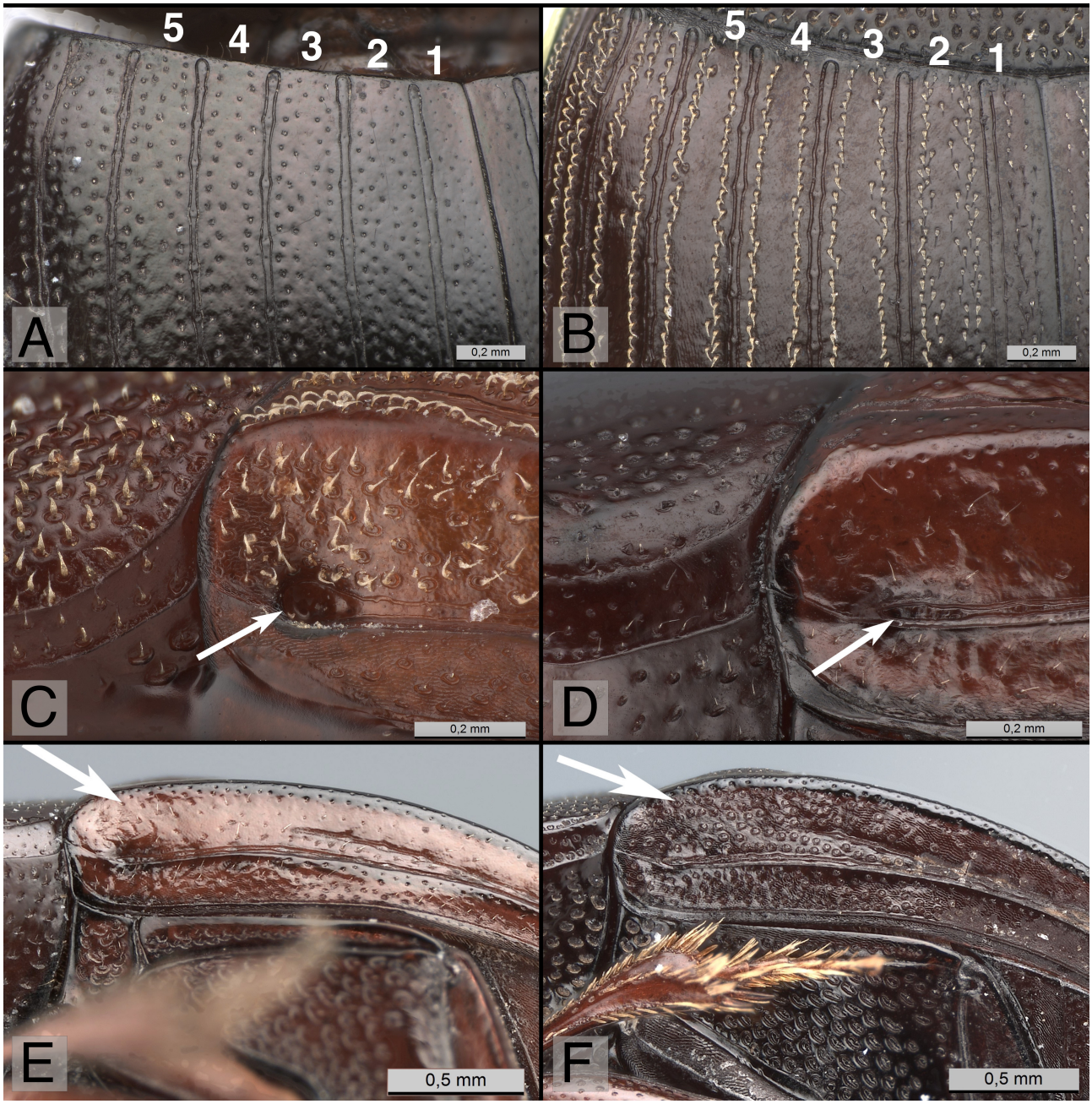

FIGURE 11. Characters used for species identification. A, dorsal elytral striae showing unaligned scattered punctures (*R. fervidus*); B, dorsal elytral striae showing two rows of punctuation on intervals 3–5 (*R. larseni*); C, basal pseudepipleural pit large and deep (*R. larseni*); D, basal pseudepipleural pit shallow and slightly larger than stria 10 (*R. fervidus*); E, basal pseudepipleural surface with irregularly distributed punctuation (*R. fervidus*); F, basal pseudepipleural surface with ocellate punctuation (*R. heurni*).

Rhytomus latidentatus Saxton & Génier, new species

urn:lsid:zoobank.org:act:8C418C61-9081-48AD-B9BB-6CBC74D23206
Figs. 4C, 4E, 7E, 8E, 10A, 12A

Name-bearing type data. Holotype ♂ (CMNC). || PAPUA NEW GUINEA: Western | Prov., P'nvang, CI RAP Survey | Camp 1. 05º29.5S 141º32.6E | 573 m. May 2013. T. Larsen ||; || Canadian Museum of | Musée canadien de la | NATURE | CMNEN 00049540 || [QR code label]; || HOLOTYPE ♂ | *Rhytomus* | *latidentatus* | Des. N. Saxton & F. Génier, 2024 || [red card].

Material examined (22 ♂♂, 12 ♀♀). PAPUA NEW GUINEA: CENTRAL PROVINCE, Kokoda Trak, Kauai River, Menari, 700 m, [09°11’30’’S, 147°37’30’’E], 12–14.viii.1976, rainforest, dung, O. Kukal—3 ♂♂, 1 ♀ paratypes (CMNC), 2 ♂♂ paratypes (MNHN); WESTERN PROVINCE, CI RAP Survey Camp 1, P’nvang, 575 m, 05°29’S, 141°32’E, v.2013, T. Larsen—1 ♂, 1 ♀ paratypes (ANIC), ♂ holotype, ♀ allotype, 14 ♂♂, 8 ♀♀ paratypes (CMNC), 1 ♂, 1 ♀ paratypes (QM).

Description. Measurements. Body length 4.5–6.3 mm, maximum body width 3.1–4.2 mm. Holotype: length 5.5 mm, maximum body width 3.9 mm. **Body.** Overall body shape in dorsal view oval, elytral edge evenly rounded from base to apex. **Head.** Clypeal edge lateral to clypeal teeth lacking emargination, clypeal teeth wide, head margin at clypeogenal suture of females slightly protruding. Dorsal parts of eyes semi-ovoid, separated by an interocular space of about 5.1 times eye width. **Pronotum.** Pronotal width to length along midline ratio 1.6, lateral pronotal edge sharply defined throughout, pronotal pubescence short and fine, pronotal basal portion along midline with fine longitudinal depression. **Elytra.** Elytral maximum width to length along suture ratio 1.0, elytral outline moderately convex in lateral view, elytral pubescence long and conspicuous, elytral surface between punctures with distinct microsculptures (Fig. 12A), basal elytral pit absent, basal surface of pseudepipleuron with irregularly distributed more or less defined punctures, interstriae 3–5 on basal fifth with two rows of punctures along striae with the odd unaligned punctures on interstriae 3 and 5 and scattered unaligned punctures on interstria 4. **Legs.** Profemoral anterior surface flat, male metatibial apicointernal teeth approximately in line with posterior tibial edge. **Pygidium.** Pygidial groove transverse, narrowed medially, and terminating in a pit at each end (Fig. 8E), surface along midline with punctures similar in density to rest of discs, pygidial surface along basal groove smooth between punctures, pygidium of female evenly convex. **Aedeagus.** Left paramere apex rounded in a dorsoventral plane (Fig. 10A). **Female genitalia.** Spermatheca with two apodemes basally and one apodeme apically.

Etymology. The specific epithet of this species is a combination of the Latin adjective “*latus*” meaning wide and the adjective “*dentatus*” meaning dentate in reference to this species’ characteristically wide clypeal teeth.

Remarks. Paulian (1985) studied four specimens of this species which he identified as “*Tesserodon heurni”* in his work on the Canthonines of New Guinea.

Rhytomus papuanus (Paulian, 1985), new combination

Fig. 7F, 8F, 10B

***Tesserodon papuanum* Paulian, 1985: 221 (original description)**

Name-bearing type data. Holotype ♂ (CMNC): || PAPUA NEW GUINEA | Wau, 1400 m. | 29.VI-2.VII.1974. S. Peck | carrion traps 18-19 ||; || PAPUA NEW GUINEA | Wau, 1400 m. | 29.vi-2.vii.74 | S. Peck, carT18-19 || [photocopy of handwritten label]; || H. & A.Howden | Collection ||; || HOLOTYPE || [red card]; || Canadian Museum of | Musée canadien de la | NATURE | CMNEN 00011856 || [QR code label]; || Tesserodon | papuanum n.sp. | R. Paulian det. || [partly handwritten]. **Studied**.

Material examined (21 ♂♂, 7 ♀♀). PAPUA NEW GUINEA: MOROBE PROVINCE, Aseki Road, 56 km W Bululo, 1750 m, 07°19’33’’S, 146°20’49’’E, 8.ii.2000, mixed montane forest litter, R.S. Anderson, (RSA2000-039a)—2 ♂♂ (CMNC); Gumi L.A. Bulolo, 2134 m, [07°11’S, 146°25’E], 18.xi.1984, infly trap, H. Roberts, (C.I.E. A16609)—1 ♂ (NHMUK); Mount Kaindi, 9 km NNW Wau, 2050 m, 07°20’24’’S, 146°40’01’’E, 6.ii.2000, montane forest litter, R.S. Anderson, (RSA2000-035b)—1 ♂ (CMNC); Wau, 1219 m, [07°20’S, 146°43’E], 1–3.vii.1974, forest litter, berlese, S. Peck—1 ♀ (CMNC); same locality, 1–3.vii.1974, H. Howden—1 ♂, 1 ♀ (MNHN); Wau, 1400 m, [07°20’S, 146°43’E], 29.vi.–2.vii.1974, carrion traps, S. Peck, (carrion traps 18-19)—♂ holotype, 12 ♂♂, 3 ♀♀ paratypes (CMNC), 2 ♂♂, 1 ♀ paratypes (MNHN); same locality, 29.vi.–2.vii.1974, carrion traps, S. Peck, (carrion trap 20)—♀ allotype (CMNC), 1 ♂ paratype (MNHN).

Redescription. **Measurements.** Body length 4.1–5.3 mm, maximum body width 2.7–3.1 mm. **Body.** Overall body shape in dorsal view oval, elytral edge evenly rounded from base to apex. **Head.** Clypeal edge lateral to clypeal teeth lacking emargination, head margin at clypeogenal suture of females slightly protruding. Dorsal parts of eyes semi-ovoid, separated by an interocular space of about 3.9 times eye width. **Pronotum.** Pronotal width to length along midline ratio 1.9, lateral pronotal edge rounded, pronotal pubescence short and fine, pronotal basal portion along midline lacking fine longitudinal depression. **Elytra.** Elytral maximum width to length along suture ratio 1.0, elytral outline moderately convex in lateral view, elytral pubescence short and fine, elytral surface between

punctures appearing glossy, at most with ill-defined microsculptures, basal elytral pit slightly wider than stria 10 and shallow, basal surface of pseudepipleuron with irregularly distributed more or less defined punctures, interstriae 3–5 on basal fifth with scattered unaligned punctures. **Legs.** Profemoral anterior surface flat, male metatibial apicointernal tooth approximately in line with posterior tibial edge. **Pygidium.** Pygidial surface along midline with punctures absent or distinctly more scattered than rest of discs, at least basally, pygidial surface along basal groove smooth between punctures (Fig. 8F), pygidium of female evenly convex. **Aedeagus.** Left paramere apex truncated apically, distinctly angular externally (Fig. 10B). **Female genitalia.** Spermatheca with two apodemes basally and one apodeme apically.

Rhytomus setulosus (Balthasar, 1965), new combination

Fig. 7G, 8G

***Tesserodon setulosum* Balthasar, 1965: 17 (original description)—**Paulian 1985: 221 (diagnosis, distribution, comment)—Bezděk & Hájek 2011: 374 (type data, comment); Gunter *et al*. 2019: 453 (distribution)

Name-bearing type data. Holotype ♀ (NMPC): || N. Guinea | Biró 1899 ||; || Sattelberg | Huon-Golf ||; || 1899 | IV.1-15 || [handwritten on verso of previous label]; || Tesserodon | setulosum | n.sp. Balth. | 63 Holotypus || [partly handwritten]. **Studied**.

Material examined (2 ♀♀)**. PAPUA NEW GUINEA**: MOROBE PROVINCE, Sattelberg, [06°29’S, 147°46’E], 1–15.iv.1899, Biró—♀ holotype, 1 ♀ paratype (NMPC) (female paratype examined via image courtesy of Jiří Hájek).

Redescription. **Measurements.** Body length 3.2 mm, maximum body width 2.3 mm. **Body.** Overall body shape in dorsal view oval, elytral edge evenly rounded from base to apex. **Head.** Clypeal edge lateral to clypeal teeth lacking emargination, head margin at clypeogenal suture of females moderately protruding. Dorsal parts of eyes semi-ovoid, separated by an interocular space of about 5.3 times eye width. **Pronotum.** Pronotal width to length along midline ratio 1.9, lateral pronotal edge sharply defined throughout, pronotal pubescence short and fine, pronotal basal portion along midline lacking fine longitudinal depression. **Elytra.** Elytral maximum width to length along suture ratio 1.0, elytral outline strongly convex in lateral view, elytral pubescence short and fine, elytral surface between punctures appearing glossy, at most with ill-defined microsculptures, basal elytral pit wide and deep, basal surface of pseudepipleuron with irregularly distributed more or less defined punctures, interstriae 3–5 on basal fifth with scattered unaligned punctures on interstriae 3 and 5 and two rows of punctures along striae with the odd unaligned punctures on interstria 4. **Legs.** Profemoral anterior surface flat. **Pygidium.** Pygidial surface along midline with punctures absent or distinctly more scattered than rest of discs, at least basally, pygidial surface along basal groove smooth between punctures, pygidium of female evenly convex (Fig. 8G).

Remarks. No male specimens known for this species.

Rhytomus sodalis Saxton & Génier, new species

urn:lsid:zoobank.org:act:7168813D-24AF-4CCA-8B46-B5168014A9E3

Figs. 7H, 8H, 10C, 12C

Name-bearing type data. Holotype ♂ (CMNC): || PAPUA NEW GUINEA: Western | Prov., P’nvang, CI RAP Survey | Camp 1. 05º29.5S 141º32.6E | 573 m. May 2013. T. Larsen ||; || Canadian Museum of | Musée canadien de la | NATURE | CMNEN 00049583 || [QR code label]; || HOLOTYPE ♂ | *Rhytomus* | *sodalis* | Des. N. Saxton & F. Génier, 2024 || [red card].

Material examined (69 ♂♂, 24 ♀♀)**. PAPUA NEW GUINEA**: WESTERN PROVINCE, CI RAP Survey Camp 1, P’nvang, 575 m, 05°29’S, 141°32’E, v.2013, T. Larsen—2 ♂♂, 1 ♀ paratypes (ANIC), 2 ♂♂, 1 ♀ paratypes (NHMUK), ♂ holotype, ♀ allotype, 23 ♂♂, 12 ♀♀ paratypes (CMNC), 2 ♂♂, 1 ♀ paratypes (MNHN), 2 ♂♂, 1 ♀ paratypes (NMPC), 1 ♂, 1 ♀ paratypes (USNM); CI RAP Survey Camp 2, P’nvang, 800 m, 05°30’S, 141°34’E, v.2013, T. Larsen—15 ♂♂, 3 ♀♀ paratypes (CMNC); CI RAP Survey Camp 3, P’nvang, 1110 m, 05°32’S, 141°33’E, v.2013, T. Larsen—19 ♂♂, 1 ♀ paratypes (CMNC), 2 ♂♂, 2 ♀♀ paratypes (QM).

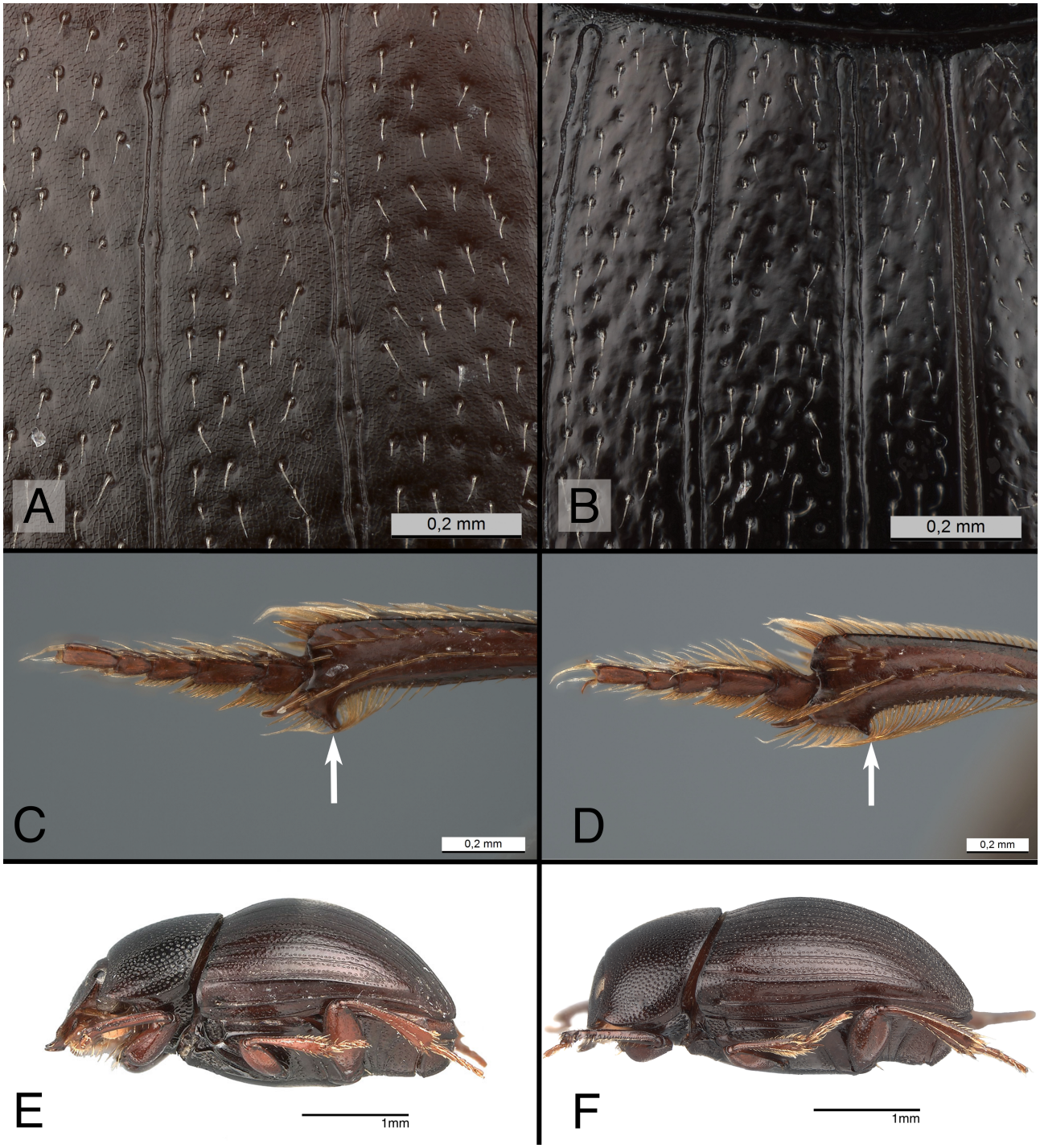

FIGURE 12. Characters used for species identification. A, elytral surface with microsculpture (*R. latidentatus*); B, elytral surface glossy (*R. fervidus*); C, male metatibial apicointernal tooth in line with posterior tibial edge (*R. sodalis*); D, male metatibial apicointernal tooth set anteriorly to posterior tibial edge (*R. larseni*); E, lateral view of strongly convex elytra (*R. setulosus*); F, lateral view of moderately convex elytra (*R. vanus*).

Description. Measurements. Body length 3.0–4.6 mm, maximum body width 2.1–2.7 mm. Holotype: body length 3.8 mm, maximum body width 2.5 mm. **Body.** Overall body shape in dorsal view elongate-oval, elytral edge slightly subangular at apical third. **Head.** Clypeal edge lateral to clypeal teeth lacking emargination, head margin at clypeogenal suture of females slightly protruding. Dorsal parts of eyes semi-ovoid, separated by an interocular space of about 3.2 times eye width. **Pronotum.** Pronotal width to length along midline ratio 1.7, lateral pronotal edge sharply defined throughout, pronotal pubescence short and fine, pronotal basal portion along midline lacking fine

longitudinal depression. **Elytra.** Elytral maximum width to length along suture ratio 1.0, elytral outline moderately convex in lateral view, elytral pubescence long and conspicuous, elytral surface between punctures appearing glossy, at most with ill-defined microsculptures, basal elytral pit wide and deep, basal surface of pseudepipleuron with irregularly distributed more or less defined punctures, interstriae 3–5 on basal fifth with two rows of punctures along striae, with at most a few scattered punctures in some individuals. **Legs.** Profemoral anterior surface flat or might appear furrowed in some individuals, male metatibial apicointernal tooth approximately in line with posterior tibial edge (Fig. 12C). **Pygidium.** Pygidial surface along midline with punctures similar in density to rest of discs, pygidial surface along basal groove with coarse transverse microsculptures (Fig. 8H), pygidium of female depressed basally. **Aedeagus.** Left paramere apex truncated apically, distinctly angular externally (Fig. 10C). **Female genitalia.** Spermatheca with two apodemes basally and one apodeme apically.

Etymology. The specific epithet of this species is a masculine noun in apposition "sŏdālis" (companion, mate, fellow) relating to the fact that it was collected along with *R. larseni* and *R. latidentatus*.

Remarks. One female specimen (excluded from type series) was discovered from the same collecting event (i.e., Camp 1, 575 m) that had coarser pronotal punctation and a barely indicated meso-metaventrite suture. This specimen likely represents a fourth species. However, because no male specimens could be found at the time of this study, we refrain from describing it.

Rhytomus vanus Saxton & Génier, new species

urn:lsid:zoobank.org:act:CD0A0711-1AC6-4D0B-8CE9-C54C31A001EA
Figs. 4D, 7I, 8I, 10D

Name-bearing type data. Holotype ♂ (CMNC): || PAPUA NEW GUINEA: Madang | Baitabag (8 km N.W.) | 100m, 30.I.2000 | 5°08'19"S 145°46'34"E | R.S.Anderson, rainforest litter | RSA2000-027 ||; || Canadian Museum of | Musée canadien de la | NATURE | CMNEN 00049581 || [QR code label]; || HOLOTYPE ♂ | *Rhytomus* | *vanus* | Des. N. Saxton & F. Génier, 2024 || [red card].

Material examined (4♂♂, 1 ♀). **PAPUA NEW GUINEA:** MADANG PROVINCE, Baitabag, 8 km NW Madang, 100 m, 05°08'19''S, 145°46'34''E, 30.i.2000, rainforest litter, R.S. Anderson, (RSA2000-027)—♂ holotype, ♀ allotype, 3 ♂♂ paratypes (CMNC).

Description. Measurements. Body length 3.3–3.6 mm, maximum body width 2.1–2.3 mm. Holotype: body length 3.6 mm, maximum body width 2.3 mm. **Body.** Overall body shape in dorsal view oval, elytral edge evenly rounded from base to apex. **Head.** Clypeal edge lateral to clypeal teeth lacking emargination, head margin at clypeogenal suture of females moderately protruding. Dorsal parts of eyes semi-ovoid, separated by an interocular space of about 4.8 times eye width. **Pronotum.** Pronotal width to length along midline ratio 1.9, lateral pronotal edge sharply defined throughout, pronotal pubescence short and fine, pronotal basal portion along midline lacking fine longitudinal depression. **Elytra.** Elytral maximum width to length along suture ratio 1.0, elytral outline moderately convex in lateral view, elytral pubescence short and fine, elytral surface between punctures with distinct microsculptures, basal elytral pit wide and deep (Fig. 4A), basal surface of pseudepipleuron with irregularly distributed more or less defined punctures or with sharply defined simple punctures (by misinterpretation), interstriae 3–5 on basal fifth with scattered unaligned punctures on interstriae 3 and 5 and two rows of punctures along striae with the odd unaligned punctures on interstria 4. **Legs.** Profemoral anterior surface flat or deeply furrowed (by misinterpretation), male metatibial apicointernal tooth approximately in line with posterior tibial edge. **Pygidium.** Pygidial surface along midline with punctures similar in density to rest of discs, pygidial surface along basal groove smooth between punctures (Fig. 8I), pygidium of female depressed apically. **Aedeagus.** Left paramere apex truncated apically, distinctly angular externally (Fig. 10D).

Etymology. *Vānus* is a Latin adjective. It is used here in the sense of "suspicious, doubtful" which pertain to the previously unrecognized status of this new species.

Key to adult mainland New Guinea *Rhytomus* species

Access to online key: https://keys.lucidcentral.org/keys/v4/rhytomus/ (click on the magic wand icon to select the best character to use first)

1 Interstriae 3–5 on basal fifth all having unaligned scattered punctures (Fig. 11A); basal pseudepipleural pit present, shallow and slightly larger than stria 10 (Fig. 11D) 2
- Interstriae 3–5 with at least one interval having two distinct rows of punctures on basal fifth (11B); basal pseudepipleural pit deep and distinctly larger than stria 10 (Fig. 11C) OR pseudepipleural pit is absent 5
2 Elytral interval 1 with basal punctures much smaller in size to those in intervals 2–3; pronotal lateral edge obsolete or sharply defined 3
- Elytral interval 1 with basal punctures similar in size and coarseness to those in intervals 2–3; pronotal lateral edge always sharply defined 4
3 Pronotal lateral edge obsolete; male clypeal edge without emargination lateral to clypeal teeth (Fig. 4B); Body length 4–5.3 mm . . . . . *Rhytomus papuanus* (Paulian, 1985)
- Pronotal lateral edge sharply defined; male clypeal edge with emargination lateral to clypeal teeth (Fig. 4A); Body length 3.6–4.1 mm . . . . . *Rhytomus howdeni* (Paulian, 1985)
4 Basal pseudepipleural surface with irregularly distributed more or less defined punctures (Fig. 11E); female pygidium depressed apically . . . . . *Rhytomus fervidus* Saxton & Génier, new species
- Basal pseudepipleural surface with sharply defined ocellate punctures (Fig. 11F); female pygidium evenly convex . . . . . *Rhytomus heurni* (Paulian, 1937)
5 Base of pronotum lacking fine longitudinal depression medially; basal pseudepipleural pit deep and distinctly larger than stria 10 (Fig. 11C); male pygidial groove not distinctly narrowed medially (Figs. 8D, H, I) 6
- Base of pronotum with fine longitudinal depression medially (Fig. E); basal pseudepipleural pit absent; male pygidial groove distinctly narrowed medially and terminating in pits (Fig. 8E) . . . . . *Rhytomus latidentatus* Saxton & Génier, new species
6 Interstriae 3, 4 and 5 having two distinct rows of punctures; elytral pubescence long and conspicuous (Fig. 11B) 7
- Interstriae 3 and 5 having unaligned and scattered punctures, interstriae 4 having two distinct rows of punctures; elytral pubescence short and fine (as in Fig. 11A) 9
7 Male metatibial apicointernal tooth approximately in line with posterior tibial edge (Fig. 12C); pygidium of female depressed basally; body length 3.0–4.6 mm . . . . . *Rhytomus sodalis* Saxton & Génier, new species
- Male metatibial apicointernal tooth set anteriorly to posterior tibial edge (Fig. 12D); pygidium of female evenly convex: body length 4.1–6.0 mm 8
8 Elytral surface between punctures dull, with distinct microsculptures (Fig. 7D, 11B); Body length 4.1–5.4 mm . . . . . *Rhytomus larseni* Saxton & Génier, new species
- Elytral surface between punctures appearing glossy, at most with ill-defined microsculptures (Fig. 6A); Body length 6mm . . . . . *Rhytomus elongatus* (van Lansberge, 1885)
9 Elytral surface appearing glossy, at most with ill-defined microsculpture (as in Fig. 12B); Elytra strongly convex in lateral view (Fig. 12E) . . . . . *Rhytomus setulosus* (Balthasar, 1965)
- Elytral surface dull, with distinct microsculpture (Fig. 12A); Elytra moderately convex in lateral view (Fig. 12F) . . . . . *Rhytomus vanus* Saxton & Génier, new species

Concluding remarks

With the description of five new species of *Rhytomus* from New Guinea, we greatly increase our knowledge of the dung beetle diversity here. Interestingly, three of these species (i.e., *R. larseni, R. latidentatus,* and *R. sodalis*) were all collected from the same or very close collection sites (Fig. 5). This level of diversity in such a small area suggests that there are many additional, undescribed species of *Rhytomus* in New Guinea and Eastern Indonesia. Additional work in the region is needed to gain a full understanding of the group's actual diversity as well as basic knowledge of the distribution and biology of this genus.

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