Bat parasites (Acari, Anoplura, Cestoda, Diptera, Hemiptera, Nematoda, Siphonaptera, Trematoda) in France (1762–2018): a literature review and contribution to a checklist

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Abstract – This paper is a bibliographical survey of records of bat parasites in France (including Corsica) between 1762 and 2018. In total, 237 scientific publications were analysed. They show that bats are infected with a large diversity of endoparasites and ectoparasites. A total of 113 parasite taxa were identified from 27 host species; in addition, six bats were not identified to the species-level. The helminth fauna of bats comprises three species of Cestoda, 15 of Trematoda, and 13 of Nematoda. Acari parasites include 53 species (in addition to 22 invalid species). Finally, insect parasites comprise 13 species of Diptera (bat flies), 12 of Siphonaptera (fleas), 3 of Hemiptera (bugs), and 1 Anoplura species. Bat taxa reported with parasites were Barbastella barbastellus, Eptesicus serotinus, Hypsugo savii, Miniopterus schreibersii, Myotis bechsteinii, M. blythii, M. capaccinii, M. dasycneme, M. daubentonii, M. emarginatus, M. myotis, M. mystacinus, M. nattereri, M. punicus, Nyctalus lasiourus, N. leisleri, N. noctula, Pipistrellus kuhlii, P. nathusii, P. pipistrellus, Plecotus auritus, P. austriacus, Rhinolophus euryale, R. ferrumequinum, R. hipposideros, R. mehelyi, Tadarida teniotis, Eptesicus sp., Myotis sp., Pipistrellus sp., Plecotus sp., Rhinolophus sp. and the species complex Pipistrellus pipistrellus/kuhlii/nathusii. As regards E. nilssonii, Vespertilio murinus (Particoloured Bat), M. alcathoe, M. escalerae, P. macrobularis and P. pygmaeus, no records were found. These published field data originated from 72 of the 96 departments in metropolitan France. The most commonly cited were Ardèche, Ariège, Bouches-du-Rhône, Haute-Savoie, Maine-et-Loire, Moselle, Meurthe-et-Moselle, Pyrénées-Orientales, Sarthe, Haute-Corse and Corse-du-Sud.

Key words: Bibliometry, Chiroptera, Host-parasite associations, Parasite biodiversity.

Résumé – Les parasites des Chiroptères (Acari, Anoplura, Cestoda, Diptera, Hemiptera, Nematoda, Siphonaptera, Trematoda) en France (1762–2018) – état des lieux bibliographique et contribution à une liste des espèces. Cet article est une étude bibliographique des signalements de parasites de chauves-souris en France (y compris la Corse) entre 1762 et 2018. Au total, 237 publications scientifiques ont été analysées. Elles montrent que les chauves-souris sont infectées par une grande diversité d’endoparasites et d’ectoparasites. Un total de 113 taxons parasites ont été identifiés parmi 27 espèces hôtes (en outre, six chauves-souris n’ont pas été identifiées au niveau de l’espèce). La faune helminthique des chauves-souris comprend trois espèces de Cestodes, 15 de Trematodes et 13 de Nématodes. Les Acariens parasites comprennent 53 espèces (en plus de 22 espèces invalides). Enfin, les insectes parasites comprennent 13 espèces de Diptères, 12 de Siphonapteres (puces), 3 d’Hémiptères (punaises) et 1 espèce d’Anoplure. Les taxons de chauves-souris signalés avec des parasites étaient Barbastella barbastellus, Eptesicus serotinus, Hypsugo savii, Miniopterus schreibersii, Myotis bechsteinii, M. blythii, M. capaccinii, M. dasycneme, M. daubentonii, M. emarginatus, M. myotis, M. mystacinus, M. nattereri, M. punicus, Nyctalus lasiourus, N. leisleri, N. noctula, Pipistrellus kuhlii, P. nathusii, P. pipistrellus, Plecotus auritus, P. austriacus, Rhinolophus euryale, R. ferrumequinum, R. hipposideros, R. mehelyi, Tadarida teniotis, Eptesicus sp., Myotis sp., Pipistrellus sp., Plecotus sp., Rhinolophus sp. et le complexe Pipistrellus pipistrellus/kuhlii/nathusii. Aucun signalement n’a été trouvé pour E. nilssonii, Vespertilio murinus, M. alcathoe, M. escalerae, P. macrobularis et P. pygmaeus. Ces données de terrain publiées proviennent de 72 des 96 départements de France métropolitaine. Les plus cités sont l’Ardèche, l’Ariège, les Bouches-du-Rhône, la Haute-Savoie, le Maine-et-Loire, la Moselle, la Meurthe-et-Moselle, les Pyrénées-Orientales, la Sarthe, la Haute-Corse et la Corse-du-Sud.
Introduction

Bats (Mammalia: Chiroptera) represent the second-most diverse order of mammals, after rodents. As of 2007, 42 bat species have been reported from Europe (Dietz et al. [84]). According to Arthur & Lemaire [16], 35 species have been unambiguously identified in France. Many aspects of the ecology of bats are under study (e.g. swarming, hunting sites, flight routes, habitat studies, acoustic ecology). One of these aspects is the study of bat parasites, which has a long history in Europe, for instance in French-speaking areas (France, Belgium). Bats are infected with a large diversity of parasites. Around the year 1999, c. 756 taxa were known to be associated with bats worldwide [167]. In Lanza’s book, a wide range of parasitic organisms were presented, belonging to 13 groups: Myconta (two taxa), Acanthocephala (three taxa), Mallophaga (one taxon, accidental exposure), Anoplura (two taxa), Heteroptera (11 taxa), Neobacteria (c. 31 taxa), Protozoa (25 taxa), Cestoda (55 taxa), Digenea (105 taxa), Nematoda (62 taxa), Acari (324 taxa), Diptera (65 taxa) and Siphonaptera (64 taxa). This includes at least ten phyla: Acanthocephala (Spiny-headed worms), Apicomplexa, Arthropoda, Ascomycota (Ascomycete fungi), Euglenozoa, Firmicutes, Nematoda, Platyhelminthes, Protobacteria and Spirochaetes. Similar findings were noted by Stiles & Nolan [235] in their “key catalogue” of bat parasites. In addition to the high diversity of bat parasites, these findings point out the predominant share, in the published records, of metazoan parasites. They also point out the issue of diseases in bats (transmission linked with their ecology) and they seemingly are able to control these infections so that they are mostly asymptomatic. Some bat parasites (e.g. bat flies) are known to be disease vectors for their hosts [83, 129, 181, 184, 192, 261].

Among the earliest works on bat parasites in France is Étienne-Louis Geoffroy’s Histoire abrégée des insectes [123], published in 1762 (Fig. 1). This book marks the starting point for research on bat parasites in France. The present paper reviews metazoan parasites reported on bats in France between 1762 and 2018, with the exception of acanthocephalan parasites. According to the Host-Parasite Database of the Natural History Museum, London [125], no bat parasites belonging to the Acanthocephala phylum are currently known in France. In addition, hyperparasites are excluded from this paper. Nevertheless, it should be noted that bat parasites have their own parasites, such as Laboulbeniales fungi associated with bat flies or viruses of haemosporidian parasites. Some of these hyperparasites have reports from France, specifically in the department of Gard (Arthrorhynchus eucampisopodes Thaxt., 1901 and A. nycteribiæ (Peyr.) Thaxt., 1931) [55, 129, 238]. The purpose of the present paper is twofold: the primary aim is to summarize the large body of published field data; and secondly to inform the reader about the geographical origin of the data and to contribute to a general overview and checklist of bat-parasite associations in France.

Methods

Initially, I used the works of nine authors: Anciaux de Faveaux [5–7], Beaucournu [28, 29], Beaucournu and Launay [37], Hürka [149], Lanza [167], Maas [185] and Szentiványi et al. [237]. The list of all the sources used in these papers offers an essential bibliographical guide. The online catalog of the Library of the Muséum National d’Histoire Naturelle (MNHN) was also used. I checked all available publications on each of the searched terms including a combination of France or the name of administrative departments (n = 111) or the names of former administrative regions of France (n = 22) with one of the generic names of the bat parasites, as mentioned in I parasiti dei pipistrelli (Mammalia, Chiroptera) della fauna italiana [167], Parasite diversity of European Myotis species with special emphasis on Myotis myotis (Microchiroptera, Vespertilionidae) from a typical nursery roost [121], Les puces de France et du bassin méditerranéen occidental [37], and Checklist of host associations of European bat flies (Diptera: Nycteribiidae, Streblidae) [237]. For the study area, see Figure 5. I searched Google Scholar, ISI Web of Science, Hyper-Article en Ligne (HAL), Biodiversity Heritage Library (BHL), Gallica, and Archives. The collated sources (n = 237) were then analysed. I then proceeded to index them in terms of their chronology, taxonomy, and geography. The validity of all the taxa found was checked using the comprehensive synonymsies provided by the Host-Parasite Database of the Natural History Museum, London [125] and the Inventaire National du Patrimoine Naturel of the Muséum National d’Histoire Naturelle (MNHN) [153]. The taxonomic works of Fain [106–108], Lanza [167], Neumann [197], Da Fonseca [72], Radovsky [212], Roy and Chauve [221, 222], Rudnick [223], Stiles and Nolan [235] and Theodor & Moscona [241] were also used. The bat classification and taxonomy, in this paper, is based on Dietz et al. (2009) and Arthur and Lemaire (2015). Authorities for the host taxa and parasites species are given in Tables 1 and 2. What follows is an overview of all bat parasites, arranged by higher taxonomic group.

1 Phylum Arthropoda Latreille, 1829

1.1 Subphylum Chelicerata Heymons, 1901

1.1.1 Subclass Acari Leach, 1817

Most of the studied papers (n = 112) deal with 75 species (53 generally recognised species and 22 invalid species) of Acari of four groups: Isodida, Mesostigmata, Trombidiformes (suborder Prostigmata), and Sarcoptiformes (Fig. 3). A total of 53 recognised species (including two subspecies) of mites and ticks were reported to be parasites of bats in France prior to 2018. Of these, two species have only been collected from the border between Switzerland and the French department of Haute-Savoie (Col de Bretolet): Spinturnix helvetiae and S. acuminatus.
These recognised species found in the literature \((n = 53)\) reported from France belong to 23 genera: *Acanthophthirius*, *Alabidocarpus*, *Argas*, *Calcarmyobia*, *Eyndhovenia*, *Hirstionysus*, *Ichoronyssus*, *Ixodes*, *Labidocarpus*, *Leptotrombidium*, *Macronyssus*, *Neomyobia*, *Neotrombicula*, *Notoedres*, *Nycteridocoptes*, *Oudemansidium*, *Paraperiglischrus*, *Pteracarus*, *Psorergates*, *Riedlinia*, *Sasatrombicula*, *Steatonyssus* and *Spinturnix*. Among this group, the most diverse genera reported in France are *Spinturnix* and *Macronyssus* (Fig. 3): these genera account for 30% of all documented Acari infections involving valid species.

Six more records reported from France without identification to species level \((n = 6)\) were found. These comprise *Dermanyssus* sp. [86], *Ichoronyssus* sp. [25], *Ixodes* sp. [178], *Neomyobia* sp. [126], *Steatonyssus* sp. [152, 212] and *Spinturnix* sp. [133]. Three other species are noted as absent from bats in western
Table 1. List of bat species and their associated metazoan parasites in France (including Corsica), based on the published literature. Authors are listed in the bibliography. See also the work titled *Les parasites métazoaires des Chiroptères de France (Acari, Anoplura, Cestoda, Diptera, Hemiptera, Nematoda, Siphonaptera, Trematoda)* : contribution à un état des lieux bibliographique (1762–2018) et à l’établissement d’une liste nationale (2019). Invalid species are listed in brackets. Records marked with an exclamation mark (!) are invalid. Records marked with a question mark (?) are dubious. They may require further clarification.

| Bat host                          | Number of parasite species reported | Parasite occurrence and citation |
|----------------------------------|------------------------------------|----------------------------------|
| *Barbastella barbastellus*       | 10 species (9 recognised species and 1 invalid species) | Acari  
| Schreber, 1774                   |                                    | Absence of *Ixodes canisuga* Johnston, 1849 [28]  
|                                  |                                    | Absence of *Pholeoixodes hexagonus* (Leach, 1815) [28] |
|                                  |                                    | [Pteroptus vespertilionis L. Duf. (=Dufour) = Pteroptus vespertilionis (Dufour, 1832)] [127, 177]  
|                                  |                                    | [Pteroptus vespertilionis] [67] |
|                                  |                                    | Acanthophthirius (Myotimyobia) pantopus (Poppel et Trouessart, 1895) [102, 114, 167, 235, 249]  
|                                  |                                    | Argas vespertilionis (Latreille, 1796) [28]  
|                                  |                                    | *Ixodes (Eschatocephalus) vespertilionis* C.L. Koch, 1844 [28, 32, 200]  
|                                  |                                    | See also [128] |
|                                  |                                    | **Chiroptera gen. sp.** 30 species  
|                                  |                                    | Acari  
|                                  |                                    | [Nyasus vespertilionis Herrmann] [257, 258]  
|                                  |                                    | [Dermatophilus vespertilionis Duègès, 1834] [94]  
|                                  |                                    | [Lepoglyphus armatus (=Hirstionyssus arcuatus (C.L. Koch, 1839)?)] [160, 177]  
|                                  |                                    | [Liponyssus setosus (Kolenati)] [72]  
|                                  |                                    | [Nycteribia vespertilionis Meig.] [12]  
|                                  |                                    | [Pteroptus vespertilionis Dufour] [120, 177]  
|                                  |                                    | [Pteroptus vespertilionis] [160]  
|                                  |                                    | Argas (Secretargas) transgariepinus White, 1846 [189]  
|                                  |                                    | *Ixodes (Eschatocephalus) vespertilionis* C.L. Koch, 1844 [45, 69, 160, 190, 197–199, 248]  
|                                  |                                    | Macronyssus uncinatus (Canestrini, 1885) [160, 177]  
|                                  |                                    | Neotrombicula autumnalis (Shaw, 1790) [62]  
|                                  |                                    | Sasatrombicula (Sasatrombicula) hexasternalae (Vercammen-Grandjean, 1963) [7]  
|                                  |                                    | Spinturnix myotis (Kolenati, 1856) [7, 65?, 167, 223, 246]  
|                                  |                                    | Spinturnix plecotina (C.L. Koch, 1839) [7]  
|                                  |                                    | Spinturnix psi (Kolenati, 1856) [7, 167, 210, 223]  
|                                  |                                    | **Diptera**  
|                                  |                                    | [Nycteribia vespertilionis Meig.] [12]  
|                                  |                                    | Nycteribia (Nycteribia) pedicularia Latreille, 1805 [170]  
|                                  |                                    | Phthiridium biarticulatum Herrmann, 1804 [173, 204]  
|                                  |                                    | Nycteribia (Nycteribia) laetissil (Leach, 1817) [148]  
|                                  |                                    | Nycteribia (Nycteribia) schmidti Schiner, 1853  
|                                  |                                    | Penicillulid (Penicillulid) dufourii (Westwood, 1834) [43]  
|                                  |                                    | **Hemiptera**  
|                                  |                                    | *Cimex dissimilis* (Horváth, 1910) [207]  
|                                  |                                    | *Cimex lectularius* Linnaeus, 1758 [28, 35]  
|                                  |                                    | *Cimex pipistrelli* Jenius, 1839 [28, 236]  
|                                  |                                    | *Cimex sp.* [28, 177]  
|                                  |                                    | **Nematoda**  
|                                  |                                    | Molinostrongylus alatus (Ortlepp, 1932) [167]  
|                                  |                                    | **Siphonaptera**  
|                                  |                                    | *Ischnopsyllus (Hexactenopsylla) hexactenus* (Kolenati, 1856) [142]  
|                                  |                                    | *Ischnopsyllus (Ischnopsyllus) intermedius* (Rothschild, 1898) [44]  
|                                  |                                    | *Ischnopsyllus (Ischnopsyllus) octactenus* (Kolenati, 1856) [219]  
|                                  |                                    | Nycteridopsylla dictena (Kolenati, 1856) ! see Beaucournu et Launay (1990; p. 314 [paper n°36])  
|                                  |                                    | [37, 146, 167, 227]  
|                                  |                                    | Nycteridopsylla pentactena (Kolenati, 1856) [204]  
|                                  |                                    | (Continued on next page)
| Bat host | Number of parasite species reported | Parasite occurrence and citation |
|----------|-----------------------------------|---------------------------------|
| Eptesicus serotinus (Schreber, 1774) | 17 species (16 recognised species and 1 invalid species) 1 innominate species | **Acari**  
Absence of Isodes canisuga Johnston, 1849 [28]  
Absence of Pholeoixodes hexagonus (Leach, 1815) [28]  
[Pteroptus vespertilionis (Dufour, 1832)] [190]  
Argas (Carios) vespertilionis (Lateille, 1802) [31, 45, 86]  
Argas (Secretargas) transgariepinus White, 1846 [45, 189]  
Argas vespertilionis (Lateille, 1796) [28, 38]  
Isodes (Eschatocephalus) vespertilionis C.L. Koch, 1844 [28, 32, 166]  
Notoedres (Notoedres) chiropetalis (Trouessart, 1896) [48, 106, 167, 250]  
Spinturnix psi (Kolenati, 1856) [48]  
**Cestoda**  
Vampirolepis acuta (Rudolphi, 1819) [158, 159, 177, 196, 255]  
Vampirolepis balci (Joyeux & Baer, 1934) [158, 159, 167, 177, 180, 196, 255]  
Vampirolepis sp./Milina sp. [86]  
**Diptera**  
Basilia (Basilia) mediterranea Húrka, 1970 [43, 167, 237]  
Basilia (Basilia) nattereri (Kolenati, 1857) [241]  
Nycteribia (Nycteribia) kolenati Theodor & Moscona, 1954 [147, 241]  
**Siphonaptera**  
Ischnopsyllus (Ischnopsyllus) intermedius (Rothschild, 1898) [29, 33, 37, 38, 142, 167, 227]  
Nycteridopsylla pentactena (Kolenati, 1856) [29, 33, 37, 164, 167]  
**Trematoda**  
Lecithodendrium linstowi Dollfus, 1931 [68, 88, 167]  
Plagiorchis vespertilionis (O.F. Müller, 1784) [68, 167]  
Prosthodendrium (Prosthodendrium) longiforme (Blaherao, 1926) [88, 167]  
Eyndhovenia euryalis (G. Canestrini, 1885) [76]  
Ichoronyssus diversipilis Vitzthum, 1920 [24]  
Ichoronyssus spinosus (Oudemans) 1902) [24, 70, 72]  
Isodes (Eschatocephalus) simplex simplex Neumann, 1906 [15, 31, 32, 45, 51, 143, 166, 167, 176] see Beaucournu (1966; p. 498) paper n°30  
Isodes (Eschatocephalus) vespertilionis C.L. Koch, 1844 [6, 28, 176] see Beaucournu (1966; p. 498) paper n°30 [200, 242]  
Macronyssus granulosus (Kolenati, 1856) [50, 167]  
Spinturnix myoti (Kolenati, 1856) [76]  
Spinturnix psi (Kolenati, 1856) [50, 63, 76, 139]  
**Cestoda**  
Milina grisea van Beneden, 1873 [68, 86, 167, 200?]  
**Diptera**  
[Noveteribia vespertilionis Meig.] [203]  
Nycteribia (Nycteribia) pedicularia Lateille, 1805 ! [85]  
Phthiridium biarticulatum Hermann, 1804 ! [85, 126, 237]  

(Continued on next page)
| Bat host | Number of parasite species reported | Parasite occurrence and citation |
|----------|-------------------------------------|----------------------------------|
| *Nycteribia (Nycteribia) kolenatii* Theodor & Moscona, 1954 | 200 |
| *Nycteribia (Nycteribia) latreillii* (Leach, 1817) | 1, 167 |
| *Nycteribia (Nycteribia) schmidlii* Schiner, 1853 | 1, 24, 28, 30, 43, 115, 149, 154, 167, 242; see also [117, 150] |
| *Nycteribia (Achrocholidia) vexata* Westwood, 1835 | [1, 43, 85, 167] |
| *Penicillidia (Penicillidia) dufouri* (Westwood, 1834) | [1, 24, 30, 237] |
| *Penicillidia (Neopenicillidia) conspicua* Speiser, 1901 | ([1, 28, 30, 115, 154, 167, 242], see also [117, 150, 237]) |
| *Nematoda* | |
| *Litomosa* | |
| *Molinostrongylus panousei* Dollfus, 1954 | [99, 167] |
| *Molinostrongylus tipula* (Beneden, 1873) | [200] |
| *Riouxgolvania rhinolophi* (Bain & Chabaud, 1968) | [21, 167] |
| *Strongylacantha glycirrhyza* van Beneden, 1873 | [99, 167, 200] |
| *Trichosomum speciosum* van Beneden, 1873 | [200] |
| See also [174] | |
| *Siphonaptera* | |
| *Nycteridopsylla pentactena* (Kolenati, 1856) | [37, 164, 167] |
| *Trematoda* | |
| *Paralecithodendrium chilostomum* (Mehlis) (=*Prosthodendrium (Prosthodendrium) chilostomum* (Mehlis, 1831) ?) | [200] |
| *Lecithodendrium granulosum* Looss, 1907 ? | [200] |
| *Mesotretes peregrinus* (Braun, 1900) | [68, 167, 188] |
| *Parabascus lepidotus* Looss, 1907 | [68, 167] |
| *Plagiorchis vespertilionis* (O.F. Müller, 1784) | [68, 167, 200, 235] |
| *Prosthodendrium (Prosthodendrium) chilostomum* (Mehlis, 1831) | [68, 167, 200, 235] |
| *Prosthodendrium parvouterus* Bhalerao, 1926 | [68, 167] |
| See also [174] | |
| *Acari* | |
| *Absence of Ixodes canisuga* Johnston, 1849 | [28] |
| *Absence of Pholeoixodes hexagonus* (Leach, 1815) | [28] |
| *Ixodes (Eschatocephalus) simplex simplex* Neumann, 1906 | [32] |
| *Spinturnix bechsteini* (Deunff, Walter, Bellido et Volleth, 2004) | [82, 130] |
| *Cestoda* | |
| *Vampirolepis balzaci* (Joyeux & Baer, 1934) | [159, 167, 177, 180, 196, 255] |
| *Diptera* | |
| *Basilia (Basilia) nana* Theodor & Moscona, 1954 | [4, 28, 30, 38, 237] |
| *Myotis bechsteinii* (Leisler in Kuhl, 1817) | 4 recognised species |
| *Myotis blythii* (Tomes, 1857) and *M. blythii oxygnathus* Monticelli, 1885 | 9 recognised species |
| *Myotis capaccinii* (Bonaparte, 1837) | 9 recognised species |
| 1 innominate species | |
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| Bat host                                                                 | Number of parasite species reported | Parasite occurrence and citation                                                                 |
|------------------------------------------------------------------------|-------------------------------------|--------------------------------------------------------------------------------------------------|
| Diptera                                                                |                                     |                                                                                                 |
| Nycteribia (Nycteribia) pedicularia Latreille, 1805                      | [1, 30, 85]                         |                                                                                                 |
| Penicillidia (Penicillidia) dafourii (Westwood, 1834)                  | [1, 237]                            |                                                                                                 |
| Siphonaptera                                                           |                                     |                                                                                                 |
| Nycteridopsylla longiceps Rothschild, 1908                             | [37, 164, 167]                      |                                                                                                 |
| Nycteridopsylla pentactena (Kolenati, 1856)                            | [37, 164, 167]                      |                                                                                                 |
| Trematoda                                                              |                                     |                                                                                                 |
| Lecithodendrium granulosum Looss, 1907                                  | [68]                                |                                                                                                 |
| Lecithodendrium linstowi Dollfus, 1931                                  | [68, 167]                           |                                                                                                 |
| Plagiorchis vespertilionis (O.F. Müller, 1784)                         | [68, 167]                           |                                                                                                 |
| Myotis dasycneme (Boie, 1825)                                          | 1 recognised species                |                                                                                                 |
| Acari                                                                  |                                     |                                                                                                 |
| Argas (Carios) vespertilionis (Lateille, 1802)                         | [6, 31, 85]                         |                                                                                                 |
| Myotis daubentonii (Leisler & Kuhl, 1817) and Myotis daubentonii natalinae | 19 species (17 recognised species and 2 invalid species) |                                                                                                 |
| Acari                                                                  |                                     |                                                                                                 |
| Absence of Isodes cansuga Johnston, 1849                               | [28]                                |                                                                                                 |
| Absence of Pholeoixodes hexagonus (Leach, 1815)                        | [28]                                |                                                                                                 |
| [Picroptus trouessartii Mégin (=Haemomyson trouessart (Mégin)?)]       | [248]                               |                                                                                                 |
| Isodes (Eschatocephalus) vespertilionis C.L. Koch, 1844                 | [28, 32]                            |                                                                                                 |
| Leptotrombidium ruscicum (Oudemans, 1902)                              | [122, 167, 177, 256]               | see also [10]                                                                                   |
| Neotrombicula autumnalis (Shaw, 1790)                                  | [8–10, 122, 167, 177, 256]          |                                                                                                 |
| Nycteridoctes poppei Oudemans, 1898                                    | [113]                               |                                                                                                 |
| Oudemansidium musca (Oudemans, 1906)                                   | [122, 167, 177]                     |                                                                                                 |
| Spinturnix andegavinus (Deunff, 1977)                                  | [76]                                |                                                                                                 |
| Myotis emarginatus (Geoffroy, 1806)                                    | 19 recognised species 2 innominate species |                                                                                                 |
| Acari                                                                  |                                     |                                                                                                 |
| Absence of Isodes cansuga Johnston, 1849                               | [28]                                |                                                                                                 |
| Absence of Pholeoixodes hexagonus (Leach, 1815)                        | [28]                                |                                                                                                 |
| Argas (Secretargas) transgariepinus White, 1846                        | [45, 189]                           |                                                                                                 |
| Argas vespertilionis (Lateille, 1796)                                  | [28]                                |                                                                                                 |
| Dermanyssus sp.                                                        | [86]                                |                                                                                                 |
| Eyndhovenia euryalis (G. Canestrini, 1885)                             | [63, 121]                           |                                                                                                 |
| Isodes (Eschatocephalus) vespertilionis C.L. Koch, 1844                 | [28, 32, 38, 136, 137, 177]         |                                                                                                 |
| Spinturnix emarginatus (Lateille, 1856)                                | [7, 76, 78]                         |                                                                                                 |
| Cestoda                                                                |                                     |                                                                                                 |
| Milina grisea van Beneden, 1873                                        | [68, 86, 167]                       |                                                                                                 |
| Diptera                                                                |                                     |                                                                                                 |
| Nycteribia (Achrocholidia) vexata Westwood, 1835                        | [23]                                |                                                                                                 |
| Nycteribia (Nycteribia) pedicularia Latreille, 1805                     | [1, 237]                            |                                                                                                 |
| Basilia (Basilia) italica Theodor, 1954                                | [4, 34]                             |                                                                                                 |
| Basilia (Basilia) nana Theodor & Moscona, 1954                         | [43, 237]                           |                                                                                                 |
| Nycteribia (Nycteribia) latreilii (Leach, 1817)                         | [22]                                |                                                                                                 |
| Bat host                        | Number of parasite species reported | Parasite occurrence and citation |
|--------------------------------|-------------------------------------|----------------------------------|
| **Hemiptera**                  | [Cimex lectularius Linnaeus, 1758](#) [253, 254] |                                   |
|                                | [Cimex dissimilis (Horváth, 1910)] [254] |                                   |
| **Nematoda**                   | [Litomosoides dogielii Bogdanov & Vladimirov, 1956](#) [19] |                                   |
|                                | [Litomosoides filaria (Beneden, 1873)] [86, 167] |                                   |
|                                | [Litomosoides ottavi iuni Lagrange & Bettini, 1948](#) [68, 167] |                                   |
| **Rictularia**                 | sp. [86] |                                   |
| **Siphonaptera**               | [Ischnopsyllus (Ischnopsyllus) simplex Rothschild, 1906](#) [29, 37, 142] |                                   |
|                                | **Trematoda**                        |                                   |
|                                | [Lechitodendrium linstowi Dollfas, 1931](#) [68, 167] |                                   |
|                                | [Plagiocirchis vespertilionis (O.F. Müller, 1784)] [68, 86, 167] |                                   |
| **Myotis myotis** (Borkhausen, 1797) | 38 species (33 recognised species and 5 invalid species) 3 in nominate species |                                   |
|                                | [Ichoronyssus sp. ?](#) [25] |                                   |
|                                | [Macronyssus rhinolophi (Oudemans, 1902)] [152, 212] |                                   |
|                                | [Argas vespertilionis (Lateille, 1796)] [28] |                                   |
|                                | [Isodes (Eschatocephalus) vespertilionis C.L. Koch, 1844](#) [23, 28, 32, 38, 154, 166] |                                   |
|                                | [Nycteridopsylla longiceps Rothschild, 1908 !](#) [228] |                                   |
|                                | [Isodes (Nycteribia) intermedius Rothschild, 1884](#) [2, 29, 33, 37, 142, 167] |                                   |
|                                | [Isodes (Nycteribia) octactenus Kolenati, 1856](#) [25, 29, 37, 167] |                                   |
|                                | [Nycteribia (Nycteribia) intermedius Rothschild, 1884](#) [2, 29, 33, 37, 142, 167] |                                   |
|                                | [Isodes (Nycteribia) octactenus (Kolenati, 1856)] [25, 29, 37, 167] |                                   |
| **Cestoda**                    | Milina grisea van Beneden, 1873 [68, 159, 167] |                                   |
|                                | [Diptera](#)                        |                                   |
|                                | [Nycteribia (Nycteribia) latreillii (Leach, 1817)] [1, 28, 30] |                                   |
|                                | [Nycteribia (Nycteribia) pedicularia Latreille, 1805](#) [25, 186] |                                   |
|                                | [Nycteribia (Nycteribia) schmidii Schiner, 1853](#) [1, 30] |                                   |
|                                | [Nycteribia (Achrochoidia) vespertilio Westwood, 1835](#) [1, 23, 25, 28, 30, 38, 43, 167] |                                   |
|                                | [Penicillidia (Neopenicillidia) conspicua Speiser, 1901](#) [25] |                                   |
|                                | [Penicillidia (Penicillidia) dufourii Westwood, 1834](#) [1, 14, 22, 28, 30, 43, 91, 186, 237, 242] |                                   |
|                                | [Nycteribia (Nycteribia) intermedius Rothschild, 1884](#) [2, 29, 33, 37, 142, 167] |                                   |
|                                | [Nycteribia (Nycteribia) octactenus (Kolenati, 1856) [25, 29, 37, 167] |                                   |
|                                | [Nycteribia (Nycteribia) intermedius Rothschild, 1884](#) [2, 29, 33, 37, 142, 167] |                                   |
|                                | [Ischnopsylla (Ischnopsylla) intermedius Rothschild, 1884](#) [2, 29, 33, 37, 142, 167] |                                   |
|                                | [Ichoronyssus sp. ?](#) [25] |                                   |
|                                | [Macronyssus rhinolophi (Oudemans, 1902)] [152, 212] |                                   |
|                                | [Argas vespertilionis (Lateille, 1796)] [28] |                                   |
|                                | [Isodes (Eschatocphalus) vespertilionis C.L. Koch, 1844](#) [23, 28, 32, 38, 154, 166] |                                   |
|                                | [Nycteridopsylla longiceps Rothschild, 1908 !](#) [228] |                                   |
|                                | [Isodes (Nycteribia) intermedius Rothschild, 1884](#) [2, 29, 33, 37, 142, 167] |                                   |
|                                | [Isodes (Nycteribia) octactenus (Kolenati, 1856)] [25, 29, 37, 167] |                                   |
| **Cestoda**                    | Milina grisea van Beneden, 1873 [68, 159, 167] |                                   |
|                                | [Diptera](#)                        |                                   |
|                                | [Nycteribia (Nycteribia) latreillii (Leach, 1817)] [1, 28, 30] |                                   |
|                                | [Nycteribia (Nycteribia) pedicularia Latreille, 1805](#) [25, 186] |                                   |
|                                | [Nycteribia (Nycteribia) schmidii Schiner, 1853](#) [1, 30] |                                   |
|                                | [Nycteribia (Achrochoidia) vespertilio Westwood, 1835](#) [1, 23, 25, 28, 30, 38, 43, 167] |                                   |
|                                | [Penicillidia (Neopenicillidia) conspicua Speiser, 1901](#) [25] |                                   |
|                                | [Penicillidia (Penicillidia) dufourii Westwood, 1834](#) [1, 14, 22, 28, 30, 43, 91, 186, 237, 242] |                                   |
|                                | [Nycteribia (Nycteribia) intermedius Rothschild, 1884](#) [2, 29, 33, 37, 142, 167] |                                   |
|                                | [Nycteribia (Nycteribia) octactenus (Kolenati, 1856) [25, 29, 37, 167] |                                   |
|                                | [Nycteribia (Nycteribia) intermedius Rothschild, 1884](#) [2, 29, 33, 37, 142, 167] |                                   |
|                                | [Ischnopsylla (Ischnopsylla) intermedius Rothschild, 1884](#) [2, 29, 33, 37, 142, 167] |                                   |
|                                | [Ichoronyssus sp. ?](#) [25] |                                   |
|                                | [Macronyssus rhinolophi (Oudemans, 1902)] [152, 212] |                                   |
|                                | [Argas vespertilionis (Lateille, 1796)] [28] |                                   |
|                                | [Isodes (Eschatocphalus) vespertilionis C.L. Koch, 1844](#) [23, 28, 32, 38, 154, 166] |                                   |
|                                | [Nycteridopsylla longiceps Rothschild, 1908 !](#) [228] |                                   |
|                                | [Isodes (Nycteribia) intermedius Rothschild, 1884](#) [2, 29, 33, 37, 142, 167] |                                   |
|                                | [Isodes (Nycteribia) octactenus (Kolenati, 1856)] [25, 29, 37, 167] |                                   |
| Bat host                  | Number of parasite species reported | Parasite occurrence and citation                                                                 |
|--------------------------|-------------------------------------|--------------------------------------------------------------------------------------------------|
| *Ischnopsyllus (Hexactenopsylla) hexactenus* (Kolenati, 1856) | 14, 29, 33, 37, 167, 228              |                                                                                                  |
| *Ischnopsyllus (Ischnopsyllus) simplex* Rothschild, 1906    | 29, 37, 85                           |                                                                                                  |
| *Nycteridopsylla pentactena* (Kolenati, 1856)               | 29, 37, 167                           |                                                                                                  |
| **Trematoda**          |                                     |                                                                                                  |
| *Lecithodendrium instowii* Dollfus, 1931                   | 68, 167                               |                                                                                                  |
| *Plagiorchis vespertilionis* (O.F. Müller, 1784)            | 86                                    |                                                                                                  |
| *Prothodendrium (Prothodendrium) chilostomum* (Mehlis, 1831) | 57, 61, 68, 167                      |                                                                                                  |
| **See also**           |                                     |                                                                                                  |
| *Myotis mystacinus* (Leisler in Kuhl, 1817)                 | 14 species (11 recognised species and 3 invalid species) |                                                                                                  |
| **Acarina**            |                                     |                                                                                                  |
| *Ixodes (Eschatocephalus) vespertilionis* C.L. Koch, 1844   | 28, 32, 38, 85                        |                                                                                                  |
| *I. vespertilionis* (Lateire, 1802)                        | 45                                    |                                                                                                  |
| *Argas (Carios) vespertilionis* (Lateire, 1796)             | 28                                    |                                                                                                  |
| *Argas vespertilionis* (Lateire, 1796)                      | 28                                    |                                                                                                  |
| *Gamassus dermanyssoïdes* (Mégnin)                         | 248                                   |                                                                                                  |
| *Pteroptus trouessarti Mégnin (=Haemomyson trouessarti (Mégnin))?* | 248                               |                                                                                                  |
| *Ischnopsyllus (Ischnopsyllus) simplex* Rothschild, 1906    | 2, 29, 33, 37, 44, 85, 142, 156       |                                                                                                  |
| *Ischnopsyllus (Ischnopsyllus) intermedius* Rothschild, 1908| 29, 37, 38, 167                       |                                                                                                  |
| *Ischnopsyllus (Ischnopsyllus) pentactena* (Kolenati, 1856) | 29, 37, 167                           |                                                                                                  |
| **Diptera**           |                                     |                                                                                                  |
| *Basilia (Basilia) italic* Theodor, 1954                    | 34, 35, 43, 237                       |                                                                                                  |
| *Basilia (Basilia) nana* Theodor & Moscona, 1954            | 241                                   |                                                                                                  |
| *Nycteribia (Nycteribia) kolenati* Theodor & Moscona, 1954  | 147, 241                              |                                                                                                  |
| **Siphonaptera**       |                                     |                                                                                                  |
| *Ischnopsyllus (Ischnopsyllus) simplex* Rothschild, 1906    | 29, 33, 37, 44, 85, 142               |                                                                                                  |
| *Nycteridopsylla longiceps* Rothschild, 1908                | 29, 37, 38, 167                       |                                                                                                  |
| *Nycteridopsylla pentactena* (Kolenati, 1856)               | 29, 37, 167                           |                                                                                                  |
| **Myotis nattereri** (Kuhl, 1817)                          | 8 recognised species                  |                                                                                                  |
| **Acarina**           |                                     |                                                                                                  |
| *Ixodes (Eschatocephalus) vespertilionis* C.L. Koch, 1844   | 28, 32                                |                                                                                                  |
| *I. vespertilionis* (Lateire, 1802)                        | 45                                    |                                                                                                  |
| *Argas vespertilionis* (Lateire, 1796)                      | 28                                    |                                                                                                  |
| *Spinturnix mystacinus* (Kolenati, 1857)                    | 14, 76, 78                            |                                                                                                  |
| **Diptera**           |                                     |                                                                                                  |
| *Basilia (Basilia) nattereri* (Kolenati, 1857)              | 4, 28, 30, 43, 187                    |                                                                                                  |
| *Basilia (Basilia) nana* Theodor & Moscona, 1954            | 4, 30, 237                            |                                                                                                  |
| *Nycteridia (Nycteridia) nattereri* Theodor & Moscona, 1954 | 28, 147                               |                                                                                                  |
| **Siphonaptera**       |                                     |                                                                                                  |
| *Ischnopsyllus (Ischnopsyllus) simplex* Rothschild, 1906    | 29, 33, 37, 44, 85, 142               |                                                                                                  |
| *Nycteridopsylla longiceps* Rothschild, 1908                | 29, 37, 167                           |                                                                                                  |
| *Nycteridopsylla pentactena* (Kolenati, 1856)               | 29, 37, 167                           |                                                                                                  |
| **Myotis punicus** Felten, Spitzenberger & Storch, 1977     | 1 recognised species                  |                                                                                                  |
| **Acarina**           |                                     |                                                                                                  |
| *Spinturnix myoti* (Kolenati, 1856)                         | 64                                    |                                                                                                  |
| **Myotis sp.**        | 4 recognised species                 |                                                                                                  |
| **Acarina**           |                                     |                                                                                                  |
| *Argas vespertilionis* (Lateire, 1796)                      | 171, 242                              |                                                                                                  |
| *Spinturnix myoti* (Kolenati, 1856)                         | 14                                   |                                                                                                  |
| **Hemiptera**         |                                     |                                                                                                  |
| *Cimex dissimilis* (Horváth, 1910)                         | 253                                   |                                                                                                  |
| **Siphonaptera**       |                                     |                                                                                                  |
| *Ischnopsyllus (Hexactenopsylla) hexactenus* (Kolenati, 1856)| 44                                    |                                                                                                  |
| **Nyctalus lasiopterus** (Schreber, 1780)                   | 1 recognised species                  |                                                                                                  |
| **Acarina**           |                                     |                                                                                                  |
| *Pteracarus pipistrellus maximus* Uchikawa, 1989            | 251                                   |                                                                                                  |
| **Nyctalus leisleri** (Kuhl, 1817)                         | 2 recognised species                  |                                                                                                  |
| **Acarina**           |                                     |                                                                                                  |
| *Argas (Carios) vespertilionis* (Lateire, 1802)             | 45                                    |                                                                                                  |
| **Siphonaptera**       |                                     |                                                                                                  |
| *Ischnopsyllus (Ischnopsyllus) intermedius* Rothschild, 1898| 44                                    |                                                                                                  |

(Continued on next page)
| Bat host                        | Number of parasite species reported | Parasite occurrence and citation                                                                 |
|--------------------------------|-------------------------------------|--------------------------------------------------------------------------------------------------|
| *Nyctalus noctula* (Schreber, 1774) | 14 species (8 recognised species and 6 invalid species) | **Acari**  
[Acarus vespertilionis Hermann, 1804 - la Mite de la chauve-souris] [135]  
[Caris vespertilionis = Argas vespertilionis (Latreille, 1796) ?] [168, 171, 201]  
[Dermanyssus coriaceus Gervais (=Hirstionyssus arcuatus (Koch, 1839)?)] [11, 13, 103, 212, 221, 222, 258, 259]  
[Haemomyson trouessarti (Mégnin) (=Leiognathus arcuatus=Hirstionyssus arcuatus (Koch, 1839)?) See [244]]  
[Pteroptus vespertilionis (Dufour, 1832)] [131, 177]  
[Pteroptus vespertilionis] [131]  
[Hirstionyssus arcuatus (Koch, 1839)] [11, 12, 103, 124, 127, 167, 177, 212, 221, 258, 259]  
Spinturnix helvetiae (Deunff, Aellen & Keller, 1986) [recorded at Col de Bretolet, at the border between France and Switzerland] [79]  
Spinturnix acuminatus (C.L. Koch, 1836) [recorded at Col de Bretolet, at the border between France and Switzerland] [79]  

**Diptera**  
Nycteribia (Nycteribia) pedicularia Latreille, 1805[85]  

**Siphonaptera**  
Ischnopsyllus (Ischnopsyllus) variabilis (Wagner, 1898) ? [37]  
Ischnopsyllus (Ischnopsyllus) elongatus (Curtis, 1832) [37, 44, 167, 204, 228?, 231!]  
Ischnopsyllus (Ischnopsyllus) intermedius (Rothschild, 1898) [3, 44]  
Nycteridopsylla eusarca Dampf, 1908 [37, 42]  

**Pipistrellus kuhlii** (Kuhl, 1817)  
9 recognised species  

**Acari**  
Absence of Ixodes canisuga Johnston, 1849 [28]  
Absence of Ixodes (Eschatocephalus) simplex simplex Neumann, 1906 [32]  
Absence of Pholeoixodes hexagonus (Leach, 1815) [28]  
Argas (Carios) vespertilionis (Latreille, 1802) [45]  
Argas vespertilionis (Latreille, 1796) [28, 166]  
Ixodes (Eschatocephalus) vespertilionis C.L. Koch, 1844 [28]  

**Siphonaptera**  
Ischnopsyllus (Hexactenopsylla) hexactenus (Kolenati, 1856) [29]  
Ischnopsyllus (Ischnopsyllus) octactenus (Kolenati, 1856) [29, 33, 37, 167]  
Ischnopsyllus (Ischnopsyllus) variabilis (Wagner, 1898) [37, 44, 142]  
Nycteridopsylla longiceps Rothschild, 1908 [37, 44, 156]  

**Pipistrellus nathusii** (Keyserling & Blasius, 1839)  
8 recognised species  

**Acari**  
Absence of Ixodes canisuga Johnston, 1849 [28]  
Absence of Ixodes (Eschatocephalus) simplex simplex Neumann, 1906 [32]  
Absence of Pholeoixodes hexagonus (Leach, 1815) [28]  
Acanthophthirius (Acanthophthirius) poppei (Trouessart, 1895) [52, 102, 114, 167, 249]  
Argas (Carios) vespertilionis (Latreille, 1802) [45]  
Argas vespertilionis (Latreille, 1796) [28]  
Ixodes (Eschatocephalus) vespertilionis C.L. Koch, 1844 [28]  

**Siphonaptera**  
Ischnopsyllus (Ischnopsyllus) octactenus (Kolenati, 1856) [29, 33, 37, 167]  
Ischnopsyllus (Ischnopsyllus) variabilis (Wagner, 1898) [2, 29, 33, 37, 44, 167]  
Nycteridopsylla longiceps Rothschild, 1908 [37, 44, 156]  

**Pipistrellus pipistrellus** (Schreber, 1774)  
23 species (17 recognised species and 6 invalid species and one species complex)  

**Acari**  
Absence of Ixodes canisuga Johnston, 1849 [28]  
Absence of Ixodes (Eschatocephalus) simplex simplex Neumann, 1906 [32]  
Absence of Pholeoixodes hexagonus (Leach, 1815) [28]  
Absence of [Pteroptus vespertilionis] [67]  
[Argas caris] [191]  
[Caris vespertilionis = Argas vespertilionis (Latreille, 1796) ?] [258]  
[Gamassus pterooides (Mégnin)] [190]  
[Haemomyson trouessarti (Mégnin) (=Leiognathus arcuatus=Hirstionyssus arcuatus (Koch, 1839)?) See [221]]  
[Laelaps (Iphis) agilis Koch, Berlese = Gamassus pterooides (Mégnin)? = Laelaps agilis C.L. Koch, 1836 ?] [244], see also [190]  

(Continued on next page)
Table 1. (Continued)

| Bat host | Number of parasite species reported | Parasite occurrence and citation |
|----------|------------------------------------|---------------------------------|
| Pteropus vespertilionis (Hermann) | [215] |
| Argas (Carios) vespertilionis (Latreille, 1802) | [31, 45, 177, 239] |
| Argas vespertilionis (Latreille, 1796) | [18, 28, 38, 67, 166] |
| Ixodes (Eschatocephalus) vespertilionis C.L. Koch, 1844 | [28, 86, 199] |
| See also [201] |
| Diptera |
| Nycteribia (Nycteribia) pedicularia Latreille, 1805 | [214, 215] |
| Basilia (Basilia) mediterranea Húrka, 1970 | [40, 43, 167] |
| Nycteribia (Nycteribia) kolenati Theodor & Moscona, 1954 | [241] |
| Nycteribia (Nycteribia) schmidli Schiner, 1853 | [147] |
| Nycteribia sp. - Complex of species Nycteribia kolenati/latreillii/pedicularia [177, 214, 215] |
| Siphonaptera |
| Ischnopsyllus (Ischnopsyllus) octactenus (Kolenati, 1856) | [2, 29, 33, 36, 37, 44, 142, 164, 167, 227] |
| Ischnopsyllus (Ischnopsyllus) variabilis (Wagner, 1898) | [33, 37, 85] |
| Nycteridopsylla ancyluris ancyluris Jordan, 1942 | [29, 37, 38, 167] |
| Nycteridopsylla longiceps Rothschild, 1908 | [2, 29, 33, 37, 85, 167] |
| Nycteridopsylla pentactena (Kolenati, 1856) | [29, 37, 38, 167] |
| Trematoda |
| Lecithodendrium linstowi Dollfus, 1931 | [68, 167] |
| Parabascus semisquamosus (Braun, 1900) | [60, 68, 167] |
| Plagiorchis vespertilionis (O.F. Müller, 1784) | [68, 86, 167] |
| Pycnoporus heteroporus (Dujardin, 1845) | [57, 61, 68, 97, 163, 167, 235] |
| Pipistrellus sp. 3 recognised species |
| Acari |
| Argas (Carios) vespertilionis (Latreille, 1802) | [45] |
| Diptera |
| Basilia (Basilia) mediterranea Húrka, 1970 | [41] |
| Penicillidia (Penicillidia) dafourii (Westwood, 1834) | [53] |
| Plecotus auritus (Linné, 1758) 16 recognised species (15 recognised species and 1 invalid species) 1 innominate species |
| Acari |
| Absence of Ixodes canisuga Johnston, 1849 | [28] |
| Absence of Ixodes (Eschatocephalus) simplex simplex Neumann, 1906 | [32] |
| Absence of Pholeoixodes hexagonus (Leach, 1815) | [28] |
| [Spinturnix vespertilionis] | [70] |
| Argas (Carios) vespertilionis (Latreille, 1802) | [45] |
| Argas vespertilionis (Latreille, 1796) | [28] |
| Ixodes (Eschatocephalus) vespertilionis C.L. Koch, 1844 | [28, 199] |
| Spinturnix plecotina (C.L. Koch, 1839) | [63, 76, 167] |
| See also [201] |
| Cestoda |
| Vampirolepis sp/Milina sp. | [86] |
| Diptera |
| Basilia (Basilia) nana Theodor & Moscona, 1954 | [28, 237] |
| Basilia (Basilia) nattereri (Kolenati, 1857) | [28, 187] |
| Phthiridium biarticulatum Hermann, 1804 | [85, 86, 237] |
| Nematoda |
| Litomosa filaria (Beneden, 1873) | [19, 167] |
| Seuratum mucronatum (Rudolphi, 1809) | [54, 86, 194] |
| Siphonaptera |
| Ischnopsyllus (Ischnopsyllus) simplex Rothschild, 1906 | [29, 37] |
| Ischnopsyllus (Ischnopsyllus) variabilis ! (Wagner, 1898) | [85] |
| Ischnopsyllus (Hexactenopsylla) hexactenus (Kolenati, 1856) | [2, 33, 37, 44, 142, 177, 227, 228] |
| Nycteridopsylla longiceps Rothschild, 1908 | [33, 37, 85, 167, 227] |
| Nycteridopsylla pentactena (Kolenati, 1856) | [29, 33, 37, 167] |
| Trematoda |
| Plagiorchis vespertilionis (O.F. Müller, 1784) | [86, 167] |
| Prothodontium sp. | [86] |

(Continued on next page)
| Bat host              | Number of parasite species reported | Parasite occurrence and citation                                                                 |
|----------------------|------------------------------------|---------------------------------------------------------------------------------------------------|
| *Plecotus austriacus* Fischer, 1829 | 7 recognised species               | Acari: Absence of *Ixodes (Eschatocephalus) simplex* Neumann, 1906 [32]                           |
|                      |                                    | Argas (Carios) *vesperilionis* (Latreille, 1802) [31]                                               |
|                      |                                    | Argas (Secretargas) *transgariepinus* White, 1846 [45, 189]                                         |
|                      |                                    | *Spinturnix plecotina* (C.L. Koch, 1839) [63, 76, 167]                                               |
|                      |                                    | See also [128]                                                                                     |
|                      |                                    | Siphonaptera: *Ixchnopsyllus (Hexactenopsylla) hexactenus* (Kolenati, 1856) [33, 37, 44]          |
|                      |                                    | *Nycteridopsylla pentactena* (Kolenati, 1856) [33, 37, 167]                                         |
|                      |                                    | Trematoda: *Lecithodendrium linstowi* Dollfus, 1931 [68, 167]                                        |
|                      |                                    | *Parabascus lepidotus* Looss, 1907 [68, 167]                                                        |
| *Plecotus* sp.       | 1 recognised species               | Nematoda: *Seuratrum mucronatum* (Rudolph, 1809) [97]                                               |
| *Rhinolophus euryale* Blasius, 1853 | 21 recognised species              | Acari: Absence of *Ixodes canisuga* Johnston, 1849 [28]                                           |
|                      |                                    | Absence of *Pholeioxodes hexagonus* (Leach, 1815) [28]                                              |
|                      |                                    | *Eyndhovenia euryalis* (G. Canestrini, 1885) [50, 63, 70, 76, 78, 105, 139, 167, 235]           |
|                      |                                    | *Ichoronyssus scutatus* (Kolenati, 1856) [68, 167]                                                 |
|                      |                                    | *Macronyssus granulosus* (Kolenati, 1856) [51, 167]                                               |
|                      |                                    | Neomyobia *slovenica* Dushábek, 1969 [50–52, 167]                                                 |
|                      |                                    | *Neotrombicula (Sasatrombicula) hexasternalae* (Vercammen-Grandjean, 1963) [51, 162, 167]       |
|                      |                                    | *Spinturnix myoti* (Kolenati, 1856) [76]                                                           |
|                      |                                    | *Spinturnix psi* (Kolenati, 1856) [76]                                                             |
| *Rhinolophus*        |                                    | Diptera: *Nycteribia (Nycteribia) pedicularia* Lateville, 1805 ! [85]                              |
| ferrumequinum        |                                    | *Nycteribia (Achrocholidia) vexata* Westwood, 1835! [85]                                           |
| (Schreber, 1774)     |                                    | *Phthiridium biarticulatum* Hermann, 1804 [28, 30, 38, 115, 167, 242]                            |
|                      |                                    | Hemiptera: *Cimex lectularius* Linnaeus, 1758? [253, 254]                                           |
|                      |                                    | Nematoda: *Litomosa ottavianii* Lagrange & Bettini, 1948 [68, 167]                               |
|                      |                                    | *Rionxogolvania rhinolophi* (Bain & Chabaud, 1968) [20, 167]                                      |
|                      |                                    | Siphonaptera: *Rhinolophopsylla unipunctata unipunctata* (Taschenberg, 1880) [2, 29, 33, 142, 167]|
|                      |                                    | Trematoda: *Lecithodendrium linstowi* Dollfus, 1931 [68, 167]                                       |
|                      |                                    | *Parabascus lepidotus* Looss, 1907 [68, 167]                                                        |
|                      |                                    | *Plagiorchis vespertilionis* (O.F. Müller, 1784) [68, 167]                                         |
|                      | 50 species                         | (44 recognised species) and 6 invalid species)                                                    |
|                      | 2 innominate species               |                                                                                                  |
|                      |                                    | Acari: Absence of *Ixodes canisuga* Johnston, 1849 [28]                                           |
|                      |                                    | Absence of *Pholeioxodes hexagonus* (Leach, 1815) [28]                                             |
|                      |                                    | *Hirstonyssus arcanus* Koch (= *Liponyssus arcanus* C.L. Koch, 1839) (pro parte) et *Macronyssus* muirius (Lucas, 1840) (pro parte) [200] |
|                      |                                    | *Pteropus vespertilionis* Hermann] (215), see also [177])                                        |
|                      |                                    | *Pteropus vespertilionis* (Dufour, 1832) [200]                                                    |
|                      |                                    | Macronyssus *rhinolophi* (Oudemans, 1902) ! [152, 212]                                             |
|                      |                                    | *Ixodes (Eschatocephalus) simplex* Neumann, 1906! [85]                                            |
|                      |                                    | Macronyssus *ellipticus* (Kolenati, 1856) ! [152, 177, 212]                                       |
|                      |                                    | According to Radovsky [212], this observation published by Husson & Daum [152] is dubious.       |
|                      |                                    | Macronyssus *longimanus* (Kolenati) ! [152, 177, 212]: according to Radovsky [212], this           |
|                      |                                    | observation published by Husson & Daum [152] is dubious.                                           |

(Continued on next page)
Table 1. (Continued)

| Bat host | Number of parasite species reported | Parasite occurrence and citation |
|----------|------------------------------------|----------------------------------|
| Alabidocarpus diceratops Lawrence, 1952 | [5, 110, 167] |  |
| Alabidocarpus megalonyx (Trouessart, 1895) | [52, 111, 167, 208, 218, 249] |  |
| Alabidocarpus minor (Rollinat & Trouessart, 1897) | [52, 111, 167, 208, 218, 249] |  |
| Argas (Carios) vespertilionis (Latreille, 1802) | [45] |  |
| Eyndhovenia euryalis (G. Canestrini, 1885) | [50, 63, 76, 78, 167] |  |
| Eyndhovenia euryalis oudemansi (Eyndhoven, 1941) | [18, 105, 252] |  |
| Ixodes (Eschatocephalus) vespertilionis C.L. Koch, 1844 | [28, 32, 38, 45, 51, 58, 154, 167, 177, 199, 200, 214, 215, 218, 229, 239] |  |
| Labidocarpus (Labidocarpus) rollinati Trouessart, 1895 | [167, 218, 232] |  |
| Neomyobia rollinati (Poppe, 1908) | [50, 52, 167] |  |
| Notoedres (Notoedres) chiropteralis (Trouessart, 1896) | [106, 109, 167, 218, 250] |  |
| Nycteridocoptes eyndhoveni Fain, 1959 | [49, 107] |  |
| Paraperiglischrus rhinolophinus (C.L. Koch, 1841) | [50, 78, 167, 235] |  |
| Psorergates rhinolophi Fain, 1959 | [108, 167] |  |
| Sasatrombicula (Sasatrombicula) hexasternalae (Vercammen-Grandjean, 1963) | [51, 162, 167] |  |
| Spinturnix psi (Kolenati, 1856) | [139, 223] |  |
| Steatonyssus spinosus Willmann, 1936 | [50, 51, 167] |  |

See also [201]

**Cestoda**

Hymenolepis sp. [86]

**Diptera**

Nycteribia vespertilionis Lateirelle [73]

**Hemiptera**

Cimex dissimilis (Horváth, 1910) [254]

Cimex lectularius Linnaeus, 1758 [253, 254]

**Nematoda**

Litomosa ottavianii Lagrange & Bettini, 1948 [19, 167]

Strongylacantha glycirrhyza van Beneden, 1873 [68, 167, 200, 243]

Trichosomum speciosum van Beneden, 1873 [200]

See also [174]

**Siphonaptera**

Iscnopsyllus (Iscnopsyllus) simplex Rothschild, 1906 [152, 177]

Iscnopsyllus (Iscnopsyllus) intermedius (Rothschild, 1898) [29]

Iscnopsyllus (Hexactenopsylla) hexactenus (Kolenati, 1856) [152]

Nycteridopsylla penticentata (Kolenati, 1856) [29, 37, 152, 164, 167, 177]

Rhinolophopsylla unipunctata unipunctata (Taschenberg, 1880) [2, 33, 38, 44, 142, 152, 156, 164, 167, 177, 227, 242]

**Trematoda**

[Paralecithodendrium chilostomum (Mehlis) (=Prosthodendrium (Prosthodendrium) chilostomum (Mehlis, 1831))] [200]

Lecithodendrium granulosum Looss, 1907 [200]

Lecithodendrium tinstowi Dollfus, 1931 [68, 167, 243]

Lecithodendrium moelldingeri (Pande, 1935) [243]

Mesotretes peregrinus (Braun, 1900) [68, 71, 88, 167, 188, 243]

Parabascus lepidotus Looss, 1907 [68, 167]

Plagiocercis vespertilionis (O.F. Müller, 1784) [68, 71, 86–88, 167, 200, 243]

Prosthodendrium (Prosthodendrium) carolinum Hurková, 1959 [167, 243]

Prosthodendrium (Prosthodendrium) chilostomum (Mehlis, 1831) [200, 243]

Prosthodendrium (Prosthodendrium) longiforme (Blalerao, 1926) [71, 167, 243]

See also [174]

**Rhinolophus hipposideros** (Bechstein, 1800) 21 species (19 recognised species and 2 invalid species) 2 innominate species

**Acarai**

Absence of Isodes canisuga Johnston, 1849 [28]

Absence of Pholeoixodes hexagonus (Leach, 1815) [28]

[Protopus vespertilionis (Dufour, 1832)] [200]
France, namely *Ixodes canisuga*, *I. ricinus*, and *Pholeoixodes hexagonus* [28]. Finally, 22 invalid taxa reported from France were found in the analysed papers. Examples for this category are *Dermanyssus murinus* (Lucas, 1840) [101, 104, 167, 195], *D. vespertilionis* Dugès, 1834 [94], *Pteroptus vespertil- lionis*, and *Spinturnix vespertilionis* (C.L. Koch) [70].

A large host group comprising the following taxa was identified with Acari infections: *Barbastella barbastellus, Eptesicus serotinus, Eptesicus sp.*, *Hypusgo savii, Minitoerpus schreiber- sii, Myotis bechsteinii, M. blythii, M. blythii oxygnathus, M. capaccini, M. dasykine, M. daubentonii, M. emarginatus, M. myotis, M. mystacinus, M. nattereri, M. punicus, Myotis sp.*, *Nyctalus lasiopterus, N. leisleri, N. noctula, Pipistrellus kuhlii, P. nathusi, P. pipistrellus, Pipistrellus sp.*, *Plecotus auritus, Rhinolophus euryale, R. ferrumequinum, R. hipposideros* and *Rhinolophus* sp. (see Tables 1 and 2).

The oldest works dealing with Acari parasitising bats in France are Geoffroy’s *Histoire abrégée des insectes* [123] and Latreille’s *Précis des caractères génériques des insectes, disposés dans un ordre naturel* [168], dated 1762 and 1797. Geoffroy mentioned the tick (found on an unidentified bat) as *Acarus fuscus ovatus, pedibulus pallidis, vespertilionis*, a taxon treated as *Caris vespertilionis* by Lamarck in the *Histoire naturelle des animaux sans vertèbres* (1839). The book of

| Bat host               | Number of parasite species reported | Parasite occurrence and citation                                                                 |
|------------------------|------------------------------------|---------------------------------------------------------------------------------------------------|
| *Rhinolophus mehelyi*  | 1 recognised species               | *Diptera*                                                                                         |
| Matschie, 1901         |                                     | *Nycteribia (Nycteribia) schmidlii* Schiner, 1853                                                 |
| *Rhinolophus sp.*      | 5 species/4 recognised species and 1 invalid species | *Acari*                                                                                            |
|                        | 1 innominate species               | *Eyndhovenia euryalis* (G. Canestrini, 1885) [51, 76]                                               |
|                        |                                     | *Ixodes (Eschatocephalus) vespertilionis* C.L. Koch, 1844 [5, 58, 126, 197]                         |
|                        |                                     | [Liponyssus setosus (Kolenati)] [72]                                                                |
|                        |                                     | *Neomyobia sp.* [126]                                                                             |
| *Tadarida teniotis*    | 1 recognised species               | *Nematoda*                                                                                        |
| (Rafinesque, 1814)     |                                     | *Litomosa ottavianii* Lagrange & Bettini, 1948 [19, 167]                                           |
|                        |                                     | *Siphonaptera*                                                                                    |
|                        |                                     | *Rhinolophopsylla uniceptinata uniceptinata* (Taschenberg, 1880) [2, 86, 142, 167, 200, 228]    |
|                        |                                     | *Trematoda*                                                                                      |
|                        |                                     | *Lecithodendrium granulosum* Looss, 1907? [200]                                                   |
|                        |                                     | [Paralecithodendrium chlostomum (Mehlis) (=Prosthodendrium (Prosthodendrium) chlostomum (Mehlis, 1831)?)] [200] |
|                        |                                     | [Mesotretes peregrinus (Braun, 1900) [68, 167, 188]                                              |
|                        |                                     | *Plagiorchis vespertilionis* (O.F. Müller, 1784) [68, 86, 167, 200]                              |
|                        |                                     | *Prosthodendrium (Prosthodendrium) chlostomum* (Mehlis, 1831) [86, 167, 200, 235]               |
| *Tadarida teniotis*    | 1 recognised species               | *Siphonaptera*                                                                                    |
| (Rafinesque, 1814)     |                                     | *Rhinolophopsylla uniceptinata uniceptinata* (Taschenberg, 1880) [44]                             |

Table 1. (Continued)
Table 2. List of bat parasites (Acari, Anoplura, Cestoda, Diptera, Hemiptera, Nematoda, Siphonaptera, Trematoda) and their hosts in France (including Corsica), based on the published literature, with reported synonyms. Authors are listed in the bibliography. See also the work entitled *Les parasites métaboîotes des Chiropètes de France (Acari, Anoplura, Cestoda, Diptera, Hemiptera, Nematoda, Siphonaptera, Trematoda) : contribution à un état des lieux bibliographique (1762-2018) et à l'établissement d'une liste nationale (2019).* Invalid species are listed in brackets. Records marked with an exclamation mark (!) are invalid. Records marked with a question mark (?) are dubious. They may require further clarification.

| Parasite species | Number of reported hosts | Bat species and citation |
|------------------|--------------------------|--------------------------|
| Acari, part I/3: generally recognised taxa (n = 53), with their reported synonyms, and records without identification to species level (n = 6) | | |
| Acanthophthirius (Myotimyobia) pantopus (Poppe et Trouessart, 1895) | 1 | Barbastella barbastellus (Schreber, 1774) [102, 114, 167, 235, 249] |
| Acanthophthirius (Acanthophthirius) poppei (Trouessart, 1895) | 1 | Pipistrellus nathusii (Keyserling & Blasius, 1839) [52, 102, 114, 167, 249] |
| Alabidocarpus diceratops Lawrence, 1952 | 1 | Rhinolophus ferrumequinum (Schreber, 1774) [5, 110, 167] |
| Alabidocarpus megalonyx (Trouessart, 1895) | 1 | Rhinolophus ferrumequinum (Schreber, 1774) [52, 111, 167, 208, 218, 249] |
| Alabidocarpus minor (Rollini & Trouessart, 1897) | 1 | Rhinolophus ferrumequinum (Schreber, 1774) [52, 111, 167, 208, 218, 249] |
| Argas pipistrellae (Audouin, 1832) = Argas vespertilionis (Lateille, 1796) | | |
| Argas transgarietipinus White, 1846 = Argas (Secretargas) transgarietipinus White, 1846 | | |
| Argas vespertilionis (Lateille, 1796) | 11 | Barbastella barbastellus (Schreber, 1774) [28] |
| | | Eptesicus serotinus (Schreber, 1774) [28, 38] |
| | | Miniopterus schreibersii (Natterer in Kuhl, 1817)? [85] |
| | | Myotis emarginatus (Geoffroy, 1806) [28] |
| | | Myotis myotis (Borkhausen, 1797) [28] |
| | | Myotis mystacinus (Leisler in Kuhl, 1817) [28] |
| | | Myotis sp. [171?, 242] |
| | | Pipistrellus kuhlii (Kuhl, 1817) [28, 166] |
| | | Pipistrellus nathusii (Keyserling & Blasius, 1839) [28] |
| | | Pipistrellus pipistrellus (Schreber, 1774) [18, 28, 38, 67, 166] |
| | | Plecotus austriacus (Fischer, 1829) [45] |
| | | Myotis mystacinus (Leisler in Kuhl, 1817) [45] |
| | | Hypsugo savii (Bonaparte, 1837) [45] |
| | | Myotis dasygneme (Boie, 1825) [31] |
| | | Myotis mystacinus (Leisler in Kuhl, 1817) [45] |
| | | Nyctalus leisleri (Kuhl, 1817) [45] |
| | | Pipistrellus kuhlii (Kuhl, 1817) [45] |
| | | Pipistrellus nathusii (Keyserling & Blasius, 1839) [45] |
| | | Pipistrellus pipistrellus (Schreber, 1774) [31, 45, 177, 239] |
| | | Pipistrellus sp. [45] |
| | | Plecotus auritus (Linné, 1758) [45] |
| | | Plecotus austriacus Fischer, 1829 [31] |
| | | Rhinolophus ferrumequinum (Schreber, 1774) [45] |
| | | See also [5, 167-169] |
| | | Eptesicus serotinus (Schreber, 1774) [31, 45, 86] |
| | | Hypsugo savii (Bonaparte, 1837) [45] |
| | | Myotis dasygneme (Boie, 1825) [31] |
| | | Myotis mystacinus (Leisler in Kuhl, 1817) [45] |
| | | Nyctalus leisleri (Kuhl, 1817) [45] |
| | | Pipistrellus kuhlii (Kuhl, 1817) [45] |
| | | Pipistrellus nathusii (Keyserling & Blasius, 1839) [45] |
| | | Pipistrellus pipistrellus (Schreber, 1774) [31, 45, 177, 239] |
| | | Pipistrellus sp. [45] |
| | | Plecotus auritus (Linné, 1758) [45] |
| | | Plecotus austriacus Fischer, 1829 [31] |
| | | Rhinolophus ferrumequinum (Schreber, 1774) [45] |
| | | See also [5, 167-169] |
| | | Calcarmyobia dusbabeki Uchikawa, 1985? |
| | | Calcarmyobia dusbabeki Uchikawa, 1985 / Calcarmyobia rhinolophia (Radford, 1940). |
| | | Calcarmyobia rhinolophia (Radford, 1940)! |
| | | Calcarmyobia rhinolophia (Radford, 1940)! |
| | | Minioptrers schreibersii (Natterer in Kuhl, 1817) [50, 51, 167] |
| | | There is only one case. According to Lanza (1999) [publication n°167], this field data published by Beron (1971) [publication n°50] is doubtful. It could be Calcarmyobia dusbabeki Uchikawa, 1985 / Calcarmyobia rhinolophia (Radford, 1940). |
| | | There is only one case. According to Lanza (1999) [publication n°167], this field data published by Beron (1971) [publication n°50] is doubtful. It could be Calcarmyobia dusbabeki Uchikawa, 1985 / Calcarmyobia rhinolophia (Radford, 1940). |
| | | Calcarmyobia rhinolophia (Radford, 1940)! |
| | | Calcarmyobia rhinolophia (Radford, 1940)! |
| | | Calcarmyobia rhinolophia (Radford, 1940)! |

(Continued on next page)
| Parasite species | Number of reported hosts | Bat species and citation |
|------------------|--------------------------|--------------------------|
| Dermanyssus coriaceus = Hirstionyssus arcuatus (Koch, 1839). See [11, 13, 221, 222] | 1 | Myotis emarginatus (Geoffroy, 1806) [86] |
| Dermanyssus sp. | | |
| Dermanyssus pipistrellae (Gervais, 1841) = Hirstionyssus arcuatus (Koch, 1839) | | |
| Diplostaspididae Kolenati, 1857 = Spinoturnix andegavinus (Deunff, 1977) according to Deunff (1977) [76] | 1 | Rhinolophus ferrumequinum (Schreber, 1774) [50, 63, 76, 78, 167] |
| Diplostaspididae | | |
| Diplostaspididae Kolenati, 1857 = Spinoturnix andegavinus (Deunff, 1977) according to Deunff (1977) [76] | 1 | Rhinolophus ferrumequinum (Schreber, 1774) [50, 63, 76, 78, 167] |
| Eschatocephalus flavipes (Koch) | 5 | Rhinolophus ferrumequinum (Schreber, 1774) [50, 63, 76, 78, 167] |
| Eschatocephalus vespertilionis C.L. Koch = Ixodes (Eschatocephalus) vespertilionis C.L. Koch, 1844 | 1 | Rhinolophus ferrumequinum (Schreber, 1774) [18?, 105, 252] |
| Eschatocephalus vespertilionis (Koch 1844) = Ixodes (Eschatocephalus) vespertilionis C.L. Koch, 1844 | 1 | Rhinolophus ferrumequinum (Schreber, 1774) [18?, 105, 252] |
| Ichoronyssus diversipilis Vitzthum, 1920 | 1 | Myotis myotis (Borkhausen, 1797)? [24, 70, 72] |
| Ichoronyssus scutatus (Kolenati, 1856) | 1 | Myotis myotis (Borkhausen, 1797)? [24, 70, 72] |
| Ichoronyssus spinosus (Oudemans) 1902) | 1 | Myotis myotis (Borkhausen, 1797)? [24, 70, 72] |
| Ichoronyssus sp. | 1 | Myotis myotis (Borkhausen, 1797)? [24, 70, 72] |
| Ixodes chiropterum Babos et Janisch, 1958 = Ixodes (Eschatocephalus) simplex simplex Neumann, 1906 | 1 | Myotis myotis (Borkhausen, 1797)? [24, 70, 72] |
| Ixodes gracilipes = Ixodes (Eschatocephalus) vespertilionis C.L. Koch, 1844 ? | 1 | Myotis myotis (Borkhausen, 1797)? [24, 70, 72] |
| Ixodes hexagonus Leach, 1815 = Pholeoixodes hexagonus (Leach, 1815) | 1 | Myotis myotis (Borkhausen, 1797)? [24, 70, 72] |
| Ixodes longipes (Lucas, 1872) = Ixodes (Eschatocephalus) vespertilionis C.L. Koch, 1844 | 1 | Myotis myotis (Borkhausen, 1797)? [24, 70, 72] |
| Ixodes (Pomerantzevella) simplex Neumann, 1906 = Ixodes (Eschatocephalus) simplex simplex Neumann, 1906 | 1 | Myotis myotis (Borkhausen, 1797)? [24, 70, 72] |
| Ixodes pospelovae Emtchuck, 1955 = Ixodes (Eschatocephalus) simplex simplex Neumann, 1906 | 1 | Myotis myotis (Borkhausen, 1797)? [24, 70, 72] |
| Ixodes siculifer Mégnin, 1880 = Ixodes (Eschatocephalus) vespertilionis C.L. Koch, 1844 | 18 | Myotis myotis (Borkhausen, 1797)? [24, 70, 72] |
| Ixodes reduvius Geer = Ixodes (Ixodes) ricinus (Linnaeus, 1758) | | |
| Ixodes (Eschatocephalus) vespertilionis C.L. Koch, 1844 | | |
| Parasite species | Number of reported hosts | Bat species and citation |
|-------------------|--------------------------|--------------------------|
| Pipistrellus nathusii (Keyserling & Blasius, 1839) [28] |  |  |
| Pipistrellus pipistrellus (Schreber, 1774) [28, 86, 199] |  |  |
| Plecotus auritus (Linné, 1758) [28, 199] |  |  |
| Rhinolophus euryale Blasius, 1853 [28, 32, 85, 166] |  |  |
| Rhinolophus ferrumequinum (Schreber, 1774) [28, 32, 38, 45, 51, 58, 154, 177, 199, 200, 214, 215, 218, 229, 239] |  |  |
| Rhinolophus hipposideros (Bechstein, 1800) [23, 28, 32, 152, 154, 199, 200] |  |  |
| Rhinolophus sp. [5, 58, 126, 197] |  |  |
| Ixodes (Eschatocephalus) simplex simplex Neumann, 1906 | 4 | Absence in Myotis blythii (Tomes, 1857) and M. blythii oxygnathus Monticelli, 1885 [32] |
| Rhinolophus ferrumequinum (Schreber, 1774) ! [85] |  |  |
| Myotis mystacinus (Leisler in Kuhl, 1817) ! [85] |  |  |
| Myotis myotis (Borkhausen, 1797) ! [85] |  |  |
| Miniopterus schreibersii (Natterer in Kuhl, 1817) ([15, 31, 32, 45, 51, 143?, 166, 167, 176] see Beaucournu [1966; p. 498] paper n°30) |  |  |
| Ixodes sp. 2 |  | Myotis myotis (Borkhausen, 1797) [178] |
| Labidocarpus megalonyx (Trouessart, 1895) = Alabidocarpus megalonyx (Trouessart, 1895) | 2 | Rhinolophus hipposideros (Bechstein, 1800) [178] |
| Labidocarpus minor (Rollinat & Trouessart, 1897) = Alabidocarpus minor (Rollinat & Trouessart, 1897) |  |  |
| Labidocarpus (Labidocarpus) rollinati Trouessart, 1895 | 2 | Rhinolophus ferrumequinum (Schreber, 1774) [167, 218, 232] |
| Leiothrix arcurata = Hirstionyssus arcuratus (Koch, 1839) |  |  |
| Leiothrix uncinitus = Macronyssus uncinitus (Canestrini, 1885) |  |  |
| Leptotrombidium (Leptotrombidium) ruscicum (Oudemans, 1902) = Leptotrombidium ruscicum (Oudemans, 1902) | 2 | Myotis daubentonii (Leisler in Kuhl, 1817) [122, 167, 177, 256] see also [10] |
| Leptos autumnalis = Neotrombicula autumnalis (Shaw, 1790) |  | Rhinolophus hipposideros (Bechstein, 1800) [161] |
| Liponyssus ellipticus = Macronyssus ellipticus (Kolenati, 1856) |  |  |
| Liponyssus euryale Canestrini = Macronyssus rhinolophi (Oudemans, 1902) |  |  |
| Liponyssus longimanus = Macronyssus longimanus (Kolenati) |  |  |
| Liponyssus spinosus Oudemans, 1902 = Ichoronyssus scutatus (Kolenati, 1856) |  |  |
| Macronyssus ellipticus (Kolenati, 1856) ! | 1 | Rhinolophus ferrumequinum (Schreber, 1774) ! [152, 177, 212] |

(Continued on next page)
Table 2. (Continued)

| Parasite species | Number of reported hosts | Bat species and citation |
|------------------|--------------------------|--------------------------|
| According to Radovsky [212], this observation published by Husson & Daum [152] is dubious. | 2 | Miniopterus schreibersii (Natterer in Kuhl, 1817) [50, 167] |
| Macronyssus granulosus (Kolenati, 1856) | 2 | Miniopterus schreibersii (Natterer in Kuhl, 1817) [50, 167] |
| Macronyssus longimanus (Kolenati) | 1 | Rhinolophus ferrumequinum (Schreber, 1774) [152, 177, 212] |
| Macronyssus uncinatus (Canestrini, 1885) | 1 | Chiroptera gen. sp. [160, 177] |
| Macronyssus rhinolophi (Oudemans, 1902) | 3 | Myotis myotis (Borkhausen, 1797)? [152?, 212?] |
| Macronyssus spinosus (Oudemans, 1902) = Ichoronyssus scutatus (Kolenati, 1856) | 1 | Rhinolophus ferrumequinum (Schreber, 1774)? [152?, 212?] |
| Myobia pantopus = Acanthophthirus (Myotimyobia) pantopus (Poppe et Trouessart, 1895) | 1 | Rhinolophus ferrumequinum (Schreber, 1774)? [152?, 212?] |
| Myobia poppei = Acanthophthirus (Acanthophthirus) poppei (Trouessart, 1895) | 1 | Rhinolophus ferrumequinum (Schreber, 1774)? [152?, 212?] |
| Neomyobia chiropterensis chiropterensis (Michael, 1884) | 1 | Rhinolophus hipposideros (Bechstein, 1800) [50, 152?, 167, 212?] |
| Neomyobia rollinati (Poppe, 1908) | 1 | Rhinolophus ferrumequinum (Schreber, 1774) [50, 52, 167] |
| Neomyobia slotenia Dusbábek, 1969 | 1 | Myotis daubentonii (Leisler in Kuhl, 1817) [8–10, 122, 167, 177, 256] |
| Neomyobia sp. | 2 | Myotis daubentonii (Leisler in Kuhl, 1817) [8–10, 122, 167, 177, 256] |
| Neotrombicula racovitzai Feider, 1970 | 1 | Eptesicus sp. [5, 118, 167] |
| Neotrombicula vandeli Kolebinova & Vercammen-Grandjean, 1971 | 1 | Rhinolophus euryale Blasius, 1853 [7, 162, 167] |
| Notoedres (Notoedres) chiropterensis (Trouessart, 1896) | 2 | Rhinolophus ferrumequinum (Schreber, 1774) [106, 109, 167, 218, 250] |
| Nycteridocoptes eyndhoveni Fain, 1959 | 1 | Eptesicus serotinus (Schreber, 1774) [48, 106, 167, 250] |
| Nycteridocoptes poppei Oudemans, 1898 | 3 | Myotis myotis (Borkhausen, 1797) [24] |
| Oudemansidium musco (Oudemans, 1906) | 1 | Myotis daubentonii (Leisler in Kuhl, 1817) [122, 167, 177] |
| Paraperiglischrus rhinolophinus (C.L. Koch) = Paraperiglischrus rhinolophinus (C.L. Koch, 1841) | 3 | Rhinolophus euryale Blasius, 1853 [50, 76, 138, 167, 235] |
| Paraperiglischrus rhinolophinus Koch, 1841 = Paraperiglischrus rhinolophinus (C.L. Koch, 1841) | 3 | Rhinolophus ferrumequinum (Schreber, 1774) [50, 78, 167, 235] |
| Paraperiglischrus rhinolophinus (C.L. Koch, 1841) | 3 | Rhinolophus hipposideros (Bechstein, 1800) [50, 138, 167, 225?, 235] |
| Periglischrus interruptus (Kolenati, 1856) = Paraperiglischrus rhinolophinus (C.L. Koch, 1841) | 1 | Nyctalus lasiopterus (Schreber, 1780) [251] |
| Pteracaris pipistrellus maximis Uchikawa, 1989 | 1 | Rhinolophus ferrumequinum (Schreber, 1774) [108, 167] |
| Prospodoctes chiropterensis (Trouessart, 1896) = Notoedres (Notoedres) chiropterensis (Trouessart, 1896) | 1 | Rhinolophus ferrumequinum (Schreber, 1774) [108, 167] |
| Psorergates rhinolophi Fain, 1959 | 1 | Rhinolophus euryale Blasius, 1853 [7, 51, 161, 167] |
| Riedlinia (Riedlinia) petarberoni (Kolebinova & Vercammen-Grandjean, 1970) | 1 | Rhinolophus euryale Blasius, 1853 [7, 51, 161, 167] |
| Sarcoptes vespertilionis = Ixodes (Eschatocephalus) vespertilionis C.L. Koch, 1844 | 1 | Rhinolophus hipposideros (Bechstein, 1800) [51, 52, 162, 167] |

(Continued on next page)
| Parasite species | Number of reported hosts | Bat species and citation |
|------------------|--------------------------|--------------------------|
| *Sasatrombicula (Sasatrombicula) hexasternalae* (Vercammen-Grandjean, 1963) | 4 | Chiroptera sp. [7] |
| | | *Rhinolophus euryale* Blasius, 1853 [51, 162, 167] |
| | | *Rhinolophus ferrumequinum* (Schreber, 1774) [51, 162, 167] |
| | | *Rhinolophus hipposideros* (Bechstein, 1800) [51, 162, 167] |
| *Spinturnix acuminatus* (C.L. Koch, 1836) | 1 | *Nyctalus noctula* (Schreber, 1774) [recorded at Col de Bretolet, at the border between France and Switzerland] [79] |
| *Spinturnix andegavina* (Deunff, 1977) | 1 | *Myotis daubentonii* (Leisler in Kuhl, 1817) [76], see also [167] |
| | | This species is treated as *Spinturnix andegavina* Deunff, 1977 by some authors [167, 209, 225]. According to Sachanowicz et al. (publication n°223; p. 49), this species “is a member of the *myoti* species group, which is actually recognised as also containing: *S. dasycnemi* (Kolenati, 1856), *S. myoti* (Kolenati, 1856), *S. bechsteini* Deunff et al. 2004, *S. emarginata* (Kolenati, 1856), and *S. mystacina* (Kolenati, 1857)”. According to Lanza [167], this taxon is actually a synonym of *Spinturnix daubentonii* (Kolenati, 1857). |
| *Spinturnix bechsteini* (Deunff, Walter, Bellido et Volleth, 2004) | 1 | *Myotis bechsteini* (Leisler in Kuhl, 1817) [82, 130] |
| *Spinturnix daubentonii* (Kolenati, 1857). This species is treated as a synonym of *Spinturnix andegavina* (Deunff, 1977) by some authors [167, 209, 225]. | | |
| *Spinturnix helvetiae* (Deunff, Aellen & Keller, 1986). | 1 | *Nyctalus noctula* (Schreber, 1774) [recorded at Col de Bretolet, at the border between France and Switzerland] [79] |
| | | In the opinion of Uchikawa et al. (1994), this taxon is actually a subspecies of *S. acuminata* (C.L. Koch, 1836). See the article entitled “Contribution to the taxonomy of the genus *Spinturnix* (Acari: Spinturnicidae), with the erection of a new genus, *Emballonuria*” (Folia Parasitologica, 41 (4), p. 295). |
| *Spinturnix emarginatus* (Kolenati, 1856) | 1 | *Myotis emarginatus* (Geoffroy, 1806) [7, 76, 78] |
| | | See also [77] |
| *Spinturnix euryalis* (G. Canestrini) = *Eyndhovenia euryalis* (G. Canestrini, 1885) | | |
| *Spinturnix morinus* (Walckenaer, 1847) = *Spinturnix myoti* (Kolenati, 1856) | | |
| *Spinturnix myoti* (Kolenati, 1856) | 8 | Chiroptera gen. sp. [7, 65, 167, 246] |
| | | *Miniopterus schreibersii* (Natterer in Kuhl, 1817) [76] |
| | | *Myotis blythii* (Tomes, 1857) and *M. blythii oxygnathus* Monticelli, 1885 [14, 76] |
| | | *Myotis capaccinii* (Bonaparte, 1837) [76] |
| | | *Myotis myotis* (Borkhausen, 1797) [14?, 76, 78, 177, 226] |
| | | *Myotis nattereri* (Kuhl, 1817) [63, 121] |
| | | *Myotis punicus* Felten, Spitzenberger & Storch, 1977 [64] |
| | | *Rhinolophus euryale* Blasius, 1853 [76] |
| | | See also [77] |
| *Spinturnix mystacinus* (Kolenati, 1857) | 1 | *Myotis mystacinus* (Leisler in Kuhl, 1817) [76, 78] |
| | | See also [77] |
| *Spinturnix nobleti* Deunff, Volleth, Keller et Aellen, 1990 | 1 | *Hypsugo savii* (Bonaparte, 1837) [81, 167] |
| *Spinturnix ouedemansii* van Eyndhoven, 1941 = *Eyndhovenia euryalis* (G. Canestrini, 1885) | | |
| *Spinturnix ouedemansii* van Eyndhoven, 1941 = *Eyndhovenia euryalis* (G. Canestrini, 1885) | | See also *Eyndhovenia euryalis ouedemansi* (Eyndhoven, 1941). |

(Continued on next page)
### Table 2. (Continued)

| Parasite species | Number of reported hosts | Bat species and citation |
|------------------|--------------------------|--------------------------|
| *Spinturnix plecotina* (C.L. Koch, 1839) | 3 | Chiroptera gen. sp. [7]  
| | | *Plecoptus auritus* (Linne, 1758) [63, 76, 167]  
| | | *Plecoptus austriacus* Fischer, 1829 [63, 76, 167] |
| *Spinturnix plecotinus* Koch, 1839 = *Spinturnix plecotina* (C.L. Koch, 1839) | | |
| *Spinturnix punctata* (Sundevall, 1833) | 1 | *Barbastella barbastellus* (Schreber, 1774) [80, 167] |
| *Spinturnix psi* (Kolenati, 1856) | 7 | Chiroptera gen. sp. [7, 167, 210?, 223]  
| | | *Eptesicus serotinus* (Schreber, 1774) [48]  
| | | *Miniopterus schreibersii* (Natterer in Kuhl, 1817) [50, 63, 76, 139]  
| | | *Myotis capaccinii* (Bonaparte, 1837) [63, 76, 121, 139]  
| | | *Myotis myotis* (Borkhausen, 1797) [76]  
| | | *Rhinolophus euryale* Blasius, 1853 [76]  
| | | *Rhinolophus ferrumequinum* (Schreber, 1774) [139, 223?]  
| | | See also [210] |
| *Spinturnix sp.* | 1 | *Myotis myotis* (Borkhausen, 1797) [133] |
| *Steatonyssus* sp. | 1 | *Myotis myotis* (Borkhausen, 1797) [152, 212] |
| *Steatonyssus spinosus* Willmann, 1936 | 1 | *Rhinolophus ferrumequinum* (Schreber, 1774) [50, 51, 167] |
| *Thrombicula autumnalis* Shaw = *Neotrombicula autumnalis* (Shaw, 1790) | | |
| *Thrombicula russica* Oudemans = *Leptotrombidium russicum* (Oudemans, 1902) | | |
| *Thrombicula russicum* = *Leptotrombidium russicum* (Oudemans, 1902) | | |
| *Trombicula muscae* = *Oudemansiadium musca* (Oudemans, 1906) | | |
| *Trombicula russicum* = *Leptotrombidium russicum* (Oudemans, 1902) | | |
| *Acarus vespertilionis* Hermann | 1 | Chiroptera gen. sp. [257, 258]  
| | | *Nyctalus noctula* (Schreber, 1774)? [90, 135] |
| *Caris vespertilionis* = *Argas pipistrellae* (Audouin)? = *Argas vespertilionis* (Lateille, 1796)? | 2? | *Pipistrellus pipistrellus* (Schreber, 1774) [191]  
| | | *Nyctalus noctula* (Schreber, 1774)? [168?, 171, 201]  
| | | *Pipistrellus pipistrellus* (Schreber, 1774)? [258]  
| | | See also [90] |
| *Dermanyssus coriaceus* Gervais (=*Hirstionyssus arcuatus* (Koch, 1839)?) | 1 | *Nyctalus noctula* (Schreber, 1774) [11, 13, 103, 212, 222, 258, 259] |
| *Dermanyssus murinus* (Lucas, 1840) | 1 | *Myotis myotis* (Borkhausen, 1797) [101, 104, 167, 183, 195] |
| *Dermanyssus vespertilionis* Dugès, 1834 | 1 | Chiroptera gen. sp. [94] |
| *Gamasus dermanyssoïdes* (Mégnin) | 1 | *Myotis mystacinus* (Leisler in Kuhl, 1817) [248] |
| *Gamasus pteroptoides* (Mégnin) | 1 | *Pipistrellus pipistrellus* (Schreber, 1774) [190] |
| The species is recognised by Da Fonseca [72], Lanza [167] and Neumann (see *A treatise on the parasites and parasitic diseases of the domesticated animals*.) Translation George Fleming, 2nd edition. Baillière Tindall, London, 1892, 574 p.; p. 99. Kramer treated the species as a synonym of *Laelaps pteroptoides* Mégnin (see the article entitled ‘Ueber Milben’, published in *Archiv für Naturgeschichte*, volume 52, issue 1, 1886, p. 251). *Tiraboschi* [244] treated the species as a synonym of *Haemomyson musculi* and *Laelaps (Iphis) agilis* Koch, Berlese. According to Rudnick [223], *Gamasus pteroptoides* (Mégnin) is not a species of the *Spinturnicidae* family. *Haemogamasus setosus* (Kolenati)] | 1 | *Rhinolophus ferrumequinum* (Schreber, 1774) [5] |

(Continued on next page)
| Parasite species                                      | Number of reported hosts | Bat species and citation                                                                 |
|-------------------------------------------------------|--------------------------|-----------------------------------------------------------------------------------------|
| [Haemomyson trouessarti (Mégnin) (=Leiognathus arcuatus (=Hirstionyssus arcuatus (Koch, 1839)? (See [167, 244]., p. 119) | 3                         | Pipistrellus pipistrellus (Schreber, 1774) [191, 244] Nyctalus noctula (Schreber, 1774) [191, 244] |
| [Laelaps (Iphis) agilis Koch, Berlese = Gamasus pteroptoides (Mégnin)? = Laelaps agilis C.L. Koch, 1836?] | 1                         | Pipistrellus pipistrellus (Schreber, 1774) ([244], see also [190])                      |
| [Leiognathus armatus (=Hirstionyssus arcuatus (C.L. Koch, 1839)?] | 1                         | Chiroptera gen. sp. [160, 177]                                                          |
| [Liponyssus arcuatus Koch (=Hirstionyssus arcuatus (C.L. Koch, 1839) (pro parte) and Steatonyssus murinus (Lucas, 1840) (pro parte) | 1                         | Rhinolophus ferrumequinum (Schreber, 1774) [200]                                        |
| [Liponyssus decussatus (Kolenati) (=Caris decussata Kolenati, 1856?)] | 1                         | Myotis myotis (Borkhausen, 1797) [23]                                                  |
| [Liponyssus setosus (Kolenati)]                       | 2                         | Chiroptera gen. sp. [72] Rhinolophus sp. [72]                                           |
| [Pteroptus trouessarti Méggin (=Haemomyson trouessarti (Méggin)?) | 2                         | Myotis daubentoni Leisler in Kuhl, 1817 [177, 248]                                      |
| [Pteroptus vesprumilis]                                | 3                         | Absence in Pipistrellus pipistrellus (Schreber, 1774) [67]                            |
| [Pteroptus vespertilious] Hermann                     | 2                         | Absence in Pipistrellus pipistrellus (Schreber, 1774) [215]                            |
| [Pteroptus vespertilious (Dufour, 1832)]              | 9                         | Absence in Pipistrellus pipistrellus (Schreber, 1774) [215]                            |
| [Spinturnix vesprumilis]                              | 2                         | Absence in Pipistrellus pipistrellus (Schreber, 1774) [215]                            |
| Myotis myotis (Borkhausen, 1797) [25]                  | 3                         | Absence in Pipistrellus pipistrellus (Schreber, 1774) [215]                            |

**Acari, part 3/3: taxa only noted as absent** *(n = 3)*

| Ixodes canisuga Johnston, 1849                      | Absence in Barbastella barbastellus (Schreber, 1774) [28] |
|------------------------------------------------------|----------------------------------------------------------|
| Absence in Eptesicus serotinus (Schreber, 1774) [28] |                                                          |
| Absence in Myotis bechsteini (Leisler in Kuhl, 1817) [28] |                                                          |
| Absence in Myotis daubentoni (Leisler in Kuhl, 1817) [28] |                                                          |
| Absence in Myotis emarginatus (Geoffroy, 1806) [28] |                                                          |
| Absence in Myotis myotis (Borkhausen, 1797) [28] |                                                          |
| Absence in Myotis mystacinus (Leisler in Kuhl, 1817) [28] |                                                          |
| Absence in Myotis nattereri (Kuhl, 1817) [28] |                                                          |
| Absence in Pipistrellus kuhli (Kuhl, 1817) [28] |                                                          |
| Absence in Pipistrellus lasius (Natterer in Kuhl, 1817) [28] |                                                          |
| Absence in Pipistrellus pipistrellus (Schreber, 1774) [28] |                                                          |
| Absence in Plecotus auritus (Linne, 1758) [28] |                                                          |
| Absence in Rhinolophus euryale Blasius, 1853 [28] |                                                          |
| Absence in Rhinolophus ferrumequinum (Schreber, 1774) [28] |                                                          |
| Absence in Rhinolophus hipposideros (Bechstein, 1800) [28] |                                                          |

| Ixodes ricinus (Linne, 1746)                        | Absence in Barbastella barbastellus (Schreber, 1774) [28] |
|-----------------------------------------------------|----------------------------------------------------------|
| Absence in Eptesicus serotinus (Schreber, 1774) [28] |                                                          |
| Absence in Myotis bechsteini (Leisler in Kuhl, 1817) [28] |                                                          |
| Absence in Myotis daubentoni (Leisler in Kuhl, 1817) [28] |                                                          |
| Absence in Myotis mystacinus (Leisler in Kuhl, 1817) [28] |                                                          |
| Absence in Myotis nattereri (Kuhl, 1817) [28] |                                                          |
| Absence in Myotis emarginatus (Geoffroy, 1806) [28] |                                                          |

(Continued on next page)
| Parasite species | Number of reported hosts | Bat species and citation |
|-----------------|--------------------------|-------------------------|
| Pholeoixodes hexagonus (Leach, 1815) | | Absence in Barbastella barbastellus (Schreber, 1774) [28] |
| | | Absence in Eptesicus serotinus (Schreber, 1774) [28] |
| | | Absence in Myotis bechsteinii (Leisler in Kuhl, 1817) [28] |
| | | Absence in Myotis daubentonii (Leisler in Kuhl, 1817) [28] |
| | | Absence in Myotis emarginatus (Geoffroy, 1806) [28] |
| | | Absence in Myotis mystacinus (Leisler in Kuhl, 1817) [28] |
| | | Absence in Myotis nattereri (Kuhl, 1817) [28] |
| | | Absence in Pipistrellus kuhlii (Kuhl, 1817) [28] |
| | | Absence in Pipistrellus nathusii (Keyserling & Blasius, 1839) [28] |
| | | Absence in Pipistrellus pipistrellus (Schreber, 1774) [28] |
| | | Absence in Plecotus auritus (Linné, 1758) [28] |
| | | Absence in Rhinolophus euryale Blasius, 1853 [28] |
| | | Absence in Rhinolophus ferrumequinum (Schreber, 1774) [28] |
| | | Absence in Rhinolophus hipposideros (Bechstein, 1800) [28] |

Siphonaptera ($n = 12$)

| Species | Hosts |
|---------|-------|
| Araeopsylla gestroi (Rothschild, 1906) | 1 |
| Ceratopsyllus hexactenus = Ischnopsyllus (Hexactenopsylla) hexactenus (Kolenati, 1856) | |
| Ceratopsyllus octactenus = Ischnopsyllus (Ischnopsyllus) octactenus (Kolenati, 1856) | |
| Ceratopsyllus pentactenus = Nycteridopsylla pentactena (Kolenati, 1856) | |
| Ceratopsyllus unipunctatus Taschenberg = Rhinolophopsylla unipunctata unipunctata (Taschenberg, 1880) | |
| Ischnopsyllus (Ischnopsyllus) elongatus (Curtis, 1832) | 1 |
| Ischnopsyllus (Hexactenopsylla) hexactenus (Kolenati) = Ischnopsyllus (Hexactenopsylla) hexactenus (Kolenati, 1856) | |
| Ischnopsyllus (Hexactenopsylla) hexactenus (Kolenati, 1856) | 9 |
| | Barbastella barbastellus (Schreber, 1774) [2, 29, 33, 37, 38, 44, 200] |
| | Chiroptera gen. sp. [142] |
| | Myotis blythii (Tomes, 1857) and M. blythii oxygnathus Monticelli, 1885? [14] |
| | Myotis mystacinus (Borkhausen, 1797) [14?, 29, 33, 37, 167, 228] |
| | Myotis sp. [44] |
| | Pipistrellus kuhlii (Kuhl, 1817) [29] |
| | Plecotus auritus (Linné, 1758) [2, 33, 37, 44, 142, 177, 227, 228] |
| | Plecotus austriacus Fischer, 1829 [33, 37, 44] |
| | Rhinolophus ferrumequinum (Schreber, 1774) [152] |
| Ischnopsyllus (Ischnopsyllus) octactenus (Kolenati, 1856) | 7 |
| | Barbastella barbastellus (Schreber, 1774) [200, 228] |
| | Chiroptera gen. sp. [219] |
| | Myotis mystacinus (Borkhausen, 1797) [25, 29, 37, 167] |
| | Pipistrellus kuhlii (Kuhl, 1817) [29, 33, 37, 167] |
| | Pipistrellus nathusii (Keyserling & Blasius, 1839) [29, 33, 37, 167] |
| | Pipistrellus pipistrellus (Schreber, 1774) [2, 29, 33, 36, 37, 44, 142, 164, 167, 177, 227] |
| | Pipistrellus sp. [142] |
Table 2. (Continued)

| Parasite species                                      | Number of reported hosts | Bat species and citation                                                   |
|-------------------------------------------------------|--------------------------|---------------------------------------------------------------------------|
| *Ischnopsyllus (Ischnopsyllus) intermedius* (Rothschild) = *Ischnopsyllus (Ischnopsyllus) intermedius* (Rothschild, 1898) |                          |                                                                           |
| *Ischnopsyllus (Ischnopsyllus) intermedius* (Rothschild, 1898) | 6                        | *Chiroptera gen. sp.* [44]                                                |
|                                                        |                          | *Eptesicus serotinus* (Schreber, 1774) [29, 33, 37, 44, 142, 167, 227]   |
|                                                        |                          | *Myotis daubentoni* (Leisler in Kuhl, 1817) [44]                         |
|                                                        |                          | *Nyctalus noctula* (Schreber, 1774) [3, 44]                               |
|                                                        |                          | *Rhinolophus ferrumequinum* (Schreber, 1774) [29]                         |
| *Ischnopsyllus (Ischnopsyllus) simplex* Rothschild, 1906 | 8                        | *Barbastella barbastellus* (Schreber, 1774) [29, 37]                     |
|                                                        |                          | *Myotis daubentoni* (Leisler in Kuhl, 1817) [44]                         |
|                                                        |                          | *Myotis mystacinus* (Leisler in Kuhl, 1817) [29, 37, 85?, 142, 156]      |
| *Ischnopsyllus (Ischnopsyllus) variabilis* Wagner = *Ischnopsyllus (Ischnopsyllus) variabilis* (Wagner, 1898) | 6                        | *Myotis daubentoni* (Leisler in Kuhl, 1817) [44]                         |
|                                                        |                          | *Nyctalus noctula* (Schreber, 1774) [37]                                 |
|                                                        |                          | *Pipistrellus kuhlii* (Kuhl, 1817) [37, 44, 142]                         |
|                                                        |                          | *Pipistrellus nathusii* (Keyserling & Blasius, 1839) [2, 29, 33, 37, 44] |
|                                                        |                          | *Pipistrellus pipistrellus* (Schreber, 1774) [33, 37, 85]                |
|                                                        |                          | *Plecotus auritus* (Linné, 1758) ! [85]                                  |
| *Nycteridopsylla ancylaris ancylaris* Jordan, 1942    | 1                        | *Pipistrellus pipistrellus* (Schreber, 1774) [33, 37, 44, 142, 157, 164] |
| *Nycteridopsylla dictena* (Kolenati, 1856) !          |                          | *Chiroptera gen. sp.! Doubtful : see Beaucournu et Launay (1990 : p. 314 [paper n°37]) [37, 146, 167, 227] |
| *Nycteridopsylla dictenus* (Kolenati, 1857) = *Nycteridopsylla dictena* (Kolenati, 1856) | 1                        |                                                                           |
| *Nycteridopsylla (Dinuceropsylla) dictena* (Kolenati, 1856) = *Nycteridopsylla dictena* (Kolenati, 1856) |                          |                                                                           |
| *Nycteridopsylla eusarca* Dampf, 1908                | 1                        | *Nyctalus noctula* (Schreber, 1774) [37, 42]                             |
| *Nycteridopsylla longiceps* Rothschild, 1908          | 10                       | *Barbastella barbastellus* (Schreber, 1774) [29, 33, 37, 167]            |
|                                                        |                          | *Myotis capaccini* (Bonaparte, 1837) [37, 164, 167]                      |
|                                                        |                          | *Myotis daubentoni* (Leisler in Kuhl, 1817) [29, 37, 167]                |
|                                                        |                          | *Myotis mystacinus* (Leisler in Kuhl, 1817) [29, 37, 38, 167]            |
|                                                        |                          | *Pipistrellus kuhlii* (Kuhl, 1817) [37, 44, 156]                         |
|                                                        |                          | *Pipistrellus nathusii* (Keyserling & Blasius, 1839) [37, 44, 167]       |
|                                                        |                          | *Pipistrellus pipistrellus* (Schreber, 1774) [2, 29, 33, 37, 85, 167]    |
|                                                        |                          | *Plecotus auritus* (Linné, 1758) [33, 37, 85, 167, 227]                 |
| *Nycteridopsylla pentactena* (Kolenati, 1856)         | 13                       | *Barbastella barbastellus* (Schreber, 1774) [2, 29, 33, 37, 44, 167, 200] |
|                                                        |                          | *Chiroptera gen. sp.* [187]                                              |
|                                                        |                          | *Eptesicus serotinus* (Schreber, 1774) [29, 33, 37, 164, 167]            |
|                                                        |                          | *Miniopterus schreibersii* (Natterer in Kuhl, 1817) [37, 164, 167]       |
|                                                        |                          | *Myotis capaccini* (Bonaparte, 1837) [37, 164, 167]                      |
|                                                        |                          | *Myotis mystacinus* (Leisler in Kuhl, 1817) [29, 37, 167]                |
|                                                        |                          | *Myotis nattereri* (Kuhl, 1817) [29, 37, 167]                           |
|                                                        |                          | *Pipistrellus nathusii* (Keyserling & Blasius, 1839) [44]                |
|                                                        |                          | *Pipistrellus pipistrellus* (Schreber, 1774) [29, 37, 38, 167]          |
|                                                        |                          | *Plecotus auritus* (Linné, 1758) [29, 33, 37, 167]                      |
|                                                        |                          | *Plecotus austriacus* Fischer, 1829 [33, 37, 167]                       |
|                                                        |                          | *Rhinolophus ferrumequinum* (Schreber, 1774) [29, 37, 152, 164, 167, 177] |
|                                                        |                          | See also [217]                                                            |

(Continued on next page)
Table 2. (Continued)

| Parasite species | Number of reported hosts | Bat species and citation |
|------------------|--------------------------|--------------------------|
| *Pulex pungens* Walckenaer (1802) (*in Faune parisienne*) = *Nycteridopsylla eusarca* Dampf, 1908 | | |
| *Pulex vespertilionis* Dugès, 1832 | 1 | *Myotis myotis* (Borkhausen, 1797) [95] |
| See also [90] | | |
| *Rhinolophopsylla unipectinata unipectinata* (Taschenberg, 1880) | 4 | *Rhinolophus euryale* Blasius, 1853 [2, 29, 33, 142, 167] |
| | | *Rhinolophus ferrumequinum* (Schreber, 1774) [2, 33, 38, 44, 142, 152, 156, 164, 167, 177, 227, 242] |
| | | *Rhinolophus hipposideros* (Bechstein, 1800) [2, 86, 142, 167, 200, 228] |
| | | *Rhinolophus sp.* [44] |
| *Diptera* (*n = 13*) | | |
| *Basilia italica* Theodor = *Basilia (Basilia) italica* Theodor, 1954 | | |
| *Basilia nana* Theodor = *Basilia (Basilia) nana* Theodor & Moscona, 1954 | | |
| *Basilia nattereri* (Kolenati) = *Basilia (Basilia) nattereri* (Kolenati, 1857) | | |
| *Basilia (Basilia) italica* Theodor, 1954 | 2 | *Myotis emarginatus* (Geoffroy, 1806) [4, 34] |
| | | *Myotis mystacinus* (Leisler in Kuhl, 1817) [34, 35, 43, 237] |
| | See also [28, 150, 167] | |
| *Basilia (Basilia) mediterranea* Hürka, 1970 | 4 | *Eptesicus serotinus* (Schreber, 1774) [43, 154, 237] |
| | | *Hypsugo savii* (Bonaparte, 1837) [41, 167, 237] |
| | | *Pipistrellus pipistrellus* (Schreber, 1774) [40, 43, 167] |
| | | *Pipistrellus sp.* [41] |
| *Basilia (Basilia) nana* Theodor & Moscona, 1954 | 5 | *Myotis bechsteinii* (Leisler in Kuhl, 1817) [4, 28, 30, 38, 237] |
| | | *Myotis emarginatus* (Geoffroy, 1806) [43, 237] |
| | | *Myotis mystacinus* (Leisler in Kuhl, 1817) [241] |
| | | *Myotis nattereri* (Kuhl, 1817) [4, 30, 237] |
| | | *Plecotus auritus* (Linné, 1758) [28, 237] |
| | See also [150, 167] | |
| *Basilia (Basilia) nattereri* (Kolenati, 1857) | 4 | *Eptesicus serotinus* (Schreber, 1774) [241] |
| | | *Myotis daubentonii* (Leisler in Kuhl, 1817) [187] |
| | | *Myotis nattereri* (Kuhl, 1817) [4, 28, 30, 43, 187] |
| | | *Plecotus auritus* (Linné, 1758) [28, 187] |
| | See also [150, 167, 237] | |
| *Brachytarsina flavipennis* Macquart, 1851 | 1 | *Rhinolophus ferrumequinum* (Schreber, 1774) [26, 40, 43, 117, 155, 237] |
| | | |
| *Celeripes biarticulata* = *Phlhidium biarticulatum* Hermann, 1804 | | |
| *Listropodia pedicularia* = *Nycteribia (Nycteribia) pedicularia* Latreille, 1805 | | |
| *Listropodia Schmidli* = *Nycteribia (Nycteribia) schmidlii* Schiner, 1853 | | |
| *Nycteribia (Achrocholidia) vexata* Westwood = *Nycteribia (Achrocholidia) vexata* Westwood, 1835 | | |
| *Nycteribia (Achrocholidia) vexata* Westwood, 1835 | 8 | *Myotis emarginatus* (Geoffroy, 1806) ! [23] |
| | | *Rhinolophus euryale* Blasius, 1853 ! [85] |
| | | *Rhinolophus ferrumequinum* (Schreber, 1774) ! [85] |
| | | *Rhinolophus hipposideros* (Bechstein, 1800) ! [85] |
| | | *Miniopterus schreibersii* (Natterer in Kuhl, 1817) [1, 85, 167] |
| | | *Myotis blythii* (Tomes, 1857) and *M. blythii oxygnathus* Monticelli, 1885 [30] |
| | | *Myotis myotis* (Borkhausen, 1797) ! [1, 23, 25, 28, 30, 38, 167] |
| | | *Myotis myotis* (Borkhausen, 1797)/*Miniopterus schreibersii* (Natterer in Kuhl, 1817) [43] |
| | See also [117, 150, 237] | |

(Continued on next page)
Table 2. (Continued)

| Parasite species | Number of reported hosts | Bat species and citation |
|------------------|--------------------------|--------------------------|
| *Nycteribia (Celeripes) biarticulata* Hermann = *Phthiridium biarticulatum* Hermann, 1804 | | |
| *Nycteribia biarticulata* = *Phthiridium biarticulatum* Hermann, 1804 | | |
| *Nycteribia blasii* (Kolenati) = *Nycteribia (Nycteribia) kolenatii* Theodor & Moscona, 1954 | | |
| *Nycteribia Celeripes Bi-Articulata* = *Phthiridium biarticulatum* Hermann, 1804 | | |
| *Nycteribia (Celeripes) biarticulata* Hermann 1804 = *Phthiridium biarticulatum* Hermann, 1804 | | |
| *Nycteribia Hermanni* Leach = *Phthiridium biarticulatum* Hermann, 1804 | | |
| *Nycteribia kolenatii* Theodor = *Nycteribia (Nycteribia) kolenatii* Theodor & Moscona, 1954 | | |
| *Nycteribia latreilli* Leach = *Nycteribia (Nycteribia) latreillii* (Leach, 1817) | | |
| *Nycteribia (Listropodia) Schmidti* Schiner = *Nycteribia (Nycteribia) schmidii* Schiner, 1853 | | |
| *Nycteribia pedicularia* = *Nycteribia (Nycteribia) pedicularia* Latreille, 1805) | | |
| *Nycteribia schmidli* = *Nycteribia (Nycteribia) schmidlii* Schiner, 1853 | | |
| *Nycteribia vespertilionis* Dufour, 1831 = *Penicillidia (Penicillidia) dufourii* (Westwood, 1834) | | |
| *Nycteribia vexata* = *Nycteribia (Achrocholidia) vexata* Westwood, 1835 | | |
| *Nycteribia (Nycteribia) kolenatii* Theodor & Moscona, 1954 | 6 | *Eptesicus serotinus* (Schreber, 1774) [147, 241] |
| | | *Miniopterus schreibersii* (Natterer in Kuhl, 1817) [200] |
| | | *Myotis daubentonii* (Leisler in Kuhl, 1817) [1, 28, 38, 43, 167, 241] |
| | | *Myotis mystacinus* (Leisler in Kuhl, 1817) [147, 241] |
| | | *Myotis nattereri* (Kuhl, 1817) [28, 147] |
| | | *Pipistrellus pipistrellus* (Schreber, 1774) [241] |
| | | See also [150, 237, 240] |
| *Nycteribia (Nycteribia) latreillii* (Leach, 1817) | 6 | *Chiroptera* gen. sp. [148] |
| | | *Miniopterus schreibersii* (Natterer in Kuhl, 1817) [1, 167] |
| | | *Myotis blythii* (Tomes, 1857) and *M. blythii oxygnathus* Monticelli, 1885 [30, 167] |
| | | *Myotis emarginatus* (Geoffroy, 1806) [22] |
| | | *Myotis myotis* (Borkhausen, 1797) [1, 28, 30] |
| | | *Myotis myotis* (Borkhausen, 1797)/*Miniopterus schreibersii* (Natterer in Kuhl, 1817) [43] |
| | | See also [147, 150, 237] |
| *Nycteribia (Nycteribia) pedicularia* Latreille, 1805 | 12 | *Chiroptera* gen. sp.? [170] |
| | | *Miniopterus schreibersii* (Natterer in Kuhl, 1817) ! [85] |
| | | *Myotis daubentonii* (Leisler in Kuhl, 1817) ! [85] |
| | | *Myotis dasycneme* (Boie, 1825) ! [85] |
| | | *Myotis emarginatus* (Geoffroy, 1806)? [23] |
| | | *Nyctalus noctula* (Schreber, 1774) ! [85] |
| | | *Pipistrellus pipistrellus* (Schreber, 1774)! [214, 215] |
| | | *Rhinolophus euryale* Blasius, 1853 ! [85] |
| | | *Rhinolophus hipposideros* (Bechstein, 1800)? [200] |

(Continued on next page)
| Parasite species                        | Number of reported hosts | Bat species and citation                                                                 |
|----------------------------------------|--------------------------|-----------------------------------------------------------------------------------------|
| Myotis blythii (Tomes, 1857)           | 7                        | Miniopterus schreibersii (Natterer in Kuhl, 1817) [1, 24, 28, 30, 43, 115, 149, 154, 167, 242] see also [117, 150, 237] |
| Myotis capaccinii (Bonaparte, 1837)    | 7                        | Miniopterus schreibersii (Natterer in Kuhl, 1817) [1, 24, 28, 30, 43, 115, 149, 154, 167, 242] see also [117, 150, 237] |
| Myotis myotis (Borkhausen, 1797)       | 7                        | Miniopterus schreibersii (Natterer in Kuhl, 1817) [1, 24, 28, 30, 43, 115, 149, 154, 167, 242] see also [117, 150, 237] |
| Nycteribia (Nycteribia) schmidii Schiner, 1853 | 7                        | Miniopterus schreibersii (Natterer in Kuhl, 1817) [1, 24, 28, 30, 43, 115, 149, 154, 167, 242] see also [117, 150, 237] |
| Nycteribia sp.                         | 3                        | Miniopterus schreibersii (Natterer in Kuhl, 1817) [1, 24, 28, 30, 43, 115, 149, 154, 167, 242] see also [117, 150, 237] |
| Nycteribia (Stylidia) biarticulata = Phthiridium biarticulatum Hermann, 1804 | 7                        | Miniopterus schreibersii (Natterer in Kuhl, 1817) [1, 24, 28, 30, 43, 115, 149, 154, 167, 242] see also [117, 150, 237] |
| [Nycteribia eparcticata]                | 7                        | Miniopterus schreibersii (Natterer in Kuhl, 1817) [1, 24, 28, 30, 43, 115, 149, 154, 167, 242] see also [117, 150, 237] |
| [Nycteribia frauenfeldi (Kolenati)] = Penicillidia (Penicillidia) dafouri (Westwood, 1834) | 7                        | Miniopterus schreibersii (Natterer in Kuhl, 1817) [1, 24, 28, 30, 43, 115, 149, 154, 167, 242] see also [117, 150, 237] |
| Nycteribosca kollari Frauenfeld, 1855 = Brachytaurus flavipennis Macquart, 1851 | 7                        | Miniopterus schreibersii (Natterer in Kuhl, 1817) [1, 24, 28, 30, 43, 115, 149, 154, 167, 242] see also [117, 150, 237] |
| Complex of species Nycteribia kolenati/latreillii/pedicularia | 7                        | Miniopterus schreibersii (Natterer in Kuhl, 1817) [1, 24, 28, 30, 43, 115, 149, 154, 167, 242] see also [117, 150, 237] |
| Penicillidia conspicua Speiser = Penicillidia (Neopenicillidia) conspicua Speiser, 1901 | 7                        | Miniopterus schreibersii (Natterer in Kuhl, 1817) [1, 24, 28, 30, 43, 115, 149, 154, 167, 242] see also [117, 150, 237] |
| Penicillidia d. dafouri (Westwood, 1834) = Penicillidia (Penicillidia) dafouri (Westwood, 1834) | 7                        | Miniopterus schreibersii (Natterer in Kuhl, 1817) [1, 24, 28, 30, 43, 115, 149, 154, 167, 242] see also [117, 150, 237] |
| Penicillidia dafouri Westwood = Penicillidia (Penicillidia) dafouri (Westwood, 1834) | 7                        | Miniopterus schreibersii (Natterer in Kuhl, 1817) [1, 24, 28, 30, 43, 115, 149, 154, 167, 242] see also [117, 150, 237] |
| Penicillidia (Neopenicillidia) conspicua Speiser, 1901 | 7                        | Miniopterus schreibersii (Natterer in Kuhl, 1817) [1, 24, 28, 30, 43, 115, 149, 154, 167, 242] see also [117, 150, 237] |
| Penicillidia (Penicillidia) dafouri (Westwood, 1834) | 7                        | Miniopterus schreibersii (Natterer in Kuhl, 1817) [1, 24, 28, 30, 43, 115, 149, 154, 167, 242] see also [117, 150, 237] |
### Table 2. (Continued)

| Parasite species | Number of reported hosts | Bat species and citation |
|------------------|--------------------------|--------------------------|
| Phthiridium biarticulatum Hermann, 1804 | 6 | Chiroptera gen. sp.? [173, 204]

* Miniopterus schreibersii (Natterer in Kuhl, 1817)? [85, 126, 237]
* Plecotus auritus (Linné, 1758) [85, 86, 237]
* Rhinolophus euryale Blasius, 1853 [28, 30, 38, 115, 167, 242]
* Rhinolophus ferrumequinum (Schreber, 1774) [1, 28, 30, 43, 85, 115, 126, 135, 151, 152, 154, 156, 175, 177, 237, 242]

* Rhinolophus hipposideros (Bechstein, 1800) [115, 126, 135, 167, 237]
  See also [47, 116, 117, 150]

Penicillidia (Penicillidia) monoceros Speiser, 1900

| Absence in Barbastella barbastellus (Schreber, 1774) | 28 |
| Absence in Eptesicus serotinus (Schreber, 1774) | 28 |
| Absence in Myotis bechsteinii (Leisler in Kuhl, 1817) | 28 |
| Absence in Myotis daubentoni (Leisler in Kuhl, 1817) | 28 |
| Absence in Myotis emarginatus (Geoffroy, 1806) | 28 |
| Absence in Myotis myotis (Borkhausen, 1797) | 28 |
| Absence in Myotis mystacinus (Leisler in Kuhl, 1817) | 28 |
| Absence in Myotis nattereri (Kuhl, 1817) | 28 |
| Absence in Pipistrellus kuhlii (Kuhl, 1817) | 28 |
| Absence in Pipistrellus nathusii (Keyserling & Blasius, 1839) | 28 |
| Absence in Rhinolophus euryale Blasius, 1853 | 28 |
| Absence in Rhinolophus ferrumequinum (Schreber, 1774) | 28 |
| Absence in Rhinolophus hipposideros (Bechstein, 1800) | 28 |

Hemiptera (n = 3)

| Cimex dissimilis (Horváth, 1910) | 4 (5?) | Chiroptera gen. sp. [207]
| Myotis emarginatus (Geoffroy, 1806) | [254] |
| Myotis myotis (Borkhausen, 1797)? | [177] |
| Myotis sp. [253] | |
| Rhinolophus ferrumequinum (Schreber, 1774) | [254] |
| See also [167, 236] |

Cimex lectularius Merrett 1667 = Cimex lectularius Linnaeus, 1758

| 1 (5?) | Chiroptera gen. sp. [28, 35]
| Myotis emarginatus (Geoffroy, 1806)? [253, 254] |
| Myotis myotis (Borkhausen, 1797)? [253, 254] |
| Rhinolophus ferrumequinum Blasius, 1853? [253, 254] |
| Rhinolophus ferrumequinum (Schreber, 1774)? [253, 254] |
| See also [167, 236] |

Cimex pipistrelli Jenins, 1839

| 1 | Chiroptera gen. sp. [28, 236] |

Cimex sp.

| 1 | Chiroptera gen. sp. [28, 177] |

Anoplura (n = 1)

Polyplax serrata (Burmeister, 1839) !

| 1 ! | Rhinolophus hipposideros (Bechstein, 1800) ! [17, 177, 216] |

Cestoda (n = 3)

| Hymenolepis acuta = Vampirolepis acuta (Rudolphi, 1819) |
| Hymenolepis balsaci = Vampirolepis balsaci (Joyeux & Baer, 1934) |
| Hymenolepis grisea = Milina grisea van Beneden, 1873 |
| Hymenolepis grisea (P.J. Van Beneden 1873) = Milina grisea van Beneden, 1873 |
| Hymenolepis sp. = Vampirolepis species |
| Milina grisea van Beneden, 1873 |

| 4 (5?) | Myotis myotis (Borkhausen, 1797) [68, 159, 167] |
| Myotis mystacinus (Leisler in Kuhl, 1817) [68, 71, 159, 196, 243] |
| Rhinolophus ferrumequinum or R. hipposideros or M. schreibersii [200] |

(Continued on next page)
| Parasite species | Number of reported hosts | Bat species and citation |
|------------------|--------------------------|--------------------------|
| *Vampirolepis acuta* (Rudolphi, 1819) | 1 | *Eptesicus serotinus* (Schreber, 1774) [158, 159, 177, 196, 255] |
| *Vampirolepis balsaci* (Joyeux & Baer, 1934) | 2 | *Myotis bechsteinii* (Leisler in Kuhl, 1817) [159, 167, 177, 180, 196, 255] |
| *Vampirolepis sp. / Milina sp.* | 2 | *Eptesicus serotinus* (Schreber, 1774) [86] |
| Allascogonoporus amphoraeformis (Mödlinger, 1930) | 1 | *Myotis daubentonii* (Leisler in Kuhl, 1817) [89, 167] |
| Distoma ascidoïdes Van Beneden, 1873 = *Prosthodendrium* (Prosthodendrium) chilostomum (Mehlis, 1831) | 1 | *Miniopterus schreibersii* (Natterer in Kuhl, 1817)? [200] |
| Distoma heteroptum (Dujardin, 1845) = *Pycnoporus heteroporus* (Dujardin, 1845) | 1 | *Miniopterus schreibersii* (Natterer in Kuhl, 1817) [200] |
| Distoma lagena Brandes, 1888 = *Lecithodendrium granulosum* Looss, 1907 | 1 (4?) | *Miniopterus schreibersii* (Natterer in Kuhl, 1817) [68, 88, 167] |
| Lecithodendrium granulosum Looss, 1907 | 10 | *Eptesicus serotinus* (Schreber, 1774) [68, 88, 167] |
| *Lecithodendrium linstowi* R.Ph Dollfus 1931 = *Lecithodendrium linstowi* Dollfus, 1931 | 1 | *Miniopterus schreibersii* (Natterer in Kuhl, 1817) [68, 88, 167] |
| Lepoderma vespertilionis (Müller) = *Plagiorchis vespertilionis* (O.F. Müller, 1784) | 1 | *Miniopterus schreibersii* (Natterer in Kuhl, 1817) [68, 88, 167] |
| Limatulum duboisi Hurkova 1961 = *Parabascus duboisi* (Hurvka, 1961) | 3 | *Miniopterus schreibersii* (Natterer in Kuhl, 1817) [68, 88, 167, 188] |
| Mesotretes peregrinus (Braun, 1900) | 3 | *Miniopterus schreibersii* (Natterer in Kuhl, 1817) [68, 71, 88, 167, 188, 243] |
| Parabascus duboisi (Hurvka, 1961) | 1 | *Myotis daubentonii* (Leisler in Kuhl, 1817) [89, 167] |
| Parabascus lepidotus Looss, 1907 | 4 | *Miniopterus schreibersii* (Natterer in Kuhl, 1817) [68, 167] |
| Parabascus semisquamosus (Braun, 1900) = *Prosthodendrium (Prosthodendrium) chilostomum* (Mehlis, 1831)? | 3 | *Miniopterus schreibersii* (Natterer in Kuhl, 1817) [68, 243] |

(Continued on next page)
Table 2. (Continued)

| Parasite species | Number of reported hosts | Bat species and citation |
|------------------|--------------------------|--------------------------|
| *Plagiorchis vespertilionis* (O.F. Müller, 1784) | 11 | Eptesicus serotinus (Schreber, 1774) [68, 167]  
Miniopterus schreibersii (Natterer in Kuhl, 1817) [68, 167, 200, 235]  
Myotis capaccinii (Bonaparte, 1837) [68, 167]  
Myotis daubentoni (Leisler in Kuhl, 1817) [89, 167]  
Myotis emarginatus (Geoffroy, 1806) [68, 86, 167]  
Pipistrellus pipistrellus (Schreber, 1774) [68, 86, 167]  
Plecotus auritus (Linné, 1758) [86, 167]  
Rhinolophus euryale Blasius, 1853 [68, 167]  
Rhinolophus ferrumequinum (Schreber, 1774) [68, 71, 86–88, 167, 200, 243]  
Rhinolophus hipposideros (Bechstein, 1800) [68, 86, 167, 200] |

Prosthodendrium carolinum J. Hurkova, 1959 = Prosthodendrium (Prosthodendrium) carolinum Hurková, 1959  
Prosthodendrium chilostoma (Mehlis, 1831) = Prosthodendrium (Prosthodendrium) chilostomum (Mehlis, 1831)  
Prosthodendrium chilostomum (Mehlis) = Prosthodendrium (Prosthodendrium) chilostomum (Mehlis, 1831)  
Prosthodendrium longiforme (Bhalerao, 1926) = Prosthodendrium (Prosthodendrium) longiforme (Bhalerao, 1926)  
Prosthodendrium (Prosthodendrium) hurkovaae Dubois, 1960  
Prosthodendrium (Prosthodendrium) chilostomum (Mehlis, 1831)  
Prosthodendrium (Prosthodendrium) hurkovaae Dubois, 1960  
Prosthodendrium (Prosthodendrium) longiforme (Bhalerao, 1926)  
Prosthodendrium parvouterus (Bhalerao, 1926)  
Pycnoporus heteroporus (Dujardin, 1845)  

Histiostrongylus tipula (van Beneden, 1873) = Molinostrongylus tipula (Beneden, 1873)  
Litomosa beaucournui Bain, 1967 = Litomosota ottavianii Lagrange & Bettini, 1948  
Litomosa desportesi Bain, 1967 = Litomosota dogielii Bogdanov & Vladimirivov, 1956  
Litomosa dogielii Bogdanov & Vladimirivov, 1956  
Litomosa filaria P.J. Van Beneden 1873 = Litomosota filaria (Beneden, 1873)  
Litomosa filaria (van Beneden) = Litomosota filaria (Beneden, 1873)  
Litomosa filaria (Beneden, 1873)  

Nematoda (*n* = 13)  

(Continued on next page)
Table 2. (Continued)

| Parasite species                      | Number of reported hosts | Bat species and citation                                      |
|---------------------------------------|--------------------------|----------------------------------------------------------------|
| Litomosa oitavianiit Lagrange & Bettini, 1948 5 | Miniopterus schreibersii (Natterer in Kuhl, 1817) [19, 167]  Myotis emarginatus (Geoffroy, 1806) [68, 167]  Rhinolophus euryale Blasius, 1853 [68, 167]  Rhinolophus ferrumequinum (Schreber, 1774) [19, 167]  Rhinolophus sp. [19, 167] |
| Molinostrongylus alatus (Orlépp, 1932)? 1? | Chiroptera gen. sp.? [167]  Miniopterus schreibersii (Natterer in Kuhl, 1817) [200]  Myotis myotis (Borkhausen, 1797) [56] |
| Molinostrongylus tipula (Beneden, 1873) 2 | Miniopterus schreibersii (Natterer in Kuhl, 1817) [200]  Myotis myotis (Borkhausen, 1797) [68] |
| Molinostrongylus ornatus (Monnig, 1927) 1 | Myotis myotis (Borkhausen, 1797) [68] |
| Molinostrongylus panousei Dollous, 1954 3 |  |
| Ophiostoma macronatum (Rudolphi, 1809) = Seuratatum macronatum (Rudolphi, 1809) |  |
| Pterygodermatites (Neopaucipectines) bovieri (Blanchard, 1886) |  |
| Rictularia bovieri = Pterygodermatites (Neopaucipectines) bovieri (Blanchard, 1886) |  |
| Strongylus tipula P.J. Van Beneden, 1873 = Molinostrongylus tipula (Beneden, 1873) |  |
| Trichosomum speciosum van Beneden, 1873 3 | Miniopterus schreibersii (Natterer in Kuhl, 1817) [200]  Rhinolophus ferrumequinum (Schreber, 1774) [200]  Rhinolophus hipposideros (Bechstein, 1800) [200] |
| Uncinaria glycirrhiza (van Beneden, 1873) = Strongylacantha glycirrhiza van Beneden, 1873 |  |

Lagréville contains an observation of *Carios* on “la Chauve-Souris noctule” (=*Nyctalus noctula* or *Nyctalus sp.*). This taxon is very likely *Argas* (*Carios*) *vespertilionis* (Lagréville, 1802). Descriptions of some species and subspecies are based on type material from France (e.g. *Spinturnix nobleti* [81], *S. bechsteini* [82], *Pteracarus pipistrellius maximus* [251], *Myobia poppei* (= *Acanthophthirius* (*Acanthophthirius*) *poppei* [249] and *Spinturnix andegavini* [76]). The majority of published data on parasites of chiropteran populations in France deal with Arachnida and similar findings were noted by Lanza [167], Kristofik & Danko [165] and Frank et al. [121] in Italy, Slovakia and other European countries.

### 1.2 Subphylum Hexapoda Latreille, 1825

#### 1.2.1 Suborder Anoplura Leach, 1815

*order Phthiraptera Haeckel, 1896*

Only one species has been reported as a bat parasite in France, *i.e.* *Polyplax serrata*. The scientist Paul Rémy (1894–1962) published in 1948 the only record; this was from *R. hipposideros* (Borkhausen, 1797) in north-eastern France at Trémont-sur-Saulx (Meuse area [177, 216]). The mentioned locality in the original paper, “Fiémont-sur-Saulx” [216], contains a typographical error. These field data, dated 1925–1926, and published in the journal *La Feuille des Naturalistes*, are surprising and dubious [Beaucournu, *in litt.*]. In fact, this species is more likely to be an ectoparasite of mammals of the Rodentia order (e.g. *Apodemus*, *Clethrionomys* and *Mus* genera) and Eulipotyphla (*Crocidura leucodon*) [98, 234]. It should be noted, however, that *Polyplax* sp. was also reported on *Rhinolophus mehelyi* by Gadziew et al., in 1990 in Eastern Europe. These are the only data on *Polyplax* sp. in Lanza’s analysis [167] and hence they may be unreliable. Rémy’s observation is not mentioned in the works of Durden & Musser [98], Ferris [119] and Hopkins [140].

#### 1.2.2 Order Diptera Linnaeus, 1758

According to Szentiványi et al., 17 species of bat flies are currently known in Europe [237]. Thirteen species of bat flies...
have been reported from France and two more records without identification to species level have been found. These are *Basilia (Basilia) italica*, *B. (Basilia) mediterranea*, *B. (Basilia) nana*, 1954, *B. (Basilia) nattereri*, *Brachytarsina flavipennis*, *Nycteribia (Achrocholidia) vexata*, *N. (Nycteribia) kolenati*, *N. (Nycteribia) latreillii*, *N. (Nycteribia) pedicularia*, *N. (Nycteribia) schmidlii*, *Penicillidia (Neopenicillidia) conspicua*, *P. (Penicillidia) dupoirii*, *Phthiridium biarticulatum*, *Nycteribia* sp. and *Nycteribia kolenati/latreillii/pedicularia* [1, 4, 12, 22–30, 34, 35, 38–41, 43, 45, 47, 53, 73, 74, 86, 91, 93, 115–117, 126, 135, 146–152, 154, 156, 167, 170, 172, 173, 175, 177, 179, 186, 187, 200, 203, 204, 206, 214,

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| Species                                      | Records |
|----------------------------------------------|---------|
| Spinturnix von Heyden, 1826                  | 11      |
| Macronyssus Kolenati, 1858                   | 5       |
| Ichoronyssus Kolenati, 1858                  | 3       |
| Eyndhovenia Rudnick, 1960                    | 2       |
| Steatonyssus Kolenati, 1858                  | 1       |
| Paraperiglischrus Rudnick, 1960              | 1       |
| Hirstonyssus Fonseca, 1948                   | 1       |
| Argas Latreille, 1795                       | 3       |
| Ixodes Latreille, 1795                      | 2       |
| Alabidocarpus Ewing, 1929,                  | 3       |
| Nycteridocoptes Oudemans, 1898               | 2       |
| Notoedres Railliet, 1893                     | 1       |
| Labidocarpus Trouessart, 1895                | 1       |
| Neomyobia Radford, 1948                     | 3       |
| Neotrombicula Hirst, 1915                   | 3       |
| Sasatrombicula Vercammen-Grandjean, 1960    | 2       |
| Calcarmyobia Radford, 1948                   | 2       |
| Acanthophthirius Perkins, 1925               | 2       |
| Riedlinia Oudemans, 1914                     | 1       |
| Psorergates Tyrrel, 1883                     | 1       |
| Pteracarus Jameson & Chow, 1952              | 1       |
| Oudemansidium Vercammen-Grandjean & Andre, 1966 | 1   |
| Leptotrombidium Nagayo, Miyagawa, Mitamura & Imamura, 1916 | 1 |

Figure 3. Number of recognised species of Acari (n = 53), per host order (n = 4) and genus (n = 23). Invalid species (n = 22 Acari) recorded in the literature (n = 237 papers) and species only noted as absent (n = 3 Acari) are not included here.
Three invalid taxa reported from France were found in the analysed papers: *Nycteribia eparticulata*, *N. vespertilions* Meig., and *N. vespertilions* Latreille. *Penicillidia* (*Penicillidia*) monoceros is noted as absent in western France [28]. Another species, *B. (Basilia) daganiae* could be distributed in France [28, 34]. As far as hosts of the bat flies (Diptera: Nycteribiidae and Streblidae) are concerned, *E. serotinus*, *H. savii*, *M. schreibersii*, *M. bechsteinii*, *M. blythii, M. capaccinii, M. daubentonii, M. emarginatus, M. myotis, M. mystacinus, M. nattereri, M. species, P. pipistrellus, Pipistrellus sp., P. auritus, R. euryale, R. ferrumequinum, R. hipposideros, and R. mehelyi* have been recorded in the literature. Jean-Frédéric Hermann’s record of *Phthiridium vespertilions*, dated 1804, is the oldest French record of a dipteran as a bat parasite [135]. The bibliographical survey of the published data (n = 111 papers) written by Szentiványi et al. has shown that ten bat fly species are known to be associated with bats in Albania, Romania, and Italy [237]. Europe’s most species-rich communities have been reported in Spain (11 species), Switzerland (11 species), Hungary (11 species) and France (13 species). As such, France has the most diverse community reported in the literature.

**Figure 4.** Histogram showing the number of studies (n = 237) per host taxon (n = 34; species: 27; complex: 1; genera: 6) during the period 1762–2018.
reported from France without identification to species level have been found (Cimex sp. on M. myotis, M. emarginatus, R. euryale, and R. ferrumequinum) [28, 177]. The first published data in the analysed literature are dated 1961 [28] when Beaucournu published his observations on Cimex sp. in the department of Maine-et-Loire. True bugs (Hemiptera: Cimicidae) using bats as hosts have not been well studied in France. Studies on bat guano deposits could provide data on the species distribution. For instance, this method provided new records of Cimex sp. and Cimex dissimilis (Horváth, 1910) in a roosting colony of M. myotis in June 2017 and June 2018 in north-eastern France [177] (about C. dissimilis in roosting colony of M. myotis, see also [121] and [224]).

1.2.4 Order Siphonaptera Latreille, 1825

Twelve species are known to be associated with bats in France. They belong to the family Ischnopsyllidae Wahlgren, 1907. The species are Araeopsylla gestroi, Ischnopsyllus (Hexactenopsylla) hexactenus, I. (Ischnopsyllus) elongatus, I. (Ischnopsyllus) intermedius, I. (Ischnopsyllus) octactenus, I. (Ischnopsyllus) simplex, I. (Ischnopsyllus) variabilis, Nyceriodopsylla anclyaris anclyaris, N. eusarca, N. longiceps, N. pentactena, and Rhinolophopsylla unipectinata unipectinata. According to Beaucournu and Launay [37], the published records of Nyceriodopsylla dictena are dubious [146, 227]. Bat fleas have been observed on 20 hosts in France [3, 14, 23, 29, 33, 36–38, 42–44, 46, 85, 86, 90, 95, 141, 142, 152, 156, 157, 167, 177, 200, 204, 219, 227, 228, 231, 242, 257]. These hosts are E. serotinus, M. schreibersii, M. blythii, M. capaccinii, M. daubentonii, M. emarginatus, M. myotis, M. mystacinus, M. nattereri, Myotis sp., N. leisleri, N. noctula, P. kuhlii, P. nathusii, P. pipistrellus, P. auritus, P. australis, R. euryale, R. ferrumequinum, R. hipposideros, Rhinolophus sp., and Tadarida teniotis. Studies on bat fleas have a long history in France and the book of Walckenaer on insects, entitled Faune parisienne, insectes ou Histoire abrégée des insectes des environs de Paris [257], may be among the earliest such works. According to the Inventaire National du Patrimoine Naturel, 91 autochthonous (indigenous) species of the Siphonaptera order have been reported in France. Species of the Ischnopsyllidae found in France represent almost 13% of fleas in the country [153].

2 Phylum Nematoda Diesing, 1861

In France, the helminth fauna of bats is varied, with more than 30 species. Nematodes recorded in bats in France are divided into three orders: Muspiceida Bain & Chabaud, 1959, Rhabditida Chitwood, 1933, and Strongyloida Molin, 1861; and six families: Oncho cercidae Leiper, 1911 (three species), Molineidae Skrjabin & Schulz, 1937 (four species), Rickett siadae Railliet, 1916 (one species), Muspiceidae Bain & Chabaud, 1959 (two species), Seuratidae Hall, 1916 (one species), and Strongylacanthidae (Yorke & Maplestone, 1926, subfamily) Chabaud, 1960 (one species). Thirteen species and two nematodes identified to genus-level have been reported: Litomosa dogieli, L. flaria, L. ottaviani, Molinostrongylus alatus, M. ornatus, M. panousei, M. tipula, Pterygodermatytes (Neopaucipectines) bovieri, Riousgolvania nycitalis, R. rhinolophi, Seuratum mucronatum, Strongylacantha glycirrhiza, Rictularia sp., Riousgolvania sp., and Trichosomum speciosum. These parasites were documented in the following bat species: M. schreibersii, M. blythii, M. emarginatus, M. myotis, Plecotus sp., Rhinolophus sp. and three species of the genus Rhinolophus (R. euryale, R. ferrumequinum, and R. hipposideros) [19–21, 54, 56, 57, 68, 75, 86, 97, 99, 167, 177, 194, 200, 211, 233, 235, 243, 245]. The original description of the rare nematode P. (Neopaucipectines) bovieri is based on material from M. myotis in France. To my knowledge, it is the first published observation in the country (dated September 1885) [56, 66, 230]. The original descriptions of Riousgolvania nycitalis and R. rhinolophi are based on material from M. blythii and R. euryale in the Netherlands and the French departments of Ariège and Pyrénées-Orientales [20, 21]. A re-description of Seuratum mucronatum was based on material from Plecotus auritus (dated 1950) in the French department of Indre-et-Loire [54]. As a comparison, according to Horvat et al. [144, 145], two Nematode species (associated with M. myotis and R. ferrumequinum) are known in Serbia to be associated with bats, whilst in Croatia, these authors noted three species.

3 Phylum Platyhelminthes Minot, 1876

3.1 Class Trematoda

Records of 15 recognised species of trematodes from bats have been found from over 17 published papers. They belong to the order Plagiorchiida La Rue, 1957 and are divided into...
three families: Lecithodendriidae Lühe, 1901 (13 species), Mesotretidae Poche, 1926 (one species), and Plagiocirhidae Lühe, 1901 (one species). These species are Allassogonoporus amphiarciformis, Lecithodendrium granulosum, L. linstowi, L. moedlingeri, Mesotretes peregrinus, Parabasurus duboisii, P. lepidotus, P. semisquamosus, Plagiochis vespertilionis, Prosthodendrium (Prosthodendrium) carolinum, P. (Prosthodendrium) hurkovaee, P. (Prosthodendrium) chilostomum, P. (Prosthodendrium) longiforme, P. parvouterus, and Pycnoporus heteroporus [1, 57, 60, 61, 68, 71, 86, 89, 163, 167, 177, 188, 200, 202, 243]. Two trematodes identified to genus-level have been reported (Lecithodendrium sp. and Prosthodendrium sp.) [86]. These parasites were documented in the following bat species: Eptesicus serotinus [68, 88, 167], Miniopterus schreibersii [68, 167, 188, 200, 235], Myotis daubentoni [89, 167], M. capaccinii [68, 167], M. emarginatus [68, 86, 167], M. myotis [57, 61, 68, 167], Pipistrellus kuhlii [86], P. pipistrellus [57, 60, 61, 68, 86, 97, 163, 167, 235], Plecotus auritus [86, 167], P. austriacus [68, 167], Rhinolophus euryale [68, 167], R. ferrumequinum [68, 86–88, 167, 188, 200, 243], and R. hipposideros [68, 86, 167, 188, 200, 235].

As a comparison, in the United Kingdom, Lord et al. [181, 182] noted four trematode species and one trematode identified to genus-level in bats. In Serbia, Horvat et al. [144, 145] noted a total of seven trematode taxa associated with bats, and only one species in Croatia. According to the Inventaire National du Patrimoine Naturel, 28 species of the family Lecithodendriidae and 27 species of the family Plagiochridae have been reported in France. Species of the Lecithodendriidae found in bats represent almost 46% of the family [153]. The observations reported in France and species of the family found in bats represent 4% of the family [153].

4 Hosts and geographical distribution of bat-parasite associations

Over a 256-year period, the 113 recognised taxa of bat parasites from France were collected from 27 bats species and six other bats that were not identified to species-level (five genera and the Pipistrellus species complex) (Figs. 2 and 4). The taxa are B. barbastellus, E. serotinus, H. savii, M. schreibersii, M. bechsteinii, M. blythii, M. capaccinii, M. dasycneme, M. daubentoni, M. emarginatus, M. myotis, M. mystacinus, M. nattereri, M. panicus, N. lasiopterus, N. leisleri, N. noctula, P. kuhlii, P. nathusii, P. pipistrellus, P. auritus, P. austriacus, R. euryale, R. ferrumequinum, R. hipposideros, R. melhelyi, T. teniotis, Eptesicus sp., Myotis sp., Pipistrellus sp., Plecotus sp., Rhinolophus sp., and the species complex Pipistrellus pipistrellus/kuhlii/nathusii. These species represent almost 79% of the bat fauna of France (including Corsica). The most commonly reported hosts, which are mentioned in more than 29 papers, are E. serotinus, R. euryale, R. hipposideros, M. schreibersii, P. pipistrellus, M. myotis, and R. ferrumequinum. However, the most cited species is the Greater horseshoe bat (R. ferrumequinum); 30% of the analysed publications deal with this species. Some bat species have no records of associated metazoan parasites in the analysed publications (n = 237), because the ecology of the host is poorly studied (E. nilssonii, Vesperilio murinus (Particoloured Bat), M. alceholo, M. escalera and P. macroballaris). In addition to this, since P. pygmaeus was identified in the 1990’s, we cannot rule out that some of the records of Pipistrellus sp. or P. pipistrellus may refer to P. pygmaeus [41, 45, 53, 58, 142].

Published field data originated from 72 French departments (Fig. 5). One of them is mentioned as a non-prospected area (department of Vosges). Indeed, there is no publication about bat parasites in this department. Associations with specified geographical locations were most commonly from Ardèche (11 papers), Ariège (13 papers), Bouches-du-Rhône (15 papers), Haute-Savoie (12 papers), Maine-et-Loire (19 papers), Moselle (11 papers), Meurthe-et-Moselle (23 papers), Pyrénées-Orientales (24 papers), Sarthe (12 papers), Haute-Corse, and

3.2 Class Cestoda

Three recognised and one innominate species of cestodes have been reported in bats from France, which makes it the richest community reported in Europe. These species are Milina grisea, Vampirolepis acuta, and V. baluaci [68, 86, 158, 159, 167, 177, 180, 196, 200, 243, 255, 262]. They belong to one family: Hymenolepididae Ariola, 1899 (Cyclophyllidea van Beneden in Braun, 1900 order). In addition to these species, one cestode identified to genus-level has been reported (Vampirolepis sp.) [86]. The description of H. baluaci is based on material from Myotis bechsteinii and Eptesicus serotinus from north-eastern France collected by the naturalist Henri Heim de Balsac (1899–1979) at a place called Buré d’Orval in Allondrelle-la-Malmaison [158, 159]. Some authors have noted that the observation was made at “Bûre” ([158] see also [142]). Joyeux & Baer’s paper on cestodes, entitled Sur quelques Cestodes de France, is the first work on the bat cestodes in France (published in 1934 in the journal Archives du Muséum national d’Histoire naturelle). Bat cestodes are not well studied, especially in France, where the most recent data from field research is almost 50 years old [68, 86, 158, 159, 167, 177, 180, 196, 200, 243, 255, 262]. France has the most diverse community reported in the literature. According to Frank et al. [121], three species are known to be associated with bats in Poland and Hungary. These authors also reported one species in Germany and two species in Austria. It is worth noting that, according to the Inventaire National du Patrimoine Naturel, 75 species of the family Hymenolepididae have been reported in France and species of the family found in bats represent 4% of the family [153].
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