



# First records of bat-associated *Cimex lectularius* (Cimicidae, Heteroptera) for Armenia and Georgia

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<http://zoobank.org/1C10736A-3846-4B75-B7D5-45EFE4C1EA7C>

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Academic editor: Levan Mumladze ♦ Received: 29 March 2023 ♦ Accepted: 24 May 2023 ♦ Published: 25 July 2023

## Abstract

Besides humans, the common bed bug *Cimex lectularius* uses bats as hosts, but no such records were available from the Southern Caucasus. Here, we record the greater horseshoe bat (*Rhinolophus ferrumequinum*) and the lesser mouse-eared bat (*Myotis blythii*) as hosts of *C. lectularius* from two Georgian and one Armenian sites. A summary of all known published records of bat-associated populations of *C. lectularius* shows they are both scattered and restricted to the Palearctic only. Observations of *C. lectularius* from bat colonies in Georgia and Armenia were made in old buildings or ruins, like churches or monasteries, but not in caves, despite a specific search. This supports previous studies suggesting that 1) bat-associations of common bed bugs are very rare outside Central Europe and 2) almost never occur in caves. We discuss climatic conditions and host preferences as possible factors for these findings and the implications for the origin of the human bed bug interaction.

## Key words

Bed bug, biogeography, ecology, ectoparasites, faunistics, host-parasite relationship, South Caucasus

## Introduction

The family Cimicidae (Heteroptera) constitutes a group of specialized haematophagous ectoparasitic insects. About two-thirds of the cimicid species are associated primarily with bats, which have been suggested to be the ancestral hosts of the family (Horváth 1913; but see Roth et al. 2019). The remaining species are associated with birds and only four cimicid species, among which the famous common bed bug *Cimex lectularius* Linnaeus, 1758, parasitize humans (Usinger 1966; Reinhardt and Siva-Jothy 2007). The Cimicidae contain about 110 species classified into 6 subfamilies and 24 genera (Henry 2017) and have a worldwide distribution. There are 17 species listed in Europe (Péricart 1996; Simov et al. 2006; Quetglas et al. 2012), in-

cluding species of the *Cimex pipistrelli* species complex (for taxonomic discussion-see Roth et al. (2018)).

Both adults and nymphs stay on the body of their host only when feeding but otherwise hide nearby in the shelter of the host (Hase 1917). Outside shelters, however, several studies report cimicids – exclusively adults and mostly females – being attached to the host body (Loye, 1985; Heise, 1988; Rupp et al. 2004; Reinhardt and Jacobs 2006; Balvín et al. 2012a). Thus, if mated females can find a new location on their own, as such studies suggest, one can speculate that even if the transport itself is a passive transport by the bats, the attachment to the host body might potentially be an intentional behavior for dispersal.

In Europe, *C. lectularius* has been found in bat colonies (Usinger 1966; Roer 1969; Morkel 1999; Balvín et

al. 2015) and occasionally also in bird nests (Günther and Niehus 1981; Vater 2015a,b; 2016). Association with bats almost exclusively occurs in bat reproduction roosts (e.g. Roer 1969) in human buildings (Balvín et al. 2015). Since their bat hosts hibernate in a different place (like caves), the bed bugs stay without their host species during the winter (e.g. Reinhardt 2012). So far, records of bat-associated *C. lectularius*, however, are rather rare outside central Europe (Balvín et al. 2015), but it is not clear whether this is due to a lack of search or a true distribution gap.

In the Southern Caucasus area, the common bed bug *C. lectularius* is well-known from human hosts/dwellings in Azerbaijan, Armenia, and Georgia (Dumas 1859, cited in Reinhardt 2014; Akramovskaya 1959; Gidayatov 1967; Zaytseva 1998; Aukema et al. 2013). But to the best of our knowledge, there are no records of cimicids related to bats as hosts in the Southern Caucasus. Here we undertook some field work and present the first records of *C. lectularius* associated with bats for the region. A detailed description of study places is given. Finally, we discuss some aspects of the ecology and distribution of *C. lectularius* associated with bats in Europe.

## Materials and methods

Material was sampled within the framework of the BMBF-funded Caucasus Barcode of Life (CaBOL) project (<https://ggbc.eu/>). The specimens were collected by hand, fixed in 96% ethanol, and later stored in a freezer under -22°C for further DNA barcoding at the University Museum Bergen. Field work took place in May 20-23 (2022) in Armenia and from May 30 to June 2 (2022) in Georgia. In total, six and eight places were visited in Georgia and Armenia, respectively (Supplementary Material 1). Seven of them were caves or tunnels, the other seven were churches or other human-made buildings.

## Investigated sites

### Georgia

Ghliana Cave: (N42.37°, E42.59°) located in the Kumistavi Village, Tskaltubo Municipality. The cave is part of the Imereti Caves Protected Areas System and is listed among the EUROBATs' underground bat sites of international importance. The total length of the cave is 1220m. In the period from April to October, the Ghliana Cave shelters one of the largest mixed bat maternity colonies in Georgia, with the number of species changing depending on the year and season. The cave is annually inhabited by lesser mouse-eared bat (*Myotis blythii* Tomes, 1857) and common bent-wing bat (*Miniopterus schreibersii* Kuhl, 1817). In some years, it also provides shelter to the greater horseshoe bat (*Rhinolophus ferrumequinum* Schreber, 1774) and the Mediterranean horseshoe bat (*Rhinolophus euryale* Blasius, 1853). Occasionally, the mixed colony is also joined by a large colony of Geoffroy's bat (*Myotis emarginatus* E. Geoffroy, 1806). The population of the bat maternity colony changes from year to year, ranging be-

tween 4000 and 8000 individuals in total. The colony size reaches its maximum in late July - early August.

Becho Cave/Tunnel: (N42.53°, E41.99°) located in the village of Alertkari, Zugdidi Municipality. The length of the tunnel is 100-120 meters, and there is a small spring inside. In the cave there is a mixed maternity colony. The colony's main population in 2021 was represented by *M. blythii* and *M. schreibersii*. However, in April 2022, the colony consisted of the same two bat species, and in addition of a small group (up to 150 individuals) of *R. ferrumequinum*. Since June 2022, the colony composition has changed and now consists of *M. blythii*, *M. schreibersii*, and a small group (up to 150 individuals) of *R. euryale*. Thus, taking all bat species together, the mixed maternity colony size can be estimated at up to 1400-1500 individuals.

Letsurtsume Cave: (N42.53°, E42.11°) located close to the Letsurtsume Village, Chkhorotsku Municipality. Letsurtsume Cave is surrounded by a small forest. There is a small spring in the cave. In the cave, there is a mixed maternity colony. The highest number of bats was recorded in summer 2014, with an estimation of 250 individuals, consisting mainly of *R. euryale* (about 200 individuals) and *M. emarginatus* (about 50 individuals). In the autumn of the same year, there was a mixed colony of *R. ferrumequinum* and *M. schreibersii* consisting of 150 individuals in total.

Gremi Church: (N42.00°, E45.66°) located close to the Gremi Village, Kvareli Municipality. In 2021, maternity colony of *R. ferrumequinum* with single individuals of *M. emarginatus* was found. The total size of the colony was estimated to be up to 400 individuals.

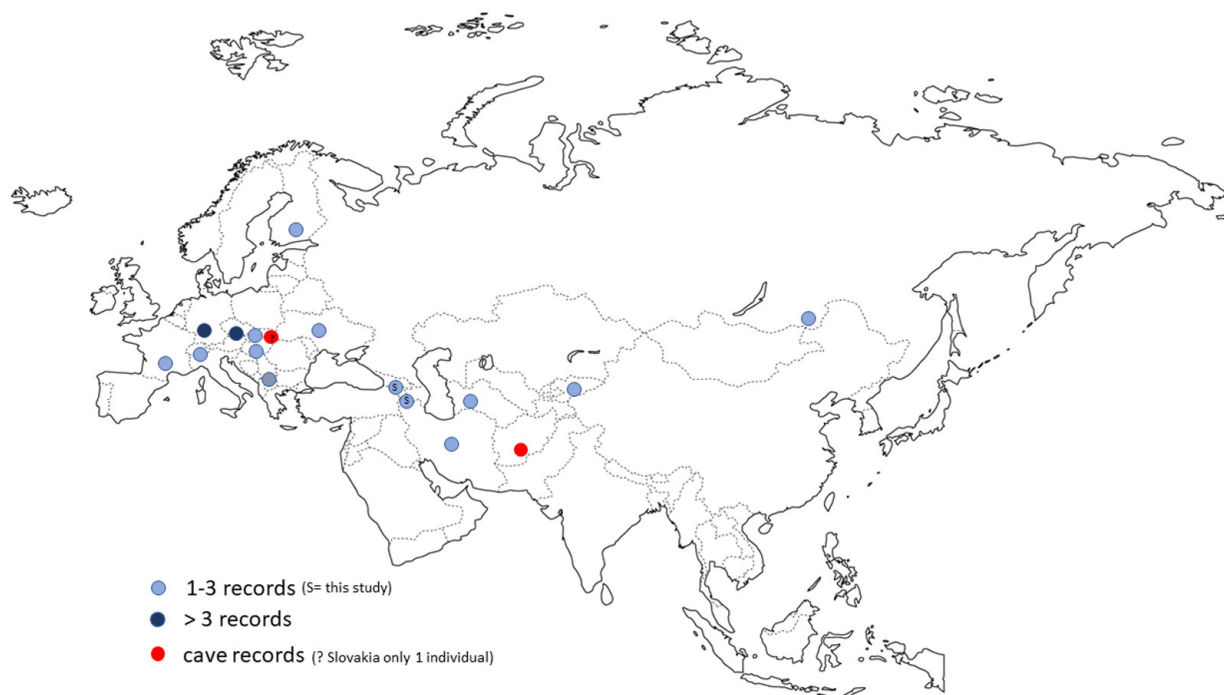
Tsminda Stepane Church: (N42.01°, E45.62°) located close to Gremi – Grzelichala villages, and it is situated in a broadleaf forest. In the church, there is a mixed maternity colony consisting of two species: *R. ferrumequinum* and *M. schreibersii*. The total number of individuals in the colony in 2021 was estimated to be about 1200.

Church near Pichkhovani Village: (N42.07°, E45.30°) is surrounded by a broadleaf forest. In the church, there is a maternity colony of *M. blythii* with about 1000-1200 individuals.

### Armenia

Arakelots Monastery: (N41.03°, E45.06°) located 3 km west of the village of Acharkut on a hill on the left bank of the Kirants River. It is located within a broadleaf forest on the slope of a forested mountain. In the monastery, there are maternity colonies of *M. blythii* and bent-wing bat (*Miniopterus pallidus* Thomas, 1907). On May 21, 2022, we found 200 bats in one of the auxiliary buildings, whereas the number of individuals recorded on August 4, 2021, was about 5,000 individuals of both species.

University Old Camp: (N40.74°, E44.81°) this camp site of the Yerevan State University is located in Dilijan city, near a tributary of the Aghstev River. Due to the mountainous climate, Dilijan and its surrounding territories are cool during the summer, and the humidity is higher compared to other cities in Armenia. The camp site has many abandoned wooden houses, where pipistrelle bats stay during the summer. In 2021, maternity colonies of common pipistrelle



**Figure 1.** Records of *Cimex lectularius* associated with bats shown for different countries in the Palearctic.

(*Pipistrellus pipistrellus* Schreber, 1774) and Kuhl's pipistrelle (*Pipistrellus kuhli* Kuhl, 1817) were found in the walls of three abandoned wooden houses. On May 21, 2022, we did not find any individuals in the area.

Getashen Cave: (N39.69°, E45.56°) located at the beginning of Gndevank Canyon on the road to Jermuk City. The canyon of Gndevank is rich in large and small caves and grottos, which are shelters for bats. The Getashen cave is a temporary shelter for some species of bats for resting after feeding, migration, or hunting. For the *R. euryale* and *R. ferrumequinum*, it is the shelter for the maternity colonies. In 2021, up to 500 individuals of these two species were registered. No bats were found there in May 2022. In different years (2007–2010), mainly in July, 200–500 individuals were recorded in the cave.

Magel Cave (Magellan Cave): (N39.71°, E45.20°) a karst cave in the Vayots Dzor region, on the road to Noravank monastery. It is one of the biggest caves in Armenia. It has been studied up to a depth of 1.7 km. This cave is used by many species of bats. The temperature inside the cave is around 8–12°C the whole year. The various halls of the cave are summer and winter habitats for *R. euryale*, *R. ferrumequinum* and other various bats. On May 22, 2022, we registered 50 bats in the hall chosen for the wintering of *R. ferrumequinum*, but there were still no bats in the hall used during the summer.

Noravank Monastery: (N39.68°, E45.23°) located in a narrow gorge of the Amaghu River near the town of Yeghegnadzor (Vayots Dzor region). The gorge is known for its tall, sheer, brick-red cliffs. A small maternity colony of Schaub's myotis (*Myotis schaubi* Kormos, 1934) was observed from the end of May to September in 2021. Since the colony was under the ceiling of the church and between the upper stones of the window, the exact number of individuals was impossible to count. In May 2022, no bats were found, but there was fresh guano, which indicated the presence of several individuals.

Areni 1 Cave: (N39.73°, E45.20°) located about two km northeast of Areni Village, between the Yerevan - Yeghegnadzor highway and the bank of the Arpa River. The cave consists of three halls, which are connected by passages. In general, the cave is known to used by 10 species of bats. Mainly there are *Myotis* species, pipistrelle bats, serotine bats, and barbastelle bats. We did not find any bats during our visit in May 2022.

Old garages: (N39.72°, E45.18°) at the end of Areni Village (Vayots Dzor region), there are abandoned garages with panel structures, which are shelters for bats. Pipistrelle bats, *M. schaubi* and David's myotis (*Myotis davidii* Peters, 1869) bats were found between the panels of these garages in different years. Pipistrelle bats were in a colony. *M. schaubi* and *M. davidii* occurred with no more than 10 individuals. Since it is not possible to count the bats between the panels, the number of bats could be higher. On May 22, 2022, only one individual of *M. schaubi* was found.

Metsamor Cave: (N40.12°/E44.18°) located in the area of the Metsamor Museum, near the ruins of the Metsamor fortress. The cave was one of the drainages canals. Now it is 50–70m deep and widens at the end. In different years, many individuals of *R. ferrumequinum*, *M. blythii*, and *M. pallidus* have been observed, mostly in April–May. On May 22, 2022, no bats were found.

### Searching approach and time spend per sampling site

Each roost was visited and examined for bugs for at least 30 minutes but usually for up to 60 minutes. One to three people were actively searching for the bugs. We used the “wwg” approach: first we checked spider webs for dead cimicids and exuviae, then the walls, and finally the ground. If possible, we tried to search the area close to the roosts/places with bats.

## Species ID and barcoding

The collected bug material is stored at the University Museum of Bergen, Norway (ZMBN). Morphological species determination was based on characters based in Usinger (1966) and Simov et al. (2006). We DNA-barcoded one specimen of *Cimex lectularius* from the church near Pichkhovani Village using the methodology of DNA extraction and PCR amplification as described in Roth et al. (2019). Primers used for amplification of the mitochondrial cytochrome c oxidase subunit I (COI) are given in Geller et al. (2013).

## Results

All specimens were identified as *Cimex lectularius*. For all specimens, the pronotum was more than 2.5–3 times as wide as long (N=4: 3.30; 3.25; 2.80; 3.35) which excludes species from the *Cimex pipistrelli*-group. The ratio of length/width of the hind femur was >3.4 (N=4: 3.70; 3.50; 3.41; 3.60) which excludes *Cimex emarginatus* Simov, Ivanova and Schunger 2006. The ID based on morphological characters was confirmed by the COI DNA barcode, which is available at Genbank with the accession number OP897494.

## Order Hemiptera

### Family Cimicidae Latreille, 1802

#### *Cimex lectularius* Linnaeus, 1758

**Materials examined.** Georgia • 2 males, 1 female, one exuviae nymph stage IV/V; Gremi Church; N42.00°, E45.66°; All individuals were dead; leg. Natradze S, Roth S; 30 May 2022. • 3 males, 2 females; Church near the Pichkhovani Village; One female was dead; leg. Natradze S, Roth S; 30 May 2022. Armenia • 2 females (dead, partly damaged), one individual of unknown sex, heavily damaged, 1 dead nymph stage V; Arekelots Monastery; N41.03°, E45.06°; leg. Ghazarayan A, Hayrapetyan T, RothS; 21 May 2022.

**Remarks.** None of the individual collected in both localities of Georgia, had taken a blood meal recently; one male still had dark spots in the gut, indicating a possible blood meal in 2022. One collected female had several eggs in the abdomen. Bugs collected in Armenia, had very small remains of blood meal, indicating some bloodmeal in 2022 or just before dying.

## Discussion

Our field work revealed the presence of bat-associated *Cimex lectularius* at three out of 14 sites. We, therefore, suggest that the previous lack of bat-associated *C. lectularius* records in the Caucasus area was a result of low search efforts. Future fieldwork is, therefore, likely to yield more sites with bat-associated *C. lectularius*.

For setting our findings in a more general context, it is worth noting that while bat- and human associated popu-

lations of *C. lectularius* seem to be well able to interbreed (DeVries et al. 2020), but there is a relatively deep genetic divide between the two host lineages (Balvín et al. 2012b; Booth et al. 2015). This genetic isolation points towards a very low degree of interbreeding, suggesting that the Caucasus area was effectively colonized by both host lineages independently. If true, the independent colonization routes of the two lineages are the reason why the human-associated lineage occurs globally but not the bat-associated one. For example, no observations of bat-associated *C. lectularius* exist from North America, where the human-associated lineage is very abundant. In fact, published records of *C. lectularius* associated with bats come only from the following countries (see Figure 1), all within the Palearctic: Afghanistan (Povolný and Usinger 1966), Czech Republic (Povolný 1957), Finland (Poppius 1912), France (Usinger and Beaucournu 1967), Germany (e.g. Eichler 1937; Roer 1969; Morkel 1999; Reinhardt 2012), Hungary (Balvín et al. 2012b), Iran (Golestan province, N37.366°, E55.982°, 27 May 2006, A. Reiter and P. Benda leg.; assigned as bat-associated bed bug based on morphology by Balvín et al. 2012a; see also Roth et al. 2019), Iraq (Abul-Hab 1979; Lanza 1999), Kyrgyzstan (Rybin et al. 1989), Russia (Dauria steppe; Dubinin 1947), Serbia (Protić and Paunović 2006, misidentified as *C. pipistrelli*), Slovakia (Usinger 1966), Switzerland (Balvín et al. 2012b), Ukraine (Balvín et al. 2012a).

Only two out of all these records, the ones from Afghanistan and the Domic Cave in Slovakia (Usinger 1966) concern findings in caves, i.e., in a natural, non-synanthropic habitats. Povolný and Usinger (1966) speculated that the former finding could represent an autochthonous bat-parasitizing population of the bed bug where humans acquired this parasite when they shared caves with bats as shelters (Horváth 1913; Usinger 1966). The status of Domic Cave as a bat roost in the past is difficult to assess. Nowadays, it is used as a summer roost for *Miniopterus schreibersii* and *Rhinolophus euryale* (Balvín, personal communication); neither species is known as a host for *C. lectularius* (Balvín et al. 2012b). It is unknown, if there ever were vital bed bug populations in that cave when it was used by Neolithic men.

The questions remaining are: 1) why is bat-associated *C. lectularius* rare in caves, and 2) why do we find a declining number of records from Central Europe to Southern Europe for both bat parasitic *Cimex* species (i.e. *C. pipistrelli*, *C. lectularius*) (Balvín et al. 2015)? A biased sampling effect cannot be excluded for many regions of the Palearctic. For Europe, however, exhaustive studies of bat roosts in Bulgarian caves have been conducted (Simov et al. 2006; Balvín et al. 2015).

Several factors, like bat host specificity of the common bed bug, habitat preferences due to climatic requirements of bed bugs, and in addition, climate preferences of the host species, are discussed as explanations for the European gradient (Simov et al. 2006; Balvín et al. 2015). For example, according to Simov (2006) the rarity of both *Cimex* spp. in bat caves might be because caves in Europe are too humid and too cold (see also Horacek 1983; Balvín et al. 2015). Human dwellings and bat boxes provide a warmer and drier alternative and more optimal summer roosts for many

bat species and, thus, for their associated bed bugs as well. However, there are variations among local populations with different preferences for either caves or human dwellings (Balvín, personal communication).

*Myotis* spp. are the main bat host for the common bed bug (Balvín et al. 2015). The lack of stable and large colonies of *Myotis* spp. in southern Europe may mean the lack of a reservoir for stable *C. lectularius* populations (Balvín et al. 2015).

In summary, the biotic and abiotic factors discussed above might explain the lack of the common bed bug in caves in some parts of Europe. The question remains open as to why there are almost no records from caves in the entire Palearctic.

Our observations of bat-associated *C. lectularius* in Armenia and Georgia are the first records for the Caucasus. Moreover, all bugs were found in old churches, despite several caves being investigated. We found small but vital (reproductive) populations of *C. lectularius* connected to the following potential host species: *Rhinolophus ferrumequinum* and *Myotis blythii*. Since there were also some single individuals of *M. emarginatus* at Gremi Church, it cannot be excluded as another host species. But given the fact that the greater horseshoe bat forms a maternity colony of about 400 individuals there, it is very unlikely. Both *Myotis* spp. are known as hosts for *C. lectularius* (Balvín et al. 2012b; Balvín et al. 2015). Records of bed bugs in *R. ferrumequinum* colonies, however, are only known from mixed colonies with other bat species (Balvín et al. 2015). Further investigation at Gremi Church should reveal if the greater horseshoe bat is really the host of *C. lectularius*, which would be a new host species.

Entomological training plus a short additional field experience for unexperienced bat researchers may increase detection rates of cimicid bugs in bat colonies. More observational contributions from bat researchers, however, would certainly improve our knowledge about the distribution and ecology of bat associated bed bugs in Europe in general and in the Caucasus region in particular.

## Acknowledgements

The project Caucasus Barcode of Life (CaBOL) – Assessing the Biodiversity of the Caucasus (ggbc.eu) on which this study is based was funded by the Federal Ministry of Education and Research under the grant number 01DK20014A. The responsibility for the content of this publication lies with the author.

We thank the members of Museum König Bonn for assistance during the field work in Armenia. Anna A. Namyatova (Zoological Institute St Petersburg) helped during the field trip in Georgia. We are very grateful to Nils Hein, the coordinator of the CaBOL project, for his engagement and management. Ondřej Balvín (Czech University of Life Sciences Prague) shared his experience about bed-bug-bat research and commented an earlier draft of the manuscript. Klaus Reinhardt (TU Dresden) and Astrid Pilz (Bergen) gave useful comments to improve the manuscript.

## References

- Abul-Hab J (1979) On the bed bugs (Hemiptera, Cimicidae) in Iraq. Bulletin of Endemic Diseases 19(1–4): 65–76.
- Akramovskaya EG (1959) True bugs (Hemiptera-Heteroptera) of the Armenian SSR. Materialy po izucheniyu fauny Armyanskoi SSR 4: 79–144. [in Russian]
- Aukema B, Rieger C, Rabitsch W (2013) Catalogue of the Heteroptera of the Palearctic Region. VI. Supplement. The Netherlands Entomological Society, Amsterdam, 629 pp.
- Balvín O, Ševčík M, Jahelková H, Bartonička T, Orlova M, Vilímová, J (2012a) Transport of bugs of the genus *Cimex* (Heteroptera: Cimicidae) by bats in western Palearctic. Vespertilio 16: 43–54.
- Balvín O, Munclinger P, Kratochvíl L, Vilímová, J (2012b) Mitochondrial DNA and morphology show independent evolutionary histories of bedbug *Cimex lectularius* (Heteroptera: Cimicidae) on bats and humans. Parasitology Research 111(1): 457–469. <https://doi.org/10.1007/s00436-012-2862-5>
- Balvín O, Bartonička T, Simov N, Paunović M, Vilímová J (2015) Distribution and host relations of species *Cimex* on bats Europa. Folia Zoologica Praha 63(4): 281–289. <https://doi.org/10.25225/fozo.v63.i4.a7.2014>
- Booth W, Balvín O, Vargo EL, Vilímová J, Schal C (2015) Host association drives genetic divergence in the bed bug, *Cimex lectularius*. Molecular Ecology 24: 980–992. <https://doi.org/10.1111/mec.13086>
- DeVries ZC, Santangelo RG, Booth W, Lawrence CG, Balvín O, Bartonička T, Schal C (2020) Reproductive compatibility among populations and host-associated lineages of the common bed bug (*Cimex lectularius* L.). Ecology and Evolution 10(20): 11090–11099. <https://doi.org/10.1002/ece3.6738>
- Dubinin VB (1947) Ecological remarks to bloodsucking bugs of the family Cimicidae of Daur steppe. Entomologičeskoje obozrenije 39: 232–246. [in Russian]
- Dumas A (1859) Reise im Kaukasus 1858–1859. In: Rödiger GFW (Eds) Lese-Kabinett, Pest, Hartleben's Verlag Expedition, 303–314.
- Eichler W (1937) Über die bei europäischen Vögeln vorkommenden Wanzenarten. Zoologischer Anzeiger 120: 267–271.
- Geller J, Meyer C, Parker M, Hawk H (2013) Redesign of PCR primers for mitochondrial cytochrome c oxidase subunit I for marine invertebrates and application in all-taxa biotic surveys. Molecular Ecology Resources 13: 851–861. <https://doi.org/10.1111/1755-0998.12138>
- Gidayatov DA (1967) True bugs (Hemiptera–Heteroptera) of the Lenkoran zone (Talysh) of Azerbaijan. Trudy Instituta Zoologii Akademii Nauk AzSSR 26: 94–155. [in Russian]
- Günther H, Niehus M (1981) *Cimex lectularius* - Freilandfund in der Pfalz. Pfälzer Heimat 32, 86.
- Hase A (1917) Die Bettwanze *Cimex lectularius* L.: ihr Leben und ihre Bekämpfung. Zeitschrift für angewandte Entomologie 4: 1–144.
- Heise G (1988) Zum Transport von Fledermauswanzen (Cimicidae) durch ihre Wirte. Nyctalus 2: 469–473.
- Henry TJ (2017) Biodiversity of Heteroptera. In: Footitt RG, Adler PH (Eds) Insect Biodiversity, John Wiley & Sons Ltd., Chichester, 279–335. <https://doi.org/10.1002/9781118945568.ch10>
- Horáček I (1983) Remarks on the causality of population decline in European bats. Myotis 21/22: 138–147.
- Horváth G (1913) La distribution géographique des cimicides et lorigine des punaises des lits. Extrait du IXe congrès international de Zoologie Tenu a Monaco, Monaco, 294–299.
- Lanza B (1999) I parassiti dei pipistrelli (Mammalia, Chiroptera) della fauna italiana. Museo Regionale di Scienze Naturali, Torino, 318 pp.

- Loye JE (1985) The life history and ecology of the cliff swallow bug, *Oeciacus vicarius* (Hemiptera: Cimicidae). *Entomologie Medicale et Parasitologie* 23: 133–139.
- Morkel C (1999) Zum Vorkommen von an Fledermäusen (Chiroptera) parasitierenden Bettwanzen der Gattung *Cimex* Linnaeus 1758 in Hessen (Heteroptera, Cimicidae). *Hessische Faunistische Briefe* 18: 38–48.
- Péricart J (1996) Family Cimicidae. In: Aukema B, Rieger C (Eds) *Catalogue of the Heteroptera of the Palaearctic region II*. The Netherlands Entomological Society, Amsterdam, 141–144.
- Poppius B (1912) *Cimex verspertilionis* n.sp. *Meddelanden af Societas pro Fauna et Flora Fennica* 38: 56–58. <https://doi.org/10.5962/bhl.part.2562>
- Povolný D (1957) Review study on cimicids (Het. *Zoologické Listy* 6 (10): 59–80. (in Czech)
- Povolný D, Usinger RL (1966) The discovery of a possibly aboriginal population of the bed bug (*Cimex lectularius* Linnaeus, 1958). *Acta Musei Moraviae, Scientiae Naturales* 51: 237–242.
- Protić Lj, Paunović M (2006) Bat bugs *Cimex dissimilis* (Horváth, 1910) (Heteroptera: Cimicidae) – the first record from Serbia. In: Aukema B (Eds) 3rd Meeting of the International Heteropterists Society, Wageningen, 18–21.
- Quetglas J, Balvín O, lučan RK, Benda P (2012) First records of the bat bug *Cacodmus vicinus* (Heteroptera: Cimicidae) from Europe and further data on its distribution. *Vespertilio* 16: 243–248.
- Reinhardt K (2012) Beobachtungen an einer überwinterten Freilandpopulation der Bettwanze *Cimex lectularius* (Heteroptera, Cimicidae). *Entomologische Nachrichten und Berichte* 56: 101–108.
- Reinhardt K (2014) *Literarische Wanzen. Eine Anthologie*. Neofelis Verlag, 270 pp.
- Reinhardt K, Jacobs DS (2006) Abundance of *Cacodmus villosus* (Stål, 1855) (Heteroptera: Cimicidae) on its host, *Neoromicia capensis* (Chiroptera: Vespertilionidae). *African Entomology* 14(2): 398–400. <https://hdl.handle.net/10520/EJC32679>
- Reinhardt K, Siva-Jothy MT (2007) Biology of the bed bugs (Cimicidae). *Annual Review of Entomology* 52: 351–374. <https://doi.org/10.1146/annurev.ento.52.040306.133913>
- Roer H (1969) Über Vorkommen und Lebensweise von *Cimex lectularius* und *Cimex pipistrelli* (Heteroptera, Cimicidae) in Fledermausquartieren. *Bonner zoologische Beiträge* 4(20): 355–359.
- Roth S, Coulianos C-C, Vinnersten TP, Roligheten E (2018) *Cimex pipistrelli* complex new to Norway and additional records of bed bug species (Cimicidae, Heteroptera) from Norway and Sweden. *Norwegian Journal of Entomology* 65: 118–126.
- Roth S, Balvín O, Siva-Jothy MT, Di Iorio O, Benda P, Calva O, Faundez EI, Anwarali Khan FA, McFadzen M, Lehnert MP, Naylor R, Simov N, Morrow EH, Willassen E, Reinhardt K (2019) Bedbugs evolved before their bat hosts and did not co-speciate with ancient humans. *Current Biology* 29: 1847–1853. <https://doi.org/10.1016/j.cub.2019.04.048>
- Rupp D, Zahn A, Ludwig P (2004) Actual records of bat ectoparasites in Bavaria (Germany). *Spixiana* 27/2: 185–190.
- Rybin N, Horáček I, Červený J (1989) Bats of southern Kirghizia: distribution and faunal status. In: Hanák V, Horáček I, Gaisler J (Eds) *European bat research 1987*. Charles University Press Prague, 421–441.
- Simov N, Ivanova T, Schunger I (2006) Bat-parasitic *Cimex* species (Hemiptera: Cimicidae) on the Balkan Peninsula, with zoogeographical remarks on *Cimex lectularius*, Linnaeus. *Zootaxa* 1190: 59–68. <https://doi.org/10.11646/zootaxa.1190.1.3>
- Usinger RL (1966) *Monograph of Cimicidae*. Thomas Say Foundation Vol. VII, illust. Entomological Society of America, College Park, 585 pp.
- Usinger RL, Beaucournu JC (1967) Sur deux *Cimex* (Insecta, Heteroptera), nouveaux pour la faune française, parasites des chauves-souris. *Annales de parasitologie humaine et comparée* 42: 269–271. <https://doi.org/10.1051/parasite/1967422269>
- Vater G (2015a) Zur Ökofaunistik der Plattwanzen (Heteroptera, Cimicidae), Teil 1.– *Entomologische Nachrichten und Berichte* 59(2): 77–84.
- Vater G (2015b) Zur Ökofaunistik der Plattwanzen (Heteroptera, Cimicidae), Teil 2. – *Entomologische Nachrichten und Berichte* 59(3/4): 217–228.
- Vater G (2016) Zur Ökofaunistik der Plattwanzen (Heteroptera, Cimicidae), Teil 3.– *Entomologische Nachrichten und Berichte* 60(1): 53–62.
- Zaytseva IF (1998) *Konspekt fauny poluzhestkokrylykh nasekomykh* (Heteroptera) Gruzii. Issue 2]. St. Petersburg, 76. [in Russian]

## Supplementary material 1

### An overview of the sampling sites

**Authors:** Ghazaryan A et al. (2023)

**Data type:** .pdf

**Explanation note.** An overview of the sampling sites: coordinates, detected specimens of *Cimex lectularius* in this study and the known bat species and their estimated numbers in each site.

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**Link:** <https://doi.org/10.3897/caucasiana.2.e104244.suppl1>