Acta Parasitologica (2024) 69:106–120
https://doi.org/10.1007/s11686-023-00732-8

REVIEW

Bat Ectoparasites (Acari, Diptera, Hemiptera, Siphonaptera) in the Grand Maghreb (Algeria, Libya, Mauritania, Morocco and Tunisia): A Literature Review and New Data

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Received: 29 May 2023 / Accepted: 26 October 2023 / Published online: 25 November 2023

Abstract

Background Arthropods parasites of bats play a crucial role in both ecological and public health contexts, as they have the potential to transmit zoonotic agents. The study aims to identify the distribution, and host-parasite associations of bat ectoparasites in the Grand Maghreb region (Algeria, Libya, Mauritania, Morocco and Tunisia), which has been largely understudied.

Methods A thorough analysis of published records was conducted and we included our own field data.

Results The checklist reveals a total of 43 ectoparasite species, encompassing a range of taxa. The list comprises 9 tick species, 11 mite species (including a chigger-mite), 11 bat fly species, 3 species of bugs, and 9 species of fleas. Extensive research efforts uncovered 141 host-parasite associations. Our data presents several new country records, documenting for the first time the presence of *Carios vespertilionis* and *Raymondia huberi* in Tunisia, *Ixodes simplex* and *Spinturnix plecotinus* in Algeria.

Conclusion By compiling and analysing available information, we have provided for the first time an up-to-date checklist of bat ectoparasites and their host associations in the region. This knowledge contributes to a better understanding of the epidemiological implications associated with bat ectoparasites, emphasizing their ecological and public health importance. The study's findings call for continued investigations and monitoring of bat ectoparasites to mitigate potential risks and safeguard both human and animal populations.

Keywords Argasidae · Fleas · Ischnopsyllidae · Ixodidae · North Africa · Nycteribiidae

Introduction

Bats (Mammalia: Chiroptera), with almost 1500 species described are the most diverse and most widely distributed mammalian group [1]. Bats are unique among mammals in their capability to truly fly, thus able to cover long distances during seasonal migrations, and their potential for very large, colonial populations as well [2]. Their ability to occupy a broad range of ecological niches as well as

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natural history traits such as a long lifespan, dense social aggregations in roosts, torpor, and high and diverse numbers of parasites distinguish them from most other mammalian groups [3]. These characteristics coupled with their strong immunity make them ideal reservoir hosts for many zoonotic pathogens [4, 5].

Ectoparasites of bats are diverse and represent several distinct evolutionary lineages [5]. According to literature, they may reduce host reproductive success and survival [6], and contribute by a pivotal transmission and maintenance of several pathogens (bacteria, protozoans or viruses), including spores of pathogenic fungi [7], among these, several infectious agents are common to humans and domestic animals [8].

The Maghreb region (also known as the Grand Maghreb or Northwest Africa) includes five countries, respectively from W to E: Mauritania, Morocco, Algeria, Tunisia, and Libya. It covers a huge surface area (6,045,741 km2), equivalent to the European Union's total land area. At a regional level, its particular geographical position is considered as biogeographical crossroads between the Mediterranean, Saharo-Sindian and Ethiopian regions. This location exhibits a great physiographic complexity and climatic diversity resulting in multiple transition zones between biomes within its boundaries. A large variety of habitat types, from temperate humid forests to the most extreme deserts on earth are to be found here. These habitat types promote a high degree of complexity and richness of fauna and flora [9].

In recent decades, bat research around the globe has become increasingly focused on understanding the interactions between bats, parasites, and pathogens given the significant role of bats in human and animal health and can be the cause of significant economic losses especially if they lead to a collapse in local bat populations, e.g., bat population crashes in North America caused by the recent often fatal white-nose syndrome [10] or by causing massive human epidemics, e.g., Ebola in Africa, Nipah in Asia, and the most recent pandemic SARS-CoV-2 which are believed to originate in bats and spread to humans and other animals [11]. Among these, there are still some regions with little information on this topic. For example, a closer look to the literature on bats in the Maghreb region, reveals a number of gaps and shortcomings related to bat parasitism. Furthermore, documentation of vector-borne diseases among native wildlife, including bats, are almost non-existent. Globally, knowledge of the ectoparasites of bats in the Maghreb region is very limited, and has always been only fragmentary.

To enhance our understanding of the bat ectoparasite community in the Maghreb region, we have performed a systematic literature review and used the extracted data to update the knowledge on the diversity, distribution and host association of these parasites. We limited our study to those ectoparasite groups which are known to regularly feed on hosts' blood and were proven (or at least suggested) to have a vectorial role for zoonotic diseases. The present checklist therefore provides a strong tool that provides useful baseline information for (i) more targeted research on parasites of bats in the region and on vector-borne diseases, and for (ii) a better under-standing of certain related epidemiological problems.

Materials and Methods

We used a three-step algorithm following Sándor *et al*. [7] for assessing the records in this paper. As a first step, a database search was conducted using the following keywords: "parasites" OR "ectoparasites" OR "ticks" OR "hard ticks" OR "soft ticks" OR "mites" OR "flies" OR "bugs" OR "fleas" OR "Ixodidae" OR "Argasidae" OR "Gastronyssidae" OR "Macronyssidae" OR "Spinturnicidae" OR "Nycteribiidae" OR "Streblidae" OR "Siphonaptera" OR "Cimicidae" AND "bats" AND "North-Africa" OR "North-West Africa" OR "Algeria" OR "Mauritania" OR "Morocco" OR "Libya" OR "Tunisia" in the following databases: Web of Science, Zoological Record, Google Scholar, PubMed, Science Direct, Global Biodiversity Information Facility (www.gbif.org), and the Biodiversity Heritage Library (www.biodiversitylibrary.org). To ensure that all publications were included, we repeated the same process using the same keywords in Spanish and French. As a further step, an analysis of the original publications was conducted, as well as a trace of the references cited in these works. This process was repeated until no new references were found. In the third step, we extracted each individual host-parasite record from the papers, noting the parasite and host species, number of collected parasite, sex and/or development stage (if) mentioned, and the location (including department/province and country). The taxonomical and binominal names of hosts were updated to those currently accepted, according to the most recent taxonomical opinions [1], while ectoparasite nomenclature followed the most recent works in their respective domains [7, 12–15].

In addition to published records, we supplemented the checklist with original, unpublished material from Algeria and Tunisia. We collected bat ectoparasites at ten different locations within these countries in 2015 and 2016, and between 2019 and 2022. Bats were captured using mist nets set up during evening at various locations such as natural corridors, above streams and water ponds, or at the entrance of roosts. Each captured bat was examined for the presence of ectoparasites. Collected ectoparasites were placed in 75% alcohol with the relevant data (bat host, locality, date, etc.). Prior to the analysis, bats were kept separate to avoid potential parasite transfers. Collected ectoparasites were identified

according to Rudnick [12], Dusbabek [13], Jobling [16], Usinger [17] and Estrada-Peña *et al*. [18].

All data were entered into a tabular database system (Microsoft Excel, Microsoft Corp., Redmond, WA, USA), and individually georeferenced to create a general distribution map.

Results and Discussion

Based on the systemic analysis of the published data between 1910 and 2022 and our original material, 505 records of 2173 ectoparasites belonging to 43 species (including 17 cases of free stages of certain tick species) were obtained from across 109 localities of the Grand Maghreb (Fig. 1), covering all studied countries. These records were extracted from a number of 53 publications from a total of 118 papers assessed in the bat-parasite reference corpus established. Listed below are the species of ectoparasites found to parasitize bats in the Grand Maghreb, along with their distribution, hosts, and relevant remarks (records for each host-parasite association are listed in Table 1).

Systematic Account

Class Arachnida

Subclass Acari

Order Ixodida

Family Argasidae Koch, 1844

Chiropterargas boueti Roubaud and Calas-Belcour, 1933, has a wide distribution, primarily on the African continent, reaching Central and South Africa, with scattered records in Central Asia and the Middle East [7, 68]. It is primarily a tick of cave dwelling tropical bats, with dominant hosts being *Rhinopoma* spp., and an extralimital occurrence in the Western Palearctic [7]. Within the Maghreb region, this species is so far known from two distinct records of free stage individuals from Morocco [20, 69] and Mauritania [19].

Secretargas transgariepinus White, 1846, is widely distributed from Africa to southern Europe, it is primarily a parasite of crevice dwelling bats [70]. Its host spectrum

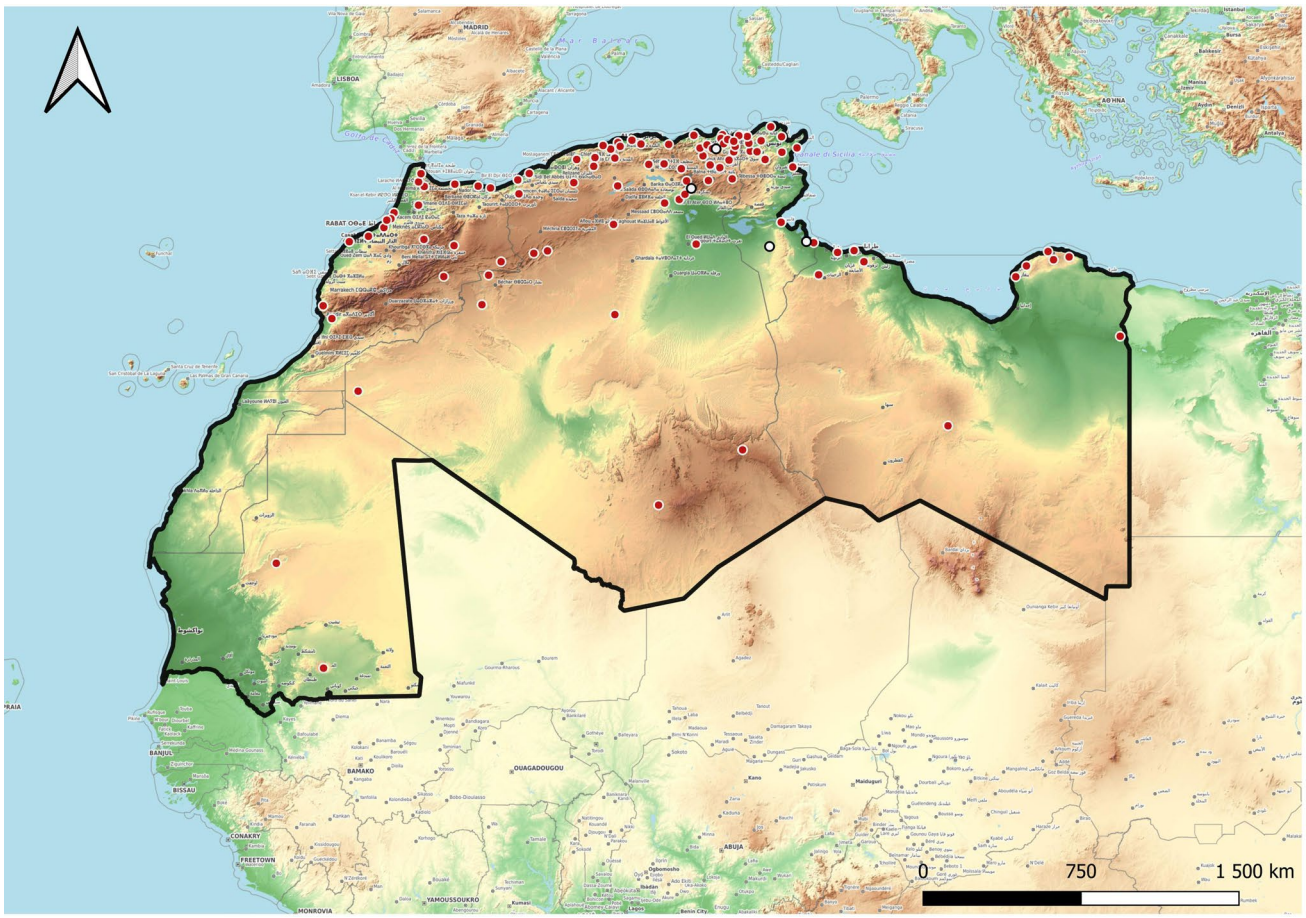

Fig. 1 Map showing the collecting localities of bat ectoparasites between 1910 and 2022, in the Grand Maghreb (red dots: published records, white dots: original records)

Table 1 List of arthropods (Acari, Diptera, Hemiptera, Siphonaptera) parasites of bats recorded in Maghreb Region, based on published data between 1910 and 2022

Parasite species	Host species	Sex/stage	Distribution	Source
Chiropterargas boueti	Free stage	UN, N	MA, MR	[19, 20]
Secretargas transgariepinus	*Eptesicus isabellinus*	A, N, L	DZ	[21, 22]
	Hypsugo savii	A, N, L	DZ, MA	[21, 23]
	Myotis mystacinus	L	MA	[23]
	Chiroptera spp.	UN	DZ	[24]
	Free stage	L	DZ	[22]
Carios vespertilionis	*Rhinopoma cystops*	L	LY	[25]
	Nyctinomus aegyptiacus	L	DZ, MA	[21, 26]
	Eptesicus isabellinus	L	LY	[25]
	Nyctalus lasiopterus	UN	MA	[27]
	Pipistrellus kuhlii	A, L	DZ, LY, **TN***	[25, 28]—Current study
	Pipistrellus pipistrellus	UN	DZ	[29]
	Plecotus christii	L	LY	[25]
	Plecotus gaisleri	L	DZ	[21]
	Free stage	UN, N	MA, MR	[19, 30, 31]
Ornithodoros coniceps	*Pipistrellus kuhlii*	L	TN	[32]
Ixodes ricinus	*Rhinolophus hipposideros*	N, L	DZ	[21]
	Tadarida teniotis	L	DZ	[21]
	Eptesicus isabellinus	UN	DZ	[21]
	Pipistrellus kuhlii	UN	DZ	[21]
Ixodes simplex	*Miniopterus schreibersii*	L	**DZ***, MA	[33]—Current study
Ixodes vespertilionis	*Rhinolophus blasii*	L	DZ	[34, 35]
	Rhinolophus euryale	L	DZ	[34]
	Rhinolophus ferrumequinum	A, L	DZ, MA	[33–35]
	Rhinolophus hipposideros	L	DZ	[36]
	Asellia tridens	L	DZ	Current study
	Miniopterus schreibersii	L	DZ	[34, 35]
	Myotis capaccinii	A, L	DZ	[21, 34]
	Myotis emarginatus	A, L	DZ	[21]
	Myotis punicus	A, N, L	DZ, MA	[21, 34, 36–38]
	Pipistrellus kuhlii	A	DZ	[35]
	Free stage	M, F, N, L	DZ, MA	[30, 36, 37, 39–42]
Rhipicephalus sanguineus s.l	*Hypsugo savii*	UN	DZ	[21]
	Myotis capaccinii	UN	DZ	[21]
	Myotis punicus	UN	DZ	[21]
Hyalomma dromedarii	*Pipistrellus kuhlii*	A	DZ	[21]
Parasteatonyssus hoogstraali	*Tadarida teniotis*	N	LY	[25]
Steatonyssus occidentalis	*Eptesicus isabellinus*	L	DZ	[34]
	Myotis punicus	L	LY	[25]
	Pipistrellus kuhlii	L	DZ	[34]
Steatonyssus periblepharus	Pipistrellus kuhlii	A, L	DZ, LY	[25, 43, 44]
Eyndhovenia euryalis euryalis	*Rhinolophus blasii*	A, L	DZ	[21, 34, 35]
	Rhinolophus ferrumequinum	A	DZ	[45]
	Rhinolophus mehelyi	A, N, L	DZ, MA	[21, 33, 34]
	Plecotus gaisleri	A	DZ	[21]
Eyndhovenia euryalis oudemansi	*Rhinolophus euryale*	A	MA	[33]
	Rhinolophus mehelyi	L	MA	[33]
Spinturnix acuminata acuminata	*Nyctalus lasiopterus*	A	MA	[33]
	Pipistrellus kuhlii	A	LY	[25]

Table 1 (continued)

Parasite species	Host species	Sex/stage	Distribution	Source
Spinturnix mystacina	*Myotis zenatius*	A, N, L	MA	[33]
Spinturnix plecotinus	*Plecotus gaisleri*	A	**DZ***, MA	[33]—Current study
Spinturnix psi	*Miniopterus schreibersii*	UN	MA	[27, 33]
Spinturnix myoti	*Tadarida teniotis*	A	LY	[25]
	Myotis capaccinii	A, L	DZ	[21]
	Myotis emarginatus	L	DZ	[21, 35]
	Myotis punicus	A, N	DZ, MA, LY, TN	[21, 34, 35]
Grandjeana mauritanica	*Rhinopoma cystops*	L	MR	[46]
Basilia daganiae	*Pipistrellus hanaki*	M, F	LY	[25, 47]
Basilia mediterranea	*Pipistrellus hanaki*	F	LY	[48]
Nycteribia latreillii	*Rhinolophus blasii*	M, F	DZ	[21, 35]
	Rhinolophus ferrumequinum	F	DZ	[35]
	Rhinolophus hipposideros	M, F	MA	[49]
	Rhinolophus mehelyi	M	MA	[50]
	Miniopterus schreibersii	M, F	DZ, MA	[35, 50]
	Myotis capaccinii	M, F	DZ	[21]
	Myotis emarginatus	M, F	DZ	[21, 34]
	Myotis punicus	M, F	DZ, MA, LY, TN	[21, 48–51]
Nycteribia pedicularia	*Rhinolophus blasii*	M	DZ	[34]
	Rhinolophus euryale	M, F	DZ	[21, 34]
	Rhinolophus ferrumequinum	M	DZ	[34, 35]
	Rhinolophus mehelyi	F	DZ, MA	[21, 50]
	Miniopterus schreibersii	M, F	DZ	[35]
	Myotis capaccinii	M, F	DZ	[51]
	Myotis punicus	UN	DZ, TN	[35, 47, 49]
Nycteribia schmidlii schmidlii	*Rhinolophus blasii*	M, F	DZ	[34]
	Rhinolophus clivosus	M, F	DZ	[21]
	Rhinolophus ferrumequinum	M, F	DZ, MA	[21, 35, 49, 50]
	Asellia tridens	M, F	DZ	[21]
	Rhinopoma cystops	M, F	DZ	[21]
	Miniopterus schreibersii	M, F	DZ, MA	[49, 50]
	Myotis capaccinii	M, F	DZ	[51]
	Myotis punicus	F	TN	[52]
	Plecotus gaisleri	M, F	DZ	[21]
Nycteribia vexata	*Rhinolophus euryale*	F	TN	[49]
	Rhinolophus hipposideros	M, F	DZ	[49]
	Rhinolophus mehelyi	M, F	MA	[50]
	Miniopterus schreibersii	M, F	MA	[50]
	Myotis punicus	M, F	DZ, MA, LY, TN	[25, 48–51]
Penicillidia conspicua	*Rhinolophus mehelyi*	UN	DZ	[27, 51]
	Miniopterus schreibersii	M	DZ, MA	[27, 49, 51]
	Myotis punicus	F	MA, TN	[27, 52]

Table 1 (continued)

Parasite species	Host species	Sex/stage	Distribution	Source
Penicillidia dufourii	*Rhinolophus blasii*	M, F	DZ	[21]
	Rhinolophus euryale	M, F	DZ, TN	[21, 47, 49]
	Rhinolophus ferrumequinum	M, F	DZ	[35, 50]
	Rhinolophus hipposideros	M, F	DZ	[49]
	Rhinolophus mehelyi	F	MA	[50]
	Asellia tridens	M, F	DZ	[21]
	Miniopterus schreibersii	M, F	DZ, MA	[21, 47, 50]
	Myotis emarginatus	M, F	DZ	[21]
	Myotis punicus	M, F	DZ, MA, TN	[47, 49–51]
Phthiridium biarticulatum	*Rhinolophus blasii*	M, F	DZ	[21, 34, 35, 48, 53]
	Rhinolophus euryale	M, F	DZ, TN	[21, 34, 48, 49, 53]
	Rhinolophus ferrumequinum	M, F	DZ, MA, TN	[21, 34, 35, 49, 52]
	Rhinolophus hipposideros	M, F	MA	[49]
	Rhinolophus mehelyi	M, F	DZ, LY	[21, 47, 48, 53, 54]
	Miniopterus schreibersii	M, F	DZ	[21, 47]
	Myotis capaccinii	M, F	DZ	[21]
	Myotis punicus	M, F	DZ, TN	[21, 47, 49, 52]
Brachytarsina flavipennis	*Rhinolophus blasii*	M, F	DZ	[21, 34, 35]
	Rhinolophus euryale	M, F	MA	[27]
	Rhinolophus ferrumequinum	F	DZ, TN	[21, 34, 35, 52]
	Rhinolophus hipposideros	M, F	DZ, MA	[27, 54]
	Rhinolophus mehelyi	M, F	DZ,	[47, 48, 50, 54]
	Miniopterus schreibersii	M, F	DZ, TN	[21, 52, 54]
	Myotis capaccinii	F	DZ	[21]
	Myotis punicus	M, F	DZ, MA	[21, 47, 50]
	Chiroptera sp.	F	DZ	[55]
Raymondia huberi huberi	*Rhinolophus clivosus*	M, F	DZ	[21]
	Nyctinomus aegyptiacus	F	DZ, **TN***	[21]—Current study
Cacodmus vicinus	*Eptesicus isabellinus*	M, F	DZ	[21]
	Pipistrellus kuhlii	M, F	DZ, LY, TN	[21, 48, 56]
	Pipistrellus pipistrellus	F	DZ	[21]
Cimex lectularius	Pipistrellus kuhlii	F	DZ, LY	[21, 57]
	Pipistrellus pipistrellus	F	DZ	[21]
Cimex pipistrelli	*Eptesicus isabellinus*	F	DZ	[21]
	Hypsugo savii	F	DZ	[21]
	Pipistrellus kuhlii	F	DZ	[21]
	Pipistrellus pipistrellus	F	DZ	[21]
Ischnopsyllus consimilis	*Pipistrellus kuhlii*	M, F	LY	[48]
Ischnopsyllus hispanicus	*Myotis zenatius*	UN	MA	[27]
Ischnopsyllus intermedius	*Eptesicus isabellinus*	F	DZ, MA, LY	[21, 27, 48, 58, 59]
	Pipistrellus pipistrellus	UN	MA	[60]
Ischnopsyllus octactenus	*Rhinolophus ferrumequinum*	F	MA, TN	[27, 50]
	Hypsugo savii	F	DZ	[21]
	Pipistrellus kuhlii	UN	DZ, MA, TN	[21, 33, 61–63]
	Pipistrellus pipistrellus	F	DZ	[34]
Nycteridopsylla longiceps	*Eptesicus isabellinus*	F	DZ	[21]
	Pipistrellus kuhlii	UN	DZ	[21, 50]

Table 1 (continued)

Parasite species	Host species	Sex/stage	Distribution	Source
Rhinolophopsylla unipectinata arabs	*Rhinolophus euryale*	F	DZ, MA, TN	[21, 63, 64]
	Rhinolophus ferrumequinum	M, F	DZ, MA, TN	[21, 27, 53, 62–66]
	Rhinolophus mehelyi	M	DZ, LY	[48, 61]
	Miniopterus schreibersii	M, F	DZ	[21, 64]
	Myotis puncius	M, F	MA, LY, TN	[27, 48, 62]
	Plecotus gaisleri	F	MA	[67]
Araeopsylla gestroi	*Tadarida teniotis*	M, F	DZ, LY	[25, 48, 53]
	Nyctinomus aegyptiacus	M, F	DZ	[21]
Synosternus cleopatrae pyramidis	*Rhinopoma cystops*	F	MA	[62]
	Tadarida teniotis	F	MA	[62]
Xenopsylla ramesis	*Rhinopoma cystops*	F	MA	[62]

Host species are listed according to family in systematic order (Rhinolophidae, Hipposideridae, Rhinopomatidae, Emballonuridae, Mollosidae, Miniopteridae and Vespertilionidae) and in alphabetic order within each family. Country abbreviation: Algeria (DZ), Libya (LY), Mauritania (MR), Morocco (MA) and Tunisia (TN). Alphanumeric designations: Male (M), F (Female), Adults (A), Nymphs (N), Larvae (L), and Unspecified/Unknown (UN)

*First record for a particular region

includes at least eight genera [7]. In this review, three bat species were found to host this soft tick in two countries, Algeria and Morocco (Table 1).

Carios vespertilionis (Latreille, 1796) is an endophilic and nocturnal species that occurs in the habitats of both migrating and nesting populations of several bat species, e.g., attics, tree holes and caves [70]. It is wildly distributed in Europe, Asia, and Africa [68]. It was found in the Maghreb region both in free stages and on six bats species belonging to the genera *Pipistrellus*, *Plecotus* and *Tadarida*, and in free stage as well. The species has 46 published records in four countries in the region (Algeria, Libya, Mauritania and Morocco), hereby we report the first individuals collected in Tunisia (2 larvae from *Pipistrellus kuhlii*, Ben Gerdane, Southern Tunisia 33.143657N, 11.191190E, 19.09.2019).

Ornithodoros (*Alectorobius*) *coniceps* (Canestrini, 1890), is the only species belonging to this genus found on bats [32, 71]. *O. coniceps* is a tick closely related to wild and domestic pigeons and is also common other birds [71]. According to the latter author, the record of this soft tick on bats comes from Tunisia, where it was found associated with *P. kuhlii* collected in a building near Tunis (Table 1). This Palearctic tick is mainly associated to habitat of its main host, pigeons, and is found in rocky areas like cliffs, wells, caves, ravines, stables, pigeon lofts as well as human habitations [72].

Family Ixodidae Koch, 1844

Ixodes ricinus (Linnaeus, 1758) is a generalist tick, associated with most groups of vertebrates and shows a European and North African distribution [73]. Species of the genera *Asellia*, *Eptesicus*, *Pipistrellus*, *Rhinolophus,* and *Tadarida* were found to be infested by this tick within the Maghreb region. *Ixodes ricinus* is considered "accidental" on bats of central Europe belonging to the genera *Rhinolophus* and *Myotis* [74].

Ixodes simplex Neumann, 1906, is an endophilic, cave dwelling tick species wide-spread in the western and eastern parts of the Mediterranean basin as well as from central Europe, where *Miniopterus schreibersii* represents its primary host [74, 75]. Within the Maghreb, it was known only from a single record originating from Morocco from *M. schreibersii* [67]. Our material consists of several individuals from Algeria, collected on the same host as in Morocco. It is a first record for the fauna of the Algeria (four larvae and three nymphs, from five individuals of *M. schreibersii*, Bir Osman, Hammam Debagh, Guelma, Algeria-36.440771N, 7.275187E, on 6 and 19.10.2022).

Ixodes vespertilionis Koch, 1844, is an oligoxenous parasite of bats from the Hipposideridae, Rhinolophidae and Vespertilionidae families, widespread throughout much of Europe, Asia and Africa [76]. It represents a typical cave-dwelling species that occurs also in similar underground environments such as mines and cellars [74]. This species was found to parasitize at least eight host species in Algeria and Morocco. Hereby we re-port the first observation on *Asellia tridens* in the region (three nymphs from two individuals of *A. tridens*, Nergine, Tebessa, Algeria—34.392014N, 7.608415E, on 25.06.2016), thus reporting also a new host-parasite association.

Rhipicephalus sanguineus [sensu lato] (Latreille, 1806) is a three-host endophilous tick, that feeds mainly on dogs and

other carnivores, but can be found also on other hosts [77]. Within the Maghreb, records originating from Algeria of this tick infesting bats were considered "as accidental" [21], where few adults were collected from three host species, *Myotis capaccinii*, *M. punicus,* and *Hypsugo savii*.

Hyalomma dromedarii Koch, 1844, has a two or a three-host lifecycle. It occurs in Mediterranean, steppe and desert climates, where it is associated to the camel, but also other domestic mammals can harbour it [78]. *Pipistrellus kuhlii* (the *deserti* form) was found to host the camel tick and was regarded as incidental [21].

Order Mesostigmata

Family Macronyssidae Oudemans, 1936

Parasteatonyssus hoogstraali (Keegan, 1956) was originally described from *Tadarida teniotis* and documented on this host in Africa, Europe, and Asia [33, 79]. It was found on *T. teniotis* in Libya (Table 1), this record representing the only report in the region, however, given the broad distribution of its primary host (and the secondary hosts, the *Pipistrellus* group, too [25]) its presence in other parts of the Maghreb is highly likely. Other parasites belonging to the latter genus are also expected e.g., *P. nyctinomi*, a specific mite to the Egyptian Free-tailed Bat, *Nyctinomus aegyptiacus* [79].

The species of the genus *Steatonyssus* genus are considered as dendrophilous oligoxenic parasites and their hosts are usually tree dwelling bat species [80]. These mites are cosmopolitan species and their host range includes other species of the families Miniopteridae and Vespertilionidae [44]. Within this genus, two species were reported on bats in the Maghreb region, *Steatonyssus occidentalis* (Ewing, 1933), and *S. periblepharus* Kolenati, 1858. The former species has been reported on three hosts from Algeria and Libya. In Europe, it was found to occur on a large spectrum of hosts of the genera *Eptesicus*, *Myotis* and *Pipistrellus* [81].

Steatonyssus periblepharus is known as specific parasite of bats of the genus *Pipistrellus*, and it has a similar distribution range to the previous species [44]. *Pipistrellus kuhlii* was found infested by this mite in Algeria and Libya. In Europe, occasional reports are known from other hosts such as bats in the family Miniopteridae, Rhinolophidae, and Vespertilionidae [80].

Family Spinturnicidae Oudemans, 1902

Eyndhovenia euryalis is a typical ectoparasite of horseshoe bats (genus *Rhinolophus*). Two subspecies have been described, namely, *E. euryalis euryalis* (Canestrini, 1885) parasitizing mainly *Rhinolophus euryale* and *E. euryalis oudemansi* (Eyndhoven, 1941) parasitizing mainly *R. ferrumequinum* [82, 83]. Maghrebian records of *E. e. euryalis* come Morocco and Algeria, where it was found on several host species (Table 1). In Europe, the host spectrum of this mite includes at least seven species of the genus *Miniopterus, Myotis* and *Rhinolophus* [83].

Eyndhovenia euryalis oudemansi has a similar host range as the previous species, with reports from two rhinolophid species, exclusively from Morocco. In Europe, *E. euryalis oudemansi* has been found on representatives of the family Rhinolophidae and occasionally Vespertilionidae [84].

Spinturnix is the most abundant and widespread genus of Spinturnicidae with over 50 species, mostly recorded from vesper bats (Vespertilionidae) in both the Old and New Worlds [84, 85]. In the Maghreb region, this genus is the most diversified of mites, where five species have been reported to date.

Spinturnix acuminata acuminata (Koch, 1836) is widespread mite in the Palearctic, and it is mostly found associated to bats of the genus *Nyctalus* [84], beside its primary hosts, it can occasionally be found on other hosts species [85]. Here, two host species of the genus *Nyctalus* and *Pipistrellus* were infested by this mite.

Spinturnix myoti (Kolenati, 1856) is one of the most prevalent wing-mites specific to bats, in particular those of the genus *Myotis*. Within the Maghreb it was found parasitizing its main host *Myotis punicus*, as well as other hosts including those belonging to the genus *Plecotus* and *Tadarida* (Table 1). *Spinturnix myoti* is restricted in Europe to three main hosts, *M. blythii, M. capaccinii,* and *M. myotis* [84]. This parasite has a wide range of distribution through the Palearctic, where it is also found on other bat species than those cited below [84].

Spinturnix mystacina (Kolenati) is so far known in the Maghreb region by a single record originating from Morocco (Table 1). This species is presumably a mite of western central Palaearctic region, with an unknown eastern boundary [85]. It parasitizes primary *M. mystacinus*, and other smaller *Myotis* species as well as bats belonging to *Eptesicus*, *Nyctalus* and *Plecotus* genera [84].

Spinturnix plecotinus (Koch, 1839) is specific to bats of the genus *Plecotus* [33], however, sporadic records on other bat species have also been reported [80]. According to our review, this mite has been so far known only from Morocco, found on *Plecotus gaisleri*. Here, we report its presence for the first time in Algeria. Our findings came from Ghoufi (Batna province, 35.0515N, 6.1670E), and consists of three parasites collected in 2016 from the same host species. *Spinturnix plecotinus* is widely distributed in Eurasia and North Africa [84].

Spinturnix psi (Kolenati, 1856) occurs first of all on different species of the genus *Miniopterus* and more rarely also on some species of the genus *Myotis* [84]. This parasite is distributed in the Palaearctic, Oriental and Australasian regions,and in Madagascar [82]. In the Maghreb,

it is found on its primary host species, *M. schreibersii* (Table 1).

Order Trombidiformes

Family Trombiculidae Ewing, 1929

Grandjeana mauritanica Kalúz and Ševčík, 2014 is a newly described species of chigger mite and the only representative of its genus in northwest Africa [46]. It was found on *Rhinopoma cystops* in Mauritania. Its presence in other parts of the Maghreb is highly likely, given that *R. cystops* has the broadest distribution range among free-tailed bats, covering deserts and dry steppes almost all-over northern Africa and the Sahel zone.

Class Insecta

Order Diptera

Family Nycteribiidae Samouelle, 1819

Basilia daganiae Theodor and Moscona, 1954 has a relatively limited range in comparison with other Western Palearctic species of bat flies. It was so far recorded only from Cyrenaica (Costal Libya) in the studied region, however, considering its known host spectrum representing all species of the genus *Pipistrellus* [86], its occurrence in other parts of the Maghreb is highly probable. *Basilia daganiae* is also known to occur in Cyprus, southern Turkey, and in several Levant countries [86].

Basilia mediterranea Hůrka, 1970 has a Western Mediterranean distribution extending to central Europe. The primary hosts of this bat fly species are bats of the genus *Pipistrellus*; however, it is occasionally found on other bat genera, e.g., *Eptesicus*, *Hypsugo* and *Plecotus* [87]. In the Maghreb region, records of this fly were reported from *Pipistrellus hanaki*, in Libya (Table 1).

Nycteribia latreillii (Leach, 1817) is widely distributed all over the distribution range of its primary host's range (*M. myotis* (Borkhausen, 1797), *M. blythii* (Tomes, 1857) and *M. punicus* Felten, 1977), however, it may also occur on other cave dwelling bats [49]. In the region, *N. latreillii* is a typical bat fly of *M. punicus*, and by far it has the largest host spectrum with eight other host species belonging to the *Rhinolophus*, *Miniopterus,* and *Myotis* genera.

Nycteribia pedicularia Latreille, 1805, has been confused with *N. latreillii* and/or *N. kolenati* for a long time [86]. It was found to infest mostly *M. capaccinii*, and also on six other host species. Throughout its range it is the typical ectoparasite of *M. capaccinii* [87]; however, it was found on several other hosts, too [88]. It is a relatively common nycteribiid, with a southerly distribution, mainly in the Balkans, Apennines, and Iberian Peninsula, with scattered records in Central Europe [88].

Nycteribia schmidlii schmidlii Schiner, 1853, is known from *M.* schreibersii and its distribution corresponds to the distributional range of this bats species, viz. central and southern Europe, the Middle East, Afghanistan, and North Africa [89]. It was collected in the region from *M. schreibersii* in Algeria, Morocco and Tunisia. Within the region *M. punicus* appears to represent its secondary host. Occasionally, this bat fly has also been found on cave dwelling bats that share the roost with its main host (Table 1). According to Hůrka [90], the host spectrum of this species includes ten other European bat species belonging to the family Rhinolophidae and Vespertilionidae. Surprisingly, bats of the family Hipposideridae and Rhinopomatidae from Algeria are found to host *N. s. schmidlii* [21].

Nycteribia vexata Westwood, 1835, is a widespread nycteribiid species in Europe, western Asia and North Africa [88]. It is an ectoparasites of the two largest *Myotis* in Europe (*M. blythii* and *M. myotis*), and it is frequently collected from other cave dwelling species present together with its primary hosts [87]. The same host preference was observed in the Maghreb region, where *M. punicus* serves as the main host (Table1).

Penicillidia conspicua Speiser, 1901, was found in very low numbers infesting *M. schreibersii* and occasionally on to two other host species of the genera *Myotis* and *Rhinolophus* (Table 1). According to the literature, this bat fly is bound to its principal host, *M. schreibersii*, and its distribution range corresponds to the occurrence rang of this host [91]. It was found frequently on *M. myotis* and other cave dwelling bat species [89].

Penicillidia dufourii Westwood, 1835, has a wide range of distribution extending from Europe, North Africa, and Asia, reaching to India [82]. Within the Maghreb region, it represents the most common nycterbiid species parasitizing primarily *M. punicus*, but also other cave dwelling species together with this species. It is generally associated with bats of the genus *Myotis*, however, it was also found on wide range of host species belonging to *Asellia, Rhinolophus* and *Miniopterus* genera, in cases where bats form mixed colonies [86].

Phthiridium biarticulatum Hermann, 1804, is a circum-mediterranean bat fly associated with cave dwelling bats and known to prefer bats of the genus *Rhinolophus* [89]. It was found to parasitize in high numbers the five *Rhinolophus* species present in the Maghreb, and also other cave dwelling bats belonging to the *Miniopterus*, *Myotis* and *Plecotus* genera (Table 1). In Europe, this fly is a typical ectoparasite of bats belonging to the genus *Rhinolophus*, with all horseshoe bat species as regular hosts. It was also collected occasionally from other cave-dwelling host species, as well from a few forest-specialist bat species during the swarming period [88].

Family Streblidae Kolenati, 1863

The family Streblidae is represented by four species in the Mediterranean area but only *Brachytarsina flavipennis* Macquart, 1851 occurs both in Europe and North Africa [92]. In older literature, it was referred to as *Nycteribosca kollari*. The host spectrum includes nine bat species, eight Mediterranean and one desert species (Table 1). According to Hůrka [92], the main hosts of this parasite are the Mediterranean *Rhinolophus* species, but it is also common on members of the genus *Myotis*.

Raymondia huberi huberi Frauenfeld, 1855, is the only representative of the genus occurring in the Maghreb, being a parasite of desert bats of this region. Formerly, the species was recorded in Algeria, on two bat species from Algerian Sahara: *R. clivosus* and *Nyctinomus aegyptiacus*, respectively. Our original material includes a female collected on *N. aegyptiacus* from southern Tunisia in Ksar Ghilane oasis on 24 October 2015. It is the first record for the fauna of this country. *Raymondia h. huberi* is a rare fly species, and was exclusively found to parasitize bats of savannahs and deserts habitats [93]. It was previously reported on *A. tridens* in the Levant and *Hipposideros tephrus* in South Africa [51, 93].

Order Hemiptera

Family Cimicidae Latreille, 1802

Cacodmus vicinus Horváth, 1934, was found infesting two host species of the genus *Pipistrellus,* as well as occasionally *Eptesicus isabellinus* (Table 1). It is a species showing a close attachment to one of the most widespread and abundant Mediterranean bat species, *P. kuhlii* [94, 95]. The record on *E. isabellinus* is rather unsurprising given that this bug can also be found on other hosts species, therefore representing a case of host-switching [95].

Cimex lectularius Linnaeus, 1758, is a well-known synanthropic species that can also infest domestic animals and humans. According to our review, *C. lectularius* was found infesting mainly hosts of the genus *Pipistrellus* in Algeria and Libya, with a few records on the genus *Myotis* (Table 1). In Europe, this species was confirmed on attic-dwelling bats of the genus *Myotis*, as well on crevice-dwelling bats of the *Eptesicus* and *Pipistrellus* genera, especially in warm nursery roosts [17, 94].

Cimex pipistrelli Jenyns, 1839, is often a roost ectoparasite of bats, which, except for the time spent engorging, mostly co-habit without physical contacts with the hosts [93]. This bat bug has a wide range of distribution in the Palaearctic region parasitizing a large host spectrum. The reports in the Maghreb came exclusively from Algeria, and it was found on crevice-dwelling bats of the *Eptesicus*, *Hypsugo* and *Pipistrellus* genera (Table 1). In Europe, *C. pipistrelli* was reported on attic-dwelling *Myotis*, as well as the crevice-dwelling populations of the *Nyctalus* and *Pipistrellus* genera [93].

Order Siphonaptera

Family Ischnopsyllidae

Ischnopsyllus consimilis Wahlgren, 1904, is a rare bat flea occurring in the eastern Mediterranean, and it is known as a typical parasite of *P. kuhlii* [96]. It was found to parasitize *P. kuhlii* from Tripolitanian Libya (Table 1). It was previously found to infest *P. pipistrellus* from Lebanon [96]. Such records are also available from Egypt and Palestine [97]. The Libyan record, represent the westernmost known locality within the distribution range of this flea species.

Ischnopsyllus hispanicus Jordan, 1942, is also a very rare bat flea belonging to the *octactenus*-group. According to Jordan [98], it was first described based on specimens collected from *M. nattereri*, from Spain (Sevilla) and in Morocco (Mazagan). No other records of this species have been made since.

Ischnopsyllus intermedius (Rothschild, 1898) was found to infest bats of the *Eptesicus* and *Pipistrellus* genera in Algeria, Morocco, Libya and Tunisia (Table 1). This flea is a Palaearctic species with a wide range of hosts: at least ten bat genera are known to host this parasite [82, 97, 99].

Ischnopsyllus octactenus (Kolenati, 1856) has a wide range extending from Spain, across all Europe and North Africa, reaching Afghanistan to the east. In the Maghreb region, it is the most commonly collected flea on three host species of the *Pipistrellus* and *Rhinolophus* genera (Table 1). According to literature, *I. octactenus* is mostly associated with bats of the genus *Pipistrellus*; however, other hosts include several species of the *Miniopterus, Myotis* and *Rhinolophus* genera [67, 97].

Nycteridopsylla longiceps Rothschild, 1908, is not only a common bat parasite across the western part of Europe but also across Turkey [100]. Within the Maghreb region, it is known only from Algeria on two hosts, *E. isabellinus* and *P. kuhlii* (Table 1). Elsewhere *P. pipistrellus* and *Plecotus auritus* are the principal hosts of *N. longiceps*, with several other common hosts known.

Rhinolophopsylla unipectinata arabs Jordan and Rothschild, 1921, is the north African subspecies of *R. unipectinata* known to parasitize mainly bats of the genus *Rhinolophus*. It was not only found to parasitize three horseshoe bats, but also other species including those belonging to the *Myotis* and *Plecotus* genera from Algeria, Morocco, Libya, and Tunisia (Table 1). Another outstanding finding of this flea on *M. schreibersii* comes from the Iberian Peninsula [67].

Araeopsylla gestroi (Rothschild, 1906) is a rare bat flea distributed in the southern brink of the western and central parts of the Palearctic, associated with bats of the genus *Tadarida* [67]. Records of this parasite came from Algeria and Libya, where it was found associated with its main host,

as well to *N. aegyptiaca* in the southern parts of this region (Table 1).

Family Pulicidae Billberg, 1820

Synosternus cleopatrae pyramidis (Rothschild 1904) is a subspecies described from Egypt, and ranges widely across North Africa and into the Middle East [62]. A single record was collected on an individual of *T. teniotis* in southern Morocco (along with records on eight rodent species). It is one of the most common fleas of rodents found in semi-desert and agricultural lands, usually away from sand, where different *Meriones* species and *Psammomys obesus* appears to be its preferred hosts [96, 97]. Its occurrence on a bat is certainly accidental.

Xenopsylla ramesis (Rothschild 1904) is a flea species parasitizing gerbillines in the deserts of the Middle East and North Africa. In the region it was recovered from *R. cystops* (Table 1) in southern Morocco and it is regarded as incidental [62].

The collected data shows poor diversity and is hardly representative for the region. If we compare Maghrebian bat ectoparasite species diversity with the number of European parasites, less than one third of the diversity was recorded (43 vs. 145, Table 2.) at a comparable number of host species (42 vs. 55). Mostly cave-dwelling Palearctic species are represented among the hosts of recorded parasites (15 out of the 17 bat species present have parasites recorded, see Table 1). In contrast, African (both Saharo-Sindian, as well Ethiopian) bat species lack parasite records. This may be caused by general ease of access to the roosts (and collecting possibilities) in case of cave dwelling and building dwelling (e.g., *P. pipistrellus*/*P. kuhlii*), coupled with the hard-to-access desert-dwelling, crevice-roosting African hosts. Hence, further surveys of bat species in the region, and especially targeted sampling of the Saharo-Sindian and Ethiopian bat species will definitely increase the number of parasite records and host-parasite relationships in the region.

In this review, we list all known data of parasites recorded on hosts derived from the Grand Maghreb, thus improving our understanding of parasite distribution and host-parasite associations in this particular region. Our review summarized 43 ectoparasite species among which 42 were reported from only 22 host species. Mites and ticks form the majority of recorded parasites with 11 and 9 species, respectively. These parasites are typically found within specific genera or host species ranges. Similar numbers of bat flies (families Nycteribiidae and Streblidae) were recorded (11 species), although this group was better covered due the affinity of dipteran species to cave-dwelling bats. These 11 dipteran species show reduced host specificity if compared to their European populations, likely due to their habit of more frequently sharing the same roosts in the Grand Maghreb, where alternative roost sites (ie., large attics, cellars, bridges and walls) are much seldom met. Shared roosts may grant easy host-switches due to high frequency of chances to meet alternative hosts [103]. Siphonaptera and Hemiptera form the smallest part of the parasite fauna with eight and three species, respectively. As temporary parasites, they primarily visit the host only to take a blood meal and thereafter leave it, thus reducing chances of encounter [94].

For all records, the parasite fauna composition differs broadly within the various hosts in the different territories. In a few cases, the same parasite species of one host were recorded simultaneously for different countries. At the territorial level, three of five countries are understudied, for example, Tunisia and Libya represent about 6% of all records, while nearly non-existent records are available from Mauritania (three records), whereas Morocco accounts for 15% of the total records, and nearly 73% of the remaining records have been obtained from Algeria (Table 2). Algeria

Table 2 Bat parasites diversity reported in the Grand Maghreb and Europe (DZ: Algeria, LY: Libya, MR: Mauritania, MA: Morocco, and TN: Tunisia)

Parasite Family	DZ	LY	MR	MA	TN	Maghreb	Europe*
Argasidae	2	1	2	3	2	4	3
Ixodidae	5	0	0	2	0	5	14
Macronyssidae	3	3	0	0	0	3	24
Spinturnicidae	2	2	0	7	1	7	13
Trombiculidae	0	0	1	0	0	1	44
Nycteribiidae	7	5	0	7	7	9	17
Streblidae	2	1	0	1	2	2	1
Cimicidae	3	2	0	0	1	3	4
Ischnopsyllidae	5	3	0	4	2	7	19
Pulicidae	0	1	0	2	0	2	7
Total	**29**	**18**	**3**	**26**	**15**	**43**	**146**

*Data extracted for Argasidae: Sándor et al. [74], Ixodidae: Sándor et al. [74], Macronyssidae: Orlova et al. [79], Spinturnicidae: Bruyndonckx et al. [91], Trombiculidae: Zajkowska et al. [101], Nycteribiidae/Streblidae: Szentiványi et al. [87], Cimicidae: Aukema and Rieger [102], Quetglas et al. [95], Ischnopsyllidae: Hopkins and Rothschild [97]. Pulicidae: Hopkins and Rothschild [61]

and Morocco exhibit the highest numbers of species with 29 and 26, respectively. In contrast, Libya and Tunisia, despite their size and the diversity of their bat fauna, have relatively smaller species counts, with 18 and 15, respectively. Mauritania, on the other hand, displays the lowest diversity, featuring only a single species (Table 2). This relatively low diversity of parasitic fauna in these three countries is likely a consequence of the limited interest within parasitological studies, particularly Mauritania, which remains a big gap.

The Grand Maghreb, and especially its southern region has obvious research gaps regarding parasite diversity, distribution, and host association. For example, of all 508 records extracted, only 83 (14%) are from latitudes below 30°N. Assuming there are 45 bat species in the Grand Maghreb [104, 105], this group remains understudied and new distributional records of bats are reported regularly. Consequently, parasite diversity number cannot be considered final and the existence of additional parasite species can be assumed given (i) the vast surface area of this region and the diversity of its ecoregions [9], and (ii) the existence of different faunal types, including Mediterranean, Saharo-Sindian, Saharo-Arabian, and Afro-Arabian as well as several endemic species composing its bat fauna.

Arthropods parasites of bats have the potential to play a crucial role in disease ecology, as they can transmit pathogens that may have an impact on animal and human health. Certain parasites, particularly species from the families Ixodidae, Streblidae, and Nycteribiidae, have been identified as carriers of numerous pathogens and can serve as significant vectors for diseases. These parasitic organisms are widely distributed among numerous hosts globally, underscoring their crucial role in the transmission of diverse diseases. To illustrate, bats in Algeria have been identified as carriers of *Bartonella* and *Coxiella*, as evidenced by detection studies [36]. Further research is necessary to investigate the role ectoparasites play in the transmission and prevalence of these pathogens.

Conclusion

The study of bat ectoparasites in the Maghreb countries has been largely disregarded, with most references to arthropod parasites of bats dating back more than seventy years. Since then, changes in nomenclature for both bats and ectoparasites have had a substantial impact on their classification. The previous references often caused alterations in species and subspecies designations, resulting in inconsistencies that need to be addressed. Here we provided an up-to-date and accurate list of arthropods ectoparasites species and their hosts in the region. We have updated the bat host species of several parasites species. However, the existing studies in this field predominantly rely on traditional taxonomy. To further enhance our understanding of species identities and distributions, it is crucial to incorporate phylogenetic research in conjunction with classic taxonomy. This combined approach would be particularly valuable in cases where distinguishing features, such as size or appendages, exhibit a continuum, allowing for a more comprehensive and accurate analysis of bat ectoparasites. In addition, knowledge of bat-parasite is important from epidemiologic point of view, too, as these arthropods are also known vectors of several zoonotic diseases. Further research is necessary to investigate the role ectoparasites play in the transmission and prevalence of these pathogens in the Grand Maghreb.

Acknowledgements We would like to thank Mohamed Rayan Guinoune for his assistance in the field, we also thank Ingo Scheffler, and the World Bat library—Geneva (http://www.ville-ge.ch/musinfo/) for facilitating access to older literature.

Author Contributions Conceptualisation: MLB and ADS, fieldwork: MLB, FK, AA, and NM, morphological identification of bats: MLB and AA, morphological identification of parasites: MLB, FK and ADS, writing of the first draft of the manuscript: MLB, data curation: MLB and ADS, data analysis and map design: MLB, review of the manuscript for important intellectual content: SA and ADM. All authors have read and approved the final manuscript.

Funding MLB was supported by the Romanian governmental scholarship E1-1/687. While working for this study, ADS was funded by Project no. TKP2020-NKA-01 implemented with the support provided from the National Research, Development and Innovation Fund of Hungary, financed under the "Tématerületi Kiválósági Program 2020" (2020-4.1.1-TKP2020) funding scheme, and also supported by OTKA K-132794 of the National Research, Development and Innovation Office.

Data Availability Data is available upon request from the corresponding author.

Declarations

Conflict of interest The authors declare that they have no competing interests. The funders had no role in the design of the study, in the collection, analyses, or interpretation of data, in the writing of the manuscript, or in the decision to publish the results.

Ethical Approval All applicable institutional, national, and international guidelines for the care and use of animals were followed.

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