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Oriental macropterous leaf-mimic pygmy grasshoppers—genera *Oxyphyllum* and *Paraphyllum* (Orthoptera: Tetrigidae) and their taxonomic assignment

JOSIP SKEJO^{1,4,*}, SUNIL KUMAR GUPTA^{2,4}, KAILASH CHANDRA²,
WAHEED ALI PANHWAR^{3,4} & DAMJAN FRANJEVIĆ¹

¹ University of Zagreb, Faculty of Science, Department of Biology, Division of Zoology, Evolution Lab, Rooseveltov trg 6, HR-10000 Zagreb, Croatia. E-mail: (JS) jskejo.biol@pmf.hr; (DF) damianf@zg.biol.pmf.hr

² Zoological Survey of India, M Block — New Alipore, IN-700053 Kolkata, India.

E-mail: (SKG) skumarento@gmail.com, (KC) kailash611@rediffmail.com

³ Shah Abdul Latif University, Faculty of Natural Sciences, Department of Zoology, Khairpur, Old National Highway PK-66020 Sindh, Pakistan. E-mail: waheed_ali_panhwar@hotmail.com

⁴ SIGTET—Special Interest Group Tetrigidae

*Corresponding author. E-mail: skejo.josip@gmail.com

Abstract

There are numerous pygmy grasshoppers (Tetrigidae) that exhibit leaf-like appearance. Leaf-mimic species can be found mainly in the subfamily Cladonotinae (tribes Cladonotini, Xerophyllini). Two leaf-mimic pygmy grasshopper species found in India, Pakistan (*Oxyphyllum pennatum* Hancock, 1909) and Borneo (*Paraphyllum antennatum* Hancock, 1913) are the only macropterous leaf-like species of Asia and were traditionally assigned to subfamily Cladonotinae. Our study present new records of these species, as well as updated descriptions. *Oxyphyllum pennatum* is recorded for the first time from Chhattisgarh (Central India), and furthermore, records from Pakistan were reviewed and confirmed. *Paraphyllum antennatum* is reported from a few localities in the mountains of Borneo (East Malaysia). New records found in online social media (Flickr, iNaturalist) were implemented. Brachypronotal specimens of *P. antennatum* are reported. After comparison with Cladonotini and Xerophyllini members, we conclude that *Oxyphyllum* and *Paraphyllum* should not be regarded Cladonotinae members. Traditional assignment was based on superficial resemblance to leaf-like Cladonotinae genera (e.g. *Phyllotettix*, *Hymenotes*, *Holoarcus*, *Xerophyllum*). However, comparison of morphological characters reveals that *Oxyphyllum* shares morphology with Tetriginae genera, while *Paraphyllum* shares morphology with Asian Metrodorinae. Here, we assign the genus *Oxyphyllum* to Tetriginae and the genus *Paraphyllum* to Metrodorinae.

Key words: Cladonotinae, Metrodorinae, Tetriginae, social media, charismatic microfauna, India, Pakistan, Borneo

Introduction

Pygmy grasshoppers (Tetridoidea) are an old Caeliferan group originating from Triassic (Sharov 1968; Flook & Rowell 1997; Flook *et al.* 1999; Song *et al.* 2015). Tetridoidea is monophyletic and monotypic taxon that includes only the family Tetrigidae (e.g. Podgornaya 1992; Tumbrinck 2014). Some authors speculated that Batrachideinae should be elevated to family rank (e.g. Flook *et al.* 1999). Pygmy grasshoppers have pronotum extended over the abdomen (being functional analogue of tegmina in covering and protecting alae), absence of arolium, two-segmented first and second tarsi and three-segmented third tarsi (Tumbrinck 2014). Due to small size, inconspicuous appearance and lack of perceptible sound production, pygmy grasshoppers are one of the least studied Orthoptera groups. Their taxonomy, ecology, and ethology are still little understood (Hochkirch *et al.* 2000). Seven subfamilies make the family, of which well known and most specious are Cladonotinae, Metrodorinae, Scelimeninae, and Tetriginae (Cigliano *et al.* 2018).

Members of the subfamily Cladonotinae Bolívar, 1887 are mostly flightless species. This subfamily comprises more than 70 genera and 250 species distributed in the tropics (Tumbrinck 2014). The main diagnostic character are the facial carinae widened into a wide scutellum (Bolívar 1887; Tumbrinck 2014). Their similarity to certain

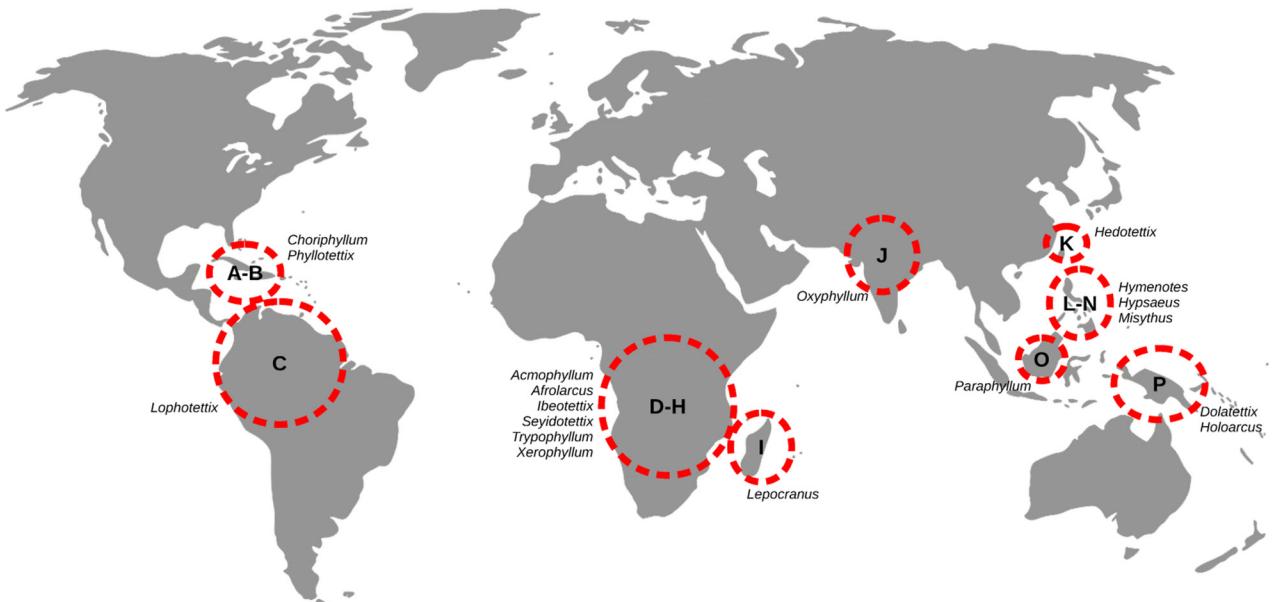


FIGURE 1. Diversity and distribution of leaf-like Tetrigidae. A. *Phyllotettix rhombeus* (Felton, 1765) (holotype, photo Tumbrinck); B. *Choriphylloides sagrai* Serville, 1838 (photo Skejo); C. *Lophotettix alticristatus* Hancock, 1909 (holotype, photo Tumbrinck); D. *Acmophyllum undulatum* Karsch, 1890 (holotype *A. nigropunctatum* Bolívar, 1905, photo Skejo); E. *Afrolarcus cf. inaequalis* (Karsch, 1890) (photo Song); F. *Ibeotettix alticrista* (photo Skejo); G. *Trypophyllum glabrifrons* Karsch, 1890 (syntype *Acmophyllum conradti* Bolívar, 1905, photo Skejo); H. *Xerophyllum platycoris simile* (paratype of *X. extensem* Hancock, 1910, photo Tumbrinck); I. *Lepocranus fuscus* Devriese, 1991 (holotype, photo Skejo); J. *Oxyphyllum pennatum* Hancock, 1909 (photo Gupta & Chandra); K. *Hedotettix cristatus* Karny, 1915 (photo Skejo); L. *Hymenotes triangularis* Westwood, 1837 (photo Tumbrinck); M. *Hypsaeus westwoodi* Bolívar, 1887 (holotype, photo Tumbrinck); N. *Misythus rectangularis* Hebard, 1923 (photo Tumbrinck); O. *Paraphyllum antennatum* Hancock, 1913 (photo Tumbrinck); P. *Holoarcus ferwillemsei* Tumbrinck, 2014 (paratype, photo Tumbrinck).

treehoppers (Auchenorrhyncha: Membracoidea) was “recognized” in the early beginnings of taxonomy and nomenclature when Felton (1765) and Linnaeus (1767) placed a cladonotin, *Phyllolettix rombeus* in the genus *Cicada*. Representatives of Cladonotinae have great morphological variability, especially in pronotal shape. Morphological variability within the group is linked to mimicry, as many of species resemble environment they live in, mimicking the surface with their rough or smooth texture, spines, projections and carinae. The subfamily is divided into two tribes (Storozhenko & Paik 2011)—Cladonotini and Xerophyllini. The Cladonotini is composed of genera with 16–17 antennal segments, high vertex lacking humeral angles, while Xerophyllini include genera with 14–15 antennal segments, depressed vertex and pronotum with strong humeral angles (see e.g. Devriese 1999). Both tribes include leaf-mimic genera with high pronotal crest (= elevated median carina).

Diversification of Tetrigoidea probably took place during Jurassic period (e.g. Sharov 1968; Song *et al.* 2015), when Earth flora was composed of mosses, ferns and conifers, of which some had leaves (megaphylls) that originated and diversified previously during Carboniferous—at least four times independently (Boyce & Knoll 2002). Leaf-mimicry in animals also originated separately several times in different animal groups, and some examples are leaf-mimic gecko (*Uroplatus phantasticus* Boulenger, 1888), leaf-mimic frog (*Ceratobatrachus guentheri* Boulenger, 1884), leaf-mimic katydids (e.g. Tettigoniidae: Pseudophyllinae, see e.g. Mugleston *et al.* 2018) and leaf-mimic pygmy grasshoppers (Tetrigidae: Cladonotini, Xerophyllini, Lophotettiginae).

Leaf-mimic Cladonotini include African *Afrolarcus* Günther, 1979 (Fig. 1E) and *Seyidotettix* Rehn, 1939, Caribbean *Choriphylum* Serville, 1838 (Fig. 1.B) and *Phyllolettix* Hancock, 1902 (Fig. 1.A), Philippine *Hymenotes* Westwood, 1837 (Fig. 1.L), *Hypsaeus* Bolívar, 1887 (Fig. 1.M), and *Misythus* Stål, 1877 (Fig. 1.N), and finally New Guinean *Dolatettix* Hancock, 1907 (inhabits also Aru island) and *Holoarcus* Hancock, 1909 (Fig. 1.P). Among Xerophyllini, leaf-mimic are African genera *Acrophylum* Karsch, 1890 (Fig. 1.D), *Trypophyllum* Karsch, 1890 (Fig. 1.G) and *Xerophyllum* Fairmaire, 1846 (Fig. 1.H). Genera *Lepocranus* Devriese, 1991 (Fig. 1.I) of Madagascar, *Oxyphyllum* Hancock, 1909 (Fig. 1.J) of India and Pakistan and *Paraphyllum* Hancock, 1913 (Fig. 1.O) of Borneo are without tribal placement (Hancock 1907; Günther 1979; Devriese 1991, 1999; Perez-Gelabert *et al.* 1999; Storozhenko & Paik 2011; Tumbrinck 2014).

Besides genera with high crest, there are numerous Cladonotinae leaf-like genera with lower crest. For example *Deltonotus* Hancock, 1904 from southern India, Sri Lanka, Indochina and China (see e.g. Hancock 1904; Storozhenko 2011), *Tuberfemurus* Zheng, 1992 from South China and Thailand (see e.g. Storozhenko & Dawwrueng 2014, 2015), *Boczkittetix* Tumbrinck, 2014 from Borneo and New Guinea, or *Dolatettix* from New Guinea are genera with low crest but still with leaf-mimic appearance (see e.g. Tumbrinck 2014). Besides Cladonotinae, there are south American *Lophotettix* Hancock, 1909 (Lophotettiginae) (Fig. 1.C), Formosan *Hedotettix cristatus* Karny, 1915 (Tetriginae: Tetrigini) (Fig. 1.K) and African *Ibeotettix alticrista* (Tetriginae: Dinotettigini) (Fig. 1.F), all species with leaf-like appearance that are not members of Cladonotinae. Generic names of many of those genera were derived from the Ancient Greek word for leaf—*φύλλον* (φύλλον) pointing their leaf-mimicry.

Two monotypic Asian genera contain macropterous species with relatively narrow scutellum compared to other Cladonotinae—*Oxyphyllum* Hancock, 1909 from India (including *O. pennatum*) and *Paraphyllum* Hancock, 1909 from Borneo (including *P. antennatum*) (Hancock 1909, 1913). *Oxyphyllum pennatum* Hancock, 1909 was described from a female holotype from India (Darjeeling), and reported only once since the description—from Pakistan (Mahmood *et al.* 2004), but since the locality is rather far from Darjeeling, the record has been considered doubtful hitherto. *Paraphyllum antennatum* Hancock, 1913 was also described from a female holotype from Borneo (Penrissen Mt.) and reported once since the description, from North Borneo (Günther 1938).

The aims of the study are (1) to report new records of *Oxyphyllum pennatum* from INDIA: Chattisgharh: Korba, (2) to re-identify the published *O. pennatum* specimen from PAKISTAN: Azad Jammu & Kashmir and present a new record from PAKISTAN, (3) to report new records of *Paraphyllum antennatum* from Borneo, (4) to critically annotate descriptions of *O. pennatum* and *P. antennatum*, and (5) to briefly compare *Oxyphyllum* and *Paraphyllum* to leaf like Cladonotini and Xerophyllini and provide preliminary data on their taxonomic placement.

Material and methods

Taxonomy, nomenclature, terminology and measurements

Taxonomy follows Orthoptera Species File [OSF] (Cigliano *et al.* 2018), database of Orthoptera taxonomy.

Nomenclature is in accordance with the International Code of the Zoological Nomenclature (ICZN 1999). Genus *Oxyphyllum* Phil. (*Embryophyta: Asteraceae: Mutisieae*) is not homonymous with *Oxyphyllum* (Metazoa), nor is genus *Paraphyllum* Lemoine (*Rhodophyta: Corallinales: Corallinaceae*) and *Paraphyllum* (Metazoa). Morphological terminology follows Devriese (1991, 1996, 1999) and Tumbrinck (2014).

Abbreviations of the pronotal projections in text are as follow and follow Skejo & Berner (2017) and Storozhenko & Pushkar (2017): FM—frontomedial, FL—frontolateral, PM—promedial, MM—metamedial, MML—metamediolateral, ML—metalateral.

Cladonotinae are divided into Cladonotini (type genus *Cladonotus*) and Xerophyllini (type genus *Xerophyllum*) according to Storozhenko & Paik (2011). Storozhenko & Paik (2011) defined diagnostic features and defined the tribe Cladonotini.

Taxonomic studies most relevant for comparison of *Oxyphyllum* and *Paraphyllum* to leaf-like Cladonotini and Xerophyllini are Tumbrinck's (2014) monograph on Cladonotinae (Cladonotini *sensu* Storozhenko) and Devriese's (1999) monograph on Xerophyllinae. Taxonomic practice follows that of Rehn (see e.g. 1904, 1930, 1952). Measurements follow Tumbrinck (2014). Measurements of museum specimens were taken in Image J software (Abràmoff *et al.* 2004) after calibration with millimetre paper.

Abbreviations used for museum collections

ANSP	The Academy of Natural Sciences of Drexel University, Philadelphia, USA,
CJT	Collection Josef Tumbrinck, Wassenberg, Germany,
CKM	Khalid Mahmood collection (destroyed), University of Poonch Rawalakot, Azad Jammu and Kashmir, Rawalakot, Pakistan,
NMW	Naturhistorisches Museum Wien, Vienna, Austria,
UMO	Oxford University Museum, Hope Entomological Collections, Oxford, UK,
ZSI	The Zoological Survey of India, Kolkata, India.

Online social media

Photographs from online social media were browsed irregularly, every few months. All the photographs of Tetrigidae found in Flickr are “deposited” in user's Josip Skejo Favourites Album (available at: <https://www.flickr.com/photos/129272508@N05/favorites>). JS commented on the photographs on which there were *Paraphyllum* specimens so authors added tag 'Paraphyllum' to their photographs and now the photographs with the tag are publicly available. A record of *Paraphyllum* found in iNaturalist webpage (<https://www.inaturalist.org/observations/13728964>) is also included in the paper.

New material collection

A specimen of *O. pennatum* (Figs. 1J, 2A, 2D, 2F-I, 3) was collected from the Korba district of Chhattisgarh [area of about 4200 km², 22.1°–22.9°N, 81.1°–82.5°E]. The district is characterized by hot and dry summers followed by the SW monsoon season, having a moist deciduous forest type dominated by sal tree—*Shorea robusta* Roth. (*Dipterocarpaceae*) interspersed with bamboo patches (*Poaceae: Bambuseae*). The specimen was collected on pebbles on the banks of the Dewan stream using an entomological net and killed by benzene vapour in a killing jar. The specimen was preserved dry and card mounted. A specimen of *O. pennatum* from PAKISTAN: Cachemine: Muzaffarabad, deposited in NMW was collected on June 18th 1953 and recently uploaded to Orthoptera Species by Josef Tumbrinck.

An image of the Chhattisgarh specimen in its natural habitat (Fig. 3) was captured using Nikon D 300S with 105 macro lens. The specimen was studied under a Leica stereozoom Microscope (Leica M205 A) and photographs were taken using the software Leica Application Suite (LAS V3.8).

Results

Taxonomic part

Subfamily Tetrinae Rambur, 1838

Genus *Oxyphyllum* Hancock, 1909

<http://orthoptera.speciesfile.org/Common/basic/Taxa.aspx?TaxonNameID=1100590>

Oxyphyllum Hancock, 1909: 393 (original description),
Oxyphyllum: Hancock 1915: 61 (listed in catalogue of Indian Tetrinidae),
Oxyphyllum: Fletcher 1921: 2 ((listed in catalogue of Indian fauna)),
Oxyphyllum: Günther 1938: 322 (included in key),
Oxyphyllum: Steinmann 1970: 85 (listed in catalogue of Oriental Tetrinidae),
Oxyphyllum: Blackith 1992: 130 (listed in catalogue of SE Asian Tetrinidae, with literature overview),
Oxyphyllum: Shishodia 1993: 182 (cited for West Bengal in catalogue),
Oxyphyllum: Yin et al. 1996: 892 (listed in catalogue),
Oxyphyllum: Otte 1997: 25 (listed in catalogue),
Oxyphyllum: Mahmood et al. 2004: 31 (new record),
Oxyphyllum: Shishodia et al. 2010: 142 (listed in check-list of Indian Orthoptera).

Type species. *Oxyphyllum pennatum* Hancock 1909, by original designation.

Remarks. Otte (1997) erroneously recorded the type species of this genus as based on monotypy, while in the original description type species was really designated by Hancock (1909).

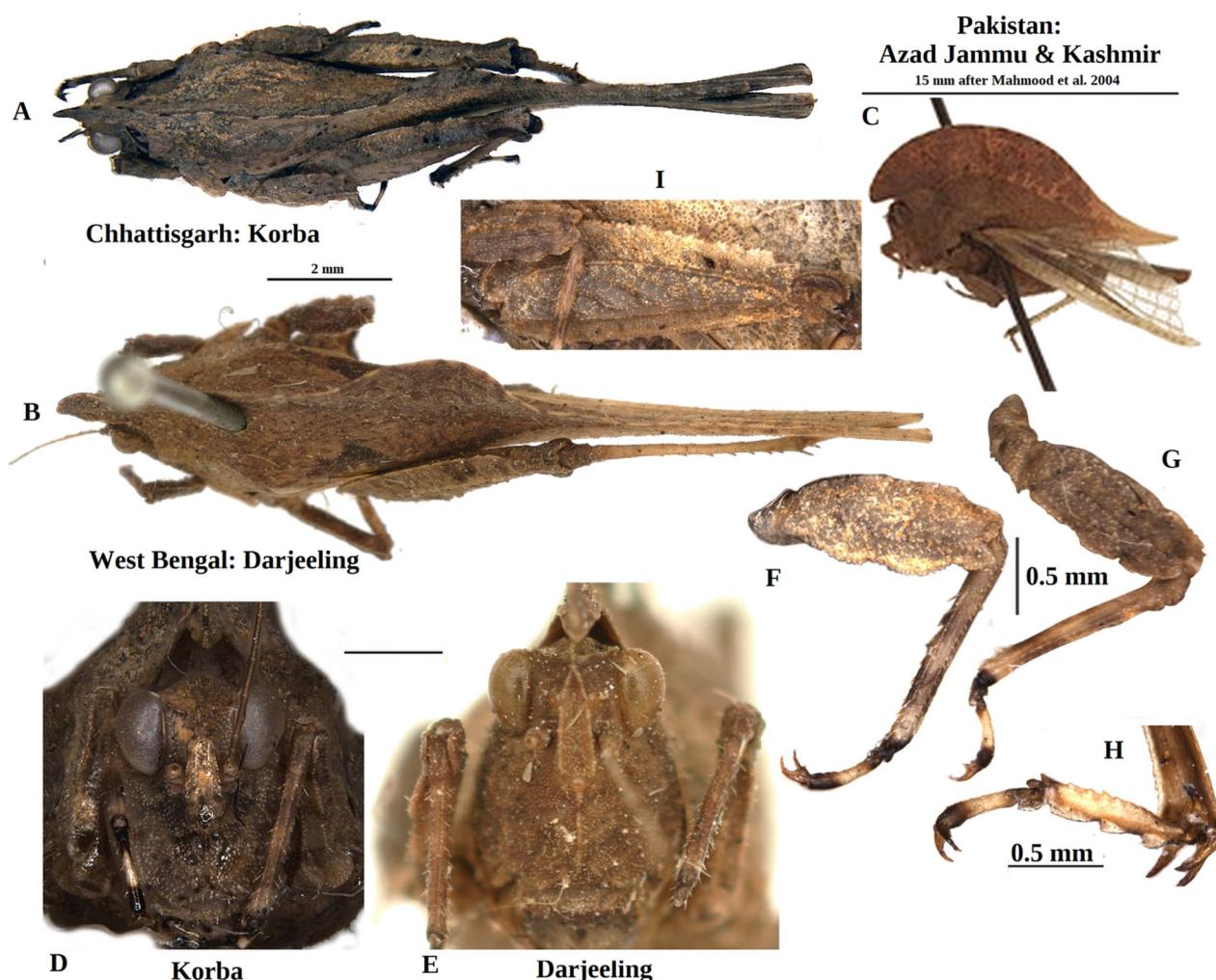


FIGURE 2. *O. pennatum*, holotype (B, E), Chhattisgarh specimen (A, D, F, G, H, I) and Azad Jammu & Kashmir specimen (D). A, B—dorsal habitus [scale bar 2 mm]; C—lateral habitus [scale bar 15 mm]; D, E—head in frontal view [scale bar 1 mm]; F—fore leg [scale bar 0.5 mm]; G—mid leg; H—tarsus of the hind leg; I—hind femur.

Composition and distribution. Type species only, inhabiting Pakistan, central and NE India.

Justification of the generic placement. Genus *Oxyphyllum* is assigned to Tetriginae because it shares diagnostic morphological characters with typical Tetriginae—*Tetrix*, *Paratettix*, and *Hedotettix*. It definitely shows closer affinity to Tetriginae than to Cladonotinae (see Table 1.). It was assigned to Cladonotinae (Hancock, 1909; Tumbrinck, 2014) because of the widened scutellum and leaf like appearance. We assign it to Tetriginae because of the following set of characters: (1) short frontal costa; (2) frontal costa bifurcation, lateral ocelli, and antennal grooves positioned high, (3) vertex prominent, (4) pronotum without pronotal projections that are arranged as recognizable FM, FL, PM, MM, MML, and ML, (5) lateral lobes of the pronotum directed downwards, slightly sideways [should be compared in future to certain Asian Metrodorinae] (6) fore and mid femora without strong teeth, undulated or weakly lobated, (7) posthumeral spots present on the disc of pronotum, (8) pulvilli of the first segment of the hind tarsi with apical teeth and (9) alae surpassing pronotal apex.

Generic diagnosis. The genus is morphologically most similar to Tetriginae genera such as *Tetrix*, *Hedotettix*, and *Paratettix*, not to *Paraphyllum*, as previously reported (e.g. Hancock 1915; Günther 1938). Antennae of *Oxyphyllum* are 12 segmented, frontal costa is short, vertex is slightly projected in front of eyes, lateral lobes are directed downwards with rounded apices, humeral angle is widely oblique or weakly angular, posthumeral spots are present, and alae surpassing tegmina. Those are characters of Asian Tetriginae, especially certain SE Asian Tetriginae taxa with dentate hind femora (see e.g. Liang & Zheng 1998). *Oxyphyllum* differs from typical Cladonotinae in not having long frontal costa and having high position of lateral ocelli. It does not exhibit horns as Xerophyllini, nor high convex vertex as Cladonotini. Furthermore, it differs from Cladonotinae members by lacking pronotal projections, weak femoral (antegenicular and genicular) teeth, elongated first tarsal segments of the hind legs, and presence of apical teeth on pulvilli of the hind tarsi. *Oxyphyllum* can be easily distinguished from other Tetriginae members by the following set of characters: median carina of the pronotum strongly elevated (leaf-like), pronotum projected over the head and covering vertex, fore femora with two weak lobes on their lower margins, mid femora with undulated dorsal margins and with three weak lobes on ventral margins, dorsal and ventral margins of the hind femora finely toothed.

Notes. The genus is monotypic, *O. pennatum* being the only species within the genus. A good description of the genus and the species was presented by Hancock (1909). Specimens examined by us do not differ from Hancock's description and are regarded conspecific with the female holotype from Darjeeling (West Bengal). Here we present updated description, measurements and photographs of morphological characters including now *O. pennatum* from Chhattisgarh. We also present a small, low quality photograph (the only available) of a female specimen from Pakistan, reported by Mahmood *et al.* (2004).

Species *Oxyphyllum pennatum* Hancock, 1909

(Figs. 1J, 2, 3)

<http://orthoptera.speciesfile.org/Common/basic/Taxa.aspx?TaxonNameID=1100591>

Oxyphyllum pennatum Hancock, 1909: 393 (original description of female holotype from India),

Oxyphyllum pennatum: Hancock 1915:61 (listed in catalogue of Indian Tetrigidae),

Oxyphyllum pennatum: Fletcher 1921: 2 (listed in catalogue of Indian fauna),

Oxyphyllum pennatum: Günther 1938: 322 (included in the key, not reviewed),

Oxyphyllum pennatum: Steinmann 1970:85 (listed in catalogue of Oriental Tetrigidae),

Oxyphyllum pennatum: Blackith 1992: 130 (listed in catalogue of SE Asian Tetrigidae, with literature overview),

Oxyphyllum pennatum: Shishodia 1993: 182 (cited for West Bengal in catalogue),

Oxyphyllum pennatum: Yin *et al.* 1996: 892 (listed in catalogue),

Oxyphyllum pennatum: Otte 1997: 25 (listed in catalogue),

Oxyphyllum pennatum: Mahmood *et al.* 2004: 31 (new record, two females reported from Azad Jammu and Kashmir),

Oxyphyllum pennatum: Shishodia *et al.* 2010: 142 (listed in checklist of Indian Orthoptera).

Material examined. 1♀ holotype INDIA: West Bengal: Darjeeling [approximately 27.026N, 88.256E] Leg. Janson (? or Samson?) 1864. wrongly labelled as ♂ by collector, det. J.L. Hancock (UMO, published in Hancock 1909, Fig. 2B, E); 1♂ INDIA: Chhattisgarh: Korba District: Kudmura range near Dewan stream (22.324806N, 83.000444E), 400 m a.s.l., 2.VI.2012. Leg. S. Kumar Gupta, Inventory Number: Reg.No.13293/H5 (Figs. 1J, 2A, D, G-I, 3) (ZSI); 1♀ PAKISTAN: Azad Jammu and Kashmir [approximately 33.996N, 73.774E] about 1050 m

a.s.l., 10.X.2001. Leg. A. Maqsood (KMC, published in Mahmood *et al.*, 2004, other female destroyed as well, Fig. 2C); 1♂ PAKISTAN: Azad Jammu and Kashmir [approximately 34.353N, 73.468E] 700-800 m a.s.l. 18.VI.1953. Det. J. Tumbrinck (NMW) [link to record <http://orthoptera.speciesfile.org/Common/specimen>ShowSpecimen.aspx?SpecimenID=145024>].

Addenda to Hancock's description. Hancock's original description is accurate. Our measurements of the holotype are in accordance with Hancock's. Since description of *O. pennatum* is publicly available online (digitalized), we do not present full re-description of the species. Important is however to add certain characters to the description on which Hancock (1909) and other scholars did not pay attention at that time. Frontal costa short. Bifurcation of the frontal costa close to the fastigium, for about one diameter of lateral ocellus. Lateral ocelli between the eyes in the middle, below bifurcation of the frontal costa. Antennae 12-segmented. Antennae 1.8 times longer than fore femur, inserted between the lower margin of the compound eyes, mid segments ~2.5 times as long as wide. Facial carinae straight or slightly undulated, scutellum between them much wider than scapus. Dorsal margins of the antennal grooves between the lower fifth of the compound eyes width. Alae surpassing pronotal apex. Pulvilli of the hind tarsi with apical teeth. Ventral margin of hind tibiae with 8 outer and 6 inner spines.



FIGURE 3. Alive male of *Oxyphyllum pennatum* Hancock, 1909 standing on a dicot leaf, from Korba (Chhattisgarh state, India). Photo Gupta & Chandra.

Colouration. Body yellowish brown; tip of antennae dark brown to black; upper margin of pronotum (= median carina in lateral view) with 23 black dots; above the tegmina discus has five black spots in two rows, upper with two spots and lower with three spots; fore and mid tibiae with two pale brown rings, junction between tibiae and tarsi, as well as the apex of tarsi with dark bands; genicular teeth of hind femora dark brown; second segment of the hind tarsi and apex of third segments with black bands; claws of all legs dark brown; alae pale green with black tinge.

Measurement in mm (HT—holotype from Darjeeling, NT—non type from Chhattisgarh). Body length (without pronotum) HT 9.51/ NT 7.3, pronotum length HT 14.98/ NT 11.22, frontal costa length HT 0.09/ NT 0.14, eye width HT 0.45/ NT 0.46, vertex width HT 0.79/ NT 0.69, scutellum width HT 0.3/ NT 0.35, scapus width HT 0.14/ NT 0.15, pronotum height HT 6.17/ NT 4.74, pronotum width (maximal, between shoulders) HT 2.76/ NT

1.89, tegmina length HT 2.16/ NT 1.61, ala length HT 12.76/ NT 9.67, alae surpassing pronotum HT 1.63/ NT 1.11, fore femur length HT 1.95/ NT 1.34, fore femur width HT 0.54/ NT 0.56, mid femur length HT 2.01/ NT 1.49, mid femur width HT 0.96/ NT 0.51, hind femur length HT 5.58/ NT 4.42, hind femur width HT 1.99/ NT 1.45, hind proximal tarsal segment HT 0.79/ NT 0.71, hind distal tarsal segment HT 0.53/ NT 0.62, pulvillus I HT 0.12/ NT 0.15, pulvillus II HT 0.17/ NT 0.19, pulvillus III HT 0.32/ NT 0.27.

Subfamily Metrodorinae Bolívar, 1887

Genus *Paraphyllum* Hancock, 1913

<http://orthoptera.speciesfile.org/Common/basic/Taxa.aspx?TaxonNameID=1100592>

Paraphyllum Hancock, 1913: 40 (original description of the genus),

Paraphyllum: Günther 1938: 322 (included in the key to Cladonotinae genera),

Paraphyllum: Blackith 1992: 133 (listed in catalogue of SE Asian Tetridoidea),

Paraphyllum: Yin *et al.* 1996: 893 (listed in catalogue of Orthoptera),

Paraphyllum: Otte 1997: 25 (listed in catalogue of Orthoptera),

Paraphyllum: Tumbrinck 2014: 350, 378 (included in the key and revision, assigned to Cladonotinae).

Type species. *Paraphyllum antennatum* Hancock 1913, by original designation.

Composition and distribution. Type species only, inhabiting Borneo.

Justification of the generic placement. The genus *Paraphyllum* is assigned to Metrodorinae because of numerous morphological features shared with Asian Metrodorinae genera, such as genera *Mazarredia* Bolívar, 1887, *Bermania* Storozhenko, 2012, *Xistra* Bolívar, 1887 and *Xistrella* Bolívar, 1909 (here provisionally, we call this group *Mazarredia* genus group) (see e.g. Bolívar 1887; Storozhenko 2012). It does not share characters with Cladonotini or Xerophyllini (see Table 1.). Other Metrodorinae groups (e.g. Malagassy and South American) are not assessed here because it was already shown that Metrodorinae represents a 'garbage can', a polyphyletic group made for easier identification of macropterous Tetrigidae with uncertain placement (Pavón-Gonzalo *et al.* 2012). Metrodorinae are often defined as a group of genera with antennae with 11-16 segments, filiform antennae without widened segments (there are numerous exceptions from this), narrow scutellum (also numerous exceptions exist), lateral pronotal lobes directed sideways and not having acute spines (also a character with numerous exceptions). It can be seen that it is not easy nor practical to define Metrodorinae. Future studies of Metrodorinae should concentrate on separating it into good evolutionary units, with combined morphological and molecular phylogeny. Shared characters in the group of Asian Metrodorinae composed roughly of genera *Bermania*, *Camelotettix* Hancock, 1907, *Mazarredia*, *Metamazarredia* Günther, 1939, *Orthotettix* Hancock, 1909, *Paraphyllum*, *Timoritettix* Günther, 1937, *Xistrella* and maybe also *Falconius* Bolívar, 1898 are: (1) 14-15 segmented antennae usually with very long medial segments and sometimes modified subapical segments, (2) short frontal costa, (3) large lateral ocelli and median ocellus, (4) elevated (to horn like) lateral and transversal carinae of the vertex in frontal view, (5) V-shaped (diagonal, obtuse angled) lateral carinae of the vertex in dorsal view, (6) elongated femora, (7) modified various parts of pronotum (humeral angles, or interhumeral carinae, or median carina, not homologous to projections in Scelimeninae and Cladonotinae), and (8) elongated first tarsal segment of the hind tarsi, having widely separated pulvilli which are not sharp.

Generic diagnosis. This genus is easily distinguished from other Asian Metrodorinae (morphologically similar genera: *Bermania*, *Camelotettix*, *Mazarredia*, *Metamazarredia*, *Orthotettix*, *Timoritettix*, and *Xistrella*) by the following set of characters: (1) median carina of the pronotum strongly elevated and compressed, high as rest of the animal, (2) dorsum of pronotum conically elevated above the tegmina, (3) interhumeral carina absent on the first sight—fused with numerous veins on leaf-like elevation, (4) head, parts of all the legs and alae black, while tegmina, pronotum, most of hind femur external surface, and abdomen bright in colouration—in females usually more orange and with longer pronotum, alae surpassing its apex, while males are brownish-green and have shorter pronotum and shorter alae, not surpassing pronotal tip.

Species *Paraphyllum antennatum* Hancock, 1913

(Figs. 10, 4)

<http://orthoptera.speciesfile.org/Common/basic/Taxa.aspx?TaxonNameID=1100593>

Paraphyllum antennata Hancock, 1913: 40 (original description of female holotype from Borneo),
Paraphyllum antennatum, Günther 1938: 322 (included in the key, new record provided),
Paraphyllum antennatum, Blackith 1992: 133 (listed in catalogue of SE Asian Tetrigidae, with literature overview),
Paraphyllum antennata, Yin *et al.* 1996: 893 (listed in catalogue of world Orthoptera),
Paraphyllum antennatum: Otte 1997: 25 (listed in catalogue),
Paraphyllum antennatum, Tumbrinck 2014: 378 (in revision, assigned to Cladonotinae, photographs of type provided).

Nomenclatural note. Hancock (1913) described the genus *Paraphyllum* without strictly defining its grammar gender. The type species epitheton is originally in feminine grammar gender (*antennata*). The word ‘paraphyllum’ is compound of Latinized Ancient Greek ‘para’ meaning *next to, near, contrary to* and ‘fyllon’ (neuter gender in standard dictionaries) meaning *leaf*. Günther (1938) cited the specific epitheton as of neuter grammar gender (*antennatum*), and all the subsequent authors followed. This is correct in nomenclatural sense. According to the ICBN (1999) Article 30. (30.1.1., 30.1.2. 30.1.3.) a genus-group name that ends in Latin, or Greek word respectively, takes the gender given for that word in standard dictionaries. ‘Paraphyllum’ is thus to be treated as a noun of neuter gender because Greek *fyllon*, Latin *phyllum* are of neuter gender. Other generic names of Tetrigidae genera ending in -phyllum are neuter (*Acromophyllum*, *Choriphyllum*, *Oxyphyllum*, *Paraphyllum*, *Trypophyllum*, *Xerophyllum*), and this should not be exception. The correct name is thus *Paraphyllum antennatum*, instead of *Paraphyllum antennata*.

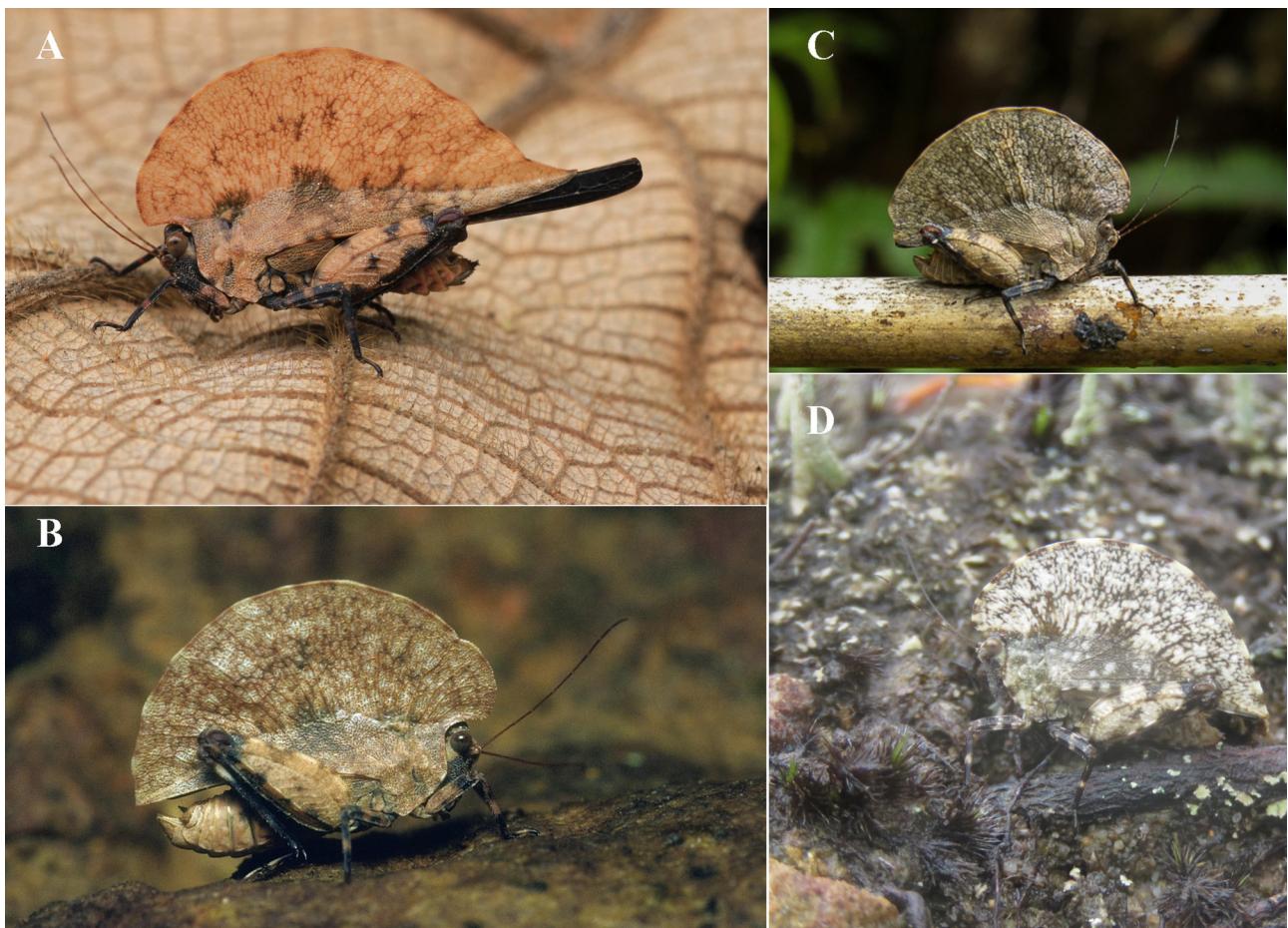


FIGURE 4. *Paraphyllum antennatum* Hancock, 1909 in natural habitats. Photos of professional photographers found in onlinesocial media (Flickr, iNaturalist). A. Macropronotal female from Mt. Trusmadi (photo A. Yakovlev), B. Brachypronotal male from Mt. Trusmadi (photo A. Sochivko). C. Brachypronotal male from Mt. Murud (photo A. Yin). D. Mesopronotal female from Mt. Alab (photo T. Pegan). Photos reproduced with permission.

Material examined. Museum material. 1♀ (macropronotal) holotype MALAYSIA: Borneo: Sarawak: Penrissen Mt. about 1000 m a.s.l. [approximately 1.1167N, 110.2167E], Leg. unknown V.1899. (labelled *Paraphyllum antennata*) det. J.L. Hancock (ANSP, published in Hancock 1913, photos of holotype available in high resolution in OSF); 1♀ (macropronotal) + 2♂♂ (macropronotal and brachypronotal—Fig. 1O) MALAYSIA: Sabah: Kinabalu NP (road in primeval forest) 1000–1800 m [approximately 6.029N, 116.550E], Leg. S. Ingrisch 5.-7.VIII.1984. Det. J. Tumbrinck (CJT). **Online social media.** 1♀ (macropronotal) MALAYSIA: Sabah: Trusmadi Mt. 1000 m a.s.l. 1.IV.2011. [approximately 5.71N, 116.42E] (link to the photography in Flickr: <https://www.flickr.com/photos/botalex/5641276873>) Photo credit: A. Yakovlev (Fig. 4.A); 1♂ (brachypronotal) MALAYSIA Sabah: Trusmadi Mt. 1000 m a.s.l. [approximately 5.71N, 116.42E] 2007. (link to the photograph in Flickr: <https://www.flickr.com/photos/botalex/4167684930/in/gallery-dominikhofer-72157632707082855/>) Photograph credit: A. Sochivko (Fig. 4.B) det. J. Skejo; 1♂ (brachypronotal) MALAYSIA: Sarawak: Pulong Tau NP: Murud Mt. [approximately 3.929N, 115.333E] Photograph credit: C. Lee (link to the photograph in AgeFotoStock <https://www.agefotostock.com/age/en/Stock-Images/Rights-Managed/MPC-00451038/1>) and also A. Yin (Fig. 4.C) (link to the photograph in Flickr <https://www.flickr.com/photos/fotosynthesys/16524051621/>) det. J. Skejo; 1♀ (mesopronotal) MALAYSIA: Sarawak: Bario 1000 m a.s.l. [approximately 3.742N, 115.469E] 6.IV.2017. Photograph credit: M. Candal (link to the photograph in Flickr: <https://www.flickr.com/photos/84942480@N03/33810198241/>) det. J. Skejo; 1♀ (brachypronotal) MALAYSIA: Sabah: Tambunan: Gunung Alab 1900 m a.s.l. [approximately 5.83N, 116.34139E] Photograph credit: Teresa Pegan (Fig. 4.D) (link to the photograph in iNaturalist: <https://www.inaturalist.org/observations/13728964>) det. J. Skejo.

Notes. The female holotype was the only published specimen for this species. More specimens (not examined by us) are likely deposited in museums, since Blackith (1992) reported pronotum (PL) and hind femur (HF) lengths for a female holotype (PL 17.0 mm, HF 8.0 mm) and a male specimen (PL 14.50 mm, HF 7.20 mm). However, Blackith (1992) did not provide any information on this male specimen. The female holotype is deposited in The Academy of Natural Sciences of Drexel University (formerly Academy of Natural Sciences of Philadelphia), USA, not in the Sarawak museum, as reported by Blackith (1992). Here we re-describe the species.

Re-description of *Paraphyllum antennatum*

(Photos of holotype from ANSP and specimens from CJT available in high resolution in OSF).

<http://orthoptera.speciesfile.org/Common/specimen/SpecimensByTaxon.aspx?TaxonNameID=1100593>

General appearance and coloration. Large, bright and smooth species of high pronotal crest. Cryptic in coloration—usually specimens have color similar to their surroundings. Pronotal crest, hind femora, and tegmina usually have bright greenish, brownish or orange tints. Parts of head and legs are darker in coloration.

Head. *In frontal view.* Eyes elongated, ovoid, Vertex as wide as an eye, concave between eyes. Eyes together with lateral carinae above level of vertex. Frontal costa long, bifurcation of frontal costa between the eyes (in the middle), paired (lateral) ocelli on each side of the facial carinae, on the lower third of the compound eye height, for about half of their diameter below the bifurcation. Scutellum wide, with weakly diverging carinae, in its widest part as wide as antennal groove. Dorsal margin of antennal groove below the lower margin of the compound eyes, on each side of scutellum. Antennae long and smooth, more than 3 times longer than fore femur, 16-segmented: 1st scapus, 2nd pedicel, 3rd to 14th very elongated segments (from 6 to 14 times as long as wide) of flagellum, apical 15th and 16th reduced, small and short. *In lateral view.* Eyes globular, strongly projected above the level of vertex and pronotal discus (except of course for its raised median carina), occipital area extremely short. Vertex and frontal costa not visible in lateral view because of strongly projected eyes. Facial carinae and scutellum projected forward, as well as antennal grooves. Palpi robust (not flattened) and hairy. *In dorsal view.* Anterior margin of the vertex not projected before the eyes, medial carina distinct, elevated in anterior half, vanishing towards anterior margin of pronotum. Fossulae shallow. Angle between transverse and lateral carinae of the vertex obtuse, resembling right angle (= L shaped carinae). It is however obtuse because of lateral carina elevation towards the supraocular lobe.

Pronotum. *In frontal view.* Lateral lobes directed downwards and slightly sideways, projected outwards slightly more than humeral angles. Pronotal discus roof like, elevation of the each side goes towards median carina in 45° angle. The highest part of pronotum (not counting compressed median carina) about two eye diameters above the level of discus (humeral angles). Median carina higher than height of rest of the body. Pronotal apex

acute. *In lateral view*. Frontal margin of the pronotum projected before the head. Median carina compressed and strongly elevated, giving the organism foliaceous, leaf or fungus like appearance. Compressed median carina full of net-like chitinous structures resembling leaf venation. Dorsal margin of the median carina finely tuberculated and weakly undulated. Prozonal and other carinae absent. Thick parts of pronotum visible in the place of promedial projection and on the basis on median carina between the shoulders. Rest of pronotum finely granulated and without projection. Three sulci present on the paranotal part of prozona. Lateral lobes directed downwards and sideways, with truncated apex. Ventral and tegminal sinuses triangular and deep, ventral deeper than tegminal. Infrascapular area narrow and long, running from the basis of tegmina to the mid of the hind femur length. Lateral area fused with dorsum (pronotal discus) and internal lateral carina weak. Pronotum reaching tip of the hind tibia where extended (macropronotal, macropterous specimens) or reaching the tip of the hind knee (brachypronotal, brachypterous specimens). *In dorsal view*. Anterior margin of the pronotum projected above the whole vertex and before the head, not covering eyes. Except for median, no distinct carinae of the pronotum. General appearance robust for flying genus, rather wide, widely rounded humeral angles. Median carina tuberculated, weakly sulcate, from $\frac{3}{4}$ of its length towards the apex carinated. Pronotal apex rounded.

Wings. Tegmina elongate, oval, with narrow and rounded apex, almost as long as mid femur and wider than the femur. Alae dark and elongated, visibly exceeding pronotal apex (macropronotal, macropterous specimens) or reaching the apex (brachypronotal, brachypterous specimens).

Legs. *Fore legs*. Femur elongated, carinated above, with wavy and finely toothed dorsal carina. Tibia rectangular in cross section and with straight margins. On the ventral inner margin of hid tibia there are 5 to 6 spines (and more transparent, spine-like hairs), while on the ventral outer margin just two (or three) apical. Dorsal margins are apparently spineless. Tibia dark with bright right in the middle. Proximal tarsal segment very short, distal elongated and with claws. *Mid legs*. Femur elongated, carinated above, with wavy and finely toothed dorsal carina. Tibia rectangular in cross section and with straight margins. On the ventral inner margin of hid tibia there are 5 to 6 spines (and more transparent, spine-like hairs), while on the ventral outer margin three. Dorsal margins spineless. Tibia dark with bright right in the middle. Proximal tarsal segment very short, distal elongated and with claws. *Hind legs*. Femur elongated, carinated above. Dorsal carina finely granulated. Antegenicular tooth triangular, genicular tooth smaller. Surface of the femur finely granulated, at least 6 to 7 low transverse ridges visible on external area. Hind tibia dark, with a pale ring close to the hind knee. On the connection of femur and tibia there are four large spines—two on the each side of the tarsus, and two below the tarsus. On the inner dorsal margin of tibia there are six triangular spines, while on the outer 7 to 9. Proximal tarsal segment longer than distal. Mid tarsal segment short. Pulvilli heteromorphic—proximal small (triangular, spine like, low), second longer (as high as the first and with angular apex), third largest (longest and slightly higher than previous two, also angular).

Abdomen. Female ovipositor short and robust, dorsal valves with 9 teeth (including apical) enlarging towards the apex. Ventral valves with 7 or 8 teeth (with apical), enlarging towards apex. Female subgenital plate square shaped, with dark triangular projection at the apex. Cerci conical and hairy. Male subgenital plate elongated and conical.

Discussion and conclusions

Indian leaf-mimic groundhopper (*O. pennatum*) is currently one of three leaf-mimic species in the subfamily Tetriginae, together with Taiwanese crested turlehopper (*Hedotettix cristatus*) and African crested groundhopper (*Ibeotettix alticrista*). On the other hand, Bornean leaf-mimic groundhopper (*P. antennatum*) is currently the only leaf-mimic Metrodorinae species. Leaf-mimicry in the Tettigoniidae evolved several times independently (Mugleston *et al.* 2018), and taken into account that there are leaf-mimic Tetrigidae from different subfamilies (Metrodorinae, Tetriginae, Lophotettiginae, Cladonotinae: Xerophyllini, Cladonotini), maybe it could be the case in this family as well.

On Himalayan leaf-mimic groundhopper (*Oxyphyllum pennatum*)

Indian *O. pennatum* was hitherto basically known solely from its type specimen—holotype female from Darjeeling

(India). Almost nothing was known on the species and its habitat. Recently, photos of holotype were digitalized and uploaded to Orthoptera Species File (Cigliano *et al.* 2018) so it became possible to identify this peculiar species.

We confirm that species inhabits India and report it from Korba (Chattisgarh) moist deciduous forest, which is for now the southernmost record of the genus and species. Records of the species from Azad Jammu (Pakistan) (Mahmood *et al.* 2004) were regarded dubious since no photographs/ drawings accompanied the record and because Azad Jammu and Kashmir is far from the type locality. We confirm identification of the specimens on the basis of hitherto unpublished photograph (Fig. 2C). We thus confirm that the species inhabits Pakistan. Our confirmation is strengthened with a new record of *O. pennatum* male from Pakistan: Muzaffarabad.

TABLE 1. Comparison of twelve morphological features of leaf-mimic Cladonotini, leaf-mimic Xerophyllini, and genera *Oxyphyllum* and *Paraphyllum*. From this comparison it is clear how different *Oxyphyllum* and *Paraphyllum* really are from other Cladonotinae.

	Leaf-mimic Cladonotini	Leaf-mimic Xerophyllini	Genus <i>Oxyphyllum</i>	Genus <i>Paraphyllum</i>
Number of antennal segments	15–17	14–15	12	16
Vertex width	very wide (usually more than 2x wider than an eye)	very wide (usually 2–3x wider than an eye)	slightly wider than an eye	slightly wider than an eye
Vertex (frontal view)	convex, elevated above the eyes	concave, deeply depressed between the eyes	almost straight, slightly depressed between the eyes	slightly depressed between the eyes
Vertex (dorsal view on carinae)	carinae more or less absent, vertex smooth	carinae strongly elevated and forming horns, anterior vertex margin truncated	carinae L shaped, frontal margin of the vertex projected	carinae V shaped, slightly elevated into low horns
Lateral ocelli	in the lower third of the compound eyes height or lower	in the lower third of the compound eyes height or lower	between the compound eyes	between the compound eyes
Frontal costa and bifurcation	frontal costa is long above the bifurcation, which is positioned very low	frontal costa is long above the bifurcation, which is positioned very low	frontal costa is short, but visible above the bifurcation, which is between the eyes	Frontal costa is short, but visible above the bifurcation, which is between the eyes
Scutellum width and shape	widened with divergent margins	widened with divergent margins	widened with parallel margins	narrow and straight
Fore and mid femora	elongated, usually with projections (teeth, tubercles), not compressed	strongly compressed and widened, dorsal and ventral margins usually bi- or trilobate	compressed, with undulated margins	elongated, with almost straight margins
Hind femora dorsal margins	with tubercles, lappets or projectons	with teeth, strong tubercles, or projections	almost smooth, toothed with fine teeth	smooth and straight
Infrascapular area	wide and decurved	narrow and triangular	narrow and straight	narrow and straight
Tegmina and alae	absent in all the species, flightless taxa	tegmina elongated, alae surpassing pronotum or shorter, able to fly	tegmina oval, alae long and able to fly	tegmina elongated, alae able to fly
Humeral angles	oblique, without projections	widely angular, usually with metalateral tubercles	obliquely angular	obliquely angular

We attribute species distribution to the Himalayan ecological region. It inhabits leaf-litter on stony and muddy basis in moist deciduous forest. Despite of pronotal crest similar to Cladonotini, Xerophyllini and *P. antennatum*, the species has rather different morphology from those groups and belong to Asian Tetriginae (see Table 1.) on the basis of 12-segmented antennae, short frontal costa, lateral lobes directed downwards, and pulvilli of the hind tarsi

bearing apical spines. In Tetrinae, species with high leaf-like median carina were already known, for example *Ibeotettix alticrista* Günther, 1979 (Fig. 1F) from Africa or *Hedotettix cristatus* Karny, 1915 (Fig. 1K) from Taiwan.

Previous authors (Hancock, 1909; Günther, 1938) did not compare *Oxyphyllum* in detail to members of Xerophyllini, Cladonotini and Tetrinae, but just to *Paraphyllum*. Because of that, these authors did not find a trace that the genus is in fact not member of Cladonotinae. After comparison to members of Indian *Paratettix*, *Euparatettix*, and *Ergatettix* we conclude that the genus does not belong to Cladonotinae, but more likely to Tetrinae (see Table 1).

On Bornean leaf-mimic groundhopper (*Paraphyllum antennatum*)

Bornean leaf-mimic groundhopper (*Paraphyllum antennatum*) was hitherto known from a single female from Penrissen Mt (Hancock 1913). Species is however not Penrissen Mt. endemic taxon (as reported in Tumbrinck 2014), but a widely distributed mountainous rainforest Bornean species. It is now known from mountains of Sabah and Sarawak—Mt. Penrissen, Mt. Trusmadi, Mt. Murud, Mt. Kinabalu, Mt. Alab and Mt. Bario.

Paraphyllum antennatum exhibits variability in pronotum and length of the hind wings. Variability of pronotum was not reported hitherto (because a single specimen was known). Some specimens are macropronotal and macropterous, meaning that their pronotum surpasses hind knees and their alae slightly surpass pronotal tip. Females from Mt. Alab and Mt. Bario are mesopronotal, meaning that they have long pronotum, but their wings do not surpass the tip of the pronotum. Males are usually brachypronotal, meaning that they have short pronotum and wings that do not surpass the pronotal apex. We report also a mesopterous male (from CJT), a specimen of long pronotum and short wings. Interestingly, pronotal apex in brachypterous specimens is not as acute as in macropterous specimens, but truncated.

From a conservation point of view, this species represents charismatic microfauna. It is often photographed and noticed by amateurs. It mimics tree mushrooms, fallen and living leaves, as well as inedible seeds. The pronotum has fine nervature-like carination composed of multiple irregular and regular 'veins'. It seems that such morphology has driven natural selection in this group (fitness better in specimens with finer carination, better resembling leaves or tree mushrooms). Millions of years of such selection may have resulted in *P. antennatum*—leaf-mimic species we know mostly from photographs found in online social media.

The genus *Paraphyllum* is here assigned to Metrodorinae on the basis of long, 16-segmented antennae, antennal grooves that are positioned low, carinae of the vertex that are V-shaped and pulvilli of the hind tarsi that are angulate (compare with e.g. Hancock 1913; Tumbrinck 2014) (see Table 1). Aforementioned characters suggest close relationships to the Asian Metrodorinae genera *Bermania*, *Camelotettix*, *Mazarredia*, *Metamazarredia*, *Orthotettix*, *Timoritettix*, and *Xistrella*. Metrodorinae of SE Asia exhibit a large variation of pronotal morphology (compare with e.g. Hancock 1907; Storozhenko 2012). The taxonomy of this group should be carefully reviewed, with emphasis on head morphology—prolongation of antennae, number of antennal segments, morphology of lateral carinae, frontal costa and scutellum.

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