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Results of ongoing mapping of *Bolbelasmus unicornis* (Schrank, 1789) (Coleoptera: Geotrupidae: Bolboceratinae): the second addendum to the biogeographical study from 2022, with a literature review and new records of *B. keithi* Miessen & Trichas, 2011 and *B. nireus* (Reitter, 1895)

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Results of ongoing mapping of *Bolbelasmus unicornis* (Schrank, 1789) (Coleoptera: Geotrupidae: Bolboceratinae): the second addendum to the biogeographical study from 2022, with a literature review and new records of *B. keithi* Miessen & Trichas, 2011 and *B. nireus* (Reitter, 1895)

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Table of Contents

Abstract

The results of ongoing research on the distribution of the European unicorn earth-borer beetle *Bolbelasmus unicornis* (Schrank, 1789) are presented, including occurrence data from 47 new localities: 15 Hungarian, 12 Croatian, 7 Romanian, 7 Slovak, 3 Ukrainian, and 2 Austrian localities. Furthermore, the fifth and most recent record of the species from Bosnia and Herzegovina is given, although dating from 1972. The first historical record of the species from a locality in Germany (Regensburg) was discovered in an overlooked work by Franz de Paula von Schrank dating from the end of the 18th century. Similarly, a record of the species from the 1950s from Moldova representing one of five localities reported from that country was discovered in an overlooked paper by Sergey Ivanovich Medvedev and Dora Samoylovna Shapiro. All new or newly discovered records have been added to four distribution maps provided in this addendum. *Bolbelasmus unicornis* is currently known from 435 localities in 20 countries, but only 12 of these countries have recent records. For each of the countries, an overview of sources with records of the species is given. An updated seasonal dynamics graph was generated based on the data complemented with new records from the countries into which the Pannonian Basin extends. In addition, new occurrence data of the very similar and probably closely related congeners *B. keithi* Miessen & Trichas, 2011 and *B. nireus* (Reitter, 1895) are presented and have been added to the distribution map of *B. unicornis* and East Mediterranean species of the genus *Bolbelasmus*. A review of the literature with records of both species is also given, as well as maps of their distribution. *Bolbelasmus nireus* is delisted from Syria based on a correction of the type locality interpretation. A table with the list of literature sources containing descriptions of immature stages of the representatives of the subfamily Bolboceratinae known to date is provided, as well as corrections for minor errors and omissions that were noted in the previous studies.

Key words: Bolboceratidae, Bolboceratinae, Bolbelasmini, zoogeography, bibliography, occurrence data, distribution maps, Western Palaearctic

Introduction

The present paper reports the results of ongoing zoogeographical research on the endangered European unicorn earth-borer beetle *Bolbelasmus unicornis* (Schrank, 1789) which is included in Annexes II and IV of the Habitats Directive of the European Union (species requiring designation of Special Areas of Conservation and species in need of strict protection, respectively) and in revised Appendix 1 of the Resolution 6 of the Bern Convention (species requiring specific habitat conservation measures) from 2011. The initial comprehensive study and addenda and corrigenda to it were published by Juřena (2022, 2023). Previously unpublished occurrence data from 58 localities in Austria, Bosnia and Herzegovina, Croatia, Germany, Hungary, Romania, Slovakia, and Ukraine are presented here, 47 of them being new. Particularly significant is the discovery of 12 new sites in Croatia, where only a single dated record (Koren 2017) was known within the last 129 years. Similarly significant is the record from the Sarajevo Canton of Bosnia and Herzegovina from 1972, which is the fifth and most recent record of the species from this country. Additionally, important historical records of the species from Germany and the Republic of Moldova were discovered in the overlooked papers by Schrank (1798) and Medvedev & Shapiro (1957). Judging from the number of known localities (Table 1) and their position on the map (Fig. 10), the Pannonian Basin and adjacent areas (especially in the east and southeast) seem to be the centre of the species' distribution. A considerable number of suitable habitats where the species has not yet been discovered can be found throughout Serbia and particularly in Romania, Moldova and Ukraine. It is very likely that *B. unicornis* is widely distributed in these countries, as in Hungary. In several countries such as Montenegro, North Macedonia, Kosovo, Greece (Macedonia and Thrace) and Russia (western regions bordering with Ukraine), the species is very likely to occur, but has not yet been confirmed by reliable records. It is probably extinct in the Czech Republic, France, Poland, and Switzerland (Juřena 2022). All the records from Sicily (e.g., Baraud 1977; Carpaneto & Piattella 1995; Sparacio 1995; Barbero & Cavallo 1999; Martín-Piera & López-Colón 2000; Agoglitta *et al.* 2006; Arnone 2010; Arnone & Massa 2010) refer to *B. vaulogeri* (Abeille de Perrin, 1898) (see Hillert *et al.* 2016; Juřena 2022), and the records from Cyprus by Keith (2002), cited by subsequent authors, and John (2007) refer to the later described *B. makrisi* Miessen, 2011 (see Miessen 2011; Hillert *et al.* 2016; Sommer *et al.* 2021a; Juřena 2022). For the distribution of *B. unicornis* and East Mediterranean *Bolbelasmus* species, see Figs 10, 15.

Bolbelasmus nireus (Reitter, 1895) and *B. keithi* Miessen & Trichas, 2011 are very similar and probably closely related congeners that substitute *B. unicornis* in the East Mediterranean. While the first species is known from Rhodes and southern Turkey, the latter is endemic to the Greek islands of Crete, Kasos and Karpathos (e.g., Hillert *et al.* 2016; Sommer *et al.* 2021a; Juřena 2023; Paulus 2023; Figs 12, 13, 15). All known records of *B. unicornis* from Crete (e.g., Heyden 1884; Oertzen 1886; Savchenko 1938; Horion 1958; Mikšić 1959) refer to *B. keithi* (see Juřena 2022),

while the records of *B. unicornis* or *B. keithi* from Rhodes (e.g., Schatzmayr 1936; Petrovitz 1959; Petersen *et al.* 2006; Hillert *et al.* 2016) refer to *B. nireus* (see Sommer *et al.* 2021a). Records of *B. nireus* from Iran (Keith 2005; Montreuil 2017) probably refer to the more recently described *B. zagrosensis* Sommer, Hillert, Hrůzová & Král, 2021 (in Sommer *et al.* 2021a). *Bolbelasmus tauricus* Petrovitz, 1973 is most likely a junior subjective synonym for *B. nireus*, as suggested by examination of type specimens by Geoffrey Miessen (2011, and remarks for *B. nireus* below). In the present paper, records from 12 new localities from Crete for *B. keithi* and four new localities from the island of Rhodes and the Mediterranean Region of Turkey for *B. nireus* are presented.

Material and methods

The concept of Bolboceratinae as a subfamily of Geotrupidae is consistent with numerous modern authors, e.g., Ratcliffe & Jameson (2004), Verdú *et al.* (2004), Jameson (2005), Smith (2006, 2009, 2024), Smith *et al.* (2006), Howden *et al.* (2007), Li *et al.* (2008, 2019), Mondaca & Smith (2008), Ocampo (2008), Lawrence *et al.* (2011), Chandra & Gupta (2012), Krikken (2013ab), Krikken & Li (2013), Nikolajev *et al.* (2016), Boilly & Vaz-de-Mello (2021), Carvalho & Vaz-de-Mello (2022), Mondaca (2023), Price & Ratcliffe (2023), Li & Wang (2024), and Vaz-de-Mello (2024).

Although Moctezuma *et al.* (2024) proposed the genus *Bolbelasmus* Boucomont, 1911 as a subgenus of *Eucanthus* Westwood, 1848, the classical concept is conserved here because of the markedly different morphology of adults as well as differing biology of the two genera (cf. Howden 1955).

The dates of Panzer's works are adopted from Bousquet (2016) and Alonso-Zarazaga & Evenhuis (2017). Panzer (1793a) is cited according to Sherborn (1902), Hillert *et al.* (2016), and Löbl & Löbl (2016). The catalogues of Megerle von Mühlfeld (1802, 1804, 1805) are cited according to Schenkling (1935).

The distributional records are divided into paragraphs according to the largest superior administrative units or traditional regions. The countries, administrative units/traditional regions, and distributional records are ordered according to their geographical position from west to east and from north to south. The following acronyms are used in the text: **CEST** = Central European Summer Time; **EEST** = Eastern European Summer Time; **EET** = Eastern European Time; **FSLG** = flying slowly low above the ground; **FMF** = faunistic map field used in grid mapping of fauna and flora in Central Europe (E.g., Zelený 1972; Novák 1989; Pruner & Míka 1996; Kolouch 2002; Fig. 9); **NP** = National Park; **PP** = Přírodní památka / Prírodná pamiatka (= Natural Monument). Unless otherwise stated, the material has been identified or revised by one of the authors.

Within the overview of references with records of *B. unicornis*, the countries are ordered from west to east and from north to south. These references include not only sources with the exact localities of the species, but also sources that merely mention the presence of the species in each country.

The following systems are used to transliterate cited literature and geographical or personal names in the Cyrillic/Greek scripts: BGN/PCGN 2013 Agreement for Bulgarian, BGN/PCGN 1996 Agreement for Greek, BGN/PCGN 1947 System for Russian, BGN/PCGN 2005 Agreement for Serbian, and BGN/PCGN 2019 System for Ukrainian.

For the distribution map of *B. unicornis* in the Czech Republic and Slovakia, the records are divided into three time periods: pre-1960, 1960–1999 and post-1999 (Fig. 9). This map was compiled by manually placing the circles in the grid map used for faunistic research in these countries in a standard free graphics software. The following time periods are used for the distribution map of Hungary and northwestern Croatia (Fig. 5) and the general distribution of the species (Fig. 10): pre-1950, 1950–1999, and post-1999. The distribution maps of *B. unicornis* and East Mediterranean species of the genus *Bolbelasmus* (Figs 12, 13, 15) were compiled using data contained in Krikken (1977), Lodos *et al.* (1999), Petersen *et al.* (2006), Miessen (2011), Miessen & Trichas (2011), Hillert *et al.* (2016), Sommer *et al.* (2021a), Juřena (2022, 2023), Paulus (2023), and new data acquired for this addendum. The latter five maps were created using the Google Maps web application by inserting specific GPS coordinates into the system. 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. The definition of the Western Palaearctic is adopted from Mitchell (2017).

Table 1 with the number of localities with the occurrence of *B. unicornis* for each country is based on the data provided by Juřena (2022, 2023) and those in this paper.

Acronyms for the persons

ABC Aleš Bezděk, České Budějovice, Czech Republic
ABZ Andrii Ivanovych Bachynskyi (Андрій Іванович Бачинський), Zalishchyky, Ukraine
AKT András Kleszó, Tard, Hungary
AMV Alexander Christian Mrkvicka, Vienna, Austria
ASB Áron Székely, Budapest, Hungary
AVC Adrian Vintilă, Constanța, Romania
BBF Bengt Åke Bengtsson, Färjestaden, Öland, Sweden
BDM Benjamin Duchaj, Monor, Hungary
BKL Bence Krajcsovszky, Lábatlan, Hungary
BLZ Boris Lauš, Zagreb, Croatia
BMB Balázs Molnár, Budapest, Hungary
BPK Balázs Pintér, Kerepes, Hungary
BTB Balázs Tóth, Budapest, Hungary
CHM Csaba Horváth, Mór, Hungary
CMI Cosmin-Ovidiu Manci, Iași, Romania
CWV † Charlotte Wewalka, Vienna, Austria
DJP Daniel Juřena, Prostějov, Czech Republic
FSC Fotis Samaritakis (Φώτης Σαμαριτάκης), Chania, island of Crete, Greece
FSP František Štěpánek, Přerov-Kozlovice, Czech Republic
FTW Florian Theves, Weingarten (Baden), Germany
FWV † Friedrich Wewalka, Vienna, Austria
GHV Georg Franz Häfner, Vienna, Austria
GML Geoffrey Miessen, Liège, Belgium
GRS Gergő Rák, Szentgál, Hungary
GSE Gábor Szerényi, Érd, Hungary
GWV Günther Wewalka, Vienna, Austria
HPV Hannes Franz Paulus, Vienna, Austria
IIS Ionuț-Ștefan Iorgu, Suceava, Romania
IMO Ivo Martinů, Olomouc, Czech Republic
ISS István Staudinger, Székesvehérvár, Hungary
JBK Jaroslav Bednář, Kralupy nad Vltavou, Czech Republic
JBZ Jelena Babić, Zagreb, Croatia
JHC Johanna Hartmann, Csákvár, Hungary
JKL † Jan Krikken (1944–2022), Leiden / Leiderdorp, Netherlands
JKN Ján Kollár, Nitra, Slovakia
JMM Jochen Martens, Mainz, Germany
JMR Juraj Matejka, Ružomberok, Slovakia
JVO Jiří Vávra, Ostrava, Czech Republic
KHE Krisztián Harmos, Eger, Hungary
KKR Konstantinos Kalaentzis (Κωνσταντίνος Καλαεντζής), city of Rhodes, island of Rhodes, Greece
LPC Levente Pribéli, Csákvár, Hungary
LPU Luka Petrokov, Umag, Croatia
MIZ Mateja Ilinić, Zagreb, Croatia
MJR Martin Jagelka, Rohožník, Slovakia
MMB Marion Mantič, Hlučín-Bobrovníky, Czech Republic
MMP Martin Mařík, Praha, Czech Republic
MSC Miroslav Snížek, Homole near České Budějovice, Czech Republic
MSL Menno Schilthuizen, Leiden, Netherlands
MSR Matúš Karol Šoltís, Ružomberok, Slovakia
NVB Nimród Varga, Budapest, Hungary
OBL Olivier Boilly, Lille, France
OSO Ondřej Sabol, Ostrava, Czech Republic

PKG Peter Kurina, Gajary, Slovakia
PKL † Petrus Jacobus (Piet) Kuijten (1925–2009), Leiden, Netherlands
PKS Petr Kylies, Slaný, Czech Republic
PSV Philip Schaffer, Vienna, Austria
RCK Roman Cséfalvay, Rohovce-Kyselica, Slovakia
RDK Ringo Dietze, Käbschütztal, Germany
RHB Roman Hergovits, Bratislava, Slovakia
RMZ † René Mikšić (1920–1986), Zagreb / Rijeka / Ilidža, former Yugoslavia
RNK Ruslan Yuriiovych Nerush (Руслан Юрійович Неруш), Kyiv, Ukraine
RSV Richard Sehnal, Velenice, Czech Republic
RVD Rober Vlk, Drnholec, Czech Republic
SCD Svätopluk Čepelák, Dlhá nad Váhom, Slovakia
SDC Steve Daniels, Cockermouth, United Kinkdom
SKD Svitlana Kiiak (Світлана Кіяк), Dniprovske near Solone, Ukraine
VKS Vítězslav Kubáň, Šlapanice, Czech Republic
VSI Valentin Szénási, Isaszeg, Hungary

Acronyms for the institutes

NHMW Naturhistorisches Museum Wien, Vienna, Austria
RMNH Naturalis Biodiversity Centre (formerly Rijksmuseum van Natuurlijke Historie), Leiden, Netherlands
UMJG Universalmuseum Joanneum, Graz, Austria

Results

Occurrence data and remarks

Bolbelasmus unicornis (Schrank, 1789)

Germany

Baden-Württemberg, Karlsruhe Region (Regierungsbezirk Karlsruhe), Karlsruhe District (Landkreis Karlsruhe), Bruchsal–Untergrombach, Michaelsberg and Habichtsbuckel Nature Reserve, ca. 49°05’32”N, 8°34’13”E, 200–220 m a.s.l., 4.vii.2022, 1 ♂ and 1 ♀ FSLG after sunset, air temperature 16°C, FTW obs.; the same site, 10.viii.2023, 2 spec. FSLG after sunset, air temperature 18°C, one week after the cessation of heavy rains, FTW obs.; the same site, 15.viii.2023, 1 ♀ FSLG after sunset, air temperature 17°C, FTW obs.; the same site, 4.vii.2024, 2 ♂♂, FSLG at 22.22–22.30 CEST after heavy rain, together with ca. 20 spec. of *Od. armiger*, air temperature 17°C, light breeze, FTW obs.

Remarks. First localised record from Germany (Regensburg) was reported by Schrank (1798)—see Corrections and additions to Juřena (2022) below. The Michaelsberg and Habichtsbuckel Nature Reserve represents the only known locality with the recent occurrences of *B. unicornis* in Germany (Juřena 2022; Theves & Bittner 2022; Bittner & Theves 2023). It is very likely that there are localities suitable for the species in the Rhineland and the Danube Region of Germany that are still waiting to be discovered.

Austria

Vienna (Wien), Lainzer Tiergarten wildlife preserve [very approx. GPS coordinates: 48°11’16”N, 16°13’56”E], 272 m a.s.l., 22.vi.2023, 1 ♂ flying ca. 1–1.5 m above the ground near several oak trees at the edge of an old natural oak forest, 22.00 CEST, air temperature ca. 25°C, just after a small summer storm, no wind, GHV & AMV obs., det. + photo, DJP rev.; the same locality, 29.vi.2023, 1 ♀ flying ca. 1–1.5 m above the ground near oak trees at the edge of an old natural oak forest, 22.45 CEST, air temperature ca. 21°C, clear, no wind, GHV & AMV obs., det. + photo, DJP rev.; Vienna (Wien)–Donaustadt, Donau-Auen NP, Festwiese, 48°11’42.13”N, 16°32’05.38”E, 154 m a.s.l., 25.v.2023, 1 ♂ crawling on a path at 17:20 CEST, PSV obs., det. + photo (Fig. 1).

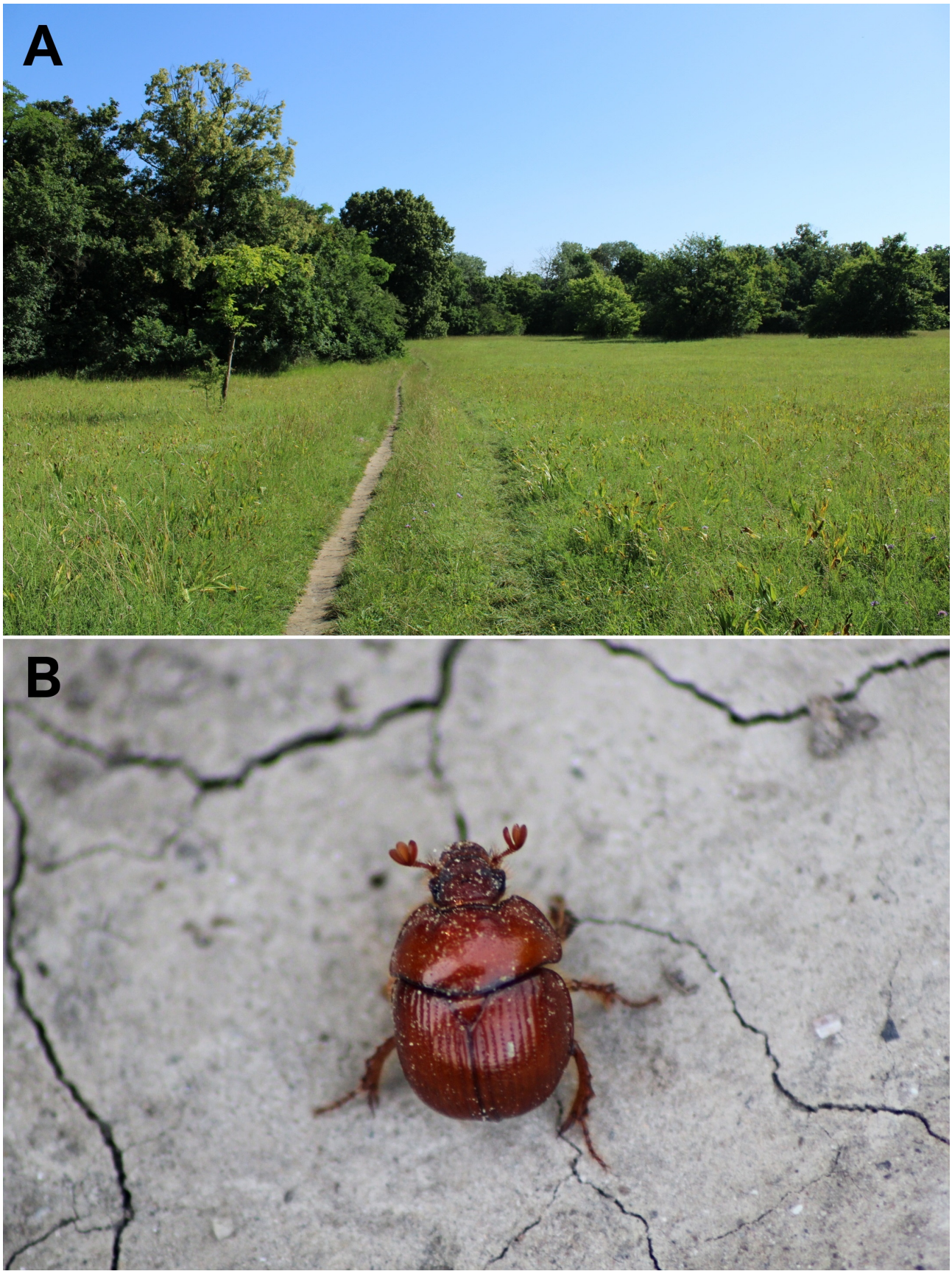

Figure 1. Finding of *Bolbelasmus unicornis* in Donau-Auen NP (Festwiese), 25.v.2023: **A,** view of the site; **B,** observed specimen (photographs by Philip Schaffer).

Remarks. Austria is the country from where *B. unicornis* was described and where the largest amount of historical literature mentioning the species is known (see Overview of references with records of *B. unicornis* below). The species has been recorded in all federal states of Austria except Salzburg, Tyrol, and Vorarlberg, which are characterised by high-mountain nature that does not suit the ecological requirements of *B. unicornis*. Gistel (1856) listed the species also from "neue Welt" in "Tyroler und Salzburger Alpen", which was obviously a confusion of locality or misidentification. Recent records have been published from Burgenland, Lower Austria, Styria, and Vienna (Paill 2007; Paill & Mairhuber 2012; Dostal 2019; Dostal & Barries 2019, 2021; Holzer 2019; Rabl *et al.* 2019; Dostal *et al.* 2021ab, 2023).

Croatia

Osijek-Baranja County (Osječko-baranjska županija), Popovac, Zlatno brdo [hill], 45°47'24.86"N, 18°40'30.11"E, 137 m, 24.v.2023, 1 ♀ FSLG after sunset, 21°C, light breeze, two days after rain, LPU obs., photo BLZ (Figs 2A–F); Popovac, Stanovi, 45°47'40.73"N, 18°40'53.12"E, 163 m a.s.l., 24.v.2023, 2 ♂♂, 1 ♀, and 1 spec. with unknown sex FSLG after sunset, 21°C, light breeze, two days after rain, BLZ obs.; Branjina, Nad mlinom, 45°48'50.76"N, 18°41'24.10"E, 91 m a.s.l., 23.v.2023, 2 ♂♂ FSLG after sunset, 22°C, light breeze, cloudy, one day after rain, LPU obs., photo BLZ (Figs 3A,B); Podolje, Vlašković, 45°49'00.96"N, 18°42'46.93"E, 140 m a.s.l., 23.v.2023, 1 ♂ FSLG after sunset, 22°C, light breeze, cloudy, one day after rain, BLZ obs. + photo (Figs 3C,D); Gajić, Filakovi, 45°49'38.32"N, 18°46'17.15"E, 144 m a.s.l., 22.v.2023, 2 ♂♂ and 6 ♀♀ FSLG after sunset, 22°C, no wind, just before the rain, BLZ & LPU obs., photo BLZ; Draž, Kraljev stol, 45°49'33.24"N, 18°47'52.08"E, 182 m a.s.l., 07.vi.2022, 5 ♂♂, 2 ♀♀, and 1 spec. with unknown sex FSLG after sunset, 22°C, no wind, just before the rain, BLZ, MIZ & JBZ obs., photo BLZ; 45°49'33.45"N, 18°47'50.54"E, 182 m a.s.l., 12.vi.2023, 2 ♂♂ FSLG after sunset, 19°C, no wind, partly cloudy, BLZ obs. + photo; Aljmaš, Botkvinac, 45°31'21.57"N, 18°56'33.57"E, 142 m a.s.l., 25.v.2023, 1 ♀ FSLG after sunset, 21°C, light breeze, partly cloudy, BLZ obs. + photo (Figs 4A,C); Aljmaš, Ćosinac, 45°31'21.57"N, 18°56'33.57"E, 102 m a.s.l., 16.vi.2023, 1 ♂♂ and 2 ♀♀ FSLG after sunset, 19°C, no wind, just before the rain, BLZ & LPU obs., photo BLZ (Figs 4B,D); Aljmaš, Glogovi, 45°31'13.31"N, 18°58'14.61"E, 164 m a.s.l., 15.vi.2023, 2 ♀♀ FSLG after sunset, 18°C, light wind, just before the rain, BLZ obs. + photo (Figs 4E,F).

Vukovar-Syrmia County (Vukovarsko-srijemska županija), Bapska, Gajevi, 45°11'58"N, 19°14'58"E, 125 m a.s.l., 21.vi.2023, 9 ♂♂, 2 ♀♀, and 1 spec. with unknown sex FSLG after sunset, quite warm, 27°C, light breeze, partly cloudy, BLZ & LPU obs., photo BLZ (Figs 3E,F); Bapska, Bagremar, 45°12'14.32"N, 19°15'46.18"E, 119 m a.s.l., 30.v.2023, 1 ♂ and 1 ♀ FSLG after sunset in light rain, 17°C, light wind, BLZ obs. + photo; Mohovo, close to the football pitch, 45°14'23.58"N, 19°13'03.54"E, 122 m a.s.l., 22.vi.2023, 1 ♂, 2 ♀♀, and 2 spec. with unknown sex FSLG after sunset, 27°C, fresh breeze, partly cloudy, BLZ & LPU obs., photo BLZ.

Remarks. Until now, only one recent record from Croatia from the County of Vukovar-Syrmia was known (Koren 2017). Most of the habitats in Croatia are severely degraded and converted to farmland (personal observations of the second author). Populations of *B. unicornis* in Slavonia have survived on narrow fragments of natural grasslands at the edges of farmlands or in a few traditional orchards with undisturbed soil cover (Figs 4A,C,E). The few preserved grasslands are subject to vegetation overgrowth as fewer and fewer livestock graze them, and they soon become overgrown with invasive plant species such as *Ailanthus altissima, Amorpha fruticosa, or Robinia pseudoacacia*. For the distribution of the species in northwestern Croatia see Fig. 5.

Bosnia and Herzegovina

Federation of Bosnia and Herzegovina (Federacija Bosne i Hercegovine / Федерација Босне и Херцеговине), Sarajevo Canton (Kanton Sarajevo / Sarajevska županija / Сарајевски кантон), Miševići (Мишевићи) near Rakovica (Раковица), 550–700 m a.s.l., iii.1972, 1 ♂, collector unknown, RMZ det., JKL det. 1976, coll. PKL deposited in RMNH (Fig. 6).

Remarks. The first record of the species for the territory of Bosnia and Herzegovina (Zavidovići env., Gostović river valley) was reported by Kendi (1910). Subsequently, only three other records were published (Mikšić 1953; Hillert *et al.* 2016), which were cited by a number of later authors (see Juřena 2022 and Overview of references with records of *B. unicornis* in this study). The above record from Miševići represents the only preserved specimen known to us from Bosnia and Herzegovina and is also the last known record from this country.

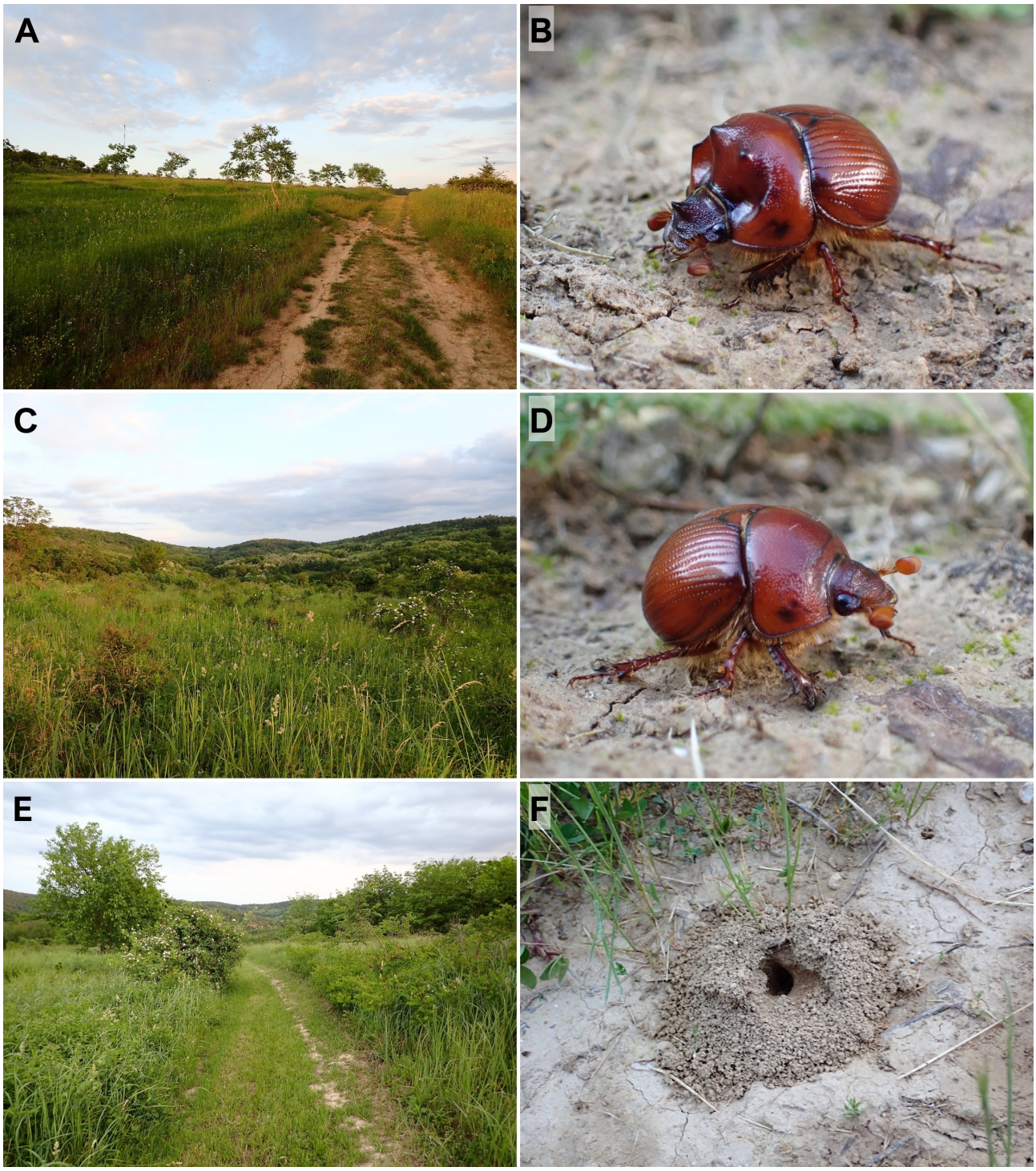

Figure 2. Habitats and observations of *Bolbelasmus unicornis* at Zlatno brdo near Popovac, 24.v.2023: **A, C, E,** sites with *B. unicornis*; **B, D,** observed male and female; **F,** burrow with push-up (photographs by Boris Lauš).

Slovakia

Bratislava Region (Bratislavský kraj), Bratislava II District (okres Bratislava II), Bratislava-Podunajské Biskupice, Kopáč Island, PP Panský diel, FMF No. 7869, ca. 48°06'05.53"N, 17°09'46.42"E, 132 m a.s.l., 26.v.2023, 6 ♂♂ and 7 ♀♀ FSLG after sunset (including 2 spec. crawling on the ground at the end of the flight time), PKG & RHB obs.; the same locality, 27.v.2023, ca. 40 spec. FSLG at 21.05–21.27 CEST (sunset: 20.36 CEST), together with more spec. of *Od. armiger* and 5 spec. of *Och. chrysomeloides*, OSO obs.; the same locality, 48°06'01.44"N, 17°09'47.32"E, 10.vi.2023, 7 ♂♂ and 3 ♀♀ FSLG in light rain at 21.25–21.57 CEST (sunset: 20.49 CEST), together with 5 spec. of *Od. armiger* and 7 spec. of *Och. chrysomeloides*, DJP & RVD obs; the same locality, ca. 48°06'05.58"N, 17°09'46.89"E,

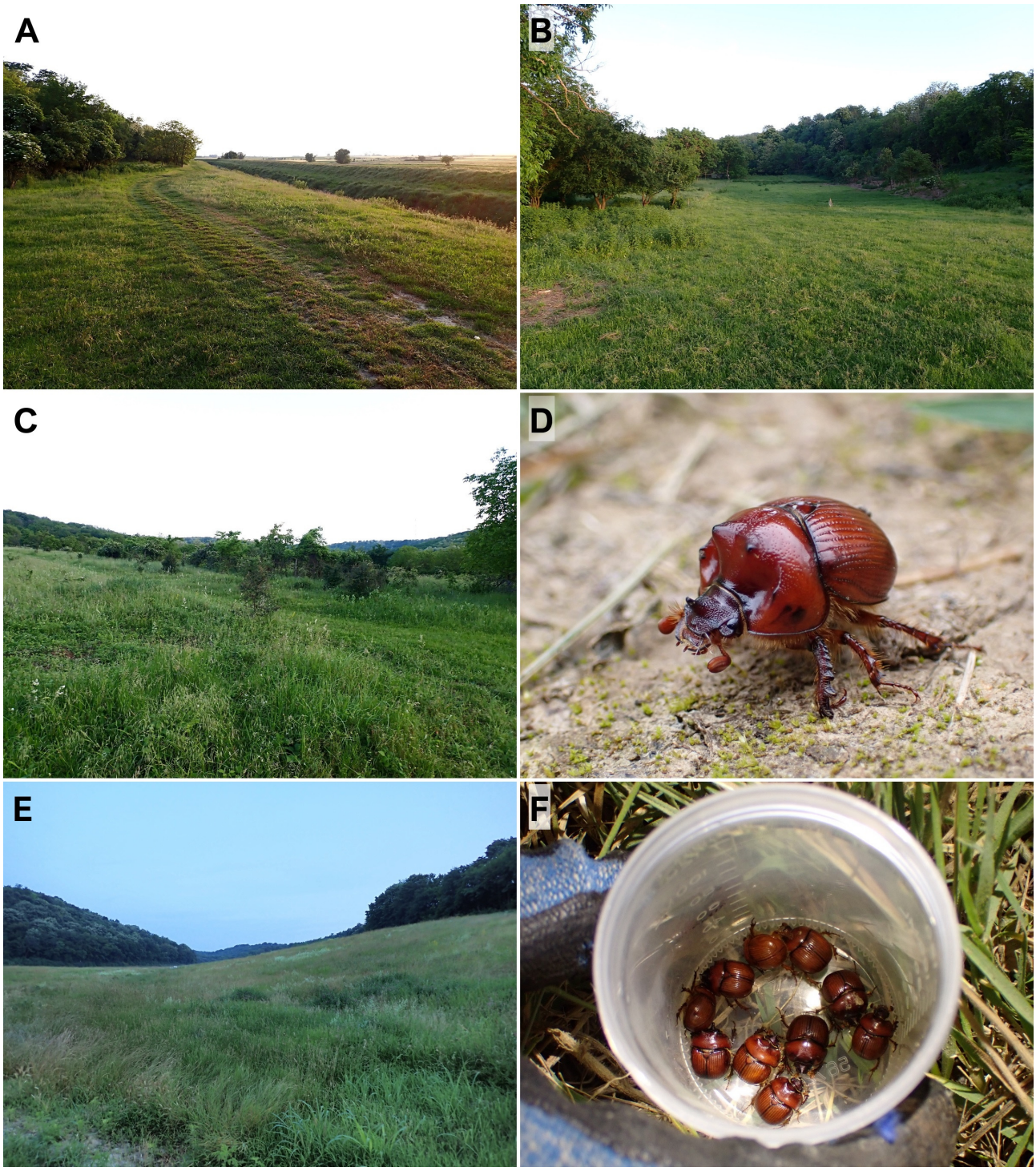

Figure 3. Sites and observed specimens of *Bolbelasmus unicornis*: **A, B,** Branjina, Nad mlinom, 23.v.2023; **C, D,** Podolje, Vlašković, 23.v.2023; **E, F,** Bapska, Gajevi, 21.vi.2023 (photographs by Boris Lauš).

8.vi.2024, 2 ♂♂ and 2 ♀♀ FSLG at 21.25–22.05 CEST (sunset: 20.53 CEST), together with several spec. of *Od. armiger* and *Och. chrysomeloides*, 22–23°C, no wind, FSP & IMO observ.

Nitra Region (Nitranský kraj), Komárno District (okres Komárno), Zlatná na Ostrove–Veľký Lél env., Veľkolélsky ostrov, FMF No. 8273, 47°44’58.54”N, 17°57’00.56”E, 110 m a.s.l., 20.viii.2023, 1 ♀, at light at 21.45 CEST (sunset: 19.54 CEST), gravel bank of the Danube River, JVO & RCK obs. + photo (Figs 7A,B); Nové Zámky District (okres Nové Zámky), Mužla–Čenkov env., flood barrier of the Danube river, FMF No. 8277, 47°46’18.69”N, 18°33’44.82”E, 110 m a.s.l., 26.vi.2023, ca. 10 burrows with push-ups, OSO obs.; the same locality, 47°46’24.86”N, 18°33’22.32”E, 110 m a.s.l., 26.vi.2023, ca. 20 burrows with push-ups, OSO obs.; outside edge of the flood barrier

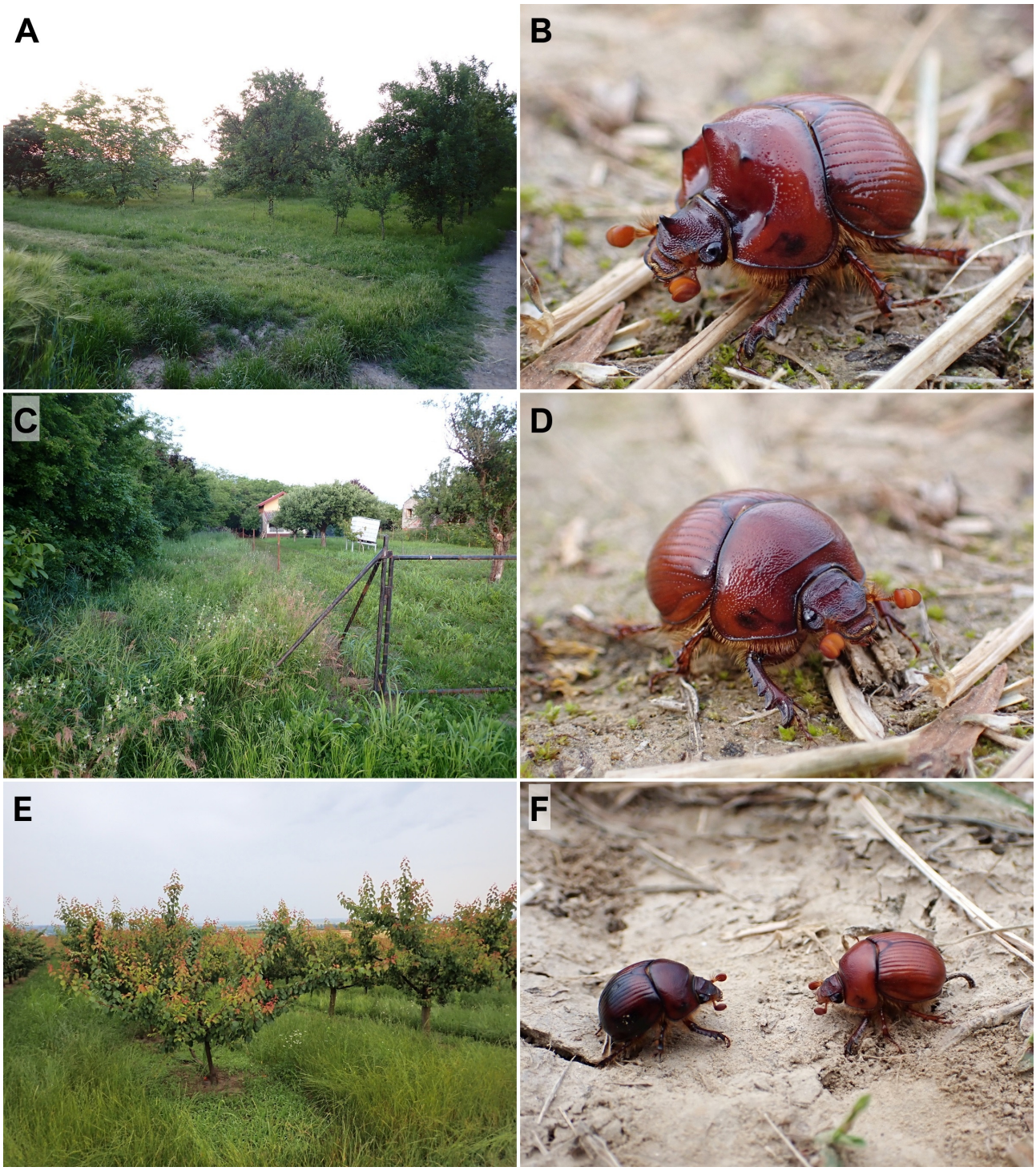

Figure 4. Sites and observed specimens of *Bolbelasmus unicornis* near Aljmaš: **A, C,** Aljmaš, Botkvinac, 25.v.2023; **B, D,** Aljmaš, Ćosinac, 16.vi.2023; **E, F,** Aljmaš, Glogovi, 15.vi.2023 (photographs by Boris Lauš).

of the Danube river, 47°46'15.94"N, 18°32'35.95"E, 108 m a.s.l., 10.viii.2023, 1 ♀ FSLG at 21.15 CEST (sunset: 20.09 CEST), RCK obs. + photo (Figs 7C,D); Nové Zámky District (okres Nové Zámky), Kamenica nad Hronom env., Čierna hora hill, FMP No. 8178, 47°50'15.33"N, 18°43'35.08"E, 198 m a.s.l., 26.vi.2023, three newly dug burrows with push-ups, OSO obs.; Levice District (okres Levice), Ipeľské Úľany env., FMP No. 7880, 48°07'40.01"N, 19°01'15.68"E, 325 m a.s.l., 30.v.2024, 1 ♀, at light at 21.45 CEST (together with 2 spec. of *Od. armiger*), 2 ♀♀ FSLG at 21.30–21.40 CEST, SCD & JKN obs.

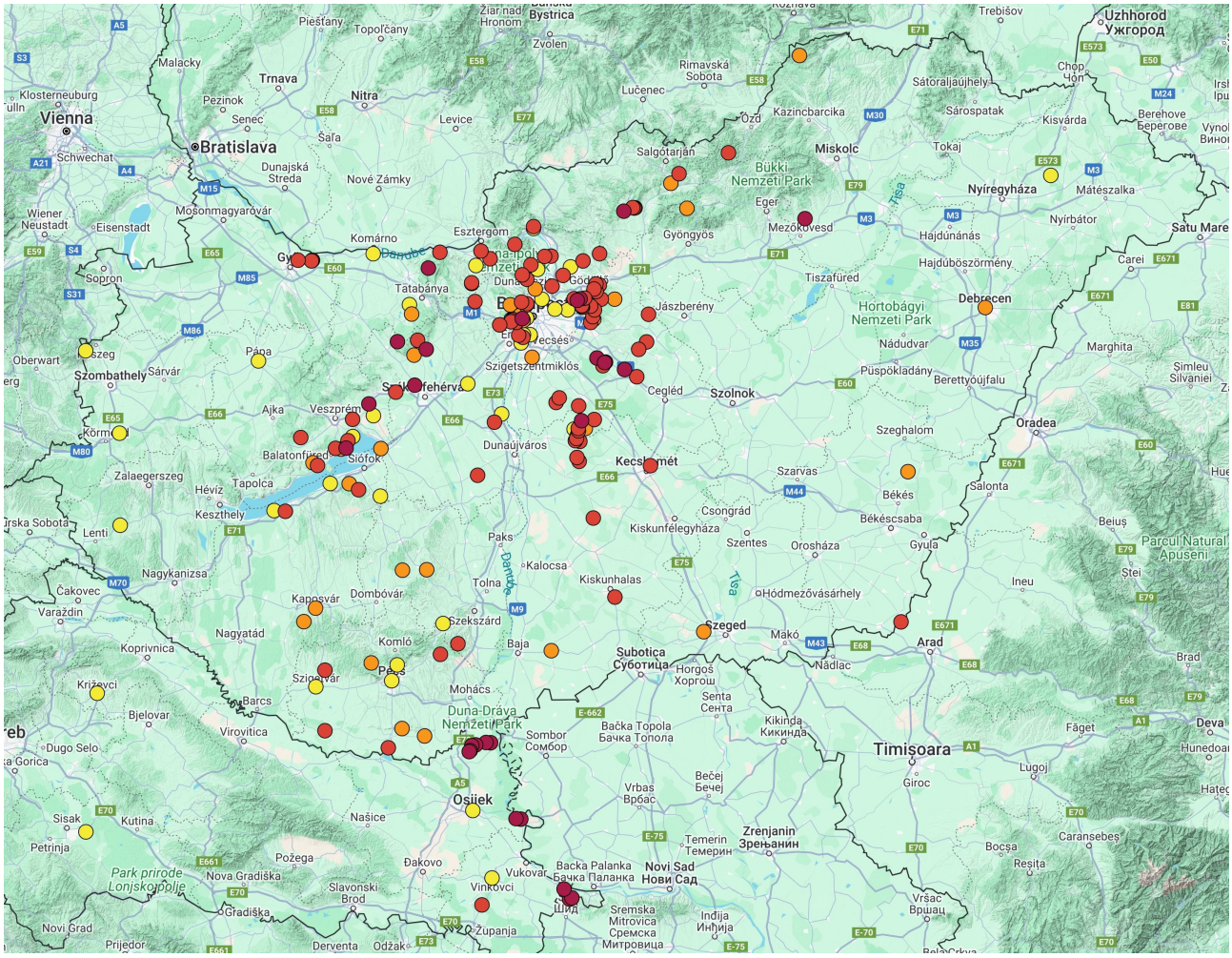

Figure 5. Distribution of *Bolbelasmus unicornis* in Hungary and northeastern Croatia (yellow circles = records before 1950; orange circles = records from 1950–1999; pale red circles = records after 1999; dark red circles = records after 1999 from sites first published in this paper).

Banská Bystrica Region (Banskobystrický kraj), Rimavská Sobota District (okres Rimavská Sobota), Hajnáčka–Buková env., FMP No. 7785, ca. 48°13’43.5”N, 19°58’13.5”E, 390 m a.s.l., 25.v.2005, 3 spec. FSLG after sunset, MMB & JVO obs.; Rimavská Sobota District (okres Rimavská Sobota), Cerová vrchovina Mts, Gemerské Dechtáre, Nízky kopec hill, FMP No. 7786, 48°14’34.59”N, 20°01’18.84”E, 260 m a.s.l., 10.vi.2024, 1 ♀ FSLG at 21.15 CEST, RCK obs.; Rimavská Sobota District (okres Rimavská Sobota), Jesenské–Barta, FMF No. 7786, ca. 48°17’40.5”N, 20°03’53.3”E, 190 m a.s.l., 17.vi.2023, 1 ♂ and 1 ♀ FSLG after sunset, VKS obs.; Rimavská Sobota District (okres Rimavská Sobota), Cerová vrchovina Mts, Jestice env., Veľké Drieňové, FMF No. 7786, 48°12’59”N, 20°02’17.7”E, 260 m a.s.l., 5.vii.2020 FSLG after sunset, MSR & JMR obs.; Rimavská Sobota District (okres Rimavská Sobota), Cerová vrchovina Mts, Jestice env., Drienkové, FMF No. 7786, 48°12’44”N, 20°02’44”E, 227 m a.s.l., 17.vi.2023, 7 spec. FSLG after sunset, together with more spec. of *Od. armiger*, ABC and RSV obs.; the same locality, 48°12’40.38”N, 20°02’50.68”E, 240 m a.s.l., 4.viii.2023, 2 ♀♀ FSLG at 21.07 CEST (sunset: 20:14 CEST), RCK obs. + photo (Figs 7E,F); Rimavská Sobota District (okres Rimavská Sobota), Figa env., FMF No. 7687, 2022–2023, number of spec. not specified, FSLG, anonymus leg. et coll.

Košice Region (Košický kraj), Trebišov District (okres Trebišov), Malý Horeš env., FMF No. 7597, 48°24’39.46”N, 21°56’41.95”E, 110 m a.s.l., 30.viii.2023, 1 ♀ FSLG at 21:10 CEST (sunset: 19:20 CEST), sand dune, RCK obs. (see Fig. 8 for a view of the site).

Remarks. Slovakia is the country with the second highest number of known localities with *B. unicornis* (see Table 1). Most of the records are from the southern border of the country (Danubian Lowland, Cerová vrchovina Mts, Slovak Karst, Eastern Slovak Lowland; Fig. 9). The largest known population is at the Panský diel Nature Monument on the Kopáč Island in the city of Bratislava (see Juřena 2022, 2023 for distributional records and photographs of the site).

Figure 6. Male of *Bolbelasmus unicornis* from Miševići near Rakovica deposited in RMNH, representing the last documented occurrence of the species in Bosnia, dorsal and lateral views (length of body 12.5 mm, labels not to scale; photographs by Yvonne van Dam, edited by Aleš Sedláček).

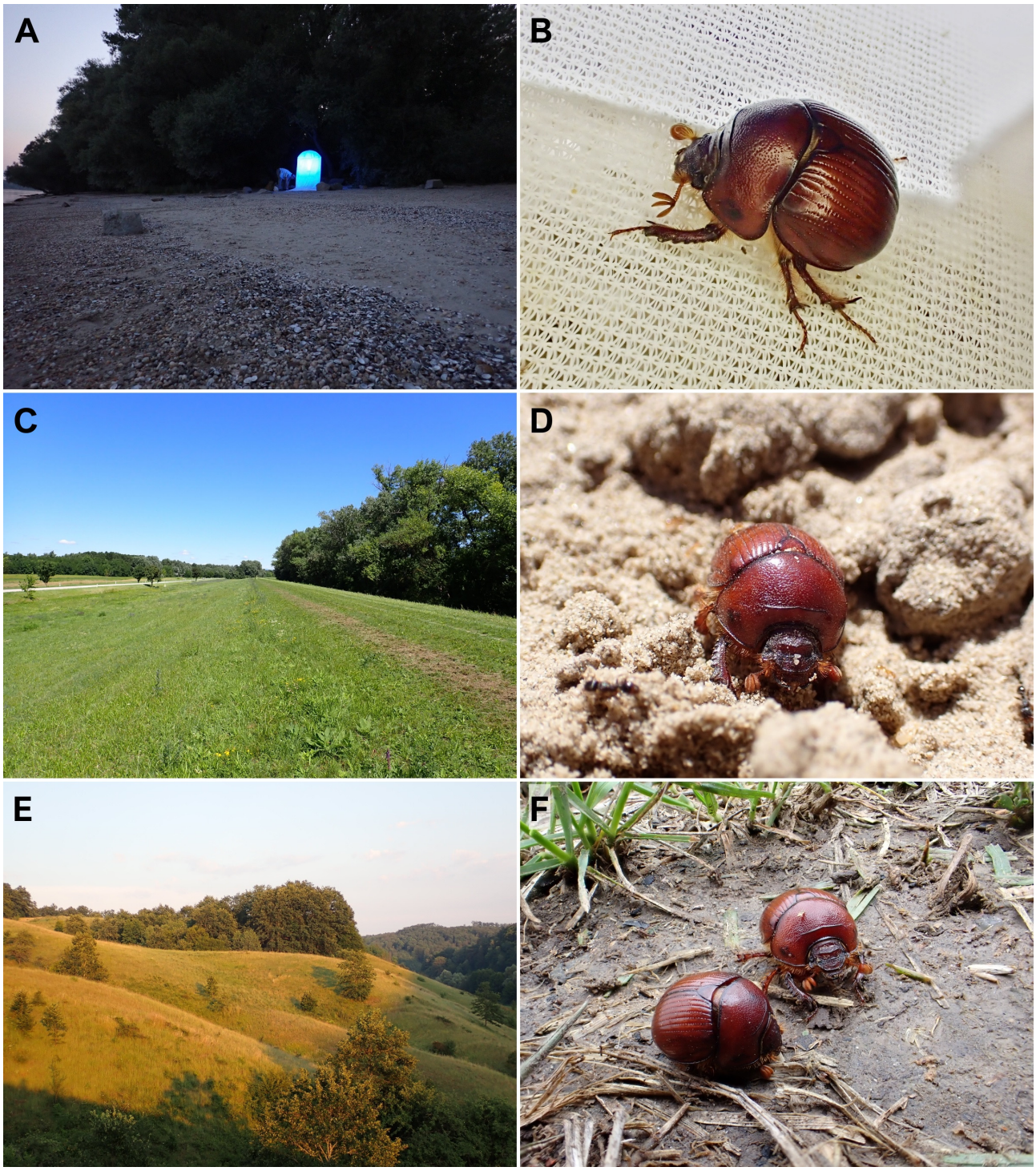

Figure 7. Sites and observed specimens of *Bolbelasmus unicornis* in Slovakia: **A, B,** Veľkolélsky ostrov near Veľký Lél, bank of the Danube River, 20.viii.2023; **C, D,** Mužla–Čenkov env., 10.viii.2023; **E, F,** Cerová vrchovina Mts, Jestice–Drienkové, 4.viii.2023 (photographs by Roman Cséfalvay).

Hungary

Central Transdanubia (Közép-Dunántúl), Veszprém County (Veszprém vármegye), Öskü env., 47°09’32”N, 18°06’06”E, 190 m a.s.l., 20.v.2023, 1 ♂, at UV light, MJR obs.; Veszprém County (Veszprém vármegye), Alsóörs env., 19.vi.2023, 1 ♀, dead on the ground, Judit Neviczki obs. + photo, VSI det., DJP rev.; Komárom-Esztergom County (Komárom-Esztergom vármegye), Tardos env., Malom Valley (Malom-völgy), 47°41’01.11”N, 18°26’29.25”E, 235 m a.s.l., 19.vi.2023, 1 ♂, at light, BKL obs., det. + photo, DJP rev.; the same locality, ca. 47°41’00.92”N, 18°26’31.13”E, ca. 240 m a.s.l., 14.v.2024, 1 ♀, at light, BKL obs., det. + photo, DJP rev.; Fejér County (Fejér vármegye), Csákvár

Figure 8. Site with *Bolbelasmus unicornis* near Malý Horeš, Eastern Slovak Lowland (photograph by Roman Cséfalvay).

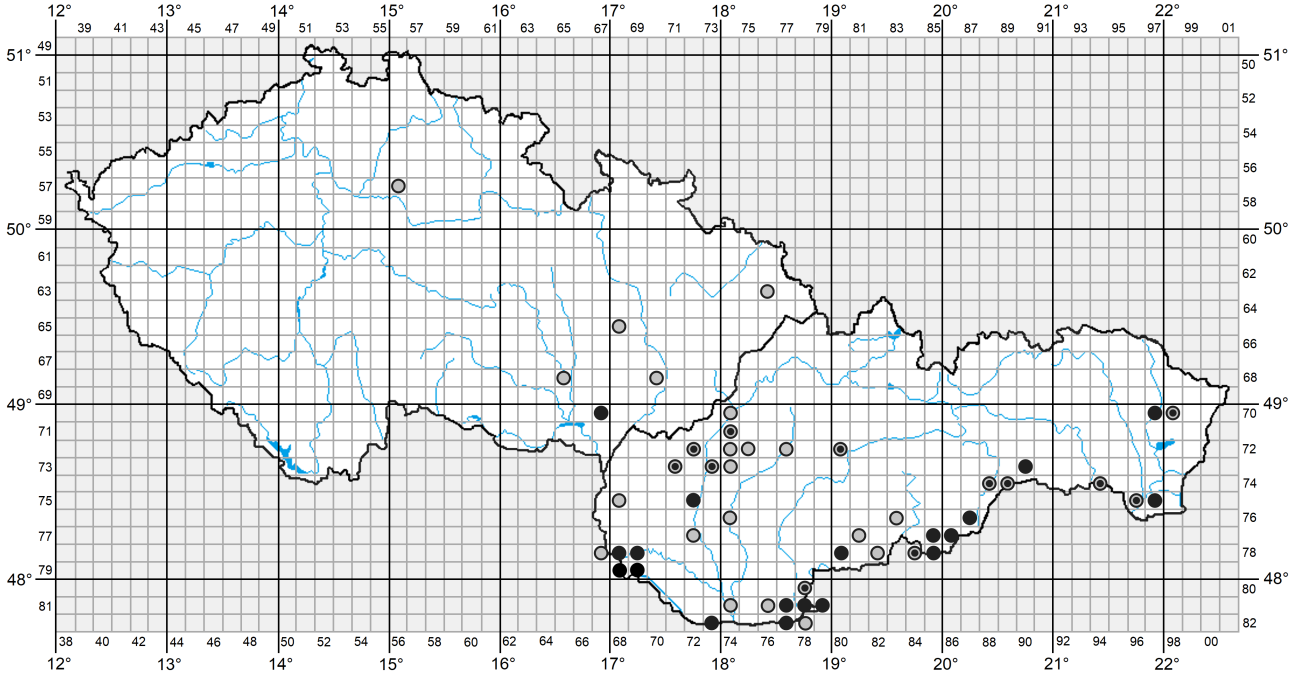

Figure 9. Distribution of *Bolbelasmus unicornis* in the Czech Republic and Slovakia (empty grey circles = records before 1960; grey circles with black centre = records from 1960–1999; solid circles = records from 2000–2024).

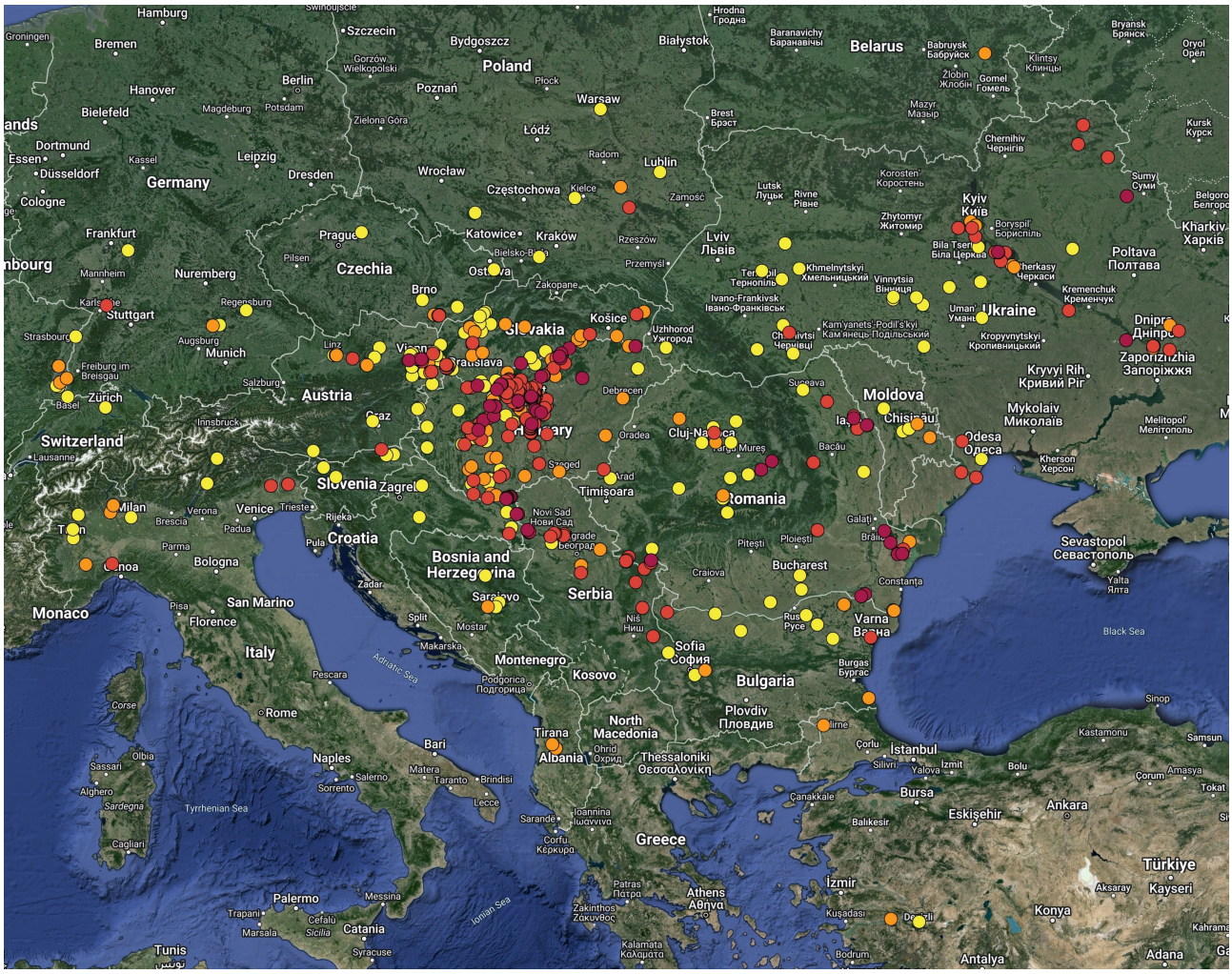

Figure 10. General distribution of *Bolbelasmus unicornis* (yellow circles = records before 1950; orange circles = records from 1950–1999; pale red circles = records after 1999; dark red circles = records after 1999 from sites first published in this paper).

env., Nagyvaskapu, 47°22’12.36”N, 18°25’45.3”E, 190 m a.s.l., 27.v.2024, 1 ♀, at light (HGLI lamp + sheet) at 21.21 CEST (sunset: 20.29 CEST), after heavy rains, JHC & LPC observ., det. + photo, DJP rev.; Fejér County (Fejér vármegye), Vértes Mts, Mór env., 47°24’01.84”N, 18°15’55.08”E, 280 m a.s.l., 31.v.2023, 1 ♂, at light, CHM obs., det. + photo, DJP rev.; Fejér County (Fejér vármegye), Moha nr. Székesvehérvár, 47°13’53.96”N, 18°21’48.17”E, 113 m a.s.l., 11.vii.2023, 1 ♂, at light, ISS & CHM obs., det. + photo, DJP rev.

Central Hungary (Közép-Magyarország), Budapest, Budapest–Széchényihegy, Virágos rét, 47°29’21.86”N, 18°58’45.03”E, 430 m a.s.l., 20.v.2022, 1 ♂, at light, NVB & ASB obs., det. + photo, DJP rev.; 47°29’20.82”N, 18°58’44.78”E, 425 m a.s.l., 21.v.2023, 1 ♂, at light, NVB & ASB obs., det. + photo, DJP rev.; Pest County (Pest vármegye), Kerepes env., Kálvária hill, 47°33’34.17”N, 19°17’37.94”E, 258 m a.s.l., 31.v.2023, 1 ♂ and 1 ♀, 1.vi.2023, 1 ♂, at light, BPK & ASB obs., det. + photo, DJP rev.; 47°33’56.65”N, 19°18’35.71”E, 295 m a.s.l., 1 ♂, at light, BPK obs., det. + photo, DJP rev.; Pest County (Pest vármegye), Monor env., 47°19’10.5”N, 19°27’00.3”E, 132 m a.s.l., Septemper 2019, 1 spec. FSLG after sunset, BMB obs. + det.; the same locality and GPS, 5.vii.2020, 1 ♂ crawling on the ground at 19.45 CEST, and 4 spec. at light (160 W mercury vapour lamp), BDM, BMB & GSE obs., det. + photo, DJP rev.; Pest County (Pest vármegye), Monor env., 47°20’13.9”N, 19°24’23.3”E, 128 m a.s.l., 3.vi.2021, 1 ♀ FSLG at 17.30 (!) CEST, BDM obs., det. + photo, DJP rev.; Pest County (Pest vármegye), Monor env., 47°19’17.3”N, 19°27’20.3”E, 132 m a.s.l., 9./10.vi.2021, 1 ♀, at light at 0.25 CEST, BDM, BMB & BTB obs., det. + photo, DJP rev.; Pest County (Pest vármegye), Pilis env., 25.v.2023, 1 ♀, anonymus obs. + photo, VSI det., DJP rev.

Southern Great Plain (Dél-Alföld), Bács-Kiskun County (Bács-Kiskun vármegye), Kunpeszér env., Forest of Peszér (Peszéri-erdő), 47°05’36.69”N, 19°19’05.59”E, 100 m a.s.l., 6.vi.2024, 5 spec. FSLG at 20.50–21.20 CEST, GRS obs., det. + photo, DJP rev.

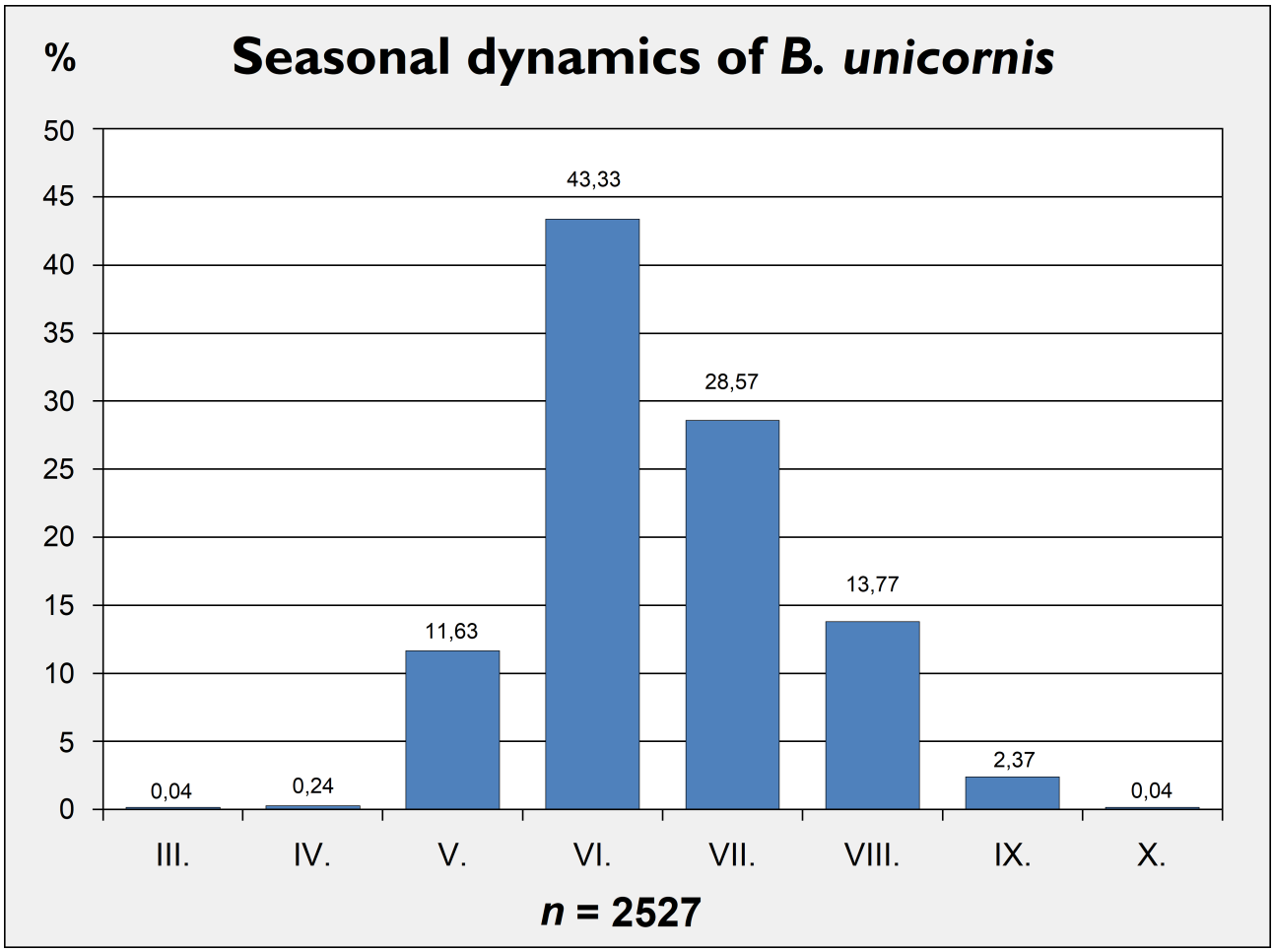

Figure 11. Seasonal dynamics of *Bolbelasmus unicornis* (the number of specimens from each country included in these statistics: Slovakia—1520; Hungary—385; Romania—200; Ukraine—180; Serbia—92; Austria—68; Croatia—51; Czech Republic—31).

Northern Hungary (Észak-Magyarország), Nógrád County (Nógrád vármegye), Buják env., Zsellérföldek, 47°54’08.22”N, 19°33’33.14”E, 290 m a.s.l., 16.vi.2023, 1 ♀ FSLG after sunset, KHE obs.; Borsod-Abaúj-Zemplén County (Borsod-Abaúj-Zemplén vármegye), Tard, Mártírok útja, 47°52’27”N, 20°35’49.66”E, 154 m a.s.l., 29.viii.2023, 1 ♀, at light (wall lamp of a residential house) at ca. 21.00 CEST (sunset: 19.27 CEST), AKT obs.

Remarks. Hungary is the country with the highest number of sites where the species was recorded (see Table 1). Most of the sites are located in the western half of the country and in the wider surroundings of Budapest. The species has so far been recorded in all counties except Jász-Nagykun-Szolnok County (Juřena 2022), where there is a lack of habitats suitable for *B. unicornis*. For the distribution of the species in Hungary see Fig. 5.

Ukraine

Kyiv Oblast (Київська область), Obukhiv Raion (Обухівський район), area between Rzhyshchiv (Ржищів) and Balyko-Shchuchynka (Балико-Щучинка), close to the Landscape Reserve of National Importance “Rzhyshchiv” (Ландшафтний заказник загальнодержавного значення «Ржищівський»), 49°58’01.68”N, 31°06’39.28”E, 168 m a.s.l., 10.vii.–5.viii.2023, 2 ♂♂, 3 ♀♀, pitfall traps, RNK leg., det. et coll.; Obukhiv Raion (Обухівський район), area between Rzhyshchiv (Ржищів) and Balyko-Shchuchynka (Балико-Щучинка), close to the Landscape Reserve of National Importance “Rzhyshchiv” (Ландшафтний заказник загальнодержавного значення «Ржищівський»), 49°57’47.24”N, 31°06’59.07”E, 160 m a.s.l., 5.viii.2023, 1 ♂, edge of the black locust (*Robinia pseudoacacia*) grove, pitfall trap, RNK leg., det. et coll.; the same locality, 49°57’34.06”N, 31°07’24.46”E, ca. 150 m a.s.l., 20.vi.–13.vii.2024, 1 ♀, Barber pitfall trap, RNK leg., det. et coll.

Sumy Oblast (Сумська область), Sumy Raion (Сумський район), Lutsykivka (Луциківка), 50°51’54.91”N, 34°22’13.26”E, 145 m a.s.l., v.2019, 1 ♂ FSLG after sunset, ABZ leg., coll. DJP.

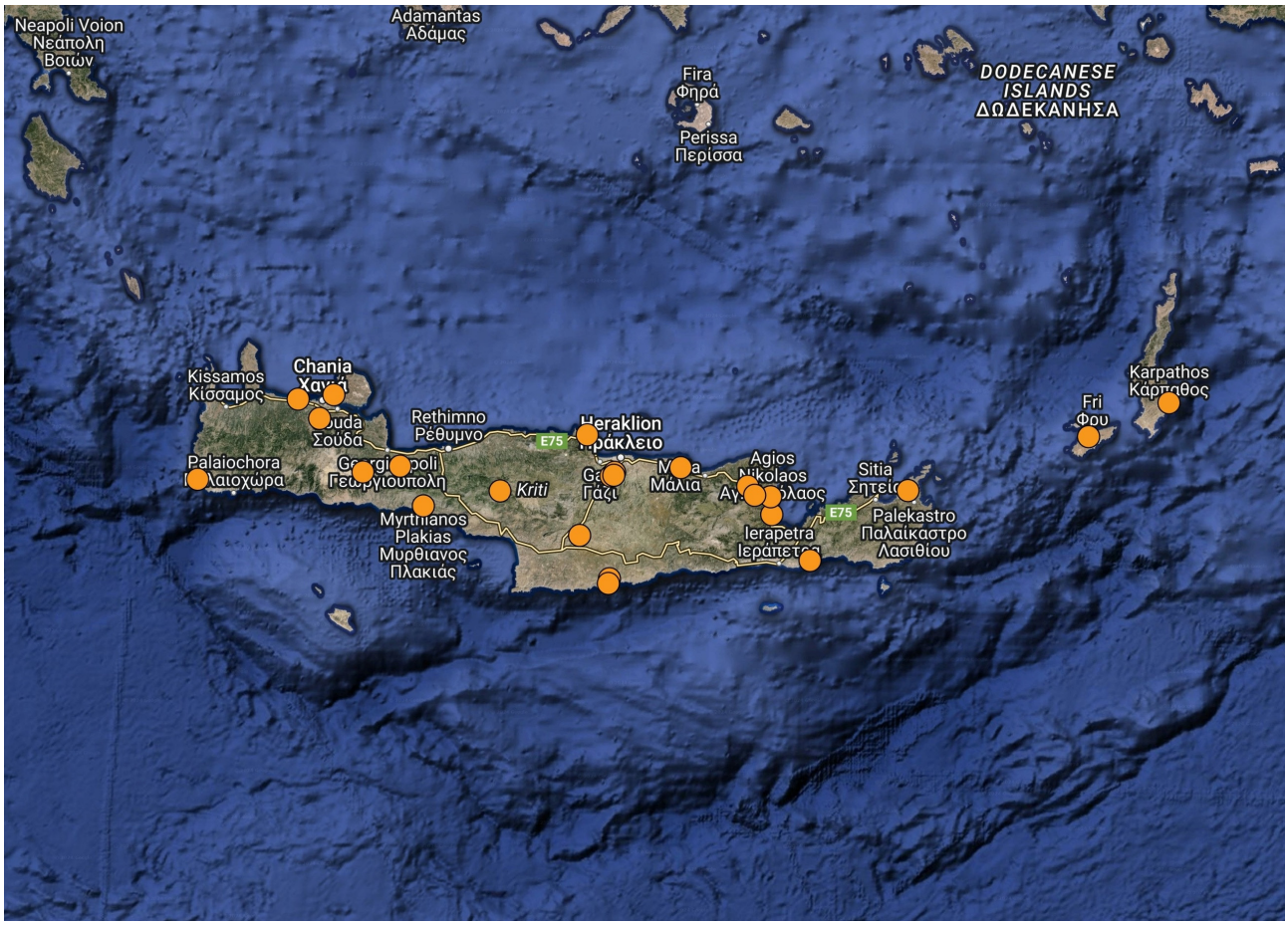

Figure 12. Distribution of *Bolbelasmus keithi*.

Dnipropetrovsk Oblast (Дніпропетровська область), Kamianske Raion (Кам'янський район), Bratske (Братське) env., Vyshnevskyi Nature Reserve (Вишневський заказник) env., 48°30'47.40"N, 34°21'08.24"E, 112 m a.s.l., 22.vii.2023, 1 ♀ FSLG at ca. 18.00 EEST (= 94 minutes before sunset!), SKD obs. + photo, DJP det.

Remarks. There are many well-preserved steppe and forest-steppe habitats suitable for *B. unicornis* throughout Ukraine but in most of them the species is still to be discovered. It is very likely that *B. unicornis* is widely distributed in the country and relatively abundant in many localities. So far it has been reliably recorded in 13 of the 25 oblasts: Cherkasy, Chernihiv, Chernivtsi, Dnipropetrovsk, Ivano-Frankivsk, Kirovohrad, Kyiv, Odessa, Poltava, Sumy, Ternopil, Vinnytsia, and Zakarpattia (Juřena 2022, 2023). Martynov (2012) also listed Volyn Oblast, but this is most likely an error based on a misinterpreted historical record from Kremenets [now in Ternopil Oblast] (Eichwald 1830), that was later cited by Hochhuth (1873) as only "Volhynien" [= Volhynian Governorate, 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]. Most of the records from the last approximately 20 years come from the Tunelna Balka tract in the city of Dnipro, an area originally of steppe character that was systematically planted with deciduous trees during the USSR era to make the slopes resistant to erosion. The species thrives very well here in the sparse forest with small clearings, dominated by oak (*Quercus* sp.), wych elm (*Ulmus glabra*), apricot (*Prunus armeniaca*), Tatarian, ash-leaved and sycamore maples (*Acer tataricum*, *A. negundo*, *A. pseudoplatanus*), black locust (*Robinia pseudoacacia*), mulberry (*Morus* sp.), European ash (*Fraxinus excelsior*), black elder (*Sambucus nigra*), and tree of heaven (*Ailanthus altissima*) (for occurrence data and photographs of the site see Juřena 2022, 2023).

Table 1. Number of known localities with *Bolbelasmus unicornis* in each country (**loc** = number of localities; **locr** = number of localities with recent occurrence, i.e., 2000–present; a cross indicates country where we consider the species to be extinct).

#	Country	loc	locr
1.	Hungary	147	89
2.	Slovakia	61	28
3.	Ukraine	46	21
4.	Romania	44	22
5.	Austria	34	11
6.	Croatia	18	14
7.	Serbia	13	9
8.	Italy	12	3
9.	Bulgaria	11	2
10.	† Czech Republic	9	1
11.	† Poland	7	1
12.	† France	6	0
13.	Germany	6	1
14.	Moldova	5	0
15.	Slovenia	4	0
16.	Bosnia and Herzegovina	4	0
17.	Turkey	3	0
18.	Albania	2	0
19.	† Switzerland	2	0
20.	Belarus	1	0
	total	**435**	**202**

Figure 13. Distribution of *Bolbelasmus nireus*.

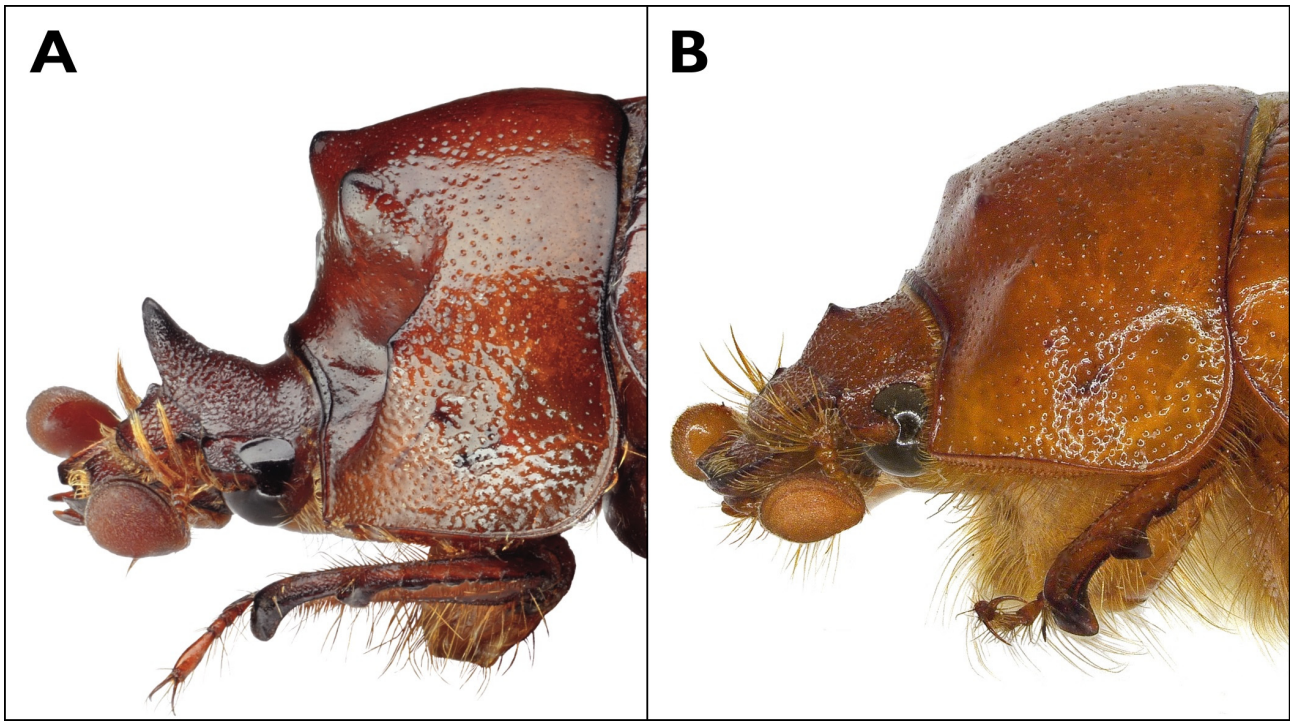

Figure 14. Examples of morphological variability in *Bolbelasmus unicornis*. **A,** typically developed male from Slovakia, Bratislava, Kopáč Island (body length 13.5 mm; photograph by Peter Kurina); **B,** poorly developed male from Austria, Hörgas near Gratwein-Straßengel, deposited in UMJG (body length 10.6 mm; photograph by Johanna Gunczy, edited by Peter Kurina).

Romania

Banat, Mehedinți County (Județul Mehedinți), Eșelnița env., Mala River Valley, 44°42'01.20"N, 22°20'19.03"E, 140 m a.s.l., 1.vi.2023, more than 10 spec. FSLG after sunset, CMI & IIS obs.

Transylvania (Transilvania), Harghita County (Județul Harghita), Porumbenii Mari env., 46°18'02.16"N, 25°07'33.24"E, 715 m a.s.l., 29.v.2018, 1 ♀ FSLG at the edge of a beech forest at ca. 19.00 CEST (= ca. 120 minutes before sunset!), CMI obs.; Harghita County (Județul Harghita); Gurghiu Mts (Munții Gurghiului), Sub Cetate / Zetevăralja, 46°27'01.17"N, 25°23'50.16"E, 590 m a.s.l., 9.vii.2021, 1 ♀ found at 22.15 EEST on the ground close to the house entrance (probably attracted to the light), IIS obs., det. + photo, DJP rev.

Western Moldavia (Moldova Occidentală), Iași County (Județul Iași), Iași–Valea Lupului, Valea lui David nature reserve, 47°11'32.28"N, 27°28'04.44"E, 75 m a.s.l., 10.vii.2021, more than 30 spec. FSLG after sunset, CMI obs.; Iași County (Județul Iași), Stânca near Comarna, 47°04'19.56"N, 27°47'51.72"E, 90 m a.s.l., 1 ♂, at light, CMI obs.

Dobruja (Dobrogea), Constanța County (Județul Constanța), Băneasa–Canaraua Fetii, 44°03'12.6"N, 27°39'12.6"E, 40 m a.s.l., 25.v.2021, 3 ♂♂ FSLG after sunset at the edge of a forest, CMI obs.; Constanța County (Județul Constanța), Negureni, 44°05'19.32"N, 27°45'02.16"E, 70 m a.s.l., 23.vi.2023, 1 ♂ FSLG after sunset, AVC obs.; Tulcea County (Județul Tulcea), Greci env., 45°13'12.72"N, 28°14'26.16"E, 140 m a.s.l., 24.vi.2021, 1 ♀, light trap, anonymus obs.; Tulcea County (Județul Tulcea), General Praporgescu env., 45°00'53.64"N, 28°23'48.48"E, 180 m a.s.l., 29.vi.2021, more than 50 spec. FSLG after sunset (although three UV traps and one illuminated canvas were installed on an area of ca. 1 ha, the beetles were not interested in these light sources), CMI obs.; Tulcea County (Județul Tulcea), Camena env., 44°48'26.28"N, 28°34'55.92"E, 135 m a.s.l., 28.vi.2020, 1 ♂, found on the ground at the edge of a forest, anonymus obs. + photo, CMI det.; Tulcea County (Județul Tulcea), Babadag Forest (Pădurea Babadag), Codru Monastery (Mănăstirea Codru) env., 44°49'04.44"N, 28°41'21.12"E, 130 m a.s.l., 22.v.2021, 1 ♀, light trap, CMI obs.; 44°48'54.72"N, 28°41'40.92"E, 105 m a.s.l., 17.vi.2021, ca. 10 spec. FSLG after sunset in light rain (just before heavy rain), IIS obs.

Remarks. There are many suitable, well-preserved sites in the Romanian lowlands and hills where the species has not yet been discovered. It is very likely that *B. unicornis* is widely distributed in the country (except in the high altitudes of the Carpathians). As the above records show, the species has substantial populations at some localities in Romania.

***Bolbelasmus keithi* Miessen & Trichas, 2011**

Greece, Crete (Κρήτη): Chania Regional Unit (Περιφερειακή ενότητα Χανίων), Agia Marina (Αγία Μαρίνα), 17.–30.v.2007, 1 ♀, JBK leg., DJP det., ex original coll. DJP, currently in coll. MMP; Chania Regional Unit (Περιφερειακή ενότητα Χανίων), Krio Nero (Κρύο Νερό) env., 35°27'30.96"N, 24°00'24.12"E, 166 m a.s.l., 1.iv.2023, 1 ♂ and 1 ♀, CMI leg., det. et coll.; Chania Regional Unit (Περιφερειακή ενότητα Χανίων), NE of Chania (Χανιά), Flora & Fauna Preservation Park (Πάρκο Διάσωσης Χλωρίδας και Πανίδας), 115–135 m a.s.l., 29.iii.2014, 1 ♀, FSC observ., det. + photo., DJP rev.; Rhetymno Regional Unit (Περιφερειακή ενότητα Ρεθύμνου), [NW of] Platanias (Πλατανιάς), ca. 450 m a.s.l., 22.–23.V.2004, 1 ♂ sitting on a rutted farm trail on the slope of an olive grove just before sunset, RSV leg., coll. PKS; Heraklion Regional Unit (Περιφερειακή ενότητα Ηρακλείου), Agia Pelagia (Αγία Πελαγία), iv.1993, 1 ♀ floating in the swimming pool, MSL leg., coll. RMNH; Heraklion Regional Unit (Περιφερειακή ενότητα Ηρακλείου), Kato Moulia (Κάτω Μούλια) env., 5.6 km NE of Gortyna (Γόρτυνα), 35°05'55.03"N, 24°59'19.55"E, 450 m a.s.l., 5.iii.2015, 1 ♀, OBL leg., coll. GML; Heraklion Regional Unit (Περιφερειακή ενότητα Ηρακλείου), 7 km N of Gortyna (Γόρτυνα), 5.iii.2015, 1 ♂ and 1 ♀, OBL leg., det. + coll.; Heraklion Regional Unit (Περιφερειακή ενότητα Ηρακλείου), Finikia (Φοινικιά) env., 6.iii.2015, 2 ♂♂, OBL leg., det. + coll.; Heraklion Regional Unit (Περιφερειακή ενότητα Ηρακλείου), S of Heraklion / Irákleio (Ηράκλειο), Lofoupoli (Λοφούπολη), 2.iii.2015, 2 ♀♀, OBL leg., coll. GML; Heraklion Regional Unit (Περιφερειακή ενότητα Ηρακλείου), Chersónisos / Hersonissos (Χερσόνησος), 10.iv.1981, 1 ♀, at light, BBF leg., coll. GML; Heraklion Regional Unit (Περιφερειακή ενότητα Ηρακλείου), Chersónisos / Hersonissos (Χερσόνησος) env., 3.iii.2015, 1 ♀, OBL leg., det. + coll.; Lasithi Regional Unit (Περιφερειακή ενότητα Λασιθίου), Nikithianos (Νικηθιανός) nr. Neapoli (Νεάπολη), 2.iv.1984, 1 spec., at light, HPV leg. et coll.; Lasithi Regional Unit (Περιφερειακή ενότητα Λασιθίου), ca. 3 km S of Agios Nikolaos (Άγιος Νικόλαος), Ammoudara (Αμμουδάρα), 14.iii.2005, 3 spec. dead in the swimming pool, HPV leg. et coll. (for incomplete data on this record see Paulus 2023); Lasithi Regional Unit (Περιφερειακή ενότητα Λασιθίου), Ferma (Φέρμα), 35°01'15.1"N, 25°51'25.5"E, 40 m a.s.l., 16.xii.2014, 1 ♂, SDC observ., det. + photo, DJP rev.

Published records: Heyden (1884; as *B. unicornis*); Oertzen (1886; as *B. unicornis*); Savchenko (1938; as *B. unicornis*); Horion (1958; as *B. unicornis*); Mikšić (1959, 1982; as *B. unicornis*); Neculiseanu *et al.* (2002; as *B. unicornis*); Trnka (2009a; as *B. unicornis*); Vasko (2009; as *B. unicornis*); Miessen & Trichas (2011; original description); Vasko & Bryhadyrenko (2011; as *B. unicornis*); Carpaneto *et al.* (2016); Hillert *et al.* (2016); Nikolajev *et al.* (2016); Dostal (2019); Glerean & Stefani (2020); Dostal *et al.* (2021b); Sommer *et al.* (2021a); Moctezuma *et al.* (2023); Paulus (2023).

Remarks. *Bolbelasmus keithi* was separated from *B. unicornis* by Miessen & Trichas (2011) and until recently was known only from the Greek islands of Crete and Kasos. Paulus (2023) newly reported it from the island of Karpathos: Pigadia / Karpathos (Πηγάδια / Κάρπαθος), 8.iv.1963, 1 spec., JMM leg., coll. HPV. If little is known about the natural history of *B. unicornis*, this applies even more so to *B. keithi*. Adults are found in the wild from December to March at low elevation sites, and from April to May at higher elevations (800–900 m a.s.l.) (Miessen 2011). In all characters, the species is very similar to *B. nireus*, *B. makrisi*, and *B. zagrosensis*, but the question of their species statuses is subject to differing opinions (these species may also be regarded as isolated populations of *B. nireus* with slight morphological differences corresponding to the considerable phenotypic plasticity known in all representatives of the genus *Bolbelasmus*—see e.g., Juřena (2022: Figs 1–3) and Fig. 15 in this addendum). The hypothesis that these are distinct species could be supported, for example, by genetic analysis, but this has not yet been carried out. The concept of the species category and its delimitation has been discussed in detail recently (e.g., Mallet *et al.* 2016, 2024; Aldhebiani 2018). For the distribution of *B. keithi* see Figs 12, 15.

***Bolbelasmus nireus* (Reitter, 1895)**

? = *B. tauricus* Petrovitz, 1973 [see remarks below]

Greece, South Aegean Region (Περιφέρεια Νοτίου Αιγαίου): island of Rhodes (Ρόδος), Ialysos (Ιαλυσός), 28.iii.2017, 1 ♂, RDK leg., OBL det. et coll.; island of Rhodes (Ρόδος), N of Sgourou (Σγουρού), ca. 36°25'02"N, 28°12'43.5"E, ca. 80 m a.s.l., 10.iii.2019, 1 ♀, at light at 21.35 EET, KKR observ., det. + photo, DJP rev.; island of Rhodes (Ρόδος), Koskinou (Κοσκινού), 2.iv.2009, 1 ♀, KKR observ., det. + photo, DJP rev.; Koskinou (Κοσκινού) env., island of Rhodes (Ρόδος), Kallithea (Καλλιθέα), ca. 36°22'48.43"N, 28°14'06.83"E, 30–100 m a.s.l., 15.xii.2021, 1 ♀, at light at 21.58 EET, KKR observ., det. + photo, DJP rev.

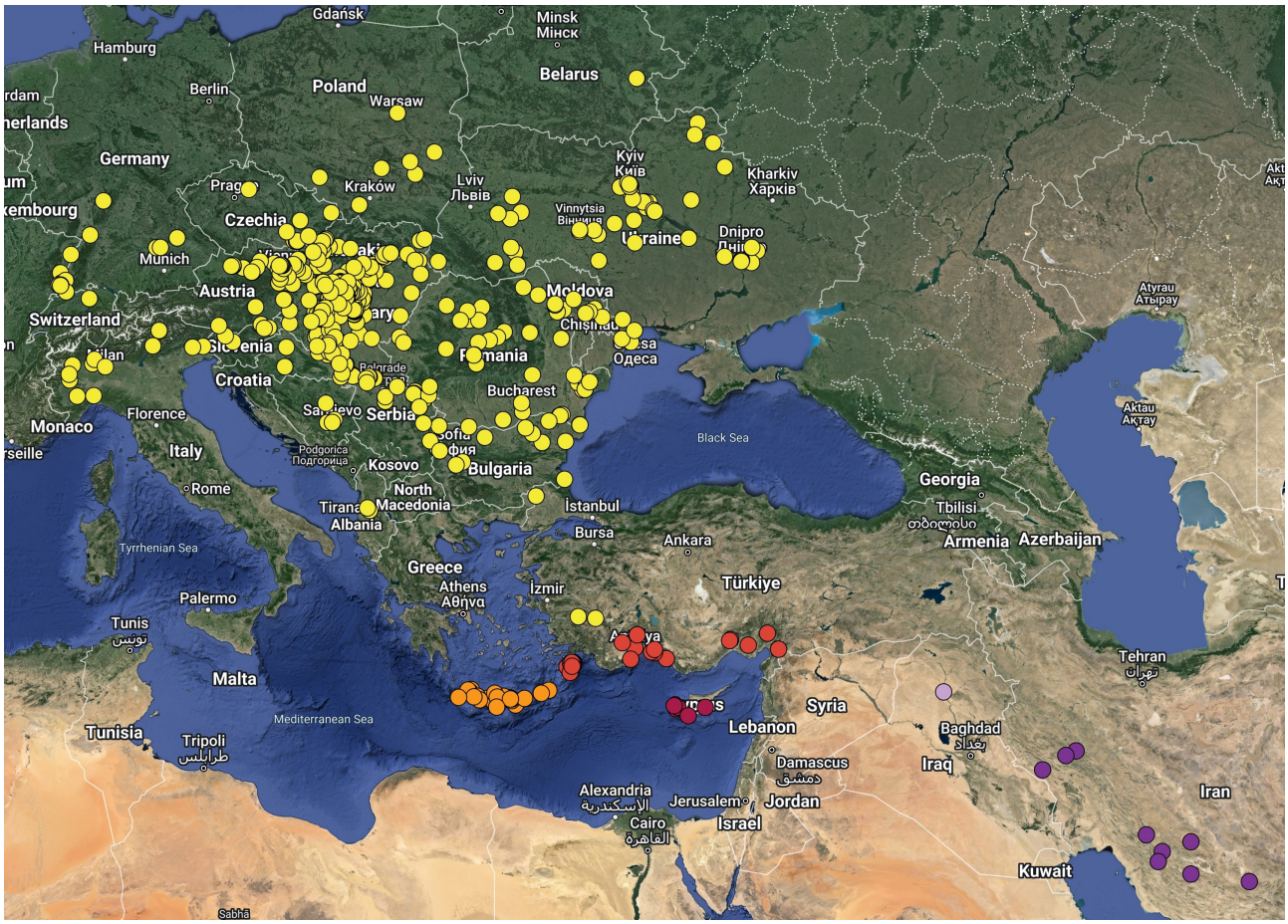

Figure 15. Distribution of *Bolbelasmus unicornis* and East Mediterranean species of the genus *Bolbelasmus* (yelow circles = *B. unicornis*; orange circles = *B. keithi*; pale red circles = *B. nireus*; dark red circles = *B. makrisi*; purple circles = *B. zagrosensis*; lilac circle = record of a female tentatively assigned to *B. nireus* by Krikken (1977) and Miessen (2011), but in need of revision).

Turkey, Mediterranean Region (Akdeniz Bölgesi): Antalya Province (Antalya İli), Antalya, iv.2002, 1 ♀, Th. de Jong leg., coll. RMNH; NE of Manavgat, 6.iii.2013, 1 ♀, and 19.iv.2015, 1 ♂, MSC leg. + coll., DJP det.; Antalya Province (Antalya İli), Alanya, 7.v.[19]65, 1 ♀ [in the hotel swimming pool], [CWV &] FWV leg., coll. NHMW, DJP det. (data specified by GWV pers. comm, 2023).

Published records: Reitter (1895; original description); Kolbe (1896); Boucomont (1912); Winkler (1929); Schatzmayr (1936; as *B. unicornis*); Paulian (1941; as *B. unicornis*); Tesař (1957; as *B. unicornis*); Paulian (1959; as *B. unicornis*); Mikšić (1959; as *B. unicornis*); Petrovitz (1959; as *B. unicornis*); Benasso (1971; as *B. unicornis*); Benasso & Stroiazzo (1973; as *B. unicornis*); Petrovitz (1973; misidentified as *B. tauricus*—see remarks below); Krikken (1977); Paulian & Baraud (1982; as *B. unicornis*); Lodos *et al.* (1999; as *B. unicornis*); Carpaneto *et al.* (2000); Nikolajev (2003b); Keith (2005); Král *et al.* (2006); Petersen *et al.* (2006; as *B. unicornis*); Carpaneto *et al.* (2016; as *B. keithi*); Hillert *et al.* (2016; part of records as *B. keithi*); Nikolajev *et al.* (2016); Glerean & Stefani (2020; as *B. keithi*); Sommer *et al.* (2021a); Moctezuma *et al.* (2023); Paulus (2023).

Remarks. The species was described from "Akbes" [= Akbez, Hassa district, Hatay Province of Turkey], where the famous Trappist monastery of Cheiklé (Notre-Dame du Sacré Cœur d'Akbès) was located and where Saint Charles de Foucauld resided in the 1890s. This was a territory that belonged to Upper Syria (Haute Syrie) at the time, which is why *B. nireus* is still erroneously listed for this country (e.g., Král *et al.* 2006; Nikolajev *et al.* 2016; Moctezuma *et al.* 2023) although no other records from present-day Syria are known. Sommer *et al.* (2021a) misinterpreted the type locality Akbes as "Maydân Akbis" [= Maydān Akbis / Maydan Ikbis / Meidan Ekbis / Midan Akbas] located nearby in the Aleppo Governorate of Syria near the border with Turkey. The species is also known from Rhodes and other provinces of southern Turkey (Antalya, Burdur, Mersin, Adana, and Osmaniye). Examination of the holotype and two paratypes of *B. tauricus* by Miessen (2011) revealed that at least both paratypes belong to *B. nireus*. Although the holotype of *B. tauricus* with the locality "Namrun" [= Namrun Castle, Çamlıyayla, Mersin Province of Turkey] showed morphological differences from *B. nireus*, it seems likely that it is also *B. nireus* in this case, given the considerable

morphological variability known in all congeners (see remarks for *B. keithi* above), since it is from the same locality as one of the two paratypes that proved to be *B. nireus*. Furthermore, there are several records of the latter species in the area. Krikken (1977), Arnone & Massa (2010), and Miessen (2011) reported the record of a female of *B. nireus* from Assur [also Aššur, Ashur, or Qal'at Sherqat], Iraq, but according to current biogeographical knowledge it could belong to *B. zagrosensis*, recently described from Iran by Sommer *et al.* (2021a). *Bolbelasmus nireus* was recently reported from two new localities in Rhodes by Paulus (2023): Prophitis Ilias (Προφήτης Ηλίας), 30.iii.1999, 1 spec., under a rock, HPV leg. et coll.; Koskinou (Κοσκινού), 30.iii.1987, 1 spec., at light, HPV leg. et coll. As in the case of *B. keithi*, individuals of *B. nireus* have been collected from December to June presumably depending on elevation (Hillert *et al.* 2016; Sommer *et al.* 2021a; data above). For the distribution of *B. nireus* see Figs 13 and 15.

Natural history, ecology, threats, and monitoring of *B. unicornis*

Bolbelasmus unicornis is a stenotopic species associated with steppe and forest-steppe habitats with natural vegetation cover in lowlands and lower hills and the average altitude of all known sites is 220 m a.s.l. (Juřena 2022). Its essential requirement is the absence of chemical pollution, and soil undisturbed by agricultural or building activities. The threat to the species lies mainly in the loss of suitable habitats through the conversion of sites to farmland and building plots. Another threatening factor is the overgrowth of sites with non-native invasive plant species, such as *Ailanthus altissima*, *Amorpha fruticosa*, and *Robinia pseudoacacia* (e.g., Chobot & Mourek 2007, 2008; Juřena 2022). Similarly, inappropriate conservation management can have a significant negative effect on *B. unicornis* populations. This includes, for example, excessive removal of native shrubs and trees from the sites or intensive grazing of livestock such as sheep (e.g., Németh 2015; Majzlan 2020a; Juřena 2022). The consequence of this inappropriate management is drying and hardening of the soil in which *B. unicornis* adults spend most of their time. Dry and hard soil is difficult for beetles to burrow in, and, in addition, hypogeous fungi, which are probably the food for adults, do not thrive in it. Given the probably very low population dynamics and female fecundity, it cannot be ruled out that, in isolated small localities, the intensive collecting individuals for the purpose of obtaining material for entomological collections or for sale may have a significant negative effect on populations of the species. Finally, the isolation of populations represents a potential threat from internal causes (Hejda 2024).

The body length of adults varies between 9.5–14.5 mm (Juřena 2022), but is typically 12.0–14.0 mm. In the wild they are usually encountered from May to September, in the southernmost parts of the range exceptionally as early as March and as late as October (see Fig. 11 for a graph of seasonal dynamics). The method for monitoring the species is very simple and is based on capturing adults during their evening flights, which start on average 35 minutes after sunset and terminate on average 60 minutes after sunset (Čepelák 1925; Juřena 2022). Only a net and a head lamp are needed to catch them. The beetles usually fly very slowly low above the ground (typically within 0.5 m above the terrain), and only after heavy rains when the soil is moist to a depth of at least 30 cm. Flying individuals are well visible in the light of a torch and are not difficult to catch with a net. The wings of the flying beetle produce a sound similar to that of the European hornet or bumblebee (Čepelák 1925; Roubal 1936; Juřena 2022; Theves & Bittner 2022), but typically weaker, sometimes the beetles even fly almost silently (Juřena 2022). Most flights have been observed in no wind or a gentle breeze with temperatures ranging from 10 to 27°C, but the optimum range has been found to be 18–24°C. Concentrations of flying individuals can vary considerably from place to place. Most flying beetles can usually be observed above trails with ruts made by agricultural machinery or above paths trodden by humans or animals (Juřena 2022). Adults of *B. unicornis* very often fly together with adults of *Odonteus armiger* (Scopoli, 1772), *Ochodaeus chrysomeloides* (Schrank, 1781), and/or *O. integriceps* Semenov, 1891 (e.g., Ghiliani 1847, 1887; Juřena *et al.* 2008; Trnka 2009b, Juřena 2022, 2023; Theves & Bittner 2022), but unlike the listed species, they are very reluctantly attracted to light sources, making light trapping completely ineffective in *B. unicornis* (the vast majority of flying individuals do not notice light sources or even show light aversion). During the day, the beetles can be dug out from their burrows, which are noticeable due to small piles of excavated soil, known as push-ups (Fig. 2F). However, these push-ups are often screened from view because sites where the species occurs are usually grassy, with dense vegetation cover. Push-ups are only clearly visible in places with exposed soil surface (Fig. 2F). Most individuals have been excavated from depths of up to 30 cm (Juřena *et al.* 2008; Juřena 2022). Occasionally, two or three specimens have been found in a single burrow, including pairs as well as individuals of the same sex (Juřena *et al.* 2008; Juřena 2022). In several cases, individuals of *Odontaeus armiger*, *Ochodaeus chrysomeloides*, and *O. integriceps* have been found in burrows together with *B. unicornis*, in almost all combinations (Juřena *et al.* 2008; Juřena 2022).

Table 2. Overview of known immature stages of bolboceratines (addition to the chapter Natural history of Bolboceratinae in Juřena 2022).

	species	immature stage(s)	author(s)
1.	***Blackbolbus frontalis*** (Guérin-Méneville, 1838)	**egg**	Houston (2011)
2.	***Blackbolbus hoplocephalus*** (Lea, 1916)	**larva, pupa**	Houston (2011)
3.	***Blackburnium reichei*** (Guérin-Méneville, 1838)	**egg, larva**	Houston (2011)
		pupa	Houston (2016)
4.	***Bolbelasmus brancoi*** Hillert & Král, 2016	**larva**	Verdú *et al.* (1998)
5.	***Bolbelasmus gallicus*** (Mulsant, 1842)	**egg**	Rahola Fabra (2004)
		larva	Verdú *et al.* (2004)
6.	***Bolbocerosoma farctum*** (Fabricius, 1775)	**larva**	Howden (1955)
7.	***Bolbocerosoma tumefactum*** (Palisot de Beauvois, 1809)	**larva**	Ritcher (1947)
8.	***Bolboleaus hiaticollis*** Howden, 1985	**egg**, **larva, pupa**	Houston (2016)
9.	***Bolborhachium anneae*** Howden, 1985	**egg**	Howden *et al.* (2007)
		larva	Howden (1985)
10.	***Bolborhachium inclinatum*** Howden, 1985	**egg**	Houston (2011)
		larva	Houston (2016)
11.	***Bolborhachium recticorne*** (Guérin-Méneville, 1838)	**egg, pupa**	Houston (2016)
		larva	Howden (1985), Houston (2016)
12.	***Bolborhachium trituberculatum*** (Bainbridge, 1842)	**egg, larva**	Houston (2011)
13.	***Eubolbitus radoszkowskii*** (Solsky, 1876)	**larva**	Nikolajev (2003a)
14.	***Eucanthus lazarus*** (Fabricius, 1775)	**larva**	Ritcher (1947)
15.	***Eucanthus subtropicus*** Howden, 1955	**larva**	Howden (1955)
16.	***Odonteus armiger*** (Scopoli, 1772)	**egg**	Arens (1922)
		larva	Medvedev (1952)
17.	***Odonteus darlingtoni*** (Wallis, 1928)	**egg, larva, pupa**	Howden (1955)
18.	***Odonteus liebecki*** (Wallis, 1928)	**larva**	Howden (1955)
19.	***Odonteus obesus*** LeConte, 1859	**larva**	Howden (1964), Ritcher (1966)
20.	***Odonteus simi*** (Wallis, 1928)	**larva**	Ritcher (1947)

Nothing is known about the diet of adults and larvae of *B. unicornis*. It is assumed that adults feed on hypogeous fungi (sporocarps, spores, and hyphae), while larvae could ingest fine soil humus, soil bacteria or perhaps do not ingest solid food at all (Juřena 2022). Immature stages are not known in *B. unicornis*. They have been described so far only in 20 species belonging to the subfamily Bolboceratinae (Table 2). The eggs of bolboceratines are extremely large compared to the size of the adults (Arens 1922; Howden 1955; Rahola Fabra 2004; Howden *et al.* 2007; Houston 2011, 2016) and are among the largest eggs known in insects (Church *et al.* 2019; Donoughe 2021). All described larvae of bolboceratines have been characterised by immobility and various degrees of degeneration, particularly vestigial appendages (e.g., simple, feeble mandibles) and a very simple form of intestine, most likely associated with reduced or even non-feeding (Houston 2011).

Adults of *B. unicornis* are capable of emitting a wide range of audible stridulatory sounds, as are representatives of most genera of the subfamily Bolboceratinae. Stridulation in *B. unicornis* was first reported by Ghiliani (1847), but the stridulatory apparatus in the genus *Bolbelasmus* was not described in detail until Arrow (1904). It is very likely that also the larvae of *B. unicornis* are capable of stridulation, as has been reported in larvae of two congeners *B. brancoi* Hillert & Král, 2016 [listed as *B. bocchus* (Erichson, 1841)] and *B. gallicus* (Mulsant, 1842) (Verdú *et al.* 1998, 2004; Rahola Fabra 2004), and in many other members of the superfamily Scarabaeoidea (e.g., Sharp 1899; Arrow 1904; Dudich 1921; Gardner 1944; Howden 1955, 1967; Edmonds & Halffter 1972, 1978; Reyes-Castillo & Jarman 1980; Monteith & Storey 1981; Palestrini & Zunino 1987; Grebennikov *et al.* 2004). The role of stridulation in bolboceratines has not yet been fully elucidated; it may be associated with inter- and intraspecific communication (e.g., Wessel 2006; Barria 2023) and deterrence of intruders or predators (e.g., Neita-Moreno *et al.* 2006; Barria *et al.*

2020, 2021). In several localities of the former Austro-Hungarian Empire (namely in present-day Slovakia, Hungary and Romania), adults of *B. unicornis* were found as a food of some birds, namely *Cuculus canorus*, *Falco vespertinus*, and *Upupa epops* (Csiki 1904, 1905, 1910; cited by subsequent authors).

Overview of references with records of *B. unicornis*

In the historical literature, *B. unicornis* was placed in various genera (*Bolboceras*, *Bolbocerus*, *Bulbocerus*, *Coprus*, *Geotrupes*, *Odontaeus*, or *Scarabaeus*), and can be found under several species names: *unicornu*(*-e*), *quadridens*, *aeneas*, *ruber*, with various authorities listed. On the problem of synonyms, see Juřena (2022).

Great Britain—erroneous reports based on misidentification by W. Skrimshire:
Skrimshire (1812), Curtis (1829 ab), Stephens (1829, 1830, 1839): Cambridgeshire, marshes between Peterborough and Wisbech. The species was subsequently recorded from England also by other authors, probably on the basis of Skrimshire's old report (e.g., Mulsant & Rey 1870, 1871ab; Sajó 1910b; Boucomont 1912; Paulian 1941; Tesař 1957; Neculiseanu *et al.* 2002; Trnka 2009a; Vasko 2009; Arnone & Massa 2010; Vasko & Bryhadyrenko 2011; Vidlička 2011).

France (90 refs):
Panzer (1802); Marseul (1857); Kampmann (1860; first localised record); Grenier (1863); Marseul (1863); Mulsant & Rey (1870, 1871ab); Marseul (1887); Acloque (1896); Barthe (1896, 1901); Döderlein (1901); Bourgeois (1904); Schilsky (1909); Sajó (1910a); Bedel (1911); Knörzer (1912); Scherdlin (1915); Huber (1916); Schaufuss (1916); Scherdlin (1920); Portevin (1931); Franz (1936); Sainte-Claire Deville (1936); Borchert (1938); Paulian (1941); Horion (1951); Tesař (1957); Horion (1958); Paulian (1959); Allenspach (1970); Benasso (1971); Benasso & Stroiazzo (1973); Franz (1974); Stebnicka (1976); Baraud (1977); Krikken (1977); Paulian & Baraud (1982); Burakowski *et al.* (1983); Koch (1989); Lumaret (1990); Gangloff (1991); Baraud (1992); Krell (1998); Drovenik & Pirnat (2003); Peslier (2004); Szwałko (2004); Zandigiacomo (2005); Agoglitta *et al.* (2006); Král (2006); Král *et al.* (2006); Petersen *et al.* (2006); Chobot & Mourek (2007, 2008); Paill (2008); Paracchini *et al.* (2008); Ruicănescu & Nițu (2008); Trnka (2009a); Arnone (2010); Arnone & Massa (2010); Brelih *et al.* (2010); Vasko (2010); Vidlička (2011); Brustel & Gouix (2012); Bunalski *et al.* (2013); Gutowski & Przewoźny (2013); Merkl (2014); Merkl *et al.* (2014); Montreuil (2014); Merkl (2015); Potocký & Majzlan (2015a); Hillert *et al.* (2016); Nikolajev *et al.* (2016); Cosandey *et al.* (2017); Koren (2017); Callot (2018); Ćurčić *et al.* (2019); Rabl *et al.* (2019); Schoolmeesters (2019); Glerean & Stefani (2020); Vasko (2020); Sommer *et al.* (2021a); Juřena (2022); Theves & Bittner (2022); Bittner & Theves (2023); Byk *et al.* (2023); Juřena (2023); Nuß & Jäger (2023); Hejda (2024); Matern (2024).

Erroneous reports obviously based on misidentification / confusion of the locality: Houlbert & Monnot (1910): "Armorique" [= Armorica, a region of Gaul between the Seine and Loire rivers that included the Brittany Peninsula]; Brustel & Gouix (2012): Savoie, Albertville.

Germany (114 refs):
Panzer (1793a, 1795); Schrank (1798; first localised record); Panzer (1802); Klug (1845); Oechsner (1854); Gerstaecker (1863); Jacquelin du Val (1863); Marseul (1863); Kraatz (1869); Mulsant & Rey (1870, 1871ab); Kittel (1879); Marseul (1887); Schilsky (1888); Acloque (1896); Fröhlich (1897); Schilsky (1909); Reitter (1909); Sajó (1910a); Boucomont (1912); Knörzer (1912); Kuhnt (1912); Huber (1916); Schaufuss (1916); Lucas (1918); Horion (1935); Ihssen (1935); Franz (1936); Schatzmayr (1936); Kuntze & Noskiewicz (1938); Savchenko (1938); Paulian (1941); Horion (1951, 1957); Panin (1957); Horion (1958); Paulian (1959); Machatschke (1969); Allenspach (1970); Benasso (1971); Franz (1974); Krikken (1977); Paulian & Baraud (1982); Burakowski *et al.* (1983); Geiser (1984); Koch (1989); Lumaret (1990); Baraud (1992); Brechtel *et al.* (1995); Geiser (1998); Köhler & Klausnitzer (1998); Krell (1998); Bunalski (1999); Bense *et al.* (2000); Klausnitzer (2000); Frank & Konzelmann (2002); Neculiseanu *et al.* (2002); Drovenik & Pirnat (2003); Jungwirt (2003); Balzer *et al.* (2004); Szwałko (2004); Böhme (2005); Jungwirt (2005); Klausnitzer (2005); Zandigiacomo (2005); Agoglitta *et al.* (2006); Král (2006); Král *et al.* (2006); Nádai (2006); Petersen *et al.* (2006); Chobot & Mourek (2007, 2008); Juřena *et al.* (2008); Paracchini *et al.* (2008); Trnka (2009a); Vasko (2009); Arnone (2010); Arnone & Massa (2010); Klausnitzer (2011); Vasko & Bryhadyrenko (2011); Brustel & Gouix (2012); Jungwirt (2012); Rößner (2012); Bunalski *et al.* (2013); Gutowski & Przewoźny (2013); Biel *et al.* (2014); Merkl (2014); Merkl *et al.* (2014); Merkl (2015); Potocký & Majzlan (2015a); Hillert *et al.* (2016); Nikolajev *et al.* (2016);

Cosandey *et al.* (2017); Kaděra (2017); Koren (2017); Müller-Kroehling (2017); Král *et al.* (2018); Ćurčić *et al.* (2019); Schoolmeesters (2019); Glerean & Stefani (2020); Schaffrath (2021); Juřena (2022); Theves & Bittner (2022); Bittner & Theves (2023); Byk *et al.* (2023); Juřena (2023); Nuß & Jäger (2023); Bleich *et al.* (2024); Hejda (2024); Lompe (2024); Matern (2024); Urban (2024).

Switzerland (42 refs):
Heer (1841ab; first localised record); Bremi-Wolf (1856); Marseul (1863); Stierlin & Gautard (1867); Mulsant & Rey (1870, 1871ab); Marseul (1887); Stierlin (1900); Kolbe (1905); Bedel (1911); Huber (1916); Schatzmayr (1936); Borchert (1938); Horion (1958); Allenspach (1970); Benasso (1971); Paulian & Baraud (1982); Lumaret (1990); Szwałko (2004); Zandigiacomo (2005); Král *et al.* (2006); Petersen *et al.* (2006); Chobot & Mourek (2007, 2008); Arnone (2010); Arnone & Massa (2010); Brustel & Gouix (2012); Gutowski & Przewoźny (2013); Merkl (2014); Hillert *et al.* (2016); Nikolajev *et al.* (2016); Koren (2017); Král *et al.* (2018); Cosandey *et al.* (2017); Ćurčić *et al.* (2019); Glerean & Stefani (2020); Juřena (2022); Byk *et al.* (2023); Juřena (2023); Hejda (2024).

Erroneous reports probably based on misidentification or confusion of the locality: Heer (1841ab), Stierlin & Gautard (1867), Stierlin (1900), Huber (1916), Borchert (1938): Canton of Ticino.

Italy (97 refs):
Panzer (1802); Cristofori & Jan (1832); Villa & Villa (1833, 1844); Ghiliani (1847; first localised record); Marseul (1857); Gredler (1863); Jacquelin du Val (1863); Costa (1864); Bertolini (1871, 1872, 1874, 1875); Heyden (1884); Ghiliani (1887); Baudi di Selve (1889); Bertolini (1891, 1899ab); Bedel (1911); Luigioni (1929); Porta (1932); Schatzmayr (1936); Borchert (1938); Horion (1958); Allenspach (1970); Benasso (1971); Benasso & Stroiazzo (1973); Franz (1974); Stebnicka (1976); Baraud (1977); Krikken (1977); Peez & Kahlen (1977); Paulian & Baraud (1982); Burakowski *et al.* (1983); Lumaret (1990); Pescarolo (1990); Baraud (1992); Carpaneto & Piattella (1995); Barbero & Cavallo (1999); Bunalski (1999); Carpaneto & Piattella (2003); Drovenik & Pirnat (2003); Pesarini (2004); Szwałko (2004); Zilioli & Pittino (2004); Zandigiacomo (2005); Agoglitta *et al.* (2006); Král (2006); Král *et al.* (2006); Nádai (2006); Petersen *et al.* (2006); Chobot & Mourek (2007); Ballerio (2008); Chobot & Mourek (2008); Paill (2008); Paracchini *et al.* (2008); Ruicănescu & Niţu (2008); Schwarz (2008); Pirnat (2009); Trnka (2009a); Arnone (2010); Arnone & Massa (2010); Vasko (2010); Vidlička (2011); Vrezec *et al.* (2011); Brustel & Gouix (2012); Bunalski *et al.* (2013); Gutowski & Przewoźny (2013); Lapini *et al.* (2013); Trizzino *et al.* (2013); Ballerio *et al.* (2014); Di Santo & Biscaccianti (2014); Merkl (2014); Stoch *et al.* (2014); Potocký & Majzlan (2015a); Carpaneto *et al.* (2016); Hillert *et al.* (2016); Nikolajev *et al.* (2016); Cosandey *et al.* (2017); Koren (2017); Kahlen (2018); Ćurčić *et al.* (2019); Schoolmeesters (2019); Glerean & Stefani (2020); Vasko (2020); Carpaneto *et al.* (2021); Glerean *et al.* (2021ab); Grignetti & La Morgia (2021); Sommer *et al.* (2021a); Juřena (2022); Bittner & Theves (2023); Byk *et al.* (2023); Juřena (2023); Hejda (2024); Matern (2024).

Erroneous reports very likely or certainly based on misidentification and/or confusion of the locality: Bertolini (1891, 1899b): Trentino-Alto Adige/Südtirol, Torcegno env.; Benasso (1971), Benasso & Stroiazzo (1973): Friuli-Venezia Giulia, Luint env.

Poland (55 refs):
Hildt (1896; first localised record); Tenenbaum (1923); Kuntze & Noskiewicz (1938); Horion (1958); Benasso (1971); Benasso & Stroiazzo (1973); Franz (1974); Stebnicka (1976); Krikken (1977); Kubicka (1981); Burakowski *et al.* (1983); Lumaret (1990); Baraud (1992); Kubisz *et al.* (1998); Bunalski (1999); Pawłowski *et al.* (2002); Drovenik & Pirnat (2003); Szwałko (2004); Zandigiacomo (2005); Agoglitta *et al.* (2006); Král (2006); Král *et al.* (2006); Nádai (2006); Petersen *et al.* (2006); Chobot & Mourek (2007, 2008); Juřena *et al.* (2008); Trnka (2009a); Arnone (2010); Arnone & Massa (2010); Bidas (2012); Brustel & Gouix (2012); Byk *et al.* (2012); Bunalski *et al.* (2013); Gutowski & Przewoźny (2013); Biel *et al.* (2014); Merkl (2014); Potocký & Majzlan (2015a); Byk *et al.* (2016); Hillert *et al.* (2016); Nikolajev *et al.* (2016); Kaděra (2017); Koren (2017); Gajdoš & Majzlan (2018); Ćurčić *et al.* (2019); Schoolmeesters (2019); Glerean & Stefani (2020); Sommer *et al.* (2021a); Juřena (2022); Bittner & Theves (2023); Byk *et al.* (2023); Juřena (2023); Nuß & Jäger (2023); Hejda (2024); Matern (2024).

Czech Republic (64 refs):
Schlögl (1883; first localised record); Kliment (1899); Schubert (1905); Zoufal (1922); Fleischer (1930); Tesař (1957); Horion (1958); Krikken (1977); Paulian & Baraud (1982); Král (1989); Lumaret (1990); Baraud (1992); Král (1993); Král & Vitner (1996); Bunalski (1999); Szwałko (2004); Chobot (2005); Hůrka (2005); Konvička *et al.* (2005); Král

(2005); Agoglitta *et al.* (2006); Král (2006); Král *et al.* (2006); Petersen *et al.* (2006); Chobot & Mourek (2007); Dušek *et al.* (2007); Mackovčin *et al.* (2007); Chobot & Mourek (2008); Juřena & Týr (2008); Juřena *et al.* (2008); Paracchini *et al.* (2008); Miko & Hošek (2009); Trnka (2009a); Arnone (2010); Arnone & Massa (2010); Brustel & Gouix (2012); Chobot (2013); Culek *et al.* (2013); Gutowski & Przewoźny (2013); Hejda (2013); Kaděra (2013); Merkl (2014); Potocký & Majzlan (2015a); Hillert *et al.* (2016); Nikolajev *et al.* (2016); Spružina (2016); Koren (2017); Král & Bezděk (2017); Kaděra (2017); Zahradník (2017); Král *et al.* (2018); Řehounek & Čížek (2018); Ćurčić *et al.* (2019); Hronová (2019); Schoolmeesters (2019); Glerean & Stefani (2020); Hruban (2020); Mariánková & Jurek (2021); Sommer *et al.* (2021b); Juřena (2022); Bittner & Theves (2023); Byk *et al.* (2023); Juřena (2023); Hejda (2024); Matern (2024).

Erroneous reports very likely or certainly based on misidentifications: Kral (1915): Bohemia, Kummer [= Hradčany near Mimoň]; Hudeček (1928, 1930): Moravia, Přerov; Hudeček (1937): Moravia: Bochoř near Přerov.

Austria (147 refs):
Schrank (1789; original description); Schneider (1792); Panzer (1793b, 1795); Illiger (1800); Sturm (1800); Megerle von Mühlfeld (1802, 1804); Duftschmid (1805; first localised record); Megerle von Mühlfeld (1805); Sturm (1805); Schultes (1807); Dejean (1821, 1833, 1836); Laporte de Castelnau (1840); Sturm (1843); Erichson (1847); Gistel (1848); Gaubil (1849); Redtenbacher (1849); Gistel & Bromme (1850); Laporte de Castelnau (1850); Gistel (1851); Westwood (1852); Gistel (1856); Marseul (1857); Reichenbach (1857); Calwer (1858); Redtenbacher (1858); Gutfleisch (1859); Jacquelin du Val (1863); Marseul (1863); Gemminger & Harold (1869); Redtenbacher (1872); Anonymus (1876); Rothschild (1876); Dalla Torre (1879); Heyden (1884); Jäger (1884); Marseul (1887); Schilsky (1888); Stierlin (1893); Holdhaus & Prossen (1901); Schilsky (1909); Bedel (1911); Dobiasch (1911); Boucomont (1912); Prossen (1913); Huber (1916); Schaufuss (1916); Lucas (1918); Franz (1936); Schatzmayr (1936); Kaszab (1937); Borchert (1938); Savchenko (1938); Pittioni (1943); Horion (1951); Schweiger (1951); Reisser (1954); Hoffmann *et al.* (1955); Petrovitz (1956); Panin (1957); Horion (1958); Allenspach (1970); Benasso (1971); Benasso & Stroiazzo (1973); Franz (1974); Krikken (1977); Franz (1983); Rößler (1989); Schmölzer (1989); Lumaret (1990); Baraud (1992); Jäch *et al.* (1994); Herzig (1997); Mitter (2000); Neculiseanu *et al.* (2002); Drovenik & Pirnat (2003); Szwałko (2004); Agoglitta *et al.* (2006); Král (2006); Král *et al.* (2006); Paill & Mairhuber (2006); Chobot & Mourek (2007, 2008); Juřena *et al.* (2008); Paill (2008); Paracchini *et al.* (2008); Schwarz (2008); Moitzi & Weigand (2009); Pirnat (2009); Trnka (2009a); Vasko (2009); Vrezec *et al.* (2011); Arnone (2010); Arnone & Massa (2010); Ressl & Kust (2010); Zettel & Rabitsch (2010); Link *et al.* (2011); Vasko & Bryhadyrenko (2011); Brustel & Gouix (2012); Paill & Mairhuber (2012); Frieß *et al.* (2013); Gutowski & Przewoźny (2013); Merkl (2014); Potocký & Majzlan (2015a); Hillert *et al.* (2016); Nikolajev *et al.* (2016); Spružina (2016); Suske *et al.* (2016); Koren (2017); Král *et al.* (2018); Ćurčić *et al.* (2019); Dostal (2019); Dostal & Barries (2019); Holzer (2019); Khutter & Mikocki (2019); Rabl *et al.* (2019); Schoolmeesters (2019); Denner (2020); Ellmauer *et al.* (2020); Gimpl *et al.* (2020); Glerean & Stefani (2020); Rabitsch *et al.* (2020); Dostal & Barries (2021); Dostal *et al.* (2021ab); Holzer *et al.* (2021); Ökoteam (2021); Schaffrath (2021); Suske *et al.* (2021); Denner (2022); Juřena (2022); Theves & Bittner (2022); Bittner & Theves (2023); Byk *et al.* (2023); Dostal (2023); Dostal *et al.* (2023); Juřena (2023); Schernhammer (2023abcd); Hejda (2024); Matern (2024).

Erroneous report based on confusion of the locality: Gistel (1856): "neue Welt" in "Tyroler und Salzburger Alpen".

Slovenia (22 refs):
Brancsik (1871; first localised record); Horion (1958); Drovenik & Pirnat (2003); Chobot & Mourek (2007, 2008); Jurc *et al.* (2008); Pirnat (2009); Brelih *et al.* (2010); Vrezec *et al.* (2011); Gutowski & Przewoźny (2013); Merkl (2014); Potocký & Majzlan (2015a); Hillert *et al.* (2016); Nikolajev *et al.* (2016); Ćurčić *et al.* (2019); Schoolmeesters (2019); Trilar (2019); Glerean & Stefani (2020); Juřena (2022); Byk *et al.* (2023); Juřena (2023); Hejda (2024).

Croatia (27 refs):
Schlosser Klekovski (1878; first localised records); Koča (1906; first dated record); Mikšić (1959, 1960, 1970, 1977, 1982); Král (2006); Chobot & Mourek (2007, 2008); Pirnat (2009); Vrezec *et al.* (2011); Brustel & Gouix (2012); Merkl (2014); Potocký & Majzlan (2015a); Hillert *et al.* (2016); Nikolajev *et al.* (2016); Koren (2017); Ćurčić *et al.* (2019); Schoolmeesters (2019); Glerean & Stefani (2020); Juřena (2022); Bittner & Theves (2023); Byk *et al.* (2023); Juřena (2023); Hejda (2024); Matern (2024).

Bosnia and Herzegovina (37 refs):
Kendi (1910; first localised record); Mikšić (1953, 1955, 1957); Horion (1958); Mikšić (1958, 1960, 1970); Benasso & Stroiazzo (1973); Mikšić (1977, 1982); Paulian & Baraud (1982); Szwałko (2004); Zandigiacomo (2005); Král (2006); Lelo (2006); Chobot & Mourek (2007, 2008); Lelo & Kašić-Lelo (2010); Brustel & Gouix (2012); Gutowski & Przewoźny (2013); Škrijelj *et al.* (2013); Merkl (2014); Milanović & Golob (2015); Milanović *et al.* (2015); Potocký & Majzlan (2015a); Hillert *et al.* (2016); Nikolajev *et al.* (2016); Koren (2017); Ćurčić *et al.* (2019); Schoolmeesters (2019); Glerean & Stefani (2020); Juřena (2022); Byk *et al.* (2023); Juřena (2023); Hejda (2024); Matern (2024).

Slovakia (90 refs):
Bolla (1859; first localised record); Rózsay (1868, 1880); Malesevics (1892); Kuthy (1898); Brancsik (1899); Kelecsényi (1900); Ortvay (1902); Brancsik (1905); Csiki (1905); Laczó (1905); Csiki (1910); Čepelák (1925); Polentz (1927); Laco (1928); Fleischer (1930); Balthasar (1933); Roubal (1936, 1938); Horion (1951); Tesař (1954); Endrődi (1957); Tesař (1957); Horion (1958); Krikken (1977); Skýpala (1978); Paulian & Baraud (1982); Král (1989); Lumaret (1990); Baraud (1992); Král (1993); Kollár & Smetana (1994); Týr (1997); Bunalski (1999); Szwałko (2004); Hůrka (2005); Majzlan *et al.* (2005); Zandigiacomo (2005); Agoglitta *et al.* (2006); Král (2006); Král *et al.* (2006); Majzlan (2006); Petersen *et al.* (2006); Chobot & Mourek (2007); Majzlan (2007); ŠOP SR (2007); Chobot & Mourek (2008); Juřena & Týr (2008); Juřena *et al.* (2008); Paracchini *et al.* (2008); Trnka (2009a); Arnone (2010); Arnone & Massa (2010); Országhová & Schlarmannová (2010); Vidlička (2011); Brustel & Gouix (2012); Byk *et al.* (2012); Gutowski & Przewoźny (2013); Kaděra (2013); Biel *et al.* (2014); Černecký *et al.* (2014); Merkl (2014); Cséfalvay (2015); Potocký & Majzlan (2015ab); Hillert *et al.* (2016); Majzlan (2016); Nikolajev *et al.* (2016); Spružina (2016); Kaděra (2017); Koren (2017); Zahradník (2017); Gajdoš & Majzlan (2018); Král *et al.* (2018); Majzlan (2018); ŠOP SR (2018); Ćurčić *et al.* (2019); Schoolmeesters (2019); Černecký *et al.* (2020); Glerean & Stefani (2020); Hudousek & Vošická (2020); Majzlan (2020ab); Juřena (2022); Theves & Bittner (2022); Bittner & Theves (2023); Byk *et al.* (2023); Juřena (2023); Hejda (2024); Matern (2024).

Hungary (136 refs):
Illiger (1800); Sturm (1800); Calwer (1858); Frivaldszky I. (1865; first localised records); Frivaldszky J. (1879ab); Sajó (1881); Török (1882); Horváth (1884; earliest and first dated record); Jäger (1884); Reitter (1892, 1893); Stierlin (1893); Viertl (1894); Kaufmann (1897); Sajó (1897); Kuthy (1898); Szlabóczky & Borbás (1900); Klapálek (1903); Csiki (1904, 1905); Wachsmann (1907); Sajó (1910ab); Kaufmann (1914ab); Huber (1916); Franz (1936); Borchert (1938); Paulian (1941); Endrődi (1956, 1957); Keve & Szijj (1957); Panin (1957); Tesař (1957); Horion (1958); Paulian (1959); Siroki (1964); Benasso & Stroiazzo (1973); Krikken (1977); Endrődi (1979); Horvatovich (1980); Paulian & Baraud (1982); Rozner I. (1984); Lumaret (1990); Baraud (1992); Bratek *et al.* (1992); Ádám (1994); Köteles & Bakonyi (1996); Ádám & Hegyessy (1998); Bunalski (1999); Sár & Horvatovich (2000); Rozner Gy. (2001); Kutasi (2002); Neculiseanu *et al.* (2002); Aszalós *et al.* (2003); Drovenik & Pirnat (2003); Merkl (2003); Szwałko (2004); Zandigiacomo (2005); Agoglitta *et al.* (2006); Enyedi (2006); Král (2006); Král *et al.* (2006); Nádai (2006); Petersen *et al.* (2006); Szél (2006); Chobot & Mourek (2007, 2008); Gaskó (2008); Jurc *et al.* (2008); Juřena *et al.* (2008); Paill (2008); Paracchini *et al.* (2008); Enyedi & Ádám (2009); Merkl & Vig (2009); Pirnat (2009); Trnka (2009a); Arnone (2010); Arnone & Massa (2010); Eichardt & Kutasi (2011); Gálhidy *et al.* (2011); Szél & Kutasi (2011); Vidlička (2011); Vrezec *et al.* (2011); Brustel & Gouix (2012); Rößner (2012); Gutowski & Przewoźny (2013); Németh (2013); Puskás & Petróczi (2013); Merkl (2014); Merkl *et al.* (2014); Merkl (2015); Németh (2015); Potocký & Majzlan (2015a); Baranyai & Fábián (2016); Carpaneto *et al.* (2016); Hillert *et al.* (2016); Nikolajev *et al.* (2016); Rozner *et al.* (2016); Spružina (2016); Vadász (2016); Kaděra (2017); Koren (2017); Pétsch & Szénási (2017); Gajdoš & Majzlan (2018); Halpern *et al.* (2018); Korda & Bartha (2018); Kovács & Szabó (2018); Král *et al.* (2018); Merkl & Szénási (2018); Szmorad *et al.* (2018); Anonymus (2019a); Bartha *et al.* (2019); Ćurčić *et al.* (2019); Dostal & Barries (2019); Merkl (2019); Pétsch & Szénási (2019); Schoolmeesters (2019); Vadász *et al.* (2019); Bócsó (2020); Deli *et al.* (2020); Glerean & Stefani (2020); Óvári (2020); Szmorad (2020); Baranyai-Nagy & Baranyai (2021); Duna-Ipoly National Park (2021); Kovács (2021); Fejes *et al.* (2022); Juřena (2022); Theves & Bittner (2022); Bittner & Theves (2023); Byk *et al.* (2023); Juřena (2023); Hejda (2024); Matern (2024).

Serbia (21 refs):
Nedyalkov (1906; first localised record); Mikšić (1959); Gradojević (1963); Guéorguiev & Bunalski (2004); Král (2006); Chobot & Mourek (2007, 2008); Gavrilović & Stojanović (2008); Arnone & Massa (2010); Merkl (2014); Potocký & Majzlan (2015a); Hillert *et al.* (2016); Ćurčić *et al.* (2019); Glerean & Stefani (2020); Juřena (2022); Bittner & Theves (2023); Byk *et al.* (2023); Juřena (2023); Hejda (2024); Kopr (2024); Matern (2024).

Albania (8 refs):
Murraj (1962; first and so far the only localised and dated records); Chobot & Mourek (2007, 2008); Potocký & Majzlan (2015a); Juřena (2022); Byk *et al.* (2023); Juřena (2023); Hejda (2024).

Belarus (8 refs):
Chobot & Mourek (2007, 2008); Ruicănescu & Niţu (2008); Potocký & Majzlan (2015a); Byk *et al.* (2023); Aleksandrowicz *et al.* (2023); Juřena (2023; first reliable localised record); Nuß & Jäger (2023).

Ukraine (94 refs):
Eichwald (1830; first localised record); Krynicki (1832); Hochhuth (1873); Cherkunov (1889); Hildt (1893, 1896); Anonymus (1897); Kulikovskiy (1897); Rybiński (1897, 1903); Łomnicki (1913); Ohloblin (1913); Tenenbaum (1923); Savchenko (1931, 1933, 1934); Kuntze & Noskiewicz (1938); Savchenko (1938); Panin (1957); Horion (1958); Medvedev (1965); Benasso (1971); Franz (1974); Stebnicka (1976); Krikken (1977); Paulian & Baraud (1982); Burakowski *et al.* (1983); Zahaikevych & Roshko (1988); Lumaret (1990); Baraud (1992); Bartenev *et al.* (1997); Bunalski (1999); Neculiseanu *et al.* (2002); Drovenik & Pirnat (2003); Martynov (2003); Szwałko (2004); Trach & Gontarenko (2005); Král (2006); Král *et al.* (2006); Vovk *et al.* (2006); Chobot & Mourek (2007, 2008); Paracchini *et al.* (2008); Ruicănescu & Niţu (2008); Schwarz (2008); Trnka (2009a); Vasko (2009); Arnone (2010); Arnone & Massa (2010); Godlevska *et al.* (2010); Vasko (2010); Gontarenko & Trach (2011); Miessen (2011); Vasko & Bryhadyrenko (2011); Vidlička (2011); Brustel & Gouix (2012); Martynov (2012); Bunalski *et al.* (2013); Gutowski & Przewoźny (2013); Merkl (2014); Potocký & Majzlan (2015a); Hillert *et al.* (2016); Kagalo *et al.* (2016); Nikolajev *et al.* (2016); Vovk *et al.* (2016ab); Koren (2017); Oskyrko & Kuzemko (2017); Sheshurak *et al.* (2018); Anonymus (2019b); Ćurčić *et al.* (2019); Kavurka *et al.* (2019); Schoolmeesters (2019); Glerean & Stefani (2020); Maniuk *et al.* (2020); Sheshurak *et al.* (2020ab); Solomakha *et al.* (2020); Vasko (2020); Kavurka & Martynov (2021); Kuzemko (2021); Sommer *et al.* (2021a); Juřena (2022); Kanarsky & Panin (2022); Sheshurak *et al.* (2022); Theves & Bittner (2022); Vasyliuk (2022); Bittner & Theves (2023); Byk *et al.* (2023); Juřena (2023); Nuß & Jäger (2023); Hejda (2024); Hubareva (2024); Matern (2024).

Romania (69 refs):
Fuss (1858); Bielz (1887); Ormay (1888); Seidlitz (1891); Kuthy (1898); Fleck (1905); Jasilkowski (1906); Montandon (1906); Csiki (1910); Petri (1910, 1912); Manolache (1930); Franz (1936); Schatzmayr (1936); Endrődi (1957); Panin (1957); Horion (1958); Benasso (1971); Benasso & Stroiazzo (1973); Franz (1974); Stebnicka (1976); Krikken (1977); Burakowski *et al.* (1983); Lumaret (1990); Baraud (1992); Bunalski (1999); Nitzu (2001); Neculiseanu *et al.* (2002); Chimişliu (2004); Szwałko (2004); Zandigiacomo (2005); Agoglitta *et al.* (2006); Král (2006); Král *et al.* (2006); Chobot & Mourek (2007); Niţu (2007); Chobot & Mourek (2008); Oprea *et al.* (2008); Ruicănescu & Niţu (2008); Schwarz (2008); Popescu & Davideanu (2009); Tatole *et al.* (2009); Trnka (2009a); Arnone (2010); Arnone & Massa (2010); Vidlička (2011); Brustel & Gouix (2012); Bădărău *et al.* (2013); Gutowski & Przewoźny (2013); Şerban (2013); Stan & Nitzu (2013); Merkl (2014); Anonymus (2015); Fusu *et al.* (2015); Potocký & Majzlan (2015a); Hillert *et al.* (2016); Nikolajev *et al.* (2016); Spružina (2016); Kaděra (2017); Koren (2017); Ćurčić *et al.* (2019); Schoolmeesters (2019); Glerean & Stefani (2020); Juřena (2022); Bittner & Theves (2023); Byk *et al.* (2023); Juřena (2023); Hejda (2024); Matern (2024).

Moldova (25 refs):
Miller & Zubowsky (1917; first localised record); Medvedev & Shapiro (1957); Panin (1957); Neculiseanu *et al.* (2002); Zandigiacomo (2005); Král *et al.* (2006); Chobot & Mourek (2007, 2008); Trnka (2009a); Brustel & Gouix (2012); Bacal *et al.* (2013); Merkl (2014); Potocký & Majzlan (2015a); Derjanschi *et al.* (2016); Hillert *et al.* (2016); Nikolajev *et al.* (2016); Ćurčić *et al.* (2019); Schoolmeesters (2019); Glerean & Stefani (2020); Juřena (2022); Bittner & Theves (2023); Byk *et al.* (2023); Juřena (2023); Hejda (2024); Matern (2024).

Bulgaria (29 refs):
Kovachev (1904; first localised records); Markovich (1909); Nedyalkov (1909); Mikšić (1959); Zaharieva-Stoilova (1974); Král & Malý (1993); Bunalski (2001); Guéorguiev & Bunalski (2004); Szwałko (2004); Král *et al.* (2006); Chobot & Mourek (2007, 2008); Paracchini *et al.* (2008); Trnka (2009a); Brustel & Gouix (2012); Gutowski & Przewoźny (2013); Merkl (2014); Hillert *et al.* (2016); Nikolajev *et al.* (2016); Ćurčić *et al.* (2019); Schoolmeesters (2019); Glerean & Stefani (2020); Juřena (2022); Theves & Bittner (2022); Bittner & Theves (2023); Byk *et al.* (2023); Juřena (2023); Hejda (2024); Matern (2024).

Turkey (23 refs):
Carpaneto *et al.* (2000); Král (2006); Král *et al.* (2006); Chobot & Mourek (2007, 2008); Paill (2008); Brelih *et al.* (2010); Vasko (2010); Vidlička (2011); Merkl (2014); Montreuil (2014); Hillert *et al.* (2016; first localised records); Nikolajev *et al.* (2016); Ćurčić *et al.* (2019); Glerean & Stefani (2020); Vasko (2020); Sommer *et al.* (2021a); Juřena (2022); Bittner & Theves (2023); Byk *et al.* (2023); Juřena (2023); Hejda (2024); Matern (2024).

Erroneous report based on misidentification: Lodos *et al.* (1999): Osmaniye Province, Kadirli (see Published records in *B. nireus*).

Corrections and additions to Juřena (2022)

Page 1, line 9 of Abstract: "several cases" should read "numerous cases".
Page 3, lines 15–16: "species in need of strict protection" should read "species requiring designation of Special Areas of Conservation and species in need of strict protection, respectively".
Page 3, line 28: "Klug (1843)" should read "Klug (1845).
Page 3, line 35: "…mistake was reported…" should read "…mistake was repeated…".
Page 4: after line 3, missing the sentence "The stridulatory apparatus of adult of *B. gallicus* was described by Arrow (1904).".
Page 4, line 19: "from east to west" should read "from west to east".
Page 5, line 10: "Glerean and Stefani 2019" should read "Glerean and Stefani 2020".
Page 9, line 33: "Stoyan Beshkov" should read "Stoyan Vladimirov Beshkov (Стоян Владимиров Бешков)"
Page 13, line 20: the record is missing "1 spec.".
Page 17, line 4: missing record "Hlohovec, ÚEV [= Special Area of Conservation] of Sedliská, no other data (Hudousek and Vošická 2020)".
Page 17, lines 8 and 12: citation of Roubal (1938) missing.
Page 18, line 33: citation of Roubal (1938) missing.
Page 19, line 15: citation of Roubal (1938) missing.
Page 25, legend to Figure 6: the author Helga Kothajová is missing for the photographs **A** and **B**.
Page 33, line 4: the following record is missing: "Elsas, Rheinebene" [= Alsace, Rhine Valley], no other data (Döderlein 1901); «"Alsace"» should read «"Alsace" or "Elsass"»; citations of Borchert (1938) and Lumaret (1990) missing.
Page 34: For Bavaria (Bayern), the following record is missing: Upper Palatinate (Oberpfalz), "Um Regensburg. Aus der Sammlung des Hrn. Senat. Harrers." [= Near Regensburg. From the collection of Mr Senator Harrer.], [ca. 340 m a.s.l.], no other data (Schrank 1798: 381).
Page 34, line 17: missing record «"Bawaria", no other data (Kuntze and Noskiewicz 1938)».
Page 35, line 2: "1 spec." should read "1 ♀".
Page 35, line 4: the record is missing "1 ♂".
Page 36, lines 6–7: "Heer 1841" should read "Heer 1841a, b".
Page 36, line 7: citation of Borchert (1938) missing.
Page 36, line 9: "Heer 1841" should read "Heer 1841a, b"; citation of Borchert (1938) missing.
Page 36, line 29: citation of Borchert (1938) missing.
Page 36, line 30: citation of Pesarini (2004) missing.
Page 37, last line: "Glerean and Stefani 2019" should read "Glerean and Stefani 2020".
Page 38, line 3: missing the following record: **Lombardia**, no other data (Villa and Villa 1844).
Page 38, line 4: citation of Pesarini (2004) missing.
Page 38, line 9: missing the following record: "Trentino", no other data (Pesarini 2004).
Page 38, line 27: citation of Pesarini (2004) missing.
Page 38, line 41: "Glerean and Stefani 2019" should read "Glerean and Stefani 2020".
Page 39, line 18: "Alpes Pedemontium" should read "Alpes Pedemontanae".
Page 39, line 29: "…no other data, 1 ♂ and 2 ♀♀…" should read "…[18]70, 1 ♂ and 1 ♀…".
Page 40, line 14: citation of Pesarini (2004) missing.
Page 40, line 17: citation of Benasso and Stroiazzo (1973) missing.
Page 41: for published data from Austria, the following text is missing: **? Tyrol (Tirol)**, no other data (Schilsky 1888, 1909)—this record does not seem likely given that this is a high mountain region, which does not correspond to the ecological requirements of *B. unicornis*.
Page 41, line 17: the following record is missing: Linz, no other data (Borchert 1938).

Page 42, line 3: "(Paill 2007;…" should read "(Paill 2008;…".
Page 42, line 16: "collector nor specified" should read "collector not specified".
Page 42, line 30: "(Paill 2007;…" should read "(Paill 2008;…".
Page 42, line 34: "…plant materials amassed by flood water, several times (according to Sturm)…" should read "…found several times after storms in detritus washed up on the lake shore…".
Page 43, line 1: the following record is missing: "Styria (Die Steyermark)", no other data, listed as "*Odontaeus aeneas* Panz." (Gistel 1856).
Page 44, line 10: "century" should read "centuries".
Page 46, line 14: citation of Borchert (1938) missing.
Page 47, line 4: citation of Borchert (1938) missing.
Page 47, line 43: citation of Siroki (1964) missing.
Page 53: the following record for Slavonia is missing: **Slavonia (Slavonija)**, no other data (Mikšić 1982).
Page 54, line 11: "the species is known" should read "the species was known".
Page 54: the following records for Bosnia and Herzegovina are missing: "Süd-Bosnien", no other data (Mikšić 1955); "BH. = Volksrepublik Bosnien-Herzegowina" (Mikšić 1957); "Bosnien", no other data (Mikšić 1982).
Page 58, line 5: the following record is missing: "Siebenbürgen" [= Transylvania], no other data (Borchert 1938).
Page 58, line 12: the following record is missing: "Nagy-Szeben" [= Sibiu], no other data (Ormay 1888).
Page 58, line 16: citation of Ormay (1888) missing.
Page 60, line 19: the following record for the **City of Chișinău (Municipiul Chișinău)** is missing: "Vadului-Voda" [= Vadul lui Vodă], 1951–1955, no other data (Medvedev and Shapiro 1957).
Page 60, lines 30–31: the sentence "Old records from another two localities are reported by Derjanschi *et al.* (2016)." should read "Old records from another three localities are reported by Medvedev and Shapiro (1957) and Derjanschi *et al.* (2016).".
Page 63, line 20: the following record for the Dnipropetrovsk Oblast is missing: Sicheslavskyi Krai (Січеславський край) [= Dnipro region], no other data (Maniuk *et al.* 2020).
Page 64, line 36: "1 ♀" should read "1 ♂".
Page 67, lines 11 and 12: "Kovachev (1905)" should read "Kovachev (1904)".
Page 71, line 4: citation of Shokhin (2011) missing.
Page 71, line 19: citation of Mikšić (1982) missing.
Page 71, line 23: citation of Benasso and Stroiazzo (1973) missing.
Page 71, line 37: citation of Medvedev and Shapiro (1957) missing.
Page 71, line 40: "…apply to Ukraine." should read "apply to Ukraine or Moldova".
Page 76, Table 9: "Glerean and Stefani 2019" should read "Glerean and Stefani 2020".
Page 77, line 33: citation of Fabre (1914) missing.
Page 79, line 9: citations of Medvedev (1952), Howden (1985), and Nikolajev (2003) missing.
Page 90, line 9: "Arens LE" should read "Arens LYe".
Page 90: missing Arrow (1904) in the list of references (see references in this paper).
Page 91: missing Benasso and Stroiazzo (1973) in the list of references (see references in this paper).
Page 92: missing Borchert (1938) in the list of references (see references in this paper).
Page 92. lines 34 and 37: "A Trencsén Vármegyei Természettudomanyi Egylet" should read "A Trencsén Vármegyei Természettudomanyi Egylet Évkönyve".
Page 96, line 8: "pp. 97–176" should read "443 pp.".
Page 96: missing Döderlein (1901) in the list of references (see references in this paper).
Page 97, line 24: "Dritter Band." should read "Dritter Band. Fünfte Lieferung.".
Page 97: missing Fabre (1914) in the list of references (see references in this paper).
Page 98, lines 10–11: for complete bibliographical notation of Franz (1974) see references in this paper.
Page 99, line 40: "Glerean P, Stefani G (2019)" should read "Glerean P, Stefani G (2020)".
Page 99, penultimate line: "…Zoologia 41: 51–62." should read "…Zoologia 41[=2019]: 51–62.".
Page 100, lines 1–5: for the correct bibliographical notation and link for Glerean *et al.* (2021) see references in this paper.
Page 100, line 25: "Heer O (1841)" should read "(Heer O (1841a)".
Page 100: missing Heer (1841b) in the list of references (see references in this paper).
Page 100, line 41: "Hildt LF (1892)" should read "Hildt LF (1893)".

Page 100, penultimate line: "Pamiętnik Fizyograficzny 12(3)" should read "Pamiętnik Fizyograficzny 12[=1892](3)".
Page 102. line 6: "1–91" should read "5–91".
Page 102: missing Hudousek and Vošická (2020) in the list of references (see references in this paper).
Page 105, line 20: "Klug JChF (1843)" should read "Klug JChF (1845)".
Page 105, line 25: "Nouvelle Série 9" should read "Nouvelle Série 11".
Page 106: for the correct bibliographical notation of Kovachev (1905[correctly 1904]) see references in this addendum.
Page 108, line 4: "A Trencsén Vármegyei Természettudomanyi Egylet" should read "A Trencsén Vármegyei Természettudomanyi Egylet Évkönyve".
Page 110: the following three bibliographical notations are missing in the list of references: Maniuk *et al.* (2020), Medvedev (1952), and Medvedev & Shapiro (1957)—see references in this paper.
Page 110, line 35: "Marseul SM" should read "Marseul SA".
Page 111: the following references are missing: Mikšić (1955, 1957, 1982)—see references in this paper.
Page 112, line 31: "Schrank, 1798" should read "Schrank, 1798 [= 1789]".
Page 112, line 32: "Schrank, 1798" should read "Schrank, 1789".
Page 113: missing Nikolajev (2003a) and Ormay (1888) in the list of references (see references in this paper).
Page 114, line 6: "Paill W (2007)" should read "Paill W (2008)".
Page 114, line 8: "Beiträge zur Entomofaunistik 8" should read "Beiträge zur Entomofaunistik 8[=2007]".
Page 115: missing Pesarini (2004) in the list of references (see references in this paper).
Page 115, lines 21–22: "Bollettino del Laboratorio di Entomologia Agraria" should read "Bollettino del Laboratorio di Entomologia Agraria "Filippo Silvestri" (Portici)".
Page 115, lines 29–36: for the correct bibliographical notation for Pirnat (2009) see references in this paper.
Page 116, lines 23: "Department" should read "Departement".
Page 117, line 24: "zum 60. Geburtstag" should read "zum 60. Geburtstage".
Page 117, line 39: "Pozsonyi…" should read "A Pozsonyi…".
Page 118, line 30–31 and 34: "Zbirnyk Prac Zoologichnoho Muzeiu" should read "Zbirnyk Prats Zoolohichnoho Muzeiu".
Page 118, last and penultimate lines: "Bollettino del Laboratorio Zoologia Generale Agraria Reale Istituto Superiore Agrario Portici" should read "Bollettino Laboratorio di Zoologia Generale ed Agraria del Reale Istituto Superiore Agrario di Portici".
Page 119: missing Schrank (1798) in the list of references (see references in this paper).
Page 121: missing Shokhin (2011) and Siroki (1964) in the list of references (see references in this paper).
Page 121, last line: "site of community importance" should read "Site of Community Importance".
Page 123, line 8: "Tenenbaum S" should read "Tenenbaum Sz".
Page 124, line 10: "administratsiya" should read "administratsiia".
Page 124, line 11: "Olesya" should read "Olesia".
Page 124, line 12: "orhanizatsiya" should read "orhanizatsiia".
Page 124: missing Villa and Villa (1844) in the list of references (see references in this paper).
Page 124. line 29: "(2005)" should read "(2006)".
Page 124, line 32: "13(1–2): 35–42" should read "13[=2005](1–2): 35–42".

Corrections and additions to Juřena (2023)

Page 210, line 31: "from east to west" should read "from west to east".
Page 211, line 13: "…and Juřena (2022)." should read "…, Juřena (2022), and present paper.".
Page 219, line 26: missing the following sentence: Neither Aleksandrovich & Pisanenko (1991) nor Aleksandrovitch *et al.* (1996) listed the species for Belarus.
Page 222: missing Aleksandrovich and Pisanenko (1991) and Alexandrovitch *et al.* (1996) in the list of references (see references in this paper).

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Recent records of *B. unicornis* in Croatia were gathered through the service "Development of monitoring programs for species and habitat types of EU interest" within the OPCC project "Development of a system to monitor the conservation status of species and habitat types", Procurement group 11: Drafting and developing a monitoring program for beetles with capacity building for stakeholders in the monitoring and reporting system.

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