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Taxonomic Revision of Pygmy Devil Genera *Almacris*, *Ginixistra*, *Tegotettix*, and *Xistra*, with Comments on *Xistrella* (Orthoptera: Tetrigidae) †

Josip Skejo [1,‡], Niko Kasalo [2,*,‡], Romeo R. Patano, Jr. [3,‡], Sergey Yu. Storozhenko [4,‡], Josef Tumbrinck [5,‡], Tomislav Domazet-Lošo [2], Victor B. Amoroso [3], Sheryl A. Yap [6] and Jadranka Škorput [7,*,‡]

1 Evolution Lab, Faculty of Science, University of Zagreb, Horvatovac 102a, 10000 Zagreb, Croatia; jskejo@biol.pmf.hr
2 Laboratory of Evolutionary Genetics, Ruđer Bošković Institute, Bijenička Cesta 54, 10000 Zagreb, Croatia; tdomazet@irb.hr
3 Center for Biodiversity Research and Extension in Mindanao, Institute of Biological Sciences, Central Mindanao University, Musuan, Maramag 8710, Philippines; romeonojrpatano@gmail.com (R.R.P.J.); victorbamoroso@gmail.com (V.B.A.)
4 Institute of Biology and Soil Science, Far East Branch of Russian Academy of Sciences, Vladivostok 690022, Russia; storozhenko@biosoil.ru
5 Auf der Hees 1, 41849 Wassenberg, Germany; j.tumbrinck@t-online.de
6 Institute of Weed Science, Entomology and Plant Pathology, College of Agriculture and Food Science, University of the Philippines Los Baños, Los Baños 4031, Philippines; sayap3@up.edu.ph
7 University Hospital Centre Zagreb, Kišpatićeva ulica 12, 10000 Zagreb, Croatia
* Correspondence: nkasalo@irb.hr (N.K.); jadranka.skorput.96@gmail.com (J.Š.)
† zoobank:urn:lsid:zoobank.org:pub:C1E8F48B-136C-4A2F-B472-F608E2080129; urn:lsid:zoobank.org:act:8115B788-393B-492B-A405-0437C19977DA; urn:lsid:zoobank.org:act:40B31705-536F-4ED7-9C27-3EB86A1916D3; urn:lsid:zoobank.org:act:80E6DD1C-7210-4726-B4A6-7C552ABEFFDE; urn:lsid:zoobank.org:act:7EA3C37F-CC3D-40EA-883A-CE6AD0F57046; urn:lsid:zoobank.org:act:DE7E971A-2014-4C19-A7B9-C6212B4F0AA2; urn:lsid:zoobank.org:act:042B3454-AA9F-467D-ABE2-436D47DC228A; urn:lsid:zoobank.org:act:757FB116-16AF-42B4-8A37-D24628AA2393; urn:lsid:zoobank.org:act:C048848F-13E4-4909-8E22-CE26BF8B0673.
‡ These authors contributed equally to this work.

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Abstract

The Philippines and the Papuan archipelagos harbor a vast diversity of pygmy grasshoppers, including the pygmy devils of the genera *Xistra* and *Tegotettix*, as well as visually similar taxa reviewed in this study. A new tribe, two new genera, a new subgenus, three new species, and 24 new or resurrected taxonomic combinations are proposed in this study. A new colorful wingless genus and species, *Almacris alleochroa* gen. et sp. nov., is described from Mindanao. Taxonomic reshuffling of the genus *Xistra* is performed—a new subgenus is described, *Tegoxistra* subgen. nov., to include *X. derijei*, *X. corniculata*, and *X. cristifera*, while the nominotypical subgenus becomes restricted to *X. gogorzae* and *X. sagittaria*. All other species previously assigned to *Xistra* are herewith moved to *Xistrella*, resulting in 20 new combinations. The genus *Ginixistra* gen. nov. (Exanimini)—whose members show remarkable similarity to Fiji-endemic *Fijixistra*—is described for *G. noveguineae*, *G. davorkae* sp. nov., and *G. novaebrittaniae* sp. nov. from New Guinea and New Britain. The new tribe Xistrellini trib. nov. is established to accommodate *Afrosystolederus*, *Bannatettix*, *Kanakacris*, *Phaesticus*, *Pseudoparatettix*, *Pseudosystolederus*, *Pseudoxistrella*, *Synalibas*, *Systolederus*, *Teredorus*, and *Xistrella*. Previous molecular phylogenetic studies have confirmed Xistrellini monophyly and suggested that the ancestor of this tribe may have originated during the Cretaceous period, approximately 127–100 million years ago (mya).

Keywords: island biogeography; pygmy grasshoppers; groundhoppers; neoteny; new species; Philippines; Mindanao; New Guinea; New Britain; Xistrellini

1. Introduction

A pygmy devil is any pygmy grasshopper (Orthoptera: Tetrigidae) in which lateral carinae of the vertex form high horns, such as in members of *Xistra* Bolívar, 1887 [1], and/or whose pronotum bears many high spines, such as in members of *Tegotettix* Hancock, 1913 [2]. The taxonomic history of the pygmy devil genus *Xistra* Bolívar, 1887 [1], the main focus of this paper, and some of its historically, or rather visually similar, genera, such as *Xistrella* Bolívar, 1909 [3] (currently in Metrodorinae, without tribal placement), *Lamellitettigodes* Günther, 1939 [4] (now in Tetriginae, without tribal placement), and *Tegotettix* Hancock, 1913 [2] (nowadays assigned to Scelimeninae: Discotettigini), is definitely a complex one [5]. As is the case with many Tetrigidae genera described from southeastern Asia, and especially from the Philippines, the genus *Xistra* also lacks a clear taxonomic definition. Most studies dealing with *Xistra* used only high horns [6,7], a highly variable trait, as the main definition of this genus, usually without a detailed comparison of other head traits, such as the position of the medial carina of the vertex in frontal view, the position of the antennal grooves, or the length of the frontal costa. The type species of *Xistra* was described from the Philippines. The Philippines has been a well-known biodiversity hotspot for Tetrigidae, where many genera and species have been described [8–10], but many others await discovery [11,12], and, of course, many await review.

Genus *Xistra* was described by Bolívar [1] based on facial traits, such as a V-shaped vertex with elevated horns, and pronotal traits, such as narrow shoulders and an elevated median carina. Originally, the genus contained eight species from southeastern Asia 1,13,14] (Table 1). Brunner von Wattenwyl [13] described one more species, and Hancock [14] transferred one species from *Paratettix* [1] to *Xistra* (Table 1).

Table 1. A brief historical overview of the classification of the genus *Xistra*. Shown is the history of 12 taxa, recognized by Bolívar, Hancock, and Günther. Nine were originally assigned to *Xistra* by Bolívar [1,15], ten by Hancock [14], and only two by Günther [16]. Traditional Bolívar's and Hancock's classifications of these species are compared with Günther's classification, and with the currently accepted Orthoptera Species File classification [5]. Species originally assigned to *Xistra* are now classified into six different genera.

Bolívar [1,15]	**Hancock** [14]	**Günther** [16,17]	**OSF** [5]
Xistra gogorzae Bolívar, 1887	*Xistra gogorzae*	*Xistra gogorzae*	*Xistra gogorzae*
Xistra corniculata (Stål, 1877)	*Xistra corniculata*	*Tegotettix corniculatus*	*Tegotettix corniculatus*
Xistra sagittaria Bolívar, 1887	*Xistra sagittaria*	*Tegotettix sagittarius*	*Tegotettix sagittarius*
Xistra impressa Bolívar, 1887	*Xistra impressa*	*Lamellitettix impressus*	*Lamellitettix impressus*
Xistra lurida Bolívar, 1887	*Xistra lurida*	*Pseudoparatettix luridus*	*Pseudoparatettix luridus*
Xistra similis Bolívar, 1887	*Xistra similis*	*Pseudoparatettix similis*	*Pseudoparatettix similis*
Xistra ochracea Bolívar, 1887	*Xistra ochracea*	*Pseudoparatettix ochraceus*	*Pseudoparatettix ochraceus*
Xistra t. tricristata Bolívar, 1898	*Xistra t. tricristata*	*Lamellitettigodes contractus tricristatus*	Syn. of *L. contractus*

Table 1. *Cont.*

Bolívar [1,15]	**Hancock** [14]	**Günther** [16,17]	**OSF** [5]
Xistra t. sumatrana Bolívar, 1898	*Xistra t. sumatrana*	Syn. of *Lamellitettigodes contractus*	Syn. of *L. contractus*
Paratettix sagittatus Bolívar, 1887	*Xistra sagittata*	*Euparatettix sagittata*	*Lamellitettigodes sagittatus*
-	*Xistra dubia* Brunner von Wattenwyl, 1893	*Xistrella dubia*	*Xistrella dubia*
-	-	*Xistra cristifera* Günther, 1935	*Tegotettix cristiferus*

Günther [16] described one more *Xistra* species, but it was later transferred to genus *Tegotettix* [18]. Apart from this change, Günther [17,18] suggested that fastigial horns originated several times and that vertex shape and tarsi shape are more relevant traits, so he moved many *Xistra* species, with and without V-shaped vertex, to other genera, such as *Lamelitettix*, *Pseudoparatettix*, *Xistrella* (Tetriginae), and *Tegotettix* (Scelimeninae). Subsequent authors had many issues in interpreting what *Xistra* is, and many species possessing horns of the vertex from Asia have been assigned to this genus without understanding the differences between *Xistra*, *Tegotettix,* and *Xistrella.*

Species assigned to *Xistra* by Bolívar, Hancock, and Günther are today assigned to the genera *Lamellitettix* Hancock, 1904 [19–21], *Lamelitettigodes* Günther, 1939 [4,22,23], *Pseudoparatettix* Günther, 1937 [17], *Tegotettix* Hancock, 1913 [2,24], *Xistrella* Bolívar, 1909 [3,25,26], while only the type species remains assigned to the genus *Xistra* [1,5,14–17,27] (Table 1).

The genus *Xistra* currently counts altogether 23 species [5] from the Philippines (1 species, the type species) [1], Cambodia (1 species) [6], PR China (19 species) [7,28–38], and Nepal (2 species) [39]. Species currently assigned to the genus *Xistra* [5] are (1) *X. angusta* Ingrisch, 2001, (2) *X. bannaensis* Deng, Wang, Mao & Li, 2022, (3) *X. brachynota* Li, Deng & Zheng, 2014, (4) *X. cambodia* Storozhenko, 2021, (5) *X. foliolata* Liang & Chen, 2010, (6) *X. gogorzae* Bolívar, 1887, (7) *X. hainanensis* Deng, 2022, (8) *X. jiulianshanensis* Zheng & Shi, 2009, (9) *X. laticorna* Zheng, 1988, (10) *X. lativertex* Zheng & Mao, 2010, (11) *X. lochengensis* (Zheng, 2005), (12) *X. longicornis* Ingrisch, 2001, (13) *X. longidorsalis* Liang & Jiang, 2004, (14) *X. medogensis* Zheng, 2005, (15) *X. nigriabdominis* Deng, 2022, (16) *X. nigrinota* Zheng & Xu, 2010, (17) *X. nigritibialis* Zheng & Jiang, 2002, (18) *X. orchotibia* Deng, Wang, Mao & Li, 2022, (19) *X. parvula* Liang & Chen, 2010, (20) *X. shilinensis* Zheng, 2015, (21) *X. strictivertex* Zheng & Ou, 2010, (22) *X. wuyishanensis* Zheng & Zeng, 2011, and (23) *X. zhengi* Deng, 2024.

For example, *Xistra corniculata* (Stål, 1877) [40] comb. resurr. and *X. sagittaria* Bolívar, 1887 [1] comb. resurr. originally belonged to *Xistra*, together with *X. cristifera* Günther, 1935 [16] comb. resurr. Günther [18] transferred all these species to the genus *Tegotettix* without justification, i.e., without a detailed morphological comparison of the type species of *Xistra* and the type species of *Tegotettix*; as a result, these species still remain assigned to the genus *Tegotettix*.

A recent paper by Patano and colleagues [24] reviewed the taxonomy of the genus *Tegotettix* and divided it into three species groups, composed of morphologically similar species, based on comparisons of head, leg, and pronotum traits. In this revision, [24] recognized that only members of *Tegotettix* (*armatus*) species groups exhibit Scelimeninae morphology, and that members of the other species groups are likely not members of this genus. The lack of comparative material prevented the authors from drawing wider conclusions on the generic placement of these species. It has become evident only now that members of the *Tegotettix* (*cristiferus*) species group share traits with the type species of

Xistra and that those members really belong to *Xistra*. The *Tegotettix* revision [24] provided a framework for the present revision of *Xistra* and *Tegotettix*, as well as for the description of *Ginixistra* gen. nov. by defining species groups based on head morphology (length of frontal costa, position of bifurcation, shape of vertex, position of the antennal grooves, shape of scutellum) and noting that they clearly belonged to different genera. Patano and colleagues [24] paved the way for future revisions of the Southeast Asian Tetrigidae, characterized by highly convergent morphologies.

Throughout its history, the genus *Xistra* has, as outlined above, lost many of its core members (Table 1) while simultaneously being filled with different unrelated species [5,29], leaving it a taxonomically useless, polyphyletic genus.

The aims of this paper are (1) to re-define the genus *Xistra* based on morphology of the type species and closely related species, and to provide an annotated identification key; (2) to re-evaluate the generic placement of the species we find not to be *Xistra* members; (3) to describe *Almacris alleochroa* Skejo, Patano, Škorput et Kasalo gen. et sp. nov. a new wingless genus and species endemic to Mindanao; (4) to describe *Ginixistra* Kasalo, Tumbrinck et Skejo gen. nov. from New Guinea and New Britain, and (5) to define the tribe Xistrellini Skejo, Storozhenko, Tumbrinck et Kasalo trib. nov. currently without any subfamily placement, for *Xistrella* and related genera.

2. Materials and Methods

We physically examined specimens mentioned in this study that are deposited in European and Philippine museums (see Abbreviations, just before the References section), including freshly collected specimens (see below). Species from PR China were examined using high-quality published photographs and original descriptions (e.g., [5,7,26,30,33,35–38,41–46]), a common practice in tetrigidology, as well as images from the Orthoptera Species File.

2.1. Fieldwork for Almacris alleochroa gen. et sp. nov. and Tegotettix derijei in Mindanao

Before the fieldwork, an approved wildlife gratuitous permit was obtained from the Department of Environment and Natural Resources for the collection of wildlife specimens (R10 2022-45). A ritual was also performed by Datus in connection with their culture and traditions. The specimens of the new genus were collected in the montane forests of Mount Balatukan at 1100 m a.s.l. (8.7221 N, 125.0226 E) and at 1210 m a.s.l. (8.7087 N, 125.0185 E) through hand picking and then placed in separate vials filled with absolute ethyl alcohol individually for long-term preservation and future molecular studies. Relevant collection data, like the place of collection, date of collection, collection number, and collector's name, were labeled and associated with the specimens in a vial. In addition, important data such as altitude, coordinates, and type of vegetation were also recorded. All collected specimens of the new genus were brought to the Central Mindanao University Museum, the Zoological section. Specimens of the new species were photographed in the field using an Olympus Tough TG-6 camera. Subsequently, specimens were brought to the museum for detailed examination under a Labomed stereo microscope equipped with a Canon camera.

2.2. Type Depository

Holotype and paratypes of *Almacris alleochroa* Skejo, Patano, Škorput et Kasalo **gen. et sp. nov.** are temporarily deposited in the Orthoptera collection of CMU, the Philippines. The holotype will be deposited in the National Museum of the Philippines.

2.3. Taxonomy and Nomenclature

Taxonomy follows the Orthoptera species file, the official world Orthoptera database [5], except for the taxonomic and/or nomenclatural changes introduced in this study. All the nomenclatural acts from our study are in accordance with the International Code of the Zoological Nomenclature [47] and its amendments [48–51].

2.4. Terminology

Terminology of the pronotal carinae follows Devriese's system [52–54], while the rest of the terminology follows [14,17,55–59].

2.5. Measurements

Measurements were taken following [9], and a total of 15 standard measurements for Tetrigidae were taken (Figure 1) using ImageJ software (version 1.54g) [60] after photographing the specimen and calibrating the scale with millimeter paper.

Measurements taken are:

BL—Body Length, measured in lateral view;
PL—Pronotum Length, measured in lateral or dorsal view;
PW—Pronotum Lobe Width, measured in dorsal view;
PH—Pronotum Height, in lateral view, between the lobe and the highest point;
FFL—Fore Femur Length, measured in lateral view;
FFW—Fore Femur Width, measured in lateral view;
MFL—Mid Femur Length, measured in lateral view;
MFW—Mid Femur Width, measured in lateral view;
HFL—Hind Femur Length, measured in lateral view;
HFW—Hind Femur Width, measured in lateral view;
VW—Vertex Width, measured in frontal view between the eyes;
EW—Compound Eye Width, maximum width measured in frontal view;
AL—Antenna Length, measured in dorsal, frontal, or lateral view;
SGPL—Subgenital plate length, measured in ventral view (only for *Almacris*);
HH—Fastigial Horn Height (new trait), measured in dorsal view, above eyes.

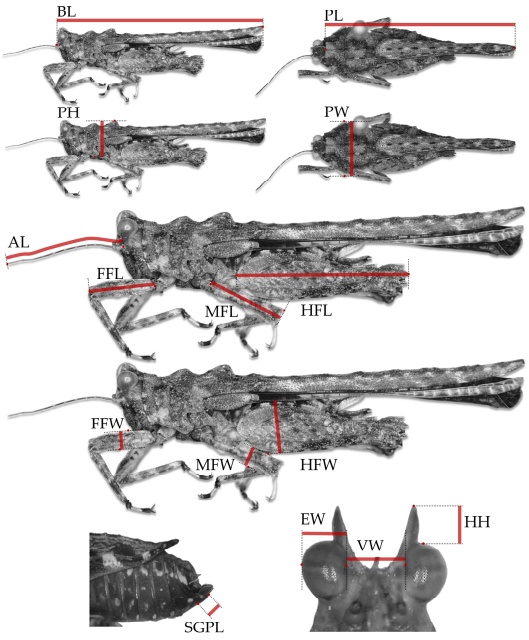

Figure 1. Measurements taken shown on the example of *Ginixistra davorkae* gen. et sp. nov. (Lateral and dorsal habitus), *Almacris alleochroa* gen. et sp. nov. (abdomen detail in lateral view), and *Xistra derijei* comb. nov. (frontal view of the head).

2.6. Structure of the Study

Genera are sorted alphabetically: *Almacris*, *Ginixistra*, *Tegotettix*, *Xistra* (divided into subgenera *Xistra* and *Tegoxistra*), and *Xistrella* with the description of Xistrellini. This study deals with *Almacris, Ginixistra*, and *Xistra* in detail, while for *Tegotettix* and Xistrellini, the study provides a brief overview of the genera taxonomy, distribution, and taxonomic issues.

3. Results

Taxonomy

Family Tetrigidae Rambur, 1838 [61]

Genus *Almacris* Skejo, Patano, Škorput et Kasalo gen. nov.
urn:lsid:zoobank.org:act:40B31705-536F-4ED7-9C27-3EB86A1916D3
(Figures 2–5)

Subfamily assignment. Without subfamily assignment.

Type species. *Almacris alleochroa* sp. nov., here designated.

Etymology. Named after Prof. Dr. Alma Baguhin Mohagan, a Philippine zoologist who greatly contributed to tetrigidology of the Philippines, and to the zoological studies in the country in general (e.g., [62–65], and a good mentor and a friend of ours. The team of Dr. Mohagan discovered and described *Xistra* (*Tegoxistra*) *derijei* (Patano, Mohagan, Tumbrinck, Amoroso et Skejo, 2021) comb. nov. a few years ago and recognized the *Xistra* problem [24]. The genus name is derived from "Alma", Ma'am Mohagan's name, and "acris", a Latinized Greek word (ἀκρίς, akris) for grasshopper. The genus name is a feminine gender noun of the third Latin declension (Nominative *Almacris*, Genitive *Almacridis*).

Descriptive diagnosis. Although the placement of this genus within the higher taxonomy of Tetrigidae cannot be confidently resolved at this time, the following set of characters differentiates it from all the other known genera. Tegmina and wings are absent. Pronotum colorful, with green and reddish tints. Two-horned vertex, formed by both the lateral and secondary carinae being weakly elevated. Frontal costa bifurcation at the middle of the eye height. Paired ocelli at the lower quarter of the eye height. The top margin of the antennal grooves is at the level of the bottom margin of the eyes. Weakly bilobate vertex anteriorly as seen in dorsal view. Vertex is very slightly narrowing anteriorly. Antennae with around 15 segments. A large crest formed by the median carina in the anterior part of the pronotum. Ovipositor minute.

The only known species, *A. alleochroa* sp. nov., resembles *Mazarredia* nymphs by pronotal hump and by striped coloration but can easily be distinguished from *Mazarredia* nymphs by its filiform antennae (with widened antennomeres in *Mazarredia* nymphs) and by all other Tetrigidae nymphs by the presence of the antegenicular notch.

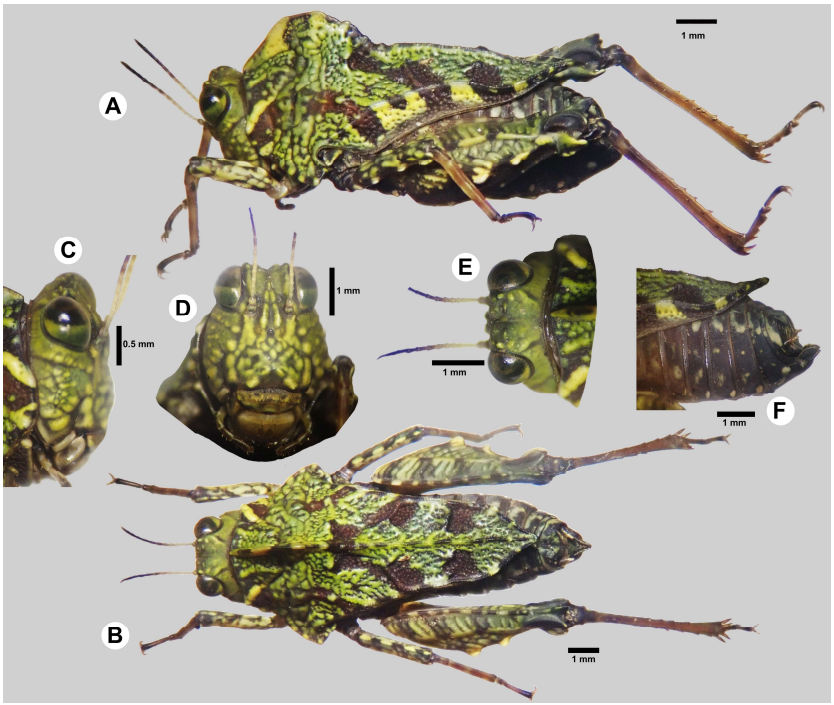

Figure 2. Holotype ♀of *Almacris alleochroa gen*. et. sp. nov. Lateral and dorsal (**A**,**B**), head in lateral view (**C**), head in frontal view (**D**), head in dorsal view (**E**), and abdominal and pronotal apex in lateral view (**F**).

Composition. Monotypic, including only *A. alleochroa* sp. nov.

Distribution. Endemic to Mindanao Island (the Philippines), known only from Mt. Balatukan

Species *Almacris alleochroa* Skejo, Patano, Škorput et Kasalo gen. et sp. n.
urn:lsid:zoobank.org:act:DE7E971A-2014-4C19-A7B9-C6212B4F0AA2
(Figures 2–5)

Figure 3. In natura photograph of a male of *Almacris alleochroa* **gen. et. sp. nov**., lateral view. Montane forest ecosystem in Mount Balatukan, Gingoog City, Misamis Oriental, Mindanao, Philippines. Photography R. Patano, Jr. on 20 January 2023.

Figure 4. In natura photograph of a male of *Almacris alleochroa* **gen. et. sp. nov**., dorsal view. Montane forest ecosystem in Mount Balatukan, Gingoog City, Misamis Oriental, Mindanao, Philippines. Photography R. Patano, Jr. on 20 January 2023.

Figure 5. In natura photographs of a male of *Almacris alleochroa* **gen. et. sp. nov**., lateral (**a**) and dorsal view (**b**). Agroforest ecosystem in Mount Balatukan, Gingoog City, Misamis Oriental, Mindanao, Philippines. Photography R. Patano, Jr. on 30 October 2023.

Type material. 1♀holotype PHILIPPINES: Mindanao: Misamis Oriental: Barangay Lunutan, Gingoog City, Mount Balatukan (montane forest) 1210 m a.s.l. 22.XII.2022. leg. R. Patano, Jr.. (CMU); 1♀paratype PHILIPPINES: Mindanao: Misamis Oriental: Barangay Lunutan, Gingoog City, Mount Balatukan (montane forest) 1210 m a.s.l. 22.XII.2022. leg. R. Patano, Jr.. (CMU); 1♂paratype PHILIPPINES: Mindanao: Misamis Oriental: Barangay Lunutan,

Gingoog City, Mount Balatukan (montane forest) 1200 m a.s.l. 20.I.2023. leg. R. Patano, Jr.. (CMU); 2♂♂paratypes PHILIPPINES: Mindanao: Misamis Oriental: Barangay Lunutan, Gingoog City, Mount Balatukan (Agroforest) 1080–1110 m a.s.l.; 29.-30.X.2023. leg. R. Patano, Jr. (CMU).

Type locality. Montane forest of the Mt. Balatukan (PHILIPPINES: Mindanao: Misamis Oriental: Barangay Lunutan, Gingoog City).

Type depository. Central Mindanao University (CMU) Orthoptera Collection, Mindanao, Philippines.

Etymology. The specific epitheton is a feminine adjective, New Latin, *alleochrous, alleochroa, alleochroum*, based on the Latinized Ancient Greek adjective, ἀλλοιόχροος ον, όα/alloiochroos, on, oa/, meaning "of varying color", "colorful".

Diagnosis. The new species is easily distinguished from all known Tetrigidae. Species diagnosis is currently inseparable from the generic diagnosis (see above).

Description.

Head

Frontal view. The vertex is nearly two times wider than an eye. The surface of the vertex is a little below the level of the upper margin of the eyes. Lateral carinae elevated, forming short horns. Secondary carinae (between the lateral and the medial carina) are elevated, forming horns a little shorter than the lateral ones. There is a V-shaped incision between the lateral and secondary horns, as well as between the secondary horns. The medial carina and frontal costa are not elevated and thus barely visible. Frontal costa bifurcation at the middle of the eye height. Facial carinae are moderately divergent ventrally. Paired ocelli at the lower quarter of the eye height. The top margin of the antennal grooves is at the level of the bottom margin of the eyes.

Lateral view. Lateral carina protruding above the eyes. The entire lateral carina is raised, with an additionally elevated medial segment in the shape of a moderately wide horn.

Dorsal view. Vertex anteriorly truncated, very slightly narrowing anteriorly. Medial carina indrawn into the vertex, giving it a bilobate look anteriorly. The medial carina is visible only in the anterior third of the vertex.

Antennae

Filiform. 15 segments visible. The proximal half of the flagellum is white, and the apical region progressively darkens.

Pronotum

Lateral view. Median carina elevated in the anterior part of the pronotum, forming a semi-circular crest that extends from the anterior margin to the level of humeral angles. Median carina is slightly elevated past this point up to the pronotal apex, where it is present but not elevated. Pronotal apex upturned. Lateral carinae are visibly elevated. Sulci are well visible across the pronotal disk. Lateral lobes are blunt and rectangular. Ventral sinus semi-oval. The infrascapular area is well-developed, extending from the ventral sinus to just before the apex; widest anteriorly, slightly narrows towards the level of the midpoint of hind femora length, then sharply narrows and continues as a thin strip towards the apex.

Dorsal view. Anterior margin semi-oval, weakly produced forwards. Prozonal carinae long, weakly converging dorsally. Lateral lobes flaring outwards. Humeral angles blunt. Interhumeral carinae unclear; short and slightly converging dorsally, connected with many sulci. Pronotum slightly narrows dorsally up to the apex, where it moderately narrows, forming a blunt spine.

Wings
Tegmina and alae absent.

Legs
Anterior femora smooth, slightly expanded proximally. Tibiae smooth. Middle femora with slightly undulate dorsal and ventral margins. Tibiae smooth. Hind femora with slightly wavy dorsal margins. Antegenicular tooth (the one before the hind knee) weak, while the genicular one (the one on the hind knee) strong. Outer margins with two tubercles. Tibiae with weak teeth. Pulvilli blunt. Tarsal claw a little shorter than the first tarsal segment.

Coloration (Figures 2–5)
Antennae white in the proximal half, black in the distal half, with a smooth transition between them. Head predominantly green with several yellowish spots on the fastigium. Occipital area marked by a yellow and a black line. Base color of the pronotum scarlet-brownish. Anterior part of the pronotal crest yellowish, posterior to it the median carina with alternating yellowish-green and brown spots/lines. Anterior third of the pronotal surface covered by a labyrinthine green pattern that resembles algal outgrowth. Posterior two thirds mainly brown, with three large blotches of green patterns that expand outwards from the median carina. Femora brown, dotted with yellowish-green spots. Tarsi pale brown, with yellowish stripes faintly visible along them.

Distribution: Endemic to Balatukan Mt. in the Island of Mindanao (the Philippines) (Figure 6).

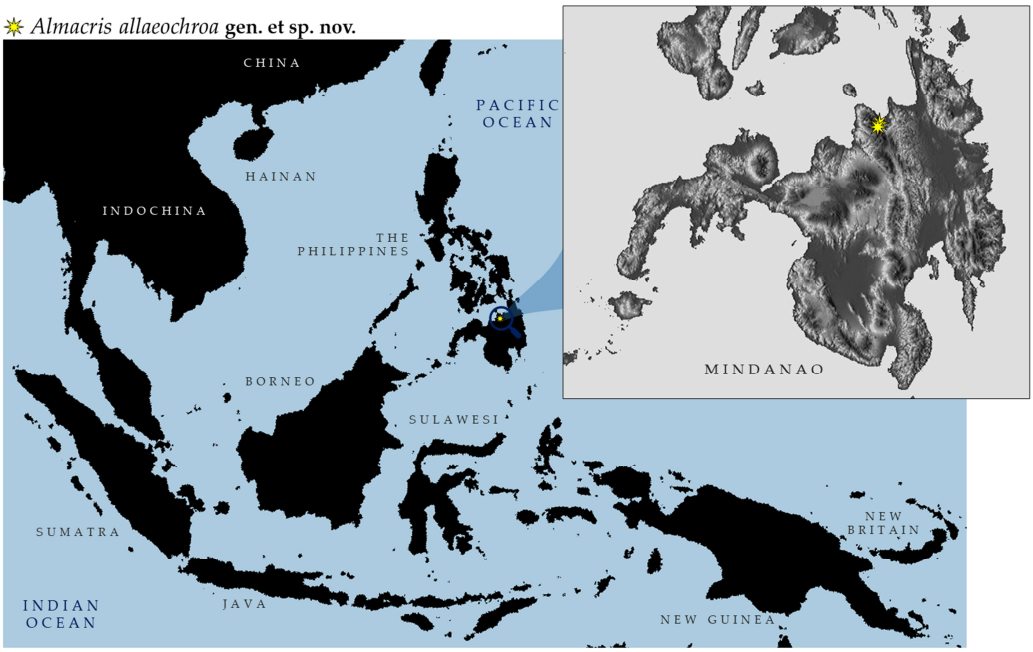

Figure 6. Distribution of *Almacris alleochroa* **gen. et. sp. nov**. Large map sourced from the website https://commons.wikipedia.org/File:Blank_Asia.png (accessed on 8 October 2025), from Wikimedia Commons, Public Domain; small map sourced from the website https://maps-for-free.com/ (accessed on 8 October 2025), OpenStreetMap, open licence.

Habitat and Ecology (Figures 7 and 8). *Almacris alleochroa* **gen. et. sp. nov.** is only known so far from Mount Balatukan, Gingoog City, Misamis Oriental (Figures 7 and 8). It is located on Mindanao's northern island and is one of those declared Key Biodiversity Areas (KBAs) of the Philippines. It is a massive, possibly active compound stratovolcano. In the Misamis Oriental province, it is the highest peak. Although the volcano has never erupted before,

it does display fumarolic activity. Specimens of the new genus were observed along the lower montane and agroforest ecosystems of the mountain.

In the lower montane forest (1200 m a.s.l.), the new species was observed dwelling on tree trunks covered with mosses of the family *Calymperaceae*. The lower montane forest ecosystem of Mount Balatukan is dominated by trees such as *Tritaxis malayana* (Hook.f.) R.Y.Yu & Welzen (family *Euphorbiaceae*) and *Goniocheton arborescens* Blume (family *Meliaceae*); ferns such as *Blechnopsis orientalis* (L.) C.Presl (family *Blechnaceae*), *Histiopteris incisa* (Thunb.) J.Sm. (family *Dennstaedtiaceae*), *Dipteris conjugata* Reinw. (family *Dipteridaceae*), *Pteridium aquilinum* (L.) Kuhn (family *Dennstaedtiaceae*), and *Nephrolepis hirsutula* (G.Forst.) C.Presl (family *Nephrolepidaceae*); and bryophytes such as *Garovaglia elegans* (Dozy & Molk.) Hampe ex Bosch & Sande Lac. (family *Ptychomniaceae*), *Leucobryum javense* (Brid.) Mitt. (family *Leucobryaceae*), and *Dicranoloma* sp. (family *Dicranaceae*), but there are also many orchids (family *Orchidaceae*), gingers (order *Gingiberales*), and many epiphytes.

Some individuals were observed in the agroforest ecosystem (1080–1110 m a.s.l.), which is dominated by rainforest trees such as *Dillenia philippinensis* Rolfe (family *Dilleniaceae*), *Hellenia speciosa* (J.Koenig) S.R.Dutta (family *Costaceae*), and *Freycinetia multiflora* Merr. (family *Pandanaceae*) but also by agricultural plants such as banana (*Musa textilis* Née, family *Musaceae*) and coffee (*Coffea arabica* L., family *Rubiaceae*). Many ferns and lesser clubmosses were observed along the ecosystem, such as *Nephrolepis falcata* (Cav.) C.Chr. (family *Nephrolepidaceae*), *Syngramma alismifolia* (C.Presl) J.Sm. (family *Pteridaceae*), *Pteridium aquilinum, Christella parasitica (L.)* H.Lév. (family *Thelypteridaceae*), and *Selaginella cupressina* (Willd.) Spring (family *Selaginellaceae*); bryophytes such as *Hymenodon sericeus* (Dozy & Molk.) Müll. Hal. (family *Orthodontiaceae*), *Isopterygium* sp. (family *Pylaisiadelphaceae*), *Dicranoloma* sp., aroids, gingers, and climbing vines. The natural habitats of *Almacris alleochroa* **gen. et sp. nov**. are gradually being converted to agricultural areas, which could lead to the extinction of the subpopulations in Mt. Balatukan, where altogether fewer than 10 individuals of this extraordinary species have been observed.

Figure 7. Natural habitat of *Almacris alleochroa* **gen. et. sp. nov.** within the montane (**upper** images) and agroforest ecosystem (**lower** images) in Mount Balatukan, Gingoog City, Misamis Oriental, Mindanao, Philippines. Photography R. Patano, Jr.

Figure 8. Panoramic view of Mount Balatukan, Gingoog City, Misamis Oriental, Mindanao, Philippines, the only known habitat of *Almacris alleochroa* **gen. et. sp. nov.** Photography R. Patano, Jr.

Measurements. See Table 2.

Table 2. Comparison of measurements of four specimens of *Almacris alleochroa* gen. et sp. nov. All measurements are in millimeters with precision to 0.05 mm.

	♀Holotype	♀Paratype	♂Paratype	♂Paratype
BL	12.70	12.50	11.0	11.30
PL	9.70	9.60	7.70	9.80
PW	5.50	5.30	4.60	5.50
PH	4.50	4.50	4.30	4.40
FFL	3.00	2.90	2.60	2.80
FFW	0.50	0.55	0.50	0.60
MFL	3.70	3.55	3.0	3.40
MFW	0.60	0.60	0.60	0.55
HFL	6.60	6.45	5.50	6.50
HFW	2.50	2.50	2.20	2.40
VW	1.10	1.10	1.00	1.00
EW	0.70	0.70	0.70	0.70
AL	3.30	3.20	2.90	3.10
SGPL	0.60	0.60	0.60	0.60

Genus *Ginixistra* Kasalo, Tumbrinck et Skejo gen. nov.
urn:lsid:zoobank.org:act:80E6DD1C-7210-4726-B4A6-7C552ABEFFDE
Tegotettix (novaeguineae) species group Günther, 1938 [18] *sensu* [24] syn. nov.

Subfamily assignment. This new genus is assigned to the tribe Exanimini Kasalo, Tumbrinck, and Skejo, 2024 [66], which is without subfamily placement within Tetrigidae. New genus is assigned to this tribe based on head morphology similarity with *Exanimus* and *Fijixistra*, recently described from Fiji [66]. This is the first winged member of Exanimini.

Type species. *Ginixistra novaeguineae* (Günther, 1938) [18] (=*Tegotettix novaeguineae* Günther, 1938), here designated.

Etymology. "*Gini-*", a simplified transliteration of Guinea, used by many Papuan languages, and "*-xistra*", referring to the similarity of this new genus to *Xistra* from the Philippines and *Fijixistra* from Fiji. The genus name is of feminine gender, as it is derived from the root *xistra*.

Diagnosis. *Ginixistra* gen. nov. is easily distinguished from other members of Exanimini by its long pronotum and by the presence of tegmina and alae. Other Exanimini members are characterized by a nanopronotal (short pronotum) and wingless morphology.

Ginixistra gen. nov. is visually similar to *Tegotettix* and *Xistra* by the following characters: (1) concave and lowered vertex with lateral carinae forming horns; (2) antennal grooves visibly below the bottom margin of the eyes; (3) pronotum with a crest above shoulders and smaller projections anterior or posterior to it, all varying from barely perceptible to distinctly expressed.

Differs from *Tegotettix* by the following characters: (1) frontal costa bifurcation a little below the middle of the eye level or further below, depending on the extent to which the vertex is lowered between the eyes (around the middle level in *Tegotettix*); (2) frontal costa approximately as long as half of eye height (shorter than half of eye height in *Tegotettix*); (3) interhumeral crest moderately developed, the anterior one weakly developed, posterior projections in the form of barely perceptible elevations of the median carina (interhumeral crest better developed in *Tegotettix*, others variable); (4) smaller size and more slender appearance: pronotal length < 16 mm in *Ginixistra* and *Xistra*, >16 mm in *Tegotettix*; pronotum width < 5 mm in *Xistra* and *Ginixistra*, >5 mm in *Tegotettix*.

Differs from *Xistra* by the following characters: (1) frontal costa bifurcation a little below the middle of the eye level or further below, depending on the extent to which the vertex is lowered between the eyes; (2) paired ocelli just above the bottom margin of the eyes (variable in *Xistra*, below the middle); (3) vertex anteriorly straight in dorsal view (rounded in *Xistra*); (4) Anterior and middle femora elongated and thin, anterior ones with weak projections on bottom margins, middle ones with three strong tubercles on bottom margins (weakly lobed femora in *Xistra*).

Description.

Head

In frontal view vertex about as wide as one eye; while in dorsal view vertex 1.35 to 1.5 times as wide as an eye. In frontal view, vertex depressed and lowest in the mid part. Lateral carinae forming horns height of which is species-specific. Frontal costa long, bifurcating between the eyes or lower. Facial carinae form scutellum narrower than scapus. Paired ocelli situated between the lower margins of the compound eyes. Top margin of the antennal groove situated below the ventral margins of the compound eyes for at least one antennal groove diameter. In lateral view, head slightly exserted above the level of pronotal discus. Fastigium not visible in lateral view. Frontal costa rounded, slightly projected forwards in lateral view. Occipital area visible. Anterior margin of vertex truncated, slightly indrawn in the mid. In dorsal view, medial carina visible in the anterior half of the vertex length. Lateral and transverse carinae of the vertex forming acute angle.

Pronotum

In lateral view median carina of the pronotum continuous from the anterior margin to the tip of pronotum; forming two humps (lower one between prozona and metazona, and higher one above the tegmina), and 4–5 low undulations behind; infrascapular area narrow; lateral area wide; tip of the lateral lobe of pronotum with truncated apex; tegminal sinus shallow, rectangular; ventral sinus deep, triangular. In dorsal view anterior margin

of pronotum straight; prozonal carina short, parallel; lateral lobes of pronotum directed sidewards; shoulders slightly widened, forming obtuse angle; interhumeral carinae short; pronotal apex truncated or slightly bilobate.

Wings

Tegmina and alae present. Tips of alae touching tips of pronotum (macropronotal state) or exceeding the tip (pauropronotal state).

Legs

Fore and mid femora with undulated margins. Mid femur with rounded or triangular projections on the ventral margin. Fore and mid tibiae rectangular in cross section. Proximal tarsal segment of the fore and mid legs much shorter than the distal one. Hind femora elongated; 3.3 to 3.55 times as long as wide. Dorsal and ventral margins without lappets. First segment of the hind tarsi visibly longer than the third. Tarsal pulvilli elongated and angular, but without apical teeth.

Composition. Three species, *Ginixistra novaeguineae*, *G. davorkae* sp. nov., and *G. novaebrittaniae* sp. nov.

Distribution. Endemic to New Guinea (*G. novaeguineae*, *G. davorkae* sp. nov.) and New Britain (*G. novaebrittaniae*) (Figure 9).

Taxonomic remarks. The original type series of the species *Tegotettix novaeguineae* Günther, 1938 [18] consists of 4 specimens mentioned in the original description [18]. Three syntypes are known (1♀syntype deposited at SMTD, 1♀syntype, and 1♂syntype deposited at MfN) and available on the OSF. The location of the last one is unknown. There are further recorded non-type specimens available on the OSF [5]. These and additional herein-published specimens are used as a basis for the description of two further species and the definition of the new genus. The genus, as delimited here, consists of three species distributed in geographically separate areas (New Britain Island, the northern and southern parts of New Guinea Island, separated by the New Guinean Highlands). The species are defined based on their differences, i.e., diagnoses, and the characters that are not mentioned are considered to conform to the diagnosis of the genus.

Figure 9. Distribution of the genus *Ginixistra* gen. nov. and its three species. Map sourced from the website https://commons.wikipedia.org/File:Blank_Asia.png (accessed on 8 October 2025), from Wikimedia Commons, Public Domain.

Species *Ginixistra novaeguineae* (Günther, 1938) [18,67]
(Figures 10 and 11)

Type material. Here, 1♀with data „PAPUA NEW GUINEA: West Sepik, Toricelli Mountains" (SMTD) is designated as the lectotype of this species (Figure 10), making the other two specimens, 1♂and 1♀from PAPUA NEW GUINEA: Mäanderberg (4.073 S, 141.657 E) (MfN) (Figure 11), paralectotypes.

Type locality. PAPUA NEW GUINEA: West Sepik: Toricelli Mountains; 3.379400 S, 142.239200 E; 600 to 780 m above sea level.

Type depository. The lectotype is deposited at SMTD, and the 2 paralectotypes at MfN.

Diagnosis. Easily distinguished from other species of the genus by the following set of characters: (1) vertex a little below the level of the eyes (noticeably below the level of the eyes in the other two species); (2) lateral carinae of the vertex barely elevated, forming barely perceptible horns (horns low in *G. davorkae* **sp. nov**., moderately high in *G. novaebritanniae* **sp. nov**.); (3) frontal costa bifurcation a little below the middle level of the eye height (at the level of the lower third of the eye height in the other two species); (4) tegmina rectangular: width/length ratio of tegmen 0.5 (0.37 or lower in the other two species); and (5) ovipositor short: dorsal valve 0.9 mm or shorter, same as in *G. novaebritanniae*, longer than 1.2 in *G. davorkae*.

Figure 10. *Ginixistra novaeguineae* (Günther, 1938) comb. nov. female lectotype from SMTD. (**a**) dorsal view; (**b**) lateral view, (**c**) frontal view, (**d**) labels. Scale bar 1 mm. Photography Sigfrid Ingrisch.

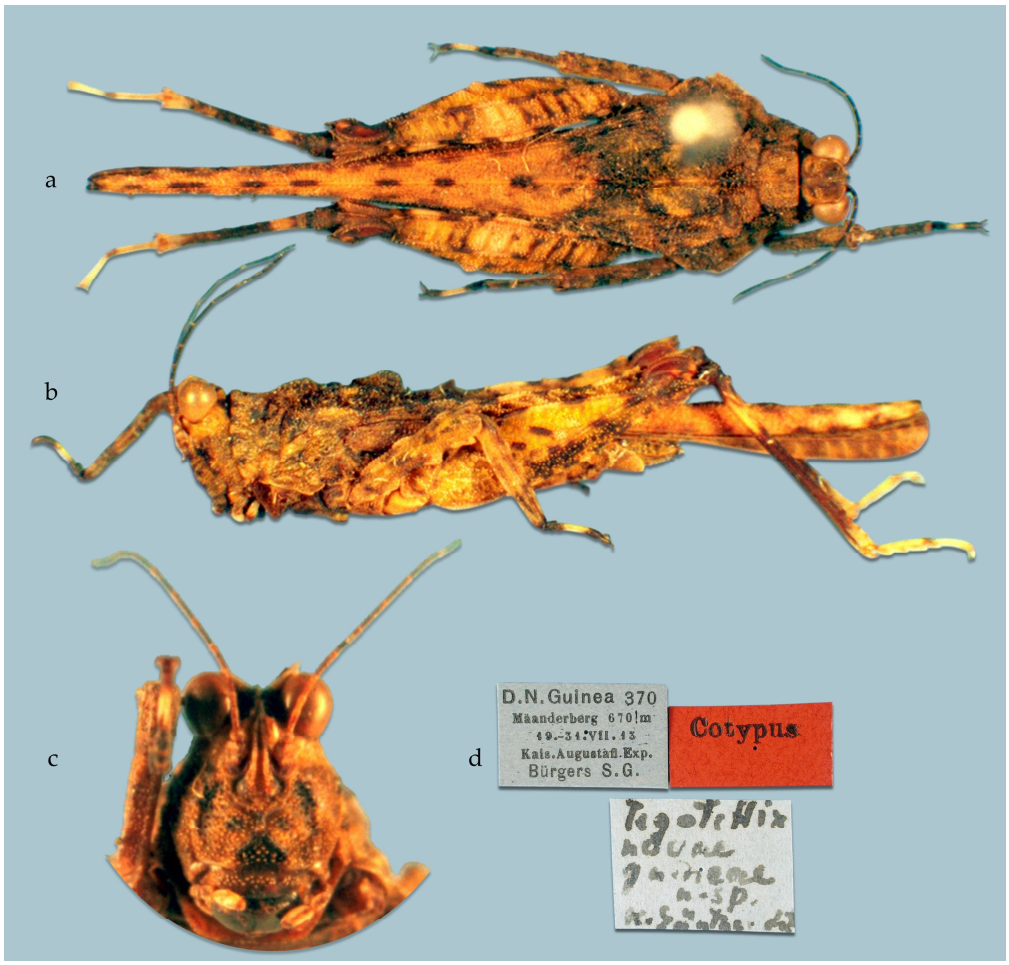

Figure 11. *Ginixistra novaeguineae* (Günther, 1938) comb. nov. female paralectotype from MfN. (**a**) dorsal view; (**b**) lateral view, (**c**) frontal view, (**d**) labels. Scale bar 1 mm. Photography Sigfrid Ingrisch.

Re-description.

Head

Frontal view. Vertex between the eyes a bit wider than one eye. Mid part of vertex slightly lower than compound eyes. Lateral carinae forming very low horns only slightly projected above the eyes. Frontal costa long, bifurcated between the compound eyes. Facial carinae weakly diverging, forming scutellum narrower than scapus. Paired ocelli situated between the lower margins of the compound eyes. Top margin of the antennal groove below the ventral margins of the compound eyes.

Lateral view. Head only slightly exserted above the level of the pronotum. Fastigium not visible. Frontal costa rounded, slightly projected forwards. Lateral carinae of the vertex are visible above the eyes as very low horns. Occipital area visible, as wide as a third of the compound eye length.

Dorsal view. Vertex about 1.5 times wider than a compound eye. Anterior margin of vertex truncated, slightly indrawn in tip of the medial carina. Medial carina visible in the anterior half of the vertex length. Lateral and transverse carinae of the vertex forming acute angle.

Pronotum

Lateral view. Median carina of the pronotum continuous from the anterior margin to the tip of pronotum; forming two triangular humps-lower between prozona and metazona and higher just above the tegmina. Furthermore there, there are 4–5 very low elevations in

metazona towards the tip. Infrascapular area narrow, with parallel margins. Lateral area wider than infrascapular, finely granulated. Tip of the lateral lobe of pronotum triangular, with truncated apex. Tegminal sinus evident, rectangularly shaped. Ventral sinus deeper than tegminal, triangularly shaped.

Dorsal view. Anterior margin of pronotum truncated, straight. Prozonal carina short, parallel. Lateral lobes of pronotum directed sidewards, with truncated apex. Shoulders slightly widened, not armed with teeth, forming obtuse angle. Interhumeral carinae present, short and a bit curved in the mid part. Pronotal apex truncated, slightly bilobate.

Wings

Tegmina and alae present. Tegmina elongated, oval, with width/length ratio about 0.5. Alae not exceeding the tip of pronotum, or slightly exceeding it (for up to 0.2 mm).

Legs

Fore legs. Fore femora with undulated margins. Fore tibiae rectangular in cross section. Second tarsal segment significantly longer than the proximal one.

Mid legs. Mid femora with less undulated dorsal margin and with more undulated ventral margin, bearing three rounded projections. Mid tibiae rectangular in cross section. Second tarsal segment significantly longer than the proximal one.

Hind: legs. Hind femora elongated; about 3.3 times as long as wide. Dorsal and ventral margins without lappets. Genicular and antegenicular teeth triangular.

First tarsal segment visibly longer than the third. Pulvilli low ang elongated, angular, but without apical teeth.

Ovipositor

Ovipositor short, dorsal valve 0.9 mm or shorter.

Distribution. Known only from the northern part of the island of New Guinea, north of the Highlands.

Habitat and Ecology. Not known.

Measurements. See Table 3.

Table 3. Comparison of measurements of three known *Ginixistra* species. For each species, it is denoted which type or non-type specimens were measured, where they are from, and in which museum they are deposited. All measurements are in millimeters with precision to 0.05 mm.

	G. novaeguineae	*G. davorkae* sp. nov.			*G. novaebritanniae* sp. nov.
Specimen	♀**Lectotype**	♀**Holotype**	♂**Paratype**	♀**Non-Type**	♀**Holotype**
Locality	**Toricelli**	**Tekadu**	**Lakekamu**	**Aru Isl.**	**New Britain Isl.**
Depository	**SMDT**	**CJT**	**CJT**	**CJT**	**CJT**
BL	14.60	14.40	13.00	15.45	15.90
PL	13.70	13.25	12.00	13.85	14.80
PW	3.85	3.90	3.35	4.10	4.10
PH	2.40	2.45	1.85	2.85	2.20
FFL	2.30	2.30	2.05	2.55	3.20
FFW	0.60	0.55	0.55	0.70	0.87

Table 3. *Cont.*

	G. novaeguineae	*G. davorkae* sp. nov.			*G. novaebritanniae* sp. nov.
Specimen	♀**Lectotype**	♀**Holotype**	♂**Paratype**	♀**Non-Type**	♀**Holotype**
Locality	**Toricelli**	**Tekadu**	**Lakekamu**	**Aru Isl.**	**New Britain Isl.**
Depository	**SMDT**	**CJT**	**CJT**	**CJT**	**CJT**
MFL	2.75	2.60	2.50	2.90	3.15
MFW	0.65	0.65	0.70	0.75	0.60
HFL	6.10	5.90	5.50	6.25	6.80
HFW	1.85	1.70	1.55	1.75	1.90
VW	0.65	0.55	0.45	0.60	0.60
EW	0.65	0.60	0.55	0.60	0.60
AL	5.25	4.80	broken	5.35	broken
HH	0.10	0.15	0.10	0.15	0.20

Taxonomic remarks. In the OSF [5], there are two nymphs from Yapen Island assigned to this species. In each, a tall pronotal crest is visible, which reduces in size as specimens go through molts [68]. It is possible that the Yapen population represents a new species of *Ginixistra,* but nothing can be said with certainty until adults are discovered. Yapen Island has been shown to be a place of high endemism in many animal and plant groups (e.g., [69–71]), but many species are also shared between mainland Papua and the island (e.g., [71–73]).

Species *Ginixistra davorkae* Kasalo, Tumbrinck et Skejo sp. nov.
urn:lsid:zoobank.org:act:042B3454-AA9F-467D-ABE2-436D47DC228A
(Figures 12–14)

Type material. 1♀holotype (Figure 12) from PAPUA NEW GUINEA: Morobe Province, Tekadu (7.63S, 146.57E) (CJT). 1♂paratype (Figure 13) from PAPUA NEW GUINEA: Gulf Province, Ivimka Research Station (7.73S, 146.50E), Lakekamu Basin. Deposited at (CJT).

Additional material (see Taxonomic remarks below). 1♀(Figure 14) INDONESIA: Aru Isl. leg. Kühne, H. (NMW), OSF collection object 1586194; code ee31b32c-cfcf-4fba-886a-ea75a0344b44.

Type locality. PAPUA NEW GUINEA: Morobe Province, Tekadu; S 7.633, E 146.567

Type depository. Currently CJT, Wassenberg, Germany.

Etymology. Named after the late Davorka Kitonić (1947-2020), a Sister of Kokoda, a friend of Papua New Guinea, traveler [74], ornithologist [75–78], philanthropist, and a great friend of J. Skejo.

Diagnosis. Easily distinguished from other species of the genus by the following set of characters: (1) vertex noticeably below the level of the eyes (same in *G. novaebritanniae*, higher in *G. novaeguineae*); (2) lateral carinae of the vertex elevated, forming low horns (horns nearly absent in *G. novaeguineae*, of medium height in *G. novaebritanniae*); (3) frontal costa bifurcation at the level of the lower third of the eye height (same in *G. novaebritanniae*, a little below the middle level in *G. novaeguineae*); (4) tegmina elongated: width/length ratio of tegmen about 0.35 (similar in *G. novaebritanniae*, 0.5 in *G. novaeguineae*); (5) ovipositor long: dorsal valve longer than 1.2 mm (0.9 mm or shorter in the other two species).

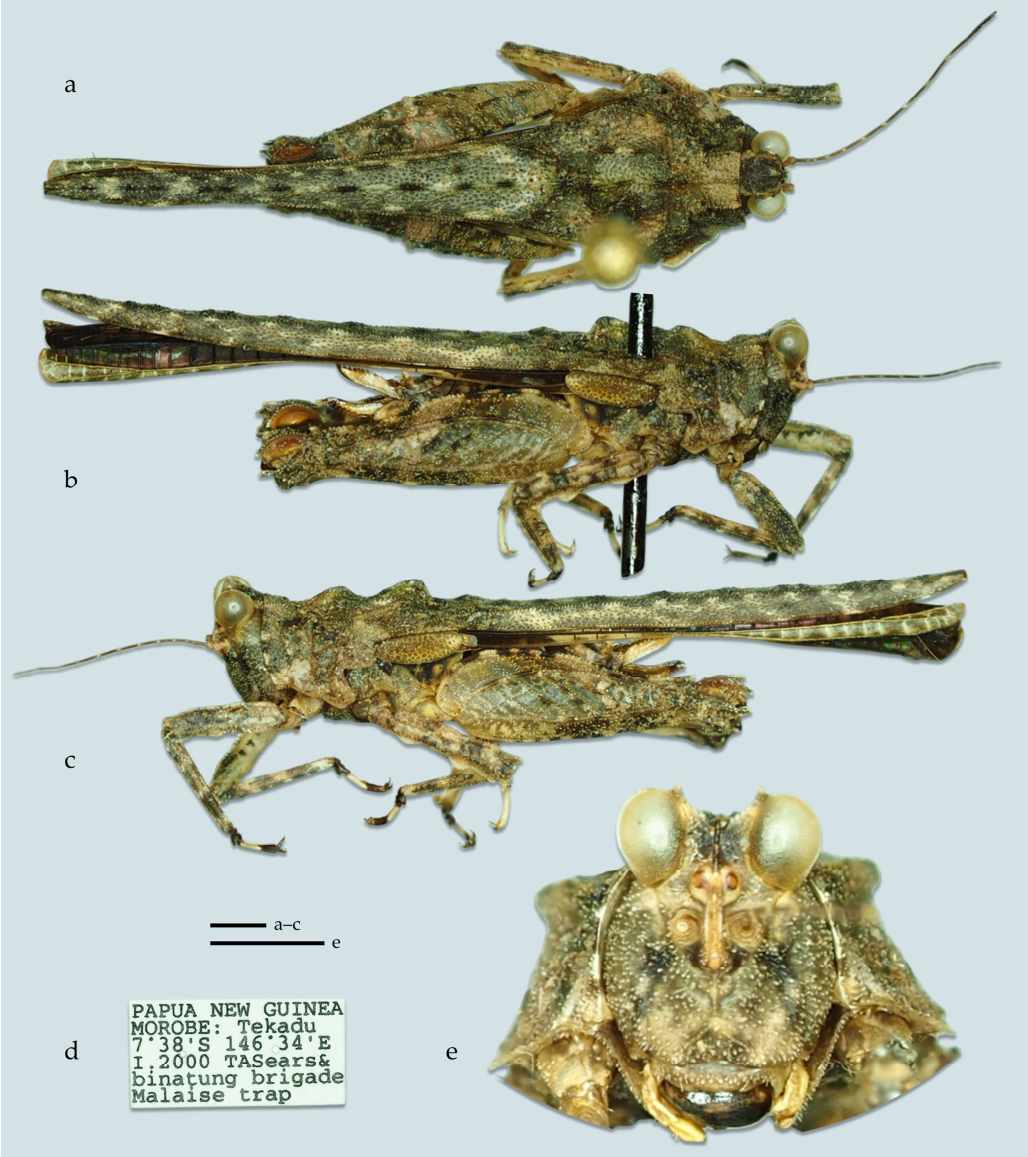

Figure 12. *Ginixistra davorkae* gen. et sp. nov. female holotype from CJT. (**a**) dorsal view; (**b**) right lateral view; (**c**) left lateral view; (**d**) labels; (**e**) frontal view. Scale bar 1 mm. Photography Josef Tumbrinck.

Figure 13. *Ginixistra davorkae* gen. et sp. nov. male paratype from CJT. (**a**) dorsal view; (**b**) right lateral view; (**c**) left lateral view; (**d**) frontal view; (**e**) labels. Scale bar 1 mm. Photography Josef Tumbrinck.

Figure 14. *Ginixistra* cf. *davorkae* gen. et sp. nov., non-type female from Aru Island, deposited in NMW. (**a**) dorsal view; (**b**) right lateral view; (**c**) left lateral view; (**d**) labels; (**e**) frontal view. Scale bar 1 mm. Photography Josef Tumbrinck.

Description.

Head

Frontal view. Vertex between the eyes a bit narrower than one eye. Mid part of vertex lower than compound eyes. Lateral carinae forming low horns only slightly projected above the eyes. Frontal costa long, bifurcated in the lower fourth of the compound eyes height. Facial carinae weakly diverging, forming scutellum narrower than scapus. Paired ocelli situated between the lower margins of the compound eyes. Top margin of the antennal groove below the ventral margins of the compound eyes.

Lateral view. Head only slightly exserted above the level of pronotum. Fastigium not visible. Frontal costa rounded, slightly projected forwards. Lateral carinae of the vertex visible above the eyes as low horns. Occipital area visible, as wide as a third of the compound eye length.

Dorsal view. Vertex 1.4 times as wide as a compound eye. Anterior margin of vertex truncated, slightly indrawn in tip of the medial carina. Medial carina visible in the anterior half of the vertex length. Lateral and transverse carinae of the vertex forming acute angle.

Pronotum

Lateral view. Median carina of the pronotum continuous from the anterior margin to the tip of pronotum; forming two triangularly rounded humps-lower one between prozona and metazona, and a bit higher one just above the tegmina; and 4–5 low elevations in metazona towards the tip. Infrascapular area narrow, with parallel margins. Lateral area wider than infrascapular, finely granulated. Tip of the lateral lobe of pronotum triangular, with truncated apex. Tegminal sinus evident, rectangularly shaped. Ventral sinus deeper than tegminal, triangularly shaped.

Dorsal view. Anterior margin of pronotum truncated, straight. Prozonal carina short, parallel. Lateral lobes of pronotum directed sidewards, with truncated apex. Shoulders slightly widened, not armed with teeth, forming obtuse angle. Interhumeral carinae present, short and a bit indrawn in the mid part. Pronotal apex truncated, slightly bilobate.

Wings

Tegmina and alae present. Tegmina elongated, oval, with width/length ratio about 0.35. Alae not exceeding the tip of pronotum or slightly exceeding it (for up to 0.2 mm).

Legs

Fore legs. Fore femora with undulated margins. Fore tibiae rectangular in cross section. Second tarsal segment significantly longer than the proximal one.
Mid legs. Mid femora with less undulated dorsal margin, and with more undulated ventral margin, bearing three circular projections. Mid tibiae rectangular in cross section. Second tarsal segment significantly longer than the proximal one.
Hind legs. Hind femora elongated; 3.45 to 3.55 times as long as wide. Dorsal and ventral margins without lappets. Genicular and antegenicular teeth triangular and sharp. First tarsal segment visibly longer than the third. Pulvilli low ang elongated, angular, but without apical teeth.

Ovipositor

Ovipositor long, dorsal valve longer than 1.2 mm.

Distribution. Known only from the southeastern part of the island of New Guinea, south of the Highlands. And from Aru? (see Taxonomic remarks below).

Habitat and Ecology. Not known.

Measurements. See Table 3.

Taxonomic remarks. In the OSF, there is a specimen from Aru that matches the diagnosis of *G. davorkae* **sp. nov.** Considering the distance from the type locality, it is possible that the Aru population represents a separate species, but there is currently no morphological proof for this. It is also possible that *G. davorkae* **sp. nov.** is a widely distributed species south of the Highlands.

Ginixistra novaebritanniae **Kasalo, Tumbrinck et Skejo sp. nov.**
urn:lsid:zoobank.org:act:757FB116-16AF-42B4-8A37-D24628AA2393
(Figure 15)

Figure 15. *Ginixistra novaebrittaniae* gen. et sp. nov. female holotype from CJT. (**a**) dorsal view; (**b**) right lateral view; (**c**) hind tarsus; (**d**) frontal view, (**e**) left lateral view. Scale bar 1 mm. Photography Josef Tumbrinck.

Type material. 1♀holotype PAPUA NEW GUINEA: Islands Region: Bismarck Archipelago: New Britain Isl.: Warongoi Valley (CJT).

Type locality. PAPUA NEW GUINEA: Islands Region: Bismarck Archipelago: New Britain (in Tok Pisin language *Niu Briten*): Gazelle Peninsula: Warongoi Valley, 100 m a.s.l.

Type depository. Currently CJT, Wassenberg, Germany.

Etymology. Genitive of Latinized "New Britain", Nova Britannia.

Diagnosis. Easily distinguished from other species of the genus by the following set of characters: (1) vertex noticeably below the level of the eyes (same in *G. davorkae*, higher in *G. novaeguineae*); (2) lateral carinae of the vertex elevated, forming horns of medium height (horns nearly absent in *G. novaeguineae*, low in *G. davorkae*); (3) frontal costa bifurcation at the level of the lower third of the eye height (same in *G. davorkae*, a little below the middle level in *G. novaeguineae*); (4) tegmina elongated: width/length ratio of tegmen about 0.37

(similar in *G. davorkae*, 0.5 in *G. novaeguineae*); (5) ovipositor short: dorsal valve shorter than 0.9 mm (same is *G. novaeguineae*, longer than 1.2 mm in *G. davorkae*).

Description.

Head

In frontal view. Vertex between the eyes as wide as one eye. Mid part of vertex lower than compound eyes. Lateral carinae forming horns projected above the eyes. Frontal costa long, bifurcated in the lower third of the compound eyes height. Facial carinae weakly diverging, forming scutellum narrower than scapus. Paired ocelli situated between the lower margins of the compound eyes. Top margin of the antennal groove below the ventral margins of the compound eyes.

In lateral view. Head a little bit exserted above the level of pronotum. Fastigium not visible. Frontal costa rounded, slightly projected forwards. Lateral carinae of the vertex visible above the eyes as pointed horns. Occipital area visible, as wide as a half of the compound eye length.

In dorsal view. Vertex 1.35 times as wide as a compound eye. Anterior margin of vertex truncated, slightly indrawn in tip of the medial carina. Medial carina visible in the anterior half of the vertex length. Lateral and transverse carinae of the vertex forming acute angle.

Pronotum

In lateral view. Median carina of the pronotum continuous from the anterior margin to the tip of pronotum; forming two high humps-lower one between prozona and metazona, and higher one just above the tegmina; and 4–5 lower humps in metazona towards the tip. Infrascapular area narrow, with parallel margins. Lateral area wider than infrascapular, finely granulated. Tip of the lateral lobe of pronotum triangular. Tegminal sinus evident, rectangularly shaped. Ventral sinus deeper than tegminal, acute.

In dorsal view. Anterior margin of pronotum truncated, straight. Prozonal carina short, almost parallel but slightly diverging. Lateral lobes of pronotum directed sidewards, with truncated apex. Shoulders slightly widened, not armed with teeth, forming obtuse angle. Interhumeral carinae present, short and parallel. Pronotal apex blunt.

Wings

Tegmina and alae present. Tegmina elongated, oval, with width/length ratio about 0.37. Alae exceeding the tip of pronotum for about 0.2 mm.

Legs

Fore legs. Fore femora with undulated margins. Fore tibiae rectangular in cross section. Second tarsal segment significantly longer than the proximal one.

Mid legs. Mid femora with moderately undulated dorsal margin bearing two low teeth, and with strongly undulated ventral margin, bearing two triangular projections. Mid tibiae rectangular in cross section. Second tarsal segment significantly longer than the proximal one.

Hind legs. Hind femora elongated, around 3.55 times as long as wide. Dorsal and ventral margins without lappets. Genicular and antegenicular teeth triangular and sharp.

First tarsal segment visibly longer than the third. Tarsal pulvilli angularly rounded, without apical teeth.

Ovipositor

Ovipositor short, dorsal valve shorter than 0.9 mm

Distribution. Known only from the island of New Britain.

Habitat and Ecology. Not known. We can assume that the species' habitat is probably similar, if not the same, to the habitat surveyed for Odonata diversity and depicted in [79]. These are wet rainforest habitats rich in creeks.

Measurements. See Table 3.

Genus *Tegotettix* Hancock, 1913 [2]
Tegotettix (armatus) species group Hancock, 1913 [2] *sensu* [24] **syn. nov**.

Subfamily assignment. Scelimeninae: Discotettigini

Type species. *Tegotettix armatus* Hancock, 1913 [2], by original designation and by monotypy (type locality: MALAYSIA: Borneo Isl.: Sarawak: Kuching. Holotype of *T. armatus* is deposited in ANSP [80].)

Redefinition. Here, *Tegotettix* is defined as a genus gathering Scelimeninae, Discotettigini species with a vertex more than two times wider than a compound eye in dorsal view; with armed, wide shoulders; and without ventrolateral projections on the lateral lobes of the pronotum. The genus from here on includes only the species that Patano et al. [24] assigned to the *Tegotettix* (*armatus*) species group, as only these belong to the Scelimeninae and Discotettigini.

Descriptive diagnosis (after [24]). *Tegotettix* is a typical Discotettiginae genus, easily distinguished from other Scelimeninae: Discotettiginae by the lack of spikes (ventrolateral projections) on the lateral lobes of pronotum. The genus bears superficial similarity to *Xistra* and *Ginixistra* **gen. nov**., whose members were previously included within *Tegotettix*. A detailed comparison with *Xistra* and *Ginixistra* **gen. nov**. is given under the *Ginixistra* **gen. nov**. diagnosis. Fastigial horns are very high and spiky. Paired ocelli are placed at the same level as the lower margins of the compound eyes. In the frontal view, the frontal costa is long and distinct, almost as long as half of the compound eye height. Facial carinae after the bifurcation diverge and have a concavity in their upper third. Prozona and prozonal carinae are well developed. Shoulders (the humeral part of the pronotum) are robust. Pronotum bears many projections on the median carina, on the discus, and on the lateral carinae. All femora are armed with teeth. Chitinous surfaces are very rough and tuberculated. Apex of the lateral lobe directed outwards but lacking VL spine.

Composition. The genus *Tegotettix* currently includes the following five species: (1) *T. armatus* Hancock, 1913 [2]; (2) *T. bufocrocodil* (Storozhenko et Dawwrueng, 2015) [81]; (3) *T. celebensis* Günther, 1937 [17]; (4) *T. siebersi* Günther, 1938 [18] [Borneo]; (5) *T. tuberculatus* (Bolívar, 1887) [1] [Sulawesi].

Distribution. Species of *Tegotettix* inhabit Indochina (*T. bufocrocodil*), Borneo (*T. armatus*, *T. siebersi*), Sulawesi (*T. celebensis*, *T. tuberculatus*), and the Philippines (one undescribed species) [5,24] (Figure 16).

Taxonomic remarks. After the update in the definition of *Xistra* and after the establishment of *Ginixistra* **gen. nov**., five species are removed from the genus *Tegotettix*, which now might represent a monophyletic unit. However, revision of this interesting corticolous genus is needed in the future when more material is available for study. The discovery of more new species is expected, as already evidenced by a new undescribed species from Mindanao (Mt. Kiamo and Mt. Kitanglad) in [24].

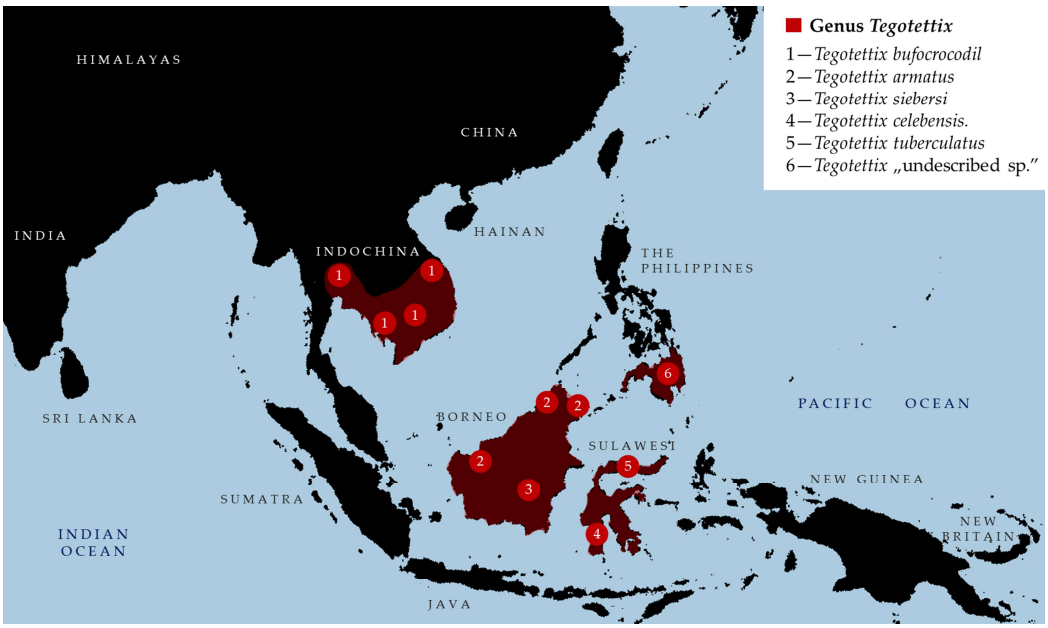

Figure 16. Distribution of the genus *Tegotettix* and its five species. Map sourced from the website https://commons.wikipedia.org/File:Blank_Asia.png (accessed on 8 October 2025), from Wikimedia Commons, Public Domain.

Measurements. Measurements of all *Tegotettix* species are shown in Table 4.

Table 4. Measurements of five known *Tegotettix* species (precision to 0.05 mm).

	T. bufocrocodil	*T. armatus*	*T. siebersi*		*T. tuberculatus*	*T. celebensis*
Specimen	♀**Holotype**	♀**Non-Type**	♀**Syntype**	♂**Syntype**	♀**Holotype**	♀**Syntype**
Locality	**Indochina**	**Borneo**	**Borneo**		**Sulawesi**	**Sulawesi**
Depository	**ZIN**	**CJT**	**SMTD**	**SMTD**	**MNCN**	**MfN**
BL	18.95	20.05	18.00	17.65	21.45	24.75
PL	17.00	18.15	17.15	16.80	20.50	23.75
PW	5.80	6.30	4.10	4.20	4.80	5.35
PH	3.65	4.75	3.15	3.00	3.55	4.80
FFL	3.10	3.35	2.65	2.35	2.60	2.85
FFW	1.20	1.20	0.85	0.65	0.70	0.95
MFL	3.60	4.10	3.10	2.70	2.65	3.40
MFW	1.40	1.60	0.65	0.75	0.70	1.05
HFL	7.55	8.30	6.50	5.60	6.80	7.45
HFW	2.45	2.50	1.80	1.75	2.10	2.40
VW	1.00	1.15	0.80	0.65	0.70	1.00
EW	0.60	0.60	0.55	0.65	0.60	0.75
AL	7.30	7.30	broken	5.65	broken	5.85
HH	0.15	0.20	0.25	0.25	0.10	0.25

Genus *Xistra* Bolívar, 1887 [1]

Subfamily assignment. Orthoptera Species File [5] assigns this genus to Metrodorinae, but we do not agree, as members of Metrodorinae have a compressed medial carina of the vertex directed forwards, and for now, they are known only to inhabit the Americas [82].

Until more evidence is presented on the taxonomic position of *Xistra*, the genus should be without a subfamily assignment

Type species. *Xistra gogorzae* Bolívar, 1887 [1] by subsequent designation by [83]

Redefinition. Head slightly dorsoventrally elongated; compound eyes and the tips of vertex above the level of the pronotum. In frontal view, medial carina of the vertex positioned just between the compound eyes, and with lateral sides of the vertex elevated. In the frontal view frontal costa bifurcation very high, with frontal costa itself being nearly invisible; *X. cristifera* being an exception with its short but visible frontal costa. Tip of the eyes visibly above the vertex. Lateral carinae projected as horns, which are in some species very low (*X. sagittaria*), while in others very high (*X. corniculata*, *X. cristifera*, *X. derijei*). Antennal grooves positioned below the lower margins of the compound eyes. Paired ocelli below the middle level of the eyes, position varies depending on the degree to which the vertex is lowered below the eyes. Scutellum slightly (*X. sagittaria*) or conspicuously widened (*X. derijei*).

Here, the *Xistra* is defined as a genus gathering species with V- or U-shaped vertex; with medial carina of the vertex positioned much lower than the dorsal margins of the compound eyes in frontal view; with lateral carinae usually elevated into high horns; and with various forms of pronotum. The genus is here defined as endemic to Borneo and the Philippines. Because of this re-definition, species from mainland Asia are excluded from this genus.

Descriptive diagnosis. Members of the genus *Xistra* are visually similar to members of *Xistrella*, but can easily be distinguished by the following traits: (1) *Xistrella* members have rectangular vertex with low horns, while *Xistra* members have V or wide U shape vertex with high horns; (2) *Xistrella* members have oval eyes in frontal view, while *Xistra* members have rounded eyes; (3) occipital area narrow in *Xistrella*, wide and elongated in *Xistra*; (4) tegminal sinus in *Xistrella* reduced, while in *Xistra* deep; and (5) elongated proximal segment of fore and mid tarsi in *Xistrella*, almost a half of the distal segment length (about a third of the distal segment length in *Xistra*).

For comparison with *Ginixistra* gen. nov., see *Ginixistra* paragraph.

Composition. Genus is divided into two subgenera and comprises five species in total. Nominotypical subgenus *Xistra* includes two species (*X.* (*Xistra*) *gogorzae* Bolívar, 1887 and *X.* (*Xistra*) *sagittaria* Bolívar, 1887 [1] **comb. resurr**.) while *Tegoxistra* subgen. nov. includes three species (*X.* (*Tegoxistra*) *corniculata* (Stål, 1877) [40] **comb. resurr**., *X.* (*T.*) *derijei* (Patano, Mohagan, Tumbrinck, Amoroso et Skejo, 2021) [24] **comb. nov**. 5) *X.* (*T.*) *cristifera* Günther, 1935 [16] **comb. resurr**.).

Distribution. Genus *Xistra* [1] is endemic to the Philippines (*X. gogorzae*, *X. sagittaria*, *X. corniculata*, *X. derijei*) and Borneo (*X. cristifera*) (Figure 17). Species transferred from *Xistra* to *Xistrella* are shown on the map of the genus *Xistrella* (Figure 18).

An annotated identification key to *Xistra* species

(**1A**) Horns of vertex low. Upper margins of antennal grooves situated slightly under the lower margins of eyes. Pronotal crest absent or very low. **subgenus *Xistra*. . .2**
(**1B**) Horns of vertex high. Top margins of the antennal grooves visibly below the bottom margins of the eyes. Pronotal crest(s) clearly visible. **subgenus *Tegoxistra*. . .3**

(**2A**) In frontal view, vertex V-shaped, narrow. In lateral view, horns of vertex visible above eyes. Pronotum is almost completely flat. ***X***. (***Xistra***) ***gogorzae*** (Figure 19)

(**2B**) In frontal view, vertex C-shaped, wide. In lateral view, horns of vertex not visible or hardly visible as a dot above eye. Pronotum has an undulation above the tegmina. ***X***. (***Xistra***) ***sagittaria*** (Figure 20)

(**3A**) Highest pronotal projection visibly higher than horns of vertex. In lateral view, dorsum of pronotum is rough. Genicular tooth large. . .**4**
(**3B**) Highest pronotal projection as high as horns of vertex. There is one in lateral view, dorsum of pronotum smooth. Genicular tooth small. ***X***. (***Tegoxistra***) ***corniculata*** **comb. resurr**. (Figure 21)

(**4A**) One high semicircular crest (projection) formed by the median carina of the pronotum visible in lateral view above the tegmina. *X*. (*Tegoxistra*) *cristifera* comb. resurr. (Figure 22)
(**4B**) Many teeth-like projection on the median carina visible in lateral view from the contact of prozona and metazona all the pronotal apex (usually >10 teeth). ***X***. (***Tegoxistra***) ***derijei*** **comb. nov**. (Figures 23 and 24)

Taxonomic remarks. The diagnoses presented in this study define the genus *Xistra* and its two subgenera in a falsifiable way. The diagnoses are based on highly similar facial morphologies, as the pronotal and leg characters are very similar among different genera but can significantly vary within them. Such characters are the presence and shape of the pronotal crest, the presence of numerous pronotal projections, the development of lateral, prozonal, and interhumeral carinae of the pronotum, sulcation of the legs, and tarsal morphologies, for which it is still unclear at which taxonomic level they could be useful. This study does not aim to resolve the ocean of problems that lie beyond *Xistra*; thus, the diagnoses are kept short and are expected to be expanded once the genera listed further in the text are revised.

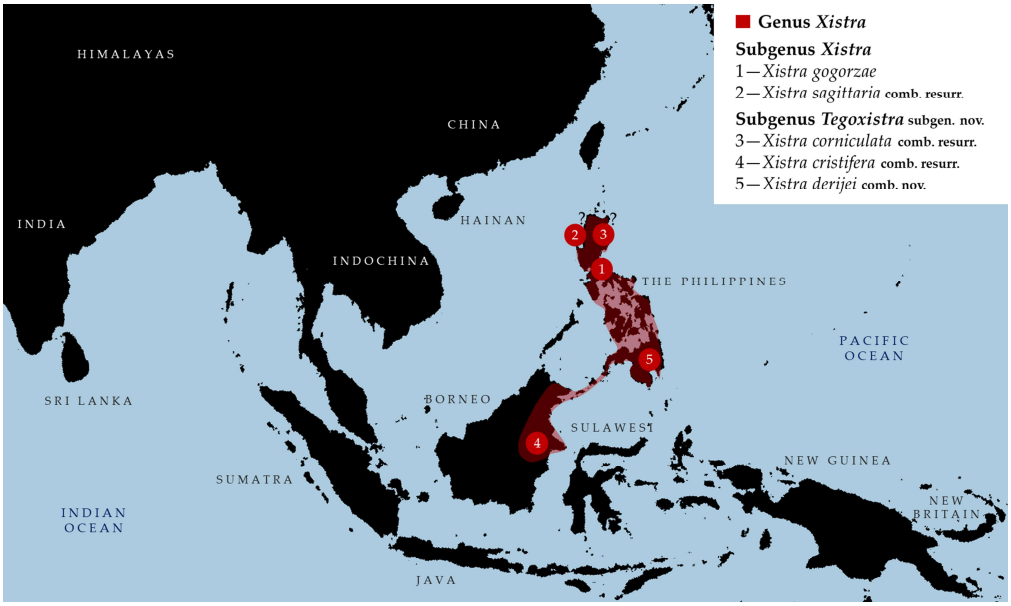

Figure 17. Distribution of the genus *Xistra* and its five species. Map sourced from the website https://commons.wikipedia.org/File:Blank_Asia.png (accessed on 8 October 2025), from Wikimedia Commons, Public Domain.

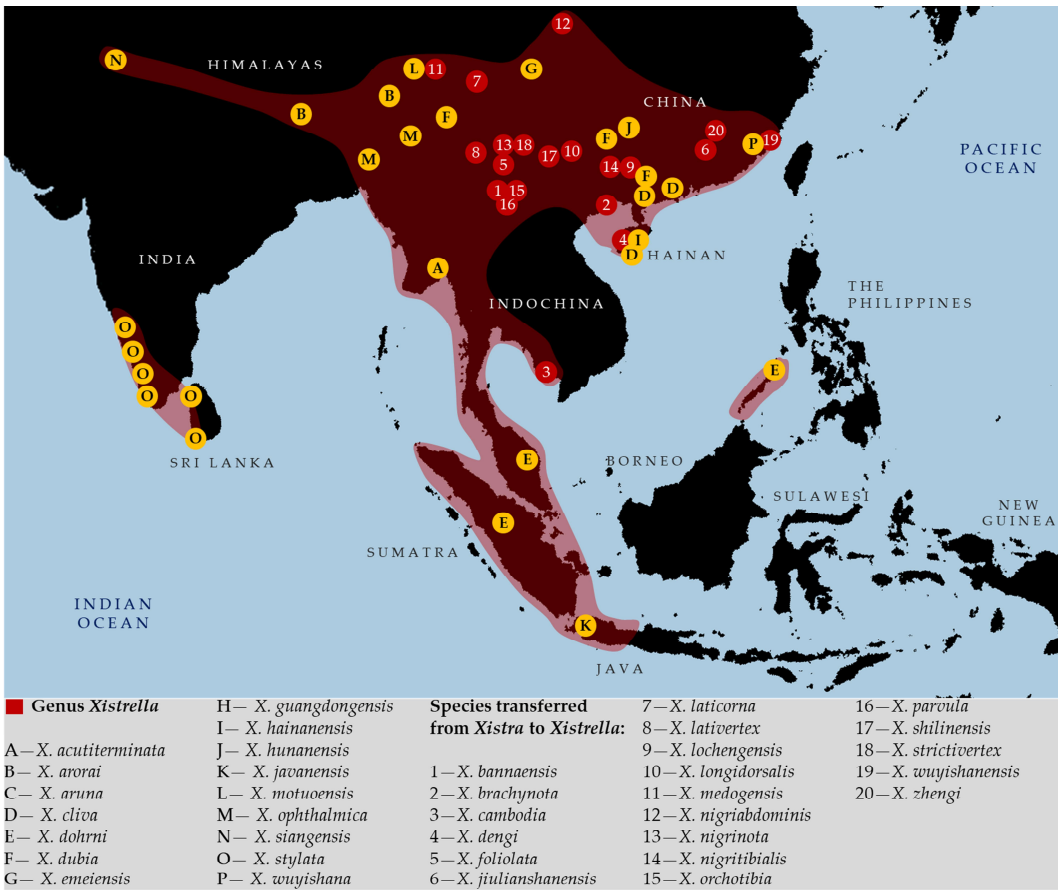

Figure 18. Distribution of the genus *Xistrella*. Yellow circles represent species hitherto assigned to the genus, while red circles represent species transferred from *Xistra*. Map sourced from the website https://commons.wikipedia.org/File:Blank_Asia.png (accessed on 8 October 2025), from Wikimedia Commons, Public Domain.

Many species are herewith transferred from *Xistra* to *Xistrella* (Figure 18). The genus *Xistra* is endemic to the Philippines and to Borneo and does not inhabit mainland Asia. We hereby transfer all Chinese species of *Xistra* (as in [5,26]) to *Xistrella*, while noting that a comprehensive revision of Xistrellini trib. nov. genera is needed (see Xistrellini paragraph below). Namely, most of the species from mainland Asia hitherto assigned to the genus *Xistra* have a rectangularly shaped vertex (species from Borneo and the Philippines have a triangular vertex), some have a vertex much narrower than an eye (species from Borneo and the Philippines have a wider vertex), and some have median carina of the pronotum former exactly like in the type species of *Xistrella*. The placement of most of these species is temporary and points to the fact that these species do not belong to the genus *Xistra.* Many mainland species assigned to *Xistra* have already been moved to *Systolederus* and *Xistrella* [7]. Some of these *Xistrella* may belong to *Bannatettix, Pseudoxistrella, Systolederus*, and even to new genera. Therefore, we will not perform a preliminary revision here but rather a comprehensive one in the future, redefining all Xistrellini genera and species based on large series. *Xistrella angusta* (Ingrisch, 2001) [39] [Nepal: Mechi: Taplejung–Terhathum District, Mitilung-Dumhan] and *X. longicornis* (Ingrisch, 2001) [39] [Nepal: Bhaktapur: Nuwakot District, Kathmandu-Trisuli] are going to be moved to *Lamellitettigodes* [Subedi et al. under review]. Also, many species that are already included in the genus *Xistrella* are probably related to this genus but do not belong to it, while others are not related to it at all.

Species moved from *Xistra* to *Xistrella* include the following [with the type locality]:

(1) *X. bannaensis* (Deng, Wang, Mao et Li, 2022) [7,38,42] **comb. nov.** [China: Yunnan: Xishuangbanna];
(2) *X. brachynota* (Li, Deng et Zheng, 2014) [7,26,36,84] **comb. nov.** [China: Guangxi: Shangsi, Shiwanshan Mt.];
(3) *X. cambodia* (Storozhenko, 2021) [6,7] **comb. nov.** [Cambodia: Kâmpôt: S part of Elephant Mts., Bokor NP, Phnom-Bokor Mt.];
(4) *X. dengi* Skejo, Kasalo, Tumbrinck et Storozhenko nom. nov. (Zoobank act urn:lsid:zoobank.org:act:C048848F-13E4-4909-8E22-CE26BF8B0673) for *X. hainanensis* (Deng, 2022) [7,26] **comb. nov.** [PR China: Hainan: Ledong, Jianfengling Mt.], homonym of *Xistrella hainanensis* Deng, 2019 [26,41];
(5) *X. foliolata* (Liang et Chen, 2010) [7,26,35,36] **comb. nov.** [China: Yunnan: Pu'er: Nanping];
(6) *X. jiulianshanensis* (Zheng et Shi, 2009) [7,26,32] **comb. nov.** [China: Jiangxi: Longnan, Jiulianshan Mt.];
(7) *X. laticorna* (Zheng, 1988) [7,26,28,29,31,36,85–88] **comb. nov.** [China: Namcha Barwa];
(8) *X. lativertex* (Zheng et Mao, 2010) [7,26,37] **comb. nov.** [China: Yunnan: Longlin];
(9) *X. lochengensis* (Zheng, 2005) [7,26,29,36,89–91] **comb. nov.** [China: Guangxi: Locheng, Pingying];
(10) *X. longidorsalis* (Liang et Jiang, 2004) [7,26,31,36,91,92] **comb. nov.** [China: Yunnan: Tianlin];
(11) *X. medogensis* (Zheng, 2005) [7,26,29,36,86] **comb. nov.** [China: Mêdog];
(12) *X. nigriabdominis* (Deng, 2022) [7] **comb. nov.** [China: Sichuan: Qingchuan (Maozhai)];
(13) *X. nigrinota* (Zheng et Xu, 2010) [26,37] **comb. nov.** [China: Yunnan: Xinping];
(14) *X. nigritibialis* (Zheng et Jiang, 2002) [7,26,93,94] **comb. nov.** [China: Guangxi: Longzhou];
(15) *X. orchotibia* (Deng, Wang, Mao et Li, 2022) [7,42] **comb. nov.** [China: Yunnan: Xishuangbanna];
(16) *X. parvula* (Liang et Chen, 2010) [7,26,35,36] **comb. nov.** [China: Yunnan: Pu'er: Nanping];
(17) *X. shilinensis* (Zheng, 2015) [7,30] **comb. nov.** [China: Yunnan: Shilin];
(18) *X. strictivertex* (Zheng et Ou, 2010) [7,26,33,36,37] **comb. nov.** [China: Yunnan: Yuanjiang];
(19) *X. wuyishanensis* (Zheng et Zeng, 2011) [7,26,30,34,36] **comb. nov.** [China: Fujian: Wuyishan];
(20) *X. zhengi* (Deng, 2024) [38] **comb. nov.** [China: Jiangxi: Ganzhou: Yudu].

Subgenus *Xistra* Bolívar, 1887 [1]

Type species. *Xistra gogorzae* Bolívar, 1887 [1] (Figure 19) by subsequent designation by Kirby [83].

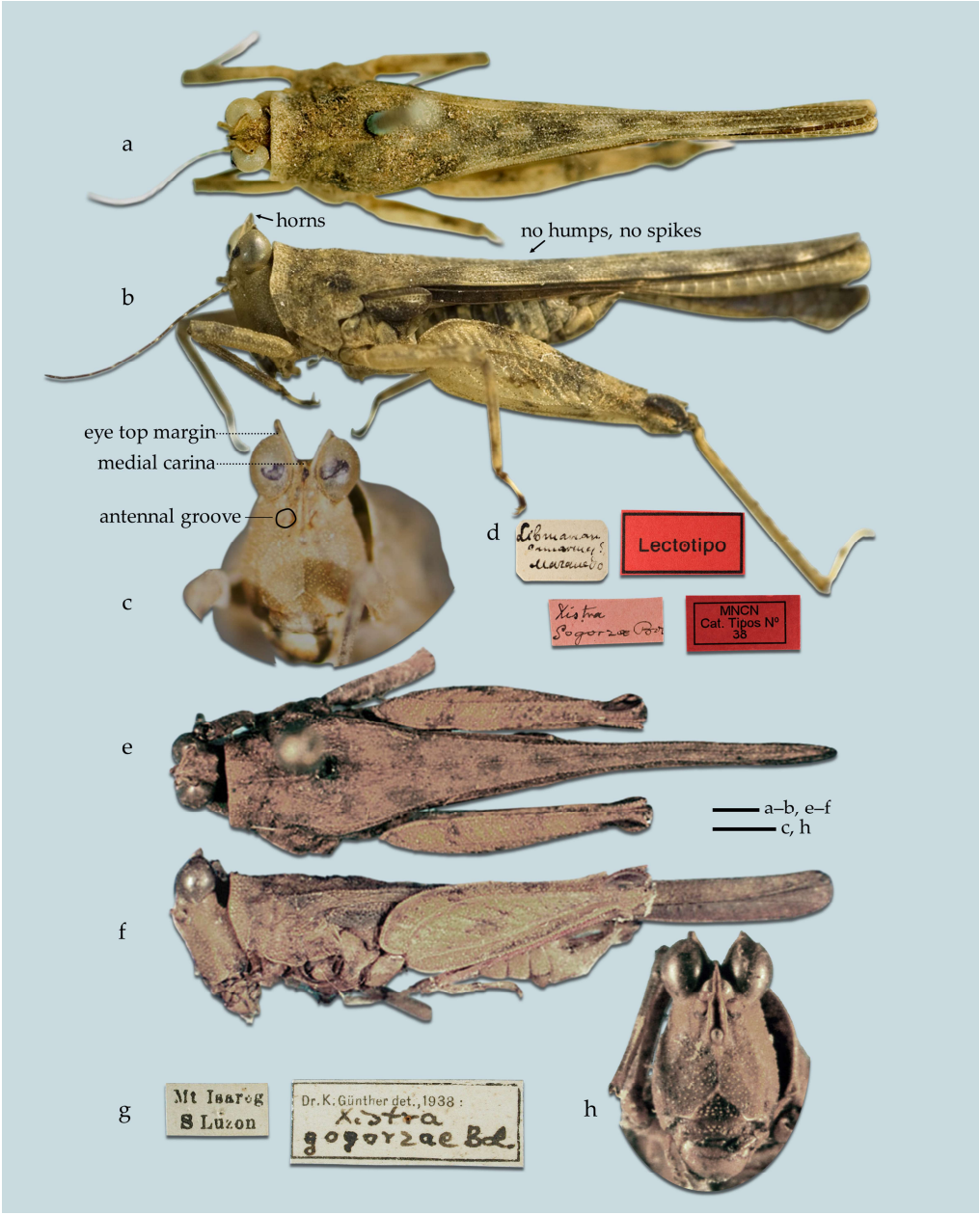

Figure 19. *Xistra* (*Xistra*) *gogorzae* Bolívar, 1887. (**a**–**d**) male holotype; (**e**–**h**) non-type male. (**a**) Dorsal view; (**b**) lateral view; (**c**) frontal view; (**d**) labels; (**e**) dorsal view; (**f**) lateral view; (**g**) labels; (**h**) frontal view. (**a**–**d**) Photography Josip Skejo & MNCN Madrid; (**e**–**h**) photography Sigfrid Ingrisch.

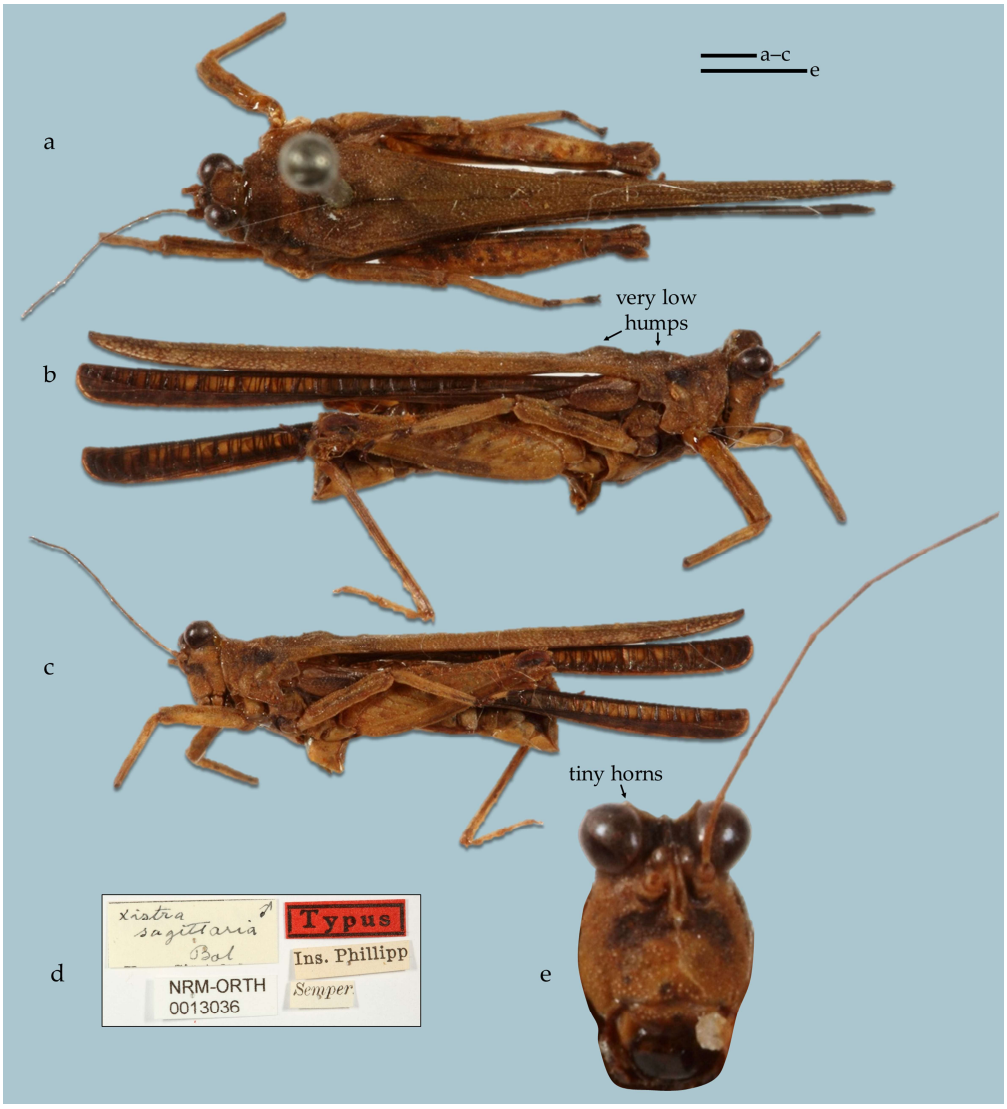

Figure 20. Holotype male of *Xistra* (*Xistra*) *sagittaria* Bolívar, 1887 from the Philippines (NHRS). Each scale bar is 1 mm. (**a**) Dorsal view; (**b**) right lateral view; (**c**) left lateral view, enlarged; (**d**) labels; (**e**) frontal view. Photography Josef Tumbrinck.

Diagnosis of the subgenus *Xistra*. Horns of the vertex weakly to moderately developed. Bifurcation of the frontal costa at the top of the face in anterior view, frontal costa nearly invisible. Top margins of the antennal grooves a little below the bottom margins of the eyes. The crest in the anterior part of the pronotum is absent or weakly developed.

Composition. Two species, *X. gogorzae* (Figure 19), and *X. sagittaria* (Figure 20).

Distribution of the subgenus *Xistra*. Endemic to the Philippines.

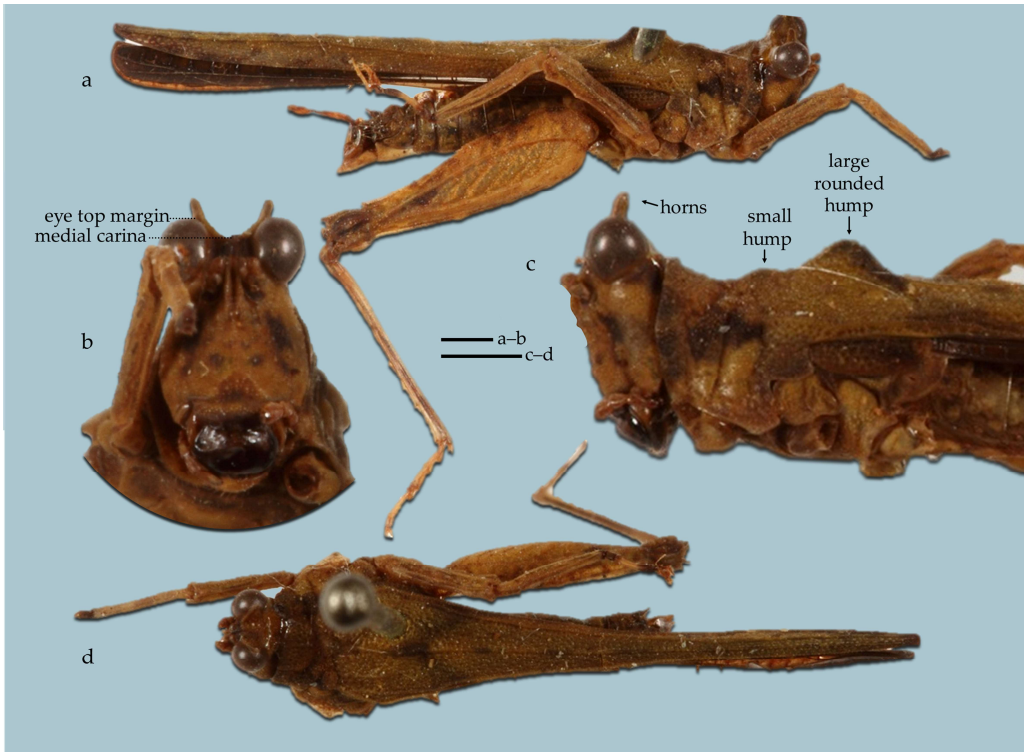

Figure 21. Holotype male of *Xistra* (*Tegoxistra*) *corniculata* (Stål, 1877) from the Philippines (NHRS). Each scale bar is 1 mm. (**a**) Syntype in right lateral view. (**b**) Head in frontal view. (**c**) Left lateral view, enlarged. (**d**) Syntype in right lateral view. Photography Josef Tumbrinck.

Subgenus *Tegoxistra* Skejo, Patano, Škorput et Kasalo subgen. nov.
urn:lsid:zoobank.org:act:7EA3C37F-CC3D-40EA-883A-CE6AD0F57046

Type species. *Tegotettix derijei* Patano, Mohagan, Tumbrinck, Amoroso et Skejo, 2021 [24] (=*X.* (*Tegoxistra*) *derijei* **comb. nov**.), here designated. Because it is the species for which the largest amount of material is available for research, we decided to designate *X. derijei* comb. nov. as the type species of this new subgenus.

Diagnosis of the subgenus *Tegoxistra* subgen. nov. Horns of the vertex are highly developed. Bifurcation of the frontal costa at the top of the face in anterior view or a little lower (in *X. cristifera*). Top margins of the antennal grooves visibly below the bottom margins of the eyes. The crest in the anterior part of the pronotum moderately developed.

Composition. Three species, *X. corniculata*, *X. derijei*, and *X. cristifera*.

Distribution. Endemic to the Philippines (*X. corniculata*, *X. derijei*), and Borneo (*X. cristifera*).

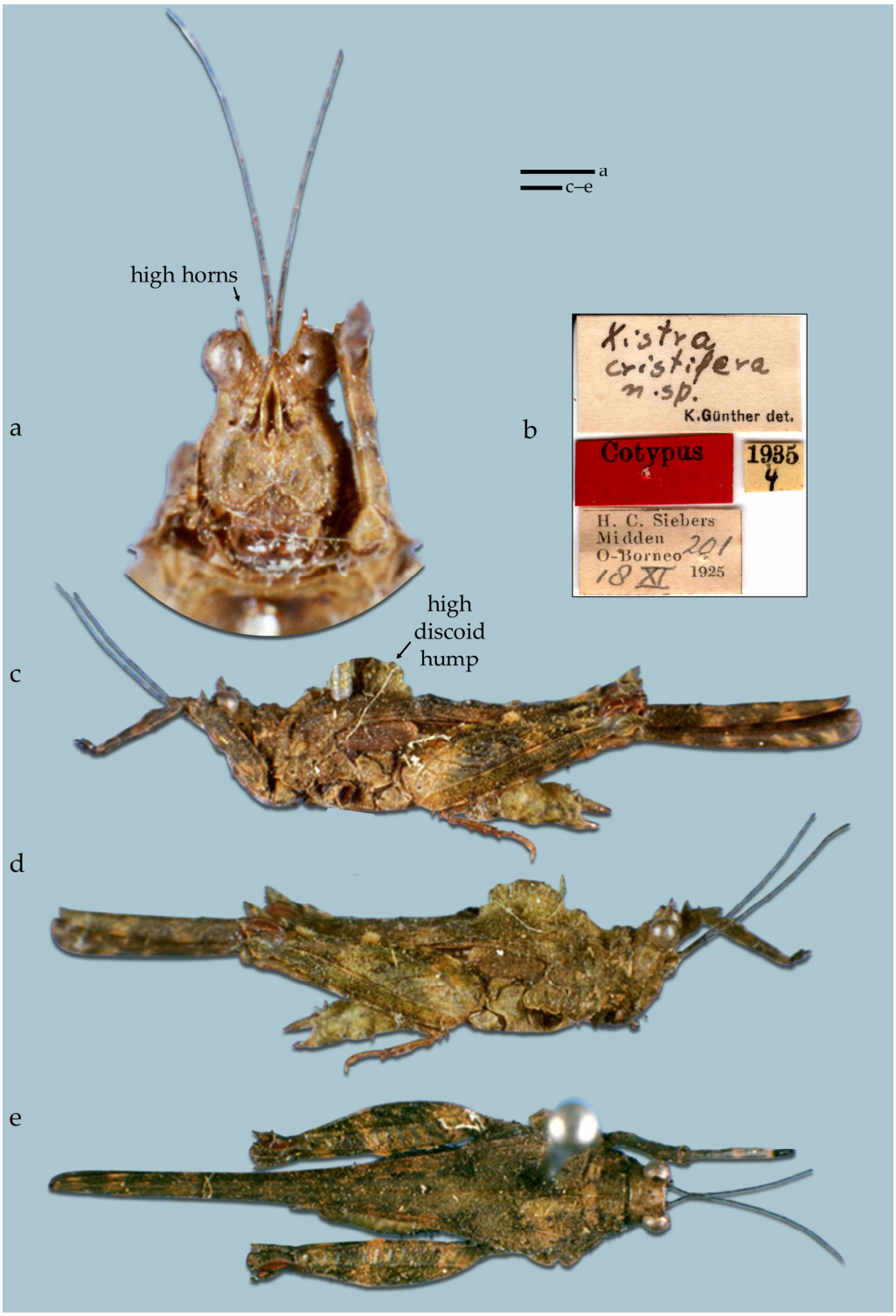

Figure 22. *Xistra* (*Tegoxistra*) *cristifera* Günther, 1935 comb. resurr. Female syntype from SMTD. (**a**) frontal view; (**b**) labels, (**c**) left lateral view; (**d**) right lateral view; (**e**) dorsal view. Head in frontal view Photography Sigfrid Ingrisch.

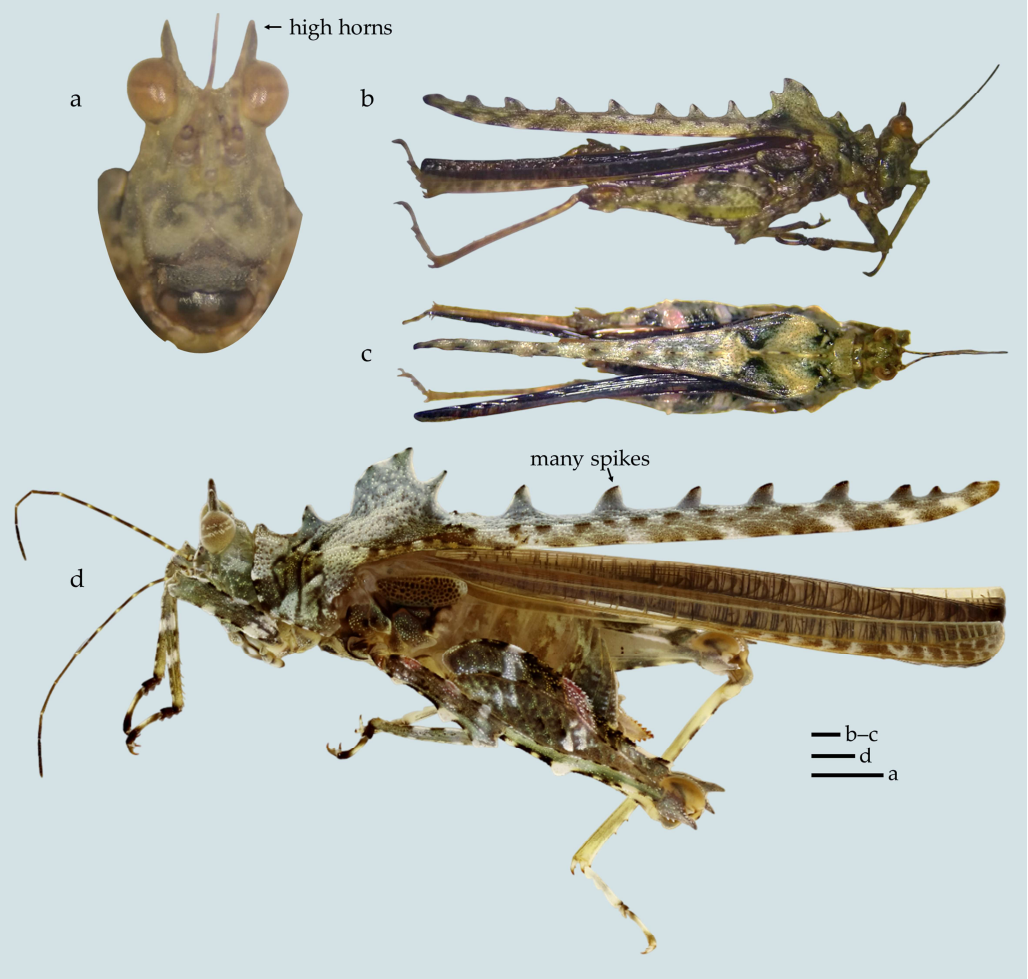

Figure 23. *Xistra* (*Tegoxistra*) *derijei* (Patano, Mohagan, Tumbrinck, Amoroso et Skejo, 2021) comb. nov. from the Philippines. (**a**–**c**) female holotype from CMU, (**d**) additional record from OSF. (**a**) frontal view, (**b**) right lateral view, (**c**) dorsal view, (**d**) left lateral view. Scale bar 1 mm. Photography (**a**–**c**) R. Patano, Jr., (**d**) Dominik Vondráček (reproduced with author's permission).

Xistra derijei **comb. nov.** was recently described from Mount Malambo [24], and here we present new records. The species was collected in Mount Natampod, Pantaron Range, Bukidnon, on 4 July 2022 (Figure 24a,b), and from Mount Balatukan, Gingoog City, Misamis Oriental, on 20 January 2023. Male and female specimens were observed mating (Figure 24c) in a branch of a sapling of an unidentified flowering plant within the lower montane forest of Mount Balatukan, Misamis Oriental. On the other hand, another male specimen was collected in Mount Natampod, perched on a shrub (*Vaccinium* sp.) within the montane forest. This is the second specimen collected in Mount Natampod, in addition to the observation reported by Patano and colleagues [24]. This implies that the species might be widely distributed across different forests and mountain ecosystems on Mindanao Island.

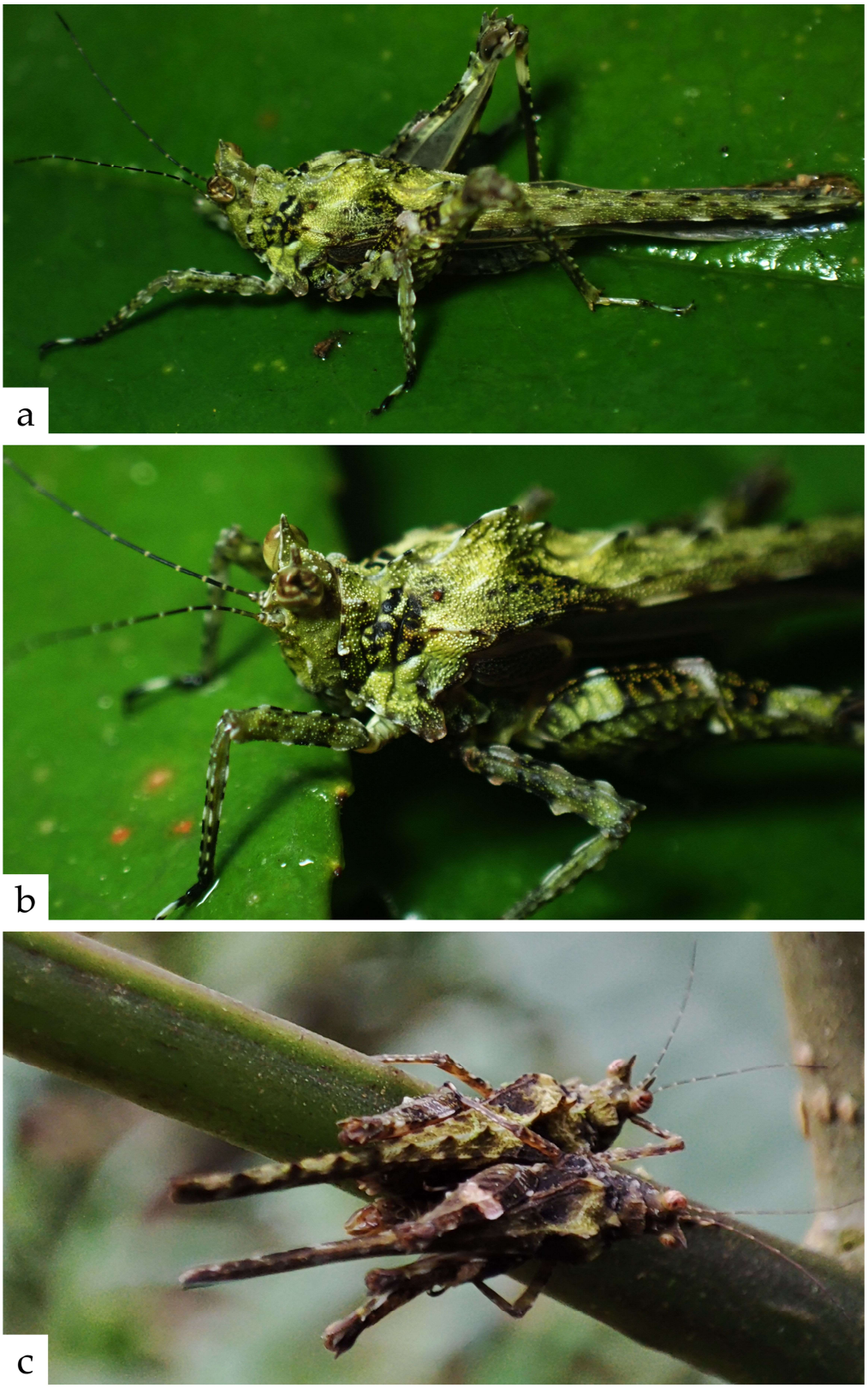

Figure 24. *Xistra* (*Tegoxistra*) *derijei* (Patano, Mohagan, Tumbrinck, Amoroso et Skejo, 2021) comb. nov., new records from Mindanao. Photography R. Patano, Jr. (**a**,**b**) Individual from Mt. Natampod; (**c**) pair from Mt. Balatukan (not mating).

Measurements. Comparative measurements of all *Xistra* species are shown in Table 5.

Table 5. Comparison of measurements of five *Xistra* species. For each species, it is denoted which type or non-type specimens were measured, and in which museum they are deposited. All measurements are in millimeters with precision to 0.05 mm. (HT = holotype, LT = lectotype, PT = paratype, ST = syntype).

	Subgenus *Xistra*			**Subgenus *Tegoxistra***				
	X. gogorzae		***X. sagittaria***	***X. derijei***			***X. corniculata***	***X. cristifera***
Specimen	**♂LT**	**♂Non-Type**	**♂HT**	**♀HT**	**♂PT**	**♀PT**	**♂HT**	**♀ST**
Locality	**Camarines Sur: Libmanan**	**Luzon: Isarog**	**Philippines: No Locality**	**Philippines: Mindanao: Davao: Marilog: Mount Malambo**			**Philippines: No Locality**	**Borneo: Central East Part**
Depository	**MNCN**	**MfN**	**NHRS**	**CMU**	**CMU**	**CMU**	**NHRS**	**SMTD**
BL	14.45	15.55	13.50	16.00	15.25	17.30	13.90	14.80
PL	13.05	13.40	12.20	14.50	13.60	15.6	12.70	13.00
PW	3.15	2.95	3.15	3.00	2.90	4.00	3.10	3.75
PH	2.30	2.15	1.85	2.10	2.85	2.95	2.10	2.40
FFL	2.45	broken	2.35	3.60	2.40	2.60	2.45	2.85
FFW	0.45	broken	0.50	0.40	0.40	0.65	0.45	0.75
MFL	2.85	broken	2.60	3.70	2.70	3.35	2.80	broken
MFW	0.65	broken	0.50	0.70	0.55	0.70	0.65	broken
HFL	6.40	6.05	5.05	5.90	5.70	6.70	5.70	6.10
HFW	1.80	1.80	1.45	2.00	1.30	2.00	1.40	1.70
VW	0.40	0.40	0.85	0.95	0.80	0.85	0.50	0.50
EW	0.75	0.70	0.70	0.80	0.70	0.65	0.55	0.65
AL	broken	broken	4.65	6.80	5.00	6.50	broken	6.00
HH	0.30	0.35	0.05	0.45	0.30	0.60	0.25	0.35

Tribe Xistrellini Skejo, Storozhenko, Tumbrinck et Kasalo trib. nov.
urn:lsid:zoobank.org:act:8115B788-393B-492B-A405-0437C19977DA

Type genus. *Xistrella* Bolívar, 1909 [3] (type species *Xistrella dromadaria* Bolívar, 1909 [3], by original monotypy).

Composition. The tribe consists of 10 genera:

(1) *Afrosystolederus* Devriese et Husemann, 2023 [95] [Africa: Liberia];
(2) *Bannatettix* Zheng, 1993 [96] [PR China; Nepal];
(3) *Kanakacris* Kasalo et Skejo, 2025 [97] [New Caledonia];
(4) *Pseudoparatettix* Günther, 1937 [17] [islands of SE Asia and Papua; Nepal];
(5) *Phaesticus* Uvarov, 1940 [98,99] [India, Indochina, PR China, Malaysia, Sumatra, Java, Borneo];
(6) *Pseudosystolederus* Günther, 1939 [4,100,101] [Madagascar];
(7) *Pseudoxistrella* Liang, 1991 [102,103] [Indochina, PR China];
(8) *Synalibas* Günther, 1939 [4] [India, Nepal, PR China, Papua];
(9) *Systolederus* Bolívar, 1887 [1,27,95,104–110] [S and SE Asia, Papua];
(10) *Teredorus* Hancock, 1907 [14,95] [Southern and Northern Americas];
(11) *Xistrella* Bolívar, 1909 [3,111] [Sri Lanka, India, Nepal, China, Indochina, Malaysia, Sumatra].

Distribution. Mostly Asia (*Bannatettix, Pseudoparatettix, Phaesticus, Pseudoxistrella, Synalibas, Systolederus, Xistrella*) but also Madagascar (*Pseudosystolederus*), New Caledonia (*Kanakacris*), Africa (*Afrosystolederus*), and Southern America (*Teredorus*). Most of the aforementioned genera require a comprehensive revision.

Description

Moderately large pygmy grasshoppers. Short and rounded vertex; in dorsal view never projected. Antennae long and filiform (most genera), or with flattened subapical antennomeres (*Phaesticus*). Dorsal margins of the antennal grooves' placement genus-specific; situated between the eyes, or at the level of the lower margins of the compound eyes, or lower. Bifurcation of the frontal costa usually around the middle of the eye height, sometimes lower. Long and relatively narrow frontal costa never forming wide scutellum. Vertex usually narrower than an eye (many *Xistrella*, *Pseudoparatettix*, *Phaesticus*, and all *Systolederus*, Synalibas, *Kanakacris*, *Pseudosystolederus*, *Afrosystolederus*, *Teredorus*), sometimes as wide as an eye or wider. Pronotal carinae, especially prozonal, reduced in many genera. First tarsal segment of the fore and mid tarsi elongated. Pulvilli of the hind tarsi are obliquely angular, without apical teeth. Nymphs of several genera (*Xistrella*, *Phaesticus*, *Pseudoxistrella*, *Pseudoparatettix*) with striped coloration.

Diagnosis. The new tribe is visually similar most similar to Tetriginae and especially to Tetrigini, a specious subfamily and Tribe whose members exhibit wide range of morphological traits. Xistrellini members are similar to Tetriginae in their slender and usually smooth appearance; paranota directed downwards; and pauropronotal state (hind wings longer than pronotum). However, Xistrellini members can generally be distinguished from Tetriginae by (1) short and rounded vertex (usually wide, rectangular or triangular in Tetriginae), (2) elongated proximal tarsal segments of fore and mid legs (not elongated in Tetriginae), (3) reduced prozonal carinae; (4) the lack of apical teeth on the pulvilli of hind tarsi, and (5) enlarged compound eyes.

Remarks on the nymphal morphology. Members of *Phaesticus* (e.g., iNaturalist observations 255283114, 235071700, 235459474, 236842858, 237243682, 228412504, 226344612, 224981610, 224600328), *Pseudoxistrella* (e.g., iNaturalist observations 147581446, 147581440, 253289656, 239757201, 214499626, 194731007), and *Pseudoparatettix* (e.g., iNaturalist observation 177970395) have very similar-looking nymphs, and it seems clear that they are related. *Xistrella* nymphs have a somewhat similar pronotal apex, but the median carina is not so uniformly elevated throughout its length, the anterior part of the pronotum does not protrude, and the vertex reaches nearly to the level of the eyes.

4. Discussion

Today, we stand a step closer to unraveling the taxonomic intricacies of three enigmatic genera of pygmy groundhoppers, *Xistra*, *Xistrella*, and *Tegotettix*. Through meticulous study, their true relationships begin to emerge with greater clarity.

The group referred to as the *Tegotettix* (*armatus*) species group by Patano and colleagues [24] is hereby regarded as only *Tegotettix* members and is confirmed to be part of the subfamily Scelimeninae, tribe Discotettigini. The closest relatives of *Tegotettix* are Asian genera *Discotettix*, *Eufalconius*, and *Paragavialidium*. They share a suite of remarkable morphological traits: (1) an exceptionally broad, rectangular vertex crowned with elevated lateral carinae rising like horns on each side; (2) a distinctive arrangement of medial and mediolateral pronotal projections; (3) wide shoulders or humeral angles marked by metalateral expansions; and (4) a long, prominent frontal costa. *Tegotettix* can be distinguished from its allies only by the presence of long, filiform antennae, the absence of a spine on its lateral lobes, and an elongated pronotum. Other species groups once placed within *Tegotettix*—namely the *T.* (*novaeguineae*) and *T.* (*cristiferus*) groups—tell a different story. These do not belong within *Tegotettix*, nor within Discotettigini, nor within Scelimeninae at all.

The *T.* (*cristiferus*) group, as Patano and colleagues [24] called it, alongside the type species *Xistra gogorzae*, truly belongs to the genus *Xistra*. This genus remains unassigned to a subfamily, and further research should be conducted to identify its sibling genera. This

genus *Xistra* is characterized, and easily distinguished from *Tegotettix*, by (1) a vertex that is relatively narrow and shaped like a V or U in frontal view, still armed with its lateral carinae; (2) pronotum with medial, but without mediolateral projections; (3) narrow/slender shoulders without mediolateral projections; and (4) a frontal costa whose bifurcation lies so high that the costa itself is short or nearly invisible.

The *T.* (*novaeguineae*) group, as defined by Patano and colleagues [24], has been assigned by us to a completely new genus, *Ginixistra* gen. nov., as its three species (*G. novaeaguineae* comb. nov., *G. davorkae* sp. nov., *G. novaebrittaniae* sp. nov.) exhibit characters different from both *Tegotettix* and *Xistra.* From *Xistra,* the new genus is easily distinguished by the lower position of the frontal costa bifurcation and longer frontal costa; straight vertex in dorsal view (rounded in *Xistra*); and toothed mid femora. From *Tegotettix* it is easily distinguished by smaller size, narrower shape, narrower vertex, the lack of mediolateral and metalateral pronotal projections, and the lack of femoral lappets. *Ginixistra* gen. nov. is assigned to the tribe Exanimini (without subfamily placement within Tetrigidae), based on similarity with *Exanimus* and *Fijixistra*, endemic to Fiji [66]. Interestingly, this is the first winged member of Exanimini and may provide important information in future research on the origin of the Tetrigidae fauna of Fiji.

4.1. Non-Binary Traits That Led to Confusion

Günther (1938) [18] transferred several *Xistra* species to *Tegotettix* based on toothed/lobed fore and mid legs, noting that *X. gogorzae* does not have lobed femora [1,18]. However, the same is true also for *X. sagittaria*, in which the femoral lobation is barely perceptible. The case is clear evidence that lobation of femora is not a simple binary character that can be used in this taxonomic group for a higher classification. Members of *Xistra*, as defined in our study, lack femoral teeth, which are typical of Discotettigini (Scelimeninae) members, to which *Tegotettix* belongs.

The presence of the pronotal crest was another reason Günther [18] transferred several *Xistra* to *Tegotettix*; however, in *X. sagittaria*, the crest is very slight, implying a range in the character from well-developed to nearly absent. It seems that the type species of *Xistra*, *X. gogorzae*, lies exactly at the end of that range, with a barely perceptible undulation in the place where other species have a crest. Even *Xistra* species with a high pronotal crest (subgenus *Tegoxistra*) lack pronotal projections typical for Discotettigini (Scelimeninae), especially frontolateral, and metalateral (ML) or humeral spikes, evident in *Tegotettix* members.

Günther [18] also mentions pronotal depression behind the shoulders, but it is unclear what he meant by this, as there are no observable depressions in the species here assigned to *Xistra,* and those that were assigned to *Tegotettix* by Günther. Possibly, Günther [18] was looking at a slight depression just after the crest, but since this trait was present in *X. gogorzae* as well, it is not clear why it would be a distinguishing trait.

Günther [18] noted that the species he transferred to *Tegotettix* are much smaller than the type species of the genus (*T. armatus*), and this size difference seems to be one of the important differences between true *Xistra* and true members of the genus *Tegotettix* (and generally with large Scelimeninae). Not only are *Tegotettix* members considerably longer than the members of *Xistra*, but, because of the widened and armed shoulders, they are also considerably wider and more robust.

Roof-like pronotum with elevated carinae, lack of wings, and wide vertex are known nymphal traits in Tetrigidae species in which adults have wings and an elongated pronotum [52]. *Almacris alleochroa* **gen. et sp. nov.** exhibits all of these traits, so it can be speculated that this may be a neotenic genus that evolved from a long-winged ancestor. Based on the similarity in the shape of the vertex, legs, pronotal crest, and characteristic

coloration, we could speculate that *Almacris* **gen. nov**. might have had a *Mazarredia*-like ancestor. Nymphs of *Mazarredia* species are colorful, apterous, and have an elevated anterior part of the pronotum. In the past, they were even described as a separate genus, *Rosacris* [68,112,113]. Nymphs of *Xistrella* [9] were previously described as a separate genus, *Pseudogignotettix* Liang, 1990 [114,115]. Hypothesis on *Almacris* **gen. nov**. paedomorphic origin requires molecular confirmation, because there are several problems with our knowledge of nymphal morphology at the moment.

For example, nymphs of *Ginixistra novaeguineae* (Günther, 1938) [18] **comb. nov.**, *Xistrella dromadaria* Bolívar, 1909 [3], and *Mazarredia fuscipes* (Stål, 1877) [40] all lack wings and have a relatively high pronotal crest in the anterior part, which becomes much lower and shorter in the adult stage. In *X. dromadaria,* the crest does not reach the anterior margin of the pronotum even in nymphs, whereas in *G. novaeguineae* **comb. nov.** it does, but it remains very low in that region. The placement of the crest in the genus *Xistra*, as defined in this paper, is more similar to that in *Xistrella* or *Tegotettix* than to that in *Almacris* **gen. nov.**

As few nymphs of SE Asian Tetrigidae have been described, a wider comparison that could possibly resolve some of our taxonomic questions cannot be made. The pronotal crest is generally considered a plesiomorphic trait [52], but available evidence suggests this rule pattern may have exceptions. For example, *Xistra gogorzae*, the type species of the genus, does not have a developed crest. Its nymphs, however, should have at least a slight crest if it is indeed related to *Tegoxistra* **subgen. n.** and to other *Xistra* species.

Homoplasy may complicate the interpretation of characters in Tetrigidae, as it happened to Günther [18] with *Xistra* and *Tegotettix*, but nymphal morphology still remains an important source of phylogenetic information in the absence of molecular data. A detailed comparison of nymphal traits may contribute to our study of morphologically similar, yet potentially distant, taxa in Southeast Asia, as well as of morphologically different, but closely related, taxa.

4.2. The Problematics of Xistrellini Taxonomy

Xistrellini is a monophyletic tribe, well supported by morphological apomorphies and also in published phylogenies [116–121]. However, most of the genera assigned to the tribe Xistrellini require urgent taxonomic revision. Despite the formal description of the tribe, the classification of its members remains inconsistent, with many species placements based on preliminary morphological assessments rather than robust phylogenetic data [5]. The transfer of Chinese species from *Xistra* to *Xistrella* solves the problem of *Xistra* taxonomy, but opens many issues in *Xistrella* taxonomy. *Xistrella*'s distinction from related genera, such as *Bannatettix*, has always been problematic, and grouping these genera into a larger unit may facilitate the revision of these genera.

The inclusion of morphologically similar but geographically distant genera—Malagasy *Pseudosystolederus*, New Caledonian *Kanakacris*, African *Afrosystolederus*, and American *Teredorus*—within this primarily Asian tribe opens further questions. Are there more genera that belong to this tribe? Placement of these genera within Xistrellini is currently based on morphological traits rather than genetic data, necessitating further molecular analyses.

Nymphal characteristics show some consistency. *Phaesticus*, *Pseudoxistrella*, and *Pseudoparatettix* nymphs all have striped coloration and share a very similar morphology, to the extent that in museum collections, *Pseudoparatettix* nymphs can be found misidentified as *Phaesticus* nymphs. Morphological variability within Xistrellini, including antennal structure, pronotal carinae, and vertex dimensions, further complicates generic delimitations. Monophyly of the tribe is supported by molecular data based on both the COI

gene and whole mitogenomes [116,121], showing high statistical backing, 97.4/99, and 1, respectively.

In the COI phylogeny *Systolederus* sp. (GMMGA439-14), *Systolederus cinaereus* (MBPT014-15), *Xistrella dohrni* (GMMGD3890-14), and *Phaesticus mellerborgi* (GMMGT2793-14) formed a monophyletic group with high statistical support (97.4/99) in [116], while mitogenomes reconstructed *Systolederus* as a paraphyletic genus within which *Phaesticus mellerborgi* is nested [121]. The ancestor of this tribe seems to have lived more than 110 (125–185) million years ago [110,121] and was, as we now understand, related to the ancestor of Tetriginae [110,117]. However, more taxonomic sampling is needed in order to assess the true position of this interesting group.

Without an integrative revision incorporating morphological, molecular, and ecological data, the current taxonomy risks perpetuating misclassifications. A comprehensive systematic reassessment is necessary to clarify generic limits, verify monophyly, and refine species placements. Until then, Xistrellini's taxonomy should be considered provisional, with caution applied in systematic and biogeographical interpretations.

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Abbreviations

The following abbreviations are used in this manuscript:

ANSP	Academy of Natural Sciences of Philadelphia, Philadelphia, USA
CJT	Collection Josef Tumbrinck, Wassenberg, Germany
CMU	Zoological Section, Central Mindanao University, the Philippines
MfN	Museum für Naturkunde, Berlin, Germany
MNCN	Museo Nacional de Ciencias Naturales, Madrid, Spain
NHRS	Naturhistoriska riksmuseet, Stockholm, Sweden
OSF	Orthoptera Species File
SMTD	Staatliches Museum für Tierkunde, Dresden, Germany

ZIN Russian Academy of Sciences, Zoological Institute, St. Petersburg, Russia

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