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1953, and a key to the Oriental and Australasian genera
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Borislav GUÉORGUIEV & Kipling WILL



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COUVERTURE / *COVER*:

Lapitchlaenius speculiferus (Fairmaire, 1879) n. comb., male specimen.

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CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)
Tél. : 33 (0)1 40 79 48 05 / Fax: 33 (0)1 40 79 38 40
diff.pub@mnhn.fr / <https://sciencepress.mnhn.fr>

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ISSN (imprimé / *print*): 1280-9551/ ISSN (électronique / *electronic*): 1638-9387

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Submitted on 30 May 2024 | Accepted on 30 September 2024 | Published on 23 May 2025

[urn:lsid:zoobank.org:pub:11740D9A-34E8-48B0-A6C9-15AB438BA100](https://zoobank.org/pub:11740D9A-34E8-48B0-A6C9-15AB438BA100)

Guéorguiev B. & Will K. 2025. — A new genus and tribal placement for *Ceneus speculiferus* Fairmaire, 1879, comments on *Grundmannius* Basilewsky, 1965, *Mirachlaenius* Facchini, 2011 and *Stenoodes* Basilewsky, 1953, and a key to the Oriental and Australasian genera of Chlaeniina Brullé, 1834 (Coleoptera, Carabidae). *Zoosystema* 47 (15): 231–259. <https://doi.org/10.5252/zoosystema2025v47a15>. <http://zoosystema.com/47/15>

ABSTRACT

The Fijian endemic species *Prosopogmus speculiferus* (Fairmaire, 1879) originally described in the tribe *Pterostichini* Bonelli, 1810 as *Ceneus speculiferus*, is reviewed. Morphological evidence places the species in the tribe Chlaeniini Brullé, 1834 and a new genus is proposed to accommodate it with the following new combination *Lapitachlaenius speculiferus* (Fairmaire, 1879) n. comb. A second species endemic to Vanuatu is also assigned to the genus *L. specularis* (Emden, 1937) n. comb. The new genus is distinguished from all other currently recognized genera of subtribe Chlaeniina Brullé, 1834 by its elytron having a medial, mirror-like area, interval 3 with large, foveate setiferous punctures, and interval 8 interrupted near the level of the elytral plica. Additionally, the pronotum disc has broad and shallow paramedial, parenthesis-like impressions that join the baso-lateral impressions. These autapomorphic morphological features provide evidence that *Lapitachlaenius* n. gen. is a derived member of the subtribe. *Grundmannius* Basilewsky, 1965, originally placed in subtribe Callistina Laporte, 1834 and recently included in Lachnophorini LeConte, 1853, is returned to Chlaeniini, and placed in the subtribe Chlaeniina. The first female of the rarely collected *Mirachlaenius barbarae* Facchini, 2011 was studied and its morphological characters are also presented. The pygidial glands, genital, and reproductive apparatus are described. *Mirachlaenius barbarae* has a distinct dorsal lobe of pygidial gland reservoir and a reservoir junction channel linking the main reservoir with the efferent duct. This pygidial gland configuration is unlike any previously reported for Chlaeniini. The genus *Stenoodes* Basilewsky, 1953 was recently moved to Chlaeniini, though its original placement was in the tribe *Oodini* La Ferté-Sénectère, 1851. The original placement is restored based on the modifications of elytral intervals 8 and 9 – present in *Stenoodes* and other oodines but absent in chlaeniines. A key to Oriental and Australasian genera of Chlaeniina is provided.

KEY WORDS

Chlaeniini,
Oodini,
Fiji,
Vanuatu,
India,
Madagascar,
Mozambique,
morphology,
new genus,
new combinations.

RÉSUMÉ

Un nouveau genre et un nouveau placement tribal pour Ceneus speculiferus Fairmaire, 1879, des commentaires sur Grundmannius Basilewsky, 1965, Mirachlaenius Facchini, 2011 et Stenoodes Basilewsky, 1953, et une clé pour les genres orientaux et australasiens de Chlaeniina Brullé, 1834 (Coleoptera, Carabidae). L'espèce endémique fidjienne *Prosopogmus speculiferus* (Fairmaire, 1879), initialement décrite dans la tribu Pterostichini Bonelli, 1810, sous le nom de *Ceneus speculiferus*, est passée en revue. Les caractères morphologiques placent l'espèce dans la tribu Chlaeniini Brullé, 1834 et un nouveau genre est proposé pour l'héberger avec la nouvelle combinaison *Lapitachlaenius speculiferus* (Fairmaire, 1879) n. comb. Une deuxième espèce endémique de Vanuatu est également attribuée à ce genre *L. specularis* (Emden, 1937) n. comb. *Lapitachlaenius* n. gen se distingue de tous les autres genres actuellement reconnus de la sous-tribu Chlaeniina Brullé, 1834 par son élytre avec une zone médiale en forme de miroir, un intervalle 3 avec de grandes piqûres sétifères fovéales et un intervalle 8 interrompu près du niveau du repli élytral. De plus, le disque du pronotum présente des impressions paramédiales larges et peu profondes, semblables à des parenthèses, qui rejoignent les impressions baso-latérales. Ces caractéristiques morphologiques autapomorphes montrent que *Lapitachlaenius* n. gen. est un membre dérivé de la sous-tribu. *Grundmannius* Basilewsky, 1965, initialement placé dans la sous-tribu Callistina Laporte, 1834 et récemment inclus dans Lachnophorini LeConte, 1853, est transféré dans les Chlaeniini et placé dans la sous-tribu Chlaeniina. La première femelle du *Mirachlaenius barbarae* Facchini, 2011, espèce rarement collectée, a été étudiée et ses caractères morphologiques sont présentés. Les glandes pygidiennes, les genitalia et les appareils reproducteurs sont décrits. Chez *M. barbarae*, le réservoir de la glande pygidiale possède un lobe dorsal distinct, et le réservoir principal est relié au canal efférent par un canal de jonction du réservoir. Cette configuration des glandes pygidiennes ne ressemble à aucune autre rapportée précédemment chez les Chlaeniini. Le genre *Stenoodes* Basilewsky, 1953 originellement classé dans les Oodini La Ferté-Sénectère, 1851, a été récemment déplacé dans les Chlaeniini. Le placement d'origine est rétabli sur la base des modifications des intervalles élytraux 8 et 9 présents chez *Stenoodes* et d'autres oodines mais absents chez les chlaeniines. Une clé des genres orientaux et australasiens de Chlaeniina est fournie.

MOTS CLÉS

Chlaeniini,
Oodini,
Fidji,
Vanuatu,
Inde,
Madagascar,
Mozambique,
morphologie,
genre nouveau,
combinaisons nouvelles.

INTRODUCTION

While revising the systematics of the pterostichine genus *Prosopogmus* Chaudoir, 1865 (Pterostichini Bonelli, 1810, Euchroina Chaudoir, 1874), one of us (KW) encountered specimens of *Ceneus speculiferus* Fairmaire, 1879. *Ceneus* Chaudoir, 1865 was originally treated as a subgenus of *Feronia* Latreille, 1817, and subsequently synonymized with *Prosopogmus* by Csiki (1930). “*Prosopogmus speculiferus*” however, does not share characteristics of the subtribe Euchroina or the tribe Pterostichini. The specimens examined have a single supraorbital seta, metepisternum laterally coadunate with the epipleuron, evident elytral plica, projecting prosternal process that fits into a deep notch in the mesosternum, abdominal ventrites 4-6 without transversely impressed sulci parallel to their bases, as well as ventral, setal pads on the male protarsomeres 1-3 of the “spongy” type – a combination of characters that is not known for any species of Pterostichini. Closer examination revealed that specimens have glabrous integument (only the typical, large tactile setae present) and the elytra have interval 3 with large, foveate setiferous punctures. Unlike oodine modifications of elytral intervals 8 and 9 (outer margin of interval 8 elevated to form a ridge, and interval 9 deepened to form a marginal furrow), these intervals are not modified along their length. This specific combination of traits is evidence that these Fijian carabids should be classified as a member of the tribe Chlaeniini Brullé, 1834, and particularly

of the subtribe Chlaeniina Brullé, 1834. These observations and a need to taxonomically place this species led to a broader review of chlaeniine and oodine taxa.

During the comparative study of chlaeniine and oodine taxa required to place this Fijian species, three peculiar, little known, and monotypic carabid genera (*Grundmannius* Basilewsky, 1965, *Mirachlaenius* Facchini, 2011 and *Stenoodes* Basilewsky, 1953), all formerly or presently referred to Chlaeniini, were investigated.

The tribe Chlaeniini is a diverse, worldwide group with more than 1200 species organized in two subtribes, Chlaeniina and Callistina Laporte, 1834 (Lorenz 2005, 2025; Bousquet 2012). In these two subtribes adults can be distinguished by the structure of the form of the galea of maxilla, presence or absence of posterolateral seta of pronotum, and presence or absence of crossed elytral epipleuron (i.e., elytral plica) (Jeannel 1949a; Basilewsky & Grundmann 1955). Larvae of Callistina can be distinguished from those of the nominate subtribe by their bifurcated pretarsus, fused sternites of abdominal segments V-VII, and several other characters (see Makarova & Makarov 1996 for character details). Chlaeniina includes nearly 96% of the species and all the genera of the tribe save two: *Callistus* Bonelli, 1810 and *Callistomimus* Chaudoir, 1872. *Grundmannius*, discussed below, was originally placed in Callistina and has recently been moved to tribe Lachnophorini LeConte, 1853 (Lorenz 2025). The bulk of species and all the 20 cur-

rently recognized extant and extinct genera of Chlaeniina are known from the Afrotropical and Oriental Regions. The following genera of the nominotypical subtribe are recorded from the Old World (Alluaud 1930; Lorenz 2005; Facchini 2011; Guéorguiev 2014; Lassalle 2015; Sciaky & Facchini 2019; Lorenz 2025): *Actodus* Alluaud, 1915 (2 sp. in Afrotropical Region), *Chlaenius* Bonelli, 1810 (1074 sp. in Holarctic, Neotropical, Afrotropical, Oriental and Australasian regions), *Eccoptomenus* Chaudoir, 1850 (3 sp. in Afrotropical Region), *Ectenognathus* Murray, 1858 (1 sp. in Afrotropical Region), *Globulipalpus* Sciaky & Facchini, 2019 (2 sp. in Afrotropical Region), *Harpaglossus* Motschulsky, 1858 (3 sp. in Afrotropical Region and 1 sp. in India), *Hololeius* La Ferté-Sénectère, 1851 (1 sp. in Oriental and Australasian regions), *Holosoma* Semenov, 1889 (11 sp. in Palaearctic part of China), *Mirachlaenius* (1 sp. from the Nilgiri Mts, India), *Parachlaenius* Kolbe, 1894 (8 sp. in Afrotropical Region), *Perissostomus* Alluaud, 1930 (2 sp. in Afrotropical Region), † *Rhopalochlaenius* Zhang, Sun & Zhang, 1994 (1 Miocene species from Shanwang, Shandong Province, China), *Rhopalomelus* Boheman, 1848 (4 sp. in Afrotropical Region), *Proclatodema* Péringuey, 1899 (1 sp. in Afrotropical Region), *Proclatus* Péringuey, 1896 (13 sp. in Afrotropical Region), *Sphodroschema* Alluaud, 1930 (4 sp. in Afrotropical Region), *Stenoodes* (1 sp. in Madagascar), *Straneomelus* Sciaky & Facchini, 2019 (2 sp. in Afrotropical Region), *Stuhlmannium* Kolbe, 1894 (1 sp. in Afrotropical Region), and *Viridagonum* Lassalle, 2015 (2 sp. in Philippines). No autochthonous representatives of the tribe have been documented from New Zealand.

In 1955, Basilewsky & Grundmann (1955) recognized two subfamilies and 11 tribes in what is today considered the tribe Chlaeniini, 10 tribes in Chlaeniinae and one tribe in Callistinae. Despite its drawbacks, this classification remains the only attempt to deal with the supra-generic system on a world basis (Davidson 1980), even now. Other authors dealing with the systematics of the group have accepted only one tribe (Bell 1960; Lindroth 1969; Davidson 1980; Habu 1987; Kirschenhofer 2010). Genera recognized by Basilewsky and Grundmann that they placed in six of 10 of their Chlaeniinae tribes are now classified as subgenera of *Chlaenius*. Currently the tribe is divided into two subtribes (Bousquet 2012) and most specialists accepted this view, though a few others (Sciaky & Facchini 2019; Serrano 2024) still follow the view of Basilewsky and Grundmann.

Based on pygidial gland secretions, Bousquet (1987, 2012) divided the *Chlaenius* species into two groups that “should be recognized either as genera or subtribes”. Members of the first group secrete various phenols as a major constituent whereas those of the second group – quinones. This chemical diversity suggests that the largest genus of the tribe may not be monophyletic. The coadunate metepisternum and elytral epipleuron observed in the subtribe Chlaeniina (including *Grundmannius*) and the tribes Oodini and Panagaenini, is lacking in Callistina, and this may be evidence that the first three groups are more closely related to each other than any of them are to the subtribe Callistina.

An analysis of the entire subtribe is beyond the scope of this contribution, as our main purposes are to establish the generic placement for *Ceneus speculiferus* Fairmaire, 1879 and its relative *Chlaenius specularis* Emden, 1937 and to contribute to the systematic understanding of *Grundmannius*, *Mirachlaenius*, and *Stenoodes*. Thus, we have examined specimens of species representing all the Palaearctic, Oriental, and Australasian genera of the subtribe except for *Viridagonum* (see “Provisional key to the Oriental and Australasian genera of Chlaeniina” below) and species of selected Afrotropical genera.

Abundant information on the morphology of the Old-World taxa of Chlaeniina exists (for instance, Sloane 1910; Andrewes 1941; Darlington 1968, 1970b; Habu 1987; a long list of works of Erich Kirschenhofer among them Kirschenhofer 2010; Ullah *et al.* 2022; etc.), and especially on Oriental and Australasian groups, which were useful in searching out the systematic position of the genera covered in this study. Some subgenera or species groups of the genus *Chlaenius* that have representatives in the geographical areas focused on have been taxonomically revised (Kirschenhofer 1998, 2002, 2003, 2005, 2013; Azadbakhsh & Kirschenhofer 2019). Most of the above sources include identification keys and provide clear morphological characterizations of the taxa treated. Although somewhat outdated, the work of Habu (1987), remains the most comprehensive taxonomic study with respect to the morphological characteristics of the genera, subgenera, and groups of species of the Chlaeniini inhabiting Oriental, Australasian and Pacific regions.

MATERIAL AND METHODS

TAXONOMIC MATERIAL

More than 300 specimens belonging to 89 species and sub-species from the Palaearctic, Afrotropical and Oriental regions were examined (Appendix 1). The material studied is preserved in the following institutions (institutional acronym and responsible curators in parentheses): Australian National Insect Collection, Canberra, Australia (ANIC, Adam Slipinski and Yu-Lingzi Zhou); Bernice Pauahi Bishop Museum, Honolulu, USA (BPBM, Jeremy Frank); California Academy of Sciences, San Francisco, California, USA (CAS, David Kavanaugh); Essig Museum of Entomology, University of California, Berkeley, California, USA (EMEC, Kipling Will); IZAS, Institute of Zoology, Chinese Academy of Science, Beijing, China (IZAS, Hongbin Liang); MNHN Muséum national d'Histoire naturelle, Paris, France (Thierry Deuve, Azadeh Taghavian); Natural History Museum, London, United Kingdom (NHMUK, Maxwell Barclay, Beulah Garner); National Museum of Natural History, Sofia, Bulgaria (NMNHS, Borislav Guéorguiev); New Zealand Arthropod Collection, Auckland, New Zealand (NZAC, Richard Leschen); South Australian Museum, Adelaide, Australia (SAMA, Ben Parslow); State Museum of Natural History in Stuttgart, Germany (SMNS, Arnaud Faille). Material from the private collection of Erich Kirschenhofer (coll. EK, Perchtoldsdorf, Austria) has been inspected, too.

TABLE 1. — Data about variation in measurements among specimens of *Lapitachlaenius speculiferus* (Fairmaire, 1879) n. comb. (values in mm). Abbreviations: **Rep.**, repository; and see Material and methods.

nr.	Locality	Rep.	BL	BW	HW	PW	PL	PA	PB	EL	EW
1♂	Viti Levu Lami	BPBM	9.70	3.50	1.90	2.80	2.00	2.00	2.30	5.70	3.50
2♂	Viti Levi Sigatoka	BPBM	10.30	3.90	2.10	3.00	2.20	2.05	2.55	6.10	3.90
3♂	Vanua Levu	NZAC	10.05	3.80	2.10	3.05	2.25	2.10	2.50	6.25	3.80
4♀	Draiba Trail	BPBM	10.00	3.70	2.00	2.90	2.10	2.05	2.40	5.80	3.70
5♀	6 mi. W. of Suva	BPBM	10.60	4.00	2.05	2.95	2.20	2.10	2.55	6.20	4.00
range			9.70-10.60	3.50-4.00	1.90-2.10	2.80-3.05	2.00-2.25	2.00-2.10	2.30-2.55	5.70-6.25	3.50-4.00

TABLE 2. — Data about ratios among specimens of *Lapitachlaenius speculiferus* (Fairmaire, 1879) n. comb. Abbreviations: **Rep.**, repository; and see Material and methods.

nr.	Locality	Rep.	PW/HW	PW/PL	PW/PA	PW/PB	PA/PB	EL/EW	EW/PW	EL/PL
1♂	Viti Levu Lami	BPBM	1.45	1.38	1.40	1.20	0.87	1.63	1.27	2.85
2♂	Viti Levi Sigatoka	BPBM	1.43	1.36	1.46	1.18	0.80	1.56	1.30	2.77
3♂	Vanua Levu	NZAC	1.45	1.36	1.45	1.22	0.84	1.64	1.25	2.78
4♀	Draiba Trail	BPBM	1.45	1.38	1.41	1.21	0.85	1.57	1.28	2.76
5♀	6 mi. W. of Suva	BPBM	1.44	1.34	1.40	1.16	0.82	1.55	1.36	2.82
range			1.43-1.45	1.34-1.38	1.40-1.46	1.16-1.22	0.80-0.87	1.55-1.64	1.25-1.36	2.76-2.85

ABBREVIATIONS

Measurements and their abbreviations are as follows: body length (BL), measured from the apex of longer mandible to apex of longer elytron; body width (BW = EW), measured along the greatest width of closed elytra (EW); width of head (HW), measured along the greatest transverse distance including eyes; pronotum width (PW), measured along its greatest width; pronotum length (PL), measured along the midline; basal width of pronotum (PB), measured along the line connecting posterior angles; apical width (PA), measured along the line connecting anterior angles; elytra length (EL), measured from the connecting point of stria 1 and basal border to the apex of left elytron.

DESCRIPTIVE PROTOCOLS AND TECHNIQUES

Observations of anatomical features and most of pictures were made using a Leica MZ12s stereomicroscope (KW) or Olympus SZX10 (BG). Line drawings of gonocoxites and photographs of mouthparts were made using a Carl Zeiss Jena Amplitval microscope. Measurements of body proportions were made using an ocular reticule. Measurements and calculated ratios for specimens examined are in the spreadsheet included in the supplementary files (Tables 1; 2).

Male genitalia and female reproductive tract and associated abdominal segments preparation followed either Guéorguiev & Liang (2020) or Will (2020), and their nomenclature followed the publications of Liebherr & Will (1998), Liebherr (2016, 2017) and Guéorguiev and Liang (*ibid.*). The nomenclature used for mandibles is that of Acorn & Ball (1991).

Habitus photos of beetles were taken as image stacks using a modified Microptics XLT digital imaging system that were then aligned and assembled with Helicon Focus version 5.3 (KW) or using Canon EOS 600D camera that were then aligned and stacked with Helicon Focus Pro 8.2.2 software (BG) and those image files were edited to enhance clarity using standard image editing software.

SYSTEMATICS

Family CARABIDAE Latreille, 1802
Subfamily HARPALINAE Bonelli, 1810
Tribe Chlaeniini Brullé, 1834
(see below, key to the adults of subtribes of Chlaeniini Brullé, 1834)

NOTES ON TRIBAL CHARACTERIZATION OF CHLAENIINI

Regarding delimitation of Chlaeniini, a tentative diagnosis was recently given by Guéorguiev (2014: 89). That included common traits for the Carabidae Conchifera (*sensu* Jeannel 1949b) as well as distinguishing tribal features.

However, in the course of the current study, we established three features of tribal significance (Guéorguiev *ibid.*), namely 1) the elytron with internal plica; 2) metepisternum laterally coadunate with elytral epipleuron; and 3) stria 7 distinct to apex, not uniformly present in all representatives of the tribe. These character states are only useful as supplemental traits given the context and restrictions provided below.

1) As stated by Jeannel (1949a) and verified herein the crossed elytral epipleuron is present in Chlaeniina (except for *Grundmannius*) and absent in Callistina.

2) The coadunate metepisternum and elytral epipleuron is a feature to consider with some caution. Based on a comprehensive study of the morphology of carabid taxa from different tribes and on an earlier statement of Habu (1956), Bousquet (1996: 449) stated that “I have found this feature in all species of oodines and panagaeines studied and in some species of Chlaeniini. Likely the character state has been secondarily lost in several chlaeniine lineages”. Ober & Maddison (2008) investigated the phylogenetic relationships among the harpalinae tribes using data from two nuclear loci and found that in most trees, oodines, chlaenines, panagaeines, and the genus *Dercylus* Laporte, 1832 form a clade. Given

KEY TO THE ADULTS OF SUBTRIBES OF CHLAENIINI BRULLÉ, 1834

1. Galea of maxilla two-segmented (Figs 2B; 11B). Tips of ultimate maxillary and labial palpomeres slightly rounded, truncate or widened (cf. Habu 1987: 7, figs 4–13). Pronotum with or without posterolateral setiferous puncture. Elytral epipleuron straight throughout or crossed (i.e., plica present) near apex 2
- Galea of maxilla one-segmented (cf. Andrewes 1921: 233, fig. 12a; Jeannel 1942: 978). Tips of ultimate maxillary and labial palpomeres acuminate (cf. Habu 1987: 7, fig. 3). Pronotum without posterolateral setiferous puncture. Elytral epipleuron straight throughout (i.e., plica absent) subtribe *Callistina* Laporte, 1834
2. Pronotum with posterolateral setiferous puncture. Lateral edge of elytral epipleuron bare. Elytral epipleuron crossed near apex. Metacoxa with only anterolateral seta subtribe *Chlaeniina* Brullé, 1834 (all genera save *Grundmannius* Basilewsky, 1965)
- Pronotum without setiferous puncture. Lateral edge of elytral epipleuron spiniferous (Fig. 11A). Elytral epipleuron straight throughout. Metacoxa with two lateral setae subtribe *Chlaeniina* (genus *Grundmannius*).

the Ober & Maddison investigations and pygidial gland defensive secretion data, Bousquet (2012: 53) then stipulated anew, now with improved evidential support, that the complex of Panagaeini – Chlaeniini – Oodini “possibly constitute a clade since the adults (except in some chlaeniines) have the metepisterna coadunate with the elytral epipleura, a synapomorphic condition that has probably been secondarily lost in some chlaeniine lineages”. However, no study has explored the distribution and extent of this character across all relevant taxa. What is known shows it is absent in representatives of the two callistine genera, *Callistus* and *Callistomimus* (see Terada & Wu 2018: 5, fig. 3H). Among the taxa from Chlaeniina we studied, the appearance of the character varies. In some species the coadunation is obvious (*Chlaeniellus* Reitter, 1908, *Chlaeniosstenus* Kuntzen, 1919), in others – less noticeable (*Amblygenius* La Ferté-Sénéctère, 1851 and some *Pleroticus* Péringuey, 1896), and it is ambiguous or appears to be lacking in some (*Callistoides*, some *Stenochlaenius* Reitter, 1908). To avoid incorrectly scoring this state care must be taken to note the condition of the specimen. If present, the state can be seen when both the sternal and elytral structures are in close proximity to each other. It is the case when the elytra are closely retracted and the lateral margin of the anterior part of the metepisternum forms a more or less distinct protrusion that covers the paired site on the medial margin of the elytral epipleuron. If the lateral margin of the metepisternum does not cover the medial margin of the elytral epipleuron then the state of the character can be difficult to ascertain though it is present. Compare the Figure 3A, B and Figure 12: the first two figures show “unnatural” states or artifacts of preservation where the metepisternum does not reach the epipleuron though both structures lie on the same level (Fig. 3A) or are concealed under the epipleuron (Fig. 3B). In Figure 12 the “natural” condition is shown – the metepisternum is tightly retracted on epipleuron.

3) In most chlaeniine genera, stria 7 is well-marked along the whole elytron length, including near the apex. However, *Callistus lunatus* and some species of *Holosoma* have stria 7 obliterated apically. In *Hololeius ceylanicus* stria 7 is usually hardly distinguishable in basal three fourths and well-perceptible on apical one fourth only.

Subtribe Chlaeniina Brullé, 1834

Chlaenides Brullé, 1834: 123.

TYPE GENUS. — *Chlaenius* Bonelli, 1810 (see Bousquet 2012: 962–963).

DIAGNOSIS OF THE SUBTRIBE. — Head with one (posterior) supraorbital setiferous puncture. Mandible without setiferous puncture in scrobe. Maxilla with two-segmented galea. Ultimate maxillary and labial palpomeres inserted centrally in penultimate palpomeres (not obliquely as in panagaeines). Pronotum with posterolateral setiferous puncture (except for *Grundmannius*), majority of taxa without anterolateral setiferous puncture, exceptionally – with one (*Chlaeniodus* Jeannel, 1949) or more (*Chlaenius leucops* Widemann, 1823, species of subgenera *Eurydactylus* LaFerté-Sénéctère, 1851 and *Pelasmomimus* Grundmann, 1955), and *Viridagonum azureoviride* Sciaky, Facchini & Anichtchenko, 2024) such punctures. Elytral intervals 8 and 9 normal throughout (without any part modified to form a furrow or ridge as in oodines). Elytral epipleuron crossed (except for *Grundmannius*) and laterally evident. Fore coxal cavities biperforate. Middle and hind femur posterior margins without notably elongate setae. Adhesive setal pads on ventral surface of male protarsomeres 1–3 of “spongy” type.

In addition, the bulk of species have elytra lacking discal setiferous punctures, with a few exceptions (*Chlaenius luisae* Gestro, 1895, *Ch. tetraphacus* Alluaud, 1918, *Grundmannius dispar*, *Lapitachlaenius speculiferus* n. comb., *Mirachlaenius barbarae*, some *Holosoma* sp., *Viridagonum lumawigi* Lassalle, 2015). Most species have also metepisternum laterally coadunate with elytral epipleuron (for manifestation of this character see the notes below) as well as mesosternum deeply concave in middle (*Grundmannius dispar* and examined species from *Callistoides* Motschulsky, 1865, *Ocybatus* LaFerté-Sénéctère, 1851 and *Pseudochlaeniellus* Jeannel, 1949 have a scarcely concave mesosternum).

Lapitachlaenius n. gen.

[url:isid:zoobank.org:act:7C063127-9D26-4B44-9D46-EEC43214085B](https://doi.org/10.21203/rs.3.rs-2806312/v1)

TYPE SPECIES. — *Ceneus speculiferus* Fairmaire, 1879: 70, here designated.

DIAGNOSIS. — Integument of body glabrous throughout except for typical sensory setae (i.e., lacking pubescence as extensively evident in most *Chlaenius* s.l. species), concolorous often with a subtle aeneous or cupreous shade; surface of elytra immaculate.

Pronotum and elytra smooth (without punctuation as in most *Chlaenius* s.l. species). Penultimate labial palpomere glabrous (also on inner margin), but with a minute seta near apex; ultimate labial palpomere fusiform in both sexes, not widened at apex, shorter than penultimate palpomere. Mentum tooth large, simple, widely rounded at apex. Antennomeres 1-3 and basal fifth to quarter of antennomere 4 glabrous; antennomere 3 just slightly longer than antennomere 4. Pronotum without anterolateral setiferous puncture, with posterior setiferous puncture about twice the width of fovea distant from posterior angle. Basal margin of elytra present, reaching base of stria 1 and/or base of parascutellar striole; parascutellar striole present, relatively long, punctiform (not linearly impressed as discal striae), reaching basal margin of elytra, not anastomosing with stria 1; interval 3 with four to seven foveate setiferous punctures; interval 8 interrupted subapically by a brief fusion of striae 7 and 8 (Fig. 4), thus it is separated in two parts, long anterior and short posterior. Prosternal process unbordered. Metepisternum with sublateral longitudinal sulcus (Fig. 3A, B). Middle tibia straight in both sexes. Tarsomeres glabrous dorsally; male protarsomeres 1-3 more or less strongly dilated; tarsal claws simple, not pectinate (pectinate in species of *Chlaenioctenus* Bates, 1892; cf. Liu *et al.* 2013).

ETYMOLOGY. — The generic name is derived from the term “Lapita”, which is the name used for the Neolithic Austronesian culture that included the people thought to be the first settlers of the islands in the region, including Viti Levu, and the Greek noun “chlaena” [χλαῖνα] (cloak, mantle). The name is treated as a Latin masculine.

DESCRIPTION

Habitus

Medium sized for chlaeniines, with elongate, slightly convex body and glabrous integument.

Chaetotaxy

Labrum anterior margin with six dorsal equidistantly spaced setae as well with a row of shorter marginal lateral setae along each side and corner (each row continues ventrally at level of medial dorsal seta). Clypeus with two lateral punctures. One supraorbital seta on each side, located near posterior eye margin. Stipes with long dorsal seta; antennomere 2 with short ventral seta. Maxilla with two-segmented galea and pointed, highly bent at apex lacinia (Fig. 2B); apical margin of ligula with a pair of large and long medial setae and two groups of three or four, rather short and small, anterolateral setae (Fig. 2C). Penultimate labial palpomere glabrous, except for single minute apical seta; ultimate labial palpomere with sparse short setae visible only at higher magnification (Fig. 1D). Mentum with two long, paramedial setae. Submentum with two long, lateral setae. Pronotum with posterior lateral setiferous punctures, each puncture far removed from angle, distant by more than twice its diameter. Elytron with four to seven discal setiferous punctures in interval 3 near stria 2, (most apical one usually smaller and less perceptible than others); parascutellar seta present, at base of striae 1 and 2, puncture large, foveate, separated from basal margin by more than one of its diameters; apical portion of stria 7 with five to seven setiferous punctures (rarely a few of them on interval 7, not in stria), apical puncture closer to suture than to apex (Fig. 4); umbilicate series consisting of 18-19 setiferous punctures of various sizes, not forming distinct

groups. Mesocoxa with one posteromedial and one lateral seta; metacoxa with one lateral seta. Protrochanter and mesotrochanter with one seta. Metafemur without posterior setae. Abdominal ventrites 3-5 without ambulatory setae; last ventrite with two marginal setae in male and four setae in female. Gonocoxite 2 with one large dorsomedial seta, one lateromedial ensiform seta, and pair of nematiform setae.

Head

Eyes conspicuously large, protruding, with short tempora and dorsal diameter longer than combined length of antennomeres 1 and 2. Frons with small, punctiform, deepened frontal impressions. Mandibles relatively short, almost as long as wide, with outer margin evenly arcuate and strongly pointed incisor teeth; right mandible (Fig. 2A), with: 1) long retinacular ridge, however without anterior retinacular tooth and posterior retinacular tooth; 2) distinct terebral tooth; and 3) well-formed premolar and molar tooth; left mandible (not figured) of similar structure as right one, but with more prominent terebral tooth, distinct posterior retinacular tooth and respectively clear posterior occlusal groove between posterior retinaculum tooth and premolar. Maxillary palpomere 4 fusiform, slightly longer than palpomere 3, nearly as long as (but considerably narrower than) maxillary palpomere 2 (Fig. 2B). Ligula with glossal sclerite dilated anteriorly and slightly down directed, its apical margin straight in middle and bent at sides, paraglossae with lobes not extended distally beyond anterior margin of glossal sclerite. Mentum tooth simple, widely round at apex, with deep paramedial pits. Submentum narrow medially (and deeply concave at point of gular apical insertion), wider laterally. Gula widened posteriorly, separated from genae by distinct gular longitudinal sutures.

Thorax

Pronotum with sides widened, convexly rounded from anterior angles to point of maximum width then almost straight to posterior angles; maximum width just before middle; pronotum base with (*L. specularis* n. comb.) or without (*L. speculiferus* n. comb.) setal fringe along edge. Lateral bead distinct, narrow anteriorly, widened posteriorly, ended just at posterior angles. Anterior margin concave, submarginal bead laterally present, lacking in medial half; anterior angles very prominent, rounded at apex. Basal margin sinuate, slightly convex laterally, subconcave medially, without marginal bead, posterior angles obtuse and widely rounded. Disc with paramedial, parentheses-like, broad, shallow impressions that join with basolateral impressions; apical transverse impression present or not, if present shallow medially; basal transverse impression absent. Prosternum with median longitudinal sulcus shallowly impressed; prosternal process elongate-rhomboid, unbordered, pointed at apex. Mesosternum deeply concave. Metepisternum longer than wide, with deep sublateral sulcus along half to entire length, with lateral border slightly convex, coadunation with epipleuron located anteriorly and medially; suture between metepisternum and metepimeron distinct.

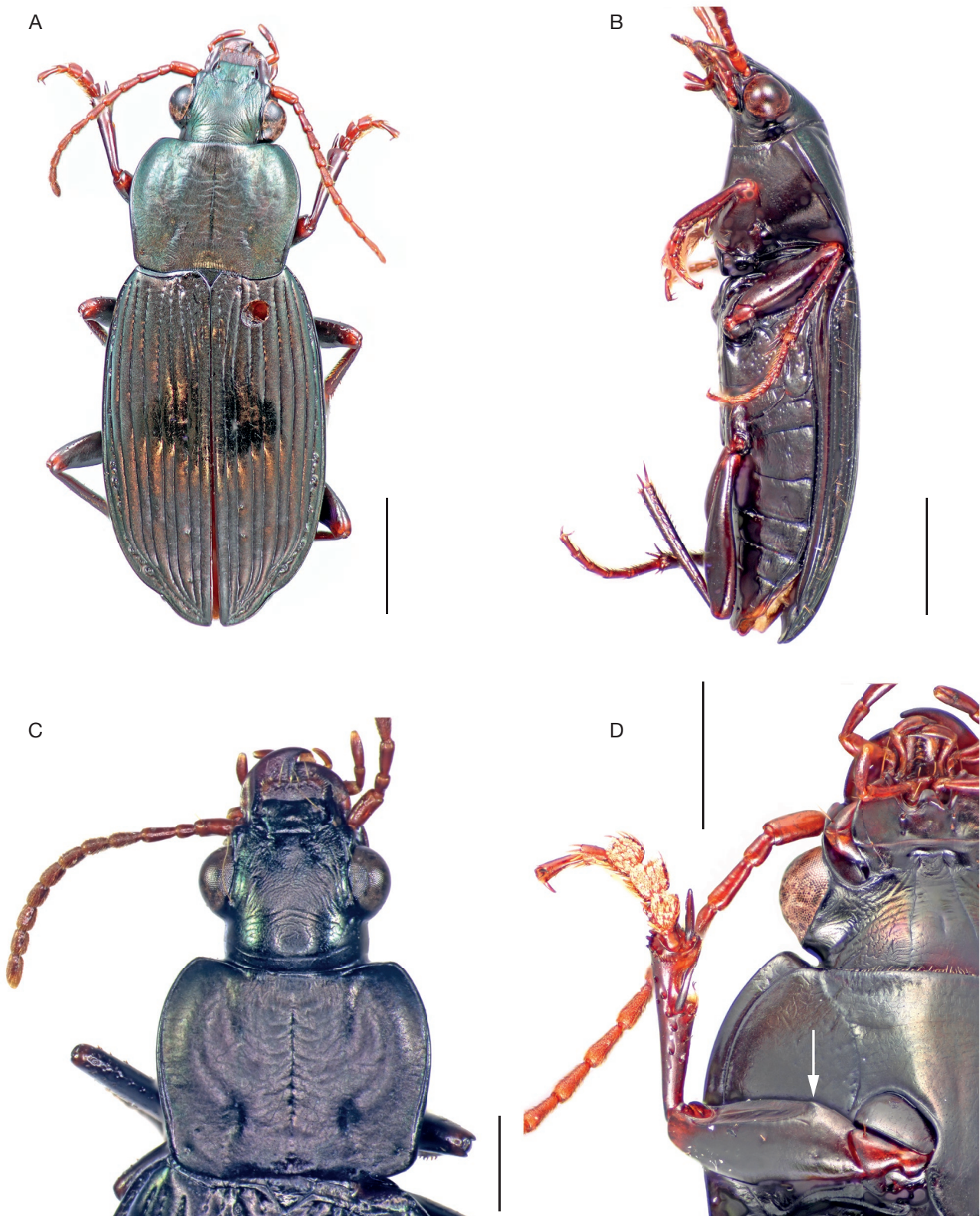


FIG. 1. — *Lapitachlaenius speculiferus* (Fairmaire, 1879) n. comb., male specimen: **A**, dorsal view; **B**, left lateral view; **C**, head and pronotum; **D**, head and fore right leg, ventral view. The **white arrow** points to the profemur ventral tooth-like tubercle. Scale bars: A, B, 2 mm; C, D, 1 mm.

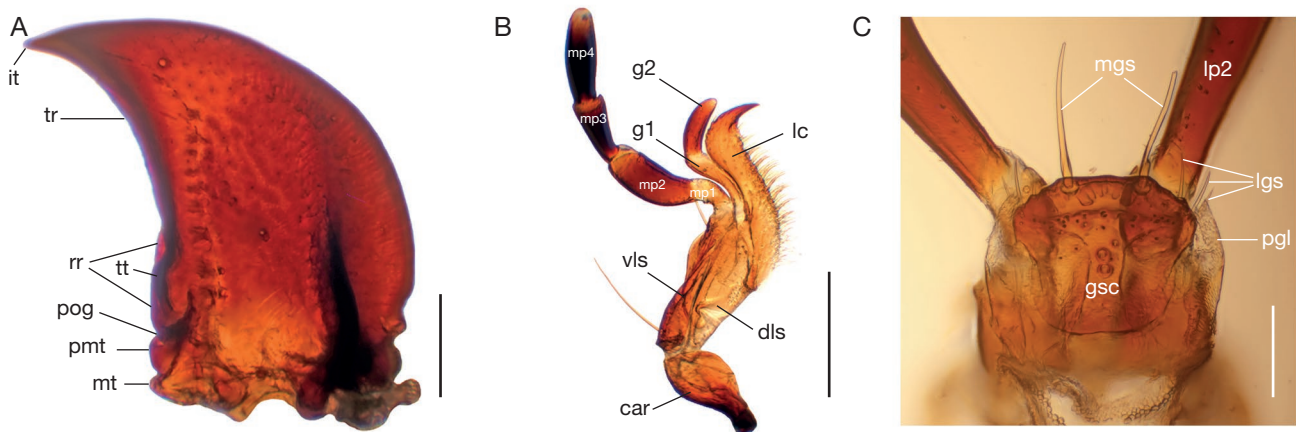


FIG. 2. — *Lapitachlaenius speculiferus* (Fairmaire, 1879) n. comb., female specimen, mouthparts: **A**, right mandible, dorsal view; **B**, right maxilla, ventral view; **C**, glossal sclerite, dorsal view. Abbreviations: **car**, cardo; **dls**, dorsal lobe of stipes; **g1**, galeomere 1; **g2**, galeomere 2; **gsc**, glossal sclerite; **it**, incisor tooth; **lc**, lacinia; **lgs**, lateral glossal seta; **mgs**, medial glossal seta; **lp2**, labial palpomere 2; **mp1-4**, maxillary palpomeres 1-4; **mt**, molar tooth; **pgl**, paraglossa; **pog**, posterior occlusal groove; **pmt**, premolar tooth; **rr**, retinaculum ridge; **tr**, terebral ridge; **tt**, terebral tooth; **vls**, ventral lobe of stipes. Scale bars: A, C, 0.2 mm; B, 0.5 mm.

Elytra

Disc subconvex. Basal margin distinct laterally, forming at humerus obtuse angle with lateral margin, ended medially at level of angular base of stria 1 (i.e., at the level of parascutellar setiferous puncture).

Legs

Profemur in male with (Fig. 1D) or without (Fig. 9) small, ventral tooth-like tubercle near base. Metacoxal basal sulcus short, ended at medial third. Mesotibial ctenidium (see Bousquet 1999: 13, 14) well-differentiated, consisting of 12-15 closely situated, subapical setae. Mesotarsomeres 1-3 and metatarsomeres in both sexes with 1-3 beneath with two rows of short and stout ventral setae and two rows of ventrolateral setae; onychium ventrally with one, rarely with two pairs of setae at apical half.

Female genitalia

See species description.

Male genitalia

See species description.

DISTRIBUTION AND DIVERSITY

The genus is endemic to the easternmost part of Melanesian Island arc and includes two species, one from the archipelago of Vanuatu and one from the archipelago of Fiji.

MONOPHYLY AND RELATIONSHIPS

At least four outstanding autapomorphies that are present in *Lapitachlaenius* n. gen., support the distinctiveness of the new genus. Three of them are features of the elytra, and one of the pronotum disc: 1) each elytron with a glistening, mirror-like area; 2) interval 3 with four to seven large, foveate setiferous punctures; 3) interval 8 distinctly interrupted into two portions along its length and 4) pronotum disc with broad and shallow paramedial, parentheses-like impressions

that join with the baso-lateral impressions. These traits along with some other peculiar features (see Diagnosis), unusual among chlaeniine carabids, provide solid basis for recognition of the new genus.

We examined selected character states and their distribution among the species of Chlaeniina from the Australasian and Oceania regions (Table 3) east of the Lydekker Line. This line demarcates the edge of the Sahul continental shelf and is used as an outermost boundary for delimitation of the typical Australasian fauna from the Oriental fauna (Beron 2015). In total, 31 representatives of the subtribe Chlaeniina Brullé, 1834 have been reported to occur east of the Lydekker Line, 20 of them are microendemic species (Table 3). These locally endemic species are known from: Micronesia, incl. Ogasawara Isl., Southern Mariana Isl. and Palau Isl. (5 species in *Chlaenius*; cf. Darlington 1970a; Kasahara 1991; Mandl 1992), New Guinea with New Britain (13 species in *Chlaenius* and *Hololeius*; cf. Sloane 1920; Darlington 1968; Azadbakhsh & Kirschenhofer 2019), Aru Islands (1 species in *Chlaenius*; Häckel *et al.* 2023), Solomon Islands (5 species in *Chlaenius*; cf. Emden 1937; Darlington 1968, 1970b), Australia (10 species of *Chlaenius* and *Hololeius*; Sloane 1920; Moore 1987), Lord Howe Island (1 species in *Chlaenius*; cf. Moore 1985, 1992), Norfolk Island (2 species in *Chlaenius*; cf. Moore 1985), New Caledonia (4 species of *Chlaenius*, cf. Fauvel 1882; Chaudoir, 1883; Heller 1916; Sloane 1920; Darlington 1968; Kirschenhofer 2002, 2015), Vanuatu (3 species in *Chlaenius* and *Lapitachlaenius* n. gen.; cf. Emden 1937; Moore 1985), Fiji (4 species in *Chlaenius* and *Lapitachlaenius* n. gen.; cf. Darlington 1968; Evenhuis 2007; present study), Samoa (2 species in *Chlaenius*; cf. Csiki 1915; Andrewes 1927), Tahiti (1 species in *Chlaenius*; cf. Darlington 1970a). No representative of the subtribe is known from New Zealand. Larochelle & Larivière (2001) stated that two Australian mainland *Chlaenius* species were introduced to Lord Howe and Norfolk Islands and that it is likely that will be discovered in New Zealand in time.

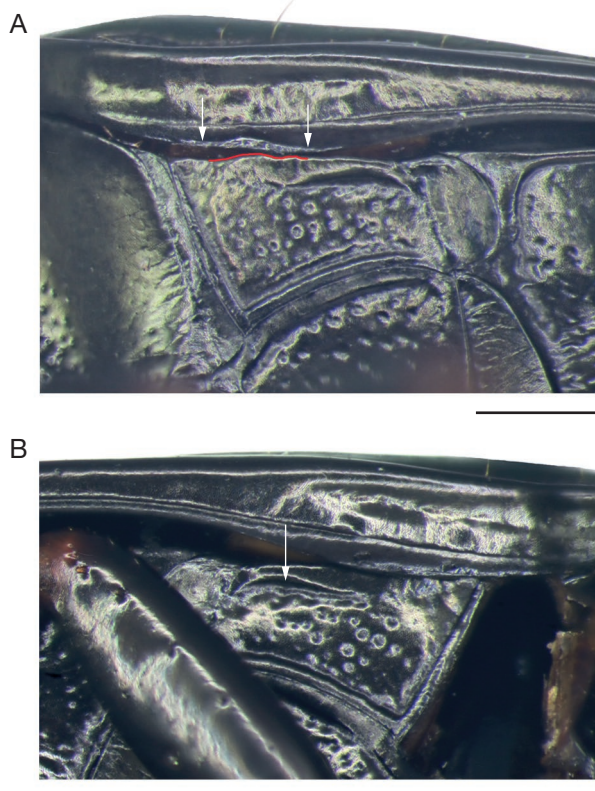


FIG. 3. — *Lapitachlaenius speculariferus* (Fairmaire, 1879) n. comb., male specimen: **A**, left metepisternum. **Arrows** mark a depression on medial margin of elytral epipleuron that usually is covered by a lateral protrusion of metepisternum – edge of the protrusion is marked by a continuous red line; **B**, right metepisternum. **Arrow** points to the sublateral longitudinal sulcus of metepisternum. Scale bars: 0.5 mm.

We found that the adults of *Lapitachlaenius* n. gen. share some specific features with the “*bimaculatus*” group of subgenus *Lissauchenius* W. S. MacLeay, 1825. The last group includes four taxa in Australasia and Oceania – *Chlaenius bimaculatus pongraczi* Jedlička, 1951, *Ch. flaviguttatus* (W. S. MacLeay, 1825), *Ch. olthofi* Darlington, 1968 and *Ch. rufifemoratus* (W. S. MacLeay, 1825) as first and third taxa are endemics in New Guinea (Table 3). Species of “*bimaculatus*” group and species of *Lapitachlaenius* n. gen. share: antennomere 3 not or only slightly longer than antennomere 4; mandibles relatively short, as long as wide, moderately arcuate towards tips (Fig. 2A); abdomen largely smooth and glabrous medially; male front femur with a small tooth-like tubercle below (Fig. 1D) (character presumed to have been secondarily lost in *L. specularis* n. comb.). For more on the distribution of the enumerated characters in some taxa of the “*bimaculatus*” group see Darlington’s (1968) “Key to species of *Chlaenius* of New Guinea”. It is assumed that the six species noted above share the state of having a simple mentum tooth that is rounded at apex. Among the taxa of “*bimaculatus*” group the simple mentum tooth is only documented in *Ch. olthofi* (Darlington *ibid.*).

A plausible hypothesis of the evolution of the genus is that there was a single, eastward, long-distance dispersal event

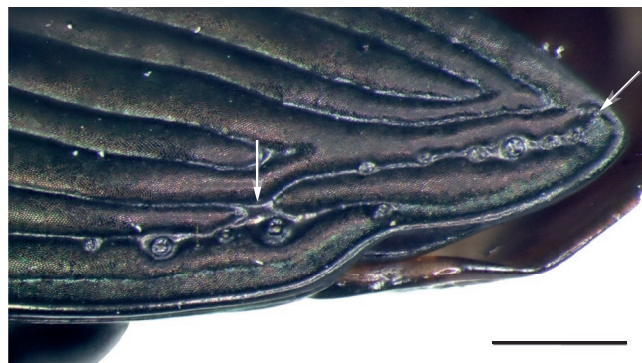


FIG. 4. — *Lapitachlaenius speculariferus* (Fairmaire, 1879) n. comb., male specimen, apical portion of stria 7 of left elytron. The **left arrow** indicates the interruption of interval 7, whereas the **right arrow** points to the terminal setiferous puncture in stria 7. Scale bar: 0.5 mm.

(Gillesbie *et al.* 2012), perhaps in the Early Miocene (or during an earlier geological epoch), of a common ancestor of *Lapitachlaenius* n. gen. and the “*bimaculatus*” group of *Lissauchenius*. Presumably, after the colonization event the lineage experienced remarkable modifications in terms of the pronotum relief, elytral relief, and elytral setiferous setation, all well before both the Fiji-Vanuatu split (Martin 2013) and then subsequently underwent species-level differentiation.

Formation of the two species is potentially a relatively recent event. It is likely the result of the separation of a widespread, ancestral population in the course of the breakup of the formerly continuous Vityaz Arc that separated into the Vanuatu and Fijian land masses, with the North Fiji Basin opening between them during the subduction processes in the Miocene (Martin 2013; Gill *et al.* 2022). The breakup of this arc acted as a significant vicariance event and driver for speciation in various groups (Liebherr 2005; Ferguson *et al.* 2023; Saxton *et al.* 2023).

Lapitachlaenius speculariferus (Fairmaire, 1879) n. comb. (Figs 1A-D; 2A-C; 3A, B; 4; 5A-D; 6; 7; Tables 1-3)

Ceneus speculariferus Fairmaire, 1879: 70 (type locality: “I. Viti.” [= Iles Viti, cf. Fairmaire, 1881]). — Fairmaire 1881: 247. — Evenhuis 2007: 6.

Prosopogmus specularifer – Csiki 1930: 566. — Lorenz 1998: 277; 2005: 264.

Prosopogmus speculariferus – Lorenz 2025: <https://www.catalogueofflife.org/data/taxon/6VZCH>.

TYPE MATERIAL. — Not examined. Should be present in MNHN, according to original description. Indications about number or sex of specimens in the type series was not included in Fairmaire’s (1879, 1881) publications.

OTHER MATERIAL EXAMINED. — Fiji • 1 ♂; Viti Levu Isl., Lami [River]; 0–200 m a.s.l.; XII.1978; N. L. H. Krauss leg.; BPBMENT 2008013406 • 1 ♀; Viti Levu Isl., Belt Road, 6 mi. W. of Suva; 29.VII.1938; E. C. Zimmerman leg.; beating shrubs; *Prosopogmus speculariferus* Fairm. det. B. P. Moore’78; BPBMENT 2008013408 • 1 ♂; Viti Levu Isl., Sigatoka [River], Sand Dunes National Park;

TABLE 3. — Records of species from subtribe Chlaeniina Brullé, 1834 on Australasia and Oceania east of the Lydekker biogeographical line. Abbreviations: **OGA**, Ogasawara Islands (= Bonin); **SMA**, Southern Mariana Islands (incl. Guam); **PAL**, Palau; **NGU**, New Guinea and Aru Islands; **ARU**, Aru Islands; **NBR**, New Britain; **SO**, Solomon Islands; **AUS**, Australia (incl. Tasmania); **LOR**, Lord Howe Island; **NOR**, Norfolk Island; **VAN**, Vanuatu (= New Hebrides); **NCA**, New Caledonia; **FIJ**, Fiji; **SAM**, Samoa; **TAH**, Tahiti; +, present; –, absent; *, endemic species/subspecies.

Species	OGA	SMA	PAL	NGU	ARU	NBR	SOL	AUS	LOR	NOR	NCA	VAN	FIJ	SAM	TAH
<i>Chlaenius</i> (<i>Callistoides</i>) <i>guttula</i> Chaudoir, 1856	–	–	–	+	–	+	–	–	–	–	–	–	–	–	–
<i>Chlaenius</i> (<i>Chlaeniellus</i>) <i>amplipennis amplipennis</i> Chaudoir, 1876	–	–	–	+	–	–	+	–	–	–	–	–	–	–	–
<i>Chlaenius</i> (<i>Chlaeniosstenus</i>) <i>daer</i> Darlington, 1968	–	–	–	*	–	–	–	–	–	–	–	–	–	–	–
<i>Chlaenius</i> (<i>Chlaeniosstenus</i>) <i>darlingensis</i> Laporte de Castelnau, 1867	–	–	–	–	–	–	–	*	–	–	–	–	–	–	–
<i>Chlaenius</i> (<i>Chlaeniosstenus</i>) <i>subcostatus</i> W.J. MacLeay, 1864	–	–	–	–	–	–	–	*	–	–	–	–	–	–	–
<i>Chlaenius</i> (<i>Haplochlaenius</i>) <i>aruensis</i> Häckel, Pašek, Kirschenhofer, 2023	–	–	–	–	*	–	–	–	–	–	–	–	–	–	–
<i>Chlaenius</i> (<i>Haplochlaenius</i>) <i>pan</i> Darlington, 1968	–	–	–	*	–	–	–	–	–	–	–	–	–	–	–
<i>Chlaenius</i> (<i>Haplochlaenius</i>) <i>ramezani</i> Azadbakhsh and Kirschenhofer, 2019	–	–	–	*	–	–	–	–	–	–	–	–	–	–	–
<i>Chlaenius</i> (<i>Lissauchenius</i>) <i>bimaculatus pongraczi</i> Jedlička, 1951	–	–	–	*	–	–	–	–	–	–	–	–	–	–	–
<i>Chlaenius</i> (<i>Lissauchenius</i>) <i>flaviguttatus</i> (W.S. MacLeay, 1825) (= <i>binotatus</i> Dejean, 1826; = <i>guttatus</i> Eschscholtz, 1833)	+	+	+	+	–	+	+	+	–	+	+	+	+	+	+
<i>Chlaenius</i> (<i>Lissauchenius</i>) <i>greensladei</i> Darlington, 1970	–	–	–	–	–	–	*	–	–	–	–	–	–	–	–
<i>Chlaenius</i> (<i>Lissauchenius</i>) <i>maculiger</i> Laporte de Castelnau, 1867	–	–	–	+	–	+	–	+	–	–	–	–	–	–	–
<i>Chlaenius</i> (<i>Lissauchenius</i>) <i>marianensis</i> Darlington, 1970	–	*	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Chlaenius</i> (<i>Lissauchenius</i>) <i>olthofi</i> Darlington, 1968	–	–	–	*	–	–	–	–	–	–	–	–	–	–	–
<i>Chlaenius</i> (<i>Lissauchenius</i>) <i>rudicollis</i> Chaudoir, 1876	–	–	–	–	–	–	–	*	–	–	–	–	–	–	–
<i>Chlaenius</i> (<i>Lissauchenius</i>) <i>rufifemoratus</i> (W.S. MacLeay, 1825) (= <i>palauensis</i> Mandl, 1992 [nec Darlington, 1970])	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–
<i>Chlaenius</i> (<i>Lissauchenius</i>) <i>tetragonoderus palauensis</i> Darlington, 1970	–	–	*	–	–	–	–	–	–	–	–	–	–	–	–
<i>Chlaenius</i> (<i>Pachydinodes</i>) <i>hamifer</i> Chaudoir, 1856 (= <i>queenslandicus</i> Sloane, 1910)	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–
<i>Chlaenius</i> (<i>Pachydinodes</i>) <i>ikedai</i> Kasahara, 1991	*	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Chlaenius</i> (<i>Pachydinodes</i>) <i>malcheri</i> Emden, 1937	–	–	–	+	–	–	+	–	–	–	–	–	–	–	–
<i>Chlaenius</i> (<i>Pachydinodes</i>) <i>mederici</i> Kirschenhofer, 2015	–	–	–	–	–	–	–	–	–	–	*	–	–	–	–
<i>Chlaenius</i> (<i>Pachydinodes</i>) <i>ophonoides</i> Fairmaire, 1843	–	–	–	–	–	–	–	+	+	+	+	+	+	–	–
<i>Chlaenius</i> (<i>Pachydinodes</i>) <i>siccus</i> Darlington, 1968	–	–	–	*	–	–	–	–	–	–	–	–	–	–	–
<i>Chlaenius</i> (<i>Pelasmomimus</i>) <i>australis</i> Dejean, 1831	–	–	–	–	–	–	–	*	–	–	–	–	–	–	–
<i>Chlaenius</i> (<i>Pelasmomimus</i>) <i>grayanus</i> White, 1841	–	–	–	–	–	–	–	*	–	–	–	–	–	–	–
<i>Chlaenius</i> (<i>incertae sedis</i>) <i>neocaledonicus</i> Chaudoir in Oberthür, 1883	–	–	–	–	–	–	–	–	–	–	*	–	–	–	–
<i>Chlaenius</i> (<i>incertae sedis</i>) <i>occultus</i> Sloane, 1907	–	–	–	+	–	+	+	–	–	–	–	–	–	–	–
<i>Chlaenius</i> (<i>incertae sedis</i>) <i>samoensis</i> Csiki, 1915	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–
<i>Hololeius ceylanicus</i> (Nietner, 1856)	–	–	–	+	–	–	–	+	–	–	–	–	–	–	–
<i>Lapitachlaenius specularis</i> (Emden, 1937) n. comb.	–	–	–	–	–	–	–	–	–	–	–	*	–	–	–
<i>Lapitachlaenius speculiferus</i> (Fairmaire, 1879) n. comb.	–	–	–	–	–	–	–	–	–	–	–	–	*	–	–

3.VI.1903; Frank Parker leg.; hand netted; FBA 028093; BPBMENT 2008013409; EMEC1411137 • 1 ♀; Viti Levu Isl., Korovisilou; 17.XI.1974; B. P. Moore leg.; ANIC • 1 ♂; Viti Levu Isl., Korovisilou; 19.IV.1979; B. P. Moore leg.; ANIC • 1 ♂, 3 ♀; Viti Levu Isl., Nausori H[igh][a]nds; B. P. Moore leg.; ANIC • 3 ♂, 1 ♀; Ovalau Island, Wainiloka; 28–30.IX.1937; J. M. Valentine leg.; ANIC • 1 ♂; Viti Levu, Naridivatu, side of Mt. Lomalagi; 5.II.1968; G. F. Gross leg.; SAMA 25-51014 • 1 ♀; Ovalau Island, Draiba Trail; 600–800 ft.; 9.VII.1938; Y. Fondo leg.; BPBMENT 2008013407 • 1 ♂; Vanua Levu, Seanganga - Ndreketi [River]; 25.X.1977; G. Kuschel leg.; Entomology Division D. S. I. R. New Zealand; Prosopogmus speculifer Fairm. det. B. P. Moore '80; NZAC.

DIAGNOSIS. — *Lapitachlaenius speculiferus* n. comb. differs clearly from its congener in the Vanuatu archipelago, by the pronotum basal edge without setal fringe, the elytral stria 7 parallel or subparallel to adjacent striae (Fig. 1A, B), the ventral side of male profemur with tooth-like tubercle near base (Fig. 1D), and the median lobe of aedeagus with longer shaft and nearly straight apical lamella (Fig. 5A–D).

ETYMOLOGY. — The name “*speculiferus*” is not a properly formed Latin word [ICZN Art. 26] though it appears to be based on the Latin word *speculifer* (-a, -um). Both *speculifer* and *speculifera* can be nouns for “mirror-bearer”. Also, these and *speculiferum* can be adjectival for “mirror-bearing”. However, since “*speculiferus*” is not

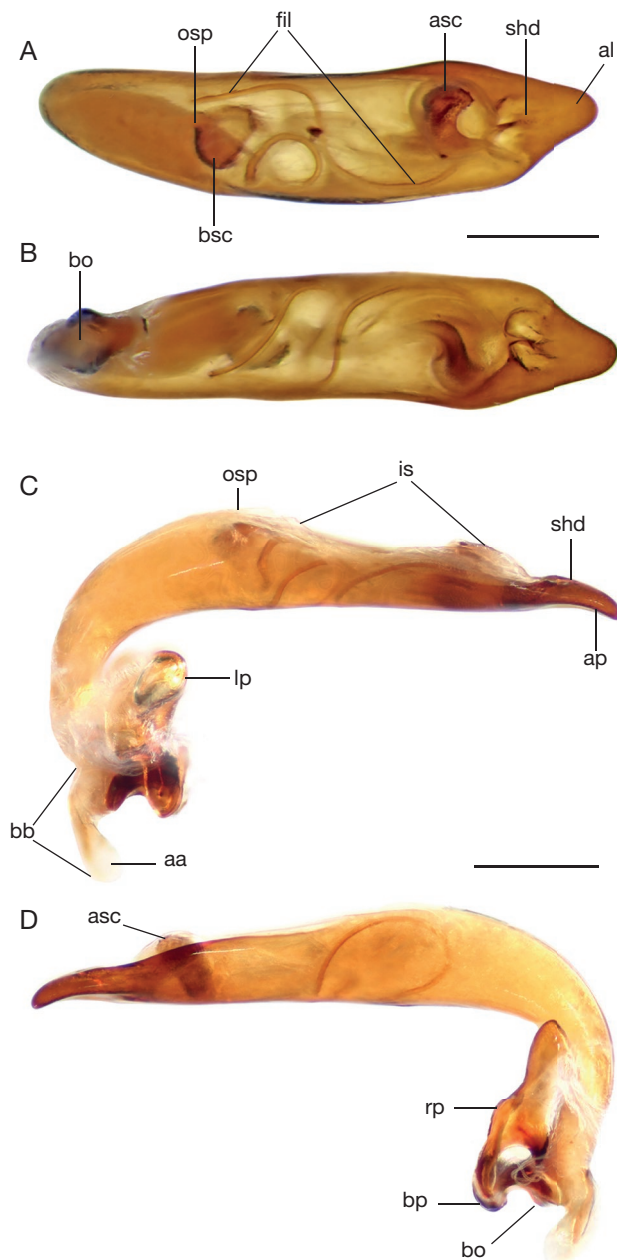


FIG. 5. — *Lapitachlaenius speculiferus* (Fairmaire, 1879) n. comb., male aedeagus: **A**, dorsal view; **B**, ventral view; **C**, left lateral view; **D**, right lateral view. Abbreviations: **aa**, apical aileron of median lobe; **al** apical lamella of median lobe; **ap**, apex of median lobe; **asc**, apical sclerite of internal sac of median lobe; **bb**, basal bulb of median lobe; **bo**, basal orifice of median lobe; **bp**, basal process of median lobe; **bsc**, basal sclerite of internal sac of median lobe; **fil**, filament of internal sac of median lobe; **is**, internal sac of median lobe; **lp**, left paramere; **osp**, proximal end of ostium of median lobe; **rp**, right paramere; **shp**, proximal end of shaft of median lobe. Scale bars: 0.5 mm.

a Latin word and Fairmaire did not specify how it was being used, it must be treated as a noun in apposition [ICZN Art. 31.2.3] that is indeclinable and retains its original spelling even if moved to a feminine genus. Csiki's (1930) use of "*Prosopogmus speculifer*" is considered an unjustified emendation and so we use Fairmaire's original spelling.

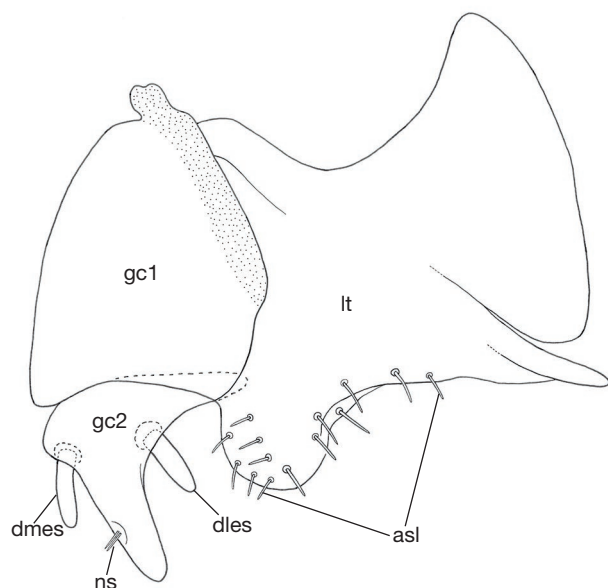


FIG. 6. — *Lapitachlaenius speculiferus* (Fairmaire, 1879) n. comb., female, left gonocoxite, ventral view. Abbreviations: **asl**, apical setae of laterotergite; **dles**, dorsolateral ensiform seta(e) of gc2; **dmes**, dorsomedial ensiform seta of gc2; **gc1**, gonocoxite 1; **gc2**, gonocoxite 2; **lt**, laterotergite of abdominal segment IX; **ns**, nematiform setae. Scale bar: 0.2 mm.

REDESCRIPTION

Habitus

Medium sized, oblong (BL: 9.70–10.60 mm, BW: 3.50–4.00 mm), dorsally with flat pronotum and slightly convex elytra, ventrally body more convex than dorsally (Fig. 1B).

Color and luster

Dorsal surface slightly aeneous or cupreous colored with a moderate to dark tone, clypeus and mandibles reddish brown, palpi, antennae, apex of femur, tibiae and tarsomeres rufous, ventral surface and remaining part of legs reddish black (Fig. 1A). Integument moderately glossy, ventrally glossier than dorsally; median part of each elytron (intervals 2 to 5) with microsculpture absent or scarcely visible, forming a transverse "mirror" region.

Microsculpture and punctuation

Dorsal surface with very distinct, well-impressed isodiametric meshes, sculpticells on elytra larger than those on head and pronotum; ventral surface with isodiametric to slightly transverse mesh microsculpture. Head dorsal surface (excl. mandibles and labrum) strigose and more or less densely micropunctate, punctures coarser and denser on frons and near eyes (Fig. 1C); genae only ventrally strigose. Pronotum smooth, without punctuation. Prosternum and mesosternum smooth; proepisternum largely impunctate, superficially punctate only medially (Fig. 1B); mesoepisternum punctate anteriorly, nearly smooth posteriorly. Metasternum most surface smooth, macropunctate only laterally; metepisternum macropunctate (Figs 3A, B). Abdominal ventrites 1–4 macropunctate and longitudinally wrinkled on sides.

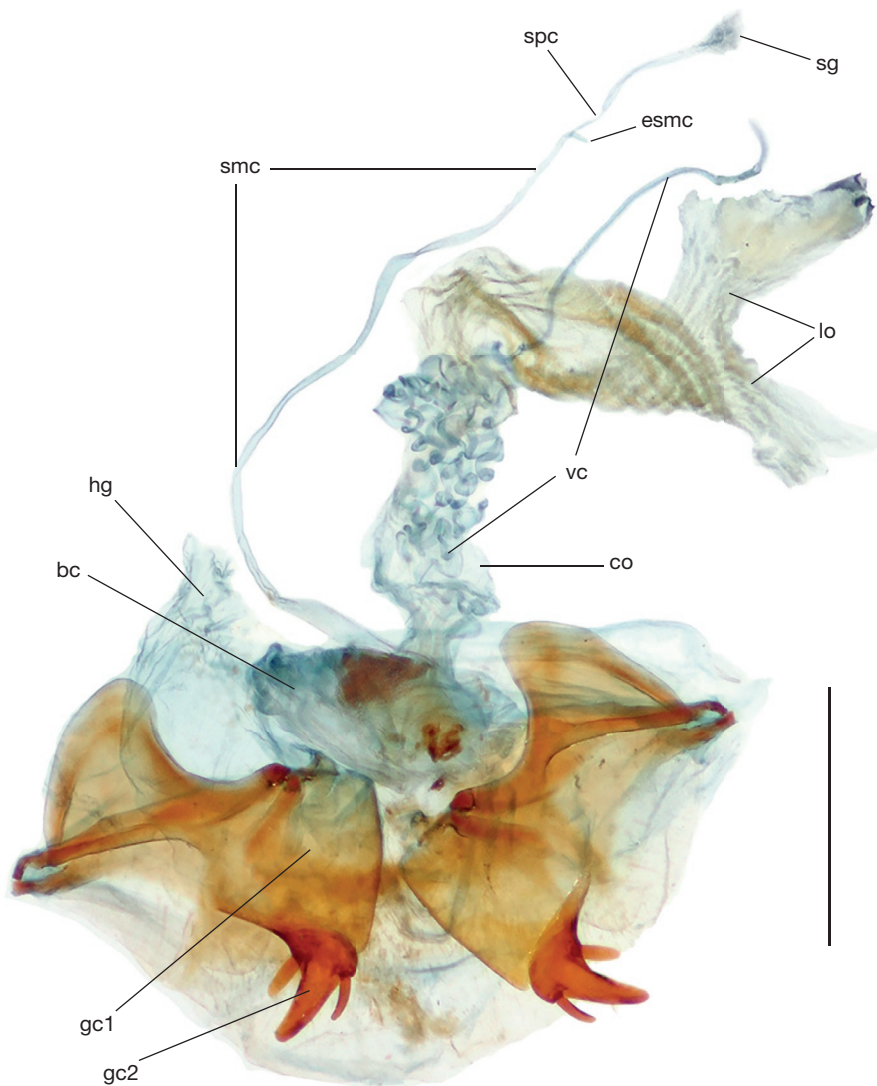


FIG. 7. — *Lapitachlaenius speculiferus* (Fairmaire, 1879) n. comb., female reproductive tract, ventral view. Abbreviations: **bc**, bursa copulatrix; **co**, common oviduct; **esmc**, end of seminal canal; **gc1**, gonocoxite 1; **gc2**, gonocoxite 2; **hg**, hindgut; **lo**, lateral oviduct(s); **sg**, spermatheca gland; **smc**, seminal canal; **spc**, spermathecal canal; **vc**, villous canal of common oviduct. Scale bar: 0.5 mm.

Head

About two-thirds width of pronotum (Table 2). Labrum rectangular, slightly concave medially, with rounded angles, as long as clypeus. Clypeus concave anteriorly, round at angles; clypeal suture reduced, thinner and shallower laterally than medially. Antenna relatively long, two last antennomeres exceeding base of pronotum, with pubescence starting from segment 4.

Thorax

Pronotum subcordate, about a third wider than long (PW/PL: 1.34-1.38); width at apex about two thirds width at broadest point and fifth-sixth or slightly more than width along basal margin (Table 2); pronotum disc depressed on most surface, just barely convex at sides anteriorly, midline distinct, impressed, about a half of pronotum length, not reaching anterior and posterior margins.

Elytra

A little more than one and a half times as long as wide (EL/EW: 1.55-1.63), about a third wider than pronotum and more than two and a half times longer than pronotum (see Table 2). Humerus not denticulate, subangulate. Marginal furrow very narrow anteriorly, appreciably broad posteriorly, with maximum width near penultimate umbilicate puncture. Apical sinuation distinct, deep.

Legs

Protibia appreciably dilated at apex, mesotibia slightly dilated at apex, metatibia with nearly parallel sides. Male protarsomeres 1-3 expanded (Figs 1A, D), 1 subtriangular, as long as wide, 2 and 3 wider than long; ventral adhesive setae present only at apical 3/4 of protarsomere 1 and entire surfaces of 2 and 3; 3 and 4 eccentrically attached to the preceding tarsomere (with basal axis of the former affixed laterally of

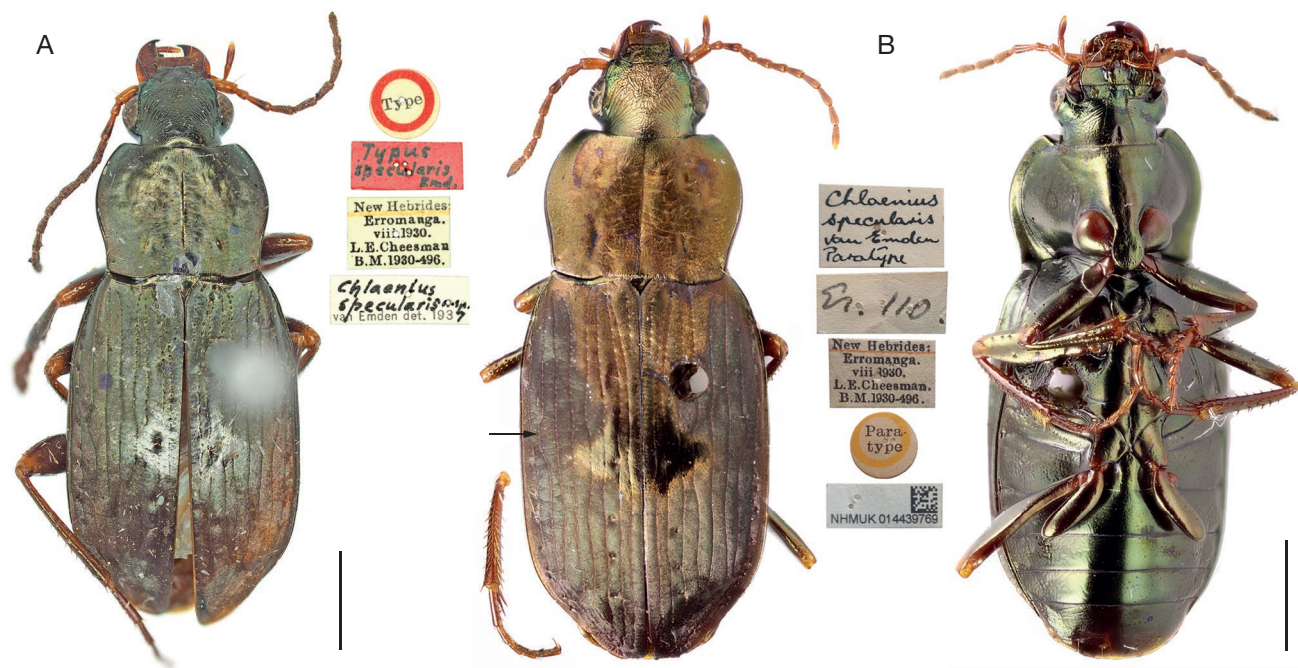


FIG. 8. — *Lapitachlaenius specularis* (Emden, 1937) n. comb., type specimens and their labels: **A**, holotype, dorsal view; **B**, female paratype, dorsal and ventral view. The black arrow in **B** indicates the bend of stria 7 at middle of left elytron. Scale bars: 2 mm.

the latter). Pro- and meso-tarsomeres 4 in both sexes from above incised on two fifths.

Female genitalia

Laterotergite with 13–15 small distal setae on posterior margin (Fig. 6). Gonocoxite 1 subconical, slightly longer than wide, apex without setae. Gonocoxite 2 scarcely curved, pointed distally, as long as wide at base, with one large dorsolateral seta, one large dorsomedial seta and two fine nematiform setae equidistant from apex and middle of gonocoxite. Spermathecal complex (Fig. 7) with a compact bursa copulatrix, with bursal sclerite on dorsal wall, and with a long, straight, undifferentiated spermatheca (receptaculum and seminal canal undistinguishable), proximally joined to bursa copulatrix; spermathecal gland small, rounded, with long spermathecal canal connected near very end of seminal canal (spermathecal canal differentiated to a narrower, short part and a broadened, longer part); common oviduct connected anteriorly to a pair of lateral oviducts and posteriorly to bursa copulatrix, its posterior and medial wall with a very long, densely coiled villous canal that distal end presents a long, free appendix and proximal end joined to distal bursa copulatrix.

Male genitalia

Median lobe of aedeagus tubular, rather long, in lateral view (Figs 5C, D) shaft bent ventrally at right angle towards a rather short and narrow basal bulb, basal bulb with an elongate and narrow apical aileron, apex long convex dorsally and concave ventrally; median lobe in dorsal view (Figs 5A, B), with broad shaft slightly curved to left, triangular apical lamella widely rounded at tip, and long ostium not reaching basal bulb;

sclerotized portion of internal sac (endophallus) with complex architecture, including a large round basal sclerite (dorsal view) located near proximal end of ostium and a thick apical saddle-like sclerite concave dorsally, convex ventrally, both sclerites connecting by a long coiled filament which apical part ends with three spikes as medial spike bifurcate at tip (ventral view). Left paramere larger than right one, elongate rather than typical “conchoid”, with apical part widely rounded; right paramere elongate, shorter and narrowed than left paramere.

BIONOMIC

Labels data for four of the five specimens indicate that they were collected near rivers and perhaps in riparian habitats, in particular these rivers are Sigatoka River, Lami River, and Rewa River on Viti Levu and Ndreketi River on Vanua Levu. Locality data for the specimen from Ovalau Island indicates that it was collected between 180 m and 240 m a.s.l. Likely this is a location in the tropical moist forests west of Draiba Village.

Lapitachlaenius specularis (Emden, 1937) n. comb. (Figs 8A, B; 9, 10; Table 3)

TYPE MATERIAL. — **Holotype.** Vanuatu • 1 ♂; Erromango Isl.; VIII.1930; L. E. Cheesman leg.; “*Chlaenius specularis* n. sp. van Emden” det. 1937; B. M. 1930–496; NHMUK.

Paratypes. Vanuatu • 1 ♂; Erromango Isl.; VIII.1930; L. E. Cheesman leg.; NHMUK 014439769 • 1 ♀; Erromango Isl.; VIII.1930; L. E. Cheesman leg.; NHMUK 015543670.

The holotype and four paratypes are stored in NHMUK. With the assistance of Dr Hongbin Liang and Dr Alexander Anichtchenko (see Acknowledgements), we were able to virtually, by means of images, investigate the holotype and two paratypes (Figs 8A, B; 9).



FIG. 9. — *Lapitachlaenius specularis* (Emden, 1937) n. comb., male paratype, prothorax and fore right leg, ventral view. The **white arrow** points to the absence of profemur ventral tooth-like tubercle. Scale bar: 1 mm.

DIAGNOSIS. — This species is distinct from *L. speculariferus* n. comb., in that stria 7 is distinctly curved outward near the middle of elytron (Fig. 8B), the pronotum basal edge with setal fringe in medial half, the ventral side of male profemur without tooth-like tubercle near base (Fig. 9) and the median lobe of aedeagus with shorter shaft and apical lamella bent to left (Figs 10B, E).

Emden (*ibid.*) stated that *L. specularis* n. comb. has the third elytral stria with 5–7 setiferous discal punctures and that its mandibles are densely wrinkled dorsally whereas specimens of its Fijian congener exhibit the third stria with 4 (very rarely with 5) punctures and the dorsal side of the mandibles only moderately wrinkled.

REMARKS

This species was described by Emden (1937) from the island of Erromango, the fourth-largest island in the Vanuatu archipelago. The author provided a rather good, for that time, description and placed it in the genus *Chlaenius*. In his discussion, Emden stressed several important features: 1) elytron with a roughly triangular specular spot, broadly reaching the suture, touching the tip of the 4th or 5th lateral striae, shiny around the 2nd punctured of the 3rd interval and the varying color nuances in and around the spot; 2) pronotum disc basal impressions continuing towards the front border as indistinct S-shaped impressions; 3) 3rd elytral stria with 5–7 engraved punctures, the first and second of which lie in the “mirror” spot; and 4) underside and upper side of body glabrous. At the end of description, the author expressed suggestion that the species may belong to a separate genus: “Die gerunzelten Mandibeln, die wohl sogar die Aufstellung einer besonderen Gattung rechtfertigen würden, und der Spiegelfleck trennen die Art von allen bekannten [The wrinkled mandibles, which would probably even justify the establishment of a separate genus, and the mirror spot separate the species from all known]”.



FIG. 10. — *Lapitachlaenius specularis* (Emden, 1937) n. comb., male paratype, abdominal segment IX and genitalia: **A**, abdominal segment IX; **B**, median lobe, left lateral view; **C**, right paramere; **D**, left paramere; **E**, median lobe, dorsal view. Scale bar: 1 mm.

The careful examination of the Emden’s description as well as images of and information about characters in the holotype and two paratypes (see the above “Type material”) show that this species shares with *Lapitachlaenius speculariferus* n. comb. all the autapomorphies of the new genus. These species appear very closely related based on their shared morphological similarities and that they inhabit very close, though isolated islands. Based on this evidence we concluded both species form a clade we treat as a genus. On the other hand, several clear distinctions between the two species (see Diagnosis under *L. speculariferus* n. comb.) are evidence that the two taxa are distinct and plausibly reproductively isolated species.

COMMENTS ON THE GENERA *GRUNDMANNIUS*, *MIRACHLAENIUS* AND *STENOODES*

Genus *Grundmannius* Basilewsky, 1965

Grundmannius Basilewsky, 1965: 223.

TYPE SPECIES. — *Ectenognathus dispar* Péringuey, 1896.

DIAGNOSIS. — Mandibles very long, subfalciform. Galea two-segmented. Pronotum without setiferous punctures. Metepisternum coadunate with elytral epipleuron. Lateral edge of elytral epipleuron spiniferous (clothed with short spines). Elytral epipleuron not interrupted by plica. Metacoxa with two lateral setae, anterolateral one and posterolateral one.

Grundmannius dispar (Péringuey, 1896) (Figs 11A–D; 12; 13A, B; 14A–E; Tables 4, 5)

Ectenognathus dispar Péringuey 1896: 521.

MATERIAL EXAMINED. — **Mozambique** • 3 ♂, 1 ♀; Cabo Delgado Province, Megaruma river near Mecufi; 6.VII.1983; P. Beron et V. Beshkov leg.; *Grundmannius dispar* Basilewsky det. Kirschenhofer 2014; BG-NMNHS-ENT-000000006143; BG-NMNHS-ENT-000000006144; BG-NMNHS-ENT-000000006145; BG-NMNHS-ENT-000000006146.

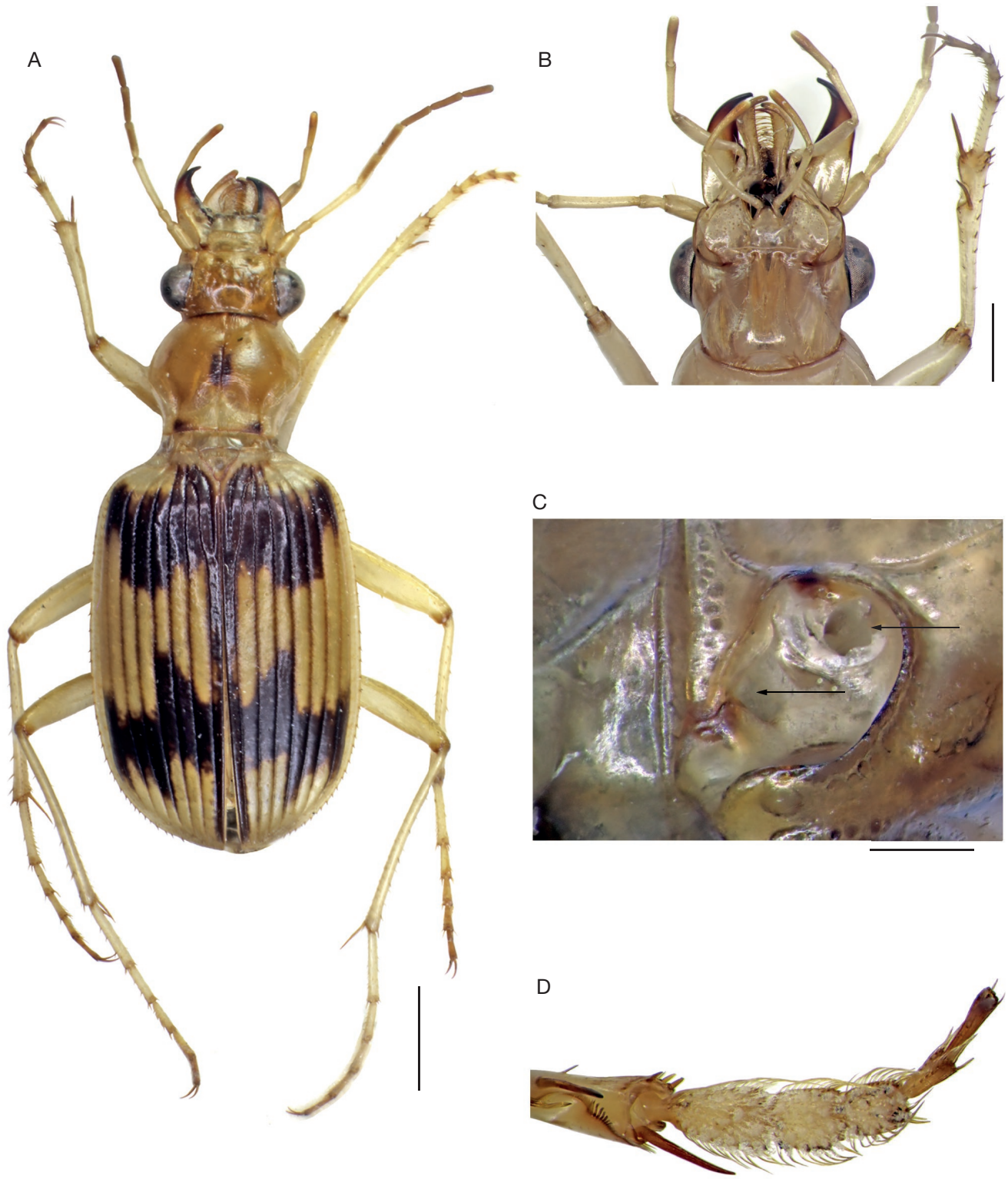


FIG. 11. — *Grundmannius dispar* (Péringuey, 1896), female specimen (A, B), male specimen (C, D): A, dorsal view; B, head, ventral view; C, right anterior coxal cavity. The **black arrows** indicate positions of two foramina; D, right protarsomeres 1-5 (claw absent), ventral view. Scale bars: A, 2 mm; B, C, 1 mm; D, 0.5 mm.

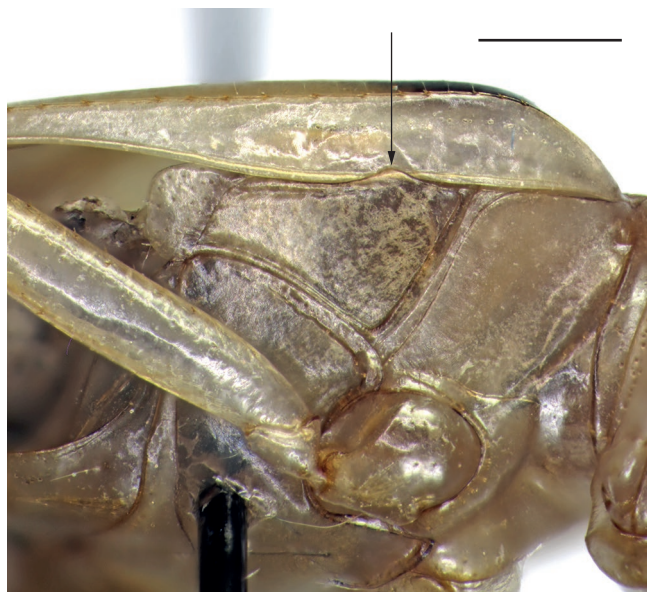


FIG. 12. — *Grundmannius dispar* (Péringuey, 1896), female specimen, right metepisternum. The **black arrow** indicates the coadunation of metepisternum with elytral epipleuron. Scale bar: 1 mm.

South Africa • 1 ♂; Transvaal, 2 mi. N. of Messina; 590 m a.s.l.; 24.III.1958; E. S. Ross & R. E. Leech leg.; CAS.

TAXONOMIC COMMENTS (BASED ON MATERIAL EXAMINED). Below we list morphological features not given in the works of Péringuey (1896) and Basilewsky (1965). A complete re-description, including a detailed description of the structures of female reproductive tract, was not possible as no fully sclerotized female individuals were available to us.

General morphology

Large specimens with glabrous integument of body, with elytra bicolored and rounded at apex; elytron with parascutellar stria not anastomosing with stria 1, base of stria 1 joining base of stria 2; lateral edge of elytral epipleuron with 32–34 short, well-visible spines more conspicuous and denser located medially and posteriorly (Fig. 11A); metathoracic flight wings long, fully developed. Antennomere 3 glabrous at low magnification but with sparse minute hairs visible at higher magnification, 3 significantly longer than antennomeres 1–2 as well as antennomere 4; maxillary palpomere 1 with very scant, hardly visible hairs, palpomeres 2–3 glabrous; galea two-segmented (Fig. 11B). Anterior coxal cavities biperforate (Fig. 11C) – a characteristic of the assemblage Chlaeniini + Oodini + Panagaeini (see Jeannel 1949a: 774, 848). Metepisternum distinctly coadunate with elytral epipleuron, with inner border 1.15–1.20 times longer than anterior border (Fig. 12). Tarsomeres 1–5 in both sexes finely grooved on dorsal side; male tarsomeres 1–3 somewhat flattened dorsally, with adhesive vestiture on ventral side of “spongy” type (Fig. 11D). Female mediotergite VIII continuous medially; ovipositor with laterotergite having about 25–30 apical setae, gonocoxite 1 having an apical fringe of four long setae and gonocoxite 2 having by one large dorsolateral and one large dorsomedial ensiform seta and two

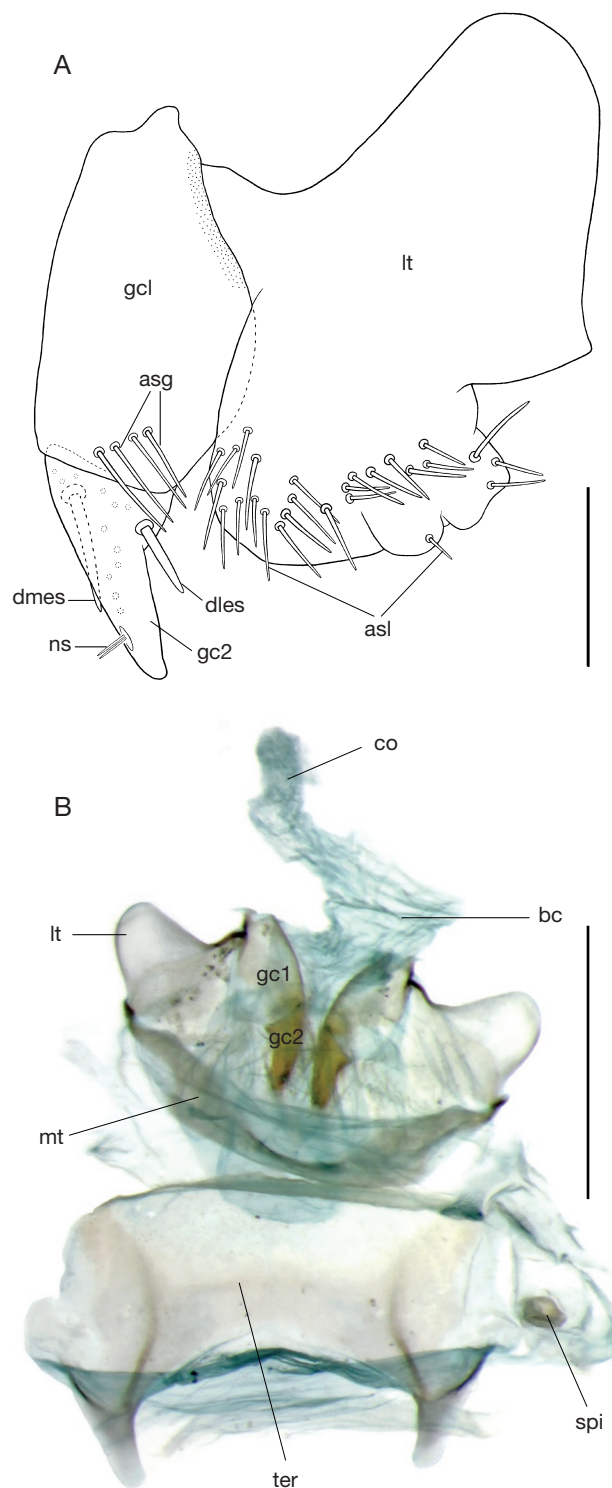


FIG. 13. — *Grundmannius dispar* (Péringuey, 1896), female genitalia: **A**, left gonocoxite, ventral view; **B**, female reproductive tract (spermatheca lacking), dorsal view plus tergum VIII, ventral view. Abbreviations: **asg**, apical setae of gonocoxite 1; **mt**, mediotergite of abdominal segment IX; **spi**, spiracle VIII of pleural membrane; **ter**, tergum VIII. Other abbreviations see Figures 6, 7. Scale bars: A, 0.2 mm; B, 1 mm.

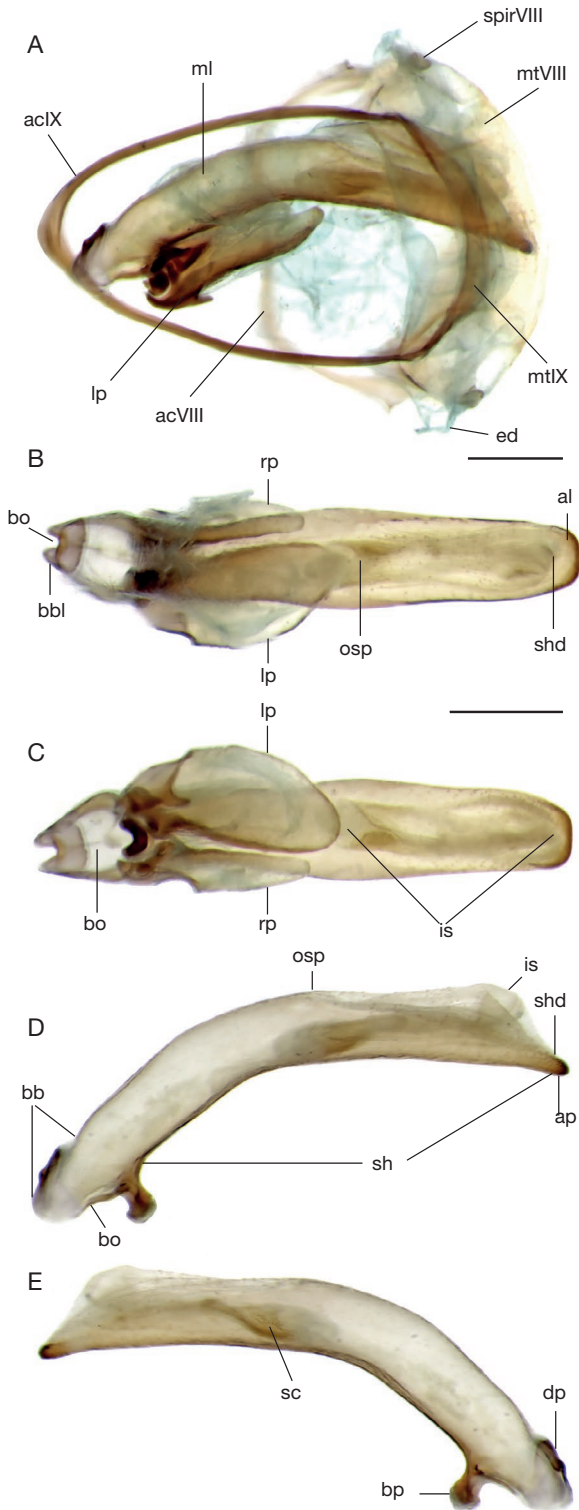


FIG. 14. — *Grundmannius dispar* (Péringuey, 1896), male genitalia: **A**, aedeagus and associated abdominal segments, dorsal view; **B**, median lobe and parameres, dorsal view; **C**, median lobe and parameres, ventral view; **D**, median lobe, left lateral view; **E**, median lobe, right lateral view. Abbreviations: **acVIII**, antecostal margin of abdominal segment VIII; **acIX**, antecostal margin of abdominal segment IX (= urite); **bbl**, lateral lobe(s) of basal bulb of median lobe; **dp**, dorsal process of basal bulb of median lobe; **ed**, efferent duct of pygidial defence gland; **mt VIII**, mediotergite of abdominal segment VIII; **mtg IX**, mediotergite of abdominal segment IX; **sc**, sclerite of internal sac of median lobe; **sh**, shaft of median lobe; **spir VIII**, spiracle of abdominal segment VIII. Other abbreviations see Figure 5. Scale bars: 0.5 mm.

nematiform setae (Fig. 13A); spermatheca with compact bursa copulatrix and wide common oviduct (Fig. 13B). Male abdominal segment VIII, with mediotergite uninterrupted medially and antecostal portion encompassing aedeagus ventrally (Fig. 14A). Plesiomorphic for Carabidae left-everting aedeagal configuration (median lobe lies on its right side in repose and left side superior) (Fig. 14A). Median lobe of aedeagus long and thin, moderately curved ventrally, with straight apex, very short apical lamella, small and very short basal bulb, proximal end of ostium near middle of shaft and internal sac with one sclerite at proximal position (Figs 14B–E). Right paramere elongate, somewhat shorter than left paramere, which is conchoid (Figs 14B, C).

Chaetotaxy

Labrum with six equidistant setae. Clypeus with two mediolateral setae. One supraorbital seta each side behind middle of eyes. Stipes with one anterior and one posterior seta. Ligula apical margin with a pair of long setae. Penultimate labial palpomere glabrous, without setae on internal margin. Mentum with two paramedial setae. Submentum with two long medial setae, without lateral setae. Elytral sensory system consisting of markedly small setiferous pores and short setae, both being barely detectable, as some pores (umbilicate series and those in apical portion of stria 7) located at or near apices of small protuberances, not in foveae, as usual in carabid beetles; parascutellar setiferous puncture small, on interval 1 near to angular base of stria 1 (but not in stria 1), seta rather short (but twice as long as discal setae); elytral intervals 1, 3, 5 and 7 with eight to twenty hardly visible, short setae, located in a row; apical portion of stria 7 with two short setae; umbilicate series consisting of 24–27 fine and hardly visible short setae. Protrochanter with long hind seta. Mesocoxa with one long posteromedial seta and one short lateral seta, with pubescent anterolateral surface; mesotrochanter with one hind seta. Metacoxa with two lateral setae, a rather long anterolateral one and a short posterolateral one; mesotrochanter without seta. Abdominal ventrites 2–5 with scarce hairs in middle; ventrites 4–5 with two long ambulatory setae; last ventrite with two setiferous punctures in male and four in female.

REMARKS

The species was described in the genus *Ectenognathus* Murray, 1858 from “Middle Limpopo”, based on single female specimen (Péringuey 1896). This generic assignment seems to have been made by Péringuey as a result of apotypic traits present in both of his species and the type species of the genus, *E. dryptoides* Murray, 1858 (Murray 1858): very long and glabrous last two joints of labial and maxillary palpomeres; simple mentum tooth, rounded at tip; long and subfalcate mandibles (*E. dryptoides* has mandibles much more falcate and curved at apex than mandibles of *G. dispar*); moderately emarginate labrum; narrow, subcordiform pronotum, with sides more or less broadly reflexed behind.

Nearly 70 years later the situation changed after more data on the morphology of Chlaeniini have been amassed. Studying one male specimen of *E. dispar* with broken protarsomeres

TABLE 4. — Distribution of character states among adults of genus *Grundmannius* Basilewsky, 1965 and tribes Chlaeniini Brullé, 1834 and Lachnophorini LeConte, 1853.

morphological characters	tribe Chlaeniini	genus <i>Grundmannius</i>	tribe Lachnophorini
shape of mandibles	subtriangular (falciform in <i>Ectenognathus</i> and <i>Pseudanomoglossus</i> , subfalciform in <i>Anomoglossus</i>)	subfalciform	markedly falciform (subfalciform in <i>Anchonoderus</i>)
tips of terminal palpomeres	acuminate (Callistina), obtuse or truncate (Chlaeniina)	obtuse	acuminate
maxillary apical palpomere	glabrous or setose	glabrous	with a sparse or dense covering of long setae (except in <i>Anchonoderus</i> , which covered by very short setae)
antennomeres 2–3	glabrous or pubescent	2 glabrous, 3 largely glabrous but on places with sparse hairs	pubescent (except in <i>Aporesthus</i> and <i>Guatemalteca</i>)
supraocular setiferous punctures	one	one	two
patch of setae ventrad subgena	absent	absent	present (except in <i>Amphithasus</i> , <i>Aporesthus</i> , <i>Guatemalteca</i> and <i>Lachnaces</i>)
pronotal lateral setiferous punctures	one (two in <i>Chlaeniodus</i> , more than two in <i>Eurydactylus</i> , none in <i>Callistina</i>)	absent	two (one in <i>Balligratus</i> , none in <i>Amphithasus</i>)
anterior coxal cavities metepisternum	biperforate coadunate with elytral epipleuron (secondarily reduced or obliterate in some lineages)	biperforate coadunate with elytral epipleuron	unknown unknown (? presumably non-coadunate)
adhesive vestiture of male protarsomere 1–3 on ventral side	of “spongy” type (rarely absent)	of “spongy” type	of “seriate” type (quadriseriate, biseriate, uniseriate or absent)
elytral epipleuron near apex	interrupted by an internal plica (Chlaeniina) or not interrupted (Callistina)	not interrupted	not interrupted
apex of elytra	rounded	rounded	obliquely truncate or subtruncate (rounded in <i>Anchonoderus</i>)
spermatheca	unipartite (with single reservoir)	unknown	bipartite
spermathecal channel junction	to apex of bursa copulatrix	unknown	to common oviduct by an elongate sclerite
gonocoxite 1	with or without apical fringe of setae	with apical fringe of setae	with apical fringe of setae

and comparing it with the type of *E. dryptoides*, Basilewsky (1965) established the genus *Grundmannius*. He made this decision because of the presence of simple, non-crossed elytral epipleuron and the absence of the lateral setiferous punctures on pronotum in the first species. Accordingly, he placed the new genus in subtribe Callistina, with species that possess the two aforementioned characters. Contrary to this, the presence of crossed elytral epipleuron in *E. dryptoides* – “the reflexed margin of the elytra, particularly towards the apex” (see Murray 1858) supports placement of this species as a member of subtribe Chlaeniina. Based on the thesis/antithesis 66(61) of Basilewsky (1950: 51) we can provide two more distinctions between the monotypic genera *Ectenognathus* and *Grundmannius*. Both the maxillary palpomeres and tarsomeres dorsally are pubescent in the former genus whereas they are glabrous in the latter genus.

Recently, Kirschenhofer (2010) supported the view of Basilewsky that the genus is a member of Callistina, but stated that *G. dispar* is a very characteristically distinct species in terms of its genital morphology and external characteristics and it should be placed in its own subtribe. Currently, *Grundmannius* is placed in tribe Lachnophorini (Lorenz 2025). Such a placement might have been based on a few external characters,

such as falciform mandibles and lack of elytral plica, which are found in lachnophorines and lacking in most chlaeniines (Table 4) as well as accepting the supposition by Chaudoir (1876: 8–9; see also Basilewsky & Grundmann 1955: 201) that *Ectenognathus* may be a lachnophorine. Additional arguments for such an assignment can be inferred from the view that the presumed basal chlaeniines and basal odacanthines (to which lachnophorines were referred before the work of Liebherr 2016) share a similar ground plan of the body and similar way of life (Baehr 1996: 263, 2005: 183).

To ascertain the relationships of *Grundmannius* the comparative method was applied, looking for similarities and differences of the morphology of adults. Two sets of characters were investigated: the first set focused on features thought to likely resolve the tribal affinity of the genus in regard to Chlaeniini and Lachnophorini (Table 4) and a second set to assign the genus subtribal position within Chlaeniini (Table 5). For character states in Lachnophorini, we carefully surveyed the works of Ball & Hilchie (1983), Liebherr (1988, 2016), Liebherr & Will (1998), Erwin & Zamorano (2014) and Moret & Ortuño (2017). In summary (Table 4), *Grundmannius* is much more similar to chlaeniines sharing with some or all of them: an obtuse tip of terminal palpomeres; glabrous

maxillary apical palpomere; glabrous antennomere 2; one supraocular setiferous puncture; biperforate anterior coxal cavities (character state unknown in lachnophorines); metepisternum coadunate with elytral epipleuron; adhesive vestiture of male protarsomeres 1-3 of “spongy” type; rounded elytral apex. Among the characters enumerated, there are three of tribal importance for Chlaeniini – the coadunate metepisternum, the adhesive vestiture of male protarsomeres 1-3, and single supraocular setiferous puncture. *Grundmannius* and Lachnophorini share only the lack of elytral plica. However, the last character state occurs in the chlaeniine subtribe Callistina.

Grundmannius dispar and representatives of the subtribe Chlaeniina share many important features not found in species of Callistina (Table 5), such as: smooth macrosculpture of cuticle; pubescence absent from integument; glabrous antennomere 2; narrow and blunt tip of ultimate palpomeres; glabrous interior side of penultimate labial palpomere; two-segmented galea; mentum tooth present; pronotal epipleuron reflexed at rear; presence of discal punctures in elytral interval 3; metepisternum coadunate with elytral epipleuron. Among taxa placed in the tribe Chlaeniini, only *G. dispar* and species of Callistina share the lack of the pronotal posterolateral setiferous punctures and elytral epipleuron not being interrupted by a plica. The character evidence supports classifying the genus as a member of the subtribe Chlaeniina, not in Callistina (cf. Basilewsky 1965). We hypothesize that the absence of the elytral epipleural plica and the lack of the posterior pronotal setiferous punctures in *Grundmannius* and Callistina represent independent character losses. The spermatheca of *G. dispar* remains unknown and given its utility in other taxa it is likely that this structure will yield evidence regarding the taxonomic position of this species within chlaeniines.

Genus *Mirachlaenius* Facchini, 2011

Mirachlaenius Facchini, 2011: 348.

TYPE SPECIES. — *Mirachlaenius barbarae* Facchini, 2011.

DIAGNOSIS. — Integument of body glabrous. Dorsal surface of body vividly metallic, bicolored. Elytra immaculate. Penultimate labial palpomere glabrous on inner border, with at most one to three very small setae at apex. Metepisternum coadunate with elytral epipleuron, with anterior border longer than inner border. Elytral epipleuron near apex interrupted by plica.

Mirachlaenius barbarae Facchini, 2011 (Figs 15; 16A, B; 17A, B)

Mirachlaenius barbarae Facchini, 2011: 349.

MATERIAL EXAMINED. — India • 1 ♀; South India, Devata, Nilgiri Hills; Stegmann leg.; SMNS 1983.

TAXONOMIC SUPPLEMENT (BASED ON SPECIMEN EXAMINED)
Added to the information noted by Facchini (2011: 348-350) in the original description based on two male specimens, we report following new morphological data. Stipes with long dorsal seta, as long as length of stipes; antennomere 2 with short ventral seta. Maxilla with two-segmented galea. Penultimate labial palpomere glabrous, except for two, minute apical ventral setae. Mentum with two long, paramedial setae; mentum tooth truncate at apex. Submentum with two very long, lateral setae. Pronotum without setal fringe along basal edge. Basal and lateral margins of elytra forming small denticle at humerus; left elytron with two

TABLE 5. — Distribution of characters in adults among the subtribes of Chlaeniini Brullé, 1834 and genus *Grundmannius* Basilewsky, 1965.

morphological characters	subtribe Chlaeniina	genus <i>Grundmannius</i>	subtribe Callistina
microsculpture of cuticle	smooth or punctate	smooth	punctate
hair cover of integument	usually present, rarely absent	absent	present
antennomeres 1-2	glabrous or pubescent	glabrous	pubescent
antennomere 3	densely or sparsely pubescent, rarely glabrous	rarely and scarce pubescent	densely pubescent
tips of ultimate maxillary and labial palpomeres	narrow, blunt or widened, blunt	narrow, blunt	narrow, acuminate
interior surface of penultimate labial palpomere	glabrous or setose	glabrous	setose
outer lobe of maxillae (= galea)	two-segmented	two-segmented	one-segmented
mentum in front	dentate	dentate	dentate (<i>Callistus</i>) or edentate (<i>Callistomimus</i>)
pronotum posterolateral setiferous puncture	present	absent	absent
pronotal epipleuron behind basal marginal border of elytra	mostly straight, rarely reflexed complete to level of stria 1 or effaced inwards	reflexed effaced inwards	straight effaced inwards
elytral lateral edge	unprotected	prickle-supplied	unprotected
discal elytral setiferous punctures in interval 3	usually absent, rarely present (a few <i>Chlaenius</i> , <i>Lapitachlaenius</i> n. gen.)	present	absent
elytral epipleuron near apex	interrupted by an internal plica	not interrupted	not interrupted
metepisternum	coadunate or not with elytral epipleuron	coadunate with elytral epipleuron	not coadunate with elytral epipleuron
number of sensory setae on metacoxa	one seta	two setae	unknown

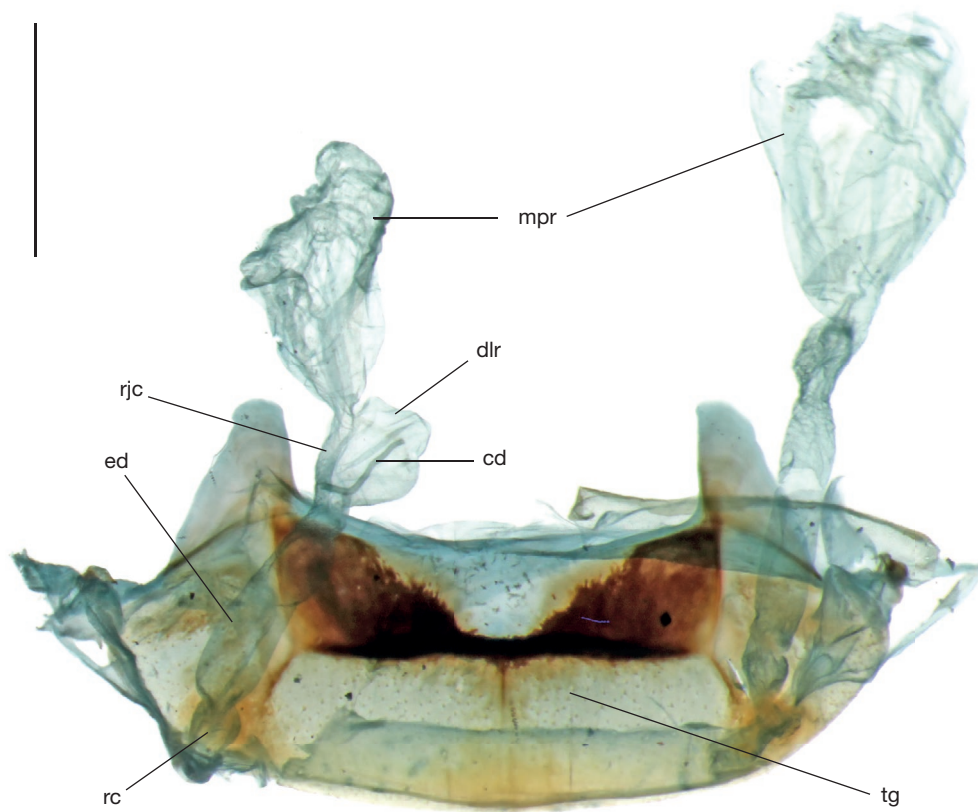


FIG. 15. — *Mirachlaenius barbarae* Facchini, 2011, female, tergum VIII with pygidial gland system (secretory lobes lacking), dorsal view. Abbreviations: **cd**, collecting duct; **dlr**, dorsal lobe of gland reservoir; **ed**, efferent duct; **mpr**, main part of gland reservoir; **rc**, reaction chamber; **rjc**, reservoir junction channel; **tg**, tergum VIII. Scale bar: 1 mm.

small, nearly imperceptible, discal setiferous punctures, first puncture in anterior fifth on interval 3 adjacent to stria 3, second puncture in center of interval 3 near apical end, closer to apex than to suture, right elytron without discal punctures (this character state in partial accordance with Facchini 2011: 350 who stated that just one discal pore was present on one of the elytra); parascutellar puncture large, foveate, at angular base of stria 1; apical portion of stria 7 with three setiferous punctures, terminal puncture closer to apex than to suture and distant from two anterior punctures; umbilicate series consisting of 21–23 setiferous punctures of various sizes. Prosternum with shallowly impressed median sulcus; prosternal process wide at apex, unbordered. Metepisternum wider than long, with anterior border longer than internal border, without sublateral longitudinal sulcus. Protrochanter with anterior seta. Mesocoxa with one posteromedial seta and one or two lateral setae; mesotrochanter with posterior seta. Metacoxa with only anterolateral seta. Metafemur without posterior setae. Abdominal ventrites 3–5 with ambulatory setae each side; last ventrite with four setae in female. Pygidial glands system with a bilobed reservoir – larger reniform lobe (main part of reservoir) and smaller spherical dorsal lobe (Fig. 15). Collecting duct arising from ventral basal part of a narrow channel (here

named “reservoir junction channel”) connecting main lobe of reservoir with efferent duct. Laterotergite with eight to ten small distal setae on posterior margin (Fig. 16A). Gonocoxite 1 broad, slightly longer than wide, apex without setae. Gonocoxite 2 elongate, slightly curved, base well protruding outward, without ensiform setae, with two close, very fine and short nematiform setae (hardly visible at highest magnification), situated in an elongate pit-like depression near apex of gonocoxite (Figs 16A, B). Spermathecal complex with small bursa copulatrix; spermatheca narrow and very long, slightly but clearly differentiated to very long seminal canal and short, coiled receptaculum (Figs 17A, B); spermathecal gland elongate, with spermathecal canal slightly differentiated, connected near middle of receptaculum; common oviduct with villous canal.

REMARKS

Since the original description (Facchini 2011), the specimen we examined is the first female and the third individual known of *M. barbarae*. Study of this material allowed us to make a contribution to the morphology of the species especially regarding the female reproductive and pygidial defensive gland structures. Additionally, we report on some external characters not discussed in the original description.

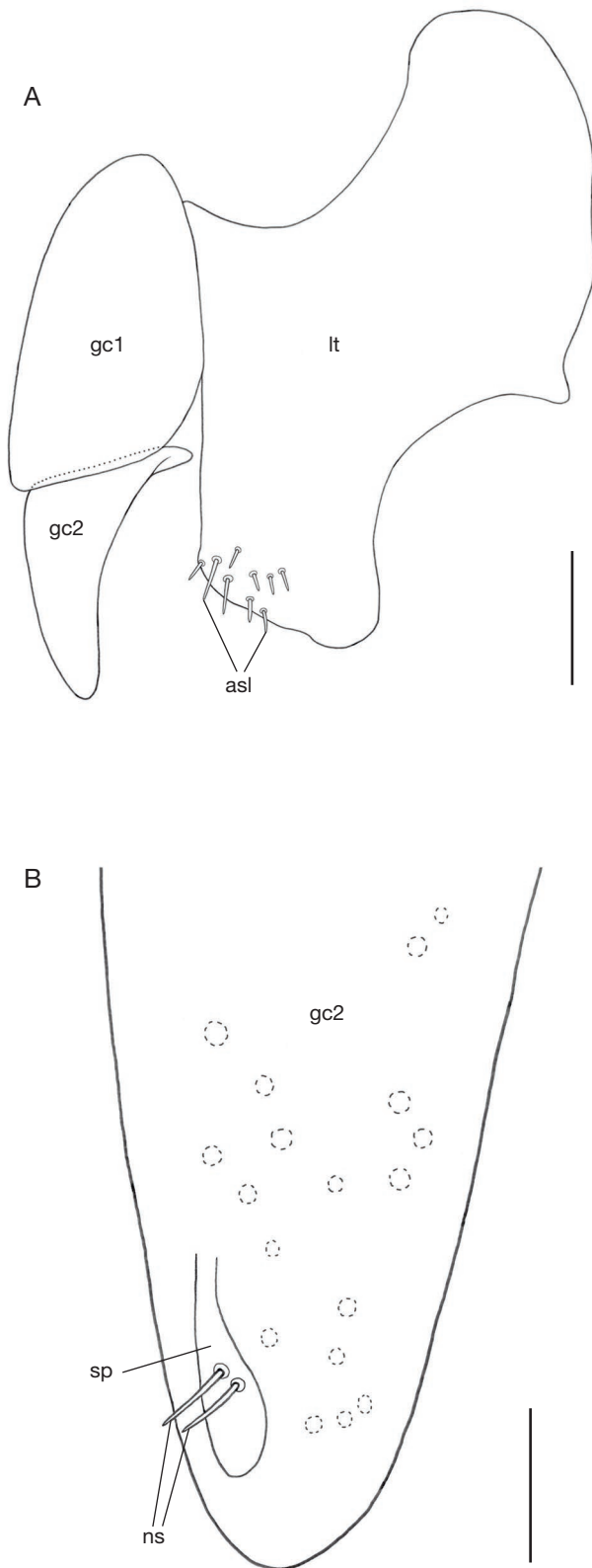


FIG. 16. — *Mirachlaenius barbarae* Facchini, 2011, female, left gonocoxite, ventral view: **A**, overall view with attached laterotergite; **B**, apical part of gonocoxite 2. Abbreviations: **asl**, apical setae of laterotergite; **gc1**, gonocoxite 1; **gc2**, gonocoxite 2; **lt**, laterotergite; **ns**, nematiform setae; **sp**, sensorial pit. Scale bars: A, 0.3 mm; B, 0.05 mm.

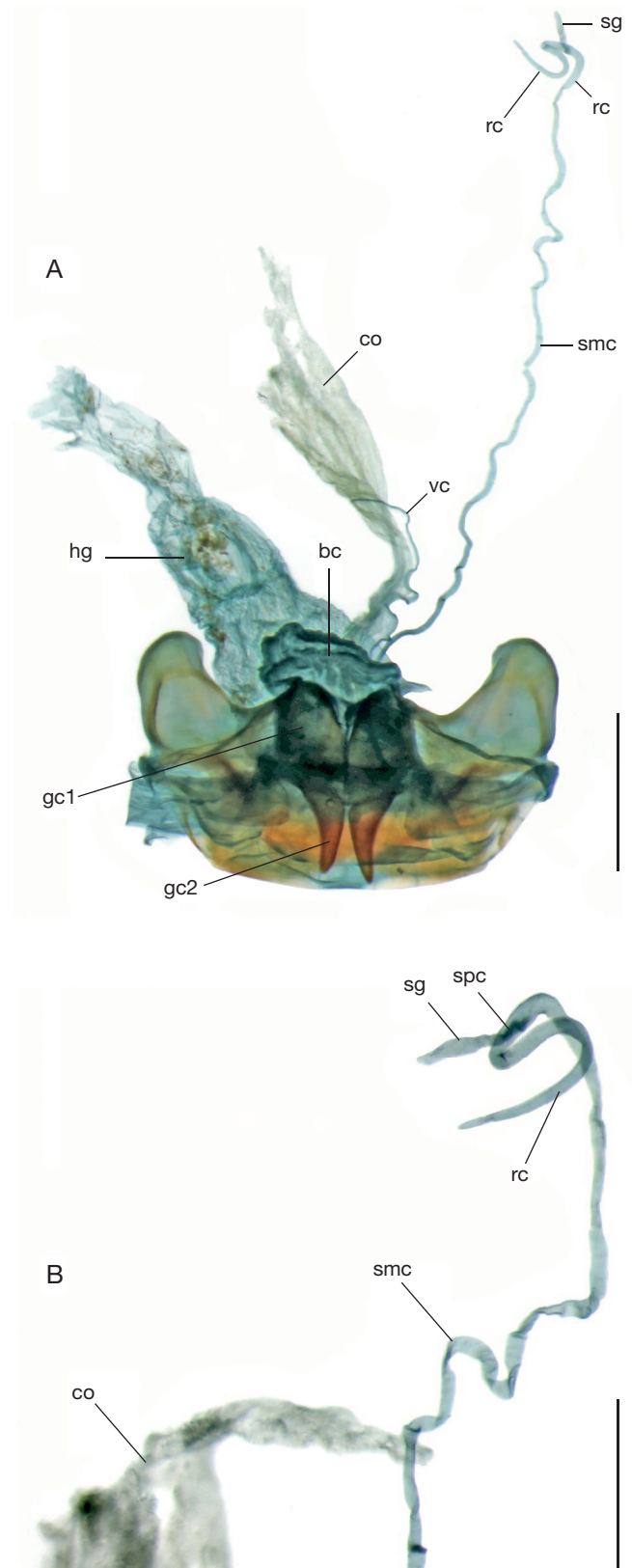


FIG. 17. — *Mirachlaenius barbarae* Facchini, 2011, female, reproductive tract, ventral view: **A**, overall view with attached gonocoxae and laterotergites of segment IX; **B**, apex of spermatheca. Abbreviations: **bc**, bursa copulatrix; **co**, common oviduct; **gc1**, gonocoxite 1; **gc2**, gonocoxite 2; **hg**, hindgut; **rc**, receptaculum; **sg**, spermathecal gland; **smc**, seminal canal; **sp**, sensorial pit; **spc**, spermathecal canal; **vc**, villous canal of common oviduct. Scale bars: A, 1 mm; B, 0.5 mm.

Forsyth (1972: 299-300) discussed a compound reservoir of the pygidial gland with a main reservoir and a dorsal lobe that occurs in the tribes Harpalini Bonelli, 1810, Licinini Bonelli, 1810, Platynini Bonelli, 1810, Anthiini Bonelli, 1813 and Dryptini Bonelli, 1810 (*ibid.* 288, fig. 42). Pygidial gland dorsal lobes are also present in Sphodrinini Laporte, 1834 (Will *et al.* 2010) and some Pterostichini (Baehr & Will 2019). Expanded and lobe-like structures on the efferent duct is known from some Abacetini Chaudoir, 1873 (Will *et al.* 2000). An independent evolution of a separate main reservoir and dorsal lobe connected by a reservoir junction channel is found in species of *Sphodrosomus* Perroud, 1864 (Pterostichini) from New Caledonia (Will 2006). A reservoir without a dorsal lobe is found in Chlaeniini and most other carabid tribes (Balestrazzi *et al.* 1985; Dazzini-Valcurone & Pavan 1980; Will 2000). Given the paucity of studies of the pygidial gland system for most species of carabids, it is not surprising that our investigation revealed a bilobed gland reservoir in the genus *Mirachlaenius*. What is even more interesting in the pygidial gland system of this genus, it is the presence of a narrow channel (Fig. 15) that links between the main reservoir and the efferent duct. This specific structure is named *reservoir junction channel*. This is the first such structure observed in Chlaeniini and among carabids the only known analogous form is that of the pterostichine *Sphodrosomus*.

Genus *Stenoodes* Basilewsky, 1953

Stenoodes Basilewsky, 1953: 55.

TYPE SPECIES. — *Stenoodes jeanneli* Basilewsky, 1953.

DIAGNOSIS. — Elytral epipleuron at apex interrupted by plica. Metepisternum coadunate with elytral epipleuron. Elytral interval 9 deep and forming a marginal furrow, more evident in posterior half, so that outer margin of interval 8 elevated to form a ridge. Integument of body, antennomeres 1-3 and palpomeres glabrous. Hind femur with one, basal posterior seta. Submedial assemblage of setae of mesotibia absent.

Stenoodes jeanneli Basilewsky, 1953 (Fig. 18A-C)

Stenoodes jeanneli Basilewsky, 1953: 55.

TYPE MATERIAL. — **Holotype.** Madagascar • 1 ♂; Ambohitsitondrona; X.1948; Michel leg.; “*Stenoodes jeanneli*, nov. gen., n. sp.”; P. Basilewsky det., 1952; MNHN.

TAXONOMIC SUPPLEMENT (BASED ON HOLOTYPE)

The following additions and specifications are added to the original description. Stipes with long and fine dorsal seta, longer than length of stipes; antennomere 2 with long ventral seta. Clypeus concave in front, with two clypeal setae; clypeus fused with frons (no frontoclypeal suture).

Mentum with two long paramedial setae. Submentum with two long lateral setae. Pronotum anterior and posterior transverse impressions barely distinct only medially; basal margin without bead, basal edge without setal fringe (Fig. 18B). Prosternum with median longitudinal sulcus shallowly impressed. Parascutellar seta present, small, located at level of elytral stria 2; parascutellar striole long, not joining elytral stria 1, almost reaching medial end of basal margin. Elytral interval 3 with two discal setiferous punctures near stria 2, first more evident, situated in medial fifth of elytral length, second, less perceptible than first, located in posterior fourth (Fig. 18A). Stria 8 distinct in anterior four-seventh where deeper than striae 1-7. Intervals 8 and 9 normal in anterior four-seventh, modified towards apex as interval 8 elevated, forming a ridge, 9 deepened and widened backwards, forming a marginal furrow (Fig. 18C). Mesotrochanter with seta. Mesotibia without submedial assemblage of setae. Metafemur with long basal posterior seta opposite metatrochanter.

REMARKS

Stenoodes was introduced for the distinctively autapomorphic species *S. jeanneli* (Basilewsky 1953). The genus was originally placed in the tribe Oodini though the author (*ibid.*) did not report on the unique modifications in elytral intervals 8 and 9 (see Introduction) that are the most recognizable morphologic features of the tribe. Recently, the genus was categorized as a representative of the tribe Chlaeniini and listed immediately after *Hololeius* (Lorenz 1998, 2005). This move was made because “*Stenoodes* was strikingly looking like an Indian *Hololeius*, that may have been unknown to Basilewsky” (Wolfgang Lorenz, pers. comm.). Careful study of the holotype of *S. jeanneli* revealed that it possesses the modifications in elytral intervals 8 and 9 typical of Oodini and that its integument is glabrous outside of the typical sensory setae, consistent with the original placement of Basilewsky (1953). The presence of a basal posterior seta on hind femur and lack of mesotibial submedial assemblage of setae (for the second character see Guéorguiev & Schmidt 2016) both are likely plesiomorphic conditions in this group of carabids. That led to supposition that *Stenoodes* is most likely an early branch in the tribe. The other oodine groups that possess basal posterior seta on metafemur are *Oodinus* Motschulsky, 1865 and *Stenocrepis* Chaudoir, 1857 (Bousquet 1996), three Australian species of *Nanodiodes* Bousquet, 1996 as well as two of the four recognized species groups of *Brachyodes* Jeannel, 1949 (unpublished data). While the representatives of the first genus are mainly restricted to the world tropical regions, with two species occurring subtropical areas of the southernmost United States, members of *Stenocrepis* inhabit the New World from southern Ontario south to Uruguay and Argentina, including the West Indies (Spence 1983; Bousquet 1996, 2012). Taxa of *Brachyodes* live mainly in the tropics of the Old World, with only a few species reaching southern skirts of the Palaearctic Region (Bousquet 2017; unpublished information).

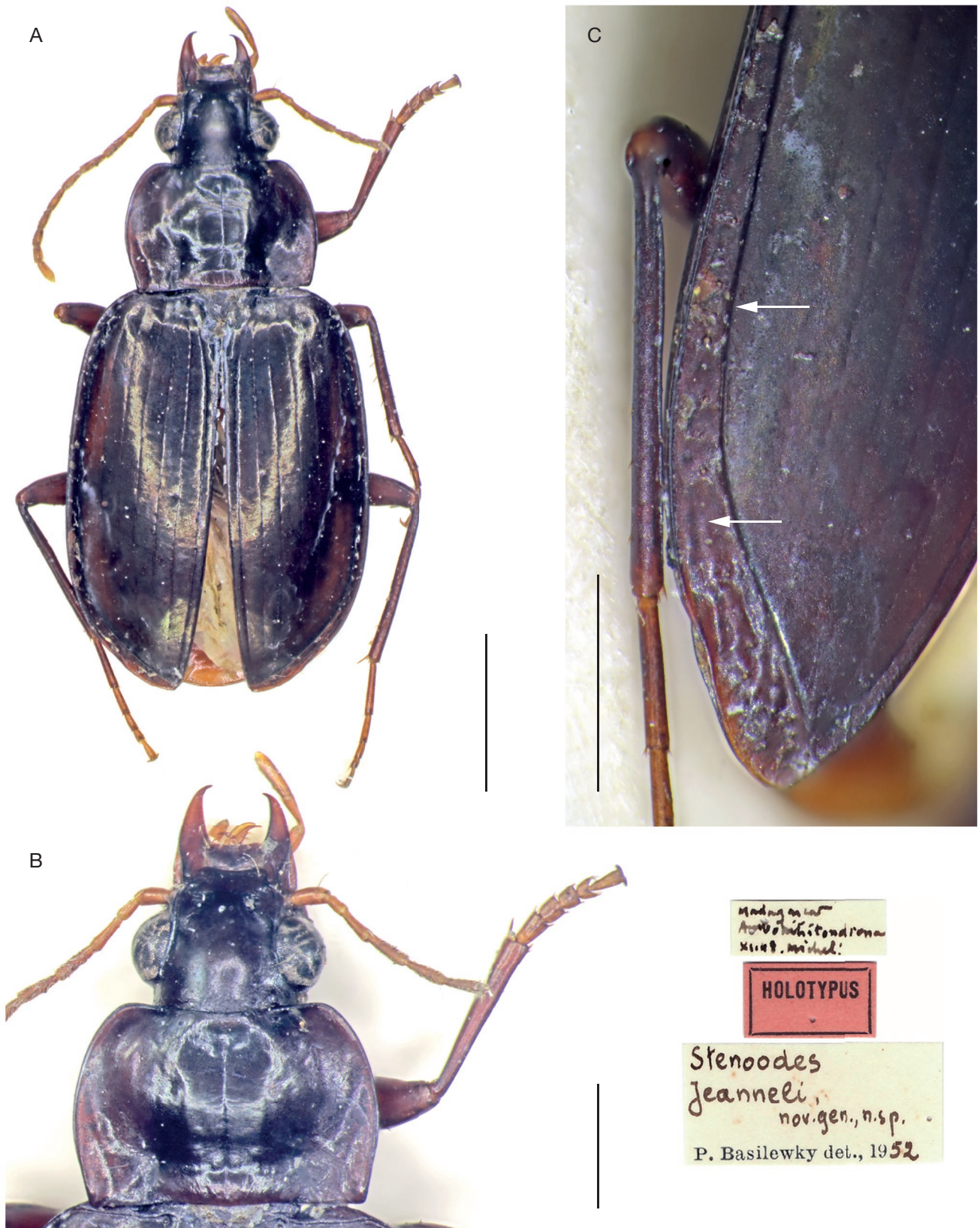


FIG. 18. — *Stenoodes jeanneli* Basilewsky, 1953, holotype and its labels, MNHN: **A**, dorsal view; **B**, head, pronotum and right front leg; **C**, posterior part of left elytron. The **upper arrow** on **C** points to the elevated outer margin of interval 8, whereas the **lower arrow** indicates the transformed into marginal furrow interval 9. Scale bars: A, 2 mm; B, C, 1 mm.

PROVISIONAL KEY TO THE ORIENTAL AND AUSTRALASIAN GENERA OF *CHLAENIINA* BRULLÉ, 1834
(BASED ON THE CHARACTERS RECORDED IN PUBLICATIONS AND OUR EXAMINED MATERIAL)

1. Dorsal surface of body more or less densely pubescent (in *Holosoma* only elytra laterally) and/or more or less coarsely punctate. Elytra maculate or immaculate 2
- Dorsal surface of body glabrous. Pronotum and elytra impunctate (excl. local micropunctations), smooth. Elytra immaculate 5
2. Elytral stria 8 deeper than striae 3–7 and 1–2 anteriorly, as deep as striae 1–2 posteriorly *Hololeius* LaFerté-Sénectère, 1851
- Elytral stria 8 shallower than or as deep as other striae 3
3. Elytral basal margin shallowly arcuate posteriorly, junction with lateral margin at humerus typically obtusely angled, rarely nearly right angled. Anterior width of metepisternum 1.2 times or less its medial length 4.
- Elytral basal margin deeply arcuate posteriorly, junction with lateral margin at humerus acutely angle. Anterior width of metepisternum 1.5 times or more its medial length *Holosoma* Semenov, 1889
4. Protarsomere 4 deeply bilobed apically. Basal margin of elytra incomplete *Viridagonum* Lassalle, 2015, in part (*V. azureoviride* Sciaky, Facchini & Anichtchenko, 2024)
- Protarsomere 4 slightly or not bilobed apically (except for subgenus *Lithochlaenius* Kryzhanovskij, 1976 of genus *Chlaenius*, which protarsomere 4 deeply bilobed apically but with basal margination of elytra incomplete, absent from medial portion; cfr. Sciaky *et al.* 2024) *Chlaenius* Bonelli, 1810
5. Ligula with apical margin excavated (cf. Chaudoir 1857; Ullah *et al.* 2022). Penultimate labial palpomere plurisetose, with row of long setae on inner border (cf. Kirschenhofer, 2010; Facchini, 2011) *Harpaglossus* Motschulsky, 1858
- Ligula with apical margin straight. Penultimate labial palpomere glabrous on inner border, with at most one to three very small and short setae at apex 6
6. Elytral striae (except for parascutellar stria) linear, well-impressed; interval 3 with large, foveate, discal setiferous punctures. Dorsal surface of body faintly metallic, unicolored *Lapitchlaenius* n. gen.
- Elytral striae punctiform, shallowly impressed; interval 3 usually without discal setiferous punctures or occasionally in *Mirachlaenius barbara*, one or two, scarcely perceptible discal punctures in interval 3. Dorsal surface of body vividly metallic, unicolored or bicolored 7
7. Dorsal surface of body unicolored, completely green. Antennae and legs bicolored. Mentum tooth at apex slightly bifid *Viridagonum* Lassalle, 2015, in part (*V. lumawigi* Lassalle, 2015)
- Dorsal surface of body bicolored, head and pronotum bluish-green, elytra red-copper. Antennae and legs unicolored, black. Mentum tooth at apex widely round *Mirachlaenius* Facchini, 2011

Acknowledgements

We express our appreciation to the curators of the collections mentioned in “Material and methods” for access to the specimens from their institutions. The first author is grateful to Erich Kirschenhofer (Perchtoldsdorf, Austria) for the identification of chaeniines in NMNHS and Wolfgang Lorenz (Tutzing, Germany) for the useful discussion and provoking his interest to study *Grundmannius dispar*. We thank Dr Hongbin Liang (Institute of Zoology, Chinese Academy of Sciences, Beijing, China) and Dr Alexander Anichtchenko (Institute of Life Sciences and Technologies, Daugavpils University, Daugavpils, Latvia) most heartily for their help in sending us pictures and information about the holotype and two paratypes of *Chlaenius specularis* on which ground we have been able to virtually investigated this species and made conclusions. Hongbin Liang also provided us morphological features useful to distinguish the species of *Chlaenius* from those of *Holosoma*.

The European Union-funded Integrated Infrastructure Initiative “Synthesys+” supported a recent visit of BG in the State Museum of Natural History in Stuttgart (application

DE-TAF-TA4-015) conducted in March 2023. Study in NMNHS was based on specimens deposited in the institution upgraded in the frames of the project DiSSCo-BG (Upgrade of the Research Infrastructure “Distributed System of Scientific Collections—Bulgaria”) funded by the National Roadmap for Research Infrastructures, Ministry of Education and Science of the Republic of Bulgaria.

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Submitted on 30 May 2024;
accepted on 30 September 2024;
published on 23 May 2025.

APPENDIX 1. — List of species and subspecies and number of specimens studied, with data for their provenance and repository.

Species and subspecies	countries	specimens	collections
<i>Callistus lunatus</i> (Fabricius, 1775)	Bulgaria, Turkey (Koru Dağları)	3	NMNHS
<i>Chlaenius</i> (<i>Achlaenius</i>) <i>varicornis</i> A. Morawitz, 1863	North Korea (Mount Myohyang)	1	coll. EK
<i>Chlaenius</i> (<i>Amblygenius</i>) <i>anthraceus</i> Alluaud, 1918	Nigeria	1	NMNHS
<i>Chlaenius</i> (<i>Amblygenius</i>) <i>episcopalis</i> Dejean, 1831 (s.l.)	Zimbabwe (Victoria Falls)	1	NMNHS
<i>Chlaenius</i> (<i>Amblygenius</i>) <i>glabratus</i> Dejean, 1831	Sudan (South Darfur)	3	NMNHS
<i>Chlaenius</i> (<i>Amblygenius</i>) <i>lioderus</i> Andrewes, 1923	India (Delhi)	1	NMNHS
<i>Chlaenius</i> (<i>Amblygenius</i>) <i>liothorax</i> Alluaud, 1934	Nigeria	1	NMNHS
<i>Chlaenius</i> (<i>Amblygenius</i>) <i>macropus</i> Chaudoir, 1876	Nepal (Lumbini)	1	coll. EK
<i>Chlaenius</i> (<i>Amblygenius</i>) <i>omochlorus</i> Andrewes, 1931	Nepal (Trisuli Bazar)	1	NMNHS
<i>Chlaenius</i> (<i>Amblygenius</i>) <i>pretiosus</i> Chaudoir, 1856	India (Delhi)	4	NMNHS
<i>Chlaenius</i> (<i>Amblygenius</i>) <i>rufomarginatus</i> Dejean, 1831	Zimbabwe (Victoria Falls)	1	NMNHS
<i>Chlaenius</i> (<i>Amblygenius</i>) <i>trachys</i> Andrewes, 1923	Sri Lanka (Dambulla)	1	NMNHS
<i>Chlaenius</i> (<i>Amblygenius</i>) sp.	Nepal (Lumbini), Sri Lanka (Dambyla)	2	NMNHS
<i>Chlaenius</i> (<i>Callistoides</i>) <i>amabilis</i> Chaudoir, 1876	Nepal (Lumbini)	3	NMNHS
<i>Chlaenius</i> (<i>Callistoides</i>) <i>malachinus</i> (Motschulsky, 1865)	India (Delhi)	1	NMNHS
<i>Chlaenius</i> (<i>Callistoides</i>) <i>tripustulatus</i> (Dejean, 1831)	Nigeria	3	NMNHS
<i>Chlaenius</i> (<i>Callistoides</i>) sp.	Sri Lanka (Dambyla)	1	NMNHS
<i>Chlaenius</i> (<i>Capsochlaenius</i>) <i>luisae</i> Gestro, 1895	Somalia	2	coll. EK
<i>Chlaenius</i> (<i>Chlaeniellus</i>) <i>atratus</i> Mandl, 1983 (s.l.)	India (Ladakh)	1	NMNHS
<i>Chlaenius</i> (<i>Chlaeniellus</i>) <i>extensus</i> Mannerheim, 1825	Turkmenistan	2	NMNHS
<i>Chlaenius</i> (<i>Chlaeniellus</i>) <i>flavipes</i> Ménétrés, 1832	Albania, Bulgaria, Turkey	8	NMNHS
<i>Chlaenius</i> (<i>Chlaeniellus</i>) <i>impressicollis</i> Chaudoir, 1876	India (Elephanta Isl.)	1	NMNHS
<i>Chlaenius</i> (<i>Chlaeniellus</i>) <i>koenigi</i> Semenov, 1888	Turkmenistan	1	coll. EK
<i>Chlaenius</i> (<i>Chlaeniellus</i>) <i>nigricornis</i> (Fabricius, 1787)	Bulgaria	3	NMNHS
<i>Chlaenius</i> (<i>Chlaeniellus</i>) <i>semiviridis</i> Andrewes, 1920	Indonesia (W Timor)	4	NMNHS
<i>Chlaenius</i> (<i>Chlaeniellus</i>) <i>stenoristus</i> Chaudoir, 1876	India (Delhi)	1	NMNHS
<i>Chlaenius</i> (<i>Chlaeniellus</i>) <i>terminatus</i> Dejean, 1826	Bulgaria	1	NMNHS
<i>Chlaenius</i> (<i>Chlaeniellus</i>) <i>tristis tristis</i> (Schaller, 1783)	Bulgaria	2	NMNHS
<i>Chlaenius</i> (<i>Chlaeniellus</i>) <i>vestitus</i> (Paykull, 1790)	Albania, Bulgaria, Greece, Turkey, Armenia	53	NMNHS
<i>Chlaenius</i> (<i>Chlaeniellus</i>) sp.	Thailand	1	NMNHS
<i>Chlaenius</i> (<i>Chlaeniodromus</i>) <i>tetraphacus</i> Alluaud, 1918	Ivory Coast	2	coll. EK
<i>Chlaenius</i> (<i>Chlaeniosstenus</i>) <i>angustatus</i> Dejean, 1831	Nigeria	1	NMNHS
<i>Chlaenius</i> (<i>Chlaeniosstenus</i>) <i>circumdatus</i> Brullé, 1835 (s.l.)	Nepal (Lumbini), Sri Lanka (Polonnaruwa), Indonesia (Mentawan Isl.)	5	NMNHS
<i>Chlaenius</i> (<i>Chlaeniosstenus</i>) <i>nitidicollis</i> Dejean, 1826	India (Delhi)	2	NMNHS
<i>Chlaenius</i> (<i>Chlaeniosstenus</i>) <i>sulcipennis sulcatulus</i> Boheman, 1848	Mozambique (Cabo Delgado)	1	NMNHS
<i>Chlaenius</i> (<i>Chlaeniosstenus</i>) <i>spoliatus spoliatus</i> (P. Rossi, 1792)	Bulgaria	5	NMNHS
<i>Chlaenius</i> (<i>Chlaenius</i>) <i>dusaultii</i> (L. Dufour, 1821) (s.l.)	Sudan (South Darfur & West Darfur), Nigeria	8	NMNHS
<i>Chlaenius</i> (<i>Chlaenius</i>) <i>festivus festivus</i> (Panzer, 1796)	Albania, North Macedonia, Bulgaria, Greece, Armenia, Iraq	18	NMNHS
<i>Chlaenius</i> (<i>Chlaenius</i>) <i>festivus velutinus</i> (Duftschmid, 1812)	Spain	3	NMNHS
<i>Chlaenius</i> (<i>Chlaenius</i>) <i>meticulosus</i> Laferté-Sénéctère, 1851	Senegal, Nigeria	2	coll. EK
<i>Chlaenius</i> (<i>Chlaenius</i>) <i>pseudocruciatulus</i> Kirschenhofer, 2009	Sudan (South Darfur)	3	NMNHS, coll. EK
<i>Chlaenius</i> (<i>Dinodes</i>) <i>cruralis</i> Fischer von Waldheim, 1829	North Macedonia	1	NMNHS
<i>Chlaenius</i> (<i>Dinodes</i>) <i>decepiens</i> (L. Dufour, 1820)	North Macedonia, Bulgaria, Greece	17	NMNHS
<i>Chlaenius</i> (<i>Epomis</i>) <i>dejeanii</i> (Dejean, 1831)	Turkey (Adana)	1	NMNHS
<i>Chlaenius</i> (<i>Epomis</i>) <i>duvaucelii</i> (Dejean, 1831)	India (Delhi)	1	coll. EK
<i>Chlaenius</i> (<i>Epomis</i>) <i>nigricans</i> Wiedemann, 1821	India (Dehradun, Delhi), Nepal (Lumbini), Sri Lanka (Polonnaruwa), Indonesia (Lombok)	8	NMNHS, coll. EK
<i>Chlaenius</i> (<i>Haplochlaenius</i>) <i>baehri</i> (Kirschenhofer, 1998)	Indonesia (Sulawesi)	1	SMNS
<i>Chlaenius</i> (<i>Haplochlaenius</i>) <i>costiger costiger</i> Chaudoir, 1856	North Korea (Kumgangsán)	1	coll. EK
<i>Chlaenius</i> (<i>Iberodinodes</i>) <i>dives</i> Dejean, 1826 (s.l.)	Spain	1	NMNHS
<i>Chlaenius</i> (<i>Lissauchenius</i>) <i>borgouensis</i> Kirschenhofer, 2007	Nigeria	2	NMNHS
<i>Chlaenius</i> (<i>Lissauchenius</i>) <i>darfurensis</i> Kirschenhofer, 2007	Sudan (West Darfur)	1	coll. EK
<i>Chlaenius</i> (<i>Lissauchenius</i>) <i>rufifemoratus</i> lynx Chaudoir, 1856	North Korea (Suyangsán Falls)	1	coll. EK
<i>Chlaenius</i> (<i>Nectochlaenius</i>) <i>canariensis seminitidus</i> Chaudoir, 1856	Israel	1	coll. EK
<i>Chlaenius</i> (<i>Nectochlaenius</i>) <i>persicus</i> L. Redtenbacher, 1850	Iran (Shiraz)	1	coll. EK
<i>Chlaenius</i> (<i>Ocybatus</i>) <i>dyrollei</i> (Laferté-Sénéctère, 1851) (s.l.)	Nigeria	2	NMNHS
<i>Chlaenius</i> (<i>Ocybatus</i>) <i>discicollis</i> (Laferté-Sénéctère, 1851)	Nigeria	2	NMNHS
<i>Chlaenius</i> (<i>Pachydinodes</i>) <i>bipustulatus</i> Boheman, 1848	Nigeria	1	NMNHS
<i>Chlaenius</i> (<i>Pachydinodes</i>) <i>pictus</i> Chaudoir, 1856	India (Delhi)	1	NMNHS
<i>Chlaenius</i> (<i>Pachydinodes</i>) <i>posticus</i> (Fabricius, 1798)	Sri Lanka (Polonnaruwa)	4	NMNHS
<i>Chlaenius</i> (<i>Pachydinodes</i>) <i>virgulifer</i> Chaudoir, 1876	India (Delhi)	1	coll. EK
<i>Chlaenius</i> (<i>Pachydinodes</i>) sp.	Sudan (South Darfur)	1	NMNHS
<i>Chlaenius</i> (<i>Pleroticus</i>) <i>buquetii hacquardi</i> Chaudoir, 1883	Zaire (Kisangani)	1	NMNHS
<i>Chlaenius</i> (<i>Prochlaeniellus</i>) <i>senegalensis</i> Dejean, 1831	Sudan (South Darfur), Nigeria	2	NMNHS
<i>Chlaenius</i> (<i>Pseudochlaeniellus</i>) <i>chitwanensis</i> Kirschenhofer, 2005	Nepal (Lumbini)	1	NMNHS
<i>Chlaenius</i> (<i>Rhopalopalous</i>) <i>janthinus</i> L. Redtenbacher, 1844	India (Jammu & Kashmir)	5	NHMUK
<i>Chlaenius</i> (<i>Rhysotrachelus</i>) <i>nepalensis</i> Hope, 1831	Nepal (Betrawati)	1	NMNHS
<i>Chlaenius</i> (<i>Sphodromimus</i>) <i>holzschuhi</i> Casale, 1984	Nepal	1	SMNS
<i>Chlaenius</i> (<i>Stenochlaenius</i>) <i>coeruleus</i> (Steven, 1809)	Turkey (Artvin)	4	NMNHS

APPENDIX 1. — Continuation.

Species and subspecies	countries	specimens collections	
<i>Chlaenius (Tomochilus) alternans</i> (Imhoff, 1843) (s.l.)	Nigeria	2	NMNHS
<i>Chlaenius (Tomochilus) carbonatus</i> Chaudoir, 1876	Senegal, Burkina Faso, Nigeria, Ethiopia	5	NMNHS, coll. EK
<i>Chlaenius (Trichochlaenius) aeneocephalus aeneocephalus</i> Dejean, 1826	Bulgaria	10	NMNHS
<i>Chlaenius</i> (unplaced) <i>rufithorax</i> Wiedemann, 1821	India	2	NHMUK
<i>Grundmannius dispar</i> (Péringuey, 1896)	Mozambique, South Africa	4	CAS, NMNHS
<i>Harpaglossus laevigatus</i> (Dejean, 1828)	“W. Africa”, Senegal	3	NHMUK, SMNS
<i>Harpaglossus opacus</i> (Chaudoir, 1857)	Eritrea, Saudi Arabia, India	7	IZAS, NHMUK
<i>Hololeius ceylanicus</i> (Nietner, 1856)	Sri Lanka, Myanmar, Indonesia (Bali), Australia	19	NMNHS, NHMUK, SMNS
<i>Holosoma hedini</i> (Andrewes, 1935)	China (Gansu)	2	NMNHS
<i>Holosoma weigoldi</i> (Heller, 1923)	China (Sichuan)	3	NMNHS
<i>Lapitachlaenius speculariferus</i> (Fairmaire, 1879) n. comb.	Fiji	17	ANIC, BPBM, NZAC, SAMA
<i>Lapitachlaenius specularis</i> (Emden, 1937) n. comb.	Vanuatu	3	NHMUK
<i>Mirachlaenius barbarae</i> Facchini, 2011	India (Nilgiri Hills)	1	SMNS
<i>Parachlaenius (Parachlaenius) eminus</i> Kolbe, 1894	Uganda, Tanzania (Bukoba)	3	NHMUK, SMNS
<i>Parachlaenius (Parachlaenius) violaceus</i> Péringuey, 1899	“E. Africa”, Zimbabwe	5	NHMUK, SMNS
<i>Proclitodema parallelum</i> Péringuey, 1899	Zimbabwe	3	NHMUK, SMNS
<i>Proclitus minor</i> Basilewsky, 1968	Nigeria (Samaru)	1	NHMUK
<i>Proclitus singularis</i> Péringuey, 1896	Zimbabwe	3	NHMUK, SMNS
<i>Rhopalomelus angusticollis</i> Boheman, 1848	South Africa	6	NHMUK, SMNS
<i>Stenoodes jeanneli</i> Basilewsky, 1953	Madagascar	1	MNHN
<i>Stuhlmannium mirabile</i> Kolbe, 1894	“E. Africa”	1	NHMUK