

New records of the land and freshwater molluscs of Gran Canaria (Canary Islands, Spain)

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Abstract

“Land and freshwater molluscs of Gran Canaria (Spain)” is an occurrence dataset containing 389 observations of 59 different taxa of land and freshwater molluscs encountered on Gran Canaria, an island central in the Canarian archipelago (Spain). Of these 59 different (sub)species, 27 are with certainty currently endemic to the island of Gran Canaria. Various sites were inspected in a period between 1988 and 2020. The dataset is published as a standardized Darwin Core Archive and includes for each observation a stable occurrence ID, scientific name, date, and location of the observation, as well as information on life stage and organism quantity. It also contains supplementary remarks on the determination and the observation itself and links to associated media. We have released this dataset to the public domain under a CC0 1.0 Universal (CC0 1.0) Public Domain Dedication. The aim is to contribute to the knowledge on the ecology and distribution of these species on the island, such that it may aid conservation and research of these organisms in the future.

Issues with the dataset can be reported at <https://github.com/BelgianBiodiversityPlatform/land-snails-occurrences>

Keywords

freshwater, Gran Canaria, observation, occurrence, open data, snails, terrestrial

Rationale

Canary Islands (Spain) is an archipelago off the coast of northwest Africa. Gran Canaria is the third-largest island and located in the centre of the archipelago (Carracedo and Troll 2016; Fig. 1). The island contains a number of endemic land snail species (e.g. Brito and Fraga 2010). Freshwater molluscs are of lesser significance, but are also present. Research on land and freshwater molluscs of the Canaries mainly goes back to the 19th century with the famous works of Webb and Berthelot (1833), Shuttleworth (1852a, 1852b), Mousson (1872), Wollaston (1878), Mabilie (1884), Odhner (1931), and others. Recent checklists are available (Groh 1985; Bank et al. 2002; Brito and Fraga 2010; Helixebas 2019) and some more recent papers are cited further in this article. Nevertheless, taxonomic research is still largely based on these old works and many species have never been found again since their description, or the ecology or proper range is not known. This, together with the threats of global warming (Luque et al. 2014) and the increase of demographic and touristic pressure (Ibáñez et al. 1997), could have (and probably already has) detrimental consequences for the survival of these species on the island (see also the assessments of IUCN Red List of Threatened Species (<https://www.iucnredlist.org/>)). Therefore, there is an urgent need for information on ecology, distribution and taxonomy. We hope that this dataset of land and freshwater snail occurrences can contribute to the knowledge on these species and ensure their survival on Gran Canaria and the Canary Islands as a whole.

Taxonomic coverage

Land and freshwater molluscs do not comprise a monophyletic taxonomic group, but are all mollusc species that live in respectively land and freshwater habitats. On land, only gastropods occur (class Gastropoda, snails and slugs) and in freshwater, both Gastropoda and bivalves (class Bivalvia) occur. No observations on bivalves are present in this dataset. The dataset includes 389 observations of 59 species and subspecies (Fig. 2) belonging to 27 genera (Fig. 3) and 18 families. Of these 59 taxa, 37 are with certainty currently endemic to the Canary Islands whereas 27 are endemic to the island of Gran Canaria in particular and 3 also occur on other islands. It is unclear whether the remaining 7 endemic taxa found on Gran Canaria also occur on other islands or not.

Species determination was mainly done during two meetings concerning the land snails of Gran Canaria organized by the Dutch Malacological Society (Nederlandse Malacologische Vereniging, NMV), coordinated by Theo Ripken. These meetings took place on 21 April 2018 and 23 February 2019 in, respectively, Leiden and Den Haag (Netherlands). Reference material and expert knowledge provided many identifications. Determinations were further based on the following articles: Alonso et al. (1995), Alonso and Ibáñez (2015b), and Yanes et al. (2011) for the genus *Napaeus*, Alonso and Ibáñez (2015a) and Valido et al. (1990) for *Insulivitrina*, Ibáñez et al. (2003) for the genus *Obelus*, Gittenberger and Ripken (1987) for the

genus *Theba*, and Hutterer and Groh (1991) for the genus *Truncatellina* (see also Langerhaert 2019). Also, Mousson (1873) (first published in 1872, see Bank et al. 2002), Wollaston (1878), Mabille (1884), Odhner (1931), Shuttleworth (1975), Groh et al. (1992), Neubert and Gosteli (2003), Serna and Gómez (2008), and Neiber (2015) were consulted. Additional information was found in Groh (1985), Bank et al. (2002), Brito and Fraga (2010), Helixebas (2019) and as well on <https://www.malacowiki.org/> and <https://www.iucnredlist.org/>. Finally, for species with a wider (European) distribution, the following works were consulted: Cameron (2008), Welter-Schultes (2012), Horsák et al. (2013), Glöer (2015), Jansen (2015), and Cadevall and Orozco (2016).

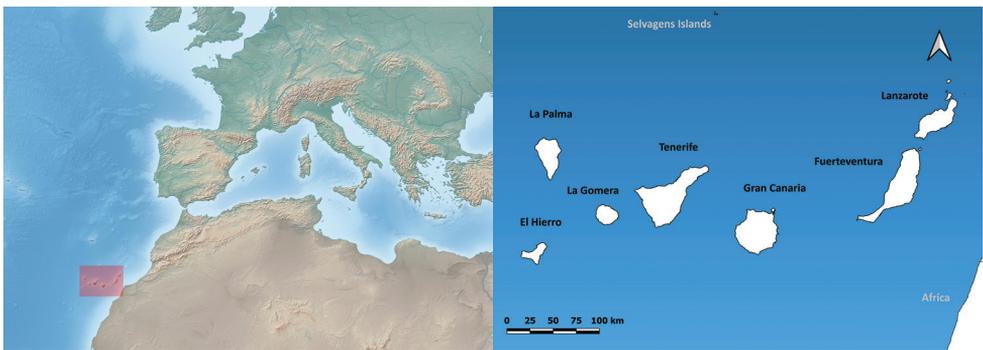


Figure 1. Map showing the Canary Islands (Spain) situated in the Western Palearctic region. Gran Canaria is located in the centre of the archipelago.

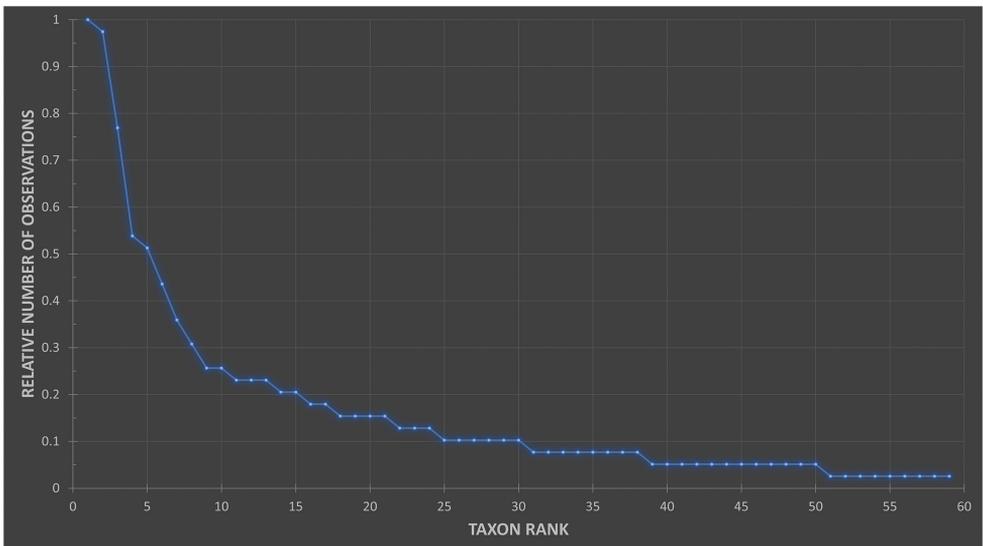


Figure 2. Graph showing the relative number of observations for each taxon. Taxon rank: 1 = most observed (sub)species, 2 = second most observed (sub)species etc.

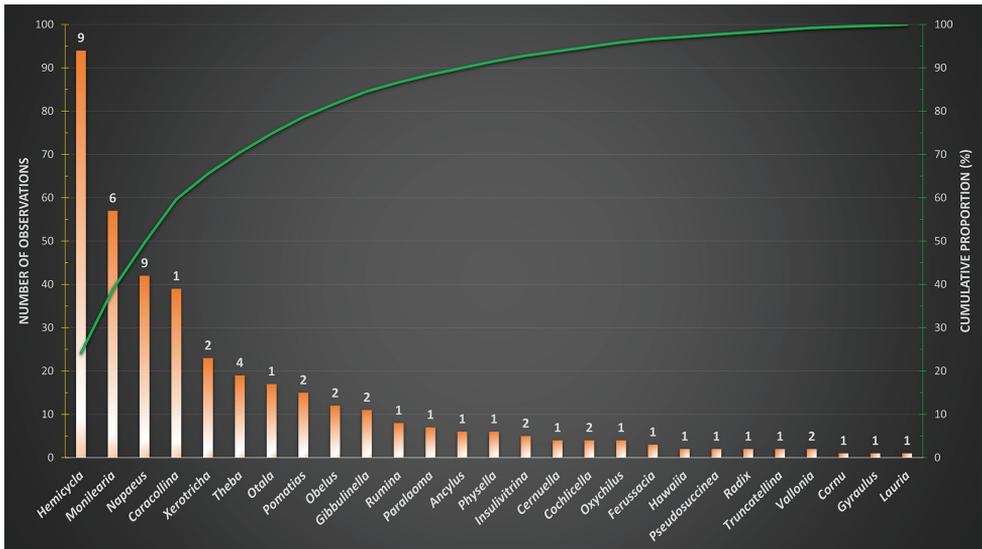


Figure 3. Graph showing the number of observations per genus and the cumulative proportion of observations. Numbers above the bars indicate the number of different taxa observed per genus.

Taxonomic ranks

Taxonomy is according to MolluscaBase eds. (2020) except for the taxon *Pomatias adjunctus* (Mousson, 1872). This species is known under the name *Pomatias canariensis* (d'Orbigny, 1840) in that database, but this name is a synonym of *Pomatias laevigatus* (Webb & Berthelot, 1833), which is a species other than *P. adjunctus* (see below; Theo Ripken personal comment; Yanes et al. 2004).

Kingdom: Animalia

Phylum: Mollusca

Class: Gastropoda

Families: Achatinidae, Enidae, Ferussaciidae, Geomitridae, Helicidae, Lauriidae, Lymnaeidae, Oxychilidae, Physidae, Planorbidae, Pomatiidae, Pristilomatidae, Punctidae, Streptaxidae, Trissexodontidae, Valloniidae, Vertiginidae, Vitrinidae

Species: *Ancylus striatus*, *Caracollina lenticula*, *Cermea virgata*, *Cochlicella acuta*, *Cochlicella barbara*, *Cornu aspersum*, *Ferussacia folliculum*, *Gibbulinella* aff. *dealbata*, *Gibbulinella* aff. *dewinteri*, *Gyraulus parvus*, *Hawaiiia minuscula*, *Hemicycla berkeleii*, *Hemicycla ethelema*, *Hemicycla* cf. *gaudryi*, *Hemicycla glasiana*, *Hemicycla guamartemes*, *Hemicycla psathyra psathyra*, *Hemicycla psathyra temperata*, *Hemicycla psathyra* cf. *temperata*, *Hemicycla saponacea*, *Hemicycla saulcyi carta*, *Hemicycla* spec., *Insulivitrina nogalesi*, *Insulivitrina parryi*, *Lauria cylindracea*, *Monilearia arguineguinensis*, *Monilearia montigena*, *Monilearia phalerata*, *Monilearia* cf. *praeposita*, *Monilearia pulverulenta*, *Monilearia tumulorum*, *Monilearia* spec., *Napaeus exilis*, *Napaeus interpunctatus*, *Napaeus isletae*, *Napaeus josei*, *Napaeus moquinianus*, *Napaeus myosotis*, *Napaeus obesatus*, *Napaeus*

validoi, *Napaeus venegueraensis*, *Napaeus* cf. *venegueraensis*, *Obelus despreauxii*, *Obelus pumilio*, *Otala lactea*, *Oxychilus draparnaudi*, *Paralaoma servilis*, *Physella acuta*, *Pomatias adjunctus*, *Pomatias* aff. *laevigatus*, *Pseudosuccinea columella*, *Radix auricularia*, *Rumina decollata*, *Theba arinagae*, *Theba geminata*, *Theba grasseti*, *Theba pisana*, *Truncatellina atomus*, *Vallonia costata*, *Vallonia pulchella*, *Xerotricha conspurcata*, *Xerotricha* aff. *orbignii*

Remarks concerning taxonomic status

Two species of *Gibbulinella* were found on the island: *Gibbulinella* aff. *dealbata* and *G.* aff. *dewinteri*. The shells of *Gibbulinella* aff. *dealbata* are wider and more solid than those of *G.* aff. *dewinteri*. These identifications were made on the meetings concerning the land snails of Gran Canaria organized by the Dutch Malacological Society where it was hypothesised that the shells found on Gran Canaria differ from those of *G. dealbata* (Webb & Berthelot, 1833) and *G. dewinteri* Bank, Groh & Ripken, 2002 from other islands. Indeed, we could find no published records of *G. dewinteri* from Gran Canaria and although this species was originally described as *Pupa* (= *Gibbulinella*) *dealbata* var. *minor* by Mousson (Bank et al. 2002), our shells are not smaller than *G. dealbata*. They are equally large, but they are slenderer. This genus should be revised on the Canary Islands.

Hemicycla gaudryi (d'Orbigny, 1839) and *H. ethelema* (J. Mabilille, 1882) show strong similarities but the shells of *H. ethelema* have a characteristic granulation. Our specimens from the Jardín Botánico Viera y Clavijo (botanical garden Tafira Alta) are old shells and it is not clear whether the granulations are lacking because the shells belong to *H. gaudryi* or because they are old and withered. Therefore, we used the name *H. cf. gaudryi*. Also, the shells were found at the overlap/edges of the distribution areas of both species but the distribution of *H. gaudryi* is not well known. Furthermore, at the meetings of Dutch Malacological Society it was stated that the correct name for this taxon should be *Hemicycla themera* (J. Mabilille, 1883) (Theo Ripken personal comment). More research is necessary on this species.

The shells designated as *Hemicycla psathyra* cf. *temperata* were found at a location outside the known range of *H. psathyra temperata* (Mousson, 1872) (northwest of the island), but we believe these shells can be contained within morphological variation of *H. psathyra temperata*. *Hemicycla psathyra* cf. *temperata* was treated together with *H. psathyra temperata* for the generation of Figs 2, 3 and thus not counted as a separate taxon.

A single shell was identified as *Hemicycla* spec. This is a juvenile shell too small for precise determination. It belongs to either *H. glasiana* (Shuttleworth, 1852) or *Hemicycla guamartemes* (Grasset, 1857). This observation was removed for the generation of Figs 2, 3 and thus not counted as a separate taxon.

In Barranco de Guayadeque, shells were found that are very convex, have an obtuse apex, and are larger than *Monilearia phalerata* (Webb & Berthelot, 1833). This description agrees nicely with the original description of *Monilearia praeposita* (Mousson, 1872) and the location agrees with the range given by the IUCN assessment of this species (Groh and Neubert 2011b). On the other hand, the IUCN status is Data Deficient and in the meetings of Dutch Malacological Society there were some doubts

on the status of this species. Therefore, we identified these shells as *M. cf. praeposita*. The fossil shells from Arinaga look like the shells from Barranco de Guayadeque but they are smaller. More research is necessary on this species.

The name *Monilearia spec.* is applied to *Monilearia* specimens where the shell is diamond shaped and has an open umbilicus. It is however not as high as *M. phalerata*. *Monilearia spec.* was observed in the northwest and from the west to the south of the island. Because of its open umbilicus and its range, this species could be *M. caementitia* (Shuttleworth, 1852). However, because we observed this species outside its known range (Groh and Neubert 2011a) and the uncertain differences with *M. persimilis* (Shuttleworth, 1852) and *M. inops* (Mousson, 1872), we identified this species as *Monilearia spec.* Comparison with reference material from museums would be helpful.

Several shells were found similar to *Napaeus venegueraensis* Artiles, Santana & Deniz, 2011 but smaller and with a more pointed top. These were designated as *N. cf. venegueraensis* and are possibly subadult shells of *N. venegueraensis*. *Napaeus cf. venegueraensis* was treated together with *N. venegueraensis* for the generation of Figs 2, 3 and thus not counted as a separate taxon.

The identifications of *Pomatias aff. laevigatus* were made in the meetings organized by the Dutch Malacological Society where it was hypothesised that the shells found on Gran Canaria differ from the *P. laevigatus* known from Tenerife. *Pomatias aff. laevigatus* is entirely smooth and occurs in the west of Gran Canaria, while *P. adjunctus* is ribbed and occurs in the northwest-northcentral part of the island. More research on this genus is needed in the Canary Islands.

Shells of *Xerotricha aff. orbignii* were found at several locations in the west of the island which look very much like *X. orbignii* (d'Orbigny, 1836), a species endemic to Tenerife. No endemic *Xerotricha* species are reported from Gran Canaria in recent checklists (Groh 1985; Bank et al. 2002; Brito and Fraga 2010; Helixebas 2019), but recent articles mention the species from Gran Canaria (Hutterer and Gittenberger 1998; Castillo et al. 2008; Wall et al. 2018). In the latter two citations the name *X. aff. orbignii* is used for these shells from Gran Canaria. Further research should reveal the relationship between *X. orbignii* from Tenerife and *X. aff. orbignii* from Gran Canaria.

Geographic coverage

The dataset comprises three trips taken to Gran Canaria (Canary Islands, Spain; Fig. 4) by the first author in the period between 2016 and 2020 and three shells of *Monilearia arguineguinensis* (Seddon & Aparicio, 1998) collected in 1988, that were obtained as a gift (WL:SNAIL:GC:OCC:00000).

Bounding box

West: 15°46,9642'W; East: 15°23,3691'W; North: 28°9,6014'N; South: 27°44,3515'N

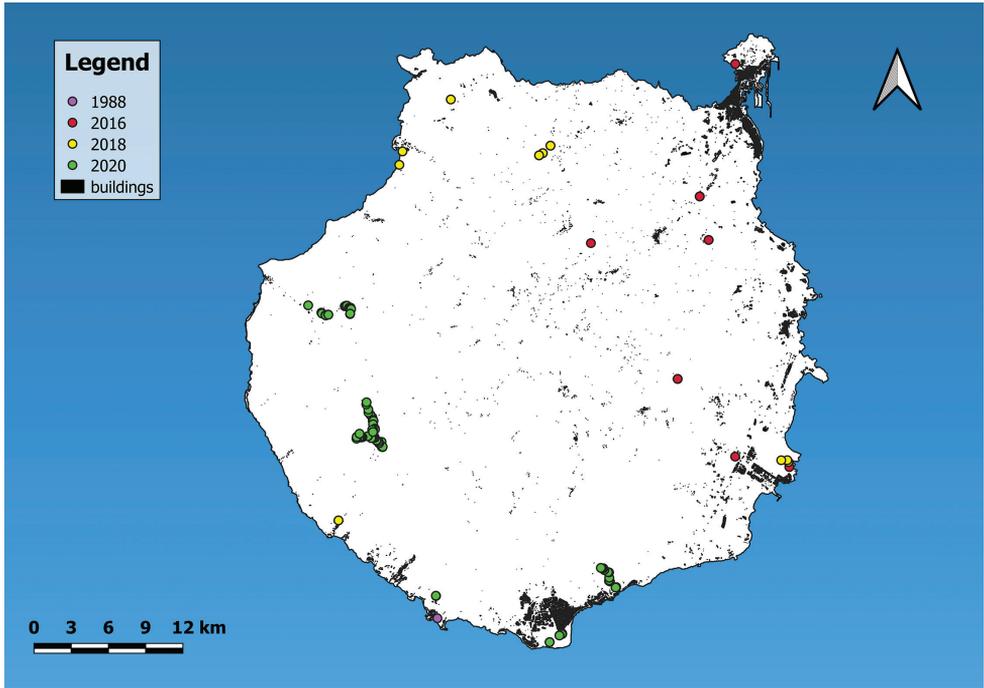


Figure 4. Map of Gran Canaria indicating all different locations in the dataset, coloured according to visiting year.

Temporal coverage

1988-04-08 to 2020-02-08

Methodology

Sampling description

Sampling was done at random along random routes. Locations were not predefined, but some regions were specifically visited because of known species richness or the occurrence of endemics. On site, observations were incidental, but microhabitats or elements that were thought to be favourable for snails were given more attention (e.g. dead wood, north facing slopes etc.). Collection of specimens was mainly done by hand on sight. In some cases, a soil sample was taken that was later examined at home.

Individuals were observed as living snails or empty shells (recent or (sub)fossil). Juveniles were treated as individuals with a shell that lack adult characteristics, like an underdeveloped peristome or the presence of a keel that is not present in adult shells. Following this practice, subadult specimen were often classified as juveniles.

Method step description

The following steps were used from data collection up to final data publication:

1. Data collection
 - Data sampling as described above
 - Species name, date, location, organism quantity, and additional remarks were noted in the field in a field notebook or entered in the app ObsMapp (Observation International 2019) (for occurrences in 2020)
 - Later, final determinations were conducted as described earlier and additional information was noted on organism quantity, location, and identification remarks
 - For shells in collection, data was kept on a label along with each specimen
 - For snails not in collection, pictures were taken in the field and data could be downloaded from <https://observation.org/> (via the app ObsMapp) for occurrences in 2020
2. All data were finally entered together as an occurrence dataset in Microsoft Excel (version 1908) and stored as an Excel Workbook (*.xlsx)
3. Standardisation of dataset to Darwin Core (Wieczorek et al. 2012) (see further)
 - Using R (R Core Team 2019) in RStudio (RStudio Team 2019)
 - Taxonomic information was added based on the scientific name and expressed in kingdom, taxonRank, and nomenclaturalCode
 - Dataset metadata information was added (language, datasetID, institutionCode, datasetName) as well as a unique taxon ID (taxonID), the license, and the rights holder (rightsHolder)
 - The final occurrence dataset was exported as a CSV-file (*.csv)
4. Data publication
 - Using the GBIF Integrated Publishing Toolkit (Robertson et al. 2014) instance at the Belgian Biodiversity Platform (<https://ipt.biodiversity.be>) (see further)
 - Complete metadata
 - Upload source data (occurrence.csv)
 - Publish on GBIF (<https://www.gbif.org/>)

Dataset

Dataset description

The following Darwin Core terms (<https://dwc.tdwg.org/terms/>) are used in the dataset: occurrenceID, family, scientificName, identificationQualifier, genus, scientificNameAuthorship, eventDate, year, basisOfRecord, lifeStage, organismQuantity, organismQuantityType, decimalLatitude, decimalLongitude, geodeticDatum, coordinateUncertaintyInMeters, locality, municipality, stateProvince, island, islandGroup, country, countryCode, recordedBy, identifiedBy, identificationRemarks, occurrenceRemarks, associatedMedia, kingdom, taxonID, language, license, rightsHolder, datasetID, institutionCode, datasetName, taxonRank, nomenclaturalCode

Object name: Land and freshwater molluscs of Gran Canaria (Spain)

Format name: Darwin Core Archive format

Format version: 1.0

Character encoding: UTF-8

Language: English

License: <https://creativecommons.org/publicdomain/zero/1.0/>

Usage norms: <https://www.inbo.be/en/norms-data-use> (Desmet et al. 2014)

Publication date: 2020-03-12

Distribution: <https://ipt.biodiversity.be/resource?r=snail-gran-canaria-occurrences>

DOI: <https://doi.org/10.15468/ny1f9n>

Data records

The data are standardized to Darwin Core (Wieczorek et al. 2012) using an R script based on the TRIAS Checklist Recipe (Reyserhove et al. 2018) with R (R Core Team 2019) in RStudio (RStudio Team 2019). The R script used for mapping the data to Darwin Core can be accessed here: <https://github.com/BelgianBiodiversityPlatform/landsnails-occurrences>. The data are published using the GBIF Integrated Publishing Toolkit (Robertson et al. 2014) instance at the Belgian Biodiversity Platform (<https://ipt.biodiversity.be>). The data are organized as an occurrence only dataset, with the occurrence core containing 389 records. The Belgian Biodiversity Platform IPT archives the data and thus serves as the data repository. The data and resource metadata are available for download in the downloads section. The versions table lists other versions of the resource that have been made publicly available and allows tracking changes made to the resource over time.

Additional information

Empty shells were collected for over 75% of the occurrences in the dataset and deposited in the private collection of first author. For 282 of the 389 observations, links to 101 images of living animals, empty shells and habitats can be found in associatedMedia.

The Darwin Core Archive creation and the publication of the data is part of the 'Integrated Biodiversity research Project' course organized in the 'Master of Science in Biology' program of Ghent University (Belgium).

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A reassessment of the genus *Oligoneuriopsis* Crass, 1947 (Ephemeroptera, Oligoneuriidae, Oligoneuriellini)

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Abstract

The distinction between the two closely related genera *Oligoneuriella* Ulmer, 1924 and *Oligoneuriopsis* Crass, 1947 has been much debated. First described from South Africa, *Oligoneuriopsis* seemed to be a clearly defined genus. However, as the known distribution of the genus widened and knowledge on it expanded, species delimitation based on morphology became less clear due to overlap in several apparently defining morphological characters, especially in the nymphs. This work attempts to reassess *Oligoneuriopsis* morphology in the context of all currently known species. The type species, *Oligoneuriopsis lawrencei* Crass, 1947 is redescribed at the imaginal and nymphal stages and a neotype is designated. The putative nymph of *Oligoneuriopsis dobbsi* (Eaton, 1912) is described based on material collected around Mt Elgon (Kenya). The adults of *Oligoneuriella orontensis* Koch, 1980 are described for the first time and the species is transferred to the genus *Oligoneuriopsis* (*Oligoneuriopsis orontensis* **comb. nov.**). Egg structure is also described for the first time for the species *Oligoneuriopsis skhounate* and *O. orontensis*. Some biogeographical considerations are also given. It is likely that more species will still be discovered, especially in Africa.

Keywords

Barcoding, generic concept, imaginal description, mayfly, neotype designation, new combination, nymphal description

Introduction

Up to the middle of the 20th century, the only oligoneuriid genus widespread in the Afrotropical realm was *Elassoneuria* Eaton, 1881. In 1947, Crass described the genus *Oligoneuriopsis* to accommodate a new species, *O. lawrencei*, from the region then known as Natal (now KwaZulu-Natal), South Africa. Crass' genus differs from *Elassoneuria*, the other genus occurring in sub-Saharan Africa, in wing venation differences in the adult stage, male genitalia features, and by the shape of the head in the nymphal stage (Crass 1947). He noted that his new genus somewhat resembles the Palearctic genus *Oligoneuriella* Ulmer, 1924 (sub. nom. *Oligoneuria* Pictet, 1843), both in nymphal and adult stages. Subsequently, Demoulin (1952) produced a key to identify the adults of Oligoneuriidae, and gave as discriminating characters 4-segmented gonostyli and dissimilar tarsal claws in *Oligoneuriopsis* vs. 3-segmented gonostyli and both tarsal claws obtuse in *Oligoneuriella* (not to be confused with *Elassoneuria*, which also has 3-segmented gonostyli and both tarsal claws obtuse). A nymph of *Oligoneuriopsis* sp. was later recorded from West Africa (Verrier 1958), but according to Demoulin (1970), this specimen belongs to the genus *Elassoneuria*. A second species of *Oligoneuriopsis* was recognized by Kimmins for a species originally described by Eaton as *Oligoneuria dobbsi* from British East Africa (now Kenya) (Eaton 1912) in which male gonostyli are 4-segmented (Kimmins 1960). Two new species were later described from South Africa, based on nymphs collected in the eastern Transvaal (now Mpumalanga) and in KwaZulu-Natal (Agnew 1973). A major advancement was the description of a new species, *Oligoneuriopsis skhounate*, from both nymphal and adult stages from Morocco, extending the known distribution of the genus all the way to North Africa (Dakki and Giudicelli 1980). The recent description of the nymph of *Oligoneuriopsis villosus* from Iran (Sroka et al. 2019) extends the distribution of this genus north-eastwards, to include Southwest Asia as well.

Dakki and Giudicelli (1980) compared *O. skhounate* to *O. lawrencei* and *O. dobbsi*, and proposed additional characters to distinguish the nymphs of *Oligoneuriopsis* from those of *Oligoneuriella*:

- posterolateral abdominal spines on segments II to VII long and going beyond the posterior margin of the tergites in *Oligoneuriella* compared to *Oligoneuriopsis* where these spines are shorter, and
- gill lamellae longer than the half length of the corresponding tergite in *Oligoneuriopsis* and shorter than the half-length in *Oligoneuriella*.

Neither of these characters holds true for separating the nymphs of these two genera, as in the three South African *Oligoneuriopsis* species, the posterolateral abdominal spines on segments II to VII extend beyond the margin of the tergites, and the gill lamellae are shorter in several species.

The first record of *O. skhounate* in the Iberian Peninsula was published by Gonzalez del Tanago and Garcia de Jalon (1983). In the same year, *O. skhounate* was reported from Algeria (Soldán and Thomas 1983), but the authors transferred it to the genus *Oligoneuriella* without much discussion, saying that “This species actually belongs to the genus *Oligoneuriella* Ulmer as apparent from wing venation and nymphal morphology (Crass 1947; Agnew 1973)”. The species was then recorded from Tunisia

(Boumaiza and Thomas 1986), and later on again from Algeria (Gagneur and Thomas 1988) but placed in the genus *Oligoneuriopsis* without generic discussion.

Due to the lack of clear distinctions between *Oligoneuriella* and *Oligoneuriopsis* nymphs, the generic concept relies mainly on male adult differences. Characters used to discriminate between the adults were proposed by Demoulin (1952). Of particular use is the number of segments composing the gonostyli, i.e., three in *Oligoneuriella* (one long proximal and two smaller apical) vs. four in *Oligoneuriopsis* (one long proximal and three smaller apical). Unfortunately, although this character is generally reliable and constant at a generic level in most mayfly families, it appears to be subject to some variation in Oligoneuriidae, as already mentioned by Eaton (1883–1888) and illustrated by Grandi (1947) for the species *Oligoneuriella rhenana* where sometimes a fourth terminal segment is present; the same has been reported by Gillies (1974) for different species of *Elassoneuria* and by Elouard (pers. comm.) for some species of *Madeconeuria*.

Another problem concerns the original description of *Oligoneuriopsis lawrencei* by Crass (1947). The gills present on the first abdominal segment supposedly lacked a lamella, being composed only of a bunch of fibrillae, the most important character fixed by the author to distinguish his new genus from *Oligoneuriella*. When describing *Oligoneuriopsis jessicae* and *Oligoneuriopsis elisabethae*, Agnew (1973) stated that first gill of both species did possess a lamella but did not mention anything about Crass' species. It was only later (Agnew 1980) that he formally confirmed that Crass' description was erroneous and that *O. lawrencei* also possessed a lamella on the ventral first gill. A second problem arose when looking at the single illustration we have of the male genitalia of *O. lawrencei* (see Crass 1947: fig. 4a), where the author has drawn penis lobes with lateral sclerite thin and hardly enlarged at the apex (proximal part of the sclerite is unfortunately not drawn), comparable to those found on different species of *Oligoneuriella* (Sowa 1973; Soldán and Landa 1977; Dakki and Giudicelli 1980; Alba-Tercedor 1983; Mol 1984). This character is quite different from what can be seen in *O. dobbsi* and *O. skhounate* where the lateral sclerite is club-shaped and enlarged at apex (Kimmins 1960; Dakki and Giudicelli 1980). As stated by Kluge (2004), the shape of the proximal part of the penis sclerite is apically pointed or bifid in *Oligoneuriopsis dobbsi* and *O. skhounate*, whereas it is saddle-shaped in all *Oligoneuriella* species (see Dakki and Giudicelli 1980 for a good comparison).

Another character to distinguish nymphs of *Oligoneuriella* and *Oligoneuriopsis* has been briefly mentioned by Demoulin (1970) and studied in more detail by Agnew (1980). In the three *Oligoneuriopsis* species from South Africa, Agnew noticed that sternites II-IV or II-V possess a well-developed tuft of long and thin setae in medio-posterior position, whereas at least some *Oligoneuriella* species possess instead a tuft of short and stout setae (Sowa 1973). In a recent phylogeny based on a combination of morphology (using *O. skhounate* from Spain), and genetics (using *O. lawrencei* from South Africa), Massariol et al. (2019) indicate that *Oligoneuriopsis* clusters separately from but closely to *Oligoneuriella* within the Oligoneuriidae, and proposed to group these two genera in a new tribe, the Oligoneuriellini.

Finally, a recent paper by Sroka et al. (2019) deals with the description of the nymph of a new *Oligoneuriopsis* species from Iran. The authors propose new diagnostic

characters to distinguish their nymphs from those of *Oligoneuriella*. They validate the discriminant character constituted by the length of medioposterior setae on the proximal sternites, which are always long in *Oligoneuriopsis* and short in *Oligoneuriella*. Two other differences are also proposed, namely a row of setae along the entire length of posterior margin of femora and outer margin of tibiae on middle and hind legs found in *Oligoneuriopsis* only.

The aim of the present paper is to investigate and confirm the generic status in reviewing all species presently known. This will also allow us to reassess the generic position of the species *Oligoneuriella orontensis* Koch, 1980, based on the rich material collected from Israel (see Yanai et al. 2020).

Materials and methods

Material was examined from South Africa, Kenya, Israel, Algeria, Tunisia, Morocco, Iran and the Iberian Peninsula. Material includes nymphs (indicated as N), female subimagos (s♀), male subimagos (s♂), female imagoes (♀) and male imagoes (♂). All studied specimens belong to the following collections: Albany Museum, Grahamstown, South Africa (**AMGS**), Museum of Zoology, Lausanne, Switzerland (**MZL**), Laboratory of Environment Biomonitoring, University of Bizerta, Tunisia (**LBE**), and Steinhardt Museum of Natural History, Tel Aviv University, Israel (**SMNH**).

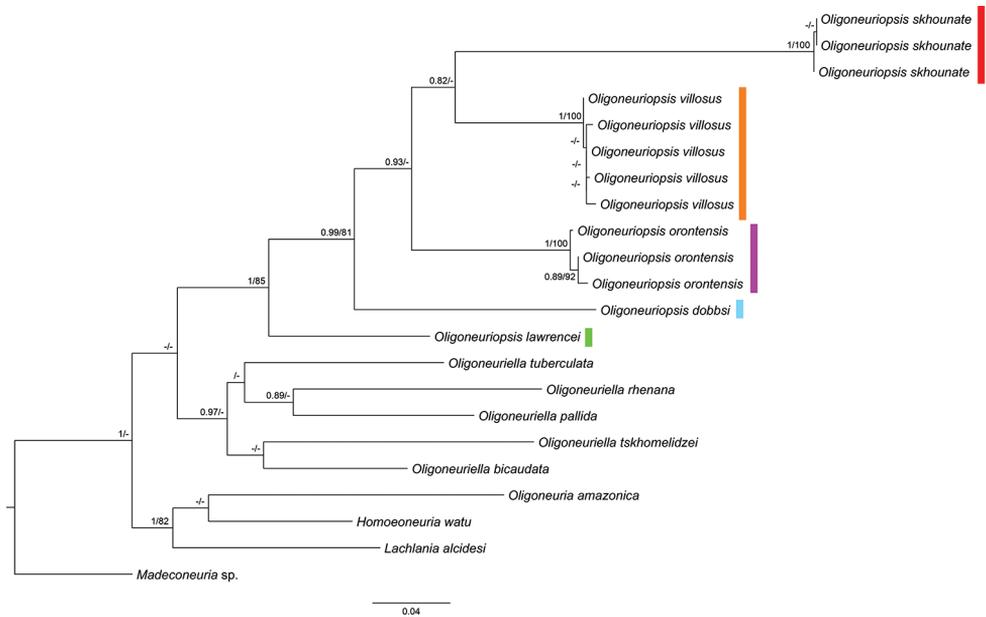
It must be mentioned that all type specimens of *Oligoneuriopsis* from South Africa described by Crass and Agnew are certainly lost (McCafferty and de Moor 1995).

For genetic analysis we used the barcoding genetic marker cytochrome *c* oxidase subunit 1 (COI). We considered available sequences of three *Oligoneuriopsis* species (*O. lawrencei*, *O. orontensis*, and *O. villosus*), to which we added newly obtained sequences of fresh specimens of *O. dobbsi* and *O. skhounate*, thus representing the great majority of the described species in the genus. We used a non-destructive method for DNA extraction, i.e., specimens were incubated overnight soaked at proteinase K to allow DNA extraction without destroying the specimen. Amplification was done using the commonly used primers HCO2198 and LCO1490 (Folmer et al. 1994), with optimal PCR conditions of initial denaturation at 95 °C for 5 min; 38 cycles of 95 °C denaturation for 40 sec, 50 °C annealing for 40 sec, and 72 °C extension for 40 sec; and final stage of 72 °C denaturation for 7 min. To clarify the generic position of *O. orontensis* and as outgroups, we also used representatives of species of the closely related genus *Oligoneuriella* and of other sibling-genera in the family (Table 1). For these taxa we retrieved mitochondrial COI sequences from NCBI GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>) and from barcode of life database (<http://www.boldsystems.org/>); accession numbers are given in Table 1.

We aligned and reconstructed the sequences in MEGA X v.10.0.5 (Kumar et al. 2018). We conducted a Maximum Likelihood (ML) analysis in RAxML v.8 (Stamatakis 2014) as implemented in raxmlGUI v.2.0 beta (Edler et al. 2019); ML analysis was performed with the GTR+G model of sequence evolution (as selected by jModelTest v.2.1.7; Durrin et al. 2012) and 100 replicates. Each inference was initiated with a

Table 1. Private identifiers of COI sequences used for the genetic analysis (GenBank accession numbers and BOLD process IDs).

Species	Database	Private identifiers
<i>Oligoneuriopsis lawrencei</i>	GenBank	MG516468
<i>Oligoneuriopsis villosus</i>	BOLD	EPHIR007-19, EPHIR008-19, EPHIR009-19, EPHIR010-19, EPHIR011-19
<i>Oligoneuriopsis orontensis</i>	GenBank	MN958842, MN958843, MN958844
<i>Oligoneuriopsis dobbsi</i>	GenBank	MT784191
<i>Oligoneuriopsis skhounate</i>	GenBank	MT784188, MT784189, MT784190
<i>Oligoneuriella tuberculata</i>	BOLD	EPHIR005-19
<i>Oligoneuriella rhenana</i>	GenBank	KY262260
<i>Oligoneuriella pallida</i>	GenBank	KU609047
<i>Oligoneuriella tskhomelidzei</i>	BOLD	EPHIR014-19
<i>Oligoneuriella bicaudata</i>	BOLD	BMIKU054-09
<i>Oligoneuria amazonica</i>	GenBank	KT201514
<i>Homooneuria watu</i>	GenBank	MG516463
<i>Lachlania alcidesi</i>	GenBank	KU609050
<i>Madeconeuria</i> sp.	GenBank	MG516465

**Figure 1.** A phylogenetic reconstruction based on Maximum Likelihood and Bayesian Inference analyses of sequences of the mitochondrial COI gene, presented on ML tree. BI posterior probabilities above 0.85 and ML bootstrap values above 70% are indicated next to the nodes.

random starting tree and nodal support was assessed with 1000 bootstrap pseudoreplicates. We conducted the Bayesian Inference (BI) analysis with MrBayes v.3.2.7a (Ronquist et al. 2012); BI analysis was performed with two simultaneous runs, each with four chains (three heated, one cold), for 2×10^6 generations with sampling every 200 generations. We monitored the standard deviation of the split frequencies between the two runs and the Potential Scale Reduction Factor (PSRF) diagnostic. The first 25% of the trees were discarded as burn-in.

Results

Figure 1 represents the phylogenetic reconstruction based on Maximum Likelihood and Bayesian Inference analyses of sequences of the mitochondrial COI gene, presented on ML tree. All *Oligoneuriopsis* species are recovered as a monophyletic clade, as are also the *Oligoneuriella* species; the former clade includes *O. orontensis*, thus supports our claim regarding its generic position (see below). Each *Oligoneuriopsis* species presents low intraspecific divergence and high interspecific values, confirming that they are all well-defined genetically. Relationships between *O. orontensis*, *O. villosus* and *O. skhounate* are not clear (BI < 0.85), but both ML bootstrap values and BI indicate that *O. lawrencei* (South Africa) is the sister species of all other *Oligoneuriopsis* species, followed by *O. dobbsi* (Kenya).

Oligoneuriopsis lawrencei Crass, 1947

Figures 2, 3, 4, 14D, 15D

Oligoneuriopsis lawrencei Crass, 1947: 53, figs 3, 4.

Material examined. Neotype: SOUTH AFRICA • 1N; Eastern Cape Province, Tributary of Tyume River, below Tor Doone, Hogsback; 32.5778°S, 26.9347°E; alt. 1445 m a.s.l.; 29 Feb. 1992; F.C. de Moor leg.; AMGS; GEN 1097A; H.M. Barber-James design., 2020. This specimen was chosen because it comes from one of Crass (1947)'s original localities.

Other material: SOUTH AFRICA • 1N; Eastern Cape Province, Tsitsa River, at “The Falls”; 31.0214°S, 28.4819°E; alt. 1140 m a.s.l.; 26 Mar. 1991; F.C. de Moor & H.M. Barber leg.; AMGS; ECR 92AE • 6N; same locality; 28 Mar. 1993; F.C. de Moor & H.M. Barber-James & K. Martens leg.; AMGS; ECR 134A • 12N; Eastern Cape Province, Nqancule River, at Waterval; 31.3672°S, 28.2167°E; alt. 1220 m a.s.l.; 24 Mar. 1991; F.C. de Moor & H.M. Barber leg.; AMGS; ECR 86A • 6N; Eastern Cape Province, Nqancule River, at Albany; 31.3486°S, 28.2153°E; alt. 1240 m a.s.l.; 5 Mar. 1991; F.C. de Moor & H.M. Barber leg.; AMGS; ECR 88A • 1N; Eastern Cape Province, Kettle Spout waterfall, Tyume River tributary, Hogsback; 32.5500°S, 26.9500°E; alt. 1835 m a.s.l.; 19 May 2007; F.C. de Moor and N. Phaliso leg.; AMGS; GEN 1845A • 3♀, 4♂, 1N; KwaZulu-Natal, Klein Mooi River, at Durleigh Farm; 29.2283°S, 29.8997°E; alt. 1392 m a.s.l.; 15 Mar. 1995; C. Dickens; AMGS; MOI 29BS • 3♀ 4♂; same locality; 3 Apr. 1995; F.C. de Moor leg.; AMGS; MOI 35B.

Male imago. Lengths. Body: up to 14.8 mm; forewing: up to 14.9 mm; cerci: up to 17.0 mm; caudal filament: up to 12.8 mm.

Vertex light brown, frontoclypeus pale cream, broadly rounded apically, compound eyes black, base of ocelli black, ocelli whitish, antennae with scape and pedicel pale cream, first segment and flagellum light brown. Pronotum light brown, margins suffused with dark brown pigmentation. Pterothorax light brown, with pale cream-col-

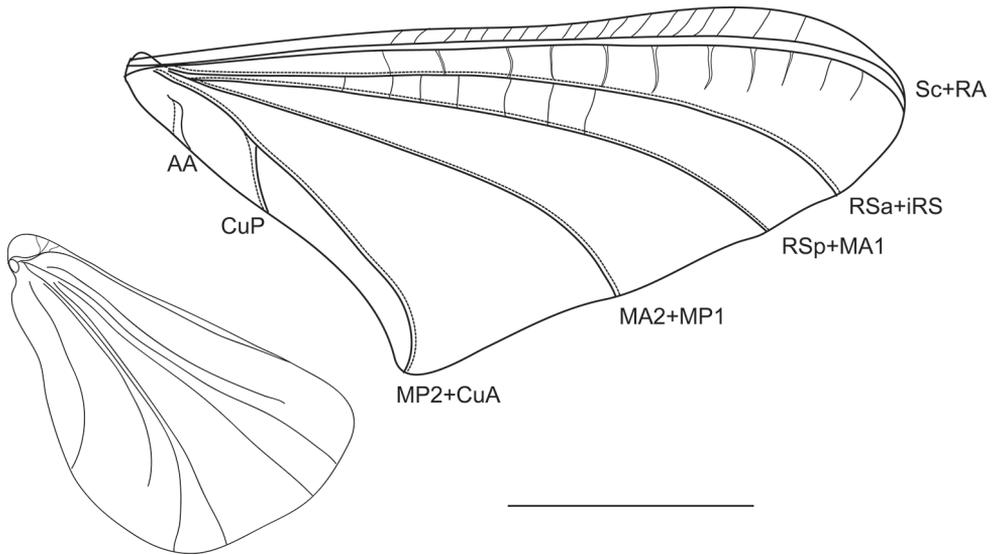


Figure 2. *Oligoneuriopsis lawrencei*, fore- and hind wings. Scale bar 0.5 mm.

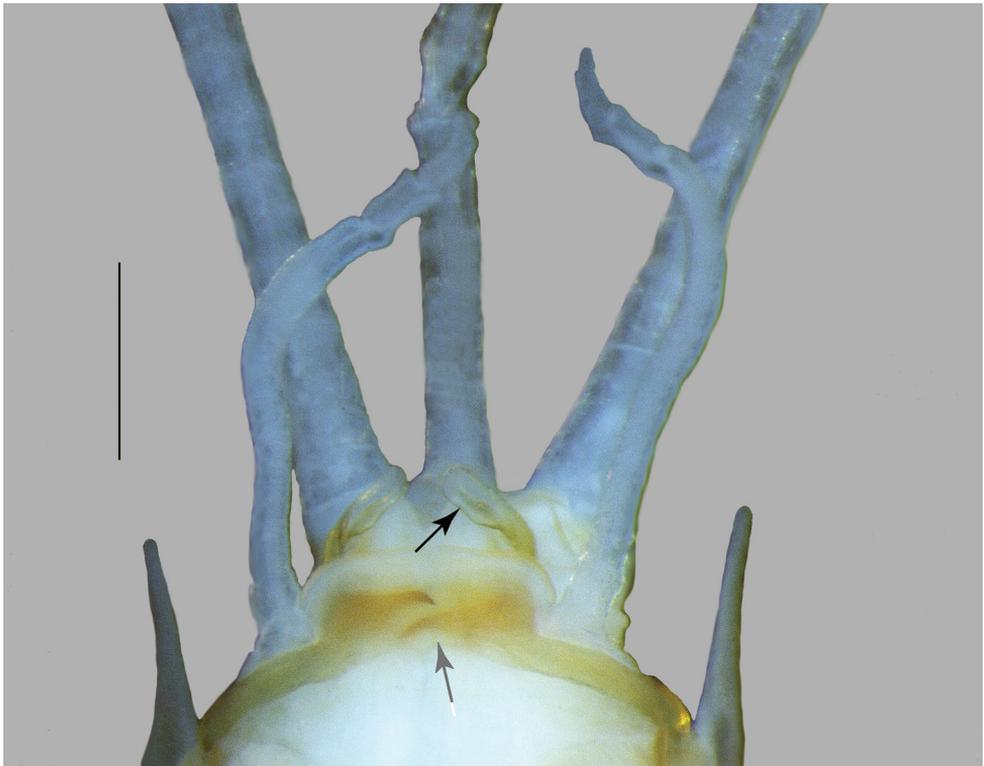


Figure 3. *Oligoneuriopsis lawrencei*, ventral view of lower abdomen of adult male, showing lateral extensions of segment IX, gonostyli and penes. Black arrow: Apex of the lateral longitudinal lobe of penis. Grey arrow: Proximal process of penis. Scale bar 0.5 mm.

oured unsclerotized line between meso and metanotal plate. Mesoscutellar filaments present. Forelegs shorter than mid or hind legs, with outer margin of femora, tibiae and tarsi dark brown, otherwise uniform pale brown colour; mid- and hindlegs cream to light brown, no distinct markings. All three pairs of legs appear to be functional. Tarsal claws paired, blunt. Wings (Fig. 2), when folded, light brown, almost whitish when unfolded. Forewing typical of the genus, with five groups of veins: Sc+RA, RSa+iRS, RSp+MA1, MA2+MP1, and a forked MP2+CuA – CuP vein. Subcostal field with numerous transversal veins, those issued from RA not reaching iRS in the distal forth of the length, those between iRS and MA1 only present in the proximal half.

Abdominal segments uniformly creamish, without distinct patterns, except tergites VII, IX, and X light brown; lateral margins with spine-shaped extensions from segment III to IX, of increasing length towards the posterior. Gonostyli whitish to grey, cerci whitish. Gonostyli 4-segmented, the basal one ca. 3 × the length of segments 2 to 4 combined. Penis lobes almost triangular, with characteristic sclerotized proximal process ending in a simple projection; apex of the lateral longitudinal lobe of penis in a small club-shaped sclerite (Fig. 3). Cerci with whorls of long setae at each junction (not figured).

Female subimago. Lengths. Body: up to 17 mm; forewing: up to 18.8 mm; cerci: up to 7 mm; caudal filament: up to 4.5 mm. Colouration as in the male; tibiae and tarsi of all legs appear to be functional. Cerci light to medium brown. Posterior margin of sternite IX deeply concave and rounded.

Nymph. Lengths. Body up to 15 mm and 18.5 mm in male and female nymphs respectively; cerci (and caudal filament) up to 9.2 mm (4.0 mm) and 10.1 mm (3.5 mm) in male and female nymphs respectively. General colouration light to medium yellow-brown (Fig. 4A), with dark brown dorso-medial markings, better developed in mature male nymphs than in immatures or females. Head (Fig. 4B) medium brown, with maculation between the compound eyes. Ventrally, head a uniform pale cream colour. Gills at base of maxillae forming a “beard” ventrally at base of head, of similar colour to head in Hogsback specimens, orientated in one plane, parallel to length of body. Pro and mesonotum medium brown, with pale cream-coloured maculae. Legs light brown, femoro-tibial articulation darker, setae of forelegs noticeably darker brown than the legs. Femur and tibia of foreleg shorter than those of mid or hind leg, in all cases, femora and tibiae subequal in length. Setae on the outer margin of mid and hind femora well developed, slightly decreasing in size and reaching the apex (Fig. 14D). Tibiae and tarsi with long, even fringe of setae along entire dorsal margin, interspersed with occasional short spine-like setae. Abdominal tergites uniformly medium brown, each with darker brown marking medially; sternites uniform pale brown, with no markings. Dense patch of posteriorly orientated setae ventromedially on abdominal sternites II–IV, much reduced patch on segments V, further reduced on VI. Gills II–VII almost subequal in size, gill I smaller. On all gills except for gill I, fibrillae shorter than lamella length. Lamella of gill I less than half the length of the fibrillar portion. Lamellae II–VII with long and thin setae on their distal inner margin (Fig. 15D). Posterolateral spines of the abdomen increasing in size posteriorly. Whole nymph (dorsal aspect) and gills as illustrated by Agnew (1980). Cerci uniformly medium brown, caudal filament paler brown.

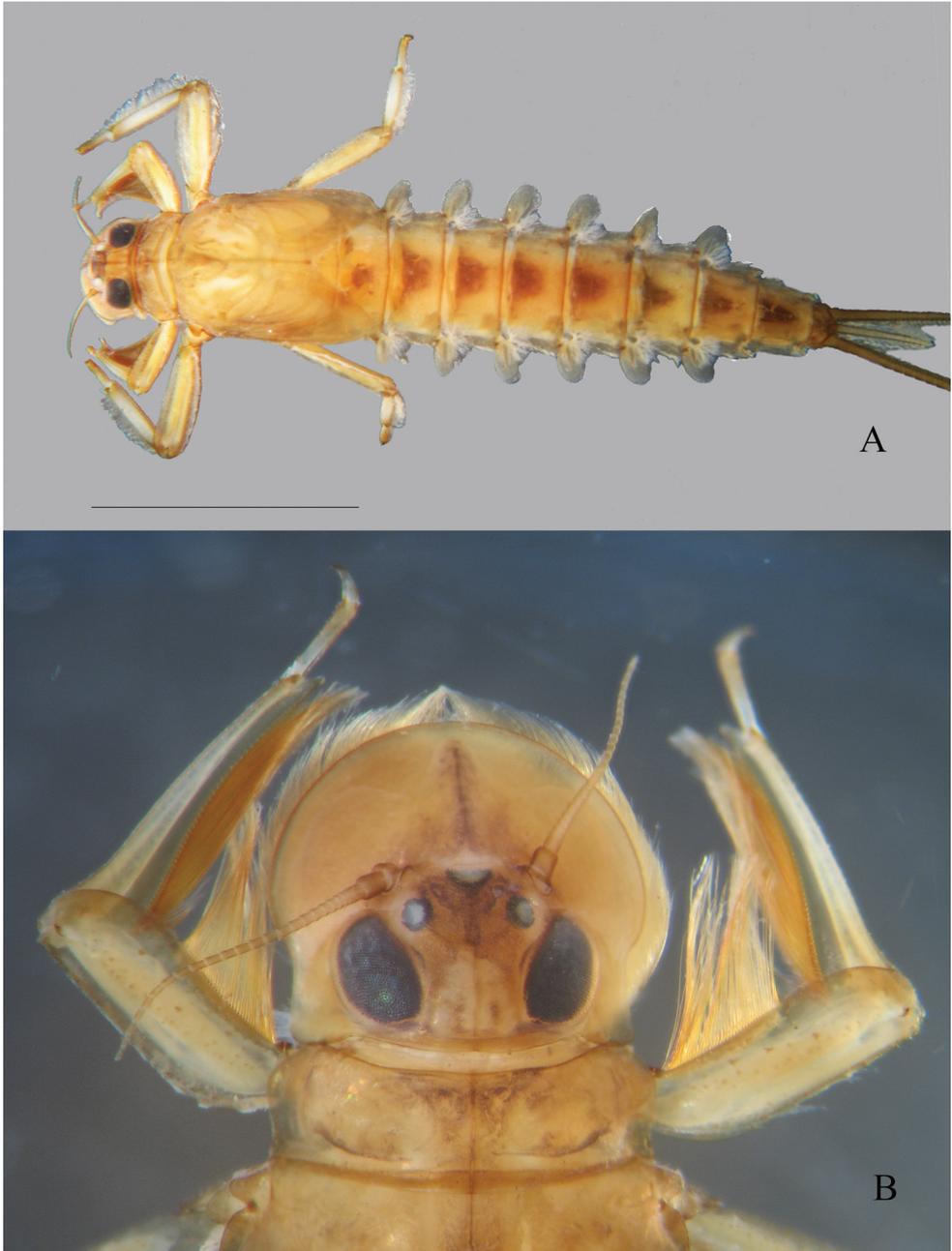


Figure 4. *Oligoneuriopsis lawrencei* **A** whole nymph, dorsal view **B** dorsal view of head. Scale bar: 5 mm (**A**).

Intraspecific variation. Specimens from KwaZulu-Natal are darker brown in colour than specimens with more southerly distribution, and first three abdominal segments darker brown in colour dorsally than remaining segments; faint paired median spots visible on the last five abdominal tergites in some KwaZulu-Natal nymphs. The head also

possesses a dark brown marking present on the frons between the ocelli, and maxillary gills are much paler in colour relative to head capsule in KwaZulu-Natal specimens.

Affinities. Winged stages were collected from the same locality as the nymphs in one instance, allowing association of the life stages. Imagos were seldom flying at the times of collection. Nymphs of *O. lawrencei* have a broadly rounded fronto-clypeal region, which easily distinguishes them from *O. jessicae* and *O. elisabethae*, both of which are more pointed in shape. Head very slightly carinate, less so than in *O. elisabethae*. Note that this is unlike the strong carination seen in *Elassoneuria*.

Habitat preference. Found under large boulders (400–500 mm diameter) in swift current, often in rivers with bedrock substrate.

Known distribution. South Africa.

Oligoneuriopsis dobbsi (Eaton, 1912)

Figures 5, 6

Oligoneuria dobbsi Eaton, 1912: 243, fig. 1 (female imago).

Oligoneuriella dobbsi: Ulmer, 1924: 32.

Oligoneuria sp.: Vayssière, 1936: 130 (nymph).

Oligoneuriopsis dobbsi: Kimmins, 1960: 276, figs 9, 10 (female and male imagos).

Oligoneuriopsis grandaeva (Navás, 1936: 125, fig. 21) (female imago).

Material examined. KENYA • 28N; Mount Elgon, Teremi upstream; 0.8973°N, 34.5973°E; alt. 2456 m a.s.l.; 13 Oct. 2019; W. Graf leg. • 23N; Mount Elgon, Teremi; 0.9094°N, 34.5994°E; alt. 2407 m a.s.l.; 13 Oct. 2019; W. Graf leg. • 13N; Mount Elgon, Kimurio upstream; 0.8913°N, 34.5892°E, alt. 2239 m a.s.l.; 11 Oct. 2019; W. Graf leg. • 46N (among them 1N – GBIFCH00890747 – sequenced); Mount Elgon, Kimurio tributary 2; 0.8956°N, 34.5878°E; alt. 2347 m a.s.l.; 8 Nov. 2019; W. Graf leg. • 15N; Mount Elgon, Kibisi upstream; 0.9028°N, 34.6175°E; alt. 2298 m a.s.l.; 9 Nov. 2019; W. Graf leg. • 8N; Mount Elgon, Kapkateny upstream; 0.8959°N, 34.5990°E; alt. 2293 m a.s.l.; 11 Oct. 2019; W. Graf leg. • 7N; Mount Elgon, Kapkateny midstream; 0.8325°N, 34.6234°E; alt. 1896 m a.s.l.; 12 Oct. 2019; W. Graf leg. • 2N; Mount Elgon, Kapkateny downstream; 0.8144°N, 34.6243°E; alt. 1660 m a.s.l.; 14 Oct. 2019; W. Graf leg.; all MZL.

Male imago. As redescribed by Kimmins (1960), with the following complement extracted from mature male nymphs: penis lobes with characteristic sclerotized proximal process ending in a simple projection; apex of the lateral longitudinal lobe of penis in a small club-shaped sclerite ca. 1.5 × larger than the lateral lobe (Fig. 5B).

Nymph. Lengths. Body up to 17 mm and 25 mm in male and female nymphs respectively; cerci (and caudal filament) up to 10 mm and 11 mm in male and female nymphs, respectively.

General colouration medium to dark brown, in general darker in mature nymphs than in immature ones (Fig. 6A). Head dark brown, with four lighter maculations



Figure 5. *Oligoneuriopsis dobbsi*, male nymph **A** hind leg **B** genitalia (sternite IX removed). Black arrows: Apex of the lateral longitudinal lobe of penis. White arrows: Proximal process of penis. Scale bar: 1 mm.

between the compound eyes, and a black marking present on the frons between the ocelli; generally also with a rounded light maculation between antennae. Ventrally, head a uniform light brown colour. Gills at base of maxillae forming a “beard” ventrally at base of head, much paler in colour relative to head capsule (Fig. 6B). Pro- and mesonotum dark brown, with lighter maculae laterally and medially. Legs light to medium brown, femoro-tibial articulation with a blackish spot. Femur and tibia of foreleg shorter than those of mid or hind leg, fore tibia longer than fore femur; on mid- and hind legs, femora and tibiae subequal in length. Setae on the outer margin of mid and hind femora well developed, slightly decreasing in size and reaching the apex (Fig. 5A). Tibiae and tarsi with long, even fringe of setae along entire dorsal margin. Abdominal tergites uniformly dark brown, each with a pair of light spots in the middle, except tergite X which bears four light spots in proximal part. Sternites medium brown, laterally dark brown, with two small pale median markings, especially visible on sternites IV to VIII. Dense patch of posteriorly orientated setae ventromedially moderately developed on abdominal sternite II, well-developed on sternites III–V, absent from other segments. Gills III–VII almost subequal in size, more than $\frac{3}{4}$ of the corresponding segment, gill II smaller, ca. $\frac{1}{2}$ the size. On all gills except for gill I, fibrillae shorter than lamella length. Lamella of gill I a little bit shorter than the length of the fibrillar portion. Lamellae II–VII with long and thin setae on their distal inner margin. Posterolateral spines of the abdomen absent of segments I and II, then increasing in size from segment III to IX, those of this last one being ca. $\frac{1}{4}$ the length of the segment.

Cerci uniformly medium brown, caudal filament paler brown towards apex.

Affinities. *Oligoneuriopsis dobbsi* male imago seems to be closely related to *O. lawrencei* from which it differs by the presence of crossveins in the proximal part of the subcostal area (see Kimmins 1960, fig. 9), as well as by the shape of the proximal



Figure 6. *Oligoneuriopsis dobbsi*, male nymph **A** in dorsal view **B** in ventral view. Scale bar: 5 mm.

process of the penis sclerite which is shorter and less pointed than in *O. lawrencei*. The supposed nymph of *O. dobbsi* presents also similarities with the one of *O. lawrencei*, but differs in several respects, namely, the absence of a slight carina on the head, the general colouration of the body, the size of gill II, smaller than the following ones in

O. dobbsi, whereas subequal to the following ones in *O. lawrencei*, the patch of setae on sternites (II) III–V in *O. dobbsi* compared to sternites II–IV (V–VI) in *O. lawrencei*, and finally the size of gill I lamella, much shorter in the latter than in *O. dobbsi*.

Remarks. The association of the nymphs from Mount Elgon with the adults described by Eaton (1912) as *Oligoneuriopsis dobbsi* is putative at the moment, because we have no rearing of the nymphs and no COI sequences from Eaton's material. However, we think this association is realistic, for the following reasons. First, male genitalia extracted from a mature nymph are compatible with those drawn by Kimmins (1960), especially the proximal process which is thick and shorter than in the other species, and the apex of the lateral longitudinal lobe of penis which is slightly clavate distally. Secondly, localities for the nymphs and adults are only distant from ca. 100 km, whereas no other *Oligoneuriopsis* populations are known in a radius of thousands of kilometres. Additional nymphal material has been collected by Laban Njoroge, National Museums of Kenya, Nairobi, from the Aberdare range of mountains in Central Kenya and one specimen from Mount Kenya. Images of these nymphs correspond completely with the nymphs of *O. dobbsi* described here. The Aberdare range is ca. 200 km east of the type locality, Kericho, while Mount Elgon is around 150 km north. It is reasonable to assume that a single species is represented in this area.

Known distribution. Kenya.

Oligoneuriopsis jessicae Agnew, 1973

Figure 7

Oligoneuriopsis jessicae Agnew, 1973: 116, fig. 1A, B (nymph).

Material examined. ESWATINI (former SWAZILAND) • 14N; Malolotja stream, Nkomati River system; 26.1167°S, 31.1144°E; alt. 1227 m a.s.l.; 3 Mar. 2003; R. Bills leg.; AMGS; GEN 1733E • 7N; Jubukweni stream near Mbuluzi, Nkomati River system; 26.2028°S, 31.1944°E; alt. 1044 m a.s.l.; 29 Mar. 2003; R. Bills leg.; AMGS; GEN 1734B • 4N; Lubuyane stream near Mnyokane, Nkomati River system; 26.1572°S, 31.2081°E; alt. 1435 m a.s.l.; 4 Apr. 2003; R. Bills leg.; AMGS; GEN 1738B.

Comments. Agnew (1973) examined material from the National Institute for Water Research (NIWR), Pretoria, and stated it would be housed in the Transvaal Museum (now known as Ditsong Museum). However, Agnew (pers. comm., 1983) indicated that when he moved from the university where he had been based, the technicians in his former laboratory discarded all of the material that he had left in his office, including all of the *Oligoneuriidae* material he had examined. Examination of mayfly material in Ditsong Museum (February 2019), and discussions with the late Curator Dr Martin Kruger[†] (pers. comm., 22 February 2019) confirmed that this material was not in this museum. As no material has since been collected from or near to the type locality (Queen River, 35 km from Barberton, 25.8200°S, 30.8100°E), no neotype has been designated.

Male and female imagos. Unknown.



Figure 7. *Oligoneuriopsis jessicae* **A** whole nymph, dorsal view **B** lateral profile, showing dorsal abdominal tubercles. Scale bar: 5 mm (**A**).

Nymph. Lengths. Body up to 20 mm and 22 mm in male and female nymphs respectively; cerci (and caudal filament) up to 14 mm (4.5 mm) and 15.8 mm (6.9 mm) in male and female nymphs respectively. General colouration pale to hazelnut brown, with small, paired paler spots in the middle of each tergum of mature nymphs in some individuals; head pale to dark brown, without markings, darker between eyes, becoming paler brown towards distal margin of head (Fig. 7A). Ventrally, head chestnut brown, gills at base of maxillae forming a pale cream coloured “beard” ventrally at base of head. Pro- and mesonotum dark brown, with pale brown marking on mesonotum, forming a distinct M-shape in mature nymphs. Legs light brown, femoro-tibial articulation darker; setae of forelegs light brown, same colour as the legs. Femur and tibia of foreleg shorter than those of mid or hind leg; in all cases, femora longer than tibiae. Coxal-femoral articulation of mid and hind legs with dark brown stripe ventrally. Setae on the outer margin of mid and hind femora well developed, tapering off slightly in length towards the apex, scattered spatulate setae over entire surface but more concentrated along margins; mid and hind tibiae and tarsi with strong fringe of fine, even setae along the outer margin. Distal end of tibiae of mid legs with three stout spines on inner side.

Abdominal tergites darker than sternites, no distinctive markings except for dorsal paired paler brown spots on each side of the midline of the tergites in mature specimens; sharply pointed dorsal tubercles present on tergites I–VII, gradually decreasing in size posteriorly (Fig. 7A); sternites uniform pale brown, with no markings. Dense patch of posteriorly orientated setae ventromedially on abdominal segments II–V, much reduced patch on segment VI. Gills II–VII almost subequal in size, gill I smaller. On all gills except for gill I, fibrillae slightly shorter than lamella length. Lamella of gill

I less than half the length of the fibrillar portion. Lamellae II–VII with long and thin setae on their distal inner margin. Posterolateral spines of the abdomen increasing in size posteriorly. Cerci and caudal filament uniformly medium brown.

Whole nymph (dorsal aspect) and gills as illustrated by Agnew (1980) and Fig. 7A. Lateral view of anterior of nymph (Fig. 7B), shows dorsal abdominal spines in profile.

Affinities. Nymphs of *O. jessicae* mainly differ from those of *O. lawrencei* by the presence of sharply pointed dorsal tubercles on tergites I–VII. The dorsal setae along the hind femur are long in *O. lawrencei*, *O. dobbsi* and *O. elisabethae*, extending to the apex of the femur, while in *O. jessicae* the setae are shorter and taper off, not reaching the apex. Gills in *O. jessicae* are shorter than the half length of the corresponding tergite, as in *O. elisabethae*, while in *O. lawrencei*, the gills reach approximately half length of the corresponding tergite, even longer in *O. dobbsi*. Adult material is needed for comparison with other species.

Habitat preference. Moss-covered stones in current. Nymphs mature in April (autumn).

Known distribution. Eswatini; South Africa: Mpumalanga near Barberton.

Oligoneuriopsis elisabethae Agnew, 1973

Figure 8

Oligoneuriopsis elisabethae Agnew, 1973: 118, fig. 1C (nymph).

Material examined. LESOTHO • 4N; Tsoelikana River; 29.9200°S, 29.0925°E; alt. 2247 m a.s.l.; 21 Jan. 1986; K. Meyer; AMGS; LES 38U • SOUTH AFRICA • 4N; KwaZulu-Natal, Umkomozana River, Sani Pass; 29.5842°S, 29.2883°E; alt. 2870 m a.s.l.; 14 Jan. 2011; T.A. Bellingan; AMGS; GEN 1978C.

Comments. As with *O. jessicae*, the material examined by Agnew has been lost. This includes VAL 606G Klip River, Vrede-Volksrust Rd. Bridge 1959/01/14 27.35806°S, 29.35000°E, Free State Province, and VAL 1061B, VAL 1062A. Klein Vaal R., at Goe-dehoop Farm 1960/03/22 26.8194°S, 30.1333°E, Mpumalanga Province, F.M. Chutter leg. As the material examined is from a different catchment to the type material, no neotype has been designated.

Male and female imago. Unknown.

Nymph. Lengths. Body up to 16.5 mm (Agnew 1973), sex-based size differences of nymphs not recorded as none of the available material is fully mature. Cerci up to 8.1 mm, caudal filament 3.3 mm. General colouration light brown (Fig. 8A). Head (Fig. 8A) light brown, with darker brown marking between bases of antennae and ocelli and a grey-brown maculation between antennae; carina on frons slightly developed. Ventrally, head a uniform light brown colour; gills at base of maxillae forming a “beard” ventrally at base of head, much paler in colour relative to head capsule (Fig. 8B). Pro and mesonotum pale brown, with darker maculae laterally. Legs light brown, femoro-tibial articulation with a blackish spot. Femur and tibia of foreleg shorter than those of

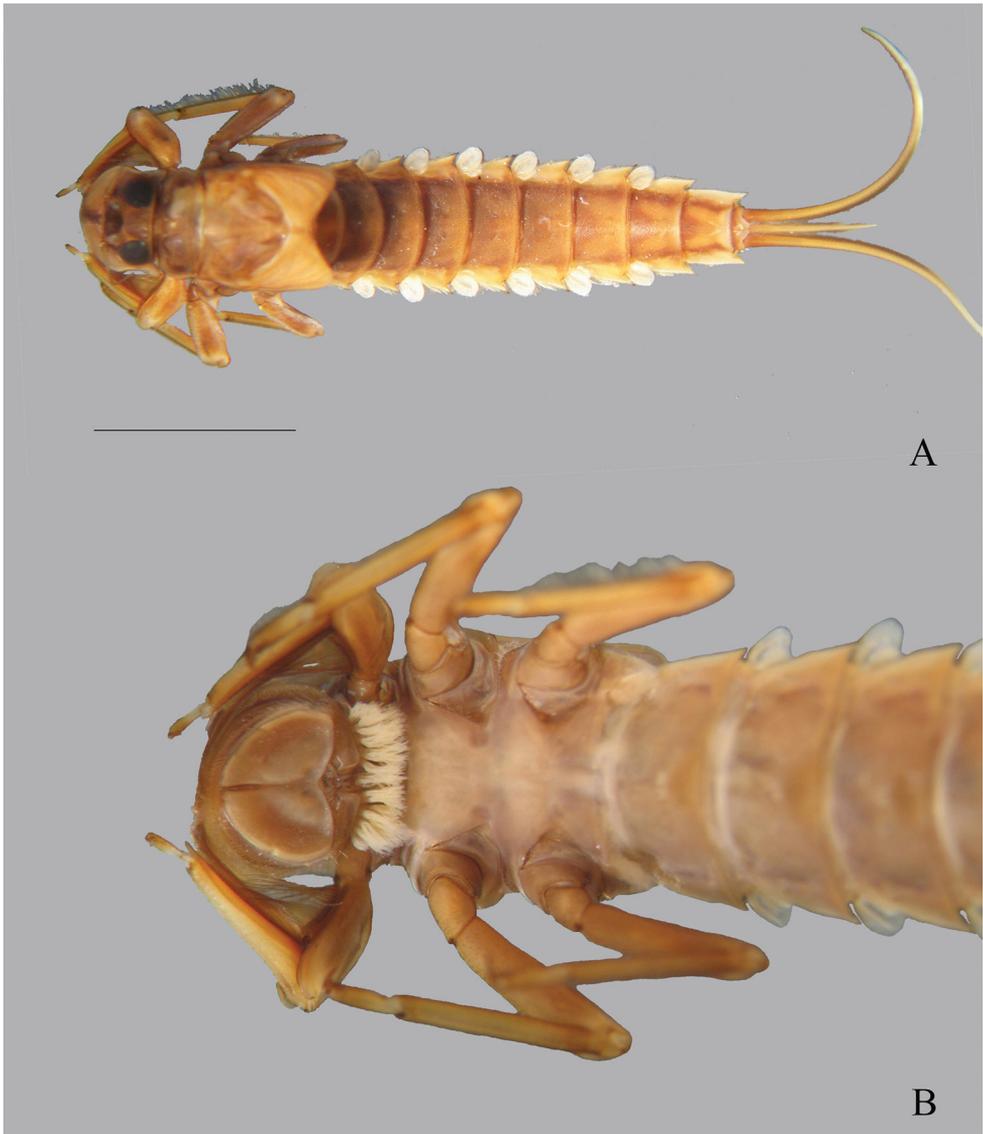


Figure 8. *Oligoneuriopsis elisabethae* **A** whole nymph (immature), dorsal view **B** dorsal view of head. Scale bar: 5 mm (**A**).

mid or hind leg; femora and tibiae of mid and hind legs of approximately equal length. Setae on the outer margin of mid and hind femora well developed, evenly distributed along length of margin; mid and hind tibiae and tarsi with well-developed fringe of even setae along the outer margin. Middle and hind legs with basal area of coxae and trochanter, and entire surface of femora covered with small, scattered, dark brown spine-like setae, extending also along ventral margins of tibiae and tarsi, as well as interspersed amongst the fringe of setae along the dorsal margins.

Abdominal tergites uniformly pale brown, no distinctive patterns except for paired pale cream-coloured markings forming a V-shaped pattern on last three abdominal segments in some specimens (Fig. 8A). Sternites uniform pale brown, with no distinctive markings (Fig. 8B). Dense patch of posteriorly orientated setae ventromedially moderately developed on abdominal sternite II, well-developed on sternites III–V, absent from other segments. Gills paler in colour than abdomen, gill I ventrally orientated, lamella less than one third the length of the fibrillar portion, gills II–VII with rounded lamella, filaments shorter than the corresponding lamella, lamella shorter than half the length of the corresponding segment. Lamellae II–VII with long and thin setae on their distal inner margin. Posterolateral spines of the abdomen of similar size on each segment, each with the tip a darker brown. Cerci uniformly medium brown, caudal filament paler brown towards apex, less than half the length of cerci.

Affinities. Nymphs of *O. elisabethae* are less flattened compared to *O. lawrencei*, and have the shortest gills relative to the abdominal tergite length of the three South African species, at ca. 1/3 of the length of the tergites. Head similar in shape to *O. jessicae* but notably different to *O. lawrencei*, which is widest medially. Lateral abdominal spines are well developed; dorsal abdominal spines as seen in *O. jessicae* are absent in *O. elisabethae*. Nymphs of *O. elisabethae* also differ from those of *O. skhounate*, *O. dobbsi*, *O. orontensis* and *O. villosus* by the reduction of the caudal filament.

Habitat preference. Found in cobble, pebble and gravel substrate in swift current.

Known distribution. Lesotho; South Africa: Free State and Mpumalanga Provinces.

Oligoneuriopsis skhounate Dakki & Giudicelli, 1980

Figures 9A, 10A, 11A–C, 12A, 14E, 15E

Oligoneuriopsis skhounate Dakki & Giudicelli, 1980: 19, figs 14–29 (male imago, nymph).

Material examined. ALGERIA • 1N (sequenced GBIFCH00763571); Oued Cherf, Medjez Amar; 36.44306°N, 7.31083°E; alt. 205 m a.s.l.; 3 Oct. 2018; B. Samraoui leg.; MZL • 2N (sequenced GBIFCH00763569–GBIFCH00763570); Oued Cherf, Dbabcha; 36.2166°N, 7.3181°E; alt. 610 m a.s.l.; 18 Oct. 2019; B. Samraoui leg.; MZL • MOROCCO • 3N; Marrakech, Palmeraie, Oued Tensift; 31.6619°N, 7.9694°W (estimated); alt. 443 m a.s.l.; 27 Apr. 1960; J. Aubert leg.; MZL • SPAIN • 4N; Pyrénées, Barbastro (Huesca), Rio Vero; 42.2400°N, 0.1278°W (estimated); alt. 1000 m a.s.l.; 24 Jun. 1956; H. Bertrand leg.; MZL • 1N; Sierra Morena, Venta de Cardenas; 38.4006°N, 3.5119°W (estimated); alt. 650 m a.s.l.; 2 Aug. 1960; J. Aubert leg.; MZL • 3N; Valladolid, Cabezon, Rio Pisuerga; 41.4650°N, 5.2297°W (estimated); alt. 650 m a.s.l.; 17 Aug. 1988; D. Studemann & P. Landolt leg.; MZL • 41N; Malaga, Cortes de la Frontera, Rio Guadairo; 36.5483°N, 5.3675°W (estimated); alt. 250 m a.s.l.; 21 Aug. 1988; D. Studemann & P. Landolt leg.; MZL • 4N, 10s♀, 17♂; same locality; 15 Sep. 1988; P. Landolt leg.; MZL • TUNISIA • 1N; Bizerte, Mateur, Oued

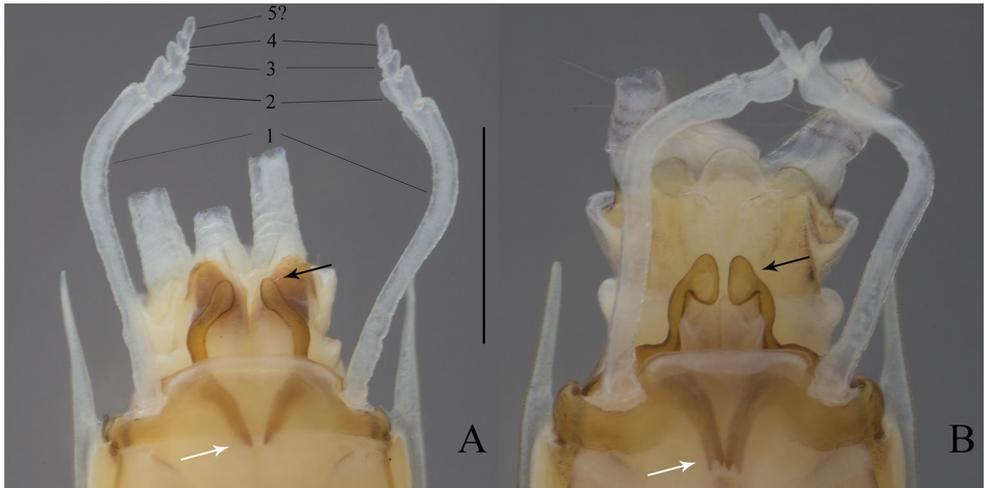


Figure 9. Genitalia of *Oligoneuriopsis* in ventral view **A** *O. skhounate* **B** *O. orontensis*. Black arrows: Apex of the lateral longitudinal lobe of penis. White arrows: Proximal process of penis. Scale bar: 1 mm.

Joumine, upstream Lake Ichkeul dam; 36.9628°N, 9.5244°E; alt. 105 m a.s.l.; 20 Nov. 2004; S. Zrelli leg.; LBE • 22N, 1s♀; same locality; 26 Jun. 2005; S. Zrelli leg.; LBE • 20N, 2s♀; same locality; 18 Jul. 2005; S. Zrelli leg.; LBE • 40N; same locality; 28 Aug. 2005; S. Zrelli leg.; LBE • 40N; same locality; 6 Sep. 2005; S. Zrelli leg.; 39 LBE, 1 MZL • 40N; same locality; 24 Oct. 2005; S. Zrelli leg.; LBE • 35N; same locality; 26 Jun. 2006; S. Zrelli leg.; 24 LBE, 11 MZL • 11N; same locality; 31 Jul. 2006; S. Zrelli leg.; LBE • 2N, 1s♀; same locality; 6 Apr. 2009; S. Zrelli leg.; MZL • 2N; same locality; 17 May 2010; S. Zrelli leg.; LBE • 5N; Tabarka, Oued Bouterfes; 36.953°N, 8.9125°E; alt. 100 m a.s.l.; 4 Jan. 2005; S. Zrelli leg.; LBE • 6N; Jandouba, Fernana, Oued Ellil; 36.7203°N, 8.7339°E; alt. 237 m a.s.l.; 28 Jul. 2005; S. Zrelli leg.; LBE • 2N; same locality; 12 Sep. 2005; S. Zrelli leg.; LBE • 4N; same locality; 29 Jul. 2006; S. Zrelli leg.; LBE • 9N; same locality; 30 Aug. 2006; S. Zrelli leg.; LBE • 10N; same locality; 26 Jun. 2008; S. Zrelli leg.; LBE • 7N; Oued Ghezala; 36.6431°N, 8.6986°E; alt. 229 m a.s.l.; 30 Aug. 2006; S. Zrelli; LBE • 5N; same locality; 21 Nov. 2009; S. Zrelli; LBE.

Male imago. Adequately described and illustrated by Dakki and Giudicelli (1980). The most important character is on the genitalia where the shape of the lateral longitudinal lobe of the penis ends in a rounded sclerite a little bit larger than the lateral lobe (Fig. 9A).

Nymph (Fig. 10A). Adequately described and illustrated by Dakki and Giudicelli (1980), with the following complements: setae on the outer margin of hind femora well developed and reaching the apex; outer margin of hind tibiae covered by a dense row of long and thin setae; lamella of gill I minute, fibrillae much longer than the lamella length; setae on distal inner margin of gills II–VII short and thin; posteromedially sternal patch of long setae present on segments (II)III–V, most developed on segments III–IV.

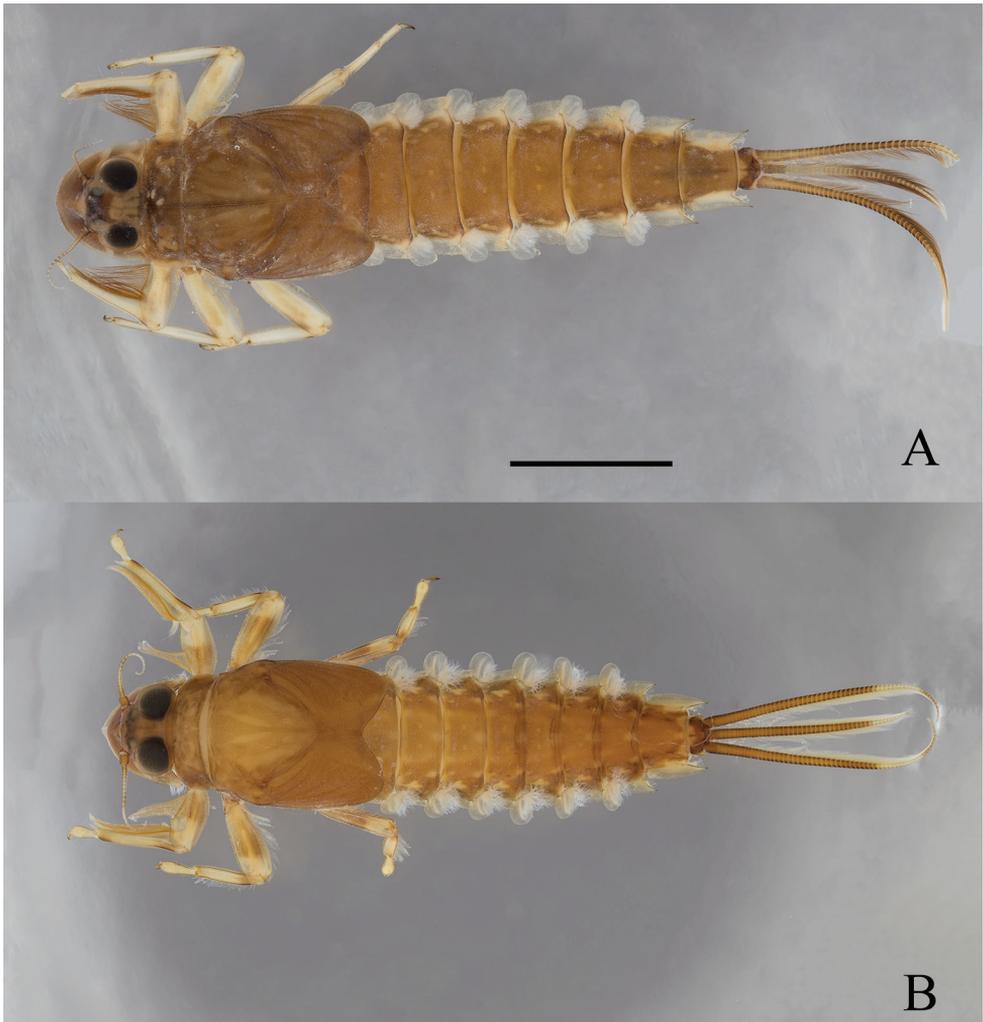


Figure 10. Habitus of *Oligoneuriopsis* nymphs in dorsal view **A** *O. skhounate* **B** *O. orontensis*. Scale bar: 5 mm.

Eggs. General shape rhomboid, ca. 280 μm long and 250 μm wide, (Fig. 11A) chorionic surface rather smooth, micropyle tagenoform, smooth, sperm guide well apparent (Fig. 11B), KCT's rather regularly arranged, ca. 10 μm of diameter, formed by coil-thread ending in a leaf-like and flat structure (Fig. 11C).

Affinities. At the male adult stage, *O. skhounate* is distinguished from *O. lawrencei* by the presence of crossveins in the proximal part of the subcostal area, and from *O. lawrencei* and *O. dobbsi* by the shape of the apex of the lateral longitudinal lobe of penis sclerite which is only slightly enlarged. In the nymphal stage, *O. skhounate* differs from *O. jessicae* by the absence of abdominal carina and from *O. lawrencei* and *O. elisabethae* by the setation of the dorsal margin of hind femora with much longer setae; it also differs from *O. dobbsi* by the size of gill I lamella, much longer in the latter.

The ecology of the nymph in North Africa is described by Bouhala et al. (2020).

Known distribution. Algeria, Morocco, Spain, Tunisia.

***Oligoneuriopsis orontensis* (Koch, 1980), comb. nov.**

Figures 9B, 10B, 11D–F, 12B, 14F

Oligoneuriella orontensis Koch, 1980: 154, figs 1–4 (nymph).

Material examined. ISRAEL • 1N; Jordan River, Ateret Fortress; 33.0032°N, 35.6286°E; alt. 63 m a.s.l.; 7 May 1990; H. Glassmann & M. Sartori leg.; MZL • 1N; same locality; 7 May 1991; H. Glassmann & M. Sartori leg.; MZL • 5N; same locality; 8 Dec. 2014; Z. Yanai leg.; SMNH • 15N, 3♂; same locality; 29 Oct. 2015; Z. Yanai & Y. Brenner leg.; SMNH • 14N; same locality; 16 May 2016; Z. Yanai & A. Charvet leg.; SMNH • 8N; same locality; 2 Jun. 2016; Y. Hershkovitz & T. Eshcoly leg.; SMNH • 3N (1N – GBIFCH00759464 – sequenced); same locality; 11 Mar. 2017; Z. Yanai & J.-L. Gattolliat leg.; MZL, SMNH • 4N (2N – GBIF-CH00664952, GBIFCH006759463 – sequenced); same locality; 27 Mar. 2019; Z. Yanai leg.; MZL, SMNH • 2N; Dan Stream, st. 6; 33.1320°N, 35.3845°E; alt. 120 m a.s.l.; 10 May 1990; A. Reuven & M. Sartori leg.; MZL • 4N; Senir (Hasbani) Stream, upstream Ma'ayan Barukh Bridge; 33.2253°N, 35.6152°E; alt. 103 m a.s.l.; 10 May 1990; A. Reuven & M. Sartori leg.; MZL • 1N; same locality; 10 May 1991; A. Reuven & M. Sartori leg.; MZL • 2N; Senir (Hasbani) Stream, downstream 'En Barukh; 33.2308°N, 35.6209°E; alt. 119 m a.s.l.; 10 May 1990; A. Reuven & M. Sartori leg.; MZL • 2s♀, 1♂; same locality; 25 Jul. 1990; A. Reuven leg.; MZL • 4s♀, 3♂; same locality; 10 May 1991; A. Reuven & M. Sartori leg.; MZL • 4N; Hermon (Banyas) Stream, Kefar Szold; 33.1301°N, 35.3832°E; alt. 100 m a.s.l.; 8 May 1991; A. Reuven & M. Sartori leg.; MZL • 1N; Jordan River, haDodot Bridge; 32.9318°N, 35.6226°E; alt. -161 m a.s.l.; 29 Jul. 2015; Y. Hershkovitz & T. Eshcoly leg.; SMNH • 2N; Jordan River, Park haYarden; 32.9091°N, 35.6235°E; alt. -203 m a.s.l.; 2 Jun. 2016; Y. Hershkovitz & T. Eshcoly leg.; SMNH • 2s♂; Senir (Hasbani) Stream, Beth Hillel; 33.1989°N, 35.6108°E; alt. 82 m a.s.l.; 6 Aug. 2020; Z. Yanai & A. Hershko leg.; SMNH.

Male imago. Lengths. Body: up to 18 mm; forewing: up to 17 mm; cerci: up to 15 mm; caudal filament: up to 13 mm.

Vertex light brown, frontoclypeus yellowish, compound eyes greyish black, base of ocelli black, ocelli whitish, antennae with pedicel light brown and flagellum medium brown.

Pronotum light brown, washed with grey. Pterothorax light brown, with a large mesonotal suture yellowish. Forelegs with outer margin of femora, tibiae and tarsi medium brown, inner margin yellowish; mid- and hindlegs yellowish, with distinct inner brown maculae on the femoro-tibial articulation; wings, when folded, light brown, almost whitish when unfolded.

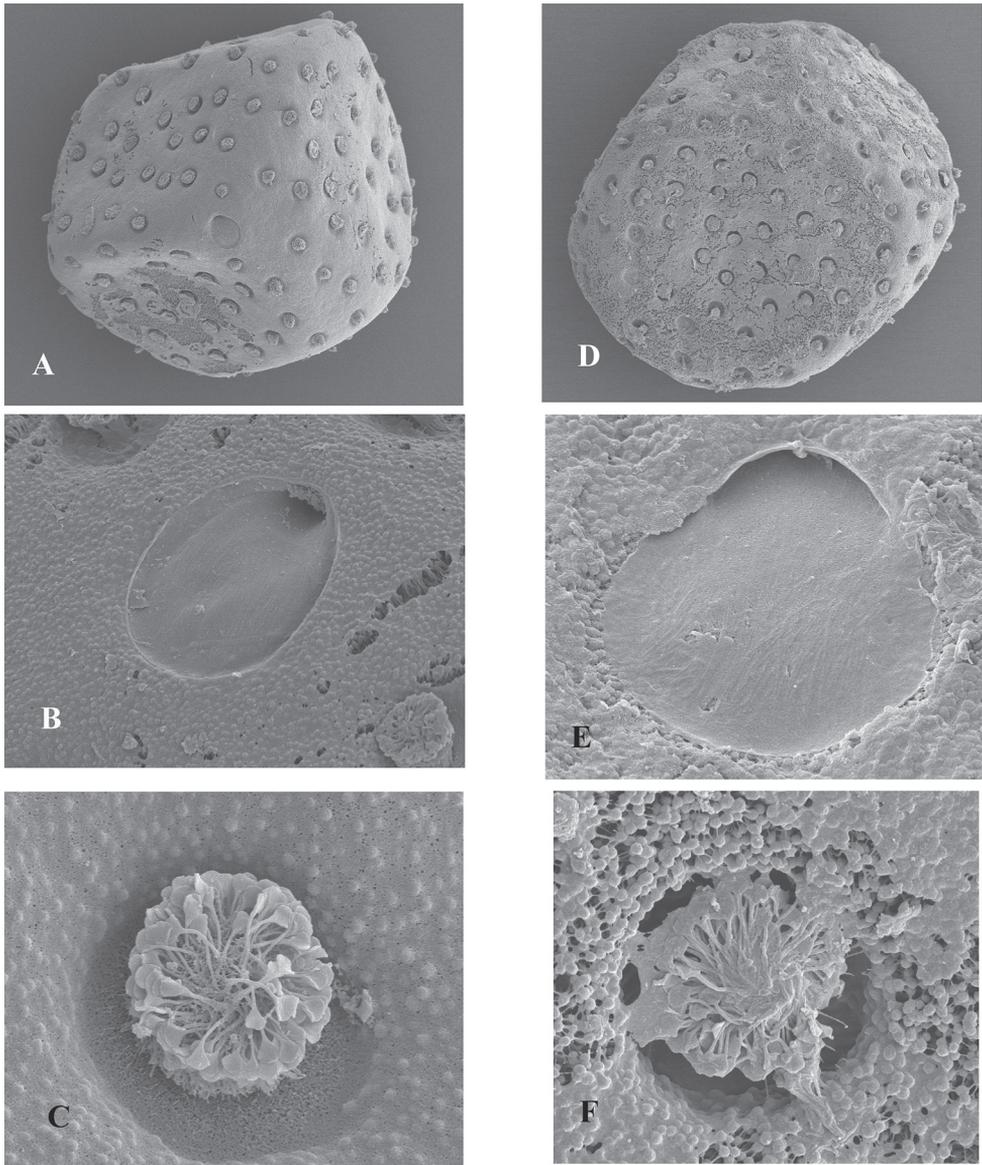


Figure 11. *O. skhounate* (A–C) and *O. orontensis* (D–F) A, D shape of the egg B, E micropyle C, F KCT's.

Abdominal segments uniformly yellowish, without distinct patterns, except sides of tergite IX, tergite X and sternite IX light brown; gonostyli and cerci whitish.

Forelegs functional, tibiae and tarsi of middle and hind legs weakly sclerotized and non-functional. Tarsal claws blunt. Forewing typical of the genus, with 5 groups of veins: Sc+RA, RSa+iRS, RSp+MA1, MA2+MP1, and a forked MP2+CuA – CuP vein. Subcostal field with numerous transversal veins, those issued from RA not reaching iRS in the distal forth of the length, those between iRS and MA1 only present in the proximal half.



Figure 12. Hind legs of *Oligoneuriopsis* in dorsal view, showing femoral and tibial setation **A** *O. skbou-nate* **B** *O. orontensis*. Scale bar: 1 mm.

Gonostyli 4-segmented, the basal one ca. $4 \times$ the length of segments 2 to 4 combined; a fifth segment can sometimes be present (Fig. 9B). Penis lobes with characteristic sclerotized proximal process ending in a bifid projection; lateral longitudinal lobe ending in a distinct club-shaped sclerite more than $2 \times$ larger than the lateral lobe. Cerci with whorls of long setae at each junction.

Female subimago. Lengths. Body: up to 23 mm; forewing: up to 21 mm; cerci: up to 7 mm; caudal filament: up to 5.5 mm.

Colouration as in the male, except antennal pedicel entirely medium brown, forefemora with outer margin sepia, tibiae and tarsi of all legs atrophied, twisted on forelegs; tarsal claws reduced to a single pointed and unsclerotized filament. Cerci light to medium brown. Posterior margin of sternite IX deeply concave and rounded.

Nymph (Fig. 10B). First described by Koch (1980) sub nomen *Oligoneuriella orontensis*.

Lengths. Body up to 14 mm and 19 mm in male and female nymphs respectively; cerci (and caudal filament) up to 7 mm (5 mm) and 9 mm (7 mm) in male and female nymphs respectively.

General colouration light to medium brown, always lighter in male nymphs. Head medium brown, yellowish between the compound eyes. Pronotum medium brown, with yellowish areas sublaterally. Pterothorax medium brown, with yellowish maculae very characteristic (see Koch 1980, fig. 4). Legs light brown, femora medium brown in the proximal half, lighter distally; femoro-tibial articulation darker, especially notable in mature nymphs. Setae on the outer margin of hind femora well developed, but not reaching the apex (if reaching it, then much smaller than the proximal ones) (Fig. 14F). Outer margin of hind tibiae without a row of long and thin setae (Fig. 12B). Abdominal tergites uniformly medium brown, each with a pair of light spots in the middle and one or two light maculae laterally; sternites with four spots on a transverse line and two



Figure 13. Genitalia of *Oligoneuriopsis* sp. from Iran in ventral view. Scale bar: 1 mm.

elongated maculae anteriorly, altogether six spots creating sort of a circle (most notable in mature nymphs). Gills II–VII almost subequal in size, gill I smaller, ventral. On all gills, fibrillae shorter or subequal to lamella length. Lamellae II–VII with long and thin setae on their distal inner margin. Posteromedially sternal patch of long and thin setae present on segments II–IV(V). Posterolateral spines of the abdomen increasing in size posteriorly. Cerci uniformly dark brown, sometimes medium brown with a wide median dark band or with apex light brown.

Eggs. General shape rhomboid, ca. 300 μm long and 270 μm wide, chorionic surface finely granulated (Fig. 11D), micropyle tageniform, smooth, sperm guide well apparent (Fig. 11E), KCT's rather regularly arranged, ca. 10 μm of diameter, formed by coil-thread ending in a leaf-like and flat structure (Fig. 11F).

Affinities. In male imagos, *O. orontensis* differ from all other known species by the apex of the lateral sclerite of the penis, which is greatly enlarged, even more than in *O.*

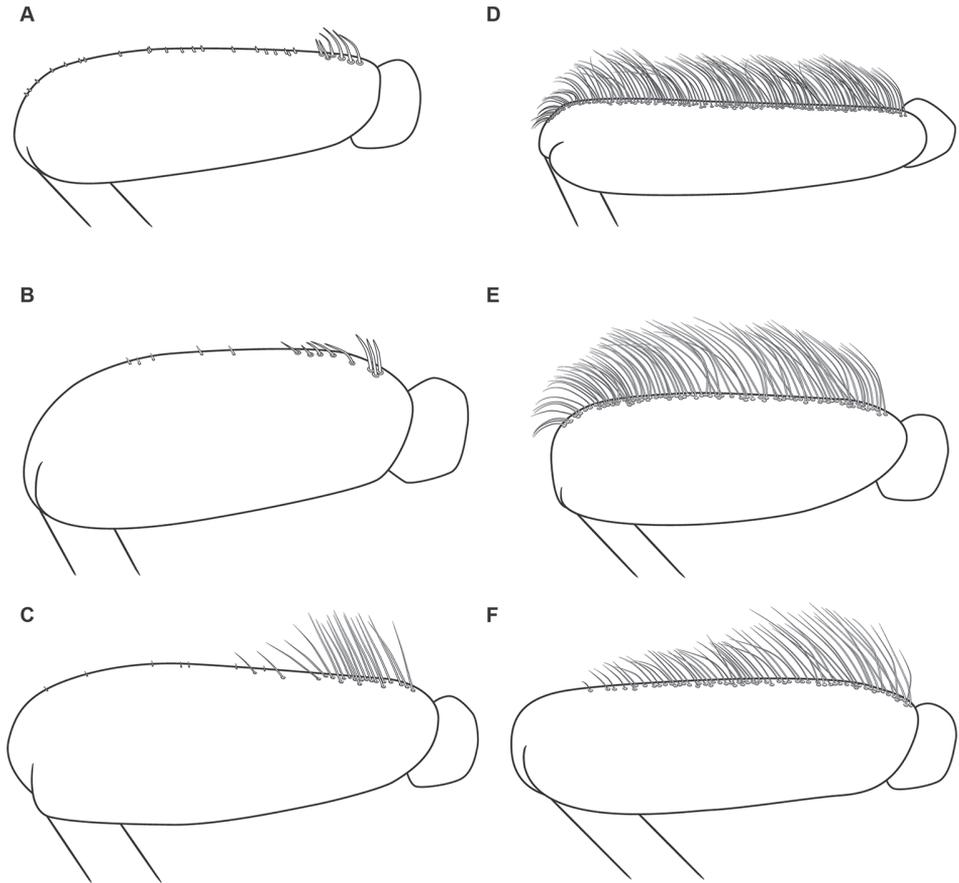


Figure 14. Hind femora of representative *Oligoneuriella* (A–C) and *Oligoneuriopsis* (D–F) species **A** *Oligoneuriella rhenana* **B** *Oligoneuriella pallida* **C** *Oligoneuriella skoura* **D** *Oligoneuriopsis lawrencei* **E** *Oligoneuriopsis skhounate* **F** *Oligoneuriopsis orontensis*.

dobbsi, and the proximal process of the penis which is bifid. Nymphs are characterized by a row of setae on the outer margin of hind femora which does not reach the apex compared to other species studied, except *O. jessicae* to some extent, and differs to all other known species by the absence of a row of setae on hind tibiae.

Habitat preference. In Israel, found in well-oxygenized streams with high water discharge and current velocity (Yanai et al. 2020). The scarcity of these habitats in the Levant may be the reason for its recent decline in Israel, and perhaps in other countries, although no recent data are available.

Known distribution. Israel, Lebanon, Syria, Turkey.

Comments. Al-Zubaidi and Al-Kayatt (1986) reported on “*Oligoneuriopsis* sp.” from northern Iraq (later cited by Abdul-Rassoul 2020). These individuals may belong either to *O. orontensis* or *O. villosus*, thus pushing distribution slightly eastwards or westwards, respectively. While both alternatives are possible in terms of ecology and geography, it is very likely that these specimens were misidentified and in fact belong

to the genus *Oligoneuriella*, the only oligoneuriid reported by the authors in the following year (Al-Zubaidi et al. 1987). Until further information is available, we ignore this report from Iraq.

***Oligoneuriopsis villosus* Bojková, Godunko & Staniczek, 2019**

Figure 15F

Oligoneuriopsis villosus Bojková, Godunko & Staniczek, 2019 in Sroka et al. 2019: 113, figs 5–8 (nymph).

Material examined. None.

Male and female imagos. Unknown.

Nymph and eggs. As described by Sroka et. al. (2019)

Affinities. The nymph of *O. villosus* can be easily differentiated from all other known species by the row of long and thin setae on the outer margin of hind femora reaching the apex, a row of long and thin setae on the outer margin of hind tibiae, posterolateral projections of abdominal segments diverging from body axis, the absence of posteromedian projections on abdominal terga, and posteromedian setae on sternites III–IV very long and dense.

Known distribution. Iran.

Comment. See comment under *O. orontensis* regarding reports from Iraq.

***Oligoneuriopsis* sp.**

Figure 13

Material examined. IRAN • 2♂; Ghilan, Sefid-rud River, close to Rudbar [Roodbar]; app. 36.817°N, 49.433°E; alt. 180 m a.s.l.; 4 Aug. 1972; W. Heinz coll. & V. Puthz leg. to MZL.

Male imago. Gonostyli 4-segmented, the basal one a little bit less than 4 × the length of segments 2 to 4 combined. Segment 2 not enlarged distally, more than 2 × longer than wide. Penis lobes with sclerotized proximal process ending in a single projection; lateral longitudinal lobe ending in a distinct club-shaped sclerite ca. 2 × larger than the lateral lobe (Fig. 13). Cerci with whorls of long setae at each junction.

Affinities. These two specimens are in bad state (legs missing, wings broken), but nevertheless we think it is important to report this finding. The shape of the genitalia is different from those of the previous species, somewhat intermediary between those of *O. skhounate* and *O. orontensis*. Second segment of gonostyli is also much slender than in the two previous species. These specimens could be the alate stages of *O. villosus*, but they are reported from a far distant place (ca 700 km); hence they could also belong to a new, undescribed species. Due to these uncertainties and the lack of proper material, we prefer mentioning it without naming it.

Known distribution. Iran.

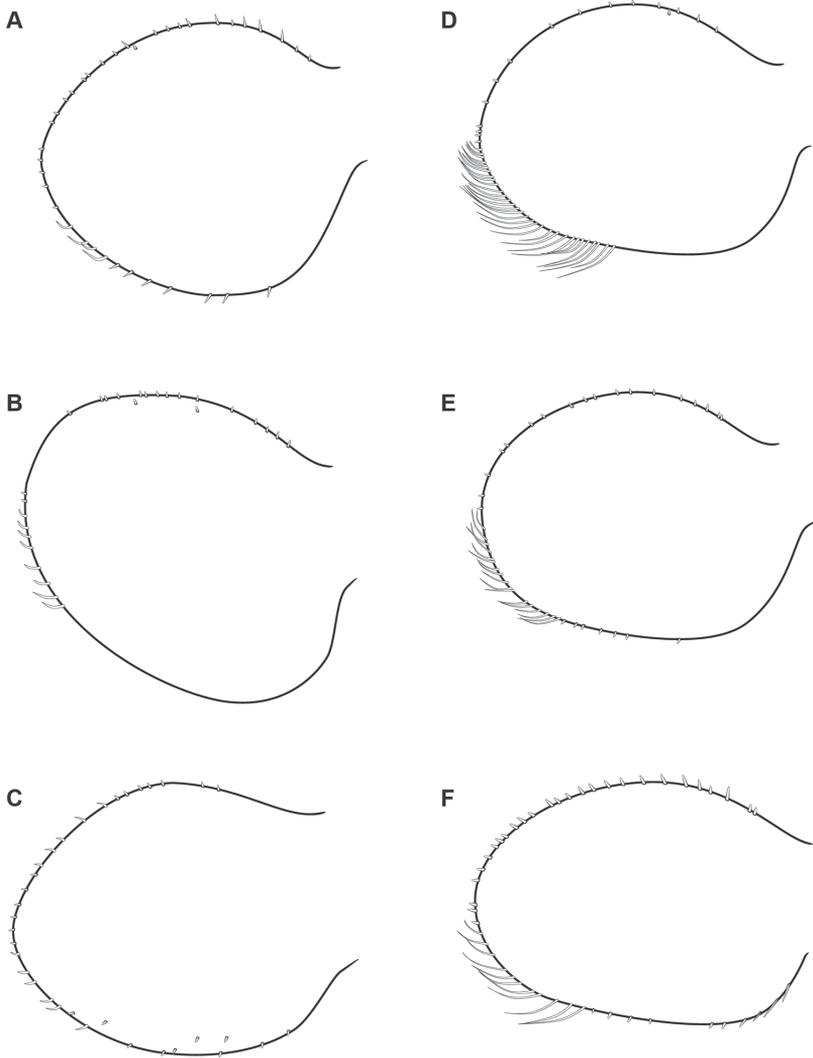


Figure 15. Outline of gill plate III of representative *Oligoneuriella* (A–C) and *Oligoneuriopsis* (D–F) species **A** *Oligoneuriella rhenana* **B** *Oligoneuriella pallida* **C** *Oligoneuriella skoura* **D** *Oligoneuriopsis lawrencei* **E** *Oligoneuriopsis skhounate* **F** *Oligoneuriopsis villosus*.

Revised diagnosis of *Oligoneuriopsis* Crass, 1947

Adult. Male gonostyli four (sometimes five)-segmented, apex of the lateral longitudinal lobe of penis club-shaped, proximal process pointed, simple or bifid; three caudal filaments, five convex longitudinal veins in forewing.

Nymph. Head usually without a carina, though a slight carina can be seen in some species (not pronounced as in *Elassoneuria*). Hind femora with a row of dense setae

reaching at least the middle of the dorsal margin. Abdominal gills shorter than or equal to length of associated abdominal segment; apically rounded and bordered by thin setae. Postero-medial patch of very long and thin setae, well developed on sternites II to IV, sometimes to sternite V or VI.

Generic affinities. As already mentioned by former authors, *Oligoneuriopsis* closely resembles *Oligoneuriella* from which it can be separated by the following characters:

In *Oligoneuriopsis* male imago, the shape of the proximal process of the penes sclerite is apically pointed or bifid, but saddle-shaped in *Oligoneuriella*, the apex of the lateral longitudinal lobe of the penis is club-shaped, enlarged at apex, but not enlarged in *Oligoneuriella*, and gonostyli are composed of four(five) segments against three (four, rarely five) in *Oligoneuriella* (including the proximal, long segment). Contrary to what Demoulin (1952) stated, there are no differences in the tarsal claw shape between the genera; they are always paired and blunt in the investigated species, as well as in all Oligoneuriidae (Kluge 2004).

In the nymphal stage, *Oligoneuriopsis* species possess a row of long and thin setae on the outer margin of the hind femora, whereas this row is absent or reduced to the proximal half of margin in *Oligoneuriella* (Fig. 14). Lamellae of gills III–V at least possess thin setae on their inner margin, whereas these setae are stout or even clavate in *Oligoneuriella* (Fig. 15). Finally, postero-medial patch of long and thin setae on proximal sternites is present in *Oligoneuriopsis*, whereas these setae are short and stout in *Oligoneuriella*.

Key to known nymphs of *Oligoneuriopsis*

- 1 Abdominal tergites I–VII with median tubercles (Fig. 7B) ***O. jessicae***
- Abdominal tergites without median tubercles **2**
- 2 Outer margin of hind tibiae without a row of long and thin setae (Fig. 12B)....
..... ***O. orontensis***
- Outer margin of hind tibiae with a row of long and thin setae (e.g., Fig. 12A) **3**
- 3 Caudal filament much shorter than cerci (Fig. 8A); frons slightly carinate (Fig. 8B) ***O. elisabethae***
- Caudal filament subequal in length to cerci (e.g., Fig. 10A); frons may or may not be slightly carinate **4**
- 4 Frons slightly carinate (Fig. 4B); lamella of gill I minute, abdominal marking as in Fig. 4A, although this can be less distinct ***O. lawrencei***
- Head without carina, lamella of gill I small but well visible; abdomen without contrasted markings (e.g., Fig. 10A) **5**
- 5 Posterolateral projections of the abdomen clearly divergent from body axis (Sroka et al. 2019, fig. 7A–B) ***O. villosus***
- Posterolateral projections of the abdomen parallel to body axis (e.g., Fig. 5B) **6**

- 6 Fibrillae of gill I as long as lamella; outer margin of hind tibiae with a row of rather short setae (Fig. 5A); body coloration dark brown (Fig. 6A) *O. dobbsi*
- Fibrillae of gill I much longer than lamella; outer margin of hind tibiae with a row of long setae (Fig. 12A); body coloration light brown (Fig. 10A)
 *O. skhounate*

Discussion

Sroka et al. (2019) proposed the presence of a row of long and thin setae on the outer margin of hind tibiae as a diagnostic character to distinguish nymphs of *Oligoneuriopsis* versus *Oligoneuriella*. Although this character is present in almost all species, it is surprisingly lacking in *O. orontensis* (Fig. 14); thus its generic value is limited.

Egg structure of *O. skhounate* and *O. orontensis* is similar to the one of *O. villosus*, as well as of *Oligoneuriella* species, but somewhat different to the one of *Oligoneuriopsis* sp. illustrated by Pescador and Peters (2007). KCT arrangement is not as dense as presented. Due to the great homogeneity in the chorionic arrangement of *Oligoneuriopsis*/*Oligoneuriella* eggs, we can suspect that the one represented by Pescador and Peters (2007) may belong to another oligoneuriid genus. In fact, it resembles much more the structure found in the Oriental oligoneuriid genus *Chromarcys* (Koss and Edmunds 1974, fig. 72).

Based on these morphological characters, a new generic concept is proposed for *Oligoneuriopsis*, meeting the need for understanding the phylogenetic position and historical development of the genus. We trust that future study of the genus (e.g., description of new species, or of unknown life stages of known species) will confirm our findings.

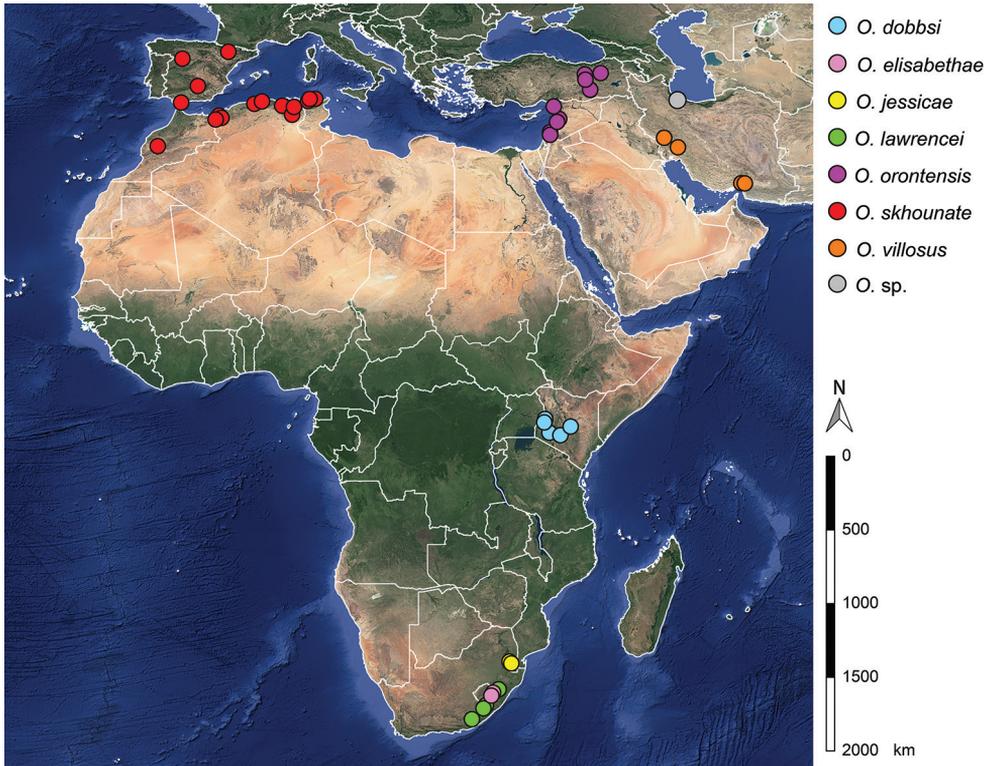
The COI tree (Fig. 1) obtained with novel and published Oligoneuriidae sequences clearly indicates that *O. orontensis* presents more genetic affinities with *Oligoneuriopsis* than with any other oligoneuriid taxon. This is also in accordance with the morphological analysis by Massariol et al. (2019, fig. 5) who recovered “*Oligoneuriella orontensis*” as the sister species of *Oligoneuriopsis skhounate*.

To date, seven species of *Oligoneuriopsis* are known. Four of them are described at nymphal and imaginal stages (*O. dobbsi*, *O. lawrencei*, *O. skhounate*, *O. orontensis*), and three only at the nymphal stage (*O. jessicae*, *O. elisabethae*, *O. villosus*). An additional, undescribed, species from Iran is mentioned here (Table 2). It is very likely that more African species will be found in future, for example, in the highlands of Zimbabwe, Mozambique, Malawi, and Tanzania, where very little research has yet been carried out.

We reconstructed the known distribution of the genus based on the material examined in this publication, and information from other sources (Eaton 1912; Koch 1980, 1988; Salur et al. 2016; Sroka et al. 2019; Bouhala et al. 2020; Yanai et al. 2020). The genus seems to be distributed in a narrow line up continental (Fig. 16), following the escarpment associated with the Great Rift Valley (Jordan Rift, Red Sea Rift, and East African Rift). In the north, this distribution branches eastwards (Iran) and westwards (North Africa and Iberian Peninsula).

Table 2. Available data and knowledge gaps for the species of *Oligoneuriopsis*.

Species	Imago described	Nymph described	COI sequenced
<i>O. dobbsi</i>	+	+	+
<i>O. elisabethae</i>		+	
<i>O. jessicae</i>		+	
<i>O. lawrencei</i>	+	+	+
<i>O. orontensis</i>	+	+	+
<i>O. skhounate</i>	+	+	+
<i>O. villosus</i>		+	+
<i>Oligoneuriopsis</i> sp. (Iran)	+		

**Figure 16.** Map with indication of all records of the eight *Oligoneuriopsis* species.

With a cluster of species recorded in South Africa, the distribution suggests a once more widely spread group that has since been restricted to cooler climate at higher altitude as Gondwanaland moved north into warmer climatic zones, isolating populations of this originally cool-adapted lineage to produce the species we see today. Massariol et al. (2019), in a global study encompassing all Oligoneuriidae genera, deduced through molecular phylogeny dating that the family had a Gondwana origin, some 150 Mya, with the lineage producing *Oligoneuriopsis* and *Oligoneuriella*, the Oligoneuriellini, arising during the early Eocene, around 50 Mya. This fits the geological history of the Great

Rift Valley: Roberts et al. (2012) indicate that uplift of the shoulders of the rift valley began during the early Eocene, some 45–40 Mya, which ties in with the estimate date of the diverging of the lineage. A possibly South African origin for *Oligoneuriopsis* can be hypothesized, with subsequent colonisation northwards through Kenya (*O. dobbsi*), then North Africa and the Iberian Peninsula (*O. skhounate*) or the Levant with an extension to the Middle East (*O. orontensis*, *O. villosus*). *Oligoneuriopsis lawrencei* being a sister-species to all other species, followed by *O. dobbsi* as a sister-species to the remaining ones (Fig. 1), support this hypothesis. A dated molecular phylogeny, involving some more conservative markers such as nuclear ones, for all *Oligoneuriopsis* species would be helpful to elucidate this. However, this is currently not possible as fresh material for most taxa is scarce.

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The authors have declared that no competing interests exist.

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Description of the new species *Coptera tonic* (Hymenoptera, Diapriidae), a pupal parasitoid of *Rhagoletis juniperina* Marcovitch (Diptera, Tephritidae), and revised partial keys to Nearctic *Coptera* Say

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Abstract

A new species of the parasitic wasp *Coptera* Say was previously distinguished from other species via correspondence between ecological (host) differences and DNA barcodes. A description and figures for *Coptera tonic* **sp. nov.**, along with revisions to existing keys that allow it to be distinguished from other Nearctic species without the aid of molecular characters, is provided in this work.

Keywords

Coptera cingulatae, *Coptera pomonellae*, Eastern red cedar, Psilini

Introduction

Coptera Say, 1836 is a genus of parasitic wasps in family Diapriidae with a near-world-wide distribution. Muesebeck (1980) recognized 29 Nearctic *Coptera* species, representing a fraction of the more than 150 species estimated to occupy this region (Mason and Garcia 2002). *Coptera* females search for hosts, usually Dipteran pupae buried shallowly in soils, by keying in on chemical signals left by the host before pupation (Granchetti et al. 2012). Females use their heads to dig up loose soil around buried pu-

pae, then drag the host to the surface and oviposit (Buckingham 1975). Hosts, when known, are primarily true fruit flies (Diptera: Tephritidae), and parasitism rates of pupae can exceed 10% (Cameron and Morrison 1977; Maier 1981), such that species in this genus have been explored as potential biological control organisms (Silvestri 1914; Hagen et al. 1980; Sivinski et al. 1998; Baeza-Larios et al. 2002; Guillén et al. 2002; Cancino et al. 2019). Further, though some *Coptera* species may be flexible in their host associations (e.g., *Coptera occidentalis* Muesebeck, 1980; Kazimírová and Vallo 1992), others are apparently limited to single fly host species and have garnered interest from evolutionary biologists interested in co-speciation (Hamerlinck et al. 2016).

Coptera species delimitation and ascertainment of host breadths have both proved challenging. These issues can be especially problematic when identifying potential bio-control species if apparent oligiphagous species are actually complexes of cryptic specialists (e.g., *Coptera silvestrii* (Kieffer, 1913); Yoder and Wharton 2002). *Coptera* are common in Malaise and pan trap collections, but they have little color variation and limited sculpturing on their sclerites, offering few landmarks for species-level identification. The last revision of the Nearctic *Coptera* (Muesebeck 1980) relied heavily on relative lengths and shapes of body parts, such that some species, as described, have much intraspecific variation. Host associations are perhaps even more challenging, as they are known only from studies where parasitized pupae have been extracted from soils – an uncommon collection technique except when specifically targeting pupal parasitoids (e.g., Buckingham 1975; Maier 1981; Hamerlinck et al. 2016).

Collections of *Coptera* from known hosts in soil, coupled with DNA barcoding (sequencing of short segments of the mitochondrial COI gene), have proved useful in distinguishing among species, determining host associations, and identifying possible new species. Collections and barcoding of *Coptera* differentiated a new species associated with the juniper maggot fly, *Rhagoletis juniperina* Marcovitch, 1915 from the apparently cryptic species *Coptera pomonellae* Muesebeck, 1980 that attacks *Rhagoletis pomonella* (Walsh, 1867) and *Rhagoletis suavis* (Loew, 1862) flies in hawthorns and walnuts, respectively (Forbes et al. 2012; Hamerlinck et al. 2016). The argument that this was a new species and not just *C. pomonellae* wasps with two divergent COI haplotype families was bolstered by ecological data: while pan trap collections underneath juniper and hawthorns included both *C. pomonellae* and the new species, *C. pomonellae* was only reared from pupae of *R. pomonella*, and the new species was only reared from *R. juniperina* pupae (Forbes et al. 2012).

Though the combination of ecological and genetic data is useful for identification of reproductively isolated groups for taxonomically-challenging groups like *Coptera* (and see: Smith et al. 2005, 2008; Condon et al. 2014; Shashank et al. 2014; Ward et al. 2020), genetic evidence of apparently cryptic species is also an opportunity to determine taxonomically informative, but previously overlooked, morphological characters (Lukhtanov et al. 2016). Further, naming species based only on DNA barcodes is unacceptable (though see Brower 2010) and morphological characters remain the cheapest and most accessible means for most researchers and naturalists to differentiate species. Here, we describe a new species of *Coptera* associated with junipers, which was discov-

ered in Forbes et al. (2012). We also provide an amendment to the existing Nearctic *Coptera* species keys such that other researchers can distinguish this species from other similar species, including *C. pomonellae*, a species with promise for biological control of the apple maggot fly (Cameron and Morrison 1977; Maier 1981). We do not attempt a full revision of the Nearctic *Coptera* at this time because – as this example shows – such an effort would be premature without additional ecological and molecular work.

Materials and methods

Study material

Collections used for study are described in Forbes et al. (2012). As part of that work, *Coptera* DNA was sampled non-destructively, such that most individuals were preserved for morphological study. Samples of the new juniper-associated *Coptera* species and *C. pomonellae* were collected via both soil pupal collections and in yellow pan traps in East Lansing, MI and Iowa City, IA in 2011. Samples of *Coptera cingulatae* Muesebeck, 1980 were collected in yellow pan traps under black cherry trees (host of *Rhagoletis cingulata*) in Rose Lake, MI and Iowa City, IA also in 2011.

Morphological descriptions and photography

We developed a character matrix of all previously described Nearctic *Coptera* based on Muesebeck (1980) and then used a Leica M125 stereomicroscope (Leica Inc., Switzerland) to record morphological characters of males and females identified via DNA barcodes as belonging to the new juniper-associated *Coptera*. Because females of the new species keyed to *Coptera pomonellae* and males of the new species keyed to *Coptera cingulatae* in the Muesebeck (1980) key, we placed particular emphasis on searching for characters that differentiated them from these two species. Terminology in the description of the new species follows Muesebeck (1980).

We used a Hitachi S-3400N (Hitachi High-Tech Corp., Tokyo, Japan) to perform scanning electron microscopy (SEM) of males and females of *C. pomonellae* and the new species. Color photographs of the same two species were photographed using a Canon EOS 60D camera with a Canon MP-E 65 mm macro lens and a Canon Macro Ring Lite MR-14EX (Canon USA, Melville, NY), mounted on a StackShot Automated Focus Stacking Macro Rail (Cognysis Inc., Traverse City, MI). Stacked images were processed using Zerene Stacker (Zerene Systems LLC., Richland, WA) and Adobe Photoshop (Adobe, San Jose, CA, USA). Measurements of relevant body parts (in mm) were made using a Leica M125 stereomicroscope (Leica Inc., Switzerland) and Leica Application Suite v4.13. Holotypes, paratypes of the new species, and additional study specimens of *Coptera pomonellae* and *Coptera cingulatae* were deposited into the collection of the University of Iowa Museum of Natural History (UIMNH; ID#s: SUI:INS:04567 – SUI:INS:04588).

Results

Taxonomy

Coptera Say, 1836

Coptera Say, 1836: 281.

Type-species. *Coptera polita* Say. By monotypy.

Coptera tonic sp. nov.

<http://zoobank.org/92F47ACC-5957-41E6-B297-80BE71905189>

Figures 1–8

Type material. *Holotype:* USA • ♀; Ingham Co., East Lansing, MI; 42.7274, -84.4777; 3 Jul. 2011; Serdar Satar; reared from soil-collected pupa of *Rhagoletis juniperina*; UIMNH ID: SUI:INS:04567.

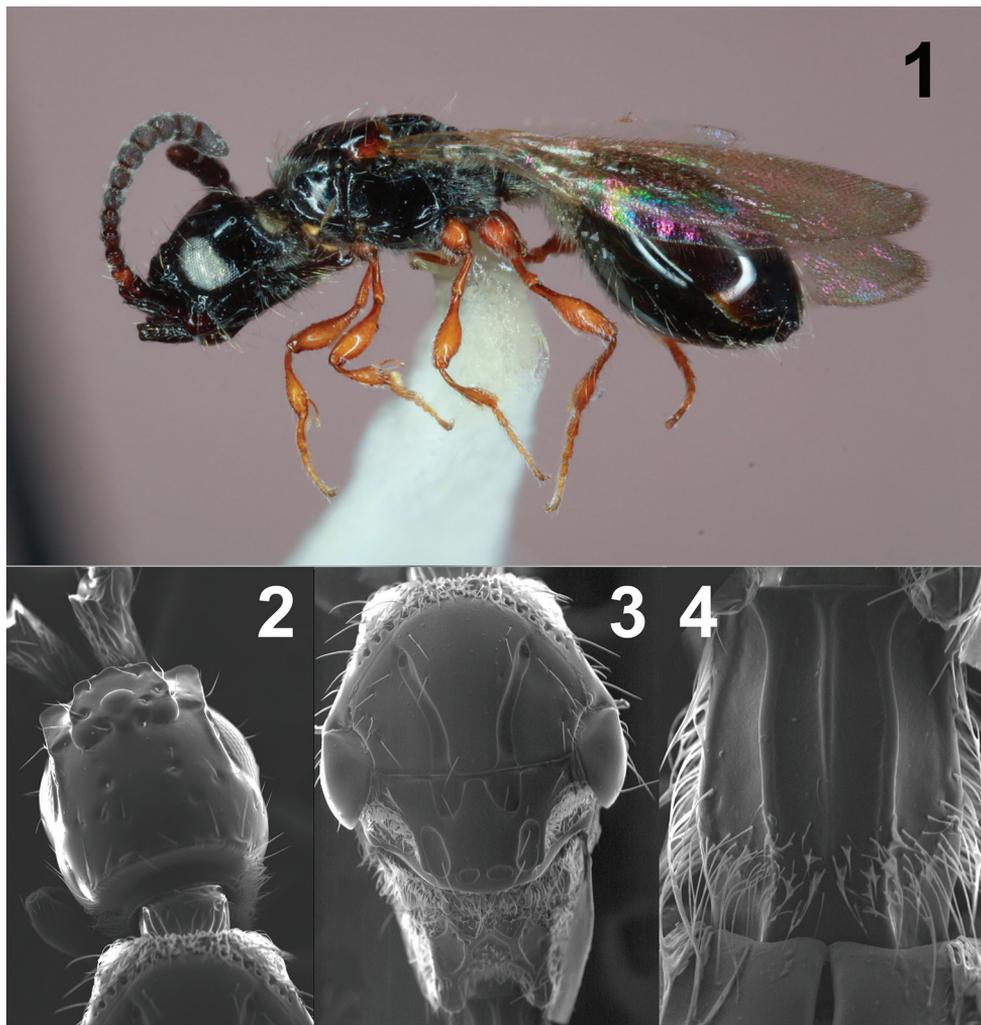
Paratypes: USA • ♀; Ingham Co., East Lansing, MI; 42.7274, -84.4777, 21 Aug. 2011; Serdar Satar; reared from pupa of *R. juniperina*, SUI:INS:04568 • 6♂; ibid; 8–9 Aug. 2011; SUI:INS:04569-04573, 04576 • ♂; ibid; 13 Aug. 2011, yellow pan trap; SUI:INS:04577 • ♀; Johnson Co., Iowa City, IA, 41.6509, -91.5603, 11 Sep. 2011, Andrew Forbes; yellow pan trap; SUI:INS:04574 • ♂; ibid; 10 Sep. 2011; SUI:INS:04565.

Diagnosis. *Coptera tonic* females (Figs 1–4) may be distinguished from female *C. pomonellae* (Figs 9–12) most readily by the distance between the apical punctures on the scutellum. In *C. tonic*, this distance is small, less than 1/2 of the shortest diameter of either puncture (Fig. 3), while in *C. pomonellae* the inter-puncture distance is subequal to the shortest diameter of each puncture (Fig. 11). Male *C. tonic* (Fig. 5) have each apical puncture partially or completely divided into two, such that there are indeterminately four apical punctures (Fig. 7), compared to the two standard punctures in male *C. pomonellae* (Fig. 15). Most flagellomeres of male *C. tonic* are 2–2.5 × longer than wide, with the apical segment 2.7–3.3 × longer than wide (Fig. 6), while the antennal segments of male *C. pomonellae* are shorter, less than 2 × as long as wide (final segment may approach 2.5 × as long as wide; Fig. 14). *Coptera tonic* of both sexes differ from *C. cingulatae* by the color of their antennae, which are dark brown to black in *C. tonic* and yellow to light brown in *C. cingulatae* (at least the first 3–4 flagellomeres; Figs 17, 18).

Description. Female. Length 3.0 – 3.1 mm; wing length 2.1 – 2.2 mm. Holotype length 3.0 mm; Holotype wing length 2.1 mm.

Color. Body (Fig. 1) black; legs, including coxae, honey yellow; antennal scape black; flagellum testaceous; eyes and 3 ocelli yellow to white; wings slightly infuscated.

Head. Head about as long as broad; dorsum of head normally with several large punctures (Fig. 2); distance from lateral ocelli to posterior margin of occiput longer

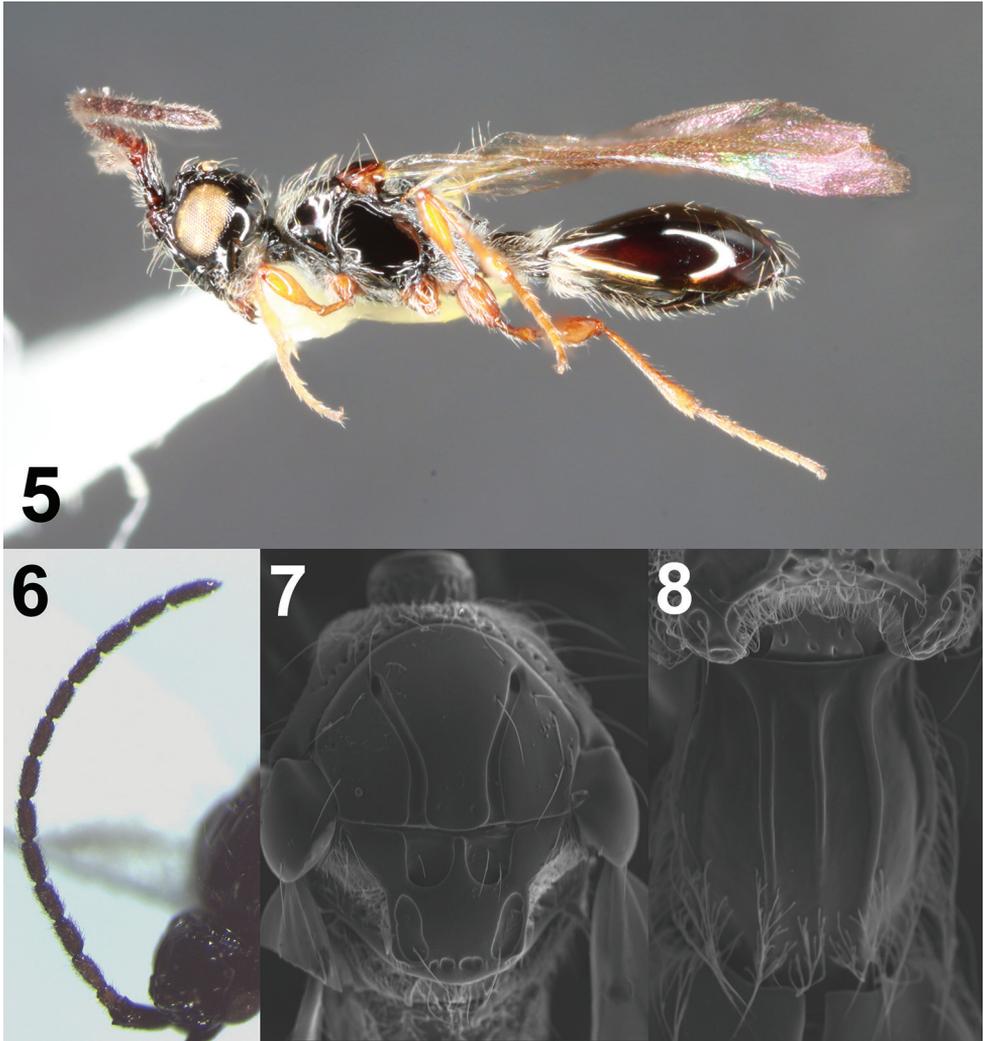


Figures 1–4. Female *Coptera tonic* **1** lateral habitus **2** dorsal view of head **3** dorsal view of mesosoma **4** dorsal view of petiole.

than eyes; temples weakly round, in lateral view nearly as wide as eyes; malar space nearly half as long as eye; antennae strongly clavate and 12-segmented; first flagellomere twice as long as wide; second and third flagellomeres less than twice as long as wide but still longer than wide; all remaining flagellomeres wider than long.

Mesosoma. Pronotum smooth. Notaulices on mesoscutum fine and slightly broadened posteriorly; scutellum weakly convex; paired punctures at apex of scutellum moderately large and separated by less than the shortest diameter of either puncture (Fig. 3); mesopleuron not impressed medially; metapleuron not impressed medially; metapleuron densely hairy.

Metasoma. Petiole of abdomen about 1.5 times as long as wide; petiole with all three dorsal longitudinal carinae strong but median one reduced on some specimens



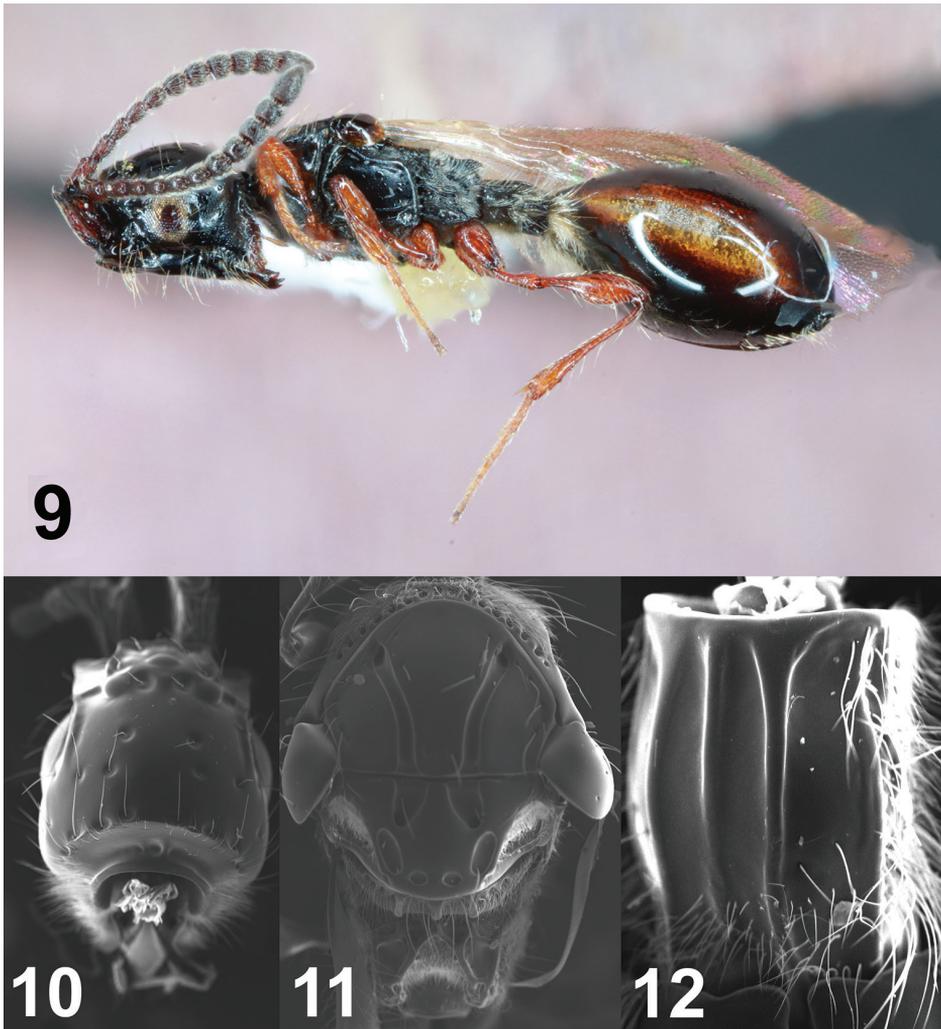
Figures 5–8. Male *Coptera tonic* **5** lateral habitus **6** antenna **7** dorsal view of mesosoma **8** dorsal view of petiole.

(Fig. 4); median sulcus of large tergite not reaching or extending beyond middle of segment; basal lateral sulci not developed.

Male. Length 2.5–3.0 mm; wing length 2.1–2.3 mm.

Color. Body black; legs (including coxae) honey yellow; antennal scape black; flagellum testaceous; eyes and 3 ocelli tan; wings slightly infuscated.

Head. Head wider than long; dorsum of head normally with several large punctures; distances from lateral ocelli to posterior margin of occiput slightly longer than eyes, temples roundly receding, in lateral view slightly narrower than eyes; malar space nearly half as long as eyes; antennae slender with uniform thickness throughout,

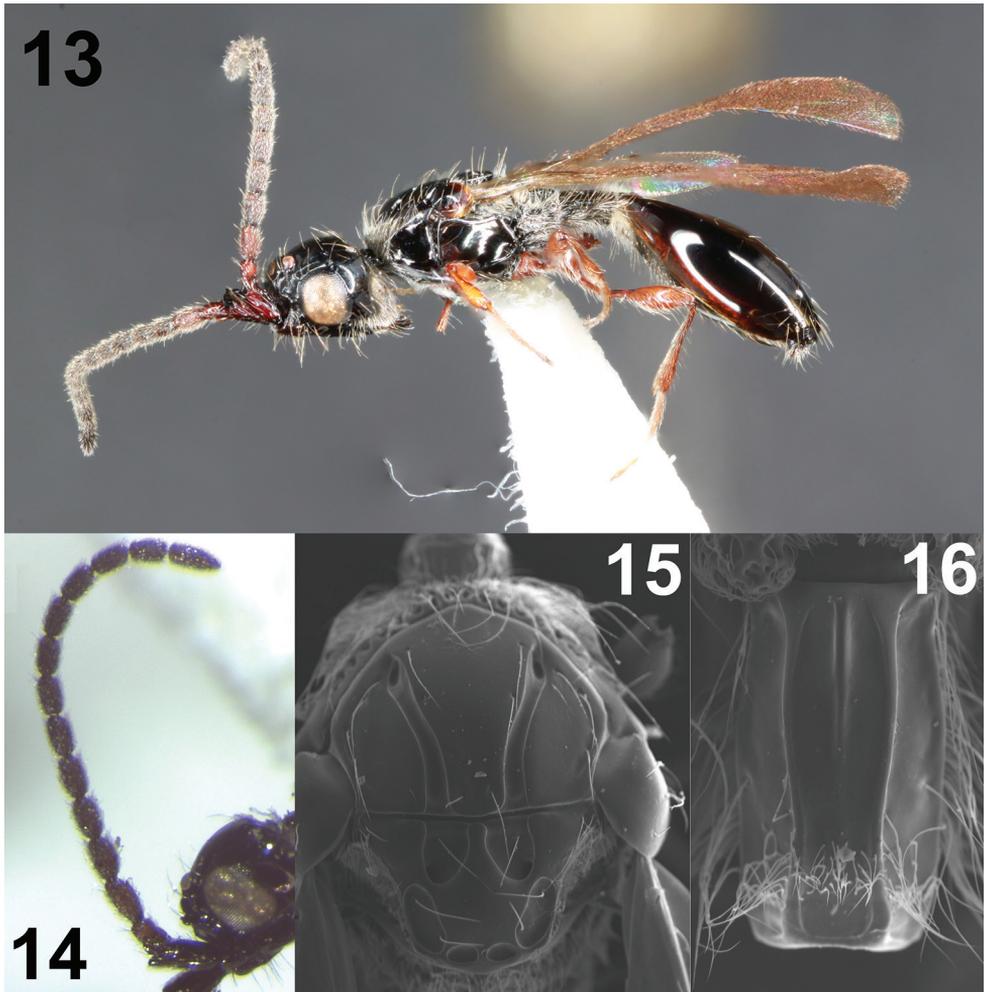


Figures 9–12. Female *Coptera pomonellae* **9** lateral habitus **10** dorsal view of head **11** dorsal view of mesosoma **12** dorsal view of petiole.

14-segmented; all flagellomeres at least twice as long as wide with apical segment about three times as long as wide (Fig. 6).

Mesosoma. Pronotum smooth. Notaulices on mesoscutum fine, slightly broadened posteriorly; scutellum flat; paired punctures at apex of scutellum each subdivided into two smaller punctures (Fig. 7), though sometimes indistinctly; mesopleuron flat, not impressed medially; metapleuron densely hairy.

Metasoma. Petiole about 1.5 times as long as wide; petiole with all three dorsal longitudinal carinae strong and complete; median sulcus of large tergite not reaching the middle of the segment; basal lateral sulci not defined.



Figures 13–16. Male *Coptera pomonellae* **13** lateral habitus **14** antenna **15** dorsal view of mesosoma **16** dorsal view of petiole.

Etymology. The species name is a noun in apposition and refers to tonic water; this parasitic wasp and tonic water are both at their best when in close association with products of *Juniperus* cones.

Ecology. *Coptera tonic* is a parasitoid of the juniper maggot fly, *Rhagoletis juniperina*, a parasite of the female cones of Eastern red cedar (*Juniperus virginiana*) and other members of genus *Juniperus*. Though oviposition has not been directly observed in *C. tonic*, these wasps have only been reared from pupae floated from soils, and not from larvae extracted from juniper cones, suggesting that attack likely occurs during the fly’s pupal stage after it has left the cone. Some pan trap collections of *C. tonic* (e.g., the female paratype labeled “Crab Apple”) were made under or near male *Juniperus*, suggesting that these wasps may use plant volatiles as an indicator for host searching.



Figures 17, 18. *Coptera cingulatae* male and female; lateral habitus.

All known adults were captured or emerged from pupae between late July and early October (Forbes et al. 2012), consistent with the phenology of *R. juniperina* pupation.

Distribution. Existing collections of *C. tonic* are limited to Iowa and Michigan. However, *Rhagoletis juniperina* is distributed across the continental United States and into southern Canada (Bush 1966, Frayer et al. 2015), so a wider distribution for *C. tonic* is possible, if not likely.

Revised partial key to Nearctic *Coptera* species

Muesebeck (1980) supplied keys to both male and female *Coptera* in the Nearctic, such that changes to both keys are necessary. We propose the following revisions to the Muesebeck (1980) key to *Coptera* females:

- 15 Antennae thickening very gradually to apices, none of flagellomeres broader than long; paired punctures at apex of scutellum usually very small and separated by more than diameter of one of them.....***polita* Say**
- Antennae more strongly clavate; preapical segments clearly wider than long (Figs 1, 9); paired punctures at apex of scutellum moderately large and separated by less than the shortest diameter of either puncture (Fig. 3) or distance is subequal to the shortest diameter of each puncture (Fig. 11). **26 (new couplet)**
- 26 Metapleuron rather thinly hairy; paired punctures at apex of scutellum separated by more than ½ of breadth of either puncture (Fig. 11)***pomonellae* Muesebeck**
- Metapleuron densely hairy; paired punctures at apex of scutellum separated by less than ½ of breadth of either puncture (Fig. 3)..... ***tonic*, new species**

We also propose the following revisions to Muesebeck's (1980) key to *Coptera* males:

- 26 Hindcoxae darkened basally; antennae and labrum black or blackish; polished disk of scutellum very small, not nearly twice as wide as unusually large lateral fovea ***tenuicornis* Muesebeck**
- All coxae yellow to orange; antennae and labrum yellow or brown, not black; polished dish of scutellum at least as broad as lateral fovea (Figs 7, 15) **28 (new couplet)**
- 28 Antennae usually largely yellow or yellowish brown, never entirely black, labrum brownish yellow. Paired punctures at apex of scutellum medium sized, widely separated..... ***cingulatae* Muesebeck**
- Flagellomeres of antennae testaceous (Fig. 6); labrum same color. Paired punctures at apex of scutellum narrowly separated and each subdivided into two smaller punctures (Fig. 7), though these sometimes partially confluent..... ***tonic*, new species**

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New records of *Celaenorrhinus pyrha* de Nicéville, 1889 and *C. munda* (Moore, 1884) from China (Lepidoptera, HesperIIDae)

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Abstract

Celaenorrhinus pyrha de Nicéville, 1889, a rare species of HesperIIDae previously known to be distributed from northeastern India to Indochina, is reported from southwestern Yunnan and southwestern Chongqing, China. A 658 bp COI gene sequence of this species is published for the first time. Although Chongqing is obviously isolated from the main distribution range, morphological characters of the specimens from this locality do not indicate a subspecies differentiation. Another rare taxon, *C. munda munda* (Moore, 1884), is also recorded from China for the first time based upon a male specimen from Cuona County in the Tibet Autonomous Region. This is the second specimen of *C. munda* from China, over 100 years after the holotype of *C. munda joka* Evans, 1949. The genitalia of both species are illustrated and described. Some taxonomic notes and a distribution map are provided as well.

Keywords

COI, distribution, fauna, female genitalia, male genitalia, subspecies

Introduction

The genus *Celaenorrhinus* Hübner, [1819] includes over 100 species worldwide (Evans 1949; Yuan et al. 2015). In China, 23 species of the genus have been recorded, most of which are distributed in southern China (Wu and Hsu 2017). In this paper, two rare taxa of the genus are added to the Chinese skipper fauna, viz. *C. pyrrha* de Nicéville, 1889 and *C. munda munda* (Moore, 1884).

Celaenorrhinus pyrrha is known from Sikkim, Bhutan through Assam to Indochina (Evans 1949; Eliot 1959; Osada et al. 1999; Kimura et al. 2011; Ek-Amnury 2012; Nakamura and Wakahara 2012; Monastyrskii and Devyatkin 2015). In the present study, it is reported from southwestern Yunnan and southwestern Chongqing in China.

Celaenorrhinus munda was recorded from China by Evans (1949) as the subspecies *C. munda joka* Evans, 1949, a subspecies based on a single specimen captured from northwestern Yunnan in 1898. No additional material of this species had been found in China since. In the present study, a male specimen of *C. munda munda* is reported from southern Tibet as the easternmost record of this subspecies and the second specimen of *C. munda* from China.

Since the genitalia structures of *Celaenorrhinus pyrrha* and *C. munda* have not been illustrated in detail except for the simple hand drawings by Evans (1949: pl. 16, B.6., fig. 8; pl. 17, B.6. fig. 19), the genitalia of both taxa are illustrated and described herein. A 658 bp COI sequence of *C. pyrrha* is also provided for DNA barcoding and future molecular studies.

Materials and methods

Morphological examination

9♂♂, 7♀♀ of *Celaenorrhinus pyrrha* and 1♂ of *Celaenorrhinus munda munda* were studied. Specimens from China are deposited in Zhengzhou University of Light Industry, and those from Thailand and Vietnam are in the private collections of Mr. Kotaro Saito (Tokyo) and Mr. Yutaka Inayoshi (Chiang Mai). Detailed information for each specimen can be found in the Results under each species.

The terminology of morphology mainly follows those of Evans (1949), Klotz (1970) and Yuan et al. (2015).

The genitalia of both sexes were examined in glycerin and photographed using an Olympus SZX7 stereomicroscope after clearing in a cold 10% NaOH solution. Images were taken with a Canon PowerShot G16 digital camera. Image post-processing was accomplished with Adobe Photoshop CS 8.0.1.

DNA extraction and sequence analysis

One leg of each dried specimen (Table 1) was used to extract genomic DNA following the protocol provided by DNeasy Blood and Tissue Kit (Qiagen, Germany). The partial

Table 1. Specimens used for sequencing and molecular analysis.

Species	Locality	Date	Sex	Voucher ID	Accession number
<i>Celaenorrhinus pyrrha</i>	China, Yunnan, Yingjiang, Jinzhuzhai	27.IV.2016	male	A56	MT997273
	China, Chongqing, Simian Mountain	16.VIII.2016	male	A57	MT997274
	China, Chongqing, Simian Mountain	16.VIII.2016	male	A58	MT997275
	China, Chongqing, Simian Mountain	16.VIII.2016	female	A59	MT997276
	China, Chongqing, Simian Mountain	16.VIII.2016	female	A60	MN443912
<i>Celaenorrhinus macrostictus</i>	Gabon, MDC Lonmin	29.I.2008	male	–	JN277521.1*
<i>Celaenorrhinus dargei</i>	Nigeria, Obudu Plateau	11.IV.2007	–	–	KP149680.1*
<i>Celaenorrhinus patula</i>	China, Tibet, Motuo	VII.2018	–	SCAU He1657	MN199383.1*

* Information downloaded from GenBank.

COI gene of 658 bp was amplified by PCR using the universal primer pairs LepF and LepR, as described by Hajibabaei et al. (2006). The PCR reactions were performed in a 20 µL mixture containing 2 µL genomic DNA, 10 µL 2×Taq mix (Vazyme Biotech, China), and 0.5 µL (10 µM) forward and reverse primers. The amplification cycle was preheating at 94 °C for 3 min, then 30 cycles of 94 °C for 1 min, 50 °C for 45 sec, and 72 °C for 1 min, and a final step of 72 °C for 10 min. The PCR products were directly sequenced by Sunya Biotech, Zhengzhou, China. Multiple sequence alignments were performed in Clustal X 2.0.12 with default parameters (Thompson et al. 1997). The creditability of COI sequences was verified by BLAST and sequences were then submitted to GenBank in NCBI.

COI sequences of *Celaenorrhinus macrostictus*, *C. dargei* and *C. patula* (Table 1) were downloaded from GenBank as outgroups for the phylogenetic analysis. The software MEGA 7.0.26 (Kumar et al. 2016) was used to calculate the Kimura-2-Parameter distance and reconstruct a neighbor-joining (NJ) tree. Node support values were estimated with 1000 bootstraps replicates.

Results

Celaenorrhinus pyrrha de Nicéville, 1889 (new record to China)

Figs 1–3

Celaenorrhinus pyrrha de Nicéville, 1889: 181. Type locality: Bhutan; Evans 1949: 95; Eliot 1959: 383; Osada et al. 1999: 188; Kimura et al. 2011: 33; Ek-Amnury 2012: 798; Nakamura and Wakahara 2012: 57; Monastyrskii and Devyatkin 2015: 72.

Material examined. Material dissected and sequenced: 1♂ 1♀, China, Chongqing, Simian Mountain, 785 m, 16 August 2016, leg. Guoxi Xue [Dissection ID CQ164, CQ165; DNA voucher ID A58, A59]; 1♂, China, Yunnan, Yingjiang, Jinzhuzhai, 27 April 2016, leg. Guoxi Xue [Dissection ID YN25, DNA voucher ID A56]. Material dissected: 1♂ 1♀, China, Chongqing, Simian Mountain, 17 June 2007, 23 September 2007, 500–1,000 m [Dissection ID CQ125, CQ67]; 1♂ 1♀, Thailand, Nan, Doi Phu Kha, 4, 18 October 1991, leg. Inayoshi Yutaka [Dissection ID Th1, Th2]. Material sequenced: 1♂ 1♀, China, Chongqing, Simian Mountain, 785 m,



Figures 1–4. Adults of *Celaenorrhinus pyrrha* and *C. munda munda*. **1–3** *C. pyrrha* **1** male, China, Chongqing, Simian Mountain, 785 m, 16 August 2016, leg. Guoxi Xue [Dissection ID CQ164, DNA voucher ID A58] **2** male, China, Yunnan, Yingjiang, Jinzhuzhai, 27 April 2016, leg. Guoxi Xue [Dissection ID YN25, DNA voucher ID A56] **3** female, China, Chongqing, Simian Mountain, 785 m, 16 August 2016, leg. Guoxi Xue [DNA voucher ID A60] **4** *C. munda munda*, male, China, Tibet, Cuona County, Lebugou, 19 June 2013, leg. Songyun Lang [Dissection ID Tib1] **a** dorsal side **b** ventral side. Scale bars: 1 cm.

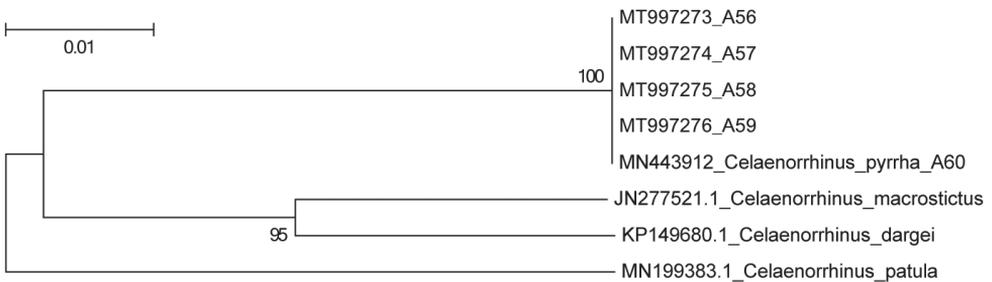


Figure 5. NJ tree based on Kimura-2-Parameter distances for the partial mitochondrial COI sequences of *Celaenorrhinus*, values at nodes represent the bootstrap support (BP) values.

16 August 2016, leg. Guoxi Xue [DNA voucher ID A57, A60]. Other material examined: **CHINA** • 1♀, Chongqing, Simian Mountain, 785 m, 16 August 2016, leg. Guoxi Xue; 2♀♀, Chongqing, Simian Mountain, 17 June 2007, 23 September 2007, 500–1,000 m. **VIETNAM** • 1♂, Lam Dong Province, near Dalat City, Nong Trai, 1,200 m, 16 August 2003, leg. Kotaro Saito; 1♂, Dalat City, Nong Trai, 10 September 2008, leg. T. Saito; 2♂♂, Dalat City, Nong Trai, 1,200 m, 12 April 2009, 24 May 2009, leg. Kotaro Saito.

Molecular analysis. A 658 bp partial COI sequence was successfully generated from each specimen used for DNA extraction (Table 1) via PCR and sequencing. The alignment of all the sequences used to perform a phylogenetic analysis is provided in Suppl. material 1. In the NJ tree (Fig. 5), the five voucher specimens were clustered into one clade, within which the mean K-2-P distance is 0 (Table 2), indicating they belong to the same species.

Description. Male genitalia (Fig. 6). In lateral view, tegumen protruding anteriorly; a small triangular plate at base of uncus; basal half of uncus pointed downwards at approximately 45°, distal half of uncus upturned and then slightly bent downwards,

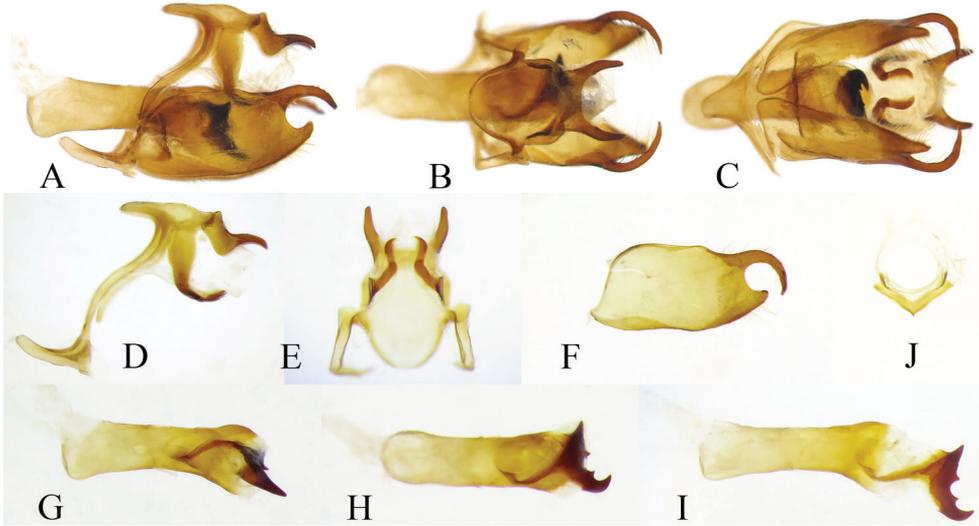


Figure 6. Male genitalia of *Celaenorrhinus pyrrha* from Chongqing [Dissection ID CQ125] **A** genital capsule, lateral view **B** genital capsule, dorsal view **C** genital capsule, ventral view **D** genital capsule, lateral view, valva and aedeagus removed **E** tegumen and gnathos, ventral view **F** right valva, inner surface **G** aedeagus, lateral view **I** aedeagus, with cornuti pulled out **H** aedeagus, dorsal view **J** juxta, posterior view.

Table 2. Uncorrected pairwise genetic distances (Kimura-2-parameter) for the COI sequences of *Celaenorrhinus* species.

	1	2	3	4	5	6	7
1. MT997273_A56							
2. MT997274_A57	0.000						
3. MT997275_A58	0.000	0.000					
4. MT997276_A59	0.000	0.000	0.000				
5. MN443912_A60	0.000	0.000	0.000	0.000			
6. MN199383.1	0.082	0.082	0.082	0.082	0.082		
7. JN277521.1	0.075	0.075	0.075	0.075	0.075	0.089	
8. KP149680.1	0.078	0.078	0.078	0.078	0.078	0.075	0.043

tapered into a sharp point; gnathos sickle-shaped, basal portion wide and elongated; saccus upturned, length about one third of the height of genitalia capsule. In dorsal view, basal half of tegumen semicircular; distal part of uncus widely bifid, tapered and bluntly pointed. In ventral view, left and right parts of gnathos separated. Distal half of valva bifid with a slender, sharply pointed dorsal branch curving downwards in lateral view and inwards in dorsal view, and a short blunt ventral branch. Aedeagus very robust; cornuti anchor shaped, extremely developed and sclerotized. Juxta V-shaped.

Female genitalia (Fig. 7). Papillae anales trapezoidal, covered with short setae. Apophyses posteriors twice as long as papillae anales. Lamella postvaginalis, lamella antevaginalis and antrum merged together, with an elongated plate on each side of ostium. Ostium round, rather large. Ductus bursae short. Bursa copulatrix decorated with longitudinal striae, composed of two big bursae, dorsal side of first one coriaceous, with a longitudinal ridge and a number of transversal grooves.

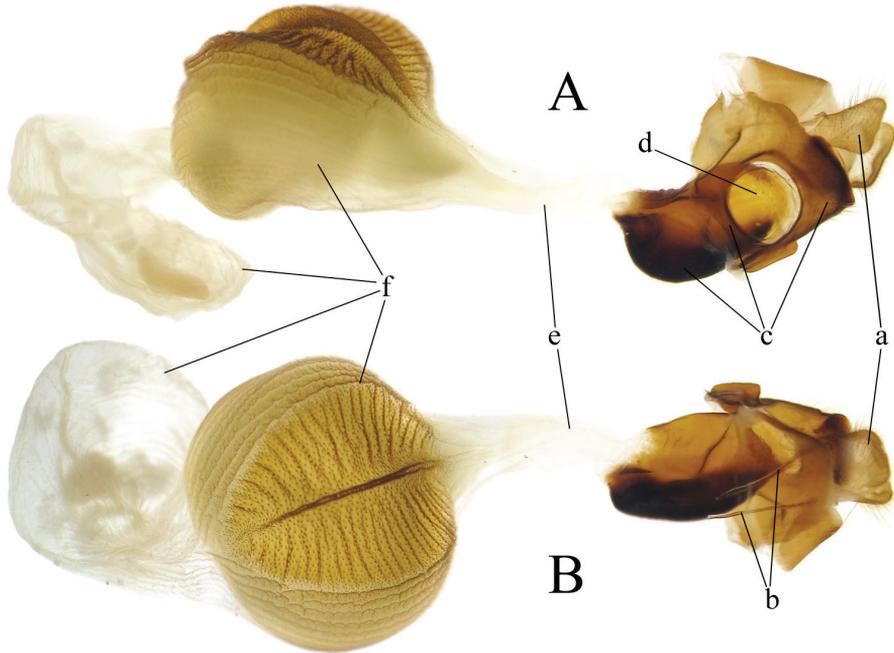


Figure 7. Female genitalia of *Celaenorrhinus pyrrha* from Chongqing [Dissection ID CQ67] **A** ventral view **B** dorsal view **a** papillae anales **b** apophyses posteriors **c** lamella postvaginalis-lamella antevaginalis-antrum complex **d** ostium **e** ductus bursae **f** bursa copulatrix.

Discussion. According to our years of field surveys, and records in the literature (Evans 1949; Eliot 1959; Osada et al. 1999; Kimura et al. 2011; Ek-Amnury 2012; Monastyrskii and Devyatkin 2015), *Celaenorrhinus pyrrha* is a rather rare species throughout its distribution range (Fig. 8). In the present study, it is reported from two localities in China: Yingjiang in southwestern Yunnan, adjacent to northern Myanmar; and the Simian Mountain in southwestern Chongqing. The latter is isolated from the known distribution range of *C. pyrrha* (Evans 1949; Eliot 1959; Osada et al. 1999; Kimura et al. 2011; Ek-Amnury 2012; Monastyrskii and Devyatkin 2015) and the discovery of this species there is totally unexpected. In the present study, some minor external variations are recognized based upon examined specimens, for example: forewing length ranges from 22.4 cm to 26.0 cm; spaces C and Sc on the dorsal side of forewing may be unmarked, or with one or two small dots above the cell spot. However, we consider these as individual variations rather than intersubspecific differences because they exist in specimens from both Chongqing and Indochina. Genitalia characters of specimens from Chongqing, Yunnan, Thailand and Vietnam are compared for both sexes. According to our observations, the specimens from Chongqing cannot be distinguished by morphological characters, and thus do not represent a separate subspecies. Even so, the geographical isolation of Chongqing compared to other localities is worthy of attention, and *C. pyrrha* can possibly be expected from Guizhou, Guangxi and eastern Yunnan.

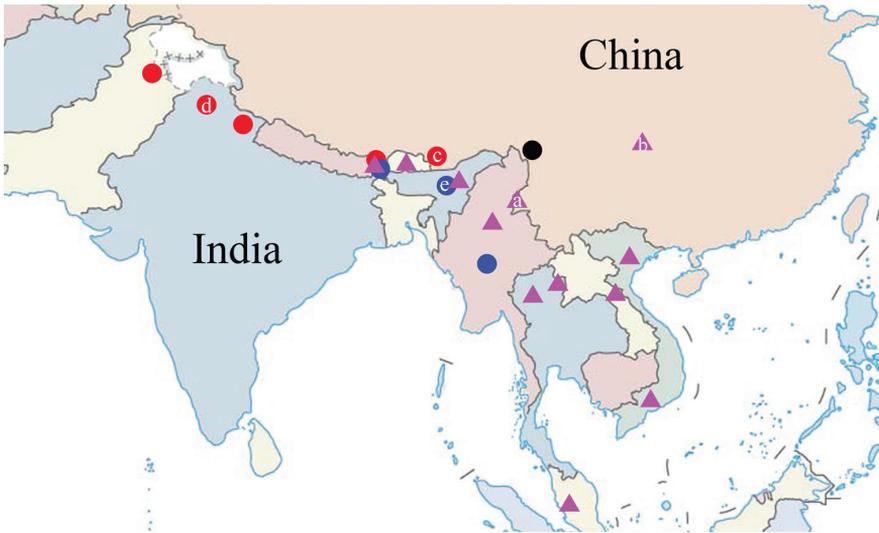


Figure 8. Distribution map of *Celaenorrhinus pyrriba* and *C. munda*. **Triangle** *C. pyrriba* **a** Yingjiang (Yunnan Province) **b** Simian Mountain (Chongqing) **Circle** *C. munda* **Red** *C. munda munda* **Blue** *C. munda maculicornis* **Black** *C. munda joka* **c** Cuona County (Tibet Autonomous Region) **d** Simla (Type locality of ssp. *munda*) **e** Khasi (Type locality of ssp. *maculicornis*).

***Celaenorrhinus munda munda* (Moore, 1884) (new record to China)**

Fig. 4

Plesioneura munda Moore, 1884: 48, type locality: Simla, India.

Celaenorrhinus munda munda; Evans 1949: 100.

Material examined. CHINA • 1♂, Tibet, Cuona County, Lebugou, 19 June 2013, leg. Songyun Lang.

Description. Male genitalia (Fig. 9). In lateral view, tegumen protruding anteriorly; base of uncus with a semi-erect process; basal half of uncus quadrangular, distal half narrow, sloped, sharply pointed; gnathos sickle-shaped, distal end reaching tip of uncus; saccus pointing slightly downwards, length about half the height of genitalia capsule. In dorsal view, basal processes of uncus triangular, central part of uncus constricted, distal half of uncus bifid, forming a pair of horn-shaped blunt points. In ventral view, left and right parts of gnathos separated. Distal portion of valva bifid, divided into a wide ventral branch and a slender dorsal branch, disto-dorsal margin of the latter with a notch; both branches subequal in length and bent inwards. Aedeagus robust, distal half bent downwards; cornuti triangular and sharply pointed, well sclerotized. Juxta ring-shaped.

Discussion. Three subspecies have been described for *Celaenorrhinus munda*, of which *C. munda joka* Evans, 1949 is only known from the type locality, Tsekou, Yunnan, where the holotype was captured in 1898 as the only known exemplar of the species from China (Evans 1949).

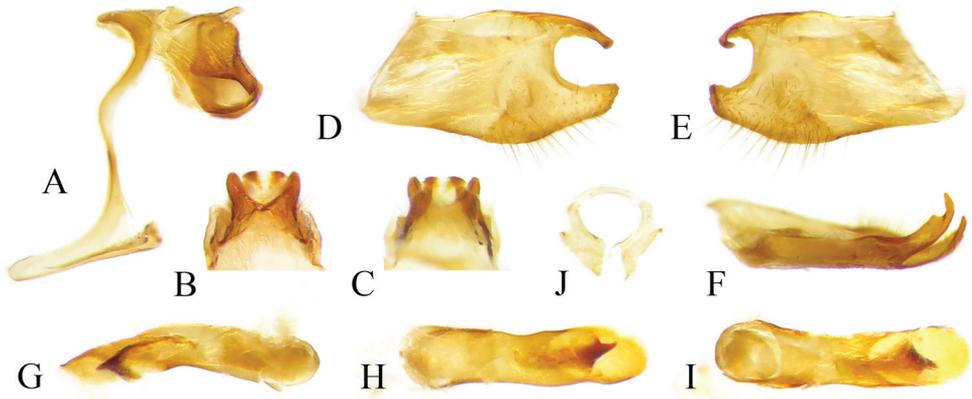


Figure 9. Male genitalia of *Celaenorrhinus munda munda* from Cuona, southern Tibet [Dissection ID Tib1] **A** genitalia capsule, lateral view, valva and aedeagus removed **B** tegumen and gnathos, dorsal view **C** tegumen and gnathos, ventral view **D** left valva, outer surface **E** left valva, inner surface **F** left valva, dorsal view **G** aedeagus, lateral view **H** aedeagus, dorsal view **I** aedeagus, ventral view **J** juxta, posterior view.

Celaenorrhinus munda maculicornis Elwes & Edwards, 1897 is distributed from Sikkim, Assam to Myanmar (Evans 1949). The record of this subspecies from Thailand by Ek-Amnuay (2006: 752, pl. 345, H49b) was considered a misidentification of *C. leucocera* (Koller, 1844) (Ek-Amnuay et al. 2007: 14), but Ek-Amnuay (2012: 800, pl. 369, H47) included it again following Pinratana (1985: 28, 120, pl. 11, fig. 37), although Kimura et al. (2011: 34) had pointed out that Pinratana's record is a misidentification. An earlier record of this subspecies from Thailand was listed by Godfrey (1930: 358) as *C. maculicornis*, but according to Kimura et al. (2011: 34) it is possibly a misidentification of *C. putra* (Moore). Devyatkin and Monastyrskii (1999) reported *C. munda maculicornis* from Vietnam for the first time based upon a female specimen, but in their later works, e.g., Monastyrskii and Devyatkin (2015), this name was not included, possibly because Dr. Devyatkin had realized that the specimen belongs to another species (Monastyrskii pers. comm. 2020). Therefore, we omit Vietnam from the distribution range of ssp. *maculicornis* (Fig. 8), since the identity of the female specimen needs further confirmation.

The nominate subspecies has been recorded from the northwestern Himalayas and Sikkim (Evans 1949). Ek-Amnuay (2006: 752, pl. 345, H49a) reported it from Thailand, but the photos of the specimens, which were provided by the second author of the present paper, actually represent *C. dhanada dhanada* (Inayoshi 2019). This mistake was corrected by Ek-Amnuay (2012: 800). Therefore, we omit Thailand from the distribution of *C. munda* in the present paper. Judging from the diagnostic characters provided by Evans (1949: 100), the specimen examined in this study belongs to *C. munda munda*. This discovery eastwardly expands the distribution range of the subspecies (Fig. 8).

Evans (1949) recorded both ssp. *maculicornis* and ssp. *munda* from Sikkim. Moreover, according to Devyatkin and Monastyrskii (1999), the two taxa are also found in Nepal, and the status of *maculicornis* remains controversial. Although differences in wing patterns of the two subspecies were clearly described by Evans (1949), the genita-

lia structures have not been illustrated and compared except for the simple hand drawing (Evans 1949: pl. 17, B.6. fig. 19). In future studies, comprehensive morphological and molecular analyses are needed to clarify the relationships of these taxa.

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Revision of the South American genus *Gaujonia* Dognin (Noctuidae, Pantheinae) with descriptions of five new genera and twenty-one new species

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Abstract

The endemic Neotropical genus *Gaujonia* Dognin is revised. Morphological characters and a phylogenetic analysis demonstrate paraphyletic relationships among the species. Four different groups are interpreted to represent four different genera. The *G. arbori* group is the only remaining clade in the genus *Gaujonia*, and the other groups have been arranged into three new genera: *Millerana* **gen. nov.**, *Oculicattus* **gen. nov.**, and *Cicadomorpha* **gen. nov.** Additionally, two other genera *Cicadomorphus* **gen. nov.**, and *Gaujoptera* **gen. nov.** were found using morphological and molecular analyses based on some specimens that were misidentified as *Gaujonia* spp. A total of five new genera, three new combinations (*Cicadomorpha vau-nigrum* Hampson, **comb. nov.**, *Oculicattus renifera* Hampson, **comb. nov.**, and *Millerana arborioides* Dognin, **comb. nov.**) and 21 new species (*Cicadomorpha ocelotus* **sp. nov.**, *Cicadomorphus chicharra* **sp. nov.**, *Cicadomorphus chuya* **sp. nov.**, *Cicadomorphus falkasiska* **sp. nov.**, *Cicadomorphus liliana* **sp. nov.**, *Gaujonia bichu* **sp. nov.**, *Gaujonia chiqyaq* **sp. nov.**, *Gaujonia kanakusika* **sp. nov.**, *Gaujonia sourakovi* **sp. nov.**, *Gaujoptera amsa* **sp. nov.**, *Millerana austini* **sp. nov.**, *Millerana cajas* **sp. nov.**, *Millerana cundinamarquensis* **sp. nov.**, *Millerana matthewsae* **sp. nov.**, *Millerana tigrina* **sp. nov.**, *Oculicattus boliviana* **sp. nov.**, *Oculicattus brehmi* **sp. nov.**, *Oculicattus inca* **sp. nov.**, *Oculicattus raizae* **sp. nov.**, *Oculicattus schmidtii* **sp. nov.**, and *Oculicattus uturunku* **sp. nov.**) are established.

Keywords

Andean Mountains, DNA barcoding, host plants, jaguar moths, Neotropics, systematics, taxonomy

Introduction

Gaujonia Dognin (Lepidoptera: Noctuidae: Pantheinae) is a poorly studied Neotropical moth genus with a distribution restricted to the Andean Mountains, from Venezuela to Bolivia. Species of this genus are known as “jaguar moths” together with species from two other genera: *Bathyra* Walker and *Lichnoptera* Herrich-Schäffer. *Gaujonia* was based on the type species of *Gaujonia arbori* Dognin from Loja, Ecuador, which previously included three other species: *G. arbosioides* Dognin, *G. renifera* Hampson, and *G. vau-nigrum* Hampson. Seitz (1919–1944) illustrated the same specimens as Hampson (1913), with the only difference being the color rendition of *G. arbori*. *Gaujonia* was not mentioned again in the literature until the check list of Poole (1989), and when Gara and Onore (1989) found that “*Gaujonia arbori*” (actually, *Millerana tigrina* sp. nov. described herein) is a pest of pines in Ecuador.

After more than a century, and with the increasing use of molecular techniques in taxonomy, it is now possible to identify many new species worldwide, and *Gaujonia* species are no exception. This study is the first in a series of revisions of Neotropical Pantheinae following the works of G. G. Anweiler and B. C. Schmidt in North America (Anweiler 2009; Schmidt and Anweiler 2010, 2020) and G. Behounek, H. L. Han and V. S. Kononenko in Eurasia (Behounek and Kononenko 2011a, b; Behounek et al. 2011–2016). This study includes re-descriptions of the four known *Gaujonia* species and descriptions of five new genera and 21 new species. Additionally, three of the previously described *Gaujonia* species are transferred to new genera.

Materials and methods

Genitalia preparation and terminology follow the protocols of Lafontaine (1987, 2004) and Schmidt and Anweiler (2020). Genitalia were stained with 10% eosin Y and examined in 30% ethanol. Only the genitalia from type specimens were mounted on slides using Euparal; the remainder were stored in vials of pure glycerin. Pinned adults were photographed prior to dissection using a camera Canon EOS Rebel T5i with a Canon EF 100 mm f/2.8 USM Macro lens. The genitalia were photographed following mounting employing a StackShot automated focus stacking macro rail with a camera Canon EOS 6D and an Infinity long-distance microscope Model K2 DistaMax.

Molecular diagnosis was performed by DNA barcoding, employing a segment from the mitochondrial cytochrome oxidase I (COI) gene for 29 species: one previously described species from *Gaujonia* sensu Hampson, 16 species newly described in this study, and the outgroup sequences of the rest of the jaguar moths along with a specimen from the type genus of *Gaujonia* (*Gaujonia arbori* Dognin) and two other unrelated genera of pantheines (*Meleneta* Smith and *Charadrya* Walker) sequences were taken from the BARCODE OF LIFE DATA SYSTEM v4 (<http://barcodinglife.com>). DNA was extracted from leg tissue removed from pinned dry specimens, and Sanger

sequencing was performed by the Canadian Centre for DNA Barcoding, Guelph, Ontario (<http://ccdb.ca>) following the protocols of Hebert et al. (2003). The sequences were concatenated and aligned using Geneious 9.1.3 (<https://www.geneious.com>). Phylogenetic trees were constructed using a maximum-likelihood (ML) analysis that was performed in IQ-TREE v. 2 to determine relationships among taxa following Nguyen et al. (2015), Hoang et al. (2018), and Minh et al. (2020). Branch support was estimated by performing 1000 replicates each for both ultrafast bootstraps (UFBoot2) ('-bb' command) and SH-aLRT test (SH-aLRT) ('-alrt' command). Phylogenetic relationships with UFBoot ≥ 95 and SH-aLRT ≥ 80 are considered to have strong support. Molecular data and photographs of the voucher specimens are available at BARCODE OF LIFE DATA SYSTEM v4 (project: Life History of Pantheinae). Sequences were submitted to GenBank (<https://www.ncbi.nlm.nih.gov/genbank>); accession numbers are listed in Suppl. material 1: Table S1.

Specimens were obtained from the following museums and collections:

CNC	Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Ontario, Canada.
CUIC	Cornell University Insect Collection, Ithaca, New York, USA.
FSU	Friedrich Schiller University of Jena, Jena, Germany.
JIM	Research Collection of Jose I. Martinez, Gainesville, Florida, USA.
MGCL	McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, Gainesville, Florida, USA.
NHMUK	The Natural History Museum (formerly British Museum [Natural History]), London, United Kingdom.
NJD	Research Collection of Nicholas J. Dowdy, Milwaukee, Wisconsin, USA.
UNAB	Universidad Nacional de Colombia sede Bogotá, Bogotá, DC, Colombia.
USNM	National Museum of Natural History, Smithsonian Institution (formerly United States National Museum), Washington, DC, USA.
TK	Research Collection of Toni Kasiske, Göttingen, Germany.
ZSM	The Zoologische Staatssammlung Muenchen, Munich, Germany.

Systematics

An exhaustive revision of Neotropical pantheines employing morphological and molecular characters shows that *Gaujonia sensu* Dognin-Hampson is a multi-genus complex. The problem with *Gaujonia* (in the broad sense) is that the species have characters that subdivide them into four genera, as defined here:

a) *arbosi* group (*Gaujonia*): represented by the type species of *Gaujonia*, *Gaujonia arbosi*, and four new species *G. bichu* sp. nov., *G. chiqyaq* sp. nov., *G. kanakusika* sp. nov., and *G. sourakovi* sp. nov., in which male wings are entirely hyaline (transparent) with a minute line of scales on the veins and margins without orbicular or reniform

spots; saccular and cucullar regions on the valva are separated; cucullar region squared and wide; aedeagus short; vesica long and wide, with two patches of thin setae; female wings hyaline with the line of scales wider than in male, with a small orbicular spot, but without a reniform spot; anal papilla wide; anterior apophysis small; appendix bursae and corpus bursae long and narrow, appendix bursae heavily sclerotized and smaller than corpus bursae.

b) *arbosioides* group (*Millerana*): represented by the type *Millerana arbosioides* misplaced originally in *Gaujonia*, and five new species: *M. austini* sp. nov., *M. cajas* sp. nov., *M. cundinamarquensis* sp. nov., *M. matthewsae* sp. nov., *M. tigrina* sp. nov., which differ from other groups in that the male antenna is serrate, whereas that of the female is filiform; wings are not hyaline; both orbicular and reniform spots are well developed; valva is simple with most species presenting an extension of the apex; aedeagus and vesica are narrow, with a band of spines surrounding the vesica near the base. Female genitalia are unknown.

c) *renifera* group (*Oculicattus*): represented by the type species *Oculicattus renifera* and seven new species: *O. boliviana* sp. nov., *O. brehmi* sp. nov., *O. inca* sp. nov., *O. raizae* sp. nov., *O. schmidti* sp. nov., and *O. uturunku* sp. nov.; males have hyaline wings and veins covered by a narrow lines of scales; orbicular spot is barely visible; reniform spot is a long horizontal black line; valva with the saccular and cucullar regions separated; cucullar region long and narrow; aedeagus long; vesica long and narrow with one patch of thin setae near the base and two patches, one on each side of tip; female wings similar to those of male with orbicular spot large and line of scales wide; anal papillae narrow; anterior apophysis long; appendix bursae and corpus bursae long, similar in size.

d) *vau-nigrum* group (*Cicadoforma*): includes the type species *Cicadoforma vau-nigrum* and a new species *C. ocelotus* sp. nov. Male wings semi-hyaline (slightly translucent) with a large conspicuous orbicular spot and a small reniform spot; valva simple; aedeagus long; vesica with small patch of spines on upper side; female wings similar to those of male, but covered with scales; anal papilla wide; anterior apophysis long; appendix bursae small; corpus bursae broad.

Unfortunately, molecular data could not be obtained for seven of the species in the *Gaujonia* complex. However, the significant amount of morphological evidence presented in this study is sufficient to justify splitting *Gaujonia sensu* Dognin-Hampson into four genera, which is corroborated by the COI gene tree (Fig. 1).

Key to the genera of the *Gaujonia* genus group based on adult male morphology

- | | | |
|---|--|--------------------------|
| 1 | Valva of male genitalia with clasper (Fig. 68) | <i>Gaujoptera</i> |
| – | Clasper absent in male genitalia (Figs 8–11, 59–67, 69–79) | 2 |
| 2 | Male genitalia with cucullar and saccular regions separated (Figs 8, 10, 64–67, 74–79) | 3 |
| – | Male genitalia with simple valva (Figs 9, 11, 59–63, 68–73) | 4 |

- 3 Antenna brownish orange; eye with copper interfacetal setae; orbicular spot small; reniform spot with large lunate marking; genitalia with cucullar region narrow; apex rounded; aedeagus long and narrow; basal area of vesica with linear patch of spines, and two other polygonal patches mesally (Figs 7, 10, 43–53, 72–79)..... *Oculicattus*
- Antenna dark brown; interfacetal setae black; orbicular spot small, sometimes barely evident; a small dot in base of cell M1 instead of reniform spot; cucullus wide with apex flattened; aedeagus wide and short; vesica with oval patches of spines only in mesal area (Figs 4, 8, 26–31, 64–67)..... *Gaujonia*
- 4 Antenna filiform, dark brown; forewing hyaline or semi-hyaline; cucullar area with a lower lobe separate from sacculus; vesica wider than aedeagus, with a wide band of small spines on its upper side (Figs 11, 12–19, 59–63) 5
- Antenna serrate, dark brown or brownish orange; forewing covered by scales; lobe not separated from sacculus area; vesica elongate with a narrow band of scattered spines surrounding vesica near base; sometimes a small patch of spines at terminal end of vesica (Figs 9, 35–42, 69–73) *Millerana*
- 5 Forewing hyaline with scales only on margins and veins; line pattern only visible from posterior margin; genitalia with remarkably wide apex and lobe; valva with outer margin presenting a series of small indentations; vesica long with patch of spines on upper side and a band of spines near base (Figs 11, 12–15, 59) *Cicadoforma*
- Forewing semi-hyaline with scattered scales all over; line pattern visible, sometimes blurry; genitalia with apex and lobe distinctively narrow; valva without indentations; vesica rounded with only a patch of spines on upper side (Figs 16–19, 60–63) *Cicadomorphus*

***Cicadoforma* gen. nov.**

<http://zoobank.org/725B4F17-CE86-4BE2-B01B-60C8EF82BED8>

Gender. Feminine.

Type species. *Gaujonia vau-nigrum* Hampson, 1913. Catalogue of Lepidoptera Phalaenae in the British Museum 13: 385, 387, pl. 235, fig. 3.

Etymology. *Cicadoforma* refers to how people in South America confuse this group with cicadas.

Included species. The genus *Cicadoforma* is established to accommodate *C. vau-nigrum*, which was previously included in *Gaujonia* because of wing pattern similarities; a new species is described in *Cicadoforma*: *C. ocelotus* sp. nov. However, there are remarkable differences in morphology and molecular characters, as shown here.

Diagnosis. *Cicadoforma* is similar to *Cicadomorphus*, not only externally, but internally as well; however, the phylogenetic analysis results showed enough evidence to separate *Cicadoforma* in a different genus from *Cicadomorphus* (Fig. 1). Nevertheless,

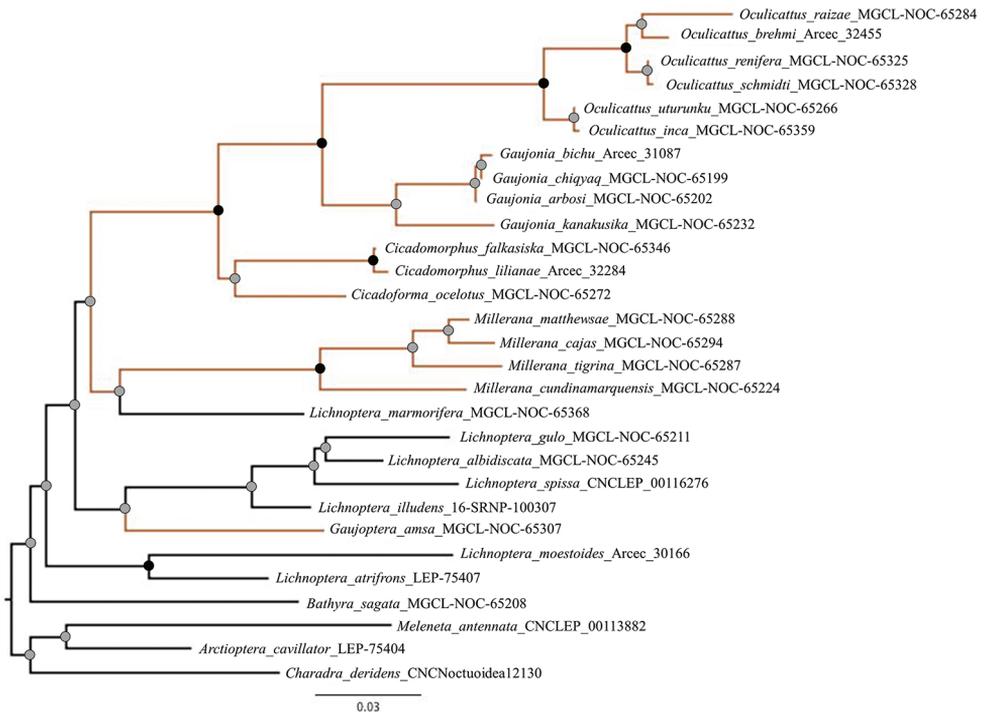


Figure 1. Maximum likelihood tree showing relationships between the *Gaujonia* genus group and the rest of the other jaguar moth genera based on the cytochrome c oxidase I gene (COI) marker. Nodes with black circles represent high support (UFBoot ≥ 95 and SH-aLRT ≥ 80). Nodes with gray circles represent low support (UFBoot < 95 and SH-aLRT < 80). Black branches constitute the outgroups.

both genera can be distinguished morphologically by the forewing, which is hyaline with scales only on margins and veins in *Cicadoforma*, whereas in *Cicadomorpha* has scales are more widely distributed on the forewing. Genitalia have some small indentations on outer margin of valva that are not present in *Cicadomorpha*; apex and lobe on valva is much wider in *Cicadoforma*; upper side of vesica with one patch of spines, and a narrow band of spines near the base are present in *Cicadoforma*. Female genitalia with square-shaped anal papillae in *Cicadoforma*; more rounded in *Cicadomorpha*. DNA barcodes show a closer relationship with *Cicadomorpha* (~ 5% divergent than with *Gaujonia* (~ 6%).

Description. Sexually dimorphic mainly in size, female slightly larger than male; forewing in male with some hyaline areas and with poorly developed pattern, whereas female forewing semi-hyaline with pattern better defined. Antenna filiform, black, or dark brown in both sexes; antenna with yellow basal line of scales; eye large, covered by long interfacetal setae; palp with black upper side and yellow underside; haustellum dark brown and reduced, but functional. Forewing with orbicular reniform spots small. Hindwing semi-hyaline with scales only on margin and veins. Male genitalia

with simple, lightly-sclerotized valva; valva wide apically with some small indentations on outer margin; clasper absent, cucullus wide, with a broad lobe extended in front of sacculus, ear-like in shape; sacculus with a small foot-like process; uncus crooked, long and wide; aedeagus short, with a simple long vesica with a broad patch of spines on upper side and a narrow band of spines at base. Female genitalia with a large square-shaped and lightly sclerotized sterigma, and a rugose, sclerotized appendix bursae; corpus bursae unsclerotized.

Immature stages. Unknown.

Biology. Unknown.

Key to species of the genus *Cicadoforma* based on adult male morphology

- 1 Thorax with small black dots; forewing with pattern well developed; orbicular spot large; vesica with spines close to base (Figs 11, 12) *C. vau-nigrum*
- Thorax with large black dots; pattern on forewing barely visible; orbicular spot small; basal area of vesica without spines (Figs 13–15, 59).... *C. ocelotus*

Cicadoforma ocelotus sp. nov.

<http://zoobank.org/B8926D26-10E1-434D-B5B5-0CBED8A385CE>

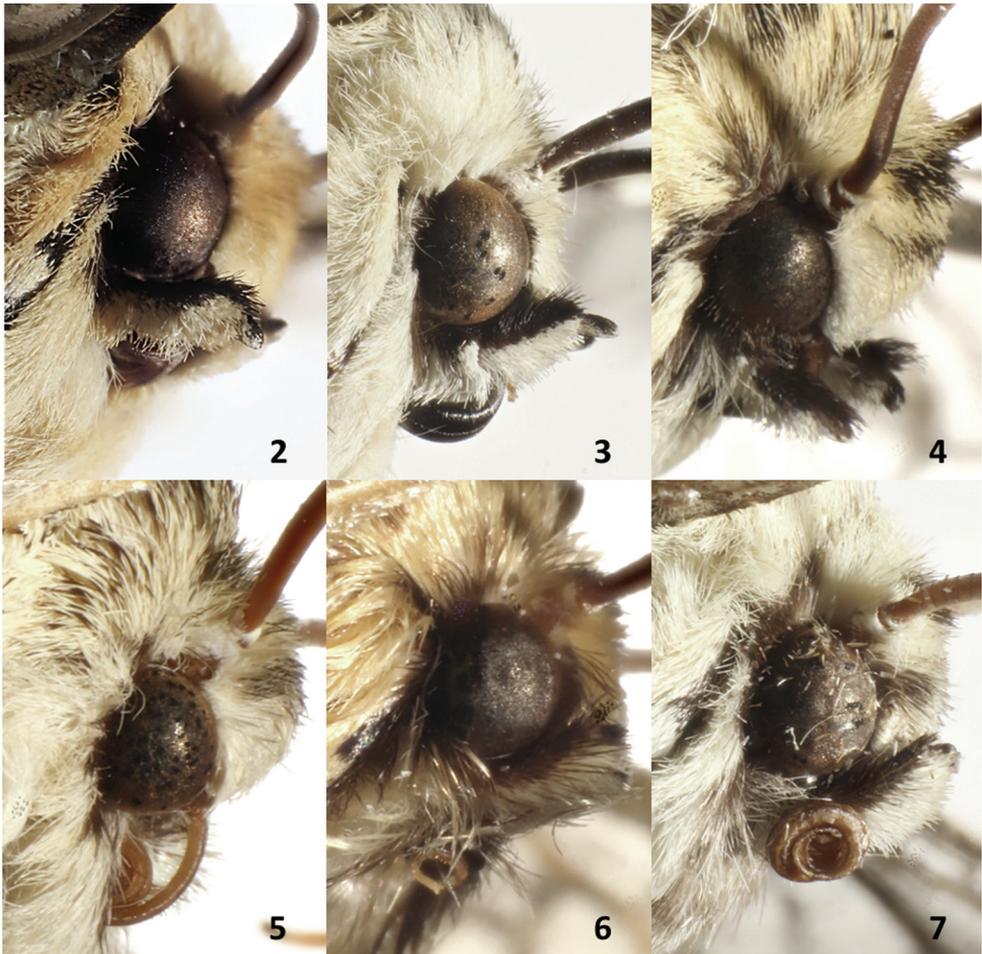
Figs 2, 13–15, 21, 59, 80, 92

Type material. Holotype ♂, **Colombia:** Colombia, Santander road Duitama-Charala, 5°58'13"N, 73°10'07"W, 15–17.III.2016, 2900 m, leg Sinyaev & Machado, coll. Dr. Ron Brechlin / UF, FLMNH, MGCL 1049088. [DNA voucher MGCL-NOC-65272] deposited in MGCL. **Paratypes** (6 ♂, 2 ♀, MGCL): **Colombia:** same collecting data as holotype (1 ♂, 1 ♀); Colombia, Boyacá Arcabuco, Vereda Peñas Blancas, 2670 m, 5°47'05"N, 73°26'17"W, 18–22.II.2015; Sinyaev, M. Márquez & J. Machado, coll. Dr. Ron Brechlin (1 ♂); Colombia, Boyacá Arcabuco, Vereda Peñas Blancas, 2670 m, 5°47'05"N, 73°26'17"W, 20–22.IV.2015; Sinyaev, M. Márquez & J. Machado, coll. Dr. Ron Brechlin (1 ♂); Colombia, Boyacá Provincia del Norte road 55 Susacon – Santa Rosita, 3050 m, 6°10'40"N, 72°43'37"W, 27–28. IV.2017, V. Sinyaev (2 ♂); Colombia, Quindío W of Salento, 1950 m, 4°38'25"N, 75°34'46"W, 9–10.III.2017, V. Sinyaev (1 ♂, 1 ♀).

Etymology. The species name *ocelotus* is derived from the characteristic yellowish orange coloration on its body, reminiscent of the color of an ocelot.

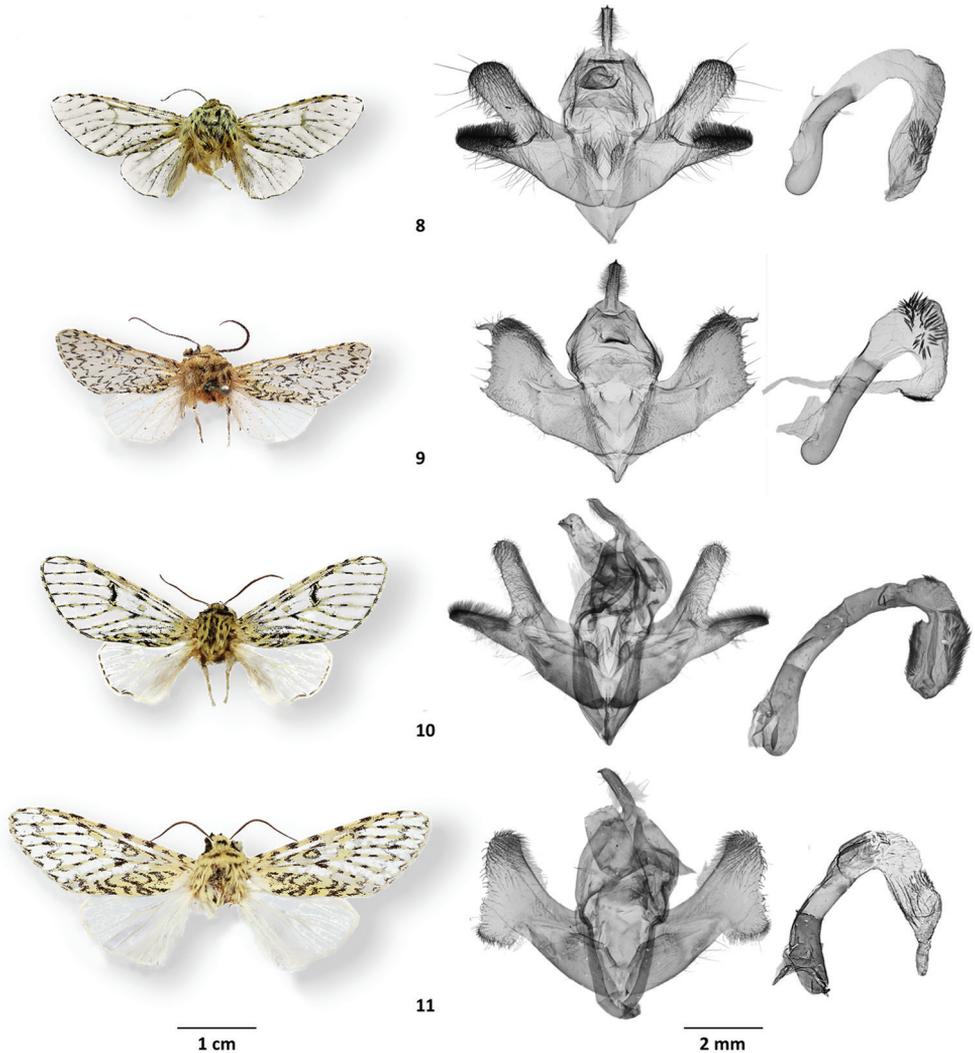
Diagnosis. *Cicadoforma ocelotus* can be distinguished from its only congener, *C. vau-nigrum*, by its remarkably brighter ground color, its larger orbicular spot, and shorter space between forewing veins R3 and R4. The valva of the male genitalia of *C. ocelotus* have concave outer margins, in contrast with the straight margin of *C. vau-nigrum*.

Description. Head. Palp short with a combination of black, yellow, and orange scales; ground color of frons orange or yellow with scattered black hair-like scales;



Figures 2–7. Adult head structure **2** *Cicadoforma ocelotus*, MGCL, Santander, Colombia **3** *Cicadomorphus falkasiska*, MGCL, Pasco, Peru **4** *Gaujonia kanakusika*, MGCL, Cundinamarca, Colombia **5** *Gaujoptera amsa*, MGCL, Cotapata, Bolivia **6** *Millerana cajas*, MGCL, Azuay, Ecuador **7** *Oculicattus renifera*, MGCL, Cusco, Peru.

antenna dark brown. **Thorax.** Yellow or orange with small spots scattered throughout dorsum. **Wings.** Forewing length: male 19–21 mm; female 25–27 mm; forewing yellow or orange scales covering veins and margins with semi-hyaline areas between them; subterminal line slightly visible; basal, antemedial, medial, and postmedial lines poorly developed, present only as small black dots on veins; reniform spot narrow with top and bottom surrounded by black scales and a small black dot in middle; orbicular spot small, elongated; female with antemedial, medial, postmedial, and subterminal lines slightly defined; reniform and orbicular spots similar to those of male; R4 almost entirely black; black V-shaped marking at base of CuA2; hindwing semi-hyaline with yellow or orange veins paler than forewing; fringe composed of short yellow or orange hair-like scales except on posterior margin, which has long,



Figures 8–11. Type specimens **8** *Gaujonia arbosi*, lectotype, USNM, Loja, Ecuador **9** *Millerana arboisoides*, holotype, USNM, Loja, Ecuador **10** *Oculicattus renifera*, holotype, NHMUK, Puno, Peru **11** *Cicadoforma vau-nigrum*, holotype, NHMUK, Tovar, Venezuela.

pale-yellow scales. **Leg.** Yellow or orange with some irregular brown spots that decrease in number from prothoracic legs to metathoracic legs. **Abdomen.** Covered by brownish orange scales that are paler than those of thorax; brown tufts in A2–A7 with tips with same color as remainder of abdomen. **Male genitalia.** Cucullus wide, lobe narrow; lobe apex rounded; apex clothed with short setae that expand over entire costal margin; sacculus base narrow; saccus relatively long, V-shaped; tegumen fairly flat; juxta U-shaped on upper side; aedeagus $3 \frac{3}{4} \times$ longer than wide with opening to vesica same width as aedeagus; vesica $1 \frac{1}{2} \times$ longer than aedeagus with a patch of spines on upper side with some conspicuous basal spines. **Female genitalia.** Anal pa-

pillae wide, petal shaped, clothed with relatively long setae; A8 membranous, relatively short; posterior apophysis almost same length as anal papilla; sterigma enlarged, lightly sclerotized, fused above ostium; anterior apophysis $\frac{7}{8}$ × shorter than posterior apophyses; ductus bursae short, strongly sclerotized and wide; posterior $\frac{3}{4}$ of appendix bursae strongly sclerotized, remainder including corpus bursae unsclerotized; corpus bursae $1\frac{1}{4}$ × longer than the appendix bursae.

Immature stages. Unknown.

Distribution. This species is only known from northern Colombia from moderate elevations from 2000–3000 m, especially in cloud forests (Fig. 92).

Biology. Unknown.

Remarks. This species is the only one in the genus group that has two different phenotypic variations, a yellow form, and an orange form, possibly due to elevation or seasonality (Figs 13–15, 21).

***Cicadoforma vau-nigrum* (Hampson), comb. nov.**

Figs 11, 12, 20, 81, 92

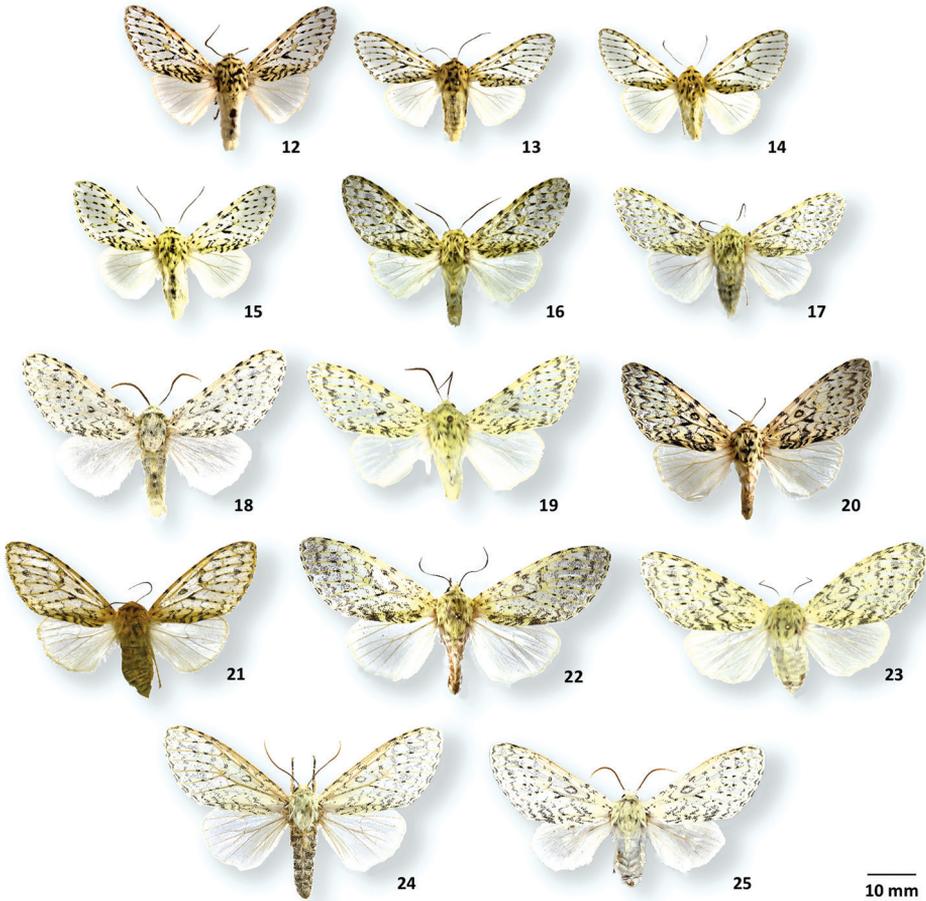
Gaujonia vau-nigrum Hampson, 1913: 387 pl. 235, fig. 3.

Type material. Holotype, ♂, Venezuela: “*Gaujonia vau-nigrum* type ♂ Hmpsn / Tovar, Venezuela Moritz / 1901-57 / Tovar Venezuela / Noctuidae ♂ Slide genitalia No. 5207 / NHMUK 010917654”, coll. G.Hampson, deposited in NHMUK. **Additional examined specimens** (8 ♂, 4 ♀, CUIC): **Venezuela:** Venezuela, Route Caracas-Colonia, Tovar, D. F., IX.1939, Rene Lichy (1 ♂); Venezuela, El Junquito, D. F., 3 Apr. 1943, coll. Rene Lichy (1 ♂); no locality given, “j.15.X.44” / Franclemont diss. #5263 (1 ♂); no locality given, “j.22.VI.47” (1 ♂); no label data (2 ♀). (2 ♂, 1 ♀, CNC): **Venezuela:** same collecting data as the first CUIC male specimens (2 ♂); Same collecting data as the second CUIC male specimens (1 ♀).

Etymology. George F. Hampson likely named this species “*vau-nigrum*” because of the black V-shaped mark at the base of CuA2.

Diagnosis. *Cicadoforma vau-nigrum* is the largest species in this genus; males have a forewing length of ca. 24–26 mm, whereas that of females is ca. 30–32 mm. This species is similar to *C. ocelotus*, but easy to distinguish by the size, and also by the orbicular spot, which is larger in *C. vau-nigrum*. Another important difference is that *C. vau-nigrum* males have hyaline wings where only the veins and margins are covered with yellow and black scales; the abdomen has dark brown tufts in the middle of A4–A7. *Cicadoforma vau-nigrum* can be differentiated from other species by the male genitalia; the vesica has two patches of spines, one near to the aedeagus and the other on the upper side of the vesica. Female genitalia have heavily sclerotized ductus bursae and appendix bursae, with the corpus bursae ca. 2 × longer than the appendix bursae and $1\frac{1}{2}$ × wider; the anterior apophyses are remarkably short, whereas the posterior apophyses are almost as long as the valva.

Immature stages. Unknown.



Figures 12–25. Adult habitus of *Cicadoforma* and *Cicadomorphus* species **12** *Cicadoforma vau-nigrum*, ♂, CNC, Tovar, Venezuela **13** *C. ocelotus*, ♂, holotype, MGCL, Santander, Colombia **14** *C. ocelotus*, ♂, paratype, MGCL, Boyacá, Colombia **15** *C. ocelotus*, ♂, paratype, MGCL, Quindío, Colombia **16** *Cicadomorphus liliana*, ♂, holotype, MGCL, Napo, Ecuador **17** *C. chuya*, ♂, holotype, MGCL, Tolima, Colombia **18** *C. falkasiska*, ♂, holotype, MGCL, Oxapampa, Peru **19** *C. chicharra*, ♂, holotype, MGCL, San Rosa, Bolivia **20** *C. vau-nigrum*, ♀, CNC, El Junquito, Venezuela **21** *C. ocelotus*, ♀, paratype, MGCL, Santander, Colombia **22** *C. liliana*, ♀, paratype, FSU, Zamora-Chinchipec, Ecuador **23** *C. chuya*, ♀, paratype, MGCL, Cochabamba, Bolivia **24** *C. falkasiska*, ♀, paratype, MGCL, Oxapampa, Peru **25** *C. falkasiska*, ♀, paratype, MGCL, Junin, Peru.

Distribution. *Cicadoforma vau-nigrum* is endemic to Venezuela, known only from the states of Vargas and Aragua at moderate elevation in the northern part of the north-western Andes (Fig. 92).

Biology. Unknown.

Remarks. The specimens that were examined were over 60 years old and DNA could not be obtained from them. The specimens from the CNC have rotting stains on the base of the wings, and one of the males is missing half of the abdomen. The only female has incomplete antennae.

Cicadomorphus gen. nov.

<http://zoobank.org/24926D2B-FFDA-41EC-8C37-1BAE0C3E0C84>

Gender. Masculine.

Type species. *Cicadomorphus lilianae* sp. nov.

Etymology. *Cicadomorphus* refers to how similar is this genus to *Cicadoforma*.

Included species. The genus contains four new species, *Cicadomorphus chicharra* sp. nov., *Cicadomorphus chuya* sp. nov., *Cicadomorphus falkasiska* sp. nov., and *Cicadomorphus lilianae* sp. nov., which were placed at first into *Cicadoforma*, but the molecular analyses place them as a sister group.

Diagnosis. *Cicadomorphus* is closed related to *Cicadoforma* genetically and morphologically (see *Cicadoforma* diagnosis).

Description. Sexually dimorphic in size, female slightly larger than male; cells of forewing with some semi-hyaline areas in male, whereas in female forewing covered by scales; line pattern conspicuous in both sexes. Antenna in both sexes dark brown, filiform with a stripe of sulfur-yellow scales basally; haustellum functional but reduced. Forewing with orbicular spot varying in size, reniform spot narrow. Hindwing semi-hyaline presenting scales only on margins and veins. Male genitalia with simple valva, lightly sclerotized lacking clasper; cucullar region with apex and ear-shaped lobe extremely narrow; saccular region with a long and narrow harpoon-shaped process; uncus hooked, broad and long; aedeagus short with simple vesica with a narrow patch of spines on upper side. Female genitalia with sterigma large, rounded, lightly sclerotized; appendix bursae rugose and sclerotized; corpus bursae transparent, not sclerotized.

Immature stages. **Egg.** Circular with soft surface with the chorion forming small square cells, which is consistent across the entire *Gaujonia* genus group. **Larva.** Passes through five to seven instars. Late instars with remarkably short secondary setae, which leave some spaces completely naked; they also present some scattered long setae especially on the prothorax, which cover the head capsule. **Pupa.** Covered by a dense cocoon. The three pair of legs are visible along with the antenna, but prothoracic legs are slightly concealed and micro-setae on the abdomen as in other pantheines, including in the other genera of the *Gaujonia* genus group.

Biology. Currently known only for *Cicadomorphus falkasiska* (see *C. falkasiska* diagnosis).

Key to species of the genus *Cicadomorphus* based on adult male morphology

- 1 Vesica gradually tapered toward apex (Figs 60, 62).....2
- Vesica wide and rounded (Figs 61, 63).....3
- 2 Thorax and forewing whitish yellow; thorax with small dots; orbicular spot small; black tufts in middle of each segment on dorsal area of abdomen; valva with ventral lobe short (Figs 17, 60) *C. chuya*
- Thorax and forewing yellow; thorax with large black spots; orbicular spot large; A1 and A3 with yellow tuft; valva with ventral large and truncated (Figs 16, 62) *C. lilianae*

- 3 Thorax and forewing greenish yellow; thorax densely covered with black dots dorsally; forewing with some hyaline areas with scales only on veins; valva with square-shaped apex; vesica with long narrow transverse band of spines (Figs 19, 63) *C. chicharra*
- Thorax and forewing pale yellow; thorax with few scattered black dots dorsally; forewing covered by scales; valva with apex rounded; vesica with short wide transverse band of spines (Figs 18, 61) *C. falkasiska*

***Cicadomorphus chicharra* sp. nov.**

<http://zoobank.org/65303202-29DE-4933-A69C-D4943042E39A>

Figs 19, 63, 92

Type material. *Holotype* ♂, **Bolivia:** Bolivia, La Paz, Santa Rosa de Lima, 16°23.6'S, 67°41.8'W, 20–22.10.2010, H = 1550 m, leg. Viktor Sinyaev & Oleg Romanov. Deposited in MGCL. *Paratypes* (2 ♂, MGCL): **Bolivia:** same collecting data as holotype.

Etymology. The word *chicharra* means cicada in the Quechua language.

Diagnosis. *Cicadomorphus chicharra* is one of the most easily identified species in the group due to its whitish yellow coloration, but also the wing pattern is thinner and paler than in related species, such as *C. lilianae*. The male genitalia have a wider vesica and narrower spine band on the upper side. Additionally, barcoding showed 2% divergence from *C. lilianae*.

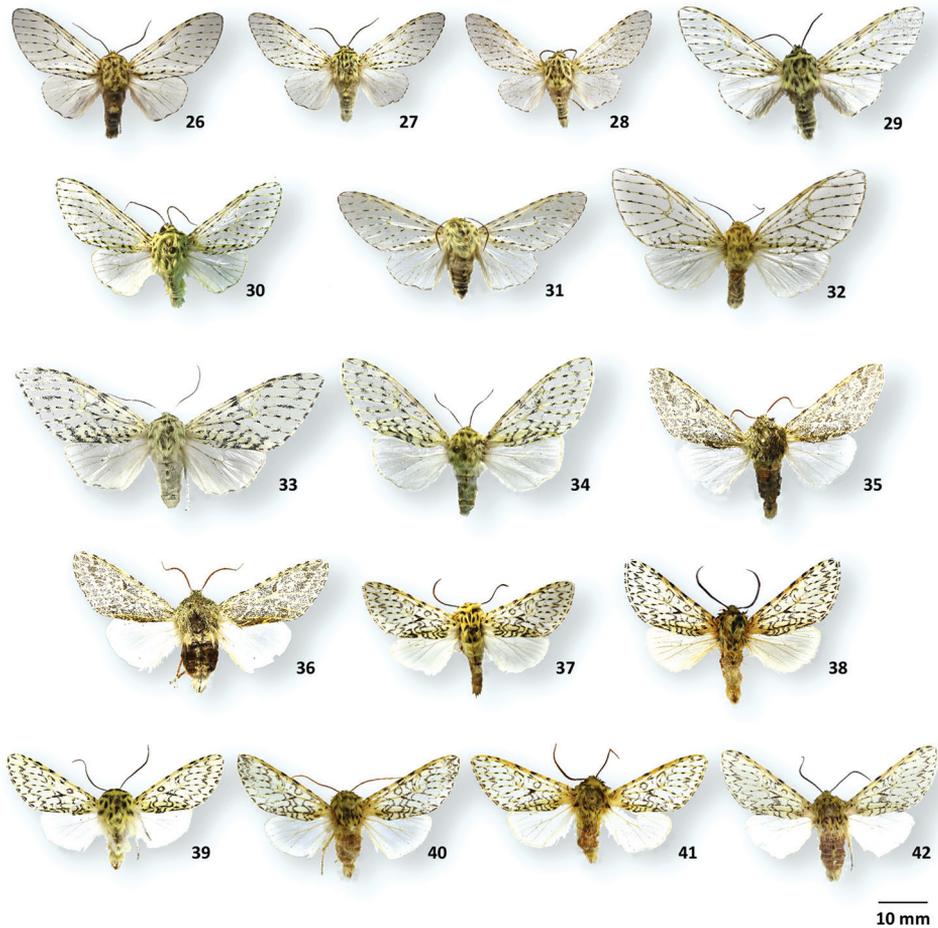
Description. *Head.* Palp with last segment black with a small white dot; frons with greenish yellow scales; antenna brownish orange. *Thorax.* Greenish yellow, with small black dots dorsally; collar with margins black. *Wings.* Forewing length: male 23–25 mm; forewing greenish yellow, semi-hyaline areas clothed by fewer greenish yellow scales; subterminal, medial, and antemedial lines slightly visible; reniform spot poorly defined; orbicular spot long; hindwing: semi-hyaline with greenish yellow veins and fringe. *Leg.* Prothoracic legs black with some patches of same color as body; mesothoracic legs and metathoracic legs greenish yellow. *Abdomen.* Greenish yellow, paler than thorax; tufts in male on A1–A6 with characteristic small black spots on A1, A5 and A6. *Male genitalia.* Cucullus wide with a wide lobe; apex, outer margin, and lobe covered by long setae; apex slightly squared; sacculus wide with needle-shaped process; tegumen narrow, unsclerotized around uncus; saccus relatively wide; juxta with U-shaped concave depression on upper side; aedeagus $\frac{2}{3}$ × as long as vesica; opening to vesica as wide as aedeagus; vesica wide with narrow transverse band of spines.

Immature stages. Unknown.

Distribution. The three specimens were found in the western zone of Bolivia at moderate elevations ca. 1500 m (Fig. 92).

Biology. Unknown.

Remarks. The holotype is in perfect condition (Fig. 19). Initially this species was confused with *Cicadomorphus lilianae*, but a rigorous morphological examination and DNA barcoding showed they were separate species.



Figures 26–42. Adult habitus of *Gaujonia*, *Gaujoptera*, and *Millerana* species **26** *Gaujonia arbori*, ♂, MGCL, Napo, Ecuador **27** *G. bichu*, ♂, holotype, FSU, Zamora-Chinchipec, Ecuador **28** *G. bichu*, ♂, paratype, FSU, Loja, Ecuador **29** *G. chiqyay*, ♂, paratype, MGCL, Marinio, Colombia **30** *G. kanakusika*, ♂, holotype, MGCL, Cundinamarca, Colombia **31** *G. sourakovi*, ♂, holotype, MGCL, Cusco, Peru **32** *G. arbori*, ♀, MGCL, Napo, Ecuador **33** *G. chiqyay*, ♀, holotype, MGCL, Marinio, Colombia **34** *G. kanakusika*, ♀, paratype, MGCL, Cundinamarca, Colombia **35** *Gaujoptera amsa*, ♂, holotype, MGCL, Cotapata, Bolivia **36** *G. amsa*, ♂, paratype, MGCL, Junin, Peru **37** *Millerana arborioides*, ♂, MGCL, Carchi, Ecuador **38** *M. austini*, ♂, holotype, CUIC, Cotopaxi, Ecuador **39** *M. matthewsae*, ♂, holotype, MGCL, Ancash, Peru **40** *M. cundinamarquensis*, ♂, holotype, MGCL, Cundinamarca, Colombia **41** *M. tigrina*, ♂, holotype, MGCL, Carchi, Ecuador **42** *M. cajas*, ♂, holotype, MGCL, Azuay, Ecuador.

***Cicadomorphus chuya* sp. nov.**

<http://zoobank.org/8A73E98E-2A87-4369-856C-5301675C5566>

Figs 17, 23, 60, 84, 92

Type material. Holotype ♂, **Colombia:** Colombia, Tolima, Nevado del Tolima, 4°36'20"N, 75°19'36"W, 2850 m, 08–11.XII.2013, leg. Victor Sinyaev & Mildred

Márquez / UF, FLMNH, MGCL 1049072, deposited in MGCL. **Paratypes** (5 ♂, 1 ♀, MGCL): **Colombia:** Colombia, Santander, km 23 rd. Barbosa – Arcabuco, 5°49'14"N, 73°30'14"W, 18–22.IX.2014, 2360 m, leg. V. Sinyaev & M. Márquez (1 ♂); **Peru:** Peru, Department Cuzco, Manu Park, San Pedro, 1800 m, III.1997, local people leg. (4 ♂); **Bolivia:** Bolivia, Cochabamba, Sierra Siberia, 16°48,3'S, 64°40,8'W, 01–02.XI.2010, H = 3060 m, leg. Viktor Sinyaev & Oleg Romanov (1 ♀).

Etymology. *Ch'uya* means pure, transparent, or glassy in the Quechua language.

Diagnosis. Although *Cicadomorphus chuya* shares some characters with *C. chicharra*, it is easy to distinguish by wing pattern; *C. chuya* is the only species that has both the terminal and subterminal lines serrated. In addition, the genitalia have the lobe reduced, and the juxta is pentagonal-shaped. The base of the lobe opens externally diagonally from the tornus to the cucullus.

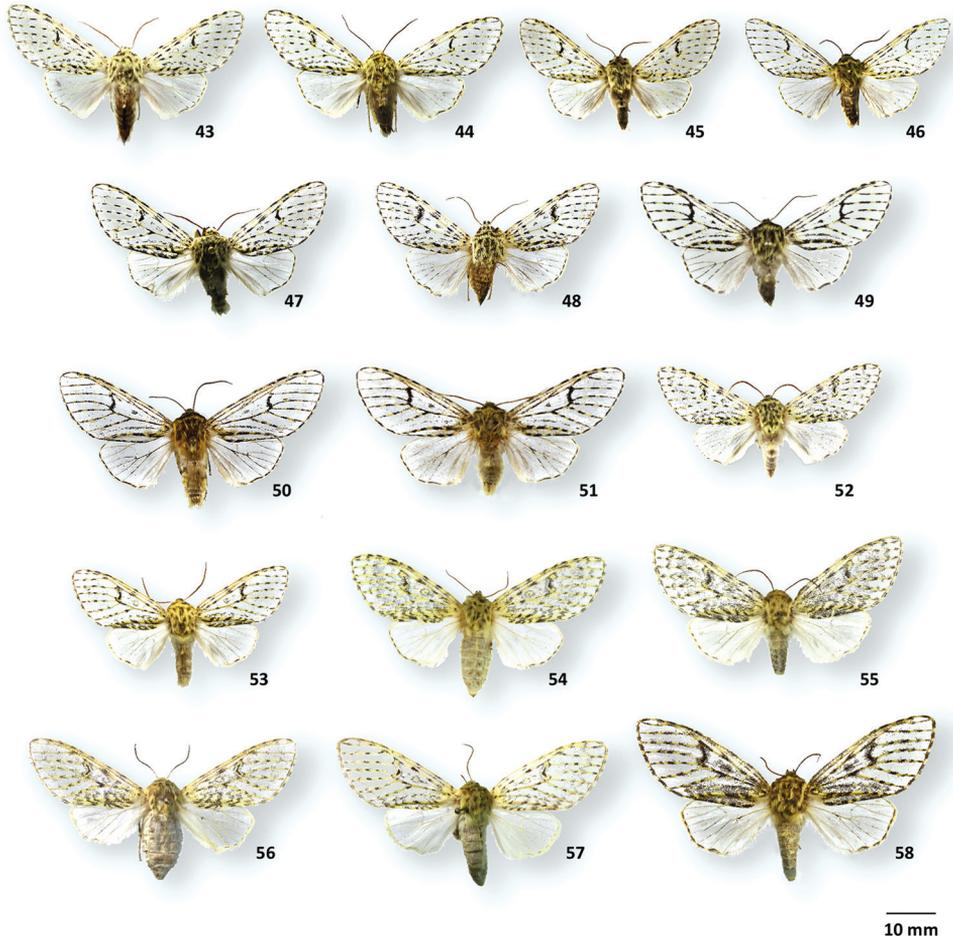
Description. Head. Third segment of palp divided with upper side black, under-side white, but white areas with a few brown spots; antenna dark brown basally, distal segments paler. **Thorax.** Whitish yellow coated with small black dots dorsally. **Wings.** Pattern in both sexes well defined and visible; forewing length: male 22–24 mm; female 29–31 mm; forewing whitish yellow with pattern somewhat blurred; nearly all lines visible and slightly blurred with exception of postmedial line, which is formed by black dots on wing veins plus some dispersed scales; subterminal and terminal lines zigzag; reniform spot relatively wide, outline poorly defined; orbicular spot medium sized and elongate; hindwing hyaline with yellow scales on fringe paler than thorax; wing veins darkened. **Leg.** Prothoracic and mesothoracic legs whitish yellow with two patches of brown scales on femur. **Abdomen.** Dorsally gray, black, and whitish yellow tufts in middle segment with A1 and A3 whitish yellow; whitish yellow ventrally. **Male genitalia.** Cucullar region wider close to apex; lobe small, almost completely covered by long setae from middle of costal margin to lobe; tooth-like protuberance barely visible; lobe diagonal to tornus of valva; saccular region relatively short with tip of process just touching tooth-like protuberance externally; saccus thin, rhomboid shaped; juxta pentagonal shaped; tegumen narrow with a small hood on base of uncus; aedeagus short and wide; opening to vesica square shaped ventrally; vesica tapered, with a large band of spines. **Female genitalia.** Anal papilla square shaped with short setae; posterior apophysis almost same size as anal papilla; anterior apophysis short; sterigma V-shaped, lightly sclerotized, above ostium; ductus bursae wide posteriorly, narrow toward appendix bursae; appendix bursae $\frac{1}{4}$ × shorter than corpus bursae; corpus bursae semi-transparent.

Immature stages. Unknown.

Distribution. Males were found in Colombia and Peru, whereas the female was found in Bolivia, all in deciduous forest habitats at moderate to high elevations from 1800–3000 m (Fig. 92).

Biology. Unknown.

Remarks. The holotype is in near perfect condition (Fig. 17) with only the right hindwing slightly bent inwards at the posterior margin. The female is missing the left antenna, otherwise the specimen is complete. The palpi in the female are broken, but still attached to the mouth parts. The female was originally thought to be a different species; however, the DNA match with the male of *Cicadomorphus chuya*.



Figures 43–58. Adult habitus of *Oculicattus* species **43** *Oculicattus renifera*, ♂, MGCL, Cusco, Peru **44** *O. renifera*, ♂, MGCL, Junin, Peru **45** *O. schmidti*, ♂, holotype, MGCL, Pasco, Peru **46** *O. schmidti*, ♂, paratype, MGCL, Junin, Peru **47** *O. inca*, ♂, holotype, MGCL, Sierra Siberia, Bolivia **48** *O. boliviana*, ♂, holotype, MGCL, Sierra Siberia, Bolivia **49** *O. uturunku*, ♂, holotype, MGCL, Morona, Ecuador **50** *O. raizae*, ♂, holotype, MGCL, Tolima, Colombia **51** *O. raizae*, ♂, paratype, ZSM, Pichincha, Ecuador **52** *O. brehmi*, ♂, holotype, FSU, Loja, Ecuador **53** *O. brehmi*, ♂, paratype, MGCL, Napo, Ecuador **54** *O. brehmi*, ♀, paratype, MGCL, Napo, Ecuador **55** *O. brehmi*, ♀, paratype, MGCL, Napo, Ecuador **56** *O. renifera*, ♀, MGCL, Cusco, Peru **57** *O. renifera*, ♀, MGCL, Cusco, Peru **58** *O. raizae*, ♀, paratype, MGCL, La Paz, Bolivia.

***Cicadomorphus falkasiska* sp. nov.**

<http://zoobank.org/894304E1-B33B-44CC-9E71-F22AA0D09ED2>

Figs 3, 18, 24, 25, 61, 83, 91A, 92

Type material. *Holotype* ♂, **Peru:** Peru, Oxapampa near Villa Rica, 2700 m, 21 Feb. 2018, coll. Falk Zahlaus / reared with *Quercus aquifolioides* & *Prunus laurocerasus* /

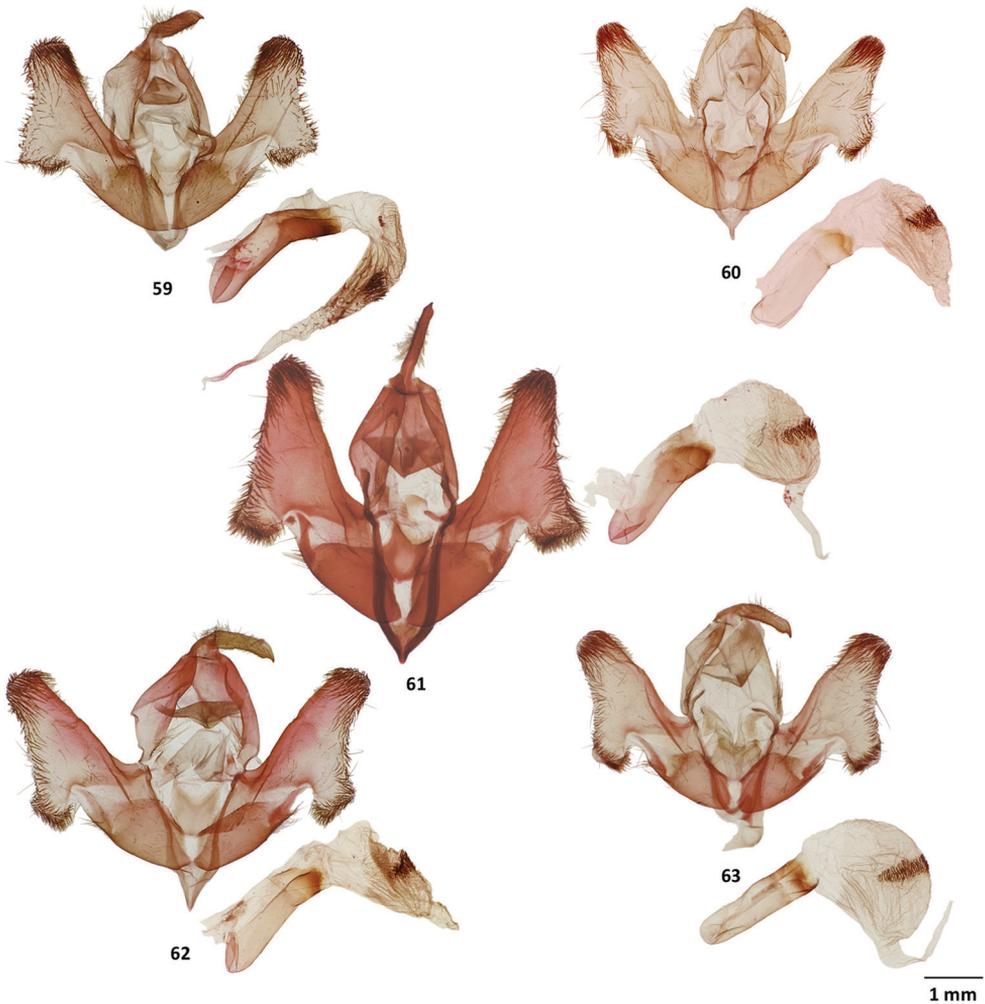
UF, FLMNH, MGCL 1049146. DNA voucher MGCL-NOC-65346 deposited in MGCL. **Paratypes** (4 ♂, 3 ♀, MGCL): **Peru:** same collecting data as holotype (2 ♂, 1 ♀); Peru-Pasco 9 km on 310° from Yapi, H = 2470 m, 10°41,8'S, 75°35,4'W, 11–13.02.2011, leg. Viktor Sinyaev & Alexander Poleschuk (2 ♂); Peru-Junin near Calabaza vill., 11°30.4'S, 74°51.7'W, 20.12.2010, H = 2722 m, leg/coll. Viktor & Svetlana Sinyaev + Vladimir Izerskiy (2 ♀). **Additional examined specimens** (2 ♂, 1 ♀, TK): **Peru:** same collecting data as holotype.

Etymology. *Falkasiska* is the combination of the names from Falk Zahlaus who collect the first female specimen and Toni Kasiske, who reared the eggs obtained from that female.

Diagnosis. *Cicadomorphus falkasiska* and *C. chicharra* share certain characters, especially in coloration and wing pattern. However, *C. falkasiska* is paler and the orbicular spot larger and outlined in black; also, the subterminal line is quite visible in *C. chicharra*, whereas in *C. falkasiska* it is inconspicuous. The male genitalia have a relatively wide aedeagus; the vesica is large and semi-rounded; the female genitalia have a wide appendix bursae and corpus bursae.

Description. **Head.** Third segment of palp in both sexes black with a pale-yellow stripe ventrally and a dot of same color dorsally; frons darker-yellow than rest of body; antenna dark brown. **Thorax.** Pale yellow with some black blurred spots, which are more visible in male than female. **Wings.** Forewing length: male 23–25 mm; female 30–32 mm; forewing pale yellow; hyaline areas in male nearly without scales, whereas forewing slightly more covered with scales in female; postmedial and subterminal lines inconspicuous in male, whereas basal, antemedial, and medial lines well defined; female with all lines weakly defined; orbicular spot large and elongate; reniform spot slightly wide, outlined with black scales and with a black dot in middle; hindwing hyaline in male, semi-hyaline in female with fringe paler yellow than forewing. **Leg.** Pale yellow with prothoracic legs with some brown patches. **Abdomen.** Whitish gray with some tufts over middle of abdomen; tufts on A1–A3 yellow with a small black dot on A2, whereas remainder tufts on other segments are black with some yellow and white scales; female with yellow tufts on A1–A4. **Male genitalia.** Cucullar region relatively wide with an axe-shaped lobe; apex round with a lobe and apex covered with quite long setae; saccular region wide with process of sacculus thin and curved; juxta flat on upper side but with a small V-shaped depression in middle; aedeagus relatively wide at opening to vesica; aedeagus ca. as long as vesica; vesica rounded with narrow transverse band of spines. **Female genitalia.** Anal papilla long and wide with posterior apophysis ca. as long as anal papilla; anterior apophysis short; sterigma large, fused above ostium; ductus bursae wide and short; and appendix bursae large, well sclerotized; corpus bursae not sclerotized $1\frac{1}{4}$ × longer than appendix bursae.

Immature stages. **Egg.** Pale yellow, turning dark brown close to emergence. **Larva.** Body black with yellowish orange verrucae and short setae; a set of long white setae on lateral verrucae, prothorax near head capsule, and on last tergite (Fig. 91A). **Pre-pupa.** Similar to last instar but with verrucae and setae dark yellow. **Pupa.** Dark brown.



Figures 59–63. Male genitalia of *Cicadoforma* and *Cicadomorphus* species **59** *Cicadoforma ocelotus*, holotype, MGCL, Santander, Colombia **60** *Cicadomorphus chuya*, holotype, MGCL, Tolima, Colombia **61** *C. falkasiska*, holotype, MGCL, Oxapampa, Peru **62** *C. liliana*, holotype, MGCL, Napo, Ecuador **63** *C. chicharra*, holotype, MGCL, San Rosa, Bolivia.

Distribution. All specimens were found in central Peru at a high altitude of ca. 2500 m or above (Fig. 92).

Biology. *Cicadomorphus falkasiska* is the only species in the genus for which immature stages are known. Adults are active throughout the year, but especially so in spring and summer. *Cicadomorphus falkasiska* feeds on *Prunus* spp. especially on *P. subcorymbosa* Ruiz ex Koehne (JIM, pers. obs.).

Remarks. Holotype (Fig. 18) and paratypes are well preserved, but three of the specimens were destroyed and only identifiable by genitalia dissection.

***Cicadomorphus lilianae* sp. nov.**

<http://zoobank.org/0B2743EF-09FA-4AB2-9850-39DFB1D3C5C4>

Figs 16, 22, 60, 82, 92,

Type material. Holotype: ♂, **Ecuador:** Ecuador, Napo, Cosanga, 2150 m, 29 Mar. 1976, coll. N. Venedictoff Holotype ♂. Deposited in MGCL. **Paratypes** (8 ♂, 3 ♀, MGCL): **Ecuador:** Ecuador, Napo + 10km Papallacta, 2730 m, 13–15 Sep. 1982, coll. N. Venedictoff (7 ♂); Ecuador: Napo, El Carmelo Barbar' 10 km, 2750 m, 19 Jan. 1985, coll. N. Venedictoff (1 ♀). (1 ♂, CNC): **Ecuador:** Ecuador, Napo province, 23 km road La Bonita, 2400 m, 7–9 Apr. 1986, coll. Stuart McKamey. (1 ♀, FSU): **Ecuador:** Ecuador, Zamora-Chinchipe Parque Nacional Podocarpus ridge forest, Bombuscaro area, Blacklight 2 × 15W (40), 04°06.84'S, 78°57.97'W, 23.iii. 2011, 19.30–20.30 h, ca. 1120 m, Gunnar Brehm leg. / DNA Barcode run 2011, COI-5P marker, University of Guelph / Arcec 32423 / [Arcec 32284] (1 ♀). **Additional examined specimens** (2 ♂ UNAB): **Colombia:** Colombia, Cundinamarca, Guasca, Choachi, Vda. El Curi, F. panes de Roka 1996 m, 02 Jun. 2013, coll. V. Raigozo (2 ♂).

Etymology. This species is named in honor of my sister Lilian Martinez Canto (1989–2017) for her love, charisma, and support offered during all her beautiful life.

Diagnosis. *Cicadomorphus lilianae* is small and the wing pattern is blurred, causing the lines to appear shapeless. The males have darker coloration than the females, and the line pattern is better defined. This species shares some features in genitalia with *C. chuya*, such as the tapered vesica.

Description. Head. Palp black, terminal segment admixed with brown and white scales; frons dark yellow basally with some black scales; female ground color pale yellow with gray scales; antenna brownish orange. **Thorax.** Ground color dark yellow with some black tufts; female same color but with gray tufts; collar with black ground color with margins yellow, female with ground color gray. **Wings.** Both sexes dark yellow, similar in pattern, nevertheless female is paler, and wing pattern is basally almost imperceptible; forewing length: male 25–27 mm; female 31–33 mm; forewing yellow with pattern in black, but blurrier, male darker; both sexes with semi-hyaline areas with some scattered dark yellow scales; both sexes with blurry lines; orbicular spot elongate, ca. same size in both sexes; reniform spot heavily outlined with black scales; hindwing hyaline with fringe yellow, but gray on posterior margin. **Legs.** Yellow, except prothoracic legs, which are brown with some black scales. **Abdomen.** Gray with yellow tufts in middle of abdomen and on each side; brown tufts on A3–A7; female abdomen yellow with some brown scales. **Male genitalia.** Cucullus wide with apex wide; costal margin without setae; outer margin sharply bent; tooth-like protuberance small; lobe with external apex large; posterior margin of lobe curved; sacculus wide with narrow process touching tooth-like protuberance; saccus thin; tegumen narrow, lightly sclerotized, barely visible around uncus; juxta wide, upper side flat; aedeagus relatively wide, V-shaped in opening; tapered vesica; band of spines with a rounded ending. **Female genitalia.** Anal papilla small; relatively wide posterior apophysis $1\frac{1}{3}$ × longer

than anal papilla; sterigma open trapezoid shaped; anterior apophysis short; ductus bursae small, well-sclerotized; appendix bursae broad, sclerotized; corpus bursae $\frac{1}{3}$ × longer than appendix bursae.

Immature stages. Unknown.

Distribution. This species has been found in Ecuador and Colombia at very variable elevations from 1100–2700 m (Fig. 92).

Biology. Unknown.

Remarks. The tip of the left antenna from the type specimen was broken during examination (Fig. 16). The paratype female is intact; however, the left orbicular spot is incomplete (Fig. 22). Otherwise, the female forewing is more brightly colored than that of the male basally where the antemedial and basal lines are almost inconspicuous. The female paratype from FSU has a different DNA voucher label from the voucher published at <http://barcodinglife.com>.

Gaujonia Dognin

Gender. Masculine.

Type species. *Gaujonia arbori* Dognin, 1891. Descriptions de Lépidoptères nouveaux. Le Naturaliste, 13: 126.

Etymology. Paul Dognin probably named this genus *Gaujonia* after Fr. Theophile Gaujon a Catholic Lazarist missionary priest and entomologist residing in Loja, Ecuador, who helped by collecting specimens for him.

Included species. Within the genus *Gaujonia* there were previously four species, however, three of the species belong to three different genera: *Gaujonia arborioides* Dognin (*Millerana arborioides* (Dognin), comb. nov.), *G. renifera* Hampson (*Oculicattus renifera* (Hampson), comb. nov.), and *G. vau-nigrum* Hampson (*Cicadoforma vau-nigrum* (Hampson), comb. nov.) based on genetic and morphological differences. Only one of the original species remains in *Gaujonia*, it being the type species *Gaujonia arbori* Dognin. However, during this revision four new species were discovered: *Gaujonia bichu* sp. nov., *Gaujonia chiqyaq* sp. nov., *Gaujonia kanakusika* sp. nov., and *Gaujonia sourakovi* sp. nov.

Diagnosis. *Gaujonia* is similar to *Oculicattus* morphologically, but it is most closely aligned genetically with *Cicadoforma* and *Cicadomorphus* (Fig. 1). The interfacetal setae of *Gaujonia* are longer than those in *Cicadoforma* and *Cicadomorphus*. Male genitalia are similar to those of *Oculicattus*, however, the cucullus is wider and slightly square in shape, whereas in *Oculicattus* the cucullus is thinner and rounded. *Gaujonia* has a short vesica and two patches of spines, whereas in *Oculicattus* the vesica is longer with three patches of spines. Female genitalia of *Gaujonia* are similar to that of *Oculicattus*, but that of *Oculicattus* is larger in size, however, the sterigma is smaller in that genus than in *Gaujonia*. DNA barcoding corroborated that *Gaujonia* is closer to *Cicadoforma* and *Cicadomorphus* (~ 6% divergent) than *Oculicattus* (~ 8%).

Description. Sexually dimorphic in size, female larger than males; forewing and hindwing hyaline with scales only on wing veins; orbicular and reniform spots in male



Figures 64–68. Male genitalia of *Gaujonia* and *Gaujoptera* species **64** *Gaujonia bichu*, holotype, FSU, Zamora-Chinchipe, Ecuador **65** *G. chiqyaq*, paratype, MGCL, Marinio, Colombia **66** *G. kanakusika*, holotype, MGCL, Cundinamarca, Colombia **67** *G. sourakovi*, holotype, MGCL, Cusco, Peru **68** *Gaujoptera amsa*, holotype, MGCL, Cotapata, Bolivia.

inconspicuous or absent, whereas female has an orbicular spot and narrow reniform spot. Antenna filiform and long haustellum dark brown; eyes hairy with long interfacetal setae. Male genitalia with saccular and cucullar regions separated and clasper absent; short-beaked uncus; aedeagus wide and vesica short with two sclerotized patches of spines on each side. Female genitalia with sterigma open wide, ductus bursae and appendix bursae are heavily sclerotized, whereas corpus bursae is not.

Immature stages. *Egg.* Circular, slightly flattened; chorion forming large square cells making the surface slightly rugose. *Larva.* Undergo from five to seven instars. Late instars with dense bands of secondary setae on the abdominal tergites, which are more scattered on the thorax; verrucae have scattered long setae; two large prothoracic

verrucae with long tufts of secondary setae *Pupa*. Similar in features to other genera in the *Gaujonia* genus group (see *Cicadomorphus* diagnosis).

Biology. The biology is known only from one species in *Gaujonia* (see *G. kanakusika* immature stages) (JIM, pers. obs.).

Key to species of the genus of *Gaujonia* based on adult male morphology

- 1 Vesica presenting short patches of spines (Figs 64–66) **2**
- Vesica showing elongated patches of spines giving the appearance of long hairs (Fig. 67) ***G. sourakovi***
- 2 Valva with apex flattened (Figs 64, 65) **3**
- Valva with apex rounded (Figs 8, 66) **4**
- 3 Forewing with V-shaped mark on base of CuA2; cucullar region widely open, almost touching saccular region (Figs 29, 65) ***G. chiqyaq***
- Forewing without V-shaped mark on base of CuA2; cucullar and saccular areas remarkably narrow (Figs 27, 28, 64) ***G. bichu***
- 4 Hindwing with fringe completely yellow with some small lines in black; cucullar region wide; vesica with two patches of spines similar in size (Figs 30, 66) ***G. kanakusika***
- Hindwing with black fringe and minute spots at the end of each vein; cucullar region narrow; vesica with two patches different in size being small patch $\frac{1}{2} \times$ smaller than the other patch. (Figs 8, 26) ***G. arbosi***

Gaujonia arbosi Dognin

Figs 8, 26, 32, 85, 93

Gaujonia arbosi Dognin, 1891: 126.

Type material. Lectotype ♂, **Ecuador:** “*Gaujonia arbosi* type ♂ Dgn. / Environs de Loja Equateur / 1993 / Type No. 30907 U.S.N.M. / Genitalia slide m, Franclemont USNM 33564”, coll. P. Dognin ♂. Deposited in USNM. **Additional examined specimens** (4 ♂, 2 ♀, MGCL): **Ecuador:** Ecuador, Napo + 10km Papallacta, 2730 m, 13–15 Sep. 1982, coll. N. Venedictoff (3 ♂); Ecuador, Napo, El Carmelo Barbar’ 10km, 2750 m, 19 Jan. 1985, coll. N. Venedictoff (2 ♀). **Colombia:** Colombia, Putumayo near San Francisco 01°07'36"N, 076°50'30"W, 25–27.01.2018, 2525m., Leg Viktor Sinjaev and Juan Machado / (1 ♂).

Etymology. Paul Dognin probably named this species *arbosi* after Fr. Mariano Arbós, a friend of Fr. Theophile Gaujon.

Diagnosis. *Gaujonia arbosi* is similar to *G. chiqyaq*, but it can be identified by coloration, which is dark yellow in *G. arbosi*. Both sexes are similar with the only difference being that the female is covered with brighter yellow scales from the fold to the posterior margin of the forewing, accenting the lines. For males the forewing length ranges from 17–19 mm and for females from 23–25 mm. Palp short and black; antenna has a stripe

of dark yellow scales from the base to the seventh antennomere; antennae are black, and longer than in *G. chiqyaq*. Male thorax dark yellow with some patches of black. Forewing with pattern similar to that of *G. chiqyaq*, but the lines on Sc+R1 and posterior margin are thicker; there is a small dot in the middle of the base of the cell M1, which is not present in *G. chiqyaq*; the V-shaped mark at the base of CuA2 smaller and thicker than in *G. chiqyaq*. The hindwing, base of M2 is angled diagonally forward to the base of the wing, fused to the base of CuA1; in *G. chiqyaq* M2 is squared and not fused with the base of CuA1; the fringe is black with few yellow scales making minute spots at the end of the veins, except the cell A2, which is completely outlined in black. The male genitalia have the cucullar region wide, slightly diagonal to the base, whereas the cucullar region in *G. chiqyaq* is wide, opened, almost touching the saccular region; the juxta is semicircular in shape; the saccus is short and wide. Female genitalia, the sterigma is peanut shaped, and the corpus bursae is $\frac{1}{8} \times$ larger than the appendix bursae. DNA Barcoding showed that *G. arbori* and *G. chiqyaq* are sister species with ca. ~ 0.3% of difference, but the morphological characters mentioned above distinguish both species.

Immature stages. *Egg.* Bright green and turning dark brown close to emergence.

Larva. Only known from the third instar, which is very similar to that of *G. kanakusika*, but the body of *G. arbori* is white with dark brown secondary setae, whereas the body of *G. kanakusika* is rather whitish yellow. *Pre-pupa.* Unknown. *Pupa.* Dark brown (Guevara and Romero 2008).

Distribution. This species is endemic to coniferous and deciduous forest of Ecuador and Colombia and can be found at high elevations above 2500 m (Fig. 93).

Biology. Guevara and Romero (2008) were the first to record the larval stages in *Gaujonia arbori* feeding on *Abnus acuminata* Kunth but they misidentified it as *Gaujonia arborioides* (now *Millerana arborioides*), even though the immature stages differ greatly between both genera (see *Millerana* immature stages). Additionally, the illustrations from Guevara and Romero (2008) lack of good quality to use for identification.

Remarks. The holotype of the species was “missing” in the P. Dognin collection (USNM), which was a female illustrated by Dognin (1894). A male was listed as the type specimen, but this is actually a different species from the illustration made by P. Dognin (Fig. 8). Presumably both specimens were used in the description of the species in his second work Dognin (1894), and is also deposited in the Dognin collection (USNM), I designated the male as the lectotype for *Gaujonia arbori* Dognin under the provisions of Article 74.1.1 of the International Code of Zoological Nomenclature (1999), whereas the female is considered a different species (see *Gaujonia chiqyaq* remarks).

Gaujonia bichu sp. nov.

<http://zoobank.org/D18A59B3-47DA-4583-9274-D4376ADE594F>

Figs 27, 28, 64, 93

Type material. *Holotype* ♂, **Ecuador:** Ecuador, Zamora-Chinchipec ca 2 km E pass El Tiro rainforest, 30 m N of road, Blacklight 2 × 15W (61), 03°59.46'S, 79°07.58'W, 3.iv.2011, | 18.45–19.45, 2630 m, coll. Lisa Lehner / DNA Barcode run 2011, COI-

5P marker, University of Guelph / Arcec 31087. [DNA voucher Arcec 31087] deposited in FSU. **Paratypes** (2 ♂, FSU): **Ecuador:** Ecuador, 8 km SE of Loja, Parque Nacional Podocarpus Cajanuma, mont. Rainforest, Blacklight 2 × 15W (50), 04°06.86'S, 79°10.48'W, 20.ix.2008, 2897 m, Florian Bodner leg / Arcec 32151 / Barcoding failed.

Etymology. The term *bichu* is used to refer to an insect or small animal in the Quechua language. Since this is the smallest species of *Gaujonia*, this name seems appropriate.

Diagnosis. *Gaujonia bichu* is closely related to *G. sourakovi*, but *G. bichu* is the smaller. The male genitalia have the valva and the saccular region narrow, and the process of the sacculus is longer and thinner.

Description. **Head.** Palp black; frons yellow with some black scales. **Thorax.** Dorsally covered by large black patches. **Wings.** Male yellow with thin spots and lines on venation; forewing length: male 15–17 mm; forewing with two V-shaped marks on base of R1+R2 and R4+R5; base of cell with small black dot on M1; five black dots on Sc+R1 with a line right on apex; half of posterior margin black; hindwing with fringe black, interrupted by a yellow dot at end of each vein. **Leg.** Prothoracic leg black with femur and tarsi presenting yellow spots; mesothoracic legs yellow with some black spots; metathoracic legs yellow. **Abdomen.** Grayish yellow with yellow and black tufts in middle of abdomen dorsally on A1–A5, remainder of abdomen covered in yellow scales. **Male genitalia.** Valva long and narrow a little swollen from middle to apex externally; sacculus narrow; sacculus process long and narrow; juxta shield-like; tegumen wide, narrower near valva; aedeagus short and narrow; vesica elongated with two oval patches, one 2 × longer than the other.

Immature stages. Unknown.

Distribution. *Gaujonia bichu* specimens were found in Ecuador in coniferous and deciduous forests at high elevations above 2500 m (Fig. 93).

Biology. Unknown.

Remarks. Three specimens are in good condition; one specimen from Loja has no black dots on the base of cell M1.

Gaujonia chiqyaq sp. nov.

<http://zoobank.org/38C22D4A-F2D3-4ED4-9A71-578970C72AF5>

Figs 29, 33, 65, 86, 93

Type material. **Holotype** ♀, **Colombia:** Colombia, Putumayo, Municipio San Francisco, Antenas on Bosque Siberia, 01°08'45"N, 76°50'43"W, 29–30.01.2018, 2940 m., Leg Viktor Sinjaev and Juan Machado / UF, FLMNH, MGCL 1049015. [DNA voucher MGCL-NOC-65199] deposited in MGCL. **Paratypes** (7 ♂, 1 ♀, MGCL): **Colombia:** Colombia, Marinio Laguna, the Cocha El Carrizo, 01°10'35"N, 77°08'13"W 25.01.2018, 2900 m., Leg Viktor Sinjaev and Juan Machado / UF, FLMNH, MGCL 1049007, [DNA voucher MGCL-NOC-65191] (1 ♂); : Colombia, Marinio Laguna, the Cocha near Encano, 01°08'10"N, 77°11'07"W, 21–24.01.2018, 2900 m., Leg Viktor Sinjaev and Juan Machado (1 ♂); : Colombia, Boyacá, Vereda El

Palmar, Parque Nacional El Virofín, 6°02'28"N, 73°13'18"W, 2114m, 25.11.2013, legit Victor Sinyaev & Mildred Márquez (2 ♂); Colombia, Border Narinio-Putumao near Pasto, 01°08'52"N, 77°05'59"W, 17–19.01.2018, 3200 m., Leg Viktor Sinyaev and Juan Machado (1 ♀); Ecuador, Pichincha, Camping Bella Vista, 2230 m, 0°00'41"S, 78°41'17"W, 19. XII 2012–7. I 2013, leg. Sinyaev & Romanov & [coll.] Dr. R. Brechlin (1 ♂); **Peru:** Peru-Junin Near Calabaza vill., 11°29,8'S, 74°51,9'W, 17.12.2010, H = 2964 m, leg/coll. Viktor & Svetlana Sinyaev + Vladimir Izerskiy (1 ♂); Peru-Junin near Calabaza vil., 11°30,5'S, 74°49,4'W, 1–2.02.2011, H = 2137 m, leg. Viktor Sinyaev & Alexander Poleschuk / UF, FLMNH, MGCL 1049018. [DNA voucher MGCL-NOC-65202] (1 ♂).

Etymology. The name *chiqyaq* means green in the Quechua language, referencing the diagnostic green coloration of this species.

Diagnosis. Beside the features mentioned above to differentiate *Gaujonia chiqyaq* from *G. arbosii*, there are also other informative characters to identify this species. The male has a narrow reniform spot outlined by black scales along the upper and lower sides, but not in the middle region. The orbicular spot is small and greenish yellow, outlined in black. The thorax has large black tufts. The female has a larger reniform spot with the same yellow coloration. Forewing transverse lines are more sharply defined and thicker than in *G. arbosii*.

Description. **Head.** Palp with last segment black; frons with a combination of black and greenish yellow scales. **Thorax.** Covered with long black tufts. **Wings.** Both sexes greenish yellow with thin spots and lines; forewing length: male: 20–22 mm; female: 28–30 mm; forewing ground color greenish yellow with small, thin lines on venation forming pattern, female with thicker and well-defined lines; orbicular spot in male small, black, but almost imperceptible; orbicular spot larger in female and elongated; reniform spot in both sexes narrow, greenish yellow, outlined in black; both sexes with hindwing venation green, and fringe black with some greenish yellow dots. **Leg.** Metathoracic and metathoracic legs black with some greenish yellow patches; hind legs greenish yellow with black shading. **Abdomen.** Brown dorsally with green tufts on A1–A3 and some black scales in middle of the green tufts; ventrally greenish yellow; female similar to male but paler in color. **Male genitalia.** Cucullar region extended close to saccular region, valva relatively narrow, slightly ridged externally on apex; saccular region rounded at base and process wide; saccus wide V-shaped; juxta rectangular concave on top; tegumen wide; aedeagus short 3 × longer than wide; basal area almost same size as apical part of vesica with two patches of spines, one 2 × narrower than the other. **Female genitalia.** Anal papilla wide, slightly ridged; posterior apophysis 1/3 × longer than anal papilla; sterigma large oval shaped, fused above ostium; anterior apophysis short; ductus bursae heavily sclerotized and connected to appendix bursae, which is sclerotized as well; appendix bursae 1/2 × narrower than corpus bursae.

Immature stages. Unknown.

Distribution. This species has a broad distribution from Ecuador to Peru between 2100–3200 m (Fig. 93).

Biology. Unknown.

Remarks. The holotype of *Gaujonia chiqyaq* closely resembles the type specimen of *Gaujonia arbori* (Fig. 33) illustrated by Dognin (1894). However, it is a different species from the lectotype of *G. arbori*, differing from it in characters of the male and female genitalia, thus it is here established as a new species. The holotype of *Gaujonia arbori* and most of the paratypes are well preserved. Guevara and Romero (2008) misidentified this species as *Gaujonia arbosioides*, which is placed in a different genus (see *Millerana arbosioides* remarks).

***Gaujonia kanakusika* sp. nov.**

<http://zoobank.org/AE542D1A-A612-4F37-922D-F48482F5D6F7>

Figs 4, 30, 34, 66, 87, 91B, 93

Type material. *Holotype* ♂, **Colombia:** Colombia, Cundinamarca, Guasca, El Chochal de Siecha, 3120 m, 28 Nov. 2019, coll. Jose I. Martinez / UF, FLMNH, MGCL 1049048. [DNA voucher MGCL-NOC-65232] deposited in **MGCL. Paratypes** (7 ♂, 2 ♀, **MGCL**): **Colombia:** Same collecting data as holotype (1 ♂); Colombia, Cundinamarca dpt, Vereda La Concepción, Bosque La Guajira, 4°47'34"N, 75°46'60"W, 8–12.XI.2014, 2910 m, leg. V. Sinyaev & M. Márquez (2 ♂); Colombia, Cundinamarca, Municipio Guasca, Alto El Paramo, 04°53'44"N, 73°45'46"W, 29–31.12.2017, 3250 m., Leg Viktor Sinjaev and Juan Machado (1 ♂); Colombia, Cundinamarca, Municipio Guasca, near Alto El Paramo, 04°53'55"N, 73°46'21"W, 22–23.02.2018, 3070 m. Leg Viktor Sinjaev and Juan Machado (3 ♂, 2 ♀)

Etymology. The name is formed from the Quechua words *kanaku* (fire) and *sika* (caterpillar), based on the immature stages of this species (Fig. 91B).

Diagnosis. This species can be differentiated from other species by the sulfur-yellow coloration of most of the body, including the abdomen.

Description. *Head.* Palp with basal and second palpal segment sulfur-yellow, last segment with white tip; frons with small black line; female with similar wing pattern, but brighter in coloration. *Thorax.* Sulfur-yellow, covered with small black dots. *Wings.* Forewing sulfur-yellow; length: male 18–20 mm; female 27–29 mm; forewing with lines visible from posterior margin to fold; basal and antemedial lines almost completely developed; no presence of a V-shaped mark; Hind wing fringe same yellow color as body. *Legs.* Prothoracic and mesothoracic legs black with some sulfur-yellow spots on joints; tarsal scales yellow and black. *Abdomen.* Sulfur-yellow with a small area of gray in middle of dorsum divided by black and yellow tufts. *Male genitalia.* Cucullus large, rounded apically; sacculus narrow with a long process; juxta shell-shaped with apices pointed; tegumen wide; saccus narrow; aedeagus short and wide; vesica 1 ½ x as long as aedeagus with two large spine patches ca. same size. *Female genitalia.* Anal papilla small, semicircular; posterior apophysis ⅓ x longer than anal papilla; sterigma narrow and large, semi-rectangular; anterior apophysis relatively long and heavily sclerotized; corpus bursae 1 ½ x longer than appendix bursae.

Immature stages. *Egg.* Completely light green, turning dark brown close to emergence. *Larva.* In general, body pale orange with dark pink verrucae and neon-orange setae on dorsal verrucae; long pale-yellow setae on lateral verrucae; inter-tergal membrane brown with white dots (Fig. 91B). *Pre-pupa.* Darker than ultimate instar. *Pupa.* Dark brown with white setae covering the whole body.

Distribution. All specimens were found in deciduous forests from the central-north Colombia between 2900–3300 m (Fig. 93).

Biology. *Gaujonia kanakusika* is the second species in this genus known to feed on *Alnus acuminata* Kunth. Adults fly year-round, mainly in summer (JIM, pers. obs.).

Remarks. Holotype (Fig. 30) and paratypes in good condition. This species was the only one whose phylogenetic placement had low support in the gene tree; however, it shares apomorphic characters with other *Gaujonia* species, so it is maintained as a *Gaujonia*.

Gaujonia sourakovi sp. nov.

<http://zoobank.org/5ADB338A-B431-4B31-8A9E-7518B2B02939>

Figs 31, 67, 93

Type material. *Holotype* ♂, **Peru:** Peru, Department Cuzco, Manu Park, San Pedro, 1800 m, Mar. 1997, coll. local people. Deposited in MGCL. **Additional examined specimens** (1 ♂, MGCL): **Peru:** Same collecting data as holotype.

Etymology. This species was found by my colleague and friend Andrei Sourakov when he was helping me locate additional specimens deposited in the MGCL, and thus I named it in his honor for his wonderful help.

Diagnosis. *Gaujonia sourakovi* differs from other species mainly in coloration, having the most lightly marked forewing in this group. The male genitalia have the apex of the cucullus rounded, the saccular region is wide, and two patches of long hair-like spines on the vesica, differing from the others which have wider and well-developed spines.

Description. *Head.* Last segment of palp black with some yellow scales; frons yellow, shaded with black scales. *Thorax.* Dark yellow with black dorsally. *Wings.* Forewing length: male 19–21 mm; forewing scales only on venation and margins; V-shaped mark at base of CuA2 widely open; dot in the middle of base of cell M1 elongated; orbicular spot small; veins lined with black; hindwing fringe black with dark yellow scales at end of each vein, whereas area on posterior margin of hindwing brown; a black line at base of vein M3. *Leg.* Prothoracic and mesothoracic legs dark brown with yellow scales on joints, whereas metathoracic legs dark yellow with some dark brown spots. *Abdomen.* Brown with scattered black scales dorsally, paler ventrally; long yellow scales laterally; black tufts with some yellow and brown scales on A1–A4. *Male genitalia.* Cucullar area narrow and curved with apex rounded; saccular region and process wide; juxta flat on upper side; tegumen wide; aedeagus $2\frac{2}{3}$ × longer than wide; basal area of vesica 4 × longer than wide and vesica almost same width with two large patches of hair-like spines, one ovoid.

Immature stages. Unknown.

Distribution. The species *Gaujonia sourakovi* was collected in a deciduous forest at 1800 m elevation in southeastern Peru (Fig. 93).

Biology. Unknown.

Remarks. One specimen has the left forewing broken at the base and a brown patch on cell R5. Right wing with some brown patches near the outer margin between the cells R5-M2. In the other specimen the wings and left valva are broken, so it is not included as a paratype.

Gaujoptera gen. nov.

<http://zoobank.org/5EBE13A2-1698-415E-AAFD-7AFEF8916772>

Gender. Feminine.

Type species. *Gaujoptera amsa* sp. nov.

Etymology. *Gaujoptera* is derived from the similarities with the genera *Gaujonia* and *Lichnoptera*.

Included species. *Gaujoptera* is monotypic, the only species is *Gaujoptera amsa* sp. nov., which was misidentified as a *Gaujonia* species; however, morphological and molecular analyses resulted in recognizing a new genus that is positioned close to the genus *Millerana* (Fig. 1).

Diagnosis. *Gaujoptera* is only known from two well-preserved male specimens and it has a close relationship with *Millerana*, not only genetically, but also by distinct morphological characters. Nevertheless, the wing pattern is more defined in *Millerana* than in *Gaujoptera*, which has a blurry pattern that is difficult to discern. In addition, the thorax is marbled with black, gray, brown, and sulfur-yellow scales, differing from species of *Gaujonia*, which have the black spots and patches well defined on the thorax. *Gaujoptera* does not have a V-shaped mark at the base of CuA2. The most important feature to differentiate *Gaujoptera* from *Gaujonia* is the presence of small clasper on the valva, similar to that of *Lichnoptera*.

Description. Forewing and hindwing dark sulfur-yellow with an inconspicuous pattern, only reniform spot visible. Hindwing hyaline with scales only on margins. Antenna filiform, with a short brownish orange haustellum; eye hairy with short interfacial setae. Male genitalia simple in male with small triangular clasper; small, curved uncus; aedeagus shorter than vesica; vesica with small spines in middle. Female unknown.

Immature stages. Unknown.

Biology. Unknown.

Gaujoptera amsa sp. nov.

<http://zoobank.org/EAE3EDDC-BED8-4CE2-8341-126A89FBAC5D>

Figs 5, 35, 36, 68, 93

Type material. *Holotype* ♂, **Bolivia:** Bolivia, Cotapata, 16°16.8'S, 67°52.6'W, 6–7.1.2010, H = 3210 m, leg/coll. Viktor & Svetlana Sinyaev + Alexei Zamesov /

UF, FLMNH, MGCL 1049124. [DNA voucher MGCL-NOC-65307] deposited in MGCL. **Paratype** (1 ♂, MGCL): **Peru:** Peru-Junin near Calabaza vill., 11°29,8'S, 74°51,9'W, 17.12.2010, H = 2964 m, leg/coll. Viktor & Svetlana Sinyaev + Vladimir Izerskiy (1 ♂). **Additional examined specimens** (6 ♂, MGCL): **Bolivia:** same collecting data as holotype. (3 ♂); **Peru:** same collecting data as paratype. (2 ♂); Peru: Dept. Junin, Cerro Pichita, Res. Sta. nr. San Ramon, 2965 m, 7–9 Apr. 2011, coll. J. B. Heppner & C. Carrera (1 ♂).

Etymology. *Amsa* is a Quechuan word that means dark, opaque, or confused.

Diagnosis. The species *Gaujoptera amsa* has similar morphological characters with species of *Millerana*, however, it is easy to identify because the thorax has no spots or patches, but is completely marbled with black, gray, brown, and sulfur-yellow scales. The forewing is dark sulfur-yellow with a blurry pattern in gray. Additionally, the genitalia have a simple valva without any lobe or protuberances, and a small clasper is present.

Description. **Head.** Palp with last segment black with few yellow scales on tip; frons marbled. **Thorax.** Marbled in black, gray, brown, and sulfur-yellow. **Wings.** Forewing length: male 18–20 mm; forewing marbled with wing pattern in gray; pattern blurry; orbicular spot barely visible in yellow; a narrow lunate marking on reniform spot; terminal lines zigzag; hindwing hyaline with sulfur-yellow fringe. **Leg.** Prothoracic and mesothoracic legs sulfur-yellow with some brown spots; tarsi brown and yellow; metathoracic legs marbled in brown and yellow with tarsi sulfur-yellow. **Abdomen.** Sulfur-yellow with a black line of tufts in middle of abdomen on A1–A5. **Male genitalia.** Valva rectangular, simple; saccular region wide; apex densely covered by setae; clasper small, triangular; juxta shell-like; tegumen narrow; uncus small; aedeagus short, almost same width as vesica; vesica ovoid with a line of minute spines in middle, positioned diagonally.

Immature stages. Unknown.

Distribution. *Gaujoptera amsa* occurs from central Peru to northern Bolivia at high elevations ca. 3000 m or above (Fig. 93).

Biology. Unknown.

Remarks. Most of the specimens are very damaged and could only be identified by genitalia examination, except the holotype and paratype (Figs 35, 36).

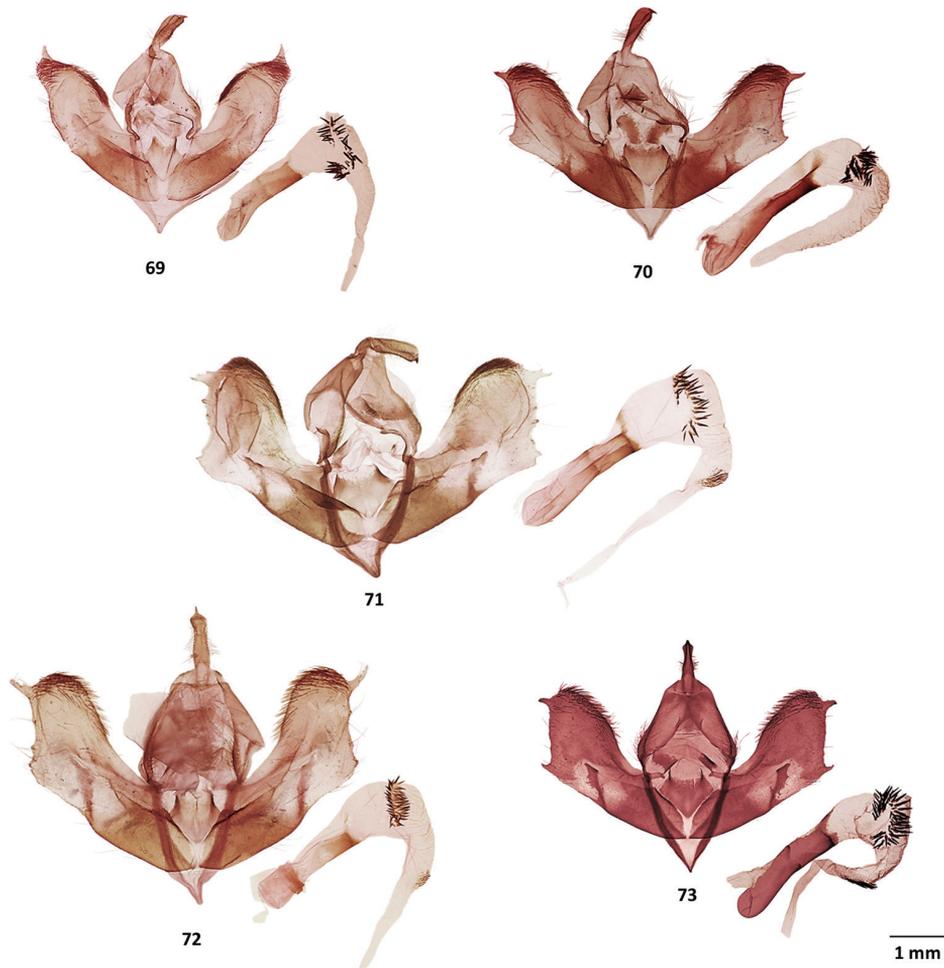
Millerana gen. nov.

<http://zoobank.org/F7EC8D53-E82F-4ECB-8896-210255E06389>

Gender. Feminine.

Type species. *Gaujonia arbosoides* Dognin, 1894. Lépidoptères de Loja et environs (équateur), descriptions d'espèces nouvelles 17: 87.

Etymology. *Millerana* is dedicated to my mentor and friend who is like a family member Dr. Jacqueline Y. Miller, an American entomologist who has worked on Lepidoptera, especially Castniidae, for nearly 40 years. However, her most important legacy has been her guidance to lepidopterists throughout the world.



Figures 69–73. Male genitalia of *Millerana* species **69** *Millerana cundinamarquensis*, holotype, MGCL, Cundinamarca, Colombia **70** *M. tigrina*, holotype, MGCL, Carchi, Ecuador **71** *M. matthewsae*, holotype, MGCL, Ancash, Peru **72** *M. cajas*, holotype, MGCL, Azuay, Ecuador **73** *M. austini*, holotype, CUIC, Cotopaxi, Ecuador.

Included species. *Millerana* is established as a new genus to include *Millerana arbosioides* Dognin originally belonged to *Gaujonia*. Additionally, five new species are recognized that were formerly confused with *M. arbosioides* because of similarities in their wing markings: *Millerana austini* sp. nov., *Millerana cajas* sp. nov., *Millerana cundinamarquensis* sp. nov., *Millerana matthewsae* sp. nov., and *Millerana tigrina* sp. nov. However, the external and internal morphology plus DNA barcoding revealed they are distinct. Females are unknown.

Diagnosis. *Millerana* is the most genetically distant genus in the *Gaujonia* genus group and is more closely related to *Gaujoptera* (Fig. 1). Externally, *Millerana* is similar

to *Cicadoforma* and *Cicadomorphus*, but smaller in size and a slightly different forewing pattern. The genitalia valva is simple as for *Cicadoforma* and *Cicadomorphus*, but much wider, with relatively long protuberances at the apex and outer margin. The vesica has a band of spines surrounding the middle area. DNA barcoding reveals that *Millerana* is distant from the other genera: *Gaujoptera* (~ 9% divergent), *Cicadoforma*, and *Cicadomorphus* (~ 18%).

Description. Orbicular spot well developed; reniform spot with small lunate marking. Forewing pale yellow with black scales, which form the forewing pattern. Hindwing with yellow scales restricted to veins and margin, extending to fringe. Antenna dark brown or brownish orange, serrate, with a stripe of pale-yellow scales on basal % of antenna. Mouthparts reduced; eyes covered by black interfacetal setae. Male genitalia: moderately sclerotized; valva wide, without clasper; apex small with a pointed extension; uncus broad, beak-like; aedeagus short, vesica with narrow band of spines around middle part of vesica.

Immature stages. *Egg.* Circular and flattened with micro-square cells formed by the chorion. *Larva.* Like many pantheines, there are five to seven instars. Late instars resemble larvae of the genus *Panthea*. Secondary setae on the abdominal tergites spine-like. White lines between the spiracles similar to those of *Panthea*. Thorax densely covered by secondary setae, with long setae on the prothorax covering head. *Pupa.* Similar to those of other species in the *Gaujonia* genus group, but remarkably smaller (see *Cicadomorphus falkasiska* immature stages) (Bollino and Onore 2001; O. Mahecha-Jiménez, pers. comm.).

Biology. *Millerana tigrina* is the only species known and is considered a pest of pine trees in Ecuador (Bollino and Onore 2001).

Key to species of the genus of *Millerana* based on adult male morphology

- 1 Valva relatively square-shaped (Figs 70–73)..... **2**
- Valva petal-like (Fig. 69) *M. cundinamarquensis*
- 2 Phallus with a band of spines on vesica close to base and another small patch of small spines apically (Figs 71–73) **3**
- Phallus with only a band of spines on vesica close to base (Fig. 70) *M. tigrina*
- 3 Antenna black; forewing with a small orbicular spot (Figs 9, 37, 38, 42) **4**
- Antenna orange; forewing with a large orbicular spot (Fig. 39) *M. matthewsae*
- 4 Cucullar region presenting outer margin with protuberances (Figs 9, 72) ... **5**
- Cucullar region without protuberances on the outer margin (Fig. 73)..... *M. austini*
- 5 Forewing with a small and elongated orbicular spot; valva with square-shaped apex (Figs 9, 37) *M. arbosioides*
- Forewing with orbicular spot rounded; valva with rounded apex (Figs 42, 72) *M. cajas*

***Millerana arbosioides* (Dognin), comb. nov.**

Figs 9, 37, 94

Gaujonia arbosioides Dognin, 1894: 87.

Type material. *Holotype* ♂, **Ecuador:** “*Gaujonia arbosioides* type ♂ Dgn. / ♂ 2700 mètres altitude, près Loja (Chonta-Cruz), 24 juin 1893 / *Gaujonia arbosioides* type ♂ Dogn., Hmpsn 15.10.12 / 1994 / Type No. 30908 U.S.N.M. / Genitalia slide m, Franclemont USNM 33565” coll. P. Dognin. Deposited in USNM. **Additional examined specimens** (2 ♂, MGCL): **Ecuador:** Ecuador, Carachi Prov., El Angel Ecological Reserve, 0°42'37"N, 78°00'12"W, 06.11.2012, H = 3560 m, Exped. Ron Brechlin & Victor Sinyaev.

Etymology. Paul Dognin likely name this species *arbosioides* in reference to its similarities to *Gaujonia arboris*, which was described previously.

Diagnosis. *Millerana arbosioides* is closely related to three species: *M. austini*, *M. cajas*, and *M. cundinamarquensis*; however, *M. arbosioides* can be recognized by the black antenna and haustellum. Forewing length in males is 16–18 mm. *Millerana arbosioides* shares more external characters with *M. cundinamarquensis*, but it can be distinguished from it by the antemedial line, which is well developed in *M. arbosioides*, the reniform spot is better defined, and the lunate marking is small; these features in *M. cundinamarquensis* are barely visible, but it presents four black tufts in the middle of 1A–4A, whereas *M. arbosioides* has three on A1–3A. The genitalia in *M. arbosioides* have a semi-squared cucullar area and some protuberances in the outer margin that are present in *M. tigrina* and *M. cajas* as well however, both species differ from *M. arbosioides* by their apexes that are rounded and their outer margins of the cucullar area, which are straighter.

Immature stages. Unknown.

Distribution. The species is known only from coniferous forests in Ecuador at very high elevations ca. 2500–3500 m (Fig. 94).

Biology. Unknown.

Remarks. One of the additional examined specimens was in very poor condition and only identifiable by genitalia examination.

***Millerana austini* sp. nov.**

<http://zoobank.org/FA2F5CB1-1F31-4006-9DA5-BA7054D91D2D>

Figs 38, 73, 94

Type material. *Holotype* ♂, **Ecuador:** Ecuador, Cotopaxi Prov., Minitrack Station paramo S of Machachi, 12,000', 10 Apr. 1958, coll. R. W. Hodges. Deposited in CUIC. **Paratypes** (4 ♂, CUIC): **Ecuador:** Same collecting data as holotype.

Etymology. The species was named after my friend Kyhl Austin, an American lepidopterist, who found this species in the dark corners of the CUIC.

Diagnosis. *Millerana austini* is similar to *M. cajas*, but it can be differentiated by the antemedial line, which is formed by a single line, whereas *M. cajas* has two. The male genitalia are without protuberances on the outer margin, except for two extensions; one near the apex and the other on the lobe; they are similar to those of *M. tigrina*; however, the outer margin of the valve is concave in *M. tigrina*.

Description. **Head.** Palp black with a small line with pale yellow underneath; frons yellow. **Thorax.** Dark yellow with dots in black. **Wings.** Forewing dark yellow with black pattern; length 17–19 mm. All lines well developed with exception of terminal line; orbicular spot circular; reniform spot incomplete, with a small lunate marking; V-shaped mark on base of CuA2 thick, black; hind wing whitish orange, veins yellowish orange. **Leg.** Prothoracic legs black with some yellow spots on joints; mesothoracic legs with some black dots on tibia; metathoracic legs yellow. **Abdomen.** Paler yellow than thorax; small tufts in black from 1A–2A. **Male genitalia.** Cucullar area wide; apex and lobe with small extensions; outer margin flat; sacculus notably wide; tegumen broad; juxta inverted, triangle-shaped; aedeagus $3\frac{1}{3}$ × longer than wide; vesica $1\frac{1}{2}$ × wider than aedeagus, gradually reduced at tip; band with large spines and thick patch of spines near apex.

Immature stages. Unknown.

Distribution. All specimens were found in a cloud forest at the north-central region of Ecuador at high elevations above 3500 m (Fig. 94).

Biology. Unknown.

Remarks. Holotype (Fig. 38) and paratypes in perfect condition.

***Millerana cajas* sp. nov.**

<http://zoobank.org/0CC0DBCA-3428-474C-B339-50C24A2776FA>

Figs 6, 42, 72, 94

Type material. **Holotype** ♂, **Ecuador:** Ecuador, Azuay Prov., Cajas Nat.Park, Road Cuenca-Pto Inca, 2°46'50"S, 79°10'58"W, 28.11.2012, H = 3615m, Exped. Ron Brechlin & Victor Sinyaev / UF, FLMNH, MGCL 1049111. [DNA voucher MGCL-NOC-65294] deposited in MGCL. **Paratype** (1 ♂, MGCL): **Ecuador:** Same collecting data as holotype.

Etymology. The only two specimens found in El Cajas National Park, Ecuador, are known.

Diagnosis. *Millerana cajas* is similar to *M. austini*. The best way to identify *M. cajas* externally is to examine the medial and postmedial lines, which are fused on the forewing. Moreover, the genitalia are very distinctive. The valva is enlarged, especially in the costal region; *Millerana cajas* has a wide apical protuberance on the valve, similar to that of *M. matthewsae*; the vesica has a distal diverticulum surrounded by a spine band.

Description. **Head.** Palp short, black and yellow, except last segment that is black with some small yellow scales; frons yellow. **Thorax.** Covered with light lemon-yellow

hair-like scales with some black spots. **Wing.** Light lemon yellow with black and gray pattern; forewing length: male 18–20 mm; forewing antemedial, medial, and subterminal lines well developed; whereas basal, postmedial, and terminal lines defined by small dots; medial line wide; orbicular spot slightly flattened; reniform spot large, incomplete, with lunate marking at base of M1 cell; V-shaped mark at base of CuA2 narrow; medial and postmedial lines fused by black scales between V-shaped mark in CuA2 and fold; hindwing whitish yellow with veins whitish orange. **Leg.** Prothoracic legs black with fuscous joints; mesothoracic and metathoracic legs yellow with a black spot on tibia; tarsi black. **Abdomen.** Paler yellow than remainder of body; tuft on middle area on A1–A5; A1–A3 black and A4–A5 yellow. **Male genitalia.** Cucullus wide, mainly in on costal area; apex with a wide extension followed by some protuberances on outer margin; saccular region wide; tegumen wide; juxta dentate, slightly curved on upper side; aedeagus $3\frac{1}{2}$ × longer than wide; opening larger than rest of aedeagus; vesica long with a distal diverticulum, which is surrounded by a band of long spines; medial area with a large patch of minute spines.

Immature stages. Unknown.

Distribution. This species was found in a deciduous forest at a high elevation in southwestern Ecuador ca. 3600 m (Fig. 94).

Biology. Unknown.

Remarks. Holotype (Fig. 42) with the right hindwing and the left forewing slightly broken; the abdomen has a spot of dead fungi; the frons has pink marker stains accidentally applied at the place where it was previously deposited. The left wings are missing in the paratype.

***Millerana cundinamarquensis* sp. nov.**

<http://zoobank.org/E138732D-E065-4421-8BDD-C51F6494882F>

Figs 39, 69, 94

Type material. **Holotype** ♂, **Colombia:** Colombia, Cundinamarca, Municipio Guasca, Alto El Paramo, 04°53'44"N, 73°45'46"W, 29–31.12.2017, 3250 m., Leg Viktor Sinjaev and Juan Machado / UF, FLMNH, MGCL 1049040. [DNA voucher MGCL-NOC-65224] deposited in MGCL. **Additional examined specimens** (1 ♂, MGCL): **Colombia:** same collecting data as holotype.

Etymology. The name is derived from the place (Department of Cundinamarca in Colombia) where this species was found.

Diagnosis. Compared with other species in *Millerana*, *M. cundinamarquensis* differs in the genitalia, in which the valva is petal-like, whereas the other two species have a rectangular valva.

Description. **Head.** Palpi short, divided by black hair-like scales on upper side and yellow underneath; last segment coated with a mix of black, white, and yellow scales; frons with sulfur-yellow scales. **Thorax.** Covered by sulfur-yellow scales with some large black spots. **Wing.** Forewing length: male 16–18 mm; forewing sulfur-yellow

with black scales defining transverse lines; antemedial, medial, and subterminal lines barely developed; basal, postmedial, and terminal lines defined by series of dots on veins; orbicular spot well-defined, oval; reniform spot blurry, with a small triangular lunate marking; CuA2 with a black V-shaped mark at base, with inferior line longer than superior line; hindwing with yellowish orange veins; fringe with pale-yellow hair-like scales; base of M2+M3 rounded. **Legs.** Yellow except prothoracic legs, which are black with pale yellow spots. **Abdomen.** Pale yellow with light-gray hair-like scales; four black tufts in the middle of A1-A4; a small pale-yellow tuft on A8 at terminus. **Male genitalia.** Cucullar area with rounded apex, apex extension claw-like; costa ovoid, covered with setae; saccular area wide; tegumen narrow and rounded; juxta with concave V-shaped depression on top; aedeagus 4 × longer than wide; opening to vesica % × total length of aedeagus; vesica long, 2 × wider than aedeagus, decreasing in width as it approaches to apex; a band of medium-size spines near basal area of vesica.

Immature stages. Unknown.

Distribution. Only two specimens are known from a cloud forest in Cundinamarca, Colombia (Fig. 94).

Biology. Unknown.

Remarks. Holotype well preserved (Fig. 39), but the other specimen, which was collected from the same location, was difficult to identify because it was practically destroyed. Thus, the identification was made by genital dissection.

***Millerana matthewsae* sp. nov.**

<http://zoobank.org/CCB1BFCF-B1ED-4ED9-A7B7-E86569702EC0>

Figs 40, 71, 94

Type material. **Holotype** ♂, **Peru:** Peru, Ancash 7 km W Yanama, 09°02,0'S, 7°32,9'W, 03.03.2011, H = 3892 m, leg. Viktor Sinyaev & Alexander Poleschuk / UF, FLMNH, MGCL 1049106. [DNA voucher MGCL-NOC-65288] deposited in MGCL. **Paratype** (1 ♂, MGCL): **Peru:** Same collecting data as holotype. **Additional examined specimens** (3 ♂, MGCL): **Peru:** Same collecting data as holotype.

Etymology. In honor of my colleague and friend Dr. Deborah Matthews-Lott, who has supported me during my travels in entomology, especially on Lepidoptera trips.

Diagnosis. *Millerana matthewsae* is closely related to *M. tigrina*; it has brownish orange antenna and can be differentiated by the wide well-defined pattern of foreign lines, and the large orbicular and reniform spots. The most distinctive character of the male genitalia is the costal margin of the valva is strongly curved upward.

Description. **Head.** Palp with long black and yellow hair-like scales; frons dark yellow. **Thorax.** Dark yellow with some black patches on dorsal area; **Wing.** Forewing length: male 18–20 mm; forewing paler yellow coloration than thorax; antemedial, medial, and subterminal lines complete; postmedial line almost complete except in area between cells of CuA1 and half of CuA2; V-shaped mark at base of CuA2 with upper line longer than lower line; terminal area covered by scattered black scales except in

M3 and CuA1 cells; orbicular spot very large, barely touching top and bottom of discal cell; reniform spot with large line marking inside of discal cell; hindwing white with veins and fringe pale yellow. **Leg.** Prothoracic and mesothoracic legs brownish orange and black with joints yellow; metathoracic legs yellow. **Abdomen.** Yellow, paler than remainder of body; dorsally with thin black tufts in middle of A1–A6 and with dark yellow tufts at A2–A3. **Male genitalia.** Cucullus wide and curved upward on costal margin; apex rounded; some protuberances in the outer margin with the upper one the largest and curved downward; sacculus wide and short; upper side of juxta has a shallow concave depression; tegumen narrow laterally; aedeagus narrow, $\frac{1}{3}$ × longer than vesica; vesica long rounded basally; Transverse band of spines near middle of vesica.

Immature stages. Unknown.

Distribution. This species has been collected only in the western zones of Peru at very high elevations almost 4000 m (Fig. 94).

Biology. Unknown.

Remarks. The holotype (Fig. 40) and the paratype have both hindwings slightly broken. The other specimens were almost destroyed with only the thorax and forewings remaining.

***Millerana tigrina* sp. nov.**

<http://zoobank.org/822C7DB2-1AFB-4CA2-9B01-0129C42AC289>
Figs 41, 70, 94

Gaujonia arbosioides Hampson, 1913 (nec. Dognin): pl. 235, fig. e2.

Gaujonia arbori Gara & Onore, 1989 (nec. Dognin): 128, figs 58, 59.

Type material. **Holotype** ♂, **Ecuador:** Ecuador, Carchi road Tulcan – El Chical, 0°48'19"N, 78°00'10"W, 12–13. II 2013, 3400 m, leg. Sinjaev & Romanov / UF, FLMNH, MGCL 1049105. [DNA voucher MGCL-NOC-65287] deposited in MGCL. **Paratype** (1 ♂, MGCL): **Ecuador:** Ecuador, Azuay Prov., Cajas Nat. Park, Road Cuenca-Pto Inca, 2°46'50"S, 79°10'58"W, 28.11.2012, H = 3615 m, Exped. Ron Brechlin & Victor Sinyaev.

Etymology. The name refers to the tigrina, *Leopardus guttulus* (Hensel), in keeping with the wild feline names, as with the other genera, since they are known as “the jaguar moths.”

Diagnosis. *Millerana tigrina* can be distinguished from *M. matthewsae* by the large, well-rounded orbicular spot. *Millerana tigrina* also has distinctive genitalia, with the valva presenting a pronounced concavity on the outer margin, forming a moon-shaped crescent.

Description. **Head.** Palp covered with hair-like scales with dorsal side black and ventral side whitish yellow; last segment black with small whitish yellow dot internally; frons yellow. **Thorax.** Covered with yellow hair-like scales with black patches. **Wing.** Forewing length: male 17–19 mm; forewing yellow with black scales forming wing

pattern; basal line barely visible; antemedial and medial lines disrupted at discal cell; reniform spot large, with small lunate marking in middle; orbicular spot rounded, almost as high as discal cell; two V-shaped marks, one at base of R1+R2, other one at base of CuA2; hindwing whitish silver with yellow fringe; veins yellow. **Leg.** Prothoracic and mesothoracic legs dark brown with some patches of black and pale yellow; metathoracic legs pale yellow with dark brown from tibia to claws. **Abdomen.** Covered with pale-yellow, hair-like scales; three small black tufts on A1–A3; a pale-yellow terminal tuft. **Male genitalia.** Outer margin of cucullar area concave, with two small protuberances, one subapical and lateral to apex and other one smaller, on lower end of lobe; saccular area wide; tegumen wider dorsally and squared; juxta concave posteriorly; aedeagus 3 × longer than wide; a diagonal opening to vesica $\frac{1}{3}$ length of aedeagus; vesica almost as long as aedeagus; transverse band of spines near base.

Immature stages. **Egg.** Bright green; turns dark green close to emergence. **Larva.** Five to seven instars; body brown with black and pale-brown secondary setae arising from pink verrucae; diagonal pinkish white lines laterally between spiracles; spiracles white; thorax covered with secondary setae; two tufts of on each side of second tergite. **Pre-pupa.** Similar to last instar, but darker and with secondary setae shorter. **Pupa.** Dark brown.

Distribution. The two specimens of *Millerana tigrina* were found in the highest elevations of the Andes in Ecuador (Fig. 94).

Biology. Only one species is known in this genus, *Millerana tigrina*, which was discussed first by Bollino and Onore (2001). Adults are active throughout the year, but mainly during summer. Larvae resemble some species of the genus *Panthea*, which also feed on pine trees. Larvae have been observed to feed on *Podocarpus magnifolius* J. Buchholz & N.E. Grayand and *Quercus humboldtii* Bonpl as well (O. Mahecha-Jiménez pers. comm.).

Remarks. The type specimen (Fig. 41) has a small patch of dead fungi on the ventral side of the abdomen. The specimen from Azuay is in poor condition but is still identifiable. This species was misidentified as the female of *Millerana arbosoides* by Hampson (1913) (as *Gaujonia arbosoides*) and Seitz (1919–1944). In addition, the larvae are reported as pine tree pests in Ecuador (Gara and Onore 1989), but was misidentified as *Gaujonia arbori*. Unfortunately, the pictures of the immature stages provided by O. Mahecha-Jiménez were not of good enough quality to be included in this revision.

***Oculicattus* gen. nov.**

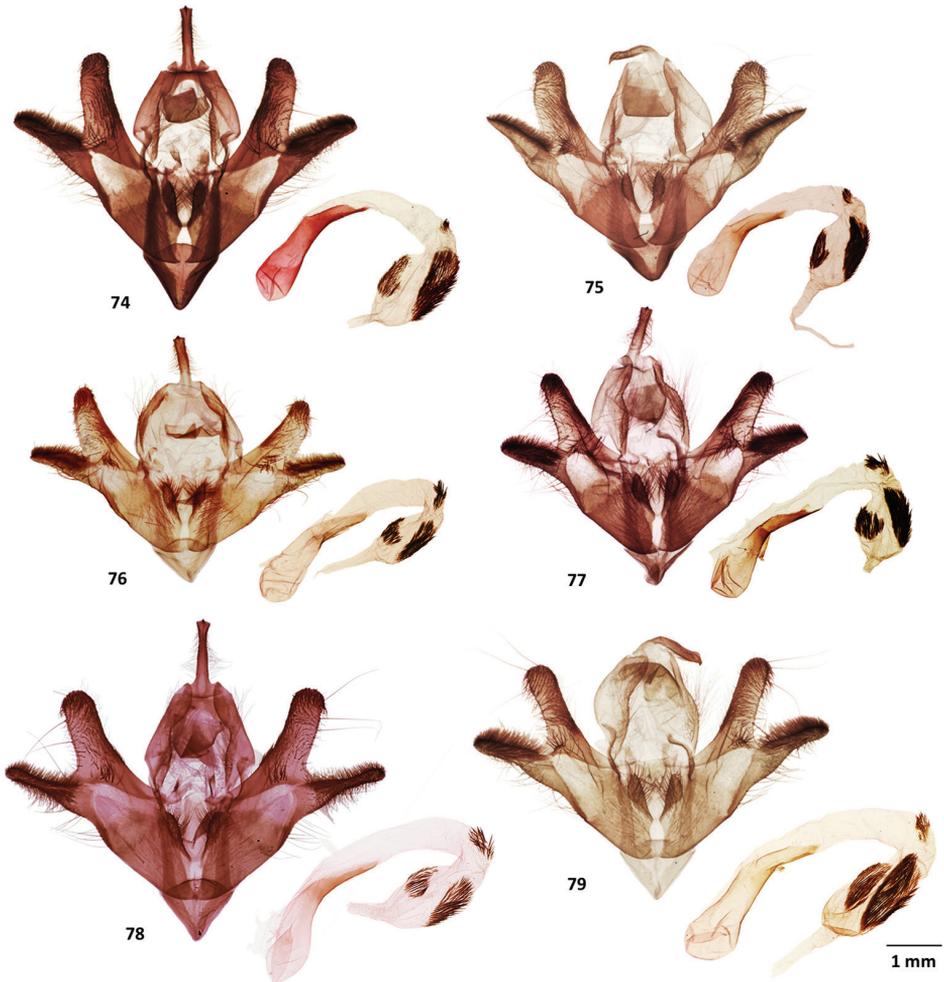
<http://zoobank.org/5372CF2B-65A3-49D9-89DC-3270DA5E8035>

Gender. Masculine.

Type species. *Gaujonia renifera* Hampson, 1913. Catalogue of Lepidoptera Phalaenae in the British Museum 13: 385, 387, pl. 235, fig. 4.

Etymology. *Oculicattus* refers to the reniform spot, which is black and surrounded with yellow scales, giving it the appearance of a cat's eye.

Included species. *Oculicattus* is a new genus established for *Gaujonia renifera* (Hampson), which was misplaced in the genus *Gaujonia*. This genus also includes six new spe-



Figures 74–79. Male genitalia of *Oculicattus* species **74** *Oculicattus inca*, holotype, MGCL, Sierra Siberia, Bolivia **75** *O. boliviana*, holotype, MGCL, Sierra Siberia, Bolivia **76** *O. uturunku*, holotype, MGCL, Morona, Ecuador **77** *O. brehmi*, holotype, FSU, Loja, Ecuador **78** *O. raizae*, holotype, MGCL, Tolima, Colombia **79** *O. schmidti*, holotype, MGCL, Pasco, Peru.

cies, *Oculicattus boliviana* sp. nov., *Oculicattus brehmi* sp. nov., *Oculicattus inca* sp. nov., *Oculicattus raizae* sp. nov., *Oculicattus schmidti* sp. nov., and *Oculicattus uturunku* sp. nov., which are morphologically and genetically distinct from the genus *Gaujonia*.

Diagnosis. *Oculicattus* can be differentiated from *Gaujonia* externally by the presence of the large reniform spot in *Oculicattus*, as well as by other features (see *Gaujonia* diagnosis).

Description. Sexually dimorphic in size, females larger than males; forewing and hindwing hyaline with sulfur-yellow and black scales covering veins and wing margins.

Forewing with a small black or sulfur-yellow orbicular spot, sometimes barely perceptible; reniform spot elongated, outlined in black; elongated black central line surrounded by sulfur-yellow outline, except for *O. raizae* and *O. uturunku*, in which the spot is entirely black. Antenna filiform, brownish orange with a sulfur-yellow band on basal to three quarters of antenna; eyes with coppery interfacetal setae. Male genitalia slightly sclerotized; valva with saccular and cucullar regions separated, without clasper; uncus long and narrow ending in beak-like tip; vesica has spine patch; vesica wider than its base, which has two patches of spines with one patch of spines larger than other. Female genitalia medium sized; lightly sclerotized rectangular-shaped sterigma; appendix bursae elongate and rugose; corpus bursae for most species approximately half size of appendix bursae.

Immature stages. Unknown.

Biology. Unknown.

Key to species of the genus of *Oculicattus* based on adult male morphology

- 1 Forewing with reniform spot poorly defined and not outlined (Figs 49–51)....2
- Forewing with well-developed and outlined reniform spot (Figs 43–48, 52, 53).....3
- 2 Thorax and forewing brownish yellow with brown pattern; valva with cucullar region wide and rounded apically; short aedeagus; wide patch of spines close to basal area (Figs 50, 51, 78) *O. raizae*
- Thorax and forewing black with some spots in sulfur-yellow; valva with cucullar area wide at basally and remarkably narrow apically; aedeagus elongate; thin patch of spines in basal area (Figs 49, 76) *O. uturunku*
- 3 Saccular process tapered to a pointed apex (Figs 75, 79)4
- Saccular process is blunt or rounded (Figs 74, 77).....5
- 4 Forewing with a small black orbicular spot and a large reniform spot; aedeagus, short, wide (Figs 48, 75) *O. boliviana*
- Forewing with a small yellow orbicular spot and a narrow reniform spot; aedeagus long, narrow (Figs 45, 46, 79) *O. schmidti*
- 5 Cucullus with same width overall; vesica long with both apical patches ovoid (Figs 10, 74)6
- Cucullar region wider at base than apex; vesica short with a truncated patch apically (Fig. 77) *O. brehmi*
- 6 Ground color grayish yellow; thorax with gray patches dorsally; A3 on abdomen with large yellow dorsal tuft; vesica short with a small patch of spines near more basal than apical; (Figs 47, 74) *O. inca*
- Ground color pale brownish yellow; brownish black spots scattered on thorax dorsally; line of black and yellow tufts on A1–A3 on dorsum of abdomen; long vesica, with a large patch of spines near the middle point of the vesica (Figs 10, 43, 44) *O. renifera*

***Oculicattus boliviana* sp. nov.**

<http://zoobank.org/AC56D195-6D14-4D26-9090-3E3B3D8235EF>

Figs 48, 75, 95

Gaujonia arbori Gowin, 2017 (nec. Dognin): pl. 47 fig. 6.

Type material. *Holotype* ♂, **Bolivia:** Bolivia, Sierra Siberia, 16 km SE Pojo, 17°49.1'S, 64°42.5'W, 14.12.2009, H = 2308 m, leg/coll. Viktor & Svetlana Sinyaev + Alexei Zamesov. Deposited in MGCL. *Paratypes* (2 ♂, MGCL): **Bolivia:** Same collecting data as holotype (1 ♂);, La Higuera, 18°47.7'N, 64°12.1'W, 19–20.12.2009, H = 2050 m, leg/coll. Viktor & Svetlana Sinyaev + Alexei Zamesov (1 ♂).

Etymology. This species is only found in Bolivia, hence the proposed name.

Diagnosis. This species can be distinguished from *O. renifera*, and *O. schmidti* by the large lunate mark in the reniform spot, being lightning bolt shaped, and by the small orbicular spot. The male genitalia have the saccular process with a sharply pointed tip; uncus thin. *Oculicattus uturunku* and *O. boliviana* share almost identical mtDNA, however, distribution and biology, in addition to morphology demonstrate that they are different species.

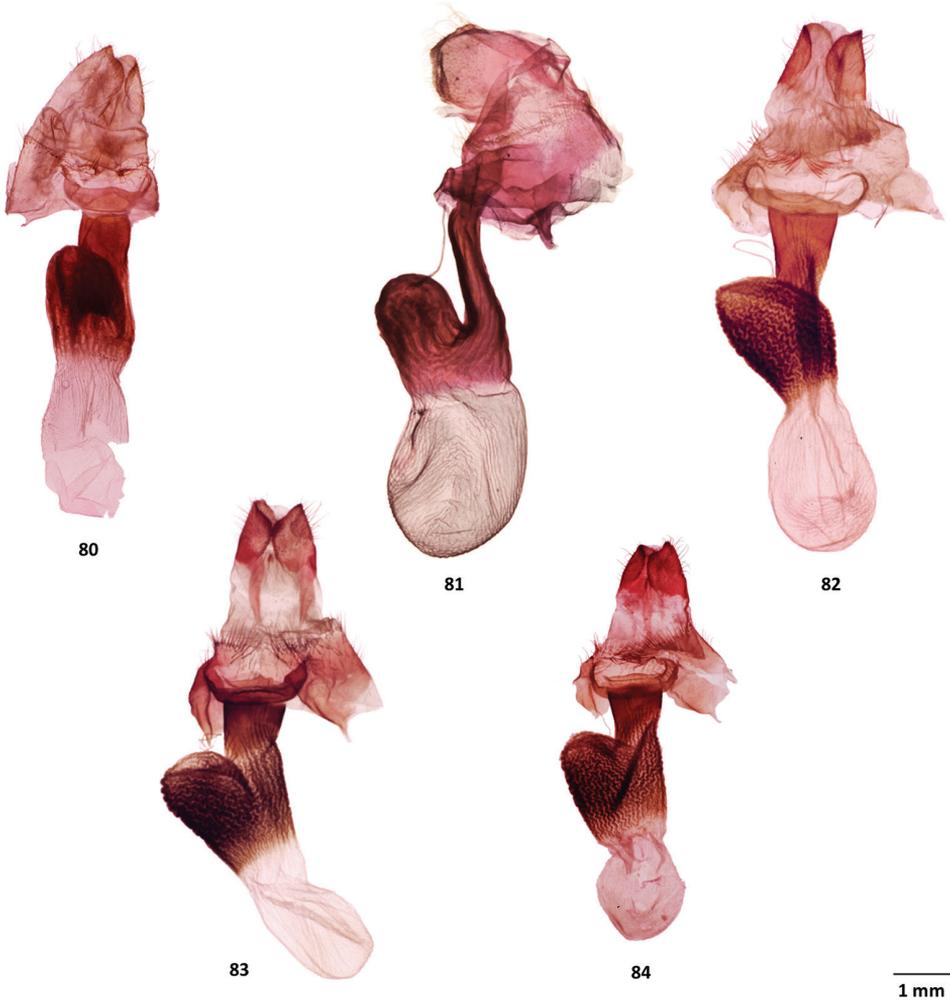
Description. *Head.* Segments of palp divided in black upper side and yellow underside; two large black spots posterior to antenna. *Thorax.* Almost entirely light yellow with some small black spots on dorsal area. *Wing.* Light yellow with wide black lines; forewing length: male 17–19 mm; forewing yellow, like rest of body, with black stripes defining pattern; reniform spot with large lightning bolt-like lunate marking; orbicular spot black, small, outlined in pale yellow; open V-shaped mark on CuA2 at base wide; fringe on hindwing light yellow with black terminal line, interrupted at the veins; posterior margin with fringe whitish yellow; vein yellow with three lines on each vein from M1 to CuA2. *Leg.* Prothoracic leg black with tibia and metatarsi yellow, whereas tarsi black, even at joints. *Abdomen.* Bright yellow with dorsal region clothed with dark brown scales; dorsal abdomen with yellow tufts and a thin black line on A1–A5. *Male genitalia.* Cucullar area wide, densely covered by hair-like setae; apex tapered; saccular area relatively narrow, ends in sharp process with a sharply pointed tip; saccular process with setae mainly confined to upper side; saccus V-shaped, considerably flat on tip; juxta flat on upper side and narrow on under side; tegumen wide; uncus thin; aedeagus $1\frac{2}{3}$ × longer than wide; vesica base $\frac{1}{2}$ × as long as vesica; two oval-shaped subapical spines patches, with small cluster of spines is near the middle of the dorsal wall of the vesica.

Immature stages. Unknown.

Distribution. The specimens were collected in south-central Bolivia at high elevations above 2000 m (Fig. 95).

Biology. Unknown.

Remarks. Holotype (Fig. 48) and paratypes are in perfect condition. This species was originally misidentified as *Gaujonia arbori* by Gowin (2017), which is endemic to Ecuador, and is here assigned to a different genus and it was photographed at Laguna Verde-Comarapa and Achira Arriba in Bolivia.



Figures 80–84. Female genitalia of *Cicadoforma* and *Cicadomorphus* species **80** *Cicadoforma ocelotus*, paratype, MGCL, Santander, Colombia **81** *C. vau-nigrum*, CNC, El Junquito, Venezuela **82** *Cicadomorphus liliana*, paratype, FSU, Zamora-Chinchi, Ecuador **83** *C. falkasiska*, paratype, MGCL, Oaxapampa, Peru **84** *C. chuya*, paratype, MGCL, Cochabamba, Bolivia.

***Oculicattus brehmi* sp. nov.**

<http://zoobank.org/8F0D6FD9-CCCF-4A0A-8EE0-B17AB28E16A4>

Figs 52–55, 77, 89, 95

Type material. Holotype ♂, **Ecuador:** Ecuador, 8 km SE of Loja, Parque Nacional Podocarpus Cajanuma, mont. Rainforest, Blacklight 2 × 15W (50), 04°06.86'S, 79°10.48'W, 20.ix.2008, 2897 m, Florian Bodner leg / DNA Barcode run 2010, COI-5P marker, University of Guelph / Arcec 32176. [DNA voucher Arcec 32455] deposited in FSU. **Paratypes** (1 ♂, FSU): **Ecuador:** Ecuador, Zamora-Chinchi Parque Na-

cional Podocarpus, Cerro Toledo, Elfin Forest, Blacklight 2 × 15W (70), 04°23.13'S, 79°07.11'W, 6.II. 2013, 19.00–22.00 h, 2938 m, Gunnar Brehm leg. / DNA Barcode run 2013, COI-5P marker, University of Guelph / leg sampled in ethanol G. Brehm, Green vial caps / [Arcec 30239] (1 ♂). (4 ♂, 2 ♀, MGCL): **Ecuador:** Ecuador, Napo + 10 km Papallacta, 2730 m, 13–15 Sep. 1982, coll. N. Venedictoff (1 ♂, 2 ♀); Ecuador, Napo, Cosanga, 2150 m, 1 Feb. 1976, coll. N. Venedictoff (3 ♂). **Additional examined specimens** (2 ♂, 1 ♀ NJD): **Ecuador:** Ecuador, Eastern slopes of the Andes, east of Quito near Cosanga, Yanayacu Biological Research Station, 2100 m, 27 Aug. 2013, “YAN13_0136”, N. J. Dowdy (1 ♂); Ecuador, Eastern slopes of the Andes, east of Quito near Cosanga, Yanayacu Biological Research Station, 2100 m, 27 Aug. 2013, “YAN13_0056”, N. J. Dowdy (1 ♂); Ecuador, Eastern slopes of the Andes, east of Quito near Cosanga, Yanayacu Biological Research Station, 2100 m, 27 Aug. 2013, “YAN13_0072”, N. J. Dowdy (1 ♀).

Etymology. The name is in honor of a great lepidopterist, Dr. Gunnar Brehm, who loaned some specimens for this research.

Diagnosis. *Oculicattus brehmi* is the smallest species in this genus; pattern formed by relative pale, thin markings. Orbicular spot small, black. There V-shaped mark at the base of CuA2 is small. Male genitalia have a tapered cucullar region, wider at the base; the saccus smaller and more tapered than in other species, and the saccular process is the second shortest in the genus with only *O. uturunku* being shorter than *O. brehmi*.

Description. Head. Wide, palp large, with last segment marbled in light yellow and black; frons pale yellowish gray; female similar to male, even in coloration. **Thorax.** Covered with dark sulfur-yellow scales and with small gray spots on dorsum. **Wing.** Pale yellow with pattern of thin dark gray lines; forewing length: male 16–18 mm; female: 21–23 mm; forewing with thin dots and stripes forming lines; lunate marking in reniform spot narrowly outlined by a thin yellow line; orbicular spot black, small; V-shaped mark at base of CuA2 small; hindwing with fringe yellow with long yellow lines between veins terminally. **Leg.** Prothoracic leg brown with joints pale yellow; mesothoracic legs marbled in brown and yellow, tarsi brown with each joint yellow; metathoracic legs yellow. **Abdomen.** Pale yellow with dorsal area gray; dorsal tufts sulfur-yellow along middle of abdomen, smaller on A1–A2, whereas A5–A8 are wide and combined with gray scales. **Male genitalia.** Cucullus tapered with small rounded apex and base wide, heavily covered with setae; sacculus wide with process long and densely clothed with setae; saccus V-shaped, and more narrowly tapered towards the end; juxta wide deeply concave posteriorly, with the outer edges sharply pointed; tegumen wide; aedeagus $1\frac{1}{4}$ × length of vesica to medial cluster of spines; vesica with small patch of spines near middle; apical part of vesica bulbous, with large tapered patch of spines on each side. **Female genitalia.** anal papilla rounded posteriorly; posterior apophysis $\frac{1}{3}$ × longer than anal papilla; anterior apophysis $\frac{2}{3}$ × shorter than posterior apophysis; sterigma crescent moon shaped; corpus bursae $\frac{1}{4}$ × longer than appendix bursae.

Immature stages. Unknown.

Distribution. This species has been recorded only in Ecuador (Fig. 95).

Biology. Unknown.

Remarks. Holotype (Fig. 52) and paratypes are in good condition; specimens from NJD were soaked in 100% ethanol with only the wings in good condition; they were kept in -80°C for molecular DNA analyses, so they are not included with the type series.

***Oculicattus inca* sp. nov.**

<http://zoobank.org/7DFAA7B1-E42A-4864-AB61-8E071D5A5C81>

Figs 47, 74, 95

Type material. *Holotype* ♂, **Peru:** Peru, Department Cuzco, Manu Park, San Pedro, 1800 m, Mar. 1997, coll. local people / UF, FLMNH, MGCL 1049174. [DNA voucher MGCL-NOC- 65359] deposited in MGCL. *Paratypes* (8 ♂, MGCL): **Peru:** Same collecting data as holotype (4 ♂); **Bolivia:** BoliviaA, Sierra Siberia 18 km SE Pojo, $17^{\circ}50.2'S$, $64^{\circ}42.1'W$, 12–13.12.2009, H = 2442 m, leg/coll. Viktor & Svetlana Sinyaev + Alexei Zamesov (2 ♂); Bolivia, La Paz, Cotapata, $16^{\circ}16.5'S$, $67^{\circ}51.6'W$, 24.10.2010, H = 3200 m, leg. Viktor Sinyaev & Oleg Romanov (1 ♂); Bolivia, La Paz, Santa Rosa de Lima, $16^{\circ}23.6'S$, $67^{\circ}41.8'W$, 20–22.10.2010, H = 1550 m, leg. Viktor Sinyaev & Oleg Romanov (1 ♂).

Etymology. This species is named after the Inca Empire, which originated in the area around Cusco.

Diagnosis. *Oculicattus inca* is similar to *O. renifera*; however, there are some morphological features that are useful to differentiate them. *O. inca* is slightly smaller, darker in coloration, the orbicular spot smaller, and wing lines are thinner than in *O. renifera*; the lunate marking in the reniform spot is not outlined in yellow. Genitalia have a wider cucullus; the juxta is flattened posteriorly, whereas in *O. renifera* the posterior margin has a V-shaped invagination. The DNA barcodes differ by 5% between the two species.

Description. *Head.* Last segment of palp divided in black upper side and yellow under side; frons yellow with some gray scales. *Thorax.* Grayish yellow with some small gray patches. *Wing.* Forewing length: male: 19–21 mm; forewing grayish yellow with markings wide; orbicular spot small, elongated, grayish yellow, outlined with black scales and with some black scales inside orbicular spot; reniform spot with lunate marking not outlined; V-shaped mark short; hindwing with fringe black, vein ends yellow, with some black scales on vein CuA2. *Leg.* Prothoracic and mesothoracic legs black anteriorly, yellow posteriorly, whereas metathoracic legs all yellow. *Abdomen.* Dorsal area brown with some yellow scales between each tergite; a large yellow tuft on A3; last abdominal segment with long yellow scales. *Male genitalia.* Cucullar and saccular regions large; saccus triangular; juxta V-shaped with posterior part flattened; vesica $1\frac{1}{2} \times$ size of aedeagus; Vesica with small patch of spines near middle of vesica; bulbous apical part of vesica with large dense patch of spines posteriorly and smaller, less dense patch anteriorly.



Figures 85–90. Female genitalia of *Gaujonia* and *Oculicattus* species **85** *Gaujonia arborisi*, MGCL, Napo, Ecuador **86** *G. chigyaq*, holotype, MGCL, Marinio, Colombia **87** *G. kanakusika*, paratype, MGCL, Cundinamarca, Colombia **88** *Oculicattus renifera*, MGCL, Cusco, Peru **89** *O. brehmi*, paratype, MGCL, Napo, Ecuador **90** *O. raizae*, paratype, MGCL, La Paz, Bolivia.

Immature stages. Unknown.

Distribution. Broadly distributed in the cloud forests in Peru and Bolivia (Fig. 95).

Biology. Unknown.

Remarks. Holotype is in perfect condition (Fig. 47). This species was originally labeled as *Oculicattus renifera*, but DNA barcoding showed that the two species are genetically distinct.

***Oculicattus raizae* sp. nov.**

<http://zoobank.org/BD31472B-72CC-4B58-B011-ED8E5339F5D4>

Figs 50, 51, 58, 78, 90, 95

Type material. *Holotype* ♂, **Colombia:** Colombia, Tolima, Nevado del Tolima, 4°36'02"N, 75°19'51"W, 2600 m, 05–07.12.2013, legit Victor Sinyaev & Mildred Márquez Martínez / UF, FLMNH, MGCL 1049101. [DNA voucher MGCL-NOC-65284] deposited in MGCL. *Paratypes* (6 ♂, 1 ♀, MGCL): **Ecuador:** Same collecting data as holotype (2 ♂); Ecuador, Carchi, El Angel Ecological Reserve, 0°45'31"N, 78°01'40"W, 7–8. XI 2012, 3320 m, leg. Sinjaev & Romanov (1 ♂); Ecuador, Carchi prov., El Moran, 0°45'50"N, 78°02'38"W, 1–3.05.2012, H = 2940 m, Exped. Ron Brechlin & Victor Sinyaev (1 ♂); Ecuador, Pichincha, Camping Bella Vista, 2230 m, 0°00'41"S, 78°41'17"W, 19.XII.2012–7.I.2013, leg. Sinjaev & Romanov & [coll.] Dr. R. Brechlin (1 ♂); Ecuador, Pichincha, Quito/Chiriboga, K40, 2480 m, 22 Mar. 1982, coll. N. Venedictoff (1 ♀); **Peru:** Peru-Junin Near Calabaza vill., 11°30,4'S, 74°51,7'W, 20.12.2010, H = 2722 m, leg/coll. Viktor & Svetlana Sinyaev + Vladimir Izerskiy (1 ♂); **Bolivia:** BOLIVIA, La Paz, Death road Coroico, 16°18.3'S, 67°48.8'W, 28–30.10.2010, H = 3060 m, leg. Viktor Sinyaev & Oleg Romanov (1 ♀). **Additional examined specimens** (1 ♂, ZSM): **Ecuador:** Ecuador, Anden Oskordillere, Prov. Pichincha, Tandayapa, Km. 3 S (Bellavista, Lodge), 2310 m, 00°03'694"N, 78°40'929"W 1–20.ix.2012, Dietl Monika + Stefan &, R. Beck leg. / BC ZSM Lep 65183 / coll. G. Behounek, grafiing bei München / "*Gaujonia renifera* ♂" (1 ♂).

Etymology. The species is dedicated to my wife, Raiza Castillo, for her love and support since the beginning of my career.

Diagnosis. *Oculicattus raizae* is closely related to *O. uturunku*; they differ from the other *Oculicattus* species by the darker color, and the unusual reniform spot that is completely brown or black. *Oculicattus raizae* can be identified by its brownish yellow coloration, and the brown forewing pattern. In the male genitalia the cucullus is longer and wider than in *O. uturunku*. Additionally, DNA barcodes are ca. 4% different.

Description. *Head.* Palp reduced in size; dorsal surface covered by brown scales, ventral surface by dark sulfur-yellow scales; frons covered by dark sulfur-yellow scales, mixed with black; female similar to male externally. *Thorax.* Dark sulfur-yellow with some brown patches. *Wing.* Forewing with dark sulfur-yellow and brown scales covering venation and margins; forewing length: male: 22–24 mm; female: 27–29 mm; antemedial, postmedial, and subterminal lines not defined; orbicular spot small, poorly-defined oblong brown spot; reniform spot brown, narrow, and barely defined; base of CuA2 with Y-shaped mark large, brown; a brown line across fold on cell at CuA2; hindwing hyaline with some dark sulfur-yellow scales on venation, but more notable along margins; a Y-shape mark at base of CuA2; some small brown lines scattered through M3+CuA1+CuA2. *Leg.* Dark sulfur-yellow with brown patches on anterior area of prothoracic legs, which is lighter on mesothoracic and metathoracic legs. *Abdomen.* Clothed in grayish yellow hair-like scales with white scales at terminus and with a dark sulfur-yellow tuft on A8. *Male genitalia.* Cucullus wide, parallel



Figure 91. A, B seventh instar larva **A** *Cicadomorphus falkasiska*, Oxapampa, Peru **B** *Gaujonia kanakusika* Cundinamarca, Colombia.

sided with the apex rounded; costal margin swollen basally; sacculus triangular with saccular process entirely coated with setae; tegumen wide; saccus broadly V-shaped; juxta small with parallel sides and a V-shaped notch posteriorly; aedeagus $3 \times$ longer than wide, with a wide opening to vesica ca. $\frac{1}{4} \times$ total length of aedeagus; vesica with basal area ca. same width that of aedeagus, and it is ventrally curved; basal area with a large patch of spines; vesica with two patches of spines on each side, one small slightly beyond middle of dorsal wall of the vesica, and truncated anteriorly, whereas other larger apically narrow, and broader towards the aedeagus. **Female genitalia.** Small and truncated apically; anal papilla with posterior apophysis $\frac{1}{4} \times$ shorter than anal papilla; anterior apophysis short; rectangular sterigma that is fused above ostium; ductus bursae wide and long; appendix bursae $\frac{2}{3} \times$ shorter than corpus bursae which is partially sclerotized at base.

Immature stages. Unknown.

Distribution. Recorded from cloud forests in Colombia, Ecuador, Peru, and Bolivia in middle and high elevations from 2000 m to above 3000 m (Fig. 95).

Biology. Unknown.

Remarks. A specimen of *Oculicattus raizae* was misidentified as *G. renifera* by G. Behounek and posted on Barcode Of Life Data System v4 (www.barcodinglife.org). Holotype (Fig. 50) and paratypes are well preserved.

***Oculicattus renifera* (Hampson), comb. nov.**

Figs 7, 10, 43, 44, 56, 57, 88, 95

Gaujonia renifera Hampson, 1913: 387, pl. 235, fig. 4.

Type material. Holotype ♂, Peru: “*Gaujonia renifera* type ♂ Hmpsn. / Agualani S. E. Peru, 9000 ft, 05’ May, G. Ockenden / 1908-159 / Noctuidae ♂ genitalia slide No. 5208 / NHMUK 010917655”, coll. G. Hampson. Deposited in NHMUK. **Addi-**

tional examined specimens (8 ♂, MGCL): **Peru:** PERU-JUNIN Near CALABAZA vil., 11°30,5'S, 74°49,4'W, 1–2.02.2011, H = 2137 m, leg. Viktor Sinyaev & Alexander Poleschuk (1 ♂); Peru, Department Cuzco, Manu Park, San Pedro, 1800 m, Mar. 1997, coll. local people (2 ♀); Peru, Cusco, Wayqecha Biological Station, 2950 m, 29 Oct 2010, coll. C. V. Covell Jr / FLMNH, MGCL 1049183 / DNA voucher MGCL-NOC- 65325 (1 ♂); **Bolivia:** BOLIVIA, SIERRA SIBERIA, 16 km SE Pojo, 17°49.1'S, 64°42.5'W, 16–17.01.2010, H = 2308 m, leg/coll. Viktor & Svetlana Sinyaev + Alexei Zamesov (2 ♂); BOLIVIA, La Paz, Cotapata, 16°16.5'S, 67°51.6'W, 24.10.2010, H = 3200 m, leg. Viktor Sinyaev & Oleg Romanov (1 ♂); BOLIVIA, La Paz, Santa Rosa de Lima, 16°23.6'S, 67°41.8'W, 20–22.10.2010, H = 1550 m, leg. Viktor Sinyaev & Oleg Romanov (1 ♂).

Etymology. George F. Hampson probably named this species *renifera* based on the characteristic reniform spot.

Diagnosis. Regarding *Ocullicattus renifera*, there is one species that is particularly similar to it (*O. inca*); however, *O. renifera* can be identifiable by its remarkably large yellow orbicular spot. The male is pale yellow, brighter yellow in the female. The forewing length in males is 19–21 mm and females 24–26 mm. Palp reduced, black with white tips; frons yellow and gray; antenna dark orange; male thorax dark yellow with scattered brownish black spots. Pattern on the forewing in male is created by black small lines and dots; the reniform spot has slightly curved and wide lunate marking. The hindwing has dark scales on the veins. The abdomen is brown with yellow scales dorsally, differing from *O. inca* in having a line of black tufts over the middle of the dorsum of the abdomen; black tufts on A1–A3 combined with yellow scales. Genitalia of male with the cucullar region narrow and the apex rounded; saccular area with the process almost same size that the cucullus; aedeagus long, almost the same size of the vesica; large patch of spines on the base of the vesica; the two spine patches large and wide similar size covering $\frac{3}{4}$ of the vesica. Genitalia in female with sterigma relatively open, with the corpus bursae almost the same size as the appendix bursae.

Immature stages. Unknown.

Distribution. *Ocullicattus renifera* is restricted to Peru and Bolivia (Fig. 95).

Biology. Unknown.

Remarks. Many of the new species are similar to this species making the process of identification difficult. The holotype is in perfect condition (Fig. 10).

***Ocullicattus schmidti* sp. nov.**

<http://zoobank.org/3A0958E1-36B7-4885-AB26-E4C210B2BB1D>

Figs 45, 46, 79, 95

Type material. *Holotype* ♂, **Peru:** Peru-Pasco 15 km SW Oxapampa, 10°42,2'S, 75°28,1'W, 10.02.2011, H = 1977 m, leg. Viktor Sinyaev & Alexander Poleschuk / UF, FLMNH, MGCL 1049179. [DNA voucher MGCL-NOC- 65328] deposited in

MGCL. **Paratypes** (6 ♂, MGCL): **Peru:** Peru, Dept. Junin, Cerro Pichita, Res. Sta. nr. San Ramon, 2165 m, 7–9 Apr. 2011, coll. J. B. Heppner & C. Carrera (2 ♂); Peru, Department Cuzco, Manu Park, San Pedro, 1800 m, Mar. 1997, coll. local people (3 ♂); **Bolivia:** Bolivia, La Paz, Cotapata, 16°16.5'S, 67°51.6'W, 24.10.2010, H = 3200 m, leg. Viktor Sinyaev & Oleg Romanov (1 ♂).

Etymology. The name of this species is in honor of my colleague and friend Dr. B. Christian Schmidt, who shared his knowledge with me about Noctuoidea without hesitation.

Diagnosis. *Oculicattus schmidti* has a set of remarkable characters that separate it from other species, such as the orbicular spot is rounded; the lunate marking of the reniform spot is incomplete, being similar to those of *Gaujonia* species; the forewing is more stylized with straighter margins. The male genitalia are similar to those of *O. boliviana*, but can be distinguished from them by the cucullar region, which is narrower than those of other species; the saccular is large and densely covered with setae; also the uncus is wider and the saccus longer than the other species of *Oculicattus*. The DNA barcode is similar to that of *O. renifera*; however, external and internal morphology reveal enough differences to identify the two species.

Description. **Head.** Palp marbled in black and white with frons yellowish gray; black patch between antennae small. **Thorax.** Covered in yellow with some black patches on dorsum. **Wing.** Forewing length: male 17–19 mm; forewing, dark yellow with well-developed lines from posterior margin to fold that look similar to those of other *Oculicattus* species; reniform spot with lunate marking narrowed in middle of base of cell M1; orbicular spot small, outlined in black, rounded; V-shaped mark on CuA2 base small, with upper line longer, extending to lower side of reniform spot; hindwing with fringe marbled in yellow and black; posterior margin with a combination of yellow and brown hair-like scales; veins yellow with two black lines in middle of veins from M2 to CuA2; black line posterior to base of CuA2. **Leg.** Prothoracic and mesothoracic legs marbled in yellow and black; metathoracic legs yellow. **Abdomen.** Dark yellow with dorsum clothed with dark brown and black scales; yellow tufts in middle of A1–A4 with a small vertical line on each tuft. **Male genitalia.** Cucullus bullhorn-like, with pointed apex heavily coated with setae; sacculus narrow with its process long and wide, densely covered with setae; terminus of saccular process tapered to apex; saccus long rhomboid-shaped, tip barely rounded; juxta shield-shaped and upper side concave; juxta with an expanded upper side; wide tegumen; aedeagus $\frac{1}{4}$ × longer than basal area of vesica, remarkable curved inwards; vesica $\frac{2}{3}$ × longer than wide; one of patches of spines on tip small slightly squared and other covering $\frac{1}{3}$ of whole vesica.

Immature stages. Unknown.

Distribution. This species is distributed from Central region of Peru and to the east region of Bolivia (Fig. 95).

Biology. Unknown.

Remarks. Holotype in perfect condition (Fig. 45), paratypes in good condition even though the forewings are slightly damaged, but they are still well preserved.

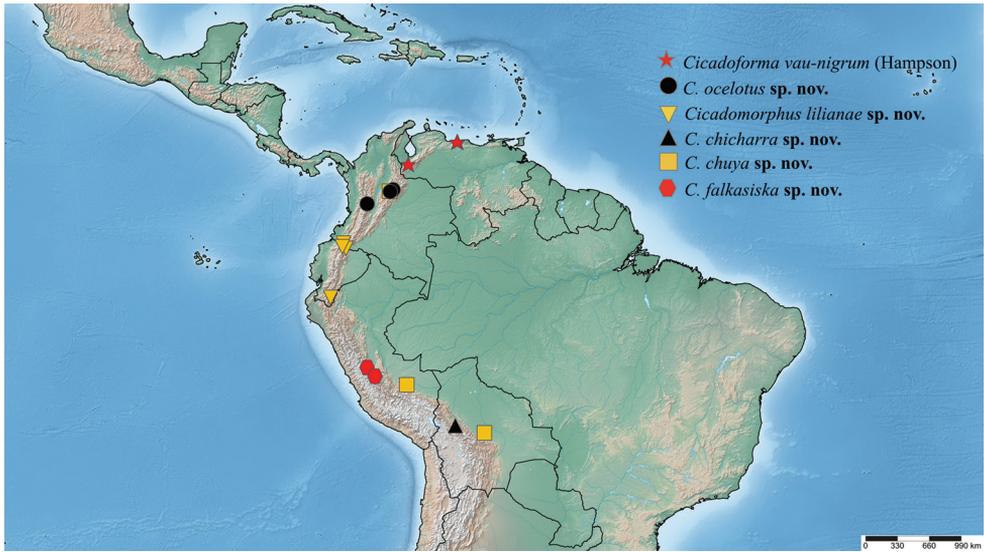


Figure 92. Distribution of examined specimens of the genera *Cicadoforma* and *Cicadomorphus*.

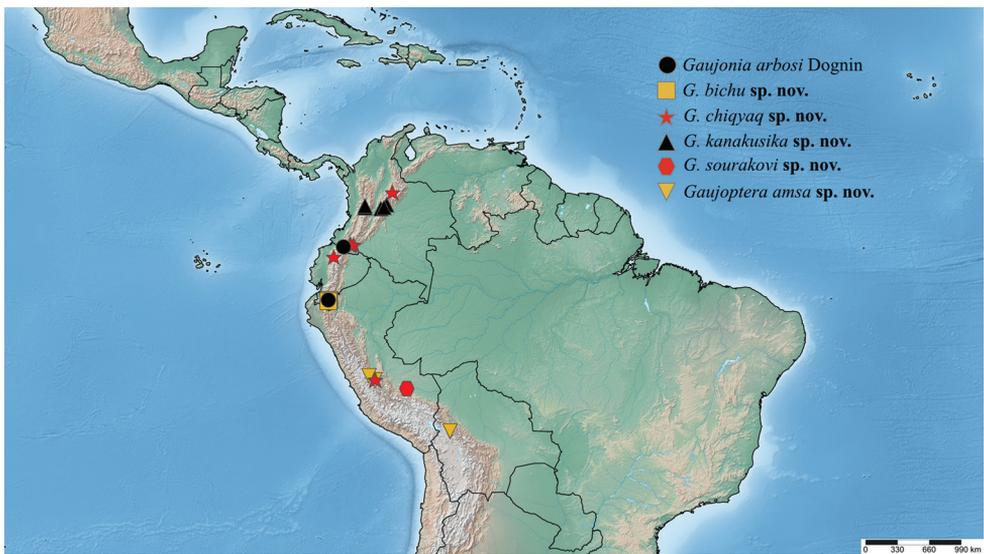


Figure 93. Distribution of examined specimens of the genera *Gaujonia* and *Gaujoptera*.

Oculicattus uturunku sp. nov.

<http://zoobank.org/6C34E855-780E-4A8F-9BF5-C1E39FE26236>

Figs 49, 76, 95

Type material. *Holotype* ♂, **Ecuador:** ECUADOR, Morona, Santiago 9km. Road Plan de Milagro – Gualaceo, 3°00'04"S, 78°30'49"W, 15.02.2012, H = 2375m,

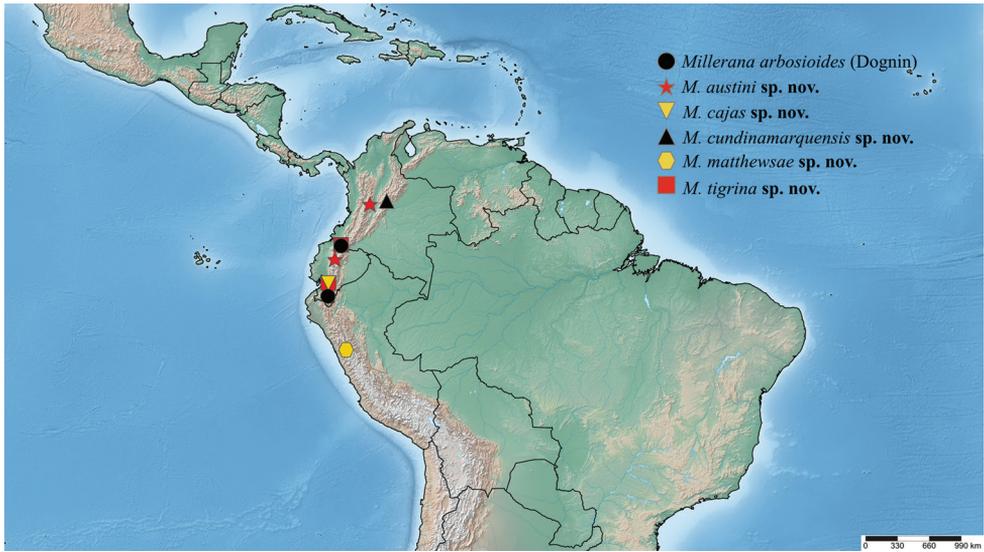


Figure 94. Distribution of examined specimens of the genus *Millerana*.

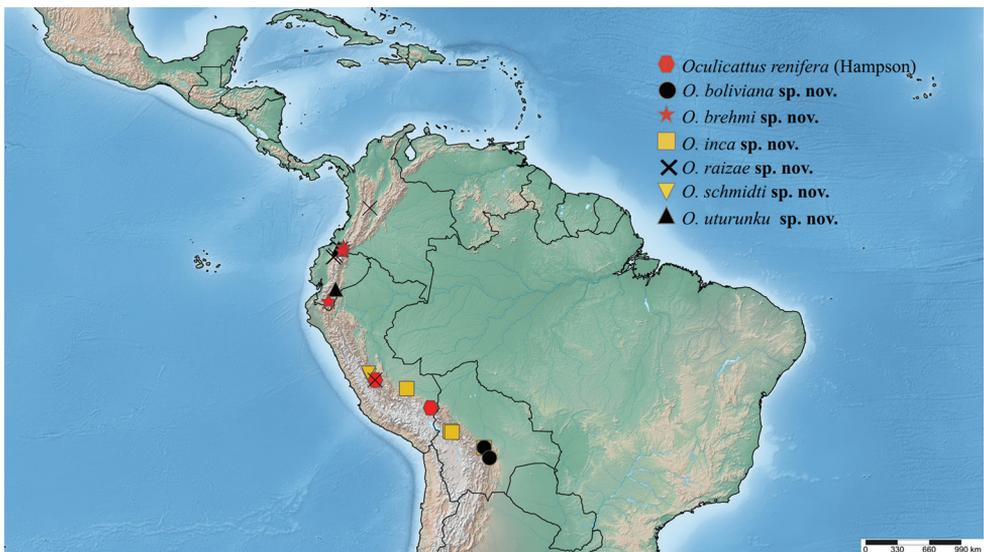


Figure 95. Distribution of examined specimens of the genus *Oculicattus*.

Exped. Ron Brechlin & Victor Sinyaev / FLMNH, MGCL 1049085. [DNA voucher MGCL-NOC- 65266] deposited in MGCL. **Paratypes** (3 ♂, MGCL): **Ecuador:** ECUADOR, CARCHI Prov., El Angel Ecological Reserve, 0°45'31"N, 78°01'40"W, 7–8.11.2012, H = 3320 m, Exped. Ron Brechlin & Victor Sinyaev (1 ♂); ECUADOR, Carchi prov., El Moran, 0°45'50"N, 78°02'38"W, 1–3.05.2012, H = 2940 m, Exped. Ron Brechlin & Victor Sinyaev (1 ♂); ECUADOR, CARCHI Prov., El Chical

– Carolinæ 0°50'20"N, 78°13'39"W, 20.11.2012, H = 2360 m, Exped. Ron Brechlin & Victor Sinyaev (1 ♂).

Etymology. The name *uturunku* makes reference to the jaguar *Panthera onca* (Linnaeus) in the Quechua language.

Diagnosis. There is only one species that has similar characters to *O. uturunku*, which is *O. raizae*. Nevertheless, they are easy to separate because the color black is predominant in *O. uturunku* and the yellow is secondary. The reniform spot is black and quite smaller, converging with long black lines making it look like an eyelash. Genitalia of the male are remarkably smaller than *O. raizae*, mainly the cucullus, which is also remarkably narrower.

Description. **Head.** Palp with last segment divided into three parts, base and tip yellow and middle area black; frons dark yellow, with a large black band between antennae. **Thorax.** Marbled in black and sulfur-yellow dorsally, and sulfur-yellow ventrally. **Wing.** Forewing length, male 20–22 mm; forewing black with some regions of sulfur-yellow; enormous black lines on veins define forewing pattern; black orbicular spot small and elongated; unusual reniform spot eyelash-like, black; black line through inferior region of discal cell barely touching base of CuA2; hindwing with black fringe and some sulfur-yellow scales at end of each vein paler than forewing, whereas that from posterior margin completely gray; veins black with some spots of sulfur-yellow. **Leg.** Prothoracic and mesothoracic legs black with some sulfur-yellow on joints, and metathoracic legs in yellow. **Abdomen.** Black with segments sulfur-yellow ventrally, whereas dorsally dark gray, paler on first three segments; A1–A3 with tufts in yellow and with some black scales. **Male genitalia.** Cucullus wider on base and apex small; costal margin curved; sacculus and process wide; saccus narrow and rhomboid-shaped; juxta square-shaped with base narrower; tegumen narrow; aedeagus 3 × longer than wide; basal area of vesica 1 ½ × longer than vesica itself; large slightly curved patch of spines close to basal area; one of patches of spines on tip small with triangular terminus and another larger covering almost ½ of vesica.

Immature stages. Unknown.

Distribution. *Oculicattus uturunku* occurs mainly in the Western Cordillera of the Andes in Ecuador. It is found at high to very high elevations (Fig. 95).

Biology. Unknown.

Remarks. Holotype (Fig. 49) and paratypes in good condition. The species *Oculicattus uturunku* has been confused with *Gaujonia* nr. *renifera* by Piñas et al. (2002). The DNA barcode is very similar to *O. schmidti* (see *O. schmidti* diagnosis)

Discussion

The Andean genus *Gaujonia* had not been properly studied since its discovery more than a century ago (Dognin 1891), and thus its life cycle and taxonomic status, were essentially unknown. Nevertheless, during this revision, I found that *Gaujonia* was not a monophyletic group, but included species representing five genera. It is worth

mentioning that the whole generic complex showed signs of mtDNA introgression or introgressive hybridization, found by studying Cytochrome c oxidase subunit I (COI), which has been observed in other groups of noctuoids even in other member of the subfamily Pantheinae (Schmidt and Sperling 2008; Anweiler 2009; Otim et al. 2018, Schmidt and Anweiler 2020).

The above morphological characters and the DNA barcode data demonstrated that the members of the *Gaujonia* genus group are sister to each other, but surprisingly despite similarities between the *renifera* and *arbosi* groups, the *arbosi* and *vau-nigrum* groups were more closely related; thus, all four groups were separated into different genera. The *arbosi* group is established now as the true *Gaujonia* due to significant differences with the other groups. Three new genera, *Millerana* gen. nov., *Oculicattus* gen. nov., and *Cicadoforma* gen. nov., are proposed for *arbosioides*, *renifera*, and *vau-nigrum* groups, respectively. In addition, there were other specimens that were misidentified as *Gaujonia* sp., but molecular and morphological analyses demonstrated that they belong to different genera (*Gaujoptera* gen. nov. and *Cicadoforma* gen. nov.). *Gaujoptera* gen. nov. was found to be closely related to the genus *Millerana* and the *Gaujonia* generic group, whereas *Cicadomorphus* gen. nov. is close to *Cicadoforma* gen. nov. In addition, the species *Gaujonia kanakusika* proved to be genetically different from the other species in the genus *Gaujonia*, however, the apomorphic characters observed in this species were not sufficient to separate this species into a different genus.

On the other hand, it was found that the *Gaujonia* genus group is represented by cryptic genera, which have similar morphology but are genetically distant, such as *Gaujonia* and *Oculicattus*, as well as *Cicadoforma* and *Cicadomorphus*. However, the same problem was observed with the molecular characters in some species groups: *Gaujonia arbosi*–*G. chiqyaq*, *Oculicattus boliviana*–*O. uturunku*, and *O. schmidti*–*O. renifera*, which showed slight differences in the COI sequences. Therefore, both morphological and molecular characters played a critical role to make an appropriate identification, not only in this genus group, but in general since there are many cryptic genera and species that are still misidentified or even undiscovered.

In addition, despite what was proposed by Schmidt and Anweiler (2020) about the closer relationship between *Arctioptera* Schmidt & Anweiler and the rest of the jaguar moths based on similar external morphology, the phylogenetic analysis placed *Arctioptera* closer to the genera *Meleneta* Smith and *Charadra* Walker. The internal morphology also shows more similar characters with the genus *Colocasia* than with the jaguar moths.

Another important discovery was that some endemic species (*Cicadomorphus falkasiska* and *Gaujonia kanakusika*) are specialists on at-risk plants such as *Alnus acuminata* Kunth and *Prunus subcorymbosa* Ruiz ex Koehne and thus are themselves vulnerable to extinction (IUCN 2019). Additionally, these species along with others, are restricted to small areas. Therefore, the group is an ideal target for conservation efforts.

Finally, it was found that larvae of *Cicadomorphus falkasiska* regurgitate a transparent highly alkaline chemical compound, which was observed to deter ants (JIM pers. obs.).

Acknowledgements

I thank Jacqueline Y. Miller and Andrew D. Warren, the MGCL at the Florida Museum of Natural History, and the University of Florida for providing the specimens and facilities for this project, as well as John B. Heppner (MGCL), Gunnar Brehm (FSU), Gottfried Behounek, Axel Hausmann (ZSM), Nick Dowdy (MPM), Kyhl Austin, and Jason Dombroskie (CUIC), who also provide additional specimens. Special thanks are due to the CNC Noctuoidea team Christian Schmidt, Donald Lafontaine and Jocelyn Gill for training me, but mainly for their kindness and support during the time of this project, and my friends Christi Jaeger (CNC), David Plotkin, and Ryan St Laurent (MGCL), who helped me with the barcoding process and the manuscript editing. I am especially indebted to Alberto Zilli at the NHMUK and Paul Goldstein at the USNM for providing the pictures of the type species. I also want to thank the following people who contributed at some point with personal loans and donations, or advising me during the process of this work: Charles V. Covell Jr., Andrei Sourakov, Debbie Matthews, Bo Sullivan, Toni Kasiske, Victor Sinyayev, Falk Zahlaus, Chris A. Johns, Oscar Mahecha-Jiménez, Francisco Serna-Cardona, Valentina Vergara-Navarro, Oscar Rojas, Juliana Torres, and Andres Gonzalez. To my wife Raiza Castillo for help me with photo editing. To National Geographic Society (EC-51416R-18) and CONACyT for financial support in part of this project.

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Supplementary material I

Table S1

Authors: Jose I. Martinez

Data type: genetic data

Explanation note: Sequences information employed in this study available at GenBank (<http://www.ncbi.nlm.nih.gov/Genbank>) and BARCODE OF LIFE DATA SYSTEM v4 (<http://barcodinglife.com>).

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Link: <https://doi.org/10.3897/zookeys.985.51622.suppl1>

Supplementary material 2

Figure S1

Authors: Jose I. Martinez

Data type: image

Explanation note: Phylogeny of *Gaujonia* and related genera based on a maximum likelihood analysis of a mitochondrial cytochrome oxidase I (COI) dataset.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/zookeys.985.51622.suppl2>

Supplementary material 3

File S1

Authors: Jose I. Martinez

Data type: sequencing data

Explanation note: FASTA file containing the alignment of all COI sequences of the taxa used in the Figure 1 and Figure S1.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/zookeys.985.51622.suppl3>

Supplementary material 4

File S2

Authors: Jose I. Martinez

Data type: phylogenetic data

Explanation note: Tree file in NEWICK format correlated with the gene tree in the Figure 1 and Figure S1.

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Four new species of the genus *Diduga* Moore, [1887] (Lepidoptera, Erebidae, Arctiinae) from China and Malaysia

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Abstract

In this paper, four species of the genus *Diduga* Moore, [1887] from China (Chongqing and Guangdong) and Malaysia (Borneo, Sabah) are described as new to science, namely *D. simianshana* **sp. nov.**, *D. chebalinga* **sp. nov.**, *D. chewi* **sp. nov.**, and *D. hollowayi* **sp. nov.** Adults of these species are illustrated in color, and images of the male and female genitalia are provided. A distribution map of the new species is provided, together with an updated checklist of all species of *Diduga*.

Keywords

Lithosiini, morphology, moth, Southeast Asia, taxonomy

Introduction

The genus *Diduga* belongs to the tribe Lithosiini in the subfamily Arctiinae, and was established by Moore ([1887], in 1884–1887), based on the type species *Diduga costata* Moore, [1887] from Dickoya, Sri Lanka. Before the establishment of the genus *Diduga*, Snellen (1879) had published a new species from India as *Pitane flavicostata*. Between 1891 and 1918, Hampson (1891, 1900, 1911, 1914, 1918) studied the genus *Diduga* and described eleven new species from the Oriental and Australian regions. After that, *D. haematiformis* Eecke, 1920 was described from Indonesia.

Subsequently, the study of the genus entered a stage of stagnation until the turn of the new century. Fang (2000) recorded *D. flavicostata* from China. Holloway (2001) reviewed the faunistics and systematics of Bornean Lithosiini and recorded five species of *Diduga*, including three new ones, namely *D. barlowi*, *D. ciliata*, and *D. dorsolobata*. More recently, Černý and Pinratana (2009), Bucsek (2012, 2014), Singh et al. (2014), Bayarsaikhan et al. (2018, 2019, 2020), Bae et al. (2019), and Bucsek (2020) have described a total of 22 new species from Southeast Asia (see checklist). To date, this genus comprises therefore 39 described species worldwide, with the majority (25) described in the past two decades.

Materials and methods

The specimens were collected using a 220V/450W mercury light and a DC black light in Chongqing Municipality (Mt. Simian), Guangdong Province (Chebaling), China, and the Borneo Jungle Girl Camp, Malaysia. Standard methods for dissection and preparation of genitalia slides were followed Kononenko and Han (2007). The vesicae were not everted and the relative position of cornuti along them is given as if they had been everted. Specimens were photographed using a Nikon D700 camera; the genitalia slides were photographed using an Olympus photo microscope controlled via Helicon Focus software, further processed in Adobe Photoshop CS6. The type materials of the new taxa are deposited in the collection of Northeast Forestry University, Harbin, China.

Abbreviations used:

NEFU Northeast Forestry University, Harbin, China
 TL Type locality
 TS Type species

Taxonomic account

Family Erebidae Leach, [1815]

Subfamily Arctiinae Leach, [1815]

Tribe Lithosiini Billberg, 1820

Genus *Diduga* Moore, [1887]

Diduga Moore, [1887]. The Lepidoptera of Ceylon 3 (4): 535. TS: *Diduga costata* Moore, [1887]. TL: Ceylon, [= Sri Lanka], Dickoya.

= *Androstigma* Hampson, 1893. Illustrations of typical specimens of Lepidoptera Heterocera in the collection of the British Museum 9: 13, 82. TS: *Diduga albicosta* Hampson, 1891. TL: India, Nilgiri Plateau.

Diagnosis. Species of *Diduga* are small in size. The proboscis is fully developed, the labial palpus is slender, directed upwards over the top of the head; the male antennae vary from ciliated to bipectinated. The tibial spurs are long.

In the male abdomen, the 8th tergite is narrowed, with long and slender apodemes (Fig. 13); and the genitalia has narrow but long lateral hairpencils in many species. The configuration of valva may vary; usually they are simple, long, slender, and tapered, or short with several distinct processes, sometimes showing bilateral asymmetry. In the female genitalia, the ductus and corpus bursae range considerably in length.

Most species have brown forewings with white or yellowish margins along the costa and distally, or forewings are medium brown with darker fasciae and stigmata. There are often various hairpencils and androconial tufts on the wings of males. In addition, the forewings have a complete set of veins arising from the cell, R_1 to R_3 , all extending to the costal margin, R_4 and R_5 have a common stem, the others are independent. In the hindwing, R_s and M_1 have a common stem, M_2 is absent, the others are independent (Fang 2000; Holloway 2001).

***Diduga simianshana* sp. nov.**

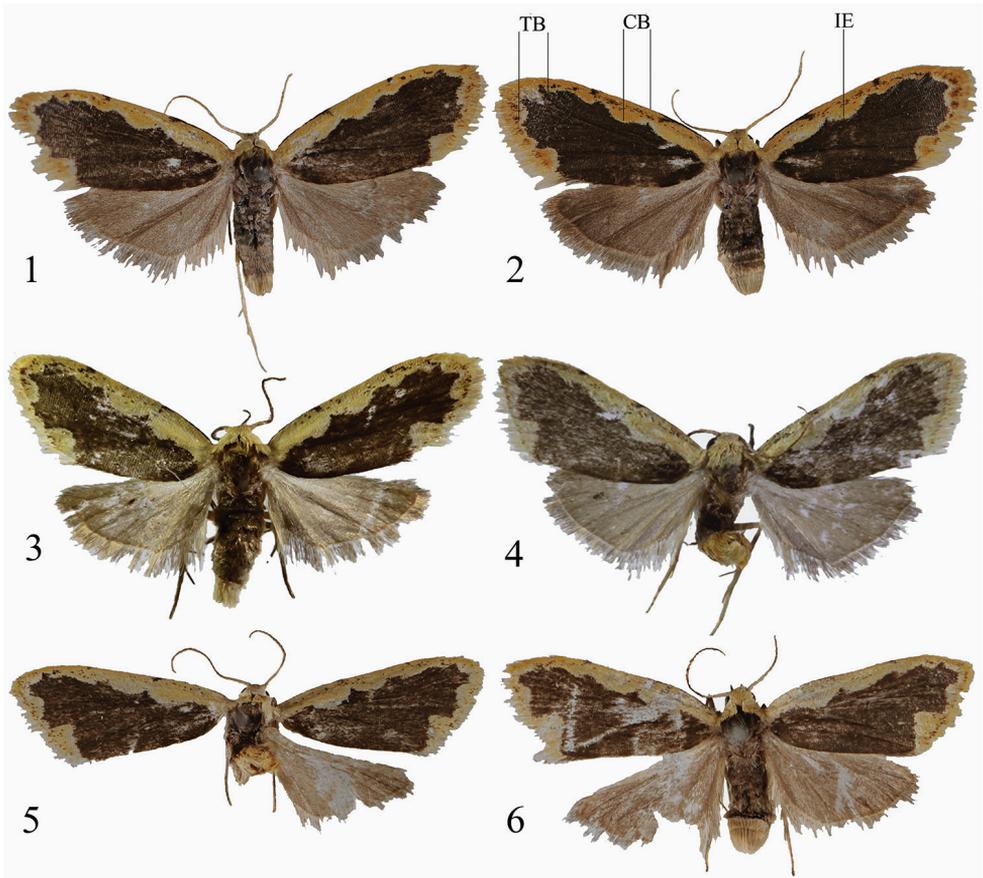
<http://zoobank.org/2598C94C-A258-4CEE-96EC-6FA25FF15A06>

Figs 1, 2, 14, 22, 28

Material examined. Holotype: CHINA: ♂; Chongqing, Jiangjin, Mt. Simian; 28.584°N, 106.356°E, elevation 1103 m; 12–13.VII.2018; leg. H.L. Han & C. Zhang; genit. prep. no. ztt-070-1; in NEFU. **Paratypes:** 3 ♀♀; same data as holotype; genit. prep. nos. ztt-073-2, ztt-074-2, ztt-080-2; in NEFU.

Diagnosis. The new species is externally similar to *D. nigridentata* Bayarsaikhan & Bae, 2019 (Figs 3, 15). It can be separated from the latter by the following characters (*D. nigridentata* details are between parentheses): the ground color of the forewing is darker; an approximate right-angled bulge at tornal area (with arched bulge); the ground color of the hindwing is darker, in the male genitalia, the two basal projections of valva are longer than tegumen (shorter); the left cucullus bears two small spines (only a single long spine); the right cucullus and costal process are fused (separated); the cornutus is long and straight (short and arched).

Description. Adult: (Figs 1, 2) Wingspan 13–14 mm. Head yellow; antenna fili-form, brown. Thorax dark brown, patagium and tegula yellow. Abdomen with pale yellow anal tuft. Forewing with dark brown ground color; costal band broad, yellow, with several small, dark brown dots, its inner edge undulated; median line absents at costa but present as a dot at the inside inner edge of costal band; terminal band of same color as costal one, inner edge of terminal band undulated, with an approximate right-angled bulge at tornus; terminal line with an admixture of brown and yellow; fringe yellow. Hindwing smoky brown, with diffuse, small, dark brown flecks; fringe pale to smoky brown, light yellow basally. **Male genitalia** (Fig. 14). Tegumen triangular, weakly



Figures 1–6. Adults of *Diduga* spp. **1** *D. simianshana* sp. nov., male, holotype, China (Chongqing) **2** ditto, female, paratype, China (Chongqing) **3** *D. nigridentata*, male (after Bayarsaikhan and Bae 2019) **4** *D. quinquicornuta*, male (after Bayarsaikhan and Bae 2019) **5** *D. chebalinga* sp. nov., male, holotype, China (Guangdong) **6** ditto, female, paratype, China (Guangdong). CB: costal band; IE: inner edge of costal band; TB: terminal band.

sclerotized, as long as uncus; the basal projections of tegumen asymmetrical, strongly sclerotized, clavate, with a triangular denticle distally; left one with large hemispherical tubercle distally, right one fist-shaped. Vinculum U-shaped, sclerotized, thick. Valva rather flat, broad, asymmetrical; the left one longer and wider; sacculus long, mostly straight, barely shorter than whole valva, saccular process curved, fingerlike, with long, sclerotized terminal spine; costa very narrow, thick, as long as valva; cucullus strongly sclerotized and tapered into elongate subtriangular process, with a long stout spine distally; the right one flat, sacculus narrow and straight, saccular process curved, fingerlike, with a shorter terminal spine; costa narrow; cucullus strongly sclerotized and tapered, with a long stout spines distally. Uncus sinuous, short and thick basally; swollen before pointed, hooked apex. Aedeagus cylindrical, smoothly curved, coecum swollen and

short, ca 1/9 as long as overall aedeagus; vesica with a small triangular cornutus, and a slender, long cornutus accompanied by a small band of hair. **Female genitalia** (Fig. 22). Ostium bursae rough and weakly sclerotized, the 8th abdominal segment shaping a deeply invaginated V-shaped ostium bursae; two triangular lobes at both sides. The posterior margin of the 7th abdominal has a distinctly sunken fold. The 6th abdominal segment slightly thickened posteriorly, with slight ridges on both sides. Ductus bursae long and narrow, twisted at middle, its posterior half strongly sclerotized, flat and straight, and anterior one membranous, partly rugose. Corpus bursae globular, membranous, with a ring-shaped signum band. Apophysis anterior rather thick, ca 5/8 as long as apophysis posterior, this slender and long. Papillae anales cone-shaped, covered with setae.

Etymology. The species is named after the type locality, Mt. Simian, Chongqing Municipality, China.

Distribution. China (Chongqing: Mt. Simian) (Fig. 28).

Habitat. The species was collected by light trap close to an evergreen broadleaf forest. The main tree species in the collecting biotope are *Engelhardia roxburghiana* Wall., 1831 and *Cunninghamia lanceolata* (Lambert) Hooker, 1827.

***Diduga chebalinga* sp. nov.**

<http://zoobank.org/43F89C07-B094-454F-946B-85BAF7C9DA71>

Figs 5, 6, 16, 23, 28

Material examined. Holotype: CHINA: ♂, Prov. Guangdong, Shaoguan, Chebaling National Nature Reserve; 24.731°N, 114.267°E, elevation 463 m; 29.IV–3.V.2019; leg. H. L. Han & J. Wu; genit. prep. no. ztt-078-1; in NEFU. **Paratype:** 1♀; same data as holotype; genit. prep. no. ztt-077-2; in NEFU.

Diagnosis. The new species is externally similar to *D. quinquicornuta* Bayarsaikhan & Bae, 2019 (Figs 4, 17, 24). It can be separated from the latter by the following characters (*D. quinquicornuta* details between parentheses): the wingspan is broader; the tegumen is thin (thick); the right costal process is long, wide, flat, and rounded distally (short, hornlike, sharp distally); the cucullus is sclerotized, thick, spoon-shaped, with a short horn distally (poorly sclerotized, club-shaped, wrinkled); the uncus is slightly swollen medially, not bending ventrally (wider and flat, hooked apex); in the female genitalia, the ostium bursae is strongly sclerotized, wrinkled, and bending to the left (weakly wrinkled, typical); the ductus bursae is curved, gradually broadening from anterior to posterior (typical, tapered); the corpus is divided into two parts, a posterior part membranous, and the anterior one globular, densely covered small flecks (long oval, anterior half with dense, small flecks, and more than 6 signa forming a vertical semicircle, posterior half membranous, smooth).

Description. Adult: (Figs 5, 6) Wingspan 13–14 mm, female larger than male. Head yellow; antenna filiform. Thorax dark brown; patagium, and tegula yellow. Abdomen brown, with pale yellow anal tuft. Forewing with dark brown ground color; costal band broad, yellow, with dispersed small, dark brown scales; its inner edge

undulated; terminal band of same color as costal one, and its inner edge undulated, with an approximately right-angled bend near tornus; terminal line with an admixture of brown and yellow; fringe yellow. Hindwing smoky brown, fringe pale to smoky brown. **Male genitalia** (Fig. 16). Tegumen triangular, thin, and narrow superiorly. Vinculum broadly V-shaped, sclerotized, thick. Valva asymmetrical and bifurcated; in the left one, basal projections of valva bifurcated, one short, the other one ca 6 times as long as the short one; sacculus thick, gradually broadening distally; saccular process narrow, smoothly arched; costa rather broad, smooth, with a curved, cone-shaped ampulla; costal process strongly sclerotized, thick, wedge-shaped; harpe short, cone-shaped, strongly sclerotized, cucullus spoon-shaped, with short, sclerotized horns distally; in the right one, sacculus weakly sclerotized, swollen, basal process lumpy; saccular process strongly sclerotized, short, sharp distally; costa broad, smooth, with a long, flat ampulla; costal process membranose; cucullus strongly sclerotized, bifurcated, one slender, rounded distally, the other one finger-shaped, distally. Uncus thick, covered with setae, slightly swollen medially, ca 7/9 as long as tegumen. Aedeagus weakly sclerotized, with small bulge at coecum; vesica with a small flecks plate at ventral part of basal. **Female genitalia** (Fig. 23). Ostium bursae broad, bent to left, with thick and sclerotized frame; lamella antevaginalis tongue-shaped. The 7th abdomere strongly sclerotized, wrinkled, densely covered with setae. Ductus bursae curved, gradually broadening posteriorly. Corpus bursae divided, anterior half globular, densely covered with small flecks, posterior half membranous, thin, and wrinkled. Papillae anales broad, covered with setae.

Etymology. The species is named after the type locality, Chebaling National Nature Reserve, Guangdong Province, China.

Distribution. China (Guangdong: Chebaling) (Fig. 28).

Habitat. The species was collected using a light trap close to a typical evergreen broadleaf forest of the mid-subtropics near the Zhangdong River. The main tree species in the collecting biotope is *Cunninghamia lanceolata* (Lambert) Hooker, 1827.

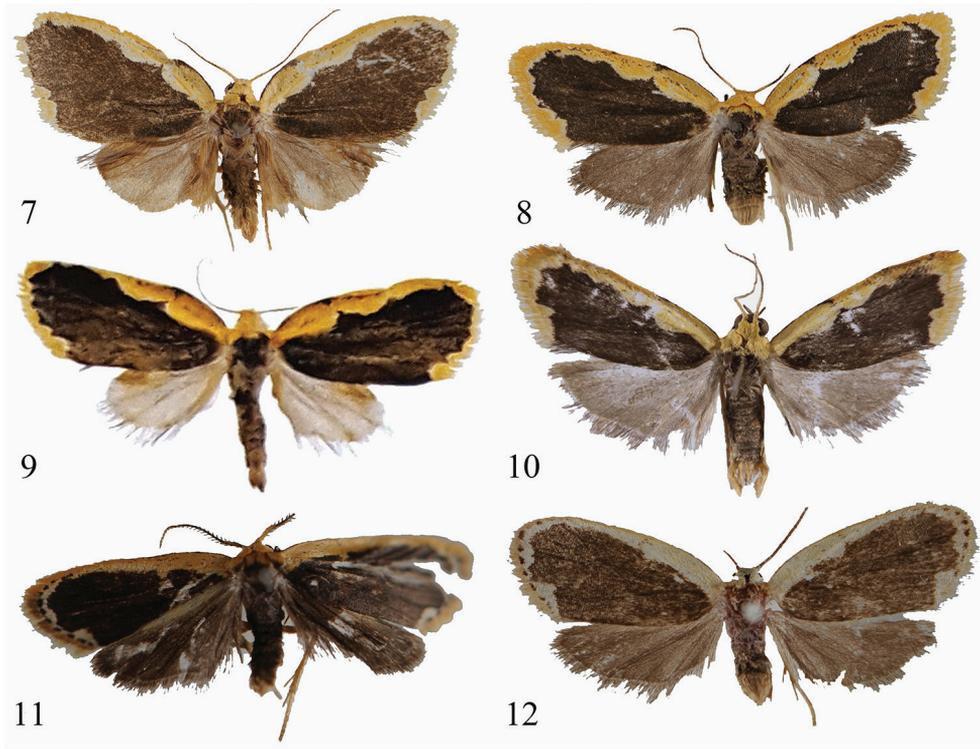
***Diduga chewi* sp. nov.**

<http://zoobank.org/74D5E4AE-3010-48D8-B167-FC83D367107>

Figs 7, 8, 18, 25, 28

Material examined. Holotype: MALAYSIA: ♂, Sabah, Borneo Jungle Girl Camp; 5.442°N, 116.451°E, elevation 1223 m; 15–20.II.2019; leg. H. L. Han; genit. prep. no. ztt-110-1; in NEFU. **Paratypes:** 1♂, 2♀♀; same data as holotype; genit. prep. nos. ztt-100-1, ztt-102-2, ztt-040-2; in NEFU.

Diagnosis. The wing pattern of the new species is similar to that of *D. trichophora* Hampson, 1900 (Figs 9, 19). It can be separated from the latter by the following characters (*D. trichophora* details are between parentheses): the forewing is broader (narrow); the male hindwing is dark grey, broad fan-shaped (pale, narrow fan-shaped); in the male genitalia, the valva termination bifurcated distally (finger-



Figures 7–12. Adults of *Diduga* spp. **7** *D. chewi* sp. nov., male, holotype, Malaysia (Borneo) **8** ditto, female, paratype, Malaysia (Borneo) **9** *D. trichophora*, male (after Bucsek 2012) **10** *D. kobkongensis*, male (after Bayarsaikhan & Bae, 2018) **11** *D. hollowayi* sp. nov., male, holotype, Malaysia (Borneo) **12** ditto, female, paratype, Malaysia (Borneo).

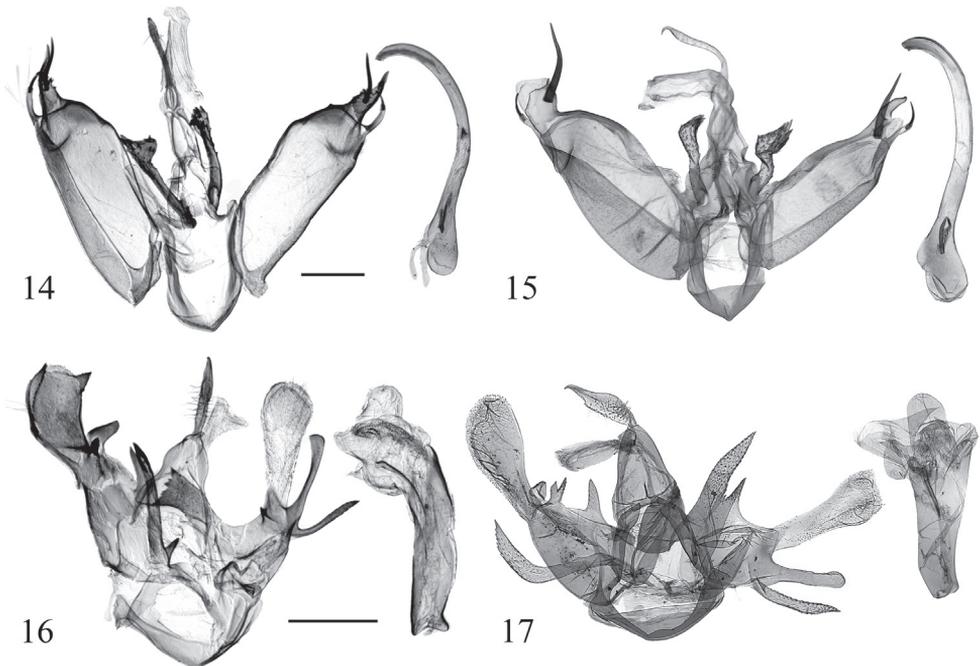
shaped, sharp distally); the coecum is typical (bifurcated); the vesica has long, narrow band of flecks (without).

Description. Adult (Figs 7, 8). Wingspan 15.5–16.5 mm. Head yellow; antenna filiform. Thorax dark brown; patagium, and tegula yellow. Abdomen dark to brown, the latter with pale yellow anal tuft. Forewing with dark brown ground color; veins and inner margin more black; costa slightly angled at 1/4 of the wing; costal band broad, yellow, with several dots and patches; its inner edge undulated; terminal band of same color as costal one, with internally facing concavity at tornus, the inner edge of terminal band undulated; terminal line and fringe yellow; ventral side of inner margin with long, brown hair tuft. Hindwing dark grey to smoky brown; costa with longer scales in male; tornus area sunken; fringe brown. **Male genitalia** (Fig. 18). Tegumen triangular, weakly sclerotized, slightly longer than uncus. Vinculum U-shaped, sclerotized. Juxta large, linguliform, weakly sclerotized, inverted harpoon-shaped. Valva approximately diamond-shaped, rather flat and symmetrical; sacculus narrow, thick and straight, 2/3 as long as valva, this terminated by long straight, sharply pointed process slightly bifurcated before apex. Uncus hooked and slender,

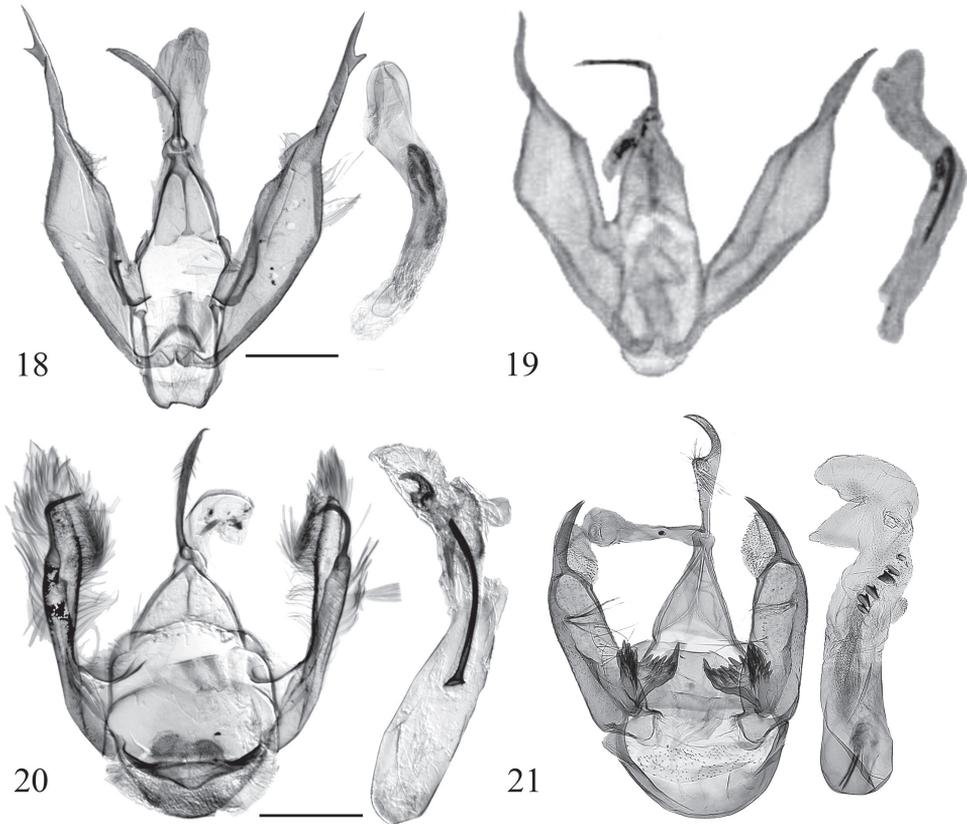


13

Figure 13. Abdomen of male adult of the genus *Diduga*.



Figures 14–17. Male genitalia of *Diduga* spp. **14** *D. simianshana* sp. nov., holotype, genit. prep. No. ztt-070-1 **15** *D. nigridentata*, 2019 (after Bayarsaikhan and Bae 2019) **16** *D. chebalinga* sp. nov., holotype, genit. prep. No. ztt-078-1 **17** *D. quinquicornuta* (after Bayarsaikhan and Bae 2019). Scale bars: 0.5 mm.



Figures 18–21. Male genitalia of *Diduga* spp. **18** *D. chewi* sp. nov., holotype, genit. prep. No. ztt-110-1 **19** *D. trichophora* (after Bucsek 2012) **20** *D. hollowayi* sp. nov., holotype, genit. prep. No. ztt-033-1 **21** *D. kobkongensis* (after Bayarsaikhan & Bae, 2018). Scale bars: 0.5 mm.

sharp distally. Aedeagus curved, short, thick; caecum slightly swollen, ca $1/4$ as long as whole aedeagus; vesica with a long cornutus and a scobinate band medially. **Female genitalia** (Fig. 25). Ostium bursae infundibuliform, weakly sclerotized. Ductus bursae narrow, flat, moderately sclerotized, sinuous anteriorly. Corpus bursae globular, membranous, with a ring-shaped signum band covered by small spines and flecks. Base of apophysis anterior is a long, inverted triangle; apophysis posterior slender, long, slightly longer than apophysis anterior; Papillae anales cylindrical, weakly sclerotized, covered with setae.

Etymology. The name “*chewi*” refers to Mr J. Chew, who is a person in charge in the camp site where the species was collected.

Distribution. Malaysia (Borneo: Sabah) (Fig. 28).

Habitat. The species was collected in a tropical rain forest area. Podocarpaceae and Myrtaceae are richest families in the collecting biotope, and mosses such as *Himantocladium plumula* (Nees) Fleisch., 1908, *Hypopterygium tamarisci* Bridel ex C.Müller, 1850, *Fissidens wichurae* Broth. & Fleisch., 1899 are also abundant.

***Diduga hollowayi* sp. nov.**

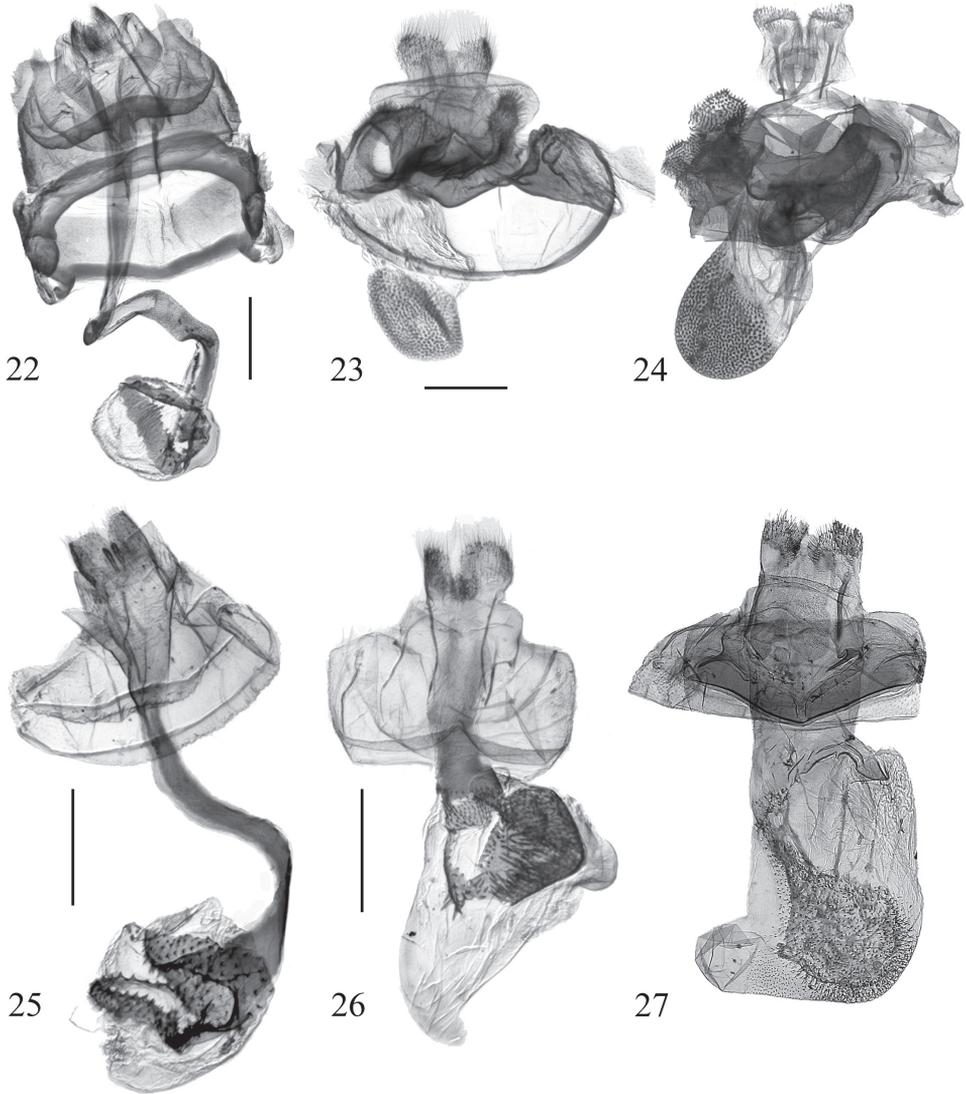
<http://zoobank.org/82C24CC3-2001-4479-B813-E3997A45C615>

Figs 11, 12, 20, 26, 28

Material examined. *Holotype*: MALAYSIA: ♂, Sabah, Borneo Jungle Girl Camp; 5.442°N, 116.451°E, elevation 1123 m; 15–20.II.2019; leg. H. L. Han; genit. prep. no. ztt-033-1; in NEFU. *Paratypes*: 1♂; same locality as holotype; 24.IV–2.V.2016; leg. H. L. Han; genit. prep. no. ztt-085-1; 7♀♀; same data as holotype; leg. H. L. Han; genit. prep. nos. ztt-034-2, ztt-083-2, ztt-096-2, ztt-097-2, ztt-099-2, ztt-103-2, ztt-104-2; in NEFU.

Diagnosis. The new species is similar to *D. kohkongensis* Bayarsaikhan & Bae, 2018 (Figs 10, 21, 27) but it can be separated from the latter by the following characters (*D. kohkongensis* details are between parentheses): the ground color of forewing is darker; the male antenna is bipectinate (ciliate); the inner edge of costal band approximately straight (undulate); the terminal line distinct, formed by brown dots (yellow); the ground color of the hindwing dark brown (grey); in the male genitalia, the editum is a small band, slightly bulging (formed by stout spines); the valva is narrow and asymmetrical (symmetrical, stout); the apical process of valva is slender, long spine-shaped, incurved inward terminally (strongly horn-shaped, weakly arched); the uncus is slender and hooked (with angular bulge ventrally); the vesica has two cornuti, one small, claw-shaped, the other long, slender, smoothly arched (a row of six irregular cornuti); in the female genitalia, the ductus bursae is narrower; the corpus bursae is approximately triangular, with a triangular signum band posteriorly (rectangular, membranous, with plate of small spines at anterior half).

Description. Adult (Figs 11, 12). Wingspan 12–13 mm, female larger than male. Head yellow; male antenna bipectinate, female antenna filiform. Thorax brown; patagium and tegula yellow, the color of female lighter. Abdomen with pale yellow anal tuft. Forewing with dark brown ground color; costal band broad, yellow to canary yellow, its inner edge nearly straight; the inner edge of terminal band undulated, with a slight right angle at tornus; terminal line conspicuous, formed by brown dots; fringe yellow. Hindwing brown, costal band light brown; fringe brown to smoky brown. **Male genitalia** (Fig. 20). Tegumen triangular, weakly sclerotized, as long as uncus. Vinculum narrow, weakly sclerotized, very broadly U-shaped, with slightly produced semicircular saccus. Juxta flat, moderately sclerotized. Valva band-shaped, weakly sclerotized, covered with setae, asymmetrical; left valva with broad and moderately sclerotized sacculus, 3/4 as long as overall valva, saccular process in shape of a long spine bent internally at ca 90°; right valva as long as left one, its saccular process like left one albeit evenly hooked internally; costa very narrow, as long as valva. Uncus slender, slightly hooked. Aedeagus membranous, cylindrical; coecum short, 1/5 as long as overall aedeagus; vesica with a small claw-shaped cornutus, and long, slender, smoothly arched cornutus subterminally. **Female genitalia** (Fig. 26). Ostium bursae flat and membranous. Ductus bursae flat, weakly sclerotized. Corpus bursae membranous, with a triangular signum band posteriorly; right part strongly sclerotized, with a signum plate covered long spines, terminally connected to ductus bursae. Apophysis anterior short, apophysis posterior ca 2 times as long as apophysis posterior. Papillae anales cylindrical, weakly sclerotized, covered with setae.



Figures 22–27. Female genitalia of *Diduga* spp. **22** *D. simianshana* sp. nov., paratype, genit. prep. No. ztt-073-2 **23** *D. chebalinga* sp. nov., paratype, genit. prep. No. ztt-077-2 **24** *D. quinicornuta* (after Bayarsaikhan and Bae 2019) **25** *D. chewi* sp. nov., paratype, genit. prep. No. ztt-102-2 **26** *D. hollowayi* sp. nov., paratype, genit. prep. No. ztt-083-2 **27** *D. kobkongensis* (after Bayarsaikhan & Bae, 2018). Scale bars: 0.5 mm.

Etymology. The species is named after Dr J.D. Holloway, who conducted outstanding lepidopterological research in Borneo.

Distribution. Malaysia (Borneo: Sabah) (Fig. 28).

Habitat. The species was collected in a tropical rain forest area. Podocarpaceae and Myrtaceae are richest families in the collecting biotope, and mosses of *Himantocladium plumula* (Nees) Fleisch., 1908, *Hypopterygium tamarisci* Bridel ex C.Müller, 1850, *Fissidens wichurae* Broth. & Fleisch., 1899 are also abundant.

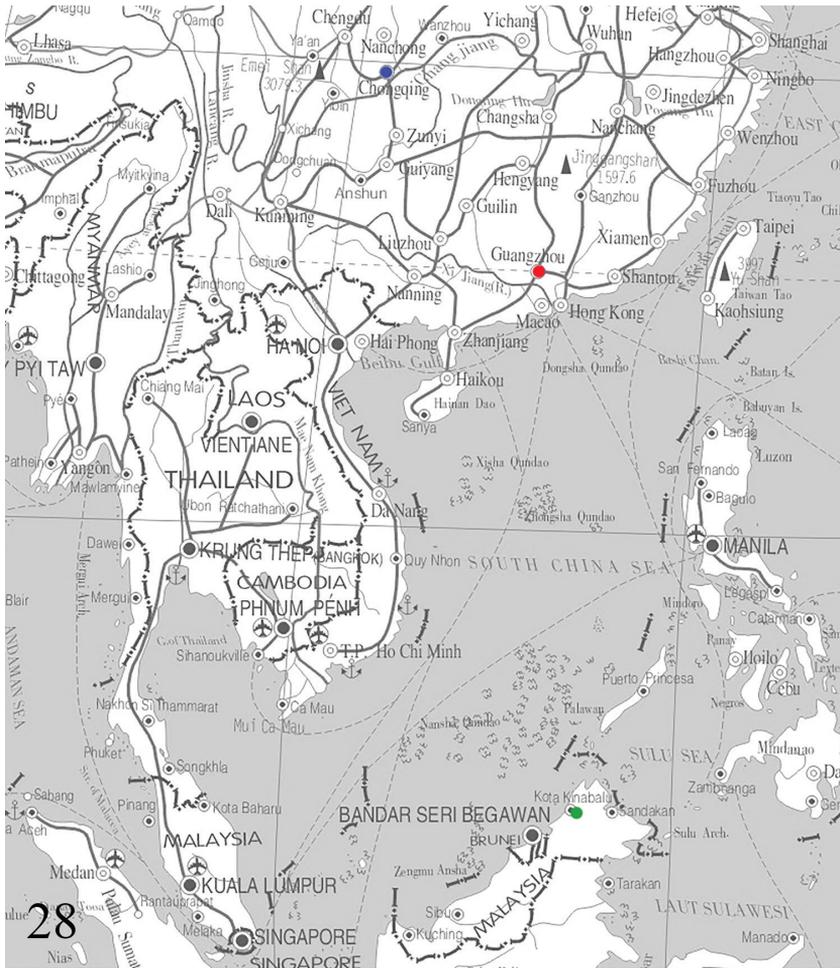


Figure 28. Collecting sites of *Diduga* spp. Key: *D. simianshana* sp. nov.: China, Chongqing, Mt Simian (blue dot); *D. chebalinga* sp. nov.: China, Prov. Guangdong, Shaoguan, Chebaling (red dot); *D. chewi* sp. nov. and *D. hollowayi* sp. nov.: Malaysia, Borneo (both green dot).

Checklist of species in the genus *Diduga* Moore, [1887], with type localities

- Diduga albicosta* Hampson, 1891 (India: Nilgiris)
Diduga albida Hampson, 1914 (New Guinea: Mimika River)
Diduga allodubatolovi Bayarsaikhan, Li & Bae, 2020 (China: Yunnan)
Diduga alternota Bucsek, 2014 (Malaysia: Pahang)
Diduga ambigua Bucsek, 2014 (Malaysia: Perak)
Diduga amoenusa Bucsek, 2012 (Malaysia: Pahang)
Diduga annulata Hampson, 1900 (Indonesia: Sambawa)
Diduga barlowi Holloway, 2001 (Borneo: Brunei)
Diduga bayartogtokhi Bayarsaikhan & Bae, 2019 (Vietnam: Vinh Phuc)

- Diduga bispinosa* Bayarsaikhan & Bae, 2018 (Cambodia: Koh Kong)
Diduga chebalinga sp. nov. (China: Guangdong)
Diduga chewi sp. nov. (Malaysia [Borneo]: Sabah)
Diduga ciliata Holloway, 2001 (Borneo: Pulo Laut)
Diduga costata Moore, [1887] (Sri Lanka: Dickoya)
Diduga cucphuonga Dubatolov & Bucsek, 2016 (North Vietnam: Ninh Binh)
Diduga dorsolobata Holloway, 2001 (Borneo: Mt. Kinabalu)
Diduga dubatolovi Bayarsaikhan & Bae, 2018 (Cambodia: Koh Kong)
Diduga excisa Hampson, 1918 (Philippines: Luzon)
Diduga flavicostata (Snellen, 1879) (India: Nilgiris)
Diduga flavifinis Bucsek, 2014 (Malaysia: Perak)
Diduga fumipennis Hampson, 1891 (India: Nilgiris)
Diduga khounngeuna Bucsek, 2020 (Laos: Ban Khoun Ngeun)
Diduga haematomiformis van Eecke, 1920 (Indonesia: West Java)
Diduga hainanensis Bayarsaikhan, Li & Bae, 2020 (China: Hainan)
Diduga hanoiensis Bayarsaikhan & Bae, 2019 (Vietnam: Hanoi)
Diduga hollowayi sp. nov. (Malaysia [Borneo]: Sabah)
Diduga iriomotensis Bae, Kishida & Bayarsaikhan, 2019 (Japan: Okinawa)
Diduga kohkongensis Bayarsaikhan & Bae, 2018 (Cambodia: Koh Kong)
Diduga luteogibbosa Bayarsaikhan, Li & Bae, 2020 (China: Yunnan)
Diduga macropilaga (Hampson, 1900) (Indonesia [Borneo]: Pulo Laut)
Diduga metaleuca Hampson, 1918 (Philippines: Luzon)
Diduga mininota Bucsek, 2014 (Malaysia: Negeri Sembilan)
Diduga nigridentata Bayarsaikhan & Bae, 2019 (Vietnam: Hanoi)
Diduga nota Bucsek, 2012 (Malaysia: Pahang)
Diduga pectinifer Hampson, 1900 (Indonesia [Borneo]: Pulo Laut)
Diduga plumosa Hampson, 1911 (Indonesia: Sambawa)
Diduga quinquecornuta Bayarsaikhan & Bae, 2019 (Vietnam: Hanoi)
Diduga rufidisca Hampson, 1898 (India: Assam)
Diduga scalprata Bayarsaikhan, Li & Bae, 2020 (China: Yunnan)
Diduga simianshana sp. nov. (China: Chongqing)
Diduga spinosusa Bucsek, 2012 (Malaysia: Perak)
Diduga trichophora Hampson, 1900 (Indonesia [Borneo]: Pulo Laut)
Diduga zetes Bucsek, 2014 (Malaysia: Perak)

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Checklist of herpetofauna in the severely degraded ecosystem of Bidong Island, Peninsular Malaysia, South China Sea

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Abstract

A herpetofaunal inventory was conducted on Bidong Island, Terengganu, Peninsular Malaysia. It incorporates data from a recent herpetological survey conducted from 1 to 3 April 2019 with reptile records from previous publications. Specimens were collected with drift-fenced pitfall traps and taxa were recorded with visual encounter surveys (VES). In total, 18 species of reptiles and amphibians were recorded, including three species of frogs, 12 species of lizards, and three species of snakes. Six species from the present survey are new records for the island.

Keywords

amphibian, Bidong Island, herpetological survey, Peninsular Malaysia, reptile, South China Sea

Introduction

The South China Sea has environmentally diverse groups of islands that have engaged researchers' attention for the past two decades (Leong et al. 2003; Grismer et al. 2004; Grismer 2006; 2011a; 2011b). The three groups of islands located off the state of Terengganu are the Perhentian, Redang and Bidong Archipelagos. Faunal studies on these islands have indicated that these subregions support high herpetological diversity and endemism (Grismer et al. 2011). The islands of Perhentian and Redang have received extensive flora and fauna research in the past (e.g., Masayuki et al. 2007; Grismer and Chan 2008; Grismer et al. 2009, 2011; David et al. 2016; Hamza et al. 2016; Pesiu et al. 2016), but several islands in this area have been overlooked where it concerns terrestrial fauna. Tamblyn et al. (2005) reported on the herpetofaunal communities on Perhentian Kecil, Perhentian Besar and Redang islands. They reported 32 species of herpetofauna (three frogs, 21 lizards and eight snakes). The expeditions by Grismer and Chan (2008) and Grismer et al. (2009) to Perhentian Besar Island resulted in the descriptions of two new species: *Cnemaspis perhentianensis* and *Tytthoscincus perhentianensis*. Subsequently, Grismer et al. (2011) reported 46 species of herpetofauna from the Perhentian and Redang archipelagos, including Tenggol Island.

The Bidong Archipelago comprises six islands with Bidong Island (Fig. 1) being the largest. It is located about 33 km to the northeast of Kuala Terengganu. The islands of Karah, Gelok and Tengkorak are situated less than 5 km from Bidong Island, while about 15 km to the east lie Yu Kecil and Yu Besar Islands.

The fauna of Bidong Island was apparently first studied by Gibson-Hill (1952) who published a record of bird species. However, other terrestrial fauna was not reported until recently. Roslan et al. (2016) surveyed the island's bat fauna, Fathihi-Hakimi et al. (2017) studied the butterfly diversity, and Grismer et al. (2014) described a new species of lizard, *Cnemaspis bidongensis*. Zakaria et al. (2017) followed up with an inventory of the island's herpetofaunal diversity in which 12 species of lizards were recorded. Their study was a rapid survey made from 31 May to 7 June 2015 limited to the Pulau Bidong Marine Nature Research Station (MNRS) area near Pantai Pasir Cina.

In this article, we report the baseline data on a collection of amphibians and terrestrial reptiles acquired during a recent survey on the western side of Bidong Island in early April 2019. This report incorporates the findings of Zakaria et al. (2017) and presents an updated inventory of the herpetofaunal diversity of Bidong Island.

Materials and methods

Study area

Bidong Island, the largest island of the Bidong Archipelago, has a land area of about one square kilometre and is 321 m above sea level at its highest point. The island was used for housing Vietnamese refugees from 1975 to 1991. The settlement area (Fig. 1)

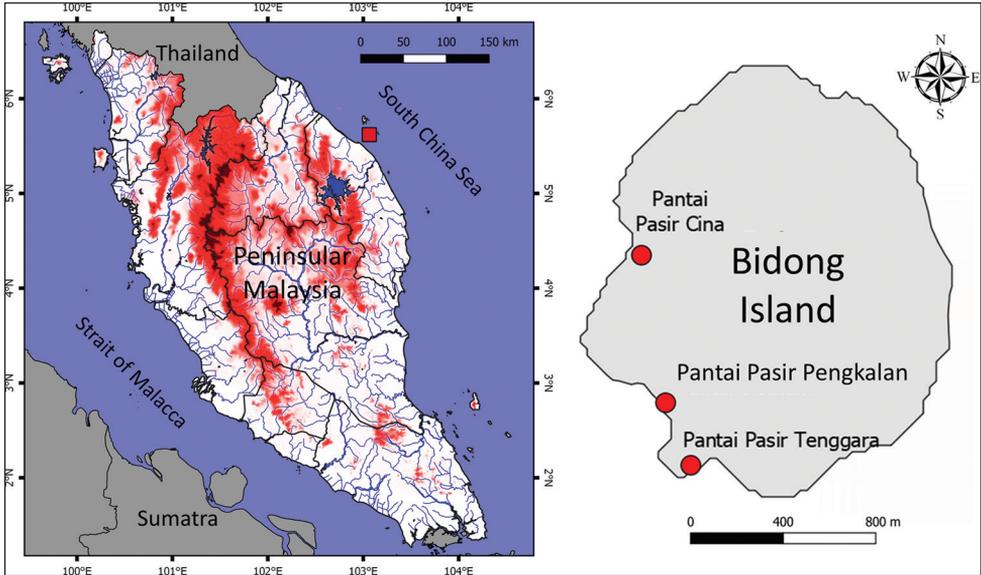


Figure 1. Map of Peninsular Malaysia (left) showing the location of Bidong Island, off the Terengganu coast, indicated by the red square. Map of Bidong Island (right) with the study locations indicated by red circles.

is situated at Pantai Pasir Pengkalan, close to Pantai Pasir Tenggara. These two beaches can be accessed via a forest trail from the western part of the island where Pulau Bidong MNRS of Universiti Malaysia Terengganu is located at Pantai Pasir Cina. This island is covered with coastal and secondary forest composed of tree species such as *Terminalia catappa*, *Vatica cineria*, *Licania splendens* and *Hibiscus tiliaceus* (Pesiou et al. 2016). The island's landscape is hilly, dominated by extensive and steep granite outcrops with a few natural but seasonal drainages.

Methods

Field surveys were conducted at the western part of Bidong Island, Terengganu, Malaysia from 1 to 3 April 2019. Study areas included chalets and research facilities, hilly areas, accessible forest trails, coastal vegetation as well as stagnant ponds near Pantai Pasir Cina ($5^{\circ}37'16''\text{N}$, $103^{\circ}3'28''\text{E}$), Pantai Pasir Pengkalan ($5^{\circ}36'53''\text{N}$, $103^{\circ}3'32''\text{E}$) and Pantai Pasir Tenggara ($5^{\circ}36'43''\text{N}$, $103^{\circ}3'36''\text{E}$). Specimens were inventoried using the following approaches: Visual Encounter Survey (VES) and drift-fenced pitfall traps. VES is an active collecting method used to sample for species richness and abundance along the survey area by an observer under a time limit condition (Crump and Scott 1994). Drift-fenced pitfall trap is a passive collecting method for sampling ground dwelling amphibians and reptiles. Two sets of drift-fenced pitfall traps were deployed randomly about 200 m from MNRS and the Vietnamese settlement area. Each set of pitfall traps consisted of three buckets assembled in a straight line with fences measuring 0.5 m high and 4 m long. Each of the buckets used were punched with two or three drainage holes. These traps were opened for two consecutive days and checked before noon.

The VES method involved active searching and was conducted during the day (10 am to 4 pm) and at night (8 pm to 11 pm) to record both diurnal and nocturnal species. Animals were caught by hand or with snake tongs. Identification of amphibians follows Berry (1975) and the latest taxonomic nomenclature was used following Amphibian Species of the World database (Frost 2020). Identification of lizards follows Grismer (2006, 2011a, 2011b) and snakes follows Das (2010) and taxonomic nomenclature follows The Reptile Database (Uetz et al. 2020). All collected individuals were examined and a representative for each species was photographed in situ. Selected specimens were kept as vouchers to confirm the occurrence of their species on the island. Specimens were fixed with 10% formalin before being stored in a 70% ethanol solution. Samples of liver tissue were stored in 100% ethanol. All voucher specimens were deposited in the General Biology Lab., Universiti Malaysia Terengganu and catalogued under UMT Zoological Collection (**UMTZC**). Unpublished records of specimens in the General Biology Lab resulting from our pilot study in 2006 were also included to produce a composite herpetofaunal checklist. In addition, the record of reptile species reported by Zakaria et al. (2017) is presented in Table 1.

In this checklist, taxonomic categories are alphabetically arranged and information for each species is presented in the following format: family name, species name, English name, notes and known distribution of the species in the offshore islands of Terengganu.

Table 1. List of terrestrial amphibians and reptiles recorded from Bidong Island, Terengganu in this study and from Zakaria et al. (2017).

Family	Species	Zakaria et al. (2017)	This study	IUCN Status
Amphibians				
Microhylidae	<i>Kaloula pulchra</i>	–	+	LC
	<i>Microhyla heymonsi</i>	–	+	LC
Rhacophoridae	<i>Polydectes leucomystax</i>	–	+	LC
Reptilians				
Agamidae	<i>Bronchocela cristatella</i>	+	+	NE
Scincidae	<i>Dasia olivacea</i>	+	+	LC
	<i>Eutropis multifasciata</i>	+	+	LC
Gekkonidae	<i>Cnemaspis bidongensis</i>	+	+	LC
	<i>Gekko cicakterbang</i>	+	+	NE
	<i>Gekko gecko</i>	+	+	LC
	<i>Gekko monarchus</i>	+	–	NE
	<i>Hemidactylus frenatus</i>	+	+	LC
	<i>Hemidactylus garnotii</i>	+	–	NE
	<i>Hemidactylus platyurus</i>	+	+	NE
	<i>Lepidodactylus lugubris</i>	+	+	NE
Varanidae	<i>Varanus salvator</i>	+	+	LC
Colubridae	<i>Lycodon capucinus</i>	–	+	LC
Pythonidae	<i>Malayopython reticulatus</i>	–	+	NE
Typhlopidae	<i>Indotyphlops braminus</i>	–	+	NE
Total no. of species/study		12	16	
Total no. of species			18	

Results

Table 1 incorporates data from this study and an earlier survey by Zakaria et al. (2017), and documents a total of 18 species of herpetofauna on Bidong Island (Table 1). These comprise three species of frogs from three genera belonging to the families Microhylidae (2 spp.) and Rhacophoridae (1 sp.); 12 species of lizards from nine genera belonging to the families Agamidae (1 sp.), Gekkonidae (8 spp.), Scincidae (2 spp.) and Varanidae (1 sp.); and three species of snakes from three genera belonging to the families Colubridae, Pythonidae and Typhlopidae with a single species in each family. The previous study by Zakaria et al. (2017) recorded two species of gekkonid lizards that were not found in the present survey. This study adds six new island records (3 amphibians and 3 snakes). Most of the herpetofauna species recorded from Bidong Island were either Least Concern (LC) or Not Evaluated (NE) according to the International Union for Conservation of Nature (IUCN) status (IUCN 2018).

Class Amphibia

Order Anura

Suborder Neobatrachia

Family Microhylidae

Kaloula pulchra Gray, 1831

Banded bullfrog

Fig. 2

Notes. The banded bullfrog is fossorial but also shelters in burrows, tree holes and beneath surface objects. On 1 April 2019, one specimen was collected in a small tree cavity about 1.5 m above ground near MNRS at night.

Distribution. This species is abundant in Peninsular Malaysia, and has also been found on Perhentian Besar, Redang and Tenggol islands (Grismer et al. 2011).

Microhyla heymonsi Vogt, 1911

Dark-sided chorus frog

Fig. 3

Notes. Many individuals were observed on the ground near puddles in grassy areas. Several males can be heard calling from the puddles. On 1 April 2019, a single specimen was collected from a stagnant puddle near MNRS at night. This specimen agrees with the morphology diagnosis by Garg et al. (2019).

Distribution. This species is not known from other islands in Terengganu.



Figure 2. *Kaloula pulchra*



Figure 3. *Microhyla heymonsi*

Family Rhacophoridae

Polypedates leucomystax (Gravenhorst, 1829)

Four-lined tree frog

Fig. 4

Notes. This species was commonly observed on the hiking trail about 10 m above sea level. Individuals were located at night perching on leaves and branches of low to medium level vegetation. One was collected on a leaf 1 m above the ground at night on 2 April 2019. It matches the diagnosis of the species by Sumarli et al. (2015).

Distribution. The four-lined tree frog is distributed throughout Perhentian Besar, Perhentian Kecil, Redang and Tenggol islands (Grismer et al. 2011).

Class Reptilia

Order Squamata

Suborder Sauria

Family Agamidae

Bronchocela cristatella (Kuhl, 1820)

Green crested lizard

Fig. 5

Notes. This striking green-coloured and diurnal lizard is active during the day and can be commonly found in open areas on bushes and trees from 1 to 3 m above the ground. On 2 April 2019, eight individuals were observed and a specimen was collected from Pantai Pasir Pengkalan. Two large individuals were seen climbing up to 3 m high on a tree near Pantai Pasir Tenggara. All examples on Bidong Island match the diagnosis of this species by Grismer (2011b).

Distribution. This agamid also occurs on Perhentian Besar, Perhentian Kecil, Pulau Lang Tengah as well as Redang islands (Grismer 2011b; Grismer et al. 2011, 2015).

Family Gekkonidae

Cnemaspis bidongensis Grismer, Wood Jr., Ahmad, Sumarli, Vazquez, Ismail, Nance, Mohd-Amin, Othman, Rizaijessika, Kuss, Murdoch & Cobos, 2014

Bidong island rock gecko

Fig. 6

Notes. *Cnemaspis bidongensis* is apparently endemic to Bidong Island where it seemed to be common. It inhabits forest in the interior of the island where it was found on rocks, twigs and tree trunks. About five individuals were observed on 1 April 2019 in the forest near MNRS. The species was described in 2014 by Grismer et al.



Figure 4. *Polypedates leucomystax*



Figure 5. *Bronchocela cristatella*

Distribution. This gekkonid has thus far been found only on Bidong Island (Grismer et al. 2014).



Figure 6. *Cnemaspis bidongensis*

***Gekko cicakterbang* (Grismer, Wood Jr., Grismer, Quah, Thy, Phimmachak, Sivongxay, Seateun, Stuart, Siler, Mulcahy, Anamza & Brown, 2019)**

Malaysian parachute gecko

Fig. 7

Notes. This gecko was occasionally observed on man-made structures in MNRS. It is nocturnal and apparently has the capability to glide from one tree to another. Until 2019, this species was thought to be conspecific with *Ptychozoon lionotum* (see Grismer et al. 2019 as *Ptychozoon cicakterbang*). *Ptychozoon* later became a subgenus of *Gekko* (see Wood et al. 2020).

Distribution. *Gekko cicakterbang* ranges throughout Peninsular Malaysia and its associated islands but in the islands off Terengganu, it has only been found on Perhentian Besar, Redang, and Bidong islands (Grismer 2011b; Grismer et al. 2011, 2019).

***Gekko gecko* (Linnaeus, 1758)**

Tokay gecko

Fig. 8

Notes. This large species of gecko was common on Bidong Island, especially at the MNRS area. Individuals observed match the diagnosis of the species by Grismer (2011b).



Figure 7. *Gekko cicakterbang*



Figure 8. *Gekko gecko*

Distribution. The Tokay Gecko has also been recorded from Perhentian Besar, Perhentian Kecil and Redang islands (Grismer 2011b; Grismer et al. 2011).

***Gekko monarchus* (Schlegel, 1836)**

Spotted-house gecko

Notes. This species was not sighted in this study but was reported by Zakaria et al. (2017).

Distribution. *Gekko monarchus* is known from Perhentian Besar, Redang and Tenggol islands (Grismer 2011b; Grismer et al. 2011).

***Hemidactylus frenatus* Schlegel, 1836**

Spiny-tailed house gecko

Notes. *Hemidactylus frenatus* is a widespread species that seems to have a preference for human settlements and disturbed forest on Bidong Island. Individuals observed match the diagnosis of this species in Grismer (2011b).

Distribution. This gekkonid is found on all of Terengganu's offshore islands except Susu Dara Kecil Island (Grismer 2011b; Grismer et al. 2011).

***Hemidactylus garnotii* Duméril & Bibron, 1836**

Garnot's house gecko

Notes. Although reported to occur on Bidong Island by Zakaria et al. (2017), none was observed in the recent study.

Distribution. This species has been observed in Kuala Aring, Kelantan (Grismer 2011b) and Karah Island near Bidong Island (Grismer, unpublished data).

***Hemidactylus platyurus* (Schneider, 1797)**

Flat-tailed house gecko

Notes. This species was observed living in syntopy with *Hemidactylus frenatus* in human settlements near MNRS. Individuals seen match the diagnosis of this species in Grismer (2011b).

Distribution. Off the Terengganu coast, Perhentian Besar Island seems to be the only other island where *Hemidactylus platyurus* has been recorded (Grismer 2011b; Grismer et al. 2011).

***Lepidodactylus lugubris* (Duméril & Bibron, 1836)**

Mourning gecko

Fig. 9

Notes. On Bidong Island, one individual was found near Pantai Pasir Pengkalan. Its appearance matches the diagnosis of the species in Grismer (2011b).

Distribution. This species has also been recorded from Susu Dara Kecil Island (Grismer 2011b; Grismer et al. 2011).

Famil Scincidae

Dasia olivacea Gray, 1839

Olive tree skink

Notes. *Dasia olivacea* is diurnal, arboreal species that can be seen basking head down on tree trunks. About three individuals were observed from 1 to 3 April 2019, and all were about 2 m high on trees. One was seen with a small, unidentified gecko in its mouth on 2 April 2019. The predation of this species on geckos was reported by Grismer (2011b) on Babi Tengah Island in Johor. Grismer (2011b) observed that this skink also feeds on large centipedes, which suggests that *Dasia olivacea* is an opportunistic feeder that does not have a specialized diet. The morphology and colour pattern of the individuals observed on Bidong Island match the diagnosis of the species by Grismer (2011b).

Distribution. This species is also recorded from Perhentian Besar, Perhentian Kecil, Redang and Tenggol islands (Grismer 2011b; Grismer et al. 2011).

Eutropis multifasciata (Kuhl, 1820)

Javan sun skink

Fig. 10

Notes. This common skink can be found across almost all habitats, including disturbed forest, open areas, human settlements and primary forest. It was very common at Pantai Pasir Pengkalan with 11 individuals being recorded during the recent survey. Specimens observed match the diagnosis of this species by Grismer (2011b).

Distribution. This skink has also been reported from Perhentian Besar, Redang, and Tenggol islands (Grismer 2011b; Grismer et al. 2011).

Famil Varanidae

Varanus salvator (Laurenti, 1768)

Water Monitor Lizard

Notes. Several individuals of this large, diurnal lizard that were seen frequently on Bidong Island from 1 to 3 April 2019, especially near MNRS, due to the availability of food at the garbage piles. They were observed foraging in the afternoon and evening before dusk. The appearance of those lizards matches the diagnosis of this species in Grismer (2011b).



Figure 9. *Lepidodactylus lugubris*



Figure 10. *Eutropis multifasciata*

Distribution. This species has been recorded on many islands off Terengganu except Susu Dara Kecil, Seringgeh and Tokong Burung Besar islands (Grismer 2011b; Grismer et al. 2011).

Suborder Serpentes

Family Colubridae

Lycodon capucinus (Boie, 1827)

Common wolf snake

Fig. 11

Notes. This nocturnal snake was common on Bidong Island where individuals were often found beneath logs, rocks and beach debris. Several individuals were observed near MNRS and Pantai Pasir Pengkalan on 1 and 2 April 2019. The individuals examined match the diagnosis of the species in Grismer et al. (2011).

Distribution. Also recorded from Perhentian Besar Island (Grismer et al. 2011).

Family Pythonidae

Malayopython reticulatus (Schneider, 1801)

Reticulated python

Notes. This large and widespread snake can be found in a wide variety of habitats and preys on large animals. A 2 m long individual was spotted at night on 2 April 2019 among grass near Pantai Pasir Pengkalan. It fits the diagnosis of the species in Grismer (2006).



Figure 11. *Lycodon capucinus*

Distribution. Also recorded from Perhentian Besar, Susu Dara Besar, Redang and Tenggol islands (Grismer et al. 2011).

Family Typhlopidae

Indotyphlops braminus (Daudin, 1803)

Common Blind Snake

Notes. This small fossorial snake resembles an earthworm and seems to occur largely in human settlements. It feeds on the larvae of ants and termites, and is known to be parthenogenic. One specimen was captured on surface debris at night on 2 April 2019 near MNRS. Its morphology matches the diagnosis of the species in Grismer (2006).

Distribution. *Indotyphlops braminus* was recorded by Grismer et al. (2011) from Perhentian Besar Island.

Discussion

Human activities are the major cause of an island's ecosystem degradation around the world (see Graham et al. 2017) and Terengganu's offshore islands are no exception. The continuous encroachment is perturbing, as anthropogenic disturbances are detrimental to terrestrial insular species (Trainor 2007). Habitat modification is one of the human activities that drive herpetofaunal species into extirpations particularly for habitat specialist species (Gibbons et al. 2000; Kanowski et al. 2006). Bidong Island has been greatly degraded by the establishment of the refugee camps from 1975 to 1991 which likely threatened its terrestrial fauna. About three quarter of the forested areas on the island has been disturbed during the Vietnamese occupancy. The natural vegetation left can be mostly found on the north-eastern and northern sides on the island. However the endemic gecko, *Cnemaspis bidongensis*, did not seem affected. Grismer et al. (2014) inferred that *C. bidongensis*, unlike most of its congeners, is not a microhabitat specialist. This could have helped its survival undeterred by the island's severely degraded ecosystem in the past. Persistence and recovery of fauna to overcome disturbances has been studied in many habitats (Gardner et al. 2007; Dent and Wright 2009; Sayer et al. 2017) but in islands this has been less addressed, particularly in Peninsular Malaysia.

It has been almost 30 years since the Vietnamese occupants left Bidong Island and the persistence of the herpetofauna to withstand the human-imposed pressure in the past is remarkable despite the great deterioration of the island's forest ecosystem. Since then, anthropogenic abandonment and forest succession may help terrestrial herpetofauna to recover (Hilje and Aide 2012; Hernandez-Ordonez et al. 2015), even more rapidly on the island (Ríos-López and Aide 2007; Herrera-Montes and Brokaw 2010; Acevedo-Charry and Aide 2019). The findings in this study have demonstrated the resiliency and persistence of this island's herpetofauna over the four years separating the two reported inventories. Yet, further tests with extensive monitoring data are required

to elucidate the shift in the community structure. Previous records of a reptile inventory in 2015 documented a total number of 12 species (Zakaria et al. 2017) and this study managed to confirm ten species out of that number. This study however, augmented the herpetofaunal study in this island by including amphibians and also adding three new records of reptiles making a total of 18 herpetofauna species for Bidong Island.

Many of the species on the island are to some extent human commensals, and some may even have been introduced with human occupation of the island. High densities of species such as *Microhyla heymonsi*, *Kaloula pulchra*, *Gekko gekko*, *Varanus salvator*, *Hemidactylus frenatus* and *Bronchocela cristatella* were also observed in this study. Anthropogenic-adapted species such as *G. gekko* and *H. frenatus* could also be accidentally introduced by humans during the arrival of the refugees on the island, which also may influence the abundance of these species on this island. Hypothetically, the abundance of these species may result from the availability of microhabitat as refugia, lack of predators, availability of food resources, human introduction and density compensation due to missing interspecific competitors in the island (Stamps and Buechner 1985; Ernst et al. 2006; Hilje and Aide 2012; Novoslov et al. 2016). Ephemeral habitats such as temporary ponds help generalist amphibians like *M. heymonsi* to thrive in harsh conditions. These ponds can be the source for natal habitat or shelters for amphibian species to recolonize back after the successional stage (Pittman et al. 2014). Lack of predation pressure also can induce the colonization of the frogs and lizards. To date, only three species of snakes are known from the island namely *Indotyphlops braminus*, *Lycodon capucinus* and *Malayopython reticulatus*. Of these, *L. capucinus* is highly likely the only predator of the frogs and lizards but again, sampling effort plays an important role to deliver accurate information on true species richness of snakes in this island because snakes are elusive. Zakaria et al. (2017) were unable to record any snakes and these new records are attributed to expanded survey areas, additional co-workers, and different sampling months.

Generally, many species that occur on this island are ubiquitous species; hence these do not require a specialized microhabitat. Reptiles in particular, have a suit of biological traits that may help them to subsist on this island such as efficiency in energy expenditure, flexibility in growth development and ability to shift diet spatially and/or temporally (see Shine and Somaweera 2019). These adaptations perhaps are the reasons for their persistence, but further studies are needed to test this. In addition, with the exception of *M. reticulatus* and *I. braminus*, large numbers of individuals of other species in Pantai Pasir Pengkalan and Pantai Pasir Cina indicated that they can be expected to be widespread throughout the island. Hence, most of these species are listed as LC in IUCN status as they are also ubiquitous on the mainland and several other islands in Terengganu.

The results of this inventory are not conclusive, as the studies done only covered several small sites of the island. Large parts of the island forest are still unexplored, thus the results may not represent the true species richness of the island. The north-eastern part of the island is rugged with steep slopes and sharp outcrops, hence has limited access during the survey. The northern, central and eastern parts of the islands' forests

are still unexplored. These large areas (which encompassed 60% of the island's landscape) are now covered by mature secondary forest and receive less human disturbance after the recovery of the forest from the past incident. Increased sampling efforts, in terms of sampling areas and sampling time, may result in the discovery of new island records, perhaps even new ground dwelling species with the installation of pitfall traps. Long-term monitoring and ecological studies are needed to realize the true diversity of herpetofauna and improve the conservation of the terrestrial herpetofauna. The herpetofauna of Bidong Island survived the catastrophic ecological event in the past, but the resilience of species to recover after land abandonment and forest succession (true species richness and population density) remains in question. Abandoned habitat from the past and intact forests need to be maintained and undisturbed to promote the persistence of this island's herpetofauna. This study provides baseline data for ecological monitoring and studies which are crucial to uncover the diversity of this insular herpetofauna and inform conservation authorities and stakeholders about current and future conservation management.

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