

Original papers

New data on the distribution of *Carios vespertilionis* Latreille, 1802 (Ixodida, Argasidae) in bats (Chiroptera) from northern Poland

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ABSTRACT. *Carios vespertilionis* Latreille, 1802 is a typical bat parasite, widely distributed in the Palearctic, Oriental and Afrotropical realms. Its localities were found throughout Poland, yet it is considerably more common in the south. Currently, 105 bats have been examined, collected in the period 1999–2017 from 27 localities in northern Poland; 102 *C. vespertilionis* larvae were noted in 6 bats of 3 species of the *Pipistrellus* genus, originating from 5 localities, of which all constitute new locality for the short-legged bat tick. Instances of *C. vespertilionis* larvae wintering in the hosts have been observed as well as occurrence of this parasite outside of bat breeding colonies.

Key words: *Carios vespertilionis*, Chiroptera, *Pipistrellus* genus, hibernate, breeding colonies, northern Poland

Introduction

The tick family Argasidae incorporates approx. 200 species of hematophagous vertebrate parasites, mainly birds and bats [1–8]. However, the level of their understanding, particularly opposed to Ixodidae ticks, is poor. Even the generic classification is controversial, despite a series of studies based on various methods, including use of molecular techniques [9–20]. According to Burger et al. [20] as many as 137 Argasidae species are of unclear status and are assigned to more than one genus. In this context, the taxonomic status of the short-legged bat tick *Carios vespertilionis* Latreille, 1802 remains unclear. According to various sources, this species is sometimes classified in the genus *Argas* [1] or *Carios* [10,21], which in turn was assigned a subgenus status of the genus *Argas* in certain publications [22,23]. However, phylogenetic research, including the latest studies based on molecular analyzes [10,20] have not proven its relationship with Argasinae (that is genus *Argas*), and indicated its belonging to the Ornithodorinae

subfamily (that is distinction of *Carios* from *Argas*). Moreover, the uniformity of *C. vespertilionis* at the specific level has been subject of discussion [24], which undoubtedly requires more extensive research concerning geographic distribution, as well as the range of host specificity and other parasite-host relationships. The short-legged bat tick is, without a doubt, a species with wide distribution in the Old World, known from numerous scattered localities [25–34]. However, full data on the distribution are lacking, particularly in the context of correlation with the host distribution, in relation to the data on the level and seasonal dynamics of infestation.

The Polish localities of *C. vespertilionis* have been recorded throughout the country, yet the southern area of Poland has been better studied in this field [28,35–40]. However, the occurrence of *C. vespertilionis* is considered a common phenomenon in breeding colonies of bats [28] from where the majority of data have been collected. At the same time, there are no data on the occurrence of these mites in other areas, outside of breeding colonies, or

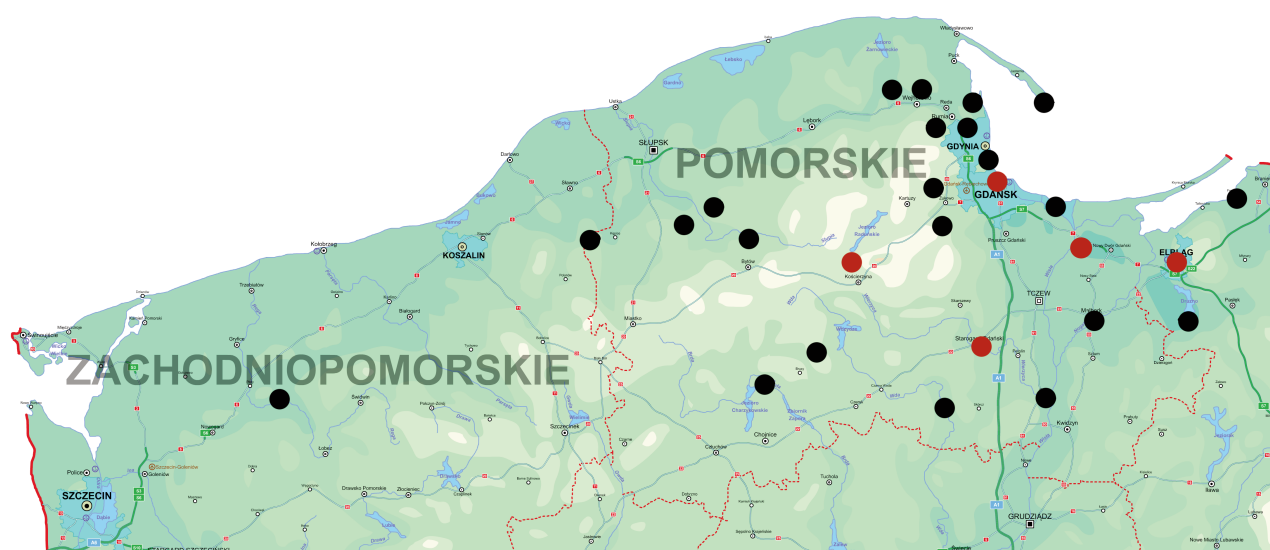


Fig. 1. The map illustrating localities of study
Black points illustrate the places where bats not infested by *C. vespertilionis* were found. Red points shows new records of *C. vespertilionis*

the occurrence in hosts in the winter period. Bats can hibernate in huge winter colonies or lonely in secluded areas, relatively inaccessible to humans, where exposure to infestation of *C. vespertilionis* is smaller. Moreover, handling of hibernating bats is usually avoided during surveys, as it leads to arousals and energy lost, thus sampling of their ectoparasites is rarely possible [41].

Materials and Methods

The study material consisted of 105 bats of the Vespertilionidae family, representing 12 species: *Eptesicus serotinus* (Schreber, 1774), *Myotis daubentonii* (Kuhl, 1817), *M. dasycneme* (Boie, 1825), *M. myotis* (Borkhausen, 1797), *M. nattereri*

(Kuhl, 1817) *Nyctalus noctula* (Schreber, 1774), *Pipistrellus nathusii* (Keyserling et Blasius, 1839), *P. pipistrellus* (Schreber, 1774), *P. pygmaeus* (Leach, 1825), *Plecotus auritus* (Linnaeus, 1758), *P. austriacus* (Fischer, 1829), *Vespertilio murinus* Linnaeus, 1758. The bats were collected in the period 1999–2017 from 27 sites of the Pomerania and the Masurian Lake District (Fig. 1). These were either individuals found dead in winter or summer roosts, or grounded outside due to various injuries that later died in captivity when rehabilitation failed. The dead bats were frozen or were stored in 70% ethyl alcohol solution. All specimens were analysed for the presence of *C. vespertilionis*, using standardized methods developed for the study of mammal parasitic arthropods [42]. The standard infestation

Table 1. The number of *Carios vespertilionis* found on bats in new localities

Collection date	Place of research GPS data	Species	Sex	Number of <i>C. vespertilionis</i>
26.07.2002	Ostaszewo 54°13'N 18°58'E	<i>Pipistrellus pipistrellus</i>	male	1
26.07.2002	Ostaszewo 54°13'N 18°58'E	<i>Pipistrellus pipistrellus</i>	female	1
02.02.2010	Elbląg 54°9'N 19°24'E	<i>Pipistrellus pipistrellus</i>	male	2
01.2012	Gdańsk 54°23'N 18°35'E	<i>Pipistrellus nathusii</i>	male	1
15.06.2012	Ogonki 54°11'N 17°49'E	<i>Pipistrellus nathusii</i>	female	1
06.07.2015	Starogard Gdański 53°59'N 18°28'E	<i>Pipistrellus pygmaeus</i>	female	96

parameters were calculated, including prevalence, mean intensity and the intensity range [43].

Results

Among the 105 examined bats, 6 were infested by short-legged bat tick, for which the name *Carios vespertilionis* has been assumed (Figs 2,3), compliant with the nomenclature used acc. to the Fauna Europaea. The total number of collected ticks was 102 (Table 1), with only larvae being found.



Fig. 2. Larvae of *Carios vespertilionis* on the female *Pipistrellus pygmaeus*



Fig. 3. Gnathosoma of larva *Carios vespertilionis*

The infestation prevalence was 5.7%, with mean intensity of 17 individuals per host and intensity range 1–96. *C. vespertilionis* was found solely on *Pipistrellus* bats, including 4 specimens on 3 *P. pipistrellus* individuals, 2 specimens on 2 *P. nathusii* individuals and 96 specimens on 1 *P. pygmaeus* individual (Table 1).

The ticks originated from 5 localities of the Pomerania, of which all constitute new localities/records of the species (Table 1, Fig. 1). Two bats (*P. pipistrellus* and *P. nathusii*), on which *C. vespertilionis* was found were collected in winter period (fed larvae were found), outside of breeding colonies (Figs 4,5).



Fig. 4. Fed larva of *Carios vespertilionis*

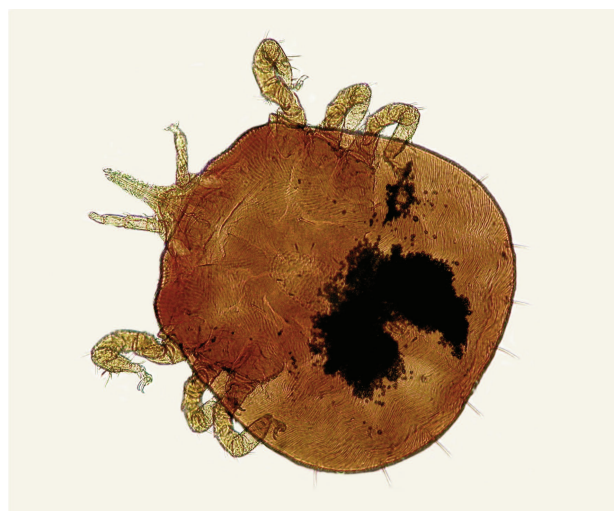


Fig. 5. Fed larva of *Carios vespertilionis* with clearly visible contents of the intestine

The short-legged bat ticks were recorded primarily from the body area of the hosts – singular specimens were found on the abdominal side, in the case of mass infestation in *P. pygmaeus*, the ticks

were located on the abdominal, as well as dorsal portion and near the head.

Discussion

Bats constitute the second largest mammalian order. Moreover, they occur in large aggregations (colonies), which undoubtedly favours the spread of parasites. Thus, they are characterized by a richness of parasitic arthropod fauna, among which the ticks are represented by Argasidae, among others. However, these are thermophilic mites, preferring mainly tropical regions, of which only few have adapted to cooler climate. Thus, only three Argasidae species have been recorded from Poland – two related to birds (*Argas reflexus* Fabricius, 1794 and *A. polonicus* Siuda et al., 1979) and the bat specific *C. vespertilionis* [28,37]. As much as the northern border for Argasidae distribution in Europe runs along the 50° of northern latitude [40], in Poland *C. vespertilionis* and *A. reflexus* cross it significantly and they are noted north of the border [28,44], although the number of localities is lower there. In the currently examined bats originating from 27 localities, *C. vespertilionis* was found only from 5 localities, at the lat. approx. 54° N (Table 1), whereas of the 38 localities previously determined for Poland as many as 36 were located more or less to the south of this boundary (47°–53°N) [28,45].

The occurrence of *C. vespertilionis* on a host in the winter period observed in the present study is not a new phenomenon, as larvae of the species have already been recorded in December [37]. However, not only the sole record of the soft ticks in the winter appears to be interesting, but the finding of larvae fed with blood. However, the lack of more extensive data from the period impedes interpretation, so as to the frequency of the phenomenon, although it is common in certain Ixodidae species wintering on hosts [46,47]. However, determination of the seasonal dynamics of *C. vespertilionis* requires considerably more extensive, long-term study covering much more abundant material.

The presented data provide evidence of *C. vespertilionis* occurrence in bats also outside of breeding colonies. However, it is unclear, that these parasites were recorded only in bats of 3 species of the *Pipistrellus* genus, while the study covered 12 bat species. Indeed, *C. vespertilionis* is considered to be a species particularly associated with *Pipistrellus* spp., yet it occurs in other Vespertilionidae, and

sporadically in other hosts, even including humans and pets [27,29,40]. And thus far it has been recorded from 14 out of 26 bat species distributed in Poland [48–50], which may indicate its high ecological adaptability [28].

References

- [1] Guglielmone A.A., Robbins R.G., Apanaskevich D.A., Petney T.N., Estrada-Peña A., Horak I.G., Shao R., Barker S.C. 2010. The Argasidae, Ixodidae and Nuttalliellidae (Acari: Ixodida) of the world: a list of valid species names. *Zootaxa* 2528: 1-28.
- [2] Dantas-Torres F., Venzal J.M., Bernardi L.F.O., Ferreira R.L., Onofrio V.C., Marcili A., Bermúdez S.E., Ribeiro A.F., Barros-Battesti D.M., Labruna M.B. 2012. Description of a new species of bat-associated argasid tick (Acari: Argasidae) from Brazil. *Journal of Parasitology* 98: 36-45. doi:10.1645/ge-2840.1
- [3] Heath A.C.G. 2012. A new species of soft tick (Ixodoidea: Argasidae) from the New Zealand lesser short-tailed bat, *Mystacina tuberculata* Gray. *Tuhinga* 23: 29-37.
- [4] Venzal J.M., Nava S., Mangold A.J., Mastropaolo M., Casás G., Guglielmone A.A. 2012. *Ornithodoros quilinensis* sp. nov. (Acari, Argasidae), a new tick species from the Chacoan region in Argentina. *Acta Parasitologica* 57: 329-336. doi:10.2478/s11686-012-0034-5
- [5] Venzal J.M., Nava S., González-Acuña D., Mangold A.J., Muñoz-Leal S., Lado P., Guglielmone A.A. 2013. A new species of *Ornithodoros* (Acari: Argasidae), parasite of *Microlophus* spp. (Reptilia: Tropiduridae) from northern Chile. *Ticks and Tick-borne Diseases* 4: 128-132. doi:10.1016/j.ttbdis.2012.10.038
- [6] Venzal J.M., González-Acuña D., Muñoz-Leal S., Mangold A.J., Nava S. 2015. Two new species of *Ornithodoros* (Ixodida; Argasidae) from the Southern Cone of South America. *Experimental and Applied Acarology* 66: 127-139. doi:10.1007/s10493-015-9883-6
- [7] Nava S., Venzal J.M., Terassini F.A., Mangold A.J., Camargo L.M.A., Casas G., Labruna M.B. 2013. *Ornithodoros guaporensis* (Acari, Ixodida: Argasidae), a new tick species from the Guaporé River Basin in the Bolivian Amazon. *Zootaxa* 3666(4): 579-590. doi:10.11646/zootaxa.3666.4.10
- [8] Barros-Battesti D.M., Landulfo G.A., Luz H.R., Marcili A., Onofrio V.C., Famadas K.M. 2015. *Ornithodoros faccinii* n. sp. (Acari: Ixodida: Argasidae) parasitizing the frog *Thoropa miliaris* (Amphibia: Anura: Cycloramphidae) in Brazil. *Parasites and Vectors* 8: 268. doi:10.1186/s13071-015-0877-3

- [9] Filippova N.A. 1966. Argasid ticks (Argasidae). Fauna of SSSR 4 (3), Zoologicheskij Institut Akademii Nauk SSSR, Moscow-Leningrad (in Russian).
- [10] Klompen J.S.H., Oliver Jr J.H. 1993. Systematic relationships in the soft ticks (Acari: Ixodida: Argasidae). *Systematic entomology* 18: 313-331. doi:10.1111/j.1365-3113.1993.tb00669.x
- [11] Black W.C., Piesman J. 1994. Phylogeny of hard- and soft-tick taxa (Acari: Ixodida) based on mitochondrial 16S rDNA sequences. *Proceedings of the National Academy of Sciences of the United States of America* 91: 10034-10038. doi:10.1073/pnas.91.21.10034
- [12] Camicas J.L., Hervy J.P., Adam F., Morel P.C. 1998. Les tiques du monde (Acarida, Ixodida): nomenclature, stades décrits, hôtes, répartition [The ticks of the world (Acarida, Ixodida): nomenclature, described stages, hosts, distribution]. Éditions de l'ORSTOM, Paris, France (in French).
- [13] Nava S., Guglielmone A.A., Mangold A.J. 2009. An overview of systematics and evolution of ticks. *Frontiers in Bioscience* 14: 2857-2877. doi:10.2741/3418
- [14] Estrada-Peña A., Mangold A.J., Nava S., Venzal J.M., Labruna M.B., Guglielmone A.A. 2010. A review of the systematics of the tick family Argasidae (Ixodida). *Acarologia* 50: 317-333. doi:10.1051/acarologia/20101975
- [15] Black W.C., Klompen J.S.H., Keirans J.E. 1997. Phylogenetic relationships among tick subfamilies (Ixodida: Ixodidae: Argasidae) based on the 18S nuclear rDNA gene. *Molecular Phylogenetics and Evolution* 7: 129-144. doi:10.1006/mpev.1996.0382
- [16] Norris D.E., Klompen J.S.H., Black W.C. 1999. Comparison of the mitochondrial 12S and 16S ribosomal DNA genes in resolving phylogenetic relationships among hard ticks (Acari: Ixodidae). *Annals of the Entomological Society of America* 92: 117-129. doi:10.1093/aesa/92.1.117
- [17] Klompen J.S.H., Black W.C., Keirans J.E., Norris D.E. 2000. Systematics and biogeography of hard ticks, a total evidence approach. *Cladistics* 16: 79-102. doi:10.1111/j.1096-0031.2000.tb00349.x
- [18] Klompen J.S.H., Lekveishvili M., Black W.C. 2007. Phylogeny of parasitiform mites (Acari) based on rRNA. *Molecular Phylogenetics and Evolution* 43: 936-951. doi:10.1016/j.ympev.2006.10.024
- [19] Mans B.J., de Klerk D., Pienaar R., de Castro M.H., Latif A.A. 2013. Correction: The mitochondrial genomes of *Nuttalliella namaqua* (Ixodoidea: Nuttalliellidae) and *Argas africanus* (Ixodoidea: Argasidae): estimation of divergence dates for the major tick lineages and reconstruction of ancestral blood-feeding characters. *PLoS One* 8: doi:10.1371/annotation/19fe1c45-57c3-4008-9733-ebdf39202075.
- [20] Burger T.D., Shao R., Labruna M.B., Barker S.C. 2014. Molecular phylogeny of soft ticks (Ixodida: Argasidae) inferred from mitochondrial genome and nuclear rRNA sequences. *Ticks and Tick-borne Diseases* 5: 195-207. doi:10.1016/j.ttbdis.2013.10.009
- [21] Vial L. 2009. Biological and ecological characteristics of soft ticks (Ixodida: Argasidae) and their impact for predicting tick and associated disease distribution. *Parasite* 16: 191-202. doi:10.1051/parasite/2009163191
- [22] Hoogstraal H. 1958. Bat ticks of the genus *Argas* (Ixodoidea, Argasidae), 3. The subgenus *Carios*, a redescription of *A.(C.) vespertilionis* (Latreille, 1802), and variation within an Egyptian population. *Annals of the Entomological Society of America* 51: 19-26. doi:10.1093/aesa/51.1.19
- [23] Roshdy M.A. 1961. Comparative internal morphology of subgenera of *Argas* ticks (Ixodoidea, Argasidae). I. Subgenus *Carios*: *Argas vespertilionis* (Latreille, 1802). *Journal of Parasitology* 47: 987-994. doi:10.2307/3275039
- [24] Hornok S., Szőke K., Tu V.T., Kontschán J., Takács N., Sándor A.D., Halajian A., Földvári G., Estók P., Plantard O., Epis S., Görföl T. 2017. Mitochondrial gene heterogeneity of the bat soft tick *Argas vespertilionis* (Ixodida: Argasidae) in the Palaeartic. *Parasites and Vectors* 10: 109. doi:10.1186/s13071-017-2037-4
- [25] Del Cacho E., Estrada-Peña A., Sanchez A., Serra J. 1994. Histological response of *Eptesicus serotinus* (Mammalia: Chiroptera) to *Argas vespertilionis* (Acari: argasidae). *Journal of Wildlife Diseases* 30: 340-345. doi:10.7589/0090-3558-30.3.340
- [26] Hillyard P.D. 1996. Ticks of north-west Europe. Field Studies Council, Linnean Society of London and the Estuarine and Coastal Sciences Association, Shrewsbury, UK.
- [27] Sylla M., Pourrut X., Faye N., Ba K., Cornet J.P., Camicas J.-L. 2004. Argasidae (Acari: Ixodida) parasites of wild and domestic animals in Senegal: 1 - Review and distribution. *Acarologia* 44: 137-149.
- [28] Siuda K., Stanko M., Piksa K., Górz A. 2009. Ticks (Acari: Ixodida) parasitizing bats in Poland and Slovakia. *Annals of Parasitology* 55: 39-45.
- [29] Krištofik J., Danko Š. 2012. Arthropod ectoparasites (Acarina, Heteroptera, Diptera, Siphonaptera) of bats in Slovakia. *Vespertilio* 16: 167-189.
- [30] Hosseini-Chegeni A., Tavakoli M. 2013. *Argas vespertilionis* (Ixodida: Argasidae): a parasite of pipistrel bat in Western Iran. *Persian Journal of Acarology* 2: 321-330. doi:10.22073/pja.v2i2.10034
- [31] Burazerović J., Čakić S., Mihaljica D., Sukara R., Čirović D., Tomanović S. 2015. Ticks (Acari: Argasidae, Ixodidae) parasitizing bats in the central Balkans. *Experimental and Applied Acarology* 66: 281-291. doi:10.1007/s10493-015-9891-6

- [32] Oba M., Omatsu T., Takano A., Fujita H., Sato K., Nakamoto A., Takahashi M., Takada N., Kawabata H., Ando S., Mizutani T. 2016. A novel Bunyavirus from the soft tick, *Argas vespertilionis*, in Japan. *Journal of Veterinary Medical Science* 78: 443-445. doi:10.1292/jvms.15-0536
- [33] Salmene I. 2016. Argasid ticks (Acari: Ixodida: Argasidae) in Latvia. *Latvijas Entomologs* 53: 125-126.
- [34] Hornok S., Szőke K., Görföl T., Földvári G., Tu V.T., Takács N., Kontschán J., Sándor A.D., Estók P., Epis S., Boldogh S., Kováts D., Wang Y. 2017. Molecular investigations of the bat tick *Argas vespertilionis* (Ixodida: Argasidae) and *Babesia vesperuginis* (Apicomplexa: Piroplasmida) reflect “bat connection” between Central Europe and Central Asia. *Experimental and Applied Acarology* 72: 69-77. doi:10.1007/s10493-017-0140-z
- [35] Rafalski J. 1954. Występowanie w Polsce kleszczy *Argas vespertilionis* Latr. i *Argas reflexus* Fabr. (Arachnida, Ixodoidea) [The occurrence of the ticks *Argas vespertilionis* Latr. and *Argas reflexus* Fabr. (Arachnida, Ixodoidea) in Poland]. *Polskie Pismo Entomologiczne* 24: 165-168 (in Polish with summary in English).
- [36] Haitlinger R. 1978. Pasożyty zewnętrzne nietoperzy Dolnego Śląska. III. Spinturnicidae, Argasidae, Ixodidae (Acarina) [External parasites of Lower Silesian bats. III. Spinturnicidae, Argasidae, Ixodidae (Acarina)]. *Wiadomości Parazytologiczne* 24: 475-490 (in Polish with summary in English).
- [37] Siuda K. 1993. Kleszcze Polski (Acari: Ixodida). Cz. 2, Systematyka i rozmieszczenie. Polskie Towarzystwo Parazytologiczne, Warszawa (in Polish).
- [38] Siuda K., Piksa K., Wiertel R., Górz A. 2000. Ticks (Acari: Ixodida) parasiting bats in Poland. *Acta Parasitologica* 45: 215.
- [39] Piksa K., Skwarek M., Siuda K. 2011. Argasid and spinturnicid mite load on swarming bats in the Tatra Mountains, Poland. *Folia Parasitologica* 58: 322-325. doi:10.14411/fp.2011.03
- [40] Nowak-Chmura M., Siuda K. 2012. Ticks of Poland. Review of contemporary issues and latest research. *Annals of Parasitology* 58: 125-155.
- [41] Ciechanowski M. 2015. Habitat preferences of bats in anthropogenically altered, mosaic landscapes of northern Poland. *European Journal of Wildlife Research* 61: 415-428. doi:10.1007/s10344-015-0911-y
- [42] Kadulski S., Izdebska J.N. 2006. Methods used in studies of parasitic arthropods in mammals. In: *Arthropods. Epidemiological importance*. (Eds. A. Buczek, Cz. Błaszak). Koliber, Lublin: 113-117.
- [43] Margolis L., Esch G.W., Holmes J.C., Kuris A.M., Schad G. 1982. The use of ecological terms in parasitology (report of an ad hoc Committee of the American Society of Parasitologists). *Journal of Parasitology* 68: 131-133. doi:10.2307/3281335
- [44] Izdebska J.N., Fryderyk S., Kentzer B. 2008. A mass occurrence of the European pigeon tick *Argas reflexus* (Acari, Argasidae) in Gdańsk. In: *Arthropods. Influence on host*. (Eds. A. Buczek, Cz. Błaszak). Akapit, Lublin: 47-50.
- [45] Orlova M. V., Zapart A. 2012. Interaction of ectoparasites in cohabitating colonies of pond bats *Myotis dasycneme* (Boie, 1825) and species of genus *Pipistrellus* from northern Poland. *Annals of Parasitology* 58: 211-215.
- [46] Izdebska J.N. 1998. Występowanie *Dermacentor reticulatus* (Acari, Ixodidae) u żubra (*Bison bonasus*) z Puszczy Białowieskiej [The occurrence of *Dermacentor reticulatus* (Fabricius, 1794) (Acari, Ixodidae) on the bison (*Bison bonasus*) from the Białowieża Primeval Forest]. *Przegląd Zoologiczny* 42: 219-221 (in Polish with summary in English).
- [47] Karbowski K., Izdebska J.N., Czapliska U., Wita I. 2003. Przypadki zimowania kleszczy z rodziny Ixodidae na żywicielach w Puszczy Białowieskiej [Cases of survival of the winter by Ixodidae ticks on the hosts in the Białowieża Primeval Forest]. In: *Stawonogi i żywiciele [Arthropods and hosts]*. (Eds. A. Buczek, Cz. Błaszak). Liber, Lublin: 77-82 (in Polish with summary in English).
- [48] Sachanowicz K., Ciechanowski M., Piksa K. 2006. Distribution patterns, species richness and status of bats in Poland. *Vespertilio* 9: 151-173.
- [49] Ciechanowski M., Bogdanowicz W. 2014. Ssaki (Mammalia). In: *Fauna Polski - charakterystyka i wykaz gatunków [Fauna of Poland - characteristics and checklist of species]*. (Eds. W. Bogdanowicz, E. Chudzicka, I. Filipiuk, E. Skibińska), Vol. 4, Muzeum i Instytut Zoologii PAN, Warszawa: 429-513 (in Polish).
- [50] Uhrin M., Hüttmeir U., Kipson M., Estók P., Sachanowicz K., Bücs S., Karapandža B., Paunović M., Presetnik P., Bashta A.-T., Maxinová E., Lehotská B., Lehotský R., Barti L., Csösz I., Szodoray-Paradi F., Dombi I., Görföl T., Boldogh S.A., Jére C., Pocora I., Benda P. 2016. Status of Savi's pipistrelle *Hypsugo savii* (Chiroptera) and range expansion in Central and south-eastern Europe: a review. *Mammal Review* 46: 1-16. doi:10.1111/mam.12050

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