ZooKeys 1105: 1–125 (2022)
doi: 10.3897/zookeys.1105.81474
https://zookeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
ZooKeys
Launched to accelerate biodiversity research

A critical review of the distribution of the endangered European earth-borer beetle *Bolbelasmus unicornis* (Coleoptera, Geotrupidae), with new records from 13 countries and observations on its bionomy

Daniel Juřena[1]

1 *Lidická 59, 796 01 Prostějov, Czech Republic*

Corresponding author: Daniel Juřena (aphodius@seznam.cz)

Academic editor: Andrey Frolov | Received 31 January 2022 | Accepted 11 May 2022 | Published 15 June 2022

http://zoobank.org/B0AD2D97-876F-4159-84E9-9A67E2E4AC76

Citation: Juřena D (2022) A critical review of the distribution of the endangered European earth-borer beetle *Bolbelasmus unicornis* (Coleoptera, Geotrupidae), with new records from 13 countries and observations on its bionomy. ZooKeys 1105: 1–125. https://doi.org/10.3897/zookeys.1105.81474

Abstract

The distribution of *Bolbelasmus unicornis* (Schrank, 1789) is critically reviewed throughout its range with emphasis on the Czech Republic and Slovakia. The species has been reliably recorded from 377 localities in 19 countries. New records are given from 152 localities of Bulgaria, Czech Republic, Germany, Hungary, Italy, Moldova, Poland, Romania, Serbia, Slovakia, Turkey, and Ukraine. For Germany, the species is recorded for the first time in 54 years. The occurrence of the species in Switzerland is confirmed by two historical specimens from Zürich. The only known historical specimen labelled "Kaukasus" is given, which could originate from Russia, where this species has not been recorded before (however, confusion of the locality label cannot be ruled out). All published faunistic data from across the range are presented here in full, in several cases supplemented by details subsequently obtained by the author. Distribution maps are compiled separately for the Czech Republic and Slovakia, and for the entire range. A separate map is also available for Hungary, where approximately one-third of the known localities are located. Statistical data concerning the flight activity of adults, seasonal dynamics for part of the distribution area, details of records and notes on the bionomy and ethology of the species are provided. Possible feeding strategies for adults and larvae of *B. unicornis* are discussed, as well as current knowledge of the natural history of various representatives of the subfamily Bolboceratinae. A monitoring method for the species is proposed.

Keywords

Asia Minor, Bolboceratinae, ethology, Europe, Palaearctic realm, zoogeography

Table of contents

Introduction

Bolbelasmus unicornis (Schrank, 1789) is a European species of earth-borer beetle extending into the western Asian part of Turkey with the centre of distribution in the

Pannonian Basin (see Faunistic records and Fig. 18). It is a medium-sized bolboceratine which was the subject of considerable interest to the insect collectors as early as the 19th century because of its interesting and attractive appearance (for male and female habitus see Figs 1–3, 21). In literature, the body length of adults is reported to be 12.0–15.0 mm (Savchenko 1938; Endrődi 1956; Panin 1957; Mikšić 1958, 1960; Medvedev 1965; Machatschke 1969; Baraud 1992; Hůrka 2005; Ballerio et al. 2014). According to measurements taken during this study on ca. 800 specimens, the body length of this species ranges between 9.5–14.5 mm. *Bolbelasmus unicornis* is considered an endangered species with bioindicator significance throughout its range (see Habitat preferences). For this reason, it has been listed as a species of special conservation in many European countries. At the instigation of Slovakia, it has been included in Annexes II and IV of the Habitat Directive of the European Union (species in need of strict protection). As very few faunistic records are known from most countries, each new record is critically important to increase our knowledge to implement appropriate conservation strategies for the species. For more than 50 years the species has not been recorded in France, Slovenia, Bosnia and Herzegovina, Albania, and Moldova. It is probably extinct in France, Switzerland, Poland, and the Czech Republic.

The species was described as *Scarabaeus unicornu* by Schrank von Paula (1789) and subsequently as *S. aeneas* by Panzer (1793a). Since the end of the 18th century, the species was often confused with *Scarabaeus quadridens* Fabricius, 1781 from India and later synonymised with it (Panzer 1793b, 1795, 1802; Illiger 1798; Duftschmid 1805; Sturm 1805, 1843; Schönherr 1806; Skrimshire 1812; Dejean 1821, 1833, 1836; Curtis 1829a, b, 1837; Stephens 1829, 1830, 1839; Eichwald 1830; Laporte de Castelnau 1840; Heer 1841). However, Illiger (1800) had already assumed that these were two distinct species. It was only Klug (1843) who separated the two species from each other, however, later authors (e.g., Erichson 1847; Gaubil 1849; Kiesenwetter and Schaum 1849; Redtenbacher 1849, 1858, 1874; Westwood 1852; Oechsner 1854; Lacordaire 1856; Calwer 1858; Fuss 1858; Gerstaecker 1863; Stierlin and Gautard 1867; Gemminger and Harold 1869; Mulsant and Rey 1871; Bertolini 1872; Jäger 1884; Seidlitz 1891; Luigioni 1929) continued to list the name *quadridens* among synonyms and often ascribed authorship of this species name to Panzer (1795). The same mistake was reported in both editions of the Catalogue of Palearctic Coleoptera (Král et al. 2006; Nikolajev et al. 2016).

Given its secretive lifestyle and lack of knowledge of effective collecting methods, the distribution and bionomy of *B. unicornis* are poorly known. Adults spend most of their time underground, with above-ground activity limited to short flight periods when they fly very close to the ground just after sunset (see Natural history of Bolboceratinae in this study). Nothing is known about the immature stages and the diet of adults and larvae. However, some authors assumed that both adults and larvae feed on hypogeous fungi (e.g., Sajó 1910a, b; Ohaus 1929; Roubal 1936; Koch 1989; Bratek et al. 1992; Merkl 2003, 2014, 2015; Nádai 2006). Adults, like in other members of the genus *Bolbelasmus*, are able to stridulate loudly, a fact first mentioned by Ghiliani (1847). Individuals of *B. unicornis* produce a wide range of sounds, varying in intensity and other characteristics depending on whether it is in response to a disturbance or part of their normal

activities (pers. obs.). In the congeneric species *B. gallicus* (Mulsant, 1842) and *B. brancoi* Hillert & Král, 2016, this ability has also been recorded in larvae (Verdú et al. 1998: *B. brancoi* listed as *B. bocchus* (Erichson, 1841); Verdú et al. 2004; Rahola Fabra 2004).

Materials and methods

The nomenclature used in this research follows Howden et al. (2007), Smith (2009), and Nikolajev et al. (2016), with corrections according to Bouchard and Bousquet (2020) and Ziani et al. (2021). The taxon *Bolbocerodema* Nikolajev, 1973 is considered here to be a subgenus of the genus *Bolbocerosoma* Schaeffer, 1906, in accordance with Krikken (1979) and Smith (2009). The concept of Bolboceratinae as a subfamily of Geotrupidae is consistent with Lawrence and Newton (1995), Verdú et al. (2004), Howden et al. (2007), and Nikolajev et al. (2016).

Faunistic records from the Czech Republic and Slovakia are divided into paragraphs beginning with a number representing the code of the faunistic square that refers to the Central European grid for mapping fauna and flora (Fig. 9; also see e.g., Zelený 1972; Novák 1989; Pruner and Míka 1996; Kolouch 2002). For other countries, the records are divided into paragraphs according to the largest superior administrative units or traditional regions. The countries, the faunistic square codes and the administrative units/traditional regions are ordered according to their geographical positions from east to west and from north to south. A question mark at the beginning of a faunistic record indicates dubious data. For protected areas in the Czech Republic and Slovakia, three acronyms are used in the text: **PP** – Přírodní památka (= Natural Monument), **PR** – Přírodní rezervace (= Nature Reserve), and **NPR** – Národní přírodní rezervace (= National Nature Reserve). The abbreviation **FSLG** means flying slowly low above the ground. The following acronyms are used for time zones: **CEST** – Central European Summer Time, and **EEST** – Eastern European Summer Time. The abbreviation representing a collector/observer (see list below) with no further details mentioned means the collector and depository are identical (leg. and coll.). All details regarding observations of adults of *B. unicornis* (in particular their flight activities) were provided by the listed participants of these observations. The material has been identified by the author, the curators of the collections, or the observers and collectors listed.

The following systems are used to transliterate cited literature and geographical or personal names in the Cyrillic and Armenian scripts: BGN/PCGN 2013 Agreement for Bulgarian, BGN/PCGN 1947 System for Russian, BGN/PCGN 2005 Agreement for Serbian, BGN/PCGN 2019 Agreement for Ukrainian, and BGN/PCGN 1981 System for Armenian.

For the distribution map of the Czech Republic and Slovakia, the records are divided into three time periods: the records before 1960, records between 1960–1999, and records after 1999 (Fig. 9). This map was compiled by manually placing the circles in the grid map used for faunistic research in these countries in standard free graphics software. For the distribution maps of Hungary and Europe, the following time peri-

ods are used: records before 1950, records between 1950–1999, and records after 1999 (Figs 12, 18). These maps were created using the Google Maps web application by inserting specific GPS coordinates into the system. GPS coordinates were obtained from collectors or providers of the sightings listed for each faunistic record. In cases where the exact GPS coordinates were not known (e.g., records from literature), the midpoint GPS coordinates of the village, town, county, or area were used.

Statistics on flights of adults were compiled for eight localities (seven Slovak and one Serbian), for which detailed data were available (Tables 1–8). A table with the same statistics was also created for the published data from the Italian locality of Cordenons (Table 9; Glerean and Stefani 2019).

The graph of seasonal dynamics was generated with data obtained from countries of the Pannonian Basin for which data on a minimum of 30 specimens were available (Fig. 19).

The dates of Panzer's works are adopted from Bousquet (2016) and Alonso-Zarazaga and Evenhuis (2017). Panzer (1793a) is cited according to Sherborn (1902), Hillert et al. (2016) and Löbl and Löbl (2016). Kuthy's book (1898) is cited following Bousquet (2016), but with some modifications.

Acronyms for the collectors, observers, and institutes

ABC Attila Balázs, Čamovce, Slovakia
ABZ Andrii Ivanovych Bachynskyi (Андрій Іванович Бачинський), Zalishchyky, Ukraine
ADW Alexander Dostal, Vienna, Austria
AGB András Gór, Biatorbágy, Hungary
AHB Adam Hergovits, Bratislava, Slovakia
AKB Attila Kotán, Budapest, Hungary
AMK András Máté, Kecskemét, Hungary
APC Alexandru-Mihai Pintilioaie, Comănești, Romania
APE Attila Pál, Érd, Hungary
APO Antonín Peutlschmid, Olomouc, Czech Republic
ARC Adrian Ruicănescu, Cluj-Napoca, Romania
ASH Aleš Sedláček, Hranice, Czech Republic
ASK Artur Anatoliiovych Shekhovtsov (Артур Анатолійович Шеховцов), Kharkiv, Ukraine
AUP Ákos Uherkovich, Pécs, Hungary
BBO Boris Bubeník Sr., Ostrava, Czech Republic
BCK Csaba Bán, Kecskemét, Hungary
BJN Jiří Brestovanský Jr., Neratovice, Czech Republic
BJO Boris Bubeník Jr., Ostrava, Czech Republic
BKL Bence Krajcsovszky, Lábatlan, Hungary
BMP Marek Bunalski, Poznań, Poland
BSP † Svatopluk Bílý, Prague, Czech Republic
BVK Bohdan Mykolaiovych Vasko (Богдан Миколайович Васько), Kyiv, Ukraine

CBE Csaba Bartha, Eger, Hungary
CBK Csaba Bíró, Kecskemét, Hungary
CKZ Csaba Kutasi, Zirc, Hungary
CMI Cosmin-Ovidiu Manci, Iași, Romania
CSB Csaba Szabóky, Budapest, Hungary
CSS Csaba Szinetár, Szombathely, Hungary
CVK Csaba Vadász, Kecskemét, Hungary
CWP Christian Wieser, Pischeldorf, Austria
DCO Dan Čagánek, Otrokovice, Czech Republic
DHH David Hrebeň, Havířov, Czech Republic
DHP David Horák, Prostějov, Czech Republic
DJP Daniel Juřena, Prostějov, Czech Republic
DKC Denis Keith, Chartres, France
DKP David Král, Prague, Czech Republic
DPB Dragan Pavićević (Драган Павићевић), Belgrade, Serbia
DPS Dmytro Protopopov (Дмитро Протопопов), Semyhiria, Ukraine
DRW Dominik Rabl, Vienna, Austria
DVB Dalibor Všianský, Brno, Czech Republic
DVH Dušan Vacík, Hranice, Czech Republic
DVZ Daniel Vít, Zlín, Czech Republic
EJB Eduard Jendek, Bratislava, Slovakia
FKD Ferenc Klecska, Dunaharaszti, Hungary
FPT Filip Pavel, Týniště nad Orlicí, Czech Republic
FSB Filip Štrba, Bratislava, Slovakia
FSP František Štěpánek, Přerov, Czech Republic
FTK Florian Theves, Weingarten (Baden), Germany
FTR Filip Trnka, Rychnov nad Kněžnou, Czech Republic
FTV Filip Trojan, Velké Němčice, Czech Republic
GAB Ádám Gór, Biatorbágy, Hungary
GPB Gergely Petrányi, Budapest, Hungary
GML Geoffrey Miessen, Liège, Belgium
GSB Győző Szél, Budapest, Hungary
HDO Hryhorii Mykolaiovych Demydov (Григорій Миколайович Демидов), Odessa, Ukraine
HMS Heinz Mitter, Steyr, Austria
HTR Hennadii Tarasenko (Геннадій Тарасенко), Rzhyshchiv, Ukraine
IIB Ionuț Ștefan Iorgu, Bucharest, Romania
IJN Ivo Jeniš, Náklo, Czech Republic
IMO Ivo Martinů, Olomouc, Czech Republic
IMP Ivan Marvan, Pardubice, Czech Republic
IPO Ivan Paloušek, Olomouc, Czech Republic
IRB Imre Retezár, Budapest, Hungary
ITV Ilja Trojan, Velké Němčice, Czech Republic

JAH † Josef Adámek, Hradec Králové, Czech Republic
JBB Jan Bezděk, Brno, Czech Republic
JCM Josef Chybík, Modřice, Czech Republic
JDB János Dobos, Budapest, Hungary
JDC Jiří Dvořák, Čelčice, Czech Republic
JHH Jiří Hájek, Hrobce, Czech Republic
JHL Jan Helešic, Lužice (near Hodonín), Czech Republic
JHM Jaromír Hanuš, Moravské Budějovice, Czech Republic
JHP Jiří Hanzlík, Přerov–Popovice, Czech Republic
JJP † Josef Jurčíček, Prague, Czech Republic
JKB Ján Kodada, Bratislava, Slovakia
JKJ Jaroslav Kaláb, Jinačovice, Czech Republic
JKO Jindřich Kuja, Olomouc, Czech Republic
JKP Josef Krošlák, Plzeň, Czech Republic
JKV Josef Kadlec, Varnsdorf, Czech Republic
JMB József Muskovits, Budapest, Hungary
JMD † Jaroslav Máslo, Dolní Radechová, Czech Republic
JMH Jan Matějíček, Hradec Králové, Czech Republic
JPH Jan Pelikán, Hradec Králové, Czech Republic
JPP Jiří Plecháč, Pecka, Czech Republic
JRC Jindřich Ryšavý Jun., České Budějovice, Czech Republic
JRS Jaroslav Resl, Sněžné (near Nové Město nad Metují), Czech Republic
JSP Jan Schneider, Prague, Czech Republic
JST József Sár, Teklafalu, Hungary
JSU Jiří Spružina, Ústí nad Labem, Czech Republic
JTK Jaroslav Turna, Kostelec na Hané, Czech Republic
JVP † Jan Vitner, Prague, Czech Republic
JZJ Jaroslav Žák, Jezernice, Czech Republic
KBB Karol Bucsek, Bratislava, Slovakia
KDO Karel Doležel, Olomouc, Czech Republic
KFW Katrin Fuchs, Vienna, Austria
KHE Krisztián Harmos, Eger, Hungary
KLP Jiří Klícha, Prague, Czech Republic
KPH Karel Pils, Hlohovec, Slovakia
KPL Krzysztof Pałka, Lublin, Poland
KPV † Karel Poláček, Vysoké Mýto, Czech Republic
KRU Květoslav Resl, Uherský Brod, Czech Republic
KVB Klára Varga Bánné, Kecskemét, Hungary
KVM Kirill Vladimirovich Makarov (Кирилл Владимирович Макаров), Moscow, Russia
KVS Václav Křivan, Štěměchy, Czech Republic
LAB László Ádám, Budapest, Hungary
LEN Ladislav Ernest, Nymburk, Czech Republic

LFI Lucian Fusu, Iași, Romania
LHI Lucian Hănceanu, Iași, Romania
LKK Ladislav Kandrnál, Kunovice (near Uherské Hradiště), Czech Republic
LKM Ľudevít Kašovský, Martin, Slovakia
LMB Levente Erik Moharos, Budakeszi, Hungary
LMN Ladislav Miško, Nové Zámky, Slovakia
LMO Luboš Mazal, Olomouc, Czech Republic
LMT Ladislav Mencl, Týnec nad Labem, Czech Republic
LNB László Nádai, Budapest, Hungary
LRL Luciano Ragozzino Lerma, Italy
MBO Michal Bednařík, Olomouc, Czech Republic
MBF Marco Bastianini, Follonica, Italy
MBP Milan Brabec, Prague, Czech Republic
MHP Marcel Hájek, Plzeň, Czech Republic
MJR Martin Jagelka, Rohožník, Slovakia
MKJ Martin Kejzlar, Jevíčko, Czech Republic
MKY Mark Yuriyevich' K'alashyan (Մարկ Յուրիևիչ Քալաշյան), Yerevan, Armenia
MLB Márk Lukátsi, Budapest, Hungary
MLS Miloš Lošťák, Šumperk, Czech Republic
MNB Martin Němec, Brno, Czech Republic
MNR Milan Nikodým, Roztoky (near Prague), Czech Republic
MOB Oto Majzlan, Bratislava, Slovakia
MPK Michal Pikner, Kněžpole (near Uherské Hradiště), Czech Republic
MPN Miloš Popović (Милош Поповић), Niš, Serbia
MPP Milan Sláma, Prague, Czech Republic
MPV Milan Pilarčík, Velké Pavlovice, Czech Republic
MRM Miklós Ringler, Munich, Germany
MRV Milan Ryšavý, Vlkoš (near Přerov), Czech Republic
MSB Milan Štrba, Bratislava, Slovakia
MSN Marko Šćiban (Марко Шћибан), Novi Sad, Serbia
MSZ Miloslav Šanda, Žatec, Czech Republic
MTM Maximilian Teodorescu, Măgurele, Romania
MTS Milan Trubačík, Staré Město (near Uherské Hradiště), Czech Republic
MVP Martin Volf, Prague, Czech Republic
MYP Vladislav Malý, Prague, Czech Republic
MZB Miroslav Zúber, Bradlec, Czech Republic
MZK Miroslav Ihorovych Zaika (Мирослав Ігорович Заїка), Kyiv, Ukraine
MZP Zdena Martinová & Zdeněk Znamenáček, Prague, Czech Republic
NKB Naďa Kazdová, Brno, Czech Republic
NPB Norbert Pometkó, Budapest, Hungary
OHS Oliver Hillert, Schöneiche bei Berlin, Germany
OKO Oleksandr Oleksandrovych Kolomeichuk (Олександр Олександрович Коломейчук), Odessa, Ukraine
OMB † Ottó Merkl, Budapest, Hungary

OSD Oleksandr Oleksiiovych Sukhenko (Олександр Олексійович Сухенко), Dnipro, Ukraine
OSO Ondřej Sabol, Ostrava–Nová Bělá, Czech Republic
OVK Oleksii Vasyliuk (Олексій Василюк), Kyiv, Ukraine
PCB Petr Čechovský, Brno, Czech Republic
PFS Péter Farkas, Ságvár, Hungary
PIL Pavel Imríšek, Louny, Czech Republic
PJH Josef Pavlas, Havířov, Czech Republic
PJL Pavel Jáchymek, Luhačovice, Czech Republic
PKB Péter Kovács, Budapest, Hungary
PKG Peter Kurina, Gajary, Slovakia
PMB Peter Mihálik, Bratislava, Slovakia
PPB Petr Pacholátko, Brno, Czech Republic
PSZ Petr Středulínský, Zlín, Czech Republic
PVP Petr Včelička, Prague, Czech Republic
PZW Petr Zábranský, Vienna, Austria
RCP † Radek Červenka, Prague, Czech Republic
RCR Roman Cséfalvay, Rohovce–Kyselica, Slovakia
REE Róbert Enyedi, Eger, Hungary
RFO † Rostislav Fornůsek, Olomouc, Czech Republic
RGM Rudolf Gabzdil, Michalovce, Slovakia
RHB Roman Hergovits, Bratislava, Slovakia
RHK Rostyslav Pavlovych Herasymov (Ростислав Павлович Герасимов), Kyiv, Ukraine
RKP Radim Klíč, Prostějov, Czech Republic
RMU Robert Machálek, Uherské Hradiště, Czech Republic
RPM Riccardo Pittino, Milan, Italy
RSG Roland Štefanovič, Galanta, Slovakia
RSP Radim Šigut, Paskov, Czech Republic
RVO † Radovan Veigler, Olomouc, Czech Republic
RZJ Renata Žáková, Jezernice, Czech Republic
SBP Sándor Bérces, Pomáz, Hungary
SBS Stoyan Beshkov, Sofia, Bulgaria
SDP Stanislav Doležal, Plzeň–Božkov, Czech Republic
SIB Sándor Ilniczky, Budapest, Hungary
SKP Jiří Skýpala, Prague, Czech Republic
SPP Serge Peslier, Perpignan, France
SRB Richard Schnürmacher, Bratislava, Slovakia
SRL Stefan Rabl, Lengenfeld, Austria
STK Serhii Vasylovych Tsykal (Сергій Васильович Цикал), Kyiv, Ukraine
SZM Stefano Ziani, Meldola, Italy
TBK Torsten Bittner, Weißenberg, Germany
TDB Tamás Deli, Békéscsaba, Hungary
TDS Tibor Danyik, Szarvas, Hungary

TGK Tomáš Grulich, Dolní Studénky–Králec, Czech Republic
TKB † Tibor Kovács Sr., Bátonyterenye–Kisterenye, Hungary
TKG Tibor Kovács Jr., Gyöngyös, Hungary
TKH Tomáš Kopecký, Hradec Králové, Czech Republic
TKK Tamás Kiss, Kecskemét, Hungary
TNB Tamás Németh, Gödöllő, Hungary
TSH Tibor Spevár, Hlohovec, Slovakia
TVP Tomáš Vendl, Prague, Czech Republic
VDP Václav Dongres, Plzeň, Czech Republic
VGG † Vadim Gennad'yevich Grachëv (Вадим Геннадьевич Грачёв), Moscow, Russia
VJP Vojtěch Jiříček, Prostějov, Czech Republic
VKK Vitalii Volodymyrovych Kavurka (Віталій Володимирович Кавурка), Kyiv, Ukraine
VKS Vítězslav Kubáň, Šlapanice, Czech Republic
VLP Jaromír Vališ, Přerov, Czech Republic
VMP Vlastimil Mihal, Přerov, Czech Republic
VPB Vilmos Polonyi, Budapest, Hungary
VRH Vladislav Řebíček, Hradištko, Czech Republic
VSI Valentin Szénási, Isaszeg, Hungary
VSK Vasyl Musiiovych Serhiienko (Василь Мусійович Сергієнко), Kyiv, Ukraine
VSM Viktor Viktorovych Strenada (Віктор Вікторович Стренада), Mykolaiv, Ukraine
VTH Vladimír Thomka, Humenné, Slovakia
VTO Viacheslav Anatoliiovych Trach (Вячеслав Анатолійович Трач), Odessa, Ukraine
VUB Viorel Ungureanu, Buzău, Romania
VVO Vladimír Vyhnálek, Olomouc, Czech Republic
VZO Vladimír Zeman, Olomouc, Czech Republic
WBW Wolfgang Barries, Vienna, Austria
WHS Walter Heinz, Schwanfeld, Germany
YHS Yurii Mykolaiovych Geriak (Юрій Миколайович Ґеряк), Sambir, Ukraine
YKL Yurii Vasylovych Kanarskyi (Юрій Васильович Канарський), Lviv, Ukraine
YKO Yevhenii Vitaliiovych Khalaim (Євгеній Віталійович Халаїм), Odessa, Ukraine
YSK Yurii Yevhenovych Skrylnyk (Юрій Євгенович Скрильник), Kharkiv, Ukraine
ZBB Zoran Božović (Зоран Божовић), Batajnica, Serbia
ZBP Zsófia Mocskonyi Bércesné, Pomáz, Hungary
ZCP Zdeněk Čermák, Prostějov, Czech Republic
ZDP † Zdeněk Doležal, Plzeň, Czech Republic
ZKB Zoltán Körmendy, Budapest, Hungary
ZKM Zdeněk Kraus, Mikulovice (near Znojmo), Czech Republic
ZLB Zdeněk Laštůvka, Brno, Czech Republic
ZVP Zdeněk Vancl, Police nad Metují, Czech Republic

BNMS Brukenthal National Museum, Sibiu, Romania
BZLA Biologiezentrum Linz, Austria
CMZC Croatian Natural History Museum, Zagreb, Croatia
CUIR Alexandru Ioan Cuza University, Iaşi, Romania
ETHZ Entomological collection of the Swiss Federal Institute of Technology, Zürich, Switzerland
FGBI Franziskaner Gymnasium Bozen, Bolzano, Italy
FMNH Finnish Museum of Natural History LUOMUS, University of Helsinki, Helsinki, Finland
GANM "Grigore Antipa" National Museum of Natural History, Bucharest, Romania
GUNU Nizhyn Gogol State University, Nizhyn, Ukraine
HNHM Hungarian Natural History Museum, Budapest, Hungary
IECA Institute of Entomology, Biology Centre of the Czech Academy of Sciences, České Budějovice, Czech Republic
IZCM Institute of Zoology of the Academy of Sciences of Moldova, Chișinău, Republic of Moldova
JHIS Jovan Hadži Institute of Biology of the Research Centre of the Slovenian Academy of Sciences and Arts, Ig, Slovenia
LKKA Landesmuseums für Kärnten, Klagenfurt am Wörthersee, Austria
MCAS Museo Civico Archeologico e di Scienze Naturali "Federico Eusebio", Alba, Italy
MCZR Museo Civico di Zoologia, Rome, Italy
MFSN Museo Friulano di Storia Naturale, Udine, Italy
MHKC Museum of Eastern Bohemia in Hradec Králové, Hradec Králové, Czech Republic
MHNG Muséum d'histoire naturelle de Genève, Geneva, Switzerland
MIZP Museum and Institute of Zoology of the Polish Academy of Sciences, Warsaw, Poland
MJMC Muzeum jihovýchodní Moravy ve Zlíně, Zlín, Czech Republic
MKPC Muzeum Komenského v Přerově, Přerov, Czech Republic
MMBC Moravian Museum, Brno, Czech Republic
MNBG Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Museum für Naturkunde, Berlin, Germany
MMGH Mátra Museum of the Hungarian Natural History Museum, Gyöngyös, Hungary
MMSH Móra Ferenc Museum, Szeged, Hungary
MNFI Natural History Museum "La Specola", Florence, Italy
MNHN Muséum national d'Histoire naturelle, Paris, France
MNSA Museum Niederösterreich, Sankt Pölten, Austria
MPGU Moscow Pedagogical State University, Moscow, Russia
MSNB Museo di Scienze Naturali dell'Alto Adige, Bolzano, Italy
MSNG Museo Civico di Storia Naturale "Giacomo Doria", Genoa, Italy
MSNM Museo Civico di Storia Naturale, Milan, Italy

MTDG Senckenberg Naturhistorische Sammlungen, Museum für Tierkunde, Dresden, Germany
MUSE Museo delle Scienze, Trento, Italy
MZLU Biological Museum, Lund University, Lund, Sweden
MZSF Musée zoologique de l'université et de la ville de Strasbourg, Strasbourg, France
NHMB Naturhistorisches Museum Basel, Switzerland
NHMD Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark
NHMK State Natural History Museum of V. N. Karazin Kharkiv National University, Kharkiv, Ukraine
NHML Natural History Museum, London, United Kingdom
NHMU National Science and Natural History Museum of the National Academy of Sciences of Ukraine, Kyiv, Ukraine
NHMW Naturhistorisches Museum Wien, Vienna, Austria
NMAG Naturmuseum Augsburg, Germany
NMBE Naturhistorisches Museum Bern, Switzerland
NMCM National Museum of Ethnography and Natural History, Chișinău, Republic of Moldova
NMEG Naturkundemuseum Erfurt, Germany
NMPC National Museum, Prague, Czech Republic
NMSB National Museum of Natural History, Sofia, Bulgaria
PMSL Slovenian Museum of Natural History, Ljubljana, Slovenia
RBIN Royal Belgian Institute of Natural Sciences, Brussels, Belgium
RMNH Naturalis Biodiversity Centre (formerly Rijksmuseum van Natuurlijke Historie), Leiden, Netherlands
SDEI Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany
SIZK I. I. Schmalhausen Institute of Zoology of National Academy of Sciences of Ukraine, Kyiv, Ukraine
SMLU State Museum of Natural History, Lviv, Ukraine
SMNK Staatliches Museum für Naturkunde Karlsruhe, Germany
SMNS Staatliches Museum für Naturkunde Stuttgart, Germany
SMOC Silesian Museum, Opava, Czech Republic
SNMS Slovak National Museum–Natural History Museum, Bratislava, Slovakia
TLMF Tiroler Landesmuseum Ferdinandeum, Innsbruck, Austria
TMLS Tekovské múzeum v Leviciach, Levice, Slovakia
UMJG Universalmuseum Joanneum, Graz, Austria
VMHS Vihorlatské múzeum Humenné, Slovakia
ZFMK Zoologishes Forschungsmuseum Alexander Koenig, Bonn, Germany
ZMNU Zoological Museum of the Taras Shevchenko National University, Kyiv, Ukraine
ZMPC Západočeské muzeum v Plzni, Plzeň, Czech Republic
ZINR Zoological Institute of Russian Academy of Sciences, Saint Petersburg, Russia
ZSMG Staatliche Naturwissenschaftliche Sammlungen Bayerns, Zoologische Staatssammlung, Munich, Germany

ZUDH Department of Nature Conservation, Zoology and Game Management, University of Debrecen, Debrecen, Hungary

Systematics

Family: GEOTRUPIDAE Latreille, 1802
Subfamily: Bolboceratinae Mulsant, 1842
Tribe: BOLBELASMINI Iablokoff-Khnzorian, 1977
Genus: *Bolbelasmus* Boucomont, 1911
Subgenus: *Bolbelasmus* Boucomont, 1911
Species: *B.* (*B.*) *unicornis* (Schrank, 1789)

Faunistic records

Czech Republic

Published data

? 5354: "Kummer" [= Hradčany near Mimoň], 1 ♂ flying in the evening, no other data (Kral 1915). Given that Kral listed several species from this locality which have never been confirmed, this record is not considered very reliable.

5756: Loučeň, 28.v.1905, 1 spec., [Augustin] Šrámek leg., Radek Červenka and Radek Dunda det., coll. NMPC (Juřena et al. 2008); note: this specimen was probably stolen from NMPC.

6865: "Kammberg b. Brünn" [probably Brno – Kohoutovice env., perhaps Kamenný vrch hill], no other data (Horion 1958). This specimen should be deposited in Georg Frey's collection in NHMB, but still on loan (Christoph Germann pers. comm., 2021).

7067: Hovorany, 6.v.1941, Jan Roubal leg. (Tesař 1957); Čejč, 28.v.1982, 1 ♀, J. Voříšek leg. (Juřena et al. 2008); Čejč env., Bílý kopec hill, [= PP Bílý kopec u Čejče, ca. 48°56'14"N, 16°59'E, ca. 200 m a.s.l.], July 1978, collector not specified (Juřena et al. 2008); Čejč env., "Mansonova step" [= "Manson's steppe", 48°55'32.1"N, 16°58'46.6"E], 1.vii.1987, 1 ♂, at light at 21.45 CEST, VJP (Juřena et al. 2008); 15.vi.1988, 1 ♂ FSLG at 21.45 CEST, ca. 20 °C, VJP (Juřena et al. 2008); 16.vi.1988, 1 ♂ flying ca. 10 cm above the ground at 21.52 CEST, ca. 10–12 °C, VJP leg., coll. DJP (Juřena et al. 2008); 17.–18.vi.1988, 2 ♀♀, JKJ (Juřena et al. 2008); 26.vi.1988, 1 ♀ was caught while trying to fly out from the grass, 21.55 CEST, MLS (Juřena et al. 2008); 29.vi.1999, 1 ♀ FSLG at 22.00 CEST, VKS (Juřena et al. 2008; Hillert et al. 2016); 3.vii.1999, 1 ♂ crawling on the footpath at 21.55 CEST, together with 1 ♂ of *Od. armiger*, RZJ leg., coll. JZJ (Juřena et al. 2008).

6568: Prostějov, [between 1878–1899, see Koleška 1985] [Karel] Kyselý leg. (Kliment 1899); Záhoří near Prostějov [probably area SW of the town, near the village of Domamyslice (6568), or Na Záhoří hill (6468), ca. 600 m NE of the vil-

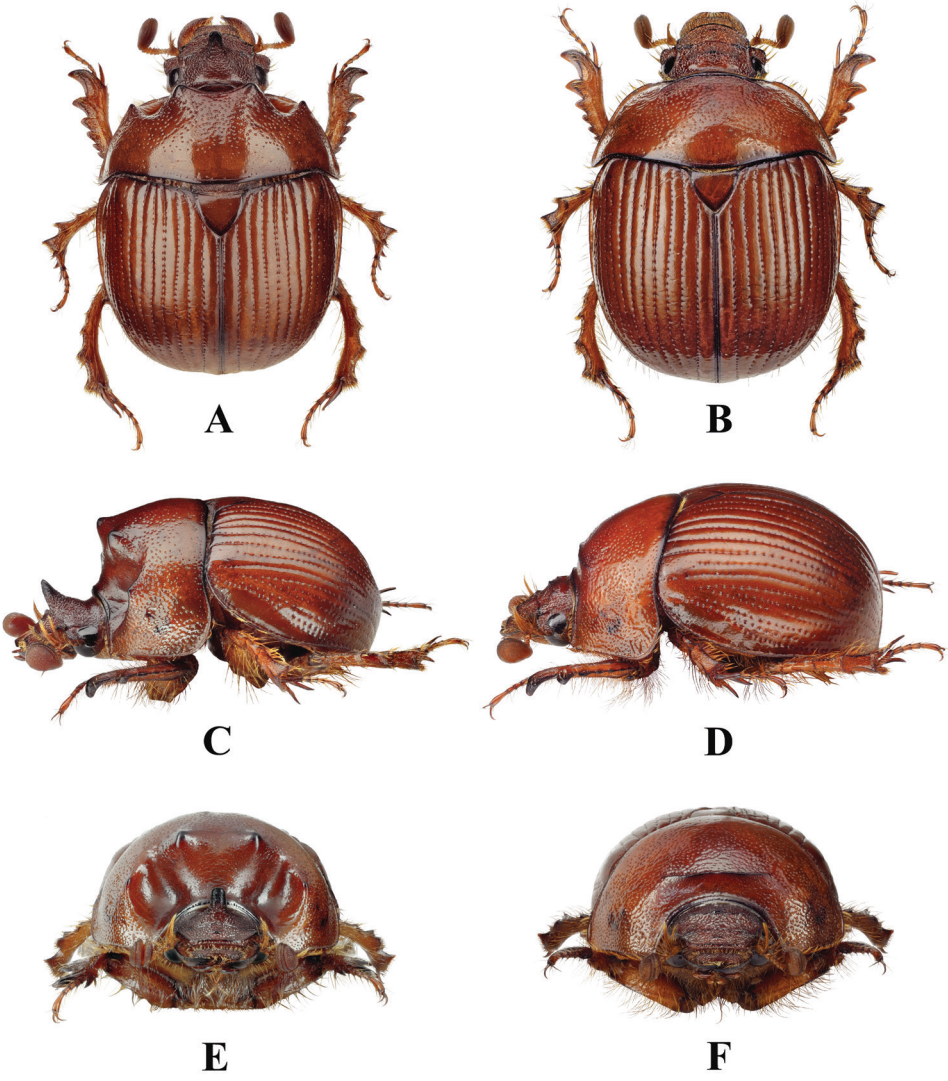


Figure 1. Habitus of *Bolbelasmus unicornis* **A** male, dorsal view **B** female dorsal view **C** male lateral view **D** female lateral view **E** male frontal view **F** female frontal view (photographs by Peter Kurina).

lage of Čelechovice na Hané – Kaple], [probably between 1878–1899], [Karel] Kyselý leg. (Fleischer 1930); "Prosznitz" [= Prostějov] (Schubert 1905; Zoufal 1922; Horion 1958); "Prossnitz" [= Prostějov], 1 ♂, [probably between 1878–1899], K[arel] Kyselý leg., coll. Georg Frey deposited in NHMB (Hillert et al. 2016).

? 6570: Přerov env. [probably Bochoř near Přerov], no other data (Hudeček 1928, 1930); Bochoř, no other data (Hudeček 1937). These two records are very doubtful. Rusty-coloured specimens of *Od. armiger* (ab. *testaceus*) labelled as *Bolbelasmus unicornis*,

Figure 2. Habitus of *B. unicornis*, male, detail. Rarely, males have a frontal horn ending in two apices (photographed specimen: "Autriche" [= Austria], "coll. Reiber", deposited in RBIN, photograph by Julien Lalanne, edited by Peter Kurina).

with black specimens of the same species, correctly labelled as *Odonteus armiger*, have been found in the Hudeček's collection in MKPC; no specimens of *B. unicornis* were discovered in this collection (Jaroslav Žák pers. comm., 2016).

6870: "Ungarisch Hradisch" [= Uherské Hradiště] env., Morava River valley, no other data (Schlögl 1883).

Material examined and new observations

7067: Bořetice env., PR Zázmoníky, 48°56'06.9"N, 16°51'20.5"E, ca. 300 m a.s.l., 1.v.1998, 1 elytron excavated from loess soil, KRU obs.; Čejč env., "Květnatá step" [= so-called Květnatá steppe, northern part of the PR Čejkovické Špidláky reserve], 48°55'22.0"N, 16°57'24.2"E, ca. 190 m a.s.l., 1.vii.1995, remains of a female excavated from a burrow of *Oryctolagus cuniculus*, KRU (VKS det., 15 October 2005); Čejč env., "Mansonova step" [= so-called "Manson's steppe"], 48°55'32.1"N, 16°58'46.6"E, ca. 210 m a.s.l., 20.vi.1986, 1 ♀ FSLG after sunset, PCB; 17.vi.1988, 1 ♀ FSLG after sunset, PCB; 21.vi.1988, 2 ♀♀ FSLG after sunset, VKS; 27.vi.1988, 8 spec. FSLG after sunset (for a photograph of one of them see Král et al. 2018), together with hundreds of spec. of *Odonteus armiger* (Scopoli, 1772), VKS; 29.vi.1988, 2 spec. FSLG after sunset, VKS; 19.vi.1989, 1 ♀ FSLG after sunset, JTK; 16.vi.1995, 1 ♂ FSLG after sunset, VKS (for partial data on this record see Hillert et al. 2016); 17.vi.1995, 1 ♂ and 1 ♀ flying slowly ca. 10 cm above the ground after sunset just after the rain, VKS; Mutěnice [= Čejč env.], "Mansonka" [= Manson's steppe], 2002, no

Figure 3. Small male of *B. unicornis* (body length: 11.5 mm) with feebly developed modifications of head and pronotum (Slovakia, Bratislava env.). The head features two small tubercles instead of the characteristic horn (photographs by Vlastimil Mihal).

other data [1 spec., anonymous collector leg. et coll.], non-public record of NDOP [= Records Database of Nature Conservation] of AOPK ČR [= Nature Conservation Agency of the Czech Republic].

6376: "Friedek Umg." [= Frýdek-Místek env.], 20.vi.1923, 1 ♀ [ex. coll. Dr Karel Samšiňák], Jos[ef] Hlisnikowski [leg.], DJP det., coll. SMOC.

Comment

In the Czech Republic, the species is known from a few localities only. Old reports by Kral (1915) from Hradčany near Mimoň and by Hudeček (1928, 1930, 1937) from Přerov and Bochoř are dubious. In this study, the species is reported for the first time

from northern Moravia on the basis of an old record from the vicinity of Frýdek-Místek. The latest record from the Czech Republic is from Čejč from 2004 and will be published with additional details at a later date (David Král pers. comm., 2021). For the distribution of the species in the Czech Republic see Fig. 9.

Slovakia

Published data

7867: [Bratislava env.,] Děvín: Kobyla [= Devínska Kobyla hill], [between 1921–1936, see Koleška 1995a], 1 spec. in horse dung, [František] Šlégl leg. (Roubal 1936; Majzlan et al. 2005); "Dévény" [= Bratislava – Devín], no other data (Endrődi 1957).

7568: Malacky, no other data (Roubal 1938).

7868: "Pozsony" or "Presburg" [= Bratislava] env., no other data (Bolla 1859; Rózsay 1868, 1880; Kuthy 1898; Ortvay 1902; Balthasar 1933; Roubal 1936; Endrődi 1957); Bratislava, June 1957, 1 ♂, collector unknown, coll. LKK (Juřena et al. 2008).

7968: Bratislava, Kopáč Island, [PR Kopáčsky ostrov], 19.v.2006, 1 spec., Malaise trap, MOB leg. (Majzlan 2006, 2007; Juřena et al. 2008).

7969: "Somorja" [= Šamorín], 10.v.1897, 1 spec. inside the digestive system of *Upupa epops*, Ernő Csiki obs. (Csiki 1905).

7371: "Pustá Ves" [= Prašník – Horná Pustá Ves or Dolná Pustá Ves], 22.vii.1984, 1 ♀, [at light], JMD leg., coll. NMPC (Hillert et al. 2016; data completed by the author).

7272: Čachtice, [probably between 1920–1938, see Koleška 1981], F[rantišek] Hajný leg., coll. JDC (Juřena et al. 2008).

7572: Hlohovec, undated [probably first half of the 20th century], 1 ♀, Várkonyi leg., coll. DKP deposited in NMPC (Juřena et al. 2008; Hillert et al. 2016).

7373: Brunovce, no other data, 1 ♀ in coll. NMEG (Hillert et al. 2016).

7074: "Liborcsa" [= Nemšová – Ľuborča], [ca. 230 m a.s.l.], undated [probably second half of the 19th century], 2 spec., Nitnausz leg. (Brancsik 1899, 1905; Balthasar 1933); "Bolessó – Pjechó" [= Bolešov – Piechov], "Branne" forest, [ca. 250–300 m a.s.l.], undated, József Laczó leg. (Laczó 1905; Laco 1928); [Trenčín –] Zlatovce [env., Malá hora hill, 48°54'43"N, 18°0'30"E, ca. 230 m a.s.l. and Vinohrady, 48°54'47.22"N, 18°1'4.68"E, ca. 250 m a.s.l.], 1.vi.–10.vii.[probably 1920s], tens of spec., Rudolf Čepelák leg. (Čepelák 1925; the site specified from Čepelák's diary – see Fig. 20); June 1926, [Rudolf] Čepelák leg., 1 ♂ in coll. JSP (Juřena et al. 2008) and 1 ♀ (ex original coll. Vladimír Balthasar) in coll. NMPC (Hillert et al. 2016; data completed by the author); Trenčín – Zlatovce [env.], 27.vi.1935, 1 ♀, collector unknown, coll. NMPC (Hillert et al. 2016); Istebník env., "Weinberg" [= Trenčín – Zlatovce env., Vinohrady, 48°54'47.22"N, 18°1'4.68"E, ca. 250 m a.s.l.], May-July 1926–1927, more spec., Georg Polentz and Rudolf Čepelák leg. (Polentz 1927).

7174: Trenčín, date not specified, old vineyard, more spec, Rudolf Čepelák, František Hajný, and Ladislav Korbel leg., and 1 spec., Jan Roubal leg. (Roubal 1936); Trenčín, no other data (Endrődi 1957); "Trencsen, Hungaria" [= Hungary, Trenčín], 1 ♂ and 1 ♀ with no other data, coll. BMP (Bunalski 1999; collection specified by Bunalski pers. comm., 2021); Trencsen [= Trenčín], no other data, 1 ♂ and 1 ♀ in coll. OHS (Hillert et al. 2016); Trenčín, no other data, 3 spec. coll. TMLS (Kollár and Smetana 1994); Trenčín, [Rudolf] Čepelák leg., no other data (Tesař 1954, 1957); Trenčín, no other data, 2 ♂♂ and 1 ♀ in coll. NMPC (Hillert et al. 2016; data specified by the author), 1 ♀ with no other data (Král et al. 2018); Trenčín, undated, 1 ♀, V[ilém] Steidl leg., ex original coll. Jan Havelka, currently in coll. NMPC (Hillert et al. 2016; data specified by the author); Trenčín, undated, 1 ♂ and 1 ♀, Dr A[lois] Richter leg., coll. NMPC (Hillert et al. 2016); Trenčín, undated, [Rudolf] Čepelák leg., 2 ♂♂ and 3 ♀♀ in coll. DKP deposited in NMPC, 3 ♂♂ in coll. MJMC [data specified by the author], 1 spec. in coll. JMH, 2 ♀♀ in coll. JSP, 1 spec. in coll. MZP, 9 ♂♂ and 10 ♀♀ in coll. NMPC, 2 ♂♂ and 1 ♀ in coll. OHS, 1 spec. in coll. SDP (Juřena et al. 2008; Hillert et al. 2016; data specified by the author); Trenčín, undated, [Ladislav] Korbel leg., 3 ♂♂, in coll. MJMC (Juřena et al. 2008; data specified by the author); Trenčín, May 1931, Dr A[lois] Richter leg., 1 ♂ in coll. JMH (Juřena et al. 2008), 1 ♀ in coll. NMPC (Hillert et al. 2016); Trenčín, June 1931, 1 ♀, Dr A[lois] Richter leg., coll. MJMC (Juřena et al. 2008; data specified by the author); Trenčín, 1960, no other data, 1 ♀ in coll. MZB (Juřena et al. 2008).

7274: "Trenčín – Inovec" [= Považský Inovec Mts, Inovec hill env.], undated [probably 1920s-1930s], 1 ♂, [Rudolf] Čepelák leg., ex original coll. Rudolf Veselý, currently in coll. NMPC (Hillert et al. 2016; data completed by the author).

7374: "Podhragy" [= Podhradie near Topoľčany], June and July 1895–1897, collector not specified (Kelecsényi 1900; Roubal 1936).

8174: "Keszegfalu" [= Keszegfalva, currently Kameničná], 25.v.1906, 1 spec. inside the digestive system of *Falco vespertinus*, Ernő Csiki obs. (Csiki 1910).

7275: Ľutov [env., Pálenice hill, ca. 48°46'57"N, 18°16'44"E, 250–300 m a.s.l.], 1.vi.–15.vii.[probably 1920s], Čepelák leg. (Tesař 1957; the site specified from Čepelák's diary – see Fig. 20).

8176: "Bátorkeszi" [= Bátorove Kosihy], June [between 1919–1923, see Koleška 1995b], 1 spec., sandy path, [Václav] Thurnher leg. (Roubal 1936; Endrődi 1957).

8177: Štúrovo (8278) [Štúrovo env., Belianské kopce hills, Modrý vrch hill env., PR Vŕšok env.], 24.v.1985, 2 spec., RFO (Týr 1997); Modrý vrch hill near Štúrovo [= Štúrovo env., Belianské kopce hills, Modrý vrch hill env., PR Vŕšok env.], 28.vi.1981, 1 ♂ and 1 ♀, 23.v.1985, 1 ♂, IJN (Juřena et al. 2008).

8178: Kamenica nad Hronom env., 47°50'29.5"N, 18°43'34.8"E, 9.vii.1980, ca. 30 spec. FSLG around midnight, PJH leg., 1 ♂ and 1 ♀ in coll. VJP, 1 ♀ in coll. ZDP deposited in ZMPC (Juřena et al. 2008; data supplemented by VJP pers. comm., 2021, and the author); 17.vii.1990, 1 ♂ and 1 ♀, 5.v.1992, 1 ♂, MTS (Juřena et al. 2008); 26.vi.1999, 1 ♂ and 1 ♀, dead on a path, JCM (Juřena et al. 2008); 24.v.2008,

2 ♀♀, at light (flew through the open window) ca. at 21.45 CEST, BBO (Juřena et al. 2008); Kamenica nad Hronom env., NPR Burdov, 47°49'32.88"N, 18°44'54.72"E, 154 m a.s.l., June 2011, 1 spec., Malaise trap, Vladimír Hošek leg. (Majzlan 2016); Kováčov, July 1985, 1 spec., ZVP (Týr 1997), 5.vii.1985, 1 spec., KPV leg., coll. JRS (Juřena et al. 2008); 4.vii.1999, 1 ♂, Karel Deneš Sr. leg., coll. DCO (Juřena et al. 2008); 29.vi.2001, 1 ♂, at light, JSU leg., coll. MSZ (Juřena et al. 2008).

8179: Chľaba env., 47°49'27"N, 18°50'57"E (the site near the confluence of the Danube and Ipeľ rivers), 103 m a.s.l., 5.vii.1975, plant materials alluviated by flooded Danube and Ipeľ rivers, 1 ♀, VKS leg. et coll., 1 ♂, PPB leg., coll. VKS (Juřena et al. 2008; data corrected by VKS pers. comm., 2021).

7781: "Plachti[n]ce" [= Horné, Stredné or Dolné Plachtince], 5.vi.1938, [Rudolf] Schwarz leg. (Tesař 1957).

7683: "Losoncz" [= Lučenec], 1877–1891, Emil Malesevics leg. (Malesevics 1892; Černecký et al. 2014); Lučenec, June [probably first half of the 20th century], Slanec leg. (Roubal 1936).

7884: Šiatorská Bukovinka, parking at the cemetery, [48°11'4"N, 19°49'33"E; 290 m a.s.l.], 8.vii.1973, 1 spec., at light (kerosene lamp), SKP leg., coll. SPP (Skýpala 1978; Juřena et al. 2008; storage of the specimen specified by Serge Peslier pers. comm., 2022)

7785: Hajnáčka [– Buková, 48°13'36.97"N, 19°58'24.11"E, steppe slope near the forest], 15.vii.1984, 1 ♀, dead on the ground, RCP (Juřena et al. 2008); 5.–8. vi.1986, 1 ♂, JMH; 18.v.1989, 1 ♂ FSLG after sunset, IMO; 5.vi.1989, 1 ♀, in flight at 21.35 CEST, IMO; 10.–11.vi.1989, 7 ♂♂ and 2 ♀♀, in flight after sunset or crawling on the ground, RVO (Juřena et al. 2008); 11.vi.1989, 1 ♂ and 2 ♀♀ FSLG after sunset, APO (Juřena et al. 2008); 24.vi.1989, 3 ♂♂ and 2 ♀♀ FSLG after sunset, MBO (Juřena et al. 2008); 27.vi.1989, 1 ♂ and 1 ♀ FSLG after sunset, RVO (Juřena et al. 2008); 1.vii.1989, 1 ♂ and 1 ♀ excavated with a garden shovel from their burrow on a steppe in the immediate vicinity of an oak forest (the burrow with push-up was localised thanks to audible stridulation of one or both specimens), VMP (Juřena et al. 2008); 6.vii.1989, 1 ♂ and 2 ♀♀ FSLG after sunset, MBO (Juřena et al. (2008); 16.vi.1990, 1 ♀ FSLG at 21.25 CEST, VJP (Juřena et al. 2008); 17.vi.1990, 1 ♂ flying at 21.28 CEST, VJP, 2 ♀♀ flying at 21.30–22.00 CEST, MNR (Juřena et al. 2008); 28.vi.1990, 1 ♂ crawling on the ground near an oak forest at 21.30 CEST, IMO (Juřena et al. 2008); 16.vi.1991, 1 ♂ and 1 ♀ FSLG at 21.25 CEST, VJP; 16.vi.1992, 3 ♂♂ and 3 ♀♀ FSLG after sunset, JDC, VJP (Juřena et al. 2008); 18.vi.1992, 1 ♂ and 1 ♀ FSLG after sunset, JDC (Juřena et al. 2008); 16.vi.1994, 2 ♂♂ FSLG after sunset, APO (Juřena et al. 2008); 28.v.1995, 1 spec., JKP (Týr 1997), 1 ♀ flying at 21.30–22.00 CEST, MNR (Juřena et al. 2008); 3.vii.1997, 3 ♀♀ FSLG at 21.30–22.00 CEST, MZP, MNR (Juřena et al. 2008); 16.vi.2009, together with *Od. armiger* and *Och. chrysomeloides*, the number of spec. and the collector name not specified (Byk et al. 2012).

7882: Kiarov, 15.–20.vi.1936, 1 ♀, [Dr Rudolf] Schwarz leg., ex original coll. Bohumil Štícha, currently in coll. NMPC (Juřena et al. 2008; Hillert et al. 2016; data completed by the author).

7277: Prievidza, forest park, 18.vii.1995, 1 ♂, RGM; (Juřena et al. 2008).

7280: Banská Bystrica, 18.v.1979, 1 ♂, collector unknown, coll. KVS (Juřena et al. 2008; Hillert et al. 2016).

7488: Silická Brezová, 3.vi.1999, 1 ♀, dead on a path crossing a steppe meadow, KDO (Juřena et al. 2008).

7390: Hrhov, 20.–21.vii.1981, 10 spec. excavated from their burrows, in a few cases together with *Od. armiger* (at a depth of up to 7 cm, the burrows changed direction from vertical to horizontal; in two cases, in one hole were two males or two females of *B. unicornis* together), LMT (Juřena et al. 2008).

7494: Slanská Huta env., 48°34'54.8"N, 21°28'31.7"E, 600 m a.s.l., 24.vii.1972, 1 ♀ crawling on the ground after sunset, ZLB obs. + photo – see Fig. 14A (Juřena et al. 2008; data specified by ZLB pers. comm., 2022).

7596: Ladmovce, 9.viii.1982, 2 ♂♂ excavated from their burrows from a depth of 8 cm, and 1 ♀ from a depth of ca. 20 cm, LMT (Juřena et al. 2008).

7097: Lackovce env., Veľká hill, [ca. 48°56'35"N, 21°58'13.5"E], 2.vii.–31.viii.2001, 2 ♂♂ and 2 ♀♀, steep forest-steppe hillside with shrubbery of *Rosa canina* and *Prunus spinosa*, pitfall traps with formaldehyde, together with more spec. of *Od. armiger*, VTH leg., coll. VMHS (Juřena et al. 2008); 16.vii.2017, 1 spec., pitfall trap with formaldehyde (48°56'37.63"N, 21°58'14.33"E), A. Macková leg. (Gajdoš and Majzlan 2018; Majzlan 2018).

7098–7099: Snina, July 1965, 1 ♂, MPP leg., coll. DKP deposited in NMPC (Hillert et al. 2016).

Material examined and new observations

7868: "Pressburg" [= Bratislava], no other data, 2 ♂♂ and 3 ♀♀ in coll. UMJG; "Hu, Pressburg" [= Hungaria, Bratislava], undated, 1 ♂, Maj[or Robert] Weber [leg.], coll. UMJG.

7868–7869: Bratislava – Podunajské Biskupice, Kopáč Island, PP Panský diel env. (Figs 4, 5), (e.g., 48°6'4.83"N, 17°9'37.55"E; 48°6'5.7"N, 17°9'48.7"E; 48°6'6.58"N, 17°9'58.21"E; 48°6'6.77"N, 17°10'2.16"E), 132–133 m a.s.l., 31.vii.2009, 1 ♀, at UV light, KBB leg., coll. DVH; 18.viii.2014, 1 ♀, at light, KBB obs.; 20.viii.2014, 1 ♂ and 1 ♀ FSLG after sunset, AHB and RHB obs.; 27.viii.2014, 2 ♀♀ FSLG after sunset, AHB obs.; 5.ix.2014, 3 ♂♂ and 2 ♀♀ FSLG after sunset, PKG and RHB obs.; 3.vi.2015, 11 ♂♂ and 4 ♀♀ flying slowly 10–20 cm above the ground after sunset, AHB and RHB obs.; 5.vi.2015, 5 ♂♂ and 1 ♀ flying slowly 10–20 cm above the ground after sunset, PKG and RHB obs.; 7.vi.2015, 4 ♂♂ FSLG after sunset, AHB obs.; 26.viii.2015, 2 ♀♀ flying slowly ca. 0.5 m above the ground at 20.20 and 20.30 CEST, DJP obs.; 28.viii.2015, 1 ♀ flying ca. 10–20 cm above the ground at 20.27 CEST, AHB obs.; 29.v.2016, 7 spec. FSLG after sunset, together with ca. 15 spec. of

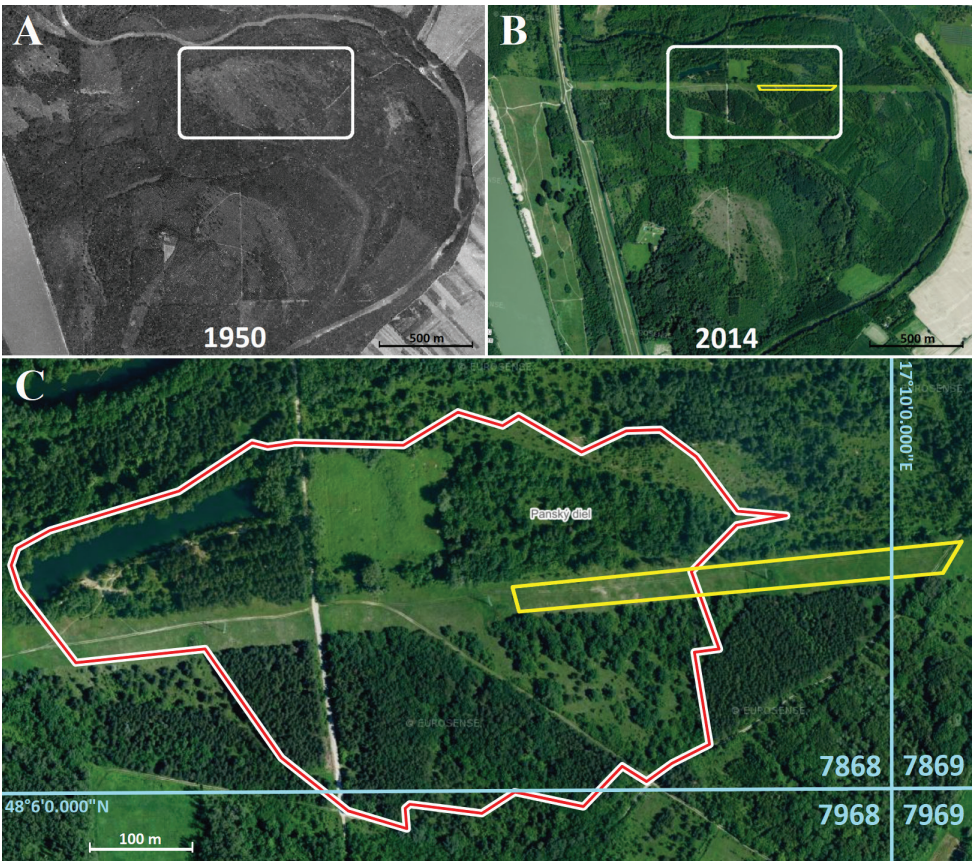


Figure 4. Bratislava, Kopáč Island (Slovakia), the area with the largest known population of *B. unicornis* in Europe before its conversion by inappropriate conservation management (removal of small trees and shrubs and introduction of intensive sheep grazing) **A** view of the site in 1950 **B** view of the site in 2014 with the area of the highest density of *B. unicornis* outlined with yellow borders **C** detail of the area with the highest density of the species with faunistic squares marked (see Materials and methods and Fig. 9).

Od. armiger, EJB, MSB and RHB obs.; 7.vi.2016, 11 spec. (4 ♂♂, 6 ♀♀ and 1 spec. not sexed) FSLG at 21.25–21.45 CEST, AHB and RHB obs. (see Table 1 for full data on the flights); 8.vi.2016, 5 spec. (4 ♂♂ and 1 spec. not sexed) flying slowly ca. 0.5 m above the ground at 21.27–21.43 CEST, together with 3 spec. of *Od. armiger*, DJP obs. (see Table 1 for full data on the flights); 18.vi.2016, 3 ♂♂ and 3 ♀♀ flying relatively slowly (but faster than 8.vi.2016) ca. 0.5 m above the ground at 21.33–21.53 CEST, DJP obs. (see Table 1 for full data on the flights); 21.vi.2016, 3 ♂♂ and 2 ♀♀ flying slowly ca. 0.5 m above the ground at 21.31–22.03 CEST, MSB obs. (see Table 1 for full data on the flights); 22.vi.2016, 2 ♂♂ and 4 ♀♀ flying slowly ca. 0.5 m above the ground at 21.21–21.57 CEST, MSB obs. (see Table 1 for full data on the flights); 23.vi.2016, 3 ♂♂ and 1 ♀ excavated from their burrows on the edge of a path crossing a forest-steppe meadow, 6 ♂♂ and 5 ♀♀ FSLG at 21.33–21.53 CEST, together

Figure 5. Bratislava, Kopáč Island, PP Panský diel (Slovakia) in 2016 (before its conversion due to inappropriate conservation management) **A–D** site details (**A** photographed by Dalibor Všianský **B–D** photographed by Ilja Trojan) **E** push-up of *B. unicornis* (photograph by Milan Štrba) **F** male excavated from its burrow (photograph by Dalibor Všianský).

with ca. 15 spec. of *Od. armiger*, DJP obs. (see Table 1 for full data on the flights); 24.vi.2016, 10 ♂♂ and 14 ♀♀ FSLG at 21.36–22.08 CEST, DJP, MSB and PKG obs. (see Table 1 for full data on the flights); 25.vi.2016, 2 ♂♂ and 5 ♀♀ FSLG at 21.28–22.08 CEST, MSB and FSB obs. (see Table 1 for full data on the flights); 26.vi.2016, 13 ♂♂ and 12 ♀♀ flying slowly up to ca. 0.5 m above the ground or relatively quickly ca. 1.5 m above ground at 21.31–22.09 CEST, together with ca. 10 spec. of *Od. armiger* and 3 spec. of *Ochodaeus chrysomeloides* (Schrank, 1781), DJP, FSB, MSB and PKG obs. (see Table 1 for full data on the flights); 27.vi.2016, 2 ♂♂ and 8 ♀♀ FSLG at 21.31–22.57 CEST, MSB and FSB obs. (see Table 1 for full data on the flights);

28.vi.2016, 2 ♂♂ and 7 ♀♀ flying slowly up to ca. 0.5 m above the ground or relatively quickly ca. 1–1.5 m above the ground at 21.28–22.48 CEST, together with 1 spec. of *Od. armiger*, DJP and PKG obs. (see Table 1 for full data on the flights); 29.vi.2016, 8 ♂♂ and 6 ♀♀ FSLG at 21.29–22.03 CEST, together with ca. 10 spec. of *Od. armiger* and 7 spec. of *Och. chrysomeloides*, DJP, PKG and MSB obs. (see Table 1 for full data on the flights); 30.vi.2016, 2 ♂♂ and 3 ♀♀ FSLG at 21.38–22.48 CEST, MSB and FSB obs.; 1.vii.2016, 1 ♀ flying slowly up to 0.5 m above the ground at 21.35 CEST, together with 1 spec. of *Od. armiger* and 1 spec. of *Och. chrysomeloides*, DJP obs.; 21.vii.2016, 25 ♂♂ and 11 ♀♀, most individuals flying slowly, some relatively quickly, up to 0.5 m above the ground, 2 spec. flying quickly ca. 1–1.5 m above the ground, at 21.09–21.51 CEST, together with more spec. of *Od. armiger* and *Och. chrysomeloides*, DJP and MSB obs. (see Table 1 for full data on the flights); 22.vii.2016, 28 ♂♂ and 23 ♀♀ flying up to 0.5 m above the ground at 21.08–21.51 CEST, together with more spec. of *Od. armiger* and *Och. chrysomeloides*, DJP and MSB obs. (see Table 1 for full data on the flights); 23.vii.2016, 26 ♂♂ and 15 ♀♀ flying up to 1 m above the ground at 21.09–21.53 CEST, together with more spec. of *Od. armiger* and *Och. chrysomeloides*, DJP and MSB obs. (see Table 1 for full data on the flights); 24.vii.2016, 38 ♂♂ and 30 ♀♀ flying mostly up to 0.5 m above the ground at 21.08–21.49 CEST, together with more spec. of *Od. armiger*, DJP, DVB, FSB and MSB obs. (see Table 1 for full data on the flights); 25.vii.2016, 14 ♂♂ and 1 ♀ FSLG at 21.06–21.41 CEST, 22 °C, light rain, no wind, FSB and MSB obs. (see Table 1 for full data on the flights); 26.vii.2016, 2 ♂♂ FSLG at 21.08–21.10 CEST, 24 °C, dry, gentle persistent wind, MSB obs.; 29.vii.2016, 6 ♂♂ and 2 ♀♀ excavated from their burrows on a loess-sandy path crossing a steppe meadow, together with 1 spec. of *Od. armiger* and 3 spec. of *Och. chrysomeloides*, DJP obs., and 10 ♂♂ and 3 ♀♀ FSLG at 21.02–21.30 CEST, 22 °C, wet vegetation, no wind, MSB obs. (see Table 1 for full data on the flights); 30.vii.2016, 1 ♂ excavated from its burrow on a loess-sandy path crossing a steppe meadow, DJP obs., and 16 ♂♂ and 21 ♀♀ FSLG at 20.53–21.56 CEST, together with ca. 20 spec. of *Od. armiger* and ca. 10 spec. of *Och. chrysomeloides*, DJP and MSB obs. (see Table 1 for full data on the flights); 7.viii.2016, 1 ♂ and 1 ♀ excavated from its burrow on a loess-sandy path crossing a steppe meadow, DJP obs., and 16 ♂♂ and 13 ♀♀ FSLG at 20.46–21.16 CEST, together with ca. 10 spec. of *Od. armiger*, 17 °C, no wind, DJP and IMO obs. (see Table 1 for full data on the flights); 8.viii.2016, 26 ♂♂ and 20 ♀♀ FSLG at 20.45–21.25 CEST, together with ca. 15 spec. of *Od. armiger* and 2 spec. of *Och. chrysomeloides*, 17–14 °C, no wind, DJP, ITV, FTV, IMO and JKO obs. (see Table 1 for full data on the flights); 13.viii.2016, 32 ♂♂ and 19 ♀♀ flying slowly up to 0.5 m above the ground at 20.40–21.01 CEST, together with ca. 30 spec. of *Od. armiger* and 7 spec. of *Och. chrysomeloides*, 19 °C, no wind, DJP, ITV and FTV obs. (see Table 1 for full data on the flights); 14.viii.2016, 2 ♂♂ and 3 ♀♀ FSLG after sunset, together with 4 spec. of *Od. armiger*, 20 °C, no wind, MSB and VKS obs.; 4.vii.2020, 1 ♂ excavated from its burrow on the edge of a path, DJP obs., 6 spec. FSLG after sunset, together with 1 spec. of *Od. armiger* and 8 spec. of *Och. chrysomeloides* DJP and FSP obs.; 6.viii.2020, 6 spec. FSLG at 21.05–21.15 CEST, FSP, IMO, PMB and VZO obs.

7968: Rusovce – Záhrady, 48°3'20.614"N, 17°9'18.014"E, 140 m a.s.l., 6.vi.2020, 1 ♂ flying ca. 10–20 cm above the ground at 21.20 CEST, small forest-steppe clearing in the forest, SRB obs. + photo (DJP det.); Bratislava – Podunajské Biskupice, Kopáč Island, PR Kopáčsky ostrov, ca. 48°5'41.97"N, 17°9'43.14"E, 132 m a.s.l., 13.vi.2006, 1 ♀, Malaise trap, MOB leg., coll. VKS; 30.v.2016, 2 ♂♂, and 3 ♀♀ FSLG after sunset, together with ca. 15 spec. of *Od. armiger*, EJB and RHB obs.; 7.vi.2016, 1 spec. FSLG after sunset, MSB obs.; 23.vi.2016, 2 ♂♂ FSLG at 21.32 and 21.38 CEST, MSB obs.; 1.vii.2016, 2 ♂♂ FSLG at 21.27 and 21.43 CEST, MSB obs.; 19.vii.2016, 4 spec. FSLG after sunset, EJB and JKB obs.; 20.vii.2016, 7 spec. FSLG after sunset, EJB and JKB obs.; ca. 48°5'39.5"N, 17°9'42.3"E, and 48°5'43.8"N, 17°9'30.4"E, 14.viii.2016, 7 spec. FSLG after sunset, DJP, ITV and VKB obs.; ca. 48°5'45.8"N, 17°9'41.9"E, 19.v.2018, 1 ♂ and 1 ♀ FSLG after sunset, MRV and VMP obs.; 9.vi.2018, 7 ♂♂ and 9 ♀♀ FSLG after sunset, together with ca. 20 spec. of *Od. armiger*, JHP, MRV and VMP obs.; 14.vii.2018, 1 ♂ and 4 ♀♀ FSLG after sunset, JRC and MRV obs.

7869–7969: "Štefánikovce" [= Rovinka near Dunajská Lužná], ca. 130 m a.s.l., May 1949, tens of spec. observed during the day sitting on the tops of the grass blades above the water on a flooded steppe meadow (after the flood), Josef Marvan obs., 2 spec. (♂ and ♀) leg., coll. IMP.

7969: Bratislava – Čunovo, PR Ostrovné lúčky (Fig. 6C, D), 48°2'28.02"N, 17°10'33.41"E, 138–139 m a.s.l., 21.vi.2016, 2 ♀♀ FSLG at 21.42 and 21.45 CEST, AHB obs.; ca. 48°2'24.5"N, 17°10'30.14"E and ca. 48°2'23.77"N, 17°10'34.47"E, 25.vii.2016, 6 ♂♂ and 4 ♀♀ flying slowly up to 0.5 m above the ground at 21.10–21.37 CEST, together with 7 spec. of *Od. armiger* and 3 spec. of *Och. chrysomeloides*, DJP obs. (see Table 2 for full data on the flights); 29.vii.2016, 1 ♂ and 1 ♀ flying quickly and 1 ♂ flying slowly up to 0.5 m above the ground at 21.11–21.25 CEST, together with 1 spec. of *Od. armiger* and 2 spec. of *Och. chrysomeloides*, DJP obs. (see Table 2 for full data on the flights); Kalinkovo env., Kalinkovská lesostep (Fig. 6A, B), 48°3'39.82"N, 17°12'37.94"E, 130 m a.s.l., 22.vi.2016, numerous ca. 2–3 weeks old burrows with push-ups weathered down, DJP and AHB obs.; 27.vii.2016, 1 ♂ and 2 ♀♀ flying up to 1 m above the ground at 21.04–21.15 CEST, together with 1 spec. of *Od. armiger*, DJP obs. (see Table 3 for full data on the flights).

7272: Višňové, Čachtický hradný vrch hill, 22.v.1988, 1 ♂ dead on a forest-steppe slope, IPO leg., coll. DJP.

7572: Hlohovec env., Nová hora near Koplotovce, 48°28'24.98"N, 17°49'21.40"E, 260 m a.s.l., 12.iv.1988, 1 ♀, accidentally dug up while turning the soil in the garden, KPH leg., coll. VKS; Hlohovec env., Mlynárska hora near Koplotovce, 48°28'6.51"N, 17°49'29.04"E, 235 m a.s.l., 4.vi.2021, 1 ♀ at light at 21.10 CEST (= 27 minutes after sunset), TSH obs.

7772: Šoporňa, [ca. 122 m a.s.l.], July 1952, 1 ♂, Kotek leg., coll. MHKC.

7373: Modrovka, [ca. 170 m a.s.l.], 15.vii.1979, 1 ♀, Mrklovský leg., coll. Ladislav Bojčuk deposited in MHKC.

7074: Trenčín – Zlatovce [env.], June 1926, [Rudolf] Čepelák leg., 1 ♂ and 1 ♀ in coll. Josef Gottwald deposited in NHMB, 2 ♀♀ in coll. Paolo Luigioni deposited

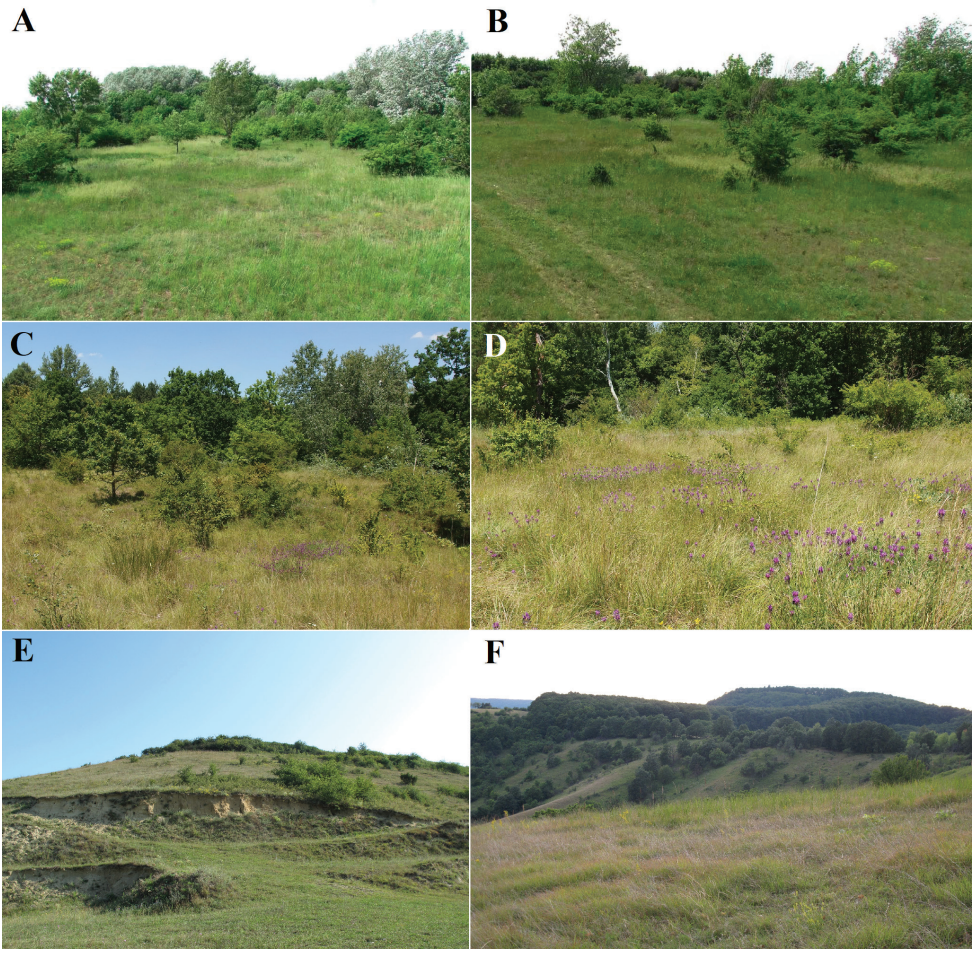


Figure 6. Slovak localities with *B. unicornis* **A, B** Kalinkovo, Kalinkovská lesostep **C, D** Čunovo, PR Ostrovné lúčky (photographs by Milan Štrba) **E** Gemerský Jablonec (photograph by Ilja Trojan) **F** Hajnáčka (photograph by Ilja Trojan).

in MCZR, 1 ♂ in coll. Zdeněk Tesař deposited in SNMS, 1 ♂ in coll. MIZP; Trenčín – Zlatovce [env.], June 1926, 1 ♀, collector not specified, coll. TLMF; [Trenčín –] Zlatovce [env.], no other data, 2 ♀♀ in coll. Zdeněk Tesař deposited in SNMS; June 1931, L[adislav] Korbel leg., 1 ♂ in coll. JJP, 1 ♀ in coll. Ladislav Daněk deposited in MHKC; June 1935, 1 ♂ and 1 ♀ (ex coll. Johann Peter Wolf), "col. Kardasch" [= Gregor Kardasch leg.], coll. ETHZ.

7174: "Trencsen Ungarn" [= Hungary, Trenčín], undated, 1 ♂ and 1 ♀ (ex coll. Engelbert Pawlik) in coll. NMPC, 1 ♂ and 1 ♀ in coll. FMNH, 2 spec. in coll. ZSMG, 1 spec. in coll. MTDG, 2 ♀♀ (ex coll. P. Franck) in coll. MIZP, 1 ♀ (ex coll. † Richard Papperitz, Peutenhausen) in coll. SMNS; Trenčín, no other data, 3 spec. in coll. NHMW, 1 ♂ in coll. MNBG, 1 spec in coll. SZM; "Trencin Slow." [= Slovakia,

Trenčín], no other data, 1 ♀ in coll. Leopold Mader deposited in MNSA; "Trenčín, Tchécoslovaquie" [= Slovakia, Trenčín], undated, 1 ♂ and 1 ♀,"coll. J[oseph] Clermont", coll. Jacques Baraud deposited in MNHN; "Slovakia Trenčín", 2.vii.[year not specified], no other data, 1 ♀ in coll. MHKC; Trenčín, undated, [Rudolf] Čepelák [leg.], 6 ♂♂ and 5 ♀♀ in coll. Leopold Mader deposited in MNSA, 5 ♂♂ and 4 ♀♀ in coll. SNMS, 3 ♂♂ and 5 ♀♀ in coll. MHNG, 2 ♂♂ and 3 ♀♀ in coll. MNBG, 3 ♂♂ and 1 ♀ (ex coll. W. Liebmann, Arnstadt) in coll. SDEI, 2 ♂♂ and 2 ♀♀ in coll. Henri Coiffait deposited in MNHN, 3 ♂♂ and 1 ♀ (ex coll. Johann Peter Wolf) in coll. ETHZ, 3 ♂♂ and 1 ♀ in coll. MHKC, 2 ♂♂ (ex coll. Sten Stockmann) in coll. FMNH, 1 ♂ and 1 ♀ in coll. MIZP, 1 ♂ and 1 ♀ in coll. SMNS, 1 ♂ in coll. RBIN, 1 ♂ in coll. Ladislav Daněk deposited in MHKC, 1 ♀ in coll. Jacques Baraud deposited in MNHN, 1 ♂ in coll. Georg Frey deposited in NHMB, 1 ♂ and 1 ♀ in coll. Vladimír Zoufal deposited in MMBC, 1 ♀ in coll. Emil Jagemann deposited in MMBC, 2 spec. in coll. ZSMG, 1 ♂ (ex coll. Antonio Porta) in coll. MSNM, 1 spec. (head and pronotum missing) in coll. RMNH, 2 ♂♂ in coll. LEN, 1 ♂ in coll. DKC, 1 ♀ in coll. VKS; Trenčín, undated [most likely late 1920s/early 1930s], Z. Zeman leg., 1 ♀ in coll. SMNS, 1 ♂ in coll. VKS; Trenčín, undated, 1 ♂, V[ilém] Steidl [leg.], coll. MIZP; Trenčín, undated, [Ladislav] Krejcárek [leg.], 2 ♂♂ and 1 ♀ in coll. TMLS (see Kollár and Smetana 1994), 1 ♀ in coll. VKS; June 1925, 1 ♂, [Rudolf] Čepelák [leg.], coll. Jan Roubal deposited in SNMS; Trenčín, 16.vi.1928, 1 ♀, [Rudolf] Čepelák leg., coll. Jan Roubal deposited in SNMS; Trenčín, 18.vi.1929, [Ladislav] Korbel [leg.], 1 ♂ and 1 ♀ (ex coll. Dr J. B. Jörger, Masans bei Chur) in coll. NHMB, 1 ♂ in coll. FMNH; Trenčín, 1931, 3 ♂♂ and 3 ♀♀, [Rudolf] Čepelák [leg.], coll. Paolo Luigioni deposited in MCZR; Trenčín, May 1931, Dr A[lois] Richter leg., 1 ♀ in coll. NMPC, 1 ♀ in coll. MJMC; "Trencsin" [= Trenčín], undated, 1 spec., S. Kardasch [leg.], coll. SMNK; Trenčín, June 1935, 1 spec., G[regor] Kardasch [leg.], coll. SMNK; Trenčín, 1936, 2 spec., [Rudolf] Čepelák [leg.], coll. SMNK; Trenčín, June 1936, 1 ♂ and 1 ♀, [Rudolf] Čepelák [leg.], coll. VKS; Trenčín, July [19]36, 1 ♂ in coll. Jan Volák deposited in MHKC.

7274: [Považský Inovec Mts], Inovec [hill env.], 1 ♂, [Ladislav] Krejcárek [leg.], coll. Josef Gottwald deposited in NHMB.

7674: Nitra [env.], 1950, no other data, 1 ♂ in coll. MHKC.

8177: Štúrovo env., Belianské kopce hills, "Hegyfarok" [= Modrý vrch], 47°49'8.09"N, 18°39'32.4, ca. 150 m a.s.l., 20.viii.2005, 1 spec., at light after midnight, 1.ix.2005, 1 spec., at light after midnight, 14.vi.2006, 2 spec., at light, 15.vi.2006, 1 spec., at light, 15.vi.2007, 1 spec., at light, 29.vii.2008, 2 spec., at light, 30.vii.2008, 1 spec., VVO obs.; Modrý vrch, PR Vŕšok, 47°49'6"N, 18°39'33"E, ca. 150 m a.s.l., 22.v.2014, 1 ♂, at light, OSO obs.; 47°49'13.5"N, 18°39'21.5"E, ca. 195 m a.s.l., 4.vi.2015, 1 ♀ at UV light at 21.30–0.30 CEST and 1 ♀ at UV light (the same trap) at 1.15 CEST (5.vi.2015), OSO obs. (moreover ca. 50 spec. of *Och. integriceps* Semenov, 1891 in the light traps were observed); 6.vi.2015, 1 ♂ FSLG after sunset, anonymous observer from the Czech Republic obs. (moreover 1 spec. of *Och. integriceps* in the light trap was observed); 47°49'9.54"N, 18°39'26.4"E, ca.

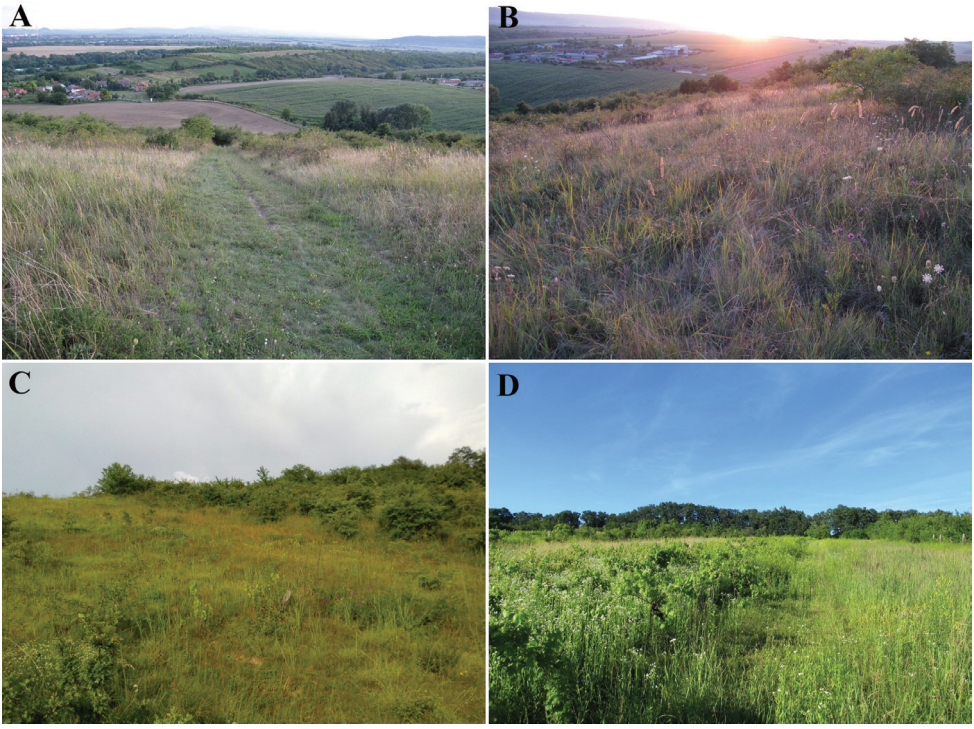


Figure 7. Biotopes of *B. unicornis* near Kamenica nad Hronom (Slovakia) **A–C** Čierna hora hill (**A, B** photographed by Ilja Trojan) **D** southwest facing slope northeast of Čierna Hora hill with old vineyards (photograph by Ondřej Sabol).

170 m a.s.l., 27.v.2015, 1 spec. FSLG after sunset, and 1 spec. at light, two anonymous observers from the Czech Republic obs.

8078: Zalaba, 47°58'8.8"N, 18°42'29.2"E, ca. 150 m a.s.l., June 1975, 1 spec. crawling on the ground on a sandy slope sparsely covered with black locust trees (*Robinia pseudoacacia*) at ca. 19.00 CEST, JAH.

8178: Bajtava, 16.vi.2006, 1 spec., at light, VVO obs.; Kamenica nad Hronom, Čierna hora hill (Fig. 7A–C), ca. 47°50'15"N, 18°43'34"E, ca. 180–190 m a.s.l., 27.vi.2009, 1 ♂ FSLG at 21.36 CEST, together with 1 ♂ a 2 ♀♀ of *Od. armiger*, OSO obs.; 5.vi.2010, 1 ♀ FSLG at 21.35 CEST, PJL obs.; 6.vi.2010, 3 ♂♂ and 1 ♀ FSLG at 21:30–21:45 CEST, and 1 ♂ at light, JHL, OSO and RSP obs. (see Table 4 for full data on the flights); 7.vi.2010, 16 spec. FSLG at 21:23–21.55 CEST, JHL, PJL, OSO and RSP obs. (see Table 4 for full data on the flights); 11.vi.2010, 4 ♂♂ flying relatively quickly ca. 1 m above the ground after sunset, light breeze to gentle breeze, DJP obs.; 12.vi.2010, 1 ♂ and 1 ♀ FSLG after sunset, light air to light breeze, DJP obs.; 26.vi.2010, 3 ♂♂ FSLG after sunset, LKK and PJL obs.; 27.vi.2010, 6 ♂♂ and 4 ♀♀ FSLG after sunset, LKK, PJL and OSO obs.; 30.vi.2010, 7 spec. FSLG after sunset, two anonymous observers from the Czech Republic obs.; 4.viii.2011, 17 spec. flying

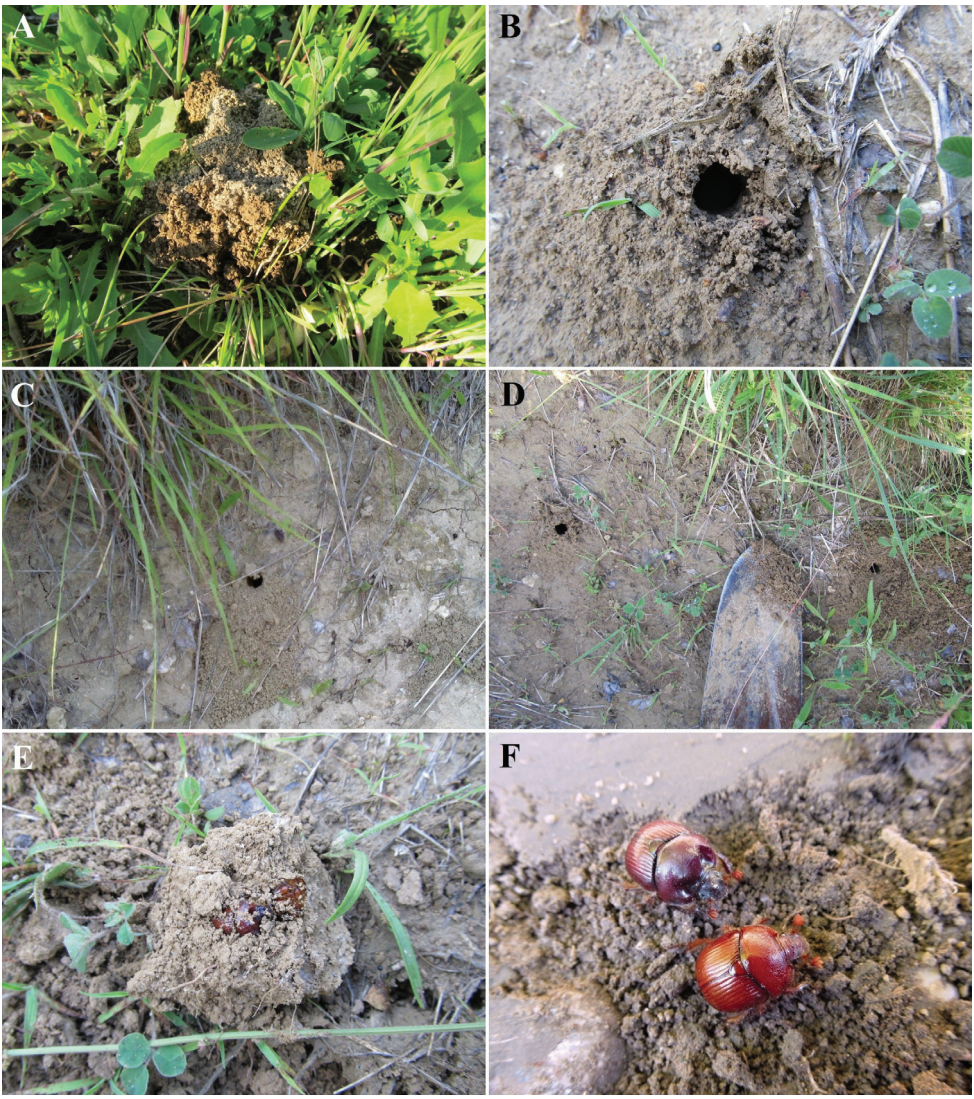


Figure 8. Excavation of *B. unicornis* at Čierna hora near Kamenica nad Hronom (Slovakia) **A–D** burrows dug by adults with push-ups (**A,B, D** photographed by Ondřej Sabol) **E, F** excavated pair (photographs by Ondřej Sabol).

very slowly ca. 20–100 cm above the ground at 20.50–21.20 CEST, DJP and PJL obs. (see Table 4 for full data on the flights); 5.viii.2011, 10 spec. FSLG at 20.50–21.10 CEST, DJP and PJL obs. (see Table 4 for full data on the flights); 6.viii.2011, 9 spec. FSLG at 20.40–21.00 CEST, DJP and PJL obs. (see Table 4 for full data on the flights); 9.viii.2011, 15 spec. FSLG at 20.45–21.05 CEST, DJP and IMO obs. (see Table 4 for full data on the flights); 11.viii.2011, 14 spec. FSLG at 20.40–21.05 CEST, DJP, RKP and DHP obs. (see Table 4 for full data on the flights); 12.viii.2011, 9 spec. FSLG at

20.40–21.05 CEST, DJP, ITV and PJL obs. (see Table 4 for full data on the flights); 13.viii.2011, 16 spec. FSLG at 20.30–21.05 CEST, DJP, ITV and PJL obs. (see Table 4 for full data on the flights); 16.viii.2011, 1 ♂ and 1 ♀ FSLG at 20.35–21.05 CEST, DJP and RKP obs. (see Table 4 for full data on the flights); 7.vi.2013, 13 ♂♂ and 9 ♀♀ FSLG at 21.20–21.45 CEST, together with 11 spec. of *Och. integriceps*, DJP, IMO and ZKM obs. (see Table 4 for full data on the flights); 8.vi.2013, 10 ♂♂ and 5 ♀♀ FSLG at 21.17–21.42 CEST, together with 3 spec. of *Od. armiger* and 12 spec. of *Och. integriceps*, DJP, IMO and ZKM obs. (see Table 4 for full data on the flights); 9.vi.2013, 3 spec. FSLG after sunset, IJN and VVO obs.; 12.vi.2013, 6 spec. excavated from their burrows, OSO obs. (Fig. 8B, D, E, F), and 15 spec. FSLG at 21.20–21.35 CEST, together with more spec. of *Od. armiger*, DJP, JZJ and OSO obs. (see Table 4 for full data on the flights); 13.vi.2013, 10 spec. excavated from their burrows under a small piles of pushed-up soil, OSO obs. (Fig. 8A), 1 spec flying ca. 1 m above the ground just before the sunset, VLP obs., and 9 spec. FSLG at 21.30–21.50 CEST, OSO, PJL, VLP and VKS obs.; 14.vi.2013, 4 spec. FSLG after sunset, DJP, DKP, LKM and VKS obs.; 15.vi.2013, ca. 490 m NNE of the hilltop of Čierna hora hill, 3 spec. FSLG at 21.30 CEST, DKP, VKS and ZKM obs., SW hillside of Čierna hora hill, 7 spec. FSLG at 21.20–21.45 CEST, two anonymous observers from the Czech Republic obs. (see Table 4 for full data on the flights); 15.vi.2013, 10 ♂♂ and 10 ♀♀ FSLG after sunset, BBO and BJO obs.; 19.vi.2013, 1 ♀ FSLG at 21.46 CEST, RMU and OSO obs.; 15.vi.2014, 1 ♀ FSLG after sunset, BBO; 17.vi.2014, 1 ♀ FSLG after sunset, BBO; 3.ix.2014, 1 ♀ excavated from its burrow (from a depth of ca. 10 cm) on a path, ONV obs., 5 ♂♂ and 3 ♀♀ flying ca. 30–100 cm above the ground at 19.52–20.07 CEST, together with 1 ♂ of *Od. armiger*, DJP and ONV obs. (see Table 4 for full data on the flights); 4.ix.2014, 3 ♂♂ and 1 ♀ excavated from their burrows (from a depth of ca. 10–25 cm) on a path, 8 ♂♂ and 5 ♀♀ FSLG at 19.51–20.16 CEST, together with 1 ♂ of *Od. armiger*, DJP and ONV obs. (see Table 4 for full data on the flights); 5.ix.2014, 1 ♂ excavated from its burrow (from a depth of ca. 8 cm) on the edge of a path, 2 ♂♂ and 2 ♀♀ flying ca. 30–80 cm above the ground at 19.47–20.04 CEST, together with 3 ♀♀ of *Od. armiger*, DJP and VKS obs. (see Table 4 for full data on the flights); 6.ix.2014, 1 ♂ and 4 ♀♀ excavated from their burrows (from a depth of ca. 10–25 cm) on a path and on a loess forest-steppe slope, DJP and VKS obs.; 9.ix.2014, 3 ♂♂ and 1 ♀ excavated from their burrows (from a depth of ca. 10 cm) on a path, DJP, JCM and IMO obs., 1 ♂ flying relatively quickly ca. 1 m above the ground at 19.43 CEST and 1 ♂ flying very slowly ca. 10 cm above the ground at 19.47 CEST, DJP and IMO obs. (see Table 4 for full data on the flights); 17.ix.2014, 2 ♀♀ excavated from their burrows (from a depth of ca. 10 cm) on a path, IMO obs.; 31.v.2015, 1 ♂ and 1 ♀ flying slowly 10–30 cm above the ground at 21.40–21.45 CEST, FTR obs.; 3.vi.2015, 1 ♂ excavated from its burrow on a loess forest-steppe slope, 1 ♀ flying slowly near the ground after sunset and 1 ♀ attracted to the light trap, APO obs.; 4.vi.2015, 1 ♂ excavated from its burrow on a loess forest-steppe slope, APO obs.; 5.vi.2015, 2 ♂♂ flying relatively quickly ca. 1 m above the ground at 21.22–21.27 CEST, together with 1 ♀ of *Od. armiger* and 1 spec. of *Och. integriceps*, DJP obs. (see Table 4 for full data on the flights); 6.vi.2015, 2 ♂♂ excavated

from a single burrow (from a depth of ca. 12 cm) and 1 ♀ excavated from another burrow (from a depth of ca. 25 cm) on a path (loess forest-steppe slope), 1 ♂ (length of body 9.5 mm!) and 1 ♀ flying relatively quickly ca. 120 cm above the ground at 21.24–21.29 CEST, together with 4 ♀♀ of *Od. armiger* and 1 spec. of *Och. integriceps*, and 1 ♂ flying slowly 10–20 cm above the ground at 21.47 CEST, DJP obs. (see Table 4 for full data on the flights); 28.v.2016, 6 spec. FSLG at 21.05–21.10 CEST, two anonymous observers from the Czech Republic obs. (see Table 4 for full data on the flights); 11.vi.2016, 2 ♂♂ and 3 ♀♀ FSLG at 21.20–21.40 CEST, JKP and VDP obs.; 47°50'4.038"N, 18°43'53.947"E, ca. 165 m a.s.l., 2.viii.2014, 1 ♂ FSLG at 21.15 CEST, RCR obs.; 47°50'9.08"N, 18°43'39.93"E, ca. 185 m a.s.l., 20.vi.2018, 4 ♂♂ and 2 ♀♀ FSLG after sunset (3 spec.) and at light (3 spec.), OSO obs.; Kamenica nad Hronom env., ca. 530 m NNE of the hilltop of Čierna hora hill, 47°50'26"N, 18°43'50.7"E, 180 m a.s.l., 30.v.2011, 1 ♀ FSLG after sunset, small steppe hillside near an oak forest, FSP obs.; Kováčov, [110 m a.s.l.], 8.viii.1965, 1 ♂, K[arel] Poláček leg., coll. MHKC; Chľaba, 11.vi.1985, 1 ♂ and 1 ♀ J. Hladný leg., coll. JZJ.

8178–8278: "Parkaň" [= Štúrovo], [ca. 110 m a.s.l.], 1934, no other data, 1 ♀ in coll. MHKC; 1940, no other data, 1 ♂ in coll. MHKC; Štúrovo, July 1967, 1 ♀, collector unknown, coll. ASH.

8179: Chľaba env., Močiar (the site near the confluence of the Danube and Ipeľ rivers), 47°49'14.53"N, 18°50'52.72"E, 110 m a.s.l., 12.vi.2014, 1 ♂ FSLG at 21.40 CEST, together with 2 ♀♀ of *Od. armiger*, OSO obs.

7785: Cerová vrchovina Mts, Hajnáčka – Buková env., ca. 48°13'51.39"N, 19°58'26.32"E, 1.vi.1978, 1 ♂ crawling on the ground in the afternoon in sunlight, IJN leg. [storage of the specimen unknown]; Cerová vrchovina Mts, Hajnáčka – Buková env., "circular pasture under vággon" [ca. 48°13'43.88"N, 19°58'15.53"E], 23.vi.1990, 1 ♀ flying at 21.28 CEST, JVP leg., ex original coll. JVP, currently in coll. NMPC; Hajnáčka – western edge of the village, 48°12'48.2"N, 19°56'52.1"E, ca. 275 m a.s.l., 7.vi.2010, 1 ♀ FSLG after sunset, together with more spec. of *Od. armiger* and *Och. chrysomeloides*, PVP obs.; 8.vi.2010, 1 spec. FSLG after sunset, together with more spec. of *Od. armiger* and *Och. chrysomeloides*, PVP obs.; Hajnáčka – Buková env., steppe hillside (former sheep pasture with low and sparse vegetation, near an oak forest), 48°13'37.24"N, 19°58'23.73"E, 340–390 m a.s.l., 27.v.2008, 5 ♀♀ FSLG at 21.10–21.35 CEST, 22 °C, no wind, together with 20 spec. of *Od. armiger* and 19 spec. of *Och. chrysomeloides*, DJP and FSP obs. (see Table 5 for full data on the flights); 28.v.2008, 1 ♀ FSLG at 21.20 CEST, 18 °C, light air – light breeze, together with 10 spec. of *Od. armiger* and 9 spec. of *Och. chrysomeloides*, FSP obs.; 29.v.2008, 1 newly hatched (light coloured) ♂ crawling on the T-shirt spread out on the ground near the edge of the forest, under an oak tree (*Quercus cerris*) at 19.55 CEST, 1 ♂ flying relatively quickly and zigzag ca. 1 m above the ground and 3 ♀♀ flying slowly ca. 0.5 m above the ground at 21.10–1.40 CEST, 21 °C, no wind to light air, together with 20 spec. of *Od. armiger* and 14 spec. of *Och. chrysomeloides*, DJP, KDO and PJL obs. (see Table 5 for full data on the flights); 30.v.2014, 1 ♂

FSLG at 21.10 CEST, 22 °C, almost no wind, together with 15 spec. of *Od. armiger* and 23 spec. of *Och. chrysomeloides*, DJP obs.; 28.vi.2009, 2 ♂♂ FSLG at 21.35 and 21.42 CEST, steppe hillside near an oak forest, together with 12 spec. of *Od. armiger* and 2 spec. of *Och. chrysomeloides*, OSO obs.; 29.vi.2009, 1 ♂ FSLG at 21.35 CEST, steppe hillside near an oak forest, together with 21 spec. of *Od. armiger* and 3 spec. of *Och. chrysomeloides*, OSO obs.; 4.vii.2009, 3 ♂♂ and 4 ♀♀ FSLG at 21.15–21.45 CEST, 22 °C, no wind, together with ca. 20 spec. of *Od. armiger* and ca. 15 spec. of *Och. chrysomeloides*, DJP and MBP obs. (see Table 5 for full data on the flights); 5.vii.2009, 1 ♂ and 2 ♀♀ FSLG at 21.15–21.30 CEST, 20 °C, no wind, together with ca. 10 spec. of *Od. armiger* and ca. 10 spec. of *Och. chrysomeloides*, DJP obs. (see Table 5 for full data on the flights); 6.vii.2009, 1 ♂ FSLG at 21:25 CEST, 21 °C, no wind, together with ca. 15 spec. of *Od. armiger* and ca. 10 spec. of *Och. chrysomeloides*, DJP obs.; 28.v.2010, 1 ♂ a 3 ♀♀ FSLG at 21.10–21.25 CEST, together with ca. 15 spec. of *Od. armiger* and ca. 25 spec. of *Och. chrysomeloides*, DJP obs. (see Table 5 for full data on the flights); 29.v.2010, 1 ♂ FSLG at 21.10 CEST, together with ca. 10 spec. of *Od. armiger*, DJP obs.; 7.vi.2010, 2 ♂♂ and 1 ♀ FSLG after sunset, FPT obs.; 48°13'30.26"N, 19°58'25.39"E, 305 m a.s.l., 20.vi.2020, 1 ♂ and 1 ♀ flying after sunset, JPH and TKH obs.; Hajnáčka, Tehliarske, 48°13'15.68"N, 19°57'45.57"E, ca. 270 m a.s.l., 8.viii.2014, 4 ♂♂ and 6 ♀♀ FSLG after sunset (ca. 21.07 CEST), RCR obs.; 8.vii.2015, 9 ♂♂ and 6 ♀♀ FSLG after sunset (ca. 21.11 CEST), RCR obs.; 29.vi.2017, 4 ♂♂ and 8 ♀♀ FSLG after sunset (ca. 21.07 CEST), RCR obs.; Hajnáčka, Lapos, 48°13'32.37"N, 19°57'50.58"E, ca. 350 m a.s.l., 24.vii.2020, 12 ♂♂ and 9 ♀♀ FSLG at 21.05–21.30 CEST, 15 °C, RCR obs.

7785–7885: Cerová vrchovina Mts, Gemerský Jablonec, 48°12'0.44"N, 19°59'24.31"E, 250–265 m a.s.l., steppe hillside with shrubbery of *Prunus spinosa* and *Rosa canina* on the hilltop, 4.vii.2009, 1 ♂ a 3 ♀♀ FSLG at 21.30–21.50 CEST, FPT and JPH obs. (see Table 6 for full data on the flights); 5.vii.2009, 3 ♂♂ a 1 ♀ FSLG at 21.30–21.50 CEST, FPT and JPH obesrv. (see Table 6 for full data on the flights); 28.v.2010, 1 ♂ and 3 ♀♀ FSLG at 21.00–21.15 CEST, ITV and MNB obs. (see Table 6 for full data on the flights); 29.v.2010, 1 ♂ and 1 ♀ FSLG after sunset, ITV and MNB obs.; 4.vi.2010, 1 ♂ FSLG at 21.30 CEST, together with 3 spec. of *Od. armiger*, ITV obs.; 8.vi.2010, 4 spec. FSLG after sunset, FPT and JPP obs.; 48°11'58.04"N, 19°59'23.71"E, 26.vi.2020, 1 spec. flying after sunset, JPH and TKH obs.; Gemerský Jablonec [env.], 5.vii.2013, 1 ♂ and 1 ♀, FPT leg., coll. GML.

7786: Cerová vrchovina Mts, Hostice – Katarínka env., 48°13'52.55"N, 20°5'0.82"E, 216 m a.s.l., small steppe hillside with rich low vegetation and shrubbery of *Prunus spinosa*, 6.vi.2010, 2 ♀♀, hovering on the spot ca. 20 cm above the ground at 21.15 and 21.30 CEST (25 spec. of *Od. armiger* and 4 spec. of *Och. chrysomeloides* were also observed at the site), DJP obs. (see Table 7 for full data on the flights); Cerová vrchovina Mts, Jestice env., 48°12'38.5"N, 20°03'07.3"E, 275 m a.s.l., 30.vi.2018, 1 ♂, 2.–3.vii.2018, 1 ♀, FPT and NKB leg., coll. GML; Jestice env., 48°12'54"N, 20°2'32"E, 6–7.vii.2019, 1 ♂ and 1 ♀ FSLG after sunset, JBB leg. (♀ in coll. IECA);

Jestice – Kökényes, 48°12'45.84"N, 20°2'50.77"E, 250 m a.s.l., 23.vi.2020, 1 ♂ flying after sunset, ABC obs.; 6.vii.2020, 1 ♂ and 1 ♀ flying after sunset, ABC obs.; Jestice – Ivánkúta env., 48°12'30.9"N, 20°5'5.37"E, 254 m a.s.l., 7.vi.2015, 2 ♂♂ FSLG at 20.25 CEST, edge of an oak forest, RCR obs.

7489: Slovak Karst, "Rakaťa" [= Rakyta Cottage] env., 48°35'29.7"N, 20°34'01.45"E, ca. 540 m a.s.l., 5.vii.1988, 1 ♀ excavated from its burrow, DKP (for partial data on this record see Hillert et al. 2016).

7390: Slovak Karst, Hrhov, E of Okrúhle hill, 48°36'48.83"N, 20°47'22.98"E, ca. 395 m a.s.l., 4.vii.1988, 2 ♂♂ excavated from their burrows, DKP (for partial data on this record see Hillert et al. 2016); Slovak Karst, Hrhov, E of Okrúhle hill, 48°36'55.5"N, 20°47'27.3"E, ca. 430 m a.s.l., 28.v.2012, 1 ♂ drowned in a puddle on the path connecting two forest-steppe meadows, MHP obs.

Comment

Slovakia is the country with the largest number of individuals found, as well as with the second largest number of known localities where the species has been recorded (52 sites). In addition to the already known localities, Endrődi (1957) mentioned Fehér Kárpátok [= The White Carpathians Mts], which most likely refers to two old records north of Trenčín (Nemšová – Ľuborča and Bolešov – Piechov) reported by Brancsik (1899, 1905), Laczó (1905), and Laco (1928). Most of the recent records are summarised by Juřena et al. (2008). New records from 26 Slovak localities are given in the present study. For the distribution of the species in Slovakia see Fig. 9.

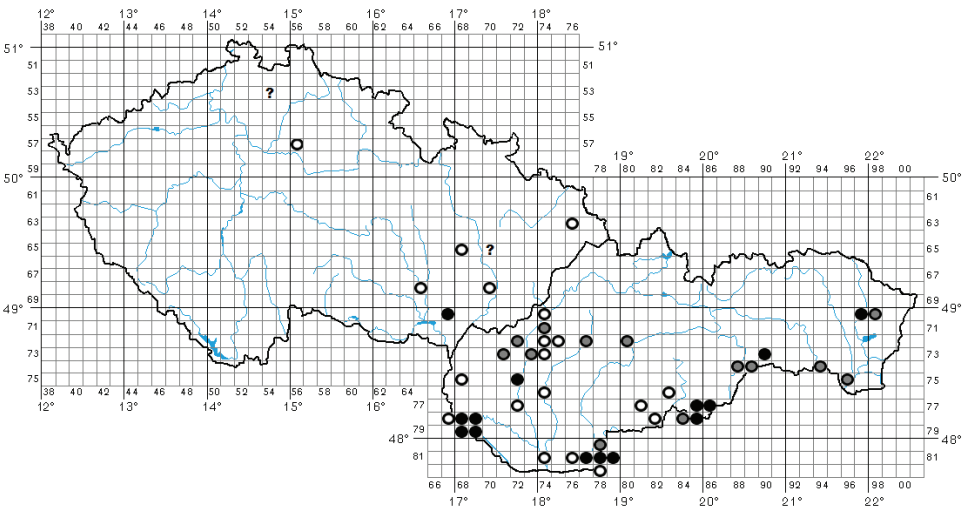


Figure 9. Distribution of *B. unicornis* in the Czech Republic and Slovakia (open circles refer to the records before 1960, open circles with a grey centre refer to the records between 1960–1999, and solid circles refer to the records after 1999; a question mark indicates a dubious record).

France

Published data

"Gallia", no other data (Panzer 1802).

"Alsace", no other data (Bedel 1911; Portevin 1931; Horion 1951; Peslier 2004; Callot 2018).

Grand Est, Bas-Rhin, Strasbourg, ca. 140 m a.s.l., "in coll. Dr Puton – Jules Bourgeois pers. comm.", no other data (Scherdlin 1915; Sainte-Claire Deville 1936; Paulian 1941; 1959 Tesař 1957; Horion 1958; Paulian and Baraud 1982; Gangloff 1991; Brustel and Gouix 2012); Haut-Rhin, Colmar, ca. 195 m a.s.l., 25.vi.1967, 1 ♂, flew through the open window attracted by light, Schlatter leg. (Gangloff 1991; Brustel and Gouix 2012); Haut-Rhin, Mulhouse, no other data (Kampmann 1860; Knörzer 1912, Schaufuss 1916; Paulian 1941, 1959; Paulian and Baraud 1982), 1 ♂, undated, [Hans W.] Kesenheimer leg. (Scherdlin 1915; Gangloff 1991; Brustel and Gouix 2012), Haut-Rhin, Mulhouse – Dornach, ca. 250 m a.s.l., no other data, Klein leg. (Scherdlin 1920; Sainte-Claire Deville 1936; Paulian 1941, 1959; Horion 1958; Paulian and Baraud 1982), August (year not specified), 1 spec., collector unknown, coll. [Édouard] Klinzig (Gangloff 1991; Brustel and Gouix 2012); Haut-Rhin, Mulhouse – Tannenwald, ca. 300 m a.s.l., undated, several spec. excavated from their burrows, Oscar Koechlin leg. (Bourgeois 1904; Knörzer 1912; Huber 1916; Sainte-Claire Deville 1936; Paulian 1941, 1959; Horion 1958; Paulian and Baraud 1982); Haut-Rhin, Riedisheim, ca. 280 m a.s.l., July 1912, 2 spec., collector not specified (Sainte-Claire Deville 1936; Horion 1958), 15.vi.1949, 1 spec., [Édouard] Klinzig leg. (Gangloff 1991; Brustel and Gouix 2012); Haut-Rhin, Baldersheim, ca. 230 m a.s.l., 26.viii.1951, 4 spec., Burglin leg., coll. [Édouard] Klinzig (Gangloff 1991; Brustel and Gouix 2012).

? Auvergne-Rhône-Alpes, Savoie, Albertville, 19th century, no other data, 1 ♂ and 1 ♀ in coll. Perroud deposited in MNHN (Brustel and Gouix 2012; according to Denis Keith pers. comm., 2020, this record is dubious – see also the comment below).

Material examined

? "S. Frankreich" [= south of France], 1 ♂ and 1 ♀, "Coll. C. Felsche, Kauf 20, 1918", coll. MTDG [locality probably mistaken].

Grand Est, "Alsatia" [= Alsace], no other data, 1 ♂ in coll. Antoine Boucomont deposited in MNHN; Bas-Rhin, Strasbourg, [ca. 140 m a.s.l.], no other data, 1 ♂ in coll. MHNG (cf. Scherdlin 1915; Sainte-Claire Deville 1936; Paulian 1941, 1959; Tesař 1957; Horion 1958; Paulian and Baraud 1982); Haut-Rhin, Mulhouse – Dornach, [ca. 250 m a.s.l.], August [year not specified], 1 ♂, coll. MZSF (see Gangloff 1991); Haut-Rhin, Riedisheim, [ca. 280 m a.s.l.], 15.vi.1949, 1 ♂, [Édouard] Klinzig [leg.], coll. MZSF (cf. Gangloff 1991); Haut-Rhin, Baldersheim, ca. 230 m a.s.l., 26.vii.1951, 2 ♀♀, collector not specified [probably Burglin leg. – see Gangloff 1991], coll. MZSF.

? Occitanie, "Francia, Montpellier", 1918, 1 ♀, Lavagne [leg.], coll. Paolo Luigioni deposited in MCZR [locality probably mistaken].

Comment

For France, *B. unicornis* was first recorded by Panzer (1802) without precise data. Up to now, it is reliably known only from Alsace, with the last record from Colmar in 1967 (Gangloff 1991). Brustel and Gouix (2012) reported two specimens from the 19th century from the Savoy Prealps (Albertville), which, according to Denis Keith (pers. comm.), is dubious and probably based on mislabelled material. The site (a mountainous area) does not meet the known requirements of the species and its occurrence here seems to be highly improbable. The same applies to the Mont Cenis specimen from the Abeille de Perrin's collection in the MNHN.

Germany

Published data

Baden-Württemberg, Markgräflerland, Neuenburg am Rhein – Grißheim, "Grißheimer Trockenaue", [ca. 47°52'18.3"N, 7°33'55.5"E, ca. 210 m a.s.l.], 2.vi.1967, 1 ♂, at light, Hans Messmer leg., photo + coll. Richard Disch (Brechtel et al. 1995; Krell 1998; Bense et al. 2000; Frank and Konzelmann 2002; Petersen et al. 2006).

Bavaria (Bayern), "Bavaria", no other data (Panzer 1793a, 1795); "Bayern", no other data (Reitter 1909; Kuhnt 1912; Huber 1916; Horion 1951; Geiser 1984); "Bavaria", no other data, 1 ♂ (ex original coll. Rudolf Veselý) in coll. NMPC (Hillert et al. 2016); Unterfranken, Aschaffenburg – Strietwald, ca. 130 m a.s.l., 1830, more spec., Dr Hoffmann leg. (Oechsner 1854; Kittel 1879; Ihssen 1935; Horion 1951, 1957, 1958) – note: Fröhlich (1897) and Knörzer (1912) consider record from Aschaffenburg to be doubtful; Oberbayern, Neuburg an der Donau – Bergheim, ca. 380 m a.s.l., 9.vii.1946, 1 spec. and 20.vii.1954, 1 spec., Rudolf Müller leg., coll. NMAG (Jungwirt 2005, 2012); ? Oberbayern, Ingolstadt, September 1892, 1 spec. K[arl] Daniel leg. (Horion 1957, 1958; Jungwirt 2005; see Material examined and new observations below).

Material examined and new observations

"Germ." [= Germany], no other data, 1 ♂ and 1 ♀ in coll. ZINR, 1 ♀ in coll. Karel Mazura deposited in MMBC.

"Germania" [= Germany], no other data, 1 ♂ in coll. Georg Frey deposited in NHMB, 1 ♂ in coll. Ladislav Bojčuk deposited in MHKC, 1 ♂ in coll. NHMD.

"Germania mer.", no other data, 1 spec in coll. ZSMG.

Baden-Württemberg, Bruchsal – Untergrombach, Michaelsberg and Habichtsbuckel Nature Reserve, ca. 49°5'32"N, 8°34'13"E, 200–220 m a.s.l., 3.vii.2021, 1 ♀, light trap, FTK and TBK obs., 4.vii.–5.viii.2021, 17 ♂♂ and 11 ♀♀ FSLG after sunset, together with more spec. of *Od. armiger* and *Och. chrysomeloides*, FTK and TBK obs. (5 spec. leg., coll. FTK, TBK and SMNK) – these records will be published with additional details at a later date (Florian Theves and Torsten Bittner pers. comm., 2021).

Bavaria (Bayern), Upper Bavaria (Oberbayern), Ingolstadt, [ca. 370 m a.s.l.], 9.ix. [18]92, 1 spec. Dr K[arl] Daniel [leg.], "Fundortverwechslung" [= locality mistaken], coll. ZSMG (see Horion 1957, 1958; Jungwirt 2005); ? Oberbayern, "Holzapfelkr." [= Holzapfelkreuth, former manor on the western outskirts of Munich], [ca. 550 m a.s.l.], 12.x.[19]12, H[ans] Kulzer [leg.], "Fundortverwechslung" [= locality mistaken], coll. ZSMG.

Comment

In addition to old records from the late 18th and the first half of the 19th centuries from Bavaria, only one record from Baden from 1967 and two records from Bavaria in 1946 and 1954 were known from Germany. Daniel's specimen from Ingolstadt and Kulzer's speci-

Figure 10. Findings of *B. unicornis* **A, B** Germany, Bruchsal – Untergrombach, Michaelsberg and Habichtsbuckel Nature Reserve, 7.vii.2021 (photographs by Torsten Bittner) **C, D** Bulgaria, Dimovo env., 26.vi.2010 (photographs by Aleš Sedláček) **E, F** Bulgaria, Oreshak env., 6.vii.2020, (photographs by Maximilian Teodorescu).

men from Munich are questionable because they bear the labels added later of "Fundortverwechslung" (= locality mistaken). The new records presented from Baden represent the first known data on the species' occurrence in Germany after 54 years (see also Fig. 10A, B).

Switzerland

Published data

Basel-Stadt (Kanton Basel-Stadt), Basel, undated, 1 spec., Ed. Bernoulli leg. (Heer 1841; Stierlin and Gautard 1867; Stierlin 1900; Huber 1916; Brustel and Gouix 2012).

? Republic and Canton of Ticino (Repubblica e Cantone Ticino), no other data, Villa [leg.] (Heer 1841; Stierlin and Gautard 1867; Stierlin 1900); given that the canton of Ticino is mountainous, this record does not seem credible (see Habitat preferences in this study).

Material examined

Canton of Zürich (Kanton Zürich), "Tigurini" [= Zürich], undated, 2 ♀♀, collector unknown, "Mus. Drews." [= Musaeum Drewseni, = ex coll. Christian Drewsen (1799–1896)], coll. NHMD (Fig. 11).

Comment

The two old records from Basel and Canton of Ticino were later considered questionable for the absence of any subsequent sightings (Allenspach 1970). Both editions of the Catalogue of Palaearctic Coleoptera (Král et al. 2006; Nikolajev et al. 2016) list Switzerland for *B. unicornis* probably on the basis of these records. *Bolbelasmus unicornis* is no longer included in the very recent checklist of Scarabaeoidea of Switzerland (Cosandey et al. 2017). The two specimens from Zürich deposited in NHMD confirm the historical occurrence of the species in the country.

Italy

Published data

"Italia", no other data (Panzer 1802).

"Italia borealis", no other data (Cristofori and Jan 1832).

Piedmont (Piemonte), no other data (Marseul 1857; Jacquelin du Val 1863; Baudi di Selve 1889; Bertolini 1899a; Bedel 1911; Luigioni 1929; Porta 1932; Horion 1958; Arnone and Massa 2010; Brustel and Gouix 2012; Carpaneto et al. 2021), 2 spec., no other data (Costa 1864), 3 ♂♂ and 1 ♀, [19th century], [Vittore] Ghiliani leg., coll. MSNG, 1 ♂, [19th century], "ex coll. Demarchi", [Flaminio] Baudi [di Selve] [leg.], coll. MSNG, 1 ♂ with no other data in coll. NMPC (Arnone and Massa

Figure 11. The only two specimens of *B. unicornis* so far known from Switzerland, deposited in NHMD (photographs by Caroline Amalie Høegh-Guldberg, edited by Peter Kurina).

2010; Ballerio et al. 2014; Hillert et al. 2016; data from MSNG specified and supplemented by Roberto Poggi pers. comm., 2021), 1 ♂, [Flaminio] Baudi [di Selve] [leg.], and 1 ♂, L. Carrara [leg.], no other data, coll. MNFI (Arnone and Massa 2010; Hillert et al. 2016); Torino env., cattle pastures, date not specified, 2 spec. flying after sunset, together with *Od. armiger* and *Och. chrysomeloides*, Vittore Ghiliani leg. (Ghiliani 1847, 1887); Torino env., June 1845, 1 spec. on the bank of the Po River after a flood, Vittore Ghiliani leg. (Ghiliani 1847, 1887); Torino, 1 spec., no other data (Horion 1958; Barbero and Cavallo 1999); Torino, alluvial materials of the Po river, ca. 230 m a.s.l., 2 spec., no other data, coll. A. Gagliardi deposited in MFSN (Barbero and Cavallo 1999; information on the storage of these specimens supplemented by Enrico Barbero pers. comm., 2021); Provincia di Cuneo, Montelupo Albese, 24.v.1978, 1 ♂, collector not specified, coll. MCAS (Barbero and Cavallo 1999; Carpaneto et al. 2016; information on the storage of this specimen specified by Enrico Barbero pers. comm., 2021); Provincia di Alessandria, Lerma, 21st century, no other data (Carpaneto et al. 2016; Glerean and Stefani 2019); Provincia di Novara, Bellinzago Novarese, Caserma

Valentino Babini env., ca. 45°33'4"N, 8°39'59"E, ca. 185 m a.s.l., 1982–1989, number of spec. not specified, Roberto Pescarolo leg. et det. (Pescarolo 1990).

Lombardy (Lombardia), no other data, (Bertolini 1872, 1899a; Luigioni 1929; Porta 1932; Horion 1958; Brustel and Gouix 2012; Carpaneto et al. 2021); "Milano" [= Milan], [ca. 120 m a.s.l.], [19th century], 1 ♂ and 1 ♀, "ex coll. A[chille] Griffini", no other data, coll. MSNG (Arnone and Massa 2010; Hillert et al. 2016; data specified by Roberto Poggi pers. comm., 2021).

Trentino-Alto Adige/Südtirol, "Tirol" [= probably Südtirol], [Stefano de] Bertolini leg. (Gredler 1863), Südtirol, no other data (Horion 1958); Provincia autonoma di Trento, Trento env., [ca. 190 m a.s.l.], September 1868, 1 [♂], plant materials alluviated by the flooded Adige River, together with *Od. armiger*, Stefano de Bertolini leg. (Bertolini 1871, 1874; note: in the first paper from 1871, Bertolini did not include *B. unicornis* in the list of identified species, but he added it in his later article from 1874) – this specimen, labelled "92", is still in the Bertolini's collection deposited in MUSE; ? Provincia autonoma di Trento, Torcegno env., "in the mountains above Torcegno", undated, 3 spec., together with *Od. armiger*, [Giovanni] Costesso leg., coll. Stefano de Bertolini (Bertolini 1891, 1899b) – this record seems improbable due to the very high altitude (ca. 1000–2300 m) of the area (cf. Habitat preferences in this study); Provincia autonoma di Bolzano, "Bozen Boden" [an urban area of Bolzano in the east of the city], [ca. 260 m a.s.l.], undated, 1 spec., coll. Vinzenz Maria Gredler (Gredler 1863; Peez and Kahlen 1977; Kahlen 2018; note: in the Gredler's collection deposited in FGBI, the space for "*Bolb. quadridens*" in the box is empty – Daniel Lorenz pers. comm., 2021; in MSNB there are no specimens of *B. unicornis* – Petra Kranebitter pers. comm., 2021); Venezia Tridentina, no other data (Luigioni 1929; Porta 1932); Trentino, no other data (Arnone and Massa 2010; Brustel and Gouix 2012).

Veneto, no other data, (Bertolini 1872, 1899a; Luigioni 1929; Porta 1932; Horion 1958; Arnone and Massa 2010; Brustel and Gouix 2012).

Friuli Venezia Giulia, Provincia di Pordenone, Magredi del Cellina, Cordenons env., ca. 116 m a.s.l., 8.ix.2018, 1 ♂ and 1 ♀, dead on a path, 9.ix.2018, 1 ♂ and 1 ♀ in flight at 20.10–20.30 CEST (air temperature 21.5 °C, humidity 81%), 1 ♀ at actinic light at 21.15 CEST (air temperature 20 °C, humidity 96%), 10.ix.2018, 1 ♂ in flight at 20.15 CEST (air temperature 19 °C, humidity 78%), 12.x.2018, 1 ♀ in flight at 20.00 CEST, 15.v.2019, 1 ♂ and 1 ♀ in flight at 21.15 CEST (air temperature 14 °C, humidity 75%), 16.v.2019, 2 ♂♂ and 1 ♀ in flight at 21.00–21.15 CEST (air temperature 17 °C), 1 ♀ crawling on the ground at 21.20 CEST, 24.v.2019, 5 ♂♂ in flight at 21.20–21.35 CEST (air temperature 20 °C, humidity 70%), 26.v.2019, 1 ♂ in flight at 21.20–21.35 CEST (air temperature 20 °C, humidity 70%), 1.vi.2019, 1 ♂ and 2 ♀♀, in flight at 21.40 CEST (air temperature 20 °C, humidity 80%), 6.vi.2019, 2 ♂♂ and 1 ♀, in flight at 21.00–21.20 CEST (air temperature 22 °C, humidity 80%), 7.vi.2019, 2 ♂♂ in flight at 21.35 CEST (air temperature 22 °C, humidity 50%), Paolo Glerean and Gabriele Stefani obs. (Glerean and Stefani 2019; for flight statistics see Table 9); Provincia di Udine, Pasian di Prato, Biotopo prati del Lavia, ca. 90 m a.s.l., 15.–31.v.2005, 1 ♀, pitfall trap, Pietro Zandigiacomo leg. (Zandigiacomo 2005; Lapini et al. 2013).

Tuscany (Toscana), no other data, coll. Dr L[ucas] von Heyden (Heyden 1884); 1 spec. with no other data (Horion 1958); 1 ♀ with no other data in coll. OHS (Hillert et al. 2016).

Material examined and new observations

"Ital." [= Italy], no other data, 1 ♀ in coll. MNBG.

"Italia borealis", 1 ♂, "ex coll. [Achille] Griffini", no other data, coll. MSNG.

"Italien" [= Italy], "coll. [Gustav] Kraatz", no other data, 2 ♂♂ and 5 ♀♀ in coll. SDEI.

"Italia", undated, 1 ♂ and 1 ♀ (ex coll. Alexander Fry), coll. NHML.

"Italia, Sella [it is not clear whether it is a geographical name or the name of a person]", no other data, 1 ♂ in coll. SDEI.

Piedmont (Piemonte), "Pedem.", [= Pedemontium, currently Piedmont], no other data, 1 ♂ in coll. RBIN; "Pedemt." [= Piedmont], no other data, 3 ♂♂ and 1 ♀ in coll. Maurice Pic deposited in MNHN; "Pedemont." [= Piedmont], no other data, 1 ♂ and 1 ♀ (ex coll. Christian Drewsen) in coll. NHMD, 1 ♂ (ex coll. Carl Gustaf Thomson) in coll. MZLU, 1 spec. in coll. NHMW; "Pedemont." [= Piedmont], undated, L[éon Marc Herminie] Fairm[aire] [leg.], 1 ♂ and 1 ♀ (ex coll. Fredrik Wilhelm Mäklin) in coll. FMNH; "Alp. Pedemont." [= Alpes Pedemontium], undated, 2 ♂♂ and 1 ♀, [Vittore] Ghiliani [leg.], coll. NHMD; "Piémont" [= Piedmont], undated, 1 ♂ in coll. Elzéar Abeille de Perrin deposited in MNHN, 1 ♀ in coll. Antoine Boucomont deposited in MNHN, 1 ♀ in coll. Jacques Baraud deposited in MNHN, 1 ♂ in coll. NMPC, 1 ♀, in coll. Alfonz Gspan deposited in PMSL, 1 ♂ (ex coll. Giacomo Doria, ex coll. Edward Bonney Nevinson) in coll. NHML; "Piemont" [= Piedmont], no other data, 1 ♂ and 1 ♀ in coll. MNBG, 1 ♂ and 1 ♀ in coll. RBIN; "Piemont" [= Piedmont], "coll. Rottenberg", 1 ♀ in coll. SDEI; "Piemont" [= Piedmont], "coll. [Carl] Felsche", 1 spec. in coll. MTDG; "Piemonte" [= Piedmont], "colezz. Alzona" [= coll. Alzona], 1 ♀ in coll. MSNM; Città metropolitana di Torino, Rivarossa, [ca. 285 m a.s.l.], no other data, 1 ♀ in coll. Leopold Mader deposited in MNSA; "Turin" [= Torino], no other data, 1 ♂ and 2 ♀♀ in coll. Sylvain Augustin de Marseul deposited in MNHN, 1 ♂ and 1 ♀ in coll. NHMD, 1 spec. in coll. ZSMG; Torino, 25.vii.[year not specified], no other data, 1 ♂ in coll. Georg Frey deposited in NHMB; Torino, "alluvioni Po" [= alluvial materials of the Po river], ca. 230 m a.s.l., 1871, 1 ♀, L. Fea leg., coll. MSNG; Torino, no other data, 1 ♂ in coll. FMNH, 1 spec. in coll. NHMW; Borgofranco d'Ivrea, [ca. 250 m a.s.l.], undated, 1 ♂, L. Demarchi leg., coll. MSNG; Provincia di Alessandria, Lerma, ca. 300 m a.s.l., May 1995, 1 ♂, in the morning accidentally dug up from the soil in the orchard; 8.iv.2014, 1 ♂, in the morning accidentally dug up from the soil in the orchard; 4.v.2014, 1 ♂ in the morning on the ground and 1 ♀ at UV light at 21.30 CEST, after several days of rain; 11.v.2014, 1 ♀, accidentally dug up from the soil in the garden at 16.00 CEST; 3.viii.2014, 1 ♀ flying around the light at 21.30 CEST; 16.v.2015, 1 ♂, at UV light at 21.30 CEST, rain in the morning and the day before, very wet, 17 °C; 17.v.2015, 1 ♂, at UV light at 21.15 CEST, wet, 17 °C; 20.vi.2015, 1 ♀, at UV light at 22.00 CEST, heavy rainfall in pre-

vious days, vegetation and soil heavily saturated with water, 17 °C; 21.vi.2015, 1 ♀, at UV light at 22.00, wet, 17 °C; 29.vi.2015, 1 ♀, at UV light at 21.50 CEST, 23 °C, LRL obs. (see Glerean et al. 2021).

Lombardy (Lombardia), Provincia di Varese, Casorate Sempione, ca. 280 m a.s.l., October 1958, 1 ♂, at light, A. Bilardo leg., ex original coll. Giovanni Mariani, currently deposited in coll. RPM (for partial data on this record see Ballerio 2008 and Ballerio et al. 2014). Note: Zilioli and Pittino (2004) reported that in 2000 Riccardo Pittino unsuccessfully attempted to rediscover the species at this locality.

Comment

In the collection of Zdeněk Tesař deposited in SNMS, there is one specimen with the locality "Tirolis", which may refer to the territory of South Tyrol (today Trentino-Alto Adige). Records from Sicily (Baraud 1977; Paulian and Baraud 1982; Carpaneto and Piattella 1995; Sparacio 1995; Barbero and Cavallo 1999; Martín-Piera and López-Colón 2000; Agoglitta et al. 2006; Trnka 2009; Arnone 2010; Alonso-Zarazaga et al. 2013; Schoolmeesters 2019; Nuß and Jäger 2020) refer to *Bolbelasmus vaulogeri* (Abeille de Perrin, 1898) (see Arnone and Massa 2010 and Hillert et al. 2016). Benasso's record from Luint, Friuli-Venezia Giulia (Benasso 1971) is apparently based on a misidentified specimen of *Bolbocerosoma* sp. (bearing an erroneous locality label), which is evident both from the drawing of the specimen and from its description; in addition, this specimen was allegedly lost (Paolo Glerean pers. comm., 2020). This study presents new records from the third known locality with a recent occurrence of the species in Italy (Lerma).

Poland

Published data

Mazovian Voivodeship (Województwo mazowieckie), Warsaw – Saska Kępa, 80–85 m a.s.l., undated, 2 spec., Antoni Waga leg. (Hildt 1896; Tenenbaum 1923; Kubicka 1981; Szwałko 2004; Byk et al. 2012, 2016).

Opole Voivodeship (Województwo opolskie), Opole County, Złotniki, ca. 155 m a.s.l., undated, 1 ♀, Ludwik Fryderyk Hildt leg. (Hildt 1896; Szwałko 2004; Byk et al. 2016).

Świętokrzyskie Voivodeship (Województwo świętokrzyskie), Kielce County, Chęciny, 1 spec., no other data, (Tenenbaum 1923; Szwałko 2004; Bidas 2012; Byk et al. 2012, 2016; for details on this record see Material examined below); Ostrowiec County, Skarbka, 9.viii.1973, 1 ♂, dug up from the soil on a meadow, A. Liana, coll. MIZP (Stebnicka 1976; Szwałko 2004; Byk et al. 2016); Sandomierz County, Góry Pieprzowe Nature Reserve, ca. 150 m a.s.l., 28.vi.2001, 1 ♀, at light, KPL (Bunalski et al. 2013).

Lublin Voivodeship (Województwo lubelskie), Lublin env., no other data, Baumgarten leg. (Hildt 1896; Szwałko 2004; Byk et al. 2016).

Material examined

Lesser Poland Voivodeship (Województwo małopolskie), Wadowice County (Powiat wadowicki), "Wadowice, Hal." [= Hałyczyna or Galicja (Galicia), Wadowice, ca. 250–300 m a.s.l.], 1 ♀, undated, Smolik [leg.], DJP det., coll. NMBE.

Świętokrzyskie Voivodeship (Województwo świętokrzyskie), Kielce County, "Góry Stokrzyskie [env.], Gałęzice, [Mt.] Góra Ostrówka" [currently the Ostrówka quarry, ca. 50°50'11.94"N, 20°24'46.38"E, ca. 250 m a.s.l.], July 1921, 1 ♂, J. Czarnocki [leg.], "Polonia, [coll.] Sz[ymon] Tenenbaum", coll. MIZP (for incomplete data on this record see Tenenbaum 1923; Szwałko 2004; Byk et al. 2012, 2016).

Comment

From Poland, only six records were known, which are summarised and specified by Byk et al. (2016). The last Polish record is from 2001 from the Góry Pieprzowe Nature Reserve (Bunalski et al. 2013). This study presents a previously unpublished historical record from Wadowice.

Austria

Published data

Upper Austria (Oberösterreich), Linz, Scharlinz, ca. 250 m a.s.l., 25.v.1936, 1 ♂, [Johann] Wirthumer leg., coll. BZLA (Mitter 2000; Schwarz 2008; sex specified by Martin Schwarz pers. comm., 2022); Linz, Weikerlsee, ca. 250 m a.s.l., 10.vii.1955, 1 ♂ and 3 ♀♀, after the flood, [Hermann] Haider leg., coll. BZLA (Mitter 2000; Schwarz 2008; sexes specified by Martin Schwarz pers. comm., 2022); Linz – Ebelsberg, bank of the Traun river, 10.vii.1954, 9 spec., F. Linzinger leg., 4 spec. in coll. HMS, 5 spec. [3 ♂♂, 2 ♀♀] in coll. BZLA, Linz env., undated, 2 spec. [1 ♂ and 1 ♀], [Emil] Munganast leg., coll. BZLA (Franz 1974; Mitter 2000; Schwarz 2008; sexes specified by Martin Schwarz pers. comm., 2022); Steyregg, ca. 250 m a.s.l., 1 ♀ with no other data, coll. BZLA (Franz 1974; Mitter 2000; Schwarz 2008; sex specified by Martin Schwarz pers. comm., 2022); bank of the Danube river between the villages of Steyregg and Pulgarn, driftwood, no other data (Dalla Torre 1879; Schwarz 2008); Saxen an der Donau, 21st century, no other data (Paill and Mairhuber 2012; Gimpl et al. 2020).

Lower Austria (Niederösterreich), no other data (Panzer 1793b; Sturm 1805); Mühling, ca. 260 m a.s.l., no other data, Arthur Schatzmayr leg. (Schatzmayr 1936; Benasso 1971); Schauboden env., Hochrieß, ca. 370 m a.s.l., end of July 1955, 1 ♂, F. X. Seidl leg., Rudolf Petrovitz det. et coll. (Ressl and Kust 2010); Melk, undated, 2 spec., [Josef] Breit leg. (Horion 1958; Franz 1974); Mödling env., Eichkogel hill., ca. 330 m a.s.l., no other data (Franz 1974; Schmölzer 1989); Weidling bei Wien, no other data (Duftschmid 1805); Wienerwald, Weidlingbach, undated, 2 spec., [Josef] Breit leg. (Horion 1958; Franz 1974); [Vienna env.,] "Donau-Auen", undated, 3 spec.,

[Franz] Blühweiss leg. (Pittioni 1943; Horion 1958); Donau-Auen National Park, Orth an der Donau env., 48°7'59.87N, 16°42'20.56"E, 145 m a.s.l., 6.–8.vii.1997, 1 ♀, plant materials alluviated by flooded Danube river, PZW obs. + photo (Paill 2007; coordinates specified by PZW pers. comm., 2009); Groß-Enzersdorf – Mühlleiten env., 48°10'34"N, 16°33'6.6"E, 159 m a.s.l., 24.vi.2019, 1 ♂ flying up to 0.5 m above the ground at 21.40 CEST, meadow adjacent to the forest, 22 °C, gentle breeze, ADW obs. + photo (Dostal 2019; Dostal and Barries 2019; Dostal et al. 2021b); Leitha Mts, Mannersdorf am Leithagebirge env., July 1900, 1 ♀ and October 1912, 1 ♀, in a forest clearing, Molitor leg. (Horion 1958; Franz 1974); Oberweiden, Sandberge Oberweiden Nature Reserve, 48°17'15.4"N, 16°49'38.5"E, ca. 155 m a.s.l., 23.viii.2019, 1 ♀ perching motionless on a path at 19.00 CEST, 25 °C, DRW and SRL leg., det et coll. (Rabl et al. 2019); Marchegg, ca. 135 m a.s.l., no other data (Franz 1974).

Vienna (Wien), no other data, coll. Dr Lucas von Heyden (Heyden 1884); no other data, (Dobiasch 1911); "Umg. Wien" [= Vienna env.], undated, 1 ♀, Ad[olf] Hoffmann [leg.], coll. ZFMK (Hillert et al. 2016); Vienna, Danube inundation area, 17.vii.1906, 3 spec., collector nor specified (Franz 1936, 1974); Vienna XXI [– Floridsdorf], August 1948, 12 spec., plant materials alluviated by flooded Danube river, [Harald] Schweiger leg. (Horion 1958); Vienna – Floridsdorf, ca. 155 m a.s.l., June 1949, 1 spec., at light in the garden, Harald Schweiger leg. (Schweiger 1951; Horion 1958; Franz 1974); Vienna env., Kahlenberg hill, no other data (Franz 1974); Vienna – Donaustadt, Fuchshäufel, 48°11'45.5"N, 16°28'57.9"E, 160 m a.s.l., 26.vi.2019, 1 ♂ flying up to 0.5 m above the ground at 21.55 CEST, 25 °C, no wind, WBW and ADW leg. + photo (Dostal 2019; Dostal et al. 2021a, b); Vienna – Donaustadt, Müllergraben, ca. 48°11'24.6"N, 16°30'42.4"E, 150 m a.s.l., 21.vi.2019, 1 spec., pitfall trap with vinegar, KFW leg. (Dostal 2019; Dostal et al. 2021a, b); Vienna – Donaustadt, Schusterau, 48°10'33.7"N, 16°32'54.7"E, 163 m a.s.l., 25.vi.2019, 1 ♀ flying up to 0.5 m above the ground at 21.50 CEST, 24 °C, no wind, WBW and ADW leg. + photo (Dostal 2019; Dostal et al. 2021a, b); Donau-Auen National Park, Untere Lobau, W of Kreuzgrund [= Lausgrund], ca. 48°9'34.52"N, 16°31'42.94"E, 152 m a.s.l., 15.vi.–9.vii.2006, 1 ♀, pitfall trap, Wolfgang Paill obs. (Paill 2007; Dostal et al. 2021b); Vienna – Donaustadt, Kreuzgrund, 48°9'36"N, 16°32'42"E, 160 m a.s.l., 12.vi.2019, one burrow, ADW and ADW obs.+ photo (Dostal 2019; Dostal et al. 2021a, b).

Burgenland, shore of Neusiedler See, plant materials amassed by flood water, several times (according to Sturm), with no further details (Petrovitz 1956); Winden am See, foot of the Zeilerberg mountain, ca. 200 m a.s.l., 3.vi.1981, 1 spec., at light, Gerhard Rößler leg. (Rößler 1989); Günser Gebirge, Rechnitz env., area of Geschriebenstein, no other data, Alfonz Freh leg. (Kaszab 1937; Horion 1958; Franz 1974); Jois env., steppe meadows north of the town, [ca. 220 m a.s.l.], 11.viii.2021, 1 ♂ flying up to 0.5 m above the ground and 1 ♀ in light trap, 21 °C, no wind, ADW and WBW obs. (Dostal and Barries 2021).

Carinthia (Kärnten), Villach, Teufelsgraben, 1 spec. with no other data (Holdhaus and Prossen 1901; Horion 1958; Paill and Mairhuber 2006); Villach env., undated, 1 spec., Arthur Schatzmayr leg. (Prossen 1913; Schatzmayr 1936; Horion 1958; Benasso 1971; Paill and Mairhuber 2006).

Styria (Steiermark), Grazer Bergland, Hörgas [near Gratwein-Straßengel], undated, 1 ♂ [10.6 mm], G[ustav] Wallaberger Sr. leg., coll. UMJG (Horion 1958; Franz 1974; Holzer 2019; sex specified by the author); Leutschach, Glanzer Klapotetzstraße 74 (Biohof Gunczy), 46°39'17.518"N, 15°31'18.03"E, ca. 370 m a.s.l., 8.ix.2018, 1 ♀, at light (flew through the open window), J. Gunczy obs., photo Gernot Kunz (Holzer 2019).

Material examined

"Styria" [= Duchy of Styria, a territory that included the modern Austrian state of Styria and the Slovenian region of Lower Styria], 1858, 1 ♂, [Eduard Albert] Bielz [leg.], coll. BNMS.

Lower Austria (Niederösterreich), "Nied. Oesterr." [= Niederösterreich], no other data, 1 ♂ in coll. NMBE; Melk, undated, 23 spec. in coll. NHMW, 1 ♂ and 1 ♀ (ex original coll. Josef Breit, Vienna) in coll. Georg Frey deposited in NHMB, 1 ♂ (ex original coll. Rudolf Petrovitz) in coll. MHNG (cf. Horion 1958 and Franz 1974); Wachau, no other data, 1 spec. in coll. NHMW; Wienerwald, Weidlingbach, undated, 2 ♂♂ (ex original coll. Josef Breit, Vienna) in coll. Georg Frey deposited in NHMB (cf. Horion 1958 and Franz 1974); "Umg. Wien" [= Vienna env.], Wienerwald, 1 spec. in coll. NHMW; "Blumau, Steinfeld" [= Blumau near Neurißhof], [ca. 250 m a.s.l.], undated, 1 ♂ (ex original coll. Rudolf Petrovitz) in coll. MHNG; [Vienna env.,] "Donau-Auen", undated, 1 ♂ and 1 ♀, F[ranz] Blühweiss leg., 1 ♂ and 1 ♀, Fr. Reiss leg., ex original coll. Rudolf Petrovitz, currently in coll. MHNG; [Vienna env.,] Donauauen, no other data, 1 ♀ in coll. TLMF, 10 spec. in coll. NHMW; [Vienna env.,] Donauauen, undated, 1 ♀, F[ranz] Blühweiss [leg.], coll. MNBG; "Marchfeld, Oberweiden", no other data, 1 ♀ in coll. MNBG; Oberweiden, Steppe [= steppe], 7.viii.1959, 1 ♀, J[osef] Gusenleitner leg., coll. BZLA.

Vienna (Wien), "Wien" [= Vienna], no other data, 2 ♀♀ in coll. Vladimír Zoufal deposited in MMBC, 1 spec. in coll. MTDG, 1 ♀ in coll. BZLA; "Wien" [= Vienna], undated, 1 ♂, J[osef] Moser leg., coll. BZLA; "Vienne" [= Vienna], no other data, 1 ♂ and 1 ♀ in coll. Albert Sicard deposited in MNHN; "Wien Umg.," [= Vienna env.], no other data, 1 ♂ in coll. Leopold Mader deposited in MNSA; "Wien, Umgebg." [= Vienna env.], undated, 1 ♀, F. Schade [leg.], coll. Jaroslav Matoušek deposited in MMBC; "Wien Umgebgebung", undated, 2 ♂♂, A[dolf] Hoffmann leg., coll. TLMF; "Umg. Wien" [= Vienna env.], undated, Ad[olf] Hoffmann [leg.], 1 ♀ (ex coll. P. Franck) in coll. MIZP, 1 ♂ in coll. SMNS, 1 ♀ in coll. Alfonz Gspan deposited in PMSL; "Hochwasser bei Wien" [= flood near Vienna], no other data, 1 ♀ (ex coll. Adolf Hoffmann) in coll. Jan Roubal deposited in SNMS; Vienna, Donau [= Danube river], Hochwasser [= flood], undated, 1 ♂ (ex original coll. Rudolf Petrovitz) in coll. MHNG; Vienna, "Donauüberschwemmung" [= flooded Danube river], September 1920, 1 spec., R. F. Lang [leg.], coll. NHMW; Vienna env., undated, 1 ♀, Carl Mandl [leg.], coll. Georg Frey deposited in NHMB; Vienna env., undated, 1 ♂, Matuschka [leg.], ex original coll. Josef Breit (Vienna), currently in coll. Georg Frey deposited in NHMB; Vienna, "Inundationsgebiet" [= inundation area of the Danube river], undated, 3 spec. (ex original coll. Herbert Franz) in coll. NHMW, 1 ♂ (ex original coll. Josef Breit, Vienna) in coll. Georg Frey deposited in NHMB; Vienna, Prater, no other data, 1 spec. in coll. NHMW.

Comment

In Austria, this species is known from six of the nine Austrian states. A recent attempt to rediscover the species at suitable sites along the Traun River in Upper Austria (Link et al. 2011) was unsuccessful, probably due to the use of inappropriate collecting methods and ignorance of the species' bionomy. This study presents previously unpublished older data from three Austrian localities.

Hungary

Published data

Western Transdanubia (Nyugat-Dunántúl), Vas County, "Molna-Szecsőd" [= Molnaszecsőd], 10.vi. [turn of the 19th and 20th century], ca. 180 m a.s.l., 1 spec. inside the digestive system of *Cuculus canorus*, Ernő Csiki obs. (Csiki 1904); Vas County, Kőszegi-hegység, no other data (Endrődi 1957); Zala County, Nova, ca. 190 m a.s.l., no other data (Endrődi 1957).

Central Transdanubia (Közép-Dunántúl), Komárom-Esztergom County, "Szőny" [a part of the current Komárom city], 6.viii.1901, 2 spec. inside the digestive system of *Upupa epops*, Ernő Csiki obs. (Csiki 1905); Komárom-Esztergom County, "Ószőny" [= Szőny, the part of the current Komárom city], ca. 105 m a.s.l., no other data (Endrődi 1957); Komárom-Esztergom County, Esztergom, 1 ♂, Sebő Endrődi leg., coll. HNHM (Endrődi 1957; Nádai 2006; sex specified by VKS pers. comm., 2020); Komárom-Esztergom County, Csolnok, no other data (Endrődi 1957), 28.v.1898, 1 ♂, Zahradka leg., coll. HNHM (Nádai 2006; sex specified by VKS pers. comm., 2020); Oroszlány env., Majkpuszta, Majki-hegy, 14.vi.1997, 1 ♀, at light. CKZ (Kutasi 2002; Nádai 2006; Eichardt and Kutasi 2011); Fejér County, Velence – Kisvelence, ca. 115 m a.s.l., July 1940, 1 ♀, Rudolf Lenczy leg., coll. HNHM (Nádai 2006; sex specified by VKS pers. comm., 2020); Fejér County, Adony, no other data (Endrődi 1957), 1 ♂, undated, Viktor Stiller leg., coll. HNHM (Nádai 2006; sex specified by VKS pers. comm., 2020).

Southern Transdanubia (Dél-Dunántúl), Somogy County, Fonyód, ca. 140 m a.s.l., undated, 1 ♂, Viktor Stiller leg., coll. HNHM (Endrődi 1957; Nádai 2006; sex specified by VKS pers. comm., 2020); Somogy County, Ordacsehi, Csehi-berek, 21.vii.2004, György Rozner leg. (Nádai 2006); Somogy County, Kaposvár, no other data (Endrődi 1957), 8.vii.1931, 1 ♂, Miklós Nattán leg., coll. HNHM (Hillert et al. 2016), 22.v.1951, 1 ♂, 3.vi.1951, 1 ♂, 4.vii.1951, 1 ♂, 31.vii.1958, 1 ♂, 19.v.1960, 1 ♀, Miklós Nattán leg., coll. HNHM (Nádai 2006; sex specified by VKS pers. comm., 2020); Somogy County, Balatonföldvár, no other data (Endrődi 1957); Somogy County, Nagyberény, 1937, 1 ♂, Ferenc Lichtneckert leg., coll. HNHM (Nádai 2006; sex specified by VKS pers. comm., 2020); Somogy County, Balatonvilágos – Balatonaliga, 1.viii.1980, collector unknown, 1 spec. in coll. HNHM (Nádai 2006; data specified by OMB pers. comm., 2020); Somogy County, Szenna, 9.vi.1998, György Rozner leg. (Rozner 2001; Nádai 2006); Tolna County, Gyulaj, 1 ♂, 1952, Jenő Győrffy leg.,

coll. HNHM (Nádai 2006; sex specified by VKS pers. comm., 2020); Tolna County, Hőgyész, 46°30'38"N, 18°25'55"E, 24.vii.1994, 1 spec. at light, collector not specified (Nádai 2006; coordinates specified by SBP, pers comm. 2021); Tolna County, Bátaapáti env., Nagy-mórágyi-völgy [valley], Quercetum, 15.vii.2004, 1 ♀, OMB leg., coll. HNHM (Nádai 2006; Hillert et al. 2016); Tolna County, Bonyhád, ca. 140 m a.s.l., 8.vii.1938, 1 spec., Nándor Vámos leg., coll. ZUDH (Enyedi 2006); Baranya County, Szigetvár, ca. 120 m a.s.l., no other data (Endrődi 1957), 1.vi.1909, remains of 1 spec., Ottó Mihók leg., coll. HNHM (Nádai 2006; data specified by VKS pers. comm., 2020); Baranya County, Sellye, finding in truffle (*Tuber* sp.), no other data (Merkl 2014); Baranya County, Pécs, no other data, (Viertl 1894; Kuthy 1898; Endrődi 1957), 1 ♂, undated, Ferenc Ehmann leg., coll. HNHM (Nádai 2006; sex specified by VKS pers. comm., 2020); Baranya County, "Szabolcs" [= Pécs – Szabolcs or Mecsekszabolcs] env., "Szarvasnóta", ca. 46°8'8"N, 18°15'46"E, beginning of June 1880, 1 ♂ and 1 ♀, the female was digging a hole into the ground at the edge of a forest footpath like *Copris*, and it seemed that the male was helping her with this work, Dr Ernő Kaufmann leg. (Kaufmann 1897, 1914a, b); Baranya County, Abaliget, 1978, no other data (Nádai 2006); Baranya County, Villányi-hegység Mts, Csukma-hegy hill, 5.v.1972, 1 spec. at light (mercury-vapor lamp), Ákos Uherkovich leg. (Horvatovich 1980; Sár and Horvatovich 2000; Nádai 2006).

Central Hungary (Közép-Magyarország), Veszprém County, Pápa env., no other data (Wachsmann 1907; Endrődi 1957), 1893, 1 ♀, Ferenc Wachsmann leg., coll. HNHM (Nádai 2006; sex specified by VKS pers. comm., 2020), June 1895, 1 ♀, Ferenc Wachsmann leg., coll. HNHM (Rozner 1984; Nádai 2006; sex specified by VKS pers. comm., 2020); Veszprém County, Balatonalmádi, 5.ix.1940, 1 ♂, Ernő Csiki leg., coll. HNHM (Rozner 1984; Nádai 2006; sex specified by VKS pers. comm., 2020); Veszprém County, Vászoly env., Öreg-hegy, 250–290 m a.s.l., 3.vii.1999, 1 spec., IRB leg. (Nádai 2006; data specified by OMB pers. comm., 2020); Veszprém County, Paloznak 17.viii.1961, Frigyes Novák leg., coll. HNHM (Rozner 1984; Nádai 2006); Veszprém County, Berhida, undated, 1 ♀, Rudolf Lenczy leg., coll. HNHM (Rozner 1984; Nádai 2006; sex specified by VKS pers. comm., 2020); Pest County, Buda hills (Budai-hegység), no other data (Frivaldszky I. 1865; Frivaldszky J. 1879a, b; Endrődi 1957); Pest County, Buda Hills, Hármashatárhegy [env.], [47°32'50.21"N, 19°0'18.77"E, ca. 390 m a.s.l.], 31.v.2004, 1 ♂, caught after sunset with a net attached to the roof of a moving car, OMB leg., coll. HNHM (Hillert et al. 2016; data specified by OMB pers. comm., 2020); Pest County, "Kis-Szent-Miklós" or "Őrszentmiklós" [= Őrbottyán – Őrszentmiklós], 1876, dry oak forest on the hill, 1 spec. on the ground in the grass in the evening (localised thanks to audible stridulation), Karoly Sajó leg. (Sajó 1881, 1897, 1910a, b), 1880s, more spec., sons of Karoly Sajó leg. (Sajó 1897, 1910b); Pest County, Sződliget, 16.vi.2005, 1 spec., Tamás Hácz leg. (Nádai 2006; data specified by OMB pers. comm., 2020); Pest County, Pilis hegység, no other data (Endrődi 1957); Pest County, Pilis hegység, Szentendre env., undated, 1 ♀, Hugó Diener leg., coll. HNHM (Nádai 2006; sex specified by VKS pers. comm., 2020); Pest County, Szigetszentmiklós, 6.vi.1954, 1 ♀, Miklós Nattán leg., coll. HNHM (Nádai 2006; sex specified by VKS pers. comm., 2020); Pest County, Dabas, no other data

(Frivaldszky 1865; Kuthy 1898; Endrődi 1957); Pest County, Dabas – Gyón env., [47°9'6.08"N, 19°18'6.84"E, ca. 100 m a.s.l.], 20.v.2012, 1 spec., at light, SIB leg. (Merkl and Szénási 2018; coordinates specified by OMB pers. comm., 2020); Pest County, Táborfalva env., shooting and training area, [47°5'52"N, 19°23'26"E, 118 m a.s.l.], 11.vii.2012, 1 spec., at light, SIB obs. (Merkl and Szénási 2018; coordinates specified by SBP pers. comm., 2021); Pest County, Gödöllő env., no other data (Pétsch and Szénási 2019); Pest County, Gödöllő env., Valkó, 22.vii.1992, 1 spec., clearing in an oak forest, László Köteles leg. (Köteles and Bakonyi 1996; Nádai 2006); Pest County, Gödöllő – Máriabesnyő, no other data (Endrődi 1957), 31.v.1912, 1 ♂, István Gurányi leg., coll. HNHM (Nádai 2006; sex specified by VKS pers. comm., 2020); Pest County, Gödöllő, 55 Erdőszél Street, [47°36'11.3"N, 19°23'23.6"E, 250 m a.s.l.], 2005, no other data, VSI leg., (Nádai 2006); Pest County, Gödöllő env., Faház-tető hill, no other data, VSI leg., (Nádai 2006); Pest County, Pécel, no other data (Kuthy 1898; Endrődi 1957; Pétsch and Szénási 2019), 1 ♀, undated, István Peregi leg., coll. HNHM (Nádai 2006; sex specified by VKS pers. comm., 2020); 47°29'11.48"N, 19°23'19.52"E, 3.vi.1972, 1 spec., IRB leg. (Nádai 2006; data specified by OMB pers. comm., 2020); Pest County, Isaszeg, no other data (Endrődi 1957; Pétsch and Szénási 2019); 29.v.1909, 1 ♂, 2.vi.1909, 1 ♂, Ottó Mihók leg., coll. HNHM (Nádai 2006; corrections and sex specified by VKS pers. comm., 2020); 1908, 1 ♀, 1909, 1 ♀, June 1917, 1 ♂, Hugó Diener leg., coll. HNHM (Nádai 2006; corrected and sex specified by VKS pers. comm., 2020); June 1929, 1 spec., Hugó Diener leg., coll. HNHM (Nádai 2006); 2008, 1 ♀, collector not specified, coll. HNHM (Hillert et al. 2016); June 2013, more spec. FSLG after sunset, TNB obs. + photo (Németh 2013); Pest County, Isaszeg, 29 Erdő Street, [47°31'23.412"N, 19°23'33.87"E, 210 m a.s.l.], 2005, VSI leg. (Nádai 2006); Pest County, Kistarcsa env., no other data (Pétsch and Szénási 2019); Pest County, Kerepes env., no other data (Pétsch and Szénási 2019); Pest County, Domony env., no other data (Pétsch and Szénási 2019); Pest County, Csévharaszt, [47°18'26"N, 19°26'26"E, 127 m a.s.l.], 14–15.viii.2001, 3 ♂♂ and 1 ♀, pitfall traps with ethylene glycol and at light, GSB leg., coll. HNHM (Nádai 2006; Szél and Kutasi 2011; Hillert et al. 2016; data specified by VKS pers. comm., 2020, and SBP pers. comm., 2021), 17.vi.2002, 1 spec., at light, SIB obs., 19.vi.2004, 1 spec., at light, SIB obs., 29.v.2005, 1 spec., at light, SIB obs. (Nádai 2006; Szél and Kutasi 2011; data specified by OMB pers. comm., 2020); Pest County, Biatorbágy, 27.vi.1999, 1 ♂, at light, AGB leg., coll. HNHM (Nádai 2006, Hillert et al. 2016; data specified by VKS pers. comm., 2020); Pest County, Nagykovácsi env., Julianna-major, 10.vi.1985, 1 spec., at light, 18.vii.1985, 1 spec., at light, Dezső Szalóki leg. (Nádai 2006); Pest County, Budakeszi, 28.v.1991, on *Glomus macrocarpum*, no other data (Bratek et al. 1992); Pest County, Budakeszi env., Hosszú-dűlő, 200 m a.s.l., 5.vi.1991, 2 ♀♀, on *Glomus macrocarpum*, *Cynodonto-Festucetum*, LAB leg. coll. HNHM (Nádai 2006; data specified by VKS pers. comm., 2020), 8.vi.1991, 2 ♀♀, on *Glomus macrocarpum*, *Cynodonto-Festucetum*, LAB leg., coll. HNHM (Nádai 2006; Hillert et al. 2016); Pest County, Budakeszi env., airport, 5.vi.1991, 1 ♀, LNB (Nádai 2006); Pest County, "Nógrádverőce" [= Verőce], Borbély-hegy hill, 1 ♂, summer 1916, municipal forest, Sebő Endrődi leg., coll. HNHM (Endrődi 1957, 1979; Nádai 2006; sex specified by VKS pers. comm., 2020); Buda

[currently western part of Budapest], "Graberl" [a historical excursion destination in the Buda surroundings], 13.v.1798 (!), 1 spec., Tóbiás Koy leg. (Horváth 1884; this record is a quotation from the unpublished diary of János Boehm, the pioneer of Hungarian entomology); Budapest, no other data (Kuthy 1898); Budapest, 22.v.1930, no other data, Hugó Diener leg. (Nádai 2006); Budapest – Hűserbiavösvölgy, 9.vi.1939, 1 ♀, József Stahulják leg., coll. HNHM (Nádai 2006; sex specified by VKS pers. comm., 2020); Budapest env., Kamaraerdő, 25.iv.1920, 1 ♂ and 30.v.1922, 1 ♀, Hugó Diener leg., coll. HNHM (Nádai 2006; data specified by VKS pers. comm., 2020); [Budapest –] Rákos, no other data (Frivaldszky 1879a, b); Budapest – Budafok, no other data (Endrődi 1957), 1 ♂ with no other data, coll. HNHM (Nádai 2006; sex specified by VKS pers. comm., 2020); Budapest – Cinkota, no other data (Endrődi 1957), July 1907, 1 ♀, Kálmán Szombathy leg., coll. HNHM (Nádai 2006; sex specified by VKS pers. comm., 2020); Budapest – Mártonhegy, 17.iii.1949, 1 ♂, József Szőcs leg., coll. HNHM (Nádai 2006; Hillert et al. 2016); Budapest – Békásmegyer, 27.vi.1954, 1 spec., 29.vi.1954, 1 spec. and 1.vii.1954, 1 spec., Attila Podlussány leg., coll. MMGH (Nádai 2006; Enyedi and Ádám 2009); Budapest – Normafa, 9.vi.1967, 1 spec., Kálmán Gaskó leg. (Nádai 2006; data specified by OMB pers. comm., 2020); Budapest – Nagytétény, undated, 1 ♂, Sebő Endrődi leg., coll. HNHM (Endrődi 1957; Nádai 2006); Budapest – Ördög-orom, 2.vi.1959, 1 spec., Kálmán Gaskó leg. (Nádai 2006; data specified by OMB pers. comm., 2020); Budapest – Rákosszentmihály, 15.viii.1930, 1 ♂, at light, Jenő Győrffy leg., coll. HNHM (Nádai 2006; data specified by VKS pers. comm., 2020); Budapest – Szépvölgy, 23.vi.1975, OMB leg. (Nádai 2006); "Pest" [currently eastern part of Budapest], no other data, 1 ♀ in coll. NMEG (Hillert et al. 2016).

Southern Great Plain (Dél-Alföld), Csongrád-Csanád County, Szeged – Kiskundorozsma env., Nagyszék, 16.–23.vi.1989, 1 spec., pitfall trap with ethylene glycol, Béla Gaskó leg., coll. MMSH (Nádai 2006; Gaskó 2008); Békés County, Bélmegyer env., Fáspuszta, 46°53'42.19"N, 21°11'8.55"E, 1967, 1 spec., at light, no other data (Merkl et al. 2014; Merkl 2015; details specified by TDS pers. comm., 2021); Békés County, Dombegyház env., Trianon border mound, 46°18'17.54"N, 21°8'43.38"E, 99 m a.s.l., 9.vi.2013, 1 ♂, pitfall trap on a narrow strip of grass with loess soil, TDS and TDB leg., coll. HNHM (Merkl et al. 2014; details specified by TDS pers. comm., 2021); Bács-Kiskun County, "Peszér" [= Kunpeszér] env., no other data (Frivaldszky 1865; Endrődi 1957); Bács-Kiskun County, Csávoly, 10.vi.1999, 1 spec., at light, collector not specified (Nádai 2006; Merkl 2015).

Northern Hungary (Észak-Magyarország), Heves County, Mátra Mts, Galyatető, 10.vii.1959, Sándor Szabó leg. (Nádai 2006); Borsod-Abaúj-Zemplén County, Aggtelek National Park, Jósvafő env., 48°29'46"N, 20°33'53"E, 300 m a.s.l., 8.vii.1980, 1 spec., Iván Gyulai leg. (Nádai 2006; data specified by OMB pers. comm., 2020 and SBP pers. comm., 2021).

Northern Great Plain (Észak-Alföld), Hajdú-Bihar County, "Debreczen" [= Debrecen] env., ca. 1860–1880, 1 spec., József Török leg. (Török 1882); Hajdú-Bihar County, Debrecen, 10.vii.1958, 2 spec., Imre Tatár leg., coll. ZUDH (Enyedi 2006); Szabolcs-Szatmár-Bereg County, "Szabolcs vármegye" [= Szabolcs County], no other data (Szlabóczky and Borbás 1900).

Material examined and new observations

Western Transdanubia (Nyugat-Dunántúl), Győr-Moson-Sopron County, Győr – Likócs env., ca. 47°42'52.5"N, 17°41'45"E, 2019, 115 m a.s.l., pitfall traps, no other data (see unpublished report for the Fertő-Hanság National Park Directorate, Anonymus 2019); Győr – Győrszentiván env., 47°42'42.17"N, 17°46'25.05"E and 47°42'51.18"N, 17°46'40.77"E, 110 m a.s.l., 10.vi.2016, 5 spec., pitfall traps, CSS and PKB leg. [storage of the specimens not specified]; 47°42'51.04"N, 17°46'40.24"E, 112 m a.s.l., 25.v.2019, 1 ♂, pitfall trap, CSS and PKB leg. [storage of the specimen not specified].

Central Transdanubia (Közép-Dunántúl), Fejér County, Csór, ca. 150 m a.s.l., 21.v.2014, 1 ♀, at light on a steppe, MPK leg., coll. DCO; 28.v.2016, 1 ♂, at light, DVZ obs.; Fejér County, Csákberény, Bucka hill, 47°20'51.65"N, 18°21'35.32"E, 230 m a.s.l., 11.vi.1987, 1 spec., at light, CSB obs.; Fejér County, Gánt env., Kövesvölgy [valley], 47°24'19.94"N, 18°22'47.67"E, 280 m a.s.l., 14.vi.2019, 1 ♀ flying after sunset, VSI obs.; Fejér County, Nagykarácsony, 46°52'49.4"N, 18°43'27.1"E, 150 m a.s.l., 2.vi.2021, 2 ♂♂ and 1 ♀ FSLG after sunset, 17–18 °C, light breeze, TDS obs.; Fejér County, Adony env., 47°5'17.2"N, 18°49'10.3"E, 120 m a.s.l., 1.vi.2021, 10 spec. FSLG after sunset, 11–15 °C, no wind, TDB and TDS obs.; Komárom-Esztergom County, Környe, no other data, 1 ♂ in coll. RBIN; Komárom-Esztergom County, Esztergom env., Kis-Strázsa-hegy hill, 47°44'59.210"N, 18°44'35.07"E, 210 m a.s.l., 23.iv.2006, 1 spec., at light (mercury-vapor lamp), VPB; Komárom-Esztergom County, Kesztölc env., 47°43'13.4"N, 18°47'43.3"E, 17.x.2014, 260 m a.s.l., 1 ♀ excavated from its burrow from a depth of 60 cm, loess steppe with abundant occurrence of *Lethrus apterus* (Laxmann, 1770), TVP (for incomplete data on this record see Hillert et al. 2016); Komárom-Esztergom County, Máriahalom env., Siklóernyő-hegy hill, 47°37'38.57"N, 18°41'20.38"E, 214 m a.s.l., 11.vi.2019, 1 ♂ and 1 ♀ flying after sunset, VSI obs. (♂ in coll. HNHM); Komárom Esztergom County, Máriahalom env., 47°37'28.3"N, 18°41'21.68"E, 190 m a.s.l., 31.vii.2020, 1 ♀, at light, BKL obs. + photo (DJP det.); Veszprém County, Nagyvázsony env., 47°1'40.73"N, 17°42'38.62"E, 315 m a.s.l., 12.vi.2009, 1 ♀ flying ca. 10 cm above the ground after sunset, KLP; 16.vi.2016, 3 ♂♂ FSLG after sunset, JHH, JPP, JSU MSZ, MPV and PIL obs.; Veszprém County, Vászoly env., Öreg-hegy, 250–290 m a.s.l., 3.vii.1999, 1 spec., IRB leg., coll. SZM; Veszprém County, Örvényes, 46°55'8.3"N, 17°48'26.07"E, 150 m a.s.l., 16.vi.2019, 1 ♀ flying after sunset, forest pasture, VSI obs.; Veszprém County, Felsőörs, Öreg-hegy, 47°0'57.59"N, 17°58'52.72"E, 214 m a.s.l., 7.viii.2018, 1 ♂, dead near the light in a garden, FKD obs. + photo (DJP det.); Veszprém County, Bakony Mts, Litér, [ca. 200 m a.s.l.], 14.vii.2014, 1 ♀, IRB leg., coll. GML.

Southern Transdanubia (Dél-Dunántúl), Somogy County, Balatonendréd, 46°50'52"N, 17°59'18"E, 174 m a.s.l., 11.v.1989, 1 ♀ excavated from its burrow together with 1 ♂ of *Od. armiger*, VRH; Somogy County, Ságvár, Jaba-völgy [valley], 46°49'28.29"N, 18°2'32.93"E, 180 m a.s.l., 25.ix.2017, 1 ♀ crawling on the

ground, PFS obs. + photo (DJP det.); Somogy County, Balatonvilágos – Balatonaliga, 10.vi.1983, 1 spec., at light, SIB obs.; Baranya County, Zselic Mts, Mozsgó, ca. 150 m a.s.l., 27.vii.2017, 1 ♂, at light, MRM; Baranya County, Drávaszabolcs, 4/c Köztársaság tér Street, 45°48'20.95"N, 18°12'43.74"E, 91 m a.s.l., 28.vi.2020, 1 ♀ dead under the lamp, JST; Baranya County, Villányi-hegység Mts, Nagyharsány env., Szársomlyó hill, ca. 145 m a.s.l., 22.v.1977, 1 ♂, at light., AUP; Baranya County, Erdősmecske, ca. 240 m a.s.l., 18.viii.2012, 1 spec., 31.vii.2016, 1 spec., 27.v.2017, 1 spec., REE obs.

Central Hungary (Közép-Magyarország), Pest County, Zsámbék, June 2016, 1 ♀, students of Department of Zoology, Charles University, Prague leg., coll. DKP deposited in NMPC; Pest County, Biatorbágy, 47°27'54.501"N, 18°51'0.515"E, ca. 190 m a.s.l., 24.vii.2021, 1 ♂, at light, GAB obs. + photo (DJP det.); Pest County, Nagymaros env., Rigó-hegy hill, 47°46'31.63"N, 18°56'11.65"E, ca. 300 m a.s.l., 21.iv.2019, 1 ♂, night sweeping, TNB leg., coll. HNHM; Pest County, Szentendre – Izbég env., 47°41'47.61"N, 19°1'40.06"E, 195 m a.s.l., 9.vi.2014, 1 spec., at light (mercury-vapor lamp), GBP and APE obs.; Pest County, Pócsmegyer env., 47°43'44.5"N, 19°6'25.7"E, 110 m a.s.l., 11.viii.2006, 1 spec., 20.vi.2008, 1 spec., 18.vi.2010, 1 spec., pitfall traps without attractant, SBP and ZBP leg., 16.ix.2014, 1 ♀, pitfall trap, SBP leg. [storage of the specimens unspecified]; Pest County, Pomáz env., Szamár-hegy hill, 47°39'28.7"N, 18°58'43.06"E, ca. 185 m a.s.l., 2.vii.2019, 1 ♂ flying after sunset, VSI obs.; Pest County, Pomáz, Majdánpola, 47°38'27.7"N, 19°0'18.61"E, 190 m a.s.l., 1. viii.2019, 1 ♂ at light (mercury-vapor lamp), SIB obs., 1 m FSLG after sunset, VSI leg., coll. HNHM; Pest County, Budakeszi env., Hosszú-dűlő, 200 m a.s.l., 5.vi.1991, 2 ♂♂ and 1 ♀, *Cynodonto-Festucetum*, on *Glomus macrocarpum*, LAB leg., coll. GML (pair) and JMB (1 ♂); Pest County, Budakeszi, 5.vi.2013, 1 spec., 6.vii.2014, 1 spec., 19.vii.2014, 1 spec., 26.vii.2014, 1 spec., 3.vi.2015, 1 spec., 28.v.2016, 1 spec., 4.vi.2018, 1 spec., all at light, SIB obs.; Pest County, Budakeszi, gliding airport, ca. 200 m a.s.l., 5.vii.1991, 1 spec., LNB leg., coll. SZM; Pest County, Budakeszi, Farkas-hegy env., gliding airport, 47°28'39.7"N, 18°54'50"E, ca. 200 m a.s.l., 6.v.2018, 2 ♂♂ flying after sunset, TNB obs. (1 ♂ in coll. HNHM); 23.v.2019, 1 m flying after sunset, 12.vi.2019, 1 ♀, night sweeping, 17.vi.2019, 1 ♂, night sweeping, 27.vi.2019, 1 ♂, night sweeping, 2.vii.2019, 1 ♀ flying after sunset, TNB obs., 22.ix.2019, 1 spec., TNB obs., 47°28'55.2"N, 18°55'6.25"E, 18.vi.2018, 2 ♂♂ and 1 ♀ flying after sunset, 20.vi.2018, 4 ♀♀ flying after sunset, 5.vii.2018, 2 ♂♂ and 3 ♀♀ flying after sunset, 10.vii.2018, 2 ♂♂ flying after sunset, 12.ix.2018, 1 ♂ excavated from its burrow, TNB leg., coll. HNHM; Pest County, Budakeszi – Nagyszénászug, ca. 47°29'11.6"N, 18°55'26.3"E, ca. 230 m a.s.l., 18.vi.2018, 1 spec., 9.vi.2019, 3 spec. in a private garden, LMB obs.; Pest County, Budaörs env., Farkas-hegy, 47°28'27.29"N, 18°56'40.42"E, ca. 335 m a.s.l., 8.vi.2019, 1 spec., OMB obs.; 22.vi.2021, 1 ♂ FSLG after sunset, VSI obs.; Pest County, Törökbálint, Nagy-Mező, 47°25'31.01"N, 18°57'31.04"E, 216 m a.s.l., 18.vi.2019, 1 ♀ flying after sunset, VSI obs.; Budapest, Tétényi-fennsík env., 47°25'2.309"N 18°58'59.332"E, 180 m a.s.l., 6.viii.2021, 1 ♂, at light, MLB obs. + photo, DJP det.; Budapest, "Pest" [currently eastern part of Budapest], no other data, 2 spec in coll. MNHN; Újpest [currently part of Budapest], undated, 1 ♂, Robert

Meusel [leg.], coll. Jože Staudacher deposited in PMSL; Budapest, no other data, 7 spec. in coll. NHMW, 2 ♂♂ and 1 ♀ (ex original coll. Josef Breit, Vienna) in coll. Georg Frey deposited in NHMB, 1 ♂ (ex original coll. Josef Breit, Vienna) in coll. Jacques Baraud deposited in MNHN, 1 ♂ in coll. MNBG, 1 ♂ in coll. DKC; Budapest, undated, [Hugó] Diener [leg.], 2 ♂♂ and 1 ♀ (ex original coll. Josef Breit, Vienna) in coll. Georg Frey deposited in NHMB, 3 spec. in coll. ZSMG, 1 spec. in coll. SMNK, 1 ♂ in coll. DKC; Budapest, Ofen [= Buda], undated, [E.] Merkl [leg.], 2 ♂♂ and 2 ♀♀ (ex coll. Stöcklein) in coll. Georg Frey deposited in NHMB; "Buda-Pesth" [= Budapest], undated, 1 ♂ and 1 ♀, E. Merkl leg., coll. NMPC; Budapest, 1890, "coll. O. Leonhard", no other data, 2 ♂♂ in coll. SDEI; Budapest, 1895, 1 ♂ and 1 ♀, [Hugó] Diener [leg.], coll. SDEI; Budapest, 1899, 2 ♀♀, [Hugó] Diener [leg.], coll. MSNG; Budapest, Hármashatárhegy Airfield, 47°33'11.133"N, 18°58'29.279"E, 276 m a.s.l., 7.vi.2019, 1 spec., NPB obs.; Pest County, Dunakeszi, gliding airport, 47°36'51.79"N, 19°8'55.91"E, 125 m a.s.l., 10.vi.2019, 1 ♀ flying after sunset, VSI obs.; Pest County, Bugyi env., Nemes-ürbő, ca. 47°10'55.9"N, 19°11'24.7"E, 92 m a.s.l., 7.vii.2018, 3 spec., Hunor Győrfy obs.; Pest County, Bugyi, Ürbőpuszta, 47°9'52.47"N, 19°10'21.22"E, 91 m a.s.l., 10.vi.2019, 1 ♂ flying after sunset, VSI obs.; Pest County, Tatárszentgyörgy env., Ordító, ca. 47°2'13.8"N, 19°17'40.2"E, ca. 95 m a.s.l., 5.vii.1999, 4 spec., AMK obs.; Pest County, Tatárszentgyörgy env., Rohanka-dűlő, 47°3'48.05"N, 19°20'26.47"E, 98 m a.s.l., date not available [end of 20th or beginning of 21st century], 1 spec. flying after sunset, AMK obs.; Pest County, Tatárszentgyörgy env., Szabad-rét, ca. 47°3'14.07"N, 19°18'1.37"E, 94 m a.s.l., 29.vi.2018, 1 spec., CVK obs.; Pest County, Tatárszentgyörgy env., Széna-dűlő, ca. 47°1'42.25"N, 19°17'26.7"E, ca. 100 m a.s.l., 21.vi.1998, 3 ♀♀, AMK obs.; Pest County, Nagytarcsa env., Küdői-hegy hill, 47°32'21.43"N, 19°19'11.77"E, 230 m a.s.l., 8.vi.2003, 1 ♂ and 2 ♀♀, at light (mercury-vapor lamp), VSI obs. (1 spec. in coll. HNHM), 47°32'13.92"N, 19°19'10.72"E, 21.iv.2006, 1 ♀, at light (mercury-vapor lamp), VSI obs., 47°31'59.96"N, 19°19'22.96"E, ca. 250 m a.s.l., 19.vi.2018, 1 ♂, night sweeping, VSI leg., coll. HNHM, 1 ♀, at UV light, SIB obs., 47°32'17.59"N, 19°19'16.03"E, 18.vi.2013, 1 ♂ and 2 ♀♀, at light (mercury-vapor lamp), 25.vii.2019, 1 ♀, at UV light, VSI obs.; Pest County, Csomád, Öreg-hegy, 47°39'29.88"N, 19°12'38.05"E, 15.vi.2002, 1 ♂ and 1 ♀, at light (mercury-vapor lamp), VSI obs. (♂ in coll. HNHM); Pest County, Gödöllő, 55 Erdőszél Street, 47°36'11.3"N, 19°23'23.6"E, 250 m a.s.l., 15.vi.2004, 1 ♂, at light (mercury-vapor lamp), VSI leg., coll. HNHM, 5.viii.2004, 1 ♀, 7.viii.2004, 1 ♀, at light (mercury-vapor lamp), VSI obs.; Pest County, Gödöllő env., Faház-tető hill, 47°37'10.12"N, 19°25'8.94"E, 255 m a.s.l., 19.v.2004, 1 m and 2 ♀♀, at light (mercury-vapor lamp), VSI obs. (1 f in coll. HNHM), 47°37'5.81"N, 19°25'9.68"E, 26.vi.2017, 1 ♀, at light (mercury-vapor lamp), VSI, TNB and AKB obs.; Pest County, Gödöllő env., Perőc-oldal, 47°34'5.754"N, 19°20'8.424"E, ca. 250 m a.s.l., 30.vi.2019, 1 ♀, Csanád Szénási leg., coll. HNHM; Pest County, Váckisújfalu, Szélesek, 47°42'40.24"N, 19°19'36.32"E, 180 m a.s.l., 24.vii.2018, 1 ♀ flying after sunset, VSI obs.; Pest County, Pest County, Galgamácsa env., Ecskendi Forest, Ördög-árok area, 47°44'20.32"N, 19°25'17.34"E, 235 m a.s.l., 5.vi.2015, 1 ♀, at light (marcury-vapor lamp), VSI obs.; Pest County, Domonyvölgy, Bárányjárás, 47°37'23.8"N, 19°24'1.94"E, 220 m a.s.l., 21.v.2004, 1 ♂

and 1 ♀, at light (mercury-vapor lamp), VSI obs. (1 spec. in coll. HNHM); Pest County, Gödöllő - Máriabesnyő env., 47°35'38.59"N, 19°24'4.82"E, ca. 190 m a.s.l., 13.vi.2013, 1 ♂, ZKB obs. + photo (DJP det.); Pest County, Isaszeg, 29 Erdő Street, 47°31'23.412"N, 19°23'33.87"E, 19.vi.2003, 1 ♂, at light, VSI obs.; Pest County, Isaszeg env., Szarkaberki-völgy [valley] 47°32'14.86"N, 19°22'11.26"E, ca. 210 m a.s.l., 27.vi.2019, 2 ♂♂ and 1 ♀ flying after sunset, VSI obs., 1 ♂, at UV light, SIB leg., coll. HNHM; 23.vi.2020, 10 spec. SIB obs.; 1.vii.2020, 1 spec., at light, SIB obs.; Pest County, Isaszeg env., Kőmalmi tölgyes, 47°33'51.65"N, 19°25'48.93"E, ca. 250 m a.s.l., 9.v.2004, 1 ♀, at light (mercury-vapor lamp), VSI leg., coll. HNHM; Pest County, Dabas, 20.v.2012, 1 spec., at light, SIB obs.; Pest County, Pécel, 5.vi.2018, 1 spec., at light, SIB obs.; Pest County, Pécel env., 47°29'49.85"N, 19°22'56.56"E, ca. 200 m a.s.l., 12.vi.2010, 1 ♂, at light (mercury-vapor lamp), JDB obs.; Pest County, Pécel env., Trianoni-emlékmű, 47°28'28.86"N, 19°22'10.78"E, ca. 255 m a.s.l., 15.iv.2015, 1 spec., LNB obs.; Pest County, Csévharaszt, 24.vi.2004, 1 spec., at light., SIB obs.; Pest County, Albertirsa env., Golyófogó-völgy [valley], 47°15'52.86"N, 19°37'59.73"E, 150 m a.s.l., 1.vii.2019, 2 ♂♂ flying after sunset, SIB and VSI obs., 2 ♀♀, at UV light, SIB obs. (1 ♀ in coll. HNHM); Pest County, Tóalmás, Boldogkáta-puszta, 47°30'22.77"N, 19°42'2.44"E, 110 m a.s.l., 28.vi.2019, 1 ♂ and 1 ♀ flying after sunset, VSI obs. (♀ in coll. HNHM), 1 spec., at light, SIB obs.; Pest County, Tápióbicske, Gombai-patak [stream] bank, 47°22'12.5"N, 19°38'43.6"E, 120 m a.s.l., 3.vii.2019, 1 ♂ flying after sunset, VSI obs.; Pest County, Tápióbicske, Felső-Tápió [stream] bank, 47°23'58.92"N, 19°41'25.29"E, 111 m a.s.l., 20.vii.2020, 1 ♂ flying after sunset, VSI obs.

Southern Great Plain (Dél-Alföld), Bács-Kiskun County, Kunpeszér env., Alsó-Peszéri-rétek, ca. 47°3'50.129"N, 19°17'57.59"E, 93 m a.s.l., 8.vi.1996, 2 ♂♂, 23.vi.1998, 1 spec., 10.vi.2002, 2 ♂♂ and 1 ♀, at light, AMK obs.; Bács-Kiskun County, Kunpeszér env., Peszéri-erdő forest, ca. 100 m a.s.l., 6.vi.1998, 6 spec., 21.vi.1999, 3 spec., 30.vi.1999, 2 ♂♂, 11.vii.1999, 1 spec., AMK obs.; 26.vi.2018, 2 spec., at light, REE obs.; 28.vi.2018, 3 spec., at light, REE and CVK obs.; 4.vii.2018, 4 spec., 5.vii.2018, 7 spec., at light, REE obs.; 6.vii.2018, 1 spec., CVK obs.; 9.vii.2020, 1 spec., 13.vii.2020, 1 spec., at light, REE obs.; 22.vii.2020, 1 spec., 29.vii.2020, 1 spec., 30.vii.2020, 5 spec., 31.vii.2020, 2 spec., 8.viii.2020, 1 spec., 16.viii.2020, 10 spec., 18.viii.2020, 7 spec., 19.viii.2020, 6 spec., 20.viii.2020, 8 spec., Botond Kozma obs.; Bács-Kiskun County, Kunadacs env., Hungarian meadow viper Conservation Centre, ca. 47°1'27.807"N, 19°17'21.286"E, ca. 100 m a.s.l., 29.vi.2018, 1 spec., Vadász Csaba obs.; Bács-Kiskun County, Kunadacs env., Hetvenholdas, ca. 47°0'56.34"N, 19°16'54.34"E, ca. 97 m a.s.l., 27.ix.2016, 1 ♀ FSLG after sunset, AMK obs.; Bács-Kiskun County, Kunadacs, Nagy-erdő forest, date not available [21st century], 1 spec. caught after sunset, AMK obs.; Bács-Kiskun County, Kunadacs, Peregi-dűlő, ca. 46°57'0.4"N, 19°17'29.4"E, 95 m a.s.l., 6.vi.2006, 1 spec., AMK obs.; Bács-Kiskun County, Kunadacs env., Szabadszállási-legelő, ca. 46°56'6"N, 19°18'15"E, 94 m a.s.l., 9.vi.2006, 1 spec., AMK obs.; Bács-Kiskun County, Páhi, Páhi-rétek, ca. 100 m a.s.l., 10.vii.2020, 3 spec., CBK and REE obs.; Bács-Kiskun County, Kiskunhalas env., pasture, 46°24'10.97"N, 19°30'33.08"E, 122 m a.s.l., 7.vi.2021, 2 ♂♂ and 1 ♀, at light just after sunset, together with 1 ♀ of *Od. armiger*, TKK obs. + photo (DJP det.); Bács-

Kiskun County, Kecskemét – Hunyadiváros, 46°55'6.114"N, 19°42'43.794"E, 115 m a.s.l., 29.vi.2021, 1 ♀, at light, BCK and KVB obs. + photo (DJP det.).

Northern Hungary (Észak-Magyarország), Nógrád County, Kozárd, village area, 47°54'53.31"N, 19°37'7.07"E, 180 m a.s.l., 28.vii.2020, 1 ♀, at light (wall lamp of a residential house), KHE obs.; Nógrád County, Kozárd env., Majorsági-hegy hill, 47°54'59.87"N, 19°36'37.52"E, ca. 240 m a.s.l., 1.viii.2020, 1 ♀ flying after sunset, KHE obs.; Nógrád County, Kozárd env., Pohánka hill, 47°54'56.21"N, 19°37'29.88"E, 225 m a.s.l., 29.vii.2020, 1 ♂ and 1 ♀ flying after sunset, KHE obs.; Nógrád County, Bátonyterenye – Kisterenye, Váci Mihály Street, 48°0'32.22"N, 19°49'46.48"E, 190 m a.s.l., 28.v.1978, 1 ♂ FSLG after sunset, TKB and TKG obs.; Heves County, Tarnalelesz env., Pataji-far, 48°7'32.66"N, 20°9'32.12"E, 475 m a.s.l., 9.vi.2016, 1 ♂, in the grass during the day, shrubby edge of an oak forest (*Quercus cerris*), CBE obs.

Comment

Approximately one-third of the known localities of the species are located in Hungary. It is known here from 18 of the 19 counties. The first record from Hungary, without further details, is given by Illiger (1800). The first dated Hungarian record is from the vicinity of Buda (Graberl, a historical excursion destination) from 1798, only nine years after the species was described (Horváth 1884). Old records are summarised by Endrődi (1957). *Bolbelasmus unicornis* has been recorded several times as food for some birds (*Cuculus canorus*, *Falco vespertinus*, and *Upupa epops*) in several localities of the

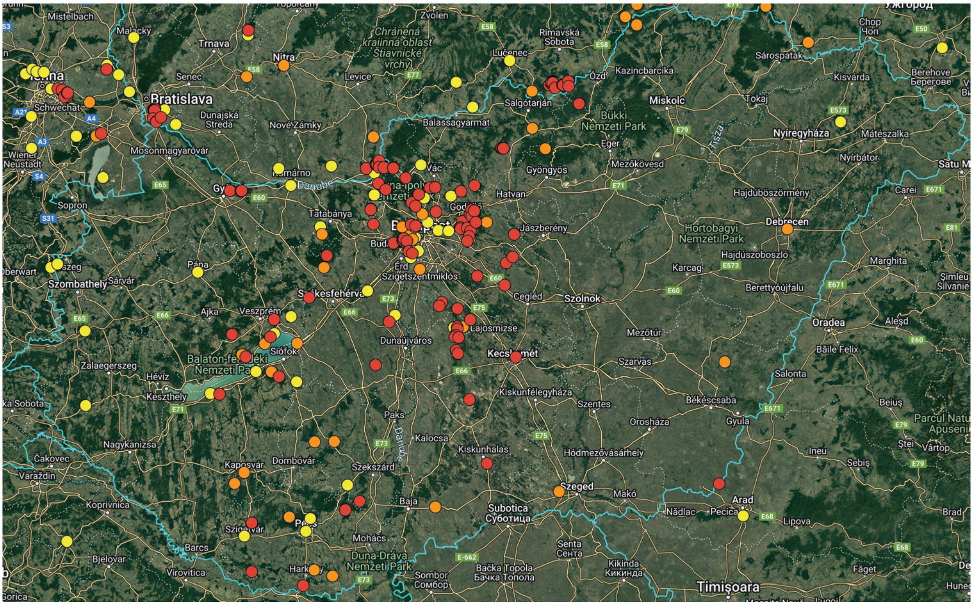


Figure 12. Distribution of *B. unicornis* in Hungary (yellow circles – records before 1950, orange circles – records between 1950–1999, red circles – records after 1999).

Austro-Hungarian Empire, including two Hungarian, two Slovak, and one Romanian locality (Csiki 1904, 1905, 1910; Madon 1930; Keve and Szijj 1957). Newer Hungarian records are summarised by Nádai (2006). Data collected by Duna-Ipoly National Park are now available online (Duna-Ipoly National Park 2021). This study presents as yet unpublished records from 68 Hungarian localities. For the distribution of the species in Hungary see Fig. 12.

Slovenia

Published data

Carniola (Kranjsko), "Carniolia, *Bolboceras quadridens* Fabr.", undated, 1 ♂, Ferdinand Joseph Schmidt leg., coll. F. J. Schmidt deposited in PMSL, Savo Brelih revid. (Brelih et al. 2010; sex supplemented by Tomi Trilar pers. comm., 2021); note: Trilar (2019) reported that there is another specimen of *B. unicornis* in the Schmidt's collection in PMSL labelled "*Athyreus kordofanus*", but the photograph makes it clear that it is a member of the genus *Athyreus*; Bohinjska Bela, 1 spec. with no other data in coll. JHIS (Brelih et al. 2010; Vrezec et al. 2011); Sorško polje, June 1900, 1 spec., Mate Hafner leg., coll. JHIS, Alja Pirnat revid. (Brelih et al. 2010; Vrezec et al. 2011).

Styria (Štajerska), "Leonhard" [= Lenart v Slovenskih goricah], no other data, 1 spec. J. N. Spitzy leg. et coll. (Brancsik 1871; Horion 1958; Brelih et al. 2010; Vrezec et al. 2011); "Marburg, Styria" [= Styria, Maribor], undated, 2 ♂♂ and 1 ♀ [Josef] Peyer [leg.], coll. J. Peyer deposited in PMSL (Brelih et al. 2010; Vrezec et al. 2011; data supplemented and specified by Tomi Trilar pers. comm., 2021).

Comment

Although there are many localities suitable for the species in Slovenia, only five old records are known from this country. The species is most likely still present here, and the reason for the absence of new data is probably the low collecting activity of the local entomologists and/or the ignorance of appropriate monitoring methods for the species. Also, a recent attempt to rediscover the species in Slovenia (Pirnat 2009) was unsuccessful mainly due to the use of inappropriate collecting methods.

Croatia

Published data

Croatia proper (Središnja Hrvatska), Moslavina [a microregion between the rivers Lonja in the south and west, Česma in the north and Ilova in the east], no other data [19th century] (Schlosser Klekovski 1878); Koprivnica-Križevci County, Križevci env., no other data [19th century] (Schlosser Klekovski 1878).

Slavonia (Slavonija), Osijek-Baranja County, Osijek env., no other data [19th century], Vukas [leg.] (Schlosser Klekovski 1878); Vukovar-Syrmia

County, Vinkovci, promenade near the Bosut river, 80 m a.s.l., 1.vi.1895, 1 ♀, caught with a net, collector not specified (Koča 1906; Mikšić 1959, 1960, 1970); Vukovar-Syrmia County, Gradište env., 45°10'33.7"N, 18°44'54.7"E, mixed lowland forest, 81 m a.s.l., 5.vi.2014, 1 ♂, at light, collector not specified (Koren 2017).

Material examined

"Chorvatsko" [= Croatia in Czech language], 1 ♂, "ex. coll. E. Hachler", no other data, coll. MMBC.

Dalmatia (Dalmacija), "Dalmatia", no other data, 1 ♀ in coll NMPC; "Dalmat." [= Dalmatia], no other data, 1 ♀ in coll. NMPC.

Comment

In Croatia, the species is known only from four old records from the 19th century. The only recent record (Gradište) is given by Koren (2017). Further historical undated specimens deposited in MMBC and NMPC are presented in this study.

Bosnia and Herzegovina

Published data

"Herzegovina", no other data, 1 ♂ in coll. ZFMK (Hillert et al. 2016).

Federation of Bosnia and Herzegovina (Federacija Bosne i Hercegovine), Zavidovići env., Gostović river valley, no other data, Károly Kendi leg. (Kendi 1910); Sarajevo, no other data (Mikšić 1953, 1958, 1960, 1970; Lelo 2006; Lelo and Kašić-Lelo 2010; Koren 2017).

Federation of Bosnia and Herzegovina (Federacija Bosne i Hercegovine) or **Republika Srpska** (Република Српска), Babin potok [river], no other data, 1 spec. in coll. René Mikšić [currently deposited in CMZC] (Mikšić 1953, 1958, 1960, 1970; Lelo 2006; Lelo and Kašić-Lelo 2010; Koren 2017).

Comment

Only four old records from Bosnia and Herzegovina have been published. No recent findings are known.

Serbia

Published data

Vojvodina (Војводина), Srem District (Сремски округ), Mt. Fruška gora (Фрушка гора), village of Vrdnik (Врдник), June 2016, 1 ♀, at light, collector unknown, coll.

DKP deposited in NMPC (Ćurčić et al. 2019); Srem District (Сремски округ), Ruma (Рума), undated, 1 ♂, [Harald] Schweiger leg., coll. MSNG (Arnone and Massa 2010; Hillert et al. 2016; collector's name specified by Roberto Poggi pers. comm., 2021); Inđija (Инђија) env., Krčedin (Крчедин), 1.vii.2013, 1 ♂, at light at 21.25 CEST, ZBB obs. + photo (Ćurčić et al. 2019; for more detailed data on this record see Material examined and new observations below); South Bačka District (Јужнобачки округ), South Bačka District (Јужнобачки округ), Mt. Fruška gora (Фрушка гора), Sremski Karlovci (Сремски Карловци) env., Stražilovo (Стражилово), 14.vii.2005, 1 ♀, at light, Dejan Stojanović obs. (Gavrilović and Stojanović 2008; Ćurčić et al. 2019); South Banat District (Јужнобанатски округ), Deliblato Sands (Делиблатска пешчара), Deliblato (Делиблато) env., Jagoda (Јагода), ca. 44°53'33"N, 21°3'2.6"E, date not specified, Zoran Gradojević leg. (Gradojević 1963; Ćurčić et al. 2019).

Belgrade District (Град Београд), Mala Ivanča (Мала Иванча) env., Grkovo (Грково), Trešnja Forest (Шума Трешња), 14.v.1986, 1 ♀ dug up beneath a hazel shrub together with *Tuber* fungi DPB leg. et coll. (Ćurčić et al. 2019); Mt. Kosmaj (планина Космај), Tresije Monastery (Манастир Тресије), 21.vi.2003, 1 ♀, dead under the lamp near a restaurant, DPB leg. et coll. (Ćurčić et al. 2019).

Southern and Eastern Serbia (Јужна и источна Србија), Bor District (Борски округ), Đerdap National Park (Национални парк Ђердап), 6 km WSW of Tekija (Текија), 27.–28.v.2014, 2 ♂♂ and 1 ♀, collector not specified, coll. DKP [deposited in NMPC] (Hillert et al. 2016; for details on this record see Material examined and new observations below); Pirot District (Пиротски округ), Bela Palanka (Бела Паланка) env., Babin Kal (Бабин Кал) env., 43°19'9"N, 22°23'23"E, 750 m a.s.l., 3.vii.2014, 1 ♂, at light, a meadow near an oak-hornbeam forest, SBS leg., coll. NMSB (Ćurčić et al. 2019); "Tsaribrod (Цариброд)" [= Dimitrovgrad (Димитровград)], no other data (Nedyalkov 1906; Mikšić 1959); Zaječar District (Зајечарски округ), village of Planinica (Планиница), 28.v.2006, 1 ♀, dug up in the garden, Siniša Ognjenović leg., coll. DPB (Ćurčić et al. 2019).

Material examined and new observations

Vojvodina (Војводина), Srem District (Сремски округ), Inđija (Инђија) env., Krčedin (Крчедин), 19.viii.2006, 2 ♂♂, at light, steppe meadow near the Danube river, LMN leg., coll. RSG and VVO; 45°10'04.5"N, 20°08'15.4"E, 98 m a.s.l., 1.vii.2013, 1 ♂, at light at 21.25 CEST, ZBB obs. + photo (for partial data on this record see Ćurčić et al. 2019); South Bačka District (Јужнобачки округ), Fruška Gora National Park (Национални парк Фрушка гора), Bukovac (Буковац) env., northern slope of Beljevo (Бељево) hill, 45°10'56.579"N, 19°53'0.802"E, 270 m a.s.l., 27.v.2019, 1 ♂, dead on the ground near the road (killed in flight by a passing car), MSN obs. + photo (Fig. 14B).

Southern and Eastern Serbia (Јужна и источна Србија), Bor District (Борски округ), Leskovo (Лесково) env., 44°18'17.28"N, 21°56'54.96"E, ca. 400 m a.s.l., 20.vi.2020, 1 ♂ crawling on the ground near the road at 18.42 CEST, MPN obs. + photo (Fig. 14C); Bor District (Борски округ), Đerdap National Park (Национални

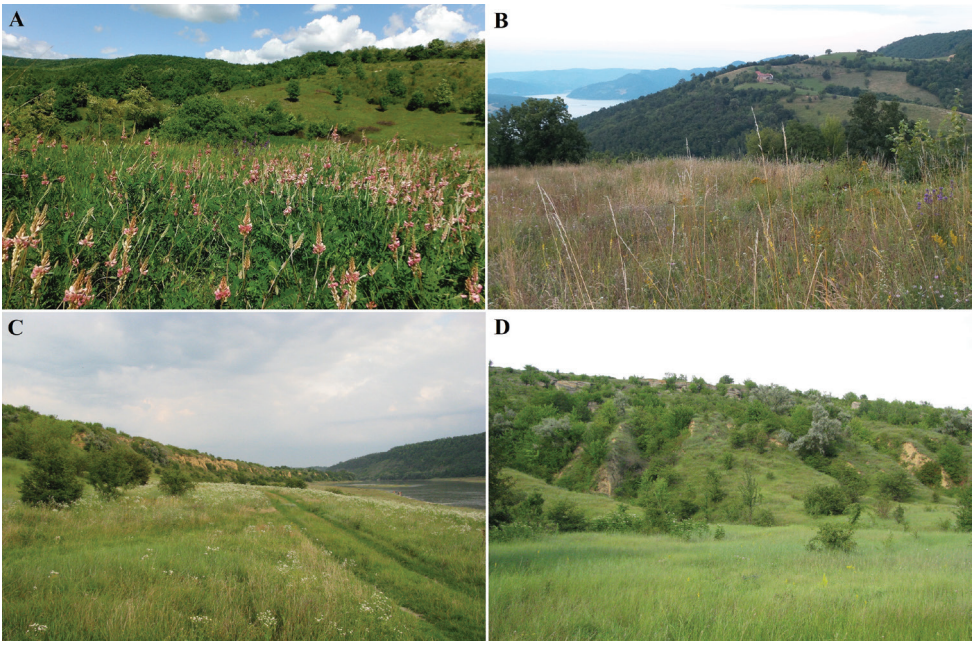


Figure 13. Localities with *B. unicornis* **A** Hungary, Kozárd env. (photograph by Krisztián Harmos) **B** Serbia, Đerdap National Park, Tekija env. (photograph by Ivo Martinů) **C, D** Ukraine, Dniester Canyon National Nature Park, Horodok env. (photographs by Yurii V. Kanarskyi).

парк Ђердап), 6 km WSW of Tekija (Текија), 44°39'19.4"N, 22°20'15.6"E, 300 m a.s.l., 27.v.2014, 1 spec. accidentally dug up while setting pitfall traps for ground beetles, RKP, 27.–28.v.2014, 51 spec. (both sexes in a ratio of 1:1) FSLG at 20.35–21.00 CEST, steppe hillside (probably former pasture, presently with tall vegetation) near an oak-beech forest, DHH (22 spec.), RKP (16 spec.), ZCP (11 spec.), TGK (1 spec.), and PSZ (1 spec.) leg., coll. OSD, DHH, DJP, DKP, GML, LMO, MBF, PSZ, RKP, TGK, VJP and ZCP (for incomplete data on this record see Hillert et al. 2016) (see Table 8 for full data on the flights); 12.–13.vii.2014, 8 ♂♂ and 12 ♀♀ FSLG at 20.43–21.15 CEST, the same place as May 27–28, RKP (11 spec.), IMO (7 spec.), MKJ (2 spec.) leg. et coll., 4 ♂♂ and 3 ♀♀ in coll. GML (see Table 8 for full data on the flights); 17.vi.2018, 1 ♂ and 2 ♀♀ FSLG after sunset, IMO, ZCP.

Comment

The known distribution of the species in Serbia was summarised by Ćurčić et al. (2019), who listed a total of 12 localities. New data from two of them (Krčedin, Tekija) and from two other new sites (Bukovac, Leskovo) are presented in this study.

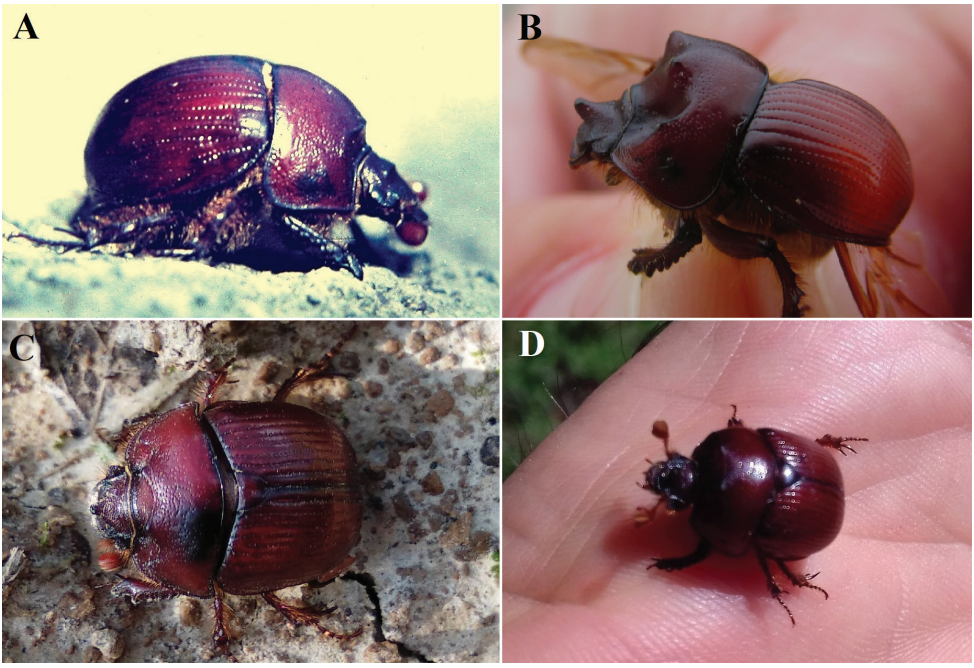


Figure 14. Findings of *B. unicornis* **A** Slovakia, Slanská Huta env., 24.vii.1972 (photograph by Zdeněk Laštůvka) **B** Serbia, Bukovac env., Beljevo hill, 27.v.2019 (photograph by Marko Šćiban) **C** Serbia, Leskovo env., 20.vi.2020, (photograph by Miloš Popović) **D** Ukraine, Semyhiria env., 3.vii.2020 (photograph by Dmytro Protopopov).

Albania

Published data

Tirana County (Qarku i Tiranës), Sauk, 10.vi.1958, 1 spec., 10.–20.vi.1961, 1 spec., Xhelo Murraj leg. (Murraj 1962); Ibë, 13.v.1959, 1 spec., 8.vi.1962, 1 spec., Xhelo Murraj leg. (Murraj 1962). Note: Murraj stated that he also found *Od. armiger* and *Och. integriceps* at both sites.

Comment

From Albania, only these records from two localities near Tirana have been published. Murraj (1962) reported that in Albania, *B. unicornis* is rare in lowland areas up to 700 m a.s.l. None of the editions of the Catalogue of Palaearctic Coleoptera (Král et al. 2006; Nikolajev et al. 2016) lists Albania for this species.

Romania

Published data

Crișana, Arad County, "Újarad" [= Arad – Aradul Nou], 28.iv.1907, 1 spec. inside the digestive system of *Falco vespertinus*, Ernő Csiki obs. (Csiki 1910).

Transylvania (Transilvania), Sălaj County, Zalău env., 3.viii.1973, 1 ♀, forest, collector unknown, coll. OHS (Hillert et al. 2016); Bistrița-Năsăud County, "Bistritz" [= Bistrița], no other data, Müller leg. (Petri 1912; Panin 1957); Bistrița-Năsăud County, Urmeniș, no other data (Panin 1957); Hunedoara County, "Nagyág" [= Săcărâmb], no other data (Bielz 1887; Kuthy 1898; Petri 1912; Endrődi 1957; Panin 1957); Sibiu County, "Mediasch" [= Mediaș], no other data, Prof. Fabini leg. (Fuss 1858), no other data, Eduard Albert Bielz leg. (Bielz 1887; Kuthy 1898; Petri 1912; Endrődi 1957; Panin 1957); Sibiu County, "Nagyszeben" or "Hermannstadt" [= Sibiu], no other data (Kuthy 1898; Petri 1912; Endrődi 1957; Panin 1957); Sibiu County, "Szenterzsébet" [= Sibiu – Gușterița], no other data (Endrődi 1957); Cluj County, "Kolozsvár" [= Cluj-Napoca], no other data (Endrődi 1957); Cluj County, "Szamosújvár" [= Gherla], no other data, Ormay leg. (Kuthy 1898; Petri 1912; Endrődi 1957; Panin 1957); Cluj County, Stufărișurile de la Sic Nature Reserve env., 2002–2004, 6 spec., forest edge, no other data (Nițu 2007; Ruicănescu and Nițu 2008; Anonymus 2015); Mureș County, "Schässburg" [= Sighișoara or Segesvár], no other data, Karl Petri leg. (Petri 1912; Endrődi 1957; Panin 1957), Sighișoara, Târnava Mare river, no other data (Ruicănescu and Nițu 2008; Tatole et al. 2009).

Western Moldavia (Moldova Occidentală), Suceava County, "Mihoweny" [= Mihoveni], 1 ♂ with no other data (Jasilkowski 1906); Vaslui County, Zorleni, no other data (Fleck 1905; Panin 1957).

Banat, Caraș-Severin County, "Gerník" [= Gârnic] env., 44°45'36.72N, 21°46'29.48"E, 620 m a.s.l., 11.–13.vi.2016, ca. 14 spec. fyling low above the ground after sunset, together with tens of spec. of *Od. armiger*, air temperature 12–15 °C, JHH, JPP, JSU MSZ, MPV and PIL obs. (Spružina 2016; data specified and corrected by JHH and JSU pers. comm., 2021).

Muntenia, Giurgiu County, Comana, no other data, Arnold Lucien Montandon leg., Jules Bourgeois det. (Montandon 1906); Bucureşti env., no other data (Manolache 1930).

Dobruja (Dobrogea), Tulcea County, Babadag [env.], [100–200 m a.s.l.], 1989–2000, no other data (Nițu 2001); Constanța County, Albești env., Hagieni Forest, ca. 50 m a.s.l., no other data, L. Székely pers. comm., 2014 (Fusu et al. 2015).

Material examined and new observations

Transylvania (Transilvania), Sibiu County, "Transsylv. Alpen" [= Transsilvanische Alpen (Carpații Meridionali)], "R.Turm Paſs" [= Roter-Turm-Pass (Pasul Turnu Roșu)], 350–450 m a.s.l., 1917, 1 ♂ and 1 ♀, Dr Maertens [leg.], coll. MNBG; Cluj County, Suatu, ca. 46°46'39"N, 23°58'24"E, ca. 365 m a.s.l., August 1997, 1 ♀, at light,

steppe hillside with sparsely scattered oak trees, ARC (for incomplete data on this record see Ruicănescu and Nițu 2008); Sibiu County, Șura Mare, [ca. 450 m a.s.l.], 28.vii.1972, 1 ♂ and 2 ♀♀, E[ckbert] Schneider [leg.], coll. Eckbert Schneider deposited in BNMS; Sibiu County, "Hammersdorf" [= Sibiu – Gușterița], [ca. 425 m a.s.l.], 17.vi.1888, [Mauritius von] Kimakowicz [leg.], coll. BNMS.

Western Moldavia (Moldova Occidentală), Bacău County, Comănești (ca. 46°25'38.5"N, 26°26'31.1"E), July 2004, 1 ♂, dead inside the collector's house (probably attracted by the light), APC; 31.vii.2010, 1 ♀, at light, APC; 8.viii.2011, 1 ♂, Barber pitfall trap, APC leg., coll. CMI; Iași County, Hârlău env., Pîrcovaci env., 47°28'28.29"N, 26°47'22.17"E, 240 m a.s.l., 24.vi.2021, 1 ♀, LHI obs. + photo (DJP det.); Iași County, Iași – Rediu, Iazul Tăutești, 47°13'33.4"N, 27°28'06.7"E, 120 m a.s.l., 28.vii.2021, 3 ♀♀, at light, MJR leg., coll. PKG; Iași County, Iași – Miroslava, Valea lui David, 47°11'38"N, 27°28'2.114"E, ca. 90 m a.s.l., 9.vii.2021, 2 ♀♀, together with 1 ♂ of *Od. armiger*, LHI obs. + photo (DJP det.); Iași County, Bârnova Forest (ca. 47°00'37.4"N, 27°33'32.8"E), 4.vii.2005, 1 ♂, found accidentally on the ground during the day, LFI leg., coll. CUIR (for incomplete data on this record see Ruicănescu and Nițu 2008; Tatole et al. 2009; Stan and Nițu 2013); Iași County, Stânca near Comarna, 47°4'11.874"N, 27°48'13.403"E, 7.vii.2017, 1 ♂, at light, CMI.

Banat, Caraș-Severin County, Svatá Helena (Sfânta Elena) env., Kulhavá skála hill env., 44°42'11.47"N, 21°43'41.49"E, 357 m a.s.l., 1.vi.2012, 1 elytron on a path going through a pasture, BJN; Caraș-Severin County, Svatá Helena (Sfânta Elena), 44°40'29.8"N, 21°42'35"E, 325 m a.s.l., 18.vi.2017, 1 ♀ FSLG after sunset, ZCP, 44°40'57.73"N, 21°42'19"E, 350 m a.s.l., 23.vi.2017, 4 spec. FSLG after sunset, ZCP obs. (1 ♂ leg. et coll.); Caraș-Severin County, Mehadia, undated [19th century], 1 ♀, "ex. coll. [Otto] Staudinger", coll. MTDG; Mehedinți County, Tisové Údolí (Eibenthal), ca. 44°32'36.7"N, 22°10'20.4"E, ca. 420 m a.s.l., 28.v.2008, 1 ♂ flying slowly up to 0.5 m above a path crossing a forest-steppe meadow at 21.45 EEST (= 40 min after sunset), JKV.

Muntenia, "Bukarest" [= Bucharest], undated, 1 ♂, V[ladimír] Zoufal leg., coll. Vladimír Zoufal deposited in MMBC; Teleorman County, Poroschia, [ca. 40 m a.s.l.], no other data, 1 ♀ in coll. GANM; Buzău County, Măgura, Mănăstirea Ciolanu [= Ciolanu Monastery], 5.vii.2014, 1 ♂, at light (160 W mercury-vapor lamp), beech forest, VUB.

Dobruja (Dobrogea), Tulcea County, Agighiol, 12.vi.1993, 1 ♀, Ioana Matache leg., coll. GANM; Tulcea County, Babadag [env.], [100–200 m a.s.l.], 20.vi.1958, 1 ♂, 20.vi.1968, 1 ♂, Nicolae Săvulescu leg., coll. GANM; 11.vii.1985, 1 ♂, at light (mercury-vapor lamp), foot of a forest-steppe loess hill, JHM leg., coll. VKS (for partial data on this record see Hillert et al. 2016); 16.v.2014, 2 ♀♀, Juhász leg., coll. GML; Tulcea County, Mănăstirea Codru [= Codru Monastery] env. (ca. 8 km S of Babadag), 44°48'55.47"N, 28°41'23.15"E, 110 m a.s.l., 6.vi.2016, 1 spec., IIB, 44°49'04.0"N, 28°40'57.9"E, 140 m a.s.l., 10.vi.2016, ca. 30 spec. FSLG after sunset, MVP obs. (1 ♂ leg., coll. NMPC); Constanța County, Băneasa – Canaraua Fetei, ca. 44°3'13.28"N, 27°40'15.07"E, ca. 115 m a.s.l., 17.vii.1965, 1 ♂, Nicolae Săvulescu leg., coll. GANM; Constanța County, Albești env., Hagieni Forest, ca. 50 m a.s.l.,

20.vi.1964, 1 ♀, collector unknown, coll. GANM; Constanța County, Hagieni, ca. 50 m a.s.l., 18.vi.1995, 1 ♀, at light, CWP leg., coll. LKKA.

Comment

For Romania, which can be considered one of the countries at the centre of the species' distribution, surprisingly small amounts of data have been published. New records from 22 Romanian localities are presented here.

Moldova

Published data

Călărași District (Raionul Călărași), Bularda near Dereneu, ca. 165 m a.s.l., 16.vi.1931, 3 ♂♂ and 4 ♀♀, Nicolai Zubowsky leg., coll. N. Zubowsky deposited in NMCM (Derjanschi et al. 2016; sex of the specimens specified by Valeriu Derjanschi pers. comm., 2021).

Ialoveni District (Raionul Ialoveni), Dănceni, ca. 170 m a.s.l., 31.v.1929, 1 ♂, Nicolai Zubowsky leg., coll. N. Zubowsky deposited in NMCM (Derjanschi et al. 2016; sex of the specimen specified by Valeriu Derjanschi pers. comm., 2021).

City of Chișinău (Municipiul Chișinău), Chișinău, [ca. 100 m a.s.l.], 20.v. and 10.vii.[between 1900–1915], no other data (Miller and Zubowsky 1917); 11.vii.1911, 1 ♀, Nicolai Zubowsky leg., coll. N. Zubowsky deposited in NMCM (Derjanschi et al. 2016; sex of the specimen specified by Valeriu Derjanschi pers. comm., 2021).

Material examined

City of Chișinău (Municipiul Chișinău), Chișinău, 20.iv.1912, 1 ♀, Nicolai Zubowsky leg., Valeriu Derjanschi det., coll. Rodion Stepanov (box No. 10) deposited in NMCM.

Anenii Noi District (Raionul Anenii Noi), Hîrbovăț env., Hîrbovăț Forest, ca. 285 m a.s.l., June 1970, 1 ♂, Rodion Stepanov leg., Valeriu Derjanschi det., coll. R. Stepanov (box No. 28) deposited in IZCM (for incomplete data on this record see Neculiseanu et al. 2002).

Comment

The first known record from Moldova (Chișinău) is mentioned by Miller and Zubowsky (1917). Old records from another two localities are reported by Derjanschi et al. (2016). The occurrence of the species in Moldova without further details is also mentioned by Panin (1957). This study presents the latest known Moldovan record from 1970.

Ukraine

Published data

"Gubernia podolska" [= Podolian Governorate (Подольская губерния) of the Russian Empire, now Ukraine] (Hildt 1892).

"Volhynien" [= Volhynian Governorate (Волынская губерния), a historical region of the Russian Empire that included almost the entire area of today's Volyn Oblast, as well as the Rivne and Zhytomyr Oblasts, northern parts of the Ternopil and Khmelnytskyi Oblasts, parts of the Podlaskie and Lublin Voivodeships of Poland and Brest Region of Belarus], undated, 2 spec., prof. Bresser leg. (Hochhuth 1873; Tenenbaum 1923; Savchenko 1931) – this record probably refers to data from Kremenets (Ternopil Oblast) reported by Eichwald (1830) – see below.

? Ivano-Frankivsk Oblast (Івано-Франківська область), Chornohora (Чорногора) [mountain range], 9.viii.1939, 1 ♂, collector unknown, coll. SIZK (Vasko 2010) – the nature of the area (high mountains) does not correspond to the known requirements of the species and its occurrence here is unlikely; it is therefore probably a mislabelled specimen.

Ternopil Oblast (Тернопільська область), Ternopil Raion (Тернопільський район), Zboriv (Зборів), 19.viii.1937, 1 ♀; collector unknown, coll. SIZK (Vasko 2010); Ternopil Raion (Тернопільський район), Ternopil (Тернопіль) env., "Gaje Tarnopolskie" [= Velyki Hai (Великі Гаї)], 26.vii.1884–1890, 1 spec., on a path, Michael Rybiński leg. et coll. (Rybiński 1897, 1903); Ternopil Raion (Тернопільський район), Ternopil (Тернопіль), no other data (Łomnicki 1913; Tenenbaum 1923; Savchenko 1938; Horion 1958); Ternopil Raion (Тернопільський район), "Zbaraż" [= Zbarazh (Збараж)] env., "Hnilice" [= Hnylytsi (Гнилиці)], no other data (Kuntze and Noskiewicz 1938); Kremenets Raion (Кременецький район), "Volhynia, Cremenezum" [= Kremenets (Кременець)] env., no other data (Eichwald 1830; Savchenko 1938).

Chernivtsi Oblast (Чернівецька область), Bukovina (Буковина), Chernivtsi Raion (Чернівецький район), Chernivtsi (Чернівці), 4 spec. with no other data (Horion 1958), 2 ♂♂ and 3 ♀♀ with no oher data, coll. K. A. Penecke deposited in ZMNU (Vasko 2010), 1 ♀ in coll. NMPC (Hillert et al. 2016).

Vinnytsia Oblast (Вінницька область), Vinnytsia Raion (Вінницький район), Vinnytsia (Вінниця) env., August 1928, 1 ♂, caught in flight in the evening, collector unknown (Savchenko 1933, 1938); Vinnytsia Raion (Вінницький район), Vinnytsia (Вінниця) env., Sabariv meadows (Сабарівські луки), no other data, 1 ♂ in coll. Yevhen Mykolaiovych Savchenko deposited in NHMU (Vasko 2010); Vinnytsia Raion (Вінницький район), Lypovets (Липовець), 24.vi.1926, 1 ♂, collector unknown, coll. Ye. M. Savchenko deposited in NHMU (Savchenko 1934, 1938; Vasko 2010); Vinnytsia Raion (Вінницький район), "Lintsi (Лінці)" [= Illintsi (Іллінці)], [ca. 215 m a.s.l.], 10.v.1905, 1 ♂ and 1 ♀, collector unknown (Savchenko 1934,

1938), 14.vi. and 19.vi. (year not specified), no other data (Savchenko 1938); Haisyn Raion (Гайсинський район), Trostianets-Podilskyi (Тростянець-Подільський) [= Trostianets (Тростянець)] env., "Zatishje" [= village of Obodivka (Ободівка)], 15.vii.1930, 1 ♀, caught in flight in the evening, V. Paliy leg., coll. Ye. M. Savchenko deposited in NHMU (Savchenko 1933, 1938; Vasko 2010).

Odessa Oblast (Одеська область), Odessa Raion (Одеський район), Odessa (Одеса), 1827–1831, no other data (Krynicki 1832; Savchenko 1938; Trach and Gontarenko 2005), Odessa Raion (Одеський район), Odessa (Одеса) env., [1825–1860], 1 ♂, undated, [prof. I. B.] Bertoldi [leg.], "coll. University of Novorossiysk" (Kulikovskiy 1897; for information on Bertoldi's collection see Sevastianov 2000, 2001), "2 spec. in coll. Gugel [or Hugel/Hügel]" (Kulikovskiy 1897); Odessa (Одеса) env., Bilhorod-Dnistrovskyi Raion (Білгород-Дністровський район), Sadove (Садове) env., Lymanskyi (Лиманський) nature reserve, ca. 46°15'19.9"N, 30°11'2.9", ca. 50 m a.s.l., 8.vi.2004, 2 ♀♀, at UV light, HDO (Gontarenko and Trach 2011; data specified by YSK pers. comm., 2021); Rozdilna Raion (Роздільнянський район), 4 km NW of Butsynivka (Буцинівка) village, 4.vi.2011, 1 ♀, at UV light, YKO leg., coll. VTO (Gontarenko and Trach 2011; sex specified by YSK pers. comm., 2021).

Kyiv Oblast (Київська область), Kiyv (Київ), old town, May 1839, 4 spec. under a dead dog, June 1870, 1 spec. on a grassy path, Johann Heinrich Hochhuth leg. (Hochhuth 1873); Kyiv (Київ) env., no other data (Cherkunov 1889); Kyiv (Київ), undated, 1 spec., prof. Jelski leg., coll. of deceased J. Wańkowicz (Hildt 1896); Kyiv (Київ), Shevchenkivskyi Raion (Шевченківський район), Nyvky Park (Парк "Нивки"), 2.viii.1998, 1 ♂, dead on the ground, BVK leg., coll. SIZK (Vasko 2010); Kyiv (Київ), Holosiivskyi Raion (Голосіївський район), Holosiyiv Forest (Голосіївський ліс) [currently Holosiivskyi National Nature Park (Національний природний парк «Голосіївський»)], near the building of Astronomical Observatory of the National Academy of Sciences of Ukraine, 6.vi.1923, 1 ♀, Ye. M. Savchenko leg., coll. Ye. M. Savchenko deposited in NHMU (Savchenko 1934, 1938; Vasko 2010); Kyiv (Київ), Holosiivskyi Raion (Голосіївський район), Holosiyiv Forest (Голосіївський ліс) [currently Holosiivskyi National Nature Park (Національний природний парк «Голосіївський»), 10.vii.1928, 1 ♀, Ye. M. Savchenko leg., coll. Ye. M. Savchenko deposited in NHMU (Savchenko 1934, 1938; Vasko 2010); Kyiv (Київ), Holosiivskyi Raion (Голосіївський район), Holosiivskyi National Nature Park (Національний природний парк «Голосіївський»), no other data (Solomakha et al. 2020); Kyiv (Київ), Holosiivskyi Raion (Голосіївський район), Lysa Hora (Лиса гора), 20.vi.1998, 1 ♀, pitfall trap, H. Uspenskyi leg., coll. BVK; 19.vi.2007, 1 ♀, pitfall trap, RHK leg., coll. SIZK (Vasko 2010; data specified by RHK pers. comm., 2021); Obukhiv Raion (Обухівський район), Hryhorivka (Григорівка), 6.vi.1928, 1 ♂, collector unknown, coll. Ye. M. Savchenko deposited in NHMU (Savchenko 1938; Vasko, 2010); Obukhiv Raion (Обухівський район), Rzhyshchiv (Ржищів) env., area of the Ecological Research Centre "Hluboki Balyky (Глибокі балики)", 49°57'44"N, 31°7'8"E, 5.–6.viii.2020, 1 spec., at light, VKK (Sheshurak et al 2020a); Bila

Tserkva Raion Raion (Білоцерківський район), village of Luka (Лука), undated [probably between 1925–1939, Bohdan M. Vasko pers. comm., 2020], 1 ♀, Jenni leg., coll. Ye. M. Savchenko deposited in NHMU (Vasko 2010).

Cherkasy Oblast (Черкаська область), Zvenyhorodka Raion (Звенигородський район), Talne (Тальне), 1 ♂ with no other data (Savchenko 1934, 1938); Cherkasy Raion (Черкаський район), Kaniv (Канів), hornbeam forest, 8.vi.1951, 1 ♀, collector not specified, coll. SIZK (Vasko, 2010); Cherkasy Raion (Черкаський район), Kaniv (Канів) env., Kaniv Nature Reserve (Канівський природний заповідник), no other data (Solomakha et al. 2020).

Chernihiv Oblast (Чернігівська область), Novhorod-Siverskyi Raion (Новгород-Сіверський район), Novhorod-Siverskyi (Новгород-Сіверський) env., 51°59'N, 33°16'E, 18.vii.2003, 1 spec., I. V. Porokhniach leg., coll. GUNU (Vovk et al. 2005, 2016; Sheshurak et al. 2018, 2020b).

Sumy Oblast (Сумська область), Shostka Raion (Шосткинський район), Matskove (Мацкове) env., ca. 51°28'48"N, 33°53'24"E, ca. 150 m a.s.l., 28.vii.2018, 1 spec., MZK (Kavurka et al. 2019).

Poltava Oblast (Полтавська область), Lubny Raion (Лубенський район), Lubny (Лубни), [ca. 160 m a.s.l.], July (year and nummber of specimens not specified), Kruhlik [leg.], coll. Provincial Museum of Poltava (Ohloblin 1913; Savchenko 1938).

Dnipropetrovsk Oblast (Дніпропетровська область), Synelnykove Raion (Синельниківський район), Raivka (Раївка), 1.viii.2000, 1 spec., A. M. Sumarokov leg. (Martynov 2003); Novomoskovsk Raion (Новомосковський район), Andriivka (Андріївка), 6.viii.1986, 1 spec., at light, A. M. Sumarokov leg. (Martynov 2003; Vasko and Bryhadyrenko 2011); Dnipro Raion (Дніпровський район), Dnipro (Дніпро) [Dnipropetrovsk until 19 May 2016], "около Днепропетровского Гослесхоза" [= near the Dnipropetrovsk State Forestry Enterprise, = Tunelna Balka (Тунельна балка) tract] (Vasko 2010; Vasko and Bryhadyrenko 2011; for detailed data see Material examined and new observations below); Dnipro Raion (Дніпровський район), Dnipro (Дніпро) [Dnipropetrovsk until 19 May 2016], 16.vi.2010, 1 ♀, collector not specified (Miessen 2011), 18.vi.2010, 1 ♀, Dementiev leg. (Brustel and Gouix 2012); Pavlohrad Raion (Павлоградський район), Kocherezhky (Кочережки) env., 21st century, no other data (Vasko and Bryhadyrenko 2011).

Material examined and new observations

Zakarpattia Oblast (Закарпатська область), Mukachevo Raion (Мукачівський район), "Schönb Ungarn" [= Hungary, Schenborn (Шенборн)], [ca. 190 m a.s.l.], "coll. Kirsch", undated, 1 ♂, coll. MTDG.

Ivano-Frankivsk Oblast (Івано-Франківська область), Kosiv Raion (Косівський район), Pistyn (Пістинь), [ca. 400 m a.s.l.], undated, 1 ♂, "A. St?kl" [the third letter is illegible] leg., coll. SMLU.

Ternopil Oblast (Тернопільська область), Chortkiv Raion (Чортківський район), "Torskie, pow[iat] Zaleszcz[yki]" [= Zalishchyky (Заліщики) Powiat,

Torske (Торське)], [ca. 250 m a.s.l.], 27.vi.[19]33, 1 ♂, collector unknown, coll. MIZP; Dniester Canyon National Nature Park (Національний природний парк «Дністровський каньйон»), Chortkiv Raion (Чортківський район), Horodok (Городок), 48°38'18.96"N, 25°50'11.04"E, ca. 140 m a.s.l., 6.vii.2018, 6 ♂♂ and 2 ♀♀ FSLG after sunset, steppe meadow on the terrace of the Dniester (Дністер) river, YKL, YHS and ABZ leg. coll. YKL and YHS (for photographs of the site see Fig. 13C, D).

Chernivtsi Oblast (Чернівецька область), Bukovina (Буковина), Chernivtsi Raion (Чернівецький район), "Czernowitz" [= Chernivtsi (Чернівці)], no other data, 1 ♂ in coll. Georg Frey deposited in NHMB, 1 ♂ and 2 ♀♀ (ex original coll. Josef Breit, Vienna) in coll. Georg Frey deposited in NHMB, 2 ♂♂ and 3 ♀♀ in coll. ZMNU, 1 ♂ and 2 ♀♀ in coll. UMJG.

Vinnytsia Oblast (Вінницька область), "Киевская г[уберния], Сквирский у[езд]" [= Kiev Governorate of the Russian Empire (disestablished 1925), Skvirsky Uyezd (incorrectly, it was actually Lipovetsky Uyezd), currently Vinnytsia Raion (Вінницький район)], "Ильинцы" [= Illintsi (Іллінці)], 14.vi.[year not specified], [ca. 215 m a.s.l.], 1 ♀, collector not specified, coll. ZINR (probably one of the two specimens mentioned by Savchenko (1938) – see published data).

Odessa Oblast (Одеська область), Bilhorod-Dnistrovskyi Raion (Білгород-Дністровський район), Karolino-Buhaz (Кароліно-Бугаз), Studentska (Студентська) railway station, ca. 46°9'56.34"N, 30°33'24.58"E, 22 m a.s.l., 15.vi.2017, 1 ♂ crawling on the ground, OKO.

Kyiv Oblast (Київська область), Bila Tserkva Raion (Білоцерківський район), "Hałajki, Kijow[ska] g[ubernia]" [= Kiev Governorate, Halaiky (Галайки)], [ca. 190 m a.s.l.], [probably 19th Century], no other data, 1 ♂ in coll. MIZP; Bucha Raion (Бучанський район), Muzychi (Музичі), ca. 160 m a.s.l., 18.vii.2006, 1 ♂, at light, M. Nesterov leg., coll. SIZK; "Kiew" [= Kyiv (Київ)], undated, 1 ♀ in Hartmann [leg.], coll. NMPC; "Kieff" [= Kyiv (Київ)], May [19]05, 1 ♂, Shelushko [leg.], coll. ZINR; Fastiv Raion (Фастівський район), Novosilky (Новосілки), ca. 180 m a.s.l., 21.vii.2012, 1 ♀, M. Nesterov leg., coll. SIZK; Obukhiv Raion (Обухівський район), Mali Dmytrovychi (Малі Дмитровичі), 50°12'59"N, 30°32'29"E, ca. 160 m a.s.l., 17.vii.2010, 1 ♂, at light, together with 1 ♂ of *Od. armiger*, VSK leg., coll. KLP; 29.v.2014, 1 ♂ and 1 ♀, at light, RHK; 25.v.2016, 1 ♂, 28.v.2016, 1 ♀, 13.vi.2020, 1 ♂ and 2 ♀♀, at light, STK; Obukhiv Raion (Обухівський район), Rzhyshchiv (Ржищів), Taras Shevchenko Park (Парк імені Тараса Шевченка), 49°57'58.1"N, 31°02'39.5"E, 112 m a.s.l., 18.ix.2021, 1 ♀ crawling on the ground at 16:22 EEST, HTR obs. + photo (DJP det.); Obukhiv Raion (Обухівський район), Rzhyshchiv (Ржищів) env., area of the Ecological Research Centre "Hlyboki Balyky (Глибокі балики)", 49°57'44.082"N, 31°7'8.094"E, ca. 150 m a.s.l., 18.vi.2021, 1 ♀, at light OVK obs. + photo + recorded an audio track of its stridulation (DJP det.); 49°57'43.729"N, 31°7'9.782"E, 19.vi.2021, 1 ♂, together with 1 ♂ and 2 ♀♀ of *Od. armiger*, OVK obs. + photo (DJP det.); Myronivka Raion (Миронівський район), Tulyntsi (Тулинці), ca. 150 m a.s.l., 9.vi.2020, 1 ♀, at

light, STK; Myronivka Raion (Миронівський район), Velykyi Bukryn (Великий Букрин) env., 49°57'13"N, 31°18'8"E, 155 m a.s.l., 27.vi.2009, 1 ♀, at light, VSK.

Cherkasy Oblast (Черкаська область), Cherkasy Raion (Черкаський район), Kaniv (Канів) env., Kaniv Nature Reserve (Канівський природний заповідник), 49°43'12"N, 31°31'19"E, ca. 200 m a.s.l., 20.vi.1984, 6 spec. excavated from their burrows, steppe slope in a hornbeam forest, KVM and VGG leg., coll. MKY and MPGU.

Kirovohrad Oblast (Кіровоградська область), Oleksandriia Raion (Олександрійський район), Semyhiria (Семигір'я) env., 49°0'29.52"N, 32°54'21.24"E, 135 m a.s.l., 2.vii.2020, 1 ♂, at light, DPS obs. + photo (Fig. 14D).

Dnipropetrovsk Oblast (Дніпропетровська область), Dnipro Raion (Дніпровський район), Dnipro (Дніпро) [Dnipropetrovsk until 19 May 2016], Tunelna Balka tract (Тунельна балка) [the name of an area with oak forest in the southern part of the city, see Fig. 15], 48°25'11.8"N, 35°02'59.8"E, 15.vii.2005, 1 ♂ and 1 ♀ excavated from their burrows near the edge of a forest path under oak tree, OSD leg., coll. OSD and SIZK; 16.vi.2006, 3 ♂♂ and 4 ♀♀ excavated from their burrows, OSD leg., coll.SIZK; 16.vii.2006, 1 ♂ and 1 ♀ excavated from their burrows, OSD; 26.vii.2006, 1 ♂ excavated from its burrow near the edge of a forest path under oak tree, OSD; 20.–25.vii.2007, 1 ♂, OSD leg., coll. SIZK; 16.–17.vi.2008, 4 ♂♂ and 5 ♀♀ excavated from their burrows + at light, OSD leg., coll. SIZK; 18.vi.2008, 1 ♀, at light, OSD leg., coll. SIZK; 1.–10.vii.2008, 3 ♂♂ and 8 ♀♀ excavated from their burrows + at light, OSD leg., coll. SIZK (for partial data on these records see Vasko 2010); 3.vi.2013, 1 ♂ and 1 ♀ excavated from their burrows, OSD leg., coll. GML; 48°25'10.7"N, 35°02'54.5"E, June 2009, 3 ♀ excavated from its burrow near the edge of a forest path under oak tree, OSD leg., coll. OSD and GML; 16.vi.2010, 1 ♀, 8.vi.2010, 1 ♂, 18.vi.2010, 1 ♂ and 1 ♀, at light, OSD leg., coll. SIZK; 48°25'02.8"N, 35°02'26.6"E, 5.vii.2014, 1 ♂, at light, OSD leg., coll. SIZK; 8.–15.vi.2014, 13 spec. excavated from their burrows near the edge of a forest path under oak trees, OSD (1 ♀ in coll. DJP); 48°25'04.8"N, 35°02'40.6"E, 6.vi.2015, 1 ♂ excavated from its burrow under oak tree, OSD leg., coll. DJP; 16.vii.2015, 1 ♂, OSD leg., coll. NHMK; 48°25'12.8"N, 35°03'00.7"E, 8.vi.2010, 1 ♂ in flight, OSD; 18.vi.2010, 1 ♂ and 1 ♀, at light, OSD; 11.vi.2015, 1 ♀, at light at 21.40 EEST (= 61 min after sunset), OSD leg., coll. DKP deposited in NMPC; 48°24'57.3"N, 35°02'33.1"E, 1.vii.2015, 1 ♂ and 1 ♀ excavated from their burrows under oak tree (distance between these two burrows was 40 cm), OSD leg., coll. DJP; 48°25'00.0"N, 35°02'22.4"E, 7.vii.2015, 1 ♂, dead on a forest path, OSD leg., coll. DJP; 48°25'01.1"N, 35°02'23.6"E, 7.vii.2015, 1 ♀ excavated from its burrow under oak tree, OSD leg., coll. DJP; 48°24'57.1"N, 35°02'13.0"E, 9.–12.vii.2015, 1 ♂ and 1 ♀, pitfall traps, OSD leg., coll. DJP and DKP (deposited in NMPC); 48°25'02.1"N, 35°02'22.6"E, 8.vi.2016, 4 ♂♂ and 3 ♀♀ excavated from their burrows under oak trees, OSD leg., coll. DJP and GML; 48°25'0.70"N, 35° 2'22.30"E, 106 m a.s.l., 10.vi.2016, more spec. excavated from their burrows, OSD leg., 5 ♂♂ and 2 ♀♀ in coll. ASK, 1 ♂ and 2 ♀♀ in coll. VSM, 1 ♀ in coll. YSK; 48°24'55.9"N, 35°02'34.7"E, 16.–17.vi.2016, 2 ♂♂ excavated from their burrows under oak trees, together with 2 ♂♂ of *Od. armiger*, OSD leg., coll. DJP;

48°24'55.50"N, 35°2'33.20"E, 111 m a.s.l., 13.–25.vi.2020, 9 ♂♂ and 4 ♀♀, OSD leg., coll. ASK; 48°24'57.6"N, 35°02'29.4"E, 100 m a.s.l., 14.vii.2021, 1 ♂ excavated from its burrow, OSD leg., coll. DJP; 48°24'57.4"N, 35°02'30.7"E, 100 m a.s.l., 14.vii.2021, 2 ♂♂ excavated from its burrow, OSD leg., coll. DJP and GML; Dnipro Raion (Дніпровський район), "Opytnoye" ("Опытное") [= Doslidne (Дослідне)], research area of the Institute of Grain Crops of NAAS of Ukraine (Інститут зернових культур НААН України), 48°22'58.2"N, 35°02'01.7"E, 143 m a.s.l., June 1978, remains of a dead specimen (elytra) on the ground near the greenhouse, OSD leg. et coll. (for partial data on this record see Vasko 2010; Vasko and Bryhadyrenko 2011).

Figure 15. Tunelna Balka tract (Ukraine), locality with abundant occurrence of *B. unicornis* **A–D** views of the site (photographs by Oleksandr O. Sukhenko) **E, F** burrows dug by adults of *B. unicornis* with push-ups (photographs by Oleksandr O. Sukhenko).

Comment

In the checklist of Ukraine (Martynov 2012), the species is listed from 12 of the 25 oblasts. The critical revision performed in the present study confirms occurrence in eleven of them with two additional ones: Sumy and Kirovohrad oblasts. Records from the Right Bank Ukraine are summarised by Vasko (2010). In the present study, new records from 15 Ukrainian localities are given, two of them (Schenborn and Semyhiria) being the first published records for the Zakarpattia and Kirovohrad oblasts, respectively.

Bulgaria

Published data

Vratsa Province (Област Враца), Oryahovo (Оряхово), no other data (Kovachev 1905).

Ruse Province (Област Русе), Vetovo (Ветово), no other data (Kovachev 1905).

Razgrad Province (Област Разград), Razgrad (Разград) env., 16.v.1905, in the barracks area, number of specimens not specified, Andrey Markovich leg, 13.vi.1907, in the vineyards, number of specimens not specified, Andrey Markovich leg. (Markovich 1909; Guéorguiev and Bunalski 2004).

Pleven Province (Област Плевен), Pleven (Плевен), April [year and collector not specified] (Nedyalkov 1909; Mikšić 1959; Guéorguiev and Bunalski 2004).

Sofia Province (Софийска област), Gorna Malina (Горна Малина) – "ДЗС" [= Държавно земеделско стопанство, area of the State Farm], ca. 650 m a.s.l., 7.vii.1969, 2 ♂♂ and 1 ♀ excavated from the soil from a depth of ca. 10 cm on a pasture (northern slope), collector not specified (Zaharieva-Stoilova 1974); Lozen Mountain (Лозенска планина), 5 km SE of German (Герман), "Germanski m." [= German Monastery of St John of Rila ("Св. Иван Рилски")], 31.v.[1]915, 1 ♂, Dr Iw[an Jossifow] Buresch [leg.], coll. NMSB (Guéorguiev and Bunalski 2004; data supplemented by Borislav Guéorguiev pers. comm., 2022; sex of the specimen corrected by the photograph).

Shumen Province (Област Шумен), Shumen (Шумен), ca. 200 m a.s.l., 1914, 2 ♂♂, Hanuš leg., coll. MYP (Král and Malý 1993).

Burgas Province (Област Бургас), "Michurin (Мичурин)" [= Tsarevo (Царево)], 29.–30.vi.1982, 1 ♂, at light., BSP (Král and Malý 1993).

Silistra Province (Област Силистра), Dulovo (Дулово) env., Karakuz forest (гора Каракуз) [note: the locality label states "Gora Kanagöl, Dulowsko"], 14.vi.1952, 1 ♀, P[encho Stefanov] Drenski leg., coll. NMSB (Guéorguiev and Bunalski 2004; data specified by Borislav Guéorguiev, 2022).

Material examined ans new observations

Vidin Province (Област Видин), Dimovo (Димово) env., steppe meadow near the Archar (Арчар) river, 43°45'28.7"N, 22°44'51.1"E, 110 m a.s.l., 26.vi.2010, 3 ♂♂

and 2 ♀♀ FSLG after sunset just before a storm, together with several spec. of *Och. chrysomeloides*, no wind, 26 °C, ASH (Fig. 10C, D).

Varna Province (Област Варна), Oreshak (Орешак) env., 43°17'50.67"N, 27°53'47.29"E, 300 m a.s.l., 6.vii.2020, 1 ♀ flying up to 0.5 m above the grass at ca. 22.00 EEST, forest-steppe clearing in an oak forest, MTM obs. + photo (Fig. 10E, F).

Comment

So far, only nine localities have been published for Bulgaria. This study presents new records from two additional sites.

Turkey (European part)

Published data

Marmara Region (Marmara Bölgesi), Edirne Province, ca. 15 km E of Edirne [according to Walter Heinz, pers. comm., these were periodically flooded meadows on the banks of the Ebros River S of Edirne], 27.iii.[19]88, 1 ♀, WHS leg., coll. DKP deposited in NMPC (Hillert et al. 2016).

Turkey (Asian part)

Published data

Aegean Region (Ege Bölgesi), Denizli Province, Denizli env., [Çürüksu River valley], "Goundely" [= Goncalı] [railway station env.], ca. 200 m a.s.l., May [19]26, 1 ♂, [Hans] Kulzer leg., coll. ZSMG (Hillert et al. 2016; locality identified by the author, year corrected by Oliver Hillert pers. comm., 2021) – see Fig. 16A.

Material examined

Aegean Region (Ege Bölgesi), Aydın Province, [Büyük Menderes River valley], "Bereketli (Denizli)" [= Bereketli near Nazilli], ca. 80 m a.s.l., 5.vii.1965, 1 ♂, [Helio] Pierotti and [Antonello] Perissinotto leg., DJP det. (2021), coll. Helio Pierotti deposited in MSNG – this record was published under a misidentification as *Bolbelasmus tauricus* Petrovitz, 1973 (Arnone and Massa 2010) – see Fig. 16B.

Comment

Only the three records mentioned above are known for Turkey. A record from Osmaniye Province (Kadirli) reported by Lodos et al. (1999) most likely refers to the related species *Bolbelasmus nireus* (Reitter, 1895) (see Miessen 2011; Hillert et al. 2016; Sommer et al. 2021).

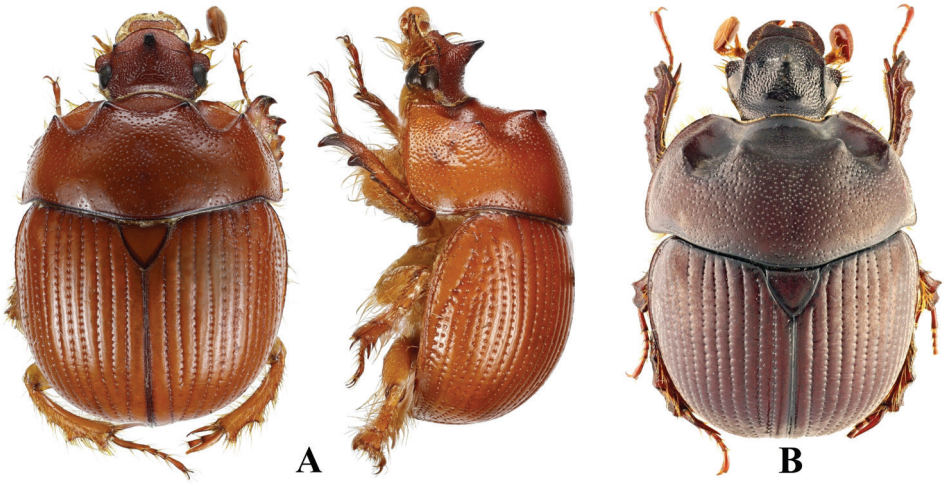


Figure 16. The only two specimens of *B. unicornis* so far known from Asia **A** Turkey, Denizli env., [Çürüksu River valley], "Goundely" [= Goncalı] [railway station env.], May [19]26, [Hans] Kulzer leg., coll. ZSMG, dorsal and lateral views, body length 12.0 mm (photographs by Michael Balke) **B** Turkey, [Büyük Menderes River valley], "Bereketli (Denizli)" [= Bereketli near Nazilli], 5.vii.1965, [Helio] Pierotti & [Antonello] Perissinotto leg., coll. MSNG, body length 12.5 mm (photograph by Marcello Romano).

Dubious faunistic records

Great Britain

Published data

East of England, Cambridgeshire, marshes between Peterborough and Wisbech, beginning of summer 1807, 1 ♂ and 1 ♀, plant materials alluviated by flooded River Nene, together with 2 ♂♂ and 3 ♀♀ of *Od. armiger*, William Skrimshire leg. (Skrimshire 1812; Curtis 1829a, b; Stephens 1829, 1830, 1839).

Comment

Skrimshire's record was probably adopted by several subsequent authors (e.g., Mulsant and Rey 1871; Sajó 1910b; Boucomont 1912; Paulian 1941; Tesař 1957; Neculiseanu et al. 2002; Trnka 2009; Vasko 2009; Arnone and Massa 2010; Vasko and Bryhadyrenko 2011; Vidlička 2011). According to Darren Mann (pers. comm. 2021), it is based on a misidentified *Od. armiger*, with no material from the British Isles. Also, Paulian and Baraud (1982) considered the report from England to be erroneous without giving any explanation. *Bolbelasmus unicornis* was no longer listed for Great Britain by the following authors: Fowler (1890), Joy (1932), Britton (1956), Jessop (1986), Mann (2012), and Lane and Mann (2016). Even in both editions of the Catalogue of

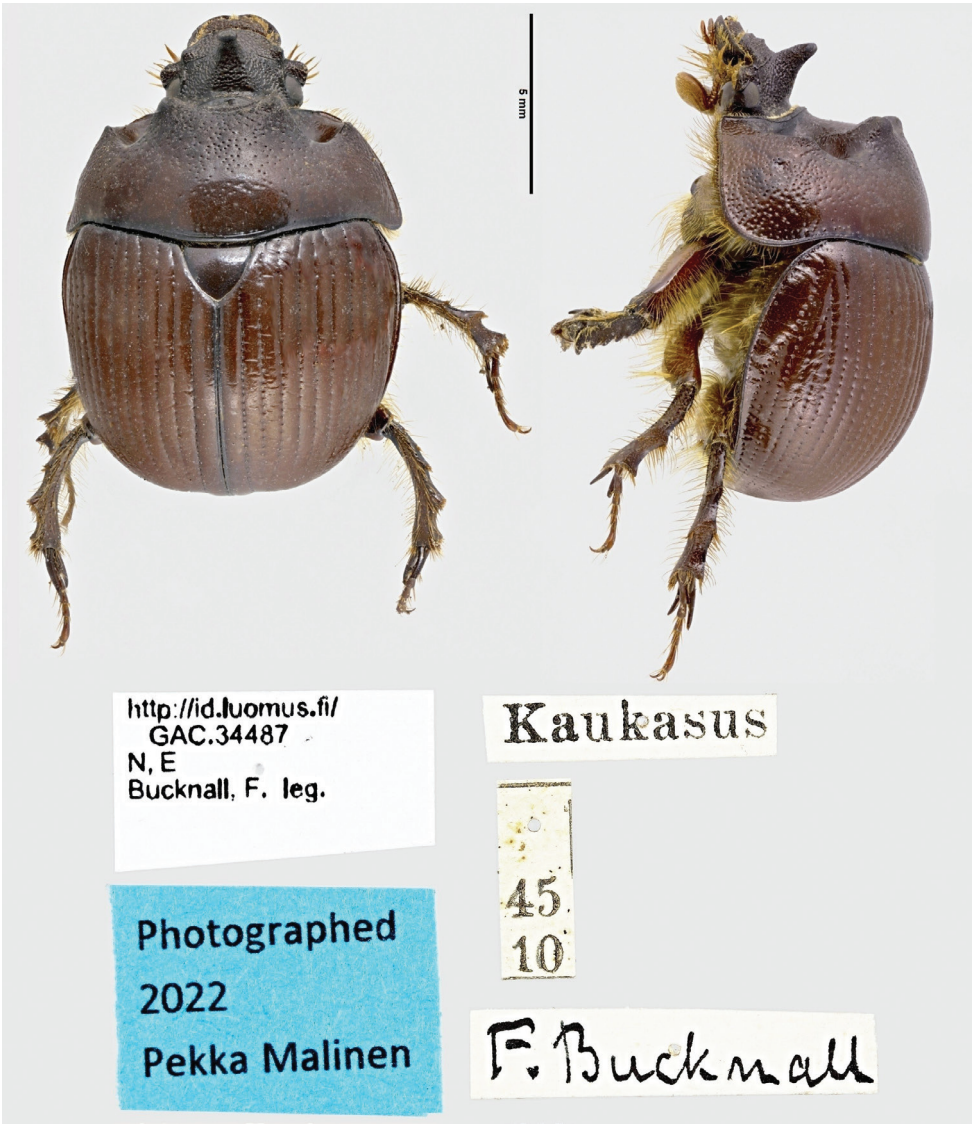


Figure 17. The only specimen of *B. unicornis* that could originate from the Caucasus region, deposited in FMNH (photographs by Pekka Malinen, edited by Peter Kurina).

Palaearctic Coleoptera (Král et al. 2006; Nikolajev et al. 2016), the United Kingdom is not listed as a country of occurrence of this species.

Country not specified [probably Russia]

Material examined

"Kaukasus" [= Caucasus], locality and date not specified, 1 ♂, F. Bucknall [leg.], coll. FMNH (Fig. 17).

Comment

This specimen represents the first record of the species from the Caucasus region. Unfortunately, country is not specified (it could be Russian part of the area, but confusion of the locality label cannot be discounted). Shokhin (2007) did not record the species from Southern Russia.

Remarks on distribution

Bolbelasmus unicornis was included in checklists, catalogues, and monographs dealing with the scarabaeoid fauna of several countries as follows: France (Montreuil 2014), Germany (Köhler and Klausnitzer 1998; Bleich et al. 2022), Italy (Ballerio et al. 2014; Carpaneto et al. 2021), Poland (Burakowski et al. 1983), Czech Republic and Slovakia (Juřena and Týr 2008; Zahradník 2017), Austria (Jäch et al. 1994), Hungary (Ádám 1994), Slovenia (Brelih et al. 2010), Bosnia and Herzegovina (Lelo 2006), former Yugoslavia (Mikšić 1970), Albania (Murraj 1962), Romania (Chimişliu 2004), Republic of Moldova (Bacal et al. 2013), Ukraine (Martynov 2012), Bulgaria (Bunalski 2001), and Turkey (Carpaneto et al. 2000). Also, it was mentioned in two editions of the Catalogue of Palearctic Coleoptera (Král et al. 2006; Nikolajev et al. 2016). For the general distribution of the species see Fig. 18.

No records are known from mainland Greece. Records from the Greek island of Crete (Heyden 1884; Oertzen 1886; Mikšić 1959; Neculiseanu et al. 2002; Trnka 2009) refer to species later described as *Bolbelasmus keithi* Miessen and Trichas 2011 (see Miessen and Trichas 2011; Hillert et al. 2016), and the records from Rhodes (Schatzmayr 1936; Paulian 1941, 1959; Tesař 1957; Mikšić 1959; Petrovitz 1959; Paulian and Baraud 1982; Petersen et al. 2006) most likely relate to *B. nireus* (see Sommer et al. 2021). The record from Greece reported by Reitter (1892) probably refers to Crete, and thus to *B. keithi*. Also, all subsequent records from Greece (Paulian 1941, 1959; Krikken 1977; Lumaret 1990; Neculiseanu et al. 2002; Szwałko 2004; Agoglitta et al. 2006; Král 2006; Král et al. 2006; Vasko 2009; Vasko and Bryhadyrenko 2011; Vidlička 2011; Brustel and Gouix 2012; Alonso-Zarazaga et al. 2013; Gutowski and Przewoźny 2013; Trizzino et al. 2013; Potocký and Majzlan 2015; Nikolajev et al. 2016; Ćurčić et al. 2019; Schoolmeesters 2019; Nuß and Jäger 2020) most likely refer to the Greek islands and thus to *B. keithi* or *B. nireus*.

Records from Cyprus (Keith 2002; Král 2006; Alonso-Zarazaga et al. 2013; Potocký and Majzlan 2015; Schoolmeesters 2019; Nuß and Jäger 2020) refer to species described as *Bolbelasmus makrisi* Miessen, 2011 (see Miessen 2011; Hillert et al. 2016; Sommer et al. 2021).

All the records from the Soviet Union and Russia (e.g., Medvedev 1965; Baraud 1992; Agoglitta et al. 2006; Král et al. 2006; Brelih et al. 2010; Brustel and Gouix 2012; Ballerio et al. 2014; Merkl 2014; Hillert et al 2016; Ćurčić et al. 2019; Schoolmeesters 2019) apply to Ukraine (Andrey V. Frolov and Liliya A. Akhmetova pers. comm.,

2020). In the second edition of the Catalogue of Palaearctic Coleoptera (Nikolajev et al. 2016), Russia is no longer listed as a country of occurrence of this species.

The species has also been listed for Belarus, Montenegro, and the Republic of North Macedonia (Chobot and Mourek 2008; Alonso-Zarazaga et al. 2013; Potocký and Majzlan 2015; Nuß and Jäger 2020), but there are no exact data from these countries, although its occurrence at least in Montenegro and North Macedonia is highly probable. Other countries where the species is highly likely to occur are Kosovo, mainland Greece (especially Macedonia and Thrace), and western Russia (e.g., Bryansk, Kursk, Belgorod and Rostov oblasts, and Krasnodar Krai). Occurrence in southern Belarus cannot be ruled out either. The species is most likely extinct in France, Switzerland, Poland, and the Czech Republic (considering the lack of suitable habitats and any new records).

Figure 18 probably does not reflect the real distribution of *B. unicornis* because of insufficient surveys in some countries. In countries such as Serbia, Romania, Moldova, Ukraine, and Bulgaria, there are probably many localities with *B. unicornis* that have not yet been discovered due to low collecting activity and the lack of application of effective collecting methods for this beetle species (see Monitoring methods below).

The northernmost known historical locality of *B. unicornis* is Warsaw (Poland), while the northernmost locality with a recent record is Novhorod Siverskyi (northern

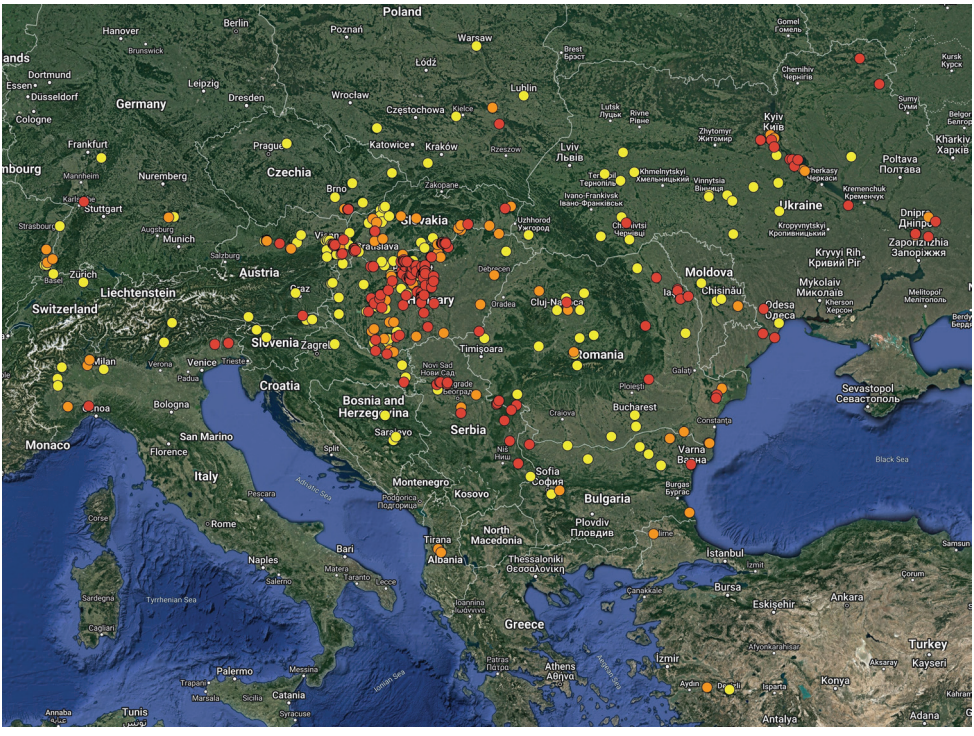


Figure 18. Distribution of B. unicornis (yellow circles – records before 1950, orange circles – records between 1950–1999, red circles – records after 1999).

Ukraine). The southernmost historical locality is Denizli (southwestern Turkey), while the southernmost recent localities are Babin Kal (Serbia) and Oreshak (Bulgaria). The westernmost historical locality is Mulhouse (Alsace, France), while the westernmost recent localities are Bruchsal (Baden, Germany) and Lerma (Piedmont, Italy). The easternmost locality with a recent record of the species is Kocherezhky (Ukraine), which is also the easternmost known point of occurrence of the species.

Natural history of Bolboceratinae

Evening flights of *B. unicornis*

Adults of *B. unicornis* spend most of their time underground. Above-ground activity is limited to short flight periods after sunset. Exceptionally, adults have been observed crawling on the ground during daylight hours (see Faunistic records). Flight statistics from each site are shown in Tables 1–8. A total of 63 periods of flights was documented at eight localities. The flights occurred in the date range from 27 May to 9 September with a total of 884 flying individuals observed. Both males and females flew, with slightly fewer females (ca. 44%). By comparison, in the congener *B. gallicus*, only 5% of the 830 individuals found were females (Rahola Fabra 2004) but in that study, these were mostly beetles excavated from their burrows. The flights of adults of *B. unicornis* started, on average, 35 minutes after sunset and terminated 60 minutes after sunset. For the start of flights, the minimum limit recorded was 23 minutes after sunset, and the maximum limit was 52 minutes after sunset. For the end of flights, the minimum and maximum limits were 35 and 86 minutes after sunset, respectively. On one occasion, a large number of specimens were observed flying around midnight (Josef Pavlas pers. obs., see Faunistic records). The average duration of flights was of 25 minutes, with the minimum and maximum limits of 4 and 63 minutes, respectively. The average air temperature during flights was 21 °C with limits of 14 and 26 °C. However, it is likely that the beetles are able to fly at lower temperatures, as has been observed, for example, in the Australian bolboceratine *Blackburnium insigne* (Lea, 1916), adults of which have been found flying to lights at 4–6 °C (Howden et al. 2007). Flights of *B. unicornis* occurred exclusively after heavy rains when the soil was moist to a depth of at least ca. 30 cm. The flights were also affected by the wind intensity. Most of the flying adults were observed when there was no wind, whereas flights did not occur at all when the wind was strong. Light rain or heavy fog had no effect on the flying beetles, and, in one case, the beetles were found flying even with moderate rain (Filip Štrba pers. comm.). Similarly, flights of adults of *Odonteus armiger* were observed during rain (Ivo Jeniš and Ilja Trojan pers. comm.). Adults of *B. unicornis* usually fly very slowly at a height of 20–50 cm above the ground, sometimes literally hovering in the same spot. However, in windy conditions they have been observed to fly faster and also at greater heights, ca. 1–2 m above the ground. Individuals flying quickly around a pile of logs at the edge of a forest were observed by the author near the village of Hajnáčka

Table 1. Data on flights of adults of *B. unicornis* at the locality of PP Panský diel. Key: BF = beginning of flights, EF = end of flights, S = sunset, S-BF = time period from sunset to the beginning of flights, S-EF = time period from sunset to the end of flights, DF = duration of flights, T = air temperature during flights.

Slovakia, Bratislava – Podunajské Biskupice, Kopáč Island, PP Panský diel									
date	***n*** **(♂/♀)**	**BF**	**EF**	**S**	**S-BF**	**S-EF**	**DF**	**T**	**note**
7.vi.2016	11 (6/5)	21.25	21.45	20.47	38 min	58 min	20 min	14 °C	heavy dew, no wind
8.vi.2016	4 (4/-)	21.27	21.43	20.48	39 min	55 min	16 min	16 °C	dew, no wind
18.vi.2016	6 (3/3)	21.33	21.53	20.54	39 min	59 min	20 min	19 °C	dew, no wind
21.vi.2016	5 (3/2)	21.31	22.03	20.54	37 min	69 min	32 min	21 °C	no wind
22.vi.2016	6 (2/4)	21.21	21.57	20.55	26 min	62 min	36 min	22 °C	no wind
23.vi.2016	11 (6/5)	21.33	21.53	20.55	38 min	58 min	20 min	23 °C	no wind
24.vi.2016	24 (10/14)	21.36	22.08	20.55	41 min	73 min	32 min	25 °C	no wind
25.vi.2016	7 (2/5)	21.28	22.08	20.55	33 min	68 min	32 min	26 °C	no wind
26.vi.2016	25 (13/12)	21.31	22.09	20.55	36 min	74 min	38 min	20 °C	light breeze
27.vi.2016	10 (2/8)	21.31	21.57	20.55	36 min	62 min	26 min	20 °C	gentle breeze
28.vi.2016	9 (2/7)	21.28	21.48	20.55	33 min	53 min	20 min	19 °C	light breeze
29.vi.2016	14 (8/6)	21.29	22.03	20.55	34 min	68 min	34 min	24 °C	light dew, no wind
21.vii.2016	36 (25/11)	21.09	21.51	20.41	28 min	70 min	42 min	24 °C	no wind
22.vii.2016	51 (28/23)	21.08	21.51	20.40	28 min	71 min	43 min	23 °C	ground mist, no wind
23.vii.2016	41 (26/15)	21.09	21.53	20.39	30 min	74 min	44 min	24 °C	light ground fog, no wind
24.vii.2016	68 (38/30)	21.08	21.49	20.38	30 min	71 min	41 min	23 °C	dew, no wind
25.vii.2016	15 (14/1)	21.06	21.41	20.37	29 min	64 min	35 min	22 °C	light rain, no wind
29.vii.2016	13 (10/3)	21.02	21.30	20.32	30 min	58 min	28 min	22 °C	light dew, no wind
30.vii.2016	37 (16/21)	20.53	21.56	20.30	23 min	86 min	63 min	24 °C	light dew, no wind
7.viii.2016	29 (16/13)	20.46	21.16	20.19	27 min	57 min	30 min	17 °C	no wind
8.viii.2016	46 (26/20)	20.45	21.25	20.17	28 min	68 min	40 min	16 °C	no wind
13.viii.2016	51 (32/19)	20.40	21.01	20.09	31 min	52 min	21 min	19 °C	no wind
n **(♂/♀)**	**519 (292/227)**		**average**		**32 min**	**65 min**	**32 min**	**21 °C**	

Table 2. Data on flights of adults of *B. unicornis* at the locality of PR Ostrovné lúčky (for abbreviations see Table 1).

Slovakia, Bratislava – Čunovo, PR Ostrovné lúčky									
date	***n*** **(♂/♀)**	**BF**	**EF**	**S**	**S-BF**	**S-EF**	**DF**	**T**	**note**
25.vii.2016	10 (6/4)	21.10	21.37	20.37	33 min	60 min	27 min	24 °C	before rain, no wind
29.vii.2016	3 (2/1)	21.11	21.25	20.31	42 min	56 min	14 min	22 °C	no wind
n	**13 (8/5)**		**average**		**38 min**	**58 min**	**21 min**	**23 °C**	

Table 3. Data on flights of adults of *B. unicornis* at the locality of Kalinkovská lesostep (for abbreviations see Table 1).

Slovakia, Kalinkovo, Kalinkovská lesostep									
date	***n*** **(♂/♀)**	**BF**	**EF**	**S**	**S-BF**	**S-EF**	**DF**	**T**	**note**
27.vii.2016	3 (1/2)	21.04	21.15	20.34	30 min	41 min	11 min	22 °C	no wind

in southern Slovakia (see Faunistic records). This phenomenon was also observed in *Od. armiger* (Ilja Trojan and Ivo Jeniš pers. comm.): adults of this species were flying around the fallen oak trunk and piles of wet logs after sunset. When disturbed, the flying specimens of *B. unicornis* either immediately fell into the grass and buried themselves or accelerated their flight, increasing the height from the ground and flying

Table 4. Data on flights of adults of *B. unicornis* at the locality of Čierná hora hill (for abbreviations see Table 1).

Slovakia, Kamenica nad Hronom env., Čierna hora hill									
date	***n*** **(♂/♀)**	**BF**	**EF**	**S**	**S-BF**	**S-EF**	**DF**	**T**	**note**
6.vi.2010	5 (4/1)	21.30	21.45	20.38	52 min	67 min	15 min	-	after the floods
7.vi.2010	16 (10/6)	21.23	21.55	20.39	44 min	76 min	32 min	-	-
4.viii.2011	17	20.50	21.20	20.18	32 min	62 min	30 min	18 °C	after ca. 10 days of persistent rainfall, ca. 2 hours after the rain has ceased, vegetation heavily soaked, no wind
5.viii.2011	10	20.50	21.10	20.16	34 min	54 min	20 min	20 °C	almost no wind
6.viii.2011	8	20.40	21.00	20.15	25 min	45 min	20 min	23 °C	almost no wind
9.viii.2011	15	20.45	21.05	20.10	35 min	55 min	20 min	17 °C	almost no wind
11.viii.2011	14	20.40	21.05	20.07	33 min	58 min	25 min	18 °C	almost no wind
12.viii.2011	9	20.40	21.05	20.05	35 min	60 min	25 min	18 °C	almost no wind
13.viii.2011	16	20.30	21.05	20.03	27 min	62 min	35 min	19 °C	almost no wind
16.viii.2011	2 (1/1)	20.35	21.05	19.58	37 min	67 min	30 min	22 °C	dry, almost no wind
7.vi.2013	22 (13/9)	21.20	21.45	20.39	41 min	66 min	25 min	18 °C	almost no wind
8.vi.2013	15 (10/5)	21.17	21.42	20.40	37 min	62 min	25 min	20 °C	light air to light breeze
12.vi.2013	15	21.20	21.35	20.43	37 min	52 min	15 min	18 °C	soil heavily saturated with water after rain, soaked vegetation
15.vi.2013	10	21.20	21.45	20.44	36 min	61 min	25 min	-	-
3.ix.2014	8 (5/3)	19.52	20.07	19.24	28 min	43 min	15 min	20 °C	light air to gentle breeze
4.ix.2014	13 (8/5)	19.51	20.16	19.22	29 min	54 min	25 min	22 °C	almost no wind
5.ix.2014	4 (2/2)	19.47	20.04	19.20	27 min	44 min	17 min	23 °C	almost no wind
9.ix.2014	2 (2/-)	19.43	19.47	19.12	31 min	35 min	4 min	22 °C	almost no wind
5.vi.2015	2 (2/-)	21.22	21.27	20.38	44 min	49 min	5 min	22 °C	almost no wind
6.vi.2015	3 (2/1)	21.24	21.47	20.39	46 min	68 min	27 min	23 °C	light air
28.v.2016	6	21.05	21.10	20.31	34 min	39 min	5 min	-	-
1.vi.2016	≈ 8	21.15	21.45	20.35	40 min	70 min	30 min	24 °C	no wind, very wet after rain
2.vi.2016	≈ 8	21.15	21.45	20.36	39 min	69 min	30 min	24 °C	no wind, very wet after rain
3.vi.2016	≈ 8	21.15	21.45	20.37	38 min	68 min	30 min	24 °C	no wind, very wet after rain
11.vi.2016	5	21.20	21.40	20.43	37 min	57 min	20 min	-	-
n	**241**	**average**			**36 min**	**58 min**	**22 min**	**21 °C**	

Table 5. Data on flights of adults of *B. unicornis* at the locality of Hajnáčka – Buková (for abbreviations see Table 1).

Slovakia, Hajnáčka – Buková									
date	***n*** **(♂/♀)**	**BF**	**EF**	**S**	**S-BF**	**S-EF**	**DF**	**T**	**note**
27.v.2008	5 (-/5)	21.10	21.35	20.26	44 min	69 min	25 min	22 °C	first or second warm day after a colder period of persistent rainfall; no wind
29.v.2008	4 (1/3)	21.10	21.40	20.29	41 min	71 min	30 min	21 °C	newly hatched, light-coloured ♂ (not included in these statistics) crawling on a t-shirt spread on the ground at the edge of the forest under an oak tree (*Quercus cerris*) at 19.55 CEST; during flights, no wind to light air
4.vii.2009	7 (3/4)	21.15	21.45	20.43	32 min	62 min	30 min	22 °C	-
5.vii.2009	3 (1/2)	21.15	21.30	20.43	32 min	47 min	15 min	20 °C	-
28.v.2010	4 (1/3)	21.10	21.25	20.26	44 min	59 min	15 min	-	♂ flying fast and high (ca 1.5–1.8 m above the ground) around a pile of logs near the edge of the forest
n **(♂/♀)**	**23 (6/17)**	**average**			**39 min**	**62 min**	**23 min**	**21 °C**	

away. This also applies to disturbances caused by too strong light source, e.g., from a headlamp. During flights, most beetles show light-aversion and avoid light sources; the individuals that were attracted to light were single cases only. These were mostly

Table 6. Data on flights of adults of *B. unicornis* at the locality of Gemerský Jablonec (for abbreviations see Table 1).

Slovakia, Gemerský Jablonec									
date	***n*** **(♂/♀)**	**BF**	**EF**	**S**	**S-BF**	**S-EF**	**DF**	**T**	**note**
4.vii.2009	4 (1/3)	21.30	21.50	20.43	47 min	67 min	20 min	-	-
5.vii.2009	4 (3/1)	21.30	21.50	20.43	47 min	67 min	20 min	-	-
28.v.2010	4 (1/3)	21.00	21.15	20.26	34 min	49 min	15 min	-	-
n **(♂/♀)**	**12 (5/7)**		**average**		**32 min**	**65 min**	**32 min**		

Table 7. Data on flights of adults of *B. unicornis* at the locality of Hostice – Katarínka (for abbreviations see Table 1).

Slovakia, Hostice – Katarínka									
date	***n*** **(♂/♀)**	**BF**	**EF**	**S**	**S-BF**	**S-EF**	**DF**	**T**	**note**
6.vi.2010	2 (-/2)	21.15	21.30	20.35	40 min	55 min	15 min	-	-

Table 8. Data on flights of adults of *B. unicornis* at the locality of Tekija (for abbreviations see Table 1).

Serbia, Tekija env.									
date	***n***	**BF**	**EF**	**S**	**S-BF**	**S-EF**	**DF**	**T**	**note**
27.v.2014	27	20.35	21.00	20.03	32 min	57 min	25 min	24 °C	after a period of persistent rainfall
28.v.2014	24	20.35	21.00	20.03	32 min	57 min	25 min	24 °C	dtto
12.vii.2014	9	20.45	21.15	20.16	29 min	59 min	30 min	19 °C	ca 5 hours after the rain; no wind
13.vii.2014	11	20.43	21.14	20.15	28 min	59 min	31 min	22 °C	full moon, clear skies, light breeze, storm in the distance
n	**71**		**average**		**30 min**	**58 min**	**28 min**	**22 °C**	

Table 9. Data on flights of adults of *B. unicornis* at the locality of Cordenons env. (for abbreviations see Table 1).

Italy, Cordenons env. (Glerean and Stefani 2019)									
date	***n*** **(♂/♀)**	**BF**	**EF**	**S**	**S-BF**	**S-EF**	**DF**	**T**	**note**
9.ix.2018	2 (1/1)	20.10	20.30	19.35	35 min	55 min	20 min	21.5 °C	humidity 81%
16.v.2019	3 (2/1)	21.00	21.15	20.34	26 min	41 min	15 min	17 °C	male crawling on the ground at 21.20 CEST
24.v.2019	5 (5/-)	21.20	21.35	20.43	37 min	52 min	15 min	20 °C	humidity 70%
6.vi.2019	3 (2/1)	21.00	21.20	20.55	5 min	25 min	20 min	22 °C	humidity 70%
n **(♂/♀)**	**13 (10/3)**		**average**		**26 min**	**43 min**	**18 min**	**20 °C**	

long-distance flights that occurred later in the night. Very rarely a few individuals did fly to the illuminated canvas just after sunset when it was not yet completely dark (Tamás Kiss, Ondřej Sabol, Tibor Spevár obs., see Faunistic records). In most Czech and Slovak localities, adults of *B. unicornis* were flying together with *Od. armiger* and *Och. chrysomeloides* or *O. integriceps* (see Faunistic records and Juřena et al. 2008). Apparently, these species almost always occur together at the sites (see also below).

Feeding and nesting behaviour of bolboceratines

More than 50 individuals of *B. unicornis* were excavated from their burrows from depths of 5–60 cm during daylight hours. The length and the shape of the burrows var-

ied, with the male burrows often changing direction from vertical to horizontal, whereas the female burrows usually descended vertically, changing direction only slightly and often leading to depths greater than those of males. In the dry periods and at the end of the season, the beetles burrow to the depths of more than 50 cm (e.g., Tomáš Vendl obs., see Faunistic records). When excavating adults, sometimes two to three individuals were found in a single burrow, even of the same sex (e.g., two males; see Faunistic records and Juřena et al. 2008). Similar observations were made, for example, by Mollandin de Boissy (1906) in the congeneric species *B. gallicus*, and by Robert J. Sim in some American *Odonteus* species (Wallis 1928). In contrast, Manee (1908) excavated ca. 100 specimens of the North American bolboceratine *Bradycinetulus ferrugineus* (Palisot de Beauvois, 1809) in North Carolina, but he never found specimens of the same sex in the same burrow. On several occasions, individuals of *B. unicornis*, *Od. armiger*, and *Och. chrysomeloides* (or *O. integriceps*) have been found together in a single burrow (see Faunistic records and Juřena et al. 2008). Similarly, Robert J. Sim found representatives of three different genera *Bolbocerosoma*, *Eucanthus*, and *Odonteus* together in a single burrow (see Wallis 1928).

As for the feeding habits of *B. unicornis*, in none of the observations made by the author was the burrow found to lead to the sporocarp of hypogeous fungus or to the mycorrhizal roots of a shrub or tree. Nothing that could be considered as their food was ever found close to the buried individuals. In contrast, the Hungarian researchers repeatedly excavated the beetles near Budapest from the immediate vicinity of sporocarps of the large-spored pea truffle *Glomus macrocarpum*, which were approximately the size of a fingernail, together with more specimens of *Od. armiger* (Bratek et al. 1992; Merkl 2003, 2014, 2015; Nádai 2006; Merkl and Vig 2009). In addition, according to Ottó Merkl (pers. comm.), an adult of *B. unicornis* was found on a sporocarp of *Tuber* sp. in the Baranya County in southwestern Hungary (see also Merkl 2014), and Ćurčić et al. (2019) reported that one specimen was excavated under a hazel shrub (*Corylus avellana*) together with sporocarps of *Tuber* sp. in the Belgrade District of Serbia. These findings support earlier hypotheses about the mycetophagy of the species (cf. e.g., Sajó 1910a, b; Ohaus 1929; Roubal 1936; Koch 1989). For *B. gallicus*, Rahola Fabra (2004) reported that the burrows of beetles often led to dead roots in various stages of decomposition, but never to the sporocarps of hypogeous fungi. This is in contrast to the observations by Fabre (1900, 1907, 1920), who found adults of *B. gallicus* on the sporocarps of *Hydnocystis arenaria* and *Tuber requienii*, and Béguin (1906), who reported finding adults on sporocarps of *Tuber aestivum*. According to Rahola Fabra (2004), even in 20 years of field observations, the natural food of *B. gallicus* could not be determined with certainty. That author reported that in captivity, adults ingested sporocarps of *Tuber melanosporum*, *Rhizopogon* sp. and *Peziza* sp., but he did not consider this as unequivocal evidence of obligate mycetophagy by the species. According to Rahola Fabra (2004), dissection studies showed that the gut of adults of *B. gallicus* contained unspecified organic matter in 60% of individuals captured in the wild. Sim (1930) found that adults of the American bolboceratine *Odonteus darlingtoni* (Wallis, 1928) stored a mass of sporocarps of ectomycorrhizal basidiomycete *Rhizopogon pachyphloes* in their burrows, and Howden (1955) reported adults of this species feeding on sporocarps of *Rh. nigre-*

scens. In the European species *Od. armiger*, Miquel and Vasko (2014) reported finding one adult feeding on a large sporocarp of *Rh. luteolus*, partially decayed, together with two individuals of *Anoplotrupes stercorosus* (Hartmann in Scriba, 1791), and another individual feeding on a sporocarp of *Glomus microcarpum*. Furthermore, these authors reported that near burrows dug by adults of *Od. armiger* kept in captivity, sporocarps of *Endogone lactiflua* were found. In contrast, adults of the genus *Eucanthus*, for example, probably do not ingest any food at all (Howden and Cooper 1977). According to Howden (2003), even adults of the genus *Bolbocerosoma* do not feed, but this is contradicted by new findings by Japanese researchers, who found that adults of *Bolbocerosoma nigroplagiatum* (C. O. Waterhouse, 1875) feed on sporocarps of arbuscular mycorrhizal fungi (Higurashi and Tanahashi 2014; Aratani 2017; Higurashi et al. 2019). Higurashi and Tanahashi (2014) reported that bits of sporocarps of *Glomus* sp. were carried to the surface of the soil by adults of *B. nigroplagiatum*, then moved to another place and subsequently drawn into burrows. Spores of these fungi were found in the intestines of dissected specimens. Bezborodov (2009) and Bezborodov and Koshkin (2014a, b) reported that adults of *Bolbocerosoma zonatum* (Nikolaev, 1973) were repeatedly found under dry horse and cow dung in the Far East of Russia, in cavities covered with white mould, thus suggesting that the adults are mycetophagous; no burrows were observed under the dung. In Australia, dissections of bolboceratines and analysis of their faeces were carried out mainly by Houston and Bougher (2010), who found that the intestines or excrement of adults of *Blackbolbus*, *Blackburnium*, *Bolboleaus* and *Bolborhachium* species contained large quantities of spores of various species of hypogeous fungi (e.g., of the genera *Amarrendia*, *Hysterangium*, and *Scleroderma*), as well as immature unidentified sporocarp tissue, unidentified ascomycetes, or glomeralean hyphae and spores with varying quantities of soil. These authors also reported that only six of 120 specimens of bolboceratines collected while in flight (i.e., those specimens taken at lights or from light traps), and only 34 of 114 bolboceratines collected from burrows had food in their intestines. It is likely that the beetles feed only intermittently and possibly spend protracted periods without a meal. In many cases, their burrows may serve to provide them only with shelter until their next foray. In several genera, Houston and Bougher (2010) found no food present in the gut, which they explained by suggesting that feeding for these beetles is likely episodic, governed by weather events, and timing may be the key to finding specimens feeding. In the case of *B. unicornis*, it was not possible to dissect the individuals to determine the intestinal contents due to its strict protection in all EU countries. In the burrows of some Australian species of the genera *Blackbolbus*, *Blackburnium*, *Bolborhachium*, and *Elephastomus*, pieces of sporocarps of *Scleroderma* sp., *Hysterangium* sp., and unspecified hypogeous fungi of the families Hymenogasteraceae and Clathraceae have been found, but with no eggs or larvae present in the vicinity (Howden et al. 2007; Houston and Bougher 2010). This suggests that these fungi were food for adults only. In burrows of both *B. gallicus* and Australian bolboceratines, adults of some species of round fungus beetles (Leiodidae) have been found on the sporocarps of hypogeous fungi (Béguin 1906; Howden et al. 2007). In the case of *B. gallicus*, this was *Leiodes cinnamomea* (Panzer, 1793). Houston

and Bougher (2010) reported that some *Scleroderma* sporocarps found in burrows of *Blackbolbus frontalis* (Guérin-Méneville, 1838) were inhabited by numerous nitidulid beetles identified as *Thalycrodes mixtum* Kirejtshuk & Lawrence, 1992, and two sporocarps identified as *Hysterangium* sp. found in soil close to a burrow of *Blackbolbus frontalis* were infested with nematodes. Mycetophagy of adults of the genus *Ochodaeus*, representatives of which were collected together with *B. unicornis*, was also recently confirmed (Huchet et al. 2022).

Immature stages have only been described in a few species of bolboceratines (Arens 1922; Ritcher 1947, 1966; Howden 1955, 1964; Verdú et al. 1998, 2004; Rahola Fabra 2004; Howden et al. 2007; Houston 2011, 2016). In *B. unicornis*, no immature stages are known, and consequently nothing is known about the larval diet. During the excavation of adults from their burrows, no immature stages were found, similar to the reported cases of excavations of North American bolboceratines (Manee 1908; Wallis 1928; Sim 1930). As for the European representatives of the genus *Bolbelasmus*, the larva has only been described in *B. brancoi* (as *B. bocchus*, Verdú et al. 1998), and *B. gallicus* (Verdú et al. 2004), but even in these species larval nutrition has not been elucidated. Eggs have been described and/or photographed in only a few species of bolboceratines (Arens 1922; Howden 1955; Rahola Fabra 2004; Howden et al. 2007; Houston 2011, 2016). They are surprisingly large compared to the size of the adults. For *B. gallicus*, Rahola Fabra (2004) reported egg dimensions to be 7.0–8.0 × 4.0 mm, but the egg photographed next to the female and scale was actually 7.0 × 4.6 mm, whereas the body length of the female was ca. 14 mm (calculated from the scale line). Howden et al. (2007) noted that two eggs of the Australian species *Bolborhachium anneae* Howden, 1985 measured 6.5 × 6.2 mm and 7.3 × 6.4 mm while two eggs of the slightly larger *B. recticorne* (Guérin-Méneville, 1838) measured 7.2 × 5.9 mm and 8.1 × 6.5 mm. The largest female of *B. anneae* measured 15.1 mm in length, while the largest female of *B. recticorne* measured 18.8 mm in length. According to Houston (2011), the eggs of another Australian bolboceratine *Blackburnium reichei* (Guérin-Méneville, 1838) weighed 45–56% as much as the females that laid them and measured 9.5–10.5 × 7.5–9.0 mm. On the other hand, the eggs of the North American bolboceratine *Odonteus darlingtoni* are not so large compared to the adults: they measure ca. 2.4 × 1.5 mm, whereas the adults are ca. 10 mm in length (Howden 1955). Similarly, for the European species *Od. armiger*, Arens (1922) reported the length of the egg to be 2.5 mm (body length of adults is usually 6–10 mm). Rahola Fabra (2004) reported that the females of *B. gallicus* have two ovaries, each composed of six ovarioles, as in other representatives of the family Geotrupidae (cf. Ritcher and Baker 1974), with only one ovariole functioning at any time, in alternating cycles (cf. Willimzik 1930). The fecundity of females of *B. gallicus* is very low (probably one to four eggs in a lifetime), nevertheless, according to Rahola Fabra (2004), populations are relatively stable; he stated that the female of *B. gallicus* fixes its giant egg to the ceiling of a small egg-shaped brood cell using soil mixed with its own excreta. All the cells found by Rahola Fabra were empty, which means that they did not contain anything that could provide food for the future larvae. Similarly, Arens (1922) reported that the brood cells with eggs of

Od. armiger contained no provision, but in a few cases he found pieces of unspecified fungi or humus in the burrows. Also, Miquel and Vasko (2014) found 16 empty brood cells of *Od. armiger*. The fact that the brood cells did not contain any material collected by females differs from what Howden (1955) observed in another species of the subfamily Bolboceratinae, where females lined their brood cells with material brought in from outside (surface humus, dried dung) that could be a food for the larva. In two species of the genus *Bolborhachium* the brood cells were filled with fine black humus, perhaps mixed with fungi (Howden 1985; Howden et al. 2007). In contrast, according to Houston (2016), the brood cells of some Western Australian bolboceratines, such as *Bolborhachium recticorne* and some congeners, were formed from darker surface soil, but no food was found. Eggs and larvae of these species collected in the field were reared in their original cells and in artificial cells made in soil. Of three instars, the first contained the already developed second instar and did not feed. Second and third instars nibbled at the walls of their cells as if feeding, grew in size, and increased their weight 2.5–3.0 times. However, they turned over little soil, ingested little solid material, and rarely passed faeces, so ingestion and digestion of 'humus' (finely divided plant detritus) is unlikely to account for all (if any) of their weight gain. As the contents of the larval intestine were hygroscopic, perhaps larvae ingest salts and/or humic and fulvic acids that enable them to absorb water (Houston 2016). This author also suggested that the soil bacteria may be a source of nutrition for the larvae. This is also consistent with Houston's finding of two newly emerged adults of *Blackburnium reichei* in closed, earthen cells at depths of 60 and 72 cm, with no traces of faecal material or uneaten provision being observed in or near these cells (Houston 2011). The hypothesis that larvae of Australian bolboceratines do not ingest solid food is supported by the description of their morphology. Houston (2011) reported that compared with free-living scarabaeoid larvae (e.g., Melolonthinae, Dynastinae, Trogidae) where the head and mandibles are strongly sclerotised and the legs well developed with strong tarsal claws, the larvae of all known bolboceratines are degenerate. According to Houston (2011), the larva of *Blackbolbus hoplocephalus* (Lea, 1916) provides the most extreme example of degeneration known to date. Its immobility and vestigial appendages (particularly its simple, feeble mandibles) suggested it was a non-feeding, resting stage. Importantly, though, the mandibles of the second instar (judging from its exuvia) were equally feeble and consistent with a no-feeding hypothesis (Houston 2011). Houston went on to point out another feature of the larvae of known bolboceratines: the relatively slender abdomen which contrasts with the swollen abdomen of many other Scarabaeoidea, suggesting at least a different feeding biology and possibly hinting at a reduction or even absence of feeding. The very simple form of the larval intestine found by Houston (2011) in *Blackburnium reichei* when compared with the intestines of larvae of other scarabaeids (e.g., Areekul 1957) and its emptiness are consistent with loss of feeding. Similarly, Higurashi and Tanahashi (2014) and Higurashi et al. (2019) recorded giant eggs, larvae, and pupae of *Bolbocerosoma nigroplagiatum* excavated from a depth of ca. 80 cm, with the larvae having poorly developed appendages (mandibles and legs). Howden (1955) reported that larvae of the North American bolboceratines *Odonteus*

darlingtoni, *O. liebecki* (Wallis, 1928), and *Bolbocerosoma farctum* (Fabricius, 1775) feed on humus, carefully sifting it from a provision of humus-rich sand filling the lower ends of burrows. This is consistent with earlier observations by Robert J. Sim, who assumed that females of *Odonteus simi* (Wallis, 1928) lay their eggs in humus formed into an elongated mass at the lower ends of the burrows (Wallis 1928).

Since we have virtually no knowledge of the diet of adults or larvae of *B. unicornis*, we can only speculate on what its diet consists of. Given the findings of Australian and Japanese researchers on related species, the likely food of adults appears to be hypogeous fungi (spores, hyphae, and sporocarps), while the food of larvae could be fine soil humus and/or soil bacteria. The previous hypothesis that the larvae of *B. unicornis* feed on sporocarps of hypogeous fungi (e.g., Bartenev et al. 1997; Nádai 2006; Juřena et al. 2008; Kaděra 2017; Németh 2015; Nuß and Jäger 2020) is not supported by observation and seems very unlikely considering the observations in other species of bolboceratines. The larval morphology of the genus *Bolbelasmus* is very similar to that of larvae of the genera *Bolbocerosoma* and *Bolborhachium* (Verdú et al. 1998, 2004), which suggests a similar way of life, including feeding habits.

Life cycles of bolboceratines

Life cycles have been documented for only a few bolboceratine species (Houston 2011, 2016). Houston (2016) found that for three Australian species (*Bolborhachium recticorne*, *Blackburnium reichei*, and *Bolboleaus hiaticollis* Howden, 1985), the period between discovery of an egg and hatching of the larva was 15–35 days. According to Houston, duration of the larval stage in *Bolborhachium recticorne* ranged from 63 to 95 days (n = 6) and for one *Blackburnium reichei* larva, it was 44 days. One larva of *Bolboleaus hiaticollis* pupated 81 days after being found while another (hatched from an egg) survived for at least 13 months before dying. Based on the Houston's data, development from egg to adult in *Bolborhachium recticorne* could require 129–159 days or more. As newly emerged adults remained in their natal cells for at least 30 days while their integuments harden and darken, total development time (egg to active adult) might require 6 months or more, according to Houston. Houston (2016) suggested the possibility that in *Bolboleaus hiaticollis*, mature larvae enter a dormant stage, thereby extending the development time even further. Houston (2011) recorded excavating a third larval instar of *Blackbolbus hoplocephalus* that remained dormant for 105 days before pupating.

Assuming that the development of *B. unicornis* is similar, it is very likely that only adults, both old and newly emerged, overwinter. This assumption is supported by numerous records where both old, dark-coloured individuals with heavily abraded teeth of fore tibiae and fresh, pale-coloured individuals with sharp protibial teeth have been recorded at the beginning of the season (pers. obs.). Some bolboceratines have overlapping generations. For example, in the genus *Odonteus*, eggs, larvae, pupae, and adults have been observed together in a single branching burrow (Jameson 2002; Staines and Staines 2020).

Seasonal dynamics of *B. unicornis*

In the Pannonian Basin, the centre of the distribution of *B. unicornis*, adults are active from May to September, exceptionally as early as April and as late as October, with a significant peak in June and the first half of July (Fig. 19). Very few data are available from the other parts of the distribution area. It appears that in the southernmost part of the range, adults may be active as early as March, which is supported, for example, by the record from East Thrace (see Hillert et al. 2016 and Faunistic records in this study). The seasonal dynamics of the species are always significantly influenced by precipitation changes during the year. It is likely that only the adults overwinter, as reported by Caillol (1913) for the congeneric species *B. gallicus* (see also Rahola Fabra 2004).

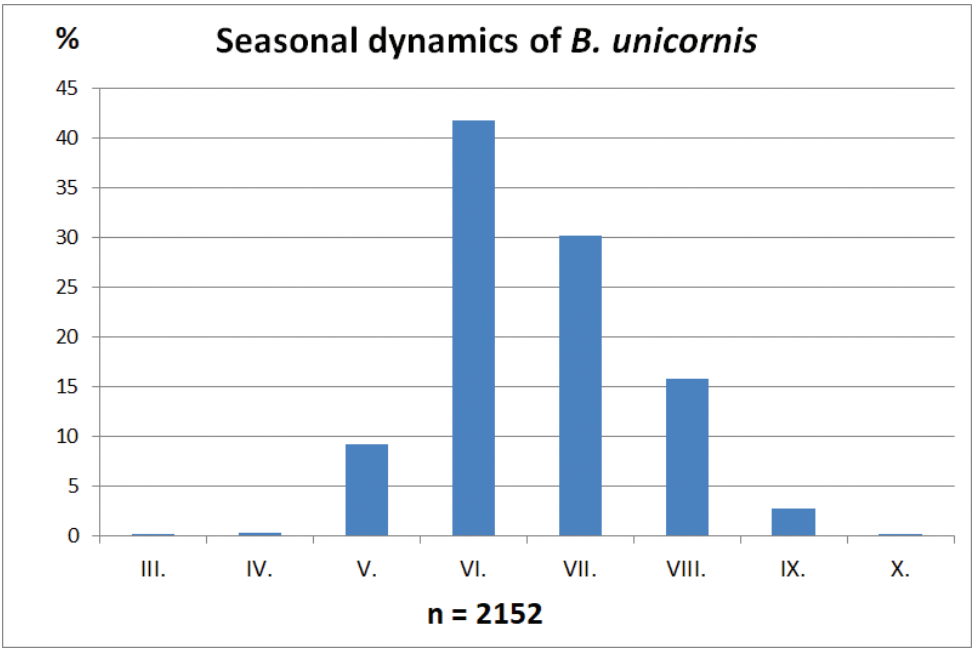


Figure 19. Seasonal dynamics of *B. unicornis* (the number of specimens from each country included in these statistics: Slovakia – 1392, Hungary – 350, Ukraine – 168, Serbia – 87, Romania – 79, Austria – 44, Czech Republic – 31).

Habitat preferences of *B. unicornis*

Bolbelasmus unicornis is a stenotopic species, characteristic of Pannonian steppes, forest-steppes and sparse deciduous forests, especially dominated by oaks. It is often found on sandy substrate (e.g., surroundings of Győr, Kiskunság National Park), sandy-loess substrate (e.g., localities around the village of Čejč), gravelly-sandy-loess substrate (e.g., Dunajské luhy Protected Landscape Area), loess substrate (e.g., wider surroundings

of Štúrovo, Cerová vrchovina Mts, Gödöllő Hills, Dniester Canyon National Nature Park) or limestone substrate (e.g., Slovak Karst, Aggtelek National Park, some localities around Budapest). Characteristic habitats are steppe or forest-steppe pastures at the edges of oak forests (e.g., Cerová vrchovina Mts, Slovak Karst), of oak-beech or beech forests (e.g., Slanské kopce hills, Đerdap National Park, some localities in Romania), oak-hornbeam or hornbeam forests (e.g., Pirot District of Serbia, Kaniv Nature Reserve in Ukraine), and of shrub zones (with e.g., *Crataegus oxyacantha*, *Prunus spinosa*, and *Rosa canina*). In the Kiskunság National Park it occurs in the Pannonic sand dune thicket (*Junipero-Populetum albae*) (Merkl 2014). Occurrences of *B. unicornis* in completely treeless habitats are known for the northern half of its range (Czech Republic, Slovakia, Hungary), while further south the species occurs in areas of more extensive forest cover (Serbia, Romania, Bulgaria). In eastern Ukraine (Dnipro City) the species occurs in sparse oak forest (Fig. 15). Also, the only known recent record from Croatia was made in forest (Koren 2017). Other typical habitats are remnants of the native steppe grasslands between vineyards, former steppe and forest-steppe pastures, remnants of steppe or forest-steppe in agricultural landscapes that have been preserved due to their inaccessibility to agricultural machinery (e.g., localities around Čejč and many sites in Hungary). In the case of hilly terrain, *B. unicornis* mainly prefers south- and southwest-facing slopes, and less frequently slopes inclined to the southeast or even to the north (e.g., Fruška Gora National Park – see Faunistic records in this study, and Gorna Malina – see Zaharieva-Stoilova 1974).

It seems that the fundamental requirement of the species is natural vegetation cover and soil undisturbed by agriculture. The same was noted by Sajó (1897), who stated that the species occurred in a dry oak forest on a hill near Kis-Szent-Miklós (currently Őrbottyán – Őrszentmiklós), but it disappeared as soon as the hill was converted to farmland. The species is probably also very sensitive to the use of chemicals in agriculture and forestry. It seems to be threatened by the overgrowth of invasive plant species such as *Robinia pseudoacacia* or *Ailanthus altissima* in steppe and forest-steppe habitats. Furthermore, the extensive removal of shrubs such as *Crataegus* sp., *Rosa canina*, *Corylus avellana*, and trees (e.g., *Quercus* spp., *Populus* spp., *Prunus spinosa*) and taller herbaceous plants, as well as too intensive sheep grazing seem to have negative effects on the presence of *B. unicornis* (cf. also Németh 2015). The largest known population of the species in Europe at the Panský diel site on Kopáč Island near Bratislava, Slovakia (Figs 4, 5) was severely decimated by the inappropriate conservation management of the site (pers. obs., cf. also Majzlan 2020).

Central European sites with substantial populations of *B. unicornis* are characterised by the occurrence of plant species such as *Quercus* spp., *Crataegus oxyacantha*, *Prunus spinosa*, *Rosa canina*, *Festuca* spp., *Thymus* spp., *Orobanche* spp., *Scabiosa ochroleuca*, *Euphorbia cyparissias*, *Achillea millefolium*, and *Artemisia* spp.

On describing the potential habitat of the related *B. gallicus* in southern France, Rahola Fabra (2004) lists the following plant species: *Quercus ilex*, *Q. coccifera*, *Q. pubescens*, *Olea europaea*, *Pinus halepensis*, *P. pinea*, *Juniperus oxycedrus*, *Buxus sempervirens*, *Cistus monspeliensis*, *C. albidus*, *Genista hispanica*, *Brachypodium retusum*, *Thymus vulgaris*, *Sedum* sp., *Coronilla glauca* and *Viburnum tinus*.

The Coleoptera that co-occur in Central European localities with *B. unicornis* include *Lethrus apterus* (Laxmann, 1770), *Odonteus armiger*, *Ochodaeus chrysomeloides*, *O. integriceps*, *Gymnopleurus* spp., *Carabus montivagus* Palliardi, 1825, *C. scabriusculus* Olivier, 1795, *Capnodis tenebrionis* (Linnaeus, 1761), *Perotis lugubris* (Fabricius, 1777), *Ptosima undecimmaculata* (Herbst, 1784), *Sphenoptera* spp., and *Agrilus albogularis* Gory, 1841 (observations by many collectors including the author).

The elevation of the sites where *B. unicornis* has been recorded varies between 20 and 800 m a.s.l. The average altitude of all known localities for which it could be at least approximately determined (n = 351) is 220 m a.s.l. It is therefore a species of lowland and lower hills.

Monitoring methods

The most effective method for monitoring this species is to capture adults during their flights after sunset with a net using a flashlight, preferably a headlamp, in suitable microhabitat. This collecting method was employed as early as the 1920s by Rudolf Čepelák (see Čepelák 1925). The effectiveness of this method is evidenced by the large number of specimens collected by him, which are still scattered in numerous collections of museums and private collectors (see Faunistic records). Typically, the flights of beetles occur in very limited areas, and the concentration of flying individuals can vary considerably from place to place. For example, more flying beetles can be observed above grassy trails with ruts made by agricultural machinery or above paths trodden by humans or animals. Flying beetles can also be detected by the hum of their wings similar to that of a flying European hornet (*Vespa crabro* Linnaeus, 1758), as reported by Čepelák (1925) and Roubal (1936). However, sometimes the beetles fly almost noiselessly (pers. obs.).

Alternatively, during the day, one may find the beetles in their burrows, which are indicated by small piles of excavated soil at the entrances (so called "push-ups"). These push-ups are similar to those of some large ground-nesting bees but the push-ups of the bees are conical, composed of uniformly loose soil about a central entrance, whereas the soil pushed up by the earth-borer beetles tends to form an irregular pile of lumps (Figs 5E, 8A–D, 15E, F). If the individual is present in the burrow, the entrance is often covered by a pile of excavated soil. An uncovered hole usually indicates that the beetle is no longer present. Similarly, if a push-up is weathered down, it is usually old and the beetle may no longer be present in the burrow. This method is less effective on grassy sites as the push-ups may be screened from view.

Light trapping appears to be ineffective to capture this species (cf. also Cséfalvay 2015), as the beetles show light-aversion during flights and avoid light sources. Only occasional specimens which may be long-distance flyers come to the light later in the night. On very rare occasions, a few individuals have been observed flying to the light (on an illuminated canvas) just after sunset. It is likely that the beetles respond differently to different light sources, something requiring further research.

Bolbelasmus unicornis is also difficult to find due to the fact that observable activity of adults (flights and digging underground tunnels with push-ups) occurs only after heavy rains, when the soil is damp and loose enough for the beetles to burrow easily. During the dry periods, when the soil is hard, and also in winter, the beetles are buried deeper in the ground and show no above-ground activity, making it very difficult to find them.

Excerpt from the diary of Rudolf Čepelák

Below is the translation of a passage on *B. unicornis* from the diary of the excellent Czech coleopterist Rudolf Čepelák (1886–1972; Fig. 20), the discoverer of an efficient method of collecting this beetle. This text was written in the second half of the 1960s (Svätopluk Čepelák pers. comm., 2021). Čepelák here supplemented and specified his previously published observations (Čepelák 1925) from sites north of Zlatovce near Trenčín, where he worked as a teacher in 1923–1939 (see Koleška 1979):

"Bolbelasmus unicornis Schrank

From 1.vi. to 15.vii. Zlatovce (Malá hora hill; Vinohrady), Ľutov (Pálenice hill), and certainly from Trenčín southwards everywhere on the south-eastern slopes.

The area of Malá hora is sparsely covered with grass, which reaches 40–50 cm in places. If it is a quiet evening (no wind), preferably without moonlight, at 9 pm they start flying about 20–30 cm above the ground. In my right hand I have a net with a handle about 10 cm long, not white but dark, and in my left hand a torch. I bend down and

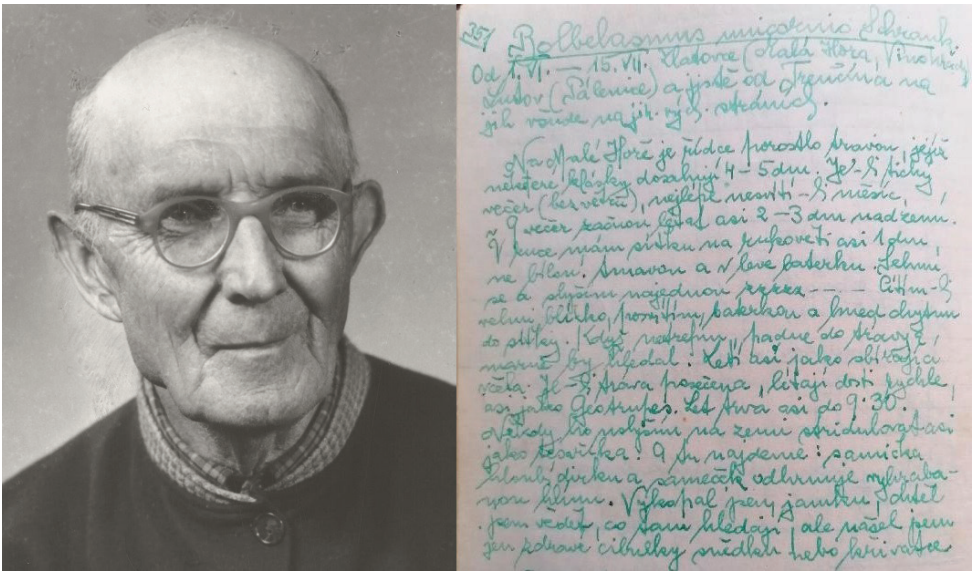


Figure 20. Rudolf Čepelák (born 16 April 1886 in Kutná Hora, Austria-Hungary, died 21 December 1972 in Český Brod, Czechoslovakia) and an excerpt from his diary with notes on collecting of *B. unicornis*.

suddenly hear 'zzzzz...'. If I feel it's very close, I shine the torch and immediately catch it with the net. If I miss, it falls into the grass, where I would look for it vainly. It flies like a bee collecting pollen. If the grass is cut, they fly quite fast, like Geotrupes. *The flights continue until ca. 9.30 pm. Sometimes I hear it on the ground, stridulating like a longhorn beetle. And then we see: the female digging a hole and the male removing away the excavated soil. I dug a hole to see what they were looking for, but all I found were healthy* Ornithogalum *or* Gagea *bulbs*."

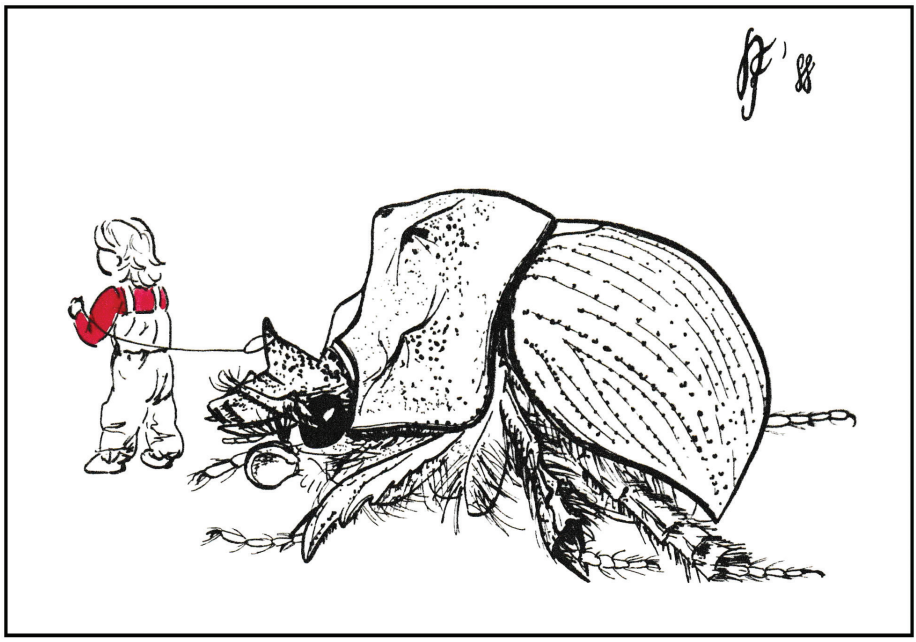


Figure 21. Drawing by Regina & David Král with the motif of *B. unicornis*, sent as PF 1988.

Acknowledgements

I would like to thank all the colleagues and staff at the institutions who provided me with their data and/or photographs (for a list of these see Materials and methods). For providing faunistic data, photographs, literature that was not easily available, and/or consultations, I thank in particular Aleš Bezděk (Institute of Entomology, Biology Centre of the Czech Academy of Sciences, České Budějovice), Vítězslav Kubáň (Šlapanice), David Král (Department of Zoology, Faculty of Science, Charles University, Prague), † Ottó Merkl (Department of Zoology, Hungarian Natural History Museum, Budapest), Valentin Szénási and Sándor Bérces (Duna-Ipoly National Park Directorate, Budapest), Sándor Ugró and Róbert Enyedi (Kiskunság National Park directorate, Kecskemét), Krisztián Harmos (Bükk National Park Directorate, Eger), Tibor

Danyik (Körös-Maros National Park Directorate, Szarvas), László Nádai (Budapest), Balázs Károlyi (Budapest), Tibor Kovács (Mátra Museum of the Hungarian Natural History Museum, Gyöngyös), Tibor Kisbenedek (Department of Natural History, Janus Pannonius Museum, Pécs), Yurii Ye. Skrylnyk (Research Institute of Forestry & Forest Melioration named after G. M. Vysotsky, Kharkiv), Yurii V. Kanarskyi and Yurii M. Geriak (Institute of Ecology of the Carpathians of the National Academy of Sciences of Ukraine, Lviv), Andrii I. Bachynskyi (Dniester Canyon National Nature Park, Zalishchyky), Bohdan M. Vasko (Department of biological methods of pest control, I. I. Schmalhausen Institute of Zoology of National Academy of Sciences of Ukraine, Kyiv), Valeriu Derjanschi and Svetlana Bacal (Institute of Zoology of the Academy of Sciences of Moldova, Chișinău), Luciano Ragozzino (Lerma), Paolo Glerean (Museo Friulano di Storia naturale, Udine), Alberto Ballerio (Brescia), Enrico Barbero (Dipartimento di Scienze della Vita e Biologia dei Sistemi, Università degli Studi di Torino), Roberto Poggi (Museo Civico di Storia Naturale "Giacomo Doria", Genoa), Michele Zilioli (Laboratorio di entomologia, Museo Civico di Storia Naturale, Milan), Roberto Casalini (Museo Civico di Zoologia, Rome), Giuseppe M. Carpaneto (Dipartimento di Scienze, Università Roma Tre, Rome), Marcello Romano (Capaci), Petra Kranebitter (Museo di Scienze Naturali dell'Alto Adige, Bolzano), Daniel Lorenz (Franziskaner Gymnasium Bozen, Bolzano), Mauro Gobbi (Museo delle Scienze, Trento), Stefano Ziani (Meldola), Riccardo Pittino (Milan), Marcello Zorzetto (Museo Civico di Storia Naturale "Silvia Zenari", Pordenone), Marco Uliana (Museo di Storia Naturale di Venezia Giancarlo Ligabue, Venice), Alain Drumont and Julien Lalanne (Royal Belgian Institute of Natural Sciences, Brussels), Antoine Mantilleri and Christophe Rivier (Muséum national d'Histoire naturelle, Paris), Henry Callot and Marie Meister (Musée Zoologique de l'Université et de la Ville de Strasbourg), Denis Keith (Muséum des Sciences Naturelles et de Préhistoire, Chartres), Christoph Germann (Biowissenschaftlichen Abteilung, Naturhistorisches Museum Basel), Guido Sabatinelli (Département d'entomologie, Muséum d'histoire naturelle, Genève), Michael Greeff (Department of Environmental Systems Science, Swiss Federal Institute of Technology, Zürich), Hannes Baur (Naturhistorisches Museum Bern, Switzerland), Harald Schillhammer (2. Zoologische Abteilung, Naturhistorisches Museum Wien, Vienna), Martin Schwarz (Entomologische Arbeitsgemeinschaft, Biologiezentrum Linz), Ulrike Hausl-Hofstätter (Abteilung Biowissenschaften – Zoologie, Universalmuseum Joanneum, Graz), Norbert Ruckenbauer (Naturkundliche Landessammlung, Museum Niederösterreich, Sankt Pölten), Andreas Eckelt (Tiroler Landesmuseum Ferdinandeum, Innsbruck), Helge Heimburg (Sammlungs- und Wissenschaftszentrum, Abteilung Zoologie, Landesmuseums für Kärnten, Klagenfurt am Wörthersee), Petr Zábranský (Institut für Forstentomologie, Forstpathologie und Forstschutz, Universität für Bodenkultur Wien, Vienna), Alexander Dostal (Vienna), Katja Neven (Staatliche Naturwissenschaftliche Sammlungen Bayerns, Zoologische Staatssammlung, Munich), Bernd Jaeger (Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Museum für Naturkunde, Berlin), Marianna Simões and Mandy Schröter (Senckenberg Deutsches Entomologisches Institut, Müncheberg),

Olaf Jäger (Senckenberg Naturhistorische Sammlungen, Museum für Tierkunde, Dresden), Alexander Riedel (Staatliches Museum für Naturkunde Karlsruhe), Arnaud Faille and Aron Bellersheim (Staatliches Museum für Naturkunde Stuttgart), Dirk Ahrens (Zoologishes Forschungsmuseum Alexander Koenig, Bonn), Roland Schultz (Senckenberg Museum für Naturkunde Görlitz), Florian Theves (Landesanstalt für Umwelt Baden-Württemberg, Karlsruhe), Torsten Bittner (Staatsbetrieb Sachsenforst, NSG-Verwaltung Königsbrücker Heide/Gohrischheide Zeithain, Königsbrück), Oliver Hillert (Schöneiche bei Berlin), Walter Heinz (Schwanfeld), Przemysław D. Szymroszczyk (Museum and Institute of Zoology of the Polish Academy of Sciences, Warsaw), Melanya Stan and Ionuț Ș. Iorgu ("Grigore Antipa" National Museum of Natural History, Bucharest), Iulia Muntean (Brukenthal National Museum, Sibiu), Cornelia Chimişliu (Department of Natural Sciences, Museum of Oltenia Craiova), Teodora Toshova (Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, Sofia), Pavel Stoev and Borislav Guéorguiev (National Museum of Natural History, Bulgarian Academy of Sciences, Sofia), Andrey V. Frolov (Zoological Institute of Russian Academy of Sciences, Saint Petersburg), Oscar Vorst (Naturalis Biodiversity Centre, Leiden), Aslak Kappel Hansen and Caroline A. Høegh-Guldberg (Natural History Museum of Denmark, University of Copenhagen, Copenhagen), Christoffer Fägerström (Biological Museum, Lund University, Lund), Hans Mejlon (Museum of Evolution, Uppsala), Sergei Tarasov, Jaakko Mattila and Pekka Malinen (Finnish Museum of Natural History LUOMUS, Helsinki), Dmitry Telnov (Department of Life Sciences, Natural History Museum, London), Darren J. Mann (Oxford University Museum of Natural History, Oxford), Roman Cséfalvay (Rohovce – Kyselica), Vladimír Janský (Slovak National Museum – Natural History Museum, Bratislava), Vladimír Smetana (Tekovské múzeum v Leviciach, Levice), Tomáš Jászay (Šariš Museum in Bardejov), Attila Balázs (Department of Forest Protection and Hunting, Faculty of Forestry and Wood Technology, Mendel University of Agriculture and Forestry, Brno), Miroslav Mikát (Museum of Eastern Bohemia in Hradec Králové, Hradec Králové), Jiří Procházka (Moravian Museum, Brno), Jan Walter (Západočeské muzeum v Plzni, Plzeň), Jiří Hájek (National Museum, Prague), Jindřich Roháček (Silesian Museum, Opava), Tomi Trilar (Slovenian Museum of Natural History, Ljubljana), Toni Koren (Association Hyla, Zagreb), Srećko Ćurčić (Institute of Zoology, Faculty of Biology, University of Belgrade, Belgrade), Yves Bousquet (Gatineau, Québec), Ondřej Sabol (Ostrava), and Aleš Sedláček (Hranice).

Many thanks also go to Peter Kurina (Gajary), Vlastimil Mihal (Přerov), Michael Balke (Zoologische Staatssammlung, Munich), Oleksandr O. Sukhenko (Dnipro), Dalibor Všianský (Brno), Maurizio Gigli (Roma), and Milan Štrba (Bratislava) for taking photographs of specimens or habitats of *B. unicornis*.

For comments on earlier drafts of the manuscript and for linguistic corrections I am very thankful to Terry F. Houston (Department of Terrestrial Zoology, Western Australian Museum, Perth). I also thank Michelle Rossini (Finnish Museum of Natural History LUOMUS, Helsinki), Andrey V. Frolov, and an anonymous reviewer for

critical comments on the manuscript, and Nathalie Yonow for the perfect cooperation in the editorial processing of this paper.

Finally, I am grateful to my teacher of entomology from my youth, Vojtěch Jiříček (Prostějov), who showed me the beetle covered in this study for the first time when I was 13 years old, and to my long-time colleague and friend Ilja Trojan (Velké Němčice), thanks to whom I returned to entomology and was able to complete this study, which I dedicate to the memory of Rudolf Čepelák, the discoverer of the most efficient collecting method for *Bolbelasmus unicornis*. I thank his grandson Svätopluk Čepelák (Dlhá nad Váhom) for providing photographs of his grandfather Rudolf and an excerpt from his entomological diary.

References

Ádám L (1994) A check-list of the Hungarian Scarabaeoidea with the description of ten new taxa (Coleoptera). Folia Entomologica Hungarica 55: 5–17. http://publication.nhmus.hu/pdf/folentom/FoliaEntHung_1994_Vol_55_5.pdf

Agoglitta R, Barbero E, Ragusa E, Zunino M (2006) Catalogo sistematico e topografico dei Geotrupidae e Scarabaeidae degradatori della Sicilia e delle isole circumsiciliane (Coleoptera: Scarabaeoidea). Boletín de la Sociedad Entomológica Aragonesa 39: 181–204. http://sea-entomologia.org/Publicaciones/PDF/BOLN39/181_204BSEA39ScarabeidaeSicilia.pdf

Allenspach V (1970) Coleoptera Scarabaeidae, Lucanidae. Insecta Helvetica. Catalogus 2. Imprimerie la Concorde, Lausanne, 186 pp.

Alonso-Zarazaga MA, Evenhuis NL (2017) Revised dating of Panzer's Faunae insectorum Germanicae initia. Deutschlands Insecten (1792–1810), based primarily on the Leipzig Book Fair Catalogs. Sherbornia 4(1): 1–8. https://digital.csic.es/bitstream/10261/194992/1/Revised_Alonso_Art2017.pdf

Alonso-Zarazaga MA, López-Colón JI, Vít S (2013) Geotrupidae. Fauna Europaea, version 2017.06. https://fauna-eu.org [accessed 3 July 2021]

Anonymus (2015) Plan de management integrat pentru siturile Natura 2000 ROSPA0104 Bazinul Fizeşuliu, ROSCI0099 Lacul Ştiucilor-Sic-Puni-Bonţida şi pentru ariile protejate de interes naţional Lacul Ştiucilor, Stufărişurile de la Sic, Valea Legiilor şi Pădurea Ciuaşului. [Integrated management plan for Natura 2000 sites ROSPA0104 Fizeşuliu Basin, ROSCI0099 Ştiucilor-Sic-Puni-Bonţida Lake, and for the protected areas of national interest Ştiucilor Lake, Stufărişurile de la Sic, and Valea Legiilor and Ciuaşului Forest]. Ministerul Mediului Apelor si Padurilor, Bucureşti, 325 pp. [in Romanian] http://www.mmediu.gov.ro/app/webroot/uploads/files/2015-12-16_PM_ROSCO0099_ROSPA0104_LW_AD.pdf [accessed 1 November 2020]

Anonymus (2019) A talajfelszíni- és egyenesszárnyú fauna alapállapot felmérése a Gönyűi-homokvidék projektterületen. [Survey of the baseline condition of the soil surface and fauna of Orthoptera in the Gönyűi Sands area]. Acrida Nature Conservation Research Ltd., Tapolca, 3 pp. [unpublished report for the Fertő-Hanság National Park Directorate,

in Hungarian] https://www.ferto-hansag.hu/upload/document/482/life-ip-grassland-hu_egyenesszarnyu-felmeres_2019_p06n.pdf [accessed 28 February 2021]

Aratani K (2017) 500 (Col.: Bolboceratidae). A record of the earth-borer beetle *Bolbocerosoma nigroplagiatum* from the island of Satsuma Iōjima [in Japanese]. Pulex 96: 732–733. http://www.agr.kyushu-u.ac.jp/lab/entomology/Pulex/Pulex_No96.pdf

Areekul S (1957) The comparative internal larval anatomy of several genera of Scarabaeidae (Coleoptera). Annals of the Entomological Society of America 50(6): 562–577. https://doi.org/10.1093/aesa/50.6.562

Arens LE (1922) K biologii *Odontaeus armiger* Scop. (Coleoptera). [On the biology of *Odontaeus armiger* Scop. (Coleoptera)]. Izvestiya Petrogradskogo Nauchnogo Instituta Imeni P. F. Lesgafta 5: 241–246. [in Russian]

Arnone M (2010) Quinto contributo alla revisione della collezione coleotterologica di Enrico Ragusa: Scarabaeoidea. Il Naturalista Siciliano 34: 61–172. http://www.sssn.it/PDF/PDF%20NS%2034/061-172.pdf

Arnone M, Massa B (2010) A new species of *Bolbelasmus* Boucomont, 1911 from Sicily (Italy). Il Naturalista Siciliano 34: 401–414. http://www.sssn.it/PDF/PDF%20NS%2034/401-414.pdf

Bacal S, Munteanu N, Toderaș I (2013) Checklist of beetles (Insecta: Coleoptera) of the Republic of Moldova. Brukenthal. Acta Musei 8(3): 415–450.

Ballerio A (2008) Insetti da proteggere: la tutela entomologica in Italia. Quaderni della Stazione di Ecologia del Civico Museo di Storia Naturale di Ferrara, 18: 21–35. https://storianaturale.comune.fe.it/modules/core/lib/d.php?c=wyHKU

Ballerio A, Rey A, Uliana M, Rastelli M, Rastelli S, Romano M, Colacurcio L (2014) Coleotteri Scarabeoidei d'Italia. Piccole Faune. Marco Serra Tarantola, Brescia. http://www.societaentomologicaitaliana.it/Coleotteri%20Scarabeoidea%20d'Italia%202014 [accessed 10 December 2020]

Balthasar V (1933) Pokus o rozbor složek fauny slovenských a podkarpatoruských coprophagních Scarabaeidů z hlediska zoogeografie na podkladě oekologickém. Ein Versuch einer Analyse der coprophagen Fauna der Karpathen-Länder auf Grund der oekologischen Zoogeographie. Časopis Učené Společnosti Šafaříkovy 7: 198–204. [in Czech with German summary]

Baraud J (1977) Coléoptères Scarabaeoidea. Faune de l'Europe occidentale: Belgique, France, Grande-Bretagne, Italie, Péninsule Ibérique. Nouvelle Revue d'Entomologie, Supplément 4: 1–352.

Baraud J (1992) Coléoptères Scarabaeoidea d'Europe. Faune de France, France et régions limitrophes, 78. Fédération Française des Sociétés de Sciences Naturelles & Société Linnéenne de Lyon, Paris – Lyon, 856 pp. https://faunedefrance.org/bibliotheque/docs/J.BARAUD(FdeFr78)Col%C3%A9opt%C3%A8resScarabaeoidea.pdf

Barbero E, Cavallo O (1999) I coleotteri scarabaeoidea degradatori (Trogidae, Geotrupidae, Scarabaeidae, Aphodiidae) del Museo civico "F. Eusebio". Alba Pompeia 20(1): 65–81.

Bartenev AF, Shatrovskiy AG, Vovk DV (1997) Obzor semeystv zhukov (Coleoptera) Ukrainy. Chast' 2. Polyphaga (Staphyliniformia: Hydrophiloidea; Scarabaeiformia: Scarabaeoidea). A synopsis of the families of beetles (Coleoptera) of Ukraine. Part 2. Polyphaga (Staphyliniformia: Hydrophiloidea; Scarabaeiformia: Scarabaeoidea). Izvestiya Kharkovskogo Ento-

mologicheskogo Obshchestva 5: 5–21. [in Russian with English Summary] https://www.zin.ru/animalia/coleoptera/pdf/bartenev_shatrovsky_vovk.pdf

Baudi di Selve F (1889) Catalogo dei Coleotteri del Piemonte. Annali della Reale Accademia d'Agricoltura di Torino 32: 51–274. https://doi.org/10.5962/bhl.title.24377

Bedel LEM (1911) Faune des Coléoptères du Bassin de la Seine. Scarabaeidae. Publications de la Société Entomologique de France 4(1): 1–164. https://gallica.bnf.fr/ark:/12148/bpt6k1176282r/f11.item

Béguin L (1906) Mœurs du *Bolboceras gallicum* Muls. (Col.). Bulletin de la Société Entomologique de France 1906(8): 93–94. https://www.biodiversitylibrary.org/item/37019#page/133/mode/1up. https://doi.org/10.3406/bsef.1906.23896

Benasso G (1971) Una specie nuova per il Friuli: *Bolbelasmus unicornis* (Schrank) (Coleoptera, Geotrupidae). Atti del Museo Civico di Storia Naturale di Trieste 27: 167–172.

Bense U, Maus C, Mauser J, Neumann C, Trautner J (2000) Die Käfer der Markgräfler Trockenaue. In: Landesanstalt für Umweltschutz Baden-Württemberg (Ed.) Vom Wildstrom zur Trockenaue. Natur und Geschichte der Flusslandschaft am südlichen Oberrhein. Verlag Regionalkultur, Ubstadt-Weiher, 347–460. https://d-nb.info/959301941/04

Bertolini S de (1871) Una inondazione dell'Adige. Notizie entomologiche. Bullettino della Società Entomologica Italiana 3(1): 41–46. https://archive.org/details/bollettinodellas-34187172soci/page/n49

Bertolini S de (1872) Catalogo sinonimico e topografico dei coleotteri d'Italia. Tipografia Cenniniana, Firenze, 263 pp. https://doi.org/10.5962/bhl.title.8783

Bertolini S de (1874) Notizie di escursioni e di cacce entomologiche II. Bullettino della Società Entomologica Italiana 6: 99–102. https://www.biodiversitylibrary.org/item/39662#page/465/mode/1up

Bertolini S de (1891) Contribuzione alla Fauna trentina dei Coleotteri. Bullettino della Società Entomologica Italiana 23: 169–217. https://www.biodiversitylibrary.org/item/55175#page/201/mode/1up

Bertolini S de (1899a) Catalogo dei Coleotteri d'Italia. Tipografia e litografia sordo-muti di L. Lazzeri, Siena, 144 pp.

Bertolini S de (1899b) I Coleotteri del Trentino. Saggio di un elenco delle specie di Coleotteri appartenenti alla regione faunistica del Trentino. Società Entomologica Italiana, Tipografia di M. Ricci, Firenze, 399 pp.

Bezborodov VG (2009) O khorologii i ekologii *Bolbocerodema zonatum* Nikolajev, 1973 (Coleoptera: Scarabaeoidea, Bolboceratidae). [On the Chorology and Ecology of *Bolbocerodema zonatum* Nikolajev, 1973 (Coleoptera: Scarabaeoidea, Bolboceratidae)]. In: Sektsiya 3. Bioraznoobraziye zhivotnykh i mikroorganizmov. Mezhdunarodnaya nauchno-prakticheskaya konferentsiya «Biologicheskoye raznoobraziye i ustoychivoye razvitiye prirody i obshchestva», posvyashchonnaya 75-letiyu KazNU im. al'-Farabi i biologicheskogo fakul'teta. [Session 3. Biodiversity of animals and microorganisms. International Scientific-Practical Conference "Biodiversity and Sustainable Development of Nature and Society" held on the occasion of the 75th anniversary of Al-Farabi Kazakh National University and the Faculty of Biology]. Almaty, 17–20. [in Russian]

Bezborodov VG, Koshkin ES (2014a) A Review of Bolboceratidae (Coleoptera, Scarabaeoidea) species from the Russian Far East. Entomological Review 94(9): 1313–1319. https://doi.org/10.1134/S0013873814090127

Bezborodov VG, Koshkin ES (2014b) Obzor vidov Bolboceratidae (Coleoptera, Scarabaeoidea) Dal'nego Vostoka Rossii. [A Review of Bolboceratidae (Coleoptera, Scarabaeoidea) species of the Russian Far East]. Zoologicheskiy Zhurnal 93: 953–959. [in Russian] https://doi.org/10.7868/S0044513414060038

Bidas M (2012) Rzadkie chrząszcze (Coleoptera) Góry Rzepki w Górach Świętokrzyskich. Rare beetles (Coleoptera) of Rzepka Mountain in Świętokrzyskie Mountains. Naturalia (Kielce) 1: 133–135. [in Polish with English summary]

Bielz EA (1887) Die Erforschung der Käferfauna Siebenbürgens bis zum Schlusse des Jahres 1886. Verhandlungen und Mittheilungen des Siebenbürgischer Vereins für Naturwissenschaften in Hermannstadt 37: 27–114. https://www.biodiversitylibrary.org/item/104997#page/425/mode/1up

Bleich O, Gürlich S, Köhler F (2022) Verzeichnis und Verbreitungsatlas der Käfer Deutschlands. World Wide Web electronic publication. www.coleokat.de [accessed 7 January 2022]

Bolla J von (1859) Beitrag zur Kenntnis der Koleopteren-Fauna Presburg's. Verhandlungen des Vereins für Naturkunde zu Presburg 4: 23–44. https://www.biodiversitylibrary.org/item/107030#page/921/mode/1up

Bouchard P, Bousquet Y (2020) Additions and corrections to "Family-group names in Coleoptera (Insecta)". ZooKeys 922: 65–139. https://doi.org/10.3897/zookeys.922.46367

Boucomont A (1912) Scarabaeidae: Taurocerastinae, Geotrupinae. In: Junk W, Schenkling S (Eds) Coleopterorum Catalogus, Pars 46. Wilhelm Junk, Berlin, 1–47. https://www.biodiversitylibrary.org/item/276306#page/393/mode/1up

Bourgeois J (1904) Catalogue des Coléoptères de la chaîne des Vosges et des régions limitrophes. Bulletin de la Société d'Histoire Naturelle de Colmar, Nouvelle Série 7: 1–93. https://doi.org/10.5962/bhl.title.8778

Bousquet Y (2016) Litteratura Coleopterologica (1758–1900): A guide to selected books related to the taxonomy of Coleoptera with publication dates and notes. ZooKeys 583: 1–776. https://doi.org/10.3897/zookeys.583.7084

Brancsik C (1871) Die Käfer der Steiermark. Verlag von Paul Cieslar, Graz, 114 pp. https://doi.org/10.5962/bhl.title.104482

Brancsik C (1899) Additamenta ad faunam Coleopterorum Comitatus Trencsiniensis. Series quarta. A Trencsén Vármegyei Természettudomanyi Egylet 21–22: 39–42. https://adt.arcanum.com/en/view/MTA_TrencsenyVmTermTudEgyletEvkonyve_1898-1899/?pg=42&layout=s

Brancsik C (1905) Enumeratio Coleopterorum in Comitatu Trencsiniensi adhuc inventorum. A Trencsén Vármegyei Természettudomanyi Egylet 27–28: 9–116. https://adt.arcanum.com/en/view/MTA_TrencsenyVmTermTudEgyletEvkonyve_1904-1905/?pg=10&layout=s

Bratek Z, Papp L, Merkl O, Takács V (1992) Föld alatti gombákon élő rovarok. [Insects living on hypogeous fungi]. Mikológiai Közlemények 31: 55–66. [in Hungarian] http://bruchiteam.nhmus.hu/Merkl/Bratek_Papp_Merkl_Takacs_fold_alattai_gombakon_elo_rovarok-mikologiai_kozlemenyek_vol_31_1_2_1992.pdf

Brechtel F, Schmid-Egger C, Neumann C, Baum F (1995) Die Trockenauen am südlichen Oberrhein. Ein Naturraum bundesweiter Bedeutung ist von Zerstörung bedroht. Naturschutz und Landschaftsplanung 27: 227–236.

Brelih S, Kajzer A, Pirnat A (2010) Gradivo za favno hroščev (Coleoptera) Slovenije. 4. prispevek: Polyphaga: Scarabaeoidea (= Lamellicornia). Material for the beetle fauna (Coleoptera) of Slovenia. 4th contribution: Polyphaga: Scarabaeoidea (= Lamellicornia). Scopolia 70: 1–386. [in Slovenian and English] http://www2.pms-lj.si/pdf/Scopolia/Scopolia-70.pdf

Britton EB (1956) Handbooks for the Identification of British Insects. Vol. V, Part 11. Coleoptera Scarabaeoidea (Lucanidae, Trogidae, Geotrupidae, Scarabaeidae). Royal Entomological Society, London, 29 pp. https://www.royensoc.co.uk/sites/default/files/Vol05_Part11_ed1.pdf

Brustel H, Gouix N (2012) La chasse aux mythes! Petite contribution cryptoentomologique sur les Coléoptères de la Directive Habitats à rechercher en France. Le Coléoptériste 15(1): 26–37. https://inpn.mnhn.fr/fichesEspece/BRUSTEL_&_GOUIX_2012_especes_DHFF_a_rechercher.pdf

Bunalski M (1999) Die Blatthornkäfer Mitteleuropas (Coleoptera, Scarabaeoidea). Bestimmung – Verbreitung – Ökologie. F. Slamka, Bratislava, 80 pp.

Bunalski M (2001) Checklist of Bulgarian Scarabaeoidea (Coleoptera). Fourth contribution to the knowledge of Scarabaeoidea of Bulgaria. Polskie Pismo Entomologiczne 70: 165–172.

Bunalski M, Sienkiewicz P, Kubasik W, Konwerski S, Pałka K (2013) Materiały do poznania rozmieszczenia chrząszczy (Coleoptera) Zachodniej Polski. Część 4. Bolboceratidae. (Contribution to the knowledge of beetles (Coleoptera) distribution in Western Poland. Part 4. Bolboceratidae). Wiadomości Entomologiczne 32: 259–265. [in Polish with English abstract] http://pte.au.poznan.pl/we/2013/35_Bunalski_I_in.pdf

Burakowski B, Mroczkowski M, Stefańska J (1983) Katalog Fauny Polski. Catalogus faunae Poloniae. Część XXIII, tom 9. Chrząszcze – Coleoptera. Scarabaeoidea, Dascilloidea, Byrrhoidea, Parnoidea. Nr. 38 «Katalogu fauny Polski». [Catalogue of the fauna of Poland. Catalogus faunae Poloniae. Part XXIII, Volume 9. Beetles – Coleoptera. Scarabaeoidea, Dascilloidea, Byrrhoidea, Parnoidea. No. 38 of the "Catalogue of the fauna of Poland"]. Państwowe Wydawnictwo Naukowe, Warsaw, 294 pp. [in Polish]

Byk A, Mokrzycki T, Dworakowski M, Bidas M (2012) Rozmieszczenie *Odonteus armiger* (Scopoli, 1772) (Coleoptera: Scarabaeoidea: Bolboceratidae) w Polsce z uwagami o jego bionomii. *Odonteus armiger* (Scopoli, 1772) (Coleoptera: Scarabaeoidea: Bolboceratidae) in Poland with some bionomical data. Wiadomości Entomologiczne 31: 100–112. [in Polish with English abstract] http://pte.au.poznan.pl/we/2012/11_byk_i_in.pdf

Byk A, Mokrzycki T, Rosa-Gruszecka A, Tylkowski S, Zamojski M (2016) Grzybolcowate (Bolboceratidae) i wygonakowate (Ochodaeidae) – aktywność, wymagania ekologiczne i metody obserwacji. (Bolboceratidae and Ochodaeidae – activity, ecological requirements and methods of observation). Studia i Materiały Centrum Edukacji Przyrodniczo-Leśnej w Rogowie 18: 124–141. [in Polish with English abstract] http://cepl.sggw.pl/sim/pdf/sim49A_pdf/Byk_i_inni.pdf

Caillol H (1913) Catalogue des Coléoptères de Provence. Deuxième partie. Société Linnéenne de Provence, Marseille, 607 pp.

Callot H (2018) Liste de référence des Coléoptères d'Alsace. Version du 30-IX-2018. Société Alsacienne d'Entomologie, Strasbourg, 107 pp. http://soc.als.entomo.free.fr/Documents%20PDF/Liste_de_Reference_des_Coleopteres_Alsace_SAE_CALLOT.pdf [accessed 20 January 2021]

Calwer CG (1858) Käferbuch. Allgemeine und specielle Naturgeschichte der Käfer Europa's. Nebst der Anweisung sie zu sammeln und aufzubewahren. Mit 1 schwarzen und 48 colorirten Tafeln. Krais & Hoffmann, Stuttgart, xxviii + 788 pp. + 49 pls. https://books.google.cz/books?id=dTTPAAAAMAAJ&hl=cs&pg=PP1#v=onepage&q&f=false

Carpaneto GM, Piattella E (1995) Coleoptera Polyphaga V (Lucanoidea, Scarabaeoidea). Checklist delle Specie della Fauna Italiana 50: 1–18. https://doi.org/10.21426/B618110438

Carpaneto GM, Piattella E, Pittino R (2000) The scarab beetles of Turkey: an updated checklist and chorotype analysis (Coleoptera, Scarabaeoidea). Biogeographia 21: 217–240. https://doi.org/10.21426/B6110170

Carpaneto GM, Rovelli V, Bologna MA, Zapparoli M (2016) *Bolbelasmus unicornis* (Schrank, 1789). In: Stoch F, Genovesi P (Eds) Manuali per il monitoraggio di specie e habitat di interesse comunitario (Direttiva 92/43/CEE) in Italia: specie animali. Manuali e linee guida 141/2016. Istituto Superiore per la Protezione e la Ricerca Ambientale, Roma, 58–59. https://www.isprambiente.gov.it/public_files/direttiva-habitat/Manuale-141-2016.pdf

Carpaneto GM, Ballerio A, Dellacasa M, Rey A, Uliana M, Ziani S (2021) Insecta: Coleoptera: Scarabeoidea. In: Bologna MA, Zapparoli M, Oliverio M, Minelli A, Bonato L, Cianferoni F, Stoch F (Eds) Checklist of the Italian Fauna. Version 1.0. Last update: 2021-05-31. https://www.lifewatchitaly.eu/iniziative/checklist-fauna-italia-it/checklist-table [accessed 31 January 2022]

Čepelák R (1925) Co jsem sbíral na Slovensku. [What I collected in Slovakia]. Acta Societatis Entomologicae Čechosloveniae 22: 110. [in Czech]

Černecký J, Galvánková J, Považan R, Saxa A, Šeffer J, Šefferová V, Lasák R, Janák M (2014) Conservation status of habitats and species of Community interest in the period of 2007–2012 in the Slovak republic. Správa o stave biotopov a druhov európskeho významu za obdobie rokov 2007–2012 v Slovenskej republike. Štátna ochrana prírody Slovenskej republiky, Banská Bystrica, 1625 pp.

Cherkunov N (1889) Spisok zhukov, vodyashchikhsya v Kiyeve i yego okrestnostyakh. Liste des coleoptères de Kiew et de ses environs. Zapiski Kiyevskago Obshchestva Yestestvoispytateley 10: 147–204. [in Russian with French title] https://books.google.cz/books?id=4axHAQAAMAAJ&hl=cs&pg=RA1-PA147#v=onepage&q&f=false

Chimişliu C (2004) Taxonomie et nomenclature actualisées concernant les espèces des Scarabéoïdés (Insecta: Coleoptera: Scarabaeoidea) en Roumanie (à l'exclusion de la fam. des Lucanidae). Revue Roumaine de Biologie, Série de Biologie Animale 47: 31–41. https://www.ibiol.ro/zoology/Volume%2047/Rev.%20roum.%20biol.%20-%20biol.%20anim.,%2047,%201-2,%202002.pdf

Chobot K, Mourek J (2008) Brouci. [Beetles]. In: Marhoul P, Turoňová D (Eds) Zásady managementu stanovišť druhů v evropsky významných lokalitách soustavy Natura 2000. [Guidelines for the management of the habitats of species in the Natura 2000 sites of European importance]. Agentura ochrany přírody a krajiny České Republiky, Prague, 65–80. [au-

thors of the part related to *Bolbelasmus unicornis* (pp. 65–66): Kubáň V, Čížek L – Vítězslav Kubáň pers. comm.] [in Czech] https://www.ochranaprirody.cz/res/archive/410/067755.pdf?seek=1544180725

Cosandey V, Chittaro Y, Sanchez A (2017) Liste commentée des Scarabaeoidea (Coleoptera) de Suisse. Alpine Entomology 1: 57–90. https://doi.org/10.3897/alpento.1.21179

Costa A (1864) Acquisti fatti durante l'anno 1862. Annuario del Museo Zoologico della Università di Napoli 2: 8–94. https://www.biodiversitylibrary.org/item/43418#page/12/mode/1up

Cristofori G de, Jan G (1832) Cataloghi sistematici e descrittivi degli oggetti di storia naturale esistenti nel museo di Giuseppe De Cristofori e Prof. Giorgio Jan contenenti il prodromo della fauna, della flora e della descrizione orittognostico-geognostica dell'Italia superiore. Sectio III.ª entomologia. Pars I.ª conspectus methodicus insectorum. Fasc. I.us Coleoptera. Giovanni Pirotta, Milano, 3 + 111 + [2] + 16 pp. https://doi.org/10.5962/bhl.title.59812

Cséfalvay R (2015) *Bolbelasmus unicornis* (Schrank, 1789) (Coleoptera, Geotrupidae). In: Janák M, Černecký J, Saxa A (Eds) Monitoring of animal species of Community interest in the Slovak Republic. Results and assessment in the period of 2013–2015. State Nature Conservancy of the Slovak Republic, Banská Bystrica, 26–27. https://daphne.sk/wp-content/uploads/2013/12/monitoring_zooANGL_web.pdf

Csiki E (1904) Biztos adatok madaraink táplálkozásáról. Positive Daten über die Nahrung unserer Vögel. Aquila 11: 270–317. [in Hungarian and German] https://www.biodiversitylibrary.org/item/87516#page/294/mode/1up

Csiki E (1905) Biztos adatok madaraink táplálkozásáról. 2. közlemény. Positive Daten über die Nahrung unserer Vögel. 2. Mitteilung. Aquila 12: 312–330. [in Hungarian and German] https://www.biodiversitylibrary.org/item/87336#page/388/mode/1up

Csiki E (1910) Biztos adatok madaraink táplálkozásáról. Hetedik közlemény. Positive Daten über die Nahrung unserer Vögel. Siebente Mitteilung. Aquila 17: 205–218. [in Hungarian and German] https://www.biodiversitylibrary.org/item/81097#page/235/mode/1up

Ćurčić SB, Pavićević D, Radović D, Vesović N, Bekchiev R, Ćurčić N, Guéorguiev B (2019) Current and predicted distribution of the rare and threatened beetle *Bolbelasmus* (*Bolbelasmus*) *unicornis* (Coleoptera: Geotrupidae) in Serbia. European Journal of Entomology 116: 413–424. https://doi.org/10.14411/eje.2019.042

Curtis J (1829a) British entomology; being illustrations and descriptions of the genera of insects found in Great Britain and Ireland: containing coloured figures from nature of the most rare and beautiful species, and in many instances of the plants upon which they are found. Vol. VI [of 16]. London, pls 242–289 + text. https://doi.org/10.5962/t.171559 [here arrangement by systematics in eight volumes]

Curtis J (1829b) A guide to an arrangement of British insects; being a catalogue of all the named species hitherto discovered in Great Britain and Ireland. [Part 1 of 8]. Richard Taylor, London, i–vi, cols 1–32.

Curtis J (1837) A guide to an arrangement of British insects; being a catalogue of all the named species hitherto discovered in Great Britain and Ireland. Second edition, greatly enlar. ged. J. Pigot and Co., Sherwood and Co., & Simpkin and Marshall, London, vi pp. + 294 cols + [1] p. https://doi.org/10.5962/bhl.title.46860

Dalla Torre KW von (1879) Die Käferfauna von Oberösterreich. Systematisches Verzeichnis der in Oberösterreich bisher beobachteten Käfer. Jahresberichte des Vereins für Naturkunde in Österreich ob der Enns zu Linz 10: 1–125. https://www.zobodat.at/pdf/VNodE_0010_0001-0125.pdf

Dejean PFMA (1821) Catalogue de la collection de coléoptères de M. le Baron Dejean. Crevot, Paris, viii + 136 + [2] pp. https://doi.org/10.5962/bhl.title.11259

Dejean PFMA (1833) Catalogue des coléoptères de la collection de M. le Comte Dejean. [Livraison 2]. Méquignon-Marvis Père et Fils, Paris, pp. 97–176. https://doi.org/10.5962/bhl.title.8771

Dejean PFMA (1836) Catalogue des coléoptères de la collection de M. le Comte Dejean. Troisième édition, revue, corrigée et augmentée. [Livraisons 1–4]. Méquignon-Marvis Père et Fils, Paris, xiv + 384 pp. https://doi.org/10.5962/t.173109

Derjanschi V, Baban E, Calestru L, Stahi N, Ţugulea C (2016) Catalogue of the N. Zubowsky entomological collection. Bons Offices, Chişinău, 296 pp.

Dobiasch E (1911) Käfer [advertisement for the sale of beetles]. Insekten-Börse 28: 363. https://www.biodiversitylibrary.org/item/47736#page/361/mode/1up

Dostal A (2019) Verbreitung des Einhorn-Trüffelkäfers *Bolbelasmus unicornis* (Schrank, 1789) (Coleoptera: Geotrupidae) in der Wiener Lobau. Wien, 12 pp. [unpublished report for Municipal Department 22 – Environmental Protection, Vienna] https://www.digital.wienbibliothek.at/wbrup/content/pageview/3292062 [accessed 2 December 2020]

Dostal A, Barries W (2019) Wiederfund des Einhorn-Trüffelkäfers, *Bolbelasmus unicornis* (Schrank, 1789) (Coleoptera: Geotrupidae), in Niederösterreich. Zeitschrift der Arbeitsgemeinschaft Österreichischer Entomologen 71: 7–11. http://www.entomologie.at/uploads/www.entomologie.at/71_2009_007-0011_dostal_barries_bolbelasmus.pdf

Dostal A, Barries W (2021) *Bolbelasmus unicornis* (Schrank, 1789) (Coleoptera: Geotrupidae): Wiederfunde im Burgenland nach 39 Jahren. Zeitschrift der Arbeitsgemeinschaft Österreichischer Entomologen 73: 31–35.

Dostal A, Barries W, Brojer M, Fuchs K, Gross H, Hovorka W, Jäch MA, Link A, Ockermüller E, Schernhammer T (2021a) Bemerkenswerte Käferfunde aus Wien (Österreich) (I) (Coleoptera). Koleopterologische Rundschau 91: 279–302. https://www.zobodat.at/pdf/KOR_91_2021_0279-0302.pdf

Dostal A, Barries W, Gross H, Fuchs K (2021b) Zur Verbreitung des Einhorn-Trüffelkäfers *Bolbelasmus unicornis* (Schrank, 1789) (Coleoptera: Geotrupidae) in der Wiener Lobau. Beiträge zur Entomofaunistik 22: 189–199.

Duftschmid CE (1805) Fauna Austriæ, oder Beschreibung der österreichischen Insekten für angehende Freunde der Entomologie. Erster Theil. Akademie Buchhandlung, Linz und Leipzig, xxxvi + 37–311 + [4] pp. https://doi.org/10.5962/bhl.title.65994

Duna-Ipoly National Park (2021) *Bolbelasmus unicornis* occurrence data. University of Debrecen, Debrecen. https://doi.org/10.48428/ADATTAR/PBMKUZ [accessed 15 December 2021]

Eichwald KE von (1830) Zoologia specialis quam expositis animalibus tum vivis, tum fossilibus potissimum Rossiae in universum, et Poloniae in specie, in usum lectionum publicarum in Universitate Caesarea Vilnensi habendarum. Pars altera, specialem podozoorum expositionem continens. Joseph Zawadzki, Vilnius, 314 pp. + 5 pls. https://doi.org/10.5962/bhl.title.51803

Eichardt J, Kutasi Cs (2011) Oroszlány a Vértes ölelésében. Oroszlány: a Town embraced by the Vértes. Tatabányai Múzem Évkönyve 2: 5–35. [in Hungarian with English abstract] https://library.hungaricana.hu/en/view/MEGY_KOME_TataBanyaiMuzeum_EK_02/?pg=6&layout=s

Endrődi S (1956) Lemezescsápú bogarak – Lamellicornia. Coleoptera IV. Magyarország Állatvilága 12. IX. kötet. 4. füzet. [Lamellicorn beetles – Lamellicornia. Coleoptera IV. Fauna Hungariae 12. IX. part, 4. issue]. Akadémiai Kiadó, Budapest, 188 pp. [in Hungarian]

Endrődi S (1957) A lemezescsápú bogarak (Lamellicornia) kárpátmedencei lelőhelyadatai. [Faunistic data on Lamellicornia of the Carpathian Basin]. Folia Entomologica Hungarica 10: 145–226. [in Hungarian] https://library.hungaricana.hu/hu/view/FoliaEntomologica_1957_10_01_12/?pg=146&layout=s

Endrődi S (1979) A Börzsöny-hegység bogárfaunája VII. Lamellicornia. (The beetle fauna of the Mts. Börzsöny. VII. Lamellicornia). Folia Historico-Naturalia Musei Matraensis 5: 25–37. [in Hungarian with English abstract] https://matramuzeum.nhmus.hu/sites/default/files/nhmusfiles/kiadvanyok/folia/vol5/27-39.pdf

Enyedi R (2006) Contributions to the Scarabaeoidea fauna of Hungary (Coleoptera: Scarabaeoidea). Folia Historico-Naturalia Musei Matraensis 30: 215–225. https://matramuzeum.nhmus.hu/sites/default/files/nhmusfiles/kiadvanyok/folia/vol30/215_225Matra.pdf

Enyedi R, Ádám L (2009) A Mátra Múzeum bogárgyűjteménye, Scarabaeoidea (Coleoptera). Collection of beetles of the Mátra Museum, Scarabaeoidea (Coleoptera). Folia Historico-naturalia Musei Matraensis 33: 133–155. [in Hungarian with English abstract] https://matramuzeum.nhmus.hu/sites/default/files/nhmusfiles/kiadvanyok/folia/vol33/13_Enyedi_Adam_Scarabaeoidea.pdf

Erichson WF (1847) Naturgeschichte der Insecten Deutschlands. Erste Abtheilung. Coleoptera. Dritter Band. Nicolaische Buchhandlung, Berlin, 641–800. https://doi.org/10.5962/bhl.title.8270

Fabre J-HC (1900) Souvenirs Entomologiques (septième série). Études sur l'instinct et les Mœurs des Insectes. Librairie Ch. Delagrave, Paris, 394 + [2] pp. https://doi.org/10.5962/bhl.title.1403

Fabre J-HC (1907) Souvenirs Entomologiques (dixième série). Études sur l'instinct et les Mœurs des Insectes. Librairie Ch. Delagrave, Paris, 353 + [2] pp. https://doi.org/10.5962/bhl.title.1403

Fabre J-HC (1920) Mœurs des Insectes. Morceaux choisis. Extraits des Souvenirs Entomologiques. 16 planches hors texte d'après les photographies de Paul-H. Fabre. Librairie Delagrave, Paris, pp. + 16 pls. http://www.rcin.org.pl/Content/49142/WA488_3920_1374_Fabre-Moeurs.pdf

Fabricius JCh (1781) Species insectorum exhibentes eorum differentias specificas, synonyma auctorum, loca natalia, metamorphosin adiectis observationibus, descriptionibus. Tomus I. Carl Ernst Bohn, Hamburg – Kiel, viii + 552 pp. https://doi.org/10.5962/bhl.title.36509

Fleck E (1905) Die Coleopteren Rumäniens (Fortsetzung). Buletinul Societății de Științe din București – România 14(1–2): 158–203. https://www.biodiversitylibrary.org/item/105609#page/164/mode/1up

Fleischer A (1930) Přehled brouků fauny Československé republiky. [Overview of beetle fauna of the Czechoslovak Republic]. Moravské museum zemské, Brno, 485 pp. [in Czech]

Fowler WW (1890) The Coleoptera of the British Islands. A descriptive account of the families, genera, and species indigenous to Great Britain and Ireland, with notes as to localities, habitats, etc. Vol. IV. Lamellicornia-Serricornia-Longicornia-Phytophaga. L. Reeve & Co., London, 411 pp. + pls 99–142. https://doi.org/10.5962/bhl.title.14423

Frank J, Konzelmann E (2002) Die Käfer Baden-Württembergs 1950–2000. Landesamt für Umweltschutz Baden-Württemberg, Karlsruhe, 521 pp. http://publikationen.ub.uni-frankfurt.de/files/12233/kaefer_1950_2000.pdf

Franz H (1936) Die thermophilen Elemente der mitteleuropäischen Fauna und ihre Beeinflussung durch die Klimaschwankungen der Quartärzeit. Zoogeographica 3: 159–320.

Franz H (1974) Die Nordost-Alpen im Spiegel ihrer Landtierwelt. Eine Gebietsmonographie. Band IV. Universitätsverlag Wagner, Innsbruck – München, 707 pp.

Frivaldszky I (1865) Jellemző adatok Magyarország faunájához. [Typical elements of the Hungarian fauna]. A Magyar Tudományos Akadémia Évkönyvei 11(4): 1–274 + [1] + 13 pls. [in Hungarian] https://adt.arcanum.com/en/view/MTA_MagyarTudomanyosAkademiaEvkonyvei_011_1864-1869/?pg=84&layout=s

Frivaldszky J (1879a) Insecta, Rovarok. Budapest s környékének jellemző rovarfajai. [Insecta, Insects. Insect species typical of the surroundings of Budapest]. In: Gerlóczy G, Dulácska G (Eds) Budapest és környéke természetrajzi, orvosi és közmivelődési leirása. [Description of the natural history, medicine and public education of Budapest and its surroundings]. A Magyar Királyi Egyetemi Könyvnyomda, Budapest, 337–403. [in Hungarian] https://doi.org/10.5962/bhl.title.95630

Frivaldszky J (1879b) Insecta, Rovarok. Budapest s környékének jellemző rovarfajai. [Insecta, Insects. Insect species typical of the surroundings of Budapest]. In: Tivadar M (Ed.) Budapest és környéke állattani tekintetben. A budapesti fauna átalános jellemzése s rövid rendszeres átnézete, a fajok lelhelyeivel és azokra vonatkozó jegyzetekkel. [Budapest and surroundings in terms of zoology. A general characterization and a brief systematic review of the fauna of Budapest, with the localities of the species and notes on them]. A Magyar Királyi Egyetemi Könyvnyomda, Budapest, 45–111. [in Hungarian] https://adt.arcanum.com/en/view/Books_22_OrvoslasTermeszetrajz_1280_Budapest_es_kornyeke_allattani_tekintetben_1088/?pg=44&layout=s

Fröhlich C (1897) Beiträge zur Fauna von Aschaffenburg und Umgegend. Die Käfer. III. Mitteilung des naturwissenschaftlichen Vereines Aschaffenburg. Gustav Fischer, Jena, vii + 158 pp.

Fuss C (1858) Beitrag zur Käferfauna Siebenbürgens. Verhandlungen und Mitteilungen des Siebenbürgischen Vereins für Naturwissenschaften zu Hermannstadt 9(1): 4–7. https://www.biodiversitylibrary.org/item/42663#page/16/mode/1up

Fusu L, Stan M, Dascălu M-M (2015) Coleoptera. In: Iorgu IȘ (Ed.) Ghid sintetic pentru monitorizarea speciilor de nevertebrate de interes comunitar din România. [Summary guide for monitoring invertebrate species of community interest in Romania]. Asocierea S.C. Compania de Consultanță și Asistență Tehnică S.R.L. & S.C. Integra Trading S.R.L., București, 44–62. [in Romanian] http://www.crayfish.ro/anexe/ghid_sintetic_monitorizare_nevertebrate.pdf

Gajdoš P, Majzlan O (2018) Pavúky (Araneae) a chrobáky (Coleoptera) lokality Lackovce – Veľký vrch pri Humennom. [Spiders (Araneae) and beetles (Coleoptera) of the locality

Lackovce – Veľký vrch near Humenné]. Entomofauna Carpathica 30(1): 25–41. [in Slovak with English abstract] http://www.ses.entomology.sk/entomofaunacarpathica/pdf/volume30/30_1_03_Gajdos_a_Majzlan_ec.pdf

Gangloff L (1991) Catalogue et Atlas des Coléoptères d'Alsace. Tome 4. Lamellicornia – Scarabaeidae, Lucanidae. Société Alsacienne d'Entomologie & Musée zoologique de l'université et de la ville de Strasbourg, 106 pp.

Gaskó B (2008) Csongrád megye természetes és természetközeli élőhelyeinek védelméről 1. Adatok az M5-ös autópálya nyomvonaláról és Szeged tágabb környékétől. [On the protection of natural and semi-natural habitats of Csongrád County 1. Data on the route of the M5 highway and the wider surroundings of Szeged]. A Móra Ferenc Múzeum Évkönyve, Természettudományi Tanulmányok (Studia Naturalia) 4: 1–394. [in Hungarian] https://library.hungaricana.hu/hu/view/MEGY_CSON_EK_Sn_04/?pg=6&layout=s

Gaubil J (1849) Catalogue synonymique des Coléoptères d'Europe et d'Algérie. Maison, Paris. 296 + [1] pp. https://doi.org/10.5962/bhl.title.53812

Gavrilović B, Stojanović D (2008) The Scarabaeidae (Coleoptera, Insecta) of Mount Fruška Gora. In: Ćurčić SB (Ed.) The Diversity of Coleoptera of the Fruška Gora National Park. Part One. Fruška Gora National Park & Directorate of Forests, Ministry of Agriculture, Forestry, and Water Management of the Republic of Serbia, Novi Sad, 89–105.

Geiser R (1984) Überblick über den gegenwärtigen Stand der faunistisch-ökologischen Erfassung der Käfer Bayerns (Coleoptera). Mitteilungen der Münchner Entomologischen Gesellschaft 74: 129–154. https://www.zobodat.at/pdf/MittMuenchEntGes_074_0129-0154.pdf

Gemminger M, Harold E von (1869) Catalogus Coleopterorum hucusque descriptorum synonymicus et systematicus. Tom. IV. Scarabaeidae. E. H. Gummi, München, 979–1346 + [8] pp. https://doi.org/10.5962/bhl.title.9089

Gerstaecker CEA (1863) Arthropoda. In: Peters WCH, Carus JV, Gerstaecker CEA (Eds) Handbuch der Zoologie. Zweiter Band. Arthropoden bearbeitet von A. Gerstaecker. Radertiere, Würmer, Echinodermen, Coelenteraten und Protozoen bearbeitet von J. Victor Carus. Wilhelm Engelmann, Leipzig, 421 pp. https://doi.org/10.5962/bhl.title.105872

Ghiliani V (1847) Mémoire sur la station de quelques Coléoptères dans les différentes régions du Piémont. Annales de la Société Entomologique de France, Deuxiéme Série 5: 83–142. https://www.biodiversitylibrary.org/item/34170#page/89/mode/1up

Ghiliani V (1887) Elenco delle specie di Coleotteri trovate in Piemonte. Annali della Accademia d'Agricoltura di Torino 29[=1886]: 195–381. https://archive.org/details/mil0112518_to0323_30_0000000/page/195

Gimpl G, Lambropoulos M, Frank G, Steiner H, Heilingbrunner G (2020) Handbuch NATURA 2000.Wald. Naturnahe Waldbewirtschaftung für ausgewählte FFH-Schutzgüter im Wald. Schwerpunkt Arten. Kuratorium Wald, Wien, 144 pp. http://natura2000.wald.or.at/wp-content/uploads/2020/10/KuratoriumWald_Natura2000_Arten_2020_web.pdf

Glerean P, Stefani G (2019) Una nuova popolazione di *Bolbelasmus unicornis* (Schrank, 1789) (Coleoptera, Geotrupidae) in Friuli Venezia Giulia (Italia nord-orientale). Gortania. Atti del Museo Friulano di Storia Naturale Botanica Zoologica 41: 51–62. http://www.civicimuseiudine.it/images/MFSN/Gortania/Gortania_41/G41_BZ_06-Glerean-Stefani.pdf

Glerean P, Ragozzino L, Ballerio A (2021) Elusive but still present in Italy: two new populations of *Bolbelasmus unicornis* (Schrank) for northern Italy. Session V. Faunistics, biogeography and conservation. XXVI Italian National Congress of Entomology, 7–11 June 2021, Torino, 83–83. [poster] https://www.cnie2020.com/wp-content/uploads/2021/07/libro_abstract_Ita.pdf

Gontarenko AV, Trach VA (2011) K faune plastinchatousykh zhukov (Coleoptera: Scarabaeoidea) Odesskoy i Nikolayevskoy oblastey. Contribution to the fauna of scarab beetles (Coleoptera: Scarabaeoidea) of the Odessa and Mykolayiv Regions. Izvestiya Kharkovskogo Entomologicheskogo Obshchestva 19(2): 20–22. [in Russian with English and Ukrainian abstracts]

Gradojević ZM (1963) Naselja Arthropoda travnih zajednica Deliblatske peščare i njihova sukcesija. [Settlements of Arthropoda of the grass communities of the Deliblato Sands and their succession]. PhD Thesis, University of Belgrade, Belgrade, Serbia, 239 pp. [in Serbian]

Gredler VM (1863) Die Käfer von Tirol nach ihrer horizontalen und vertikalen Verbreitung verzeichnet. J. Eberle, Bozen, iv + [1] + 491 pp. https://www.digitale-sammlungen.de/de/view/bsb10307384?page=9

Guéorguiev BV, Bunalski M (2004) Critical Review of the Families Glaresidae, Lucanidae, Trogidae, Bolboceratidae, Geotrupidae, Hybosoridae and Ochodaeidae in Bulgaria (Coleoptera: Scarabaeoidea). Acta Zoologica Bulgarica 56(3): 253–275.

Gutowski JM, Przewoźny M (2013) Program NATURA 2000 jako narzędzie ochrony chrząszczy (Coleoptera) w Polsce. Natura 2000 as a tool to conserve beetles (Coleoptera) in Poland. Wiadomości Entomologiczne 32(Supplementum): 5–40. [in Polish with English abstract] http://pte.au.poznan.pl/we/2013/supl_Gutowski_Przwozny.pdf

Heer O (1841) Die Kaefer der Schweiz, mit besonderer Berücksichtigung ihrer geographischen Verbreitung. Erster Theil, Dritte Lieferung [VI. Classe: Clavicornia, VII. Classe: Palpicornia, VIII. Classe: Lamellicornia]. Neue Denkschriften der Allgemeinen Schweizerischen Gesellschaft für die Gesammten Naturwissenschaften 5(4): 1–79. https://www.biodiversitylibrary.org/item/39559#page/403/mode/1up

Heyden L von (1884) Coleopterologische Ausbeute des Baron H. v. Maltzan von der Insel Creta. Deutsche Entomologische Zeitschrift 28: 363–368. https://www.biodiversitylibrary.org/page/33120005#page/367/mode/1up

Higurashi T, Tanahashi K (2014) Geotrupidae feeding on hypogeous fungi [in Japanese]. The 5th Annual Meeting of the Coleopterological Society of Japan. The Abstracts of Presentations 2014: 13.

Higurashi T, Tanahashi K, Okuyama Yu (2019) Feeding behavior and lifecycle of mycophagous dung beetles feeding on arbuscular mycorrhizal sporocarps: possibility of spore dispersion by insects. Abstract of the 66th Annual Meeting of the Ecological Society of Japan, March 2019, Kobe. [in Japanese with English title] https://www.esj.ne.jp/meeting/abst/66/W03-2.html [accessed 1 July 2021]

Hildt LF (1892) Przyczynek do fauny chrząszczów podolskich. [A contribution to the fauna of the beetles of Podolia]. Pamiętnik Fizyograficzny 12(3): 209–235. [in Polish] https://www.biodiversitylibrary.org/item/172438#page/499/mode/1up

Hildt LF (1896) Żuki czyli gnojowce krajowe. [Beetles of the region]. Pamiętnik Fizyograficzny 14(3): 153–228. [in Polish] https://www.biodiversitylibrary.org/item/150360#page/391/mode/1up

Hillert O, Arnone M, Král D, Massa B (2016) The genus *Bolbelasmus* in the western and southern regions of the Mediterranean Basin (Coleoptera: Geotrupidae: Bolboceratinae). Acta Entomologica Musei Nationalis Pragae 56(1): 211–254. https://www.aemnp.eu/data/article-1625/1606-56_1_211.pdf

Hochhuth IH [= JH] (1873) Enumeration der in den russischen Gouvernements Kiew und Volhynien bisher aufgefundenen Käfer (Fortsetzung v. Bulletin 1872, N° 4). Bulletin de la Société Impériale des Naturalistes de Moscou 46(1): 124–164. https://www.biodiversitylibrary.org/item/107118#page/130/mode/1up

Holdhaus K, Prossen T (1901) Verzeichnis der bisher in Kärnten beobachteten Käfer. Carinthia II 91: 92–106. https://www.zobodat.at/pdf/CAR_91_0092-0106.pdf

Holzer E (2019) Erstnachweise und Wiederfunde für die Käferfauna der Steiermark (XVII) (Coleoptera). Joannea Zoologie 17: 149–170. https://www.zobodat.at/pdf/JoanZoo_17_0149-0170.pdf

Horion A (1951) Verzeichnis der Käfer Mitteleuropas (Deutschland, Österreich, Tschechoslowakei) mit kurzen faunistischen Angaben. 2. Abteilung: Clavicornia, Teredilia, Heteromera, Lamellicornia, Phytophaga, Rhynchophora. Alfred Kernen Verlag, Stuttgart, 277–536.

Horion A (1957) Bemerkungen zur Scarabaeiden-Fauna von Südbayern. Nachrichtenblatt der Bayerischen Entomologen 11: 105–109. https://www.zobodat.at/pdf/NachBlBayEnt_006_0105-0109.pdf

Horion A (1958) Faunistik der Mitteleuropäischen Käfer. Band VI: Lamellicornia (Scarabaeidae – Lucanidae). A. Feyel, Überlingen – Bodensee, xxiv + 343 pp.

Horváth G (1884) Egy mult századbeli napló. [A diary from the last century]. Rovartani Lapok 1: 217–223. [in Hungarian] https://www.biodiversitylibrary.org/item/103929#page/245/mode/1up

Horvatovich S (1980) Hazánk faunájára új és ritka bogárfajok a Dél- és Nyugat-Dunántúlról (Coleoptera) II. Für die Fauna Ungarns neue und seltene Käferarten aus Süd- und West-Transdanubien (Coleoptera) II. A Janus Pannonius Múzeum Évkönyve 24: 33–43. [in Hungarian with English abstract and German summary] https://library.hungaricana.hu/hu/view/MEGY_BARA_JPM_evkonyv_1979/?pg=34&layout=s

Houston TF (2011) Egg gigantism in some Australian earth-borer beetles (Coleoptera: Geotrupidae: Bolboceratinae) and its apparent association with reduction or elimination of larval feeding. Australian Journal of Entomology 50(2): 164–173. https://doi.org/10.1111/j.1440-6055.2010.00794.x

Houston TF (2016) Brood cells, life-cycle stages and development of some earth-borer beetles in the genera *Bolborhachium*, *Blackburnium* and *Bolboleaus* (Coleoptera: Geotrupidae), with notes on captive rearing and a discussion of larval diet. Austral Entomology 55(1): 49–62. https://doi.org/10.1111/aen.12151

Houston TF, Bougher NL (2010) Records of hypogeous mycorrhizal fungi in the diet of some Western Australian bolboceratine beetles (Coleoptera: Geotrupidae, Bolboceratinae). Australian Journal of Entomology 49(1): 49–55. https://doi.org/10.1111/j.1440-6055.2009.00720.x

Howden HF (1955) Biology and taxonomy of the North American beetles of the subfamily Geotrupinae with revisions of the genera *Bolbocerosoma*, *Eucanthus*, *Geotrupes* and *Peltotrupes*. Proceedings of the United States National Museum 104: 151–319. https://doi.org/10.5479/si.00963801.104-3342.151

Howden HF (1964) The Geotrupinae of North and Central America. Memoirs of the Entomological Society of Canada 96(Supplement 39): 1–91. https://doi.org/10.4039/entm9639fv

Howden HF (1985) A revision of the Australian beetle genera *Bolboleaus* Howden & Cooper, *Blackbolbus* Howden & Cooper, and *Bolborhachium* Boucomont (Scarabaeidae: Geotrupinae). Australian Journal of Zoology, Supplementary Series 111: 1–179. https://doi.org/10.1071/AJZS111

Howden HF (2003) Subfamilia Geotrupinae. In: Morón MA (Ed.) Atlas de los escarabajos de México. Coleoptera: Lamellicornia. Vol. II. Familias Scarabaeidae, Trogidae, Passalidae y Lucanidae. Argania editio, Barcelona, 102–106.

Howden HF, Cooper JB (1977) The generic classification of the Bolboceratini of the Australian region, with descriptions of four new genera (Scarabaeidae: Geotrupinae). Australian Journal of Zoology, Supplementary Series 50: 1–50. https://doi.org/10.1071/AJZS050

Howden HF, Howden A, Holloway G (2007) Digging down under: Australian Bolboceratini, their habits and a list of species (Coleoptera: Scarabaeoidea: Geotrupidae). Zootaxa 1499(1): 47–59. https://doi.org/10.11646/zootaxa.1499.1.2

Huber A (1916) Die wärmeliebende Tierwelt der weiteren Umgebung Basels. Archiv für Naturgeschichte 82(7): 1–120. https://www.biodiversitylibrary.org/item/47768#page/351/mode/1up

Huchet J-B, Azoulay L, Danay O, Ezov N, Perman I, Friedman A-L, Shaltiel-Harpaz L (2022) *Ochodaeus berytensis* Petrovitz (Coleoptera: Ochodaeidae), a new pest of the truffle *Tuber aestivum* in Upper Galilee, Israel. Journal of Applied Entomology 00: 1–6. https://doi.org/10.1111/jen.13027

Hudeček L (1928) Entomologie (Motýlové, brouci, mřížokřídlí, rovnokřídlí, síťokřídlí, polokřídlí). Zvláštní otisk z „Vlastivědy župy olomoucké“. [Entomology (Lepidoptera, Coleoptera, Pseudoneuroptera, Orthoptera, Neuroptera, Hemiptera). Special print from “Natural History of the Olomouc County”]. J. Slovák, Kroměříž, 48 pp. [in Czech]

Hudeček L (1930) Entomologie. Brouci – Coleoptera. [Entomology. Beetles – Coleoptera]. In: Černý N, Pelíšek R (Eds) Vlastivěda střední a severní Moravy. Vlastivěda župy olomoucké. Díl I. Přírodní památky střední a severní Moravy. Vlastivědné příručky. Svazek I. [Natural history of Central and Northern Moravia. Natural history of the Olomouc County. Part I. Natural monuments of Central and Northern Moravia. Natural history guides. Volume I.]. Vydavatelství sdružení učitelstva župy olomoucké, Kroměříž, 360–376. [in Czech]

Hudeček L (1937) Jižní a jiné vzácné druhy hmyzu, pozorované ve střední a severní Moravě. [Southern and other rare species of insects, observed in central and northern Moravia]. Časopis Vlasteneckého Spolku Musejního v Olomouci 50: 151–153. [in Czech]

Hůrka K (2005) Brouci České a Slovenské republiky. Beetles of the Czech and Slovak Republics. Nakladatelství Kabourek, Zlín, 390 pp. [in Czech and English]

Ihssen G (1935) Beiträge zur Kenntnis der Fauna von Südbayern (3). Entomologische Blätter 31(2): 42–48.

Illiger JKW (1798) Verzeichniss der Käfer Preussens. Entworfen von Johann Gottlieb Kugelann Apotheker in Osterode. Ausgearbeitet von Johann Karl Wilhelm Illiger. Mit einer Vorrede des Professors und Pagenhofmeisters Hellwig in Braunschweig, und dem angehängten Versuche einer natürlichen Ordnungs- und Gattungs-Folge der Insekten. Johann Jacob Gebauer, Halle, xlii + [1] + 510 + [1] pp. https://doi.org/10.5962/bhl.title.125071

Illiger JKW (1800) Olivier's Entomologie oder Naturgeschichte der Insekten mit ihren Gattungs- und ArtMerkmalen, ihrer Beschreibung und Synonymie. Käfer. Uebersetzt und mit Zusätzen und Anmerkungen durchgängig begleitet. Erster Theil. Karl Reichard, Braunschweig, xvi + 309 pp. + 2 pls. https://doi.org/10.5962/bhl.title.120818

Jäch MA, Adlbauer K, Barries W, Cate P, Franz H, Geiser E, Geiser R, Holschuh C, Kirschenhofer E, Kreissl E, Novak G, Probst J, Reiser P, Schillhammer H, Schmid H, Schödl S, Suppantschitsch W, Wewalka G, Zábranský P, Zelenka W (1994) Rote Liste der gefährdeten Käfer Österreichs (Coleoptera). Grüne Reihe des Bundesministeriums für Umwelt, Jugend und Familie 2: 107–200. https://www.zobodat.at/pdf/Gruene-Reihe-Lebensministerium_2_0107-0200.pdf

Jacquelin du Val PNC (1863) Catalogue de la famille des scarabéides. In: Jacquelin du Val PNC, Fairmaire L, Migneaux J (Eds) Manuel Entomologique. Genera des Coléoptères d'Europe comprenant leur classification en familles naturelles, la description de tous les genres, des Tableaux synoptiques destinés à faciliter l'étude, le Catalogue de toutes les espèces, de nombreux dessins au trait de caractères et plus de quinze cents types représentant un ou plusieurs insectes de chaque genre dessinés et peints d'après nature avec le plus grand soin. Tome troisième. A. Deyrolle, Paris [1859–1863], 126–138. https://doi.org/10.5962/bhl.title.35866

Jäger G (1884) C. G. Calwers Käferbuch. Naturgeschichte der Käfer Europas zum Handgebrauche für Sammler. Julius Hoffmann & K. Thienemann, Stuttgart, [2] + lvi + 667 + [1] pp. + 50 pls. https://doi.org/10.5962/bhl.title.66959

Jameson ML (2002) Family 29. Geotrupidae Latreille 1802. In: Arnett Jr RH, Thomas MC, Skelley PE, Frank JH (Eds) American Beetles. Volume 2. Polyphaga: Scarabaeoidea through Curculionoidea. CRC Press, Boca Raton, 23–27. https://doi.org/10.1201/9781420041231

Jasilkowski SB (1906) Weitere Coleopterenfunde aus der Bukowina (Fortsetzung). Insekten-Börse 23: 87–88. https://www.biodiversitylibrary.org/page/43817504

Jessop L (1986) Handbooks for the Identification of British Insects. Vol. 5, Part 11. Dung Beetles and Chafers Coleoptera: Scarabaeoidea. New edition. Royal Entomological Society, London, 53 pp. https://www.royensoc.co.uk/sites/default/files/Vol05_Part11.pdf

Joy NH (1932) A Practical Handbook of British Beetles. Volume 1. H. F. & G. Witherby, London, xxvii + 622 pp.

Jungwirt D (2005) Kommentierte Checkliste der Lamellicornia Bayerns (Coleoptera, Scarabaeoidea). Facetta 23–24: 28–44. https://www.zobodat.at/pdf/Facetta_23-24_0028-0044.pdf

Jungwirt D (2012) Die Blatthornkäfer des Naturmuseums Augsburg (Insecta, Coleoptera, Lamellicornia). Bericht der Naturforschenden Gesellschaft Augsburg 64: 32–55. https://www.zobodat.at/pdf/Ber-Naturf-Ges-Augsburg_064_2012_0032-0055.pdf

Juřena D, Týr V (2008) Seznam listorohých brouků (Coleoptera: Scarabaeoidea) České republiky a Slovenska. Checklist of Scarabaeoidea (Coleoptera) of the Czech Republic and Slovakia. Klapalekiana 44(Supplementum): 3–15. [in Czech with English abstract and summary]

Juřena D, Týr V, Bezděk A (2008) Příspěvek k faunistickému výzkumu listorohých brouků (Coleoptera: Scarabaeoidea) na území České republiky a Slovenska. Contribution to the faunistic research on Scarabaeoidea (Coleoptera) in the Czech Republic and Slovakia. Klapalekiana 44(Supplementum): 17–176. [in Czech with English abstract and summary] http://hdl.handle.net/11104/0177252

Kaděra M (2017) Chrobák jednorohý. [Earth-borer beetle *Bolbelasmus unicornis*]. Naše Příroda 2017(5): 24–27. [in Czech] http://nasepriroda.cz/artkey/npr-201705-0003.php

Kahlen M (2018) Die Käfer von Südtirol. Ein Kompendium. Veröffentlichungen des Naturmuseum Südtirol. Nr. 13. Naturmuseum Südtirol, Bozen, 602 pp.

Kampmann FE (1860) Catalogus Coléopterorum vallis rhenanæ alsatico-badensis. Bulletin de la Société d'Histoire Naturelle de Colmar 1: 29–75. https://www.numistral.fr/ark:/12148/bpt6k9637896x/f33.item

Kaszab Z (1937) A Kőszegi hegység bogárfaunájának alapvetése. Grundlagen zur Kenntnis der Käferfauna des Kőszeget Gebirges. Vasi Szemle 4(3): 161–185 [A Kőszegi Múzeum Közleményei 1(2): 1–27]. [in Hungarian with German summary] http://real-j.mtak.hu/9652/1/MTA_DunantuliVasiSzemle_1937.pdf

Kaufmann E (1897) Jellemző magyarországi Coleopterák. II. [Typical Hungarian Coleoptera. II.]. Rovartani Lapok 4: 151–153. [in Hungarian] https://www.biodiversitylibrary.org/item/54389#page/19/mode/1up

Kaufmann E (1914a) Képek a Mecsek-hegység bogárvilágából. [Pictures from the beetle world of the Mecsek Mountains]. Különlenyomat a Mecsek Egyesület 1913-iki évkönyvéből [Special print from the 1913 yearbook of the Mecsek Association], Pécs, 35 pp. [in Hungarian]

Kaufmann E (1914b) Pécs város és Baranyavámegye bogárfaunája. [The beetle fauna of the city of Pécs and the Baranya County]. Pécs-Baranyamegyei Múzeum-Egyesület, Pécs, 94 pp. [in Hungarian]

Kavurka VV, Zaika MI, Popov HV, Lazarev IYe (2019) Novi znakhidky pavukopodibnykh (Arachnida), bahatonizhok (Myriapoda) ta komakh (Insecta), zanesenykh do Chervonoi knyhy Ukrainy. [New records of arachnids (Arachnida), millipedes (Myriapoda) and insects (Insecta), listed in the Red Book of Ukraine]. In: Akimov IA, Kharchenko VO, Kostiushyn VA, Vasyliuk OV (Eds) Materialy do 4-ho vydannia Chervonoi knyhy Ukrainy. Tvarynnyi svit. Tom 3. [Materials for the 4th edn. of the Red Book of Ukraine. Fauna. Volume 3]. Schmalhausen Institute of Zoology of National Academy of Sciences of Ukraine & Ukrainian Nature Conservation Group, Kyiv, 134–141. [in Ukrainian] https://pub.flowpaper.com/docs/http://uncg.org.ua/wp-content/uploads/2019/11/Mater.-do-ChKU_tvaryny-3_2019_compressed.pdf#page=135

Keith D (2002) Contribution à la connaissance des Scarabaeoidea du Proche et du Moyen Orient (10e note) sur la faune de Chypre. Biocosme Mésogéen 19(1–2): 21–30.

Kelecsényi K (1900) Ujabb adatok Nyitramegye bogár-faunájához. [New data on the beetle fauna of Nitra County]. A Nyitravármegyei Orvos-Gyógyszerészi és Természettudományi Egyesület Évkönyve 5[1897–1900]: 42–57. [in Hungarian]

Kendi K (1910) Adatok Bosnyákország bogárfaunájához. [Data on the beetle fauna of Bosnia]. Rovartani Lapok 17: 6–12. [in Hungarian] https://www.biodiversitylibrary.org/item/103059#page/414/mode/1up

Keve A, Szijj J (1957) Distribution, biologie et alimentation du Faucon kobez *Falco vespertinus* L. en Hongrie. Alauda 25(1): 1–23. https://www.biodiversitylibrary.org/item/293533#page/5/mode/1up

Kittel G (1879) Systematische Uebersicht der Käfer, welche in Baiern und der nächsten Umgebung vorkommen. (Fortsetzung). Correspondenz-Blatt des Zoologisch-Mineralogischen Vereines in Regensburg 33: 39–40. https://www.biodiversitylibrary.org/item/43470#page/45/mode/1up

Kiesenwetter EAH von, Schaum HR (1849) Catalogus coleopterorum Europae. Bautzen, 82 + [7] pp. https://www.biodiversitylibrary.org/item/47880#page/5/mode/1up

Kliment J (1899) Čeští brouci. Dílo o broucích Čech, Moravy a Slezska. [Czech beetles. A study on beetles of Bohemia, Moravia and Silesia]. J. Kliment, Německý Brod, xvi + 811 pp. [in Czech] https://kramerius5.nkp.cz/view/uuid:28e81840-2dc5-11de-a5a9-000d606f5dc6?page=uuid:96b33db0-e365-11e6-8010-005056827e51

Klug JChF (1843) Die Coleopteren-Gattungen: *Athyreus* und *Bolboceras*, dargestellt nach den in der Sammlung hiesiger Königl. Universität davon vorhandenen Arten. Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin 1843(1): 21–57 + pls 1–2. https://www.biodiversitylibrary.org/item/92691#page/51/mode/1up

Knörzer A (1912) Deutschlands wärmste Gegenden und ihre Insektenfauna. Bulletin de la Société d'Histoire Naturelle de Colmar, Nouvelle Série 9: 1–24. https://doi.org/10.5962/bhl.title.8778

Koča G (1906) Popis tvrdokrilaca (kornjaša) Vinkovačke okoline. Enumeratio coleopterorum circa Vinkovce inventorum. Glasnik Hrvatskoga Naravoslovnoga Društva 17: 119–212. [in Croatian] https://www.biodiversitylibrary.org/item/42301#page/129/mode/1up

Koch K (1989) Die Käfer Mitteleuropas, Ökologie. Band 2. Goecke & Evers, Krefeld, 382 pp.

Köhler F, Klausnitzer B (1998) Entomofauna Germanica. Band 1. Verzeichnis der Käfer Deutschlands. Entomologische Nachrichten und Berichte (Beiheft 4): 1–185.

Koleška Z (1979) Seznam biografií československých entomologů (entomologové nežijící) – 15. pokračování. Šlégl František. [Biographies of Czechoslovak entomologists (entomologists deceased) – Part 15. Šlégl František]. Klapalekiana 31(Supplementum): 578. [in Czech]

Koleška Z (1981) Seznam biografií československých entomologů (entomologové nežijící) – 15. pokračování. Thurnher Václav, Ing. [Biographies of Czechoslovak entomologists (entomologists deceased) – Part 15. Thurnher Václav, Ing.] Klapalekiana 31(Supplementum): 623. [in Czech]

Koleška Z (1985) Seznam biografií československých entomologů (entomologové nežijící). I. Pokračování 7. Kyselý Karel. [Biographies of Czechoslovak entomologists (entomologists deceased). I. Part 7. Kyselý Karel]. Zprávy Československé Společnosti Entomoogické při ČSAV 21(Supplementum A): 236. [in Czech]

Koleška Z (1995a) Seznam biografií československých entomologů (entomologové nežijící) – 15. pokračování. Šlégl František. [Biographies of Czechoslovak entomologists (entomologists deceased) – Part 15. Šlégl František]. Klapalekiana 31(Supplementum): 578. [in Czech]

Koleška Z (1995b) Seznam biografií československých entomologů (entomologové nežijící) – 15. pokračování. Thurnher Václav, Ing. [Biographies of Czechoslovak entomologists (entomologists deceased) – Part 15. Thurnher Václav, Ing.]. Klapalekiana 31(Supplementum): 623. [in Czech]

Kollár L, Smetana V (1994) Skarabeusovité (Coleoptera, Scarabaeidae) v zbierkach Tekovského múzea v Leviciach. (Scarab beetles (Coleoptera, Scarabaeidae) in the collections of Tekov museum in Levice). Acta Musei Tekoviensis Levice 2: 63–80. [in Slovak with English abstract] https://www.muzeumlevice.sk/images/dokumenty/zborniky/Z2/z2-08-Kollar.pdf

Kolouch LR (2002) Kartografické čtverce – možnost jejich stanovení z mapových podkladů. Cartographic squares – possibility of their designation from maps. Malacologica Bohemoslovaca 1: 7–9. [in Czech with English summary] https://doi.org/10.5817/MaB2002-1-7

Koren T (2017) The status and occurrence of *Bolbelasmus unicornis* Schrank, 1789 (Coleoptera: Geotrupidae) in Croatia. Acta Zoologica Bulgarica 69(1): 139–142. https://www.acta-zoologica-bulgarica.eu/downloads/acta-zoologica-bulgarica/2017/69-1-139-142.pdf

Köteles L, Bakonyi G (1996) First record on the Scarabaeoidea (Coleoptera) fauna of Gödöllő (Hungary). Folia Entomologica Hungarica 57: 97–104. http://publication.nhmus.hu/pdf/folentom/FoliaEntHung_1996_Vol_57_97.pdf

Kovachev VT (1905) Prinos kam izuchavaneto na entomologichnata fauna na Bulgaria. [Contribution to the study of the Bulgarian insect fauna]. Godishnik Rusenskata Gimnaziya 1904–1905: 3–12. [in Bulgarian]

Kral H (1915) Die Käfer aus dem Gebiete des Kummergebirges. Mitteilungen aus dem Vereine der Naturfreunde in Reichenberg 42: 49–100.

Král D (2006) Metodika monitoringu evropsky významného druhu chrobák jednorohý (*Bolbelasmus unicornis*). [Monitoring methods for earth-borer beetle *Bolbelasmus unicornis*, the species of European importance]. Agentura ochrany prírody a krajiny ČR, Prague, 7 pp. [in Czech]

Král D, Malý V (1993) New records of Scarabaeoidea (Coleoptera) from Bulgaria. Acta Societatis Zoologicae Bohemicae 57: 17–29. https://www.zoospol.cz/ixadmin/app/webroot/uploads/15-12-2017/1993/1993%201.pdf

Král D, Löbl I, Nikolajev GV (2006) Family Bolboceratidae Mulsant, 1842. In: Löbl I, Smetana A (Eds) Catalogue of Palaearctic Coleoptera. Volume 3. Scarabaeoidea – Scirtoidea – Dascilloidea – Buprestoidea – Byrrhoidea. Apollo Books, Stenstrup, 82–84. http://www.apollobooks.dk/palaearcticcoleoptera.htm

Král D, Bezděk A, Juřena D (2018) Coleoptera: Scarabaeoidea: Geotrupidae, Trogidae, Glaresidae, Lucanidae, Ochodaeidae, Glaphyride. Icones insectorum Europae centralis. Folia Heyrovskyana. Serie B 32: 1–28. https://www.zin.ru/animalia/coleoptera/pdf/kral_bezdek_jurena_2018-icones.pdf

Krell F-Th (1998) Familienreihe Lamellicornia. In: Lucht W, Klausnitzer B (Eds) Die Käfer Mitteleuropas 15 (4. Supplementband). Goecke & Evers, Krefeld, 285–295.

Krikken J (1977) The genus *Bolbelasmus* Boucomont in Asia, with notes on species occurring in other regions (Coleoptera: Geotrupidae). Zoologische Mededelingen 51: 278–292. https://repository.naturalis.nl/pub/319326/ZM1977051017.pdf

Krikken J (1979) The genus *Bolbocerosoma* Schaeffer in Asia (Coleoptera: Geotrupidae). Zoologische Mededelingen 54: 35–51. https://repository.naturalis.nl/pub/318362/ZM1979054003.pdf

Krynicki I [= J] [= Krinitskiy IA] (1832) Enumeratio Coleopterorum Rossiae meridionalis et praecique in Universitatis Caesareae Charkoviensis circulo obvenientium, quae annorum 1827–1831 spatio observavit. Bulletin de la Société Impériale des Naturalistes de Moscou 5: 65–179 + pls ii–iii. https://www.biodiversitylibrary.org/item/124268#page/71/mode/1up

Kubicka A (1981) Scarabaeids (Coleoptera, Scarabaeidae) of Warsaw and Mazovia. Memorabilia Zoologica 34: 145–164. https://rcin.org.pl/dlibra/publication/25816/edition/36733/content

Kuhnt P (1912) Illustrierte Bestimmungstabellen der Käfer Deutschlands. Ein Handbuch zum genauen und leichten Bestimmen aller in Deutschland vorkommenden Käfer. Mit 10 000, alle wichtigen Bestimmungsmerkmale illustrierenden Text-Abbildungen. E. Schweizerbart'sche Verlagsbuchhandlung Nägele & Dr. Sproesser, Stuttgart, vii + 1138 pp.

Kulikovskiy EA (1897) Materialy dlya fauny Coleoptera Yuzhnoy Rossii. Die Käferfauna v. Süd-Russlands. Zapiski Novorossiyskago Obshchestva Yestestvoispytateley 21: 1–278. [in Russian]

Kuntze R, Noskiewicz J (1938) Zarys zoogeografii polskiego Podola. Versuch einer Zoogeographie des polnischen Podoliens. Prace naukowe, dział II., tom IV. Wydawnictwo Towarzystwa Naukowego we Lwowie, Lviv, vii + 538 pp. [in Polish with German summary] https://baza.biomap.pl/en/getpdf/4574_Kuntze_et_Noskiewicz_1938.pdf

Kutasi Cs (2002) Védett bogarak (Coleoptera) a Vértes-hegységből és környékéről. [Protected beetles (Coleoptera) from the Vértes mountain range and its surroundings]. Limes 2002(1): 35–45. [in Hungarian] https://adt.arcanum.com/en/view/Limes_2002/?pg=238&layout=s

Kuthy D (1898) A Magyar birodalom állatvilága. A Magyar birodalomból eddig ismert állatok rendszeres lajstroma. Fauna regni Hungariae. Animalium Hungariae hucusque cognitorum enumeratio systematica. Editio separata. III. Arthropoda (Insecta, Coleoptera). Királyi Magyar Természettudományi Társulat, Budapest, 213 pp. [in Hungarian and Latin] http://eprints.edk.oee.hu/534/1/hk_153_magyar_birodalom_allatvilaga_opt.pdf

Laco [= Laczó] J (1928) Fauna chrobákov z okolia Bolešov-Piechova neďaleko Trenčína, Slovakia. Fauna Coleopterorum ex pagu Bolešov-Piechov prope Trenčín, Slovakia. In: Laco [= Laczó] J (Ed.) Chrobákoveda. Vol. III. Popis nových chrobákov. Fauna chrobákov Slovenska, župy Trenčianskej, okolia Bratislavy a okolia Bolešov-Piechov. [Coleopterology. Vol. III. Description of new beetles. Fauna of the beetles of Slovakia, the county of Trenčín, the vicinity of Bratislava and the vicinity of Bolešov-Piechov] Jozef Laco [= József Laczó] [litography], Bratislava, 1–35. [chapters paginated separately] [in Slovak and Latin] https://sk.wikipedia.org/wiki/Chrob%C3%A1koveda

Lacordaire Th (1856) Histoire naturelle des insectes. Genera des Coléoptères ou exposé méthodique et critique de tous les genres proposés jusqu'ici dans cet ordre d'insectes. Tome

troisième contenant les familles des Pectinicornes et Lamellicornes. Roret, Paris, 594 pp. https://doi.org/10.5962/bhl.title.8864

Laczó J (1905) Kirándulás a bolessói erdőkben fekvő csepkőbarlanghoz. [Excursion to the stalactite cave in the Bolešov forests]. A Trencsén Vármegyei Természettudomanyi Egylet 27–28: 251–255. [in Hungarian]

Lane SA, Mann DJ (2016) A review of the status of the beetles of Great Britain. The stag beetles, dor beetles, dung beetles, chafers and their allies – Lucanidae, Geotrupidae, Trogidae and Scarabaeidae. Species Status 31: 1–118. http://publications.naturalengland.org.uk/file/6560814490714112

Lapini L, Dorigo L, Glerean P, Giovannelli MM (2013) Status di alcune specie protette dalla direttiva habitat 92/43/CEE nel Friuli Venezia Giulia (Invertebrati, Anfibi, Rettili, Mammiferi). Gortania. Atti del Museo Friulano di Storia Naturale Botanica Zoologica 35: 61–139. http://www.civicimuseiudine.it/images/MFSN/Gortania/Gortania%2035_BZ/GORT35%2061-139%20Lapini%20LR.pdf

Laporte de Castelnau FLNC (1840) Histoire naturelle des insectes Coléoptères, avec une introduction renfermant l'anatomie et la physiologie des animaux articulés, par M. Brullé; ouvrage accompagné de 155 planches gravées sur acier représentant plus de 800 sujets. Tome deuxième. P. Duménil, Paris, 563 + [1] pp. + 38 pls. https://doi.org/10.5962/bhl.title.35290

Lawrence JF, Newton Jr AF (1995) Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names). In: Pakaluk J, Ślipiński SA (Eds) Biology, Phylogeny, and Classification of Coleoptera: Papers Celebrating the 80th Birthday of Roy A. Crowson. Museum i Instytut Zoologii PAN, Warsaw, Poland, 779–1006. https://www.zin.ru/animalia/coleoptera/pdf/lawrence_newton_1995_families_and_subfamilies_coleoptera_part-1.pdf

Lelo S (2006) Popis balegara (Insecta: Scarabaeoidea) Bosne i Hercegovine. Checklist of dung beetles (Insecta: Scarabaeoidea) of Bosnia and Herzegovina. Prilozi Fauni Bosne i Hercegovine 2: 8–31. [in Bosnian with English abstract] http://faunabih.com/wp-content/uploads/2018/09/No.-002c.pdf

Lelo S, Kašić-Lelo M (2010) Biodiverzitet listorožaca (Insecta: Coleoptera: Scarabaeoidea) Bosne i Hercegovine. Biosistematski prijegled podatakasa preliminarnim kartama rasprostranjenja. [Biodiversity of scarab beetles (Insecta: Coleoptera: Scarabaeoidea) of Bosnia and Herzegovina. Biosystematic overview of data with preliminary distribution maps]. Udruženje za inventarizaciju i zaštitu životinja, Ilijaš, 70 pp. [in Bosnian]

Link A, Mitter H, Ockermüller E, Hauser E 2011: Untersuchungen zum Vorkommen der beiden FFH-Arten *Bolbelasmus unicornis* (SCHRANK 1789) und *Cucujus cinnaberinus* (SCOPOLI 1763) im Natura 2000-Gebiet „Untere Traun". Linz, 23 pp. [unpublished report for the Nature Conservation Department of Upper Austria, Linz]

Löbl I, Löbl D (2016) References. In: Löbl I, Löbl D (Eds) Catalogue of Palaearctic Coleoptera. Volume 3: Scarabaeoidea – Scirtoidea – Dascilloidea – Buprestoidea – Byrrhoidea. Revised and Updated Edition. Brill, Leiden & Boston, 627–961. https://doi.org/10.1163/9789004309142_004

Lodos N, Önder F, Pehlivan E, Atalay R, Erkin E, Karsavuran Y, Tezcan S, Aksoy S (1999) Faunistic studies on Scarabaeoidea (Aphodiidae, Cetoniidae, Dynastidae, Geotrupidae, Glaphyridae, Hybosoridae, Melolonthidae, Ochodaeidae, Rutelidae, Scarabaeidae) (Coleoptera) of western Black Sea, central Anatolia and Mediterranean regions of Turkey. Department of Plant Protection, Faculty of Agriculture, University of Ege, İzmir, 63 pp.

Łomnicki MA (1913) Wykaz chrząszczów czyli Tęgopokrywych (Coleoptera) ziem polskich. (Catalogus coleopterorum Poloniae). [List of beetles or coleopterans (Coleoptera) of Poland (Catalogus coleopterorum Poloniae)]. Kosmos 38: 21–155. [in Polish] https://baza.biomap.pl/en/getpdf/5282_Lomnicki_MA_1913.pdf

Luigioni P (1929) I Coleotteri d'Italia. Catalogo sinonimico-topografico-bibliografico. Memorie della Pontificia Accademia delle Scienze – I Nuovi Lincei, Serie II 13: 1–1130.

Lumaret J-P (1990) Atlas des Coléoptères Scarabèides Laparosticti de France. Série des Inventaires de Faune et de Flore 1: 1–419. https://bibliotheques.mnhn.fr/EXPLOITATION/infodoc/ged/viewportalpublished.ashx?eid=IFD_FICJOINT_IFAFL_S000_1980_T001_N000_1

Machatschke JW (1969) Familienreihe Lamellicornia. In: Freude H, Harde KW, Lohse GA (Eds) Die Käfer Mitteleuropas, Band 8. Teredilia, Heteromera, Lamellicornia. Goecke & Evers, Krefeld, 265–371.

Madon P (1930) Pics, Grimpereaux, Sittelles, Huppes; leur régime (fin). Alauda, Série 1 2(3–4): 206–240. https://www.biodiversitylibrary.org/item/291971#page/56/mode/1up

Majzlan O (2006) Faunistické príspevky zo Slovenska (Coleoptera) 2. Faunistic notes on beetles (Coleoptera) 2. from Slovakia. Naturae Tutela 10: 195–200. [in Slovak with English abstract] http://www.ses.entomology.sk/prace/pdf-prace/fauna-2.pdf

Majzlan O (2007) Chrobáky (Coleoptera) PR Ostrov Kopáč pri Bratislave. Beetles (Coleoptera) of the Nature Reserve Ostrov Kopáč near Bratislava. In: Majzlan O (Ed.) Príroda ostrova Kopáč. Fytoterapia OZ pri Pedagogickej fakulte UK, Bratislava, 151–196. [in Slovak with English abstract]

Majzlan O (2016) Chrobáky (Coleoptera) v Národnej prírodnej rezervácii Burdov. Beetles (Coleoptera) in the Burdov National Nature Reserve. Ochrana Prírody 27: 48–88. [in Slovak with English abstract] http://www.sopsr.sk/publikacie/ved_casopis_OP_27_final.pdf

Majzlan O (2018) Faunistické príspevky zo Slovenska – Coleoptera 13. Faunistic notes on beetles from Slovakia – Coleoptera 13. Naturae Tutela 22: 245–248. [in Slovak with English abstract] https://www.smopaj.sk/sk/documentloader.php?id=2155&filename=naturae%20tutela_22_2%20na%20internet.pdf

Majzlan O (2020) Chrobáky (Coleoptera) pod pohorím Burda (južné Slovensko). Beetles (Coleoptera) under the Burda Mountains (south Slovakia). Naturae Tutela 24: 47–70. [in Slovak with English abstract] https://www.smopaj.sk/sk/documentloader.php?id=2707&filename=naturae%20tutela%2024_2%20net.pdf

Majzlan O, Rychlík I, Korbel L (2005) Chrobáky (Coleoptera). In: Majzlan O (Ed.) Fauna Devínskej Kobyly. [Fauna of Devínska Kobyla]. Asociácia priemyslu a ochrany prírody, Bratislava, 89–114. [in Slovak]

Malesevics E (1892) Losoncz faunája, vagyis az 1876. év őszétől, az 1891. év végeig talált és maghatározott állatfajok rendszeres felsorolása és a fauna jellemzése. [Fauna of Lučenec,

a systematic review of the species found and identified from the autumn of 1876 to the end of 1891, and the characterization of the fauna]. A Losonci Magyar Királyi Állami Főgymnasium Értesítője 1891–1892: 3–47. [in Hungarian] https://adt.arcanum.com/en/view/Losonc_18594_AllamiFoGimnazium_18615_1891/?pg=4&layout=s

Manee AH (1908) Some Observations at Southern Pines, N. Carolina. Entomological News and Proceedings of the Entomological Section of the Academy of Natural Sciences of Philadelphia 19: 459–462 + pls xx–xxi. https://www.biodiversitylibrary.org/item/20252#page/525/mode/1up

Mann DJ (2012) Family Geotrupidae Latreille, 1802. In: Duff AG (Ed.) Checklist of Beetles of the British Isles. 2nd Edn. Pemberley Books, Iver, 55–55. https://www.coleoptera.org.uk/sites/www.coleoptera.org.uk/files/imce/coleoptera/checklist2012.pdf

Manolache CI (1930) Colecţia Coleopterelor din laboratorul de Zoologie Descriptivă din Bucureşti donată de W. Knechtel senior. [Collection of Beetles of the laboratory of Descriptive Zoology in Bucharest donated by W. Knechtel senior]. Buletinul Societăţii Studenţilor în Ştiinţe Naturale din Bucuresti: 1: 18–20. [in Romanian]

Markovich A (1909) Prinos za nasekomnata fauna v Razgradska okolnost. [Contribution to the insect fauna in the Razgrad surroundings]. Sbornik za Narodni Umotvoreniya, Nauka i Knizhnina 25(3): 1–20 [articles paginated separately]. [in Bulgarian] http://digilib.nalis.bg/xmlui/handle/nls/26358

Martín-Piera F, López-Colón JI (2000) Coleoptera – Scarabaeoidea I. Fauna Ibérica. Vol. 14. Museo Nacional de Ciencias Naturales & Consejo Superior de Investigaciones Científicas, Madrid, 526 + [1] pp.+ pls 117–123 + [1] p. http://www.fauna-iberica.mncn.csic.es/english/publicaciones/fi14.php

Martynov VV (2003) Novye i interesnye nakhodki plastinchatousykh zhukov (Coleoptera: Scarabaeoidea) na territorii Ukrainy. New and interesting records of Lamellicorn beetles (Coleoptera: Scarabaeoidea) from Ukraine. Izvestiya Kharkovskogo Entomologicheskogo Obshchestva 10[= 2002](1–2): 51–56. [in Russian with English summary] https://www.zin.ru/Animalia/coleoptera/pdf/martynov_2002.pdf

Martynov VV (2012) Kontrolnyy spisok plastinchatousykh zhukov (Coleoptera: Scarabaeoidea) fauny Ukrainy. A checklist of lamellicorn beetles (Coleoptera: Scarabaeoidea) of the Ukraine. Izvestiya Kharkovskogo Entomologicheskogo Obshchestva 20(2): 11–44. [in Russian with English and Ukrainian abstracts] http://www.irbis-nbuv.gov.ua/cgi-bin/irbis_nbuv/cgiirbis_64.exe?C21COM=2&I21DBN=UJRN&P21DBN=UJRN&IMAGE_FILE_DOWNLOAD=1&Image_file_name=PDF/Vkhet_2012_20_2_5.pdf

Marseul SM de (1857) Catalogue des Coléoptères d'Europe. Paris, xvi +200 pp. https://doi.org/10.5962/bhl.title.66031

Medvedev SI (1965) 26. Sem. Scarabaeidae – plastinchatousyye. [26th family: Scarabaeidae – scarab beetles]. In: Bey-Biyenko GYa (Ed.) Opredelitel nasekomykh evropeyskoy chasti SSSR v pyati tomakh. II. Zhestokrylyye i veyerokrylyye. [The key to the identification of insects of the European part of the USSR in five volumes. II. Coleoptera and Strepsiptera]. Nauka, Moskva-Leningrad, 166–208. [in Russian] https://www.zin.ru/animalia/coleoptera/pdf/Part_vol2pp160-208.pdf

Merkl O (2003) Bogarak. Futrinkák, cincérek, katicabogarak és más bogárcsaládok a Kárpát-medencében. [Insects. Ground beetles, longhorn beetles, ladybird beetles and other beetle families in the Carpathian Basin]. Kossuth Kiadó, Budapest, 112 pp. [in Hungarian]

Merkl O (2014) Szarvas álganéjtúró *Bolbelasmus unicornis* (Schrank, 1789). [Earth-borer beetle Bolbelasmus unicornis (Schrank, 1789)]. In: Haraszthy L (Ed.) Natura 2000 fajok és élőhelyek Magyarországon. [Natura 2000 species and habitats in Hungary]. Pro Vértes Közalapítvány, Csákvár, 243–245. [in Hungarian] https://termeszetvedelmikezeles.hu/adatlap-allatok?showAll=0&id=833

Merkl O (2015) Szarvas álganéjtúró *Bolbelasmus unicornis* (Schrank, 1789). [Earth-borer beetle *Bolbelasmus unicornis* (Schrank, 1789)]. In: Deli T, Danyik T (Eds) A Körös-Maros Nemzeti Park állatvilága. Gerinctelenek. A Körös-Maros Nemzeti Park természeti értékei II. [Fauna of the Körös-Maros National Park. Invertebrates. Natural values of the Körös-Maros National Park II]. Körös-Maros Nemzeti Park Igazgatóság, Szarvas, 388–389. [in Hungarian]

Merkl O, Szénási V (2018) A Turjánvidék Natura 2000 terület déli részének bogárfaunája (Coleoptera). The beetle (Coleoptera) fauna of the southern part of the Turjánvidék Natura 2000 site. Rosalia 10: 509–638. [in Hungarian with English abstract] http://turjanvidek.hu/media/statikus/Rosalia_10_pp_509-638.pdf

Merkl O, Vig K (2009) Bogarak a Pannon régióban. [Beetles in the Pannonian region]. B. K. L. Kiadó, Szombathely, 494 pp. [in Hungarian]

Merkl O, Ködöböcz V, Deli T, Danyik T (2014) Bogárfaunisztikai adatok a Dél-Tiszántúlról (Coleoptera). Faunistic data to the beetles from the south-eastern Great Hungarian Plain (Coleoptera). Crisicum 8: 99–152. [in Hungarian with English abstract] http://real.mtak.hu/126102/1/99_152_Merkl_Crisicum_8_2014.pdf

Miessen G (2011) Quelques commentaires sur le genre *Bolbelasmus* Boucomont, 1911 et description d'une nouvelle espèce de Chypre. Lambillionea 111: 109–119.

Miessen G, Trichas A (2011) Description d'un nouveau *Bolbelasmus* Boucomont, 1911 du sud de l'Archipel Egéen (Coleoptera, Scarabaeoidea, Bolboceratidae). Lambillionea 111: 182–188.

Mikšić R (1953) Fauna Insectorum Balcanica. Scarabaeidae. 15. Beitrag zur Kenntnis der Scarabaeiden. 15. Prilog poznavanju Scarabaeidae. Godišnjak Biološkog Instituta u Sarajevu 6: 49–281. [in German and Bosnian]

Mikšić R (1958) Scarabaeidae Jugoslavije. Prvi dio. [Scarabaeidae of Yugoslavia. First part]. Naučno društvo Bosne i Hercegovine, Odjeljenje privredno-tehničkih nauka, 150 pp. [in Bosnian]

Mikšić R (1959) Dritter Nachtrag zur „Fauna Insectorum Balcanica – Scarabaeidae" (30. Beitrag zur Kenntnis der Scarabaeiden). Godišnjak Biološkog Instituta Univerziteta u Sarajevu 12: 47–136.

Mikšić R (1960) Die Scarabäiden Jugoslawiens. Systematische Monographie. I. Teil. Biološki Glasnik 13: 313–343.

Mikšić R (1970) Katalog der Lamellicornia Jugoslawiens (Insecta – Coleoptera). Institut za Šumarstvo, Sarajevo, 71 pp.

Miller E, Zubowsky N (1917) Materialy po entomologicheskoy faune Bessarabii. [Materials on the insect fauna of Bessarabia]. Trudy Bessarabskago Obshchestva Yestestvoispytateley i Lyubiteley Yestestvoznaniya 6(1914–1915): 119–150. [in Russian]

Miquel ME, Vasko BN [= BM] (2014) A study of the association of *Odonteus armiger* (Scopoli, 1772) (Coleoptera: Geotrupidae) with the European rabbit. Journal of Entomology and Zoology Studies 1(6): 157–167. https://www.entomoljournal.com/vol1Issue6/Issue_Dec_2013/31.2.pdf

Mitter H (2000) Die Käferfauna Oberösterreichs (Coleoptera: Heteromera und Lamellicornia). Beiträge zur Naturkunde Oberösterreichs 8: 3–192. https://www.zobodat.at/pdf/BNO_0008_0003-0192.pdf

Mollandin de Boissy R (1906) Communications. Sur *Bolboceras gallicum* Muls. (Col.). Bulletin de la Société Entomologique de France 1906(13): 178. https://doi.org/10.3406/bsef.1906.23946

Montandon AL (1906) Notes sur la faune entomologique de la Roumanie. Buletinul Societății de Științe din București – România 15: 30–80. https://www.biodiversitylibrary.org/item/39574#page/36/mode/1up

Montreuil O (2014) Bolboceratidae. In: Tronquet M (Ed.) Catalogue des Coléoptères de France. Association Roussillonnaise d'Entomologie, Perpignan, 376–376.

Mulsant E, Rey C (1871) Histoire naturelle des Coléoptères de France. Lamellicornes – Pectinicornes. A. Deyrolle, Paris, [4] + 735 + [1] + 42 + [3] pp. , 3 pls. https://doi.org/10.5962/bhl.title.8758

Murraj Xh (1962) Kontribut për faunën e krahëfortëve (Coleoptera) të vendit tonë. Contribution à la faune des Coléoptères en Albanie. Buletin i Universitetit Shtetëror të Tiranës, Seria Shkencat Natyrore 16: 118–128. [in Albanian with French summary]

Nádai L (2006) A Bolboceratinae alcsalád magyarországi fajainak lelőhelyadatai (Coleoptera, Scarabaeoidea: Geotrupidae). Hungarian localities of the species of Bolboceratinae (Coleoptera, Scarabaeoidea: Geotrupidae). Folia Historico-Naturalia Musei Matraensis 30: 205–210. [in Hungarian with English abstract] https://matramuzeum.nhmus.hu/sites/default/files/nhmusfiles/kiadvanyok/folia/vol30/205_210Matra.pdf

Neculiseanu Z, Dănilă A, Cilipic G (2002) Lista insectelor rare și amenințate cu dispariția din Republica Moldova. *Bolbelasmus unicornis* Schrank, 1798. [List of rare and endangered insects in the Republic of Moldova: *Bolbelasmus unicornis* Schrank, 1798]. SalvaEco, Chișinău. [in Romanian] https://www.salvaeco.org/insecte/page/bolbelasmus_unicornis.php [accessed 4 December 2021]

Nedyalkov N (1906) Prinos kam entomologichnata fauna na Bulgaria. [A contribution to the Bulgarian insect fauna]. Periodichesko Spisanie na Bulgarskoto Knizhnovno Druzhestvo v Sofia 17[=1905]: 404–439. [in Bulgarian] http://digilib.nalis.bg/xmlui/handle/nls/28595

Nedyalkov N (1909) Peti prinos kam entomologichnata fauna na Bulgaria. [Fifth contribution to the Bulgarian insect fauna]. Sbornik za Narodni Umotvoreniya, Nauka i Knizhnina 25(3): 1–37 [articles paginated separately]. [in Bulgarian] http://digilib.nalis.bg/xmlui/handle/nls/26358

Németh T (2013) Trip reports, VI.2013, Isaszeg. Hungarian Natural History Museum, Department of Zoology, Budapest. http://coleocoll.nhmus.hu/kepek/TRIPREPORTS/Reports/2013.VI.Isaszeg_english.html [accessed 15 December 2020]

Németh T (2015) Szarvas álganéjtúró. [Earth-borer beetle *Bolbelasmus unicornis*]. Élet és Tudomány 70: 1119. [in Hungarian] http://epa.oszk.hu/02900/02930/00135/pdf/EPA02930_elet_es_tudomany_2015_35.pdf

Nikolajev GV, Král D, Bezděk A (2016) family Geotrupidae Latreille, 1802. In: Löbl I, Löbl D (Eds) Catalogue of Palaearctic Coleoptera. Volume 3: Scarabaeoidea – Scirtoidea – Dascilloidea – Buprestoidea – Byrrhoidea. Revised and Updated Edition. Brill, Leiden – Boston, 33–52. https://doi.org/10.1163/9789004309142_003

Niţu E (2001) Edaphic and subterranean Coleoptera from the Dobrogean karstic areas (Romania). A zoogeographic approach. Mitteilungen aus den Hamburgischen Zoologischen Museum und Institut 98: 131–169.

Niţu E (2007) Studii eco-faunistice asupra asociaţiilor de coleoptere edafice din zona Sic-Păstăraia (Câmpia Transilvaniei). Eco-faunistic studies on the soil Coleoptera in the Sic-Păstăraia area (Transylvanian Plane). Analele Institutului de Cercetări şi Amenajări Silvice 50: 153–167. [in Romanian with English abstract] http://www.editurasilvica.ro/analeleicas/50/1/nitu.pdf

Novák I (1989) Seznam lokalit a jejich kódů pro síťové mapování entomofauny Československa. [List of localities and their codes for grid mapping of entomofauna of Czechoslovakia]. Zprávy Československé Společnosti Entomologické při ČSAV 25: 3–84. [in Czech]

Nuß M, Jäger O (2020) Vierzähniger Mistkäfer (*Bolbelasmus unicornis* Schrank, 1789). Insekten Sachsen. https://www.insekten-sachsen.de/pages/TaxonomyBrowser.aspx?id=188691 [accessed 22 April 2022]

Oechsner G (1854) Die Käfer der Umgegend Aschaffenburgs. Ein Beitrag zu den Lokalfaunen Bayerns. Programm der königlichen Landwirtschafts- und Gewerbs-Schule zu Aschaffenburg zur Feier ihrer öffentlichen Schlussprüfung und Preisevertheilung im Schuljahre 1853 in 1854. Wailandt, Aschaffenburg, iv. + 48 pp. http://digital.bib-bvb.de/view/bvb_single/single.jsp?dvs=1639010751724~0&locale=cs&VIEWER_URL=/view/bvb_single/single.jsp?&DELIVERY_RULE_ID=39&bfe=view/action/singleViewer.do?dvs=&frameId=1&usePid1=true&usePid2=true

Oertzen E von (1886) Verzeichniss der Coleopteren Griechenlands und Cretas, nebst einigen Bemerkungen über ihre geographische Verbreitung und 4 die Zeit des Vorkommens einiger Arten betreffenden Sammelberichten. Berliner Entomologische Zeitschrift 30: 189–293. https://www.biodiversitylibrary.org/item/100061#page/231/mode/1up. https://doi.org/10.1002/mmnd.18870300211

Ohaus F (1929) Aus der Praxis des Käfersammlers. XII. Über das Sammeln und Züchten von Mistkäfern. Koleopterologische Rundschau 15: 141–150. https://www.zobodat.at/pdf/KOR_15_1929_0141-0150.pdf

Ohloblin [= Ogloblin] DO (1913) Materialy k izucheniu Coleoptera Poltavskoy gub. Contribution à la faune des Coleopteres de la gouvernement de Poltawa. Yezhegodnik Yestestvenno-Istoricheskago Muzeya Poltavskago Gubernskago Zemstva 1: 29–36. [in Russian with French title]

Ortvay T (1902) Pozsony vármegye és a területén fekvő Pozsony, Nagyszombat, Bazin, Modor s Szentgyörgy városok állatvilága. Állatrajzi és állatgazdaságtörténeti monografia. Első kötet: állatrajzi rész. [The fauna of Bratislava County and the cities of Bratislava, Trnava, Pezinok, Modra and Svätý Jur. Zoological and zoohistorical monograph. Volume 1: zoological part]. K. Stampfel, Pozsony [= Bratislava], xvi + 647 + [1] pp. [in Hungarian]

Paill W (2007) Wiederfund von *Bolbelasmus unicornis* (SCHRANK, 1789) in den Wiener Donauauen (Coleoptera: Scarabaeoidea: Geotrupidae). (Rediscovery of *Bolbelasmus unicornis* in Vienna's Lobau). Beiträge zur Entomofaunistik 8: 165–171. https://www.zobodat.at/pdf/BEF_8_0165-0171.pdf

Paill W, Mairhuber C (2006) Checkliste und Rote Liste der Blatthornkäfer und Hirschkäfer Kärntens mit besonderer Berücksichtigung der geschützten Arten (Coleoptera: Trogidae, Geotrupidae, Scarabaeidae, Lucanidae). Carinthia II 196/116: 611–626. https://www.zobodat.at/pdf/CAR_196_116_0611-0626.pdf

Paill W, Mairhuber C (2012) Käfer der FFH-Richtlinie in Niederösterreich. Basisdatenerhebung FFH-Käfer Niederösterreich (RU5-S, 845/001-2009). ÖKOTEAM – Institut für Tierökologie & Naturraumplanung OG, Graz, 48 pp. https://www.noe.gv.at/noe/Naturschutz/BDE_Kaefer_2012.pdf

Panin S (1957) Coleoptera: familia Scarabaeidae (subfamiliile: I Coprinae, II Geotrupinae, III Aphodiinae, IV Aegialinae, V Hybosorinae, VI Ochodaeinae, VII Orphninae, VIII Troginae, IX Glaphyrinae, X Sericinae, XIII Hoplinae, XIV Dynastinae, XV Valginae, XVI Trichiinae şi XVII Cetoniinae). Fauna Republicii Populare Romîne. Insecta. Volumul X. Fascicola 4. Editura Academiei R.P.R., Bucureşti, 316 pp. + 36 pls. [in Romanian]

Panzer GWF (1793a) Beyträge zur Geschichte der Insekten. Symbolae Entomologicae. I. Theil. Johan Jakob Palm, Erlangen, 24 pp. + 6 pls.

Panzer GWF (1793b) Faunae insectorum Germanicae initia. Deutschlands Insecten. Heft 12. Felsecker, Nürnberg, 24 pp. + 24 pls. https://doi.org/10.5962/bhl.title.15007

Panzer GWF (1795) Deutschlands Insectenfaune oder entomologisches Taschenbuch für das Iahr 1795. Entomologia Germanica exhibens insecta per Germaniam indigena secundum classes, ordines, genera, species adiectis synonymis, locis, observationibus. I. Eleuterata. Cum tabulis aeneis. Felsecker, Nürnberg, [32] + 370 + [2] pp. + 12 pls. https://doi.org/10.5962/bhl.title.11756

Panzer GWF (1802) Beyträge zur Geschichte der Insekten. Johann Euseb Voets Beschreibungen und Abbildungen hartschaalichter Insecten. Coleoptera Linn. Aus dem Original getreu übersetzt mit der in selbigem fehlenden Synonymie und beständigen Commentar versehen von D. Georg Wolffgang Franz Panzer. Fünfter Theil. Mit zwölf Kupfertafeln. Symbolae Entomologicae. Johann Jacob Palm, Erlangen, [2] + 114 pp. + 12 pls. https://doi.org/10.5962/bhl.title.65761

Paulian R (1941) Coléoptères Scarabéides. Faune de France 38. Paul Lechevalier et Fils, Paris, 240 pp. https://faunedefrance.org/bibliotheque/docs/R.PAULIAN(FdeFr38)Scarabeides1.pdf

Paulian R (1959) Coléoptères Scarabéides. (Deuxième édition, revue et augmentée). Faune de France 63. Éditions Paul Lechevalier, Paris, 298 pp. https://faunedefrance.org/faune-63

Paulian R, Baraud J (1982) Faune des Coléoptères de France II. Lucanoidea et Scarabaeoidea. Encyclopédie Entomologique 43. Éditions Lechevalier S.A.R.L., Paris, 477 pp.

Peez A von, Kahlen M (1977) Die Käfer von Südtirol. Faunistisches Verzeichnis der aus der Provinz Bozen bisher bekannt gewordenen Koleopteren. Selbstverlag des Tiroler Landesmuseum Ferdinandeum, Innsbruck, 525 pp. https://www.zobodat.at/pdf/VeroeffFerd_57_BL_0001-0525.pdf

Pescarolo R (1990) Ricerche sui coleotteri della Valle del Ticino. La Rivista Piemontese di Storia Naturale 11: 81–104. http://www.storianaturale.org/anp/PDF%20ANP/11_1990_Pescarolo_Ricerche%20sui%20Coleotteri%20della%20Valle%20del%20Ticino_81-104.pdf

Peslier S (2004) Clé de détermination illustrée des Geotrupidae de France (Coleoptera, Scarabaeoidea). Revue de l'Association Roussillonnaise d'Entomologie 13: 1–9. https://r-a-r-e.fr/wp-content/uploads/2019/10/2004-XIII-1.pdf

Petersen B, Vischer-Leopold M, Wurst C (2006) *Bolbelasmus unicornis* (Schrank, 1789). In: Petersen B, Ellwanger G (Eds) Das Europäische Schutzgebietssystem Natura 2000. Ökologie und Verbreitung von Arten der FFH-Richtlinie in Deutschland, Band 3: Arten der EU-Osterweiterung. Bundesamt für Naturschutz, Bonn-Bad Godesberg, 85–89.

Petri K (1912) Siebenbürgens Käferfauna auf Grund ihrer Erforschung bis zum Jahre 1911. Siebenbürgishen Verein für Naturwüssenschaften zu Hermannstadt, Hermannstadt, ix + [1] + 376 pp. https://doi.org/10.5962/bhl.title.8978

Petrovitz R (1956) Die koprophagen Scarabaeiden des nördlichen Burgenlandes. Wissenschaftliche Arbeiten aus dem Burgenland, Heft 13. Burgenländisches Landesmuseum, Eisenstadt, 24 pp. https://www.zobodat.at/pdf/Wiss-Arbeiten-Burgenland_013_0001-0024.pdf

Petrovitz R (1959) Beitrag zur Scarabeiden – Fauna der Insel Rhodos. Bollettino del Laboratorio di Entomologia Agraria 17: 124–130.

Pétsch N, Szénási V (2019) (Eds) A HUDI20023 Gödöllői-dombság kiemelt jelentőségű természetmegőrzési terület Natura 2000 fenntartási terve. [Conservation plan for the Natura 2000 priority protected area HUDI20023 Gödöllő Hills]. Duna-Ipoly Nemzeti Park Igazgatóság, Budapest, 126 pp. [in Hungarian] http://dinp.nemzetipark.gov.hu/_user/browser/File/Natura2000/Godolloi_dombsag_Natura2000_fenntartasi_terv_egyeztetesi_anyag.pdf

Pirnat A (2009) Govnač vrste *Bolbelasmus unicornis*. [Earth-borer beetle *Bolbelasmus unicornis*]. In: Vrezec A (Ed.) Izvajanje spremljanja stanja populacij izbranih ciljnih vrst hroščev v letu 2008 in 2009 in zasnova spremljanja stanja populacij izbranih ciljnih vrst hroščev. [Implementation of population monitoring of selected target beetle species in 2008 and 2009, and design of population monitoring of selected target beetle species]. Nacionalni inštitut za biologijo, Ljubljana, and Notranjski muzej Postojna, 113–125. [in Slovenian] http://www.natura2000.si/fileadmin/user_upload/knjiznica/raziskave/Hrosci_monitoring_koncno_porocilo_09.pdf

Pittioni E (1943) Die Käfer von Niederdonau: Die Curti-Sammlung im Museum des Reichsgaues Niederdonau, II. Silphidae – Pythidae. Niederdonau – Natur und Kultur 23: 67–130.

Polentz G (1927) Coleopterologische Streifzüge um Trentschin (Slowekei). Zeitschrift für Entomologie 15: 9–15.

Porta A (1932) Fauna Coleopterorum Italica. Vol V. – Rhynchophora-Lamellicornia. Anthribidae, Brenthidae, Curculionidae, Nemonychidae, Ipidae, Lucanidae, Scarabaeidae. Stabilimento Tipografico Piacentino, Piacenza, 476 pp.

Portevin G (1931) Histoire naturelle des Coléoptères de France. Tome II. Polyphaga: Lamellicornia, Palpicornia, Diversicornia. Encyclopédie Entomologique, Série A, XIII. Paul Lechevalier & Fils, Paris, vi. + [2] + 542 + [1] pp. + pls vi–x. https://documentcloud.adobe.com/link/review?uri=urn:aaid:scds:US:9cd3ab47-d65e-4f06-91cc-7e075579a1c4

Potocký P, Majzlan O (2015) Metodika monitoringu hubára jednorohého *Bolbelasmus unicornis* (Schrank, 1789) (Coleoptera, Geotrupidae). [Monitoring methods for the earth-borer beetle *Bolbelasmus unicornis* (Schrank, 1789) (Coleoptera, Geotrupidae)]. Štátna ochrana prírody SR Banská Bystrica, 15 pp. [in Slovak] https://www.biomonitoring.sk/Monitoring/MonitoringMethodology/DownloadFile/33 [accessed 12 September 2021]

Prossen T (1913) I. Nachtrag zum Verzeichnisse der bisher in Kärnten beobachteten Käfer (3. Fortsetzung und Schluß). Carinthia II 103/23: 74–85. https://www.zobodat.at/pdf/CAR_103_23_0074-0085.pdf

Pruner L, Míka P (1996) Seznam obcí a jejich částí v České republice s čísly mapových polí pro síťové mapování fauny. List of settlements in the Czech Republic with associated map fields codes for faunistic map system. Klapalekiana 32(Supplementum): 1–115. [in Czech with English abstract]

Rabl D, Rabl S, Rabl Ch (2019) Ein neuer Nachweis von *Bolbelasmus unicornis* (Schrank, 1789) (Coleoptera: Geotrupidae) aus dem Naturschutzgebiet Sandberge Oberweiden, Niederösterreich. A new record of *Bolbelasmus unicornis* (Schrank, 1789) (Coleoptera: Geotrupidae) from the nature reserve Sandberge Oberweiden, Lower Austria. Beiträge zur Entomofaunistik 20: 252–254. https://www.zobodat.at/pdf/BEF_20_0252-0254.pdf

Rahola Fabra P (2004) Biologie de *Bolbelasmus gallicus* (Mulsant, 1842) (Coleoptera: Geotrupidae: Bolboceratinae) dans le Department du Gard (Languedoc, sud de la France). Elytron 17: 37–46.

Redtenbacher L (1849) Fauna Austriaca. Die Käfer. Nach der analytischen Methode. Carl Gerold, Wien, xxvii + 883 pp. + 2 pls. https://doi.org/10.5962/bhl.title.37851

Redtenbacher L (1858) Fauna Austriaca. Die Käfer. Nach der analytischen Methode. Zweite, gänzlich umgearbeitete, mit mehreren Hunderten von Arten und mit der Charakteristik sämmtlicher europäischen Käfergattungen vermehrte Auflage. Mit zwei Kupfertafeln. Carl Gerold's Sohn, Wien, cxxxvi + 1017 pp. + 2 pls. https://doi.org/10.5962/bhl.title.9570

Redtenbacher L (1874) Fauna Austriaca. Die Käfer, nach der analytischen Methode. Dritte, gänzlich umgearbeitete und bedeutend vermehrte Auflage. Erster Band. Mit zwei Kupfertafeln. Carl Gerold's Sohn, Wien, 564 pp. https://doi.org/10.5962/bhl.title.9061

Reitter E (1892) Bestimmungs-Tabelle der Lucaniden und coprophagen Lamellicornen. XXIV. Heft. Edmund Reitter, Brno, 230 pp. https://www.zobodat.at/pdf/MON-ECOL_0020_0001-0230.pdf

Reitter E (1909) Fauna Germanica. Die Käfer des Deutschen Reiches. II. Band. Nach der analytischen Methode bearbeitet. Mit 70 Text-Illustrationen und 40 Farbendrucktafeln, zusammengestellt und redigiert von Dr. K. G. Lutz. K. G. Lutz' Verlag; Stuttgart, 392 pp. + pls 41–80. https://www.zin.ru/animalia/coleoptera/pdf/reitter_band_ii_text.pdf

Ressl F, Kust T (2010) Naturkunde des Bezirkes Scheibbs. Tierwelt 4. Wissenschaftliche Mitteilungen aus dem Niederösterreichischen Landesmuseum 20: 11–436. https://www.zobodat.at/pdf/WM_20_0011-0436.pdf

Ritcher PO (1947) Larvae of Geotrupinae with keys to tribes and genera (Coleoptera: Scarabaeidae). Bulletin of the Kentucky Agricultural Experiment Station 506: 1–27. https://dspace.gipe.ac.in/xmlui/bitstream/handle/10973/36161/GIPE-037617.pdf?sequence=3&isAllowed=y

Ritcher PO (1966) White grubs and their allies. A study of North American scarabaeoid larvae. Studies in entomology number four. Oregon State University Press, Corvallis, 219 pp. https://ir.library.oregonstate.edu/downloads/nk322k13b

Ritcher PO, Baker ChW (1974) Ovarioles numbers in Scarabaeoidea (Coleoptera: Lucanidae, Passalidae, Scarabaeidae). Proceedings of the Entomological Society of Washington 76: 480–494. https://www.biodiversitylibrary.org/item/55199#page/510/mode/1up

Rößler G (1989) Bemerkenswerte Käferfunde aus dem nördlichen Burgenland (Carab., Halipl., Dytisc., Hydraen., Hydroph., Staph., Coccin., Scarab., Ceramb., Curcul.). Entomologische Blätter 85: 126–127.

Roubal J (1936) Katalog Coleopter (brouků) Slovenska a Podkarpatské Rusi na základě bionomickém a zoogeografickém a spolu systematický doplněk Ganglbauerových „Die Käfer von Mitteleuropa" a Reitterovy „Fauna Germanica". Díl II. Catalogue des Coléoptères de la Slovaquie et de la Russie Subcarpathique d'après les documents et zoogéographiques ainsi que supplément systématique au Ganglbauer „Die Käfer von Mitteleuropa" et Reitter „Fauna Germanica". Tome II. Učená Společnost Šafaříkova, Bratislava, viii + 434 pp. [in Czech with French introduction]

Roubal J (1938) Thermophile Coleopteren der Slovakei (mit besonderer Berücksichtigung der xerothermicolen Arten) und ihr Eindringen nordwärts der Donau nebst Ergänzung des Lebensbildes der betreffenden Biotope durch andere, nicht exclusiv thermophile Arten. Festschrift zum 60. Geburtstag von Professor Dr. Embrik Strand 4: 405–437.

Rozner I (1984) A Bakony hegység lemezescsápú bogárfaunájának alapvetése I. (Coleoptera: Trogidae & Scarabaeidae). [Fauna of Trogidae and Scarabaeidae (Coleoptera) of the Bakony Mountains I]. Folia Musei Historico-Naturalis Bakonyiensis 3: 71–124. [in Hungarian] https://library.hungaricana.hu/hu/view/SZAK_BAKO_Btmk_03_1984/?pg=72&layout=s

Rozner Gy (2001) Somogy megye dögbogár, sutabogár és lemezescsápú bogár faunája (Coleoptera: Silphidae, Histeridae, Lamellicornia). [Fauna of carrion beetles, clown beetles and lamellicorn beetles (Coleoptera: Silphidae, Histeridae, Lamellicornia) in the Somogy county]. Natura Somogyiensis 1: 161–167. [in Hungarin with English abstract] https://doi.org/10.24394/NatSom.2001.1.161

Rózsay E (1868) Catalogus coleopterorum Posonii et Cassoviae inventorum. A Pozsonyi Királyi Katolikus Főgymnasium Értesítvénye 1867–1868: 13–20. [in Hungarian with Latin title] https://adt.arcanum.com/en/view/Pozsony_28386_KathFogymnasium_28401_1867/?pg=12&layout=s

Rózsay E (1880) Enumeratio Coleopterorum Posoniensium. Adalék Pozsony rovarfaunájának ismeretéhez. [An addition to the knowledge of the insect fauna of Bratislava]. Pozsonyi Természettudományi és Orvosi Egylet Közleményei 1873–1875: 25–54. [in Hungarian with Latin title] https://www.biodiversitylibrary.org/item/192931#page/33/mode/1up

Ruicănescu A, Niţu E (2008) 4011 *Bolbelasmus unicornis*. In: Goriup P (Ed.): Natura 2000 in Romania. Species fact sheets. Ministry of Environment and Sustainable Development,

Bucharest, 302–303. [in English and Romanian] https://www.crayfish.ro/anexe/SpeciesFactSheetsFeb08.pdf

Rybiński M (1897) Wykaz chrząszczów nowych dla fauny galicyjskiej. [List of beetles new to the Galician fauna]. Sprawozdanie Komisyi Fizyograficznej 32(2): 46–62. [in Polish] https://www.biodiversitylibrary.org/item/129225#page/301/mode/1up

Rybiński M (1903) Wykaz chrząszczów zebranych na Podolu galicyjskiem przy szlaku kolejowym Złoczów-Podwołoczyska w latach 1884–1890. [List of beetles collected in Galician Podolia alongside the Zolochivka-Pidvolochysk railway line in 1884–1890]. Sprawozdanie Komisyi Fizyograficznej 37(2): 57–175. [in Polish] https://www.biodiversitylibrary.org/item/129184#page/301/mode/1up

Sainte-Claire Deville J (1936) Catalogue raisonné des Coléoptères de France. L'Abeille 36(2): 161–264.

Sajó K (1881) Daten zur Insekten-Statistik von Kis-Szent-Miklós (Pester Komitat, Bezirk: Waitzen). Zeitschrift für Entomologie Breslau 8: 40–65. https://www.biodiversitylibrary.org/item/213874#page/62/mode/1up

Sajó K (1897) Beitrag zu den Lautäusserungen der Käfer. Illustrierte Wochenschrift für Entomologie 2: 544. https://www.biodiversitylibrary.org/item/98743#page/564/mode/1up

Sajó K (1910a) A szarvasgombák. [The truffles]. Uránia 11: 204–212. [in Hungarian] http://real-j.mtak.hu/10710/1/MTA_Urania_1910.pdf

Sajó K (1910b) Aus der Käferwelt. Mit Rücksicht auf die Beziehungen der Kerfe zur menschlichen Kulturgeschichte. Theodor Thomas, Leipzig, 89 pp.

Sár J, Horvatovich S (2000) Lemezescsápú bogarak (Coleoptera: Lamellicornia) a Villányi-hegységből. Lamellicornia (Coleoptera) from the Villány Hills, South Hungary. Dunántúli Dolgozatok Természettudományi Sorozat 10: 215–222. [in Hungarian with English abstract] https://library.hungaricana.hu/hu/view/MEGY_SOMO_Osborokas_10/?pg=216&layout=s

Savchenko YeM (1931) Beitrag zur Kenntnis der Scarabaeidenfauna Wolyniens. Trudy Pryrodnycho-Tekhnichnoho Viddilu 5: 43–62.

Savchenko YeM (1933) Ohlyad zhukiv-lystorozhtsiv (Coleoptera, Scarabaeidae) Podillya. Uebersicht der Podolischen Blatthornkäfer (Coleoptera, Scarabaeidae). Zbirnyk Prac Zoologichnoho Muzeiu 12: 121–143. [in Ukrainian with German summary]

Savchenko YeM (1934) Fauna zhukiv-lystorozhtsiv (Coleoptera, Scarabaeidae) Kyivshchyny ta yii zooheohrafichnyi kharakter. Fauna der Blatthornkäfer (Scarabaeidae) des Kyjiwer Gebiets und deren zoogeographischer Charakter. Zbirnyk Prac Zoologichnoho Muzeiu 13: 41–85. [in Ukrainian with German and Russian summaries]

Savchenko YeM (1938) Materialy do fauny URSR – plastynchastovusi zhuky (Coleoptera, Scarabaeidae). Beitrag zur Blatthornkäferfauna (Coleoptera, Scarabaeidae) Ukr. SSR. Vydavnytstvo Akademii Nauk URSR, Kyiv, 208 pp. [in Ukrainian with Russian and German summaries]

Schatzmayr A (1936) Risultati scientifici delle cacce entomologiche di S.A.S. il principe Alessandro Della Torre e Tasso nelle isole dell'Egeo. VI. Scarabaeidae. Bollettino Laboratorio Zoologia Generale Agraria Reale Istituto Superiore Agrario Portici 30: 9–23.

Schaufuss C (1916) Calwer's Käferbuch. Einführung in die Kenntnis der Käfer Europas. Band II. E. Schweizerbart'sche Verlagsbuchhandlung Nägele & Dr. Sproesser, Stuttgart, 7pp. 710–1390 + pls 21–48. https://doi.org/10.5962/bhl.title.39556

Scherdlin P (1915) Supplément au Catalogue des Coléoptères de la chaîne des Vosges et des régions limitrophes. Bulletin de la Société d'Histoire Naturelle de Colmar, Nouvelle Série 13: 293–590. https://doi.org/10.5962/bhl.title.8778

Scherdlin P (1920) Deuxième supplément au Catalogue des Coléoptères de la chaîne des Vosges et des régions limitrophes. Bulletin de la Société d'Histoire Naturelle de Colmar, Nouvelle Série 15: 1–255. https://doi.org/10.5962/bhl.title.8778

Schlögl L (1883) Die Coleopteren-Fauna aus dem Marchthale bei Ung. Hradisch (Schluß.). Programm des K. K. Real- und Ober-Gymnasiums in Ungarisch Hradisch in Mähren 1882/1883: 3–30.

Schlosser Klekovski JK (1878) Fauna kornjašah Trojedne Kraljevine. Svezak drugi. [The beetle fauna of the Triune Kingdom. Volume two]. Jugoslavenska akademija znalosti i umjetnosti, Zagreb, 343–726. [in Croatian] http://library.foi.hr/knjige/knjiga1.aspx?B=1&C=X00383&fl=t

Schmölzer K (1989) Beitrag zur Kenntnis der Käferfauna des Eichkogels (NÖ). Sitzungsberichte der Akademie der Wissenschaften Mathematisch-Naturwissenschaftliche Klasse 197: 223–286. https://www.zobodat.at/pdf/SBAWW_197_0223-0286.pdf

Schönherr CJ (1806) Synonymia Insectorum, oder: Versuch einer Synonymie aller bisher bekannten Insecten; nach Fabricii Systema Eleutheratorum geordnet, mit Berichtigungen und Anmerkungen, wie auch Beschreibungen neuer Arten und illuminirten Kupfern. Erster Band. Eleutherata oder Käfer. Erster Theil. Lethrus – Scolytes. Heinr. A. Nordström, Stockholm, xxii + 293 pp. + [1] + 3 pls. https://doi.org/10.5962/bhl.title.66107

Schoolmeesters P (2019) Scarabs: World Scarabaeidae Database (version Jan 2019). In: Roskov Y, Ower G, Orrell T, Nicolson D, Bailly N, Kirk PM, Bourgoin T, DeWalt RE, Decock W, Nieukerken E van, Zarucchi J, Penev L (Eds) Species 2000 & ITIS Catalogue of Life, 2019 Annual Checklist. Naturalis, Leiden. https://www.catalogueoflife.org/annual-checklist/2019 [accessed 19 October 2021]

Schrank von Paula F (1789) Entomologische Beobachtungen. Der Naturforscher 24: 60–90. http://ds.ub.uni-bielefeld.de/viewer/image/2108412_024/65

Schubert F (1905) Die Coleopteren-Fauna von Prosznitz und Umgebung. Jahres-Bericht der Deutschen Landes-Oberrealschule zu Prosznitz 30: 3–27.

Schwarz M (2008) Pilotprojekt: Grundlagen für den Schutz ausgewählter Insektengruppen in Oberösterreich. Abteilung Naturschutz des Landes Oberösterreich, Linz, 159 pp. https://www.zobodat.at/pdf/GUTNAT_0669_0001-0159.pdf

Schweiger H (1951) Käferfang bei Nacht. Entomologisches Nachrichtenblatt Österreichischer und Schweizer Entomologen 3: 193–198. https://www.zobodat.at/pdf/ZAOE_3_0193-0198.pdf

Seidlitz GCM von (1891) Fauna Transsylvanica. Die Kaefer (Coleoptera) Siebenbürgens. Mit 1 Tafel. Hartung, Königsberg, lvi + 192 + 914 pp. + 1 pl. https://doi.org/10.5962/bhl.title.123006

Sevastianov VD (2000) Poperednii opys kolektsii zhukiv I. B. Bertoldi. Preliminary description of I. B. Bertoldi's beetles collection. Visnyk Odeskoho Natsionalnoho Universytetu 5: 295–298. [in Ukrainian with Russian and English summaries] http://dspace.onu.edu.ua:8080/bitstream/123456789/16882/1/295-298.pdf

Sevastianov VD (2001) Poperednii opys kolektsii zhukiv I. B. Bertoldi (povidomlennia druhe). The preliminary description of I. B. Bertoldi's beetles collection (the second report). Visnyk Odeskoho Natsionalnoho Universytetu 6: 222–226. [in Ukrainian with Russian and English summaries] http://dspace.onu.edu.ua:8080/bitstream/123456789/16516/1/222-226.pdf

Sherborn CD (1902) Index animalium sive index nominum quae ab A.D. MDCCLVIII generibus et speciebus animalium imposita sunt societatibus eruditorum adiuvantibus. Sectio prima. A kalendis Ianuariis, MDCCLVIII usque ad finem Decembris, MDCCC. Cambridge, lix + 1071 pp. https://doi.org/10.5962/bhl.title.159249

Sheshurak PN, Voblenko AS, Kavurka VV, Berest ZL, Nazarov NV (2018) Bespozvonochnyye, vnesonnyye v krasnuyu knigu Ukrainy, vstrechayushchiyesya na territorii Chernigovskoy oblasti. [Invertebrates included in the Red Book of Ukraine found on the territory of Chernihiv Oblast]. In: Akimov IA, Kharchenko VO, Kostiushyn VA, Vasyliuk OV (Eds) Materialy do 4-ho vydannia Chervonoi knyhy Ukrainy. Tvarynnyi svit. Tom 2. [Materials for the 4th edn. of the Red Book of Ukraine. Fauna. Volume 2]. Schmalhausen Institute of Zoology of National Academy of Sciences of Ukraine, Kyiv, 367–381. [in Russian] http://mail.izan.kiev.ua/RedBook18_T2_web.pdf#page=368

Sheshurak PN, Voblenko AS, Kavurka VV, Nazarov NV (2020a) Nakhodki nasekomykh, vnesënnykh v prilozheniya Konventsii ob okhrane dikoy fauny i flory i prirodnykh sred obitaniya v Yevrope (Bernskoy konventsii), na territorii Ukrainy. [Faunistic records of insect species included in the Annexes of the Berne Convention on the Conservation of European Wildlife and Natural Habitats in the territory of Ukraine]. In: Kuzemko AA, Sadohurska SS, Holdin PYe, Kavurka VV, Kutsokon YuK, Nekrasova OD, Vasyliuk OV, Prylutskyi OV, Rusin MYu (Eds) Znakhidky vydiv roslyn, tvaryn ta hrybiv, shcho znakhodiatsia pid okhoronoiu, v Ukraini. Seriia: «Conservation Biology in Ukraine». Vypusk 19. Records of protected animal, plant and fungi species in Ukraine. Series: «Conservation Biology in Ukraine», Issue 19. TVORY, Vinnytsia, 613–626. [in Russian] https://uncg.org.ua/wp-content/uploads/2021/01/New_FC-Ed_REDbook_2020_BOOK_print-1.pdf

Sheshurak PN, Voblenko AS, Kavurka VV, Nazarov NV (2020b) Bespozvonochnyye, vnesënnyye v prilozheniya Konventsii ob okhrane dikoy fauny i flory i prirodnykh sred obitaniya v Yevrope (Bernskoy konventsii), vstrechayushchiyesya na territorii Chernigovskoy oblasti. [Invertebrates included in the Annexes of the Berne Convention on the Conservation of European Wildlife and Natural Habitats, found in the territory of the Chernihiv Oblast]. In: Kuzemko AA, Sadohurska SS, Holdin PYe, Kavurka VV, Kutsokon YuK, Nekrasova OD, Vasyliuk OV, Prylutskyi OV, Rusin MYu (Eds) Znakhidky vydiv roslyn, tvaryn ta hrybiv, shcho znakhodiatsia pid okhoronoiu, v Ukraini. Seriia: «Conservation Biology in Ukraine». Vypusk 19. Records of protected animal, plant and fungi species in Ukraine. Series: «Conservation Biology in Ukraine», Issue 19. TVORY, Vinnytsia, 583–612. [in Russian] https://uncg.org.ua/wp-content/uploads/2021/01/New_FC-Ed_REDbook_2020_BOOK_print-1.pdf

Shokhin IV (2007) Materialy k faune plastinchatousykh zhukov (Coleoptera, Scarabaeoidea) Yuzhnoy Rossii. Contribution to the fauna of lamellicorn beetles (Coleoptera, Scarabaeoidea) of Southern Russia, with some nomenclatural changes in the family Scarabaeidae. Kavkazskiy Entomologicheskiy Byulleten' 3(2): 105–185. [in Russian with English abstract] https://doi.org/10.23885/1814-3326-2007-3-2-105-185

Sim RJ (1930) Scarabæidæ, Coleoptera; Observations on species unrecorded or little-known in New Jersey. Journal of the New York Entomological Society 38: 139–147. https://www.biodiversitylibrary.org/item/206060#page/173/mode/1up

Skrimshire W (1812) Remarks on some rare Insects found during a Flood at Wisbech. The Transactions of the Entomological Society of London 1: 315–322. https://books.google.cz/books?id=EMwEAAAAQAAJ&pg=PA70&lpg=PA70&dq=skrimshire,+entomological+transaction&source=bl&ots=mxGokrV7Je&sig=ACfU3U33j33N-gwnwbHUHwqwR3yRJlhLgw&hl=cs&sa=X&ved=2ahUKEwiO2KyQhbzuAhUMxBQKHXVWClkQ6AEwAHoECAEQAg#v=onepage&q=skrimshire%2C%20entomological%20transaction&f=false

Skýpala J (1978) K poznání motýlů československé části Cérové vrchoviny (Lepidoptera). Zur Kenntnis der Schmetterlingsfauna des tschechoslowakischen Teiles von Cérová vrchovina (Lepidoptera). Zprávy Československé Společnosti Entomologické při ČSAV 14: 115–118. [in Czech with German abstract]

Smith ABT (2009) Checklist and Nomenclatural Authority File of the Scarabaeoidea of the Nearctic Realm including Canada, the continental United States, and the northern Mexican states of Baja California, Baja California Sur, Chihuahua, Coahuila de Zaragoza, Durango, Nuevo Leon, Sinaloa, Sonora, Tamaulipas, and Zacatecas. Version 4 – released 22 April 2009. Ottawa, 97 pp. https://unsm-ento.unl.edu/SSSA/Nearctic-Scarabs4.pdf

Solomakha IV, Konishchuk VV, Mudrak OV, Mudrak HV (2020) A Study of the Emerald Network objects in Ukrainian Forest-Steppe of Dnieper Ecological Corridor. Ukrainian Journal of Ecology 10(2): 209–218. https://www.ujecology.com/articles/a-study-of-the-emerald-network-objects-in-ukrainian-foreststeppe-of-dnieper-ecological-corridor.pdf

Sommer D, Hillert O, Hrůzová L, Král D (2021) *Bolbelasmus* (*Bolbelasmus*) *zagrosensis* (Coleoptera: Scarabaeoidea: Bolboceratidae), a new species from Iran, along with an updated key to the western Palaearctic species of the subgenus. Zootaxa 4920(3): 380–394. https://doi.org/10.11646/zootaxa.4920.3.4

Sparacio I (1995) Coleotteri di Sicilia. Parte prima. L'Epos, Palermo, 233 pp.

Spružina J (2016) Zápisky z terénního deníku: Banát 15.6.–16.6.2016. [Field diary notes: Banat 15.6.–16.6.2016]. Příspěvky k Ústecké Vlativědě 14: 33–35. [in Czech] http://www.muzeumusti.cz/CMSUpload/Clanek_1328/prispevky14%20web.pdf

Staines CL, Staines SL (2020) An annotated checklist of the Coleoptera of the Smithsonian Environmental Research Center: the Scarabaeoidea. Banisteria 54: 87–98. https://virginianaturalhistorysociety.com/banisteria/pdf-files/ban54/An_annotated_checklist_Coleoptera_SERC_III_Staines.pdf

Stan M, Nițu E (2013) New data on the knowledge of beetle fauna (Insecta: Coleoptera) in the "Bârnova-Repedea Forest" site of community importance (ROSCI 01235, Iaşi, Roma-

nia). Travaux du Muséum National d'Histoire Naturelle "Grigore Antipa" 56(1): 33–44. https://doi.org/10.2478/travmu-2013-0003

Stebnicka Z (1976) Żukowate – Scarabaeidae. Grupa podrodzin: Scarabaeidae laparosticti. Klucze do oznaczania owadów Polski. Część XIX. Zeszyt 28a. [Beetles – Scarabaeidae. Subfamily group: Scarabaeidae laparosticti. Keys to the identification of insects of Poland. Part XIX. Volume 28a]. Państwowe Wydawnictwo Naukowe, Warsaw, 139 pp. [in Polish] https://baza.biomap.pl/pl/getpdf/KdOOP_Coleoptera_Scarabaeidae_laparosticti_cz_XIX_zesz_28a_nr_89.pdf

Stephens JF (1829) A systematic catalogue of British insects: being an attempt to arrange all the hitherto discovered indigenous insects in accordance with their natural affinities. Containing also the references to every English writer on entomology, and on the principal foreign authors. With all the published British genera to the present time. Insecta mandibulata. Ordo I. Coleoptera. Baldwin & Cradock, London, xxxiv + [ii] + 416 + 388 pp. https://doi.org/10.5962/bhl.title.8987

Stephens JF (1830) Illustrations of British entomology; or, a synopsis of indigenous insects: containing their generic and specific distinctions; with an account of their metamorphoses, times of appearance, localities, food, and economy, as far as practicable. Mandibulata. Vol. 3. Baldwin & Cradock, London, 374 + [5] pp. + pls xvi–xix. https://doi.org/10.5962/bhl.title.8133

Stephens JF (1839) A manual of British Coleoptera, or beetles; containing a brief description of all the species of beetles hitherto ascertained to inhabit Great Britain and Ireland; together with a notice of their chief localities, times and places of appearances, etc. Longman, Orme Brown, Green, and Longmans, London, xii + 443 pp. https://doi.org/10.5962/bhl.title.59227

Stierlin G (1900) Fauna coleopterorum helvetica. Die Käfer-Fauna der Schweiz nach der analytischen Methode. 1. Teil. Bolli & Böcherer, Schaffhausen, 667 pp. https://doi.org/10.5962/bhl.title.8772

Stierlin G, Gautard V von (1867) Fauna coleopterorum helvetica. Die Käfer-Fauna der Schweiz. Stierlin & Gautard, Schaffhausen – Vevey, 372 pp. https://www.e-rara.ch/zut/content/zoom/19074197

Sturm J (1805) Deutschlands Fauna in Abbildungen nach der Natur mit Beschreibungen. V. Abtheilung. Die Insecten. Erstes Bändchen. Käfer. Mit 20 illuminirten Kupfertafeln. Jacob Sturm, Nürnberg, 10 + xxxxiiii + 271 pp. + 20 pls. https://doi.org/10.5962/t.173057

Sturm J (1843) Catalog der Kæfer-Sammlung von Jacob Sturm. Mit 6 ausgemalten Kupfertafeln. Jacob Sturm, Nürnberg, xii + 386 pp. + 6 pls. https://doi.org/10.5962/bhl.title.37837

Szél Gy, Kutasi Cs (2011) Bogarászati kutatások Csévharaszt és Vasad térségében (Coleoptera). [Research on beetles in the area of Csévharaszt and Vasad (Coleoptera)]. Rosalia 6: 303–351. [in Hungarian]

Szlabóczky I, Borbás V (1900) Szabolcs vármegye állatvilága (Fauna). [Fauna of Szabolcs County]. In: Borovszky S (Ed.) Magyarország vármegyéi és városai (Magyarország monografiája). A magyar korona országai történetének, földrajzi, képzőművészeti, néprajzi, hadügyi és természeti viszonyainak, közművelődési és közgazdasági állapotának. Enziklopédiája. Szabolcs vármegye. [Counties and towns of Hungary (Monograph of Hungary). The history, geography, art, ethnography, military and natural conditions, culture and economy of the countries of the Hungarian crown. Encyclopaedia. Szabolcs County]. „Apollo" irodalmi társaság, Budapest, 245–252. [in Hungarian] https://adt.arcanum.com/en/view/Borovszky_Szabolcs/?pg=280&layout=s

Szwałko P (2004) *Bolbelasmus unicornis* (Schrank, 1879). In: Głowaciński Z, Nowacki J (Eds) Polska Czerwona Księga Zwierząt. Bezkręgowce. Polish Red Data Book of Animals. Invertebrates. Instytut Ochrony Przyrody PAN, Kraków. [in Polish with English abstract] https://www.iop.krakow.pl/pckz/opisc7fc.html?id=180&je=pl [accessed 24 January 2021]

Tatole V, Iftime A, Stan M, Iorgu E-I, Iorgu IŞ, Oţel V (2009) Speciile de animale Natura 2000 din România. [Natura 2000 animal species of Romania]. Imperium Print, Bucureşti, 174 pp. [in Romanian]

Tenenbaum S (1923) Przybytki do fauny chrząszczów Polski od roku 1913. [Additions to the beetle fauna of Poland since 1913]. Rozprawy i Wiadomości z Muzeum Imienia Dzieduszyckich 7–8: 136–186. [in Polish] https://rcin.org.pl/dlibra/publication/152779/edition/122396/content

Tesař Z (1954) Přehled československých druhů čeledi Geotrupidae. [Overview of Czechoslovak species of the family Geotrupidae]. Časopis Národního Musea, Oddíl Přírodovědný 123(2): 204–214. [in Czech]

Tesař Z (1957) Brouci listorozí – Lamellicornia. Díl II. Scarabaeidae – vrubounovití. Laparosticti. Fauna ČSR 11. Nakladatelství Československé akademie věd, Prague, 326 pp. + 16 pls. [in Czech with German and Russian summaries]

Török J (1882) Debreczen Rovarfaunája. [Insect fauna of Debreczen]. In: Zelizy D (Ed.) Debreczen szabad királyi város egyetemes leirása. [General description of the free royal city of Debrecen]. Városi Könyvnyomda, Debreczen [= Debrecen], 181–213. [in Hungarian] https://adt.arcanum.com/en/view/CsaladHely_MonografiaVaros_DebreczenSzabadKiralyiVarosEgyetemesLeirasa/?pg=198&layout=s

Trach VA, Gontarenko AV (2005) Zhuki navozniki (Coleoptera: Scarabaeoidea: Troginae, Geotrupinae, Ochodaeinae, Aphodiinae, Scarabaeinae) Odesskoy oblasti. The dung beetles (Coleoptera: Scarabaeoidea: Troginae, Geotrupinae, Ochodaeinae, Aphodiinae, Scarabaeinae) of the Odessa region. Izvestiya Kharkovskogo Entomologicheskogo Obshchestva 12[=2004](1–2): 77–85. [in Russian with English summary]

Trilar T (2019) (Ne)spregledano iz Prirodoslovnega muzeja Slovenije. Bledi glivar (*Bolbelasmus unicornis*). [(Un)overlooked from the Natural History Museum of Slovenia. Earth-borer beetle *Bolbelasmus unicornis*]. Trdoživ 8(1): 29. [in Slovenian] http://www.dlib.si/stream/URN:NBN:SI:doc-3LL5QXXK/1246b1ee-4bea-48db-874c-ff9875df6711/PDF

Trizzino M, Audisio P, Bisi F, Bottacci A, Campanaro A, Carpaneto GM, Chiari S, Hardersen S, Mason F, Nardi G, Preatoni DG, Vigna Taglianti A, Zauli A, Zilli A, Cerretti P (2013) Gli artropodi italiani in Direttiva Habitat: biologia, ecologia, riconoscimento e monitoraggio. Quaderni Conservazione Habitat. 7. Corpo Forestale dello Stato, Ufficio per la Biodiversità, Roma, 256 pp. https://www.mite.gov.it/sites/default/files/archivio/biblioteca/protezione_natura/artropodi_italiani_dir_habitat.zip

Trnka F (2009) *Bolbelasmus unicornis* – chrobák jednorohý. [Earth-borer beetle *Bolbelasmus unicornis*]. [in Czech] http://www.naturabohemica.cz/bolbelasmus-unicornis [accessed 6 September 2021]

Týr V (1997) Příspěvek k faunistice brouků nadčeledi Scarabaeoidea (Coleoptera) Čech, Moravy a Slovenska. Contribution to the faunistics of Scarabaeoidea (Coleoptera) of Bohemia, Moravia and Slovakia. Klapalekiana 33: 239–247. [in Czech with English abstract]

Vasko BM (2009) *Bolbelasmus unicornis* (Schrank, 1789) – Bolbeliazm odnorohyi. [Earth-borer beetle *Bolbelasmus unicornis* (Schrank, 1789)]. In: Akimov IA (Ed.) Chervona knyha

Ukrainy. Tvarynnyi svit. [Red Book of Ukraine. Fauna]. Hlobalkonsaltynh, Kyiv, 111–111. [in Ukrainian] https://redbook.land.kiev.ua/111.html

Vasko BM (2010) Fauna i ekologiya plastinchatousykh zhukov (Coleoptera: Scarabaeoidea) Pravoberezhnoy Ukrainy. Fauna and ecology of Lamellicornia beetles (Coleoptera: Scarabaeoidea) of the Right-Bank Ukraine. Izvestiya Kharkovskogo Entomologicheskogo Obshchestva 18(1): 4–86. [in Russian with English summary]

Vasko BM, Bryhadyrenko VV (2011) *Bolbelasmus unicornis* (Schrank, 1789) – Bolbeliazm odnorohyi. [Earth-borer beetle *Bolbelasmus unicornis* (Schrank, 1789)]. In: Pakhomov OYe (Ed.) Chervona knyha Dnipropetrovskoi oblasti (Tvarynnyi svit). [Red Book of the Dnipropetrovsk Oblast (fauna)]. Dnipropetrovska oblasna derzhavna administratsiya, Dnipropetrovskyi natsionalnyi universytet Olesya Honchara & Dninronetrovska oblasna orhanizatsiya Vseukrayinskoi ekolohichnoi lihy, Dnipropetrovsk, 104–104. [in Ukrainian] http://pernatidruzi.org.ua/books/ck/ck_dnipropetrovks.pdf

Verdú JR, Galante E, Lumaret J-P (1998) Description de la larve de *Bolbelasmus bocchus* (Erichson) et position systematique du genre. Annales de la Société Entomologique de France 34: 245–251. https://gallica.bnf.fr/ark:/12148/bpt6k6136676b/f31.item

Verdú JR, Galante E, Lumaret J-P, Cabrero-Sañudo FJ (2004) Phylogenetic analysis of Geotrupidae (Coleoptera, Scarabaeoidea) based on larvae. Systematic Entomology 29(4): 509–523. https://doi.org/10.1111/j.0307-6970.2004.00256.x

Vidlička Ľ (2011) Článkonožce. (Arthropods). In: Halčinová K (Ed.) Atlas druhov európskeho významu pre územia NATURA 2000 na Slovensku. The Atlas of Species of European Interest for NATURA 2000 Sites in Slovakia. Slovenské múzeum ochrany prírody a jaskyniarstva, Liptovský Mikuláš, 138–233. [in Slovak and English]

Viertl A (1894) II. Természetrajzi rész. I. Pécs és környékének faunája. 3. Coleoptera, Lepidoptera. [II. Natural history. I. The fauna of Pécs and its surroundings. 3. Coleoptera, Lepidoptera]. In: Ágh T (Ed.) Emléklapok Pécs sz[abad] kir[ályi] város múltjából és jelenéből. [Memories of the past and present of the free royal city of Pécs]. József Taizs, Pécs, 39–72. [in Hungarian]

Vovk DV, Sheshurak PN, Nazarov NV (2005) K izucheniyu plastinchatousykh zhukov (Coleoptera: Scarabaeoidea) Chernigovskoy oblasti Ukrainy. To the study of Scarab beetles (Coleoptera: Scarabaeoidea) of the Chernigov region of Ukraine. Izvestiya Kharkovskogo Entomologicheskogo Obshchestva 13(1–2): 35–42. [in Russian with English summary]

Vovk DV, Sheshurak PN, Nazarov NV (2016) Plastinchatousye zhuki (Coleoptera: Scarabaeoidea) Chernigovskoy oblasti (Ukraina). The scarab beetles (Coleoptera: Scarabaeoidea) of Chernihiv Region (Ukraine). Ukrayinskyi Entomolohichnyi Zhurnal 11(1–2): 91–98. [in Russian with Ukrainian and English abstracts] http://irbis-nbuv.gov.ua/cgi-bin/irbis_nbuv/cgiirbis_64.exe?C21COM=2&I21DBN=UJRN&P21DBN=UJRN&IMAGE_FILE_DOWNLOAD=1&Image_file_name=PDF/Uej_2016_1-2_13.pdf

Vrezec A, Pirnat A, Kapla A, Polak S, Vernik M, Brelih S, Drovenik B (2011) Pregled statusa in raziskanosti hroščev (Coleoptera) evropskega varstvenega pomena v Sloveniji s predlogom slovenskega poimenovanja. Status and knowledge about beetles (Coleoptera) of European conservation importance in Slovenia with proposal of Slovenian nomenclature. Acta Ento-

mologica Slovenica 19: 81–138. [in Slovenian with English abstract] http://www2.pms-lj.si/pdf/Acta/AES_19-2_1_Vrezec.pdf

Wachsmann F (1907) Pápa és vidékének bogárfaunája. [Beetle fauna of Pápa and its surroundings]. Rovartani Lapok 14: 11–23. [in Hungarian] https://www.biodiversitylibrary.org/item/53352#page/15/mode/1up

Wallis JB (1928) Revision of the genus *Odontaeus*, Dej. (Scarabaeidae, Coleoptera). The Canadian Entomologist 60: 119–128, 151–l56, 168–176. https://doi.org/10.4039/Ent60119b-5

Westwood JO (1852) Descriptions of some new or imperfectly known Species of *Bolboceras*, Kirby. Transactions of the Linnean Society of London 21: 19–30 + pls 3–4. https://doi.org/10.1111/J.1096-3642.1852.TB00496.X

Willimzik E (1930) Über den Bau der Ovarien verschiedener coprophager Lamellicornien und ihre Beziehung zur brutpflege. Zeitschrift fur Morphologie und Oekologie der Tiere 18(4): 669–700. https://doi.org/10.1007/BF00418156

Zaharieva-Stoilova B (1974) Scarabaeidae ot Sredna i Istochna Stara planina. Scarabaeidae von dem mittleren und dem östlichen Balkangebirge. Izvestiya na Zoologicheskiya Institut s Muzey 41, 123–139. [in Bulgarian with German and Russian summaries]

Zahradník P (2017) Seznam brouků (Coleoptera) České republiky a Slovenska. Check-list of beetles (Coleoptera) of the Czech Republic and Slovakia. Lesnická práce, Kostelec nad Černými lesy, 544 pp. [in Czech and English]

Zandigiacomo P (2005) Nuovo rinvenimento di *Bolbelasmus unicornis* (Schrank) (Coleoptera, Geotrupidae) in Friuli Venezia Giulia. Bollettino della Società Naturalisti "Silvia Zenari" 29: 75–79.

Zelený J (1972) Návrh členění Československa pro faunistický výzkum. Entwurf einer Gliederung der Tschechoslowekei für Zwecke der faunistischen Forschung. Zprávy Československé Společnosti Entomologické při ČSAV 8: 3–16. [in Czech with German abstract]

Ziani S, Bezděk A, Krell F-Th, Sommer D (2021) Authorship and date of publication of the name *Scarabaeus stercorosus* (currently *Anoplotrupes stercorosus*) (Coleoptera: Scarabaeoidea: Geotrupidae). Zootaxa 5067(4): 593–599. https://doi.org/10.11646/zootaxa.5067.4.7

Zilioli M, Pittino R (2004) Un reperto eccezionale: *Lucanus tetraodon* Thunberg in Lombardia (Coleoptera, Lucanidae). Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale in Milano 145: 301–306. https://www.biodiversitylibrary.org/item/269606#page/303/mode/1up

Zoufal V (1922) Fauna brouků Prostějovského okresu. [Beetle fauna of the Prostějov district]. Věstník Klubu Přírodovědeckého v Prostějově 18: 5–21. [in Czech]

ZooKeys 1105: 127–164 (2022)
doi: 10.3897/zookeys.1105.85055
https://zookeys.pensoft.net

CATALOGUE

A peer-reviewed open-access journal
ZooKeys
Launched to accelerate biodiversity research

Catalogue of primary types of Neotropical *Myotis* (Chiroptera, Vespertilionidae)

Roberto Leonan M. Novaes[1], Don E. Wilson[2], Ricardo Moratelli[1]

1 *Fundação Oswaldo Cruz, Fiocruz Mata Atlântica, R. Sampaio Correa s/n, Taquara, 22713-560, Rio de Janeiro, Brazil* **2** *Smithsonian Institution, National Museum of Natural History, Division of Mammals. 10th St. & Constitution Ave. NW, 20013-7012, Washington, DC, USA*

Corresponding author: Roberto Leonan M. Novaes (robertoleonan@gmail.com)

Academic editor: DeeAnn Reeder | Received 7 April 2022 | Accepted 6 May 2022 | Published 15 June 2022

http://zoobank.org/D98F9EE8-C804-4A5D-BAB5-664446AF8EE0

Citation: Novaes RLM, Wilson DE, Moratelli R (2022) Catalogue of primary types of Neotropical *Myotis* (Chiroptera, Vespertilionidae). ZooKeys 1105: 127–164. https://doi.org/10.3897/zookeys.1105.85055

Abstract

Myotis comprises a diverse group of vespertilionid bats with worldwide distribution. Neotropical *Myotis* have an accentuated phenotypic conservatism, which makes species delimitation and identification difficult, hindering our understanding of the diversity, distribution, and phylogenetic relationships of taxa. To encourage new systematic reviews of the genus, a catalogue of the primary types and names is presented, current and in synonymy, for Neotropical *Myotis*. Currently 33 valid species (and three subspecies) are recognized, and their primary types are deposited in 12 scientific collections in the USA (30 types), Brazil (two types), England (two types), and France (one type). The names of 29 Neotropical *Myotis* species currently in synonymy were found. However, it is possible that some synonyms represent independent evolutionary lineages, considering recent results provided by taxonomic revisions.

Resumo

Myotis compreende um grupo diverso de morcegos vespertilionídeos amplamente distribuídos ao redor do planeta. *Myotis* neotropicais têm um acentuado conservatismo fenotípico, o que dificulta a delimitação e identificação de espécies a partir de caracteres morfológicos, criando barreiras para a compreensão da diversidade, distribuição e relações filogenéticas entre os táxons. Visando encorajar novas revisões sistemáticas para o gênero, é apresentado este catálogo de nomes e tipos primários, válidos e sob sinonímia, para *Myotis* neotropicais. Atualmente, são reconhecidas 33 espécies válidas (e três subespécies) e seus tipos estão depositados em 12 coleções científicas nos EUA (30 tipos), Brasil (2 tipos), Inglaterra (2 tipos) e França (1 tipo). Compilamos 29 nomes de espécies de *Myotis* atualmente sob sinonímia. Entretanto, é possível que alguns desses sinônimos possam representar linhagens evolutivas independentes, considerando resultados recentes de revisões taxonômicas.

Keywords
Myotinae, taxonomy, type locality, type specimen, vespertilionid bats, zoological nomenclature

Palavras-chave
espécime-tipo, localidade-tipo, morcego vespertilionídeo, Myotinae, nomenclatura zoológica, taxonomia

Introduction

Taxonomy is the discipline of Biology responsible for describing, classifying, and naming organisms, as well as hypothesize about the evolutionary relationships between taxa (Tancoigne et al. 2011). Therefore, understanding and organizing biological diversity is the primary task of the taxonomist. Taxonomic studies have profound implications in virtually all areas of the biological sciences, such as ecology, evolution, genetics, and epidemiology, in addition to directly influencing public policies focused on health and environment (Cracraft 2002; Pearson et al. 2011; Cook et al. 2020). Furthermore, knowing the real diversity of organisms on our planet is critical for the sustainable use of natural resources and for the management and conservation of species (May 1988), especially in the current biodiversity crisis, where the rate of extinction indicates that we are witnessing a sixth mass extinction (Ceballos et al. 2015, 2017).

Species are the central unit of taxonomy and the association between an unambiguous scientific name and a species is of paramount importance for a reliable biological information system (Wheeler 2004). For that, the existence of primary types, which are those specimens designated as the name-bearing representative of a species is essential. In addition to serving as a reference point for the existence of any organism, type-specimens are a particularly important source of information for scientists to track and unravel the taxonomic history of biologically complex groups, such as bats of the genus *Myotis* Kaup, 1829.

Myotis is the most speciose genus of bats and the second largest genus of mammals, with more than 140 extant species (MDD 2021). It is also the genus with the greatest area of distribution among non-human mammals (Moratelli et al. 2019a). The greatest diversity and abundance of *Myotis* is reported in temperate and subtropical areas (Nowak 1994; Moratelli et al. 2019a). However, recent systematic reviews have indicated that there is a high diversity of *Myotis* in the Neotropics (e.g., Larsen et al. 2012; Moratelli et al. 2011a, 2013, 2016, 2017, 2019b; Carrión-Bonilla and Cook 2020; Novaes et al. 2021a, b, c). Nevertheless, our knowledge of species limits, name validity, and distributional boundaries for several Neotropical *Myotis* species remains incipient.

Part of the taxonomic hurdle is due to the accentuated morphological conservatism and lack of specimen series covering all geographic distributions (Menu 1987; Smith et al. 2012; Moratelli et al. 2019a). On the other hand, molecular studies have revealed the existence of more independent evolutionary lineages than species recognized from morphology-based taxonomy (Larsen et al. 2012; Novaes et al. 2021a, b). This indicates the existence of hidden diversity possibly composed of multiple cryptic species, which challenges the delimitation of species and raises the need for new systematic reviews, especially those based on multiple lines of evidence.

To contribute to the organization of systematic knowledge about this genus, and to support future studies of taxonomy, we present a catalogue of the primary types of Neotropical *Myotis*. Later, we briefly comment on the validity and distribution of some species.

Materials and methods

The catalogue was mostly compiled by analysis of the specimens deposited in 12 biological collections: American Museum of Natural History (New York, USA), Field Museum of Natural History (Chicago, USA), Louisiana State University Museum of Natural Science (Baton Rouge, USA), Museum of Texas Tech University (Lubbock, USA), Museum of Vertebrate Zoology at University of California (Berkeley, USA), Kansas University Biodiversity Institute and Natural History Museum (Lawrence, USA), Natural History Museum, Los Angeles County (Los Angeles, USA), Smithsonian's National Museum of Natural History (Washington D.C., USA), Natural History Museum, London (London, UK), Zoologisches Staats-Sammlung München (Munich, Germany), Muséum National D'Histoire Naturelle (Paris, France), Muséum d'Histoire Naturelle (Geneva, Switzerland), Museu de Zoologia da Universidade de São Paulo (São Paulo, Brazil), Universidade Federal Rural do Rio de Janeiro (Seropédica, Brazil). When it was not possible to visit the collection to examine the type specimen, the information was retrieved from the original species descriptions or other available bibliography (e.g., LaVal 1973; Carter and Dolan 1978; Carrión-Bonilla and Cook 2020) and by direct consultation with the curators of the collections. Abbreviations of biological collections cited in the text are available below.

ALP Universidade Federal Rural do Rio de Janeiro, Seropédica, Brazil;
ANSP Academy of Natural Sciences of Drexel University, Philadelphia, USA;
AMNH American Museum of Natural History, New York, USA;
BMNH Natural History Museum, London, UK;
FMNH Field Museum of Natural History, Chicago, USA;
KU Natural History Museum, Kansas University, Lawrence, USA;
LACM Natural History Museum, Los Angeles County, Los Angeles, USA;
LSU Louisiana State University Museum of Natural Sciences, Baton Rouge, USA;
MHNG Muséum d'Histoire Naturelle, Geneva, Switzerland;
MNHN Muséum National D'Histoire Naturelle, Paris, France;
MSB Museum of Southwestern Biology, University of New Mexico, Albuquerque, USA;
MVZ Museum of Vertebrate Zoology, University of California, Berkeley, USA;
MZUSP Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil;
RNH Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands;
TTU Museum of Texas Tech University, Lubbock, USA;
USNM Smithsonian's National Museum of Natural History, Washington D.C., USA;
ZSM Zoologisches Staats-Sammlung München, Munich, Germany.

The list of *Myotis* species adopted here is based on systematic reviews conducted for the genus *Myotis* in the Neotropical region (i.e., LaVal 1973; Bogan 1978; Moratelli et al. 2019a, b; Carrión-Bonilla and Cook 2020; Novaes et al. 2021a, b, c). Following LaVal (1973), we excluded species from the definition of Neotropical *Myotis* when their distributions extend from the Nearctic into the Neotropics. Geographical coordinates of type localities were retrieved, when available, directly from the original publications or by consulting the museum database and the gazetteer of Gardner (2008). In cases where they were not available, we used proximal coordinates of the locality from the search in the USA's National Geospatial – Intelligence Agency (https://geonames.nga.mil/namesgaz/). We follow the International Code of Zoological Nomenclature (ICZN 1999) as a reference for the categories of type specimens.

The list of names was divided in two parts, the first with accounts of name-bearing type specimens of currently recognized species; and the second with accounts of name-bearing type specimens in synonymy. The accounts were arranged chronologically, following the date of taxa description. The format of accounts was inspired by Fisher and Ludwig (2015), but with modifications. Each account reads as follows: (i) Current name (for recognized species) or original published name (for names in synonymy) followed by the author's or authors' names; (ii) Original citation, including publication, volume, pages, and year of publication; (iii) Taxonomy, species original published name if different from the currently name, followed by information on subspecies, if any; (iv) Type designation as holotype, lectotype, paralectotype, neotype, or syntype, including collection number, age and sex, date collected and collector(s) name(s), and preparation of specimen; (v) Type locality: Verbatim locality as given in the original description or neotype designation, published restrictions, and supplementary data. Abbreviations are used for miles (mi), kilometers (km), feet (ft), and meters (m); (vi) Remarks, with additional information is provided as needed, but especially to explain types designated subsequent to description.

Results

Name-bearing type specimens of recognized species

For the 33 species (and three subspecies) of Neotropical *Myotis* currently recognized (Table 1), primary types are deposited in 12 zoological collections in the USA (eight collections), Brazil (two collections), England (one collection) and France (one collection). The USA is home to 30 primary types of Neotropical *Myotis*, while Brazil and England are home to two primary types each and France to one type specimen. The collections with the largest number of primary types are the Smithsonian's National Museum of Natural History (11 types), followed by the American Museum of Natural History (eight types), both in the USA. The other collections have 1–4 type specimens each (Fig. 1).

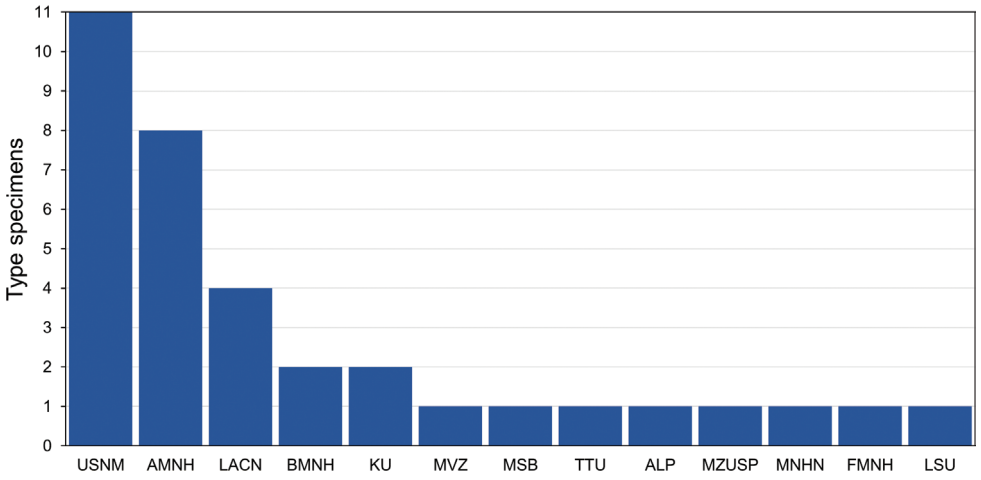


Figure 1. Number of primary type specimens of Neotropical *Myotis* deposited in zoological collections. The name of the institution for each acronym shown in the graph is described in the methods.

Of all recognized Neotropical *Myotis* types, 28 are holotypes, six are neotypes, and one is syntype. Only one taxon lacks a type specimen (*M. nigricans osculati*), which presumably was destroyed. About 95% of the type specimens are preserved as skin and skull, with mandible; while only 5% are preserved in fluid (usually alcohol 70°GL). Most types (80%) are in a good condition, with complete skulls and untorn skin. The other 20% are damaged, especially the oldest ones. Damages include broken skulls, loss of bone elements, or torn skins (Figs 2–8).

Below is an annotated list of Neotropical *Myotis* species (organized in chronological order of description), with information about the primary specimen types and the type locality. We include a map containing the geographical point of all type localities (Fig. 9).

Myotis ruber (É. Geoffroy, 1806)

Annales du Muséum d'Histoire Naturelle 8: 187–205.

Taxonomy: Described as *Vespertilio ruber* by Geoffroy Saint-Hilaire (1806: 204). Treated as monotypic (Wilson 2008; Moratelli et al. 2019a).

Neotype: USNM 115097, adult male collected on May 22, 1901 by W. Foster; skull, mandible, and skin.

Type locality: Sapucay (= Sapucai, Paraguarí), Paraguay (25°40'S, 56°57'W; ca. 200 m a.s.l.) by neotype designation (LaVal 1973: 45).

Remarks: The holotype was not specified by the author, who based his description on the Azara's (1801) "chauve-sourris cannelle". LaVal (1973) noted that D. C. Carter did not locate the specimen at the Muséum National d'Histoire Naturelle (Paris, France) or in any other European museum, concluding that it was lost or destroyed. The neotype was designated by LaVal (1973: 45), following the same reasoning presented for *M. albescens* (see below).

Table 1. Valid species and subspecies of Neotropical *Myotis* including information on their primary types.

Species	Type specimen	Proximal type locality
M. albescens	Neotype AMNH 205195	Paraguarí, Paraguay
M. armiensis	Holotype MSB 262089	Chiriquí, Panamá
M. atacamensis	Neotype USNM 391786	Tarapacá, Chile
M. attenboroughi	Holotype USNM 540693	St. John Parish, Tobago Island
M. bakeri	Holotype MVZ 136907	Lima, Peru
M. carteri	Holotype LACM 36876	Jalisco, Mexico
M. caucensis	Holotype AMNH 32787	Valle del Cauca, Colombia
M. chiloensis	Neotype FMNH 24029	Chiloé Island, Chile
M. clydejonesi	Holotype TTU 109227	Sipaliwini, Suriname
M. cobanensis	Holotype AMNH 145017	Alta Verapaz, Guatemala
M. diminutus	Holotype USNM528569	Los Ríos, Ecuador
M. dinellii	Holotype BMNH 0.7.9.4	Tucumán, Argentina
M. dominicensis	Holotype USNM 113564	Dominica
M. elegans	Holotype KU 88398	Veracruz, Mexico
M. findleyi	Holotype USNM 512417	Islas Tres Marías, Mexico
M. handleyi	Holotype USNM 370932	Distrito Federal, Venezuela
M. izecksohni	Holotype ALP 6675	Rio de Janeiro, Brazil
M. keaysi	Holotype AMNH 15814	Puno, Peru
M. larensis	Holotype AMNH 130709	Lara, Venezuela
M. lavali	Holotype MZUSP 18762	Pernambuco, Brazil
M. levis	Syntype MNHN 1997-1805	Southern Brazil
M. martiniquensis	Holotype AMNH 214062	Tartane, Martinique
M. midastactus	Holotype AMNH 211156	Beni, Bolívia
M. moratellii	Holotype USNM 513482	Los Ríos, Ecuador
M. nesopolus	Holotype USNM 101849	Curaçao, Netherlands Antilles
M. n. nigricans	Neotype LACN 36877	Rio de Janeiro, Brazil
M. n. extremus	Holotype USNM 77670	Chiapas, Mexico
M. n. osculati	Not located	Eastern Ecuador
M. nyctor	Holotype KU 109473	St. Thomas Parish, Barbados
M. o. oxyotus	Neotype LACN 36878	Carchi, Ecuador
M. o. gardneri	Holotype LSU 12924	San José, Costa Rica
M. pampa	Holotype AMNH 205471	Artigas, Uruguay
M. pilosatibialis	Holotype LACN 36879	Francisco Morazán, Honduras
M. riparius	Holotype USNM 310255	Darién, Panamá
M. ruber	Neotype USNM 115097	Paraguarí, Paraguay
M. simus	Holotype BMNH 8.5.12.2	Loreto, Peru

Myotis albescens (É. Geoffroy, 1806)

Annales du Muséum d'Histoire Naturelle 8: 187–205.

Taxonomy: Described as *Vespertilio albescens* by Geoffroy Saint-Hilaire (1806: 204–205). Treated as monotypic (Moratelli and Oliveira 2011; Moratelli et al. 2019a).

Neotype: AMNH 205195, adult female collected on June 2, 1963 by M. D. Tuttle; skull, mandible, complete post-cranial skeleton and skin.

Type locality: Yaguarón, Paraguarí, Paraguay (25°33'S, 57°17'W; ca. 200 m a.s.l.) based on neotype designation (LaVal 1973: 26).

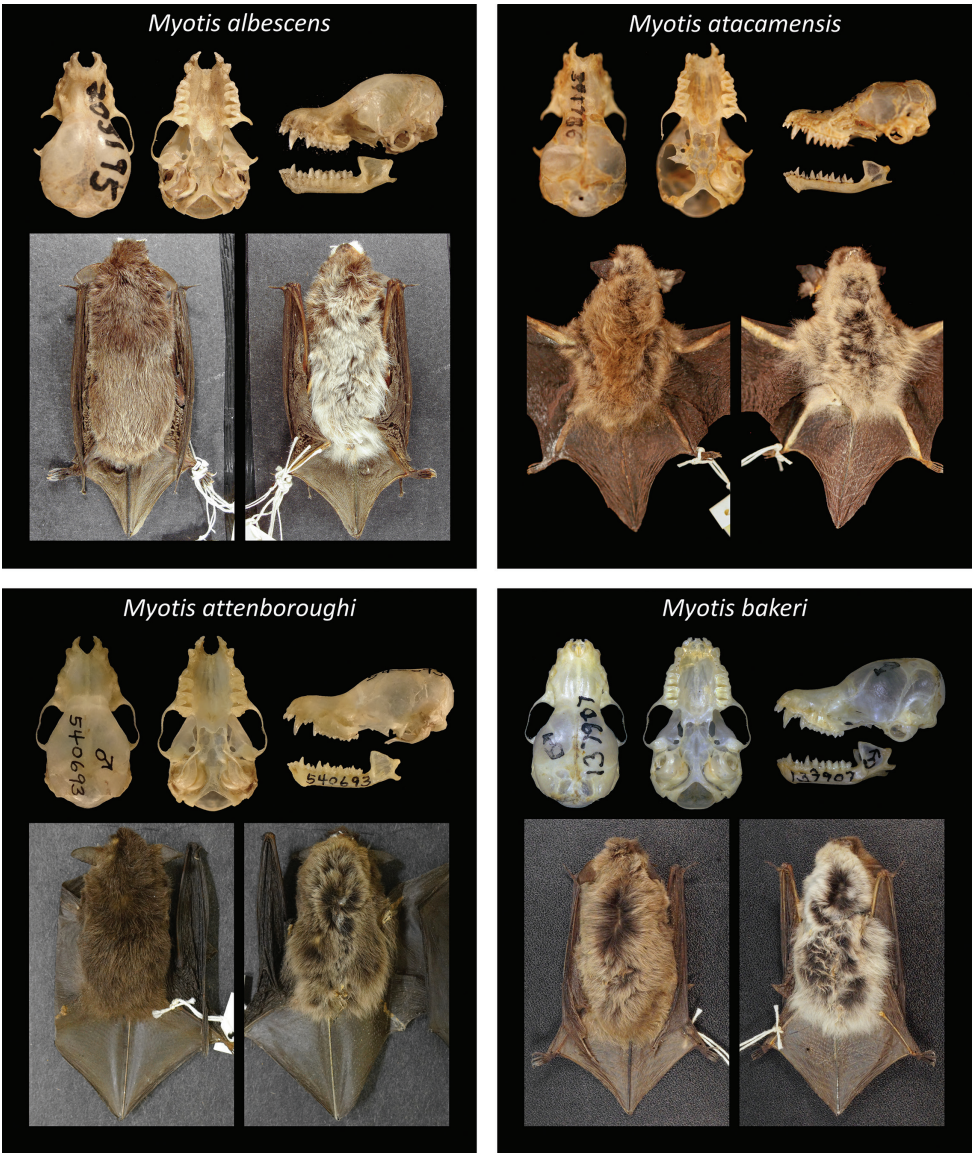


Figure 2. Some type specimens from valid species of Neotropical *Myotis*: AMNH 205195, neotype of *M. albescens*; USNM 391786, neotype of *M. atacamensis*; USNM 540693, holotype of *M. attenboroughi*; MVZ 136907, holotype of *M. bakeri*.

Remarks: The holotype was not specified by the author, who based his description on the Azara's (1801) "chauve-souris donzième". LaVal (1973) noted that D. C. Carter was unable to locate a specimen in European zoological collections from Azara's expedition. According to Cabrera (1958), É. Geoffroy based his description of *Phyllostoma lineatum* (currently *Platyrrhinus lineatus*) on specimens collected in Paraguay and listed

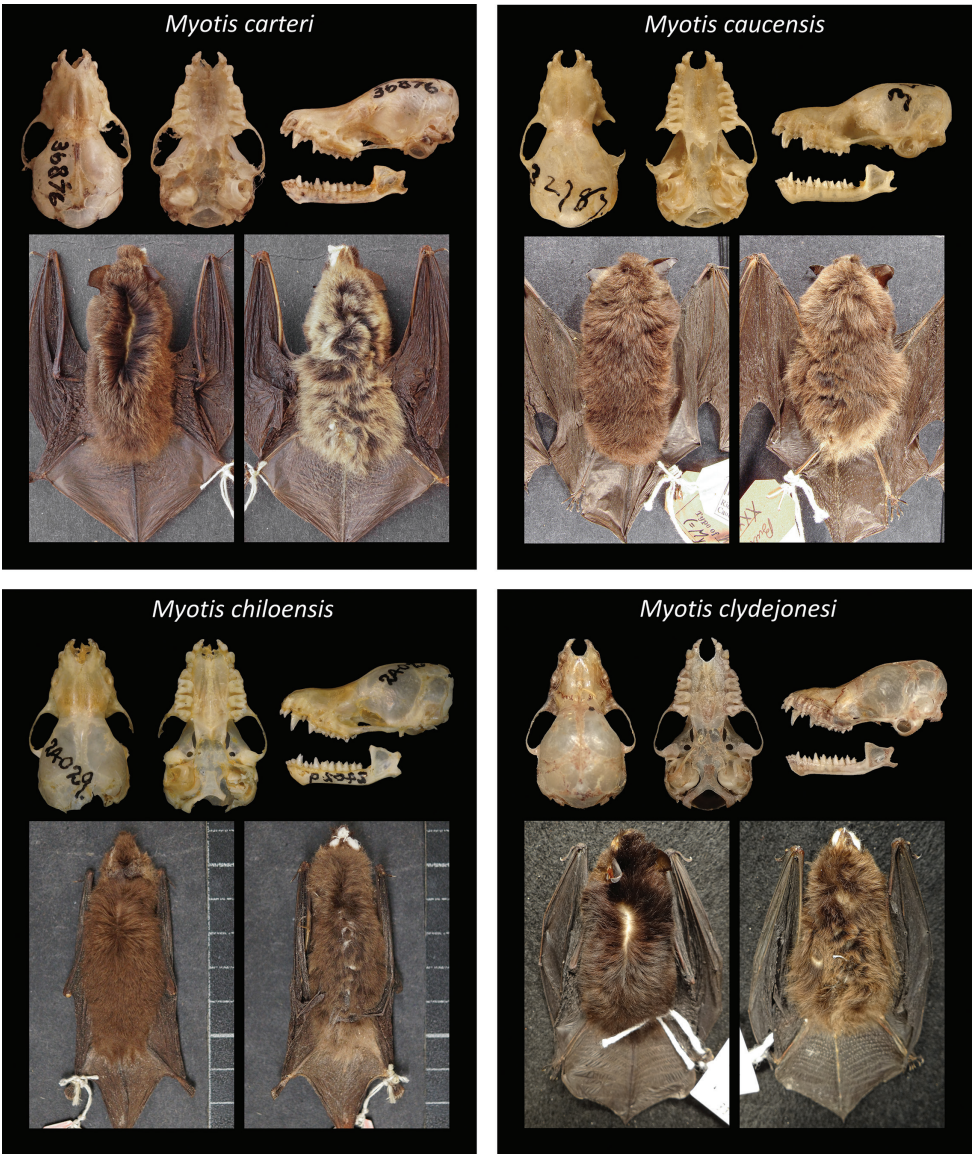


Figure 3. Some type specimens from valid species of Neotropical *Myotis*: LACM 36876, holotype of *M. carteri*; AMNH 32787, holotype of *M. caucensis*; FMNH 24029, neotype of *M. chiloensis*; TTU 109227, holotype of *M. clydejonesi*.

by Azara (1801) in the same publication in which he listed the specimen that Geoffroy described as *Vespertilio albescens*. Cabrera stated that the specimen of *P. lineatum* was destroyed. LaVal (1973: 26) considered that the type specimen of *V. albescens* met the same fate and designated a neotype.

Myotis nigricans (Schinz, 1821)

Taxonomy: Originally *Vespertilio nigricans* Schinz, 1821. We follow Bogan (1978) and Moratelli et al. (2019a) in recognizing three subspecies, and in treating *M. carteri* as a distinct species, instead of a subspecies of *M. nigricans*.

Myotis nigricans nigricans (Schinz, 1821)

In "Das tierreich eingetheilt nach dem Bau der thiere als Grundlage ihrer Naturgeschichte und der vergleichenden Anatomie von dem Herrn Ritter von Cuvier, volume 1". Saugethiere und Vögel, Stuttgart and Tübingen, 894 pp.

Taxonomy: Described as *Vespertilio nigricans* by Schinz (1821: 179).

Neotype: LACM 36877, adult female collected on October 14, 1968 by A. L. Peracchi; skull, mandible, and skin.

Type locality: Seropédica, 42 km S Rio de Janeiro, Brazil (22°45'S, 43°41'W; 33 m a.s.l.).

Remarks: The species was described based on a specimen collected by Prinz Maxilian zu Wied-Neuwied at Fazenda do Agá, near the Rio Iritiba, Espírito Santo, Brazil. Miller and Allen (1928) were not able to confirm the existence of this specimen. From a personal communication of D. C. Carter, that he could not locate it in among the important collection of Wied's Brazilian specimens at the American Museum of Natural History, LaVal (1973: 9) presumed it has been lost and designated a neotype.

Myotis nigricans osculati (Cornalia, 1849)

In "Vertebratorum synopsis in Museo Mediolanense extantium que per novam orbem Cajetanus Osculati collegit annis 1846–47–1848 (…)". Typographia Corbetta, Modoetiae, 16 pp.

Taxonomy: Described as *Vespertilio osculati* by Cornalia (1849: 11).

Type specimen: None. The specimen used in the original description was collected by G. Osculati between 1846 and 1848. Osculati's collection deposited in the Museo di Storia Naturale di Milano, Italy, in 1848, was destroyed during World War II (Cagnolaro and Violani 1988; Moratelli et al. 2013).

Type locality: Eastern Ecuador.

Myotis nigricans extremus Miller & Allen, 1928

Bulletin of the United States National Museum 144: 1–218.

Taxonomy: Described as *Myotis nigricans extremus* by Miller and Allen (1928: 181).

Holotype: USNM 77670, adult female collected by the E. W. Nelson and E. A. Goldman on March 1, 1896; skull, mandible, and skin.

Type locality: Huehuetán, Chiapas, Mexico (15°01'N, 92°22'W; 91 m a.s.l.).

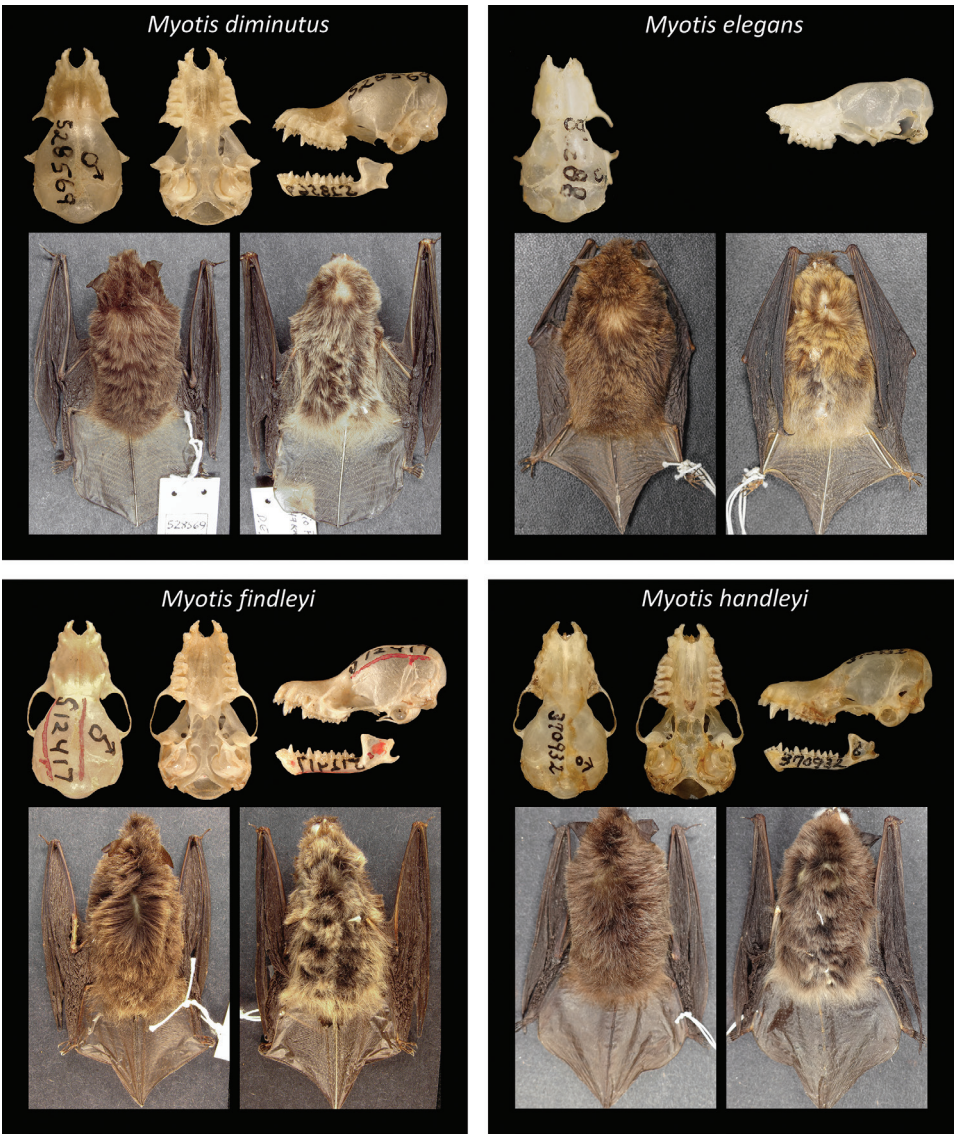


Figure 4. Some type specimens from valid species of Neotropical *Myotis*: USNM528569, holotype of *M. diminutus*; KU 88398, holotype of *M. elegans*; USNM 512417, holotype of *M. findleyi*; USNM 370932, holotype of *M. handleyi*.

Myotis levis (I. Geoffroy, 1824)

Annales de Sciences Naturelles de Paris 3: 440–447.

Taxonomy: Described as *Vespertilio levis* by Geoffroy Saint-Hilaire (1824: 444); currently monotypic (Moratelli et al. 2019a).

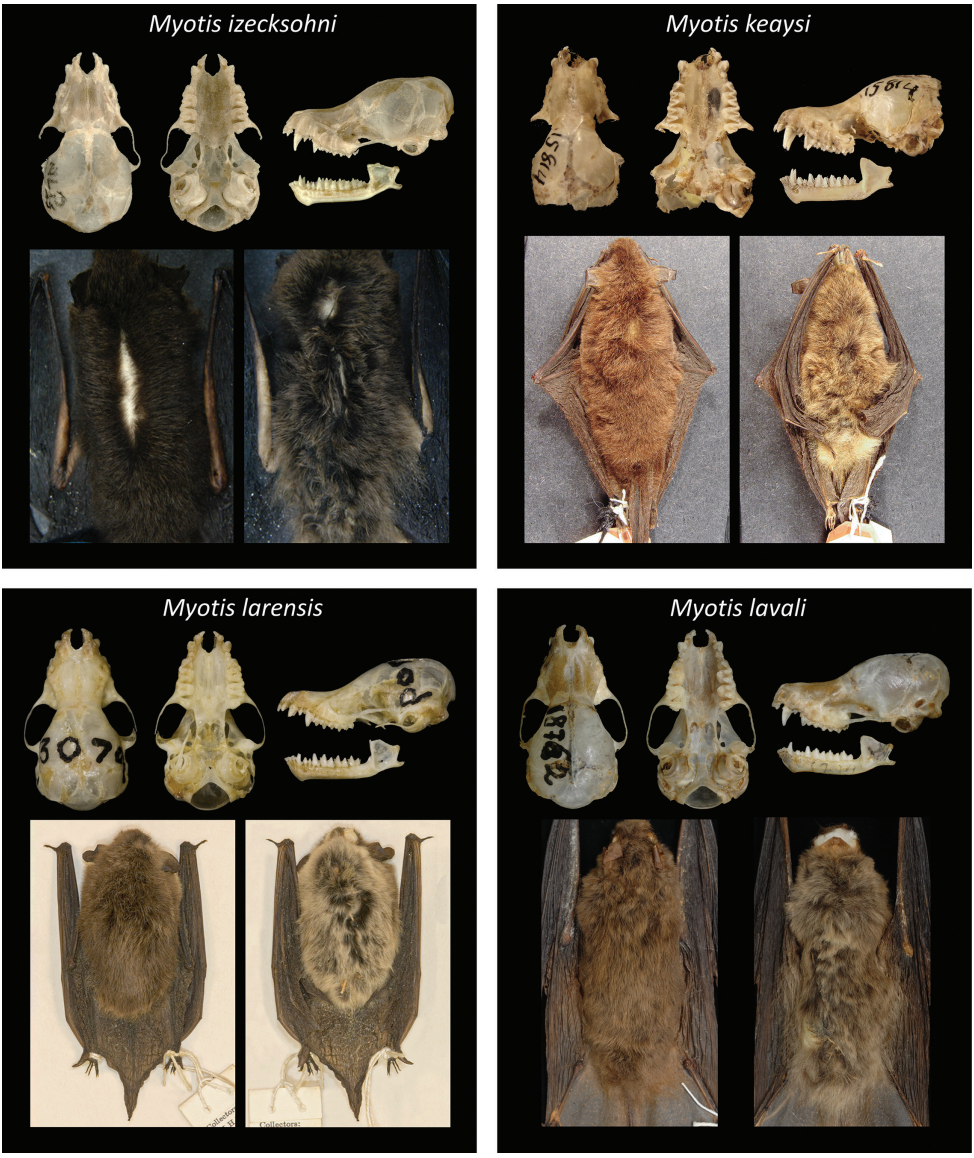


Figure 5. Some type specimens from valid species of Neotropical *Myotis*: ALP 6675, holotype of *M. izecksohni*; AMNH 15814, holotype of *M. keaysi*; AMNH 130709, holotype of *M. larensis*; MZUSP 18762, holotype of *M. lavali*.

Syntype: MNHN type 203 (also referred to as MNHN 1997-1805), adult, sex unknown, collected by A. Geoffroy Saint-Hilaire (date not specified); mounted specimen, with skull removed and severely damaged.

Type locality: Southern Brazil.

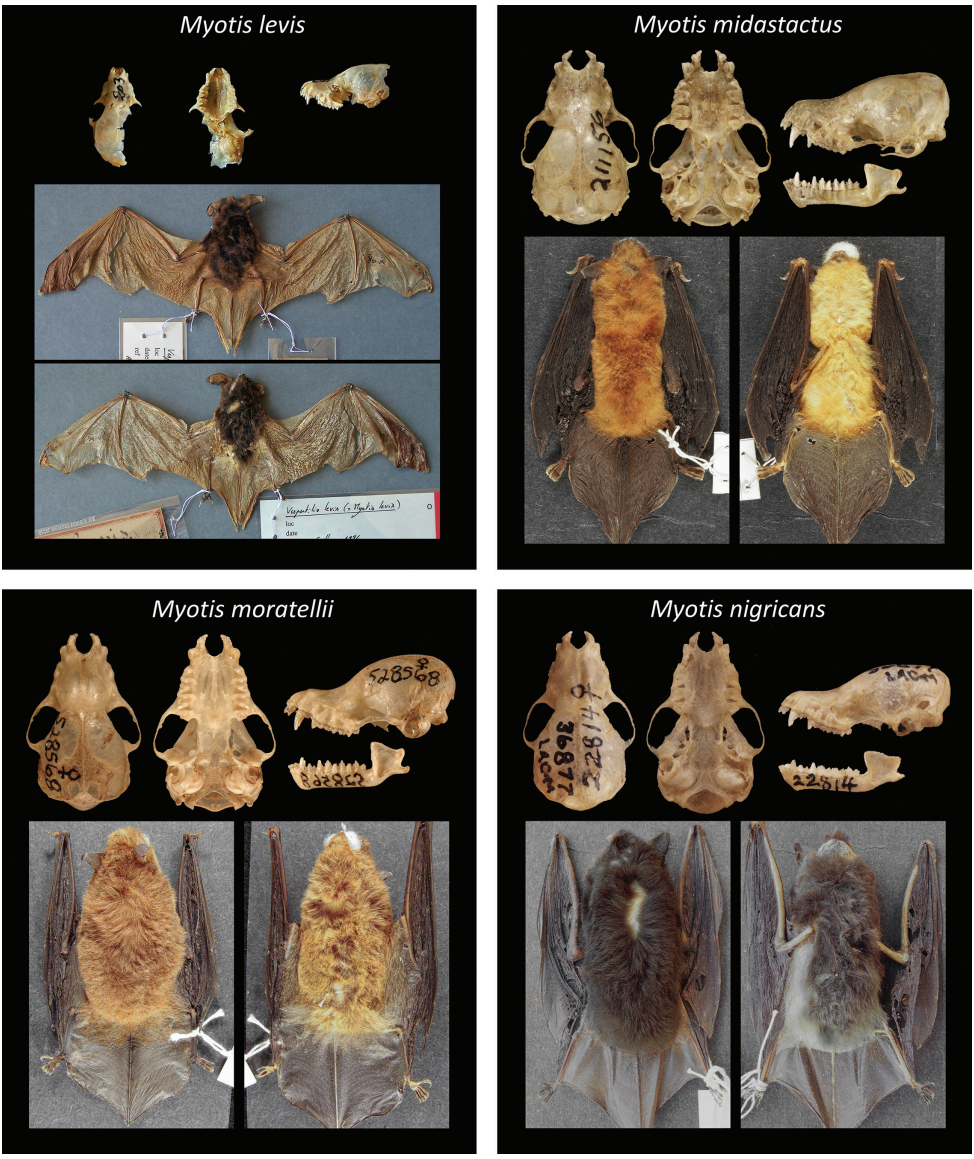


Figure 6. Some type specimens from valid species of Neotropical *Myotis*: MNHN 1997-1805, syntype of *M. levis*; AMNH 211156, holotype of *M. midastactus*; USNM 513482, holotype of *M. moratellii*; LACN 36877, neotype of *M. nigricans*.

Myotis chiloensis (Waterhouse, 1840)

In "The zoology of the voyage of the H.M.S. Beagle, under the command of Captain Fitzroy, R.N., during the years 1832 to 1836". Smith, Elder and Co, London, 97 pp.

Taxonomy: Described as *Vespertilio chiloensis* by Waterhouse (1840: 5); currently monotypic (Novaes et al. 2018; Moratelli et al. 2019a).

Figure 7. Some type specimens from valid species of Neotropical *Myotis*: LACN 36878, neotype of *M. oxyotus*; AMNH 205471, holotype of *M. pampa*; LACN 36879, holotype of *M. pilosatibialis*; USNM 310255, holotype of *M. riparius*.

Neotype: FMNH 24029, adult female collected by J. Vera in 1923; skull partially damaged, mandible, and skin.

Type locality: Cucao, Chiloé Island, Los Lagos, Chile (42°38'S, 74°06'W; sea level).

Remarks: The original description was based on a specimen collected in January 1836 by Lieutenant Sullivan and given to C. R. Darwin during the H. M. S. Beagle

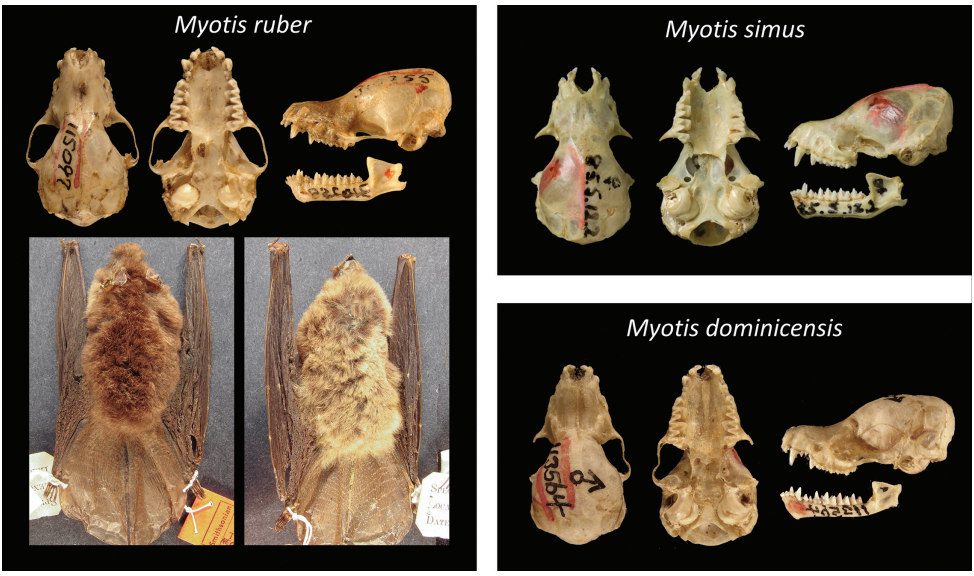


Figure 8. Some type specimens from valid species of Neotropical *Myotis*: USNM 115097, neotype of *M. ruber*; BMNH 8.5.12.2, holotype of *M. simus*; USNM 113564, holotype of *M. dominicensis*.

voyage. Miller and Allen (1928) were unable to locate the specimen. LaVal (1973: 43) presumed it lost and designated a neotype.

Myotis oxyotus (Peters, 1866)

Taxonomy: Originally *Vespertilio oxyotus* Peters, 1866. We follow LaVal (1973) and Moratelli et al. (2019a) in recognizing two subspecies.

Myotis oxyotus oxyotus (Peters, 1866)

Monatsberichte der Königlichen Preussische Akademie des Wissenschaften zu Berlin 1867: 16–25.

Taxonomy: Originally *Vespertilio oxyotus* as described by Peters (1866: 19).

Neotype: LACM 36878, adult female collected by D. C. Carter on July 4, 1964; skull, mandible, and skin.

Type locality: Gruta Rumichaca, 2 mi E La Paz, Carchi, Ecuador (00°29'N, 77°50'W; ca. 2,600 m a.s.l.).

Remarks: The original description was based on an adult female preserved in spirit at "Zoologischen Cabinet zu München" (Peters 1866). Presumably this "Zoologischen Cabinet" is the same as the current Zoologische Sammlung des Bayerischen Staates (= Zoologische Staatssammlung München) in Munich, Germany. LaVal (1973) noted that D. C. Carter was unable to locate the holotype there in 1966, and he pointed out that many specimens in the museum in Munich were destroyed during World War II, and must be presumed lost. Therefore, LaVal (1973: 41) designated a neotype.

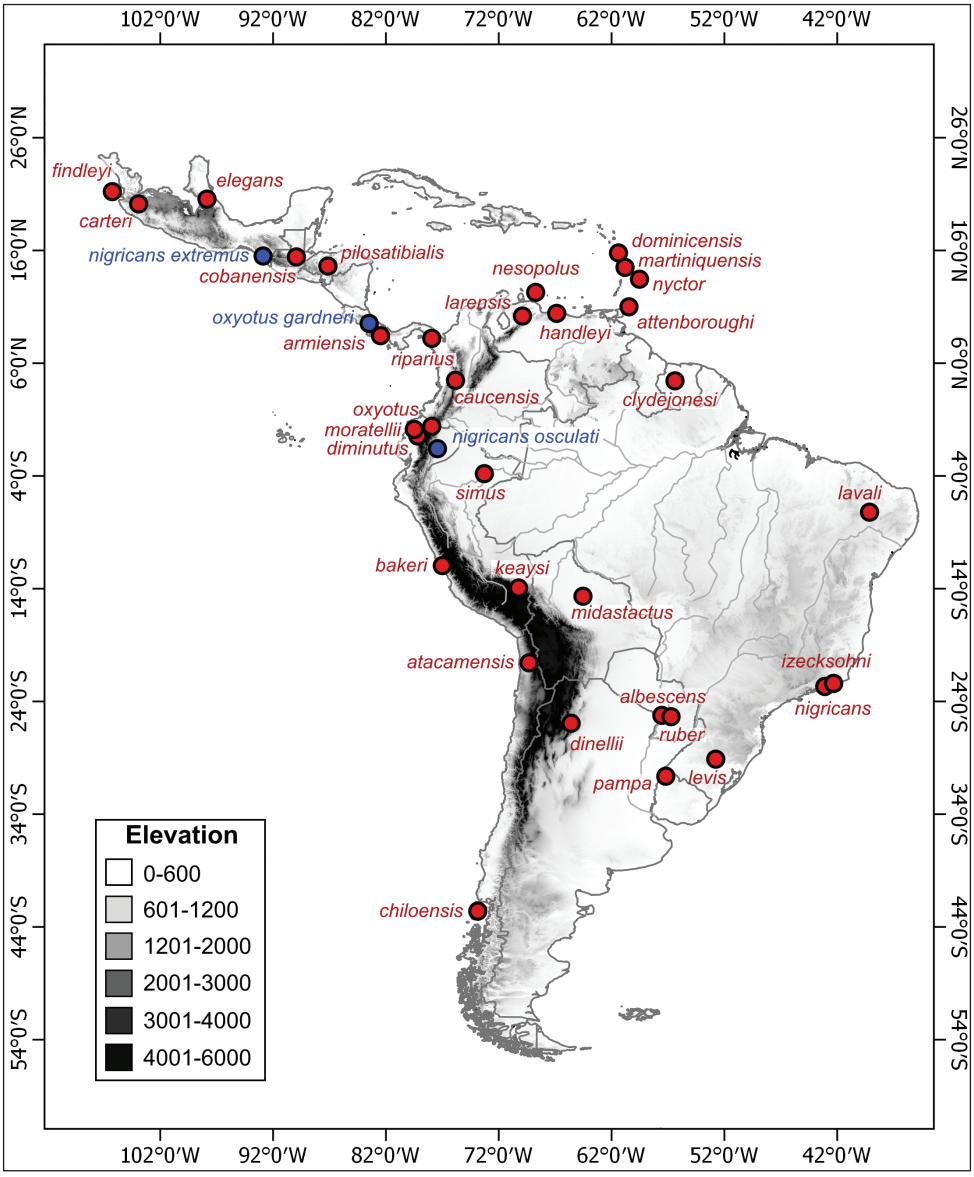


Figure 9. Type localities of the currently valid species (red) and subspecies (blue) of Neotropical *Myotis*.

Myotis oxyotus gardneri LaVal, 1973

Bulletin of the Natural History Museum of Los Angeles County 15: 1–54.

Taxonomy: Described as *Myotis oxyotus gardneri* by LaVal (1973: 42).

Holotype: LSU 12924, adult male collected by A. L. Gardner on May 8, 1967; skull, mandible, baculum, and skin.

Type locality: Fila La Maquina, ca. 7.5 km E Canaan, San José, Costa Rica (09°27'N, 83°32'W; 2,610 m a.s.l.).

Myotis atacamensis (Lataste, 1892)

Actes de la Société Scientifique du Chili 1: 70–91.

Taxonomy: Described as *Vespertilio atacamensis* Lataste (1892: 79); currently monotypic (Moratelli et al. 2019a).

Neotype: USNM 391786, adult female collected by W. Mann and S. Mann in January 1944; skull partially damaged, mandible, and skin.

Type locality: Near Minimini, Tarapacá, Chile (19°10'S, 69°41'W; 1,800 m a.s.l.).

Remarks: The original description was based on three syntypes, probably collected in February 1885 in San Pedro de Atacama, Antofagasta, Chile, and deposited at Museo Nacional de Historia Natural (Santiago, Chile), including a mounted specimen (number 277), a skull (number 1007), and a fluid preserved specimen (number 276). LaVal (1973) argued these specimens are lost or, more probable, were destroyed. Novaes et al. (2022: 3) designated a neotype.

Myotis nesopolus Miller, 1900

Proceedings of the Biological Society of Washington 13: 123–127.

Taxonomy: Described as *Myotis nesopolus* by Miller (1900: 123). Treated as monotypic (Novaes et al. 2021a).

Holotype: USNM 101849, adult male collected by L. J. Guthrie on November 4, 1899; complete specimen preserved in alcohol.

Type locality: Near Willemstad, Curaçao, Netherlands Antilles (12°07'N, 68°52'W, ca. 35 m a.s.l.).

Myotis simus Thomas, 1901

Annals and Magazine of Natural History (ser. 7) 7: 189–193.

Taxonomy: Described as *Myotis simus* by Thomas (1901: 541). Currently monotypic (Moratelli et al. 2011b, 2019a).

Holotype: BMNH 8.5.12.2, adult female collected in 1876 by W. Davis; body preserved in alcohol (skin is faded and the dorsum and venter have blocks of hair losses) with skull and mandible removed, being partially damaged.

Type locality: Thomas (1901) indicates Sarayacu (06°44'S, 75°06'W; Carter and Dolan 1978), Peru, as type-locality. Later, LaVal (1973) added Rio Ucayali, Loreto, Peru, 100 m a.s.l.

Myotis dominicensis Miller, 1902

Proceedings of the Biological Society of Washington 15: 243–244.

Taxonomy: Described as *Myotis dominicensis* by Miller (1902: 243). Currently monotypic (Moratelli et al. 2019a).

Holotype: USNM 113564, adult male collected by H. S. Branch on July 18, 1901; body preserved in alcohol, skull and mandible removed.

Type locality: Island of Dominica.

Myotis dinellii Thomas, 1902

Annals and Magazine of Natural History (ser. 7) 10: 493–494.

Taxonomy: Described as *Myotis dinellii* by Thomas (1902: 493), treated as subspecies by LaVal (1973), and as species by Miranda et al. (2013) and Moratelli et al. (2019a). Monotypic (Moratelli et al. 2019a).

Holotype: BMNH 0.7.9.4, adult female collected by L. Dinelli on April 7, 1899; skull severely damaged, mandible missing, and skin.

Type locality: Tucumán, Argentina.

Myotis keaysi J.A. Allen, 1914

Bulletin of the American Museum of Natural History 33(29): 381–389.

Taxonomy: Described as *Myotis ruber keaysi* by Allen (1914: 383). Monotypic (Mantilla-Meluk and Muñoz-Garay 2014; Moratelli et al. 2019a).

Holotype: AMNH 15814, adult male collected by H. H. Keays on December 2, 1899; skull severely damaged and skin.

Type locality: Inca Mines, Puno, Peru (13°30'S, 70°00'W, 1,830 m a.s.l.).

Myotis caucensis J.A. Allen, 1914

Bulletin of the American Museum of Natural History 33(29): 381–389.

Taxonomy: Described as *Myotis caucensis* by Allen (1914: 386). Currently monotypic (Moratelli et al. 2013, 2019a).

Holotype: AMNH 32787, adult male collected by L. E. Miller on November 29, 1911; skull, mandible, and skin

Type locality: Rio Frío, Cauca River, Valle del Cauca, Colombia (04°09'N, 76°17'W; 1,066 m a.s.l.).

Myotis cobanensis Goodwin, 1955

American Museum Novitates 1744: 1–5.

Taxonomy: Described as *Myotis velifer cobanensis* by Goodwin (1955: 2), but considered as a full species by de la Torre (1958) and Hall (1981). Monotypic (Moratelli et al. 2019a).

Holotype: AMNH 145017, adult male collected by T. Larson on June 21, 1946; skull, mandible, and skin.

Type locality: Cathedral at Cobán, Alta Verapaz, Guatemala (15°28'S, 90°22'W; 1,305 m a.s.l.).

Myotis riparius Handley, 1960

Proceedings of the United States National Museum 112: 459–479.

Taxonomy: Described as *Myotis simus riparius* by Handley (1960: 466), raised to the species level by LaVal (1973). Treated as monotypic (Moratelli et al. 2019a).

Holotype: USNM 310255, an adult female (USNM 310255) with one embryo (7 mm crown-rump) collected by C.O. Handley and B.R. Feinstein on February 9, 1959; skull, mandible, and skin.

Type locality: Tacarcuna Village, Río Pucro, Darién, Panamá (07°51'N, 77°43'W, 945 m.a.s.l.).

Myotis elegans Hall, 1962

University of Kansas Publications, Museum of Natural History 14(13): 161–164.

Taxonomy: Described as *Myotis elegans* by Hall (1962: 163). Currently monotypic (Moratelli et al. 2019a).

Holotype: KU 88398, adult female collected by P.L. Clifton on September 24, 1961; skull severely damaged, mandible missing, and skin.

Type locality: 12.5 mi N of Tihuatlán, Veracruz, Mexico (20°41'N, 97°30'W; 90 m a.s.l.).

Myotis carteri LaVal, 1973

Bulletin of the Natural History Museum of Los Angeles County 15: 1–54.

Taxonomy: Described as *Myotis nigricans carteri* by LaVal (1973: 13), and elevated to the species level by Bogan (1978). Monotypic (LaVal 1973; Bogan 1978).

Holotype: LACM 36876, adult male collected by D. C. Carter on January 19, 1960; skull, mandible, baculum, and skin.

Type locality: 16 mi NE of Tamazula, Jalisco, Mexico (19°41'N, 103°14'W; 1,500 m a.s.l.).

Myotis larensis LaVal, 1973

Bulletin of the Natural History Museum of Los Angeles County 15: 1–54.

Taxonomy: Described as full species by LaVal (1973: 44), but posteriorly treated as subspecies of *M. nesopolus* by Genoways and Williams (1979). Novaes et al. (2021a) raised *M. larensis* to species level. Monotypic (LaVal 1973; Novaes et al. 2021a).

Holotype: AMNH 130709, adult female collected by G. H. H. Tate on March 23, 1938; skull, mandible, and skin.

Type locality: Rio Tocuyo, Lara, Venezuela (10°16'N, 69°56'W; 500 m a.s.l.).

Myotis martiniquensis LaVal, 1973

Bulletin of the Natural History Museum of Los Angeles County 15: 1–54.

Taxonomy: Described as *Myotis martiniquensis* by LaVal (1973: 35). Monotypic (Moratelli et al. 2019a).

Holotype: AMNH 214062, adult female collected by H. Beatty on March 15, 1967; body in alcohol, skull and mandible removed.

Type locality: Ca, 6 km E La Trinité, Tartane, Martinique (14°45'N, 60°54'W; ca. 65 m a.s.l.).

Myotis pilosatibialis LaVal, 1973

Bulletin of the Natural History Museum of Los Angeles County 15: 1–54.

Taxonomy: Described as *Myotis keaysi pilosatibialis* by LaVal (1973: 24), and raised to the species level by Mantilla-Meluk and Muñoz-Gray (2014). Treated as monotypic (Moratelli et al. 2019a).

Holotype: LACM 36879, adult male collected by R.K. LaVal and R. Valdez on July 26, 1969; skull, mandible, and skin partially damaged.

Type locality: 1 km W Talanga, Francisco Morazán, Honduras (14°24'N, 87°05'W; 750 m a.s.l.).

Myotis nyctor LaVal & Schwartz, 1974

Caribbean Journal of Science 14: 189–192.

Taxonomy: Described as *Myotis nyctor* by LaVal and Schwartz (1974: 190). Currently monotypic (Moratelli et al. 2019a).

Holotype: KU 109473, adult male collected by D. C. Leber and A. Schwartz on February 16, 1961; skull, mandible, and skin.

Type locality: Cole's Cave, Saint Thomas Parish, Barbados (13°11'N, 59°34'W; 270 m).

Myotis findleyi Bogan, 1978

Journal of Mammalogy 59(3): 519–530.

Taxonomy: Described as *Myotis findleyi* by Bogan (1978: 524). Currently monotypic (Bogan 1978).

Holotype: USNM 512417, adult male collected by C. B. Robbins on March 14, 1976; skull, mandible, and skin.

Type locality: Isla Maria Magdalena, Islas Tres Marias, Nayarit, Mexico (21°27'N, 106°25'W; ca. 300 m).

Myotis diminutus Moratelli & Wilson, 2011

Mammalian Biology 76: 608–614.

Taxonomy: Described as *Myotis diminutus* by Moratelli and Wilson (2011a: 609). Monotypic (Moratelli and Wilson 2011a; Moratelli et al. 2019a).

Holotype: USNM 58569, sub-adult male collected by D. E. Wilson on February 11, 1979; skull, mandible, and skin.

Type locality: Río Palenque Science Center, 47 km S (by road) from Santo Domingo, Los Rios, Ecuador (00°35'S, 79°21'W; ca. 150 m).

Myotis izecksohni Moratelli, Peracchi, Dias & Oliveira, 2011

Mammalian Biology 76: 592–607.

Taxonomy: Described as *Myotis izecksohni* by Moratelli et al. (2011a: 597). Currently monotypic (Moratelli et al. 2011a, 2019a).

Holotype: ALP 6675, adult male collected by D. Dias on June 25, 2005; skull, mandible, complete post-cranial skeleton, and skin.

Type locality: Fazenda Maria Brandina, Tinguá Biological Reserve, Rio de Janeiro, Brazil, (22°36'S, 43°27'W; 760 m).

Myotis lavali Moratelli, Peracchi, Dias & Oliveira, 2011

Mammalian Biology 76: 592–607.

Taxonomy: Described as *Myotis lavali* by Moratelli et al. (2011a: 602). Currently monotypic (Moratelli et al. 2011a, 2019a).

Holotype: MZUSP 18762, adult male collected by M. R. Willig on April 3, 1977; skull, mandible, and skin.

Type locality: 6 km S of Exu, Pernambuco State, Brazil (07°30'S, 39°43'W; 523 m).

Myotis handleyi Moratelli, Gardner, Oliveira & Wilson, 2013

American Museum Novitates 3780: 1–36.

Taxonomy: Described as *Myotis handleyi* by Moratelli et al. (2013: 11) Currently monotypic (Moratelli et al. 2013, 2019a).

Holotype: USNM 370932, adult male collected by the Smithsonian Venezuela Project team on August 19, 1965; skull, mandible, and skin.

Type locality: Pico Ávila, 5 km northeast of Caracas, Distrito Federal, Venezuela (10°33'N, 66°52'W; 2,092 m).

Myotis midastactus Moratelli & Wilson, 2014

Journal of Mammalogy 95: E17–E25.

Taxonomy: Described as *Myotis midastactus* by Moratelli and Wilson (2014: E19). Currently monotypic (Moratelli and Wilson 2014; Moratelli et al. 2019a).

Holotype: AMNH 211156, adult male collected by S. Anderson on September 9, 1965; skull, mandible, complete post-cranial skeleton, and skin.

Type locality: Cercado, Río Mamoré, Beni, Bolívia, ca. 23 km W of San Javier (14°34'S, 64°55'W, 160 m).

***Myotis clydejonesi* Moratelli, Wilson, Gardner, Fisher & Gutiérrez, 2016**

Special Publications, Museum of Texas Tech University 65: 49–66.

Taxonomy: Described as *Myotis clydejonesi* by Moratelli et al. (2016: 56). Currently monotypic (Moratelli et al. 2016, 2019a).

Holotype: TTU 109227, adult female collected by H. H. Genoways on January 23, 2008; skull, mandible, skin, and tissue (TK 151465).

Type locality: Raleigh Falls, Sipaliwini, Suriname (04°43'N, 56°12'W; 55 m).

***Myotis attenboroughi* Moratelli, Wilson, Novaes, Helgen & Gutiérrez, 2017**

Journal of Mammalogy 98: 994–1008.

Taxonomy: Described as *Myotis attenboroughi* by Moratelli et al. (2017: 997). Currently monotypic (Moratelli et al. 2017, 2019a).

Holotype: USNM 540693, adult male collected on April 4, 1981 by G. S. Morgan, L. K. Gordon and F. A. Harrington; skull, mandible, and skin.

Type locality: Charlottesville, 1 km N of Pirate's Bay, Saint John Parish, Tobago Island, Republic of Trinidad and Tobago (ca. 11°19'N, 60°33'W; sea level).

***Myotis bakeri* Moratelli, Novaes, Carrión & Wilson, 2019**

Special Publications, Museum of Texas Tech University 71: 239–256.

Taxonomy: Described as *Myotis bakeri* by Moratelli et al. (2019b: 241). Currently monotypic (Moratelli et al. 2019b).

Holotype: MVZ 137909, adult male collected by M. L. Hawes on July 30, 1969; skull, mandible, and skin.

Type locality: 7 km SE of Chilca, Lima, Peru (12°33'S, 76°41'W; ca. 250 m).

***Myotis armiensis* Carrión-Bonilla & Cook, 2020**

Therya 11: 508–532.

Taxonomy: Described as *Myotis armiensis* by Carrión-Bonilla and Cook (2020: 515). Currently monotypic (Carrión-Bonilla and Cook 2020).

Holotype: MSB 262089, adult male collected by J.A. Cook and collaborators on March 20, 2012; skull, mandible, complete post-cranial skeleton, and skin.

Type locality: Las Nubes Ranger Station, Parque Internacional La Amistad, District of Bugaba, Province of Chiriquí, Panamá (08°53'N, 82°36'W; 2,214 m).

***Myotis pampa* Novaes, Wilson & Moratelli, 2021**

Vertebrate Zoology 71: 711–722.

Taxonomy: Described as *Myotis pampa* by Novaes et al. (2021b: 716), who considered it monotypic.

Holotype: AMNH 205471, adult female collected by M. D. Tuttle in January, 1963; skull, mandible, and skin.

Type locality: Ca. 6 km NW from Belén, Artigas, Uruguay (30°37'S, 57°50'W; 32 m elevation).

Myotis moratellii Novaes, Cláudio, Carrión, Abreu, Wilson, Maldonado & Weksler, 2021

Journal of Mammalogy 103: 1–20.

Taxonomy: Described as *Myotis moratellii* by Novaes et al. (2021c: 10), who considered it monotypic.

Holotype: USNM 513482, adult male collected by A. L. Gardner on July 22, 1976; skull, mandible, and skin, all well-preserved.

Type locality: Vinces Canton, 3 km NE of Puerto Nuevo, Los Ríos, Ecuador (01°15'S, 78°31'W; 15 m elevation).

Name-bearing type specimens of species in synonymy

There are at least 29 names currently in synonymy of recognized species (Table 2). Fourteen names are junior synonyms of *M. nigricans*, three are under *M. albescens*, three under *M. chiloensis*, two under *M. ruber*, one under *M. atacamensis*, one under *M. oxyotus*, and one under *M. simus*. Below is an annotated list of these names (in chronological order), with information about the primary specimen types, their preservation, and the type localities.

Vespertilio leucogaster Schinz, 1821

In "Das tierreich eingetheilt nach dem Bau der thiere als Grundlage ihrer Naturgeschichte und der vergleichenden Anatomie von dem Herrn Ritter von Cuvier, volume 1". Saugethiere und Vögel, Stuttgart and Tübingen, 894 pp.

Taxonomy: Described as *Vespertilio leucogaster* (currently allocated to *Myotis*) by Schinz (1821: 180). Currently a junior synonym of *Myotis albescens* (Miller and Allen 1928; LaVal 1973; Wilson 2008).

Lectotype: AMNH 385, adult (undetermined sex) collected by Maximilian, Prinz zu Wied-Neuwied (date not specified); taxidermized skin and skull not removed (see Avila-Pires 1965).

Type locality: Mucurí, Bahia, Brazil.

Vespertilio brasiliensis Spix, 1823

In "Simiarum et Vespertilionum brasiliensium species novae (…)". Typis Francisci Serephici Hübschmanni, Monaco, xvi + 72 pp.

Taxonomy: Described as *Vespertilio brasiliensis* (currently allocated to *Myotis*) by Spix (1823: 63). Currently a junior synonym of *Myotis nigricans* (Miller and Allen 1928; Wilson 2008).

Table 2. Names under synonymy of valid species of Neotropical *Myotis*, including information on their primary types.

Nomenclatural types	Type specimen	Synonymy	Proximal type locality
argentatus	Holotype KU 19228	*M. albescens*	Veracruz, Mexico
isidori	Holotype? MNHN 1997-1806	*M. albescens*	Corrientes, Argentina
leucogaster	Lectotype AMNH 385	*M. albescens*	Bahia, Brazil
punensis	Holotype AMNH 36263	*M. albescens*	Guayas, Ecuador
nicholsoni	Holotype FMNH 50783	*M. atacamensis*	Arequipa, Peru
aelleni	Holotype MHNG 1486.76	*M. chiloensis*	Chubut, Argentina
arescens	Holotype FMNH 24396	*M. chiloensis*	Valparaiso, Chile
gayi	Not located	*M. chiloensis*	Los Lagos, Chile
alter	Holotype BMNH 0.6.29.23	*M. levis*	Paraná, Brazil
nubilus	Holotype? ZSM 121	*M. levis*	Southern Brazil
polythrix	Syntypes MNHN 842, 843	*M. levis*	Rio Grande do Sul, Brazil
arsinoe	Holotype RNH 17635	*M. nigricans*	Suriname
bondae	Holotype AMNH 14587	*M. nigricans*	Santa Marta, Colombia
brasiliensis	Not located	*M. nigricans*	Brazil
chiriquensis	Holotype AMNH 18736	*M. nigricans*	Chiriquí, Panama
concinnus	Syntypes ANSP 1114, 1115	*M. nigricans*	San Salvador, El Salvador
dalquesti	Holotype KU 23839	*M. nigricans*	Veracruz, Mexico
esmeraldae	Holotype AMNH 33239	*M. nigricans*	Esmeraldas, Ecuador
exiguus	Holotype ANSP 5626	*M. nigricans*	Panamá, Panama
hypothrix	Holotype? MNHN 1903-41	*M. nigricans*	Beni, Bolivia
maripensis	Holotype AMNH 17069	*M. nigricans*	Bolívar, Venezuela
mundus	Holotype ANSP 1829	*M. nigricans*	Zulia, Venezuela
parvulus	Lectotype RNH 17621	*M. nigricans*	Brazil
spixi	Not located	*M. nigricans*	Brazil
splendidus	Holotype? ZSM 142	*M. nigricans*	US Virgin Islands
thomasi	Not located	*M. oxyotus*	Napo, Ecuador
cinnamomeus	Not located	*M. ruber*	Paraguay
kinnamon	Holotype? MNHN 1997-2056	*M. ruber*	Minas Gerais, Brazil
guaycuru	Holotype ALP 9277	*M. simus*	Mato Grosso do Sul, Brazil

Type specimen: No specimen was designated by the author. Just like Carter and Dolan (1978), we have not found any reference specimens deposited in European collections.

Type locality: Brazil.

Remarks: The original name combination is preoccupied by *Vespertilio brasiliensis* Desmarest, 1822 (currently *Eptesicus brasiliensis*), hence, Fischer (1829) replaced it by *Vespertilio spixii*.

Vespertilio polythrix I. Geoffroy, 1824

Annales de Sciences Naturelles de Paris 3: 440–447.

Taxonomy: Described as *Vespertilio polythrix* (currently allocated to *Myotis*) by Geoffroy Saint-Hilaire (1824: 443). Currently a junior synonym of *Myotis levis* (LaVal 1973; Wilson 2008).

Syntypes: MNHN 842 (adult, undetermined sex), MNHN 843 (adult male), ZMB 3911 (adult, undetermined sex) collected by A. Geoffroy Saint-Hilaire, date not specified. All specimens are skins taxidermized (faded) with skull not removed.

Type locality: Rio Grande do Sul or Minas Gerais, Brazil.

Remarks: According to Turni and Kock (2008), the name *polythrix* is a nomen oblitum, due to page priority. This is the first available name (p. 443), whereas *levis* (nomen protectum) is on page 444 in Geoffroy's publication (1824).

Vespertilio spixii Fischer, 1829

In "Synopsis mammalium". Stuttgardtiae: J. G. Cottae, xlii + 752 pp.

Taxonomy: This name was proposed in replacement for *Vespertilio brasiliensis* Spix, 1823, considering that this name was preoccupied by *Vespertilio brasiliensis* Desmarest, 1822 (= *Eptesicus brasiliensis*). Currently a junior synonym of *Myotis nigricans* (Miller and Allen 1928; Cabrera 1958; Wilson 2008).

Vespertilio parvulus Temminck, 1840

In "Monographies de mammalogie ou description de quelques genres de mammifères dont les espèces ont été observées dans les différens musées de l'Europe". E. d'Ocagne et A. Bertrand, Paris, 141–272.

Taxonomy: Described as *Vespertilio parvulus* (currently allocated to *Myotis*) by Temminck (1840: 246). Currently a junior synonym of *Myotis nigricans* (Miller and Allen 1928; LaVal 1973; Wilson 2008).

Lectotype: RNH 17621, adult, sex undetermined, collected by J. Natterer (date not specified); skull severely damaged and skin faded.

Type locality: Brazil.

Vespertilio arsinoe Temminck, 1840

In "Monographies de mammalogie ou description de quelques genres de mammifères dont les espèces ont été observées dans les différens musées de l'Europe". E. d'Ocagne et A. Bertrand, Paris, 141–272.

Taxonomy: Described as *Vespertilio arsinoe* (currently allocated to *Myotis*) by Temminck (1840: 247). Currently a junior synonym of *Myotis nigricans* (LaVal 1973; Wilson 2008).

Holotype: RNH 17635, adult female (collector and date of capture are unknown); skull partially damaged and skin faded.

Type locality: Surinam.

Vespertilio hypothrix d'Orbigny & Gervais, 1847

In "Voyage dans l'Amérique méridionale (…). P. Bertrand/Strasbourg: V. Levrault, Paris 4: 1–32.

Taxonomy: Described as *Vespertilio hypothrix* (currently allocated to *Myotis*) by d'Orbigny and Gervais (1847: 14). Currently a junior synonym of *Myotis nigricans* (Miller and Allen 1928; Cabrera 1958; Wilson 2008).

Holotype: MNHN AC 1903-41, sex, age, collector, and date undetermined; stretched skin only.

Type locality: Moxos [Beni], Bolivia.

Vespertilio isidori d'Orbigny & Gervais, 1847

In "Voyage dans l'Amérique méridionale (…)". P. Bertrand/Strasbourg: V. Levrault, Paris 4: 1–32.

Taxonomy: Described as *Vespertilio isidori* (currently allocated to *Myotis*) by d'Orbigny and Gervais (1847: 16). Currently a junior synonym of *Myotis albescens* (Miller and Allen 1928). However, based on observations made by Carter and Dolan (1978), Wilson (2008) did not include this name in the synonym list for *M. albescens* (see discussion in Remarks section)

Holotype: Probably MNHN 1997-1806, adult, sex undetermined; skull (damaged), mandible, and skin.

Type locality: Corrientes, Argentina.

Remarks: Rode (1941) indicated the specimen MNHN 865 as the holotype. However, Carter and Dolan (1978) show that there was confusion when interpreting a Cadre number, used to guide visitors about a specimen on display in the museum, with the catalog number. Thus, Carter and Dolan indicate that this is not the type specimen of this name and have not found any other specimen in collections in Europe that could be. One of us (RM) found the supposed specimen used for the description by d'Orbigny and Gervais deposited in the mammal collection of the Muséum National D'Histoire Naturelle, Paris, France. The presumable holotype (MNHN 1997-1806) is an adult (sex undetermined). The skull reassembles *M. albescens*, but the color pattern of the skin is not a Neotropical *Myotis*.

Vespertilio splendidus Wagner, 1855

In "Die säugthiere in abbildungen nach der natur mit beschreibungen von Dr. Johann Christian Daniel von Schreber (…)". T.O. Weigel, Leipzig, xxvi + 810 pp.

Taxonomy: Described as *Vespertilio splendidus* (currently allocated to *Myotis*) by Wagner (1855: 148). Currently a junior synonym of *Myotis nigricans* (see Carter and Dolan 1978; Wilson 2008).

Holotype: ZSM 142, adult of undetermined sex, probably collected by A. F. W. Schimper (date not specified); skin only, slightly faded.

Type locality: St. Thomas [American Virgin Islands (Carter and Dolan 1978)].

Vespertilio nubilus Wagner, 1855

In "Die säugthiere in abbildungen nach der natur mit beschreibungen von Dr. Johann Christian Daniel von Schreber (…)". T. O. Weigel, Leipzig, xxvi + 810 pp.

Taxonomy: Described as *Vespertilio nubilus* (currently allocated to *Myotis*) by Wagner (1855: 752). Currently a junior synonym of *Myotis levis* (see LaVal 1973; Wilson 2008).

Holotype: ZSM 121, subadult, sex undetermined; collector and date of capture are unknown; skin taxidermized with skull not removed.

Type locality: Brazil.

Vespertilio cinnamomeus Wagner, 1855

In "Die säugthiere in abbildungen nach der natur mit beschreibungen von Dr. Johann Christian Daniel von Schreber (…)". T. O. Weigel, Leipzig, xxvi + 810 pp.

Taxonomy: Wagner (1855: 755) proposed the name *Vespertilio cinnamomeus* as a substitute for *Vespertilio ruber* É. Geoffroy, 1806 believing that "chauve-sourris cannelle" from Azara (1801) was a *Noctilio* Linnaeus, 1766. However, Miller and Allen (1928) resolved Wagner's misunderstanding, indicating that both the name *ruber* and *cinnamomeus* were based on the same specimen. Currently a junior synonym of *Myotis ruber* (see Miller and Allen 1928; LaVal 1973; Wilson 2008).

Vespertilio kinnamon Gervais, 1856

In "Animaux nouveaux ou rares recueillis pendant l'expédition dans les parties centrales de l'Amérique du Sud (…)". P. Bertrand, Paris, 25–88.

Taxonomy: Described as *Vespertilio kinnamon* (currently allocated to *Myotis*) by Gervais (1856: 84). Currently a junior synonym of *Myotis ruber* (Miller and Allen 1928; Cabrera 1958).

Holotype: MNHN 1997-2056, adult male collected on 1844 (collector not specified); skin only.

Type locality: Capela Nova, Minas Gerais, Brazil.

Vespertilio mundus H. Allen, 1866

Proceedings of the Academy of Natural Sciences of Philadelphia 18: 279–288.

Taxonomy: Described as *Vespertilio mundus* (currently allocated to *Myotis*) by Allen (1866: 280). Currently a junior synonym of *Myotis nigricans* (Miller and Allen 1928; LaVal 1973; Wilson 2008).

Holotype: ANSP 1829 (=USNM 5547), subadult female collected by S. Hayes (date not specified), currently deposited in the mammal collection of the Academy of Natural Sciences of Drexel University (Philadelphia, USA); complete specimen preserved in alcohol with skin faded.

Type locality: Maracaibo, Venezuela.

Vespertilio concinnus H. Allen, 1866

Proceedings of the Academy of Natural Sciences of Philadelphia 18: 279–288.

Taxonomy: Described as *Vespertilio concinnus* (currently allocated to *Myotis*) by Allen (1866: 281). Currently a junior synonym of *Myotis nigricans* (Miller and Allen 1928; Cabrera 1958; LaVal 1973; Wilson 2008).

Syntypes: ANSP 1114 and ANSP 1115, are adult females, collected by J. Leidy (date not specified); Body preserved in alcohol with skin faded, skull and mandible removed.

Type locality: San Salvador, El Salvador.

Vespertilio exiguus H. Allen, 1866

Proceedings of the Academy of Natural Sciences of Philadelphia 18: 279–288.

Taxonomy: Described as *Vespertilio exiguus* (currently allocated to *Myotis*) by Allen (1866: 281). Currently a junior synonym of *Myotis nigricans* (Miller and Allen 1928; Cabrera 1958).

Holotype: ANSP 5626 (= USNM 5373), adult female collected by S. Hayes (date not specified) is currently deposited in the mammal collection of the Academy of Natural Sciences of Drexel University (Philadelphia, USA); complete specimen preserved in alcohol with skin faded.

Type locality: Aspinwall, NG. (= Colón, Panama).

Vespertilio gayi Lataste, 1892

Actes de la Société Scientifique du Chili 1: 70–91.

Taxonomy: Described as *Vespertilio gayi* (currently allocated to *Myotis*) by Lataste (1892: 79), currently considered a junior synonym of *Myotis chiloensis* (Miller and Allen 1928; Cabrera 1958; Wilson 2008).

Type specimen: None. We did not access the original publication describing the species. However, no specimens from Lataste that could match the description of *M. gayi* are available in collections in Europe or South America. Probably, these specimens are lost.

Type locality: Valdivia, Chile.

Myotis thomasi Cabrera, 1901

Boletín de la Sociedad Española de Historia Natural 1: 367–373.

Taxonomy: Described as *Myotis thomasi* by Cabrera (1901: 370). Currently a junior synonym of *Myotis oxyotus* (Miller and Allen 1928; LaVal 1973; Wilson 2008).

Type specimen: None. The original description was based on an adult female preserved in alcohol that, according to the author, was deposited in the mammal collection of the Museo Nacional de Ciencias Naturales (Madrid, Spain). However, a voucher number for the specimen was not listed by Cabrera (1901). Nevertheless, Carter and Dolan (1978) did not find the representative specimen in the MNCN collection and suspect that when moving to Argentina, A. Cabrera would have taken the type specimens. There are no specimens of *Myotis* that can represent the type of *M. thomasi* in the Museo de La Plata (Itatí Olivares, pers. comm.). We presume that probably this type specimen is lost.

Type locality: In the original description, Cabrera (1901) argued that he did not have reliable data on the geographical origin of the specimen, but that it was probably from southern Brazil. Later, Cabrera (1902) corrected this to "Archidona [sobre el citado río], Napo, Ecuador".

***Myotis chiriquensis* J.A. Allen, 1904**

Bulletin of the American Museum of Natural History 20: 29–80.

Taxonomy: Described as *Myotis chiriquensis* by Allen (1904: 77). Currently a junior synonym of *Myotis nigricans* (Miller and Allen 1928; Cabrera 1958; LaVal 1973; Wilson 2008).

Holotype: AMNH 18736, adult female, collected by J. H. Batty on October 16, 1901; skull, mandible, and skin.

Type locality: Boquerón, Chiriquí, Panama.

***Myotis punensis* J.A. Allen, 1914**

Bulletin of the American Museum of Natural History 33(29): 381–389.

Taxonomy: Described as *Myotis punensis* by Allen (1914: 383). Currently a junior synonym of *Myotis albescens* (see Moratelli and Wilson 2011b).

Holotype: AMNH 36263, sub-adult male collected by W.B. Richardson on May 8, 1913; skull (partially damaged), mandible, and skin.

Type locality: Isla Puna, Guayaquil, Guayas, Ecuador.

***Myotis bondae* J.A. Allen, 1914**

Bulletin of the American Museum of Natural History 33(29): 381–389.

Taxonomy: Described as *Myotis bondae* by Allen (1914: 384). Currently a junior synonym of *Myotis nigricans* (Miller and Allen 1928; Cabrera 1958; LaVal 1973; Wilson 2008).

Holotype: AMNH 14587, adult of undetermined sex, collected by H. H. Smith in June 1898; skull, mandible, and skin.

Type locality: Bonda, Santa Marta, Colombia.

***Myotis maripensis* J.A. Allen, 1914**

Bulletin of the American Museum of Natural History 33(29): 381–389.

Taxonomy: Described as *Myotis maripensis* by Allen (1914: 385). Currently a junior synonym of *Myotis nigricans* (Miller and Allen 1928; Cabrera 1958; LaVal 1973; Wilson 2008).

Holotype: AMNH 17069, adult female collected by S. M. Klages on December 13, 1909; skull, mandible, and skin.

Type locality: Maripa, Venezuela.

***Myotis esmeraldae* J.A. Allen, 1914**

Bulletin of the American Museum of Natural History 33(29): 381–389.

Taxonomy: Described as *Myotis esmeraldae* by Allen (1914: 385). Currently a junior synonym of *Myotis nigricans* (Miller and Allen 1928; Cabrera 1958; Wilson 2008).

Holotype: AMNH 33239, adult male, collected by W. B. Richardson on November 5, 1912; skull, mandible, and skin.

Type locality: Esmeraldas, Ecuador.

Myotis chiloensis alter Miller & Allen, 1928

Bulletin of the United States National Museum 144: 1–218.

Taxonomy: Described as a subspecies of *Myotis chiloensis* by Miller and Allen (1928). Currently a junior synonym of *Myotis levis* (LaVal 1973; Wilson 2008).

Holotype: BMNH 0.6.29.23, adult female collected by G. Grillo (date not specified); body in alcohol, skull and mandible removed.

Type locality: Palmeira, Paraná, Brazil.

Myotis nigricans nicholsoni Sanborn, 1941

Field Museum of Natural History, Zoological Series 27: 371–387.

Taxonomy: Described as a subspecies of Myotis nigricans by Sanborn (1941: 382). Currently a junior synonym of *Myotis atacamensis* (LaVal 1973; Wilson 2008).

Holotype: FMNH 50783, adult male collected by C. C. Sanborn on October 17, 1939; skull, mandible, and skin, all well-preserved.

Type locality: Hacienda Chucarapi, Tambo Valley, Arequipa, Peru.

Myotis chiloensis arescens Osgood, 1943

Field Museum of Natural History, Zoological Series 30: 1–268.

Taxonomy: Described as a subspecies (Osgood 1943: 55), but currently considered a junior synonym of *Myotis chiloensis* (LaVal 1973; Wilson 2008).

Holotype: FMNH 24396, adult male collected by J. A. Wolffsohn on January 1, 1925; skin only.

Type locality: Hacienda Limache, Valparaíso, Chile.

Myotis guaycuru Proença, 1943

Revista Brasileira de Biologia 3: 313–315.

Taxonomy: Described as *Myotis guaycuru* by Proença (1943: 314), but currently considered a junior synonym of *Myotis simus* (Wilson 2008; Moratelli et al. 2011b).

Holotype: ALP 9277, an adult female collected in 1940 by Scientific Committee of the Oswaldo Cruz Institute, headed by L. Travassos; body preserved in fluid (severely damaged), with the skull (including mandible) removed and complete.

Type locality: Rio Miranda, Salobra, Mato Grosso do Sul, Brazil.

***Myotis argentatus* Dalquest & Hall, 1947**

University of Kansas Publications, Museum of Natural History 1(12): 237–244.

Taxonomy: Described as a full species by Dalquest and Hall (1947: 239). Currently a junior synonym of *Myotis albescens* (see LaVal 1973).

Holotype: KU 19228, adult male collected by W. W. Dalquest on February 2, 1947; skull, mandible, and skin.

Type locality: 14 km SW of Coatzocoalcos, Veracruz, Mexico (30 m elevation).

***Myotis nigricans dalquesti* Hall & Alvarez, 1961**

University of Kansas Publications, Museum of Natural History 14(4): 69–72.

Taxonomy: Described as a subspecies of *Myotis nigricans* by Hall and Alvarez (1961: 71), but currently considered a junior synonym of *Myotis nigricans* (LaVal 1973).

Holotype: KU 23839, adult male collected by W. W. Dalquest on January 5, 1948; skull, mandible, and skin.

Type locality: 3 km E of San Andrés Tuxtla, Veracruz, Mexico (304 m elevation).

***Myotis aelleni* Baud, 1979**

Revue Suisse de Zoologie 86(1): 267–278.

Taxonomy: Described as a full species by Baud (1979: 268), but currently considered a junior synonym of *Myotis chiloensis* (Novaes et al. 2018).

Holotype: MHNG 1486.76, adult male collected by A. Kovacs on December 19, 1975; body preserved in alcohol, skull and mandible removed.

Type locality: El Hoyo de Epuyen, 42°10'S, 71°21'W (230 m elevation), Provincia de Chubut, Argentina.

Discussion

Myotis is the most speciose bat genus in the Neotropics, with 33 species recognized currently (Bogan 1978; Moratelli et al. 2019a, b; Novaes et al. 2021a, b, c). Several species' descriptions and revalidations have been recently proposed (e.g., LaVal 1973; Moratelli et al. 2011a, 2013, 2016, 2017, 2019b; Novaes et al. 2018, 2021a, b, c), and the evidence available points in the direction of hidden diversity (Clare et al. 2007; Larsen et al. 2012; Novaes et al. 2018; Carrión-Bonilla and Cook 2020). In this scenario of intense taxonomic change, a careful assessment of all name-bearing types is essential to the correct application of names to newly identified lineages and other nomenclatural acts. Below, we point out some nomenclatural issues still associated with name-bearing types of Neotropical *Myotis*.

Since its description, *Myotis nigricans* has been treated as a widely distributed species, and several subspecies have been recognized by different authors. However, recent

studies have merged evidence indicating that *M. nigricans* is composite, as currently recognized, representing a complex of allopatric species (Moratelli and Wilson 2011a; Moratelli et al. 2011a, 2016, 2017, 2019b; Novaes et al. 2021b). The name *nigricans* seems to apply to Atlantic Forest populations from southeastern Brazil and southern South America, considering the type locality (Moratelli and Wilson 2011a; Moratelli et al. 2013, 2017). Therefore, it is necessary to reassess the taxonomic status of populations from tropical Mexico, Central America, and northern South America currently recognized as *M. nigricans* (and its subspecies). In this case, names currently treated under synonymy might apply to these potential new taxa.

Currently, 14 names are under synonymy of *M. nigricans* and can be available to use after a careful taxonomic review that considers the examination of type specimens. An example is the name *Vespertilio splendidus* Wagner, 1855 (= *Myotis splendidus*), described based on a specimen from "St. Thomas" (Wagner 1855). Carter and Dolan (1978) indicated the type locality as "St. Thomas [American Virgin Islands]", which was followed by subsequent authors (e.g., Wilson 2008). However, *Myotis* apparently does not occur either on the US Virgin Islands (Bacle et al. 2008) or on the nearest Caribbean islands (Puerto Rico, British Virgin Islands, Anguilla; Timm and Genoways 2003; Genoways et al. 2007). On the other hand, "St. Thomas" is a locality on the Caribbean Island of Barbados, where *M. nyctor* is the only species known to occur (Novaes et al. 2021a). Based on this scenario, *Myotis splendidus* is a very rare (or extinct) species (and unique representative of the genus) on the US Virgin Islands; or the geographical origin of the holotype of *Myotis splendidus* is Barbados, not US Virgin Islands, and the name is the senior synonym of *Myotis nyctor*. In any case, *Myotis splendidus* is unlikely to be a synonym for *Myotis nigricans*, considering the biogeographical history of colonization of the Caribbean, where each island has its own unique species of *Myotis*, and there is no evidence of the occurrence of *M. nigricans* as recognized by Moratelli et al. (2017) and Novaes et al. (2021a).

Another important issue is the validity of some names occasionally found in the literature on *Myotis* taxonomy. In their catalogue of type specimens of neotropical bats deposited in selected European museums, Carter and Dolan (1978) listed "*Vespertilio carbonarius* Wagner" based on a specimen (ZSM 124) from Brazil obtained by J.F. Brandt, whose label reads "*Vespertilio carbonarius* Wagn. / 1843 / Brandt / Brasil". This specimen (taxidermized skin with skull not removed) was examined by us and it resembles *M. riparius* in size and the fur texture, length, and coloration. However, as with Carter and Dolan (op cit.), we were also unable to locate the publication with the species description. It is not impossible that this name was formally published (considering the vast, and sometimes rare, production of Wagner). However, if a publication containing the species description is found, we suggest that *Vespertilio carbonarius* should be treated as a *nomen oblitum*, following article 23.9.1 from ICZN (1999).

For another example, Cornalia (1849) assigned the name "*Vespertilio quixensis* Osculati" to the synonymy of *Vespertilio osculati* (= *Myotis nigricans osculati*). In an introduction to the facsimile reprint of Cornalia's (1849) publication, Cagnolaro and Violani (1988) recommended treating *V. quixensis* as a *nomen nudum*, but the name became

available in the combination *Phyllostomus quixensis* Osculati, 1854: 53. It is possible that the description of *quixensis* appeared in the first edition of the Osculati's publication; however, we have not been able to examine that publication due to its rarity.

Myotis comprises a diverse group in number of species compared to other neotropical bat genera. However, its species richness does not reflect its phenotypic diversity, characterized by a low morphological differentiation (Ghazali et al. 2017; Moratelli et al. 2019a). Due to the large number of species names proposed, this catalogue puts together information on name-bearing types of species treated as valid or under synonymy as an aid for future taxonomic works.

Acknowledgements

The following curators and collection staff provided access to specimens under their care: A.L. Peracchi (Universidade Federal Rural do Rio de Janeiro, Brazil); M. de Vivo and J.G. Barros (Museu de Zoologia da Universidade de São Paulo, Brazil); N. Simmons and E. Westwig (American Museum of Natural History, USA); B. Patterson, W. Stanley and R. Banasiak (Field Museum of Natural History, USA); J.A. Esselstyn (Museum of Natural Sciences at Louisiana State University, USA); R. Baker and H. Garner (Museum of Texas Tech University, USA); C. Conroy (Museum of Vertebrate Zoology at University of California, USA); R.M. Timm and M. Eifler (Natural History Museum of the Kansas University, USA); J. Dines (Natural History Museum of Los Angeles County, USA); K. Helgen, D. Lunde, and L. Gordon (National Museum of Natural History, USA); R.P. Miguez (Natural History Museum, London, UK); M. Hiermeier (Zoologisches Staats Sammlung München, Germany); C. Callou, C. Denys, J.-M. Pons (Muséum National D'Histoire Naturelle, France). G.S.T. Garbino (Universidade Federal de Viçosa, Brazil) provided access to information about Ángel Cabrera's publications. N.S. Gilmore (Museum of the Academy of Natural Sciences of Drexel University, USA) and A.L.G. Rodríguez (Museo Nacional de Ciencias Naturales, Spain), Itatí Olivares provided access to information about specimens deposited in Museo de La Plata, (Buenos Aires, Argentina). G. Bardelli (Sezione di Zoologia dei Vertebrati, Museo di Storia Naturale di Milano, Italy) provided information about Gaetano Osculati's collection. This work was partially supported by the Smithsonian Institution, USA, Conselho Nacional de Desenvolvimento Científico e Tecnológico, Brazil (CNPq 313963/2018-5) and Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro, Brazil (FAPERJ; E-26/200.967/2021) through grants to RM and DEW. RLMN has received support from FAPERJ (E-26/204.243/2021).

References

Allen H (1866) Notes on the Vespertilionidae of Tropical America. Proceedings. Academy of Natural Sciences of Philadelphia 18: 279–288. https://biostor.org/reference/127631

Allen JA (1904) Mammals from southern Mexico and Central and South America. Bulletin of the American Museum of Natural History 20: 29–80. http://hdl.handle.net/2246/662

Allen JA (1914) New South American bats and a new octodont. Bulletin of the American Museum of Natural History 33: 381–389. http://hdl.handle.net/2246/1820

Avila-Pires FD (1965) The type specimens of Brazilian mammals collected by Prince Maximilian zu Wied. American Museum Novitates 2209: 1–21.

Azara F (1801) Essais sur l'histoire naturelle des quadrupèdes de la province du Paraguay. Paris: Charles Pougens, vol. 1, 366 pp; vol. 2, 499 pp. https://doi.org/10.5962/bhl.title.112568

Bacle J-P, Lindsay KC, Kwiecinski GG (2008) Bats of St. Thomas and St. John U.S. Virgin Islands: priority conservation measures for species of greatest concern. Occasional Paper of the Island Resources Foundation 60: 1–13.

Baud FJ (1979) *Myotis aelleni*, nov. sp., chauve-souris nouvelle d'Argentine (Chiroptera: Vespertilionidae). Revue Suisse de Zoologie 86: 267–278. https://doi.org/10.5962/bhl.part.82292

Bogan MA (1978) A new species of *Myotis* from the Islas Tres Marias, Nayarit, Mexico, with comments on variation in *Myotis nigricans*. Journal of Mammalogy 59(3): 519–530. https://doi.org/10.2307/1380228

Cabrera A (1901) Descripción de tres nuevos mamíferos americanos. Boletín de la Sociedad Española de Historia Natural 1: 367–373.

Cabrera A (1902) Nota sobre el verdadero "hábitat" del "*Myotis Thomasi*". Boletín de la Sociedad Española de Historia Natural 2: 293.

Cabrera A (1958) Catálogo de los mamíferos de América del Sur. Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia". Ciencias Zoológicas 4: 1–308.

Cagnolaro L, Violani C (1988) Introduction to the anastatic reprint of "Vertebratorum synopsis…" by E. Cornalia (1849). Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano 129: 433–434.

Carrión-Bonilla CA, Cook JA (2020) A new bat species of the genus *Myotis* with comments on the phylogenetic placement of *M. keaysi* and *M. pilosatibialis.* Therya 11(3): 508–532. https://doi.org/10.12933/therya-20-999

Carter DC, Dolan PG (1978) Catalog of type specimens of Neotropical bats in selected European museums. Special Publications. Museum Texas Tech University Press 15: 1–136. https://doi.org/10.5962/bhl.title.142635

Ceballos G, Ehrlich PR, Barnosky AD, García A, Pringle RM, Palmer TM (2015) Accelerated modern human–induced species losses: Entering the sixth mass extinction. Science Advances 1(5): e1400253. https://doi.org/10.1126/sciadv.1400253

Ceballos G, Ehrlich PR, Dirzo R (2017) Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. Proceedings of the National Academy of Sciences of the United States of America 114(30): E6089–E6096. https://doi.org/10.1073/pnas.1704949114

Clare EL, Lim BK, Engstrom MD, Eger JL, Hebert PDN (2007) DNA barcoding of Neotropical bats: Species identification and discovery within Guyana. Molecular Ecology Notes 7(2): 184–190. https://doi.org/10.1111/j.1471-8286.2006.01657.x

Cook JA, Arai S, Armién B, Bates J, Carrión-Bonilla C, Cortez MBS, Dunnum JL, Ferguson AW, Johnson KM, Khan FAA, Paul DL, Reeder DM, Revelez MA, Simmons NB, Thiers

BM, Thompson CW, Upham NS, Vanhove NPM, Webala PW, Weksler M, Yanagihara R, Soltis PS (2020) Integrating biodiversity infrastructure into pathogen discovery and mitigation of emerging infectious diseases. Bioscience 70(7): 531–534. https://doi.org/10.1093/biosci/biaa064

Cornalia E (1849) Vertebratorum synopsis in Museo Mediolanense extantium que per novam orbem Cajetanus Osculati collegit annis 1846–47–1848: speciebus novis vel minus cognitis adjectis nec non discriptionibus atque iconibus illustratis. Typographia Corbetta, Modoetiae, 16 pp, 1 pl. [reprinted in 1988 in Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano 129: 435–452, but with original pagination, and with introduction by L. Cagnolaro and C. Violani]

Cracraft J (2002) The seven great questions of systematic biology: An essential foundation for conservation and the sustainable use of biodiversity. Annals of the Missouri Botanical Garden 89(2): 303–304. https://doi.org/10.2307/3298558

d'Orbigny A, Gervais P (1847) Mammifères. In: d'Orbigny A (Ed.) Voyage dans l'Amérique méridionale (le Brésil, la République orientale de l'Uruguay, la République Argentine, la Patagonie, la République du Chili, la République de Bolivia, la République du Pérou), exécuté pendant les années 1826, 1827, 1828, 1829, 1830, 1831, 1832 et 1833. P. Bertrand/Strasbourg; V. Levrault, Paris 4: 1–32. [+ 23 pls] https://doi.org/10.5962/bhl.title.100771

Dalquest WW, Hall ER (1947) A new bat (genus *Myotis*) from Mexico. University of Kansas Publications. Museum of Natural History 1: 237–244.

de la Torre L (1958) The status of the bat *Myotis velifer cobanensis* Goodwin. Proceedings of the Biological Society of Washington 71: 167–170. https://biostor.org/reference/83550

Fischer JB (1829) Synopsis mammalium. Stuttgardtiae: J. G. Cottae, [xlii +] 752 pp.

Fisher RD, Ludwig CA (2015) Catalog of type specimen of recent mammals: Orders Didelphimorphia through Chiroptera (excluding Rodentia) in the National Museum of Natural History, Smithsonian Institution. Smithsonian Contributions to Zoology 644: 1–110. https://doi.org/10.5479/si.19436696.644

Gardner AL (2008) Gazetteer of marginal localities. In: Gardner AL (Ed.) Mammals of South America, vol. 1: marsupials, xenarthrans, shrews, and bats. University of Chicago Press, Chicago, 581–628. https://doi.org/10.7208/chicago/9780226282428.001.0001

Genoways HH, Williams SL (1979) Notes on bats (Mammalia: Chiroptera) from Bonaire and Curaçao, Dutch West Indies. Annals of the Carnegie Museum 48: 311–321.

Genoways HH, Pedersen SC, Phillips CJ, Gordon LK (2007) Bats of Anguilla, northern Lesser Antilles. Occasional Papers of Texas Tech University 270: 1–12. https://doi.org/10.5962/bhl.title.156960

Gervais P (1856) Deuxième mémoire. Documents zoologiques pour servir a la monographie des chéiroptères Sud-Américains. In: Gervais P (Ed.) Mammifères. In: Castelnau F (Ed.) Animaux nouveaux ou rares recueillis pendant l'expédition dans les parties centrales de l'Amérique du Sud, de Rio de Janeiro a Lima, et de Lima au Para; exécutée par ordre du gouvernement français pendant les années 1843 a 1847, sous la direction du comte Francis de Castelnau. P. Bertrand, Paris, 25–88. https://doi.org/10.5962/bhl.title.86371

Ghazali M, Moratelli R, Dzeverin I (2017) Ecomorph evolution in *Myotis* (Vespertilionidae). Journal of Mammalian Evolution 24(4): 475–484. https://doi.org/10.1007/s10914-016-9351-z

Goodwin GG (1955) Mammals from Guatemala, with description of a new little brown bat. American Museum Novitates 1744: 1–5.

Hall ER (1962) A new bat (*Myotis*) from Mexico. University of Kansas Publications. Museum of Natural History 14: 163–164.

Hall ER (1981) The mammals of North America. John Wiley & Sons, New York, [xv +] 600 pp. [+ 90]

Hall ER, Alvarez T (1961) A new subspecies of the black myotis (bat) from eastern Mexico. University of Kansas Publications. Museum of Natural History 14: 69–72.

Handley CO (1960) Descriptions of new bats from Panama. Proceeding of the United States Nacional Museum 112: 459–479. https://doi.org/10.5479/si.00963801.112-3442.459

ICZN (1999) International Code of Zoological Nomenclature. 4th edn. London, 305 pp.

Larsen RJ, Knapp MC, Genoways HH, Khan FAA, Larsen PA, Wilson DE, Baker RJ (2012) Genetic diversity of Neotropical *Myotis* (Chiroptera: Vespertilionidae) with an emphasis on South American species. PLoS ONE 7(10): e46578. https://doi.org/10.1371/journal.pone.0046578

Lataste F (1892) Etudes sur la faune chilienne. II—Note sur les chauve souris. Actes de la Société Scientifique du Chili 1: 70–91.

LaVal RK (1973) A revision of the Neotropical bats of the genus *Myotis*. Natural History Museum of Los Angeles County. Science Bulletin 15: 1–54.

LaVal RK, Schwartz A (1974) A new bat of the genus *Myotis* from Barbados. Caribbean Journal of Science 14: 189–192.

Mantilla-Meluk H, Muñoz-Garay J (2014) Biogeography and taxonomic status of *Myotis keaysi pilosatibialis* LaVal, 1973 (Chiroptera: Vespertilionidae). Zootaxa 3793(1): 60–70. https://doi.org/10.11646/zootaxa.3793.1.2

May RM (1988) How many species are there on Earth? Science 241(4872): 1441–1449. https://doi.org/10.1126/science.241.4872.1441

MDD (2021) Mammal Diversity Database (Version 1.7). Zenodo. http://doi.org/10.5281/zenodo.4139818

Menu H (1987) Morphotypes dentaires actuels et fossiles des chiroptères. Palaeovertebrata 17: 77–150.

Miller GS (1900) Three new bats from the Island of Curaçao. Proceedings of the Biological Society of Washington 13: 123–127.

Miller GS (1902) A new bat from the Island of Dominica. Proceedings of the Biological Society of Washington 15: 243–244.

Miller GS, Allen GM (1928) The American bats of the genera *Myotis* and *Pizonyx*. Bulletin – United States National Museum 144(144): 1–128. https://doi.org/10.5479/si.03629236.144.i

Miranda JMD, Bernardi IP, Sponchiado J, Passos FC (2013) The taxonomic status of *Myotis levis levis* and *Myotis levis dinellii* (Mammalia: Chiroptera: Vespertilionidae). Zoologia 30(5): 513–518. https://doi.org/10.1590/S1984-46702013000500007

Moratelli R, Oliveira JA (2011) Morphometric and morphological variation in South American populations of *Myotis albescens* (Chiroptera: Vespertilionidae). Zoologia 28(6): 789–802. https://doi.org/10.1590/S1984-46702011000600013

Moratelli R, Wilson DE (2011a) A new species of *Myotis* Kaup, 1829 (Chiroptera, Vespertilionidae) from Ecuador. Mammalian Biology 76(5): 608–614. https://doi.org/10.1016/j.mambio.2010.10.003

Moratelli R, Wilson DE (2011b) The identity of *Myotis punensis* (Chiroptera: Vespertilionidae). Zoologia 28(1): 115–121. https://doi.org/10.1590/S1984-46702011000100016

Moratelli R, Wilson DE (2014) A new species of *Myotis* (Chiroptera, Vespertilionidae) from Bolivia. Journal of Mammalogy 95(4): 17–25. https://doi.org/10.1644/14-MAMM-149

Moratelli R, Peracchi AL, Dias D, Oliveira JA (2011a) Geographic variation in South American populations of *Myotis nigricans* (Schinz, 1821) (Chiroptera, Vespertilionidae), with the description of two new species. Mammalian Biology 76(5): 592–607. https://doi.org/10.1016/j.mambio.2011.01.003

Moratelli R, Peracchi AL, Oliveira JA (2011b) Morphometric and morphological variation in *Myotis simus* Thomas (Chiroptera, Vespertilionidae), with an appraisal of the identity of *Myotis guaycuru* Proença based on the analysis of the type material. Zootaxa 2985(1): 41–54. https://doi.org/10.11646/zootaxa.2985.1.3

Moratelli R, Gardner AL, Oliveira JA, Wilson DE (2013) Review of *Myotis* (Chiroptera, Vespertilionidae) from northern South America, including description of a new species. American Museum Novitates 3780(3780): 1–36. https://doi.org/10.1206/3780.2

Moratelli R, Wilson DE, Gardner AL, Fisher RD, Gutiérrez EE (2016) A new species of *Myotis* (Chiroptera, Vespertilionidae) from Suriname. Special Publications of Texas Tech University 65: 49–66.

Moratelli R, Wilson DE, Novaes RLM, Helgen KM, Gutiérrez EE (2017) Caribbean *Myotis* (Chiroptera, Vespertilionidae), with description of a new species. Journal of Mammalogy 98(4): 1–15. https://doi.org/10.1093/jmammal/gyx062

Moratelli R, Burgin C, Cláudio VC, Novaes RLM, López-Baucells A, Haslauer R (2019a) Family Vespertilionidae (Vesper Bats). In: Wilson DE, Mittermeier AR (Eds) Handbook of the mammals of the world, vol. 9. Bats. Lynx Edicions, Barcelona, 716–981.

Moratelli R, Novaes RLM, Carrión-Bonilla C, Wilson DE (2019b) A new species of *Myotis* (Chiroptera, Vespertilionidae) from Peru. Special Publications of Museum of Texas Tech University 71: 239–256.

Novaes RLM, Wilson DE, Ruedi M, Moratelli R (2018) The taxonomic status of *Myotis aelleni* Baud, 1979 (Chiroptera, Vespertilionidae). Zootaxa 4446(2): 257–264. https://doi.org/10.11646/zootaxa.4446.2.5

Novaes RLM, Cláudio VC, Larsen RJ, Wilson DE, Weksler M, Moratelli R (2021a) The taxonomic status of *Myotis nesopolus larensis* (Chiroptera, Vespertilionidae) and new insights on the diversity of Caribbean Myotis. ZooKeys 1015: 145–167. https://doi.org/10.3897/zookeys.1015.59248

Novaes RLM, Cláudio VC, Carrión-Bonilla C, Abreu EF, Wilson DE, Maldonado JE, Weksler M (2021b) Variation in the *Myotis keaysi* complex (Chiroptera, Vespertilionidae), with description of a new species from Ecuador. Journal of Mammalogy 2021: gyab139. https://doi.org/10.1093/jmammal/gyab139 [online first]

Novaes RLM, Wilson DE, Moratelli R (2021c) A new species of *Myotis* (Chiroptera, Vespertilionidae) from Uruguay. Vertebrate Zoology 71: 711–722. https://doi.org/10.3897/vz.71.e73146

Novaes RLM, LaVal RK, Wilson DE, Moratelli R (2022) Redescription of *Myotis atacamensis* (Chiroptera, Vespertilionidae) with neotype designation. Zoologia 39: e21026. https://doi.org/10.1590/s1984-4689.v39.e21026

Nowak RN (1994) Walker's bats of the world. The Johns Hopkins University Press, Baltimore, 287 pp.

Osgood WH (1943) The mammals of Chile. Field Museum of Natural History, Zoological Series 30: 1–268. https://doi.org/10.5962/bhl.title.3842

Pearson DL, Hamilton AL, Erwin TL (2011) Recovery plan for the endangered taxonomy profession. Bioscience 61(1): 58–63. https://doi.org/10.1525/bio.2011.61.1.11

Peters W (1866) Über einige neue oder weniger bekannte Flederthiere. Monatsberichte der Königlichen Preussische Akademie des Wissenschaften zu Berlin 1867: 16–25.

Proença AMC (1943) "Myotis guaycurú" n.sp., morcego proveniente de Salobra, Estado do Mato Grosso (Microchiroptera, Vespertilionidae). Revista Brasileira de Biologia 3: 313–315.

Rode P (1941) Catalogue des types de memmifères du Muséum National d'Histoire Natuelle. II. Ordre des Chiroptères. Muséum National d'Histoire Naturelle, Zoology Series 20: 23–27.

Saint-Hilaire G (1806) Mémoire sur le genre et les espècies de Vespertilion, l'un des genres de la famille des chauve-souris. Annales du Muséum d'Histoire Naturelle 8: 187–205. https://biostor.org/reference/135512

Saint-Hilaire G (1824) Sur les Vespertilions du Brésil. Annales de Sciences Naturelles de Paris 3: 440–447.

Sanborn CC (1941) Descriptions and records of Neotropical bats. Field Museum of Natural History, Zoological Series 27: 371–387.

Schinz HR (1821) Das tierreich eingetheilt nach dem Bau der thiere als Grundlage ihrer Naturgeschichte und der vergleichenden Anatomie von dem Herrn Ritter von Cuvier, volume 1. Saugethiere und Vögel, Stuttgart and Tübingen, 894 pp.

Smith T, Habersetzer J, Simmons NB, Gunnell GF (2012) Systematics and paleobiogeography of early bats. In: Gunnell GF, Simmons NB (Eds) Evolutionary history of bats: fossils, molecules, and morphology. Cambridge University Press, Cambridge, 23–66. https://doi.org/10.1017/CBO9781139045599.003

Spix J (1823) Simiarum et Vespertilionum brasiliensium species novae: ou histoire naturelle des especies nouvelles de singes et de chauves-souris observées et recueillies pendant le voyage dans l'intérieur de Bresil. Typis Francisci Serephici Hübschmanni, Monaco, [xvi +] 72 pp. https://doi.org/10.5962/bhl.title.157804

Tancoigne E, Bole C, Sigogneau A, Dubois A (2011) Insights from Zootaxa on potential trends in zoological taxonomic activity. Frontiers in Zoology 8(1): e5. https://doi.org/10.1186/1742-9994-8-5

Temminck CJ (1840) Treizième monographies sur les cheiroptères vespertilionides formant les genres Nyctice, Vespertilion et Furie. In: Monographies de mammalogie ou description de quelques genres de mammifères dont les espèces ont été observées dans les différens musées de l'Europe. E. d'Ocagne et A. Bertrand, Paris, 141–272.

Thomas O (1901) New *Myotis*, *Artibeus*, *Sylvilagus* and *Metachirus* from South America. Annals and Magazine of Natural History (Serie 7) 9: 189–193. https://doi.org/10.1080/00222930108678512

Thomas O (1902) On Azara's "Chauve-souris onzième" (*Myotis ruber*, Geoff.) and a new species allied to it. Annals and Magazine of Natural History (Serie 7) 10: 493–494. https://doi.org/10.1080/00222930208678708

Timm RM, Genoways HH (2003) West Indian mammals from the Albert Schwartz collection: Biological and historical information. Scientific Papers, Natural History Museum. The University of Kansas 29: 1–47. https://doi.org/10.5962/bhl.title.8485

Turni H, Kock D (2008) Type specimens of bats (Chiroptera: Mammalia) in the collections of the Museum für Naturrrrkunde, Berlin. Zootaxa 1869(1): 1–82. https://doi.org/10.11646/zootaxa.1869.1.1

Wagner JA (1855) Die säugthiere in abbildungen nach der natur mit beschreibungen von Dr. Johann Christian Daniel von Schreber. Supplementband. Fünfte Abtheilung: Die Affen, Zahnlücker, Beutelthiere, Hufthiere, Insektenfresser und Handflügler. T.O. Weigel, v. 5 Leipzig, [xxvi +] 810 pp.

Waterhouse GR (1840) Mammalia. In: Waterhouse GR, Darwin CR (Eds) The zoology of the voyage of the H.M.S. Beagle, under the command of Captain Fitzroy, R.N., during the years 1832 to 1836. Smith, Elder and Co, London, 97 pp.

Wheeler QD (2004) Taxonomic triage and the poverty of phylogeny. Philosophical Transactions of the Royal Society of London – Series B, Biological Sciences 359(1444): 571–583. https://doi.org/10.1098/rstb.2003.1452

Wilson DE (2008) Genus *Myotis* Kaup 1829. In: Gardner AL (Ed.) Mammals of South America, vol. 1: marsupials, xenarthrans, shrews, and bats. University of Chicago Press, Chicago, 468–481.

ZooKeys 1105: 165–208 (2022)
doi: 10.3897/zookeys.1105.82495
https://zookeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
ZooKeys
Launched to accelerate biodiversity research

Hexatoma crane flies (Diptera, Limoniidae) of Korea

Sigitas Podenas[1,2], Sun-Jae Park[3], Hye-Woo Byun[3], Virginija Podeniene[2]

1 *Nature Research Centre, Akademijos str. 2, LT–08412 Vilnius, Lithuania* **2** *Instute of Biosciences, Life Sciences Centre of Vilnius University, Sauletekio str. 7, LT–10257 Vilnius, Lithuania* **3** *Animal Resources Division, National Institute of Biological Resources, Incheon 22689, Republic of Korea*

Corresponding author: Sigitas Podenas (sigitas.podenas@gamtc.lt)

Academic editor: Gunnar Kvifte | Received 19 February 2022 | Accepted 5 April 2022 | Published 15 June 2022

http://zoobank.org/BEE6D442-CB16-4294-BA09-19873BBB283E

Citation: Podenas S, Park S-J, Byun H-W, Podeniene V (2022) *Hexatoma* crane flies (Diptera, Limoniidae) of Korea. ZooKeys 1105: 165–208. https://doi.org/10.3897/zookeys.1105.82495

Abstract

Hexatoma Latreille, 1809 is a large genus of short-palped crane flies with a worldwide distribution. Accounting for more than 60 percent of global species, 362 extant species occur in Asia. Prior to our study, *Hexatoma* crane flies on the Korean Peninsula (both the Democratic People's Republic of Korea and the Republic of Korea) had been studied for 90 years starting in 1930, but only three species had been recorded, with one of them being a misidentification. This study adds six species to the fauna of the Korean Peninsula, all of which belong to the subgenus *H.* (*Eriocera*) Macquart, 1838. General information on genus and subgenus morphological characters is presented in this paper, with a redescription of each species based on Korean specimens, as well as illustrations of both sexes, the elevation range, the period of activity, habitat information, general distribution, and a distribution map for the Korean Peninsula. Three species *H.* (*E.*) *ilwola* Podenas, **sp. nov.**, *H.* (*E.*) *pianigra* Podenas, **sp. nov.** and *H.* (*E.*) *serenensis* Podenas, **sp. nov.** are described as new to science. *Hexatoma* (*E.*) *lygropis* (Alexander, 1920) is deleted from the Korean species list as a misidentification. This publication is a continuation of our previous work on short-palped crane flies (Limoniidae) from Korea.

Keywords

East Palaearctic, Limnophilinae, North Korea, South Korea, Taiwan, taxonomy

Introduction

Investigations into Korean short-palped crane flies, family Limoniidae (Diptera), began more than a century ago with the first specimens collected as early as 1915 (Podenas et al. 2019). The first publication on that group of insects, with four descriptions of new species, was written by Ch. P. Alexander (Alexander 1934a). He described 49 species from Korea, most of them from the northern part of the peninsula, now the Democratic People's Republic of Korea (North Korea) (Podenas 2013). Nearly eighty years later, in 2012, further investigations into the Limoniidae crane flies on the Korean Peninsula were initiated by the authors of this publication and researchers from the National Institute of Biological Resources in Incheon, the Republic of Korea (South Korea). Prior to those studies, 95 species of Limoniidae were recorded from the North and South Koreas (Podenas 2013), the new findings summarized in the National List of Species of Korea a few years later (Cho 2019), this already including 144 species.

The original description of the genus *Hexatoma* (Latreille 1809) was based on a male of a single species *H. nigra* Latreille, 1809. It listed just antennal and wing venation characters, such as a 6-segmented antenna, two short basal antennomeres, an especially short subglobular pedicel, four long cylindrical flagellomeres and an open discal cell with parallel veins reaching the wing margin. Recently, the genus has been divided into six subgenera. All of them have sexually dimorphic antennae, with the male antennae longer than that of female. In some species, the male antenna is several times longer than the body. Wing venation, especially a closed or open discal cell, is used for discrimination of subgenera. Male terminalia are comparatively simple, with a wide epandrium, usually elongate gonocoxite, two pairs of gonostyli and a simple aedeagus. On the other hand, in more tropical and subtropical regions, *Hexatoma* are distinguished on striking color patterns of the body and wings.

The genus has a worldwide distribution and includes 596 extant species (Oosterbroek 2022). *Hexatoma* is especially diverse in Asia, from where we know 362 species.

Larvae of all known Palaearctic *Hexatoma* species are aquatic, most of them developing in rivers with sandy or gravel bottoms, some Nearctic species developing in bogs (Alexander 1920) while the mating behavior includes swarming of males above the water surface observed during collecting trips in Asia.

The second publication on Korean crane flies (Alexander 1934b) included the original description of *H. masakii*, a species endemic to South Korea. These specimens were collected in 1930 by I. Tabashi. The last specimens of that species were collected in 1954 in an area close to the type locality. At the beginning of our studies, three species of *Hexatoma* had been recorded from the Korean Peninsula (Cho 2019), including another endemic species, *H.* (*E.*) *pernigrina* Alexander, 1938, that had been described from North Korea. Added in 1971 (Kim 1971), these three species also included *H. lygropis* (Alexander, 1920) that was a misidentification of *H. pernigrina*.

Commensing our studies, we expected a high diversity of *Hexatoma* crane flies in Korea due to the abundance of suitable habitats, specifically rivers with sandy or gravel bottoms.

Since 2012, crane flies have been collected annually in different localities, at different times and using different methods throughout the country. Despite original and subsequent descriptions of East Palearctic species over a long period of time, some of these species were known only from the original descriptions and no illustrations were available. The aim of our study was to document, redescribe, illustrate, and prepare keys for all Korean crane fly species identified to date. In this article, we provide photographs of important taxonomical details, such as antennae, wings and male and female terminalia. We also include distribution maps of the Korean species, as well as a key for all the species of the Korean Peninsula. This publication is a continuation of our previous work on short-palped crane flies (Limoniidae) from Korea. We plan similar treatments of the subfamily Chioneinae and the family Pediciidae which potentially could yield many more species for the Peninsula.

Materials and methods

Crane flies available for this study (Table 1) are preserved in these scientific collections: the Hungarian Natural History Museum, Budapest, Hungary (**HNHM**), specimens collected in 1971 in North Korea by S. Horvatovich and J. Papp; Korea University, Seoul, South Korea (**KU**), specimens collected in 1973–2015 in South Korea by entomologists and students of Korea University; the National Institute of Biological Resources (**NIBR**), Incheon, South Korea, specimens collected in 2011–2019 in South Korea mostly by the authors of this publication; the Snow Entomological Museum, University of Kansas, Lawrence, KS, USA (**SMEK**), specimens collected in 1954 in South Korea by Dr. G. W. Byers; the United States National Museum, the Smithsonian Institution, Washington DC, USA (**USNM**), specimens collected in 1930–1940 in the central and northern parts of the Korean Peninsula (now North and South Koreas) by I. Tabashi and A. M. Yankovsky; the Natural History Museum, London, United Kingdom (**NHMUK**), comparative material; Naturalis biodiversity center, Leiden, Netherlands (**Naturalis**), comparative material; and Nature Research Center, Vilnius, Lithuania (**NRC**), comparative material.

Adult crane flies were collected in various ways, including by insect nets, with Malaise traps, LED light traps, black light traps, Mosquito Magnet traps (Pro Model, Woodstream Corp., Lititz, PA), New Jersey traps and at light sources. Some specimens were preserved dry in envelopes in the field and were later mounted at the laboratory on their side on a paper point, with legs generally surrounding the insect pin. Other specimens were preserved in 96% ethanol (ETOH). Some specimens were slide mounted in Euparal; the genitalia of males and ovipositors of females were cleared overnight in approximately 10% potassium hydroxide (KOH) and preserved in microvials filled with glycerol on the same pin as the dry insect, or on a separate pin if the crane fly was preserved in ETOH.

Table 1. Collecting sites in Korea.

Locality	Year	Coordinates (N*, E*)	Collector	Method	Collection
S. Korea, Suigen, Chosen	1930	37°16.00'N, 127°01.00'E	I. Tabashi	Net	USNM
N. Korea, Ompo (Onbo, Hamgyeongbuk-do,Gyeongsung-gun)	1937 1938 1939	41°30.81'N, 129°34.69'E	A. M. Yankovsky	Net	USNM
N. Korea, Seren Mts. (Hamgyeongbuk-do, Gyeongsung-gun)	1938	41°41.24'N, 129°18.55'E	A. M. Yankovsky	Net	USNM
N. Korea, Kankyo Nando, Puksu Pyaksan (Yanggang-do, Pungseo-gun, Mt. Buksubaeksan)	1939	40°41.99'N, 127°42.96'E	A. M. Yankovsky	Net	USNM
N. Korea, Chonsani (Yanggang-do, Daehongdan-gun)	1940	41°59.62'N, 128°45.15'E	A. M. Yankovsky	Net	USNM
S. Korea, #12, Hwy. #20, 8 mi. SW of Kangnung (Gangwon-do, Gangneung, Seongsan-myeon, Eoheul-ri)	1954	37°42.00'N, 128°47.00'E	G. W. Byers	Net	USNM, SMEK
S. Korea, #25, #26 Central National Forest, 18 mi. NE Seoul (Gyeonggi-do, Namyangju-ai, Sudong-myeon, Naebang-ri)	1954	37°44.89'N, 127°17.62'E	G. W. Byers	Net	SMEK, USNM
N. Korea, Prov. South Pyongan, Pyongyan, Hotel garden	1971	39°00.63'N, 125°45.10'E	S. Horvatovich, J. Papp	Net	HNHM
S. Korea, Gyeonggi-do, Paju-si, Aengmubong	1973	37°45.46'N, 126°55.65'E	Y. Kim	Net	KU
S. Korea, Gyeonggi-do, Pocheon-si, Soheul-eup, Gwangneung Forest	1973	37°45.05'N, 127°09.70'E	O. Lee	Net	KU
S. Korea, Seoul, Mt. Suraksan	1974	37°41.79'N, 127°04.93'E	–	–	KU
S. Korea, Gyeongsangbuk-do, Yeongju-si, Punggi-eup, Samga-ri, Mt. Sobaeksan	2000 2001	36°55.28'N, 128°30.33'E	–	–	KU
S. Korea, Gyeongsangbuk-do, Bonghwa-gun, Mt. Seondalsan	2000 2001	37°02.38'N, 128°42.55'E	–	–	KU
S. Korea, Gyeongsangbuk-do, Yeongyang-gun, Ilwol-myeon, Yonghwa-ri, Mt. Ilwolsan, Yonghwasa Temple	2001	36°48.71'N, 129°07.55'E	–	–	KU
S. Korea, Jeollabuk-do, Namwon, Sannae-myeon, Buun-ri, Namwonsi Sannaemyeon Baemsagol	2009	35°21.21'N, 127°34.95'E	S. W. Jung	Net	KU
S. Korea, Gangwon-do, Jeongseon-gun, Imgye-myeon, Dojeon-ri	2011	37°32.15'N, 128°54.17'E	H.-W. Byun et al.	Malaise trap	NIBR
S. Korea, Gangwon-do, Pyeonchang-gun, Jinbu-myeon, Dongsan-ri, Odaesan NP	2012	37°44.26'N, 128°35.50'E	S. Podenas	Net	NIBR
S. Korea, Jeollanam-do, Gurve, Masan-myeon, Hwangjeon-ri	2013	35°14.62'N, 127°29.38'E	S. Podenas, H.-W. Byun	Net	NIBR
S. Korea, Gangwon-do, Chuncheon, Dongsan-myeon, Bongmyeong-ri, KNU experimental Forest	2014	37°46.74'N, 127°48.94'E	S. Podenas	Net	NIBR
S. Korea, Gyeonggi-do, Gapyeong-gun, Buk-myeon, Jeokmok-ri	2014	37°58.61'N, 127°26.59'E	D.-G. Kim, M.-D. Baek, H.-D. Gang, Ch. Uy	Net	KU
S. Korea, Gyeonggi-do, Gapyeong-gun, Buk-myeon, Jeokmok-ri, Garim-gyo (Br.)	2015	37°58.55'N, 127°26.49'E	Y. J. Bae	Malaise trap	KU
S. Korea, Jeollanam-do, Gurye-gun, Toji-myeon, Naeseo-ri, Piagol valley	2015 2016 2019	35°16.31'N, 127°34.29'E 35°16.40'N, 127°34.15'E 35°15.50'N, 127°34.93'E 35°15.95'N, 127°34.85'E 35°16.03'N, 127°34.66'E	S. Podenas	Net	NIBR
S. Korea, Gyeongsangbuk-do, Gyeongju-si, Yangbuk-myeon, Janghang-ri	2016	35°45.74'N, 129°21.84'E	S. Podenas, H. M. Baek	Net	NIBR
S. Korea, Gyeonggi-do, Yangpyeong, Cheongun-myeon, Dowon-ri	2017	37°32.70'N, 127°47.69'E	S. Podenas	At light	NIBR
S. Korea, Gyeonggi-do, Paju-si, Gunnae-myeon, Jeongja-ri, Warrior Base Training Area	2017	37°55.07'N, 126°44.50'E	T.A. Klein, H.-C. Kim	NJ trap	NIBR

Information on the examined material is given as it is on the labels, except coordinates, altitudes and measurement units which are given according to journal requirements. Also given are any additional labels kept with the specimen or additional notes

on the same label, such as "metatype" written by Dr. Ch. P. Alexander, who originally described the species. For specimens collected by S. Podenas and his colleagues, the collecting date on the label is followed by a number in brackets. Different localities where insects were collected on the same date were given separate numbers and all information from those localities, whether in the field notes, databases, photographs, or other locality information, were marked with the specific number. Specimens are arranged according to the collecting date.

Prior to these studies all East Palaearctic and most Oriental species of *Hexatoma* (*Eriocera*) were studied and photographed. Special attention was payed to species recorded from neighbouring countries, like China, Japan, and Russia. Only four East Palaearctic species were not accessible to the authors of this publication and other entomologists who kindly helped with illustrations or photographs. These species are *H*. (*E*.) *caesia* (Savchenko, 1979), *H*. (*E*.) *cleopatroides* (Men, 2015) (Men and Yu 2015), *H*. (*E*.) *flavimarginata* (Yang, 1999), and *H*. (*E*.) *superba* (Savchenko, 1976) (Savchenko and Krivolutskaya 1976), but Chinese species are well illustrated and included in the key that covers all Chinese species (Men and Yu 2015), and Russian species also are included in the key and described in detail (Savchenko and Krivolutskaya 1976).

Crane flies were observed using an Olympus SZX10 dissecting microscope. Photographs were taken with a Canon EOS R5 digital camera through a Canon MP–E 65 mm macro lens and through Mitutoyo M Plan Apo 10× and 20× lenses mounted on the same camera.

The terminology of adult morphological features generally follows that of Cumming and Wood (2017), de Jong (2017) for terminology of wing venation.

The general distribution of species is given according to Oosterbroek (2022).

Taxonomy

Hexatoma Latreille, 1809

Hexatoma Latreille 1809: 260; Edwards 1938: 63 (in key), 64 (descriptive note), pl. 3, fig. 14; Alexander 1948: 528 (in catalogue); Ishida 1959: 2 (in key); Savchenko and Krivolutskaya 1976: 76 (note on distribution); Savchenko 1983: 67 (note on distribution); Savchenko 1986: 337–342 (redescription), figs 96, 173–179; Savchenko 1989: 118–119 (redescription), figs 58–60.
Nematocera Meigen 1818: 209, pl. 7, figs 1–4.
Anisomera Meigen 1818: 210, pl. 7, figs 5–8.
Peronecera Curtis 1836: 589, figs 2–7; Enderlein 1936: 22 (in key), fig. 41.
Trimacromera Enderlein 1936: 23 (in key), fig. 43.

Type species. *Hexatoma nigra* Latreille, 1809 (southern Europe).

Description. Medium-sized to large crane flies with body length 6.5–32.0 mm and wing length 7.5–21.0 mm. Body coloration varies from yellow or orange to brown and black, some species have very distinct coloration.

Head. Rounded posteriorly without neck–like extension. Vertex wide with distinct tubercle. Length of antenna varies from short, hardly reaching wing base, if bent backwards, to very long, when it exceeds body length up to 4×. Antennae sexually dimorphic. Males usually have longer antennae than females, but that is because of elongated basal segments of the male flagellum. Antenna has reduced number of segments, less than typical 14–16-segmented antenna of most short–palped crane flies, often male antenna 6- or 7-segmented, that of female 8–11-segmented. Verticils missing or indistinct, but male flagellum often with two longitudinal rows of short erect spines medially.

Thorax. Some species with very setose thorax, setae could be long, dense, and erect. Some species with more dense and longer pubescence in males than in females. Prothorax very narrow but wide. Mesonotal prescutum usually without, sometimes with, small indistinct tubercular pits, pseudosutural fovea small. Prescutum and presutural scutum with three or four longitudinal stripes. Pleuron usually without stripes, could be bare or setose, depending on species. Meron usually big, thus middle and posterior coxae widely separated. Wing long and narrow, patternless or with very distinct pattern, sometimes completely dark, even black, but often with light "window" in the middle, stigma present or missing. Macrotrichiae missing on wing cells. Arculus present, humeral vein close to arculus. Vein Sc long, reaching wing margin far beyond branching point of Rs, sc-r slightly before tip of Sc. Radial sector with two or three branches reaching wing margin. R_1 short, nearly transverse, or slightly elongate, R_3 and R_4 diverging. Cell r_3 with long stem. Cell m_1 present or missing; two, three or four branches of M reaching wing margin. Discal cell present or missing. Position of cross-vein m-cu differs according to species. Vein CuP usually slightly arched at distal part, anal vein long, slightly sinuous or arched, reaching wing margin close to the level of Rs base. Anal angle distinct, widely rounded. Wing cells without macrotrichiae. Wing squama setoseless. All legs with tibial spurs, usually fore leg with single spur, middle and posterior legs with two spurs each. Claw simple or with single subbasal spine.

Abdomen. Tergites with paired transverse sutures. Male terminalia approximately as wide as the rest of the abdominal segments, slightly elongate. Epandrium (ninth tergite) wider than longer, posterior margin simple without additional structures. Each gonocoxite elongate, two pairs of terminal gonostyli, the shape of which are only slightly variable among different species. Aedeagus simple, short, and straight. Ovipositor usually with long and narrow cerci and hypovalvae, distal part of cercus slightly raised upwards, acute. Some species with shortened ovipositor bearing fleshy cerci and hypovalvae.

596 species belong to the genus *Hexatoma* worldwide, they are divided into six subgenera:

H. (*Eriocera*) Macquart, 1838 (556 extant and three fossil species),
H. (*Cladolipes*) Loew, 1865 (three species, one of them with two subspecies),
H. (*Coreozelia*) Enderlein, 1936 (one Western Palearctic species),
H. (*Euhexatoma*) Alexander, 1936 (one Oriental species),
H. (*Hexatoma*) Latreille, 1809 (23 species, one of them with two subspecies),

H. (*Parahexatoma*) Alexander, 1951 (12 species, Afrotropics only) (Oosterbroek 2022).

Six fossil species are described from the Eocene, three of them in *H*. (*Eriocera*), three not assigned to subgenera (Evenhuis 2014).

Key to subgenera of the genus *Hexatoma* Latreille

1 Radial sector with three branches (Figs 2–6, 16, 24, 25, 29, 35, 43, 48, 51, 56) **2**

– Radial sector with two branches (Fig. 1)... ***Hexatoma* (*Cladolipes*) Loew, 1865**

2 Discal cell present (Figs 2–4, 16, 24, 29, 35, 43, 48, 51, 56), missing in exceptionally rare cases in atypical specimens (Fig. 25), 3 (Figs 2, 3, 24, 25, 29, 48, 51) or 4 (Figs 4, 16, 35, 43, 56) branches of M reaching wing margin **3**

– Discal cell missing, two branches of M reaching wing margin (Figs 5, 6) **5**

3 Supernumerary cross-veins missing in cells r_3, r_4 and r_5 (Figs 2, 3, 16, 24, 25, 29, 35, 43, 48, 51, 56)..... **4**

– Supernumerary cross-veins in cells r_3, r_4 and r_5 (Fig. 4) .... ***Hexatoma* (*Euhexatoma*) Alexander, 1936**

4 Vein Sc reaching wing margin beyond Rs branching point, R_2 beyond fork of R_3 and R_4 (Figs 3, 16, 24, 25, 29, 35, 43, 48, 51, 56) .... ***Hexatoma* (*Eriocera*) Macquart, 1838**

– Vein Sc reaching wing margin at Rs branching point, R_2 at fork of R_3 and R_4 (Fig. 2)..... ***Hexatoma* (*Coreozelia*) Enderlein, 1936**

5 Ovipositor short with fleshy valves... ***Hexatoma* (*Hexatoma*) Latreille, 1809**

– Ovipositor with long and slender valves..... ..... ***Hexatoma* (*Parahexatoma*) Alexander, 1951**

***Hexatoma* (*Eriocera*) Macquart, 1838**

Hexatoma (*Eriocera*) Macquart, 1838: 78, pl. 10, fig. 2; Alexander 1948: 528–529 (in catalogue); Ishida 1959: 2 (in key); Savchenko 1983: 67 (note on distribution); 1986: 342–344 (descriptive note), figs 174,1–2, 176,1–3, 178,1–2; 1989: 121 (descriptive note), figs 58,1, 59,1–2, 60,1.

Caloptera Guerin–Meneville 1831: 20 (nom. obl.).

Eriocera Macquart 1838: 78; Edwards 1921: 67–70 (redescription), pl. 10, figs 1–12.

Evanioptera Guerin–Meneville 1838: 287.

Pterocosmus Walker 1848: 78.

Allarithmia Loew 1850: 36, 38.

Oligomera Doleschall 1857: 387.

Physecrania Bigot 1859: 123.

Arrhenica Osten Sacken 1860: 243–244.

Penthoptera Schiner 1863: 220.

Androclosma Enderlein 1912: 34–35, fig. U.
Globericera Matsumura 1916: 471.
Coreozelia Enderlein 1936: 22 (in key), fig. 40.

Type species. *Hexatoma macquarti* (Enderlein, 1912) (= *Eriocera nigra* Macquart, 1838, = *Hexatoma macquarti* (Enderlein, 1912)) (Brazil).

Description. Most characters as for the genus. Medium-sized to large crane flies with body length 6.5–32.0 mm and wing length 7.5–21.0 mm. Most species dark colored, but some could be orange-yellow (e.g., *H. masakii* Alexander, 1934).

Head. Rounded, vertex with distinct tubercle. Antennae sexually dimorphic. Male antenna longer than that of female, sometimes few times longer than body, 6- or 7-segmented, female antenna 8–11-segmented. Verticils missing or indistinct, but male flagellum often with two longitudinal rows of short erect spines.

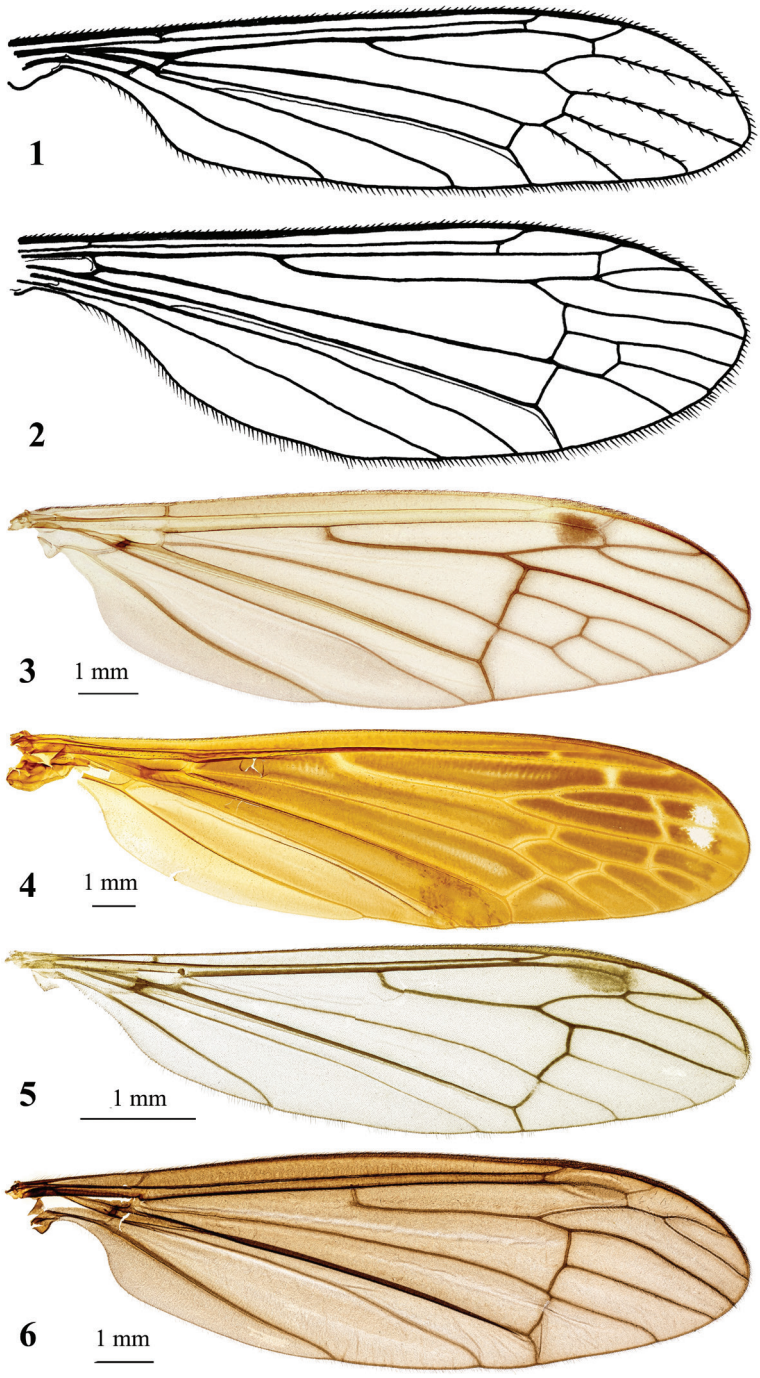
Wing. Radial sector with three branches, discal cell always present, three or four branches of M reaching wing margin.

Terminalia. Male terminalia slightly elongate, not wider than preceding abdominal segments. Epandrium transverse, posterior margin slightly concave. Gonocoxite elongate with two pairs of terminal gonostyli. Outer gonostylus long, narrow with spine-shaped apex. Inner gonostylus long, fleshy, and setose. Aedeagus simple, usually short, and straight (Figs 7–9, 17, 18, 22, 23, 30, 31, 40, 44, 52, 53), but could be long (Figs 36, 37) and arched (Figs 57, 58). Paramere usually two–branched and variable among species. Ovipositor with long and narrow cercus and long hypovalva, distal part of cercus slightly raised upwards, acute, some species with subapically dilated hypovalva.

Subgenus *H.* (*Eriocera*) includes 556 extant species (seven of them with two subspecies each). It has a worldwide distribution with the highest diversity in the Oriental region, 286 species (four of them with two subspecies each), the Neotropics, 143 species, and the Eastern Palearctic, 65 species. Thirty-three species (one of them with two subspecies) are recorded from Nearctic, 29 species (one with two subspecies) from Afrotropics, five species from Australasia, and four species from West Palaearctic (Oosterbroek 2022). Three fossil species are described from Eocenian Baltic amber (Evenhuis 2014).

List of Korean *Hexatoma* crane flies

Hexatoma (*Eriocera*) *gifuensis* Alexander, 1933
Hexatoma (*Eriocera*) *ilwola* Podenas, sp. nov.
Hexatoma (*Eriocera*) *masakii* Alexander, 1934
Hexatoma (*Eriocera*) *pernigrina* Alexander, 1938
Hexatoma (*Eriocera*) *pianigra* Podenas, sp. nov.
Hexatoma (*Eriocera*) *serenensis* Podenas, sp. nov.
Hexatoma (*Eriocera*) *stackelbergi* Alexander, 1933
Hexatoma (*Eriocera*) *ussuriensis* Alexander, 1934



Figures 1–6. *Hexatoma* wings **1** *H.* (*Cladolipes*) *simplex* (Loew, 1865) **2** *H.* (*Coreozelia*) *cimicoides* (Scopoli, 1763) **3** *H.* (*Eriocera*) *gifuensis* Alexander, 1933 **4** *H.* (*Euhexatoma*) *triphragma* Alexander, 1936, holotype **5** *H.* (*Hexatoma*) *khasiensis* Alexander, 1962, holotype **6** *H.* (*Parahexatoma*) *angustatra* Alexander, 1963, holotype. Scale bars: 1.0 mm. (**1** redrawn after Mendl (1979) and Savchenko (1989); **2** redrawn after Slipka (1949)).

Key to Korean species of the genus *Hexatoma* Latreille

1 Entire body, including legs and wings, coal black (Figs 26, 33) **2**
– Body patterned with brown, gray, or orange (Figs 10, 12, 21, 41, 45, 47, 50) ... **3**
2 Wing cell m_1 missing (Fig. 29). Gonocoxite short and wide, length just slightly exceeds width (Figs 30, 31). Cercus of ovipositor comparatively short, triangular (Fig. 32). Wing length up to 15.0 mm ..... ***Hexatoma* (*Eriocera*) *pernigrina* Alexander, 1938**
– Wing cell m_1 present (Fig. 35). Gonocoxite long and narrow, length few times exceeds width (Figs 36, 37). Cercus of ovipositor long, parallel-sided (Fig. 38). Wing length above 16.0 mm ..... ***Hexatoma* (*Eriocera*) *pianigra* Podenas, sp. nov.**
3 Male **4**
– Female **9**
4 Wing cell m_1 present (Figs 16, 43). Wing length above 16.0 mm **5**
– Wing cell m_1 missing (Figs 3, 24, 25, 48, 51). Wing length up to 13.0 mm ... **6**
5 Antenna 3× as long as the rest of the body (Fig. 41). Cell m_1 distinctly longer than its stem (Fig. 43) ... ***Hexatoma* (*Eriocera*) *serenensis* Podenas, sp. nov.**
– Antenna distinctly shorter than the rest of the body (Fig. 12). Cell m_1 approximately as long as its stem (Fig. 16) ..... ***Hexatoma* (*Eriocera*) *ilwola* Podenas, sp. nov.**
6 Antenna at least twice as long as entire body, usually more than that (Figs 10, 21, 50) **7**
– Antenna not reaching wing root if bent backwards ..... ***Hexatoma* (*Eriocera*) *stackelbergi* Alexander, 1933**
7 Abdomen orange yellow (Fig. 21). Costal wing area darkened (Figs 24, 25). Outer gonostylus with hook-shaped apex (Figs 22, 23) ..... ***Hexatoma* (*Eriocera*) *masakii* Alexander, 1934**
– Abdomen brown or dark brown (Figs 10, 50). Costal wing area not darker than the rest of the wing (Figs 3, 51) **8**
8 Paramere with dorsal branch parallel-sided, lower branch wide, plate-shaped, anterior apodeme of aedeagus with wide lateral lobes (Figs 8, 9) ..... ***Hexatoma* (*Eriocera*) *gifuensis* Alexander, 1933**
– Paramere with dorsal branch wedge-shaped, lower branch elongate, anterior apodeme of aedeagus without lateral plates (Figs 52, 53) ..... ***Hexatoma* (*Eriocera*) *ussuriensis* Alexander, 1934**
9 Abdomen orange yellow. Costal wing area darkened (Figs 24, 25) ..... ***Hexatoma* (*Eriocera*) *masakii* Alexander, 1934**
– Abdomen brown or dark brown (Figs 45, 47). Costal wing area not darker than the rest of the wing (Figs 3, 16, 43, 48, 51) **10**
10 Wing cell m_1 missing (Figs 3, 48, 51) **11**
– Wing cell m_1 present (Figs 16, 43) **13**

11 Wing stigma distinct, dark brown (Figs 3, 51) **12**
– Wing stigma very small, nearly missing (Fig. 48) .... ***Hexatoma* (*Eriocera*) *stackelbergi* Alexander, 1933**
12 Wing stigma elongate, oval, radial sector arched at base (Fig. 51)..... .....***Hexatoma* (*Eriocera*) *ussuriensis* Alexander, 1934**
– Wing stigma approximately as long as wide, radial sector angulate at base (Fig. 3)..... ***Hexatoma* (*Eriocera*) *gifuensis* Alexander, 1933**
13 Thorax brown (Fig. 13). Cell m_1 approximately as long as its stem (Fig. 16) . .....***Hexatoma* (*Eriocera*) *ilwola* Podenas, sp. nov.**
– Thorax gray (Fig. 42). Cell m_1 distinctly longer than its stem (Fig. 43) .... ***Hexatoma* (*Eriocera*) *serenensis* Podenas, sp. nov.**

***Hexatoma* (*Eriocera*) *gifuensis* Alexander, 1933**
Figs 3, 7–11, 59

Hexatoma (*Eriocera*) *gifuensis* Alexander 1933: 153–155, pl. 1, figs 15–16, pl. 2, fig. 33.

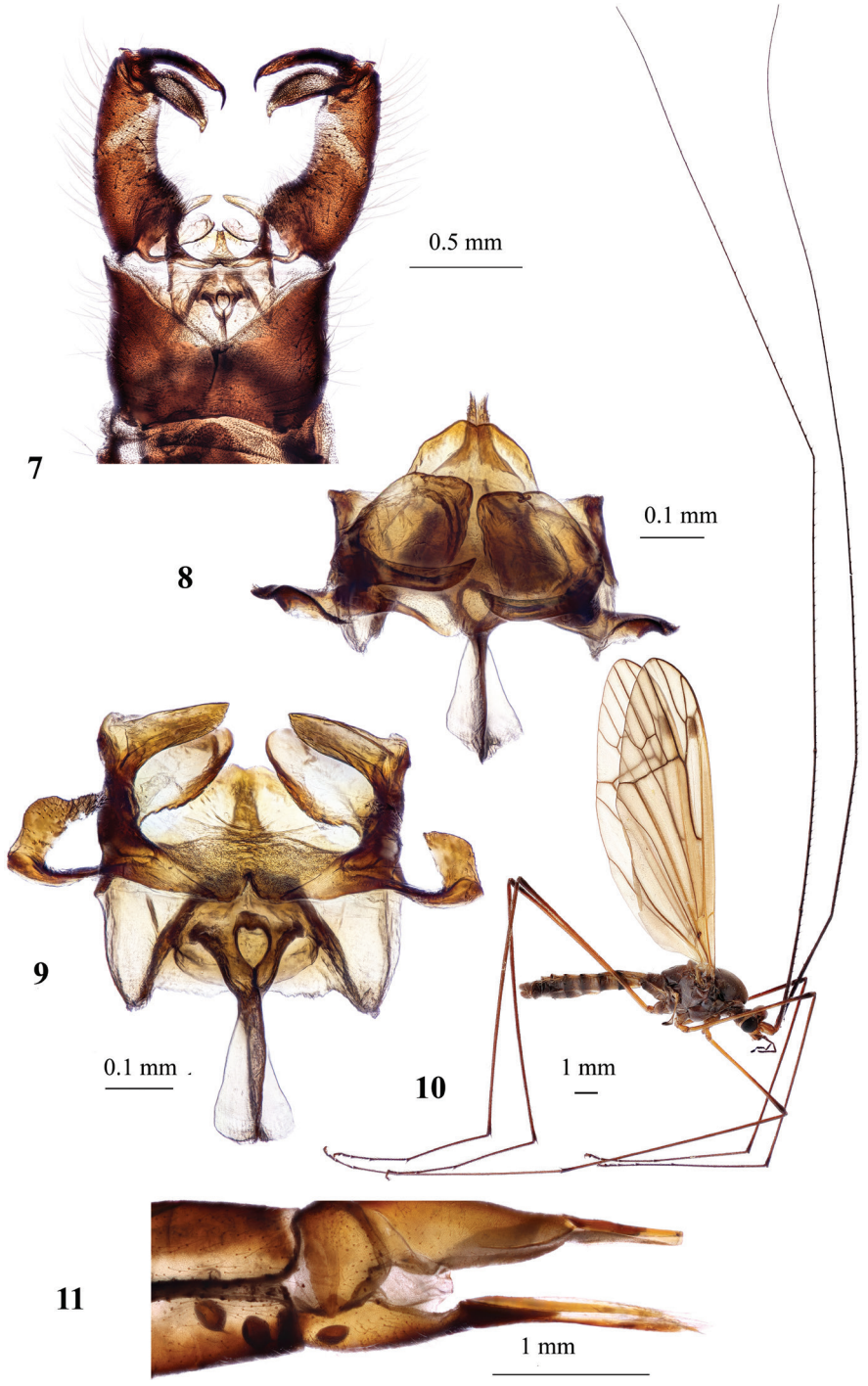
Type material examined. ***Holotype***, male (wing and genitalia slide mounted), **Japan**, Gifu, 6 June 1931, Kariya leg. (USNM). ***Allotype***, female (antenna, wing and ovipositor slide mounted on same slide as holotype), topotypic (USNM).

Other examined material (Fig. 59). **South Korea**, 1 female (in ETOH), Gyeonggi–do, Paju–si, Gunnae–myeon, Jeongja–ri, Warrior Base Training Area, 37°55.07'N, 126°44.50'E, alt. 20 m, 18 July 2017, T. A. Klein, H.–C. Kim leg., NJ trap (NIBR); 1 female, 1 specimen, sex unknown (in ETOH), same collection data as for preceding, 25 July 2017 (NIBR); **Japan**, 1 male (marked as metatype; antenna, leg and wing slide mounted), Shikoku, Matsuyama, Iyo, 14 September 1947, T. Ishihara leg. (USNM); 1 male (pinned, genitalia in microvial with glycerol), Niigata, 16 August 2021, coll. D. Kato (NRC).

Description. ***Body*** dark brown. Male body length 9.5 mm, wing length 14.3 mm. Female body length 12.5–13.5 mm, wing length 12.0–12.2 mm.

Head. Dark brown, postero–laterally yellowish. Vertical tubercle large, dark brown, yellowish laterally. Eyes widely separated, distance between them at the base of the antennae nearly the same as length of both basal antennomeres. Male antenna 47.3 mm long, ~ 3× as long as the entire body (Fig. 10). Antennal scape elongate, nearly cylindrical, brownish yellow with short and erect dark brown setae dorsally and ~ 3× as long as pedicel. Pedicel small, subglobular, brownish yellow. Rostrum brown. Palpus and mouth parts dark brown.

Thorax. Cervical sclerites dark brown. Pronotum short but wide, brown. Prescutum and presutural scutum grayish brown with three longitudinal dark brown stripes. Medial stripe separated anteriorly by narrow grayish line, which is missing posteriorly. Tubercular pits missing, pseudosutural fovea brown. Dorsopleural membrane dark brown, yellowish anteriorly. Postsutural scutum with each lobe



Figures 7–11. *Hexatoma* (*Eriocera*) *gifuensis* Alexander, 1933 **7** male genitalia, dorsal view **8** aedeagal complex, fronto–dorsal view **9** aedeagal complex, dorsal view **10** male, general vew **11** ovipositor, lateral view (tip of cercus broken). Scale bars: 0.5 mm (**7**); 0.1 mm (**8, 9**); 1.0 mm (**10, 11**).

brown with concave elongate dark brown spot in middle, area between lobes brown. Scutellum dark brown, lighter along posterior margin. Mediotergite entirely brown. Pleuron uniformly dark brown. Episternum bare, setoseless. Meron comparatively small, second and third pairs of legs close together. Wing (Fig. 3) with brownish tinge, costal area darker, all veins narrowly surrounded with darker brownish. Stigma distinct, dark brown, short, just slightly longer than wide. Veins brown, yellow in costal area. Venation: Sc long, reaching wing margin slightly beyond r-m, sc-r approximately at r-m. Radial sector long, nearly straight, slightly arched or angulate at base, if angulate then with very short spur. Free end of R_1 concave, R_2 close to R_1 apex. R_3 and R_4 diverging towards wing margin, cell r_3 with long stem, which is half as long as Rs. Cross-vein r-m distinct, transverse, in alignment with basal deflection of M_1 (base of discal cell). Discal cell 1.8× longer than wide. Cross-vein m-cu slightly beyond base of discal cell. Vein CuP distinctly curved at distal part, thus cell cup gets wider towards wing margin. Anal vein long, slightly concave in middle, apex reaching wing margin at the level of Rs base. Anal angle wide, posterior margin widely rounded. Halter pale with black knob and slightly darkened base of stem. Length of male halter 1.5 mm, that of female 1.3 mm. Coxae dark brown dorsally, yellowish ventrally and posteriorly. Trochanters obscure yellow. Femur yellow with narrowly blackened distal part. Tibia brownish yellow with narrowly darkened apex. Basal tarsomere brownish with yellow base, remainder of tarsus brown to dark brown or black. Covered with long dense dark brown setae. Male femur I: 5.5 mm long, II: 4.3 mm, III: 7.9 mm, tibia I: 7.9 mm, II: 9.9 mm, III: 11.3 mm, tarsus I: 7.4 mm, II: 10.3 mm, III: 7.2 mm. Tibia of fore leg with single apical spur, tibiae of middle and hind pairs of legs with two apical spurs each.

Abdomen. Tergites dark brown, narrowly yellow laterally, with two pairs of transverse indistinct sutures. Sternites dark brown along middle, yellow laterally. Male terminalia (Fig. 7) dark brown to black. Epandrium wider than long, posterior margin with deep and wide V-shaped emargination. Gonocoxite elongate, 2× longer than wide at base, dorsal surface with narrow pale stripe across middle. Two pairs of long narrow gonostyli. Outer gonostylus sclerotized, long, slightly arched, apex spine-shaped. Inner gonostylus elongate, fleshy and setose, spindle shaped. Paramere bilobed, outer lobe elongate, knife-shaped, distal part slightly arched, lower lobe wide, plate-shaped (Figs 8, 9). Aedeagus simple, short and straight, bifid at apex. Aedeagal sheath completely covers aedeagus dorsally. Anterior apodeme long with membranous lobes along both sides, extending far beyond frontal margin of aedeagal sheath. Ovipositor (Fig. 11) brownish yellow, valvae long and narrow.

Elevation range in Korea. Ca. 20 m altitude.

Period of activity in Korea. Second half of July.

Habitat. Unknown. Attracted to light.

General distribution. Honshu and Shikoku islands of Japan. Recorded in the Korean Peninsula for the first time.

***Hexatoma* (*Eriocera*) *ilwola* Podenas, sp. nov.**
http://zoobank.org/B06AD1FA-08E1-4074-AA77-2AF768A9EA48
Figs 12–19, 60

Type material examined (Fig. 60). ***Holotype***, male (in ETOH), **South Korea**, Gyeongsangbuk–do, Yeongyang–gun, Ilwol–myeon, Yonghwa–ri, Mt. Ilwolsan, Yonghwasa Temple, 36°48.71'N, 129°07.55'E, alt. 510 m, 6 August 2001 (KU). ***Paratypes***: **North Korea**, 1 female (pinned), Ompo, alt. 230 m, 28 August 1939, A. Yankovsky leg. (USNM); **South Korea**, 1 female (in ETOH), topotypic (KU); 2 females (in ETOH), Gyeongsangbuk–do, Yeongju–si, Punggi–eup, Samga–ri, Mt. Sobaeksan, 36°55.28'N, 128°30.33'E, alt. 400 m, 13 August 2001 (KU); 1 female (pinned), Gangwon–do, Chuncheon–si, Dongsan–myeon, Bongmyeong–ri, KNU experimental forest, 37°46.74'N, 127°48.94'E, alt. 230 m, 22 August 2014 (1), S. Podenas leg. (NIBR).

Diagnosis. Large brownish gray species with body length 19.0–31.8 mm. Rostrum brown. Head and thorax with short and scarce pubescence. Male antenna reaching to approximately middle of abdomen if bent backwards. Prescutum and presutural scutum with four distinct dark brown stripes. Wing translucent with distinct stigma. Cell m1 present. Halter with dark knob. Femur yellow with narrowly blackened distal part. Abdominal sternites yellowish. Epandrium of male genitalia with wide V-shaped emargination. Gonostyli approximately equal in length. Posterior margin of inner gonostylus rounded, apical part slightly arched. Paramere V-shaped. Aedeagus simple, short, straight. Ovipositor with nearly straight cercus. Hypovalva long, distal part widened and setose, apex distinctly narrows into setiforme structure.

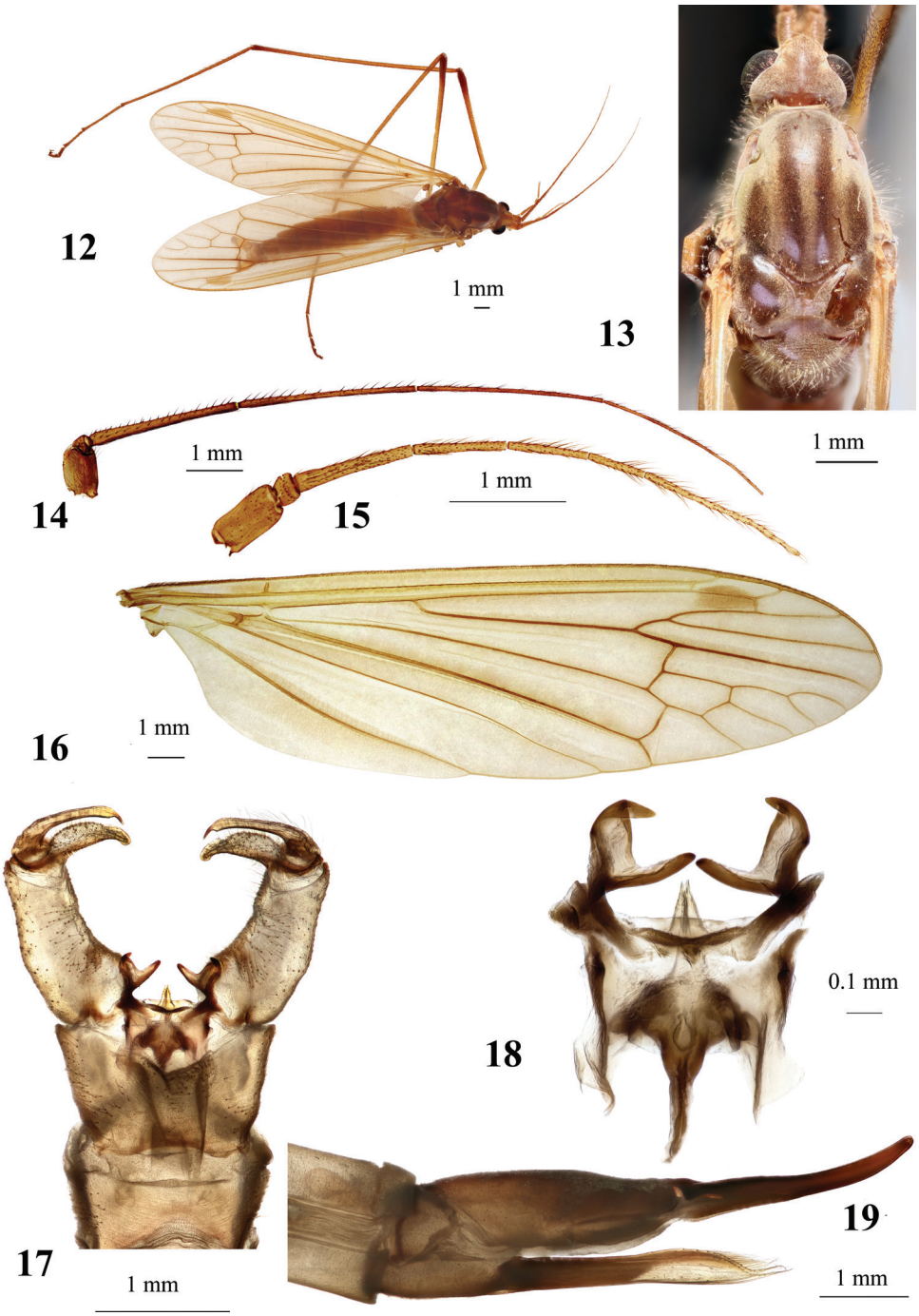
Etymology. Species is named after type locality, Ilwol mountain.

Description. Body coloration brownish gray. Body length of male 19.0 mm, female 23.0–31.8 mm, wing length of male 20.8 mm, female 16.3–20.6 mm.

Head (Fig. 13). Dark brown, dusted with gray, pale gray along eye margin, densely covered with short erect brown setae dorsally. Vertical tubercle large, rounded, with indistinct median vita, reddish brown fronto-laterally above base of antenna. Eyes widely separated in both sexes, distance between them at base of antennae equals to length of scape and pedicel taken together. Male antenna (Fig. 14) entirely brown, 7-segmented, 12.4 mm long, reaching to approximately middle of abdomen if bent backwards. Scape large, twice as long as wide, sparsely dusted with gray. Pedicel subglobular. Flagellomeres with two parallel lines of short spines medially. Basal flagellomere approximately as long as head and both basal antennomeres taken together, remaining flagellomeres getting longer towards apex of antenna. Female antenna (Fig. 15) 11-segmented, 4.8–6.5 mm long, reaching wing base if bent backwards. Scape elongate, cylindrical, 1.6× longer than wide and 3× as long as pedicel. Pedicel wider than long. Basal flagellomere 1.75× as long as scape, remaining flagellomeres decreasing in length, apical segment elongate, approximately as long as preceding segment. Comparative length of flagellomeres slightly varies depending on specimen. Short spines that are present on male flagellum are completely missing on female antenna. Rostrum, palpus and mouth parts brown, just distal palpomeres somewhat darker.

Thorax. Cervical sclerites brown, dusted with gray. Pronotum much wider than long, gray with narrowly yellowish anterior margin. Prescutum light bluish gray, presutural scutum bluish gray laterally, brownish gray posteriorly. Prescutum and presutural scutum with four distinct dark brown stripes (Fig. 13) and covered with comparatively sparse medium long erect yellowish setae, that are less dense and shorter than in *H. aequinigra*, but denser and longer than in *H. superba*. Area separating medial stripes approximately as wide as stripe itself. Tubercular pits small, close to each other at anterior part of sclerite, pseudosutural fovea small, brownish. Postsutural scutum with each lobe dark brown with gray margins. Area between lobes brown. Scutellum dark brown, dusted with gray, posterior and lateral margins gray and covered with long yellow setae. Mediotergite gray because of dense pruinosity, dark brown posteriorly. Pleuron brown dorsally, whitish gray ventrally, covered with fine yellowish setae. Wing (Fig. 16) slightly iridescent, with brownish tinge, yellowish in costal area and at base. No other dark spots except elongate stigma. Veins light brown. Macrotrichiae on distal veins very scarce, nearly missing. Venation: humeral vein slightly before arculus, Sc very long, reaching wing margin distinctly beyond branching point of R_{2+3} and R_4, sc-r close to the apex of Sc. Rs long and nearly straight, arched at base. Free end of R_1 elongate, R_2 twice its own length before apex of R_1. R_3 and R_4 diverging, cell r_3 with stem, which is nearly as long as m-cu. Cross-vein r-m distinct, transverse, slightly beyond base of discal cell. Discal cell 2× longer than wide. Cross-vein m-cu at middle of discal cell length. Anal vein long, slightly concave in the middle, apex distinctly beyond the level of Rs base. Anal angle wide, posterior margin widely rounded. Stem of halter grayish brown with yellowish base, knob dark brown. Length of male halter 2.4 mm, that of female 1.9–2.3 mm. Coxae brownish yellow, densely covered with whitish–bluish gray pruinosity and long yellowish setae. Posterior coxa somewhat darker. Trochanters obscure yellow. Femur yellow with narrowly blackened distal part. Tibia brownish yellow with slightly darkened apex. Tibia of fore leg with single apical spur, tibiae of middle and hind pairs of legs with two apical spurs each. Basal tarsomere light brown with darker distal part, remainder of tarsus brown to dark brown. Male femur I: 9.5 mm long, II: 11.5 mm, III: 15.7 mm, tibia I: 14.0 mm, II: 9.5 mm, III: 17.0 mm, tarsus I: 16.2 mm, II: 12.7 mm, III: 12.0 mm. Female femur I: 9.0–10.5 mm long, II: 10.0–11.5 mm, III: 14.0–14.2 mm, tibia I: 11.0–12.2 mm, II: 10.0–10.4 mm, III: 13.0–13.5 mm, tarsus I: 11.0–12.0 mm, II: 8.5–10.2 mm, III: 7.8–8.5 mm long. Claw dark brown basally, reddish brown distally, simple, without spines.

Abdomen. Tergites dark brown, dusted with gray, narrowly orange along lateral margin, posterior margin narrowly orange starting from fourth tergite. All tergites with two pairs of transverse sutures and covered with very short yellowish setae. Sternites dark brown basally, obscure yellow laterally and posteriorly, dusted with gray. Male terminalia (Fig. 17) brownish yellow, slightly narrower than pregenital segments. Epandrium wider than long, posterior margin with wide V-shaped emargination. Gonocoxite elongate, slightly more than twice as long as wide at base, dorsal surface uniformly sclerotized. Two pairs of long narrow gonostyli. Outer



Figures 12–19. *Hexatoma* (*Eriocera*) *ilwola* Podenas, sp. nov. **12** holotype, male, dorsal view **13** head and thorax, dorsal view, paratype, female **14** male antenna, holotype **15** female antenna, paratype **16** female wing, paratype **17** male genitalia, dorsal view, holotype **18** aedeagal complex, dorsal view **19** ovipositor, lateral view, paratype. Scale bars: 1.0 mm (**12–17, 19**); 0.1 mm (**18**).

gonostylus sclerotized, long, slightly arched, apex distinctly narrowed and spine-shaped. Inner gonostylus elongate, fleshy and setose, posterior margin rounded, apical part slightly arched. Paramere (Fig. 18) bifid, V-shaped, dorsal branch wider at base, tip folded, ventral branch straight and narrow. Aedeagus simple, short, and straight, protruding through aedeagal sheath in dorsal view, apex bifid. Anterior apodeme long and narrow, extending forward beyond frontal margin of aedeagal sheath. Female pregenital segment and ovipositor orange (Fig. 19). Tenth tergite elongate. Cercus slightly darker at base, nearly straight, rounded apex, distal part slightly raised upwards, very apex pale. Hypovalva long, parallel-sided at ~ 2/3 from base, distal part widened and setose, reaching to ~ 1/3 of cercus, apex distinctly narrows into setiforme structure.

Elevation range. From slightly above 200 m to slightly above 500 m.

Period of activity. Whole of August.

Habitat. Sandy and rocky margins of medium–sized mountainous rivers covered with deciduous forest and scarce grassy vegetation (Fig. 20).

Distribution. Korean Peninsula.

Remarks. *Hexatoma ilwola* sp. nov. is most similar to *H. aequinigra* Alexander, 1934b, which is described and known only from the southern part of the Far East of Russia. *Hexatoma aequinigra* was described from the female, which is distinctly bigger than that of *H. ilwola* sp. nov. *Hexatoma aequinigra* has dense and long pubescence on head and thorax, while it is short and scarce in *H. ilwola* sp. nov. *Hexatoma aequinigra* has dark brown basal antennomeres, which are paler in *H. ilwola* sp. nov. *Hexatoma aequinigra* has pale yellow halter with dark brown knob, while the halter of *H. ilwola* sp. nov. is grayish brown with dark brown knob. Abdominal sternites of *H. aequinigra* are dark brown, but widely yellowish in *H. ilwola* sp. nov. Another similar species is *H. sachalinensis*, which is also known from the Far East of Russia, but it has a brownish black rostrum, dark brown femora, and brownish black tibiae. The rostrum of *H. ilwola* sp. nov. is brown, the legs yellow to brownish yellow. Unfortunately, the male of *H. aequinigra* is unknown and the male terminalia of *H. sachalinensis* have not been illustrated, thus comparison of the structure of male terminalia is not possible at the moment.

***Hexatoma* (*Eriocera*) *masakii* Alexander, 1934**

Figs 21–25, 61

Hexatoma (*Eriocera*) *masakii* Alexander 1934b: 48, pl. 1, fig. 18.

Type material examined. ***Holotype***, male (pinned, antennae, legs and wing slide mounted), **South Korea**, Suigen, Chosen, 14 August 1930, I. Tabashi leg. (USNM).

Other examined material. South Korea, 7 males (pinned), #26, Central National Forest, 18 mi. NE of Seoul, 37°44.89'N, 127°17.62'E, alt. 110 m, 14 August 1954, G. W. Byers leg. (SMEK, USNM).

Figure 20. Habitat of *Hexatoma* (*Eriocera*) *ilwola* Podenas, sp. nov., KNU experimental forest.

Description. ***Body***. Thorax brown, head, and abdomen orange-yellow (Fig. 21). Male body length 9.5–11.5 mm, wing length 9.0–10.2 mm.

Head. Orange-yellow, narrowly grayish along posterior eye margin, sparsely covered with short erect brown setae. Vertex with distinct uniformly pale orange-yellow tubercle. Eyes widely separated in male, distance between them at base of antennae nearly the same as length of both basal antennomeres. Male antenna 8-segmented, 16.0–19.5 mm long, ~ 2× as long as wing (Fig. 21). Scape short and wide, approximately as long as wide, 3× as long as pedicel, nearly cylindrical, brownish yellow, covered with few very short brown setae. Pedicel small, subglobular, brownish yellow. Basal flagellomere very long, cylindrical, pale yellow with narrowly dark brown apex. Second flagellomere brownish yellow, darker at base and apex. Remaining flagellomeres brown. Apical segment elongate, subcylindrical, more than twice as short as preceding. All flagellomeres covered with dense erect whitish pubescence and scattered short dark brown setae, length of which less than pubescence on two basal flagellomeres, slightly exceeds length of pubescence on base of third flagellomere, and 2–3× longer on remainder of flagellum. Rostrum orange-yellow. Palpus and mouth parts dark brown.

Thorax. Cervical sclerites and pronotum dark brown. Prescutum blackened. Presutural scutum and prescutum semi-polished dark brown, covered with scattered short brown setae and very sparse brownish pruinosity, longitudinal stripes missing. Tubercular pits missing, pseudosutural fovea distinct. Dorsopleural membrane yellow frontally. Postsutural scutum with each lobe blackish, area between lobes polished

dark brown. Scutellum brown, sparsely dusted with brownish pruinosity. Mediotergite brown, darkened posteriorly. Pleuron brown, very sparsely dusted with gray. Episternum bare, setoseless, ventral margin of katepisternum blackish. Meron well developed, second and third pairs of legs staying apart. Wing (Figs 24, 25) iridescent, brownish, with brown frontal margin. Brown area extends through costal area, stigma and reaches vein R_4. Indistinct darkenings surrounding cord and distal margin of discal cell. Veins brown. Venation: Sc very long, reaching wing margin slightly before branching point of R_{2+3} and R_4, sc-r shortly beyond branching point of Rs. Radial sector long, nearly straight, slightly arched at base. Free end of R_1 longitudinal, R_2 twice its own length beyond branching point of R_{2+3} and R_4. R_3 and R_4 slightly diverging at wing margin, cell r_3 with long stem, which is twice as long as R_{2+3}. Cross-vein r-m distinct, transverse, at base of discal cell. Discal cell nearly twice as long as wide, sometimes open due to reduction of cross-vein m-m (Fig. 25). Cross-vein m-cu at ~ 1/3 of discal cell. Anal vein long, slightly sinuous, apex reaching wing margin slightly before the level of Rs base. Anal angle wide, posterior margin widely rounded. Halter black with pale base. Length of male halter 1.5–1.7 mm. Coxae brown to dark brown, fore coxa yellowish postero–ventrally. Fore trochanter yellowish, middle and hind trochanters yellowish dorsally, brownish ventrally. Femur brownish yellow with pale yellow base and conspicuous black apical ring. Tibia brownish yellow with narrowly infuscate apex. Basal tarsomere brownish with yellow base, remainder of tarsus brown to dark brown or black, covered with long dense dark brown setae. Tibia of fore leg with single apical spur, tibiae of middle and hind pairs of legs with two apical spurs each. Male femur I: 5.2–6.5 mm long, II: 5.0–6.0 mm, III: 5.9–6.0 mm, tibia I: 6.0–8.3 mm, II: 6.4–6.5 mm, III: 7.7–8.0 mm, tarsus I: 7.2–8.5 mm, II: 5.2–6.3 mm, III: 4.5–5.8 mm. Claw simple, without spines.

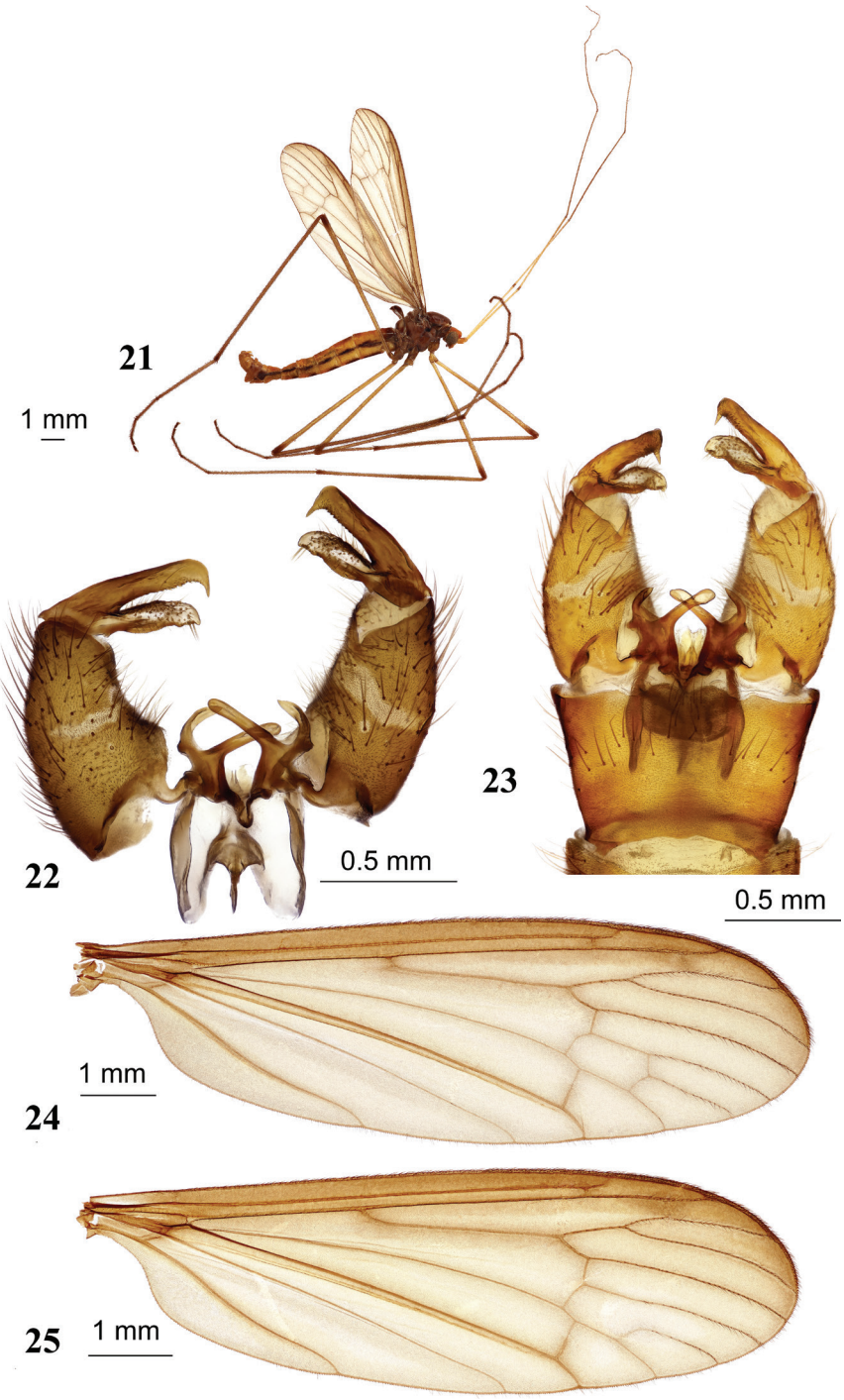
***Abdomen*.** Abdominal segments orange yellow. Tergite laterally narrowly blackened, with paired transverse suture at ~ 1/3 of length. Sternite with lateral margin narrowly blackened and with longitudinal spot in the middle. Eight sternite without black spot in the middle. Lateral and ventral abdominal lines interrupted at posterior margins of segments. Whole ninth segment compact, making genital ring, yellow dorsally, pale brown ventrally. Male genitalia (Figs 22, 23) brownish yellow to pale brown. Epandrium wider than long, posterior margin with two low wide lobes separated by shallow emargination. Gonocoxite twice as long as wide, slightly wider at base, without additional lobes. Outer gonostylus long and narrow, sclerotized, with sharp apical spine turned mesally, inner margin finely serrated. Inner gonostylus long, fleshy, setose. Paramere with two long narrow arms. Aedeagus simple, short, and straight, apex bifid. Anterior apodeme long and narrow, but extending forward less than lateral margins of aedeagal sheath.

Elevation range in Korea. Slightly above 100 m.

Period of activity in Korea. Middle of August.

Habitat. Unknown.

General distribution (Fig. 61). Endemic to South Korea (erroneously listed for North Korea by Oosterbroek (2022)). May be extinct due to urban development; not



Figures 21–25. *Hexatoma* (*Eriocera*) *masakii* Alexander, 1934 **21** male, lateral view **22** male genitalia with ninth segment removed, dorsal view **23** male genitalia, dorsal view **24** male wing **25** male wing variation with open discal cell. Scale bars: 1.0 mm (**21, 24, 25**); 0.5 mm (**22, 23**).

one specimen was found in the tens of thousands we collected. However, it is difficult to collect *Hexatoma* adults: you need to be at the right place and at the right time to catch them or to see them swarming.

Hexatoma (*Eriocera*) *pernigrina* Alexander, 1938

Figs 26–32, 62

Hexatoma (*Eriocera*) *pernigrina* Alexander 1938: 159, pl. 1, fig. 21.

Type material examined. ***Holotype***, male (pinned), **North Korea**, Ompo, alt. 140 m, 14 June 1937, A. Y. Yankovsky leg. (USNM). ***Paratypes***: **North Korea**, 1 male, 1 female (on same pin as holotype), 1 male, 5 females (pinned, antenna, hind leg, wing and terminalia of male slide mounted), topotypic (USNM).

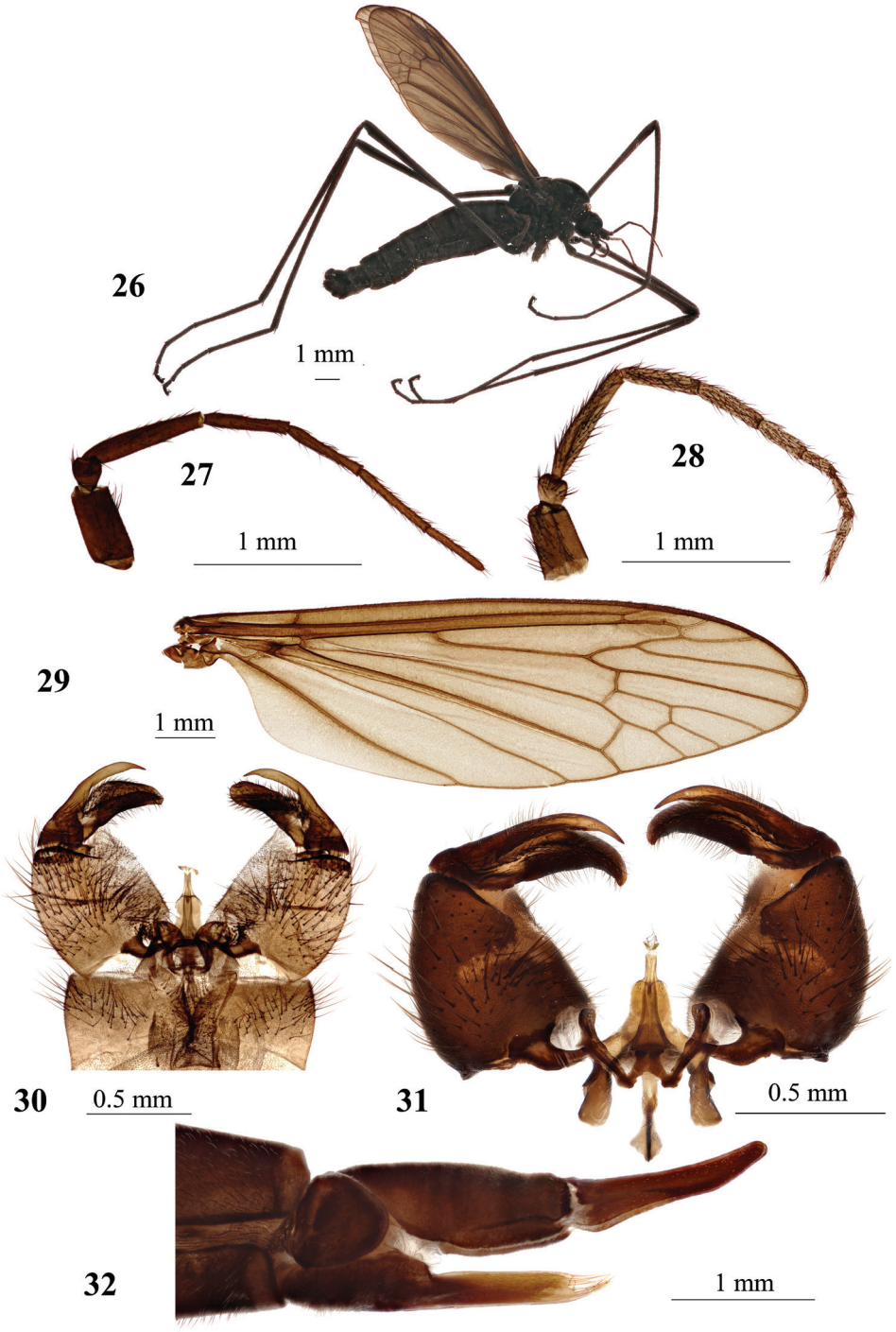
Other examined material. North Korea, 6 males, 2 females (pinned), Ompo, alt. 90 m, 9 June 1937, A. Y. Yankovsky leg. (USNM); 1 male, 1 female (pinned), Ompo, alt. 50 m, 28 May 1938, A. Y. Yankovsky leg. (USNM); 1 male (pinned), Chonsani, alt. 920 m, 22 June 1940, A. Y. Yankovsky leg. (USNM); **South Korea**, 1 male, 1 female (pinned), #12, Hwy. #20, 8 mi. SW of Kangnung, 37°42.00'N, 128°47.00'E, alt. 590 m, 8 June 1954, G. W. Byers leg. (SMEK, USNM); 1 female (pinned), Gyeonggi–do, Paju–si, Aengmubong, 37°45.46'N, 126°55.65'E, alt. 550 m, 6 June 1973, Yuseok Kim leg. (KU); 1 male (pinned), Gyeonggi–do, Pocheon–si, Soheul–eup, Gwangneung Forest, 37°45.05'N, 127°09.70'E, alt. 180 m, 10 June 1973, Okjin Lee leg. (KU); 1 male (pinned), Seoul, Mt. Suraksan, 37°41.79'N, 127°04.93'E, alt. 570 m, 4 June 1974 (KU); 1 male (in ETOH), Gyeongsangbuk–do, Yeongju–si, Punggi–eup, Samga–ri (downstream), Mt. Sobaeksan, 36°55.28'N, 128°30.33'E, alt. 400 m, 14 May 2000 (KU); 1 female (in ETOH), Gyeongsangbuk–do, Bonghwa–gun, Mt. Seondalsan, 37°02.38'N, 128°42.55'E, alt. 1220 m, 5 September 2000 (KU); 2 females (in ETOH), same collection data as for preceding, 4 July 2001 (KU); 1 male, 1 female (in ETOH), same collection data as for preceding, 15 September 2001 (KU); 1 male, 1 female (in ETOH), Jeollabuk–do, Namwon, Sannae–myeon, Buun–ri, Namwonsi Sannaemyeon Baemsagol, 35°21.21'N, 127°34.95'E, alt. 830 m, 27 May 2009, S. W. Jung leg. (KU); 1 male (in ETOH), Gangwon–do, Jeongseon–gun, Imgye–myeon, Dojeon–ri, 37°32.15'N, 128°54.17'E, alt. 760 m, 24 May – 23 June 2011 (1), H.–W. Byun et al. leg., Malaise trap (NIBR); 1 female (in ETOH), Gangwon–do, Pyeonchang–gun, Odaesan NP, 37°44.26'N, 128°35.50'E, alt. 730 m, 22 June 2012 (03), S. Podenas leg. (NIBR); 3 males, 2 females (pinned), 7 males, 6 females (in ETOH), Jeollanam–do, Gurve, Masan–myeon, Hwangjeon–ri, 35°14.62'N, 127°29.38'E, alt. 100 m, 8 May 2013 (1), S. Podenas, H.–W. Byun leg. (NIBR); 20 males, 15 females (in ETOH), Gyeonggi–do, Gapyeong–gun, Buk–myeon, Jeokmok–ri, 37°58.61'N, 127°26.59'E, alt. 310 m, 22 May 2014, D.–G. Kim, M.–D. Baek, H.–D. Gang, Ch. Uy leg. sweeping (KU); 1 male, 2 females (in ETOH), Gyeonggi–do, Gapyeong–gun, Buk–myeon, Jeokmok–ri, Garim–gyo (Br.), GERC–H, 37°58.55'N, 127°26.49'E, alt. 310 m, 24–30 May 2015, Y. J. Bae leg., Malaise trap (KU);

1 male (in ETOH), Gyeonggi–do, Gapyeong–gun, Buk–myeon, Jeokmok–ri, Garim–gyo (Br.), GERC–F, 37°58.55'N, 127°26.49'E, alt. 310 m, 7–13 June 2015, Malaise trap (KU); 2 males, 1 female (in ETOH), Gyeonggi–do, Gapyeong–gun, Buk–myeon, Jeokmok–ri, Garim–gyo (Br.), GERC–G, 37°58.55'N, 127°26.49'E, alt. 310 m, 6–12 May 2015, Y. J. Bae leg., Malaise trap (KU); 4 females (pinned), Gyeongsangbuk–do, Gyeongju–si, Yangbuk–myeon, Janghang–ri, 35°45.74'N, 129°21.84'E, alt. 330 m, 28 May 2016 (1), S. Podenas, H. M. Baek leg. (NIBR); 1 female (pinned), Jeollanam–do, Gurye–gun, Toji–myeon, Naeseo–ri, Piagol valley, 35°16.31'N, 127°34.29'E, alt. 490 m, 3 June 2016 (02), S. Podenas leg. (NIBR); 1 female (pinned), Jeollanam–do, Gurye–gun, Toji–myeon, Naeseo–ri, Piagol valley, 35°16.40'N, 127°34.15'E, alt. 550 m, 3 June 2016 (3), S. Podenas leg. (NIBR); 2 males (pinned), 1 female (in ETOH), Gyeonggi–do, Yangpyeong, Cheongun–myeon, Dowon–ri, 37°32.70'N, 127°47.69'E, alt. 220 m, 29 May 2017, S. Podenas leg., at light (NIBR).

Description. ***Body*** coloration opaque black (Fig. 26). Body length of male 11.5–12.0 mm, female 16.3–19.8 mm, wing length of male 10.0–11.0 mm, female 10.6–15.0 mm.

Head. Opaque black dorsally, dull black ventrally, sparsely covered with erect black setae. Vertex with small tubercle. Eyes widely separated in both sexes, distance between them at base of antennae nearly the same as length of scape. Antenna black at base, turning dark brown towards apex, 7-segmented in male (Fig. 27) (some specimens with fissure in the middle of the last segment, thus antenna looks 8-segmented), 2.6–4.0 mm long, extending to approximately middle of prescutum if bent backward. Female antenna (Fig. 28) 3.0–4.0 mm long. Scape elongate, nearly cylindrical, 1.7× longer than wide, 3× as long as pedicel, pedicel widened distally, bearing a few setae. Flagellomeres elongate, sub–cylindrical, narrower towards apex of antenna, covered with sparse short setae, length of which approximately as width of respective segments. Length of I–V flagellomeres decreases in all specimens, but length ratio varies individually (1.00/0.65 ± 0.02/0.56 ± 0.07/0.41 ± 0.09/0.26 ± 0.04) (mean ± standard deviation). Rostrum black, semi–polished, with few long apical setae. Palpus and mouth parts black.

Thorax. Cervical sclerites and pronotum black. Prescutum and presutural scutum opaque black with four semi–polished stripes, areas between stripes covered with dense short setae. Tubercular pits missing, pseudosutural fovea black, semi-polished. Postsutural scutum with each lobe black covered with grayish pruinosity, area between lobes polished-black. Scutellum dull black with narrow transverse wrinkles. Mediotergite black, laterally covered with grayish pruinosity. Pleuron black, sparsely dusted with gray. Wing (Fig. 29) dark brown, slightly iridescent, with blackish costal area. Stigma same color as darkening along frontal wing margin. Veins dark brown. Venation: humeral vein just slightly before arculus, Sc very long, reaching wing margin slightly beyond branching point of R_{2+3} and R_4, sc-r shortly before branching point of R_{2+3} and R_4. Rs long, slightly arched at base. Free end of R_1 short and oblique, R_2 3× its own length before apex of R_1. R_3 and R_4 diverging, cell r_3 with long stem, which slightly exceeds m-cu in length. Cross-vein r-m distinct,



Figures 26–32. *Hexatoma* (*Eriocera*) *pernigrina* Alexander, 1938 **26** male, lateral view **27** male antenna **28** female antenna **29** male wing **30** male genitalia, dorsal view **31** male genitalia with ninth segment removed, dorsal view **32** ovipositor, lateral view. Scale bars: 1.0 mm (**26–29, 32**); 0.5 mm (**30, 31**).

transverse, at base of discal cell. Length of discal cell slightly more than twice its width. Cross-vein m-cu slightly before middle of discal cell. Anal vein long, slightly concave at middle, apex slightly beyond the level of Rs base. Anal angle wide, posterior margin widely rounded. Halter black throughout. Length of male halter 1.4–1.7 mm, that of female 1.5–1.7 mm. Whole leg, including coxa and trochanter, black. Tibia of fore leg with single apical spur, tibiae of middle and hind pairs of legs with two apical spurs each. Male femur I: 5.0–5.2 mm long, II: 6.4–6.5 mm, III: 6.8–7.5 mm, tibia I: 5.7–6.0 mm, II: 5.8–6.0 mm, III: 6.8–7.0 mm, tarsus I: 6.0–6.2 mm, II: 5.5–5.8 mm, III: 5.5–6.0 mm. Female femur I: 4.3–6.5 mm long, II: 4.7–5.0 mm, III: 8.0–9.0 mm, tibia I: 4.7–5.2 mm, II: 2.7–4.4 mm, III: 5.2–6.0 mm, tarsus I: 5.0–5.7 mm, II: 3.5–4.4 mm, III: 3.5–6.0 mm. Claw with subbasal spine.

Abdomen. Abdominal segments black with narrowly grayish posterior margin. Posterior segments dusted with gray, more densely on sternites. Tergites with paired transverse sutures frontally. Male terminalia (Figs 30, 31) black, narrower than pregenital segments. Epandrium wider than long, posterior margin with two short blunt–apexed lobes separated by wide but shallow V-shaped emargination. Gonocoxite slightly longer than wide, slightly arched, without additional lobes. Outer gonostylus long and narrow, sclerotized, pointed and slightly arched. Inner gonostylus slightly longer than outer gonostylus, wide, fleshy, setose. Paramere long and narrow, with distal part curved mesally. Aedeagus simple, short, and straight, tip with brush of few setae. Anterior apodeme long with triangullar lobes on both sides, extending far beyond frontal margin of lateral lobes of aedeagal sheath. Ovipositor (Fig. 32) black with distal part of cercus brown. Tenth tergite elongate. Cercus nearly straight, comparatively stout, narrowing distally, apex rounded, ventral margin slightly sinuous. Hypovalva long, parallel-sided, reaching only base of cercus, blunt apex, apical setae longer ventrally than dorsally.

Elevation range in Korea. From less than 50 m to more than 1200 m.

Period of activity in Korea. From beginning of May through to middle of September.

Habitat. Margins of mountainous small- and medium-sized streams densely covered with deciduous forests. Species is attracted to light.

General distribution (Fig. 62). Endemic to the Korean Peninsula.

Hexatoma (*Eriocera*) *pianigra* Podenas, sp. nov.

http://zoobank.org/5F5B56FA-5ACA-47B6-97BF-DDCACFDE7513
Figs 33–38, 63

Type material examined (Fig. 63). ***Holotype***, male (Fig. 33) (pinned), **South Korea**, Jeollanam–do, Gurye–gun, Toji–myeon, Naeseo–ri, Piagol valley, 35°15.95'N, 127°34.85'E, alt. 450 m, 3 June 2016 (1), S. Podenas leg. (NIBR). ***Paratypes***: **South Korea**, 1 female (pinned), #25, Central National Forest 18 miles NE of Seoul,

14 August 1954, G. W. Byers leg, (USNM); 1 female (pinned), Jeollanam–do, Gurye–gun, Toji–myeon, Naeseo–ri, Piagol valley, 35°15.50'N, 127°34.93'E, alt. 310 m, 29 June 2015 (2), S. Podenas leg. (NIBR); 1 female (pinned), Jeollanam–do, Gurye–gun, Toji–myeon, Naeseo–ri, Piagol valley, 35°16.03'N, 127°34.66'E, alt. 460 m, 27 June 2019 (3), S. Podenas leg. (NIBR).

Diagnosis. Large black species (Fig. 33) with body length 14.0–31.5 mm. Male antenna reaching to base of halter if bent backwards. Prescutum and presutural scutum with three distinct stripes. Wing brown with distinct stigma and darkened costal area. Cell m_1 present. Legs dark brown to black. Abdomen entirely black. Epandrium of male genitalia with slightly concave posterior margin. Gonocoxite 2.6× longer than wide. Inner gonostylus wide, slightly arched, swollen in the middle. Paramere arched. Aedeagus simple, long, narrow, straight. Ovipositor brown.

Etymology. The species is named after the type locality, the Pia River, and for the black color of the body (= *nigra*).

Description. Body coloration black, semi-polished. Body length of male 14.0 mm, female 26.5–31.5 mm, wing length of male 16.3 mm, female 17.8–21.0 mm.

Head. Black, densely covered with brownish gray pruinosity and scattered short erect black setae. Eyes marginated by narrow whitish gray. Vertical tubercle large, rounded, with indistinct medial groove, concolorous with the rest of the head. Eyes widely separated in both sexes, distance between them at the base of antennae equal to length of scape. Male antenna 7-segmented, 5.2 mm long, reaching to approximately base of halter if bent backwards. Scape large, 2× as long as wide, 4× as long as pedicel, dark brown to blackish, sparsely dusted with brownish. Pedicel wider than long, black. Flagellum entirely black, densely covered with semi–erect black setae. Basal flagellomere longer than both basal antennomeres taken together and slightly longer than second flagellomere, third flagellomere longest, apical segment very small, button-shaped. Female antenna (Fig. 34) 11-segmented, 6.5–7.0 mm long, reaching wing base if bent backwards, entirely black. Rostrum dark brown, dusted with grayish. Palpus and labellum black, dusted with grayish brown pruinosity.

Thorax. Cervical sclerites dark brown dorsally, brown laterally, densely dusted with gray. Pronotum dark brown, postero–lateral angle polished rusty brown. Prescutum and presutural scutum densely dusted with orange–brownish gray, with three distinct stripes, medial stripe laterally semi-polished dark brown, divided along middle with densely dusted area, lateral stripe polished black. Tubercular pits missing, pseudosutural fovea black, semi-polished. Postsutural scutum with each lobe black, sparsely dusted. Area between lobes densely covered with pruinosity. Scutellum dark brown, densely dusted, covered with sparse short erect setae. Mediotergite dark brown densely dusted with grayish brown. Pleuron dark brown, dusted with grayish brown. Wing (Fig. 35) brown, dark brown along frontal margin and along cubital vein, iridescent, stigma dark brown, elongate, but not very distinct because of dark background. Veins brown to dark brown. Macrotrichiae on distal veins very scarce, nearly missing. Venation: humeral vein slightly before arculus, Sc very long, reaching wing margin distinctly beyond branching

point of R_{2+3} and R_4, sc-r at branching point of R_{2+3} and R_4. Rs long, slightly arched at base. Free end of R_1 elongate, R_2 2× its own length before apex of R_1. R_3 and R_4 diverging, cell r_3 with long stem, which is approximately as long as m-cu. Cross-vein r-m distinct, transverse, at base of discal cell. Discal cell slightly more than 2× as long as wide. Cell m_1 approximately as long as its stem or slightly shorter. Cross-vein m-cu at ~ 1/4 of discal cell length. Anal vein long, slightly sinuous, apex beyond the level of Rs base. Anal angle wide, posterior margin widely rounded. Entire halter dark brown except pale brown base of stem. Length of male halter 2.0 mm, that of female 2.0–2.2 mm. Coxa dark brown densely dusted, trochanter dark brown, femur dark brown to black with narrowly brownish base, remainder of leg dark brown to black. Tibia of fore leg with single apical spur, tibiae of middle and hind pairs of legs with two apical spurs each. Legs covered with short dense semi-erect setae. Male femur I: 9.0 mm long, II: 11.5 mm, III: 13.0 mm, tibia I: 11.7 mm, II: 10.5 mm, III: 13.7 mm, tarsus I: 11.8 mm, II: 9.2 mm, III: 8.7 mm. Female femur I: 10.0–10.5 mm long, II: 12.0–12.5 mm, III: 12.0–14.0 mm, tibia I: 11.2–11.5 mm, II: 11.0 mm, III: 10.5–15.5 mm, tarsus I: 11.5–11.7 mm, II: 8.7–9.0 mm, III: 8.4–8.5 mm. Claw rusty brown with subbasal spine.

Abdomen. Male abdomen black, semi-polished, dusted with brownish pruinosity, covered with erect sparse whitish setae, longer on sternites, shorter on tergites. Posterior margins of tergites and sternites narrowly grayish. Tergites with two pairs of transverse sutures. Female abdomen dark brown, coloration of sternites slightly varies individually from brown to dark brown, in some females basal sternites pale brown, in some seventh sternite pale brown to yellowish brown. Male terminalia (Figs 36, 37) dark brown, gonocoxites rusty medially, outer gonostylus pale brown. Epandrium wider than long, posterior margin slightly concave. Gonocoxite elongate, 2.6× longer than wide. Two pairs of long narrow gonostyli. Outer gonostylus sclerotized, point–apexed and slightly arched, apical part at right angle to longitudinal axis of gonostylus. Inner gonostylus approximately as long as outer gonostylus, wide, fleshy, and setose, slightly arched, swollen at middle. Paramere with two long and narrow arms, dorsal arm slightly arched, ventral nearly straight, longer than dorsal. Aedeagus very long, narrow, simple, straight. Anterior apodeme long and narrow, extending forward beyond lateral lobes of aedeagal sheath. Ovipositor (Fig. 38) brown. Tenth tergite elongate, blackish basally, brownish distally and laterally. Cercus round–apexed, distal part slightly raised upwards, brown, polished, blackened at base. Hypovalva long, parallel-sided to approximately middle, slightly swollen subapically, reaching to ~ 1/3 of cercus, pointed apex, with long setae along dorsal margin distally.

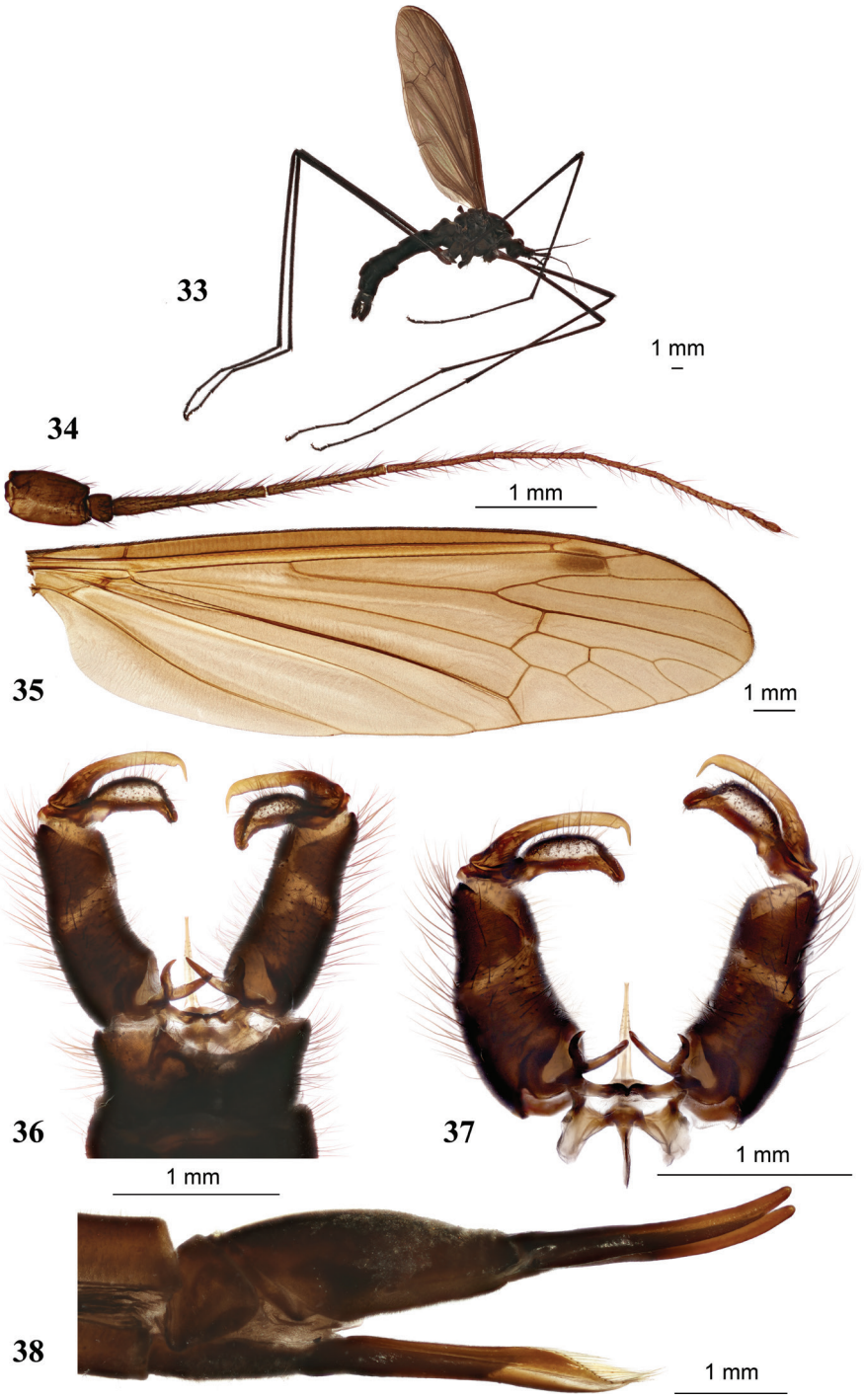
Elevation range. 300–500 m.

Period of activity. From beginning of June through to mid–August.

Habitats. Mountainous medium–sized rivers with sandy or fine gravel covered margins surrounded by dense mixed forests (Fig. 39).

Distribution. South Korea.

Remarks. There are a few black *Eriocera* species with cell m_1 recorded from territories close to the Korean Peninsula, but some of them have unknown males. Among those with males described, the male terminalia are usually unstudied and separation of them is mostly



Figures 33–38. *Hexatoma* (*Eriocera*) *pianigra* Podenas, sp. nov. **33** holotype, male, lateral view **34** female antenna, paratype **35** female wing, paratype **36** male genitalia, dorsal view, holotype **37** male genitalia with ninth segment removed, dorsal view **38** ovipositor, paratype. Scale bars: 1.0 mm.

based on external features such as coloration or comparative length of separate structures. *Hexatoma aequinigra* Alexander, 1934b is known only from the female, the size and general appearance of which is similar to that of *H. pianigra* sp. nov., but the species can be easily separated by leg coloration, the femur of *H. pianigra* sp. nov. is black with a narrowly brownish base, while that of *H. aequinigra* is yellow with only the tip blackened. *Hexatoma atripes* Alexander, 1934b is also described from the female only, the measurements of which are also close to *H. pianigra* sp. nov., but the halter has a yellow stem and blackened knob, while the halter of *H. pianigra* sp. nov. is entirely black. The male of *H. issikii* (Alexander, 1928) is somewhat larger than *H. pianigra* sp. nov., it has a yellow mesonotum, a pleuron with a broad stripe and a yellow halter with only the knob blackened. All these structures are completely black in *H. pianigra* sp. nov. *Hexatoma lygropis* (Alexander, 1920) is a somewhat larger species with a velvety black body, *H. pianigra* sp. nov. is semi-polished with a sparse cover of pruinosity. *Hexatoma nigrotrochanterata* (Alexander, 1932) is similar in size to *H. pianigra* sp. nov., but both species can be easily separated based on leg coloration. The femur of *H. pianigra* sp. nov. is black, while that of *H. nigrotrochanterata is* yellow with only the apical part blackened. *Hexatoma pieliana* Alexander, 1940 is described from the female with the male unknown, but it can be easily separated from *H. pianigra* sp. nov., because it has yellow legs and orange yellow abdominal sternites. Males of *H. imperator* Alexander, 1953b, *H. jozana* (Alexander 1924), *H. longeantennata* (Lackschewitz, 1964), *H. pallidibasis* Alexander, 1953a, *H. sachalinensis* (Alexander, 1924), *H. stricklandi* (Edwards, 1921) and *H. superba* Savchenko, 1976 have long antennae, which are at least close to the body length, but usually a few times that. Two other similar species, *H. fumidipennis* (Alexander,

Figure 39. Type locality of *Hexatoma* (*Eriocera*) *pianigra* Podenas, sp. nov., Jirisan National Park, Piagol valley.

1927) and *H. morula* Alexander, 1923, are described from Sichuan, China. *Hexatoma fumidipennis* is dull gray and bigger than *H. pianigra* sp. nov. with a clear wing except a distinctly darkened costal area. *Hexatoma morula* generally looks more like *H. pianigra* sp. nov., but is much smaller with a wider wing and distinct differences in wing venation, especially the long vein Sc reaching slightly beyond R_2, while it is just slightly beyond the branching point of R_{2+3} and R_4 in *H. pianigra* sp. nov.

***Hexatoma* (*Eriocera*) *serenensis* Podenas, sp. nov.**
http://zoobank.org/A5691FAE-C487-460B-9A01-59148A694183
Figs 40–46, 64

Type material examined (Fig. 64). ***Holotype***, male (Fig. 41) (pinned), **North Korea**, Seren Mts., alt. 610 m, 18 July 1938, A. M. Yankovsky leg. (USNM). ***Paratypes*: North Korea**,1 male, 1 female (pinned) (Fig. 45), topotypic (USNM).

Diagnosis. Large crane fly with body length 16.0–23.5 mm. Body dark brown, densely dusted with gray. Male antenna ~ 3× as long as the whole body. Prescutum and presutural scutum with four stripes. Wing clear with dark stigma. Cell m_1 present. Abdominal tergites dark brown, lateral margins brownish orange. Male gonocoxite nearly 3× as long as width at base. Inner gonostylus nearly parallel-sided, distal part smoothly narrows to blunt apex. Aedeagus simple, short, straight. Paramere with long narrow branches widely separate at base. Ovipositor brownish orange.

Etymology. Species is named after type locality, the Seren mountains.

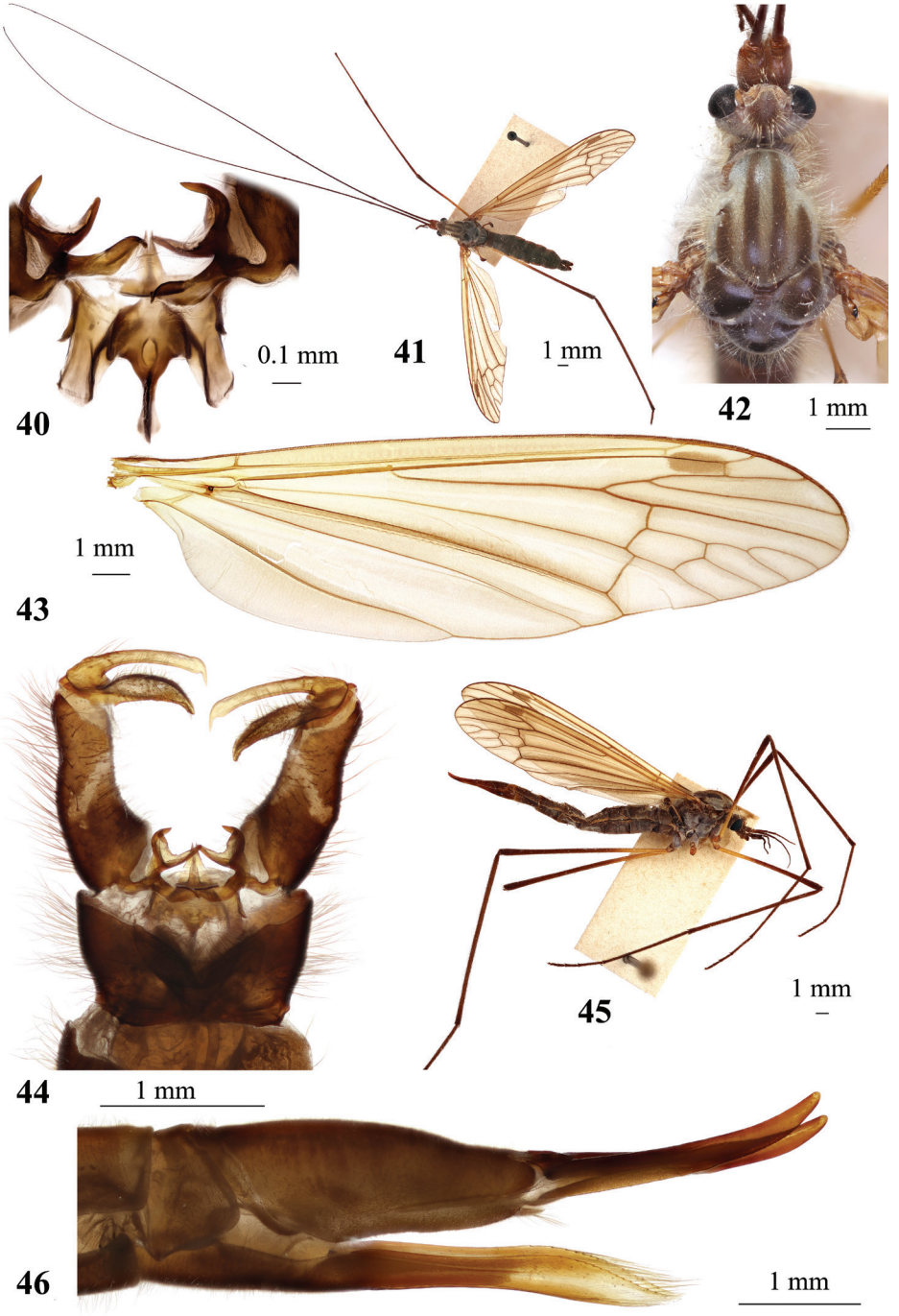
Description. ***Body*** coloration dark brown densely dusted with gray pruinosity. Body length of male 16.0–16.5 mm, female 23.5 mm, wing length of male 19.0–20.5 mm, female 20.0 mm.

***Head*.** Gray due to dense pruinosity, densely covered with long yellowish erect setae in male, pubescence less dense and distinctly shorter in female. Vertical tubercle large, rounded, dark brown, densely covered with long yellowish erect setae. Area between bases of antennae and tubercle brownish yellow. Eyes widely separated in both sexes, distance between them at base of antennae equals length of scape and pedicel taken together. Male antenna 7-segmented, 50.0–50.3 mm long, ~ 3× as long as entire body (Fig. 41). Scape large, 1.7× long than wide, dark brown at base, brownish orange at distal half, sparsely dusted with gray. Pedicel short and wide, more than twice as wide as long, brownish yellow. Flagellum entirely dark brown, flagellomeres with two parallel lines of short spines medially. Basal flagellomere longer than head and thorax taken together, second–fourth segments getting longer, length ratio of first to fourth segments 1.0: 1.5: 2.4: 3.0, apical segment very small button-shaped. Female antenna 11-segmented, 5.7 mm long, reaching wing base, if bent backwards. Scape 0.68 mm long, brown with dark brown base, dusted with gray, nearly cylindrical. Pedicel 0.16 mm long, cup-shaped, pale brown. Flagellomeres elongate, subcylindrical, covered with dark brown setae, single row of spine-shaped setae only on basal flagellomere, length of 1–5 flagellomeres respectively 1.07 mm, 0.73 mm,

0.68 mm, 0.64 mm, 0.56 mm. Rostrum brown, paler ventrally. Palpus and mouth parts dark brown.

Thorax. Cervical sclerites dark brown, densely dusted with gray dorsally. Pronotum gray, lateral angle brownish orange-yellow. Prescutum and presutural scutum brownish gray, pale gray laterally with four distinct dark brown stripes (Fig. 42), covered with dense long erect yellowish setae dorsally, whitish laterally in male, pubescence less dense and distinctly shorter in female. Area separating medial stripes as wide as stripe itself. Tubercular pits very small, close to each other at frontal margin of sclerite, pseudosutural fovea comparatively small, orange posteriorly, dark brown frontally. Postsutural scutum with each lobe bluish gray with widely dark brown central area. Area between lobes gray. Scutellum dark brown, dusted with gray, more densely along posterior margin, covered with very long and dense whitish erect setae posteriorly and laterally. Mediotergite dark brown, gray pruinosity denser frontally, fronto–lateral corner yellowish. Pleuron whitish gray, silvery brown dorsally, densely covered with long erect yellowish setae. Wing (Fig. 43) brownish, darker along frontal margin and along cubital vein, iridescent, with distinct dark brown elongate stigma. Veins brown. Macrotrichiae on distal veins very scarce, nearly missing. Venation: humeral vein at same level as arculus, Sc very long, reaching wing margin distinctly beyond branching point of R_{2+3} and R_4, sc-r at branching point of R_{2+3} and R_4. Rs long and nearly straight, slightly arched at base. Free end of R_1 elongate, R_2 3× its own length before apex of R_1. R_3 and R_4 diverging, cell r_3 with long stem, which slightly exceeds m-cu in length. Cross-vein r-m distinct, transverse, at base of discal cell. Discal cell twice as long as wide. Cross-vein m-cu at ~ 1/4 of discal cell length. Anal vein long, slightly concave at middle, apex far beyond the level of Rs base. Anal angle wide, posterior margin widely rounded. Stem of halter orange-yellow, knob dark brown. Length of male halter 2.0–2.1 mm, that of female 2.1 mm. Coxa gray covered with dense long erect setae, trochanter brown dusted with gray. Fore and middle femora of male yellow before middle, brown to dark brown beyond middle, posterior femur dark brown with ~ 1/3 yellow at base. Femur of female dark brown with only ~ 1/4 yellow at base, yellow area subequal on all legs. Tibia brown with narrowly yellowish base and dark brown apex. Tibia of fore leg with single apical spur, tibiae of middle and hind pairs of legs with two apical spurs each. Tarsal segments brown to dark brown. Male femur I: 7.0 mm long, II: 8.5–9.3 mm, III: 14.0–15.0 mm, tibia I: 12.5 mm, II: 10.0–10.1 mm, III: 13.8–14.5 mm, tarsus I: 14.3 mm, II: 6.3 mm, III: 9.0 mm. Female femur I: 8.5 mm long, II: 10.0 mm, III: 13.5 mm, tibia I: 11.0 mm, II: 9.5 mm, III: 14.0 mm, tarsus I: 11.5 mm, II: 9.2 mm. Claw orange with dark brown apex bearing subbasal spine.

Abdomen. Tergites dark brown with dense cover of gray pruinosity, dusting less intense along middle and posterior margin, covered with long erect yellowish setae. Basal tergite with brownish orange frontal margin, remaining tergites narrowly gray along posterior margin. Lateral margins brownish orange. Second tergite with two distinct pairs of transverse sutures, remaining tergites with second pair less distinct. Sternites dark brown dusted with gray, narrowly orange laterally, each with paired transverse suture at base. Male terminalia (Fig. 44) dark brown, narrower



Figures 40–46. *Hexatoma* (*Eriocera*) *serenensis* Podenas, sp. nov. **40** aedeagal complex, dorsal view, paratype **41** holotype, male, dorsal view **42** head and thorax, dorsal view, holotype, male **43** male wing, paratype **44** male genitalia, dorsal view, paratype **45** female, lateral view, paratype **46** ovipositor, lateral view, paratype. Scale bars: 0.1 mm (**40**); 1.0 mm (**41–46**).

than pregenital segments. Epandrium wider than longer, posterior margin concave. Gonocoxite elongate, nearly 3× as long as width at base, dorsal surface with oblique narrow membranous suture. Two pairs of long narrow gonostyli. Outer gonostylus sclerotized, long, parallel-sided, apex distinctly narrowed and spine-shaped. Inner gonostylus elongate, fleshy and setose, nearly parallel-sided, distal part smoothly narrows to blunt apex. Paramere (Fig. 40) bifid, U-shaped, with long narrow branches widely separate at base. Aedeagus simple, short, and straight, bifid at apex. Anterior apodeme long and narrow, with small lateral lobes on each side, extending forward beyond frontal margin of lateral lobe of aedeagal sheath. Female pregenital segment (Fig. 45) and ovipositor (Fig. 46) orange. Tenth tergite elongate. Cercus slightly darker at base, nearly straight, rounded apex, distal part slightly raised upwards, very apex pale. Hypovalva long, parallel-sided at ~ 2/3 from base, distal part widened and setose, reaching to ~ 1/3 of cercus.

Elevation range. Slightly above 600 m.

Period of activity. Mid-July.

Habitat. Unknown.

Distribution. North Korea, Seren Mountains.

Remarks. *Hexatoma serenensis* sp. nov. is most similar to *H. superba* Savchenko, 1976, which is described and known only from Kunashir Island, Russia (Table 2). *Hexatoma serenensis* sp. nov. is also similar to *H. aequinigra* from Eastern Siberia, but female of *H. aequinigra* has dense and long pubescence on head and thorax, when that is short and scarce in *H. serenensis* sp. nov., femur of *H. aequinigra* female yellow with just distal sixth or less blackened, when femur of *H. serenensis* sp. nov. yellow only at ~ 1/4 from base. Distal wing veins with macrotrichiae nearly missing in *H. serenensis* sp. nov. and *H. superba*, but abundant in *H. aequinigra*. In general, female of *H. serenensis* sp. nov. looks closer to female of *H. superba*, male to *H. aequinigra*. Unfortunately male terminalia of *H. superba* aren't described or illustrated, male of *H. aequinigra* unknown, thus comparison of structure of male terminalia isn't possible at the moment.

Table 2. Comparison of *Hexatoma aequinigra*, *H. superba*, and *H. serenensis* sp. nov.

Character	*H. aequinigra*	*H. superba*	*H. serenensis* sp. nov.
Pubescence of female head	dense and long	scarce and medium-long	medium-long
Vertical tubercle	reddish on either side of midline of vertical tubercle	same color as rest of the head, brownish gray	dark brown, rest of the head gray
Male antenna	–	slightly more than twice as long as body	3.5× as long as body
Pubescence of thorax	dense and long	scarce and medium-long	dense and long
Area separating medial prescutal stripes	slightly wider than the stripes	distinctly narrower than stripes	as wide as stripes
Lateral margin of prescutum	suffused with pale brown	with additional dark spot	uniformly pale gray
Femur	yellow, tip narrowly blackened	basal 1/3 brownish yellow	basal 1/2 brownish yellow
Cell m_1	as long as its stem	as long as 1/2 of its stem	as long as its stem
Abdominal tergites	female dark brown with yellowish brown lateral margin	male uniformly dark brown	male dark brown with brownish orange lateral margin
Female body length (mm)	33	26–27	23.5
Macrotrichiae on distal wing veins	abundant	missing	missing

***Hexatoma* (*Eriocera*) *stackelbergi* Alexander, 1933**
Figs 47–49, 65

Hexatoma (*Eriocera*) *stackelbergi* Alexander 1933: 152–153, pl. 1, fig. 14; Savchenko 1983: 67 (short note on distribution); 1989: 123 (short note on distribution); Podeniene and Gelhaus 2015: 104–107 (descriptions of larva and pupa), figs 29–38.

Type material examined. ***Paratype***, male (antenna, fore leg, and both wings slide-mounted), **Russia**, E. Siberia, Ussuri, Tigrowaja, Suchan distr., 43°15.00'N, 133°00.00'E, [alt. 250 m], 11 June1927, Stackelberg leg. (USNM).

Other examined material (Fig. 65). **North Korea**, 1 female (pinned, fragments of ovipositor in microvial on same pin), Kankyo Nando Puksu Pyaksan, alt. 1830 m, 29 July 1939, A. Yankovsky leg. (USNM).

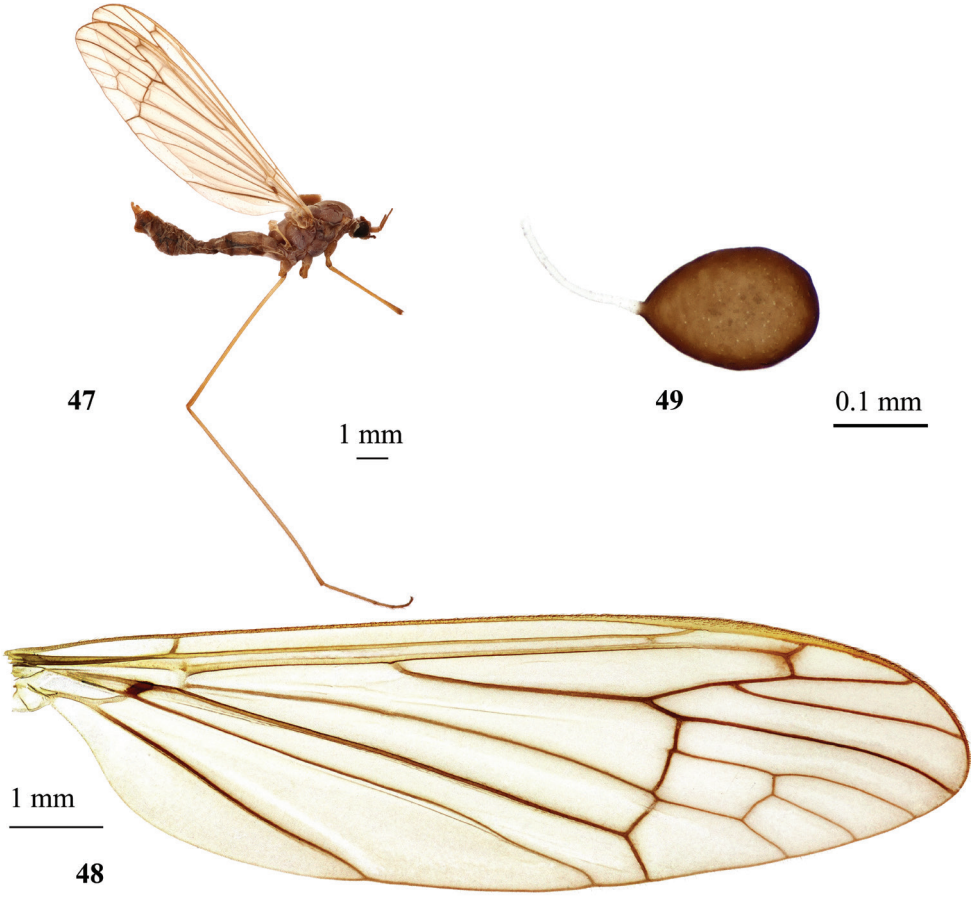
Description. ***Body*** coloration brownish gray (Fig. 47). Body length of female 8.8 mm, wing length 10.4 mm.

Head. Gray, Brownish gray anteriorly, pale gray posteriorly, covered with short whitish erect setae. Vertical tubercle large, divided by medial grove longitudinally. Eyes widely separated, distance between them at base of antennae approximately equals to length of scape. Basal segments of antenna brown. Scape elongate, 1.6× longer than wide, 2.7× as long as pedicel, darker at base, dusted with gray. Pedicel short, subglobular. Basal flagellomere 1.6× longer than scape, nearly cylindrical, second flagellomere 0.6× as long as basal. Flagellomeres covered with short semi–erect whitish pubescence. Rostrum very short, dark brown, palpus black, labella pale brown.

Thorax. Cervical sclerites pale brown, dusted with gray. Pronotum much wider than long, yellowish brown with gray dusting. Prescutum and presutural scutum gray with three darker brown longitudinal stripes and covered with sparse short whitish setae. Medial stripe separated longitudinally by narrow darker line. Tubercular pits missing, pseudosutural fovea small, pale brown. Postsutural scutum with each lobe gray with indistinct darker brownish spots anteriorly, at middle and posteriorly. Scutellum brownish or yellowish gray with longer yellowish setae along posterior margin. Mediotergite brownish gray, more brownish posteriorly. Pleuron gray with brownish spots where gray pruinosity scarcer. Laterotergite with dense long yellowish setae posteriorly. Wing (Fig. 48) slightly iridescent, subhyaline, with pale grayish tinge, yellowish in costal area and at base. Stigma missing except darkening around R_1 and R_2. All veins surrounded by brownish, but no other spots. Veins brown, yellowish at wing base, except distinctly dark brown axillary vein. Macrotrichiae on distal veins missing. Venation: humeral vein slightly before arculus, Sc long, reaching wing margin slightly beyond branching point of Rs, sc-r at or slightly before branching point of Rs. Rs long, slightly arched, short spurred at base in paratype. Free end of R_1 short and oblique, R_{2+3} just slightly exceeds R_2 in length. R_3 and R_4 diverging, ~ 2.5× as long as its stem. Cross-vein r-m distinct, in alignment with basal deflection of M_{1+2} (base of discal cell). Discal cell slightly more than twice as long as wide. Cross-vein m-cu very slightly beyond base of discal cell (branching point of M). Vein CuP curved at distal

part, thus cell cua gets wider towards wing margin. Anal vein long, slightly sinuous, reaching wing margin slightly before or at same level as Rs base. Anal angle wide, posterior margin widely rounded. Halter with stem and knob yellow, base of stem brownish. Length of female halter 1.2 mm. Coxae brown anteriorly, grayish yellow posteriorly, covered with short erect whitish setae. Trochanters obscure yellow. Femur with basal half pale yellow, distal brown. Tibia and tarsus brown to dark brown. Tibia of posterior leg with two apical spurs. Female femur I: 3.0 mm long, III: 5.5 mm, tibia III: 8.0 mm, tarsus III: 3.5 mm. Claw yellowish at base, blackish at apex, with subbasal spine.

Abdomen. Tergites brown, dusted with gray, with one pair of transverse sutures, covered with short yellowish setae. Sternites yellowish brown. Male hypopygium large, black, epandrium wider than long, polished black (Alexander 1933). Ovipositor yellowish brown. Spermatheca (Fig. 49) brown with small paler dots, ovoid.



Figures 47–49. *Hexatoma* (*Eriocera*) *stackelbergi* Alexander, 1933 **47** female, lateral view **48** female wing **49** spermatheca. Scale bars: 1.0 mm (**47, 48**); 0.1 mm (**49**).

Elevation range. Above 1800 m in Korea, ca. 250 m in Russia.

Period of activity. Late August in Korea, middle of June in the Far East of Russia.

Habitat. Unknown in Korea. Larvae of this species develop in the bottom gravel of large and medium size rivers. Last instar larvae and pupae can be found in the riparian zone, usually in gravel, sand or under stones in Mongolia (Podeniene and Gelhaus 2015).

General distribution. Far East of Russia and Mongolia. Recorded on the Korean Peninsula for the first time.

Remark. *Hexatoma stackelbergi* was known only from three type specimens, all males, listed in Alexander (1933). The male genitalia were not illustrated and we had no possibility to study them. This is the first record not only for Korea, but it is also the first specimen besides the types and the first female. Unfortunately, it has badly damaged terminalia, thus a more detailed study of the ovipositor is not possible at this time.

***Hexatoma* (*Eriocera*) *ussuriensis* Alexander, 1934**

Figs 50–53, 66

Hexatoma (*Eriocera*) *ussuriensis* Alexander 1934a: 341–343, pl. 1, fig. 22, pl. 4, fig. 49; Savchenko 1983: 68 (short note on distribution); 1989: 123 (short note on distribution); Przhiboro et al. 2009: 221–228 (distribution and habitats); Podeniene and Gelhaus 2015: 107–112 (descriptions of larva and pupa), figs 39–53.

Type material examined. ***Paratypes*: Russia**, male (antenna, fore leg, wing, and genitalia slide–mounted), E. Siberia, Ussuri, Bikin, river Bikin, 8 July 1927, Martynov leg. (USNM); 1 specimen, sex unknown (pinned), Ussurian district, river Bikin, station Bikin, 8–9 July 1927, Martynov leg. (USNM); 1 male (pinned), same collection data as for preceding, 9 July 1927 (USNM).

Other examined material (Fig. 66). **North Korea**, teneral male (pinned), Prov. South Pyongan, Pyongyan, Hotel garden, 5 August 1971, No 141, S. Horvatovich et J. Papp leg. (HNHM).

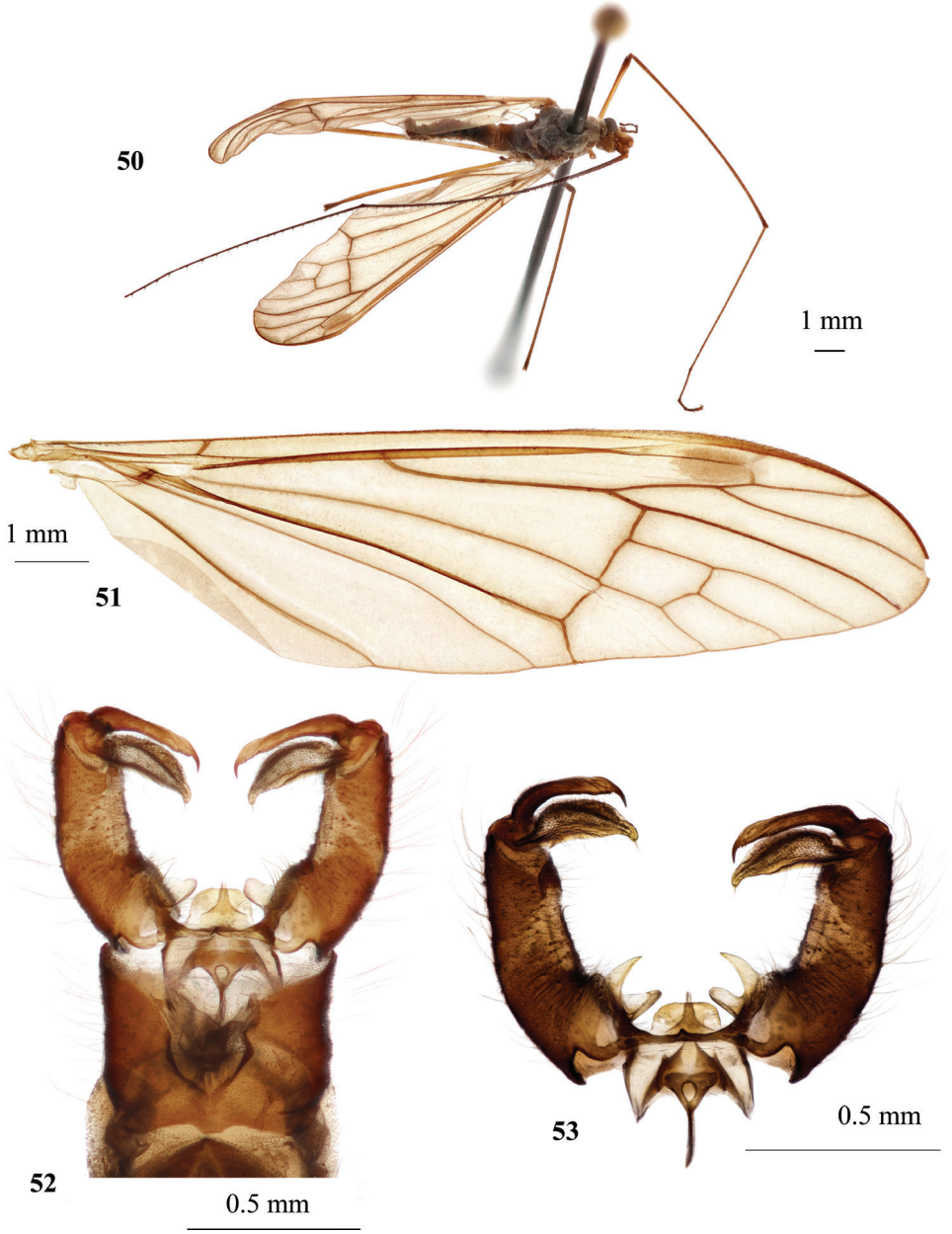
Description. ***Body*** coloration gray to dark brown (Fig. 50). Male body length 7.5 mm, wing length 12.5 mm.

***Head*.** Brownish gray, narrowly pale gray along eye margin, covered with whitish erect setae. Vertical tubercle very large, rounded, brown, dusted with grayish yellow postero-dorsally, without polished black summit mentioned in original description (Alexander 1934a), polished black area also missing in studied topotypic paratypes. Tubercle reaches beyond middle of scape. Eyes widely separated, distance between them at base of antennae equal to length of scape and pedicel taken together. Male antenna 18.9 mm long, distinctly longer than the entire body. Scape very large, elongate, obscure yellow with darkened and dusted dorsal surface. Pedicel very short, ring-shaped, yellow. Flagellum black with base of first flagellomere narrowly brownish. Flagellomeres with two parallel rows of short spines. Basal flagellomere 4.2 mm long, with 19 spines in each row and sparse short whitish pubescence between them, second

flagellomere 6.0 mm long with 24 spines, third flagellomere 7.2 mm long with 21 spines. Rostrum brownish yellow with few long erect setae dorsally, palpus dark brown to blackish, labella black.

Thorax. Cervical sclerites brown, dusted with gray. Pronotum much wider than long, dark brown with gray dusting. Prescutum and presutural scutum gray with four distinct dark brown longitudinal stripes and covered with comparatively sparse long whitish setae. Area separating medial stripes slightly narrower than the stripes themselves. Tubercular pits missing, pseudosutural fovea small, polished–brown. Postsutural scutum with each lobe gray with dark brown central area, which also dusted with gray. Area between lobes dark brown anteriorly, pale posteriorly. Scutellum gray with pale fronto-lateral angle. Mediotergite brown, dusted with gray. Pleuron gray, posterior margin of anepimeron with dense long yellowish setae. Wing (Fig. 51) slightly iridescent, with pale brownish tinge, yellowish in costal area and at base. Stigma distinct, oval, dark brown. Small but distinct dark spot surrounds axillary vein at wing base. Cord, distal margin of discal cell and distal longitudinal veins surrounded by indistinct brownish areas. Veins brown, yellowish at wing base. Macrotrichiae on distal veins missing. Venation: humeral vein slightly beyond arculus, Sc very long, reaching wing margin distinctly beyond r-m but before branching point of R_{2+3} and R_4, sc-r at the level of r-m. Rs long and nearly straight, arched at base. Free end of R_1 oblique, R_2 and R_{2+3} equal in length. R_3 and R_4 diverging, cell r_3 with long stem, which is approximately half length of Rs. Cross-vein r-m distinct, slightly oblique, in alignment with basal deflection of M_{1+2} (base of discal cell). Discal cell 1.5× longer than wide. Cross-vein m-cu very slightly beyond base of discal cell (branching point of M). Vein CuP distinctly curved at distal part, thus cell cua gets wider towards wing margin, but nearly parallel-sided from base to ~ 2/3 of its length. Anal vein long, slightly concave at middle, apex at same level as Rs base. Anal angle wide, posterior margin widely rounded. Stem of halter pale to brownish, knob dark brown. Length of male halter 1.2 mm. Coxae from brown dorsally to yellow ventrally, covered with gray pruinosity and long yellowish setae. Trochanters obscure yellow. Femur yellow with narrowly dark brown apical part. Tibia yellowish brown with narrowly darkened apex. Tibia of fore leg with single apical spur, tibiae of middle leg with two apical spurs. Tarsus brown at base, dark brown at distal end. Male femur I: 3.2 mm long, II: 4.5 mm, III: 7.5 mm, tibia I: 7.5 mm, II: 5.7 mm, tarsus I: 7.0 mm. Claw yellowish brown with subbasal spine.

Abdomen. Two basal tergites brown, remaining dark brown with narrowly brownish yellow lateral margins. Three basal sternites grayish brown, remaining getting darker towards apex, lateral margins brownish to grayish yellow. Abdominal segments covered with long whitish setae, that are denser laterally. Male terminalia (Figs 52, 53) brownish, ninth segment narrower than rest of the abdomen. Epandrium wider than long, posterior margin with wide V-shaped emargination. Gonocoxite elongate, nearly 3× as long as wide at base, dorsal surface with lighter transverse area at middle which extends from less sclerotized mesal surface. Two pairs of long narrow gonostyli. Outer gonostylus sclerotized, long, slightly arched, apex distinctly narrowed and spine-shaped, mesal surface with small serration distally. Inner gonostylus elongate, fleshy and setose, apical part distinctly narrower, rounded apex. Paramere with two



Figures 50–53. *Hexatoma* (*Eriocera*) *ussuriensis* Alexander, 1934 **50** male, dorsal view **51** male wing **52** male genitalia, dorsal view **53** male genitalia with ninth segment removed, dorsal view. Scale bars: 1.0 mm (**50, 51**); 0.5 mm (**52, 53**).

lobes, dorsal lobe wedge-shaped, ventral lobe elongate with rounded distal margin. Aedeagus simple, short, and straight, apex just slightly protrudes beyond frontal margin of aedeagal sheath in dorsal view. Anterior apodeme long and narrow, without lateral lobes, extending far forward.

Elevation range. Ca. 20 m in Korea. 30 m to 650 m in Russia, Japan, and Mongolia (Przhiboro et al. 2009).

Period of activity. Beginning of August in Korea. June–July in Russia, Japan, and Mongolia (Przhiboro et al. 2009).

Habitat. Unknown in Korea. Shores of different types of running waters, from shores of large- and medium-sized rivers on plains to medium-sized and small rivers in the foothills in boreal forest, mixed forest, forest-steppe, and steppe landscape zones in Russia and Mongolia (Przhiboro et al. 2009). Both sexes are attracted to light (Przhiboro et al. 2009). Larvae of this species develop only on the bottom of large and medium sized rivers. Last instar larvae and pupae can be found in the riparian zone, usually in gravel, sand or under stones in Mongolia (Podeniene and Gelhaus 2015).

Distribution. Eastern part of Russia, Mongolia and Hokkaido Island, Japan. Recorded on the Korean Peninsula for the first time.

***Hexatoma* (*Eriocera*) *lygropis* (Alexander, 1920)**
Figs 54, 56–58

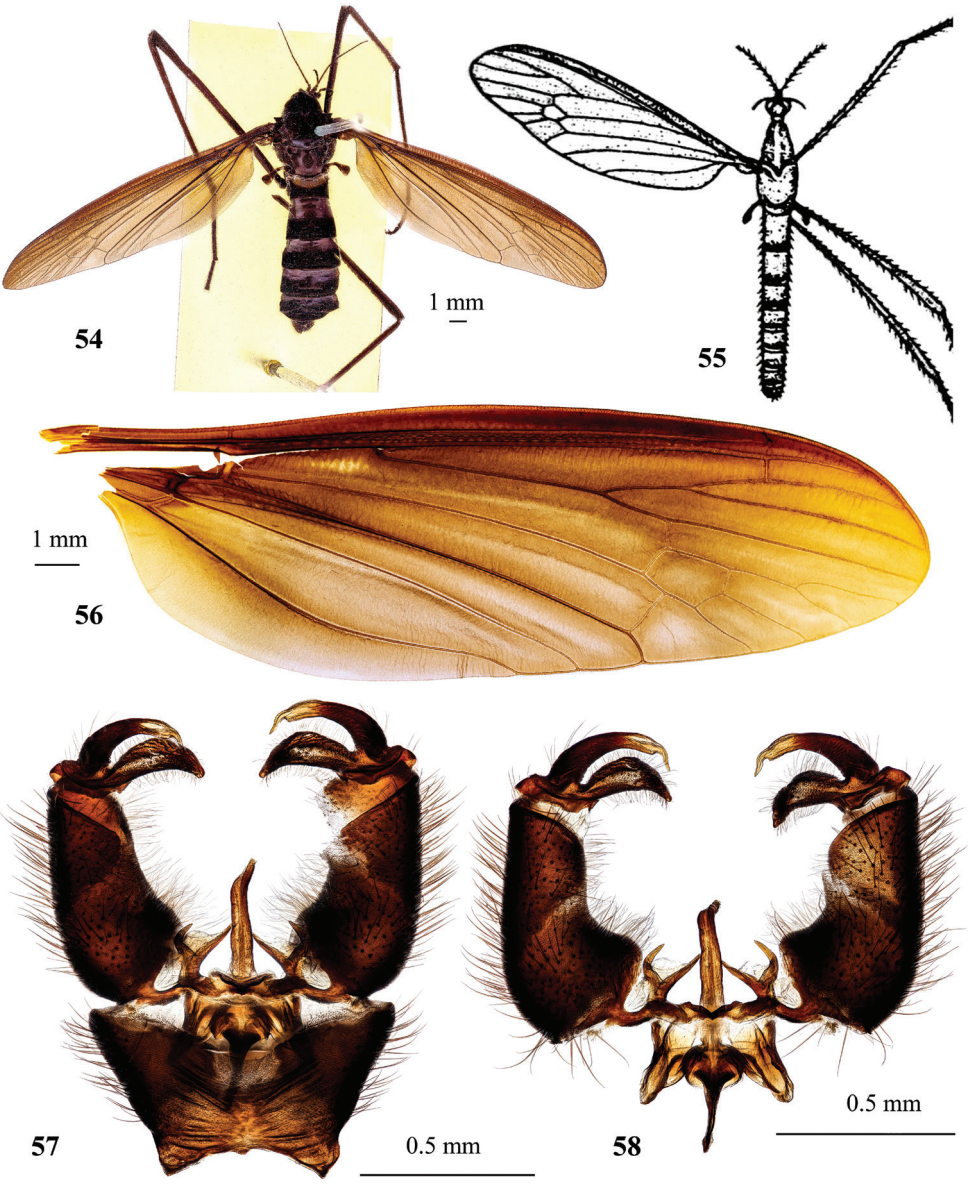
Type material examined. ***Paratype***, male (pinned, wing slide–mounted), **China**, Formosa [Taiwan], Koshun, 25 April – 25 May 1918, J. Sonan, K. Miyake, M. Yoshino leg. (USNM).

Other examined material. **China**, 2 males, 1 female (pinned), Formosa [Taiwan], Koshun, 25 April – 25 May 1918, J. Sonan, K. Miyake, M. Yoshino leg. (NHMUK) (Fig. 54); 1 male (pinned), Formosa [Taiwan], [Kaohsiung County – label in Chinese] (NHMUK).

Remark. The first record of this species from Korea is that of Kim (1971). Unfortunately, no information was listed on which specimen(s) that record had been made, but the illustration (fig. 36) shows a species which is different from *H. lygropis* (Fig. 55). The most obvious difference is the missing cell m_1, while *H. lygropis* has a well–developed cell m_1. The Korean University collection, on which Kim's (1971) publication was based, has a few *Hexatoma* specimens identified as *H. lygropis*, but all of them are in fact *H. pernigrina*, which also has no cell m_1. All other records of that species are based only on Kim (1971). Based on this, we exclude *H. lygropis* from the Korean species list. *Hexatoma lygropis* is endemic to Taiwan.

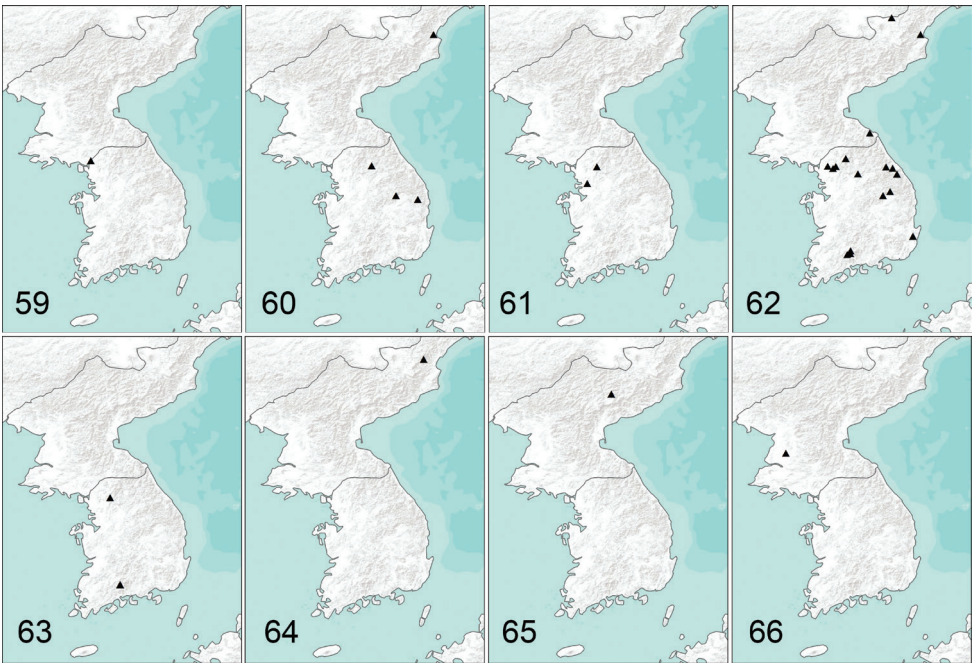
Discussion

Crane flies belonging to the genus *Hexatoma* Latreille, 1809 (Diptera, Limoniidae) are very diverse in the Eastern Palaearctic, the fauna of which includes 72 species (Oosterbroek 2022). Despite a 90 year history of research into these crane flies on the Korean Peninsula, dating back to 1930, only three species were listed on the most



Figures 54–58. *Hexatoma* (*Eriocera*) *lygropis* (Alexander, 1920) **54** male, dorsal view **55** erroneous image of *H. lygropis* on which were based all Korean records **56** male wing **57** male genitalia, dorsal view **58** male genitalia with ninth segment removed, dorsal view. Scale bars: 1.0 mm (**54, 56**); 0.5 mm (**57, 58**). (**55** after Kim (1971)).

recent species list of Korea (Cho 2019), this covering both North and South Korea. Due to the abundance of habitat suitable for *Hexatoma* in Korea, it was expected that more species should occur, but the genus is rather difficult and problematic taxonomically, with many Asiatic species known only from type specimens, with some of them



Figures 59–66. Sampling localities of Korean *Hexatoma* (*Eriocera*) **59** *H.* (*E.*) *gifuensis* Alexander, 1933 **60** *H.* (*E.*) *ilwola* sp. nov. **61** *H.* (*E.*) *masakii* Alexander, 1934 **62** *H.* (*E.*) *pernigrina* Alexander, 1938 **63** *H.* (*E.*) *pianigra* sp. nov. **64** *H.* (*E.*) *serenensis* sp. nov. **65** *H.* (*E.*) *stackelbergi* Alexander, 1933 **66** *H.* (*E.*) *ussuriensis* Alexander, 1934.

described from females only. Male terminalia and wing venation, which are often used for discriminating species in other genera of Limnophilinae crane flies, are rather uniform in most *Hexatoma* and lack good identifying characters, thus raising the probability of misindentifications and prompting the urgent need of revision of local species at least. Based on material from all the scientific collections that were available for our study, and on our personal collecting, we were able to add six new species to the Korean species list, three of which were new to science. One species, endemic to Taiwan, was deleted from the Korean species list as a misidentification. New detailed photographs of the most important taxonomical characters and a provided identification key will be useful not only for researchers of Korean insects, but also for researchers from neighboring countries, such as China, Japan, and Russia, all of which are currently making good progress in the research into crane flies.

Acknowledgements

Our warmest thanks to all Korean friends and colleagues who helped us during our visits to South Korea and all those who helped to collect crane flies. We are very grateful to Professor Y.J. Bae for the specimens from Korea University, Seoul, the Republic of

Korea; to J.C. Thomas for help with Korean specimens from the University of Kansas, U. S. A.; to Dr F. Shockley and Dr T. Dikow (USNM) and Dr J.K. Gelhaus (Academy of Natural Sciences of Drexel University, U. S. A.) for the possibility to use specimens from the USNM collections. Dr Duncan Sivell for the possibility to use specimens from the Natural History Museum, London, United Kingdom and Pasquale Ciliberti for the specimens from the Naturalis biodiversity center, Leiden, Netherlands; Dr Daichi Kato, Echigo–Matsunoyama Museum of Natural Sciences, 'Kyororo', Tôkamachi, Japan for the specimens donated to the NRC. Special thanks are also extended to colleagues from the Nature Research Centre, Lithuania: to Jos Stratford who checked the language, to Dr M. Dagys for his help in preparing distribution maps, and R. Markevičiūtė who helped with plates. We are very grateful for Dr Jukka Salmella and Dr J.K. Gelhaus for comments on earlier version of the manuscript.

This work was supported by a grant from the National Institute of Biological Resources (NIBR), funded by the Ministry of Environment (MOE) of the Republic of Korea (NIBR202002112). This research received support from the SYNTHESYS+ Project http://www.synthesys.info/ which is financed by European Community Research Infrastructure Action under the H2020 Integrating Activities Programme, Project number 823827.

References

Alexander CP (1920) New or little-known crane-flies from Formosa (Tipulidae, Diptera). Annals of the Entomological Society of America 13(3): 249–270. https://doi.org/10.1093/aesa/13.3.249

Alexander CP (1923) Undescribed crane–flies in the Paris national museum (Tipulidae, Diptera): Part IV. Asiatic species. Bulletin du Muséum National d`Histoire Naturelle 1(28): 295–299. [part]

Alexander CP (1924) New or little–known crane flies from northern Japan (Tipulidae, Diptera). Philippine Journal of Science 24: 531–611.

Alexander CP (1927) Undescribed crane–flies from the Holarctic region in the United States national museum. Proceedings of the United States National Museum 72(2): 1–17. https://doi.org/10.5479/si.00963801.72-2698.1

Alexander CP (1928) New or little–known Tipulidae from eastern Asia (Diptera). III. Philippine Journal of Science 36: 455–485.

Alexander CP (1932) New or little–known Tipulidae from eastern Asia (Diptera). XI. Philippine Journal of Science 49: 105–136.

Alexander CP (1933) New or little–known Tipulidae from eastern Asia (Diptera). XV. Philippine Journal of Science 52: 131–166.

Alexander CP (1934a) New or little–known Tipulidae from eastern Asia (Diptera). XVI. Philippine Journal of Science 52: 305–348.

Alexander CP (1934b) New or little–known Tipulidae from eastern Asia (Diptera). XXI. Philippine Journal of Science 55: 19–60. https://doi.org/10.1093/aesa/27.1.55

Alexander CP (1938) New or little–known Tipulidae from eastern Asia (Diptera). XL. Philippine Journal of Science 67: 129–166.

Alexander CP (1940) New or little–known Tipulidae from eastern China. Part III. Notes d'Entomologie Chinoise 8: 1–28.

Alexander CP (1948) Notes on the tropical American species of Tipulidae (Diptera). IV. The primitive Hexatomini: *Paradelphomyia*, *Austrolimnophila*, *Epiphragma*, *Lecteria*, *Polymera*, and allies. Revista de Etologia 19: 149–190.

Alexander CP (1951) New or little-known crane-flies from Madagascar (Tipuloidea, Diptera). Part I. Memoires de l'Institute Scientifique de Madagascar (A) 5: 33–63.

Alexander CP (1953a) Records and descriptions of Japanese Tipulidae (Diptera). Part I. The crane-flies of Shikoku. I. Philippine Journal of Science 82: 21–75.

Alexander CP (1953b) Records and descriptions of Japanese Tipulidae (Diptera). Part II. The crane-flies of Shikoku. II. Philippine Journal of Science 82: 141–179.

Alexander CP (1962) New exotic crane-flies (Tipulidae: Diptera). Part VI. Entomological News 73: 209–216.

Alexander CP (1963) The crane flies of Madagascar in the natural history museum, Basel, collected by Fred Keiser (Ptychopteridae and Tipulidae; Diptera). Verhandlungen der Naturforschenden Gesellschaft in Basel 74: 181–229.

Bigot JMF (1859) Order VII, Dipteres. In: Voyage au Gabon. Histoire naturelle des insectes et des arachnides recueillis pendant un voyage fait au Gabon en 1856 et en 1857 par M. Henry C. Deyrolle sous les auspices de MM. le Comte de Mniszech et James Thomson precedee de lhistoire du voyage par M. James Thomson. Archives Entomologiques (Thomson) 2: 346–376.

Cho G (2019) National species list of Korea. III. Insects (Hexapoda). National Institute of Biological Resources, Incheon, 989 pp.

Cumming JM, Wood DM (2017) Adult morphology and terminology. In: Kirk-Spriggs AH, Sinclair BJ (Eds) Manual of Afrotropical Diptera. Volume 1. Introductory chapters and keys to Diptera families. Suricata 4. South African National Biodiversity Institue, Pretoria, 107–151.

Curtis J (1836) British entomology: being illustrations and descriptions of the genera of insects found in Great Britain and Ireland: containing coloured figures from nature of the most rare and beautiful species, and in many instances of the plants upon which they are found. Richard and John E. Taylor, London, vol. 13, 578–625.

de Jong H (2017) 14. Limoniidae and Tipulidae (crane flies). In: Kirk–Spriggs AH, Sinclair BJ (Eds) Manual of Afrotropical Diptera. Volume 2. Nematocerous Diptera and lower Brachycera. Suricata 5. South African National Biodiversity Institue, Pretoria, 427–477.

Doleschall CL (1857) Tweede bijdrage tot de kennis der dipterologische fauna van Nederlandsch Indie. Natuurkundig Tijdschrift voor Nederlandsch Indie 14: 377–418.

Edwards FW (1921) The Old–World species of Eriocera in the British museum collection (Diptera, Tipulidae). Annals & Magazine of Natural History 9(8): 67–99. https://doi.org/10.1080/00222932108632559

Edwards FW (1938) British short-palped craneflies. Taxonomy of adults. Transactions of the Society for British Entomology 5: 1–168.

Enderlein G (1912) Studien uber die Tipuliden, Limoniiden, Cylindrotomiden und Ptychopteriden. Zoologische Jahrbucher. Abteilung fur Systematik, Geographie und Biologie der Tiere 32: 1–88.

Enderlein G (1936) 22. Ordnung: Zweiflugler, Diptera. In: Brohmer P, Erhmann P, Ulmer G (Eds) Tierwelt Mitteleuropas 6(2), Insecta 3, Abt. 16: 1–259.

Evenhuis N (2014) Family Limoniidae. In: Catalogue of the fossil flies of the world (Insecta: Diptera). http://hbs.bishopmuseum.org/fossilcat [accessed 23 Oct. 2020]

Guerin–Meneville FE (1831) Insectes. In: Duperrey LI (Ed.) Voyage autour du monde, execute par ordre du Roi, sur la corvette de sa majeste La Coquille etc. Histoire naturelle, zoologie. Atlas, 1–21.

Guerin-Meneville FE (1838) Premiere division. Crustaces, arachnides et insectes. Div. 1: 1–216, 217–319 (= livrs. 25, 26). In: Duperrey LI (Ed.) Voyage autour du monde, execute par ordre du Roi, sur la corvette de sa majeste La Coquille etc. Zoologie 2(2): 1–319.

Ishida H (1959) The catalogue of the Japanese Tipulidae, with the keys to the genera and subgenera (Diptera). V. Limoniinae, Tribe Hexatomini. Science Report of the Hyogo University of Agriculture, Serie. Nature and Science 4(1): 3–11.

Kim CW (1971) Family 1. Blepharoceridae – Family 11. Cecidomyiidae; Family 13. Xylophagidae – Family 24. Dolichopodidae. Illustrated encyclopedia of fauna and flora of Korea, 12, Insecta 4: 643–678, 758–824.

Lackschewitz P (1964) New and little–known palaearctic crane-flies of the family Limoniidae (Diptera, Tipuloidea). Entomologicheskoe Obozrenie 43: 710–733. [In Russian]

Latreille PA (1809) Genera crustaceorum et insectorum secumdum ordinem naturalem in familias disposita, iconibus exemplisque plurimis explicata. Tomus Quartus et Ultimus. A. Koenig, Parisiis et Argentorati [= Paris and Strasbourg] 4: 1–399. https://doi.org/10.5962/bhl.title.65741

Loew H (1850) Über den Bernstein und die Bernsteinfauna. Programm K. Realschule zu Meseritz 1850: 3–44. https://doi.org/10.5962/bhl.title.98386

Loew H (1865) Über die bisher beschriebenen europaischen Anisomera-Arten. Zeitschrift fur die Gesammten Naturwissenschaften 26: 395–426.

Macquart J (1838) Dipteres exotiques nouveaux ou peu connus. Tome premier. 1re partie. Roret, Paris, 5–221. Journal version: Memoires de la Societe Royale des Sciences, de l Agriculture et des Arts, de Lille 2: 9–225. https://doi.org/10.5962/bhl.title.15792

Matsumura S (1916) Thousand insects of Japan. 2. Tokyo: 185–474. [In Japanese]

Meigen JW (1818) Systematische Beschreibung der bekannten europaischen zweiflugeligen Insekten. Gedrukt bei Beaufort Sohn, Aachen, vol. 1, [i–xxxvi,] 324 pp. https://doi.org/10.5962/bhl.title.13731

Men Q-L, Yu D-P (2015) One new species of the subgenus *Hexatoma* (*Eriocera*) Macquart (Diptera, Limoniidae) from China, with a key to Chinese species. ZooKeys 477: 157–171. https://doi.org/10.3897/zookeys.477.7570

Mendl H (1979) Neue und bisher erst wenig bekannte Limoniiden aus dem Mittelmeergebiet (Diptera, Nematocera, Limoniidae). Spixiana 2: 167–185.

Oosterbroek P (2022) Catalogue of the Craneflies of the World (CCW). https://ccw.naturalis.nl/ [accessed 23 Oct 2020]

Osten Sacken CR (1860) New genera and species of North American Tipulidae with short palpi, with an attempt at a new classification of the tribe. Proceedings. Academy of Natural Sciences of Philadelphia 1859: 197–254.

Podenas S (2013) Infraorder Tipulomorpha. In: Kim S-K (Ed.) National list of species of Korea (Insecta: Diptera I). Dongjin Publishing Company, Seoul, 1–36.

Podenas S, Seo HY, Kim T, Hur JM, Kim A-Y, Klein TA, Kim HC, Kang TH, Aukstikalniene R (2019) *Dicranomyia* crane flies (Diptera: Limoniidae) from Korea. Zootaxa 4595(1): 1–110. https://doi.org/10.11646/zootaxa.4595.1.1

Podeniene V, Gelhaus JK (2015) Review of the last instar larvae and pupae of *Hexatoma* (*Eriocera*) and *Hexatoma* (*Hexatoma*) (Diptera, Limoniidae, Limnophilinae). Zootaxa 4021(1): 93–118. https://doi.org/10.11646/zootaxa.4021.1.4

Przhiboro AA, Paramonov NM, Bazova N (2009) Distribution of *Hexatoma* (*Eriocera*) *ussuriensis* Alexander (Diptera: Limoniidae). In: Lantsov V (Ed.) Crane flies. History, taxonomy and ecology (Diptera: Tipulidae, Limoniidae, Pediciidae, Trichoceridae, Ptychopteridae, Tanyderidae). Memorial volume dedicated to Dr. Charles Paul Alexander (1889–1981), Dr. Bernhard Mannheims (1909–1971) and Dr. Evgeniy Nikolaevich Savchenko (1909–1994). Zoosymposia 3: 221–228. https://doi.org/10.11646/zoosymposia.3.1.18

Savchenko EN (1979) Supplements and corrections to the limoniid–flies fauna (Diptera, Limoniidae) of south Kuriles and south Sakhalin. Vestnik Zoologii 1979(1): 23–29. [In Russian with English summary]

Savchenko EN (1983) Limoniidae of South Primorye. Akademiy Nauk Ukrainskoy SSR, I.I. Schmalhausen Institute of Zoology of Academy of Sciences of Ukraine, Naukova Dumka, Kiev, 156 pp. [In Russian]

Savchenko EN (1986) Komary–limoniidy [limoniid–flies]. (General description, subfamilies Pediciinae and Hexatominae). Fauna Ukrainy 14(2): 1–380. [In Russian]

Savchenko EN (1989) Komary–limoniidy fauny SSSR [Limoniidae fauna of the USSR]. Determination tables of superspecies taxa with catalogue survey of species. Akadimiya Nauk Ukrainian SSR, I.I. Schmalhausen Institute of Zoology of Academy of Sciences of Ukraine, Naukova Dumka, Kiev, 377 pp. [In Russian]

Savchenko EN, Krivolutskaya GO (1976) Limoniidae of the south Kuril Islands and south Sakhalin. Akadimiya Nauk Ukrainian SSR, Kiev, 160 pp. [In Russian]

Schiner JR (1863) Vorlaufiger Commentar zum dipterologischen Theile der Fauna austriaca. V. Wiener Entomologische Monatschrift 7: 217–226. [concl.]

Scopoli JA (1763) Entomologia carniolica exhibens insecta carnioliae indigena et distributa in ordines, genera, species, varietates, methodo Linnaeana. Ioannis Thomae Trattner, Vindobonae [= Vienna], 424 pp. https://doi.org/10.5962/bhl.title.34434

Slipka J (1949) Species of the subfamily Hexatominae, new for Czechoslovakia. Casopis Ceske Spolecnosti Entomologicke 46: 180–183. [In Czech with English summary]

Walker F (1848) List of the specimens of dipterous insects in the collection of the British museum. Publisher Edward Newman, 9, Devonshire St. Bishopsgate, London, Vol. 1, 229 pp. https://doi.org/10.5962/bhl.title.57902

Yang D (1999) One new species of Limoniidae from Jigongshan, Henan (Diptera: Tipuloidea). In: Shen X, Shi Z (Eds) Insects of the Funiu Mountains Region. Vol. 1. China Agriculture Science and Technology Press, Beijing, 41–43.