Zootaxa 5217 (1): 001–064
https://www.mapress.com/zt/

Monograph

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.5217.1.1
http://zoobank.org/urn:lsid:zoobank.org:pub:86CD1EDF-8C38-4A90-888A-185B8481A6ED

ZOOTAXA

5217

Spiky pygmy devils: revision of the genus *Discotettix* (Orthoptera: Tetrigidae) and synonymy of Discotettiginae with Scelimeninae

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Magnolia Press
Auckland, New Zealand

Accepted by R. Mariño-Pérez: 1 Nov. 2022; published: 6 Dec. 2022

JOSIP SKEJO, TARAS I. PUSHKAR, NIKO KASALO, MARKO PAVLOVIĆ, MAKS DERANJA, KARMELA ADŽIĆ, MING KAI TAN, FRAN REBRINA, AMIRA AQILAH MUHAMMAD, NURUL ASHIKIN ABDULLAH, RAZY JAPIR, ARTHUR Y. C. CHUNG & JOSEF TUMBRINCK
SPIKY PYGMY DEVILS: REVISION OF THE GENUS *DISCOTETTIX* (ORTHOPTERA: TETRIGIDAE) AND SYNONYMY OF DISCOTETTIGINAE WITH SCELIMENINAE
(*Zootaxa* 5217)

64 pp.; 30 cm.

6 Dec. 2022

ISBN 978-1-77688-648-7 (paperback)

ISBN 978-1-77688-649-4 (Online edition)

FIRST PUBLISHED IN 2022 BY

Magnolia Press

P.O. Box 41-383

Auckland 1041

New Zealand

e-mail: magnolia@mapress.com

https://www.mapress.com/zt

ISSN 1175-5326 (Print edition)

ISSN 1175-5334 (Online edition)

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Abstract

Spiky pygmy devils (Tetrigidae: Discotettiginae) are, because of the spiky pronotal projections and widened subapical antennal segments, among the most unique pygmy grasshoppers in Southeast (SE) Asia. The taxonomy of the group was unclear in the past, so this study brings a taxonomic and biographical review of the genus *Discotettix* Costa, 1864. New terminology of the pronotal projections is proposed for Scelimeninae. All valid species hitherto included in the genus are redescribed; a new genus is established for *Discotettix shelfordi* Hancock, 1907, *Disconius* Skejo, Pushkar et Tumbrinck **gen. n.**, so a new combination is established for the species (*Disconius shelfordi* **comb. n.**). New synonymy is established: *Discotettix selysi* Bolívar, 1887 = *Discotettix selangori* Mahmood, Idris et Salmah, 2007 **syn. n.** Three new species are described and a key to *Discotettix* species is provided. The genus now includes seven species (1) *Discotettix aruanus* Skejo, Pushkar et Tumbrinck **sp. n.** from Aru; (2) *D. belzebuth* (Serville, 1838) from Borneo; (3) *D. doriae* Bolívar, 1898 **stat. resurr.** from the Mentawai islands; (4) *D. kirscheyi* Skejo, Pushkar, Tumbrinck et Tan **sp. n.** from Northeast (NE) Borneo; (5) *D. scabridus* (Stål, 1877) endemic to Mindanao and Samar; (6) *D. selysi* Bolívar, 1887 from Sumatra and Peninsular Malaysia; (7) *D. sumatrensis* Skejo, Pushkar et Tumbrinck **sp. n.** endemic to southern Sumatra. Moreover, *Discotettix* is again subdivided into two subgenera: *Mnesarchus* Stål, 1877 **stat. resurr.** (*D. scabridus*) and nominotypical one (other species). Widened antennal segments are the only character common to all Discotettiginae genera, but this trait does not have great taxonomic importance, as it is homoplastic, meaning that it appeared in distant Tetrigidae groups independently. *Discotettix* is herewith transferred to the subfamily Scelimeninae and accordingly, the subfamily Discotettiginae Hancock, 1907 **syn. n.** becomes a junior synonym of the subfamily Scelimeninae Bolívar, 1887. The tribe Discotettigini **stat. resurr.**, on the other hand, gathers corticolous genera of the Scelimeninae (*Austrohancockia* Günther, 1938, *Bidentatettix* Zheng, 1992, *Disconius* **gen. n.** *Discotettix, Eufalconius* Günther, 1938, *Gibbotettix* Zheng, 1992, *Paragavialidium* Zheng, 1994, *Gavialidium* Saussure, 1862, and *Tegotettix* Hancock, 1913), while the tribe Scelimenini becomes restricted to amphibious taxa. All taxa are described and amply depicted with both museum specimens and *in situ* photographs. An identification key is provided. The morphology and function of widened antennae in Discotettigini are discussed.

Key words: Scelimenini, Discotettigini, *Disconius, doriae, aruanus, kirscheyi, sumatrensis,* pronotal projections, terminology, new species, flattened antennae, SE Asia, Sundaland, new taxa, new synonymy

Introduction

The small pygmy grasshopper subfamily Discotettiginae (Orthoptera: Tetrigidae) with the type genus *Discotettix* Costa, 1864 was established by Hancock in 1907 to include the genera from the Old World with widened subapical antennal segments, namely *Discotettix* Costa, 1864, *Ophiotettix* Walker, 1871 (=*Tettigodina* Bolívar, 1887), *Arulenus* Stål, 1877, *Hirrius* Bolívar, 1887, and *Phaesticus* Uvarov, 1940 (=*Phaestus* Bolívar, 1887) (Hancock 1907a). The type genus, *Discotettix*, has not been systematically reviewed since Günther (1937; 1938). Currently, only *Arulenus, Discotettix, Hirrius,* and *Kraengia* Bolívar, 1909 are placed in Discotettiginae (Skejo 2017; Zha *et al.* 2021; Cigliano *et al.* 2022). Since the establishment of the subfamily, the shape of the antennal segments has been used as the main and practically the only diagnostic character, treated as an apomorphy, uniting the genera into this subfamily. However, the value of this trait seems to be problematic. According to this character, Discotettiginae are similar to Tripetalocerinae Bolivar, 1887, but differ by the number of antennomeres: 8 in Tripetalocerinae, 11–15 in Discotettiginae; and by their shape, where only subapical antennomeres are considerably widened and flattened in Discotettiginae, while Tripetalocerinae have all the antennomeres except the basal and apical widened and flattened triangularly (Storozhenko 2013, Tumbrinck 2014). There were many problems with Discotettiginae taxonomy (Skejo & Caballero 2016; Skejo & Bertner 2017; Günther 1937, 1938) and many genera were transferred subsequently to other subfamilies. For example, *Ophiotettix* and *Rosacris* Bolívar, 1931 are now assigned to Metrodorinae (Bolívar 1931, Skejo 2016, Tumbrinck & Skejo 2017, Kasalo 2022), while *Phaesticus* Uvarov, 1940 (Liang & Zheng 1984, 1998) currently lacks subfamily placement (Zha *et al.* 2021).

The originally monotypic genus *Discotettix* was established by Costa in 1864 as follows: *"Abito de'Tettix, dai quali principalmente differisce per le antenne, di cui i due articoli che precedono i tre apicali sono compressi e dilatati a foggia di foglioline. Il protorace poi si prolunga al di là del capo in un corno rivolto in sopra, oltre allo essere fornito di molte spine corte e robuste, altre dorsali, altre laterali"*[1]. The genus included a single species,

1 Looks like *Tettix*, mainly differs from it by the antennae, two segments of which [are situated] before the three apical, [are] compressed and dilated in a foliaceous shape. The pronotum extends above the head like a horn [= *frontomedial projection*] directed above,

described in the same paper, *Discotettix armatus* Costa, 1864 (species number "1696", just after *Tettix bufo*). The previously described species *Discotettix belzebuth* (=*Tetrix belzebuth* Serville, 1838) was not mentioned in Costa's paper (until 2016, the reference in Cigliano *et al.* 2022 was wrong). Thus, *Tetrix belzebuth* cannot be the type species of the genus. The type species of the genus is *D. armatus* by monotypy (ICZN, 1999, art. 68.3). The type locality of *D. armatus* is Borneo Island. The species *Tetrix belzebuth* (hitherto believed to be from Java Island) was described by Serville (1838), and the specimen Serville examined had large and long spines (= projections) on the dorsal and lateral surfaces: "*Prothorax dépassant l'abdomen de près de trois lignes, très-rugueux en dessus, fort dilaté sur les côtés antérieurement; ces côtés bordés chacun de trois épines; l'antérieure pointue; la seconde très-petite et obtuse; la troisième plus grande que la première, portée par un appendice ou lame assez large et aplatie: carène médiane peu saillante, chargée de trois gros mamelons, terminés par une épine; les deux premiers rapprochés l'un de l'autre, le troisième éloigné. Disque du prothorax ayant en outre, de chaque côté de la carène, un mamelon analogue à ceux que porte cette dernière; ce disque est bordé antérieurement sur ses côtés, de quelques petites épines, dont la dernière plus grande; bord antérieur du prothorax ayant au milieu, une corne épaisse, droite, cylindrique, bifide au bout, débordant la tête en avant, de plus d'une ligne… Les antennes manquent*"[2]. Blackith (1992) and Otte (1997) noted that the type species of *Discotettix* is *Tetrix* (sic!) *armatus* by subsequent designation by Willemse (1939a or 1939b), while Yin *et al.* (1996) mentioned *Discotettix belzebuth* as the type species of this genus. Willemse (1930) lists *Tetrix belzebuth* as the genotype (type species) of the genus. There is no mention of *Discotettix* in Willemse (1939a; 1939b).

Stål (1877) established the monotypic genus *Mnesarchus* Stål, 1877: «*Tettigi affine genus, antennis prope apicem dilatatis, pronoto dorso tuberculis magis minusve elevatis, inter quae tria vel quattuor in carina media anterius posita, angulis posticis loborum lateralium pronoti productis, acuminatis, margine dentatis vel serratis, distinguendum*»[3]. The genus included a single species, described in the paper, *Mnesarchus scabridus* from the Philippines. True difference between *Discotettix* and *Mnesarchus* was absent from the aforementioned diagnosis of the genus and mentioned only in the description of the *M. scabridus*: tuberculum [*frontomedial projection*] on anterior margin [of the pronotum] small: *"tuberculo ad marginem apicalem posito parvo"*. Willemse (1930) synonymized *Mnesarchus* with *Discotettix*. The first to revise the genus *Discotettix* was Bolívar (1887), who divided the genus into two groups: one with projected anterior pronotal margin (*D. belzebuth* and *D. selysi*), and the other group with truncated anterior margin (*D. scabridus*). Bolívar (1887) noted that all the *D. belzebuth* material he examined came from Borneo, and he did not have any specimens from Java. Bolívar was not sure about the origin of *D. scabridus* because, in his opinion, the nymphs of *D. belzebuth* can be very similar in morphology to *D. scabridus*. Eleven years later, Bolívar (1898) described one more species of the genus—*Discotettix doriae* from Mentawai islands near Sumatra. Günther (1938) synonymized *D. doriae* with *D. selysi*. Hancock (1907b) described *D. shelfordi* from Borneo as a species with a smooth pronotal surface and with a truncated anterior margin of pronotum. According to the characteristics listed for the species, it does not belong to this genus and its true taxonomic position should be ascertained. The last major changes within the taxonomy of the genus were made in 2007 when Mahmood *et al.* described two new species within the genus: *D. adenanii* and *D. selangori*. *Discotettix adenanii* was discussed in Kočárek *et al.* (2015) and synonymized with *D. belzebuth*.

This study aims to redescribe the genus *Discotettix*, present an annotated identification key for *Discotettix* species, and redescribe each species assigned to the genus. Furthermore, we describe three new *Discotettix* species, (1) *D. kirscheyi* Skejo, Pushkar, Tumbrinck et Tan **sp. n.** from Borneo, (2) *D. sumatrensis* Skejo, Pushkar et Tumbrinck **sp. n.** from Sumatra, and (3) *D. aruanus* Skejo, Pushkar et Tumbrinck **sp. n.** from Aru. Finally, we aim to describe a new genus for *D. shelfordi.*

[pronotum] additionally being equipped with many short strong spines, on both dorsal and lateral surfaces.

2 Pronotum surpassing abdomen for about three lines [= 6.4 mm], very rough above, considerably dilated in the anterior part; this part bears all of the three spines; [1] anterior acuminate [= *frontomedial projection*]; [2] second very small and obtuse [= *promedial*]; [3] third larger than the first one [= 1st *metamedial*][;] supported by an appendix or rather large and flattened lamina: slightly prominent medial carina, bearing three big warts, ending in a spine [*medial projections*]; the first two close one to another, the third distant. Disc of the pronotum additionally having on each side carina, wart similar to later [*metalateral projection* of humeral angle]; disc bordered in anterior side by few small spines, the last larger [*frontolateral projections*]; anterior edge of the prothorax with the median, thick horn [*frontomedial projection*], straight, cylindrical, excised at apex, covering head forward for more than one line. Antennae missing.

3 The genus of characters similar to *Tetrix*, antennae near apex widened, dorsal surface of pronotum granulated, more or less raised and wrinkled in three or four places in the anterior part of the medial carina, posterior sides of the pronotal lateral lobes protruded, acuminate, margin dentate or serrate, distinct.

Material and methods

This study is based on a detailed analysis of literature data, type specimens, hitherto published and unpublished museum material, as well as photographs from social networks such as iNaturalist, Facebook, Flickr, ProjectNoah, and eBay. All photographs in this article are used with the permission of their authors. Specimens for the study were photographed using different cameras. Photographs of all type specimens were uploaded to the Orthoptera Species File (Cigliano *et al.* 2022) (abbreviated to OSF further in the text). All the information related to the photographs is written below the figures. Synonymy, type material, type locality, additional examined material, distribution data, and re-description are provided for each species, together with additional notes, when necessary.

Organization of an annotated list. The following information is, where applicable, given for the *Discotettix* species: (i) the name of the species, the figure in which it appears, and the proposed vernacular name; (ii) an overview of the literature regarding the species, including its synonymy and the summary of key points contained in each reference; (iii) the type locality, together with comments elucidating any detected discrepancies; (iv) nomenclatural notes; (v) identification notes; (vi) the lectotype designation; (vii) detailed information on the examined material, separated into sections for the type material, additional physical material, and the material obtained from online social media; (viii) the etymology of the species name (for newly described species); (ix) the updated distribution of the species, together with comments based on literature and novel observations; (x) taxonomic notes based on literature and novel observations; (xi) the specific diagnosis (together with the subgeneric diagnosis in the case of *Mnesarchus*) with an explicit focus on differences between similar species; (xii) the (re)description of the species; and (xiii) the morphometric data.

Museum abbreviations are given as follow:

AMS—Australian Museum, Sydney, New South Wales, Australia;
CJT—Josef Tumbrinck's Collection, Wassenberg, Germany;
FRC—Forest Research Center (Sepilok), Sabah Forestry Department, East Malaysia
MFN—Museum für Naturkunde (Naturkundemuseum or Humboldt-Museum), Berlin, Germany;
MHNG—Muséum d'Histoire Naturelle Geneva, Geneva, Switzerland;
MNCN—Museo Nacional de Ciencias Naturales, Madrid, Spain;
MNHN—Muséum National d'Histoire Naturelle, Paris, France;
MCSN—Museo Civico di Storia Naturale «G. Doria», Genova, Italy;
NCB—Nederlands Centrum voor Biodiversiteit, Leiden, the Netherlands;
NCM—Norwich Castle Museum Collections, Norwich, the United Kingdom;
NHMUK—Natural History Museum, London;
NHRS—Naturhistoriska Riksmuseet, Stockholm, Sweden;
NMNH NASU—National Museum of Natural History, National Academy of Sciences of Ukraine, Kyiv, Ukraine;
OUMNH—Oxford University Museum of Natural History (Hope Ent. Coll.), Oxford, the United Kingdom;
SMTD—Staatliche Naturhistorische Sammlung Dresden, Museum für Tierkunde, Dresden, Germany;
UKM—Universiti Kebangsaan Malaysia, Bangi, Selangor, Malaysia;
ZISP—Zoological Institute of the Russian Academy of Sciences, St.-Petersburg, Russia;
ZFMK—Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany;
ZMUH—Zoologisches Museum Hamburg, University of Hamburg, Hamburg, Germany;
ZRC—Zoological Reference Collection, Lee Kong Chian Natural History Museum, Singapore

Taxonomy and nomenclature. Taxonomy follows Cigliano *et al.* (2022). Nomenclature agrees with the International Code of the Zoological Nomenclature (ICZN 1999).

Morphological terminology.

For each part of the body, it is denoted which studies presented an informative terminology followed in the current study. Joint descriptions of the species' characters for both males and females are given, and if there are differences between the sexes, these are noted in the text.

Antennae (Fig. 1). Terminology follows the work of Kuřavova *et al.* (2017), which examined the *Discotettix belzebuth* antennae in detail. The terminology is used in this study as follows: 1st antennomere scapus, 2nd antennomere pedicel, 3rd to 6th basal antennomeres of the flagellum, 7th and 8th central or subapical antennomeres of the flagellum, 9th enlarged apical antennomere, and 10th to 13th reduced apical antennomeres of the flagellum (usually the borders not well visible under the stereomicroscope, easily discernible seen under SEM; Kuřavova *et al.* 2017). The terminology of the *Discotettix* antennae shown in Skejo (2017: Fig. 15) is undoubtedly wrong, as too many basal segments were suggested to exist.

Head. Terminology follows Tumbrinck (2014) with updates from Muhammad *et al.* (2018).

Pronotal carinae. Terminology follows Devriese (1991), updated in Devriese (1999) and with changes made by Tumbrinck (2014).

Pronotal projections (Fig. 2)**.** Herewith we present a new terminology for the pronotal projections (protuberances) based on their location on the pronotal surface relative to the pronotal carinae (Fig. 2). There are two groups of projections, the **dorsal group** on the surface of the pronotal disc, and the **marginal group** on the margins of the pronotum. The dorsal group contains ***medial projections*** on the medial pronotal carina, and ***mediolateral projections*** on both sides of the pronotal disc, between the medial and lateral carinae. The marginal group consists of ***frontal projections*** on the anterior margin of the pronotum, and ***lateral projections*** on the extralateral, humero-apical, external lateral carinae, and ***ventrolateral projections*** **(VL)** on the ventral margin of the pronotal lateral lobes (paranota). Projections are furthermore divided into **prozonal** and **metazonal**. The prozona ends approximately where the humero-apical and interhumeral carinae begin, and the mentioned carinae are situated in the frontal part of metazona, strictly caudad to the last ***promediolateral*** (**PML**) projection. The **frontal group** includes the ***frontomedial*** (**FM**), and three pairs of ***frontolateral*** (**FL**) projections (**FL1, FL2, FL3)**. The **medial group** includes ***promedial*** (**PM**) projections in the prozona and four ***metamedial*** (**MM**) projections in the metazona (**MM1**, **MM2**, **MM3**, **MM4**). The **mediolateral group** includes two pairs of ***promediolateral*** (**PML**) projections in the prozona and five pairs of ***metamediolateral*** (**MML**) projections in the metazona. The **lateral group** includes two pairs of ***prolateral*** (**PL**) ***projections*** in the prozona (**PL1**, **PL2**) and ***metalateral*** (**ML**) projection(s) or a tubercle on the humeral angles. The ***ventrolateral projection*** (**VL**) is the projected part of the lateral lobe.

Legs. Terminology follows Tumbrinck (2014) with updates from Muhammad *et al.* (2018).

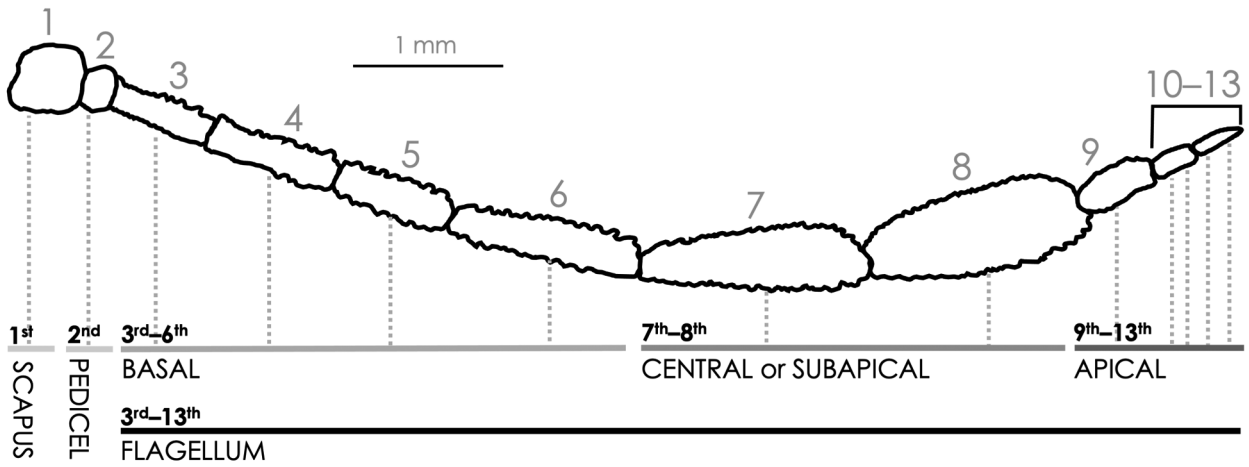

FIGURE 1. *Discotettix belzebuth* (Serville, 1838), morphology of antennae. The first segment is scapus, the second is pedicel, and the rest are flagellum antennomeres. Drawing by Josip Skejo after the figure in Kuřavova *et al.* (2017). Scale bar = 1 mm.

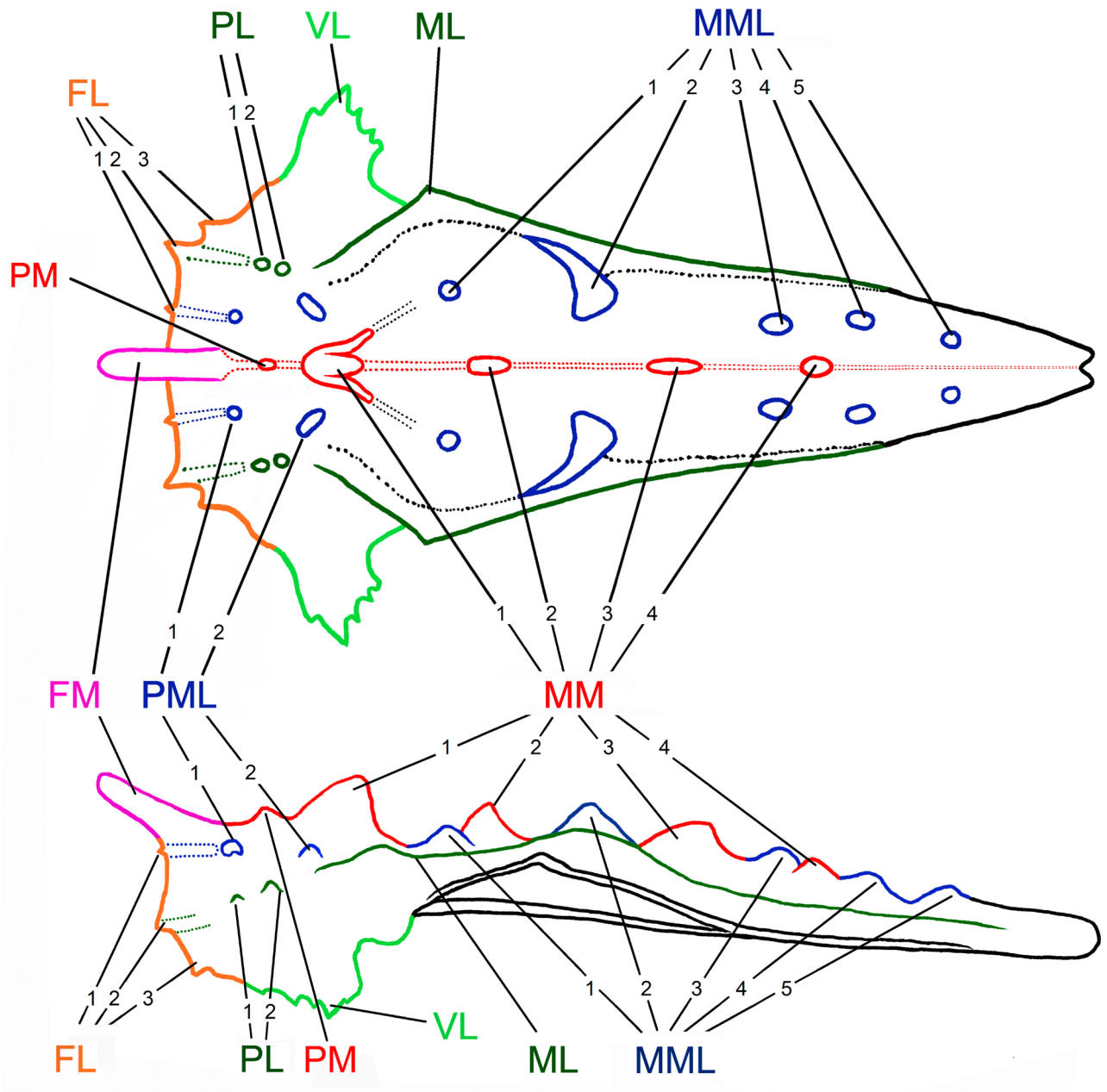

FIGURE 2. *Pronotum* projections of *Discotettix sumatrensis* Skejo, Pushkar et Tumbrinck **sp. n.** numbered and named according to the proposed terminology: FL1—first frontolateral, FL2—second frontolateral, FL3—third frontolateral, FM—frontomedial, ML—metalateral, MM1—first metamedial, MM2—second metamedial, MM3—third metamedial, MM4—fourth metamedial, MML1—first metamediolateral, MML2—second metamediolateral, MML3—third metamediolateral, MML4—fourth metamediolateral, MML5—fifth metamediolateral, PL1—first prolateral, PL2—second prolateral, PM—promedial, PML1—first promediolateral, PML2—second promediolateral, and VL—ventrolateral.

Measurements. Measurements were performed in ImageJ software (Wayne Rasband, Research Services Branch, National Institute of Mental Health, Bethesda, MD, USA) after manual calibration with millimeter paper. All measurements are given in millimeters. Abbreviations used for the measurements and indices of the species are given alphabetically:

AnL—antenna length;

AgW—antennal groove width;

As-L/W—widest antennal segment length/ width;

BL—body length (from the frontal costa to the apex of the subgenital plate);

EW—compound eye width;
fFL—fore femur length;
fFW—fore femur width;
hFL—hind femur length;
hFW—hind femur width;
mFL—mid femur length;
mFW—mid femur width;
OvL—ovipositor length;
PnL—pronotum length;
PnW—pronotal width (max., between the lateral lobes);
PrzW—prozona width (between extralateral carinae);
PrzL—prozona length (including frontal projection);
ScW—scapus width;
SW—frontal ridge (= scutellum) width;
T1L/T3L—hind femur: first tarsal segment length / third tarsal segment length;
TL—tegmen (visible part) length;
TW—tegmen (visible part) width;
VW—vertex width.

Results

Taxonomy

Family Tetrigidae Rambur, 1838

Subfamily Scelimeninae Bolívar, 1887

Discotettiginae: Steinmann 1970, Storozhenko 2013, Tumbrinck 2014, **syn. n.**
Discotettigiae: Hancock 1907a, Hancock 1907b, Willemse 1930, Günther 1938, **syn. n.**
Discotettinae: Otte 1997, Mahmood *et al.* 2007, **syn. n.**
Discotettigidae: Liang et Zheng 1998, Zheng 2005, Deng *et al.* 2007, **syn. n.**

Notes. Herewith proposed definition of Scelimeninae is different from recent literature. Bolívar (1887) created the section (now subfamily) to include all Tetrigidae species with outwardly directed spines. Günther (1938) defined two groups within Scelimeninae—1) "Scelimenae verae" to include what are now Scelimeninae, i.e., the genera related to the type genus *Scelimena*, and 2) "Scelimenae spuriae" to include genera with lateral spines that are not closely related to the genus *Scelimena*. These "Scelimenae spuriae" are what we know today as tribes Criotettigini and Thoradontini. Kevan (1966) was the one to create the tribes Scelimenini, Thoradontini, Discotettigini, and Criotettigini. Thoradontini and Criotettigini were already then (Kevan 1966) defined as tribes for the taxa from the heterogeneous genera of section "Scelimenae spuriae". Adžić *et al*. (2020) confirmed the existence of two related tribes, Thoradontini and Criotettigini, which do not belong to Scelimeninae. The current definition of Discotettigini is very different from the Kevan's (1966) definition, which was unfortunately based on a very partial list of genera by Günther (1955), so it may be regarded as the start of a highly chaotic taxonomy in Otte (1997) and later in Orthoptera Species File (Cigliano *et al.* 2022). Criotettigini and Thoradontini require revision and might be synonymous. Liang & Zheng (1998) and consequent Chinese authors ignored the taxonomic treatment by Kevan (1966), which we regard as useful, as far as the genera related to the type genus are included in the tribe. Muhammad *et al.* (2018) provided the most recent treatment for Scelimeninae: Scelimenini, which we follow in this paper.

Composition and distribution (sensu Günther 1938, with additions from Muhammad *et al.* 2018). The subfamily currently counts 180 species within 23 genera. The tribe Scelimenini includes amphibious Asian and Papuan taxa with flat pronotum (genera *Amphibotettix* Hancock, 1906, *Euscelimena* Günther, 1938, *Indoscelimena* Günther, 1938, *Paramphibotettix* Günther, 1938, *Platygavialidium* Günther, 1938, *Scelimena* Serville, 1838, *Tagaloscelimena* Günther, 1938, and *Tefrinda* Bolívar, 1906), while the tribe Discotettigini **stat. resurr.** gathers

Asian and Papuan corticolous taxa with undulated pronotum (genera *Austrohancockia* Günther, 1938*, Bidentatettix* Zheng, 1992, *Disconius* Skejo, Pushkar et Tumbrinck, **gen. n.** *Discotettix* Costa, 1864, *Eufalconius* Günther, 1938, *Gavialidium* Saussure, 1862, *Gibbotettix* Zheng, 1992, *Kraengia* Bolívar, 1909, *Paragavialidium* Zheng, 1994, *Tegotettix* Hancock, 1913). Genera *Zhengitettix* Liang, 1994, *Hebarditettix* Günther, 1938, *Falconius* Bolívar, 1898, and *Dengonius* Adžić, Deranja, Franjević et Skejo, 2020 are of uncertain position within Scelimeninae, while *Arulenus* Stål, 1877 and *Hirrius* Bolívar, 1887 do not belong to this subfamily and should be removed from it, thus remaining without subfamily assignment for now.

Tribe Discotettigini Hancock, 1907 stat. resurr.

Discotettigiae: Hancock 1907a: 5; 1907b: 213; Willemse 1930: 4, 7; Günther 1938: 301.
Discotettigini: Kevan 1966: 380.
Discotettiginae: Steinmann 1970: 216; Storozhenko 2013: 158; Tumbrinck 2014: 349.
Discotettinae: Otte 1997: 32; Mahmood *et al.* 2007: 1275.
Discotettigidae: Liang & Zheng 1998: 23; Zheng 2005: 15; Deng *et al.* 2007: 400.

Type genus: *Discotettix* Costa, 1864.

Differential diagnosis. The tribe Discotettigini is a sister tribe to Scelimenini; their representatives share many apomorphies inherited from the common ancestor. The main difference is the shape of the pronotum (elongated, flat, and hydrodynamic in Scelimenini; and robust, wrinkled, and cryptic in Discotettigini; Rebrina *et al.* in preparation), as well as the shape of the fore and mid femora (elongated in Scelimenini, short and toothed in Discotettigini), and the shape of the hind tibia and tarsi (widened into a paddle in Scelimenini, while of regular shape in Discotettigini). Scelimenini members have shorter projections of the pronotal disc in comparison to Discotettigini members. Discotettigini are mostly corticolous, and Scelimenini members are mostly amphibious grasshoppers (e.g., Muhammad *et al*. 2018).

Description. Head. Antenna with 11–15 antennomeres, filiform or with widened preapical segments (Fig. 1). Frontal costa visible above the bifurcation; the bifurcation and the lateral ocelli placed low, between the compound eyes, in line with the lower margin or visibly below the compound eye; the antennal groove located below the lower margins of the compound eyes; lateral carinae of the vertex more or less elevated; anterior margin of the vertex truncated, slightly indrawn from the level of the outer margin of the compound eyes; fossula present; medial carina of the vertex visible in the upper third cephalad (Fig. 5C).

Pronotum. Prozonal, extralateral, median, humeral and lateral carinae present; interhumeral carinae present, but sometimes not visible because of the pronotal projections in their place. Pronotum strongly granulated and wrinkled, armed with numerous strong projections (**FM**, **FL**, **PM**, **MM1**, **MM2**, **MML1, MML2**, and **ML**) that can be of different shapes and sizes: low, high, and wart-like or high triangular, saw-like, or spine-like protuberances. Paranota triangular, laterally projected, usually bearing strong **VL** projection, sometimes without a spine (Figs 2, 5A, B).

Legs. Dorsal and ventral margins of all the legs with small, medium-sized, or large teeth. Tibiae rectangular in cross-section, not widened into the paddles. The dorsal margin of the fore and mid femora carinated. Hind tarsi not widened into a paddle (Fig. 29B).

Composition and distribution. The tribe gathers corticolous Scelimeninae genera with an undulated pronotum, and without widened hind tibiae. Altogether, 10 genera and 68 species are herewith assigned to this tribe, and these are *Austrohancockia* (19 species in PR China, China, and Taiwan), *Bidentatettix* (2 species in PR China), *Disconius* **gen. n.** (1 species in Borneo) *Discotettix* (7 species in Peninsular Malaysia, Sumatra, Borneo, Mindanao, Aru), *Eufalconius* (1 species in Peninsular Malaysia), *Gavialidium* (2 species in Sri Lanka and Southern India), *Gibbotettix* (13 species in PR China), *Kraengia* (1 species in Sulawesi), *Paragavialidium* (14 species in PR China), and *Tegotettix* (8 species in Indochina, Borneo, Philippines, Sulawesi, New Guinea) (Muhammad *et al.* 2018, this study).

Genus *Discotettix* Costa, 1864

Discotettix: Costa 1864: 59; Bolívar 1887: 306; Rehn 1904: 670; Hancock 1907a: 6; Hancock 1907b: 213; Kirby 1910: 2; Willemse 1930: 7; Steinmann 1970: 216; Blackith 1992: 46; Yin *et al.* 1996: 866; Otte 1997: 32; Mahmood *et al.* 2007: 1275; Kočárek *et al.* 2015: 288–294.

Mnesarchus Stål, 1877: 55; synonymized with *Discotettix* by Bolívar (1887).

Type species: *Discotettix armatus* Costa, 1864, by original monotypy, a junior synonym of *Discotettix belzebuth* (Serville, 1838).

Nomenclatural note. Many authors recently treat *tettix* as a noun originally of feminine gender. It is incorrect, as in all the Ancient Greek dictionaries the noun "*tettix, tettigos* or *tettikos, ʰo"* is of masculine gender. The word "*tetrix, tetrigos, ʰe"* is however of feminine gender in Ancient Greek. Latreille (1802) introduced the name *Tetrix* (vernacular tétrix), but did not explain why he used the Ancient Greek name of a bird (*tetrix* is the Ancient Greek name of the Pipit, still present in the name of the Black Grouse *Tetrao tetrix*). Since then, the name Grouse Locust has been coined in the US, while the vernacular name pygmy grasshoppers has become more widely used. Even if Latreille did not want to relate pygmy grasshoppers to the bird and randomly invented the word "*tetrix*", he used the word as feminine gender, which has to be followed (ICZN 1999, Art. 30.1.4.2). *Tettix* is a masculine Ancient Greek word for grasshopper, introduced by Berthold (1827) as an (unjustified) emendation of Latreille's name. The epitheta of all the Tetrigidae species whose genus is coined out from the word *tettix* should be in the grammatic masculine gender.

Diagnosis. The genus can be distinguished from all the other genera by the following set of characters: (I) frontal costa bifurcates between the lower third of the compound eye height (bifurcates below the lower third in other Discotettigini), (II) scutellum narrower than scapus (of the same width or wider in *Gavialidium, Paragavialidium,* and *Tegotettix*), (III) antenna 13-segmented (15-segmented in *Gavialidium, Paragavialidium,* and *Tegotettix*), (IV) subapical antennal segments widened (filiform in most of Discotettigini), (V) margins of the antenna saw-like (smooth in most of other Discotettigini).

Comparison to former Discotettiginae genera. Among the former Discotettiginae genera (see Skejo 2017) the genus is similar to *Kraengia* and certain members of the genus *Hirrius*, i.e., *H. montanus* Günther, 1937 and *H. sarasinorum* Günther, 1937 from Sulawesi. *Discotettix* is similar to *Kraengia* in the general arrangement of pronotal protuberances (**FM**, **FLs**, **MM**, **ML**). However, in *Discotettix* the lower part of the lateral pronotal lobe is directed outwards forming a spine-like **VL** projection, while in *Kraengia* the lower part of the lateral pronotal lobe has a truncated margin. **ML** is more or less distinct in *Discotettix* species, while fully reduced in *Kraengia,* the humeral angle being obtuse. Additionally, *Discotettix* can be distinguished from *Kraengia* by the following set of characters: (1) 13 antennal segments (11 in *Kraengia*), (2) large body size (more than 11 mm in *Discotettix*, less than 9 mm in *Kraengia*), (3) presence of tegmen and wing in all *Discotettix* species (*Kraengia* is wingless), and (4) distinct prozona with carinae (in *Kraengia* prozona is very short and carinae are usually not distinct). *Discotettix* can be distinguished from *Hirrius montanus* and *H. sarasinorum* by the following characteristics: (1) dorsal surface of the pronotum with protuberances and projections (in *Hirrius* the pronotum is almost flat, medial, mediolateral, and lateral projections are considerably reduced in size, hump-like or fully absent); (2) the lower part of the lateral lobe of the pronotum forms a sharp spine-like or saw-like **VL** projection (**VL** spine wanting or weak in *Hirrius*); (3) tegmen and wing visible (not visible in *Hirrius*).

Comparison to similar Scelimeninae: Discotettigini genera. The genus is morphologically similar to other Discotettigini genera, especially winged *Bidentatettix, Disconius* **gen. n.**, *Gavialidium, Eufalconius, Paragavialidium*, and *Tegotettix*. Of all the mentioned genera, *Discotettix* is most similar to *Disconius*. From all the genera except for the *Disconius*, *Discotettix* can be easily distinguished by the widened antennomeres, while from *Disconius* it can be distinguished by the visible FM (reduced in *Disconius*), by tuberculated median carina (continuous in *Disconius*) and by strong FLs (almost absent in *Disconius*).

Redescription of the genus *Discotettix*

General features. Medium and large sized species, robust in appearance. All the surfaces rough and granulated, rugose; pronotal disc wrinkled with numerous small tubercles and protuberances of different sizes and shapes. Macropronotal.

Coloration. Body color dark brown, ferruginous brown, or with brighter tints of brown; pronotal projections darker or differently colored than the rest (e.g., reddish or yellowish). Antenna black or dark brown, sometimes with pale-colored joints between the segments or with yellowish apical segments. Maxillary palpi dark brown, sometimes with darker distal margins of the last segment, or black with pale-colored joints between the segments. The visible part of the tegmen dark brown without spots. Legs dark brown except more or less distinct pale rings on tibia and tarsi and whitish 1st tarsal pads.

Head. Head not elevated above the pronotum *in lateral view*. *In dorsal view,* the fastigium of the vertex considerably broader than a compound eye; the anterior margin of the fastigium truncated, widely excised, with protruded medial carina of the vertex, reaching not far from the anterior margin of a compound eye. *In frontal view*, the vertex slightly concave, indrawn from the considerably raised lateral carinae on the level of the upper margin of a compound eye; the medial carina of the vertex distinct in the anterior part of the vertex. Fossula present. Supraocular lobe absent. Lateral ocelli at the level of lower margin or between the compound eyes. Median ocellus far below the level of the lower margin of a compound eye, just between the facial carinae in the place where they end. Antennal groove just above the median ocellus, below or on the level of the lower margin of a compound eye. Frontal costa narrow, with the bifurcation a bit above or between the lateral ocelli. Frontal costa bifurcates into slightly divergent facial carinae forming a narrow scutellum, in lateral view with two concavities: the first large between the lateral ocelli and the second smaller below the antennal grooves. Maxillary palpi flattened. Compound eye in frontal view subglobular, in lateral and dorsal view drop-like, not protruding above the pronotum in lateral view. The occipital area between the eye and the anterior margin of the pronotum narrow, partly visible (more often not) from above (Fig. 5C). Antenna 13-segmented (but in male looks like 12-segmented, because 13th segment very small and not visible under an optical microscope, only under SEM). Antennal segments as follows: 1st massive scapus; 2nd large pedicel; 3th to 6th basal elongated antennomeres; 7th and 8th central or subapical antennomeres, widened; apical 9th small; 10th to 13th apical segments small, very reduced in comparison to others (Fig. 1).

Pronotum. Pronotum wrinkled and granulated, covered by numerous small tubercles and larger projections. Posterior process of the pronotum slender, surpassing the hind knee for about a half of the hind femur length or more (macropronotal); covering the whole abdomen. Disc of pronotum: 1) more or less depressed behind the well-developed shoulder and gradually descending backward, or 2) almost at the same level along all length, without distinct depression behind the shoulder, and not descending backward. General arrangement of pronotal disc projections: pronotum with 4–7 unpaired projections of variable size on the medial carinae (**FM** and 3–6 *medial projections*); 1–3 pairs of **FL** projections; 1–7 pairs of more or less distinguished *mediolateral projections*; 1–3 pairs of *lateral* and a pair of more or less distinct **VL** (better seen in profile). In some species, some of the projections lacking or reduced. Prozona subsquare or wider than long (not taking into account **FM**). Anterior margin of pronotum truncated or projected, with a small or a large **FM** directed mainly upwards or forwards, sometimes covering a part of or the whole vertex. Prozonal and extralateral carinae in the prozona distinct, more or less elevated, surpassing the anterior margin of the pronotum as dentiform **FL1** and **FL2**, where **FL2** more distinct. **FL3** dentiform, small and weak, sometimes indistinct. Median carina behind FM extended along the whole length of the pronotum, with 3–6 unpaired *medial* projections[4] of variable size, more or less distinct (seen very well in profile). **PM** small and triangular. **MM1** large and triangular. **MM2**, **MM3,** and **MM4** decreasing in size towards the apex of the pronotum (sometimes **MM3** and **MM4** reduced). **MM5** present only in a few specimens of *D. belzebuth*. Usually, 1–7 pairs of the mediolateral projections increase in size towards MML1 (largest) and then decrease towards the tip of the pronotum (**PML1**<**PML2**<**MML1**>**MML2**>**MML2**>**MML4**>**MML5**). **PML1** more or less distinct; **PML2** distinct; **MML1** small; **MML2** large; **MML3**, **MML4,** and **MML5** small, decreasing caudad (sometimes 1–3 of these posterior projections reduced). **PL1** and **PL2** small and triangular. **ML** more or less sharp, usually projected outwards. Interhumeral carinae indistinct, weak. External lateral carinae raised upwards above the base of the tegmen, in the posterior half smooth, not reaching the apex of the pronotum. Internal lateral carinae smooth, weak, usually indistinct. The infrascapular area triangular, as wide as the mid femur, fused to the lateral area. Lateral area narrower than the infrascapular and running towards the apex of the pronotum. The apex of the posterior pronotal process in the dorsal view shallowly excised or rounded. Hind margin of the pronotal lateral lobe bisinuate, ventral sinus deep, tegminal sinus small. The lower part of the lateral lobe with serrate anterior and posterior margins. **VL** elongated as spine-like, directed strongly outwards, sometimes forward or even slightly backward, but never downward (Figs 2, 5A, B).

4 The description of medial, mediolateral and lateral projections is given in the order from the anterior to the posterior part of the body.

Wings. The visible part of the tegmen oval and elongated. Hind wing with scalloped inner margin, usually shorter than the pronotal process, not reaching its apex.

Legs. Femora robust, compressed laterally; with smooth or rough surface; dorsal and ventral margins finely or roughly serrate (Fig. 29B); genicular teeth visible on the knees; additional one to three teeth present on each margin. Fore and mid tarsi with distal segments longer than the proximal ones. Both sides of the upper margin of the hind femur finely serrated with distinct or indistinct lappets. Lateral area of the hind femur bears weak carinae with net-like elevations and outgrowths, especially on the ventro-external carina. Genicular teeth equal to or larger than the antegenicular. Hind tibia in dorsal view very slightly widened in basal and apical part. Both sides of the dorsal margin of the hind tibia finely serrated, usually with a few outer and large inner teeth. 1st tarsal segment of the hind leg longer than 3rd (without claws); 1st and 2nd basal pads of 1st tarsal segment short and triangular, 3rd (apical) elongated (Fig. 1).

Abdominal apex. Male subgenital plate in ventral view triangular, longer than wide (Fig. 31A, B). Female subgenital plate in ventral view subsquare. Ovipositor elongated or robust. Valves of the ovipositor narrow, serrate (Fig. 31C, D). Epiproct in females as long as wide near the base, apex pointed. Cerci conical with narrowly rounded apex.

Composition and classification. The genus *Discotettix* is divided into two subgenera: (1) nominotypical *Discotettix* (type species *D. armatus* = *D. belzebuth*) characterized by a long FM projected over the vertex; and (2) *Mnesarchus* Stål, 1877 **stat. resurr.** (type species *Mnesarchus scabridus* = *Discotettix scabridus*) characterized by a minute FM, not projected over the vertex. The subgenus *Discotettix* includes six species. One species formerly assigned to *Discotettix,* that is *D. shelfordi*, has been transferred to a new genus, *Disconius* Skejo, Pushkar et Tumbrinck **gen. n.** The distribution of all the species is presented in Fig. 3.

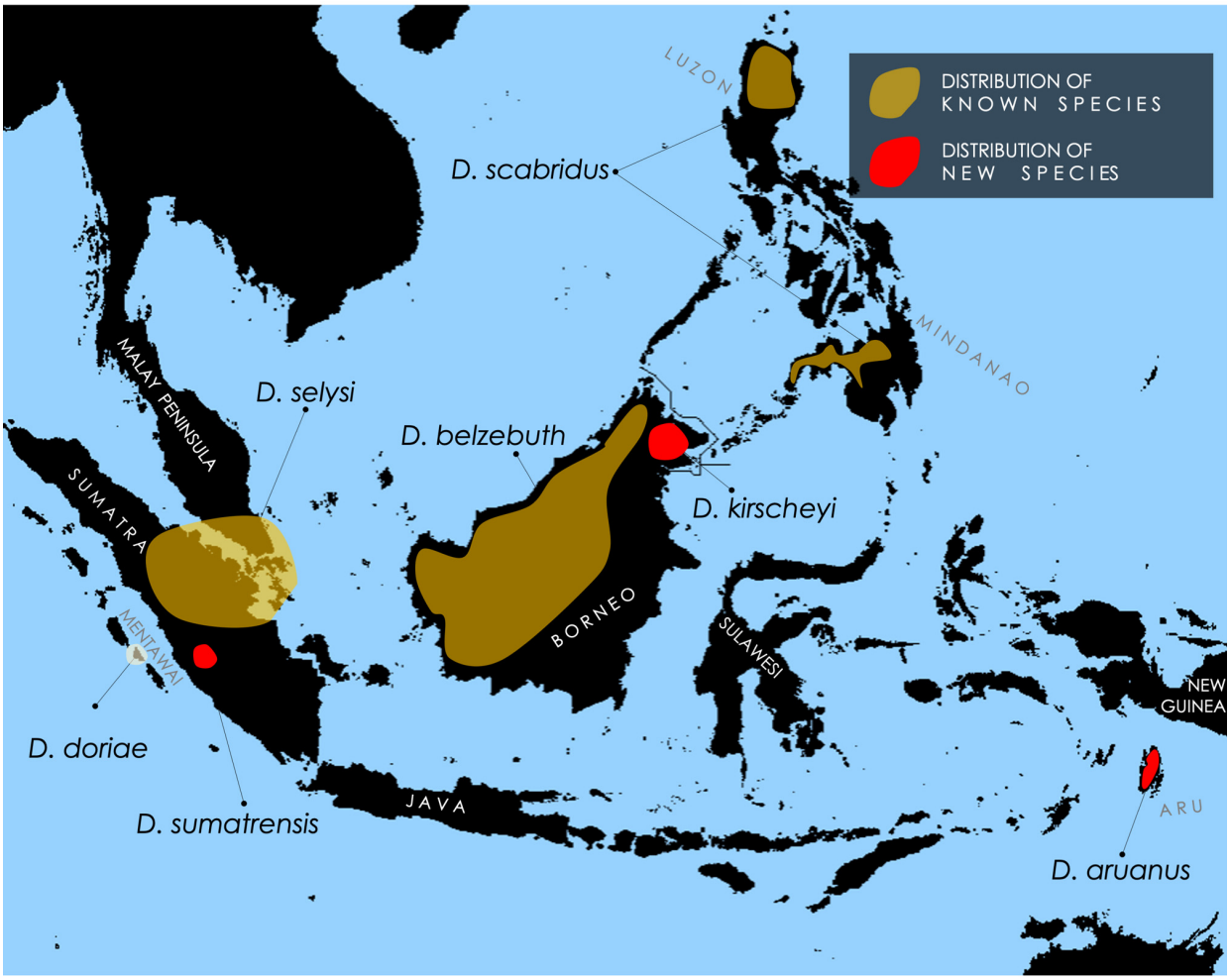

FIGURE 3. Distribution map of *Discotettix* species.

The annotated checklist of *Discotettix* species

1) *Discotettix (Discotettix)* ***aruanus*** Skejo, Pushkar et Tumbrinck **sp. n.** [Aru: Tanahbesar],

2) *Discotettix (Discotettix)* ***belzebuth*** (Serville, 1838) [Borneo, Java(?)],

3) *Discotettix (Discotettix)* ***doriae*** Bolívar, 1898 **stat. resurr.** [Mentawai: Sipora],

4) *Discotettix (Discotettix)* ***kirscheyi*** Skejo, Pushkar, Tumbrinck et Tan **sp. n.** [Northeastern Borneo],

5) *Discotettix (Discotettix)* ***selysi*** Bolívar, 1887 [Peninsular Malaysia, Sumatra],

6) *Discotettix (Discotettix)* ***sumatrensis*** Skejo, Pushkar et Tumbrinck **sp. n.** [Southern Sumatra],

7) *Discotettix (Mnesarchus)* ***scabridus*** (Stål, 1877) [Philippines: Mindanao, Samar].

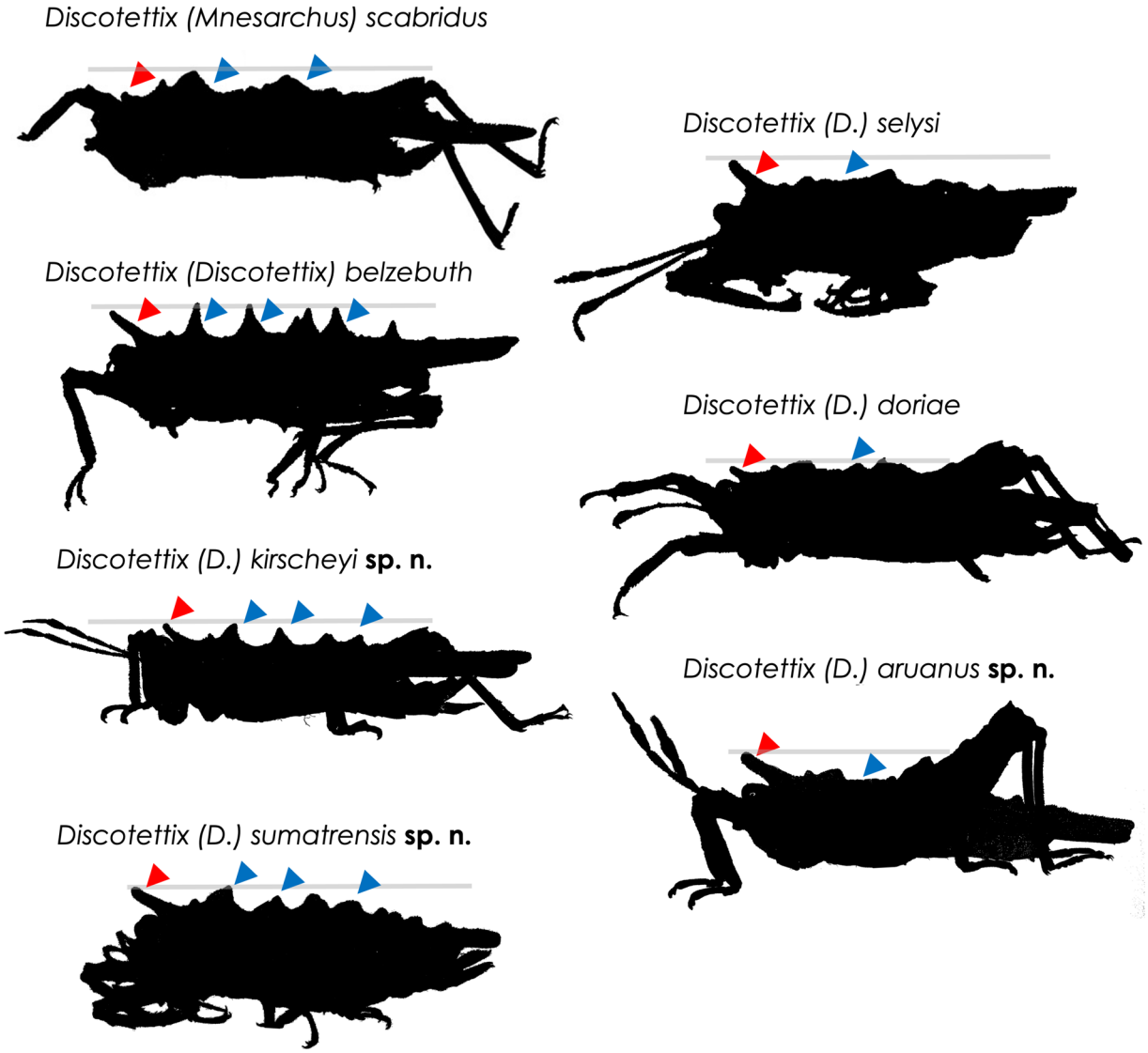

FIGURE 4. The silhouettes of *Discotettix* species. The silhouettes are not to scale. The red arrow points to FM (frontomedial projection of the anterior margin of the median carina of the pronotum), while blue arrows point to the morphology of the dorsum (only one arrow if the dorsum is flattened, while more arrows show projections to be compared).

A key for the identification of *Discotettix* subgenera and species (Fig. 4)

1A) FM not projected above the vertex in lateral view (red arrow in Fig. 4). Shoulders unarmed. (Subgenus *Mnesarchus*). The Philippines. . . . . ***D.* (*M.*) *scabridus***
1B) FM projected above the vertex in lateral view (red arrow in Fig. 4). Shoulders armed with ML. (Subgenus *Discotettix*). **2**

2A) Dorsum of the pronotum with high projections, as high or almost as high as the FM (compare the grey line in Fig. 4). 3
2B) Dorsum of the pronotum flattened, usually no projection higher than the FM (gray line in Fig. 4, exception is *D. doriae* where FM is reduced). **5**

3A) FM small (red arrow in Fig. 4). Dorsum of the pronotum with triangular projections (blue arrows in Fig. 4). Widest antennomere 8th. NE Borneo . . . . . ***D.* (*D.*) *kirscheyi* sp. n.**
3B) FM large (red arrow in Fig. 4) **4**

4A) Dorsum of the pronotum with high spikes (blue arrows in Fig. 4). Widest antennomere 8th. Borneo . . . . . ***D.* (*D.*) *belzebuth***
4B) Dorsum of the pronotum with triangular projections (blue arrows in Fig. 4). Widest antennomere 7th. Sumatra. . . . . . ***D.* (*D.*) *sumatrensis* sp. n.**

5A) FM small, not exceeding the head (red arrow in Fig. 4). Mentawai Isl . . . . . ***D. (D.) doriae***
5B) FM large, directed more upwards than forwards, usually not exceeding the head (red arrow in Fig. 4). **6**

6A) Larger species, pronotum length more than 20 mm in females. PM and MM1 lower and more oblique. Sumatra, Peninsular Malaysia. . . . . ***D.* (*D.*) *selysi***
6B) Smaller species, pronotum length less than 17 mm in females. PM and MM1 elevated and more triangular. Aru Isl.. . . . . ***D.* (*D.*) *aruanus* sp. n.**

An annotated list of subgenera and species with descriptions of new taxa

Subgenus *Discotettix* Costa, 1864

Discotettix (as nominotypical subgenus): Kevan 1966: 380.

Taxonomic notes. Two previously synonymized genera, *Discotettix* and *Mnesarchus*, have been recognized as distinct subgenera by Kevan (1966) and we agree with such a decision. Type species, synonymy, and description of nominotypical subgenus are given under the genus *Discotettix* (see above). The differences from the subgenus *Mnesarchus* are given below.

Composition. The nominotypical subgenus consists of six species, three of which are described below.

Discotettix (Discotettix) belzebuth (Serville, 1838) (Figs 5–14)

Vernacular name: Bornean Spiky Pygmy Devil

Tetrix belzebuth Serville, 1838: 759 [original description, type locality: originally Java but actually probably Borneo].
Tettix belzebuth: Stål 1873: 152 [listed in the catalog].
Discotettix belzebuth: Bolívar 1887: 306 [included in the revision]; Rehn, 1904: 670 [new records]; Hancock 1907a: 6 [included in the revision]; Hancock 1907b: 213 [new records]; Kirby 1910: 2 [included in the catalog]; Hancock 1913: 39 [new records]; Willemse 1930: 8 [new records]; Günther 1938: 301 [included in the revision]; Steinmann 1970: 216 [listed in the catalog]; Blackith 1992: 46 [listed in the catalog]; Yin *et al.* 1996: 866 [listed in the catalog], Otte 1997: 32 [listed in the catalog], Kočárek *et al.* 2015: 289 [new records, data on variability]; Kuřavova *et al.* 2017: 120–128 [data on the antennae morphology]; Tan & Wahab 2018: 123 [new records in Brunei Darussalam].
Discotettix armatus Costa, 1864: 59 [original description, type locality: Borneo]; synonymized by Bolívar (1887).
Discotettix adenanii Mahmood *et al.,* 2007: 1276 [original description, type locality: Borneo: Kuching]; synonymized by Kočárek *et al.* (2015).

Type locality. According to the original description the type locality is Java, but since no locality label is present under the holotype (the only found specimen originating from Serville's collection in MNHN), we believe that the specimen originates from Borneo, from where the majority of the records of this species are. In MNCN, there are four specimens labeled 'Java' so it is not fully clear whether this species is/was present on Java. Borneo Island is the

type locality of *D. armatus*, which is the type species of the genus *Discotettix* (a junior synonym of *D. belzebuth*). The type specimen of *D. belzebuth* was considered lost, but was found in March 2016 by JS in MNHN. For *D. armatus,* we believe that the specimen still exists in the Naples collection (Italy), but we were not able to contact the Museum or to get information on Costa's collection.

Material examined.

Type material. HOLOTYPE of *D. belzebuth* 1♀ (locality, date and collector labels missing), red label 'TYPE' and Günther's label '*Discotettix belzebuth* Serv. K. Günther det.' present (MNHN); **PARATYPE of *D. adenanii*** 1♂ Malaysia: Sarawak: "Adanan Bukra", Gunung Serapi 3.VI.1988. (UKM) (according to Kočárek *et al.* (2015) the holotype and the rest of the type series has probably been destroyed).

Additional museum material. 2♀♀, 1♂ **Borneo: Malaysia**: **Sarawak**: Mattang Collector Frivaldsky, det. J. Skejo (MNCN); 1♀, 2♂♂ Borneo: Malaysia: Sarawak Collector Mjöberg, det. J. Tumbrinck (NHRS); 1♀ Borneo: Malaysia: Sarawak: Bidi 1908. Collector. C. J. Brooks, det. J. Tumbrinck (NCM); 1♂ Borneo: Malaysia: [Sarawak, Bidi] Collector: C. J. Brooks, det. J. Tumbrinck (NCM); 1♀ Borneo: Malaysia: Sarawak: 75 km S of Miri Town, Niah Nat. Park [100 m a.s.l., forest around Niah Great Cave] 30.III.2012. Collectors A.V. Gorochov and M. Berezin, det. J. Skejo et T. Pushkar (ZISP); 2♀♀ **Borneo: Malaysia: Sabah**: Kina-Balu-Gebirge Collector: Waterstradt, det. Hancock (AMS)*;* 1♀ Borneo: Malaysia: Sabah: Kinabalu NP: Poring [forest clearing] 8.VIII.1984. Collector S. Ingrisch, det. S. Ingrisch (CJT); 2♀♀, 2♂♂ Malaysia: Sabah [labeled Nord-Borneo Collector Waterstradt det. J. Skejo (MNCN)**;** 3♂♂ Borneo: Malaysia: Sabah: Pajau River, Collector Mjöberg, det. J. Tumbrinck (NHRS); 1♂ Borneo: Malaysia: Sabah: Kajan River Collector Mjöberg, det. J. Tumbrinck (NHRS); 1♀, 2♂♂ Malaysia: Sabah [on original label written North Borneo] Collector: Watterstradt, det. K. Günther (SMTD); 1♀ Borneo: Malaysia: Sabah: Batu Niah 4.VIII.1984. Collector S. Ingrisch, det. S. Ingrisch (ZFMK); 1♀ Borneo: Malaysia: Sabah: Kinabalu NP: Poring: Bergil 10.IV.1997. [6º5'N, 116º33'E] [collected by fogging] Collector A. Floren, det. J. Tumbrinck (ZFMK); 1♀ Malaysia: Sabah: Crocket Range, 80 km S of Kota Kinabalu City [environment of the village Ula Kumanis at 800 m a.s.l.] 5 – 10.V.2006. Collector A. Sochivko, det. J. Skejo et T. Pushkar (ZISP); 1♀, 3♂ Borneo: Malaysia: Sabah: [original labels „Nord Borneo, Kina-Balu-Gebirge [at 1500 m a.s.l.] Collector Waterstradt, det. Brunner von Wattenwyl (ZISP); 1♀ Malaysia: Sabah: Mt. Trus Madi: Tambunan distr [975 m a.s.l.] 25.IV–10.V.2006, Collector P. Udivichenko, det. J. Skejo et T. Pushkar (ZISP); 4♂♂ Malaysia: Sabah: Mt. Trus Madi: Tambunan district [975 m a.s.l.] 25.IV–10.V.2006. Collector P. Udivichenko, det. J. Skejo et T. Pushkar (ZISP); 2♀, 2♂ Borneo: Malaysia: Sabah: Mt. Trus Madi [1000 m a.s.l.] 13.–25.V.2007. Collector A.V. Gorochov, det. J. Skejo et T. Pushkar (ZISP); 1♀ Borneo: Malaysia: Sabah: Mt. Trus Madi [1200 m a.s.l.] 13–24.I.2007. Collector A. Sochivko, det. J. Skejo et T. Pushkar (ZISP); 1♂ label '99. 10064.' [without specified data] det. J. Skejo (MNCN); 1♂ [without specified data] det. J. Skejo (MNCN); 1♀, 1♂ Malaysia: Borneo [without specified other data] (NMNH NASU); 2♀♀ **Indonesia: Kalimatan**: Kalimantan Timur [= East]: Marah 12.XI.1925. Collector: H. C. Siebers, det. K. Günther (SMTD); 1 nymph (sex unteterminable) Indonesia: Kalimatan: West Kalimatan: Pontianak det. J. Skejo (MNCN); 2♀♀, 2♂♂ **Indonesia: Java** [without other data specified] det. J. Skejo (MNCN);

Additional material from online social media. All the records of *D. belzebuth* from iNaturalist may be found on the following link: https://www.inaturalist.org/observations?taxon_id=637240 (all records submitted by July 2022 are shown in Table 1); while for Flickr, ProjectNoah, and SpinelessWonders all the observations (Figs 6–14) are listed in the Table 1.

TABLE 1. Observations of the Bornean Spiky Pygmy Devil (*Discotettix belzebuth* (Serville, 1838)) from iNaturalist, Flickr, ProjectNoah and SpinelessWonders.

iNaturalist Location	**Date**	**Observer**	**iNaturalist observation number**
Bahagian Miri, Sarawak, Malaysia	12.III.2011.	frank375	58447945
Ranau, Sabah, Malaysia	31.VII.2020.	simonenderby	55198104
Amo, Brunei	3.X.2018.	tjeales	51338313
Marudi, Sarawak, Malaysia	3.X.2016.	frogstail	48878758
Keningau, Sabah, Malaysia	3.V.2019.	song88180	41576629
Marudi, Sarawak, Malaysia	27.VII.2017.	chenshu	39791524

.....Continued on the next page

TABLE 1. (Continued)

Location	Date	Observer	iNaturalist observation number
Kuching, Sarawak, Malaysia	8.III.2019.	frankcanon	38750215
Marudi, Sarawak, Malaysia	16.X.2019.	kinmatsu	38500714
Marudi, Sarawak, Malaysia	16.X.2019.	kinmatsu	38500706
Marudi, Sarawak, Malaysia	16.X.2019.	kinmatsu	38500698
Bahagian Miri, Sarawak, Malaysia	11.V.2018.	squiresk	38409095
Sebuyau, Sarawak, Malaysia	8.V.2018.	squiresk	38373431
Marudi, Sarawak, Malaysia	11.X.2019.	kinmatsu	37776967
Tambunan, Sabah, Malaysia	15.V.2011.	entomokot	36537963
Marudi, Sarawak, Malaysia	7.XII.2011.	hlormel	34836639
Marudi, Sarawak, Malaysia	3.VII.2019.	roeyo	29366988
Bahagian Miri, Sarawak, Malaysia	27.II.2019.	kinmatsu	21514086
Miri, Sarawak, Malaysia	5.VII. 2018.	amanda222	14100141
Malinau, Kalimantan Utara, Indonesia	24.II.2006.	christianlangner	11313877
Lundu, Sarawak, Malaysia	14.VII.2016.	subirshakya	8507421
Ranau, Sabah, Malaysia	9.VI.2009.	nashuagoats	5428136
Kubah, Sarawak, Malaysia	26.I.2017	sullivanribbit	5117700
Sarawak, Malaysia	10.VI.2016.	sohkamyung	3769218

Flickr			
Location	**Date**	**Observer**	**Det.**
Ulu Temburong NP [= National Park], Brunei Darussalam	27.I.2015.	Kateřina Kuřavová	Kateřina Kuřavová
Sabah, Malaysia	07.I.2007.	Arthur Anker	Josip Skejo
Gunung Gading NP, Sarawak, Malaysia, Borneo	19.XI.2008.	Paul Bertner	Josip Skejo
Gunung Mulu, Sarawak, Malaysia, Borneo	19.XII.2016.	Michael Candel	Michael Candel
Gunung Mulu NP, Sarawak, Malaysia, Borneo	26.II.2007.	Paul Bertner	Josip Skejo
Gunung Mulu NP, Sarawak, Malaysia, Borneo	3.XI.2015.	Bernard Dupont	Josip Skejo
Gunung Mulu NP, Sarawak, Malaysia, Borneo	2.XI.2015.	Bernard Dupont	Josip Skejo
Deer Cave Boardwak, Gunung Mulu, Sarawak, Malaysia, Borneo	16.IX.2015.	Bernard Dupont	Josip Skejo
Gunung Mulu NP, Sarawak, Malaysia, Borneo	23.II.2007.	Bernard Dupont	Josip Skejo
Gunung Mulu NP, Sarawak, Malaysia, Borneo	29.IV.2013.	Arthur Anker	Josip Skejo
Gunung Mulu NP, Sarawak, Malaysia, Borneo	25.II.2007	Bernard Dupont	Josip Skejo
Kubah NP, Sarawak, Malaysia, Borneo	uploaded on 28.VI.2011.	Melvin Yeo	Josip Skejo
Sarawak, Malaysia, Borneo	12.I.2012.	Arthur Anker	Josip Skejo

.....Continued on the next page

TABLE 1. (Continued)

ProjectNoah			
Location	**Date**	**Observer**	**Det.**
Gunung Gading, Sarawak, Malaysia, Borneo	7.V.2014	Dandoucette	Josip Skejo
SpinelessWonders			
Location	**Date**	**Observer**	**Det.**
Niah NP, Sarawak, Malaysia, Borneo		David Knowles	Josip Skejo

Distribution. The species is widespread in Borneo (many data from Malaysian and Brunei part, but few from the Indonesian part, probably due to the lack of research) and adjacent small islands (such as Labuan). This species was previously considered widely distributed on all the Greater Sunda Islands of the Malay Archipelago, namely on Borneo, Java, and Sumatra (Serville 1838; De Haan 1843; Rehn 1904; Hancock 1907a; 1907b; Günther 1938; Mahmood *et al.* 2007; Kočárek *et al.* 2015; Tan & Wahab 2018). Distribution of the species in Java was/is possible, as in the Bolívar's collection in MNCN Madrid there are several specimens labeled 'Java', but its presence nowadays should be confirmed as there have been no records for more than a century. The species is not present in Sumatra (De Haan 1843), with De Haan's (1843) records likely belonging to *D. selysi*, which was not described at the time.

Taxonomic notes. *Discotettix adenanii* is considered a junior synonym of *D. belzebuth*. Seven well-developed pronotal projections (Mahmood *et al.* 2007) are the diagnostic character of *D. belzebuth* as well. Günther (1938) pointed out the variability of this polymorphic species with certain specimens that are not easy to identify as *D. belzebuth*, but as a form with certain characteristics somewhat similar to *Kraengia*. The description of *D. adenanii*, on the other hand, completely fits *D. belzebuth* description and diagnosis. Variability of the species can be observed solely by comparison of Bolívar's drawing (Hancock, 1907a: 6) with Günther's *D. belzebuth* figure (1938: p. 301, Fig. 2). Kočárek *et al.* (2015) examined type specimen of *D. adenanii* and the variability of the pronotal morphology in *D. belzebuth* populations collected in different parts of Borneo, showing that all the studied specimens fit the variability of *D. belzebuth*. We agree with the conclusion of Kočárek *et al.* (2015) that *D. adenanii* is a pure synonym of *D. belzebuth*.

Diagnosis. This is the species with the highest (in lateral view) and spikiest/sharpest pronotal projections in the entire genus and by its general appearance it can readily be distinguished from all the other species of the genus. It is somewhat similar to *D. kirscheyi* Skejo, Pushkar, Tumbrinck et Tan **sp. n.** from NE Borneo, and to *D. sumatrensis* Skejo, Pushkar et Tumbrinck **sp. n.** from Sumatra. From *D. scabridus* the new species can be separated by the following characters: (I) bifurcation of the frontal costa between the eyes (on the lower margin of the compound eyes in *D. scabridus*), (II) **FM** high and developed (present as a small tubercle in *D. scabridus*), (III) **MM** elevated into spines (lower and saw-like in *D. scabridus*), (IV) **MML** elevated into spines (present as low and triangular, compressed elevations in *D. scabridus*), (V) **ML** strong and long, tooth-like (absent in *D. scabridus*), (VI) interscapular area with parallel margins (wide and triangular in *D. scabridus*). *Discotettix belzebuth* can be separated from *D. selysi, D. doriae,* and *D. aruanus* Skejo, Pushkar et Tumbrinck **sp. n.** by the following characters: (I) more than one well-developed protuberance on the pronotal disc, (II) long frontomedial projection of the anterior margin of the pronotum, (III) fore and mid femora are more slender, (IV) antennal segments are more specialized in morphology than in *D. selysi*, the widest and the most flattened is the 10th segment (unlike the 9th segment in *D. selysi* and *D. doriae*). From *D. sumatrensis* Skejo, Pushkar et Tumbrinck **sp. n.** the species can be easily separated by the following characteristics: (I) larger body size, (II) all antennae segments are of black/dark color, (III) the 8th antennal segment is the widest one (unlike the 7th segment in *D. sumatrensis* Skejo, Pushkar et Tumbrinck **sp. n.**), (IV) the hind femur bears small lappets. *D. kirscheyi* Skejo, Pushkar, Tumbrinck et Tan **sp. n.** can be easily separated from *D. belzebuth* by the following set of characters: (I) in *D. kirscheyi* Skejo, Pushkar, Tumbrinck et Tan **sp. n.** antennae with more robust segments gradually become wider distally, not as specialized as in *D. belzebuth*, (II) *D. kirscheyi* Skejo, Pushkar, Tumbrinck et Tan **sp. n.** has short **FM**, not covering the whole head as in *D. bellzebuth*, (III) projections on the dorsal surface of the pronotum are smaller in *D. kirscheyi* Skejo, Pushkar, Tumbrinck et Tan **sp. n.**, (IV) *D. kirscheyi* **sp. n.** has weak **ML**, (V) *D. kirscheyi* **sp. n.** has robust and serrated fore and mid femora, not as slender as in *D. belzebuth* and (VI) *D. kirscheyi* **sp. n.** has smaller body size.

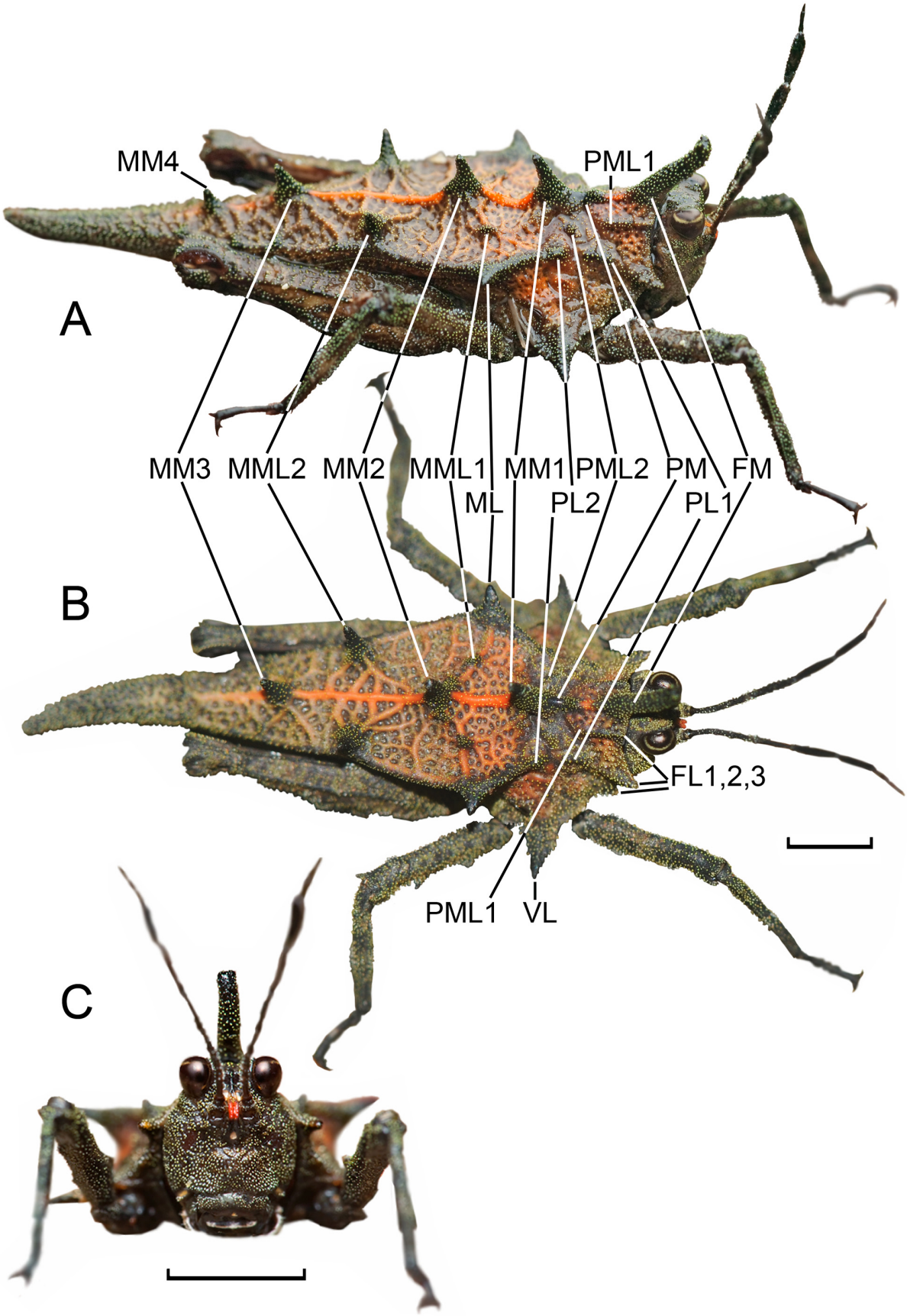

FIGURE 5. *Discotettix belzebuth* (Serville, 1838). A. dorsolateral view; B. dorsal view; C. frontal view. Photographs by Melvin Yeo. Reproduced with the author's permission. Scale bar = 2 mm.

FIGURE 6. *Discotettix belzebuth* (Serville, 1838) in its natural habitat among moss in Sarawak, Malaysia, Borneo. Photographed on April 29, 2013, by Arthur Anker. Reproduced with the author's permission. Photograph available at link: https://www.flickr.com/photos/artour_a/50961987378.

FIGURE 7. Adult female of *Discotettix belzebuth* (Serville, 1838) in her natural habitat on the bark in the Mulu National Park, Sarawak, Malaysia, Borneo. Note that pronotum looks similar to the tree bark in coloration because it is rich in overgrowth of epizoic organisms. Photographed by Bernard Dupont on November 3, 2015. Reproduced with the author's permission. The photograph is available at the link: https://www.flickr.com/photos/berniedup/23074185173.

FIGURE 8. Adult female of *Discotettix belzebuth* (Serville, 1838) in her natural habitat on the bark in the Gunung Mulu National Park, Sarawak, Malaysia, Borneo. Note that pronotum looks similar to the tree bark in coloration because it is rich in overgrowth of epizoic organisms. Photographed by Bernard Dupont on October 28, 2015. Reproduced with the author's permission. The photograph is available at the link https://www.flickr.com/photos/berniedup/22754517337.

FIGURE 9. Adult male and female of *Discotettix belzebuth* (Serville, 1838) in their natural habitat on the bark in the Gunung Mulu National Park, Sarawak, Malaysia, Borneo. Note that pronotum looks similar to the tree bark in coloration because it is rich in overgrowth of epizoic organisms. Photographed by Bernard Dupont on February 26, 2007. Reproduced with the author's permission. The photograph is available at the link: https://www.flickr.com/photos/berniedup/6731079763.

FIGURE 10. Adult female of *Discotettix belzebuth* (Serville, 1838) in her natural habitat on the bark in the Gunung Mulu National Park, Sarawak, Malaysia, Borneo. Photographed by Paul Bertner on November 19, 2008. Reproduced with the author's permission. The photograph is available at the link https://www.flickr.com/photos/rainforests/3495912894.

FIGURE 11. Adult of *Discotettix belzebuth* (Serville, 1838) in lateral view in its natural habitat on the bark in Kubah, Sarawak, Malaysia, Borneo. Photographed by Frank Deschandol on June 5, 2019. Reproduced with the author's permission. The photograph is available at the link: https://www.flickr.com/photos/55114263@N00/48088112106/.

FIGURE 12. Adult of *Discotettix belzebuth* (Serville, 1838) in dorsal view in its natural habitat on the bark in Kubah, Sarawak, Malaysia, Borneo. Photographed by Frank Deschandol on June 5, 2019. Reproduced with the author's permission. The photograph is available at the link: https://www.flickr.com/photos/55114263@N00/48079513827.

FIGURE 13. Adult of *Discotettix belzebuth* (Serville, 1838) in its natural habitat on the bark in Kubah, Sarawak, Malaysia, Borneo. Photographed by Frank Deschandol on March 8, 2019. Reproduced with the author's permission. The photograph is available at the link: https://www.flickr.com/photos/55114263@N00/47427023271/.

FIGURE 14. Adult of *Discotettix belzebuth* (Serville, 1838) in its natural habitat on the bark in Sarawak, Malaysia, Borneo. Photographed by Chien Lee on September 14, 2021. Reproduced with the author's permission. The photograph is available at the link: https://www.flickr.com/photos/25872797@N02/51523708155.

Redescription.

General characters. Medium to large sized, robust, species (13.01–17.02 mm), texture granulated, rugose; pronotum wrinkled, with numerous small tubercles, medium-sized and large protuberances on dorsal and lateral sides. Epizoic symbiotic bryophytes and algae are often present on the pronotal surfaces, so usually the specimens are characterized by cryptic colors (Figs 8, 10). Macropronotal.

Coloration. Coloration variable: from black and dark brown to brighter tints of brown: grayish, greenish, yellowish, reddish, somewhat purple; pronotal projections usually darker. The entire body, including antennae, may be of the same color, except brightly colored frontal carina on the head and the median carina of pronotum, while fore and mid tibiae and tarsi usually bear 1–3 lighter rings. Maxillary palpi black with pale colored joints between the segments (Figs 5–14).

Head. In dorsal and frontal view, vertex 2.21–2.76 times as wide as an eye. Fossula elliptic and deep.

The lower margin of the lateral ocelli a bit below the level of the lower margin of a compound eye. In frontal view, frontal costa narrow, bifurcated above lateral ocelli into subparallel, finely granulated facial carinae forming a very narrow scutellum. Scutellum slightly narrower than the antennal groove. Antennal groove below the lower margin of the compound eye (Fig. 5C). Antenna with 13 antennomeres. A detailed description of the antennal morphometrics and morphology was published recently by Kuřavová *et al.* (2017). Antennal segments as follows: scapus (1st antennomere) and pedicel (2nd antennomere) massive; basal segments (3rd to 6th) elongated and circular in cross-section; central or subapical segments (7th and 8th) strongly widened, pennate, 8th being the widest antennal segment (in holotype 2.22 times as long as wide); apical segment 9th much smaller than the subapical and much larger than the rest of the apical segments; apical segments 10th to 13th reduced, very small, and borders between them barely visible. Antennomeres 3rd to 9th bearing saw-like margins, because of the presence of large basiconic sensilla (Fig. 10). When the body and the antennae are covered with algae and moss, the 8th segment is always free of epizoic organisms (Fig. 10).

Pronotum. Pronotum wrinkled and granulated, covered in numerous small tubercles and larger projections. The posterior process of the pronotum slender, surpassing the hind knee for about half of the hind femur length. Disc of the pronotum at almost the same level along all length, and unlike other species of the genus, without a distinct depression behind the shoulder. Pronotum not descending backward. Morphology of the pronotal disc variable, usually with 4–7 unpaired projections of variable size on the median carina (**FM**, **PM**, and 2–5 **MMs**); 2–3 pairs of **FL**; 4–7 pairs of more or less distinct **PMLs** and **MMLs**; 3 pairs of **PLs** and **MLs**; and a pair of **VL**. Prozona short, subsquare. The anterior margin of the pronotum projected as a large digitate **FM** directed upwards and forwards above the head, covering the whole area of the fastigium of the vertex. **FM** often decurved with excised apex. Prozonal carinae slightly elevated, surpassing the anterior margin of the pronotum as dentiform **FL1**. Extralateral carinae elevated, surpassing anterior margin of pronotum as dentiform **FL2**. **FL3** dentiform, small and weak, more distinct than **FL1**. Median carina extended along the whole length of the pronotum, tuberculated, but with smooth areas. Median carina bearing **FM** and 3–6 of large digitate *medial* projections well seen in profile. **PM** small, distinct in about a third of the examined specimens. **MM1, MM2, MM3,** and **MM4** large and digitate (MM1<MM2>MM3>MM4). **MM4** well visible in most of the specimens, but in some completely reduced. **MM5** present as a spike in about every tenth specimen, but usually very small and almost invisible. Among mediolateral projections, **PML1** is a small tubercle**,** almost indistinct; **PML2** small; **MML1** small; **MML2** large; **MML3** and **MML4** distinct in a few examined specimens. **PL1** and **PL2** elongated, small, and almost indistinct. In the metazona humero-apical carinae forms a sharp humeral angle, projected outwards as strong spine-like or digitate **ML**. Interhumeral carinae hardly observable because of numerous net-like elevations and tubercles present in the whole disc. The apex of pronotum blunt, and shallowly excised. The lower part of the lateral lobe with finely serrate anterior and coarsely serrate posterior margin, elongated as **VL** of variable shapes from sharp spine-like to saw-like form, directed strongly outwards or in rare cases somewhat backward (Fig. 5A, B).

Wings. The visible part of tegmen elongated and oval. Hind wing long, often not reaching the pronotal apex.

Legs. Femora more or less robust, and compressed laterally, but elongated in comparison to other species. The rough surface of the legs usually bears outgrowths and tubercles of variable size and sharpness. The dorsal and ventral margins serrate. Genicular teeth visible on all the knees, and additionally 1–3 weak teeth present on the dorsal and ventral margins of the fore and mid femora. Hind femur with small lappets on both dorsal and ventral margins. Lateral area of the hind femur with net-like elevations and weak carinae, ventro-external carina with teeth-like outgrowths. Genicular teeth of the hind femora larger than the antegenicular. Both sides of the dorsal margin of the hind tibia finely serrated, additionally with 4–5 outer and 3–4 inner larger teeth.

Abdominal apex. Female subgenital plate with a triangular protrusion in the middle of the posterior margin. Ovipositor of variable shapes, usually elongated, but can be more robust, probably due to the ecological factors.

Measurements. **BL** ♂♂13.1–15.01 mm, ♀♀14.3–17.02 mm; **PnL** ♂♂16.04–19.14 mm, ♀♀18.5–22.34mm; **PnW** ♂♂7.99–8.24 mm, ♀♀9.04–9.66 mm; **AnL** ♂♂6.88–7.8 mm, ♀♀7.11–7.99 mm; **TL** ♂♂1.9–2.54 mm, ♀♀2.1–3.01 mm; **TW** ♂♂0.78–1.14 mm, ♀♀0.99–1.23 mm; **fFL** ♂♂3.29–4.46 mm, ♀♀4.1–5.16 mm; **fFW** ♂♂0.77–1.01 mm, ♀♀0.89–1.02 mm; **mFL** ♂♂3.49–4.72 mm, ♀♀4.2–5.09 mm; **mFW** ♂♂0.98–1.02 mm, ♀♀0.99–1.11 mm; **hFL** ♂♂6.99–10.03 mm, ♀♀8.1–10.28 mm; **hFW** ♂♂2.28–3.45 mm, ♀♀2.26–3.24 mm; **OvL** ♀♀1.38–2.11 mm; **AnL/fFL** ♂♂1.58–2.09, ♀♀1.55–1.71; **VW** ♂♂1.02–1.48 mm, ♀♀1.35–1.91 mm; **EW** ♂♂0.38–0.49 mm, ♀♀0.46–0.82 mm; **VW/EW** ♂♂2.21–2.52, ♀♀2.31–2.76; **SW** ♂♂0.31–0.37 mm, ♀♀0.32–0.42 mm; **AgW** ♂♂0.19–0.34 mm, ♀♀0.29–0.41 mm; **ScW** ♂♂0.21–0.29 mm, ♀♀0.23–0.28 mm; **SW/AgW** ♂♂1.46–1.51, ♀♀1.41–1.56; **SW/ScW** ♂♂1.20–1.47, ♀♀1.21–1.35; **As—L/W** ♂♂2.41–3.1, ♀♀2.39–3.12; **PrzW** ♂♂3.35–3.59 mm, ♀♀4.59–4.82 mm; **PrzL** ♂♂3.7–4.11 mm, ♀♀4.29–4.99 mm; **Prz—W/L** ♂♂0.85–0.9, ♀♀0.84–0.91; **TL/TW** ♂♂2.85–3.17, ♀♀2.88–3.11; **mFW/TW** ♂♂0.81–1.29, ♀♀0.87–1.24; **fFL/fFW** ♂♂4.11–5.41, ♀♀4.12–5.22; **mFL/mFW** ♂♂4.21–5.01, ♀♀4.28–4.91; **hFL/hFW** ♂♂3.01–3.67, ♀♀3.19–3.59; **T1L/T3L** ♂♂0.89–1.25, ♀♀0.9–1.11.

Discotettix (Discotettix) selysi Bolívar, 1887 (Figs 15–17)

Vernacular name: Sumatran Unicorn Pygmy Devil

Discotettix selysi Bolívar, 1887: 307 [original description, type locality: Sumatra]; Hancock 1907a: 6 [listed in catalog]; Kirby 1910: 2 [listed in catalog]; Willemse 1930: 207 [new records], Günther 1938: 301 [partim; new records] Blackith 1992: 46 [listed in catalog], París 1994: 236 [data on the type specimens]; Yin *et al.* 1996: 866 [listed in the catalog]; Otte 1997: 32 [listed in the catalog].
Discotettix selangori Mahmood *et al.*, 2007: 1276 [original description, type locality: Selangor]; **syn. n.**
Discotettix selangorei: Mahmood *et al.* 2007: 1275 [lapsus calami].
Acridium (*Tetrix*) *belzebuth* (nec Serville): De Haan 1843: 166 [reported for Sumatra, misidentification].

Type locality. Sumatra: Padang Panjang (= originally "Padang Pandjang" on the label) [approximate coordinates 0.45S, 100.416667E].

Note on *Discotettix selysi* identification history. The species was recorded by De Haan (1843) for the first time under the name *D. belzebuth*, since only *D. belzebuth* was described at the time (*D. selysi* being described 44 years later). De Haan's (1843) drawing of *D. belzebuth* agrees in morphology with *D. selysi*. The author, in the description, noted the possession of only one well distinctive anterior pronotal projection. Examination of specimens confirmed that De Haan's records of *D. belzebuth* from Sumatra belong to *D. selysi* and there is no evidence of the presence of *D. belzebuth* on the island.

Material examined.

Type material. SYNTYPES of *D. selysi* 1♂ Indonesia: Sumatra: Padang Panjang (= on the label "Padang Pandjang") Collector H. Rolle [the type lacks antennae] (**Fig. 16**) (MNCN); 1♂ Indonesia: Sumatra 25.XII. [18]84. Soerian (MHNG). **HOLOTYPE of D. *selangori*** 1♂ Malaysia: Selangor: leg. Brokurtak (UKM), Sabah Forestry Department, East Malaysia).

Misidentified museum material. Identified by Günther (1938) as *D. selysi*: 1♂ Indonesia: Sumatra: west coast, Anai Kloof [500 m a.s.l.] 1926. Collector E. Jacobson, det. K. Günther (SMTD); (5–6) 2♀♀ Indonesia: Sumatra: Excell. v. Studf., collector and date unknown, det. K. Günther (MFN); Identified by De Haan (1843) as *D. belzebuth*: 1♂ + 2♀♀ + 2 nymphs (sex indeterminable) Indonesia: Sumatra: Bat. Sing. [= W Sumatra Isl., Mt. Singgalang volcano] (collector and date not specified in labels), as *D. selysi* det. J. Skejo et J. Tumbrinck (**Fig. 16**) (NCB-RMNH);

Additional museum material. 2♀♀ Indonesia: Sumatra: Maninjau, Puncak, Lawang [600–950 m a.s.l. forest] 17.IV.1995. Collector Sigfrid Ingrisch, det. J. Tumbrinck (CJT, ZFMK); 3♂♂ Indonesia: Sumatra: Mt. Tandikat [600–900 m a.s.l.] VII.2009. Collector Jakl, det. J. Tumbrinck (ZMUH); 1♂ Indonesia: Sumatra: North Sumatra Prov., Roburan Dolok, Panyabungan Selatan, Mandailing, Natal Regency (bamboo stand) 0°44'52.83''N 99°31'30.68''E [723 m a.s.l.] 7.X.2019. Collector Fajar Kaprawi, det. J. Tumbrinck (CJT);

Additional material from online social media. 2 specimens, sex unidentifiable (lateral and dorsal habitus) Malaysia: Peninsular Malaysia: Kuala Lumpur XII.2014. Photographer Pang Way, det. J. Skejo et J. Tumbrinck

(**Figs 17, 18)** (**Facebook**).

Distribution. This species inhabits the rainforests of southern Peninsular Malaysia and of Sumatra, where it can be found on tree bark and roots (Bolívar 1887; Hancock 1907a; Günther 1938; Mahmood *et al.* 2007, our data).

Taxonomic notes on *Discotettix selangori* and *D. doriae*. The description and the measurements of the recently described *Discotettix selangori* Mahmood, Idris et Salmah, 2007 (type locality Malaysia: Selangor) completely fit that of *D. selysi*. The new name for the *D. selysi* population on the Malaysian peninsula does not provide any new information thus we synonymize *D. selangori* **syn. n.** with *D. selysi*. The authors of the former were not aware of *D. selysi* morphological variability and distribution. In the description (Mahmood *et al.* 2007), the epitheton was "selangori", while in the key and under the drawing it was written as "selangorei" (Mahmood *et al.* 2007). As the first reviewers, according to the ICZN, we pick *selangori* as the original spelling, while "*selangorei"* is considered a misspelling. We do not agree with Günther's (1938) synonymy of *D. doriae* and *D. selysi*, since a few clear morphological differences can be found (small FM in *D. doriae*, and swollen antennal segment in *D. doriae*) thus we regard *D. doriae* as a separate species with its own traits and distribution (see a paragraph on *D. doriae*).

Diagnosis. The species is morphologically similar to its congeners that do not have strong pronotal projections of the disc, i.e. to *D. doriae* from Mentawai and *D. aruanus* from Aru Isl. *Discotettix selysi* can be distinguished from *D. doriae* by the following set of characters: (1) *D. doriae* has **FM** small and narrow, covering vertex only partially, while in *D. selysi* **FM** is large, long, and covering entire vertex); (2) *D. doriae* is of smaller body size (pronotum length only 16 to 17 mm in females) than *D. selysi* (pronotum longer than 20 mm in females); (3) *D. doriae* has shorter and stouter antennae with swollen 6th, 7th and 8th antennal segments, while *D. selysi* does not have swollen segments and (4) *D. selysi* has more elongated and slender fore and mid femora, while *D. doriae* has strong teeth on their ventral and dorsal margins. From *D. aruanus* **sp. n.,** *D. selysi* can be distinguished by (I) different shape of the antennae (margins stronger, more saw-like in *D. aruanus*); (II) different shape of FM (not exceeding the head in *D. selysi*, exceeding the head in *D. aruanus* **sp. n.**); (III) less elevated and less triangular PM and MM1; (IV) legs more robust and toothed in *D. selysi* than in *D. aruanus* **sp. n.**, and (V) by larger body size (pronotum length more than 20 mm in females of *D. selysi*, while less than 17 mm in females of *D. aruanus* **sp. n.**). The species is easily distinguished from *D. sumatrensis* **sp. n.** from Sumatra, *D. belzebuth* from Borneo, *D. kirscheyi* **sp. n**. from NE Borneo by the lack of strong spines on the pronotal disc and from the Filipino *D. scabridus* by numerous characters: (I) bifurcation of the frontal costa between the eyes (on the lower margin of the compound eyes in *D. scabridus*), (II) **FM** high and developed (present as a small tubercle in *D. scabridus*), (III) reduced **MM**, not highly protruded (higher, compressed and saw-like in *D. scabridus*), (IV) lateral and humeral carinae are granulated (toothed in *D. scabridus*) and (V) larger body size. From *D. belzebuth, D. selysi* can be easily separated by (I) less widened antennal segments, (II) **FM** being the only large medial projection (disc of pronotum with many spine-like **MM**, **ML** and **MML** in *D. belzebuth*), (III) smoother lateral and humeral carinae (not as equipped and toothed as in *D. belzebuth*), (IV) hind femora bearing large lappets, (V) fore and mid femora being more armed and stouter, **FM** shorter and not decurved as in *D. belzebuth*. From *D. sumatrensis* **sp. n.** the species can be distinguished by (I) completely black antennae, (II) **FM** being the only large medial projection, pronotum without elevated **MM**, **ML** and **MML** and (III) larger body size. *Discotettix kirscheyi* **sp. n.** has (1) smaller **FM** than *D. selysi*, (II) larger **MM1** and **MM2**, (II) higher **MML2s**, (III) more robust fore and mid femora with stronger lobes, (IV) less specialized subapical antennal segments, (V) and is smaller in size. Finally, from *D. doriae* the species can be separated by (I) longer **FM**, (II) more slender appearance, (III) not swollen subapical antennal segments, and (IV) larger body size.

Redescription (Fig. 15).

General features. Large-sized and relatively robust species (16–20 mm). Body finely granulated; pronotum slightly rugose, with numerous small tubercles and net-like elevations. The chitinous surfaces are smooth and without tubercles in places, while the rest is strongly granulated. The anterior part of the pronotum bears several strong protuberances, while other projections are reduced (Fig. 15). Macropronotal.

Coloration. The general color dark brown, but may be of brighter tints of brown or even dark greenish. Pronotal carinae and projections darker and of a different color than the rest of the body. Median pronotal carina from dark orange to bright red (Figs 16, 17). Antennae completely black or dark brown. Maxillary palpi dark brown. The visible part of the tegmen dark brown without any spots. Legs dark brown except for more or less distinct pale rings on tibiae and tarsi. The body usually covered with algae that give a greenish appearance to the specimens. After preservation in alcohol or drying the greenish color disappears.

Head. In dorsal and frontal view, vertex 2.3 times as wide as an eye. Lateral carinae considerably raised and

granulated. Fossula deep, but not easily observable because it is covered by large **FM** of the anterior pronotal margin. Lateral ocelli situated just below the level of the lower margin of a compound eye. Antennal groove significantly below the lower margin of a compound eye. In frontal view, frontal costa bifurcated at the level of lateral ocelli into facial carinae, forming narrow parallel scutellum (Fig. 15E). Antennal groove slightly wider than the frontal costa. Antenna 13-segmented (but in male looks like 12-segmented, because the 13th segment is very small and not visible under an optical microscope, only under SEM): scapus (1st antennomere) and pedicel (2nd antennomere) massive; basal segments (3rd to 6th) elongated and circular in cross-section; central or subapical segments (7th and 8th) strongly widened, pennate, 8th being the widest antennal segment (about 2.7–2.8 times as long as wide); apical segment 9th elongated and pennate, smaller than the subapical and much larger than the rest of the apical segments; apical segments 10th to 13th reduced, very small, and borders between them barely visible. Antennomeres 3rd to 9th bearing saw-like margins, because of the presence of the large basiconic sensilla. When the body and the antennae are covered with algae and moss, the 8th segment is always free of epizoic organisms.

Pronotum. Pronotum rugose and granulated with numerous small tubercles and net-like elevations, but in some parts smooth and without tubercles (parts of the pronotal disc and some intervals of the median carina of the pronotum). The anterior part of the pronotum bears large **FM**, and a few medium-sized and small protuberances. The posterior process of the pronotum slender, surpassing hind knees for more than a half-length of the hind femur or less. The disc of the pronotum almost completely flat. A small depression on the disc positioned between the near bases, then the disc becomes slightly elevated again. Caudad, pronotum gradually descending. Disc rich in net-like elevations, more distinct in the places of the interhumeral carinae. The median carina of the pronotum bears unpaired projections of variable size: high and digitate **FM**, directed upwards and forwards above the head and covering the whole area of the fastigium of the vertex; small triangular **PM,** a bit larger triangular **MM1**, small **MM2**; and completely reduced **MM3** and **MM4**. Prozona subsquare. Prozonal and extralateral carinae in prozona distinct, surpassing anterior margin of pronotum as dentiform small **FL1** and larger **FL2**, **FL2**. **FL3** small, dentiform. Behind the **FM** medial carina extended along the whole length of pronotum from the anterior margin to the pronotal apex, slightly undulated by the low aforementioned projections. **PML1** small, **PML2** even smaller. **MML1** almost indistinct; **MML2** distinct; **MML3** very small, while **MML4** and **MML5** completely indistinct. **PL1** and **PL2** small. Humeral angle obtuse with pointed apex. **ML** small, reduced. Pronotum apex narrow, shallowly excised. The lower part of the lateral pronotal lobe with serrate anterior and posterior margins, elongated as spine-like **VL**, directed strongly outwards and backward (Fig. 15A, B).

Wings. The visible part of the tegmen elliptical. Hind wing with scalloped inner margin, a few millimeters shorter than the apex of the pronotal process. In living specimens, the tegmina are covered by photosynthetic microbes (most probably algae and cyanobacteria), so are greenish in appearance.

Legs. Fore and mid femora relatively robust, compressed laterally; with dorsal and ventral margins serrated with genicular tooth on the knees and additional 2–3 strongly projected and sharp teeth on each margin. Hind femur with wrinkled margins, one small protuberance situated on the ventral external carina. Genicular tooth large, while antegenicular tooth almost indistinct. Both sides of the dorsal margin of the hind tibia finely serrated, with 3–4 outer and 1–3 inner larger teeth.

Abdominal apex. Male subgenital plate in lateral view about two times as long as high. Female subgenital plate in ventral view with a longitudinal keel in the median region and with a triangular protrusion in the middle of the posterior margin. Ovipositor robust, dorsal valvae robust, ventral valvae slender; all valvae serrate.

Measurements. BL ♂♂14.41–14.88 mm, ♀♀16.01–16.28 mm; **PnL** ♂♂17.85–18.35 mm, ♀♀20.46–21.11 mm; **PnW** ♂♂8.06–8.14 mm, ♀♀9.27–9.48 mm; **AnL** ♂♂7.68–7.22 mm, ♀♀7.18–7.49 mm; **TL** ♂♂2.44–2.51 mm, ♀♀2.78–2.91 mm; **TW** ♂♂0.77–0.81 mm, ♀♀1.03–1.11 mm; **fFL** ♂♂4.49–4.55 mm, ♀♀5.07–5.12 mm; **fFW** ♂♂0.78–0.84 mm, ♀♀0.92–0.94 mm; **mFL** ♂♂4.52–4.71 mm, ♀♀4.77–5.01 mm; **mFW** ♂♂0.99–1.01 mm, ♀♀1.03–1.14 mm; **hFL** ♂♂8.51–8.68 mm, ♀♀9.97–10.12 mm; **hFW** ♂♂2.65–2.72 mm, ♀♀3.05–3.2 mm; **OvL** ♀♀1.39–1.43 mm; **AnL/fFL** ♂♂1.68–1.7, ♀♀1.59–1.69; **VW** ♂♂1.01–1.05 mm, ♀♀1.36–1.48 mm; **EW** ♂♂0.39–0.47 mm, ♀♀0.51–0.71 mm; **VW/EW** ♂♂2.23–2.49, ♀♀2.43–2.67; **SW** ♂♂0.32–0.36 mm, ♀♀0.33–0.42 mm; **AgW** ♂♂0.21–0.33 mm, ♀♀0.34–0.39 mm; **ScW** ♂♂0.22–0.27 mm, ♀♀0.24–0.29 mm; **SW/AgW** ♂♂1.49–1.53, ♀♀1.44–1.58; **SW/ScW** ♂♂1.21–1.45, ♀♀1.2–1.34; **As–L/W** ♂♂2.69–2.78, ♀♀2.71–2.81; **PrzW** ♂♂3.44–3.52 mm, ♀♀4.68–4.71 mm; **PrzL** ♂♂3.93–4.01 mm, ♀♀4.74–4.79 mm; **Prz–W/L** ♂♂0.86–0.88, ♀♀0.98–1.02; **TL/TW** ♂♂2.91–3.09, ♀♀2.7–2.88; **mFW/TW** ♂♂1.19–1.25, ♀♀0.98–1.09; **fFL/fFW** ♂♂5.42–5.61, ♀♀5.51–5.71; **mFL/mFW** ♂♂4.32–4.66, ♀♀4.46–4.63; **hFL/hFW** ♂♂3.21–3.28, ♀♀3.21–3.27; **T1L/T3L** ♂♂1.01–1.08, ♀♀1.01–1.02.

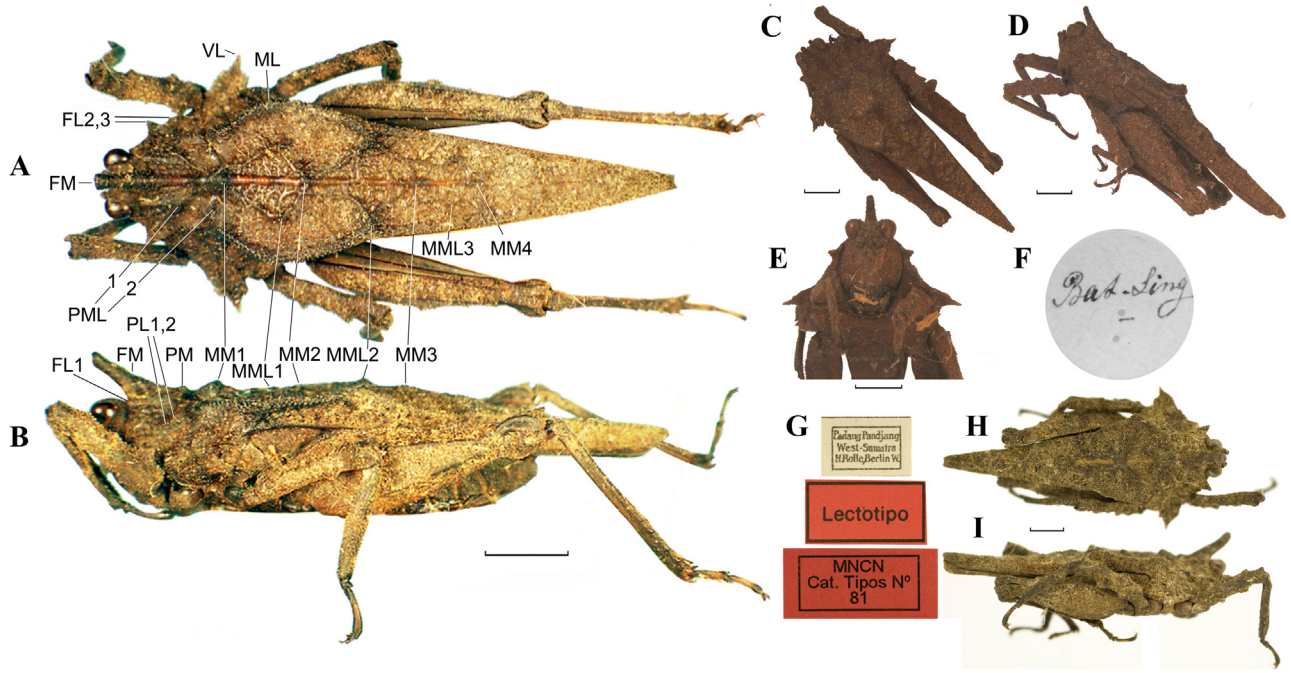

FIGURE 15. Old museum material and syntype of *Discotettix selysi* Bolívar, 1887. A, B. Male from SMTD, W Sumatra (photograph by S. Ingrisch, reproduced with the author's permission), scale bar = 2 mm; C–F. De Haan's (1843) '*D. belzebuth*' specimens from Sumatra: Mt. Singgalang, selected female from NCB (photograph by Luc Willemse, reproduced with author's permission), scale bar = 5 mm; G–I. Syntype male from MNCN with labels, W Sumatra: Padang Panjang (copyright Josip Skejo & MNCN), pronotum length 15,45 mm.

FIGURE 16. *Discotettix selysi* Bolívar, 1887 in its natural habitat in Peninsular Malaysia. Photograph by Pang Way, close to Kuala Lumpur in December 2014. Reproduced with the author's permission.

FIGURE 17. *Discotettix selysi* Bolívar, 1887 in Peninsular Malaysia on the photographer's fingertip. Photograph by Pang Way, close to Kuala Lumpur in December 2014. Reproduced with the author's permission.

Discotettix (Discotettix) doriae Bolívar, 1898 stat. resurr. (Fig. 18)

Vernacular name: Mentawai Unicorn Pygmy Devil

Discotettix doriae Bolívar, 1898: 80 [original description, type locality: Mentawai: Sipura]; Hancock 1907a: 6 [listed in the catalog]; Kirby 1910: 2 [listed in the catalog]; Willemse 1930: 207 [listed in the catalog]; París 1994: 236 [data on type series]; Muhammad *et al.* 2018: 20.

Discotettix selysi (partim): Günther 1938: 302 [synonymized *D. doriae* with *D. selysi*; it is not accepted here]; Blackith 1992: 46 [listed in the catalog]; Yin *et al.* 1996: 866 [listed in the catalog]; Otte 1997: 32 [listed in the catalog].

Type locality. Indonesia: Sumatra: Mentawai: Sipura Island

Material examined.

Type material. LECTOTYPE (Fig. 18) 1♀ Mentawei: Sipora, Sereinu [= Indonesia: Mentawai: Sipura island] V.–VI.[18]84. Leg. E. Modigliani (MCSN); **PARALECTOTYPE** 1♀ Mentawei: Sipora, Sereinu [= Indonesia: Mentawai: Sipura island] V.–VI.[18]84. Leg. E. Modigliani (MNCN).

Distribution. This species inhabits the rainforest of the small island of Sipura (845 km^2), the smallest of the four large islands of the Mentawai Archipelago, west of Sumatra. Only two females of this species have been known hitherto.

Diagnosis. This species is morphologically similar to *D. selysi* from Sumatra and the Malayan peninsula and to *D. aruanus* **sp. n.** from the Aru Islands because of the presence of low projections, or absence of the high ones, flat dorsum of the pronotum, and coloration. It seems to be closely related to *D. selysi*, but can be easily recognized from the latter by the following set of characters: (1) **FM** small and narrow, covering vertex only partially (in *D. selysi* it is large, long, and covering entire vertex), (2) smaller body size (females have a slightly shorter body and pronotum than the ones of *D. selysi*), (3) shorter and stouter antennae with swollen 6th, 7th and 8th antennal segments (no swollen segments in *D. selysi*), and (4) stronger teeth of the fore and mid femora. From *D. aruanus* **sp. n.** from Aru Island, which also seems related to *D. selysi* and *D. doriae*, *D. doriae* can be easily told apart by the much smaller **FM** (large and reaching in front of the head in *D. aruanus* **sp. n.**), and much stouter and more armed fore

and mid femora (less armed in *D. aruanus* **sp. n.**). From *D. sumatrensis* **sp. n.** inhabiting neighboring Sumatra, the species can be separated by (1) dark antennae with stouter antennomeres, (2) lower projections, especially **FM** and **MMs**, (3) larger body size (approximately 2 mm longer), and (4) stouter femora. For comparison with other species (*D. belzebuth* and *D. kirscheyi* from Borneo and *D. scabridus* from the Philippines), please consult the diagnosis of *D. selysi*, where a comparison to all the species of the genus *Discotettix* has been given, as well as the detailed diagnoses of *D. scabridus* and *D. belzebuth* containing comprehensive comparisons.

Redescription. (Fig. 18)

General features. Medium-sized (about 15 mm), robust species. Body finely granulated; pronotum rugose, with numerous small tubercles and net-like elevations, in parts smooth and without tubercles, anterior part of the pronotum bearing a few larger protuberances (Fig. 18). Macropronotal.

Coloration. Body dark brown. Carinae and projections darker than the rest of the body. Median pronotal carina with orange patches. Antenna dark brown, without pale colored parts. Maxillary palpi dark brown. The visible part of the tegmen dark brown and without any pale spots. Legs brown except for the pale rings on tibiae and tarsi. The body probably covered with epizoic symbionts, just as in other species, giving an animal greenish camouflage when alive, after preservation in alcohol and/or drying the green color disappears.

Head. In dorsal and frontal view, vertex 2.21–2.36 times as wide as the eye. Lateral carinae raised and granulated. Fossula deep. Lateral ocelli situated just below the level of the lower margin of the compound eye. Antennal groove significantly below the lower margin of the compound eye. In frontal view, frontal costa bifurcated into facial carinae, forming a scutellum with narrow and parallel borders, bifurcation just above the level of lateral ocelli. Antennal groove slightly wider than frontal costa. Antenna 13-segmented, all segments robust in comparison to other species of the genus: scapus (1st antennomere) and pedicel (2nd antennomere) massive; basal segments (3rd to 5th) robust, less elongated than in other species of the subgenus *Discotettix*, and circular in cross-section; basal segment 6th widened and swollen; central or subapical segments (7th and 8th) strongly widened, pennate and swollen, 8th being the widest antennal segment (about 2.6 times as long as wide); apical segment 9th elongated and pennate, but smaller than the subapical and much larger than the rest of the apical segments; apical segments 10th to 13th reduced, very small, and borders between them barely visible. Antennomeres 3rd to 9th bearing saw-like margins, but weaker than in the other species of the subgenus (Fig. 18C).

Pronotum. Pronotum rugose, granulated, with numerous tubercles and net-like elevations, somewhere smooth and without tubercles (some parts of the pronotal disc and parts of the median carina of the pronotum). The anterior margin of the pronotum bearing a medium-sized **FM**, smaller than in the other species of the subgenus *Discotettix*. The posterior process of the pronotum surpassing the hind knees for at most a half-length of a hind femur. Disc of the pronotum with a small depression between the tegminal bases, then slightly elevated again. Caudad, pronotum gradually descending backward. Net-like elevations of omnipresent on the pronotal disc, all along the median carina of the pronotum and connecting it to all other carinae and the projections of the dorsal surface of the pronotum. Net-like elevations very distinct in the interhumeral region of the disc. The median carina of the pronotum continuous from the anterior margin to the pronotal apex, undulated irregularly because of the projections. The median carina of the pronotum bearing four unpaired projections of variable size: medium-sized digitate **FM**, directed upwards and forwards and covering the fastigium of the vertex (but not completely); **PM** small and triangular; **MM1** large and triangular; **MM2** and **MM3** evident, but decreasing in size caudad, **MM4** reduced. Prozona subsquare. Prozonal and extralateral carinae in prozona distinct, surpassing anterior margin of pronotum as dentiform **FL1** and **FL2**, with **FL2** more distinct. **FL3** dentiform, small, and weak. Among the *mediolateral* projections **PML1** more or less distinct; **PML2** very small; **MML1** small; **MML2** large; **MML3 v**ery small; **MML4** and **MML5** wanting. **PL1** and **PL2** present as small triangular tubercles forming posterior elongation of the extralateral carinae in the line joining the humero-apical carinae. Humeral angle obtuse with pointed apex. **ML** present, but reduced. Pronotal apex narrow, shallowly excised. The lower part of the lateral pronotal lobe with serrate anterior and posterior margins, elongated as spine-like **VL**, directed strongly outwards and backward (Fig. 18A, B).

Wings. Tegmina and alae present and visible. The visible part of tegmen elliptical, granulated, and tuberculated. Hind wing not reaching apex of pronotum, a few millimeters of length are lacking to touch the tip.

Legs. Fore and mid femora robust, compressed laterally, dorsal and ventral margins serrated; with genicular tooth on the knees and additionally with two to three sharp teeth on the dorsal and ventral margin. Mid femora with stronger teeth than the fore femora. Hind femur with lappets, and a small protuberance situated on the ventral external carina. The genicular tooth large, while the antegenicular one small. Both sides of the dorsal margins of the hind tibia finely serrated, with 3–4 outer and 1–3 inner large teeth.

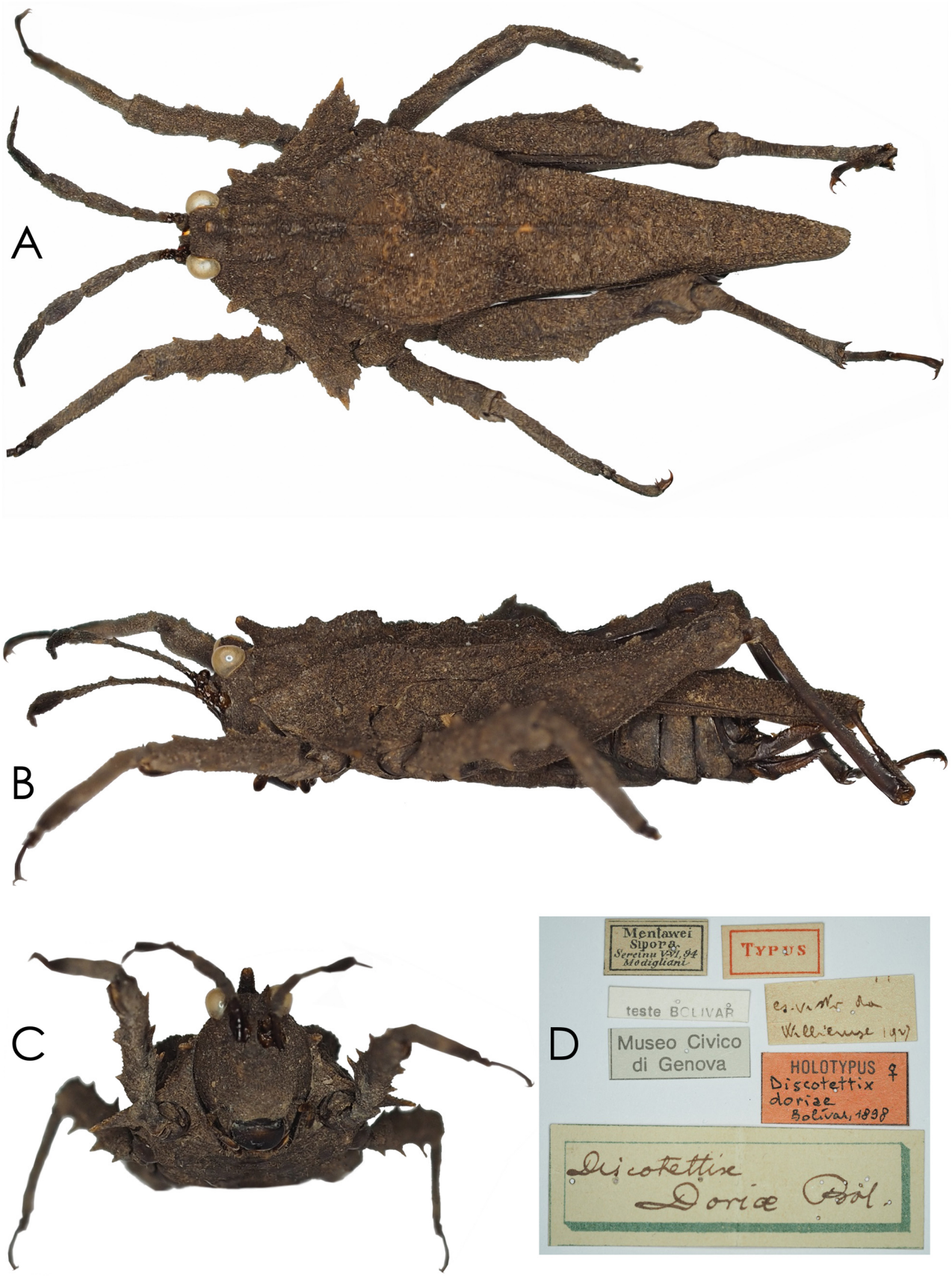

FIGURE 18. Female lectotype of *Discotettix doriae* Bolívar, 1898, **nom. resurr.** from Metawai Island. Lectotype is deposited in MCSN. A. Dorsal view, B. Lateral view, C. Frontal view, and D. Labels, pronotum length 16.19 mm. Photographs by Josef Tumbrinck.

Abdominal apex. Female subgenital plate in ventral view with a triangular protrusion in the middle of the posterior margin. Ovipositor robust, dorsal valvae robust, ventral slender, and serrate. Cerci robust, hairy, with a long tip.

Measurements (♀♀ only). **BL** 14.51–14.79 mm; **PnL** 16.06–17.01 mm; **PnW** 8.45–8.61 mm; **AnL** 6.88–7.01 mm; **TL** 1.93–2.11 mm; **TW** 0.75–0.91 mm; **fFL** 3.86–4.01 mm; **fFW** 0.78–0.82 mm; **mFL** 3.47–3.61 mm; **mFW** 0.86–0.93 mm; **hFL** 7.59–8.01 mm; **hFW** 2.68–2.73 mm; **OvL** 1.62–1.71 mm; **AnL/fFL** 1.75–1.81; **VW** 1.18–1.23 mm; **EW** 0.51–0.55 mm; **VW/EW** 2.21–2.36; **SW** 0.26–0.31 mm; **AgW** 0.31–0.34 mm; **ScW** 0.21–0.27 mm; **SW/AgW** 0.67–0.81; **SW/ScW** 1.19–1.24; **As–L/W** 2.59–2.63; **PrzW** 3.44–3.51 mm; **PrzL** 2.22–2.38 mm; **Prz–W/L** 1.47–1.60; **TL/TW** 2.57–2.90; **mFW/TW** 1.08–1.09; **fFL/fFW** 4.03–4.12; **mFL/mFW** 4.01–4.51; **hFL/hFW** 2.91–3.22; **T1L/T3L** 1.02–1.04.

Discotettix (Discotettix) aruanus **Skejo, Pushkar et Tumbrinck sp. n. (Figs 19–20)**
Vernacular name: Aruan Unicorn Pygmy Devil

Type locality: Indonesia: SE Moluccas: Aru Island: Wokam: 10–15 km NEE of Wakua.

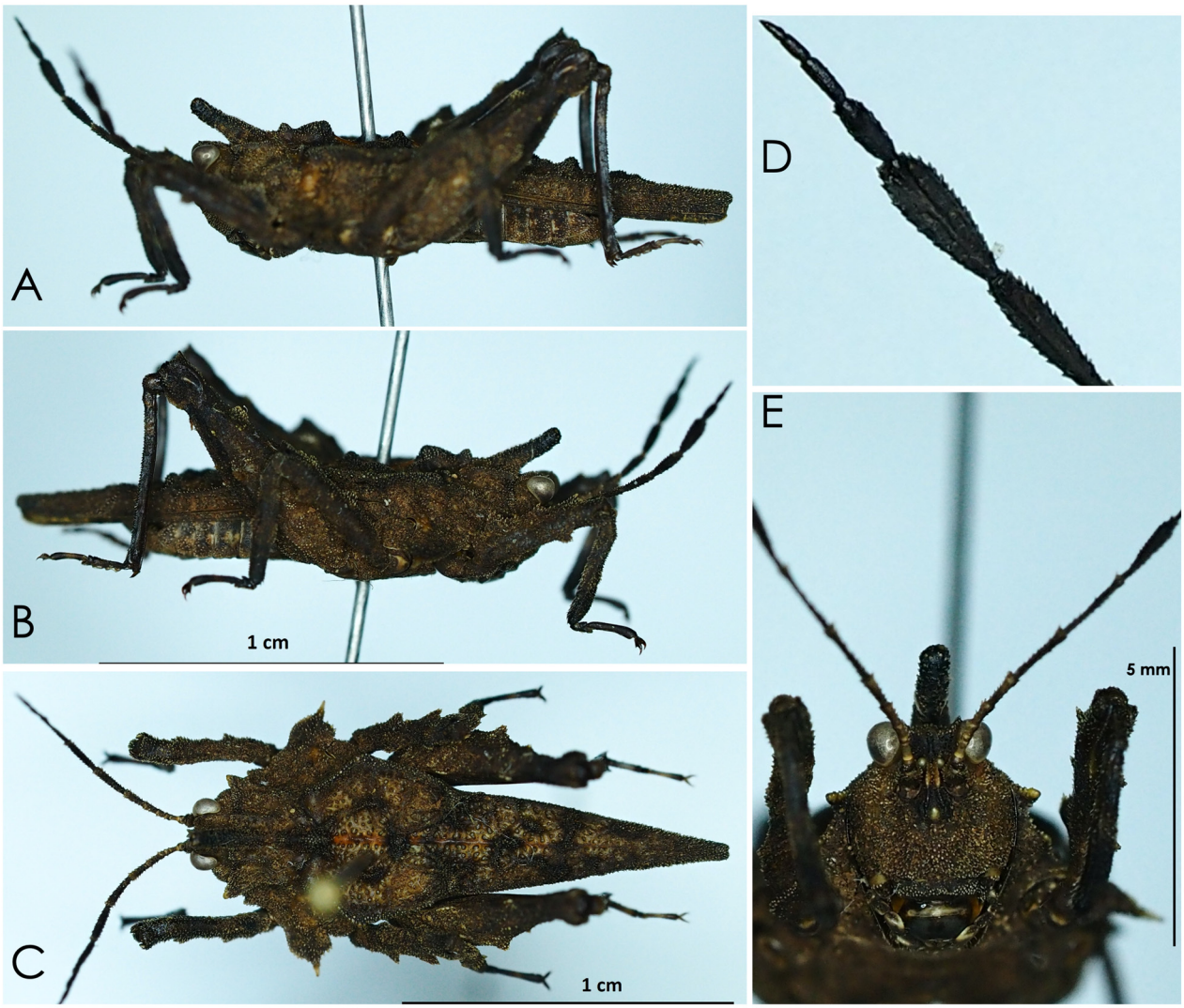

FIGURE 19. Female holotype of *Discotettix aruanus* Skejo, Pushkar et Tumbrinck **sp. n.** A. left lateral view; B. right lateral view; C. dorsal view; D. antenna detail; E. head in frontal view. The holotype is deposited in ZMUH. Photographs by Josef Tumbrinck.

Material examined.

Type material. HOLOTYPE (Fig. 19) 1♀ Indonesia: SE Moluccuas: Aru Island, S coast of Wokam I., 10–15 km NEE of Wakua vill., 0–50 m alt. 21–30.I.2015., St. Jakl leg. (ZMUH); **PARATYPE (Fig. 20)** 1♀ Indonesia: SE Moluccuas: Aru Island, S coast of Wokam I., 10–15 km NEE of Wakua vill., 0–50 m alt. 21–30.I.2015., St. Jakl leg. (FM broken in this specimen) (ZMUH). **Type series depository.** Zoologisches Museum Hamburg, Germany.

Type series depository. Zoologisches Museum Hamburg, Germany (ZMUH).

Etymology. Named after the island of Aru. The specific epitheton is a masculine gender adjective in the Nominative case made from the Latinisation of the name Aru (*aruanus, aruana, aruanum*).

Distribution. This species is known to inhabit the Peninsula of Wokam (Wokam Palau), a part of the island of Aru in the southeastern Moluccas. This is the easternmost species of the genus *Discotettix*.

Specific diagnosis. The new species is very similar to *Discotettix selysi* from the southern Malaysian peninsula and from Sumatra. It shares many traits with *D. selysi*, but a few subtle differences exist. Due to morphological differences among *D. aruanus*, *D. selysi* and *D. doriae* (Fig. 21) and because of high geographical isolation, *D. aruanus* **sp. n.** is proposed as a new species within the genus *Discotettix,* and not a subspecies of *D. selysi*. From *D. doriae* this species is easily separated by (I) the large **FM** covering the whole vertex and being produced even in front of the head (in *D. doriae* **FM** is much smaller) and (II) by much longer antennae without swollen segments. From *D. selysi*, the new species can separated by the following set of characteristics: (I) **FM** somewhat larger and in dorsal and lateral views projected before the head (in *D. selysi*, there are specimens without and with long projected **FM**); (III) **MMLs** more elevated than in *D. selysi*; (IV) **PM** and **MM1** more elevated and more triangular (usually lower and more oblique in *D. selysi*); (V) **VL** spine more distinct in *D. aruanus* **sp. n.** because the posterior lobe of the lateral pronotal lobe has smaller spikes than in *D. selysi* (in *D. selysi* some specimens are similar to *D. aruanus*); (VI) femora more slender in *D. aruanus* **sp. n.** than in *D. selysi;* and (VII) humeral angles more projected in *D. selysi* (well visible in frontal view), and infrascapular area thus wider in *D. selysi* than in *D. aruanus* **sp. n.** For a comprehensive comparison with other species of the genus please consult the diagnoses of *D. scabridus* and *D. belzebuth.*

Description (holotype).

General features. Medium-sized, robust species (body length 11.5–13.5 mm in females, pronotum length about 16.5 mm); pronotum granulated and wrinkled, with numerous small tubercles and net-like elevations. The chitinous surfaces are smooth and without tubercles in some places of the dorsum, while the rest is strongly granulated. One large digitate **FM** on the anterior margin and numerous small triangular protuberances on the dorsal and lateral sides of the pronotum. Almost the entire body (except the eye, labrum, fore and mid tarsi, second and third segments of hind tarsus, and inner side of the hind femur) covered with numerous small tubercles (Figs 19, 20). Only the macropronotal form is known.

Coloration. Body dark brown, only some parts of the pronotal net-like elevations orange-red in color. Antenna dark brown, almost black. Proximal segments of the palpi light brown, and distal black. The visible part of the tegmen dark brown and without spots. Legs dark brown with lighter rings and patches. Fore and mid femora and tibiae dark brown with numerous small tubercles with somewhat lighter apices; fore and mid tarsi black, second segment with a light ring in the middle; 1st tarsal pads whitish, claws brown. Hind femur dark brown with numerous small tubercles with lighter apices. Hind tibia dark brown with two weak light rings, one in the basal part, and another in the distal third. 1st tarsus of hind leg pale brown, pads whitish; third segment pale brown with a dark ring in its distal part, claws brown. Tergites, sternites, epiproct, and cerci dark brown.

Head. In dorsal and frontal view, vertex 1.7 times as wide as an eye. In frontal view, lateral carinae of the vertex considerably raised and granulated. Fossula elliptic and deep, but not easily observable because it is covered by large **FM** of the anterior pronotal margin. Lateral ocelli situated just below the level of the lower margin of a compound eye. Antennal groove significantly below the lower margin of a compound eye. In frontal view frontal costa bifurcated at the level of lateral ocelli into facial carinae, forming narrow parallel scutellum. Scutellum narrower than the antennal grove and the scapus (Figs 19E, 20E). Antenna elongated 13-segmented: scapus (1st antennomere) and pedicel (2nd antennomere) massive; basal segments (3rd to 6th) elongated and circular in cross-section; central or subapical segments (7th and 8th) strongly widened, pennate, 8th being the widest antennal segment (about 2.8–3 times as long as wide); apical segment 9th elongated and pennate, smaller than the subapical and much larger than the rest of the apical segments; apical segments 10th to 13th reduced, very small, and borders between them barely visible. Antennomeres 3rd to 9th bear strong saw-like margins, likely because of the presence of large basiconic sensilla (Figs 19D, 20D).

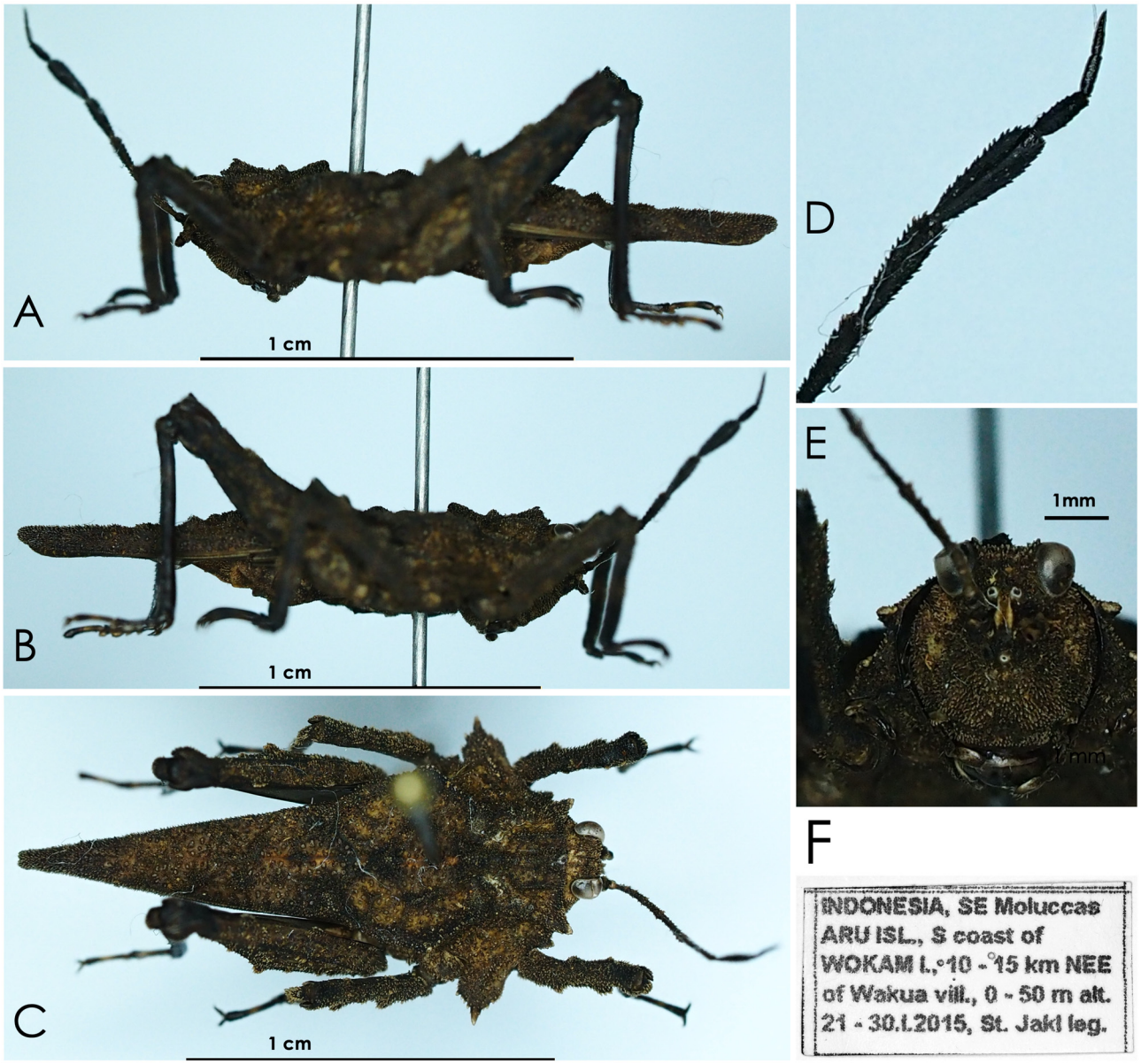

FIGURE 20. Female paratype of *Discotettix aruanus* Skejo, Pushkar et Tumbrinck **sp. n.** A. left lateral view; B. right lateral view; **C.** dorsal view; D. antenna detail; E. head in frontal view; F. collection labels. The paratype is deposited in ZMUH. Photographs by Josef Tumbrinck.

Pronotum. Pronotum rugose and granulated with numerous small tubercles and net-like elevations, but in some parts smooth and without tubercles (parts of the pronotal disc and some intervals of the median carina of the pronotum). The anterior part of the pronotum bears one large **FM**, and a few medium-sized and small protuberances. The posterior process of the pronotum slender, surpassing the hind knees for more than a half-length of the hind femur (macropronotal form). The disc of the pronotum is visually flat, but upon a closer inspection, many triangular elevations (*projections*) may be observed. A depression is visible on the pronotal disc positioned between the bases of the tegmina, then the disc becomes slightly elevated again. Caudad, pronotum gradually descending. The pronotal disc is rich in chitinous net-like elevations, more distinct in the interhumeral region. Medial carina extended along the whole length of the pronotum from the anterior margin to the pronotal apex, slightly undulated by the unpaired projections of variable size: the largest is high and digitiform massive **FM**, directed upwards and forwards above and before the head and covering the whole area of the fastigium of the vertex; triangular **PM,** a large triangular **MM1**, small triangular **MM2**; small **MM3,** and almost completely reduced **MM4**. Prozona subsquare. Prozonal and extralateral carinae in the prozona distinct, surpassing anterior margin of the pronotum as a small dentiform

FL1 and large **FL2**, which is also well visible in frontal view. **FL3** small and dentiform. **PML1** and **PML2** small. **MML1** and **MML2** distinct; **MML3** very small; **MML4** and **MML5** indistinct. **PL1** and **PL2** small. Humeral angle obtuse with a pointed apex. **ML** small, reduced. Pronotum apex narrow, shallowly excised in the middle. The lower part of the lateral pronotal lobe bearing small teeth on the anterior and the posterior margins, with the middle region elongated as a large spine-like **VL**, directed mostly outwards and slightly backward (Figs 19A–C, 20A–C).

Wings. Tegmina partly covered, not as easily discernible as in *D. doriae* and *D. selysi*. The visible part of the tegmen elliptical. Hind wing not reaching the pronotal tip for a few millimeters.

Legs. Fore and mid femora elongated, but with robust armature on the dorsal and ventral margins. Fore and mid femora compressed laterally; with dorsal and ventral margins serrated with genicular tooth on the knees and additional 2–3 strongly projected and sharp teeth on each margin. Hind femur bearing small lappets on dorsal and ventral margins and one small protuberance on the ventral external carina. Genicular tooth large, while antegenicular tooth very small. Both sides of the dorsal margin of the hind tibia finely serrated, with 3–4 outer and 1–3 inner larger teeth.

Abdominal apex. Female subgenital plate in ventral view bearing a longitudinal keel in the middle and has a triangular protrusion in the middle of the posterior margin. Ovipositor, in ventral view, seems to be elongated, but dorsal valvae are not visible because of the decurvation of the pronotal tip, which is directed downward. Ventral valvae are elongated, but for example in *D. selysi* the dorsal are more robust, which can be expected in *D. aruanus* **sp. n.** as well.

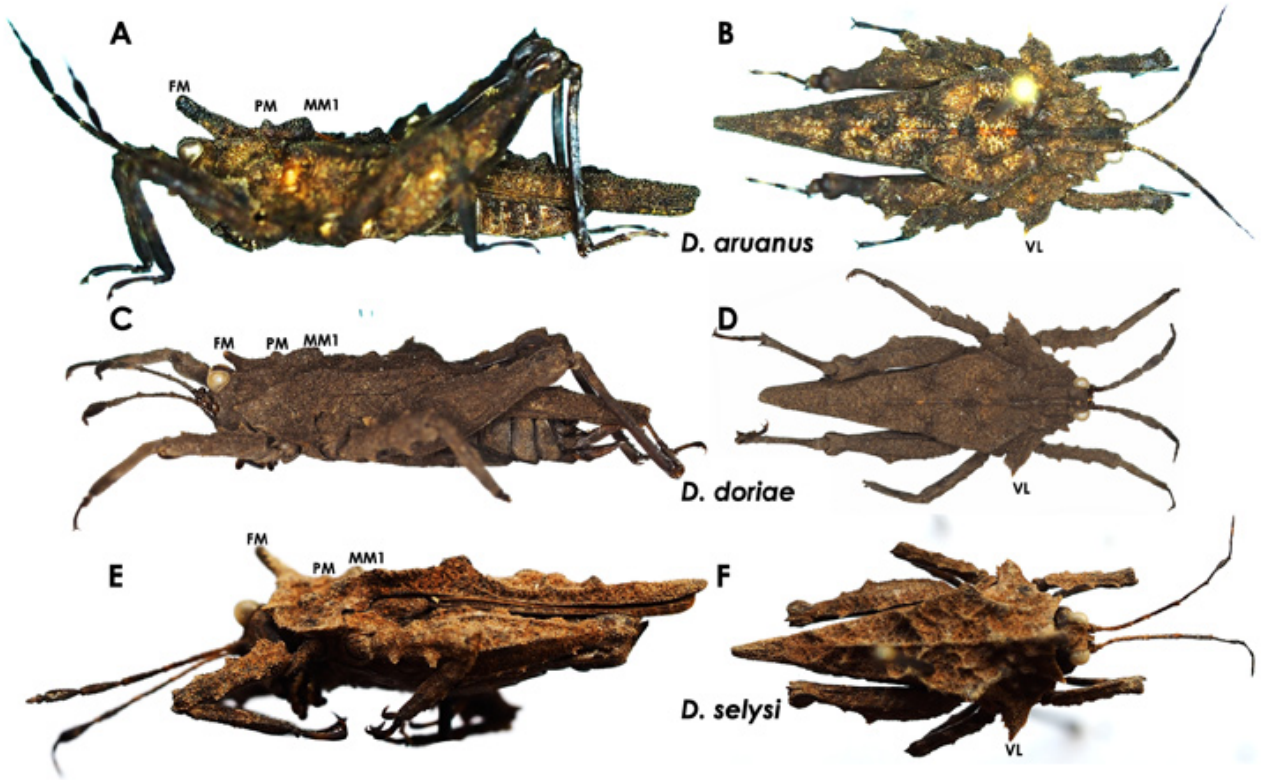

FIGURE 21. *Discotettix* spp. with flattened pronotum. A, B. *D. aruanus* Skejo, Pushkar et Tumbrinck **sp. n.**, holotype female; C, D. *D. doriae* Bolívar, 1898, **nom. resurr.**, syntype female; E, F. *D. selysi* Bolívar, 1887, syntype male; left: body in lateral view; right: body in dorsal view. Frontomedial (FM), promedial (PM), the first metamedial projection (MM1), and the ventrolateral (VL) projections are marked.

Measurements (♀♀ only, HT—holotype, PT—paratype). BL HT 13.45 mm, PT 11.80 mm; **PnL** HT 16.29 mm, PT 14.94 mm (without FM); **PnW** HT 8.40 mm, PT 8.49 mm; **AnL** HT 6.74 mm, PT 7.10 mm; **TL** HT 1.4 mm, PT 1.0 mm; **TW** HT 0.4 mm, PT 0.3 mm; **fFL** HT 4.40 mm, PT 4.22 mm; **fFW** HT 0.90 mm, PT 0.72 mm; **mFL** HT 4.41 mm, PT 4.21 mm; **mFW** HT 0.88 mm, PT 0.75 mm; **hFL** HT 8.63 mm, PT 7.42 mm; **hFW** HT 2.50 mm, PT 1.98 mm; **OvL** HT (Not visible, more than 1 mm), PT (not visible, more than 1 mm); **AnL/fFL** HT 1.51, PT 1.68; **VW** HT 1.00 mm, PT 1.05 mm; **EW** HT 0.59 mm, PT 0.61 mm; **VW/EW** HT 1.7, PT 1.7; **SW** HT 0.23

mm, PT 0.26 mm; **AgW** HT 0.45 mm, PT 0.40 mm; **ScW** HT 0.42 mm, PT 0.38 mm; **SW/AgW** HT 0.5, PT 0.65; **SW/ScW** HT 0.55, PT 0.68; **As—L/W** HT 2.8, PT 3.0; **PrzW** HT 3.71 mm, PT 3.43 mm; **PrzL** HT 1.85 mm, PT 1.78 mm; **Prz—W/L** HT 2.00, PT 1.92; **TL/TW** HT 3.5, PT 3.3; **mFW/TW** HT 2.2, PT 2.5; **fFL/fFW** HT 4.9, PT 5.6; **mFL/mFW** HT 5.0, PT 5.8; **hFL/hFW** HT 3.4, PT 3.7; **T1L/T3L** HT 1.1, PT 1.1.

Discotettix (Discotettix) kirscheyi Skejo, Pushkar, Tumbrinck et Tan sp. n. (Figs 22–29)

Vernacular name: Kirschey's Spiky Pygmy Devil

Discotettix belzebuth (Serville, 1838) [partim]: all older records from NE Borneo need revision

Type locality. Borneo: Malaysia: East Sabah: Sepilok, lowland.

Material examined.

Type material. HOLOTYPE (Fig. 22) 1♀ Borneo: Malaysia: East Sabah: Sepilok XI.1994. (ZFMK); **PARATYPES (Fig. 23)** 2♂, 1♀ Borneo: Malaysia: East Sabah: Kawag Forest Reserve, N5.04861, E117.07355, 118.6±8.7 m.a.s.l., 14.V.2022, 19h27, on tree trunk, leg. M.K. Tan, T. Robillard & R. Japir, SBH.22.76–78 (ZRC); 1♂, 2♀ Borneo: Malaysia: East Sabah: Kawag Forest Reserve, N5.05020, E117.98286, 134.7±6.8 m.a.s.l., 14.V.2022, 13h16, on leaf litter on track, leg. M.K. Tan, SBH.22.69–71 (FRC); 1♂ Borneo: Malaysia: East Sabah: Sepilok: Rainforest Discovery Centre, N5.87414, E117.93782, 96.8±6.8 m.a.s.l., 18.V.2022, 21h28, foliage of seedling near ground, leg. M.K. Tan & T. Robillard, SBH.22.155 (FRC); 1♂ Borneo: Malaysia: East Sabah: Tabin Wildlife Reserve, N5.19465, E118.50310, 92.7±7.5 m.a.s.l., 15.V.2022, 20h01, on foliage near ground, leg. M.K. Tan, T. Robillard & R. Japir, SBH.22.86 (ZRC); 1♀ Borneo: Malaysia: Sabah state (North Borneo), env. of Kinabatangan, 29.II.2008, leg. V.G. Bezborodov (ZISP); 1♀ Borneo: Malaysia: Borneo: East Sabah: Sepilok, 1–6.II.2014, leg. M. Berezin (ZISP).

Additional material from online social media. 1♀ Borneo: Malaysia: East Sabah: Sepilok **(Fig. 27)** photo: T. Kirschey; 2♂♂, 1♀ Borneo: Malaysia: East Sabah: Danum Valley, 04.II.2011. photo: A. Anker (Flickr) **(Figs 25, 26)**; 1 adult Borneo: Malaysia: East Sabah: Danum Valley, 08.II.2014. photograph: P. Bertner (Flickr); 1 adult Borneo: Malaysia: East Sabah: Tawau district, 03.IV.2009. photo: author unknown (found in the album 'Fauna of Sabah') (Flickr); 1 adult Borneo: Malaysia: East Sabah: Kinabatangan River Area 26–27.XI.2016. photograph: C. Odonnell (Facebook); 1 adult Borneo: Malaysia: East Sabah: near the Tawau Hills Park 21.IV.2018. photograph: A. Bouma (Facebook) **(Fig, 29)**; 1 adult Borneo: Malaysia: East Sabah: Tawau Hills Park (4.34N, 117.89E) observed by Sustainable Strategies Network (@hobatahalmahera) on 22.I.2020. (inaturalist.org/observations/37844288) **(Fig. 24)**; 1♂ Borneo: Malaysia: East Sabah: Kinabatangan (5.44N, 117.75E) observed by @simben on 21.VII.2016. (inaturalist.org/observations/102814348) **(Fig. 28)**.

Material that likely belongs to this species but was not checked by the authors. 1♀ Borneo: Malaysia: Sabah state (North Borneo), env. of Kinabatangan, 29.II.2008, leg. V.G. Bezborodov (ZISP).

Type series depository. Museum Alexander Koenig in Bonn (ZFMK).

Etymology. Named after the German biologist Tom Kirschey, our friend and a well-known researcher of the Oriental region, who currently serves as the Head of the International Peatlands and Southeast Asia Programme at NABU (Naturschutzbund Deutschland) headquarters.

Distribution and habitat. The species is restricted to NE Borneo, East Sabah. It is found in Danum Valley (and adjacent Kawag Forest Reserve), Tabin Wildlife Reserve, Tawau Hills, Sepilok District, and around the Kinabatangan River Area. The species inhabits the rainforest, where it can be found on the bark of the roots and trunks of trees, among leaf litter, and sometimes on the foliage of seedlings near the ground. According to the photographer, biologist Tom Kirschey, who observed the species in its natural habitat in the lowlands and the mountains of Sepilok, the microhabitat of *D. kirscheyi* are the roots of the big (old) trees close to pools filled with rain water **(Fig. 28)**. The distribution areas of this species and that of *D. belzebuth* do not appear to overlap.

Diagnosis. The species is similar to *D. belzebuth,* but can be easily distinguished from the latter by the following set of characters: (1) **FM** shorter, narrower, and directed more upwards, not covering the entire vertex as in *D. belzebuth*, which has a large and long digitate **FM** covering the entire vertex, (2) pronotal projections are much shorter, and not as spiky as in *D. belzebuth*, but stouter and triangular, (3) femora are stouter and bear stronger teeth than observed in *D. belzebuth*, and (4) tegmina are smaller, partly covered and not as evident and wide as in *D. belzebuth*.

Description (holotype).

General features. Medium-sized, robust species (body length 14.82 mm); pronotum granulated and wrinkled, with one digitate **FM** on anterior margin and numerous triangular protuberances on dorsal and lateral sides. Almost the whole body (except the eye, labrum, fore and mid tarsi, second and third segments of hind tarsus, and inner side of the hind femur) covered with numerous small tubercles. Macropronotal.

FIGURE 22. Female holotype of *Discotettix kirscheyi* Skejo, Pushkar, Tumbrinck et Tan **sp. n.** and its labels. **A**. dorsal view, B. right lateral view, C. left lateral view, D. ventral view; right: E. head in frontal view, F. holotype labels.

Coloration. Body dark brown, almost completely covered by numerous small tubercles. Pronotum, projections, and protuberances dark brown (Figs 23–26, 28, 29). Antenna dark brown, almost black. Proximal segments of the palpi light brown, and distal segments black. The visible part of the tegmen dark brown and without spots. Legs dark brown with lighter rings and patches. Fore and mid femora and tibiae dark brown with numerous small tubercles with lighter apices, fore and mid tarsi black, second segment with a light ring in the middle; 1st tarsal pads whitish, claws brown. Hind femur dark brown with numerous small tubercles with lighter apices. Hind tibia dark brown with two weak light rings, one in the basal part, and another in the distal third. 1st tarsus of hind leg pale brown, pads whitish; third segment pale brown with a dark ring in its distal part, claws brown. Tergites, sternites, epiproct, and cerci dark brown.

Head. In dorsal and frontal view, vertex 1.95 times as wide as an eye. Fossula elliptic and deep. Lateral ocelli at the level of the lower margin of a compound eye. In frontal view, frontal costa narrow, bifurcated slightly above lateral ocelli into finely granulated facial carinae, forming a narrow scutellum. Scutellum slightly narrower than antennal groove (Fig. 22E). Antennal groove considerably below the lower margin of the compound eye. Antennae 13-segmented, short in appearance compared to *D. belzebuth*: scapus (1st antennomere) and pedicel (2nd antennomere) massive; basal segments (3rd to 6th) elongated, but shorter than in *D. belzebuth*, and circular in cross-section; central or subapical segments (7th and 8th) strongly widened, pennate, 8th being the widest antennal segment (about 3–4 times as long as wide), but only slightly wider than the 7th; subapical segments less widened than in the other species of the subgenus *Discotettix*; apical segment 9th small and pennate, smaller than the subapical and much larger than the rest of the apical segments; apical segments 10th to 13th reduced, very small, and borders between them barely

visible. Antennomeres 3rd to 9th bearing saw-like margins, because of the presence of large basiconic sensilla. When the body and the antennae are covered with algae and moss, the 8th segment is free of epizoic organisms.

Pronotum. Pronotum wrinkled and granulated, covered by numerous small and medium-size tubercles. The posterior process of the pronotum extended beyond the hind knees for less than half of the hind femur length. Disc of the pronotum slightly depressed behind the well-developed shoulder. Pronotum with 5(–7) unpaired projections of variable size on median carina (digitate **FM** and 4 to 6 *medial projections*), 3 pairs of **FL**, up to 7 pairs of more or less distinct *mediolateral projections*, 3 pairs of *lateral projections,* and a pair of **VL** (well seen in profile). Prozona robust, wider than long (because of the short **FM**). Anterior margin of pronotum projected into a medium-sized digitate **FM** protuberance directed mainly upwards than slightly forwards, and not covering the whole vertex above. Prozonal and extralateral carinae forming small **FL1** and larger **FL2**, more distinct. **FL3** dentiform. Behind the **FM** medial carina extended along the whole length of pronotum, with 5 unpaired large and small *medial* projections (well visible in profile). **PM** triangular and smaller than other *medial* projections. **MM1** is the largest projection; **MM2** and **MM3** distinct, while **MM4** and **MM5** small. **PML1** and **PML2** distinct, tubercle-like. **MML1** and **MML2** large and triangular; **MML3**, **MML4,** and **MML5** smaller, decreasing in size caudad. **MML4** and **MML5** sometimes absent. **PL1** and **PL2** triangular, tubercle-like. **ML** sharp and triangular. The apex of the posterior pronotal process in dorsal view shallowly excised. The lower part of the lateral lobe with serrate anterior and posterior margins, elongated as spine-like **VL**, with saw-like margins, directed outwards (Fig. 22A–C).

Wings. The visible part of the tegmen small, oval with a tuberculated surface, visible part 2.57 times as long as wide; the ratio of the maximum width of the mid femur (without teeth)/visible part of tegmina width 1.21. Hind wing not reaching the apex of the posterior pronotal process, ending a few millimeters before the tip.

FIGURE 23. *Discotettix kirscheyi* Skejo, Pushkar, Tumbrinck et Tan **sp. n.**, male paratype SNH.22.155 in the natural habitat, Sepilok, Sabah, Malaysia, Borneo. Photograph by Ming Kai Tan.

Legs. Femora robust, compressed laterally, surface rough, dorsal, and ventral margins roughly serrate. Fore and mid femora bearing one genicular tooth on knees on each margin, and additionally 3 strong teeth on upper carina and 2–3 on lower margin, almost equal in size; teeth on fore femur equal or larger than on mid femur. Upper and lower margin of hind femur finely serrated, with 2 lappets on each margin, and with numerous small tubercles. Lateral area of hind femur with weak carinae that have up to 3 outgrowths, especially in ventro-external carina. Genicular teeth larger than antegenicular. teeth. Fore femur length/width ratio 4.69. Mid femur length/ width ratio 3.94. Hind femur length/width ratio 3.28. Both sides of the upper margin of the hind tibia finely serrated, with 2–3 outer and 2–3 inner larger teeth (spines).

Abdominal apex. Male subgenital plate in ventral view with shallowly excised apex, slightly longer than wide. Female subgenital plate in ventral view with a keel in middle and with a triangular protrusion in the middle of posterior margin. Ovipositor elongated, upper valve 5.0 times as long as wide. The lower valve of ovipositor about 6.0 times as long as wide (maximal width). Cerci stout, with thin apex, hairy.

Measurements. All the measurements of *Discotettix kirscheyi* **sp. n.** are given in the Table 2.

FIGURE 24. *Discotettix kirscheyi* Skejo, Pushkar, Tumbrinck et Tan **sp. n.** in the natural habitat. Photograph by Sustainable Strategies Network (@hobatahalmahera in iNaturalist). CC BY-NC-SA 4.0 Licence. The photograph is available on the link: https://www.inaturalist.org/observations/37844288.

FIGURE 25. Male of *Discotettix kirscheyi* Skejo, Pushkar, Tumbrinck et Tan **sp. n.** in the natural habitat, Danum Valley, Sabah, Malaysia, Borneo. Photograph by Arthur Anker. Reproduced with the author's permission. The photograph is available on the link: https://www.flickr.com/photos/artour_a/6204630856/.

FIGURE 26. Male and female of *Discotettix kirscheyi* Skejo, Pushkar, Tumbrinck et Tan **sp. n.** in the natural habitat, Danum Valley, Sabah, Malaysia, Borneo. Photograph by Arthur Anker. Reproduced with the author's permission. The photograph is available at the link: https://www.flickr.com/photos/artour_a/5563149548/.

FIGURE 27. The natural habitat of *Discotettix kirscheyi* Skejo, Pushkar, Tumbrinck et Tan **sp. n.** in Sepilok, a secondary lowland dipterocarp forest. Photograph by Tom Kirschey. Reproduced with the author's permission.

FIGURE 28. Male of *Discotettix kirscheyi* Skejo, Pushkar, Tumbrinck et Tan **sp. n.** in natural habitat, Kinabatangan, Sabah, Malaysia, Borneo. Photograph by @simben and available on iNaturalist on the link https://www.inaturalist.org/observations/102814348. Reproduced with the author's permission.

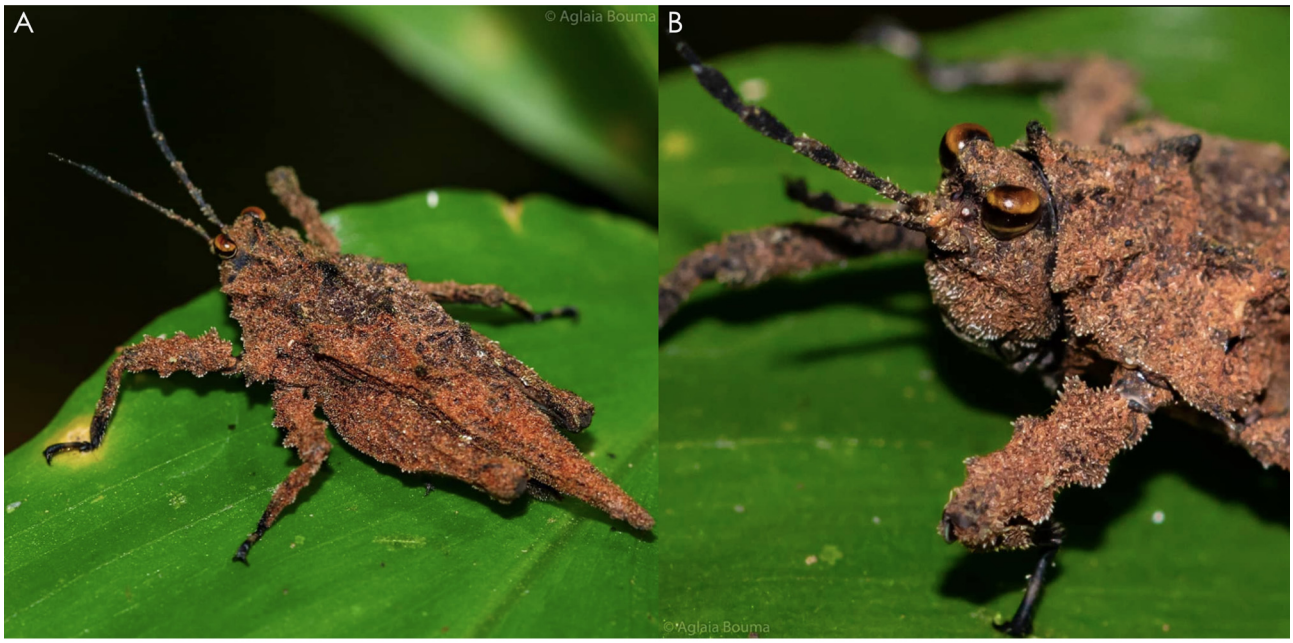

FIGURE 29. *Discotettix kirscheyi* Skejo, Pushkar, Tumbrinck et Tan **sp. n.** in a natural habitat near Tawau Hills Park in Sabah, Malaysia, Borneo. A. Dorsolateral habitus; B. head and pronotum detail. Photograph by Aglaia Bouma. Reproduced with the author's permission.

TABLE 2. Kirschey's Spiky Pygmy Devil (*Discotettix kirscheyi* Skejo, Pushkar, Tumbrinck et Tan sp. n.) measurements of female holotype (♀HT) and male and female paratypes (♂ PT and ♀PT). All the measurements are given in millimeters.

		SBH.2 2.76	SBH.2 2.77	SBH.2 2.86	SBH.2 2.69	SBH.2 2.155	SBH.2 2.70	SBH.2 2.71	SBH.2 2.78
	♀HT	♂ PT	♂ PT	♂ PT	♂ PT	♂ PT	♀ PT	♀ PT	♀ PT
BL	14.82	10.8	9.5	10.1	10.5	11.5	12.4	13.1	11.9
PnL	15.6	13.7	13.3	13.5	13.6	15.2	15.4	16.2	15.0
PnW	6.76	6.2	6.4	5.7	5.8	6.3	6.9	6.9	7.0
AnL	6.11	5.9	-	5.8	5.1	5.7	-	5.7	6.0
TL	1.8	1.5	1.5	1.6	1.5	1.8	1.8	2.0	1.9
TW	0.7	0.5	0.5	0.5	0.5	0.7	0.6	0.6	0.8
fFL	3.75	3.2	3.2	3.2	2.7	2.9	2.9	3.9	3.6
fFW	0.8	0.8	0.9	-	0.8	0.8	1.0	0.9	0.9
mFL	3.35	3.3	3.1	3.0	3.4	3.4	3.3	3.5	4.0
mFW	0.85	0.8	0.8	0.7	0.8	0.8	0.7	0.6	0.8
hFL	7.54	6.6	6.3	6.3	6.3	6.5	7.0	7.3	7.3
hFW	2.3	2.1	2.2	2.0	2.0	2.1	2.3	2.4	2.3
OvL	2.1	NA	NA	NA	NA	NA	-	1.2	1.1
AnL/fFL	1.63	1.8	-	1.8	1.9	2.0	-	1.5	1.7
VW	1.07	0.9	1.0	0.9	1.0	1.1	1.1	1.1	1.1
EW	0.55	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.7
VW/EW	1.95	1.6	1.7	1.6	1.7	1.8	1.9	1.9	1.7

		SBH.2 2.76	SBH.2 2.77	SBH.2 2.86	SBH.2 2.69	SBH.2 2.155	SBH.2 2.70	SBH.2 2.71	SBH.2 2.78
	♀HT	♂ PT	♂ PT	♂ PT	♂ PT	♂ PT	♀ PT	♀ PT	♀ PT
SW	0.25	0.2	0.2	0.2	0.2	0.2	0.3	0.2	0.3
AgW	0.39	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3
ScW	0.31	0.3	0.3	0.3	0.3	0.3	0.4	0.2	0.3
SW/AgW	0.64	0.7	0.7	0.7	0.7	0.7	1	0.7	1
SW/ScW	0.81	0.7	0.6	0.7	0.8	0.7	0.9	0.9	0.8
As-L/W	3.31	4.0	-	3.3	4.3	3.8	-	3.6	3.0
PrzW	3.6	3.1	3.1	2.9	3.2	3.2	3.5	3.7	3.7
PrzL	1.85	2.0	2.0	1.7	2.0	2.1	2.0	2.4	2.1
Prz-W/L	1.95	1.5	1.6	1.7	1.6	1.5	1.7	1.5	1.7
TL/TW	2.57	2.9	2.8	3.0	2.8	2.8	2.9	3.5	2.4
mFW/TW	1.21	1.5	1.4	1.4	1.5	1.2	1.2	1.1	1.0
fFL/fFW	4.69	4.0	3.6	-	3.1	3.7	3.1	4.1	4.1
mFL/mFW	3.94	4.3	4.1	4.2	4.4	4.5	4.6	5.6	5.0
hFL/hFW	3.28	3.1	2.9	3.1	3.1	3.1	3.0	3.0	3.2
T1L/T3L	0.91	1.0	1.0	0.9	1.0	1.0	0.9	1.1	1.1

***Discotettix (Discotettix) sumatrensis* Skejo, Pushkar et Tumbrinck sp. n. (Figs 30–32)**
Vernacular name: Sumatran Spiky Pymgy Devil

Type locality. Indonesia: Sumatra: Jambi province, 35 km N of Sungai Penuh, NP Kerinci-Seblat, Mt. Kerinci, 1500–2000 m a.s.l.

Material examined.

Type material. HOLOTYPE: 1♀ Indonesia: Sumatra: Jambi province, 35 km N of Sungai Penuh, NP Kerinci-Seblat, Mt. Kerinci, 1500–2000 m a.s.l. 8–22.XI.1999. Leg. A.V. Gorochov (Figs 30, 31) (ZISP); **PARATYPES:**1♀, 1♂ Indonesia: Sumatra: Jambi province, 35 km N of Sungai Penuh, NP Kerinci-Seblat, Mt. Kerinci, 1500–2000 m a.s.l. 8–22.XI.1999. Leg. A.V. Gorochov (Figs 30, 31) (ZISP).

Type series depository. ZISP: Orthoptera collection of the Zoological Institute of the Russian Academy of Sciences (St. Petersburg), Russia.

Additional material. 1♂ Indonesia: Sumatra: Siolak Daras.: Korinchi Valley (= Kerinci) 3100 ft. (= 945 m a.s.l.) III.1914. identified as *D. selysi* by K. Günther, photographs (Fig. 32) barcode NHMUK012498526 available at https://data.nhm.ac.uk/dataset/56e711e6-c847-4f99-915a-6894bb5c5dea/resource/05ff2255-c38a-40c9-b657-4ccb55ab2feb/record/8248606 (NHMUK).

Etymology. The new species is named *sumatrensis* (adjective masculine, third, vocal declension) after the type locality, Sumatra Island.

Distribution and habitat. The species is currently known only from Mt. Kerinci, Sumatra, the highest vulcano in Indonesia and the Sumatra's highest peak (above 1500 m). The mountain is surrounded by lush forest. It is an isolated mountain, so there is a chance of *D. sumatrensis* being a local endemic. Distribution is shown in Fig. 3.

Specific diagnosis. The species is morphologically similar to *D. kirscheyi* **sp. n.** from Borneo and can be easily distinguished from other species. From *D. scabridus* the species differs by: (I) frontal costa bifurcates between the eyes, (II) **FM** well developed, (III) **MM** triangular and elevated, (IV) **MML** triangular and elevated, (V) lateral and humeral carinae granulated. The species can be distinguished from *D. belzebuth* by the following characters: (I) smaller body size, (II) peculiar coloration of antennae with lighter colored segments, (III) antenna with 7th segment being the widest (not the 8th as in most of the other species), (IV), pronotum with smaller triangular projections, except the digitate **FM**, (V) hind femur with large lappets (smaller in *D. belzebuth*), and (VI) ovipositor generally

slenderer than in *D. belzebuth*. The species differs from *D. selysi* by (I) peculiar coloration of antennae with lighter colored segments, (II) widened antennal segments narrower than in *D. selysi*, (III) pronotal disc with numerous triangular protuberances and (IV) large lappets of hind femur (medium sized in *D. selysi*). The species is similar to *D. kirscheyi* **sp. n.** but can be easily distinguished from the mentioned by (I) longer **FM**, (II) stronger pronotal projections, (III) specialized and colorful antennal segments and (VI) smaller body size.

Holotype description. (Figs 30, 31)

General features. Medium sized, robust species (body length 11.7–13.5 mm); pronotum granulated and wrinkled, with one digitate **FM** on anterior margin and numerous triangular protuberances on dorsal and lateral sides. Almost the entire body (except eye, labrum, fore and mid tarsi, second and third segments of hind tarsus, inner side of the hind femur) covered with numerous small tubercles (Figs 31, 32). Macropronotal.

Coloration. Body dark brown, almost completely covered by numerous small tubercles with lighter apices. Pronotum dark brown with darker projections and protuberances, tubercle-shaped **ML** of humeral angles on shoulders lighter. Antenna darkish with yellowish colored apical segments (after widened segments 8th black with yellowish apex, 9th yellow, 10th–13th black. Maxillary palpi dark brown. The visible part of the tegmen dark brown and without spots. Legs generally dark brown with lighter rings and patches. Fore and mid femora and tibiae dark brown with numerous small tubercles with lighter apices, fore and mid tarsi darkish, second segment with light ring near middle; 1st tarsal pads whitish, claws brown. Hind femur dark brown with numerous small tubercles with lighter apices. Hind tibia in ♀ dark brown with two light rings, one in basal part, and another—in distal third; while in ♂ blackish brown, with weak (not distinguishable) light rings. 1st tarsus of hind leg darkish, with light colored ring near apex, pads whitish; third segment blackish brown with a light ring near the middle, claws brown. Tergites, sternites, epiproct, and cerci dark brown.

Head. In dorsal and frontal views, vertex 2.6 times in ♂, 2.5 times in ♀ as wide as an eye. Fossula deep. Lateral ocelli situated at the level of the lower margin of the compound eye. In frontal view, frontal costa narrow, bifurcated between the lateral ocelli into a distinctly divergent, finely granulated facial carinae, concave in about the middle of its length, forming sand-clock-shaped scutellum. Frontal costa in ♂ 1.6 times, in ♀ 1.5 times, wider than antennal groove, 1.25 times in ♂, 1.2 times in ♀ as long as antennal groove width. Antennal groove considerably below the lower margin of a compound eye (Fig. 30B). Antenna 13-segmented: scapus (1st antennomere) and pedicel (2nd antennomere) massive; basal segments (3rd to 6th) dark, elongated and circular in cross-section; central segment 7th strongly widened and the widest antennal segment (3–3.6 times as long as wide), 8th segment reduced, weakly pennate, dark, and with yellow apex; apical segment 9th small, yellow, elongated, and pennate, smaller than the subapical and much larger than the rest of the apical segments; apical segments 10th to 13th again dark reduced, small, elongated in comparison to other species of the subgenus, and the borders between them barely visible. Antennomeres 3rd to 9th bearing saw-like margins, because of the presence of large basiconic sensilla.

Pronotum. Pronotum wrinkled and granulated, covered by numerous small and medium-size tubercles. Posterior process of pronotum extended beyond hind knees for less than half of hind femur length. Disc of the pronotum depressed behind the well-developed shoulder, slightly descending backwards. Pronotum with 6 unpaired projections of variable size on medial carina (large digitate **FM** and 5 medium-sized *medial*), 3 pairs of **FL** projections, 7 pairs of more or less distinct *mediolateral*, 3 pairs of *lateral* and 1 pair of **VL** projections (well seen in profile). Prozona subsquare: prozonal length/width ratio 1.0 in ♂, 1.15 in ♀. Anterior margin of pronotum projected into a large digitate **FM** protuberance directed mainly forwards than upwards, covering whole vertex above. Prozonal and extralateral carinae in the prozona surpassing the anterior margin of the pronotum as dentiform **FL1** and **FL2**. **FL2** more distinct. Downwards, at the anterior margin of the pronotum less developed dentiform **FL3**. Behind **FM** medial carina extended along the whole length of the pronotum, with 5 unpaired large and small *medial* projections (better seen in profile): behind digitate **FM**, in the prozona, first small triangular **PM** protuberance. Next large triangular protuberance, between spinae of lateral lobes—**MM1**, then **MM2**, **MM3** and **MM4**) protuberances, generally decreasing in size towards apex of pronotal process (sometimes posterior projection almost wanting). Smaller and lower then medial: 7 distinct double triangular **MML**. *Mediolateral* projections in the prozona present as more or less distinct **PML1** double tubercle as a posterior elongation of prozonal carinae, and on same line **PML2** double tubercle near border between prozona and metazona. Small **MML1** between the shoulders, and large **MML2** projection on the place where most Tetrigidae (Tetriginae) species have a posthumeral spot. Next three—**MML3**, **MML4** and **MML5** smaller, decreasing caudad. In the prozona lateral projections present as small double triangular **PL1** and **PL2** tubercles situated between the sulci on the line joining extralateral and humero-apical carinae.

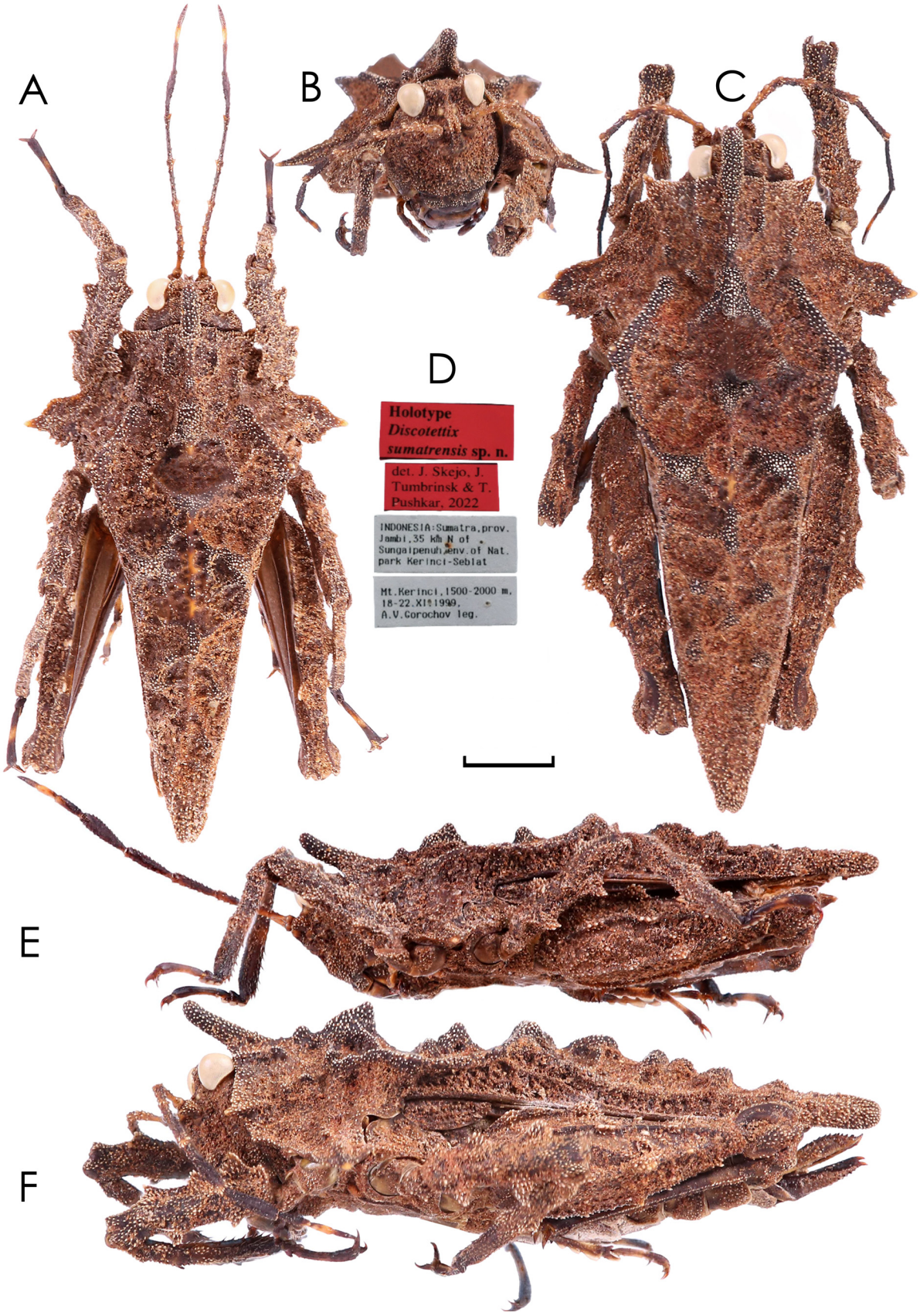

FIGURE 30. *Discotettix sumatrensis* Skejo, Pushkar, et Tumbrinck **sp. n.** A, E) male paratype; B–D, F) female holotype. A: Paratype dorsal view, B. Holotype frontal view, C. Holotype dorsal view, D. Holotype labels, E. Paratype in lateral view. F. Holotype in lateral view. Specimens photographs by V. Loktionov, lables photograph by Sergey Storozhenko. Reproduced with the author's permission. Scale bar = 2 mm. C. Labels.

In metazona, humero-apical carinae forming moderately sharp humeral angle, projected outwards as a small **ML** tubercle of humeral angle, behind this point joining the external lateral carinae. Apex of posterior pronotal process in dorsal view shallowly excised. Lower part of lateral lobe with serrate anterior and posterior margins, elongated as spine-like **VL**, directed outwards (Fig. 30A, C, E, F).

Wings. Visible part of tegmen slightly elongated, oval with champlevé surface, visible part 3.2 times as long as wide in ♂ and 2.9 in ♀; ratio of maximum width of mid femur (without teeth) / visible part of tegmina width 1.6 times in ♂ and 1.29 times in ♀. Hind wing almost reaching the apex of the posterior pronotal process (ending 1.2–1.3 mm before it).

Legs. Femora robust, compressed laterally, surface from smooth to rough, dorsal and ventral margins roughly serrate. Fore and mid femora bearing one genicular tooth on the knees on each margin, and additionally 3 strong teeth on the upper carina and 2–3 on the lower margin, lower usually smaller than upper; teeth on fore femur equal or smaller than on mid femur. Upper and lower margin of hind femur finely serrated, with 2–3 lappets on each margin, and with numerous small tubercles. Lateral area of hind femur with weak carinae that have 2–3 outgrowths, especially in ventro-external carina. Genicular teeth larger than antegenicular. Fore femur length/width ratio 3.9 in ♂ and 3.8 in ♀. Mid femur length/width ratio 4.1 in ♂ and 4.2 in ♀. Hind femur length/width ratio 3.0 in ♂ and 3.2 in ♀. Both sides of the upper margin of hind tibia finely serrated, additionally with 2–3 outer and 2–3 inner (bit larger) teeth.

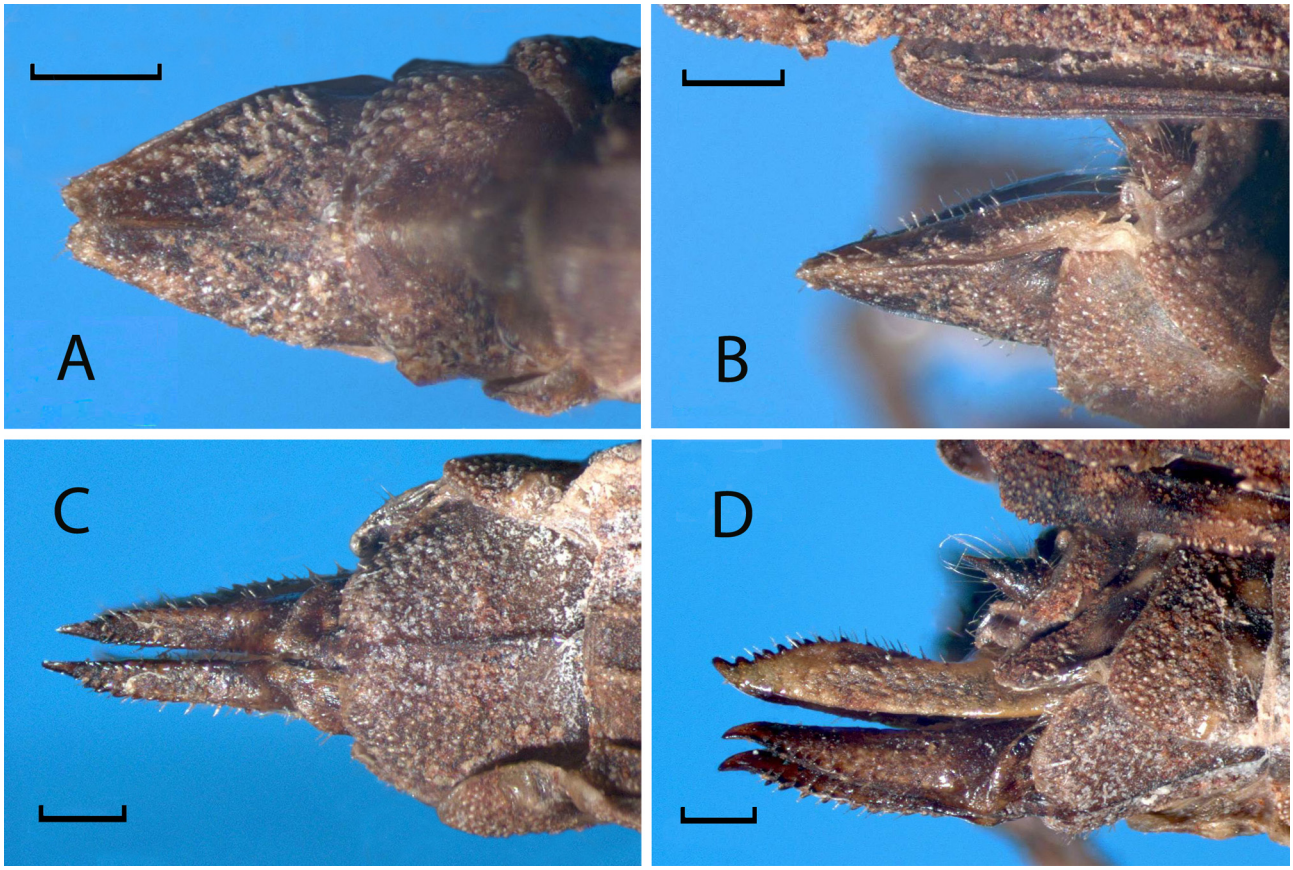

FIGURE 31. Abdominal apex of *Discotettix sumatrensis* Skejo, Pushkar, et Tumbrinck **sp. n.** A, B. male paratype; C, D. female holotype. Photographs by Sergey. Storozhenko. Reproduced with the author's permission. Scale bar = 0.5 mm.

Abdominal apex. Male subgenital plate in ventral view with shallowly excised apex, 1.4 times as long as wide, in lateral view 2.4 times as long as tall (Fig. 31A, B). Female subgenital plate in ventral view with triangular protrusion in middle of posterior margin. Ovipositor elongated, upper valve 5.0 times as long as wide. Lower valve of ovipositor 6.0 times as long as wide (maximal width) (Fig. 31C, D). Cerci length/width ratio near base 1.8 in ♀ and 1.9 in ♂.

Measurements (male paratype and female holoype). **BL** ♂11.7 mm, ♀13.5 mm; **PnL** ♂12.8 mm, ♀15.6 mm; **PnW** ♂6.63 mm, ♀7.86 mm; **AnL** ♂7.2 mm, ♀7.2 mm; **TL** ♂1.6 mm, ♀2.0 mm; **TW** ♂0.91 mm, ♀1.1 mm; **fFL**

♂3.5 mm, ♀3.8 mm; **fFW** ♂0.89 mm, ♀1.01 mm; **mFL** ♂3.3 mm, ♀3.8 mm; **mFW** ♂0.8 mm, ♀0.91 mm; **hFL** ♂6.4 mm, ♀7.5 mm; **hFW** ♂2.13 mm, ♀2.49 mm; **OvL** ♀2.4 mm; **AnL/fFL** ♂2.05, ♀1.89; **VW** ♂1.91 mm, ♀2.05 mm; **EW** ♂0.73 mm, ♀0.82 mm; **VW/EW** ♂2.6, ♀2.5; **SW** ♂0.36 mm, ♀0.41 mm; **AgW** ♂0.23 mm, ♀0.27 mm; **ScW** ♂0.29 mm, ♀0.23 mm; **SW/AgW** ♂1.6, ♀1.5; **SW/ScW** ♂1.25, ♀1.2; **As—L/W** ♂3.6, ♀3.3; **PrzW** ♂4.11 mm, ♀5.62 mm; **PrzL** ♂4.09 mm, ♀4.91 mm; **Prz—W/L** ♂1, ♀1.15; **TL/TW** ♂3.2, ♀2.9; **mFW/TW** ♂1.6, ♀1.29; **fFL/fFW** ♂3.9, ♀3.8; **mFL/mFW** ♂4.1, ♀4.2; **hFL/hFW** ♂3, ♀3.2; **T1L/T3L** ♂1.15, ♀1.07.

FIGURE 32. *Discotettix sumatrensis* Skejo, Pushkar, et Tumbrinck **sp. n.**, male from NHMUK (012498526). A. right lateral view; B. dorsal view; C. labels. Photography NHMUK, copyright The Trustees of the Natural History Museum, London.

Subgenus *Mnesarchus* Stål, 1877, nom. resurr.

Mnesarchus Stål, 1877: 55; synonymized with *Discotettix* by Bolívar (1887).
Mnesarchus (as subgenus of *Discotettix*): Kevan 1966: 380.
Discotettix (partim): Bolívar 1887: 306; Kirby 1910: 2 [listed in the catalog]; Blackith 1992: 46 [listed in the catalog]; Yin *et al.* 1996: 866 [listed in the catalog], Otte 1997: 32 [listed in the catalog].

Type species: *Mnesarchus scabridus* Stål, 1877, by original monotypy.

Taxonomic notes. The genus *Mnesarchus* have been synonymized with *Discotettix* by Bolívar (1887). Kevan (1966) recognized it as distinct subgenus but later *Mnesarchus* has been considered a synonym of *Discotettix* again (Blackith, 1992; Yin *et al.*, 1996; Otte, 1997). The type species is morphologically very different from other *Discotettix* members and is thus assigned to its own subgenus, *Mnesarchus*. It can be easily separated from other species of the genus by the set of the following characters: (I) frontal costa bifurcates at the lower margin of the compound eyes (bifurcation is in the lower third of the compound eyes in *D. aruanus* **sp. n.**, *D. belzebuth, D. doriae, D. kirscheyi* **sp. n.**, *D. selysi*, and *D. sumatrensis* **sp. n.**), (II) **FM** present as a low tubercle (developed and elevated in *D. aruanus* **sp. n.**, *D. belzebuth, D. doriae, D. kirscheyi* **sp. n.**, *D. selysi*, and *D. sumatrensis* **sp. n.**), (III) **MM** laterally compressed and elevated (spine-like in *D. belzebuth,* triangular protrusions in *D. sumatrensis* **sp. n.**, *D. kirscheyi* **sp. n.**, while very low in *D. aruanus* **sp. n.**, *D. doriae* and *D. selysi*), (IV) **MML** low and triangular, compressed elevations (spine-like in *D. belzebuth,* triangular protrusions in *D. sumatrensis* **sp. n.,** similarly formed in *D. selysi*), (V) interscapular area triangular, with large concavity (similarly to *D. selysi,* and *D. sumatrensis* **sp. n.**, almost parallel in *D. belzebuth*), (VI) lateral and humeral carinae strongly toothed (similar to *D. belzebuth*, granulated in *D. selysi,* and *D. sumatrensis* **sp. n.**), (VII) weak **ML** (almost absent in *D. scabridus*, while well visible in other species), (VIII) **VL** complex, with a few spines (in other species usually with one main spine, and a saw-like margin) and (IX) tegmen more elongated (**TL/TW** > 5) than in the other species of the genus (**TL/TW** < 3.5).

Composition. The type species of *Mnesarchus* is the only species presently assigned to this subgenus.

Discotettix (Mnesarchus) scabridus (Stål, 1877) (Fig. 33)

Vernacular name: Filipino Spiky Pygmy Devil

Mnesarchus scabridus Stål, 1877: 55 [original description, type locality: the Philippines]; Casto de Elera 1895: 207.
Discotettix scabrides: Hancock 1907a [lapsus calami].
Discotettix scabridus: Bolivar 1877: 307 [in revision]; Kirby 1910: 2 [listed in the catalog]; Günther 1938: 302 [in revision]; Yin *et al.* 1996: 866 [listed in the catalog]; Blackith 1992: 46 [listed in the catalog]; Otte 1997: 32 [listed in the catalog].
Discotettix (*Mnesarchus*) *scabridus*: Kevan 1966: 380 [new records].

This is the type species of the subgenus *Mnesarchus* and the only species presently assigned to this subgenus. The species diagnosis and the description may hence be used as subgeneric diagnosis and description of *Mnesarchus*.

Type locality. The Philippines (without exact locality).

Lectotype designation. The lectotype for this species is designated herewith, that being the female deposited in NHRS, under the inventory number NRM-ORTH 00112879, designated by J. Tumbrinck. The lectotype bears the red label 'lectotypus'. Lectotype designation is important because of the future analysis of intraspecific differences among *D. scabridus* populations in Mindanao and other islands that could result in the discovery of new species or subspecies. Since Tetrigidae species are usually morphologically well-defined, the lectotype may provide a basis for the identification of the nominotypical and/or already described taxon.

Material examined.

Type material. LECTOTYPE (Fig. 33): ♀ Ins. Philipp. Collector: Semper, det. C. Stål, inventory number NRM-ORTH 00112879 (NHRS); labeled *Mnesarchus scabridus*; here designated.

Additional museum material. 2♀♀ the Philippines, Mindanao, Zambaonga, date uknown, Collector: W. Schultze, det. K. Günther (SMTD); 1♂ Ins. Philipp. Collector: Semper, det. K. Günther (MFN); 1♀, 1♂ the Philippines, Mindanao, Pt. Bango, det. J. Tumbrinck (NHRS); 1♀ labeled '100.4115' (MNCN) det. J. Skejo; 1♀ nymph, 2♂♂ the Philippines, Mindanao, Zambonga Del Norte, VIII.2020. Collector: Sandayong, det. J. Tumbrinck (ZMHU); 1♀, 1♂ the Philippines, Luzon, N-Luzon Island, Hueva, Belance, III.2014, det. J. Tumbrinck (ZMHU);

Additional material from eBay. 3♀♀ the Philippines, Mindanao, Zambaonga del Sur, IX.2013. Collector: unknown (not in museum) (found on eBay on 18.VI.2016) det. J. Skejo; 2♂♂, 2♀♀ the Philippines: Samar Collector: unknown (not in museum) (found on eBay on 21.VII.2016) det. J. Skejo; 4♀♀ the Philippines: Mindanao: Bukidnon Collector: unknown (not in museum) (found on eBay on 04.VIII.2016) det. J. Skejo; 1♂ the Philippines: Mindanao: Davao Collector: unknown (not in museum) (found on eBay on 15.VIII.2016) det. J. Skejo; 3♀♀ the Philippines: Mindanao: Surigao unknown (not in museum) (found on eBay on 01.IX.2016) det. J. Skejo.

Distribution. This species inhabits the Philippines, where it has been reported from the islands of Mindanao, Samar, and Luzon. Numerous records from Mindanao, while few from Luzon might indicate that the species has higher abundance in Mindanao.

Subgeneric diagnosis of *Mnesarchus* and specific diagnosis of *Discotettix scabridus*. The species is morphologically very different from other *Discotettix* members and is thus assigned to its own subgenus, *Mnesarchus*. It can be easily separated from other species of the genus by the set of the following characters: (I) frontal costa bifurcates on the lower margin of the compound eyes (bifurcation is in the lower third of the compound eyes in *D. aruanus* **sp. n.**, *D. belzebuth, D. doriae, D. kirscheyi* **sp. n.**, *D. selysi*, and *D. sumatrensis* **sp. n.**), (II) **FM** present as a low tubercle (developed and elevated in *D. aruanus* **sp. n.**, *D. belzebuth, D. doriae, D. kirscheyi* **sp. n.**, *D. selysi*, and *D. sumatrensis* **sp. n.**), (III) **MM** laterally compressed and elevated (spine-like in *D. belzebuth,* triangular protrusions in *D. sumatrensis* **sp. n.**, *D. kirscheyi* **sp. n.**, while very low in *D. aruanus* **sp. n.**, *D. doriae* and *D. selysi*), (IV) **MML** low and triangular, compressed elevations (spine-like in *D. belzebuth,* triangular protrusions in *D. sumatrensis* **sp. n.**, similarly formed in *D. selysi*), (V) interscapular area triangular, with large concavity (similarly to *D. selysi,* and *D. sumatrensis* **sp. n.**, almost parallel in *D. belzebuth*), (VI) lateral and humeral carinae strongly toothed (similar to *D. belzebuth*, granulated in *D. selysi,* and *D. sumatrensis* **sp. n.**), (VII) weak **ML** (almost absent in *D. scabridus*, while well visible in other species), (VIII) **VL** complex, with a few spines (in other species usually with one main spine, and a saw-like margin) and (IX) tegmen more elongated (**TL/TW** > 5) than in other species of the genus (**TL/TW** < 3.5).

Redescription (Fig. 33).

General features. Medium-sized flattened species (body 12.3–12.75 mm) (15–17 mm cited in the original description, but in this measurement, pronotum was probably included as well), relatively robust in dorsal view. The entire body finely granulated, rugose; pronotum wrinkled and with numerous small tubercles and medium-sized projections. Macropronotal form.

Coloration. Body color from almost black, dark brown, and ferruginous brown to yellowish-brown. Pronotal protuberances usually colored in different colors (black, reddish, yellow, whitish) and often different in color from the rest of the pronotal surface. Antenna with pale colored joints between the antennomeres; scapus, pedicel, basal and medial segments dark brown, while subapical and apical even darker. Maxillary palpi dark brown, sometimes with even darker distal margins of the last segments. The visible part of the tegmen dark brown, without spots. Tibiae and tarsi with unclear pale colored rings.

Head. In dorsal and frontal view, vertex 2.4–2.65 times as wide as the eye. Lateral carinae of the vertex granulated. Lateral ocelli situated at the level of the lower margin of the compound eye. In frontal view, frontal costa narrow, bifurcating a bit above the lateral ocelli into slightly divergent facial carinae forming a very narrow scutellum. Antennal groove slightly wider than the scutellum, situated just below the lower margin of the compound eye (Fig. 33C). Antenna 13-segmented (in male seems 12-segmented, because 13th segment very small and not visible under an optical microscope, only under SEM): scapus (1st antennomere) and pedicel (2nd antennomere) massive; basal segments (3rd to 6th) elongated and circular in cross-section; central or subapical segments (7th and 8th) widened, weakly pennate, 7th and 8th antennal segments almost equal in width (2–2.4 times as long as wide); apical segment 9th elongated, but much smaller than the subapical and much larger than the rest of the apical segments; apical segments 10th to 13th reduced, very small, and borders between them barely visible. Antennomeres 3rd to 9th bear weak saw-like margins (weaker than in the other species of the genus), because of the presence of large basiconic sensilla. Antennomeres of *D. scabridus* are less significantly widened than in other species of the genus and less saw-like in appearance, supposedly because of fewer or smaller basiconic sensilla.

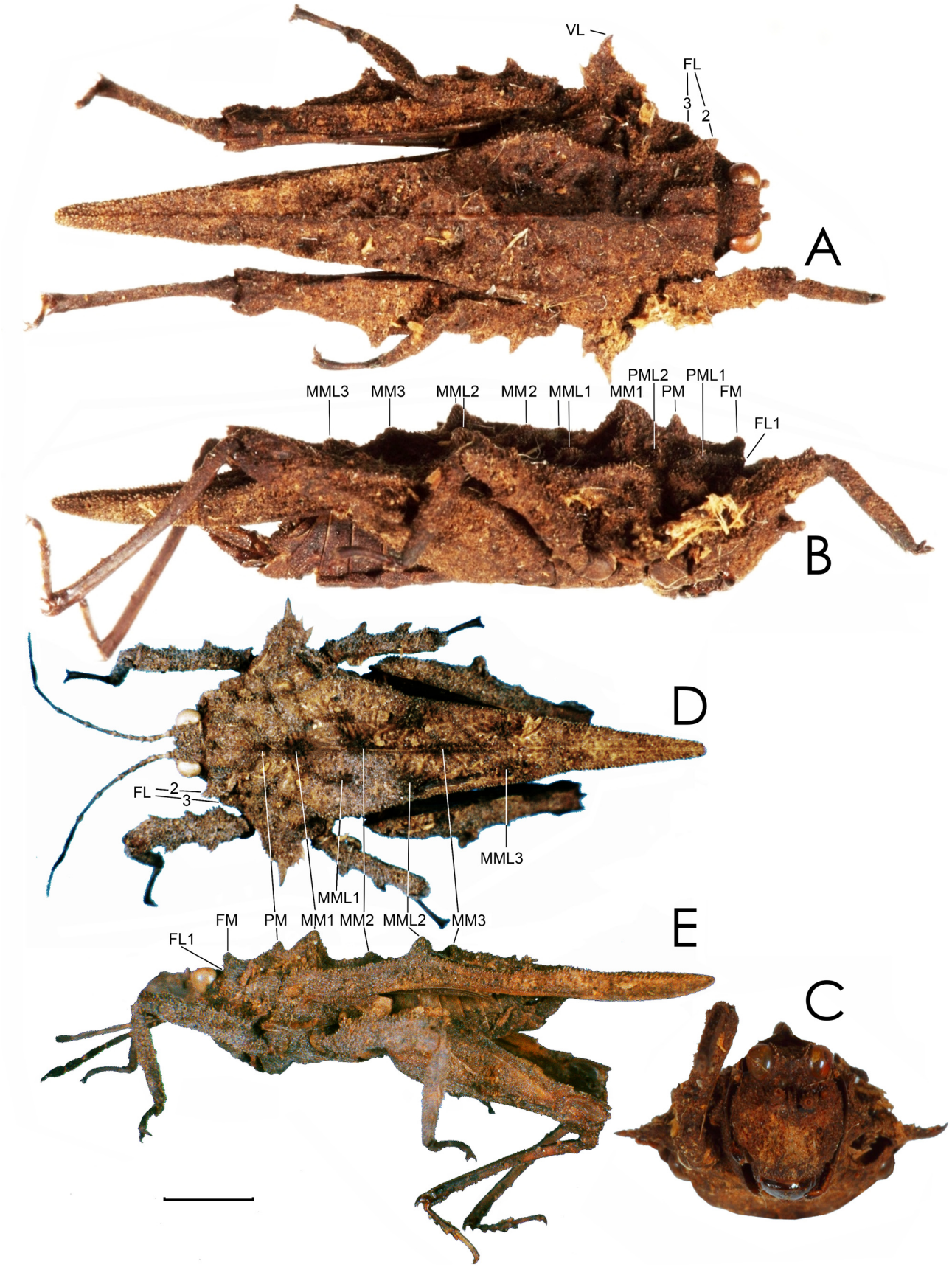

FIGURE 33. *Discotettix scabridus* (Stål, 1877). A–B, E) lectotype female from the Philippines, in NHRS: A. dorsal view; B. lateral view; C. frontal view (photograph by Josef Tumbrinck); D–E). male from the Philippines in MfN: D. dorsal view; E. lateral view (photograph by Sigfrid Ingrisch, reproduced with the author's permission).

Pronotum. Pronotum wrinkled and granulated, covered in numerous small tubercles, medium-sized and large triangular protuberances. The posterior process of the pronotum slender, surpassing the hind knee for about half the length of the hind femur (macropronotal form). Disc of the pronotum a bit depressed behind the well-developed shoulder, gradually descending backward. Pronotum with 5 unpaired projections of variable size on the medial carina (**FM**, **PM** and 3 **MMs**), three pairs of **FLs**, two pairs of more or less distinguished **PMLs,** and two of **MMLs**; three pairs of *lateral* and a pair of **VL** (well visible in profile). Anterior margin of the pronotum truncated, with small **FM** directed upwards. **FM** considerably lower than in the other species of the genus. Prozonal carina elevated and decurved caudad in the direction of the median carina, in females projected anteriorly as a small dentiform **FL1**. Extralateral carinae distinct in males, saw- or fan-like and elevated along the entire length much more than the prozonal carina, surpassing the anterior margin of the pronotum as a dentiform **FL2**. **FL3** weak, but distinct. Prozona of variable length, from subsquare to wider than long, but still very short when compared to other species of the genus. Behind the **FM** median carina extended along the whole length of pronotum. **PM** larger than **FM**, and **MM1** larger than **PM1**. **MM2** medium-sized in males or small in females. **MM3** lies in the middle of pronotum length, in females as large as **PM**, while in males smaller. **MM4** small and indistinct. **PML1** and **PML2** very small. **MML1** small, situated between the shoulders. **MML2** large. **MML3** very small, better visible in females than in males. **MML4** almost indistinct in both sexes. **PL1** and **PL2** small and triangular tubercles between the sulci on the line joining the extralateral carinae and the humero-apical carinae. **ML** reduced, almost absent. The apex of the posterior pronotal process very narrow, and rounded; in females weakly excised. The posterior part of the pronotal process (about a fifth of the pronotum length) directed slightly upwards or in the level of the rest of the pronotum. The lower part of the lateral lobe with serrate margins (2–3 larger teeth on the posterior margin, and numerous smaller teeth on the anterior margin), elongated as strong spine-like **VL** directed outwards and slightly forwards (Fig. 33A, B, D, E).

Wings. The visible part of the tegmen shaped quite elongated oval, lower side slightly curved. The tegmen is not always visible. Based on the photographs, it is hard to say whether tegmina are visible or not, in both sexes they can be noticed only after careful examination under the stereomicroscope. Hind wing present, visible under pronotum, not reaching the apex of the pronotum.

Legs. Femora robust and compressed laterally. Dorsal and ventral margins of the fore and the mid femora roughly serrate, with genicular tooth on knees, and additionally with 1–3 strongly projected teeth on each margin. Teeth of ventral margin projected outwards and downwards. Hind femur with small teeth on the dorsal and ventral margins; one large tooth projected outwards situated on the ventro-external carina. Genicular and antegenicular teeth small, but recognizable. Both sides of the dorsal margins of the hind tibia finely serrated, additionally with 5–8 outer and 2–4 inner bit larger teeth. The first tarsal segment of the hind leg slightly longer than the third segment.

Abdominal apex. Ovipositor elongated.

Measurements. BL ♂10.56 mm, ♀♀12.31–12.74 mm; **PnL** ♂14.99 mm, ♀♀15.48–16.52 mm; **PnW** ♂8.16 mm, ♀♀7.99–8.95 mm; **AnL** ♂5.08 mm, ♀♀6.89–7.01 mm; **TL** ♂2.49 mm, ♀♀2.51–2.7 mm; **TW** ♂0.49 mm, ♀♀0.47–0.52 mm; **fFL** ♂3.45 mm, ♀♀3.86–4.01 mm; **fFW** ♂0.84 mm, ♀♀0.68–0.77 mm; **mFL** ♂3.52 mm, ♀♀3.42–3.93 mm; **mFW** ♂0.84 mm, ♀♀0.76–1.01 mm; **hFL** ♂6.69 mm, ♀♀7.39–7.91 mm; **hFW** ♂2.05 mm, ♀♀2.16–2.22 mm; **OvL** ♀♀1.39–1.55 mm; **AnL/fFL** ♂1.48, ♀♀1.68–1.72; **VW** ♂0.93 mm, ♀♀1.11–1.18 mm; **EW** ♂0.49 mm, ♀♀0.42–0.49 mm; **VW/EW** ♂1.9, ♀♀2.51–2.65 mm; **SW** ♂0.22 mm, ♀♀0.19–0.23 mm; **AgW** ♂0.39 mm, ♀♀0.31–0.36 mm; **ScW** ♂0.25 mm, ♀♀0.18–0.21 mm; **SW/AgW** ♂0.64, ♀♀0.51–0.7; **SW/ScW** ♂1.48, ♀♀0.96–1.02; **As—L/W** ♂2.41, ♀♀2.06–2.11; **PrzW** ♂3.25 mm, ♀♀3.18–3.24 mm; **PrzL** ♂2.41 mm, ♀♀1.34–1.74 mm; **Prz—W/L** ♂1.35, ♀♀1.84–2.41; **TL/TW** ♂5.08, ♀♀4.68–5.71; **mFW/TW** ♂1.75, ♀♀0.47–0.51; **fFL/fFW** ♂4.01, ♀♀5.18–5.34; **mFL/mFW** ♂4.09, ♀♀3.88–3.91; **hFL/hFW** ♂3.26, ♀♀3.49–3.66; **T1L/T3L** ♂1.14, ♀♀1.22–1.31.

Genus *Disconius* Skejo, Pushkar et Tumbrinck gen. n.

Type species: *Discotettix shelfordi* Hancock, 1907 (= *Disconius shelfordi* **comb. n.**).

Justification for the establishment of the new genus. Head and pronotum morphology of *Disconius shelfordi* **comb. n.** differs too widely from other *Discotettix* species for it to be regarded as a member of the latter genus, so a new monotypic genus is established for this species, *Disconius* Skejo, Pushkar et Tumbrinck **gen. n.** Fastigial horns

are lower, while the bifurcation of the frontal costa, lateral ocelli and antennal grooves have a much higher position than in any *Discotettix* species. Unlike **FM** and high pronotal projections in *Discotettix*, *Disconius* **gen. n.** lacks elevated **FM** (present as a small tubercle on the anterior pronotal margin); **FL1** and **FL3** are not strongly projected forwards as in *Discotettix,* and the strongest projections are **ML** of the shoulders area (similar to *Tegotettix*). The new genus is assigned to the subfamily Scelimeninae and to the tribe Discotettigini **stat. resurr.** on the basis of the width of the vertex (wide) and the weak elevation of the lateral carinae of the vertex; the typical arrangement of the pronotal projections (**FM**, **MM**, **MML**, **ML**); armed femora; and not widened hind tibiae and tarsi. The new genus is similar and likely related to the genera *Tegotettix* and *Discotettx*, but also superficially resembles *Falconius*. From *Tegotettix* and *Falconius* it can be easily distinguished by widened antennal segments, while from *Discotettix,* to which it was formerly assigned, it can be distinguished by a number of characteristics stated above. Molecular and comprehensive morphometric comparison of *Disconius shelfordi* **comb. n.** with large series of *Discotettix, Tegotettix,* and *Falconius* specimens is needed in the future, to elucidate the evolution of this curious taxon.

Composition and distribution. A monotypic genus, including only *Disconius shelfordi* (Hancock, 1907) **comb. n.**, known only from northern Borneo.

Etymology. Because of the former taxonomic placement within *Discotettix*, and because of the superficial similarity to certain members of the genus *Falconius* due to its slender appearance and the shape of the pronotal projections, the names of two genera were combined into *Disconius*, meaning that this is both *Discotettix*-like and *Falconius*-like genus.

Differential diagnosis. For the comparison with *Discotettix*, from which *Disconius* **gen. n.** has been removed, see the justification above, as well as the diagnosis of the genus *Discotettix*. From the genus *Tegotettix* (including *T. armatus* and *T. bufocrocodil*) the genus can be separated by head morphology—lateral ocelli positioned higher, frontal costa short before the bifurcation, vertex not bearing high horns, antennae with widened subapical antennal segments, and tibiae not armed. From the genus *Falconius*, *Disconius* **gen. n.** can be separated by the arrangement of the pronotal projections, the lack of flattened hind tarsi, and by widened apical segments of the antennae.

Description.

Head. Frontal costa bifurcation between the compound eyes; scutellum narrower than scapus; upper margin of the antennal groove above the lower margins of the compound eye; lateral (paired) ocelli between the compound eyes; eyes protruded above the vertex Antennae 15-segmented (1st scapus; 2nd pedicel; basal 3rd–7th elongated; central or subapical 8th weakly compressed, 9th elongated and strongly compressed; 10th compressed; apical segment 11th small; apical 12th–15th reduced, smooth and cylindrical). Vertex wider than a compound eye. Lateral carinae of the vertex in frontal view weakly elevated, medial carina of the vertex visible, anterior margin of the vertex slightly indrawn.

Pronotum. Body robust, the ratio of the humeral angles' width to the prozonal width more than 3.5. Anterior margin of the pronotum truncated or slightly excised, without strongly elevated **FM**; prozonal carinae distinct and parallel; extralateral carinae strong, with **FL2** as a small elevation; **FL3** weak; medial carina continuous along all the pronotum, tuberculated; **MM** high compressed elevations; **PMLs** and **MMLs** distinct; **MML2** well developed as a high tubercle; **ML** triangular protrusion with a tubercle on its tip; interhumeral carinae distinct; interscapular area distinct and with parallel margins; lateral area as wide as the interscapular area; humero-apical, humeral, and lateral carinae with triangular or spine-like projections; **VL** protruded as a weak spine; paranota triangular; dorsum of the pronotum without *Discotettix*—characteristic net-like elevations, but still rough.

Legs. Fore and mid femora carinated above, armed with a few small teeth on the dorsal and ventral margins; the dorsal margin of hind femora strongly armed; ventral margin with undulated carinae; the external surface of the hind femora with recognizable transverse ridges; hind tibia finely, densely serrate with numerous small teeth, but without large teeth; distal part of the hind tibia slightly widened, proximal tarsal segment slightly widened; first and the third tarsal segments of the hind legs almost equal in length; pulvilli typical for Scelimenini—first two angular and the third obtuse.

Disconius shelfordi (Hancock, 1907), comb. n. (Figs 34–36)
Vernacular name: Bornean Fallen Pygmy Devil

Discotettix shelfordi Hancock, 1907b: 214 [original description, type locality: Borneo]; Kirby 1910: 575 [listed in the catalog]; Günther 1938: 303 [in review]; Yin *et al.* 1996: 866 [listed in the catalog]; Blackith 1992: 47 [listed in the catalog]; Otte 1997: 32 [listed in the catalog].

Type locality. Malaysia: Borneo: Kuching

Note on the syntypes. The species description was based on two syntypes (male and female) labeled as "NW Borneo: Kuching, 22.IX.1899, Collector Dyak (Bornean native), det. J.L. Hancock" and kept in the Oxford University Museum. As both specimens have been collected at the same locality and date, it is unlikely that they belong to different species. Thus, there is no need for lectotype designation.

Material examined.

Type material. SYNTYPE 1♀ NW Borneo: Kuching, 22.IX.1899., Collector Dyak, det. J. L. Hancock **(Fig. 34)** (OUMNH); **SYNTYPE** 1♂ NW Borneo: Kuching, 22.IX.1899., Collector Dyak, det. J. L. Hancock (OUMNH);

Additional museum material. 2♀♀, 1♂ Indonesia: NE Borneo: Pajau River, leg. Mjöberg, det. J. Tumbrinck **(Fig. 35)** (NHRS).

Additional material from online social media (iNaturalist): 1 adult Borneo: Malaysia: N Sarawak: Marudi (N4.041847, E114.8144) observed 15.X.2019., submitted on 5.II.2020. Photograph by Kinmatsu Lin (@kinmatsu), available at link inaturalist.org/observations/38326084 **(Fig. 36)**.

Distribution: Known only from N Borneo; in Sabah from the surroundings of Kuching (type locality) and from the region of the Pajau River; and from Sarawak reported from Marudi (Hancock 1907b; our data).

Redescription. (Figs 34, 35)

General features. Medium-sized species (body length 14.0–15.8 mm) (in the original description stated as 17.5–19 mm, but it meant from the tip of the head to the tip of the pronotum*)*, relatively slender. The entire body finely granulated, covered by numerous small tubercles and with a few larger ones on the margins of the pronotal disc and the lateral lobes; in lateral view the pronotum almost flat, except for the median carina undulated by a few small wart-like and medium-sized semicircular compressed protuberances (Figs 34, 35). Macropronotal form.

Coloration. Body color from dark brown and ferruginous brown to brown with an inexpressive grayish tint. Some parts of the body pale colored, previously yellowish: tubercles on the margin of the disc and lateral lobe of pronotum, **VL** and **ML**, connections of dark antennal segments, patches on femora, more or less distinct ring in the middle of fore and mid tibiae, two rings (I) in basal and (II) distal third of the hind tibia, distal segments and claws of fore and mid tarsi, and usually yellowish hind tarsus (except for the darker connections of tarsal segments). Living specimens have much more vivid coloration than the museum material. It is visible that the dorsum of the pronotum has an alternation of dark and pale tones (see iNaturalist observation in Material examined).

Head. In dorsal and frontal view, vertex about 2.4 times as wide as the eye. Fossula visible, but not deep. Lateral ocelli situated between the compound eyes. The antennal groove situated at the level of the lower margin of the compound eye (in males) or a bit below (in females). In frontal view frontal costa narrow, bifurcates a bit above the lateral ocelli into a slightly divergent facial carinae, slightly concave inside in medium length and forming a narrow hour-glass shaped scutellum (Figs 34C, 35C). Antennal groove considerably wider than scutellum. Antennae 15 segmented, long. Antennomeres are shaped as follows: scapus (1st antennomere) massive; pedicel (2nd antennomere) large, basal antennomeres (3rd to 7th) elongated, 7th being extremely elongated; central or subapical segments 8th to 10th pennate, 8th slightly widened, while 9th, and 10th significantly widened and flattened; apical segment 11th small; while apical segments 12th to 15th reduced in size, filiform.

Pronotum. Pronotum finely granulated, covered by numerous small and few larger tubercles on the margin of the disc and the lateral lobe of the pronotum; almost flat, except for the wrinkled and scalloped median carina with small wart-like and medium-sized, compressed laterally, semicircular protuberances (different in specimens from different geographical populations); posterior process of pronotum very long, surpassing the hind knee for more than a half hind femur length (macropronotal form). Disc of the pronotum almost of the same height in the anterior part, slightly depressed behind the level of the tegmen apex and gradually descending backwards. Morphology of the pronotal projections variable. Pronotum with 5 unpaired projections of variable size on medial carina (**FM** and 4 *medial projections*); 2–3 pairs of **FL**; a pair of **VL** (better seen in profile); while among the *mediolateral* and *lateral* projections only one projection distinct per group. Prozona very short. Anterior margin of pronotum truncated,

bearing small and weak triangular **FM** directed more upwards, then forwards. Prozonal and extralateral carinae low, tuberculated, not forming sharp saw-like or fan-like ridge, with small **FL1** and more distinct dentiform. **FL3** indistinct. Behind **FM** medial carina extended along the whole length of the pronotum, low, bearing four more or less distinct *medial* projections of variable size (well visible in lateral view). **PM** triangular, equal to or larger than **FM** and joined with the latter as a continuous two-humped structure in specimens of some populations. **MM1**, large. **MM2** is the largest and the most massive projection, usually compressed laterally as a semicircular triangular protuberance. **MM3** relatively large, while **MM4** almost indistinct, marked by spot and darker than rest of the pronotal disc surface. Unlike in *Discotettix* species, *Disconius shelfordi* **comb. n**. has only one distinct projection from the mediolateral group, **MML2**, situated in the place where most Tetrigidae (Tetriginae) species have a posthumeral spot. Similar to the previous projections' group, only one projection exists from *the lateral* group of the projections. In the metazona the humero-apical carinae forms a moderately sharp humeral angle, projected outwards as a small **ML** tubercle of the humeral angle, much larger than other tubercles along the margin of the pronotal disc and the lateral lobe; and behind this point the humero-apical carinae is joining the external lateral carinae. The apex of the posterior pronotal process in the dorsal view shallowly excised. The lower part of the lateral lobe with smooth anterior and posterior margins, without smaller teeth. The lateral lobe elongated as spine-like **VL**, directed exactly outwards, blunt (Figs 34A, B, 35A, B).

Wings. The visible part of the tegmen elongated and oval, distinctly acuminate towards the apex, about 2.75 times as long as wide. Hind wings reach the apex of the pronotal process.

Legs. Femora relatively slender, compressed laterally, and finely granulated, with numerous small teeth-like tubercles on the whole surface. Fore and mid femora bearing a hardly noticeable genicular tooth on the knees, and additionally 1–3 small teeth on the dorsal and ventral margin. Hind femur significantly compressed laterally, finely granulated, without any lappets on dorsal and ventral margins, smooth, and not bearing any recognizable outgrowth on the external carinae. Genicular and antegenicular teeth small. Both sides of the dorsal margin of the hind tibia only finely serrated, without any large teeth.

Abdominal apex. Male subgenital plate in ventral view about 1.5 times as long as wide, in lateral view about 2 times as long as tall. Ovipositor elongated.

Observed variability and differences found among populations, with implications for taxonomy. In the different populations of *D. shelfordi* **comb. n.**, we have observed that the projections of the pronotum differ in size and shape. For example, among the specimens from the banks of the Pajau river the pronotum projections are much more expressed than in the specimens from Kuching (the type locality of the species). This primarily applies to lower and weaker medial protuberances in the specimens from Kuching. Especially **FM** and **PM** are quite small and wart-like, **MM** is medium size and slightly compressed laterally. In specimens from the Pajau river **FM** and **PM** are well expressed, and form a continuous double-hump structure. Other **MMs** are much more expressed, and more compressed laterally, they have semicircular form, especially the largest **MM2**. Only the examination of a larger series will allow drawing conclusions about the specific value of the aforementioned traits.

Measurements (female syntype and a non-type male). BL ♂13.99 mm, ♀15.87 mm; **PnL** ♂18.74 mm, ♀20.81 mm; **PnW** ♂7.35 mm, ♀7.42 mm; **AnL** ♂9.39 mm, ♀9.68 mm; **TL** ♂2.43 mm, ♀2.62 mm; **TW** ♂0.85 mm, ♀0.96 mm; **fFL** ♂3.22 mm, ♀3.33 mm; **fFW** ♂0.57 mm, ♀0.62 mm; **mFL** ♂4.01 mm, ♀4.15 mm; **mFW** ♂0.55 mm, ♀0.61 mm; **hFL** ♂7.99 mm, ♀8.76 mm; **hFW** ♂2.34 mm, ♀2.71 mm; **OvL** ♀1.41 mm; **AnL/fFL** ♂2.91, ♀2.9; **VW** ♂1.1 mm, ♀1.29 mm; **EW** ♂0.45 mm, ♀0.53 mm; **VW/EW** ♂2.44, ♀2.43; **SW** ♂0.14 mm, ♀0.19 mm; **AgW** ♂0.39 mm, ♀0.47 mm; **ScW** ♂0.26 mm, ♀0.38 mm; **SW/AgW** ♂0.36, ♀0.4; **SW/ScW** ♂0.54, ♀0.5; **As-L/W** ♂2.35, ♀2.62; **PrzW** ♂3.18 mm, ♀3.47 mm; **PrzL** ♂1.5 mm, ♀1.71 mm; **Prz-W/L** ♂2.12, ♀2.03; **TL/TW** ♂2.86, ♀2.73; **mFW/TW** ♂0.65, ♀0.64; **fFL/fFW** ♂5.65, ♀5.37; **mFL/mFW** ♂7.29, ♀6.8; **hFL/hFW** ♂3.41, ♀3.23; **T1L/T3L** ♂1.27, ♀1.19.

FIGURE 34. *Disconius shelfordi* (Hancock, 1907), **comb. n.**, lectotype female from N Borneo: Kuching, in UOMNH. A. dorsal view; B. lateral view; C. head in frontal view; and labels. Photographs by A. Spooner & K. Child. Reproduced with the author's permission. Scale bar = 2 mm.

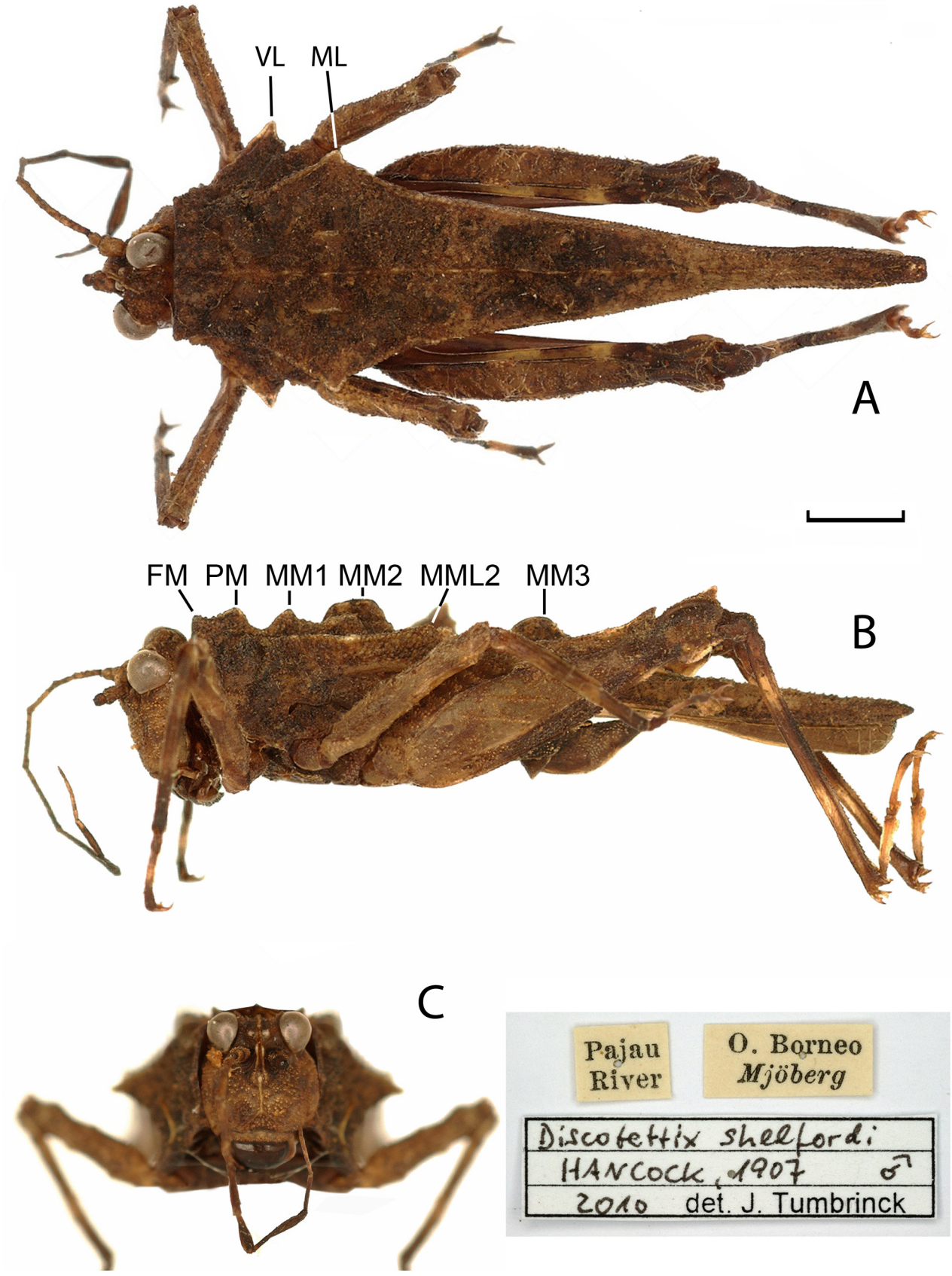

FIGURE 35. *Disconius shelfordi* (Hancock, 1907), **comb. n.**, male from N Borneo: Pajau River, in NHRS. A. dorsal view. B. lateral view. C. head in frontal view, and labels. Photographs by Josef Tumbrinck. Scale bar = 2 mm.

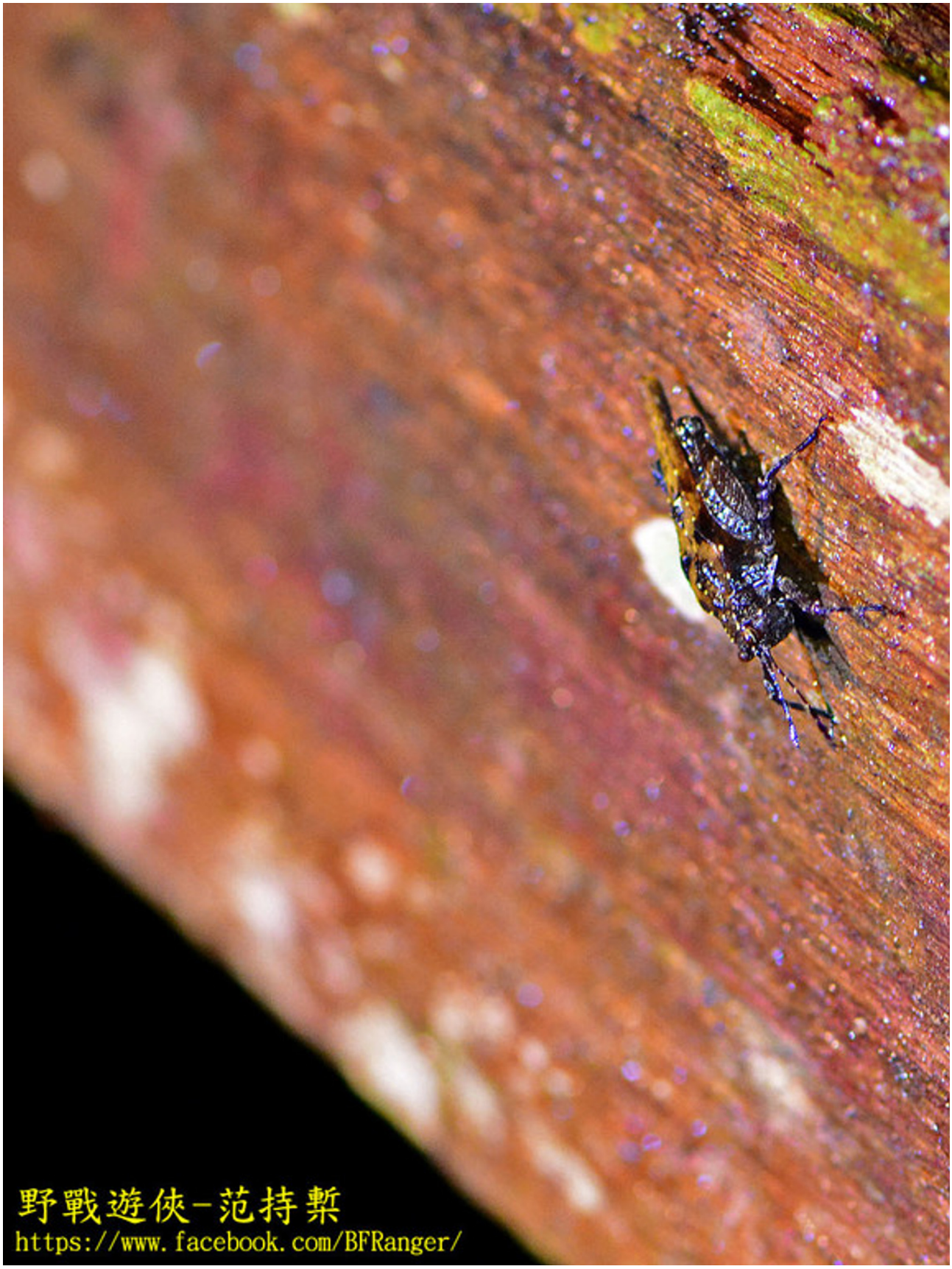

FIGURE 36. Adult *Disconius shelfordi* (Hancock, 1907), **comb. n.** in the natural habitat. Photograph by Kinmatsu Lin (@ kinmatsu). Reproduced with the author's permission. Available at the link: inaturalist.org/observations/38326084.

Discussion

Revisited taxonomy and biogeography of *Discotettix* and *Disconius* gen. n.

The genus *Discotettix* now contains seven species and is divided into two subgenera. The subgenus *Mnesarchus* contains a single species—*D. (M.) scabridus* from the Philippines (islands of Mindanao, Samar, and Luzon), while the nominotypical subgenus, *Discotettix*, contains six species, namely *D. (D.) aruanus* Skejo, Pushkar et Tumbrinck **sp. n.**, *D. (D.) belzebuth, D. doriae* **stat. resurr.**, *D. (D.) kirscheyi* Skejo, Pushkar, Tumbrinck et Tan **sp. n.**, *D. (D.) selysi,* and *D. (D.) sumatrensis* Skejo, Pushkar et Tumbrinck **sp. n.**, from Peninsular Malaysia, Sumatra, Mentawai Isls., Borneo, and Aru.

Type specimens of all the species were examined by the authors, except for *D. armatus*, the type species of the genus *Discotettix* and a supposed synonym of *D. belzebuth*. While the historic synonymization of the species and the original description leave no doubt that *D. armatus* belongs to the genus *Discotettix*, the fact that we could not examine this species is still problematic. Considering that the species was described from Borneo, there are three distinct possibilities as to its true identity: it could truly be a synonym of *D. belzebuth*, it could be a distinct species, or it could be a species of which *D. kirscheyi* Skejo, Pushkar, Tumbrinck et Tan **sp. n.** is a junior synonym. If the type locality of *D. armatus* is NE Borneo, which is not specified in Costa's (1864) description, the latter option is a real possibility. With that in mind, the work that has been done on *D. kirscheyi* Skejo, Pushkar, Tumbrinck et Tan **sp. n.** represents an extensive hypothesis against which the scarce original material can be compared and fitted into its rightful place. Thus, with this paper, we have made the penultimate step towards resolving the identity of *D. armatus*, the last one being to examine the type material. Despite our considerable efforts to do so, our queries made between 2016 and 2021 remain unanswered by the curators of the Museo Zoologico dell'Università "Federico II" (MZFN) in Napoli. Currently, the Bornean Spiky Pygmy Devil (*D. belzebuth*) is known to be a species with a variable number of pronotal spikes, widespread in central, western, and northern Borneo, but its range does not overlap with that of the smaller species with lower (in lateral view) spikes, the Kirschey's Spiky Pygmy Devil (*D. kirscheyi* Skejo, Pushkar, Tumbrinck et Tan **sp. n.**).

The Mentawai Unicorn Pygmy Devil (*D. doriae* **nom. resurr.**) is once again regarded as a valid species, as the review of the available material showed clear differences among this species, *D. selysi*, and *D. aruanus* Skejo, Pushkar et Tumbrinck **sp. n.** On the other hand, *D. selangori* **syn. n**. from southern Peninsular Malaysia has been synonymized with *D. selysi*, as no differences were found between the two. *Discotettix selysi* also inhabits Sumatra, and if in the future any morphometric or molecular differences are found between the Malayan and Sumatran populations, *D. selangori* **syn. n.** might be regarded as a subspecies of *D. selysi*. A species from northern Borneo, previously assigned to the genus *Discotettix*, has been moved to a newly established genus *Disconius* and is now known as the Bornean Fallen Pygmy Devil (*D. shelfordi* **comb. n.**). Three species new to science are proposed, as the examined material did not meet the diagnostic criteria of other species: (1) Sumatran Spiky Pygmy Devil endemic to southern Sumatra (*D. sumatrensis* Skejo, Pushkar et Tumbrinck **sp. n.**), (2) Kirschey's Spiky Pygmy Devil endemic to northeastern Borneo (*D. kirscheyi* Skejo, Pushkar, Tumbrinck et Tan **sp. n.**), and (3) Aruan Unicorn Pygmy Devil endemic to Aru Island close to New Guinea (*D. aruanus* Skejo, Pushkar et Tumbrinck **sp. n.**).

For this study, we examined a large amount of museum specimens and photographs of living individuals, taken by amateur and professional photographers. By examining a wide range of different material, we arrived at conclusions that significantly expand the current knowledge on morphology, variability, and distribution of the genus *Discotettix*. Notable new findings are the first records of *D. (M.) scabridus* from Luzon, the northern large island of the Philippines; and a new species from Aru Island (*D. aruanus* Skejo, Pushkar et Tumbrinck **sp. n.**), which lies some 130 km SSW of New Guinea, and extraordinary 2000 km E of the other species' areas of distribution. Interestingly, *D. aruanus* Skejo, Pushkar et Tumbrinck **sp. n.** is morphologically very similar to *D. selysi*, despite the great geographical separation and supposedly long isolation of the populations of the two species, inferred from the fact that Aru is geographically primarily associated with the Australian plate and has been a part of a single landmass together with Australia and New Guinea when the sea level was lower, the last time during the Pleistocene (Linthout *et al.* 1997; Ludt & Rocha 2015). One possible explanation for the similarity of *D. selysi*, *D. doriae,* and *D. aruanus* Skejo, Pushkar et Tumbrinck **sp. n.** could be their recent origin, which could be tested by molecular phylogeny and the molecular clock and would mean that the ancestral population of *D. aruanus* was established through dispersal to the Aru Island, without land connection. The alternative hypothesis that may be tested using the

same methodology is that the flattened morphology observed in *D. selysi, D. doriae,* and *D. aruanus* Skejo, Pushkar et Tumbrinck **sp. n.** represents the ancestral, plesiomorphous morphology within the genus *Discotettix*. In other words, we propose two alternate hypotheses: long isolation hypothesis *vs.* recent origin hypothesis.

The end of Discotettiginae

After comprehensive comparisons of Scelimeninae genera (Storozhenko & Dawwrueng 2015; Skejo 2017; Storozhenko 2017; Skejo & Bertner 2017; Muhammad *et al.* 2018; Adžić *et al.* 2020; Regul 2022), it has become clear that key traits characterizing this subfamily are: (i) the low position of the antennal grooves, (ii) the low position of the frontal costa bifurcation and lateral ocelli, (iii) elevated lateral carinae of the vertex, (iv) indrawn anterior margin of the vertex, (v) the presence of the pronotal projections arranged as **FM**, **FLs**, **PM**, **MMs**, **PMLs**, **MMLs**, **MLs**, and **VLs**, and (vi) toothed dorsal and ventral margins of fore, mid and hind femora. *Discotettix* was included in the catalog of Scelimeninae genera (Muhammad *et al.* 2018) as, even then, mounting evidence suggested its rightful taxonomic place within Scelimeninae. The synonymization of Discotettiginae and Scelimeninae was not conducted at the time as this act would assign many genera of dubious placement to the latter subfamily (Muhammad *et al.* 2018). This revision was postponed until the problematic genera have been reviewed and correctly assigned. *Arulenus* was excluded from Discotettiginae by Skejo & Caballero (2016), *Ophiotettix* transferred to Metrodorinae by Tumbrinck & Skejo (2017), *Rosacris* transferred to Metrodorinae by Skejo (2016) and recognized as a senior synonym of *Metamazarredia* Günther, 1939 by Kasalo (2022), *Phaesticus* excluded from Discotettiginae by Zha *et al.* (2021), and only *Hirrius* remains to be revisited.

After more than a century and numerous revisions of individual genera, it is finally demonstrated that the subfamily Discotettiginae, established by Hancock (1907a) to include genera with widened antennal segments, is polyphyletic in nature, as its main diagnostic character represents a homoplasy. Thus, widened antennal segments, used as a simple trait, have no value in defining higher groups in Tetrigidae. However, when antennae are treated adequately and recognized as a complex trait, the shape and the number of antennal segments may be used in the suprageneric taxonomy of Tetrigidae, exemplified by the diagnostic criteria of Batrachideinae, Lophotettiginae, Tripetalocerini, or Clinophaestini (Skejo 2017; Cigliano *et al.* 2022).

Herewith we assign the genera *Discotettix, Disconius* Skejo, Pushkar et Tumbrinck **gen. n.**, and *Kraengia* to the tribe Discotettigini **stat. resurr.**, together with the genera *Austrohancockia* Günther, 1938, *Bidentatettix* Zheng, 1992, *Eufalconius* Günther, 1938, *Gibbotettix* Zheng, 1992, *Paragavialidium* Zheng, 1994, *Gavialidium* Saussure, 1862, and *Tegotettix* Hancock, 1913. The abovementioned genera lack the paddle-like hind tibiae, which separates them from the members of the tribe Scelimenini, namely *Amphibotettix* Hancock, 1906, *Euscelimena* Günther, 1938, *Indoscelimena* Günther, 1938, *Paramphibotettix* Günther, 1938, *Platygavialidium* Günther, 1938, *Scelimena* Serville, 1838, *Tagaloscelimena* Günther, 1938, and *Tefrinda* Bolívar, 1906. Widened hind tibiae and tarsi of Scelimenini are used as paddles for swimming and diving. *Discotettix* is morphologically most similar to the genera *Bidentatettix, Eufalconius, Paragavialidium*, and *Tegotettix,* which inhabit areas north of the *Discotettix* distribution area. *Discotettix* is easily distinguished from these genera by widened antennae, but some species of *Discotettix*, especially *D. scabridus*, appear very similar to certain members of *Paragavialidium* and *Bidentatettix* when characters other than antennae are considered. With the placement of Discotettigini within Scelimeninae, a prerequisite for more thorough research into the relationships among the genera within this subfamily is provided at last.

A summary of the morphology and the function of the *Discotettix* antennae

Research on the morphology and function of antennae in *Discotettix* has been performed as a result of an inspiring case of idea sharing among researchers. The senior author (JS) started the discussion on ResearchGate, entitled "*Has anybody investigated the function of antennae with flattened anteapical/subapical segments (in e.g., Hemiptera:* Dalader*, Orthoptera: Discotettiginae)*?" (ResearchGate 2016), which sparked Kuřavova *et al.* (2017) to study the morphology of *D. belzebuth* antennae in detail. The research was conducted using the electron microscope and revealed four types of sensilla, confirming important sensory function of the antennae. The coeloconic sensilla are

situated only on the ventral side of the antennal segments, while the other three types (placoid, basiconic (type I and II), and Böhm) appear on both sides. Each of them has a different spatial per-segment distribution, with the type II basiconic sensilla being taxonomically the most interesting as their position on the lateral margins of antennal segments gives *D. belzebuth*, together with the rest of the genus, its characteristic antennae with saw-like margins, which are present in both sexes without significant differences. Interestingly, the widened segments neither bear more sensilla nor are they placed differently than in other segments. The key differentiating property of the widened segments is their surface being profusely covered by prominences and cuticular plates (Kuřavova *et al.* 2017).

The diversity of antennal morphology of acridoid grasshoppers (Acridoidea), with their flattened, clubbed, foliaceous, and variously colored subapical segments can be readily observed (Cigliano *et al.* 2022). In a number of cases, the function of these modifications is intraspecific signaling, for example in courtship (Berger & Gottsberger 2010). Similar modifications are present outside of Orthoptera as well, for example in Hemiptera. The species of the extant genus *Dalader* Amyot et Serville, 1843 and the extinct genus *Gyaclavator kohlsi* Wappler, Guilbert, Wedmann et Labandeira, 2015 (Wappler *et al.* 2015) possess antennae that are remarkably similar to those found in the genus *Discotettix*.

Until a comprehensive ecological study is performed, we can only offer hypotheses providing potential explanations to the morphological peculiarities of the genus *Discotettix*. Considering that the widened antennae do not bear more sensilla than the 'typical' ones, their shape could represent an adaptation associated with camouflage, as they visually fit in with the animals' corticolous-mossy habitat and make them harder to spot. For example, the shape and size (sometimes even the color) of the antennae found in the members of this genus resemble moss sporangia, which, coupled with protective coloration and unique body shape, could provide a significant advantage in the given habitat. The efficiency of *Discotettix* camouflage is likely further facilitated by mosses, algae, fungi, and lichens growing on the surface of their pronotum. The extent of this mutualistic relationship represents a very promising research opportunity because it could go beyond zoohoria, phoresy or epibiosis, and could in fact be more akin to the one observed between sloths and the algae inhabiting their hair (Pauli *et al.* 2014). In conclusion, widened antennal segments appear in several evolutionarily independent groups (different subfamilies of Tetrigidae, Acridoidea, Hemiptera, Coleoptera), and thus by themselves do not carry much taxonomic information. For Tetrigidae, this issue is finally put to rest but the questions pertaining to ecology remain. Those *pygmy walking gardens*, invisible to an inpatient eye, have yet to reveal their greatest secrets.

Acknowledgments and authors' contribution

The authors are grateful to Andrej Gorochov who provided specimens of the new species *Discotettix sumatrensis*; to Tom Kirschey for providing habitat photographs of the new species *D. kirscheyi*; to A. Radchenko, V. Korneyev, and Hojun Song for the valuable comments; to Mercedes Paris from MNCN Madrid and Simon Poulain from MNHN Paris for the help with the examination of the old type series; to Martin Husemann for help with photographing *D. belzebuth* holotype in MNHN Paris; to V. Loktionov for taking photographs of the new species *D. sumatrensis*; to the colleagues who participated in a very fruitful discussion on *Discotettix* flattened antennae morphology and function on ResearchGate platform; to the photographers Arthur Anker, Paul Bertner, Aglaia Bouma, Frank Deschandol, Bernard Dupont, Tom Kirschey, Chien Lee, Kinamatsu Lin, Kurt Orion, Pang Way, Melvin Yeo, Simben (inaturalist @simben), Sustainable Strategies Network, and all the others who took beautiful photos of *Discotettix* specimens; to Tony Robillard and Mohamad Azizan Bin Asidi for field assistance during the discovery of *D. kirscheyi*; to anonymous reviewers who, with their comments, contributed to this manuscript. This study was part of Josip Skejo's Master Thesis "Taxonomic revision of the pygmy devils (Tetrigidae: Discotettiginae) with online social media as a new tool for discovering hidden diversity" defended in 2017—so thanks to Damjan Franjević and Axel Hochkirch for valuable comments during mentoring of the thesis—as well as a part of Josef Tumbrinck's and Josip Skejo's project funded by OSF 'Digitalization of Tetrigoidea types in European Musea'. The permission for research in Sabah by Ming Kai Tan was granted by the Sabah Biodiversity Centre (JKM/MBS.1000-2/3 JLD.3 (99) and JKM/MBS.1000-2/2 JLD.10 (179)); Osman Bangkong [the District Forestry Officer (DFO) of Lahad Datu]; Geungnong Ah Jing (the assistant DFO of Lahad Datu); and Jackly Ambrose (the DFO of Ulu Segama-Malua). The work of Ming Kai Tan was supported by the Orthoptera Species File Grant 2019 under the taxonomic research project titled "Contribution to the species diversity and acoustic data on Orthoptera from Sandakan (Borneo, East Malaysia,

Sabah)". The study was Josip Skejo's idea. Authors who are equal in their contributions are Josip Skejo, Taras I. Pushkar, Niko Kasalo, and Josef Tumbrinck. Most of the study has been written by Josip Skejo with the great help of Niko Kasalo, and with species description editing by Marko Pavlović; Taras I. Pushkar was involved in species descriptions, and proposed the new terminology of pronotal projections and protuberances; Josef Tumbrinck helped with species descriptions and measurements; Marko Pavlović sorted material from online social media; Ming Kai Tan helped with *D. kirscheyi* description and measurements; all the other authors (Maks Deranja, Karmela Adžić, Fran Rebrina, Amira Aqilah Muhammad, Nurul Ashikin Abdullah, Razy Japir, Arthur Y. C. Chung) helped with the descriptions, measurements, fieldworks, biogeographical analysis and organization of the manuscript. Many many thanks to non-anonymous reviewers (Hendrik Devriese and Sergey Storozhenko) who made this study better.

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