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From the Steppe to the Desert: Survey of Band-Winged Grasshoppers from Mongolia (Orthoptera: Acrididae: Oedipodinae) Based on Material from 50 Years of Expeditions

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From the steppe to the desert: Survey of band-winged grasshoppers from Mongolia (Orthoptera: Acrididae: Oedipodinae) based on material from 50 years of expeditions¹

L.-S. Dey, M. Seidel, D. Lkhagvasuren & M. Husemann

Abstract

The steppe regions of Mongolia have a rich grasshopper fauna. Especially, the short-horned (Caelifera) grasshopper family Acrididae with the subfamilies Gomphocerinae (slant-faced grasshoppers) and Oedipodinae (band-winged grasshoppers) show a high diversity and abundance. This study reviews the Mongolian fauna of band-winged grasshoppers based on collection data of 50 years of expeditions of the German-Mongolian research cooperation. These collection data (assembled between 1962 and 2019) were used to generate a faunistic overview of Oedipodinae species for the region. In total 740 specimens belonging to 16 species were reported. Based on the collected material, study of the types and the original species descriptions following species were synonymized: *Bryodema gebleri mongolica* ZUBOWSKY, 1900 **syn. nov.** with *Bryodema gebleri* (FISCHER von WALDHEIM, 1836), as well as *Oedaleus asiaticus* BEY-BIENKO, 1941 **syn. nov.** with *Oedaleus decorus* (GERMAR, 1825). Based on the generated dataset the region around Khustai National Park and the Great Lakes Depression in North-West-Mongolia were evaluated as the most species-rich spots of Oedipodinae.

Key words: Angaracris, Bryodema, Bryodemella, Compsorhipis, Celes, Oedaleus, Sphingonotus, Orthoptera, species richness, distribution

1. Introduction

The large steppes of Mongolia harbour a high diversity of insects. Grasshoppers are one of the most abundant groups in these habitats; specifically, the Acrididae occur in large numbers. Within the Acrididae, the Gomphocerinae, also known as slant-faced grasshoppers, and the Oedipodinae, or band-winged grasshoppers are specifically diverse in grasslands. Both groups share a cryptic morphology, but they differ in their habitat preferences, with the Oedipodinae generally requiring more open areas. Oedipodinae grasshoppers are one of the most diverse and widespread subfamilies of Acrididae (Orthoptera) (SONG et al. 2018), with ca. 800 species and a worldwide distribution. Due to their young age and high diversity they represent an interesting system for evolutionary, as well as ecological questions (e.g. CHANDRA 1982, FRIES et al. 2007, GUZMAN & CONFALONIERI 2010, HOCHKIRCH & HUSEMANN 2008, HUSEMANN et al. 2012, LIGHTFOOT *ET AL*. 2010, OTTE 1972, 1981; PENER & ORSHAN 1980). One of the main diversity hotspots of the subfamily are the large steppe regions of Central Asia.

Since the early the 20th century Russian researchers have worked on the Central Asian grasshopper fauna (e.g. BEY-BIENKO et al. 1963, BENEDIKTOV 2011, MISTSHENKO 1937, SERGEEV 1992; STOROZHENKO et al. 2017, UVAROV 1966). However, most of their studies focused on the former Soviet Union providing only little data on Mongolia and other neighbouring countries (GOROCHOV et al. 1989, MISTSHENKO 1968, 1974). Moreover, much of the literature on Mongolian Orthoptera was published in local journals and hence relatively little is known about these outside of Central Asia. This started to change with larger international collaborations and expeditions to the country. In 1961, German scientists from Halle and Gatersleben in Germany began to collaborate with the newly founded Committee of Science of Mongolia (now Mongolian Academy of Science); they started a new era of exploring the Asian fauna and flora (STUBBE et al. 1981). Although many

¹ Ergebnisse der Mongolisch-Deutschen Biologischen Expeditionen seit 1962, Nr. 361.

expeditions of foreign scientists were performed in Mongolia in the years before, most of the collected material was exported and little scientific progress was made within the country. Consequently, one main objective of this new cooperation was to establish a scientific collaboration with Mongolia (Ulan-Bator) leading to the establishment of a reference collection of the Mongolian flora and fauna within the country. The first expeditions to southern and western Mongolia by the German-Mongolian cooperation took place in 1962 and 1964. Since then annual or biennial expeditions to Mongolia were organized and performed by this cooperation. Material of all groups of animals and plants were collected and split between the institutes in Ulan-Bator (MAS; NUM) and the MLU Halle-Wittenberg University (ZNS). Some of the material collected by K. Günther during the expeditions was deposited in the Natural History Museum Berlin (MfN) (GÜNTHER 1962, 1971). In this study, he reports the material of Oedipodinae collected during these expeditions and deposited in the ZNS and private collections to provide an overview of the diversity of this subfamily in Mongolia and review the status of some taxa.

1. Material and Methods

740 specimens of the subfamily Oedipodinae were collected between 1964 and 2019 (total number of sites = 108). 59 % (435 specimens) of the material was collected on four field surveys of the authors (LSD & DL) between 2015 and 2019. Further material collected between 1962 and 2015 is deposited in the Zoological Collection of the Martin-Luther-University of Halle-Wittenberg (ZNS). Material collected by K. Günther, deposited in Natural History Museum Berlin (MfN) was not included, because two manuscripts regarding this material are already published (GÜNTHER 1962, 1971). A list of all studied material and sampling locations is provided in Table 1. All specimens were identified by the authors based on keys by BEY-BIENKO 1930, BEY-BIENKO & MISTSHENKO 1963, MISTSHENKO 1937, STOROZHENKO et al. 2017. If possible, investigated individuals were compared with type material. All available images of type material were uploaded to the Orthoptera Species File (CIGLIANO et al. 2020). Photos of one female and one male specimen of each identified species were taken at Centre of Natural History (CeNak) Hamburg using a custom-made DUN Inc. stacking system with a Canon EOS 5DSr and a 100 mm lens. Images were edited using Gimp v. 2.10.0 (KIMBALL et al. 2018) and Inkscape v. 0.92.3 (THE INKSCAPE DEVELOPMENT TEAM 2018).

Coordinates of all sampling locations were obtained from Google maps. Distribution maps for all species were created using QGis v. 2. 18. 23 (QGIS DEVELOPMENT TEAM 2020). A background layer was downloaded in 30 arc-sec resolution from the GADM database (GLOBAL ADMINISTRATIVE AREAS 2012) available from the Natural Earth website (https://www.natura-learthdata.com) and from Worldwildlife.org (OLSON et al. 2001). Based on all records a heat map of species diversity was constructed using R (R CORE TEAM 2019) and the packages "sf" (PEBESMA 2018), "dplyr" (WICKHAM et al. 2019), "ggplot2" (WICKHAM 2016), "scico" (PEDERSEN & CRAMERI 2018), "rnaturalearth" (SOUTH 2017a), "purrr" (HENRY & WICKHAM 2019), "smoothr" (STRIMAS-MACKEY 2018), "rnaturalearthdata" (SOUTH 2017b) and "lwgeom" (PEBESMA 2019). Grid cell size was fixed at 0.8 units.

BMNH	British Museum of Natural History London (England)
MAS	Mongolian - Academy of Sciences (Ulan-Bator, Mongolia)
MfN	Museum für Naturkunde Berlin (Germany)
MHNG	Muséum d'histoire naturelle de la Ville de Genève (Switzerland)
MNHN	Muséum national d'histoire naturelle Paris (France)
NUM	National University of Mongolia (Ulan-Bator, Mongolia)
RAS	Russian Academy of Sciences
SMNS	Staatliches Museum für Naturkunde Stuttgart (Germany)
SZMN	Siberian Zoological Museum Novosibirsk (Russia)
ZIN	Zoological Institute RAS St. Petersberg (Russia)
ZNS	Zentralmagazin naturwissenschaftlicher Sammlungen der Martin-Lu-
	ther Universität Halle-Wittenberg (Germany)
	MAS MfN MHNG MNHN NUM RAS SMNS SZMN ZIN

Table 1: Compared species lists provided by this study, the manuscript by GÜNTHER (1971) and the Orthoptera Species File (CIGLIANO et al. 2020)

Species	this study	GÜNTHER (1971)	CIGLIANO et al. (2020)
Andrea gorochovi MISTSHENKO, 1989			х
Angaracris barabensis (PALLAS, 1773)	х	х	х
Bryodema gebleri (FISCHER VON WALDHEIM, 1836)	х	х	
Bryodema kozlovi BEY-BIENKO, 1930			х
Bryodema luctuosum luctuosum (STOLL, 1813)	х	х	х
Bryodema miramae miramae BEY-BIENKO, 1930			х
Bryodema nigripennis MISTSHENKO & GOROCHOV, 1989			х
Bryodemella (Bryodemella) holdereri (KRAUSS, 1901)	х	х	
Bryodemella (Bryodemella) tuberculata tuberculata (FABRICIUS, 1775)	х	х	х
Bryodemella (Marikovskiella) orientale orientale (BEY-BIENKO, 1930)		х	х
Bryodemella (Marikovskiella) orientale simulans (STEBAEV, 1964)		х	
Bryodemella (Marikovskiella) zaisanicum fallax (BEY-BIENKO, 1930)		х	
Celes skalozubovi skalozubovi ADELUNG, 1906	х	х	х
Compsorhipis bryodemoides BEY-BIENKO, 1932	х	х	х
Compsorhipis davidiana (SAUSSURE, 1888)			х
Compsorhipis orientalis CHOGSOMZHAV, 1989	х		х
Epacromius pulverulentus (FISCHER VON WALDHEIM, 1846)		х	х
Epacromius tergestinus tergestinus (MEGERLE VON MÜHLFELD, 1825)		х	х
Helioscirtus moseri moseri SAUSSURE, 1884		х	
Leptopternis gracilis (EVERSMANN, 1848)			х
Leptopternis iliensis UVAROV, 1925		х	
Oedaleus decorus (GERMAR,1825)	х	х	х
Oedaleus infernalis SAUSSURE, 1884			х
Psophus stridulus (LINNAEUS, 1758)			х
Sphingoderus carinatus (SAUSSURE, 1888)		х	х
Sphingonotus (Sphingonotus) beybienkoi MISTSHENKO, 1937 /		х	х
Sphingonotus (Sphingonotus) elegans MISTSHENKO, 1937 /	х	х	х
Sphingonotus (Sphingonotus) lucidus MISTSHENKO, 1937			
Sphingonotus (Sphingonotus) coerulipes UVAROV, 1922	х		
Sphingonotus (Sphingonotus) gobicus CHOGSOMZHAV, 1975	х		х
Sphingonotus (Sphingonotus) halophilus BEY-BIENKO, 1929		х	
Sphingonotus (Sphingonotus) mongolicus SAUSSURE, 1888	х		х
Sphingonotus (Sphingonotus) nebulosus nebulosus (FISCHER VON	х	х	х
Sphingonotus (Sphingonotus) obscuratus latissimus UVAROv, 1925	х	х	х
Sphingonotus (Sphingonotus) rubescens (WALKER, 1870)	х		
Sphingonotus (Sphingonotus) tzaidamicus MISTSHENKO, 1937	х		
Stethophyma grossum (LINNAEUS, 1758)			х
TOTAL	17	20	26

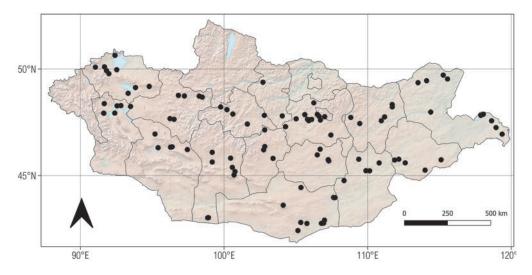


Fig. 1: Distribution map showing all visited sampling locations presented in this study, sampling bias could be observed in the South-Western and Northern areas of Mongolia (see table 2, appendix).

3. Results

3.1. Taxonomic changes

Bryodema gebleri (FISCHER von WALDHEIM, 1836) - valid species

Oedipoda gebleri FISCHER von WALDHEIM, 1836: 346 [original combination].

Bryodema gebleri: ZUBOWSKI (1898): 98 [new combination].

Thrinchus baicalensis FISCHER von WALDHEIM, 1846 - Junior subjective synonym

Thrinchus baicalensis FISCHER von WALDHEIM, 1846: 263 [original combination]. Synonymized with *B. gebleri* by KIRBY (1910: 261).

Bryodema baicalensis: FIEBER (1854): 202 [new combination].

Bryodema gebleri mongolica ZUBOWSKY, 1900 - New junior subjective synonym

Bryodema gebleri mongolica ZUBOWSKY, 1900 syn. nov.

Bryodema gebleri var. mongolica ZUBOWSKY, 1900: 17 [original combination].

Bryodema gebleri mongolicum: CHOGSOMZHAV (1975): 43 [unjustified emendation]

Bryoderma mongolicum: ZHANG, WANG & YIN 2006: 17 [unjustified elevation to species level]

Remarks

The subspecies *B. gebleri mongolica* only differs from the nominate form in the colour of the hind tibia (violet to blue in *B. gebleri mongolica*, while reddish in *B. gebleri gebleri*) and no further morphological differences were described or could be observed from the investigated specimens. Studies on other Orthoptera suggest that colour, in this case that of the hind tibia, may show high intraspecific variation (HAGEN 1982, SCHENNUM & WILLEY 1979, STOROZHENKO et al. 2017). GÜNTHER (1971) states a specifically high variability in both subspecies of *B. gebleri* and

notes that intermediate forms are found in some regions. Moreover, the subspecies do not seem to have specific habitat preferences or represent distinct geographic units. Individuals of both morphs were collected at the same location (e.g. 46.136433N, 99.177505E; 47.694874N, 96.51888E). Therefore, intraspecific variation seems to be more reliable than the presence of several subspecies at the same location and hence supports the formal synonymizing of *B. gebleri* mongolica with *B. gebleri gebleri*. The type location of the nominate form is in Siberia (Altai Mts., Katun Mt) and of *B. gebleri* mongolica is Siberia, Altay, Chuiskaia steppe. The close proximity of both type locations further supports the synonymy.

Oedaleus decorus (GERMAR, 1825) - valid species

Acrydium decorum GERMAR, 1825: pl. 10:12, tab. 17 [original combination]

Oedaleus nigrofasciatus (DEGEER, 1773): KIRBY (1910): 225 [unjustified synonymization of *Acrydium decorum* with *O. nigrofasciatus*]

Oedaleus decorus (GERMAR, 1825): UVAROV (1923): 69 [changed original species name *A. decorum* with *O. decorus*]

Oedaleus asiaticus BEY-BIENKO, 1941 - New junior subjective synonym

Oedaleus asiaticus BEY-BIENKO, 1941 syn . nov.

Oedaleus asiaticus BEY-BIENKO, 1941 New junior subjective synonym.

Oedaleus asiaticus BEY-BIENKO, 1941: 153 [original combination]

Oedaleus decorus asiaticus: RITCHIE (1981): 126 [new subspecific status]

Remarks

Oedaleus asiaticus BEY-BIENKO, 1941 has been treated variably as species or subspecies of *O. decorus* by different authors in the past. Morphologically *O. asiaticus* is similar to *O. decorus* and according to the original description, it differs only in its body size, the thickness and posterior margin of the hind wing fascia, as well as the internal surface of the epiphallic bridge. However, RITCHIE (1981) found differences between the two taxa in a variety of morphometric measurements and suggested that species status may be justified. Yet, the species generally show high variability in most traits. The distributions of both species are overlapping (RITCHIE 1981). Based on molecular results (COI, HUANG et al. 2013, HUSEMANN & DEY unpubl.) both taxa represent a single molecular Operational Taxonomic Unit (mOTU) without any differentiation. As no clear diagnostic differences between the species can be found *O. asiaticus* will be synonymized with *O. decorus*.

3.2. Species records and Discussion

The 740 specimens were determined into 16 species and one species group. We therefore recovered 46 % of the species recorded by the Orthoptera Species File (OSF, (CIGLIANO et al. 2020) for the country and 60 % of the species identified by GÜNTHER (1971) in our dataset. Table 1 shows all species recorded by this study compared to GÜNTHER (1971) and the Orthoptera Species File (CIGLIANO 2020); newly introduced synonyms are considered. In contrast to GÜNTHER (1971) the following species were not recorded during the survey: *Bryodemella (Marikovskiella) orientale orientale* (BEY-BIENKO, 1930), *Bryodemella (Marikovskiella) zaisanicum fallax* (BEY-BIENKO, 1930), *Epacromius pulverulentus* (FISCHER von WALDHEIM, 1846), *Epacromius tergestinus tergestinus* (MEGERLE von MÜHLFELD, 1825), *Helioscirtus moseri moseri* SAUSSURE, 1884, *Leptopternis iliensis* UVAROV, 1925 and *Sphingoderus carinatus* (SAUSSURE, 1888). In turn, *Compsorhipis orientalis* CHOGSOMZHAV, 1989, *Sphingonotus (Sphingonotus) coerulipes* UVAROV, 1922, *Sphingonotus* (Sphingonotus) gobicus CHOG-SOMZHAV, 1975, *Sphingonotus* (Sphingonotus) mongolicus SAUSSURE, 1888, *Sphingonotus* (Sphingonotus) rubescens (WALKER, 1870) and Sphingonotus (Sphingonotus) tzaidamicus MISTSHENKO, 1937 were recorded, which were not included in GÜNTHER's (1971) study (see table 1). The most abundant species in the dataset was *Angaracris barabensis* (PALLAS, 1773) which was collected in almost all biome types in high numbers. In contrast *Celes skalozubovi skalozubovi* ADELUNG, 1906 was just collected once in the Khustai National Park. Altogether, species belonging to four tribes were recorded. Just one species found at one location belongs to the tribe Oedipodini (*Celes skalozubovi skalozubovi*). *Oedaleus decorus* (GERMAR, 1825) was the only caught Locustini present at 22 locations. Furthermore eight species of Sphingonotini from 21 locations and seven species of Bryodemini from 92 locations were collected. According to this, the most abundant tribe of Oedipodinae grasshoppers are the Bryodemini. In the following detailed information about the investigated species and their collection locations are provided.

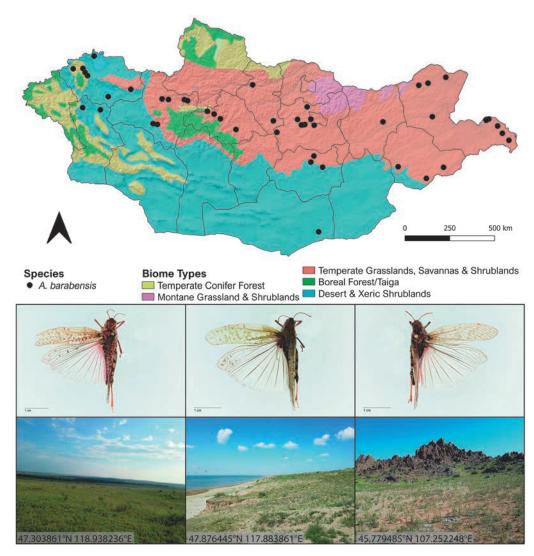


Fig. 2: Sampling locations and specimens of Angaracris barabensis collected in Mongolia.

Angaracris barabensis (PALLAS, 1773) – Figure 2

Angacris barabensis is known as a widely distributed species in Northern and Central Asia. The species seems to be the most abundant Oedipodinae in the temperate grasslands of Mongolia. and it was collected at almost every location in steppe habitats. It shows high morphological variation with different hind wing colours and patterns, including red, yellow, green or colorless hind wings, with many, few or without melanistic patterns at the hind and forewings. The different morphs were formerly thought to be 14 independent species (A. acrohylina BI, 1986; A. hospes (FISCHER von WALDHEIM, 1846); A. lugubris (FISCHER von WALDHEIM, 1846); A. morulimarginis HUANG, 1981; A. morulipennis ZHENG & REN, 1994; A. neimongolensis ZHENG & HAN, 1998; A. nigrimarginis ZHENG & REN, 1993; A. nigripennis LIAN & ZHENG, 1984; A. rhodopa (FISCHER von WALDHEIM, 1836); A. rhodoptila (KARNY, 1908); A. roseipennis (KRAUSS, 1901); A. hunbergi (STAL, 1861) and A. ulashanicus LI, 1981). These were synonymized with A. barabensis by CHILDEBAEV et al. (2013) and STOROZHENKO et al. (2017). The syntypes of *A. barabensis* were collected in western Siberia, Barabinskaya steppe. Neotypes were designated by S. Storozhenko and are deposited in the Zoological Collection of St. Petersburg (ZIN) (collection location: Altaisky Krai, Kliuchevckov Ravon, Severka: 7, August 1922). In this study data of 199 specimens collected at 43 locations (40 % of the total visited locations) were included. The findings suggest, that the species prefers temperate grasslands and forest edges with steppe vegetation.

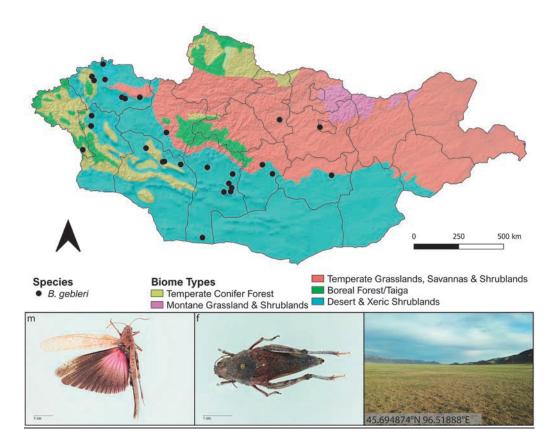


Fig. 3: Sampling locations and specimens of Bryodema gebleri collected in Mongolia.

Bryodema gebleri (FISCHER von WALDHEIM, 1836) - Figure 3

This species is one of the largest band-winged grasshoppers occuring in Mongolia (body size: female: ~32-42 mm; male: ~25-32 mm). Its distribution range includes most of Central Asia. 138 individuals of this species at 28 locations (26 % of the total visited locations) with different habitat characteristics were collected. The species was found only in small numbers at most locations. It occurs in temperate and montaine grasslands, forest edges, as well as desert areas. The type depository of the nominate subspecies is unknown, yet it seems likely that it is deposited at the Zoological Collection of St. Petersburg (ZIN), where the type material of *B. gebleri mongolica* **syn. nov.** is also deposited.

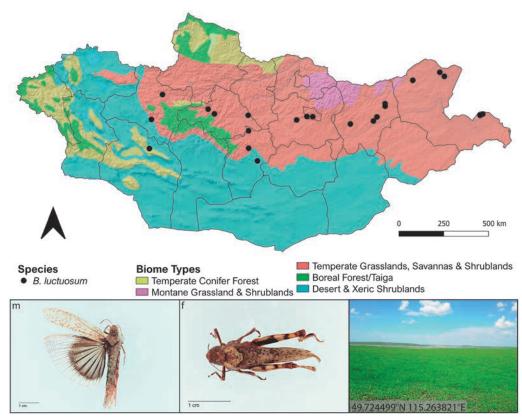


Fig. 4: Sampling locations and specimens of *Bryodema luctuosum luctuosum* collected in Mongolia.

Bryodema luctuosum luctuosum (STOLL, 1813) - Figure 4

Bryodema luctuosum is split into two subspecies *B. luctuosum luctuosum* and *B. luctuosum inda* SAUSSURE, 1884. Both subspecies are present in Asia; while *B. luctuosum inda* is distributed in India and the sourrounding countries, the nominate form is found in Central Asia. In Mongolia the species is very common in steppe habitats. Altogether 58 individuals from 22 locations (20 % of the total visited locations) were recorded. According to the generated distribution map, the species prefers temperate grasslands, but it is also present at the edges of temperate conifer forests and in steppe islands within desert zones. The type location is just recorded as Siberia; the type depository is unknown.

Bryodemella holdereri (KRAUSS, 1901) - Figure 5

This species morphologically resembles *Bryodemella tuberculata* (FABRICIUS, 1775), but can be distinguished by the larger body size, the brighter reddish hind wings and a distinct venation of the hind wings. Interestingly, the species can be found syntopic with *B. tuberculata*; both species were found to be present together at several locations (e.g. 47.939045 N, 100.61386 E; 47.87765 N, 102.806735 E), and moreover some specimens with intermediate traits. Hence, the two species may represent the two extremes of intraspecific morphological variation, or young species which are still able to hybridize. Further studies, including genetic analyses need to be performed to answer this question. Altogether 28 specimens from 14 locations (13 % of the total visited locations) of this phenotype were recorded. GÜNTHER (1971) lists it as one of the most widespread species in the country. He states that the species is often found on slopes with gravel and loose vegetation, most often close to water bodies. The type specimen was described from China, Huangyuan County, Qinghai Lake, Chengguan [China, Koko-nor Lake, Donkir] and is deposited in the Natural History Museum Stuttgart (SMNS).

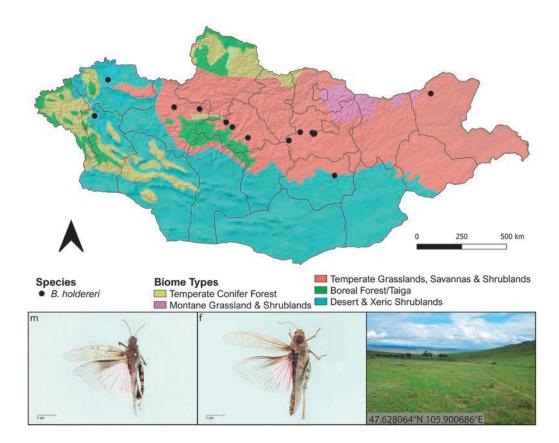


Fig. 5: Sampling locations and specimens of Bryodemella holdereri collected in Mongolia.

Bryodemella tuberculata tuberculata (FABRICIUS, 1775) – Figure 6

This species is one of the most common Oedipodinae in Central Asia. It is found from Central Europe to Korea. While most populations in Europe are extinct since the early 20th century due to habitat loss (BAZYLUK 2000, BUDRYS & PAKALNIŠKIS 2007, HIRNEISEN 2003, REINHARDT et al. 2005), the species is still very widespread in Asia (DEY et al. submitted). Further studies have to shed light on the decrease and extinction of the species in Europe. The species is split into two subspecies: Bryodemella tuberculata tuberculata which is found from Central and Northern Europe to Central Asia and B. t. bavarica (ZACHER, 1919) which is endemic to the Alps. The Central and Eastern Asian populations were assigned to Bryodemella t. diluta (STOLL, 1813). Accordingly, GÜNTHER (1971) lists the subspecies B. t. diluta (STOLL, 1813) for Mongolia. However, the subspecies is now considered to be a synonym of B. t. tuberculata (KIRBY, 1910; SERGEEV et al., 2020), which is also supported as no morphological characters divide both subspecies and they share an overlapping distribution range. The subspecies B. t. tuberculata was recorded from grasslands and at the edge of forests. Altogether 39 individuals from 12 locations (11% of the total visited locations) were sampled; it was never present in desert areas. Bryodemella t. tuberculata was described by FABRICIUS in 1775; the types are considered lost; a Neotype was designated by Harz in 1975 from Germany, Bremen, Oldenbüttel (deposited in the Muséum d'Histoire Naturelle de la Ville de Genève (MHNG); HARZ 1975).

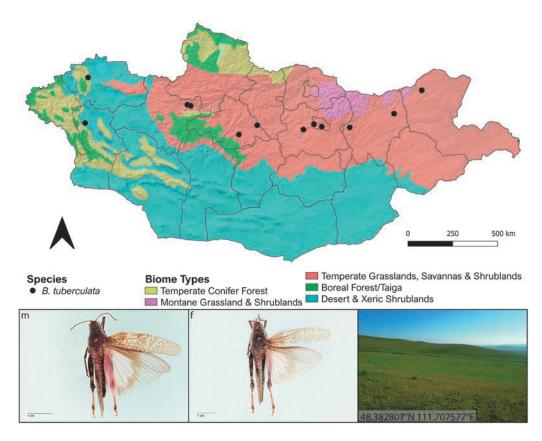


Fig. 6: Sampling locations and specimens of *Bryodemella tuberculata tuberculata* collected in Mongolia.

Compsorhipis bryodemoides BEY-BIENKO, 1932 – Figure 7

This species is very common in Mongolia and adjacent countries. However, up to now, just a few sampling locations were published. The species was frequently collected during the surveys in Mongolia. 61 individuals from 18 locations (17 % of the total visited locations) were collected. *Compsorhipis bryodemoides* shows a clear habitat preference for desert areas with sparse vegetation. GÜNTHER (1971) listed it for pebbly and rocky desert-steppes. The type location is Mongolia at the middle reaches of the Tuijn-gol River, Nalha. The holotype is deposited at the Zoological Collection of St. Petersburg (ZIN).

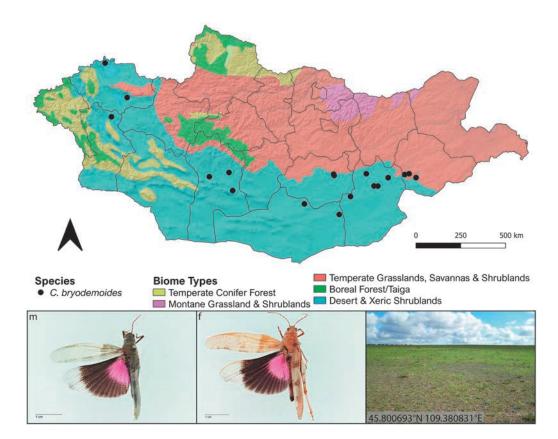


Fig. 7: Sampling locations and specimens of Compsorhipis bryodemoides collected in Mongolia.

Compsorhipis orientalis CHOGSOMZHAV, 1989 - Figure 8

This species so far has rarely been documented. Only two studies with information regarding this species have been published (CHOGSOMZHAV 1989, YIN & WANG 2005). The first is the original description, which contains only a few morphological features (red hind tibia and relatively thick antennae) to distinguish it from other species of the genus (CHOGSOMZHAV 1989); the second is a reference of the type location from Eastern Gobi Aimag (YIN & WANG 2005). The lack of morphological features for clear identification and missing records makes the status of this species questionable. Based on the few morphological differences to the other species of Compsorhipis, further identification was not possible. However, C. orientalis was found syntopic at the same location as C. bryodemoides, which only differs in the colour of hind tibiae (pale yellow). Hence, the two species may be conspecific. Further analyses using molecular methods are necessary to clarify its status. Similar to C. bryodemoides, C. orientalis is restricted to desert areas with sparse vegetation. 15 specimens from nine locations (8 % of the total visited locations) were recorded. Up to now, the species is just known from Mongolia. The type location is close to the collecting site in Eastern Mongolia (45.238959 N, 109.87863 E, close to the Aimag-Center Sainschand). The species is described from Mongolia. Eastern Gobi Aimag, type depository is unknown.

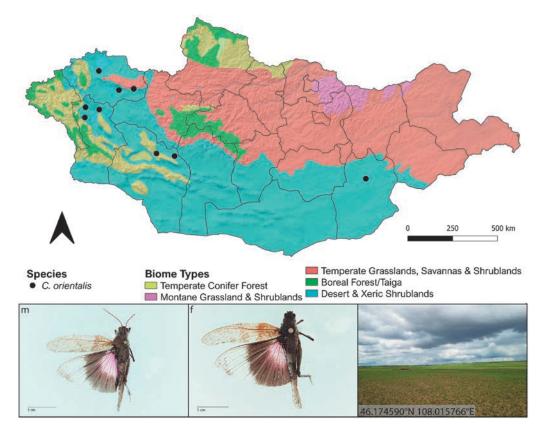


Fig. 8: Sampling locations and specimens of Compsorhipis orientalis collected in Mongolia.

Celes skalozubovi skalozubovi ADELUNG, 1906 - Figure 9

This species is distributed across Central Asia. In Mongolia it seems rather rare; just a single individual was found during the surveys. Although the sampling location Khustai National Park was frequently visited, the species was just found once in 2017. Species of the genus prefer temperate grasslands in hilly and mountainous regions (BUZZETTI et al. 2010, IORGU et al. 2008, ZINENKO & STRIGANOVA 2009). GÜNTHER (1971) found the species on hot and dry slopes with loose vegetation, where specimens were sometimes hiding under rocks. The type specimen comes from Russia (Tobolsk) and is deposited in the Zoological Collection St. Petersburg (ZIN).

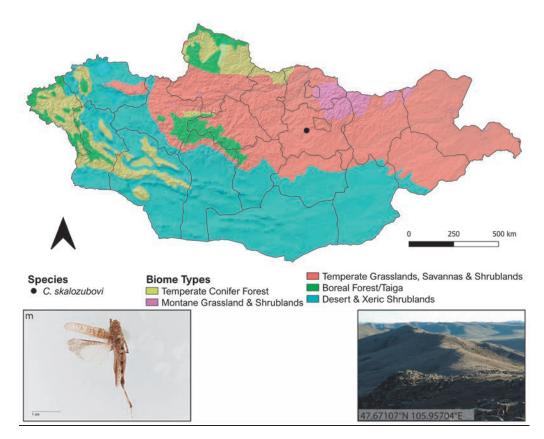


Fig. 9: Sampling location and specimen of Celes skalozubovi skalozubovi collected in Mongolia.

Oedaleus decorus (GERMAR, 1825) - Figure 10

Oedaleus decorus is one of the most widespread Oedipodinae species worldwide. Its distribution ranges from China and Russia in the east to Algeria, Spain and France in the west (BOCZKI 2007, KUŘAVOVÁ 2015, RITCHIE 1980, SCHMIDT 1997). During the expeditions 96 individuals at 22 locations in Mongolia (20 % of the total visited locations) were collected. The type location of *O. decorus* is Dagestan, North Caucasus; the type is deposited at the Natural History Museum London (BMNH). Syntypes of *O. asiaticus* are collected from Buriatia, Kiakhta, Ust'-Kiran in Russia and are deposited at the Zoological Collection of St. Petersburg (ZIN).

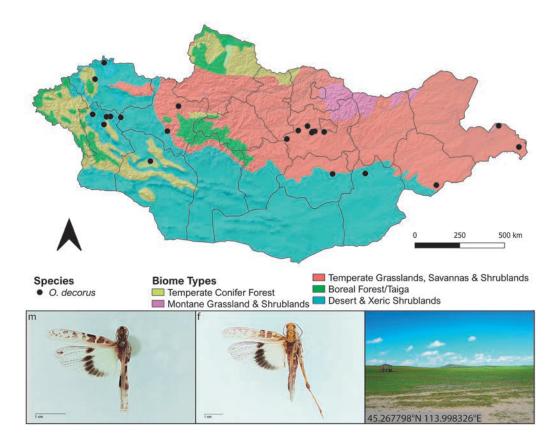


Fig. 10: Sampling locations and specimens of Oedaleus decorus collected in Mongolia.

<u>Sphingonotus (Sphingonotus) beybienko MISTSHENKO, 1937 / S. (S.) lucidus MISTSHENKO, 1937 / S. (S.) elegans MISTSHENKO, 1937 complex – Figure 11</u>

Because of the rather subtle morphological differences, which show variation and overlap between species, *S.* (*S.*) beybienkoi, *S.* (*S.*) lucidus and *S.* (*S.*) elegans were treated here as a species group. According to the species descriptions and identification keys (BEY-BIENKO & MISTSHENKO 1951, MISTSHENKO 1937) the females of the species can be differentiated by the shape of the eyes, and the number of veins branching off of the median vein in the apical part of the forewing. *S.* (*S.*) beybienkoi is defined by round eyes and 1-2 branches; while *S.* (*S.*) lucidus has oval eyes and 3-4 branches. *S.* (*S.*) elegans is also defined by oval eyes and three branches (MISTSHENKO 1937). Unfortunately, the diagnostic traits of females of the species are overlapping and hence not many specimens could be identified with certainty. Males cannot be identified with current keys at all. Hence, the status of the species will have to be clarified in future studies. Altogether, 58 individuals of this group at 16 locations (15 % of the total visited locations) were collected, and all in desert habitats and xeric shrublands.

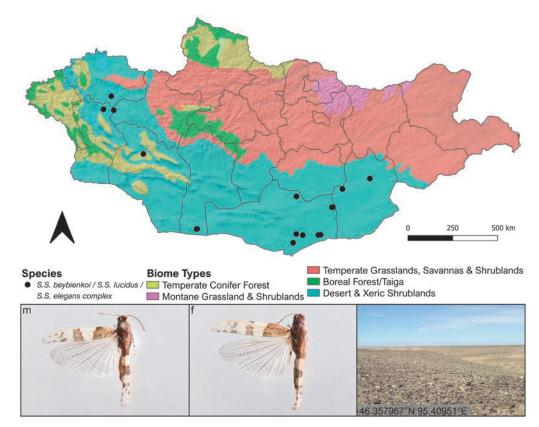


Fig. 11: Sampling locations and specimens of the group of *Sphingonotus* (*Sphingonotus*) beybienko, S. S. lucidus, S. S. elegans (not clearly identifiable) collected in Mongolia.

In general *Sphingonotus (Sphingonotus) beybienkoi* is considered as one of the most common Sphingonotini in Mongolia (MISTSHENKO 1937, GÜNTHER 1971). The species is known to be widespread in Central Asia and has been recorded from Kazakhstan, China and Mongolia. The type material is deposited in the Zoological Collection of St. Petersburg (ZIN). MISTSHENKO (1937) described the species from Mongolia (southern Mongolia, Baishintu, S. Ala-Shan). The Ala-Shan desert is covering parts of southern Mongolia and northern China. Unfortunately,

georeferencing of the location Baishintu within this desert area was not possible. Hence, it remains unclear, if the species was described from Mongolia or China. *S. (S.) lucidus* is known from only a few specimens and so far has only been found in Tadzhikistan. GÜNTHER (1971) does not list the species for Mongolia; some of the investigated specimens seem to match the species, but the identification is uncertain. The type material is deposited in the Zoological Collection of St. Petersburg (ZIN); the type location is Tadzhikistan (Pamir Mts., Sardy, Gunt River). *S. (S.) elegans* is known to be present in Kazakhstan and Turkmenistan and was listed by GÜNTHER (1971) for Mongolia. The type location is Turkmenistan (Kaakhka); the types are deposited in the Zoological Collection of St. Petersburg (ZIN).

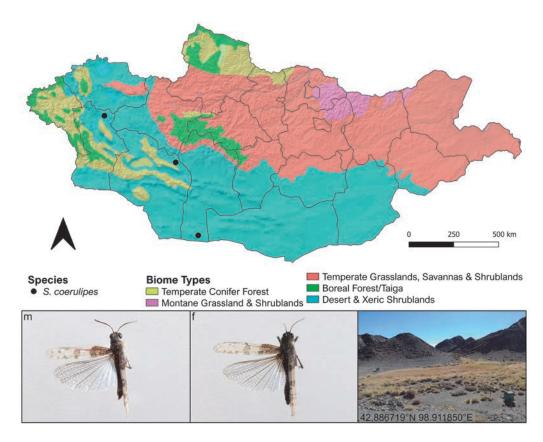


Fig. 12: Sampling locations and specimens of *Sphingonotus (Sphingonotus) coerulipes* collected in Mongolia.

Sphingonotus (Sphingonotus) coerulipes UVAROV, 1922 - Figure 12

Sphingonotus (Sphingonotus) coerulipes was found at three locations during the surveys. The species lives in deserts and xeric shrublands on stony to somewhat sandy ground. We collected six individuals at three locations during the field trip in 2017 (3 % of the total visited locations). The species is widespread in Central Asia. Four subspecies are described, which are geographically separated. Sphingonotus (Sphingonotus) coerulipes coerulipes UVAROV, 1922 was described from Iran. The holotype was collected in Qazvin Province and is deposited at the British Museum of Natural History in London (BMNH); Sphingonotus (Sphingonotus) coerulipes dja-konovi MISTSHENKO, 1937 is known from Turkey and Ukraine, the type specimen was collected

in Crimea, between Otuzy and Kozy, Echki-Dag and is deposited in the Zoological Collection of St. Petersburg (ZIN); *Sphingonotus (Sphingonotus) coerulipes kermanicus* PREDTECHENSKII, 1937 is endemic to Iran; the type location is northern Kerman. The type is deposited in the Zoological Collection of St. Petersburg (ZIN). *Sphingonotus (Sphingonotus) coerulipes uvarovianus* BEY-BIENKO, 1926 is endemic to Kazakhstan; the type was collected in Kazakhstan, Zaisan Lake and is assumed to be deposited in Omsk, with no further detail on the institution. Because of lacking material for morphological comparison no further identification of the specimens from Mongolia at the subspecific level was possible.

Sphingonotus (Sphingonotus) gobicus CHOGSOMZHAV, 1975 – Figure 13

Sphingonotus (Sphingonotus) gobicus is one of the morphologically best defined Sphingonotini without a wing band. The species is very small (body length: female: ~14-15.5 mm; male: ~11-14.5 mm) and has large eyes. A clear diagnostic trait are the three dark bands on the inner site of the hind femora. Up to now just small number of known records and a limited number of preserved specimens from museum collections are known. 15 specimens from three locations (~3 % of the total visited locations) were collected during field trips to Mongolia in 2017. The holotype of the species was collected in Mongolia, Bajanchongor-Aimag, Shar-Hulsnii-Bulag (43.308698° N 97.776054° E) and is deposited in the MAS Mongolia.

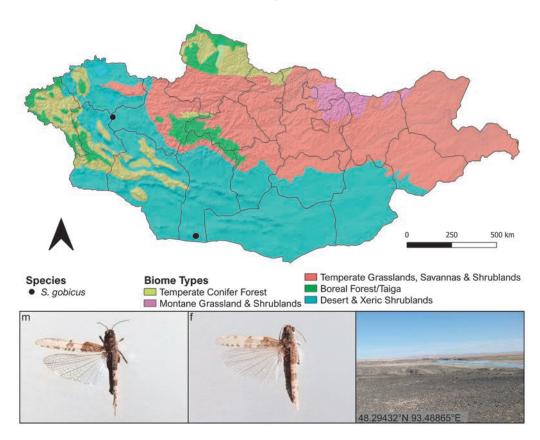


Fig. 13: Sampling locations and specimens of *Sphingonotus (Sphingonotus) gobicus* collected in Mongolia.

Sphingonotus (Sphingonotus) mongolicus SAUSSURE, 1888 – Figure 14

Sphingonotus (Sphingonotus) mongolicus was one of the most rarely found Sphingonotini during the surveys. Only four individuals from one location in the Gobi Gurvan Saikhan National park in 2015 were recorded. The species could be identified by its characteristic bluish hind wings with a curved, fairly wide band. S. (S.) mongolicus is distributed from Mongolia to Kamchatka. It was described by Saussure from Mongolia in 1888 without a specified type location. A syntype is deposited in the Muséum d'Histoire Naturelle de la Ville de Genève (MHNG).

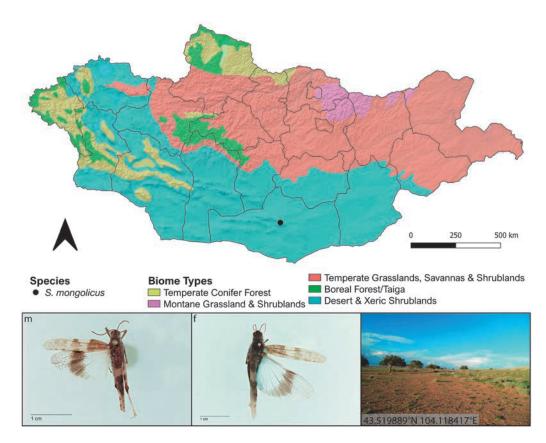


Fig. 14: Sampling location and specimens of *Sphingonotus (Sphingonotus) mongolicus* collected in Mongolia.

Sphingonotus (Sphingonotus) nebulosus nebulosus (FISCHER von WALDHEIM, 1846) - Figure 15

Sphingonotus (Sphingonotus) nebulosus is one of the most colourful Oedipodinae worldwide. It has several subspecies distributed across Asia, which differ mostly in their hind wing colours (violet, pinkish, green or bluish hindwings with a typical wing band shape). While the species is quite common in southern Asia, it is hard to find at its northern distribution range. The Gobi Desert represents one of the most northern locations it has been found (DEY et al. 2018, MEDETOV 2017, PRAVDIN 1969). Five individuals of the subspecies *Sphingonotus* (*Sphingonotus*) nebulosus at a stony mountain canyon were collected during the field surveys of this study. The subspecies was described from Kazakhstan (Songaria). The type depository is unknown.

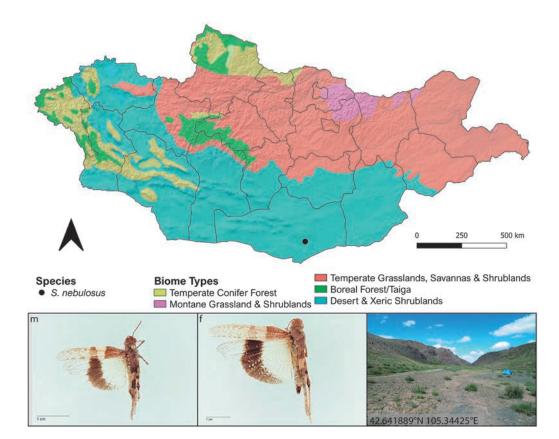


Fig. 15: Sampling locations and specimens of *Sphingonotus (Sphingonotus) nebulosus nebulosus collected* in Mongolia

Sphingonotus (Sphingonotus) obscuratus latissimus UVAROV, 1925 – Figure 16

Sphingonotus (Sphingonotus) obscuratus is divided into six subspecies, distributed across northern Africa, South-East Asia up to western Asia. Mongolia represents the eastern distribution margin of the species. Until now the subspecies *S. (S.) obscuratus latissimus* was recorded from South-West Mongolia (several locations) by GOROCHOV et al. (1989), GÜNTHER (1971) and MISTSHENKO (1968). The subspecies is defined by the unique shape of its hind wing band. It appears to be rather stenoecious and is only found in rocky areas within the Gobi Desert. The species was recorded only three times (3 % of the total visited locations) with a total number of six individuals. The type location is Kazakhstan (Semiretchye). The type depository is the British Natural History Museum in London (BMNH).

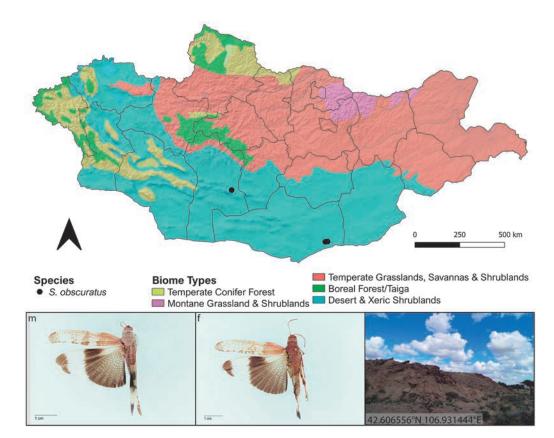


Fig. 16: Sampling locations and specimens of *Sphingonotus (Sphingonotus) obscuratus latissimus* collected in Mongolia.

Sphingonotus (Sphingonotus) rubescens (WALKER, 1870) – Figure 17

Sphingonotus rubescens has a wide distribution range spreading from the Cape Verde Islands across northern Africa, the Middle East and Central Asia and Mongolia. In northern Africa, the species can be found in many habitat types. It is more restricted in Mongolia. Altogether six subspecies are described:

- S. (S.) r. rubescens (WALKER, 1870) which was described from Wadi Genneh (Egypt), but type material is unfortunately lost;
- *S. (S.) r. afghanicus* MISTSHENKO, 1937 which is endemic to Afghanistan, type location is Barizendan (Afghanistan) and deposition is the Zoological Collection of St. Petersburg (ZIN);
- *S. (S.) r. burri* CHOPARD, 1936 is endemic to the Cape Verde islands, type location is Fogo (Cape Verde), types are deposited in the NHM Paris (MNHN);
- S. (S.) r. fallax MISTSHENKO, 1937 was described from Jammu-Kashmir, Nubra River (Northern India), types are deposited in the Zoological Collection of St. Petersburg (ZIN);
- S. (S.) r. fasciatus MISTSHENKO, 1937 the type specimen was described from Nono-Voskresenovka (Kazakhstan) and deposited in the Zoological Collection of St. Petersburg (ZIN);
- S. (S.) *r. subfasciatus* BEY-BIENKO, 1951 was described from Lake Issyk-Kul (Kyrgyzstan), unfortunately the type depository is unknown, topotypes are deposited in the Siberian Zoological Museum Novosibirsk (SZMN).

The species is easily confused with other species of the *S.* (*S.*) caerulans- and *S.* (*S.*) coerulipesgroups, but is characterized by hyaline wings and an s-shaped intercalary vein. Six specimens at five locations (5 % of the total visited locations) were collected suring the field trips.

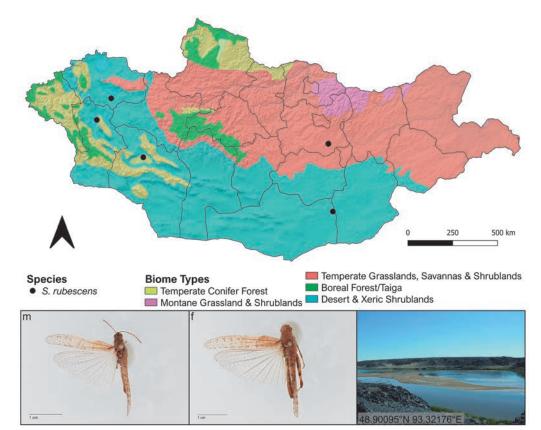


Fig. 17: Sampling locations and specimens of *Sphingonotus (Sphingonotus) rubescens* collected in Mongolia.

Sphingonotus (Sphingonotus) tzaidamicus MISTSHENKO, 1937 – Figure 18

Sphingonotus (Sphingonotus) tzaidamicus was recorded five times within the dataset from three locations (3 % of the total visited locations) with five specimens in total. The species is distributed in Central Asia preferring open areas with sparse vegetation and stony or sandy underground (MISTSHENKO 1937). The type of the species was described from China (eastern Tsaidam, Barun-Tzaraka Range) and is deposited in the Zoological Collection of St. Petersburg (ZIN).

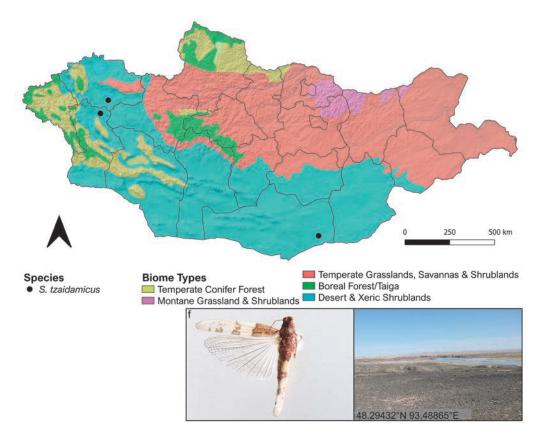


Fig. 18: Sampling locations and specimens of *Sphingonotus (Sphingonotus) tzaidamicus* collected in Mongolia.

3.3. Species richness

The species richness for Oedipodinae grasshoppers was calculated for different regions of Mongolia based on the collected distribution data (fig.19). The analysis shows the highest diversity around Ulan-Bator and in the lake-rich western Mongolian region. In this region up to six species were recorded per cell. High species richness may result of the presence of several biome types and water bodies in this region. Yet, it may also be largely caused by sampling bias, as also suggested by decreasing species richness in the vicinity of country borders, which are rarely visited.

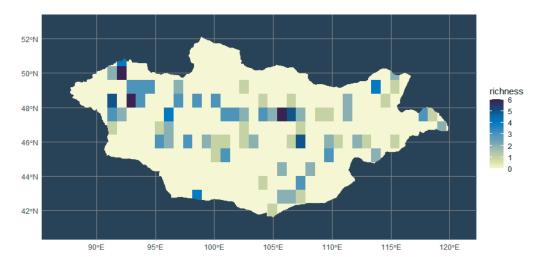


Fig. 19: Calculated species richness based on 740 records of Oedipodinae grasshoppers from Mongolia with a used grid cell size of 0.8. Species richness is shown as color gradient from white to dark blue (white = 0 species; dark blue = 6 species). Regions with no species recorded represent sampling gaps.

3.4. Conclusions

Although sampling was performed at many locations in Mongolia, large areas are still are missing (fig. 1). This is also reflected in a relatively large number of species, which are known from the country, but were not encountered in the sampleset: Andrea gorochovi MISTSHENKO, 1989; Bryodema kozlovi BEY-BIENKO, 1930; Bryodema miramae miramae BEY-BIENKO, 1930; Bryodema nigripennis MISTSHENKO & GOROCHOV, 1989; Bryodema orientale orientale (BEY-BIENKO 1930); Bryodema orientale simulans STEBAEV, 1964; Bryodema zaisanicum fallax (BEY-BIENKO, 1930); Compsorhipis davidiana (SAUSSURE, 1888); Epacromius pulverulentus (FISCHER von WALDHEIM, 1846); Epacromius tergestinus tergestinus (MEGERLE von MÜHLFELD, 1825); Locusta migratoria (LINNAEUS, 1758); Leptopternis gracilis (EVERSMANN, 1848); Leptopternis iliensis UVAROV, 1925; Helioscirtus moseri SAUSSURE, 1884; Oedaleus infernalis SAUSSURE, 1884; Psophus stridulus (LINNAEUS, 1758); Sphingonotus halophilus BEY-BIENKO, 1929; Sphingoderus carinatus (SAUSSURE, 1888) and Stethophyma grossum (LINNAEUS, 1758) (GÜNTHER 1971, CIGLIANO et al. 2020). GÜNTHER (1971) had in total 4098 individuals at his disposal, a much larger number than the specimens investigated in this study. In his studies he lists several of the species as rather rare. Nevertheless, this study contributes several new records for Mongolia and hence increases the knowledge on the fauna of Oedipodinae in the country. Further investigations, also including the fauna of neighbouring countries, need to be performed to better understand the distributions of these taxa.

Based on the performed analyses of the collected material and study of type material the following species were synonymized: *Bryodema gebleri mongolica* ZUBOVSKI, 1900 **syn. nov.** of *Bryodema gebleri* (FISCHER von WALDHEIM, 1836), as no clear differences between the subspecies were detected and both subspecies occur sympatrically. Moreover, *Oedaleus asiaticus* BEY-BIENKO, 1941 **syn. nov.** was synonymized with *Oedaleus decorus* (GERMAR, 1825), a synonymy already suggested by RITCHIE (1981) and confirmed by genetic data. The status of *Bryodemella holdereri* (KRAUSS, 1901) needs to be reconsidered in the future, as the species is morphological very similar to *Bryodemella tuberculata tuberculata* (FABRICIUS, 1775) and both taxa can be found sympatrically at several locations. The same is true for some species within the genus *Sphingonotus*, which will be studied with molecular tools in the future.

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Apendix

Table 2: Oedipodinae grasshopper species collected during surveys to Mongolia and their sampling locations (all locations are visualized in fig. 1)

Latitude	Longitude	Angaracris barabensis	Bryodema gebleri	Bryodema luctuosum luctuosum	Bryodemella holdereri	Bryodemella tuberculata tuberculata	Celes variabilis	Compsorhipis bryodemoides	Compsorhipis orientalis	Oedaleus decorus	S. S. beybienkoi/ S. S. lucidus/ S. S. elegans complex	Sphingonotus coerulipes	Sphingonotus gobicus	Sphingonotus mongolicus	Sphingonotus nebulosus	Sphingonotus obscuratus latissimus	Sphingonotus rubescens	Sphingonotus tzaidamicus
42.2225	105.14408										х							
42.58880	105.77										х							
42.59458	106.77983										х					х		
42.60655	106.93144										х					х		
42.64188	105.34425										х				х			
42.75862	106.99446																	х
42.88055	98.8614		х															
42.88216	98.863633										х		х					
42.88748	98.9118										х	х	х					
43.51988	104.11842													х				
43.89708	107.66208										х							
43.9055	107.72817										х						х	
43.91211	107.62156							х										
44.40766	105.35611							х			х							
44.75169	108.35585							х			х							
45.01051	100.25352		х															
45.02860	100.69696		х					х								х		
45.20021	100.76205		х															
45.23369	110.13685							х			х							
45.23895	109.87863							х	х									
45.26779	113.99833	х								х								
45.40592	100.57567		х															

Table 2 continuing

1	r		1		1	1	1	1	1	1	1		1	1	1	1	1	
Latitude	Longitude	Angaracris barabensis	Bryodema gebleri	Bryodema luctuosum luctuosum	Bryodemella holdereri	Bryodemella tuberculata tuberculata	Celes variabilis	Compsorhipis bryodemoides	Compsorhipis orientalis	Oedaleus decorus	S. S. beybienkoi/ S. S. lucidus/ S. S. elegans complex	Sphingonotus coerulipes	Sphingonotus gobicus	Sphingonotus mongolicus	Sphingonotus nebulosus	Sphingonotus obscuratus latissimus	Sphingonotus rubescens	Sphingonotus tzaidamicus
45.62015	110.79885	Ì						x		-								
45.62296	112.61696							x										
45.66625	99.178856							x										
45.71861	107.29175							x										
45.76186	111.88111							x										
45.77291	115.11445	х																
45.77948	107.25225	х	х		х			х		х								
45.80069								х		х								
45.80158		х						х										
45.83626	100.82331		х															
45.84178	103.41129		х	х														
45.85453	100.45655							х										
46.01213	106.49194	х																
46.13643	99.177505		х															
46.25533	102.75913		х															
46.26827	97.446815		х						х			х						
46.28603	106.68976	х																
46.35796	95.40951									х	х						х	
46.38181	96.27138		х						х									
46.39974	96.3862		х	х														
46.41541	102.83617			х														
46.92613	91.082046		х															
46.95108	107.43864																х	
46.99282		х								х								
46.99676	95.194431		Х															

Table 2 continuing

Latitude	Longitude	Angaracris barabensis	Bryodema gebleri	Bryodema luctuosum luctuosum	Bryodemella holdereri	Bryodemella tuberculata tuberculata	Celes variabilis	Compsorhipis bryodemoides	Compsorhipis orientalis	Oedaleus decorus	S. S. beybienkoi/ S. S. lucidus/ S. S. elegans complex	Sphingonotus coerulipes	Sphingonotus gobicus	Sphingonotus mongolicus	Sphingonotus nebulosus	Sphingonotus obscuratus latissimus	Sphingonotus rubescens	Sphingonotus tzaidamicus
47.19430	102.83315			х														
47.30386	118.93824	х																
47.34692	104.28503	х			х					х								
47.47122	101.62091	Х			х	Х												
47.49574	109.44978			Х														
47.62377	118.63003	Х																
47.62684	110.94969			х														
47.62806	105.90069				Х					Х								
47.65841	106.70806	Х								Х								
47.67107	105.95704	Х		х	х		х			Х								
47.67315	105.87237	Х																
47.68777	106.09908	х	<u> </u>	<u> </u>	<u> </u>	<u> </u>	<u> </u>	<u> </u>		х		<u> </u>	<u> </u>			<u> </u>		
47.6925	105.81183	<u> </u>	<u> </u>	<u> </u>	<u> </u>	х	<u> </u>	<u> </u>		<u> </u>		<u> </u>	<u> </u>			<u> </u>		
47.69320	105.81099				х													
47.69487	96.51888	х	х	х	<u> </u>	<u> </u>	<u> </u>	<u> </u>		х		<u> </u>	<u> </u>			<u> </u>		
47.98468	92.39198									х								\square
48.03231	114.38769	х	<u> </u>	<u> </u>	<u> </u>	<u> </u>	<u> </u>	<u> </u>		<u> </u>		<u> </u>	<u> </u>			<u> </u>		
48.14519		х	<u> </u>	х	х	<u> </u>	<u> </u>	<u> </u>		<u> </u>		<u> </u>	<u> </u>			<u> </u>		
48.25241	103.877		х															
48.26857	99.764565	х	<u> </u>	<u> </u>	<u> </u>	<u> </u>	<u> </u>	<u> </u>		<u> </u>		<u> </u>	<u> </u>			<u> </u>		
48.27335	111.7126	<u> </u>		х														\square
48.29432	93.48865	<u> </u>	<u> </u>	<u> </u>	<u> </u>	<u> </u>	<u> </u>	<u> </u>		х	х	<u> </u>	х			<u> </u>	х	
48.32235	92.551644	<u> </u>	<u> </u>	<u> </u>	<u> </u>	<u> </u>	<u> </u>	<u> </u>	х	х		<u> </u>	<u> </u>			<u> </u>		
48.33323	92.81828	<u> </u>						х		х	х	х						х
48.38280	111.70758			х		х												

Table 2 continuing

Latitude	Longitude	Angaracris barabensis	Bryodema gebleri	Bryodema luctuosum luctuosum	Bryodemella holdereri	Bryodemella tuberculata tuberculata	Celes variabilis	Compsorhipis bryodemoides	Compsorhipis orientalis	Oedaleus decorus	S. S. beybienkoi/ S. S. lucidus/ S. S. elegans complex	Sphingonotus coerulipes	Sphingonotus gobicus	Sphingonotus mongolicus	Sphingonotus nebulosus	Sphingonotus obscuratus latissimus	Sphingonotus rubescens	Sphingonotus tzaidamicus
48.42477	91.65891	х	х		х				х	х								
48.46079	106.2514	х																
48.72501	98.47725	х			х	х												
48.77071	98.269883	х																
48.77806	97.239265	х		х						х								
48.80373	96.8224	х			х	х												
48.90095	93.32176										х						х	х
49.72449	115.26382	х		х														
49.79195	91.980845	х																
49.92685	91.815663	х	х			х				х								
49.96848	92.529228		х		х				х									
50.08483	91.042728	х																
50.09930	91.676319	х	х															
50.61108	92.406657	х	х					х		х								