The Fossil Record of Bats (Mammalia: Chiroptera) in Greece

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1 Introduction

At present, bats (Order Chiroptera) are the second most diverse mammalian order after the rodents, with more than 1100 living species (>20% of the total extant species) distributed worldwide (apart from the poles and some isolated islands) (Simmons 2005a, b). Despite the abundant information on modern bats, their fossils are rare mostly because of their small and delicate skeleton (Gunnell and Simmons 2005). However, their distribution is universal with the oldest chiropteran fossils coming from the early Eocene of Europe (Coimbra District, Portugal), North America (Wyoming, USA), South America (Chubut, Argentina), Africa (Chambi, Tunisia or El Kohol, Algeria), Oceania (Queensland, Australia), and Asia (Gujarat, India) (Tabuce et al. 2009; Simmons et al. 2008; Tejedor et al. 2005; Sigé 1991; Ravel et al. 2011; Hand et al. 1994; Smith et al. 2007). It is evident that the appearance of Chiroptera in early Eocene is sudden, almost global, and it seems to be an isochronous event (Smith et al. 2007). Nevertheless, some of the most important questions that have yet to be answered are the temporal, geographical, and phylogenetic origins of Chiroptera.

Regarding the Greek region, recent zoological studies recorded 32 chiropteran species (Hanák et al. 2001). In the fossil record, the earliest documented chiropteran specimens come from the early Miocene locality of Lapsarna, Lesvos (Vasileiadou and Zouros 2012; Vasileiadou et al. 2017).

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E. Vlachos (ed.), *Fossil Vertebrates of Greece Vol. 2*,
https://doi.org/10.1007/978-3-030-68442-6_4

2 Historical Overview

The knowledge concerning the fossilized chiropteran faunas in Greece is still limited, and the Greek archive of fossilized Chiroptera is sparse. The studies so far have mainly conducted basic systematics, usually on a limited amount of specimens, and there are several factors that did not lead researchers to work with fossil Chiroptera. First, the process for the collection of microfossils requires the use of specialized equipment (sieves), unlimited water supply, etc. (for more details on the collection of microfossils and relevant information about the study of micromammals see van den Hoek Ostende 2003), which was rarely used at paleontological excavations, as researchers that worked on fossil material from the Greek region, organized excavations mainly for large mammals. Moreover, even when researchers were looking for microfossils, the chances of retrieving fossil Chiroptera were low, due to the fact that most excavations have taken place in open sites and not caves, the natural habitat for a plethora of bats. If we take all the above into account, in addition to the difficulty of the fossilization of chiropteran remains, this sparsity can be partly explained. However, the Greek archive of fossilized Chiroptera spans from early Miocene until Early/Middle Holocene. The localities where Chiroptera are documented in their faunal lists are given in Box 1.

Box 1

Early Miocene
Lapsarna, Lesvos (Vasileiadou and Zouros 2012; Vasileiadou et al. 2017)

Early/Middle Miocene
Antonios, Chalkidiki (Vasileiadou and Koufos 2005; Koufos 2006)

Late Miocene
Elaiochoria 2, Chalkidiki (Horáček 1991; Hulva et al. 2007; Sigé et al. 2014), Mytilinii, Samos (Revilliod 1922)

Miocene/Pliocene
Nea Silata, Chalkidiki (Vasileiadou et al. 2003; Koufos 2006), Maramena, Serres (Schmidt-Kittler et al. 1995; Koufos 2006)

Late Pliocene
Tourkobounia 1, Athens (Reumer and Doukas 1985)

Early Pleistocene
Tourkobounia 2, 3, 5, Athens (Reumer and Doukas 1985), Vathy, Kalymnos (Kuss 1973; Kotsakis et al. 1979)

Middle Pleistocene
Latomi 1, Chios (Storch 1975; Kotsakis et al. 1979), Petralona Cave, Chalkidiki (Sickenberg 1964, 1971; Kretzoi 1977; Kretzoi and Poulianos 1981; Horacek and Poulianos 1988; Tsoukala 1989)

(continued)

Late/Middle Pleistocene
Varkiza 1, 2, Athens (van de Weerd 1973)

Late Pleistocene
Kalamakia Cave, Lakonia (Harvati et al. 2013; Darlas and Psathi 2016; Kolendrianou et al. 2020), Loutra Almopias Cave, Pella (Chatzopoulou et al. 2001; Chatzopoulou 2003, 2005; Tsoukala et al. 2006; Piskoulis 2018, 2019, 2020), Naxos, Cyclades (van der Geer et al. 2014), Kharoumes 5, Lasithi (Kuss 1970; Mayhew 1977; Dermitzakis 1977; Doukas and Papayianni 2016), Liko, Chania (Mayhew 1977; Dermitzakis 1977; Doukas and Papayianni 2016), Bate Cave, Rethymno (Kotsakis et al. 1976)

Late Pleistocene/Early Holocene
Franchthi Cave, Argolis (Stiner and Munro 2011), Anonymous Cave of Schisto at Keratsini, Piraeus (Mavridis et al. 2013)

Holocene
Charkadio Cave, Tilos (Symeonidis et al. 1973; Kotsakis et al. 1979), Vraona Cave, Attica (Symeonidis et al. 1980)

Early/Middle Holocene
Sarakenos Cave, Boeotia (Pereswiet-Soltan 2016)

Box 2

The Loutra Almopias Cave (LAC) is located in Pella, Macedonia (Northern Greece) at the eastern slopes of Mount Voras (2524 m), about 120 km northwest of Thessaloniki. The cave is developed on the northern slope of the V-shaped gorge of Thermopotamos Stream, on the altitude of 540 m. The coordinates of the site are: N 40°58.267′, E 021°54.850′. The accumulation of sediments in the cave was in cyclic intervals (clastic and chemical sediments). The fossiliferous bed is mainly brown gravelly sand of fluvial origin. Thousands of Late Pleistocene faunal remains were collected during the excavation and through sieving procedure. The cave-site has yielded abundant faunal remains comprised of large and small mammals, birds, fish, and reptiles. The major part of the large mammalian material belongs to the cave bear (Tsoukala et al. 2006). Thirty species of rodents, insectivores, and lagomorphs have been recognized within the floor sediments providing a remarkable diversity to the LAC microfauna (Chatzopoulou 2014).

Regarding the chiropteran fauna of Loutra Almopias Cave (for more information about it, see Box 2), it is worth to mention that it is currently under study within the framework of the doctorate thesis of the first author. Here are presented the first preliminary results (up to date) of the chiropteran fauna, based on fossil specimens that have been retrieved from the sediments of the cave's floor (Fig. 1).

Fig. 1 Finding chiropteran fossils from Loutra Almopias Cave: (**a**) chiropteran tooth (in circle) found in the sieved sediments, (**b**) screening the sieved sediments for microremains, (**c**) box containing cataloged chiropteran fossils, (**d**) over 3000 of cataloged specimens found in the sieved sediments, (**e**) overview of collected microremains, and (**f**) drawing of specimens with the use of camera lucida

3 Phylogenetic Relationships

Chiroptera is clearly distinguished from other mammalian taxonomic groups because of their ability for powered flight and, for most of the bats, to echolocate (Gunnell and Simmons 2005; Simmons 2005b; Teeling et al. 2005). Despite the fact of being the only known mammals with the aforementioned characteristics, the monophyly of Chiroptera was largely debated since the late 1980s (Gunnell and Simmons 2005 and references therein); however, the intensification of research related to this topic and, thus, the acquirement of plethora of data (morphological, DNA hybridization and nucleotide sequence data), eventually further supported the hypothesis that all chiropteran taxa have a common (flying) ancestor (Gunnell and Simmons 2005; Teeling et al. 2005).

Table 1 All chiropteran families, extinct and extant. As classification above family level is still a matter of dispute, only the most widely accepted distinct families are presented (after Gunnell and Simmons 2005; Miller-Butterworth et al. 2007; Simmons et al. 2008; Lack et al. 2010). Chiropteran families present in the fossil record of Greece are indicated with boldface

Extinct families	Extant families		
Icaronycteridae	Pteropodidae	Emballonuridae	Furipteridae
Archaeonycteridae	**Rhinolophidae**	Myzopodidae	Natalidae
Palaeochiropterygidae	Hipposideridae	Mystacinidae	Molossidae
Hassianycteridae	**Megadermatidae**	Phyllostomidae	**Vespertilionidae**
Tanzanycteridae	**Rhinopomatidae**	Mormoopidae	**Miniopteridae**[a]
Philisidae	Craseonycteridae	Noctilionidae	Cistugidae[a]
Onychonycteridae	Nycteridae	Thyropteridae	

[a]Miniopteridae and Cistugidae are distinct families according to Miller-Butterworth et al. (2007) and Lack et al. (2010), respectively

The aforementioned debate, resulted in the abandonment of the traditional division of Chiroptera into two sub-orders—Megachiroptera (one extant family of non-echolocating Old World fruit bats) and Microchiroptera (19 extant families of echolocating bats) (Gunnell and Simmons 2005; Simmons 2005b)—and led to the establishment of the sub-orders of Yinpterochiroptera, which includes Pteropodidae, Rhinolophidae, Hipposideridae, Megadermatidae, Craseonycteridae and Rhinopomatidae (Springer et al. 2001), and Yangochiroptera, which includes the remaining chiropteran families (Gunnell and Simmons 2005). Accordingly, echolocation in bats was evolved separately for either the two sub-orders or once with Pteropodidae (Old World fruit bats) losing it at a later stage (Teeling et al. 2005; Simmons 2005b).

As stated in the Introduction, Chiroptera appear in the fossil record during the early Eocene. New data on the phylogeny of fossil bats indicate that Onychonycteridae is the basal family for the order Chiroptera, with the rest of the extinct and extant families being sister groups (Simmons et al. 2008). The chiropteran families (20 extant and seven extinct) up to date are given in Table 1. In respect to the Greek chiropteran faunas, no phylogenetic analyses have been carried out until now. As a result, no comments can be made on the phylogeny of Greek bats.

4 Distribution

Even though the fossil record of Chiroptera is a not well-studied subject in Greece, there are quite a few localities across different regions of the country. All localities are East of Pindus Mountain Range (the absence of fossiliferous localities West of Pindus Mountain Range is because of its uplift and the absence of sedimentary basins). Out of 23 localities (Fig. 2), six are in the geographic region of Macedonia (Loutra Almopias Cave, Maramena, Antonios, Petralona Cave, Nea Silata,

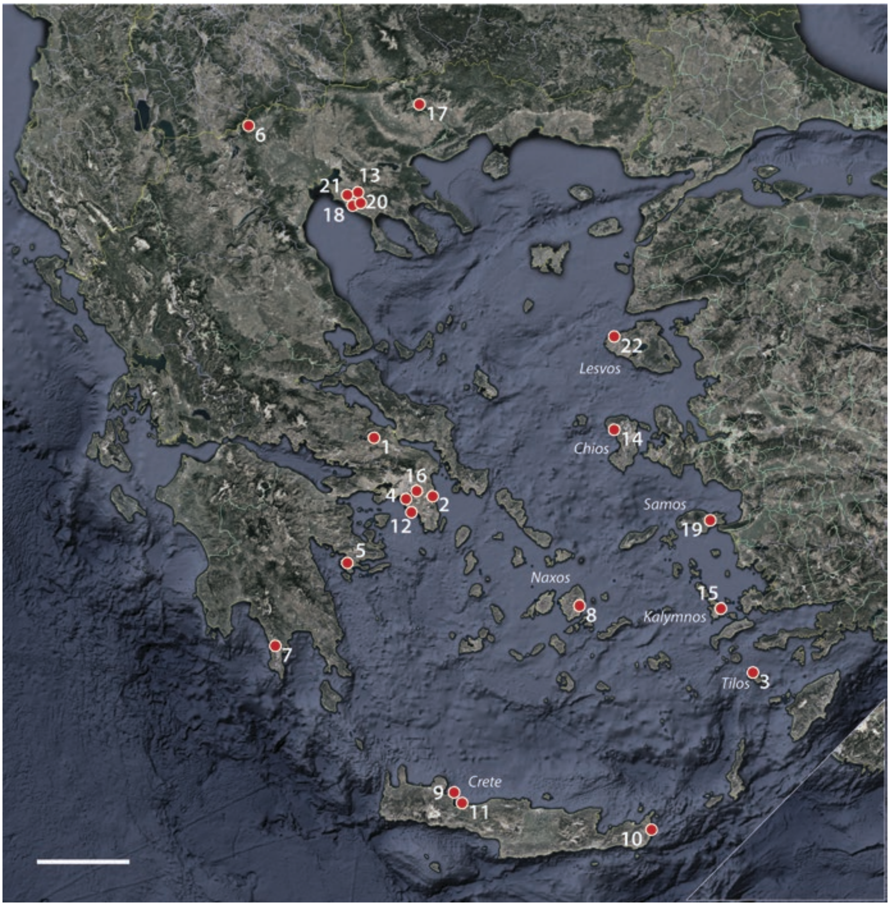

Fig. 2 Map with all the localities, where Chiroptera have been described/recorded: **1** Sarakenos Cave, **2** Vraona Cave, **3** Charkadio Cave, **4** Anonymous Cave of Schisto at Keratsini, **5** Franchthi Cave, **6** Loutra Almopias Cave, **7** Kalamakia Cave, **8** Naxos, **9** Liko Cave, **10** Kharoumes 5, **11** Bate Cave, **12** Varkiza 1 and 2, **13** Petralona Cave, **14** Latomi 1, **15** Vathy village, **16** Tourkobounia 1, 2, 3 and 5, **17** Maramena, **18** Nea Silata, **19** Mytilinii, **20** Elaiochoria 2, **21** Antonios, **22** Lapsarna. See Appendix for more information. Image exported from Google Earth Pro © 2019, map data from US Dept. of State Geographer, SIO, NOAA, U.S. Navy, NGA, GEBCO, image from Landsat/Copernicus. Scale bar equals 80 km, North faces upward

Elaiochoria 2), three of North Aegean Islands (Lapsarna, Latomi 1, Mytilinii), six of Central Greece (Sarakenos Cave, Anonymous Cave of Schisto at Keratsini, Tourkobounia 1, Tourkobounia 2, 3, 5, Vraona Cave, Varkiza 1, 2), two of Peloponnese (Franchthi Cave, Kalamakia Cave), one of Cyclades (Naxos) two of Dodecanese Islands (Vathy village, Charkadio Cave), and three of Crete (Liko, Bate Cave, Kharoumes 5). Further details on all localities are given in the Appendix.

5 Systematic Paleontology

As Chiroptera is the only known mammal group capable of self-powered flight, there are several morphological characteristics that can easily distinguish them from other extant and extinct mammals. Most importantly, their forelimbs and hind limbs are highly specialized for flight (wings) and upside-down roosting respectfully (Gunnell and Simmons 2005 and references therein). In addition to that, the chiropteran families that evolved echolocation have multiple specializations of their auditory system (Gunnell and Simmons 2005 and references therein). As described in the Introduction, complete chiropteran fossils are extremely rare, limiting their study mostly from their dental elements (including mandibles and maxillae) and humeri, which can be easily fossilized due to their harder nature (Sevilla 2016). All the above have morphological characteristics that allow paleontologists to identify fossil specimens up to species level. The identifications that follow were based on the aforementioned characteristics. Moreover, because of the limited information on most of the localities containing chiropteran fossils in Greece, this section contains information only up to the generic level. For further details on the mentioned species, see Simmons (2005a), Dietz et al. (2009), etc. *Samonycteris* is the only extinct chiropteran genus/species named from Greece (Revilliod 1922). It is also worthy to note that one extant chiropteran species, *Myotis alcathoe*, has been named from Greece (von Helversen et al. 2001).

Chiroptera Blumenbach, 1779[1]

Rhinolophidae Gray, 1825

Type Genus *Rhinolophus* Lacépède, 1799.

***Rhinolophus* Lacépède, 1799**

Type Species *Vespertilio ferrum-equinum* Schreber, 1774.

Included Taxa *Rhinolophus* gr. *delphinensis* Gaillard, 1899, *Rhinolophus ferrumequinum* Schreber, 1774 (Greater Horseshoe Bat) (Fig. 3a, b), *Rhinolophus ferrumequinum topali* Kretzoi 1977, *Rhinolophus* (cf.) *hipposideros* Bechstein, 1800 (Lesser Horseshoe Bat) (Fig. 3c, d), *Rhinolophus euryale* Blasius, 1853 (Mediterranean Horseshoe Bat), *Rhinolophus* (cf.) *mehelyi* Matschie, 1901 (Mehely's Horseshoe Bat) (Fig. 3f), *Rhinolophus blasii* Peters, 1866 (Blasius's

[1] For the purpose of this chapter, we follow Simmons (2005a). We are aware that new species have been described since then, however, as plenty of them are still under discussion and because the purpose of this chapter is not to provide an updated taxonomy of extant Chiroptera, we follow the last widely accepted valid work of this kind.

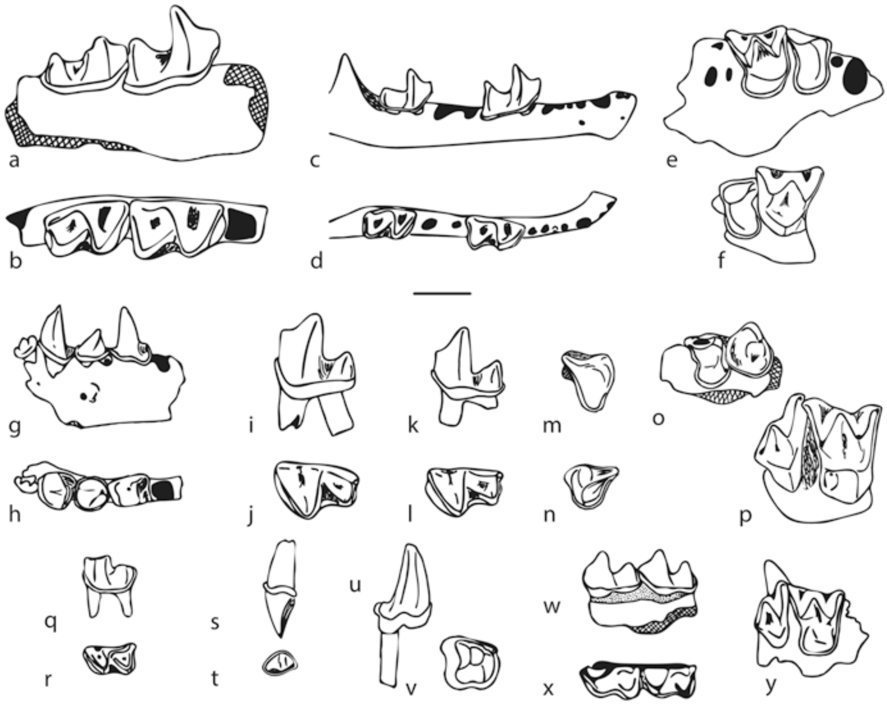

Fig. 3 (**a**, **b**) *Rhinolophus ferrumequinum* (LAC 20600) right partial hemimandible in labial (**a**) and occlusal (**b**) view, (**c**, **d**) *Rhinolophus hipposideros* (LAC 16660) right partial hemimandible in labial (**c**) and occlusal (**d**) view, (**e**) *Rhinolophus* sp. (LAC 17496) right partial hemimaxilla in occlusal (**e**) view, (**f**) *Rhinolophus mehelyi* (LAC 16667) left partial hemimaxilla in occlusal (**f**) view, (**g**, **h**) *Rhinolophus mehelyi/euryale/blasii* (LAC 16744) left partial hemimandible in labial (**g**) and occlusal (**h**) view, (**i**, **j**) *Myotis myotis* (LAC 22236) left m3 in labial (**i**) and occlusal (**j**) view, (**k**, **l**) *Myotis blythii* (LAC 22232) left m3 in labial (**k**) and occlusal (**l**) view, (**m**) *Myotis blythii* (LAC 20468) right P4 in occlusal (**m**) view, (**n**) *Myotis emarginatus* (LAC 20473) left P4 in occlusal (**n**) view, (**o**) *Vespertilio murinus* (LAC 16379) right partial hemimaxilla in occlusal (**o**) view, (**p**) *Nyctalus noctula* (LAC 19325) right partial hemimaxilla in occlusal (**p**) view, (**q**, **r**) *Barbastella barbastellus* (LAC 17977) left m1 in labial (**q**) and occlusal (**r**) view, (**s**, **t**) *Pipistrellus pipistrellus* (LAC 18052) left C in labial (**s**) and occlusal (**t**) view, (**u**, **v**) *Eptesicus serotinus* (LAC 21077) right p4 in labial (**u**) and occlusal (**v**) view, (**w**, **x**) *Barbastella barbastellus* (LAC 16371) left partial hemimandible in labial (**w**) and occlusal (**w**) view, and (**y**) *Miniopterus schreibersii* (LAC 16383) right partial hemimaxilla in occlusal (**y**) view

Horseshoe Bat), *Rhinolophus mehelyi/euryale/blasii* (Fig. 3g, h), *Rhinolophus* sp. (Fig. 3e), *Rhinolophus* sp. I (euryale group), *Rhinolophus* sp. II, *Rhinolophus* sp. III.

Comments *Rhinolophus* appears in the fossil record during late Eocene–Oligocene at Quercy, France (Sigé 1978). Five Horseshoe Bat species can be found nowadays in Greece (Hanák et al. 2001; Simmons 2005a). All of those species are also present in the Greek fossil record, including *R.* gr. *delphinensis*, a fossil species that appears in the European fossil record, between MN 6 and MN 15 (Ziegler 2003). *R.* gr. *del-*

phinensis is present in Elaiochoria 2, *R. ferrumequinum* and *R. hipposideros* are present in Sarakenos Cave, *R. hipposideros* and *R. blasii* are present in Charkadio Cave, *R. ferrumequinum*, *R. hipposideros*, *R. euryale*, *R. mehelyi*, *R. blasii*, *R. mehelyi/euryale/blasii*, and *Rhinolophus* sp. are present in Loutra Almopias Cave, *Rhinolophus* sp. is present in Kalamakia Cave, *R. ferrumequinum topali*, *R.* cf. *hipposideros*, *R.* cf. *mehelyi*, *Rhinolophus* sp. I (euryale group), II and III are present in Petralona Cave.

Vespertilionidae Gray, 1821

Type Genus *Myotis* Kaup, 1829.

Comments Vesper Bats appear in the fossil record during early Eocene (Miller-Butterworth et al. 2007). Several species have been identified in the Greek fossil record at different taxonomic levels. Vespertilionidae sp.1 and sp.2 are present at Nea Silata.

★*Samonycteris* Revilliod, 1922

Type Species ★*Samonycteris majori* Revilliod, 1922.

Included Taxa *Samonycteris majori* Revilliod, 1922.

Comments Major (1891) assigned an incomplete chiropteran skull retrieved from the late Miocene Mytilinii basin (Samos) as Chiroptera indet. Later on, Revilliod (1919) refers to this specimen for the first time as *S. majori*, while its description was published in 1922 by the same author. *Samonycteris* has a single robust upper incisor and its skull has a morphological resemblance to that of *Otonycteris* and/or *Eptesicus*, which, however, differs in several morphological features (e.g., the cochlea) and is also a little smaller than the latter (Revilliod 1922; Horáček 1991). *S. majori* is a monotypic taxon.

Myotis Kaup, 1829

Type Species *Vespertilio myotis* Borkhausen, 1797.

Included Taxa *Myotis myotis* Borkhausen, 1797 (Greater Mouse-eared Bat) (Fig. 3i, j), *Myotis blythii* Tomes, 1857 (Lesser Mouse-eared Bat) (Fig. 3k–m), *Myotis blythii oxygnathus* Monticelli, 1885, *Myotis bechsteinii* Kuhl, 1817 (Bechstein's Bat), *Myotis emarginatus* Geoffroy, 1806 (Geoffroy's Bat) (Fig. 3n), *Myotis capaccinii* Bonaparte, 1837 (Long-fingered Bat), *Myotis* cf. *daubentonii* Kuhl, 1817 (Daubenton's Bat), *Myotis mystacinus*? Kuhl, 1817 (Whiskered Bat), *Myotis myotis/blythii*, *Myotis* sp., *Myotis* sp. I, *Myotis* sp. II, cf. *Myotis* (small sized).

Comments *Myotis* appears in the fossil record during early Oligocene (Gunnell et al. 2017). Ten to eleven Mouse-eared Bat species currently inhabit the Greek region (Hanák et al. 2001), and some of them are also present in the fossil record. *M. blythii* and *M. myotis/blythii* are present in Sarakenos Cave, *Myotis* sp. is present in Vraona Cave, *M. blythii* and *Myotis* sp. are present in Charkadio Cave, *M.* cf. *blythii* is present in Kalamakia Cave, *M. myotis*, *M. blythii*, *M. bechsteinii*, *M. emarginatus*, *M. capaccinii*, *M. mystacinus*?, *M. myotis/blythii* and *Myotis* sp. are present in Loutra Almopias Cave, *M. myotis*, *M. blythii* ssp., *M. blythii oxygnathus*, *M. emarginatus*, *M.* cf. *daubentonii*, *Myotis* sp. I and II are present in Petralona Cave,[2] cf. *Myotis* (small sized) is present in Elaiochoria 2.

Nyctalus Bowdich, 1825

Type Species *Nyctalus verrucosus* Bowdich, 1825 (= *Vespertilio leisleri* Kuhl, 1817).

Included Taxa *Nyctalus lasiopterus*? Schreber, 1780 (Greater Noctule Bat), *Nyctalus leisleri* Kuhl, 1817 (Leisler's Bat), *Nyctalus noctula* Schreber, 1774 (Noctule Bat) (Fig. 3p).

Comments *Nyctalus* appears in the fossil record during the Oligocene (Horáček 2001). Three Noctule Bat species can be found nowadays in the Greek region (Hanák et al. 2001; Simmons 2005a). In the fossil record of Greece, *N. noctula* is present in Sarakenos and Loutra Almopias Caves, *N.* cf. *noctula* is present in Petralona Cave, *N. lasiopterus*? and *N. leisleri* are present only in Loutra Almopias Cave.

Pipistrellus Kaup, 1829

Type Species *Vespertilio pipistrellus* Schreber, 1774.

Included Taxa *Pipistrellus pipistrellus* Schreber, 1774 (Common Pipistrelle Bat) (Fig. 3s, t), *Pipistrellus*(?) sp.

Comments *Pipistrellus* appears in the fossil record during Middle Pleistocene (Horáček and Jahelková 2005). Four Pipistrelle Bat species can be found nowadays in the Greek region (Hanák et al. 2001; Simmons 2005a). In the Greek fossil record,

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[2] *M. blythii oxygnathus* is described for the first time by Kretzoi (1977). He states in his description of this taxon that "*Though there are some differences in comparison with the living European form, the material at our disposal is not enough to define the subspecific distinction*." Later on, Horacek and Poulianos (1988) add *M. blythii* in the chiropteran faunal list of Petralona Cave; however, they state that their "*sample is too small to enable a detailed comparison as to its subspecific relationship that undoubtedly is quite a complicated (cf.* oxygnathus*,* punnicus*,* omari *that may come in consideration in the Mediterranean region)*." Consequently, *M. blythii* should be considered a different subspecies from *M. blythii oxygnathus* (most possibly its nominal subspecies *M. blythii blythii*).

P. pipistrellus is present in Loutra Almopias Cave, *Pipistrellus*(?) sp. is present in Petralona Cave, and *Pipistrellus* sp. is present in Kalamakia Cave.

Hypsugo Kolenati, 1856

Type Species *Vespertilio savii* Bonaparte, 1837.

Included Taxa *Hypsugo savii* Bonaparte, 1837 (Savi's Pipistrelle Bat).

Comments *Hypsugo* was included in *Pipistrellus* until mid-1980s, however, since then it gained separate generic status (Horáček and Hanák 1985). One Asian Pipistrelle Bat species can be found nowadays in the Greek region (Hanák et al. 2001), which is also present in the Greek fossil record. *H. savii* is present only in Petralona Cave.

Vespertilio Linnaeus, 1758

Type Species *Vespertilio murinus* Linnaeus, 1758.

Included Taxa *Vespertilio murinus* Linnaeus, 1758 (Parti-colored Bat) (Fig. 3o).

Comments *Vespertilio* appears in the fossil record during the Pliocene (Gunnell and Simmons 2005). One Parti-colored Bat species can be found nowadays in the Greek region (Hanák et al. 2001), which is also present in the Greek fossil record. *V. murinus* is present in Loutra Almopias and Petralona Caves.

Eptesicus Rafinesque, 1820

Type Species *Eptesicus melanops* Rafinesque, 1820 (= *Vespertilio fuscus* Beauvois, 1796).

Included Taxa *Eptesicus serotinus* Schreber, 1774 (Serotine Bat) (Fig. 3u, v), *Eptesicus* sp.

Comments *Eptesicus* appears in the fossil record during the early Miocene (Gunnell and Simmons 2005). Three Serotine Bat species can be found nowadays in the Greek region, with *E. bottae* only present in Rhodes (Hanák et al. 2001; Simmons 2005a), and at least one of them is also present in the Greek fossil record. *E. serotinus* is present in Loutra Almopias and Sarakenos Caves, *Eptesicus* sp. is present in Petralona Cave.

Barbastella Gray, 1821

Type Species *Vespertilio barbastellus* Schreber, 1774.

Included Taxa *Barbastella barbastellus* Schreber, 1774 (Western Barbastelle Bat) (Fig. 3q, r, w, x).

Comments *Barbastella* appears in the fossil record during the Early Pleistocene (Rydell and Bogdanowicz 1997). One Barbastelle Bat species can be found nowadays in the Greek region (Hanák et al. 2001), which is also present in the Greek fossil record. *B. barbastellus* is present only in Loutra Almopias Cave.

Plecotus Geoffroy, 1818

Type Species *Vespertilio auritus* Linnaeus, 1758.

Included Taxa *Plecotus austriacus* Fischer, 1829 (Gray Long-eared Bat), *P. auritus/austriacus*.

Comments *Plecotus* appears in the fossil record during the middle Miocene (Gunnell and Simmons 2005). Three Long-eared Bat species are currently present in the Greek region (Hanák et al. 2001). *P. austriacus* is present in the fossil record of Charkadio Cave and *P. auritus/austriacus* is present in the fossil record of Loutra Almopias Cave.

Miniopteridae Mein and Tupinier, 1977[3]

Type Genus *Miniopterus* Bonaparte, 1837.

Miniopterus Bonaparte, 1837

Type Species *Vespertilio ursinii* Bonaparte, 1837 (= *Vespertilio schreibersii* Kuhl, 1817).

Included Taxa *Miniopterus schreibersii* Kuhl, 1817 (Schreibers' Bent-winged Bat) (Fig. 3y).

Comments *Miniopterus* appears in the fossil record during middle Miocene (Horáček et al. 2013). One Bent-winged Bat species can be found nowadays in Greece (Hanák et al. 2001), which is also present in the Greek fossil record. *M. schreibersii* is present in Loutra Almopias Cave, Petralona Cave, and Vathy village.

Rhinopomatidae Bonaparte, 1838

Type Genus *Rhinopoma* Geoffroy, 1818.

[3] For details on the classification of this family, see Sect. 3 and references therein.

***Rhinopoma* Geoffroy, 1818**

Type Species *Vespertilio microphyllus* Brünnich, 1782.

Included Taxa *Rhinopoma* aff. *hardwickii* Gray, 1831 (Lesser Mouse-tailed Bat).

Comments The Mouse-tailed Bats (*R.* aff. *hardwickii*) appear in the fossil record during Late Miocene at Elaiochoria 2, Greece, which is the earliest and sole occurrence of this family in Europe (Hulva et al. 2007).

Megadermatidae Allen, 1864

Type Genus *Megaderma* Geoffroy, 1810.

Included Taxa cf. Megadermatidae gen. and sp. indet. (False Vampire Bats).

Comments The False Vampire Bats appear in the fossil record during late Eocene (Agnarsson et al. 2011). Fossils of Megadermatidae have been retrieved from several European sites (Gunnell and Simmons 2005), including Greece. cf. Megadermatidae gen. and sp. indet. is present in Antonios.

Chiroptera indet.

Comments Undetermined species of Chiroptera (also mentioned as "Chiroptera," "Bats," etc.) have been found at Anonymous Cave of Schisto at Keratsini, Franchthi Cave, Loutra Almopias Cave, Naxos, Liko, Kharoumes 5, Bate Cave, Varkiza 1, 2, Latomi 1, Tourkobounia 1, 2, 3, 5, Vathy village, Maramena, and Lapsarna.

6 Concluding Remarks

It is evident that the fossil record of Chiroptera is not well-studied in Greece, with sparse finds and most of the works reaching up to generic level. Nevertheless, the following taxa have been identified in Greece: *Rhinolophus* gr. *delphinensis*, *Rhinolophus ferrumequinum*, *Rhinolophus ferrumequinum topali*, *Rhinolophus* (cf.) *hipposideros*, *Rhinolophus euryale*, *Rhinolophus* (cf.) *mehelyi*, *Rhinolophus blasii*, *Rhinolophus mehelyi*/*euryale*/*blasii*, *Rhinolophus* sp., *Rhinolophus* sp. I (euryale group), *Rhinolophus* sp. II, *Rhinolophus* sp. III, *Samonycteris majori*, *Myotis myotis*, *Myotis* (cf.) *blythii* (ssp.), *Myotis blythii oxygnathus*, *Myotis bechsteinii*, *Myotis emarginatus*, *Myotis capaccinii*, *Myotis* cf. *daubentonii*, *Myotis mystacinus*?, *Myotis myotis*/*blythii*, *Myotis* sp., *Myotis* sp. I, *Myotis* sp. II, cf. *Myotis* (small sized), *Nyctalus lasiopterus*?, *Nyctalus leisleri*, *Nyctalus* (cf.) *noctula*, *Pipistrellus pipistrellus*, *Pipistrellus*(?) sp., *Hypsugo savii*, *Vespertilio murinus*, *Eptesicus serotinus*, *Eptesicus* sp., *Barbastella barbastellus*, *Plecotus austriacus*, *Plecotus auritus*/*austriacus*, *Miniopterus schreibersii*, *Rhinopoma* aff. *hardwickii*, cf.

Megadermatidae gen. and sp. indet., Vespertilionidae sp.1, Vespertilionidae sp.2, and Chiroptera indet.

Rhinopoma aff. *hardwickii* from Late Miocene site Elaichoria 2 is the earliest and sole occurrence of Rhinopomatidae in Europe and consequently Greece. Furthermore, the study of Chiroptera from Loutra Almopias Cave, which is presented here for the first time as an updated preliminary list of taxa, will give us the first complete chiropteran record in the Greek region. In addition, the revision of the existing specimens retrieved from the localities mentioned herein might allow us to reach to a more detailed identification. In any case, the acquisition of new material and basic systematic study will give us the opportunity to carry out more targeted research on this relatively unexplored topic (i.e., phylogenetic analysis) that will allow us to extent our knowledge on the chiropteran evolution in the Balkan Peninsula.

Acknowledgments This research (P.P.) is co-financed by Greece and the European Union (European Social Fund; ESF) through the Operational Programme "Human Resources Development, Education and Lifelong Learning" in the context of the project "Strengthening Human Resources Research Potential via Doctorate Research" (MIS-5000432), implemented by the State Scholarships Foundation (ΙΚΥ). We would also like to thank Prof. E. Tsoukala (supervisor), Prof. P. Sevilla and Prof. D. Kostopoulos (members of the Ph.D. committee of the first author) for their continuous help and support. We would also like to thank Prof. V. Popov for his critical review that helped on the improvement of the manuscript.

Appendix

List of fossil localities with occurrences of Chiroptera in Greece. Locality numbers refer to the collection numbers of the PaleoBiology Database (PBDB). Type localities are marked with boldface

Localities[PBDB no]	Age (MN)	Taxon
Sarakenos Cave[203845]	Early/Middle Holocene	*Rhinolophus ferrumequinum*[1] *Rhinolophus hipposideros*[1] *Myotis blythii*[1] *Myotis myotis/blythii*[1] *Nyctalus noctula*[1] *Eptesicus serotinus*[1]
Vraona Cave[183139]	Holocene	*Myotis* sp.[2]
Charkadio Cave[182809]	Holocene	*Rhinolophus hipposideros*[3] *Rhinolophus blasii*[3] *Myotis blythii*[3] *Myotis* sp.[3] *Plecotus austriacus*[3]
Anonymous Cave of Schisto at Keratsini[203846]	Late Pleistocene/Early Holocene	Chiroptera indet.[4]
Franchthi Cave[182709]	Late Pleistocene/Early Holocene	Chiroptera indet.[5]

(continued)

Localities[PBDB no]	Age (MN)	Taxon
Loutra Almopias Cave[203847]	Late Pleistocene, Torringian (MNQ 26)	*Rhinolophus ferrumequinum*[a] *Rhinolophus hipposideros*[a] *Rhinolophus euryale*[a] *Rhinolophus mehelyi*[a] *Rhinolophus blasii*[a] *Rhinolophus mehelyi/euryale/blasii*[a] *Rhinolophus* sp.[a] *Myotis myotis*[a] *Myotis blythii*[a] *Myotis bechsteinii*[a] *Myotis emarginatus*[a] *Myotis capaccinii*[a] *Myotis mystacinus*?[a] *Myotis myotis/blythii*[a] *Myotis* sp.[a] *Nyctalus lasiopterus*?[a] *Nyctalus leisleri*[a] *Nyctalus noctula*[a] *Pipistrellus pipistrellus*[a] *Plecotus auritus/austriacus*[a] *Vespertilio murinus*[a] *Eptesicus serotinus*[a] *Barbastella barbastellus*[a] *Miniopterus schreibersii*[a] Chiroptera indet.[a]
Kalamakia Cave[184245]	Late Pleistocene	*Myotis* cf. *blythii*[6] *Pipistrellus* sp.[6] *Rhinolophus* sp.[6]
Naxos[203848]	Late Pleistocene	Chiroptera indet.[7]
Liko Cave[92902]	Late Pleistocene	Chiroptera indet.[8]
Kharoumes 5[204088]	Late Pleistocene	Chiroptera indet.[9]
Bate Cave[183122]	Late Pleistocene	Chiroptera indet.[10]
Varkiza 2[204167]	Late/Middle Pleistocene	Chiroptera indet.[11]
Varkiza 1[204166]	Late/Middle Pleistocene	Chiroptera indet.[11]
Petralona Cave[183123]	Middle Pleistocene	*Rhinolophus ferrumequinum topali*[12] *Rhinolophus* cf. *hipposideros*[12] *Rhinolophus* cf. *mehelyi*[12] *Rhinolophus* sp. I (*euryale* group)[12] *Rhinolophus* sp. II[12] *Rhinolophus* sp. III[12] *Myotis myotis*[12] *Myotis blythii* ssp.[12] *Myotis blythii oxygnathus*[12] *Myotis emarginatus*[12] *Myotis* cf. *daubentonii*[12] *Myotis* sp. I[12] *Myotis* sp. II[12] *Nyctalus* cf. *noctula*[12] *Pipistrellus*? sp.[12] *Hypsugo*[12] *savii*[12] *Vespertilio murinus*[12] *Eptesicus* sp.[12] *Miniopterus schreibersii*[12]

(continued)

Localities[PBDB no]	Age (MN)	Taxon
Latomi 1[204077]	Middle Pleistocene	Chiroptera indet.[13]
Vathy village	Early Pleistocene	*Miniopterus schreibersii*[14] Chiroptera indet.[14]
Tourkobounia 3–5[34592]	Late Pliocene, Early Biharian (MNQ 19)	Chiroptera indet.[15]
Tourkobounia 2[34767]	Late Pliocene, Early Biharian (MNQ 19)	Chiroptera indet.[15]
Tourkobounia 1[34589]	Late Pliocene, Early Villanyian, MN 16	Chiroptera indet.[15]
Maramena[32189]	Miocene/Pliocene, Late Turolian/Early Ruscinian (MN 13/14)	Chiroptera indet.[16]
Nea Silata[191612]	Miocene/Pliocene, Late Turolian/Early Ruscinian (MN 13/14)	Vespertilionidae sp.1[17] Vespertilionidae sp.2[17]
Mytilinii[202120]	Late Miocene (MN 12)	***Samonycteris majori***[18]
Elaiochoria 2[219100]	Late Miocene, Early Turolian (MN 10/11)	*Rhinolophus* gr. *delphinensis*[19], *Rhinopoma* aff. *hardwickii*[19] cf. *Myotis* (small sized)[19]
Antonios[73861]	Early/Middle Miocene, Orleanian (MN 4/5)	cf. Megadermatidae gen. and sp. indet.[20]
Lapsarna[186558]	Early Miocene, Orleanian, MN 4	Chiroptera indet.[21]

[1]Pereswiet-Soltan (2016), [2]Symeonidis et al. (1980), [3]Symeonidis et al. (1973), [4]Mavridis et al. (2013), [5]Stiner and Munro (2011), [6]Kolendrianou et al. (2020), [7]van der Geer et al. (2014), [8]Mayhew (1977), [9]Kuss (1970), [10]Kotsakis et al. (1976), [11]van de Weerd (1973), [12]Horacek and Poulianos (1988), [13]Storch (1975), [14]Kuss (1973), [15]Reumer and Doukas (1985), [16]Schmidt-Kittler et al. (1995), [17]Vasileiadou et al. (2003), [18]Revilliod (1922), [19]Hulva et al. (2007), [20]Vasileiadou and Koufos (2005), [21]Vasileiadou and Zouros (2012)
[a]This study

References

Agnarsson I, Zambrana-Torrelio CM, Flores-Saldana NP, May-Collado LJ (2011) A time-calibrated species-level phylogeny of bats (Chiroptera, Mammalia). PLoS Curr 3:RRN1212

Chatzopoulou K (2003) The Late Pleistocene small mammal fauna from Loutra Aridea Bear-cave (Pella, Macedonia, Greece). Atti Mus Civ Stor Nat Trieste 49:35–45

Chatzopoulou K (2005) The small mammal fauna from the Loutra Aridea bear-Cave (Pella, Macedonia, Greece) with emphasis on the third chamber. Abh Nathist Ges Nürnberg 45:57–64

Chatzopoulou K (2014) The micromammals of the Quaternary deposits from cave A, Loutra Almopias (Pella, Northern Greece), Stratigraphy-Taphonomy-Paleoenvironment. Dissertation. Aristotle University of Thessaloniki, Thessaloniki

Chatzopoulou K, Vasileiadou A, Koliadimou K, Tsoukala E, Rabeder G, Nagel D (2001) Preliminary report on the Late Pleistocene small mammal fauna from the Loutraki Bear-cave (Pella, Macedonia, Greece). Cad Lab Xeol Laxe 26:485–495

Darlas A, Psathi E (2016) The middle and upper Paleolithic on the western coast of the Mani Peninsula (southern Greece). In: Harvati K, Roksandic M (eds) Paleoanthropology of the Balkans and Anatolia: Human evolution and its context. Springer, Dordrecht, pp 95–117

Dermitzakis M (1977) The quarternary fossil mammals in the caves and karstic-holes of Crete island and their significance. Bull Speleol Soc Grece 14:152–190

Dietz C, Nill D, von Helversen O (2009) Bats of Britain, Europe and Northwest Africa. A & C Black Publishers, London, pp 1–400

Doukas CS, Papayianni K (2016) Small mammals in the Plio/Pleistocene sediments of Greece. In: Harvati K, Roksandic M (eds) Paleoanthropology of the Balkans and Anatolia: Human evolution and its context. Springer, Dordrecht, pp 291–302

Gunnell GF, Simmons NB (2005) Fossil evidence and the origin of bats. J Mamm Evol 12:209–246

Gunnell GF, Smith R, Smith T (2017) 33 million year old *Myotis* (Chiroptera, Vespertilionidae) and the rapid global radiation of modern bats. PLoS One 12:e0172621

Hanák V, Benda P, Ruedi M, Horáček I, Sofianidou TS (2001) Bats (Mammalia: Chiroptera) of the Eastern Mediterranean. Part 2. New records and review of distribution of bats in Greece. Acta Soc Zool Bohem 65:279–346

Hand S, Novacek M, Godthelp H, Archer M (1994) First Eocene bat from Australia. J Vert Paleontol 14:375–381

Harvati K, Darlas A, Bailey SE, Rein TR, El Zaatari S, Fiorenza L, Kullmer O, Psathi E (2013) New Neanderthal remains from Mani peninsula, southern Greece: the Kalamakia middle Paleolithic cave site. J Hum Evol 64:486–499

Horáček I (1991) Enigma of *Otonycteris*: ecology, relationship, classification. Myotis 29:17–30

Horáček I (2001) On the early history of vespertilionid bats in Europe: the Lower Miocene record from the Bohemian Massif. Lynx NS 32:123–154

Horáček I, Hanák V (1985) Generic status of *Pipistrellus savii* (Bonaparte, 1837) and remarks on systematics of the genus *Pipistrellus*. Bat Res News 26:62

Horáček I, Jahelková H (2005) History of the *Pipistrellus pipistrellus* group in Central Europe in light of its fossil record. Acta Chiropterol 7:189–204

Horacek I, Poulianos N (1988) Further data on bats of the Early Pleistocene site, Petralona, Greece. Abstracts of the 2nd Panellenic congress of anthropology, Athens, 27–29 May 1988

Horáček I, Maul LC, Smith KT, Barkai R, Gopher A (2013) Bat remains (Mammalia, Chiroptera) from the Middle Pleistocene site of Qesem Cave, Israel, with the first Pleistocene record of fruit bats in the Mediterranean region. Palaeontol Electron 16:1–23

Hulva P, Horáček I, Benda P (2007) Molecules, morphometrics and new fossils provide an integrated view of the evolutionary history of Rhinopomatidae (Mammalia: Chiroptera). BMC Evol Biol 7:165

Kolendrianou M, Ligkovanlis S, Maniakas I, Tzortzi M, Iliopoulos G (2020) The Palaeolithic cave of Kalamakia (Mani Peninsula), Greece: new insights on the palaeoenvironment using microvertebrates and mesowear analysis of ruminant teeth. Heliyon 6:e03958

Kotsakis T, Melentis J, Sirna G (1976) Seconda spedizione paleontologica Lincea nell'isola di Creta (1975). Rend Accad Naz Lincei 223:3–10

Kotsakis T, Petronio C, Sirna G (1979) The quaternary vertebrates of the Aegean islands: palaeogeographical implications. Ann Geol Pays Helleniques 30:31–64

Koufos GD (2006) The Neogene mammal localities of Greece: faunas, chronology and biostratigraphy. Hellenic J Geosci 41:183–214

Kretzoi M (1977) The fauna of small vertebrates of the Middle Pleistocene at Petralona. Anthropos 4:131–143

Kretzoi M, Poulianos NA (1981) Remarks on the middle and lower Pleistocene vertebrate fauna in the Petralona Cave. Anthropos 8:57–72

Kuss SE (1970) Abfolge und Alter der Pleistozänen Säugetierfaunen der Insel Kreta. Ber Nat forsch Ges Freiburgi Br 60:35–83

Kuss SE (1973) Die pleistozänen Säugetierfaunen der ostmediterranen Inseln. Ihr Alter und ihre Herkunft. Ber Naturf Ges Freiburg Br 63:49–71

Lack JB, Roehrs ZP, Stanley Jr CE, Ruedi M, Van Den Bussche RA (2010) Molecular phylogenetics of *Myotis* indicate familial-level divergence for the genus *Cistugo* (Chiroptera). J Mammal 91:976–992

Major CF (1891) Considérations nouvelles sur la faune des Vertébrés du Miocène supérieur dans l'île de Samos. C R Hebd Séances Acad Sci 113:608–610

Mavridis F, Kormazopoulou L, Papadea A, Apostolikas O, Yamaguchi D, Tankosic Z, Kotzamani G, Trantalidou K, Karkanas P, Maniatis Y, Papagianni K, Lambropoulos D (2013) Anonymous cave of Schisto at Keratsini, Attika: a preliminary report on a diachronic cave occupation from the Pleistocene/Holocene transition to the Byzantine times. In: Mavridis F, Jensen JT (eds) Stable places and changing perceptions: cave archaeology in Greece. Archaeopress, Oxford, pp 248–284

Mayhew DF (1977) The endemic Pleistocene murids of Crete I-II. P K Ned Akad B Phys 80:182–214

Miller-Butterworth CM, Murphy WJ, O'brien SJ, Jacobs DS, Springer MS, Teeling EC (2007) A family matter: conclusive resolution of the taxonomic position of the long-fingered bats, *Miniopterus*. Mol Biol Evol 24:1553–1561

Pereswiet-Soltan A (2016) First record of serotine bat *Eptesicus serotinus* (Chiroptera: Vespertilionidae) from Early-Mid Holocene in Southern Europe (Beotia–Greece). Hystrix It J Mamm 27(2)

Piskoulis P (2018) *Rhinolophus ferrumequinum* (Chiroptera): tooth size variation from late to latest Pleistocene of Loutra Almopias Cave (Macedonia, Greece) XXXIV Jornadas de Paleontologia & IV Congresso Ibérico de Paleontologia, Vila Real (Portugal), 26–29 Sep 2018

Piskoulis P (2019) Late Pleistocene bats (Mammalia: Chiroptera) from Loutra Almopias Cave (Pella, Macedonia, Greece): preliminary results. 4th International meeting of early-stage researchers in palaeontology, Cuenca (Spain), 11–14 Jun 2019

Piskoulis P (2020) Potential precipitation-driven body size differentiation of *Rhinolophus ferrumequinum* from the Late to latest Pleistocene of Loutra Almopias Cave A (Pella, Macedonia, Greece). N Jb Geol Paläont Abh 297:311–323

Ravel A, Marivaux L, Tabuce R, Adaci M, Mahboubi M, Mebrouk F, Bensalah M (2011) The oldest African bat from the early Eocene of El Kohol (Algeria). Naturwissenschaften 98:397–405

Reumer JWF, Doukas CS (1985) Early Pleistocene Insectivora (Mammalia) from Tourkobounia (Athens, Greece). P K Ned Akad B Phys 88:111–121

Revilliod P (1919) L'état actuel de nos connaissances sur les chiroptères fossiles (note préliminaire). C R Soc Sci Phys Nat Genève 36:93–96

Revilliod P (1922) Contribution a l'étude des chiroptères des terrains tertiaires. Troisième partie et fin. Mém Soc Paléont Suisse 45:133–195

Rydell J, Bogdanowicz W (1997) *Barbastella barbastellus*. Mamm Species 557:1–8

Schmidt-Kittler N, de Bruijn H, Doukas K (1995) The vertebrate locality Maramena (Macedonia, Greece) at the Turolian-Ruscinian boundary (Neogene). 1. General introduction. Münchner Geowiss Abh A 2:9–18

Sevilla P (2016) Bats from Azokh caves. In: Fernández-Jalvo Y, King T, Yepiskoposyan L, Andrews P (eds) Azokh cave and the transcaucasian corridor. Springer, Dodrecht, pp 177–189

Sickenberg O (1964) Die Säugetierfauna der Höhle Petralona bei Thessaloniki (Vor. Mit.). Geol Geophys Res 9:1–16

Sickenberg O (1971) Revision der Wirbeltierfauna der Höhle petralona (Griech. Mazedonien). Ann Geol Pays Helleniques 23:230–264

Sigé B (1978) La poche à phosphate de Ste-Néboule (Lot) et sa faune de vertébrés du Ludien supérieur. 8. Insectivores et Chiroptères. Palaeovertebrata 8:249–268

Sigé B (1991) Rhinolophoidea et Vespertilionoidea (Chiroptera) du Chambi (Eocèneinférieur de Tunisie). Aspects biostratigraphique, biogéographique et paléoécologique de l'origine des chiroptèresmodernes. N Jb Geol Paläont Abh 182:355–376

Sigé B, Mein P, Jousse H, Aguilar JP (2014) Un nouveau Rhinopomatidae (Chiroptera) du Paléokarst miocène de Baixas (Pyrénées-Orientales, France); apport zoogéographique. Geodiversitas 36:257–282

Simmons NB (2005a) Order Chiroptera. In: Wilson DE, Reeder DM (eds) Mammal species of the world: a taxonomic and geographic reference, vol 1. JHU Press, Baltimore, MD, pp 312–529

Simmons NB (2005b) An Eocene big bang for bats. Science 307:527–528
Simmons NB, Seymour KL, Habersetzer J, Gunnell GF (2008) Primitive Early Eocene bat from Wyoming and the evolution of flight and echolocation. Nature 451:818–821
Smith T, Rana RS, Missiaen P, Rose KD, Sahni A, Singh H, Singh L (2007) High bat (Chiroptera) diversity in the Early Eocene of India. Naturwiss 94:1003–1009
Springer MS, Teeling EC, Madsen O, Stanhope MJ, de Jong WW (2001) Integrated fossil and molecular data reconstruct bat echolocation. Proc Natl Acad Sci U S A 98:6241–6246
Stiner MC, Munro ND (2011) On the evolution of diet and landscape during the Upper Paleolithic through Mesolithic at Franchthi Cave (Peloponnese, Greece). J Hum Evol 60:618–636
Storch G (1975) Eine Mittelpleistozäne Nager-Fauna von der Insel Chios, Ägais (Mammalia, Rodentia). Senckenberg Biol 56:165–189
Symeonidis N, Bachmayer F, Zapfe H (1973) Grabungen in der Zwergelefanten-Höhle "Charkadio" auf der Insel Tilos (Dodekanes, Griechenland). Ann Naturhistor Mus Wien 77:133–139
Symeonidis N, Bachmayer F, Zapfe H (1980) Ergebnisseweiterer Grabungen in der Höhle von Vraona (Attika, Griechenland). Ann Geol Pays Helleniques 30:291–299
Tabuce R, Antunes MT, Sigé B (2009) A new primitive bat from the earliest Eocene of Europe. J Vert Paleontol 29:627–630
Teeling EC, Springer MS, Madsen O, Bates P, O'brien SJ, Murphy WJ (2005) A molecular phylogeny for bats illuminates biogeography and the fossil record. Science 307:580–584
Tejedor MF, Czaplewski NJ, Goin FJ, Aragón E (2005) The oldest record of South American bats. J Vert Paleontol 25:990–993
Tsoukala E (1989) Contribution to the study of the Pleistocene fauna of large mammals (Carnivora, Perissodactyla, Artiodactyla) from Petralona Cave (Chalkidiki, N. Greece). Dissertation, Aristotle University of Thessaloniki. Sci Ann School Geol 1(8):1–360
Tsoukala E, Chatzopoulou K, Rabeder G, Pappa S, Nagel D, Withalm G (2006) Paleontological and stratigraphical research in Loutra Arideas Bear Cave (Almopia Speleopark, Pella, Macedonia, Greece). Sci Ann School Geol 98:41–67
van de Weerd A (1973) Rodentia from two Pleistocene fissure fillings near Athens. P K Ned Akad B Phys 76:148–166
van den Hoek Ostende LW (2003) Fossils explained 42. Micromammals. Geol Today 19:70–76
van der Geer AA, Lyras GA, van den Hoek Ostende LW, de Vos J, Drinia H (2014) A dwarf elephant and a rock mouse on Naxos (Cyclades, Greece) with a revision of the palaeozoogeography of the Cycladic Islands (Greece) during the Pleistocene. Palaeogeogr Palaeoclimatol Palaeoecol 404:133–144
Vasileiadou K, Koufos GD (2005) The micromammals from the Early/Middle Miocene locality of Antonios, Chalkidiki, Greece. Ann Paleontol 91:197–225
Vasileiadou K, Zouros N (2012) Early Miocene micromammals from the Lesvos Petrified Forest (Greece): preliminary results. Palaeobiodiv Palaeoenviron 92:249–264
Vasileiadou KV, Koufos GD, Syrides GE (2003) Silata, a new locality with micromammals from the Miocene/Pliocene boundary of the Chalkidiki peninsula, Macedonia, Greece. Deinsea 10:549–562
Vasileiadou K, Böhme M, Neubauer TA, Georgalis GL, Syrides GE, Papadopoulou L, Zouros N (2017) Early Miocene gastropod and ectothermic vertebrate remains from the Lesvos Petrified Forest (Greece). Pal Z 91:541–564
von Helversen O, Heller KG, Mayer F, Nemeth A, Volleth M, Gombkötö P (2001) Cryptic mammalian species: a new species of whiskered bat (*Myotis alcathoe* n. sp.) in Europe. Naturwissenschaften 88:217–223
Ziegler R (2003) Bats (Chiroptera, Mammalia) from Middle Miocene karstic fissure fillings of Petersbuch near Eichstätt, Southern Franconian Alb (Bavaria). Geobios 36:447–490