

Bats (Mammalia: Chiroptera) of the Eastern Mediterranean and Middle East. Part 7. The bat fauna of Crete, Greece

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Received August 28, 2009; accepted September 18, 2009

Published October 12, 2009

Abstract. A complete list of bat records available from Crete is presented, based on both literature data and new records obtained during recent field studies. Distribution maps and summaries of the distributional characteristics of particular species are provided. From the island of Crete, at least 622 confirmed records of 17 bat species are known; viz., *Rhinolophus ferrumequinum* (Schreber, 1774) (87 record localities), *R. hipposideros* (Borkhausen, 1797) (74), *R. blasii* Peters, 1866 (41), *Myotis blythii* (Tomes, 1857) (48), *M. emarginatus* (Geoffroy, 1806) (22), *M. aurascens* Kuzjakin, 1935 (11), *M. capaccinii* (Bonaparte, 1837) (20), *Eptesicus serotinus* (Schreber, 1774) (19), *Hypsugo savii* (Bonaparte, 1837) (45), *Pipistrellus hanaki* Hulva et Benda, 2004 (32), *P. nathusii* (Keyserling et Blasius, 1839) (2), *P. kuhlii* (Kuhl, 1817) (67), *Nyctalus leisleri* (Kuhl, 1817) (3), *Plecotus macrobullaris* Kuzjakin, 1965 (5), *P. kolombatovici* Đulić, 1980 (13), *Miniopterus schreibersii* (Kuhl, 1817) (31), and *Tadarida teniotis* (Rafinesque, 1814) (102). *Nyctalus leisleri* is reported here from Crete for the first time and *Pipistrellus nathusii*, whose previous record was based on echolocation call recordings only, was confirmed by finding of an individual. Cretan form of *Pipistrellus hanaki* was found to be morphologically and genetically unique and therefore described as a separate subspecies, *P. hanaki creticus* subsp. nov.

Distribution, taxonomy, echolocation, Balkans, Mediterranean, *Pipistrellus*

INTRODUCTION

Crete is the largest island of Greece and the fifth largest of the Mediterranean islands after Sicily, Sardinia, Cyprus and Corsica, with a total surface of 8.261 km². The main characteristic of the island's geomorphology is the high percentage of mountainous regions, with 39% of its surface being above 400 m a. s. l., 12.5% above 800 m and 1.6% above 1600 m. There are three main mountain massifs in Crete: Lefka Ori in the western part, Psiloreitis (Idi) in the central part and Lasithiotika Ori in the eastern part. The highest summits of the island are found in the Lefka Ori and Psiloreitis Mts (2.456 m). 58 more summits over 2000 m a. s. l. can be found in the island, 56 of them situated in the Lefka Ori Mts (Fig. 1).

Crete is situated in the centre of the South Aegean Arc, just north of the collision zone between the African and European tectonic plates. According to Dermitzakis & Papanikolaou (1981) and Le Pichon & Angelier (1981), intense fragmentation and the first subdivisions of the Hellenic Arc that started in the middle Miocene (15–11 Ma), transformed the southern parts of 'Aegaiida' (the united land mass comprising what is today the Hellenic peninsula and the Aegean Sea) into

separated island forms. Although Meulenkaamp et al. (1988) dated these events back to the late Oligocene (26 Ma) and controversy about the periods and duration of land connections of Crete with neighbouring continental areas still exists, it seems quite sure that Crete has been fully isolated since 5 Ma.

The mountains of Crete are fairly new in geological time. Until the early Pliocene (5 Ma), the highest peak did not exceed 500 m a. s. l., but pronounced uplifts that took place during the Pleistocene (1.5 Ma) resulted in the formation of the present bold relief (Meulenkaamp et al. 1994). A wide array of rock types can be found on the island, with limestone (Platy marbles, Tripali marbles and Tripolitsa rocks) prevailing. The extensive erosion and karstification of these carbonate rocks has led to the formation of several hundreds of caves and potholes (Platakis 1974, Fassoulas et al. 2007), which, along the numerous steep cliffs and gorges, provide suitable roosting sites for bats. Crete has been characterised as a ‘miniature continent’ (Rackham & Moody 1996), since its great geomorphological variability is accompanied by a vast variety of habitats and climatic factors, ranging from the insular character of coastal areas to a fully continental character of the higher parts of its mountains.

The most common vegetation type in Crete is phrygana (low shrubs). It can be found from sea level to the mountain tops with the most characteristic species being *Sarcopoterium spinosum*, *Coridothymus capitatus*, *Phlomis* spp., *Cistus* spp., *Genista acanthoclada*, *Calicotome villosa*, and *Euphorbia* spp. in the lowlands and *Berberis cretica*, *Rhamnus saxatilis*, *Prunus prostrata*, and *Satureja spinosa* in the higher situated areas. Phrygana is intermixed with maquis which may reach the altitude of 600 m a. s. l. The most common maquis species are *Ceratonia siliqua*, *Pistacia lentiscus*, *P. terebinthus*, shrub-like *Quercus coccifera*, *Juniperus phoenicea*, *J. oxycedrus*, *Erica arborea*, etc. In Crete, the tree line reaches the altitudes of 1600–1800 m a. s. l., with the most common tree species being *Pinus brutia*, *Quercus coccifera*, *Cupressus sempervirens*, and *Acer sempervirens*. Clear altitudinal zonation, such as evergreen broadleaved-deciduous forests / conifers, does not exist in Crete (Rackham & Moody 1996). Above the tree line only scarce, small cushion-like shrubs can be found.

In biogeographical terms, Crete consists of a mosaic of Mediterranean, Aegean, Greek and Anatolian elements, which are remnants from older times when the island was united with the

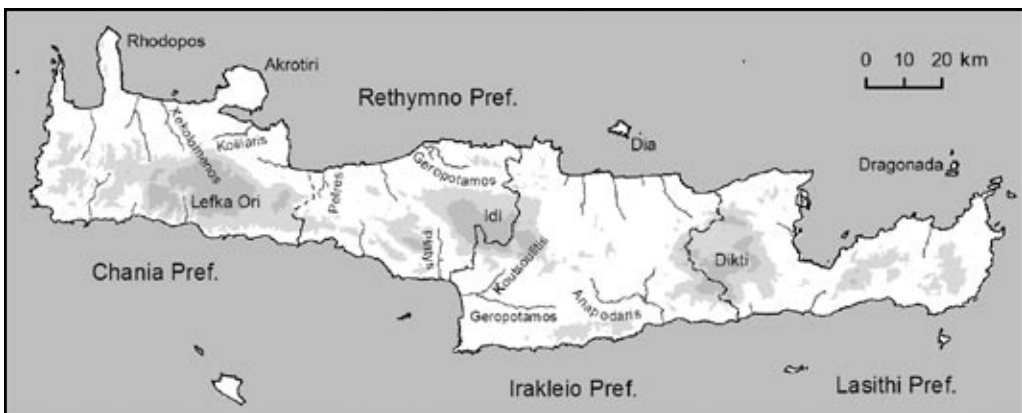


Fig. 1. General map of Crete showing political division and main geographical features (pale shaded – area above 600 m a. s. l., dark shaded – area above 1200 m a. s. l.).

corresponding land masses. Furthermore, high percentage of endemism occurs in plants (Turland et al. 1995), molluscs (Vardinoyannis 1994), insects (Trichas 1996) and other animal groups. Regarding mammals, the pre-Holocene fauna of the island seems rather unbalanced, characterised by the absence of equids, suids, bovids and carnivores, with the exception of the otter *Lutrogale cretensis* (Symeonides et Sondaar, 1975), while many large mammals (e.g. elephants, deer and hippopotamuses) developed dwarf forms there (van der Geer et al. 2006). The early Holocene arrival of man in the island caused a dramatic turnover in the mammal fauna, as a result of hunting and/or introduction of anthropophilous species. Today, the only representative of the ancient mammal fauna of Crete is *Crociodura zimmermanni* Wettstein, 1953, the only mammal species endemic to Greece (Masseti 1999).

Unlike other mammalian groups, bats have not been studied systematically in Crete until most recently, although the first published observation of bats in a roost comes from 1700 when Pitton de Tournefort (1717) found bats in the Labyrinth, a famous ancient mine at Gortys in the southern part of Crete. This observation was later interpreted as of *Myotis murinus* [*M. blythii*] by Raulin (1869b), however, no fact supports this identification but the presence of the species in the underground system almost 150 years later. However, Raulin (1869b) was the first author to bring specific bat records from the island; in 1845 he found *Myotis blythii* (reported under *M. murinus*) and *Miniopterus schreibersii* in the underground system of the Labyrinth and *M. blythii* in the Katholiko Monastery in the Akrotiri peninsula in northwestern Crete. Almost twenty years later Doria (1887) noted a finding of *Rhinolophus blasii* from another famous underground site, the Milatos cave. However, this report remained overlooked for more than a century.

The first detailed survey on mammals of Crete was undertaken by Bate (1905) who among 16 mammalian species mentioned also four species of bats, of which *Rhinolophus ferrumequinum* and *R. hipposideros* for the first time. For almost half a century the Bate's (1905) review remained the only reliable source of data on contemporary mammal fauna of Crete (Table 1). Pohle (1953) gathered data from German collectors who visited the island in the 1930s and 1940s and gave records of six bat species, for the first time he reported findings of *Eptesicus serotinus* and *Pipistrellus kuhlii* from Crete. Kahmann (1959) reported his own findings of six bat species from Crete, re-discovering *Rhinolophus blasii* (as he overlooked the record by Doria 1887), and for the first mentioning two species from the island, *Tadarida teniotis* and *Pipistrellus pipistrellus* [*P. hanaki*]. Kahmann & Çağlar (1960) mentioned occurrence of *Myotis capaccinii* in Crete, however, the detailed data on the record were published later by Kock (1974b). Martens (1967) reported records of five bat species from Crete, including the first record of *Plecotus austriacus* [*P. kolombatovici*].

Pieper (1977) analysed an enormous material of *Tyto alba* pellets from Crete and among almost 1300 individuals of mammalian prey he identified 151 specimens of 11 bat species; by this way he detected *Myotis emarginatus*, *Hypsugo savii*, and *Plecotus auritus* [*P. macrobullaris*] in the island for the first time. The last two bat species have been reported from Crete only recently; von Helversen (in Mitchell-Jones et al. 1999) mapped distribution of *Myotis mystacinus* [*M. aurascens*] in the Akrotiri peninsula and Skiba (2007) recorded a call of *Pipistrellus nathusii* at the Kourna Lake.

In a review of all available bat records from Greece, Hanák et al. (2001) compiled 120 records of 15 bat species from Crete (Table 1), including new records of 11 species. This review documented the first period of gathering of occasional findings rather than of a serious and systematic research of Cretan bat fauna. The review summarised basic knowledge on composition of the fauna but did not give any close look at its biological or taxonomical characteristics.

With the exception of two taxonomic revisions (though obviously based on limited comparative material used) by Iliopoulou-Georgudaki (1979) and Iliopoulou-Georgudaki & Ondrias (1986),

Table 1. Composition of the bat fauna of Crete and the number of records of particular species according to subsequent reviews. In brackets are noted the records known at the time of publishing of the respective review but not included into it; in parentheses are the records published under different taxonomic opinion but here considered to belong under the respective species (see the species chapters for details). The distribution of bats in Crete is in the review by von Helversen (in Mitchell-Jones et al. 1999) expressed by covering of squares 50×50 km; here it is expressed as a relative representation of abundance as follows: + = 1–2 squares covered, ++ = 3–4 squares, +++ = 6–8 squares, ++++ = >8 squares

species	Bate 1905	Pohle 1953	Kahmann 1959	Ondrias 1965	von Helversen 1999	Hanák et al. 2001	present review
<i>Rhinolophus ferrumequinum</i>	1	1	2	4	++	20	87
<i>Rhinolophus hipposideros</i>	1	2	7	7	+++	16	74
<i>Rhinolophus blasii</i>	– [1]	– [1]	1 [+1]	1 [+1]	++	9	41
<i>Myotis blythii</i>	1	1	1	1	+++	13	48
<i>Myotis emarginatus</i>	–	–	–	–	++	5	22
<i>Myotis aurascens</i>	–	–	–	–	(+)	1	11
<i>Myotis capaccinii</i>	–	–	–	1	+	1	20
<i>Eptesicus serotinus</i>	–	1	1	1	++	4	19
<i>Hypsugo savii</i>	–	–	–	–	++	10	45
<i>Pipistrellus hanaki</i>	–	–	(1)	(1)	(+)	(3)	32
<i>Pipistrellus nathusii</i>	–	–	–	–	–	–	2
<i>Pipistrellus kuhlii</i>	–	3	10	4	++++	11	67
<i>Nyctalus leisleri</i>	–	–	–	–	–	–	3
<i>Plecotus macrobullaris</i>	–	–	–	–	(+)	(1)	5
<i>Plecotus kolombatovici</i>	–	–	–	–	(+)	(3)	13
<i>Miniopterus schreibersii</i>	1	2	2	1	+++	6	31
<i>Tadarida teniotis</i>	–	–	3	3	++++	17	102
No. of species	4 [+1]	6 [+1]	9	10	15	15	17

which brought the description of *Rhinolophus ferrumequinum creticus*, the Cretan bat fauna has not been analysed from the phylogenetic point of view. However, individual samples of Cretan origin were included in some recent broad scale revisions of Mediterranean bat taxa, results of which refined the list of Cretan bats and supplemented it with *Plecotus macrobullaris* (Juste et al. 2004), *Plecotus kolombatovici* (Kiefer & von Helversen 2004b), *Myotis aurascens* (Benda & Tsytsulina 2000, Benda & Karataş 2005), and *Pipistrellus hanaki* (Hulva et al. 2007). Concerning the fauna of Crete, all these papers rather raise new questions about its composition and relations than elucidate taxonomic situation of the respective populations in the island. Moreover, some species, like *Myotis capaccinii* or *M. aurascens*, remained documented from the island by a single record only.

With respect to this, we undertaken an intensive research of bats in Crete in 2004–2008 and gathered around 450 new records of all previously known bats and also found one species new for the island. Here, we present a review of all available bat records from Crete as well as some additional data on bat biology from the island. Large part of the records presented here come from the doctoral thesis by Georgiakakis (in prep.). We also included records from the unpublished theses by Georgiakakis (2003) and Galanaki (2006). With this paper we continue the series of summaries of bat fauna of the Eastern Mediterranean already published (Benda & Horáček 1998, Hanák et al. 2001, Benda et al. 2003, 2006, 2007) and emphasise the insular characteristics of the fauna of Crete. We have recently studied also the bat fauna of Cyprus (Benda et al. 2007), i.e. of the island of a similar size and biogeographic relations, so we had a good opportunity to compare the faunas of Crete and Cyprus as well as their characteristics, since the methodical approaches to the study of the two faunas were identical.

MATERIAL AND METHODS

Records

The lists of records (arranged in alphabetical and/or chronological orders) include, for each item, the following information: prefecture name (in spaced types), name of the locality (each record is primarily listed by a name of the nearest settlement or notable physical feature) [in brackets, number of locality as indicated in the map], and/or description of record site, date, number of recorded bats with indication of their sex, age and physiological condition (for details see Abbreviations below). Correctness of place names was verified according to Stamatelatos & Stamatelatou-Vamva (2001). Transliteration of place names to Latin script was made according to the ISO 843:1997 standard. Maps were created using Microsoft Access 2007 and ArcMap v9.2. For the evaluation of seasonal distribution and to demonstrate possible shifts between seasons with different abundance of potential prey in the island conditions, respectively, we divided the records more or less arbitrarily as follows: summer season = 1 April – 31 October, winter season = 1 November – 31 March.

Morphological analysis

For morphological comparisons, we used museum specimens which were examined as described in previous studies (see Benda et al. 2006). The specimens were measured in a standard way with the use of mechanical or optical callipers. Dental dimensions were taken on cingulum margins. The examined museum material is mentioned in the respective species chapters, the lists of comparative materials were published by Benda & Horáček (1995), Benda & Ivanova (2003) and Benda et al. (2004a, b, 2006, 2007). For the evaluated external and cranial measurements see Abbreviations. Statistical analyses were performed using the Statistica 6.0 software. Other methodological details or aspects are described in the chapters concerning taxonomic notes on the respective species.

Genetic analysis

Total genomic DNA from tissue samples (pectoral muscle or wing biopsy) was extracted using DNA Blood and Tissue kit (Qiagen). Partial sequence of control region (comprising part of central conserved domain and second hypervariable domain) was amplified with primers L16517 and HSC (Fumagalli et al. 1996). PCR was performed in 20 µl reactions containing 1× Taq buffer (Promega), 2.5 mM MgCl₂, 200 µM dNTPs, 0.5 µM primers, 1u Taq polymerase (Promega) and ca. 20 ng template DNA. The protocol contained predenaturation step (94 °C, 3 min), then 10 cycles of denaturation (94 °C, 1 min), annealing (68 °C with touchdown 0.5 °C every cycle, 1 min), and extension (72 °C, 1 min), followed by 25 cycles with 63 °C annealing temperature and a final extension step (72 °C, 4 min). The fragments were excised from agarose gels (QIAquick Gel Extraction Kit, Qiagen), sequenced with PCR primers and analyzed in 3130 Genetic Analyzer. Sequences were aligned by ClustalW and cut to the length 303 bp. The genetic relationships were visualized by median-joining method (Bandelt et al. 1999) computed in the program Network 4.2.0 (www.fluxus-engineering.com).

Field recordings and sound analysis

Acoustic recordings were made using a portable ultrasound detector D-1000x (Pettersson Elektronik, Inc.) set on time-expansion mode with a sampling rate of 500 kHz, a pretrigger of 3 seconds and a posttrigger of 2 seconds. All analysed echolocation sequences of *Pipistrellus hanaki* were recorded in free flight under natural conditions at sites where the species was captured by mistnetting. To ensure species identification echolocation call sequences of 14 captured *Pipistrellus hanaki* were recorded during hand release and echolocation calls were analysed. These calls showed the same distribution of end-frequencies as those of foraging bats. However, since the release sequences often showed a predominance of short echolocation calls, these sequences were not furthermore used. Ten echolocation call sequences of *Rhinolophus ferrumequinum* were recorded having the bat in hand and the microphone held in a distance of 1 m to record the resting frequency (unchanged from Doppler-shift compensation).

The recordings were analysed with the software SELENA (© University of Tuebingen, Germany). A 512 pt. FFT with Hamming window was used for analyses. Oscilograms, power spectra and spectrograms were evaluated. For each echolocation call, the following parameters of the call were measured: pulse duration (PDUR), start frequency (SF), end frequency (EF, both SF and EF at –30 dB below the peak power spectral intensity), and inter-pulse interval (IPI, the time between two consecutive calls). Only search phase calls in free flight were measured and only sequences with good recording quality (a dynamic range of more the 30 dB) were selected.

In total, we analysed 25 call sequences (300 calls) of *Pipistrellus hanaki* (in addition 14 release call sequences with 212 calls were analysed and used for comparison but not included in further analyses) and 10 call sequences with 150 calls of *Rhinolophus ferrumequinum*.

ABBREVIATIONS

Collection acronyms

CDIS = Christian Dietz private collection, Horb, Germany; MHNG = Natural History Museum, Geneva, Switzerland; NHMC = Natural History Museum of Crete, Irakleio, Greece; NMP = National Museum (Natural History), Prague, Czech

Republic; NMW = Natural History Museum, Vienna, Austria; SMF = Research Institute and Museum Senckenberg, Frankfurt am Main, Germany; ZFMK = Zoological Institute and Museum Alexander Koenig, Bonn, Germany.

Measurements

EXTERNAL MEASUREMENTS. LC = head and body length; LCd = tail length; LAt = forearm length; LPol = thumb length (without claw); LA = auricle length; LTr = tragus length; LaFE = horseshoe width; G = body weight.

CRANIAL MEASUREMENTS. LCr = greatest length of skull (incl. the praemaxilla in *Rhinolophus*); LCb = condylobasal length; LCc = condylocanine length; LaZ = zygomatic width; LaI = width of interorbital constriction; LaInf = infraorbital width; LaN = neurocranium width; LaM = mastoidal width; ANc = neurocranium height; ACr = skull height; LBT = largest horizontal length of tympanic bulla; I¹I¹ = rostral width between first upper incisors (excl.); CC = rostral width between upper canines (incl.); P⁴P⁴ = rostral width between largest upper premolars (incl.); M³M³ = rostral width between third upper molars (incl.); I¹M³ = length of upper tooth-row between I¹ and M³ (incl.); CM³ = length of upper tooth-row between C and M³ (incl.); M¹M³ = length of upper tooth-row between M¹ and M³ (incl.); CP⁴ = length of upper tooth-row between C and P⁴ (incl.); LMD = condylar length of mandible; ACo = height of coronoid process; I₁M₃ = length of lower tooth-row between I₁ and M₃ (incl.); CM₃ = length of lower tooth-row between C and M₃ (incl.); M₁M₃ = length of lower tooth-row between M₁ and M₃ (incl.); CP₄ = length of lower tooth-row between C and P₄ (incl.).

DENTAL MEASUREMENTS (taken from bats of the *Pipistrellus pipistrellus* group only). LI¹ = mesiodistal length of first upper incisor; LI² = mesiodistal length of second upper incisor; LC¹ = mesiodistal length of upper canine; LaC¹ = palatolabial width of upper canine; LP³ = mesiodistal length of first upper premolar (P³); LP⁴ = mesiodistal length of second upper premolar (P⁴); LaP⁴ = palatolabial width of second upper premolar (P⁴); ACin = height of the mesiopalatal cingular cusp of the second upper premolar (P⁴); LM¹ = mesiodistal length of first upper molar (M¹); LaM¹ = palatolabial width of first upper molar (M¹); LM³ = mesiodistal length of third upper molar (M³); LaM³ = palatolabial width of third upper molar (M³); LI₁ = mesiodistal length of first lower incisor; LI₃ = mesiodistal length of third lower incisor; LC₁ = mesiodistal length of lower canine; LP₃ = mesiodistal length of first lower premolar (P₃).

Other abbreviations

a = adult; A = alcoholic preparation; B = stuffed skin (balg); coll. = collected; det. = detected by a bat-detector; EF = end frequency at -30 dB below the peak power spectral intensity; f = female; F = frozen specimen; G = pregnant; ind. = individual of sex unidentified or indeterminable; IPI = inter-pulse interval; j = juvenile; m = male; M = mean; max., min. = dimension range margins; med = median; net. = netted; obs. = observed; PDUR = pulse duration; rec. = a call recording collected; s = subadult; S = skull; SD = standard deviation; SF = start frequency at -30 dB below the peak power spectral intensity; trap. = trapped.

LIST OF SPECIES

Rhinolophus ferrumequinum (Schreber, 1774)

RECORDS. **Original data:** C h a n i a: Agia, old building [1], 29 April 2008: obs. 1 ind.; - Agia Eirini, above a stream [2], 18 August 2008: net. 1 ma; - Alikampos, Skala cave [3], 30 December 2004: obs. ca. 40 inds., 7 February 2008: obs. ca. 40 inds.; - Anopoli, Porolagos, pine forest [4], 19 September 2002: det. & rec. 3 inds.; - Azogyres, Zoure cave [5], 8 October 2007: obs. 2 inds.; - Champatha, Vennidon cave [6], 11 April 2005: obs. 50 inds., 2 July 2005: net. 2 ma, 1 fa, 1 September 2005: obs. ca. 30 inds., 28 October 2005: obs. 2 inds., 4 April 2007: net. 2 ma, 1 fs, 11 fa, 12 May 2007: net. 29 inds., 21 July 2007: det. & rec. several inds.; - Episkopi, pumping station [7], 3 October 2004: net. 1 m, 1 f, 22 January 2005: obs. 1 ind.; - Fylaki, Psimaki cave [8], 21 September 2006: obs. ca. 50 inds., 21 March 2008: det. & rec. several inds.; - Katholiko monastery (Fig. 12), Agiou Ioanni cave [9], 28 April 2008: net. 1 ma, 27 May 2008: net. 1 ma, det. & rec. 2-3 inds.; - Kolymvari, mine above the village [10], 29 September 2006: obs. 2 inds., 9 October 2006: net. 1 ma, 1 fs (NMP 91119 [S+A], 91120 [A]), 13 July 2008: net. 2 ma; - Koumares, 4 km NE, Panagias Arkoudiotissas cave [11], 28 September 2006: net. 1 ma (NMP 91048 [S+A]); - Krya Vrissi, old house [12], 16 June 2003: obs. 2 inds., 13 April 2004: obs. 3 inds.; - Limni, pond [13] (Fig. 51), 19 August 2008: net. 1 fs; - Myloniana, Koulieri cave [14], 2 May 2005: net. 1 ma, 17 fa, 1 fs, 2 September 2005: obs. ca. 23 inds., 24 July 2007: net. 1 ma, 2 mj, 17 faL, 3 fj; - Nopigeia, gallery [15], 6 November 2008: obs. ca. 80 inds.; - Omalos Plateau, Tzani cave [16], 1 October 2006: net. 2 ma (NMP 91177, 91178 [S+A]), det. 1 ind., 17 August 2008: net. 1 ma, 2 fs; - Perivolias, Mamaloukou cave [17], 3 September 2005: obs. 3 inds.; - Rodopos peninsula, cave [18], 5 February 2008: obs. 1 ind.; - Samaria, old village [19], 6 July 2008: obs. 4 inds.; - Sougia, gypsum mine [20], 14 March 2006: obs. 1 ind.; - Stavros, Lera cave [21], 26 December 2005: net. 3 ma, 1 fa; - Theriso, Sarakinias cave [22], 8 October 2007: obs. a colony of 5 inds. (exam. 4 fa, coll. 2 f; NMP 92294 [S+A], 92295 [A]), net. 2 ma, 5 fa (coll. 1 m; NMP 92296 [S+A]); - Theriso, scrubland (close to Panagia) [23], 4 October 2002: det. & rec. 3 inds.; - Vafes, Kalamato cave [24], 30 December 2004: obs. several inds.; - Vafes, Kryoneridas cave [25], 30 December 2004: obs. 39 inds., 2 January 2005: net. 10 fa, 6 January 2008: obs. & exam. 1 ma, 8 fa, 1 fs, 6 January 2008: obs. 27 inds.; - Voukolies, mine on the way to Sebronas [26], 27 December 2004: obs. 1 ind.; - Vryses Kydonias, Keras

Spiliotissas cave [27], 30 December 2004: obs. ca. 100 inds., 2 January 2005: coll. bones (NHMC FC7722), 21 October 2007: obs. 30 inds. – *I r a k l e i o*: Alithini, Meires cave [28], 11 January 2006: obs. 9 inds., 25 May 2007: obs. several inds.; – Amnisos, Eileithyas cave [29], 4 October 2006: net. 1 ma (NMP 91189 [S+A]), det. several inds.; – Ampelouzou, gorge, mines [30], 19 May 2007: obs. 1 ind., 26 January 2008: obs. 1 ind., 6 April 2008: obs. 4 inds., 17 May 2008: obs. several inds. (exam. 1 fa, coll. 1 mummy; NHMC FC11141); – Ano Asites, Agiou Charalampou gorge [31], 22 May 2008: det. & rec. several inds.; – Ano Asites, Nykteridospilios cave [32], 27 July 2004: net. 3 ma, 6 mj, 3 fa, 4 fs, 3 fj, 6 October 2004: obs. 102 inds., 18 October 2004: net. 8 ma, 2 fa, 6 fs, 5 December 2004: net. 7 ma, 2 fa, 2 fs, 8 February 2005: obs. 14 inds., 28 February 2005: net. 9 ma, 2 fa, 1 fs, 5 April 2005: net. 7 ma, 12 fa, 7 April 2005: obs. 61 inds., 23 April 2005: net. 2 ma, 2 fa, 1 fs, 30 May 2005: net. 16 faG, 3 fa, 3 fs, 14 June 2005: obs. ca. 104 ad.+155 juv. inds., 29 July 2005: net. 5 ma, 19 mj, 7 faL, 1 fa, 3 fs, 21 fj, 1 August 2005: obs. ca. 150 inds., 3 October 2005: obs. 62 inds., 7 October 2005: obs. 100 inds., 20 October 2005: net. 9 ma, 1 fa, 4 fs, 10 December 2005: obs. 75 inds., 8 February 2006: obs. 51 inds., 14 May 2006: obs. ca. 100 inds., 19 August 2006: obs. ca. 200 inds., 31 January 2007: obs. ca. 80 inds.; – Ano Fortetsa, gallery under a school [33], 12 April 2003: obs. ca. 20 inds., 9 May 2003: obs. ca. 10 inds., 20 May 2003: obs. ca. 10 inds., 22 June 2003: obs. 2 inds., 25 November 2003: obs. 3 inds., 27 January 2004: obs. 1 ind., 13 March 2004: obs. 5 inds., 26 May 2004: obs. 8 inds., 10 August 2004: obs. 5 inds., 10 August 2004: net. 2 m, 1 fs; – Astrakoi, gorge [34], 3 June 2008: det. & rec. several inds., 14 August 2008: net. 2 fa; – Damasta, scrubland [35], 5 June 2008: det. & rec. 1 ind.; – Faistos, Geropotamos river [36], 28 February 2008: det. & rec. 1 ind.; – Giouchtas hill, Stravomyti cave [37], 28 August 2007: obs. 5 inds., 16 September 2007: det. & rec. several inds., 30 September 2007: obs. 10 inds., 30 December 2007: obs. ~250 inds., 17 January 2008: obs. 1 ind., 18 May 2008: det. & rec. several inds., 7 June 2008: net. 1 ma, 1 ms, 22 June 2008: det. & rec. several inds.; – Kamaraki, Chainospilios cave [38], 19 November 2006: obs. 2 inds.; – Kamilari, gallery [39], 17 December 2005: obs. 2 inds.; – Kavrochori, Gazanos river [40], 3 July 2008: det. & rec. several inds.; – Laloumas, Koutsoulitis river, under a Venetian bridge [41], 26 August 2007: det. & rec. several inds., 29 May 2008: det. 1 ind., 16 June 2008: det. & rec. several inds.; – Marathos, Arkalospilios cave [42], 22 February 2006: obs. 5 inds.; – Marathos, Doxas cave [43], 14 October 2007: obs. 1 ind.; – Plouti, Gortynas Labyrinth mine [44], 16 January 2005: obs. 1 ind., 24 May 2007: obs. 4 inds.; – Plouti, Mikro Labyrinthaki mine [45] (Fig. 45), 16 January 2005: obs. 4 inds., 7 October 2007: net. 1 ma (NMP 92291 [S+A]), 25 May 2008: obs. 1 ind.; – Rouva forest [46], 4 June 2008: det. & rec. 1 ind.; – Sarchos, Chonos cave [47], 16 January 2005: obs. 32 inds., 21 January 2005: net. 2 ma, 1 ms, 20 May 2005: net. 8 fa, 2 fs, 10 June 2005: obs. several inds., 1 December 2005: net. 9 ma, 4 ms, 3 fs, 21 December 2005: obs. 45 inds., 19 March 2006: obs. 20 inds., 14 May 2006: obs. ca. 110 inds., 14 June 2006: obs. 40 juv. inds., 19 August 2006: obs. ca. 100 inds., 22 August 2006: net. 1 fa, 1 fj, 9 September 2006: net. 1 ma, 13 fa, 17 November 2006: obs. 15 inds., 15 December 2006: obs. 80 inds., 18 March 2007: obs. 6 inds., coll. 12 mummies (NHMC FC10244), 30 June 2007: obs. ca. 65 inds. (ad.+juv.), 27 January 2008: obs. 14 inds. (exam. 10 ma, 1 fs); – Spilia, Agia Eirini chapel, 2 km S of Knossos, above a brook [48], 26 May 2008: det. 1 ind.; – Tylisos, Kamilari cave [49], 16 June 2005: obs. ca. 260 inds. (ad.+juv.), 20 January 2006: obs. ca. 330 inds., 3 February 2006: obs. ca. 150 inds., net. 4 ma, 23 March 2006: net. 4 ma, 2 ms, 2 fa, 7 April 2006: obs. ca. 100 inds., net. 1 ma, 5 fs, 7 fa, 16 May 2006: obs. ca. 20 inds., net. 3 ma, 1 fa, 3 fs, 12 June 2006: net. 1 ma, 1 faG, 12 July 2006: net. 3 ma, 15 mj, 2 faL, 21 fs, 23 September 2006: obs. ca. 50 inds. (exam. 6 ma, 8 fa), 6 November 2006: obs. ca. 220 inds., 16 December 2006: obs. ca. 200 inds., 23 March 2007: net. 14 ma, 4 fa, 8 fs, 4 April 2007: obs. ca. 100 inds., 20 April 2007: net. 5 ma, 2 fa, 3 fs, 28 July 2007: net. 2 ma, 4 mj, 3 fa, 1 fs, 3 fj, 23 October 2007: net. 6 ma, 3 fa, 2 fs, 13 April 2008: net. 2 ma, 6 ms, 3 fa, 5 fs; – Vorizia, olive grove [50], 8 July 2008: det. & rec. 1 ind. – *L a s i t h i*: Agios Georgios, at the Megalo Katofygi cave [51], 5 September 2004: det. & rec. several inds.; – Gra Lygia, Mpramianos river dam [52], 21 May 2003: obs. & coll. 1 faG (NHMC FC4876 [A]; leg. M. Ivović); – Kritsa, Gaidourotrypa cave [53] (Fig. 2), 14 October 2007: obs. & coll. 1 fa (NMP 92319 [S+A]), 31 May 2008: net. 2 ma (NMP 92342, 92343 [S+A]); – Milatos, Milatou cave [54], 2 November 2004: obs. 2 inds. (exam. 1 fa, coll. 1 ms; NHMC FC5868 [F]), 7 October 2006: net. 4 ma, 2 ms, 1 fa, 2 fs (NMP 91101–91103, 91105, 91199, 91200 [S+A]), 91104, 91106, 91107 [A]), 12 August 2007: obs. ca. 20 inds., 27 December 2007: obs. 83 inds. (exam. 5 m, 4 fa, 1 fs); – Pefkoi, Vreiko cave [55], 23 November 2007: obs. 5 inds. (exam. 2 fa); – Vrahasi, Peristeras cave [56], 13 January 2002: obs. 2 inds. – *R e t h y m n o*: Agios Ioannis, Platis river [57], 26 May 2007: det. & rec. several inds.; – Archaia Eleftherna, Aravanes oak forest [58] (Figs. 3, 22), 12 August 2008: trap. 2 ma, 1 fa; – Doxaro, Mougri cave [59], 24 January 2003: obs. 2 inds., 11 November 2004: net. 2 ma, 9 ms, 1 fs, 18 January 2006: obs. ca. 30 inds., 7 June 2006: obs. 5 inds., 9 November 2007: obs. ca. 40 inds.; – Erfoi, cave [60], 3 April 2005: obs. ca. 220 inds., 17 May 2006: obs. 5 inds., 28 December 2006: obs. ca. 280 inds., 29 February 2008: net. 10 ma, 1 ms; – Gallos river gorge, old watermill [61], 24 April 2008: obs. ca. 30 inds., 12 June 2008: obs. ca. 35 inds.; – Gerani, Geraniou cave [62], 6 October 2006: net. 1 ma (NMP 91195 [S+A]), 8 October 2007: obs. & coll. 1 fa (NMP 92293 [S+A]); – Lefkogeia, at a Venetian bridge ca. 3 km E of the Kato Preveli Monastery [63], 30 May 2008: net. 1 faG (NMP 92332 [S+A]), det. & rec. 1 ind.; – Melidoni, Gerontospilios cave [64], 23 February 2006: obs. 15 inds.; – Monastiraki, Genianos stream [65], 2 June 2008: net. 1 faG, det. & rec. 4 inds.; – Myloi, abandoned village [66], 12 June 2008: obs. ca. 20 inds.; – Patsos, Agiou Antoniou cave [67], 3 October 2006: net. 1 fs (NMP 91188 [S+A]); – Prinos, Prinou cave [68], 21 May 2005: det. & rec. several inds., 1 March 2006: obs. several inds., 18 November 2006: det. & rec. several inds., 11 October 2007: net. 11 ma, 11 fs, 19 June 2008: net. 6 ma, 2 faL; – Rou-

meli, Geropotamos river [69], 16 April 2006: obs. 3 inds., 15 February 2008: det. & rec. 1 ind., 26 June 2008: det. & rec. several inds.; – Roumeli, Geropotamos river, watermill [70], 5 July 2006: obs. ca. 500 inds. (ad.+juv.), 21 September 2006: obs. ca. 25 inds.; – Siripidiana, olive grove [71], 22 February 2008: det. & rec. 1 ind.; – Zoniana, Sfentoni cave [72], 12 August 2008: obs. & exam. 1 m. – **Published data:** C h a n i a: Agia Triada [= Agias Triadas] monastery [73], 15 August 1971: 1 f (Hanák et al. 2001); – Azogyres bei Paläochora [= Palaiochora], cave [= Zoure cave] [5], 13 March 1965: 3 inds. (Martens 1967); – Haniá [= Chania] [74], Summer 1971: 1 fa (Hanák et al. 2001); – Limni Kourna [= Mouri, Kourna lake] [75], 2 May 2003: det. 1 ind. (Skiba 2007); – Katholiko monastery, caves [9], 13 March 1965: 6 inds. (Martens 1967); Moni Katholiko – Agios St. Ioannis [= Katholiko monastery, Agiou Ioanni cave], 4 May 2003: det. 2 inds. (Skiba 2007); – Mt. Goría Monastery [= Kolymvari, Gonias monastery] [76], 1 m, 2 f (Miller 1912, Theodor 1967); NW coast, cave close to the sea, March 1904: 3 inds. (Bate 1905); – Paläochora [= Palaiochora], mine [77], 13 March 1965: 1 ind. juv. (mummy) (Martens 1967); – Topolia, cave Aghia Sophia [= Agias Sofias cave] [78], 16–17 March 1965: 2 inds. (Martens 1967); – Topolia [79], 1973–1975: 14 inds. (from owl pellets) (Pieper 1977); – Vafes, Kalamatu [= Kalamato] cave [24], 15 January 1968 (Beron 1970). – I r a k l e i o: Ag. [= Agio] Pnevma [80], 1973–1975: 1 ind. (from owl pellets) (Pieper 1977); – Amoudara, small cave [= Linoperamata, at the Almyros river spring, small cave] [81], 8 July 1995: obs. 1 ind. (Hanák et al. 2001); – spilaion Lavrinthou, resp. cave ‘Labyrinth’ [= Plouti, Gortynas Labyrinth mine] [44], 3 inds. (Iliopoulou-Georgudaki 1977), 8 August 1973: 2 m, 1 f (Iliopoulou-Georgudaki 1979, Iliopoulou-Georgudaki & Ondrias 1986); Gortis, labyrinth [= Plouti, Gortynas Labyrinth mine], 1 ind. (Hanák et al. 2001); – Sarchos [82], 1973–1975: 10 inds. (from owl pellets) (Pieper 1977). – L a s i t h i: spilaion Milatou, resp. cave ‘Milatos’ [= Milatou cave] [54],



Fig. 2. The Gaidourotrypa cave near Kritsa, eastern Crete. A roost of *Rhinolophus ferrumequinum* and *R. hipposideros*, foraging site of *Myotis blythii*, *Hypsugo savii*, *Pipistrellus kuhlii*, and *Tadarida teniotis* (photo by Z. Bendová).



Fig. 3. Typical aspect of a Cretan mountain habitat in the Aravanes oak forest near Archaia Eleftherna. The vegetation on the ground is heavily grazed. Foraging habitat of *Rhinolophus ferrumequinum*, *Pipistrellus hanaki* and *Hypsugo savii* (photo by C. Dietz).

1 ind., resp. 1 f (Iliopoulou Georgudaki 1977, Iliopoulou-Georgudaki & Ondrias 1986); Milatos Spilia [= Milatos, Milatou cave], 28 April 2004: det. 15–20 inds. (Skiba 2007); – Megalo Katafygi, 14–15 km SW Sitia [51], osteological remnants (Boettger 1962, 1963, Martens 1967); – Piskokefalo, cave [83], 22 March 1958: 1 f (Kahmann 1959); – Sitia [84], 1 ind. (Felten et al. 1977); – Starochori [= Stavrochori] [85], 12 inds., resp. 5 m, 7 f, 1 juv. (Iliopoulou-Georgudaki 1977, Iliopoulou-Georgudaki & Ondrias 1986). – R e t h y m n o: Gerani, rocky canyon [86], 16 July 1995: det. 1 ind. (Hanák et al. 2001); – Melidoni Andro [= Melidoni, Gerontospilios cave] [65], 30 April 2003: det. 40–50 inds. (Skiba 2007); – Rethimnon, resp. Rethymnon [= Rethymno] [87], 20 April 1975: 1 ind. (Felten et al. 1977, Kock 1989).

COMMENTS. *Rhinolophus ferrumequinum* is the most common bat species in continental Greece, Bulgaria and Turkey (Benda & Horáček 1998, Hanák et al. 2001, Benda et al. 2003) and similarly, it is one of the most common bats in Crete. Since at least 87 record sites are currently known from the island (Fig. 4), the species represents the second most frequently recorded bat in Crete after *Tadarida teniotis* (Table 1). The occurrence of *R. ferrumequinum* was evidenced in all parts of the island, in altitudes from the sea level up to medium elevated areas exceeding even 1000 m a. s. l. Although *R. ferrumequinum* inhabits a wide range of sites of Crete in the summer season, it prefers rather lower altitudes (median 200.0 m, n=61). In the winter period it occurs in slightly more elevated sites (median 234.0 m, n=34), though the total range of the known winter sites lies lower than that of the summer sites, between 5–548 m a. s. l. only (Table 2).

Majority of the records of *R. ferrumequinum* in Crete are associated with underground spaces (50 sites, i.e. 57.5%), both natural caves (40) and mines (10), they include both findings of bats in their roosts and nettings/recordings of emerging and/or swarming individuals. However, eight record sites (9.2%) are represented by overground man-made shelters (most often old houses). Altogether 22 records (25.3%) refer to foraging bats, either recorded by an ultrasound detector

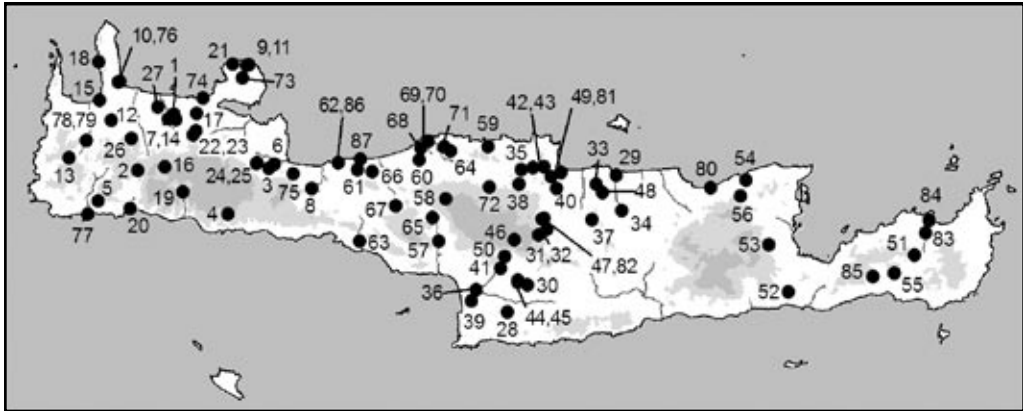


Fig. 4. Records of *Rhinolophus ferrumequinum* (Schreber, 1774) in Crete.

and/or netted in the areas not directly related to their roosts. Pieper (1977) reported findings of this bat in owl pellets from three sites in Crete (3.4%).

In eight cases we recorded aggregations of *R. ferrumequinum* representing nursery colonies (both directly observed and indirectly assumed), four of them were situated in natural caves (composed of 20–250 inds.), one in a mine (Ano Fortetsa, around 10 inds.; however, this record is rather related to a transient aggregation), and three in abandoned buildings (20–500 inds.). Winter aggregations of bats were recorded solely in natural caves (at least in 13 cases, besides the records of wintering solitaries), they were composed of up to 330 individuals (on average 85 inds.). However, no true hibernants were found in the Nykteridospilios cave at Ano Asites studied comprehensively by Galanaki (2006), or elsewhere in the island.

R. ferrumequinum is the most widespread bat in Greece (Hanák et al. 2001), it was recorded in all geographical parts of the country, including northern and southern mainland regions and many islands; Hanák et al. (2001) reviewed records from Thasos, Lesbos, Skyros, Euboea, Siros, Paros, Kos, Rhodes, Crete and Corfu. Von Helversen (in Mitchell-Jones et al. 1999) mentioned an additional unspecified record from northern Cyclades (Andros/Tinos). Mitchell-Jones et al. (1999) showed this bat to be widely distributed in the European Mediterranean and sub-Mediterranean, including numerous islands (Mallorca, Menorca, Corsica, Elba, Sardinian archipelago, Sicily, Malta, many Dalmatian islands). In Cyprus, *R. ferrumequinum* was found to be the fourth most common bat (Benda et al. 2007), though occurring in rather more elevated areas than in Crete.

TAXONOMY. Miller (1912) was the first to evaluate Cretan samples of *R. ferrumequinum* and attributed them to the nominotypical form. Ondrias (1965) assigned all then Greek records including the Cretan ones to this form too. Felten et al. (1977) included one specimen from Crete in their analysis of Mediterranean populations and made the same conclusion as the previous authors.

Iliopoulou-Georgudaki & Ondrias (1986) compared a sample of 17 specimens from Crete to literature data and their own samples from mainland Greece; on the basis of differences in nine cranial and external dimensions as well as in pelage coloration – Cretan samples were found to be relatively small and pale – they described a separate subspecies, *R. ferrumequinum creticum* (type locality: Cave “Milatos” [= Milatou cave], Lasithi, Crete). Since the authors did not specify the name *creticum* as a noun, its form should be corrected to *creticus* according to the generic name

Table 2. Altitudinal distribution of particular bat species in Crete; for the definition of seasons see Methods, for abbreviations see p. 110

	all records					summer records					winter records				
	n	min	max	M	med	n	min	max	M	med	n	min	max	M	med
all sites	229	0	1650	349.0	223.0										
<i>Rhinolophus ferrumequinum</i>	85	5	1025	262.1	210.0	61	5	1025	285.3	200.0	34	5	548	235.7	234.0
<i>Rhinolophus hipposideros</i>	69	10	1510	348.4	260.0	48	21	1464	365.6	260.0	27	10	1510	322.6	277.0
<i>Rhinolophus blasii</i>	40	10	1500	315.7	237.5	28	10	1500	376.8	312.5	16	10	480	194.6	193.5
<i>Myotis blythii</i>	48	0	1650	423.5	262.5	37	0	1650	465.2	260.0	5	30	1650	1009.0	1450.0
<i>Myotis emarginatus</i>	22	5	600	213.9	204.5	18	5	600	200.6	150.0	—	—	—	—	—
<i>Myotis aurascens</i>	11	5	1464	342.2	96.0	10	5	1464	366.8	115.0	—	—	—	—	—
<i>Myotis capaccinii</i>	20	2	1025	159.4	93.0	20	2	1025	159.4	93.0	2	116	260	188.0	188.0
<i>Eptesicus serotinus</i>	18	10	1490	362.9	207.5	13	30	1490	454.2	206.0	—	—	—	—	—
<i>Hypsugo savii</i>	45	0	1490	414.1	250.0	41	0	1490	416.1	260.0	2	233	860	546.5	546.5
<i>Pipistrellus hanaki</i>	32	2	1025	380.2	356.5	28	2	1025	370.5	333.5	6	26	940	453.2	356.5
<i>Pipistrellus nathusii</i>	2	2	65	52.5	52.5	—	—	—	—	—	—	—	—	—	—
<i>Pipistrellus kuhlii</i>	57	3	815	176.0	80.0	51	5	815	166.1	70.0	4	3	490	282.0	317.5
<i>Nyctalus leisleri</i>	3	240	600	381.7	305.0	—	—	—	—	—	—	—	—	—	—
<i>Plecotus macrobullaris</i>	5	265	1490	925.8	1025.0	—	—	—	—	—	—	—	—	—	—
<i>Plecotus kolombatovici</i>	13	15	1490	478.8	396.0	10	15	1490	515.0	440.5	2	350	480	415.0	415.0
<i>Mintopterus schreibersii</i>	30	5	1025	275.5	221.5	24	10	1025	272.2	205.0	8	116	782	341.5	268.5
<i>Tadarida teniotis</i>	100	0	1600	425.5	333.5	79	0	1600	455.6	400.0	19	5	1450	319.6	140.0

Table 3. Basic biometric data [in mm] on examined Cretan and comparative samples of *Rhinolophus ferrumequinum* (Schreber, 1774); for abbreviations see p. 110

	n	Crete				n	Cyprus				n	Balkans			
		M	min	max	SD		M	min	max	SD		M	min	max	SD
LC	26	68.5	38	74	6.647	11	65.6	60	70	4.251	95	65.7	55	73	3.613
LCd	26	42.0	35	48	3.156	10	36.9	33	41	2.601	95	38.6	27	49	3.278
LAt	26	55.92	54.3	58.8	1.374	15	55.81	53.0	58.0	1.462	99	57.69	54.8	62.0	1.435
LA	26	26.20	25.30	27.60	0.656	11	23.39	21.5	25.8	1.499	94	23.48	19.0	26.0	1.159
LCr	21	23.40	22.83	23.88	0.264	8	24.12	23.58	24.65	0.364	74	23.79	22.70	24.82	0.406
LCc	21	20.46	20.04	20.86	0.232	9	20.86	20.46	21.12	0.219	104	20.69	19.88	21.76	0.340
LaZ	21	12.18	11.64	12.84	0.263	9	12.38	12.12	12.71	0.182	105	12.11	11.27	12.86	0.299
LaI	21	2.43	2.24	2.88	0.184	9	2.39	2.08	2.68	0.179	109	2.52	2.09	3.04	0.185
LaN	21	9.33	9.15	9.61	0.134	9	9.50	9.18	9.73	0.167	106	9.42	8.05	10.18	0.248
ANc	21	6.92	6.39	7.58	0.254	9	7.22	6.90	7.52	0.186	104	6.91	6.19	7.43	0.258
CC	21	6.59	6.34	6.86	0.141	9	6.83	6.63	7.08	0.145	107	6.58	5.89	7.22	0.208
M ³ M ³	21	8.61	8.44	8.88	0.115	9	8.68	8.47	9.02	0.178	108	8.64	7.95	9.07	0.209
CM ³	21	8.58	8.42	8.75	0.093	9	8.82	8.54	9.09	0.190	109	8.63	6.63	9.08	0.251
LMd	21	15.57	15.13	16.13	0.254	9	16.01	15.75	16.48	0.263	109	15.72	14.94	16.48	0.301
ACo	21	4.00	3.76	4.18	0.113	9	4.08	3.76	4.28	0.146	109	3.98	3.43	4.40	0.169
CM ₃	21	9.27	9.04	9.43	0.120	9	9.48	8.92	9.78	0.266	109	9.28	8.72	9.73	0.193

gender (ICZN 1999: Art. 31.2; see Koopman 1994, Ransome in Mitchell-Jones et al. 1999, Hanák et al. 2001). However, the name was used for the first time (as a nomen nudum and in its erroneous form) already by Iliopoulou-Georgudaki (1979). The valid endemic status of the Cretan subspecies *R. f. creticus* was mostly accepted by subsequent authors; see Koopman (1994), Ransome (in Mitchell-Jones et al. 1999), Gaisler (2001a), Csorba et al. (2003) and Simmons (2005).

Table 4. Results of statistic comparison (ANOVA) of Cretan set of *Rhinolophus ferrumequinum* (Schreber, 1774) samples with comparative sets; for abbreviations see p. 110

	Crete vs. Balkans			Crete vs. Cyprus		
	df	F	p	df	F	p
LC	119	8.384	*	35	1.838	
LCd	119	21.394	**	34	20.302	**
LAt	123	31.945	**	39	0.050	
LA	118	130.670	***	35	64.246	***
LCr	93	17.307	**	27	34.698	**
LCc	123	9.000	**	28	19.684	**
LaZ	124	0.986		28	4.287	*
LaI	128	3.765		28	0.281	
LaN	125	2.371		28	8.547	*
ANc	123	0.036		28	10.444	*
CC	126	0.050		28	18.596	**
M ³ M ³	127	0.504		28	2.025	
CM ³	128	0.680		28	21.119	**
LMd	128	4.872	*	28	18.806	**
ACo	128	0.244		28	2.399	
CM ₃	128	0.050		28	9.769	*

Describing the new subspecies, Iliopoulou-Georgudaki & Ondrias (1986) compared their samples from Crete properly only with bats from mainland Greece, i.e. population then considered a separate subspecies, *R. f. martinoi* Petrov, 1941. The subspecific status of the latter form was however convincingly doubted by Kryštufek (1993) and de Paz (1995), who found the larger individuals of the Balkan populations to be inhabitants of climatically rather extreme conditions and their dimensional differences from the nominotypical form of western and central Europe running along a cline. Moreover, de Paz (1995) included a sample of *R. ferrumequinum* from Crete into his analysis of West Palaearctic populations; although he did not make any suggestion concerning the position of Cretan bats, his results clearly placed them among other European samples and doubted their peculiar position. Hence, Hanák et al. (2001) considered the separate position of *R. f. creticus* an open question as the proposed diagnostic specificities of the Cretan form were not sufficiently supported by large scale comparisons with representatives of surrounding populations. A similar opinion was also mentioned by Dietz et al. (2007).

Since the subspecies *creticus* was defined clearly on biometric traits (Iliopoulou-Georgudaki & Ondrias 1986), we compared basic metric characters of the newly collected specimens from Crete (see Records above) with samples from southern and central Europe, Asia Minor, Cyprus and northwestern Africa, i.e. representatives of the nominotypical form sensu Kryštufek (1993), Koopman (1994), Ransome (in Mitchell-Jones et al. 1999), Csorba et al. (2003), Simmons (2005) and Benda et al. (2006), to test justification of the separate position of Cretan populations in situation when the form *martinoi* is generally not accepted any more. However, the comparison of external and cranial measurements (Tables 3, 4, Figs. 5, 6) showed the Cretan bats to be a part of Mediterranean and sub-Mediterranean European populations of *R. ferrumequinum*, comparable

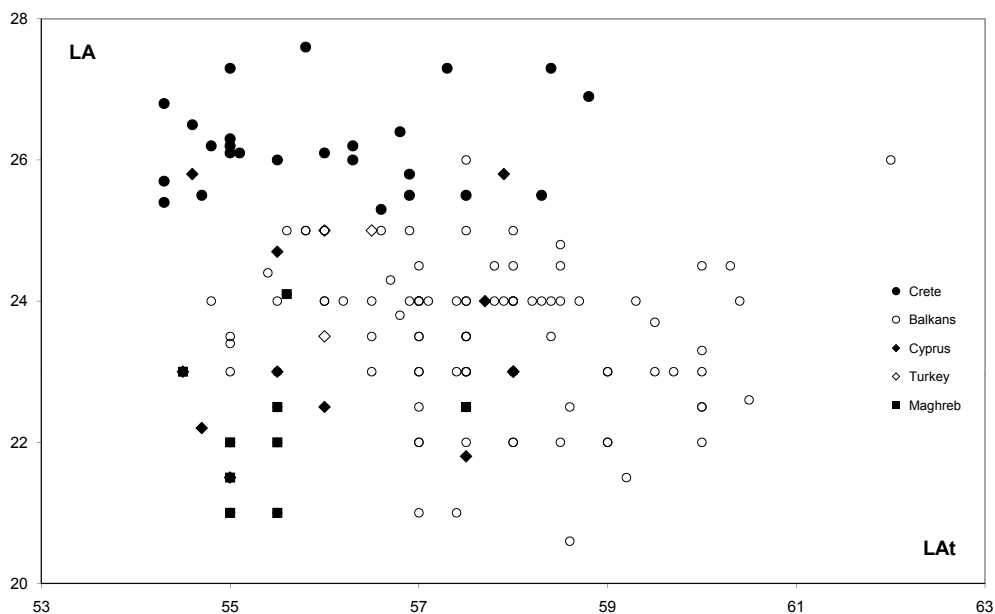


Fig. 5. Bivariate plot of examined Cretan and comparative samples of *Rhinolophus ferrumequinum* (Schreber, 1774): forearm length (LA) against the ear length (LA).

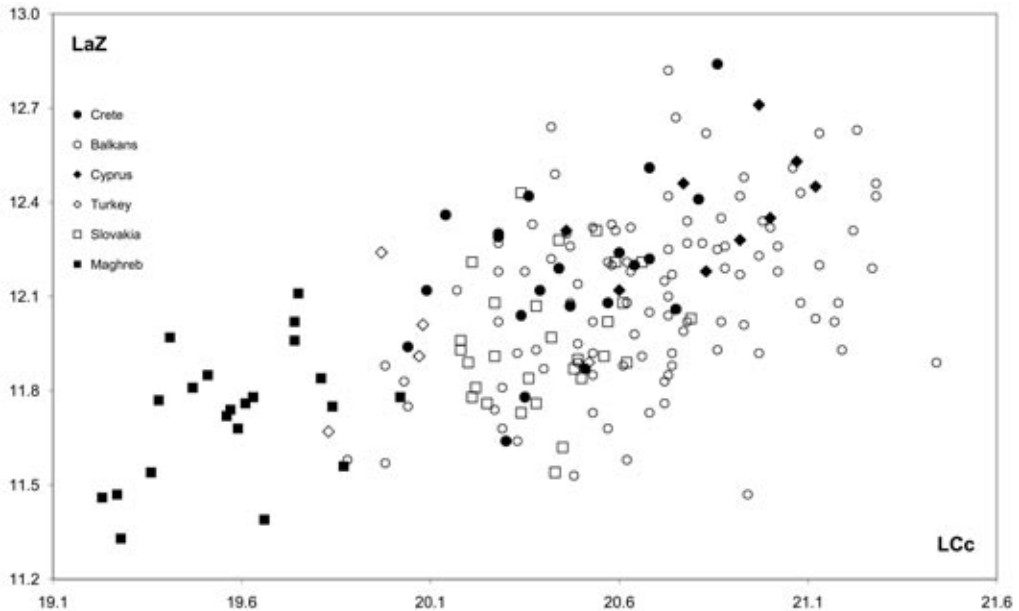


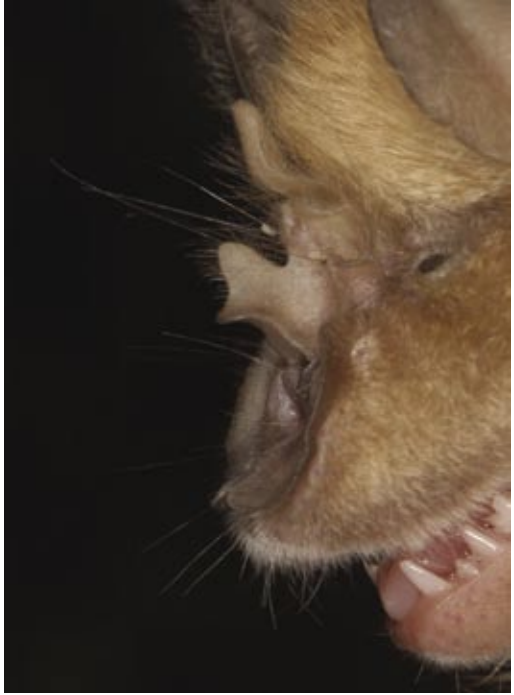
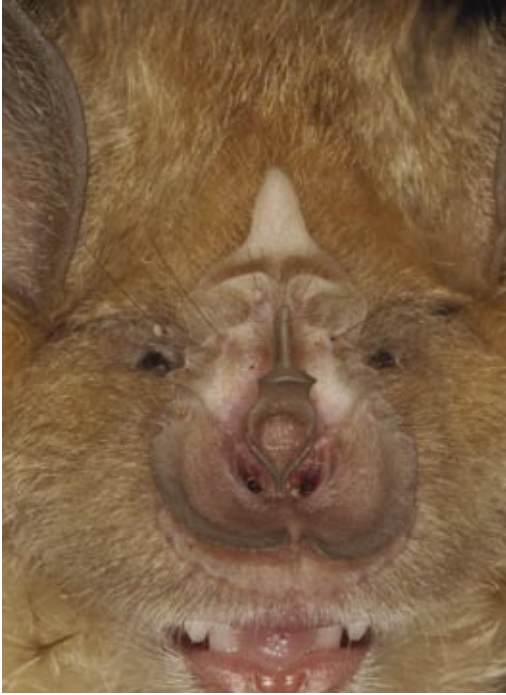
Fig. 6. Bivariate plot of examined Cretan and comparative samples of *Rhinolophus ferrumequinum* (Schreber, 1774): condyloacanine length of skull (LCc) against zygomatic width of skull (LaZ).

in dimensions also to those from Cyprus and the Mediterranean Levant (see also the data by Benda et al. 2006).

Iliopoulou-Georgudaki & Ondrias (1986) presented a significant difference between mainland Greek and Cretan samples in the forearm length; our comparison showed Cretan individuals to be very similar in this dimension to other compared samples (Fig. 5). Although the Balkan and Cretan sample sets on average differed from each other in this and other external dimensions and the ANOVA test indicated significant differences between the samples, the mensural ranges of these dimensions largely overlap. The Cypriot samples agree in their forearm lengths with those of the Cretan bats, the statistic test did not show any level of significance (Table 4). On the other hand, though the Cretan samples more or less conform in their forearm lengths to all other compared samples from the Mediterranean, they differ clearly from all other bats in their ear length; the range of this dimension almost does not overlap with those of other samples (Fig. 5). Since this dimension was taken by one author (PB) in most of the samples (complete Cretan, Cypriot and Maghrebian sample sets, and part of the Balkan set), this difference cannot be explained by a difference in the sizing technics.

Furthermore the CF-frequency of the echolocation calls of Cretan *R. ferrumequinum* recorded in handheld position (resting frequency unchanged from Doppler-Shift compensation) were by their mean at 81.4 kHz and thus similar or only moderately higher than those from mainland Greece (77–81 kHz; Heller & von Helversen 1989) and Bulgaria (78–82 kHz; own data).

Figs. 7–10. Nose-leaves of the Cretan horseshoe bats (all photos by C. Dietz). 7, 8 (above) – *Rhinolophus ferrumequinum* (Schreber, 1774). 9, 10 (below) – *Rhinolophus hipposideros* (Borkhausen, 1797). 7, 9 (right) – antero-dorsal views. 8, 10 (left) – semi-lateral views.



In skull dimensions the Cretan bats clearly conform to other bats from the European and Asian Mediterranean and sub-Mediterranean (Table 3). The Cretan samples completely overlap in their dimensional ranges with available population samples from Greece, Bulgaria, Slovakia, Turkey and Cyprus, which together form a common cluster, quite distinct from the cluster of small Maghrebian bats (Fig. 6). However, bats from the Maghreb are considered to belong to the same taxon as the European continental populations (Koopman 1994, Gaisler 2001a, Csorba et al. 2003).

In conclusion, the comparison of dimensions and echolocation call parameters of a larger set of specimens of *R. ferrumequinum*, coming from a broader area of the Mediterranean Basin, places the Cretan representatives into a group of other samples from the European and Asian Mediterranean arboreal zone (incl. central Europe). The ear length is the only dimension, in which Cretan specimens were found to be relatively and absolutely distinct from other compared populations of the north-Mediterranean bats, a difference not being reflected in differences of basic echolocation call parameters. Otherwise the Cretan population was not evidenced to be exclusive in other dimensions. Hence, this finding does not support the assignment of the Cretan *R. ferrumequinum* population to a separate subspecies suggested by Iliopoulou-Georgudaki & Ondrias (1986). Such a conclusion is favoured also by preliminary results of genetic analyses (Kûs 2007, Benda et al. in press, Georgiakakis unpubl. data). Therefore, we consider the Cretan populations of *R. ferrumequinum* to represent a part of the European populations of the nominotypical form and the name *Rhinolophus ferrumequinum creticum* Iliopoulou-Georgudaki et Ondrias, 1986 a mere synonym of *Vespertilio ferrumequinum* Schreber, 1774 (= *Rhinolophus ferrumequinum ferrumequinum*).

***Rhinolophus hipposideros* (Borkhausen, 1797)**

RECORDS. Original data: C h a n i a: Agia Eirini, gorge [1], 24 April 2008: obs. 1 ind.; – Alikampos, Skala cave [2], 30 December 2004: obs. 3 inds., 7 February 2008: obs. 6 inds.; – Champatha, Vennidon cave [3], 23 January 2005: obs. 2 inds., 11 April 2005: obs. 3 inds., 28 October 2005: obs. 1 ind., 21 July 2007: det. & rec. several inds.; – Fylaki, Psi-maki cave [4], 21 September 2006: obs. 5 inds.; – Kandanos, chapel [5], 3 November 2008: obs. 3 inds.; – Kastelos, cave [6], 20 February 2006: obs. 1 ind.; – Katholiko monastery, Achyrosopilios cave [7], 28 April 2008: obs. & exam. 1 fa; – Krya Vrisi, old house [8], 16 June 2003: obs. 3 inds., 13 April 2004: obs. 2 inds.; – Mouselas river, Argyroupoli, old building [9], 17 August 2008: obs. 3 inds. (exam. 1 fa); – Myloniana, Koulieri cave [10], 2 May 2005: net. 1 fa, 24 July 2007: net. 1 ma, 3 faL; – Perivolia, Mamaloukou cave [11], 26 December 2004: obs. 1 ind., 2 May 2008: obs. & exam. 1 m; – Samaria, Agios Georgios chapel [12], 4 June 2005: obs. ca. 100 inds., 5 July 2008: obs. ca. 20 ad.+3 juv. inds. (exam. 1 ma, 2 ms, 1 faG, 5 faL, 1 fa, 1 fs); – Samaria, old village [13], 6 July 2008: obs. 1 ind.; – Sfinari, Neraidospilia cave [14], 5 November 2006: obs. 1 ind.; – Sougia, gypsum mine [15], 23 March 2008: obs. & exam. 1 m, 2 fa; – Theriso, cave [16], 23 January 2005: obs. 1 ind.; – Theriso, Sarakinas cave [17], 8 October 2007: net. 2 ma, 7 fa (coll. 2 m, 2 f, NMP 92297–92300 [S+A]); – Vafes, Kalamato cave [18], 30 December 2004: obs. several inds.; – Vafes, Kryoneridas cave [19], 30 December 2004: obs. 6 inds., 2 January 2005: net. 4 fa, 6 January 2008: obs. 15 inds. (exam. 10 ma, 1 fs); – Voukolies, mine at the way to Sebronas [20], 27 December 2004: obs. 1 ind.; – Zourva, cypress forest [21], 26 October 2002: det. & rec. 2 inds. – I r a k l e i o: Alithini, at the Meires cave [22], 25 May 2007: det. & rec. several inds.; – Ano Asites, Nykteridospilios cave [23], 3 November 2004: obs. 7 inds., 3 December 2004: obs. 5 inds., 5 December 2004: net. 1 m, 22 February 2005: obs. 9 inds., 28 February 2005: net. 1 ma, 5 April 2005: net. 2 ma, 1 fa, 7 April 2005: obs. 3 inds., 8 June 2005: obs. 1 ind., 29 July 2005: net. 2 ma, 1 faL, 1 fj, 23 September 2005: obs. 6 inds., 7 October 2005: obs. 8 inds., 20 October 2005: net. 1 ma, 10 December 2005: obs. 5 inds., 19 August 2006: obs. 2 inds., 31 January 2007: obs. 3 inds.; – Astrakoi, gorge [24], 3 June 2008: det. & rec. several inds.; – Avdou, Agias Foteinis cave [25], 10 October 2007: net. 1 ma (NMP 92303 [A]), obs. & det. 5 inds.; – Giouchtas hill, Stravomyti cave [26], 16 September 2007: det. & rec. few inds., 18 May 2008: det. & rec. several inds.; – Gonies, Tsakalou pothole [27], 25 March 2006: obs. 3 inds.; – Kamaraki, Chainospilios cave [28], 16 December 2005: obs. 6 inds., 19 November 2006: obs. 5 inds., 9 October 2006: obs. several inds., 10 August 2007: net. 1 fa, 17 January 2008: obs. 11 inds., 5 June 2008: obs. 1 ind.; – Keri hill, at a pothole [29], 10 September 2006: det. & rec. 2 inds.; – Laloumas, Koutsoulitis river [30], 26 August 2007: det. & rec. several inds., 3 December 2007: det. & rec. several inds., 16 June 2008: det. & rec. several inds.; – Laloumas, village [31], 29 May 2008: obs. 4 inds. (exam. 1 faL, 1 juv.), 16 June 2008: obs. 3 ad.+1 juv. inds. (exam. 1 ma, 1 faG); – Laloumas, Koutsoulitis river, small concrete building at a Venetian bridge [32], 29 May 2008: obs. 2 inds. (ad.+juv.); – Marathos, Doxas cave

[33], 14 October 2007: obs. torpid 1 ind.; – Plouti, at the Gortynas Labyrinth mine [34], 16 January 2005: obs. 5 inds., 24 May 2007: det. & rec. 3 inds.; – Plouti, Mikro Labyrinthaki mine [35] (Fig. 45), 7 October 2007: obs. & coll. 1 ms (NMP 92290 [A]); – Sarchos, Chonos cave [36], 16 January 2005: obs. 5 inds., 20 May 2005: net. 1 ma, 10 June 2005: obs. several inds., 26 November 2005: obs. several inds., 1 December 2005: net. 2 ma, 1 ms, 1 fa, 21 December 2005: det. & rec. several inds., 19 March 2006: obs. 2 inds., 22 August 2006: net. 2 m, 9 September 2006: net. 2 fa, 15 December 2006: obs. 4 inds., 18 March 2007: obs. 4 inds., 27 January 2008: net. 4 ma, 14 February 2008: det. & rec. several inds.; – Tylisos, close to the Kamilari cave [37], 13 April 2007: det. & rec. 1 ind.; – Tylisos, Kamilari cave [38], 3 February 2006: det. & rec. several inds., 23 March 2006: det. & rec. 2 inds., 7 April 2006: obs. 1 ind., 9 April 2008: det. & rec. several inds.; – Venerato, Agios Fanourios chapel, at a creek [39], 9 June 2008: det. & rec. 1 ind.; – Vorizia, olive grove [40], 21 February 2008: det. & rec. 1 ind., 8 July 2008: det. & rec. 1 ind. – L a s i t h i: Kritsa, Gaidourotrypa cave [41] (Fig. 2), 14 October 2007: obs. & coll. 1 ma (NMP 92320 [S+A]), 31 May 2008: obs., det. & rec. 2 inds.; – Lithines, Agiou Antoniou cave [42], 14 August 2004: obs. 1 ind.; – Milatos, Milatou cave [43], 7 October 2006: net. 1 ms, 1 fa (NMP 91197, 91198 [S+A]), 27 December 2007: obs. 3 inds. (exam. 2 m); – Riza, Krygiospilios cave [44], 6 February 2000: coll. 1 ind. (NHMC FC4892 [bones]); – Sitanos, Exo Latsidi cave [45], 13 October 2007: net. 1 ma (NMP 92317 [S+A]), obs. 4–5 flying inds. – R e t h y m n o: Agios Yakinthos (Idi Mts.), Agiou Yakinthou chapel [46], 15 June 2008: obs. 1 ind.; – Agridia, at a cave [47], 27 May 2008: det. & rec. 5 inds.; – Archaia Eleftherna, Aravanis oak forest [48] (Fig. 3, 22), 9 October 2002: det. & rec. 1 ind.; – Doxaro, Mougri cave [49], 18 January 2006: obs. 1 ind.; – Erfoi, cave [50], 3 April 2005: obs. 14 inds., 28 December 2006: obs. 5 inds.; – Fourfouras, water reservoir [51], 3 November 2007: obs. 2 inds.; – Gerani, Geraniou cave [52], 6 October 2006: obs. & coll. 1 ms, 1 fs (NMP 91193, 91194 [S+A]), 8 October 2007: obs. & coll. 1 ms (NMP 92292 [A]); – Lefkogeia, at a Venetian bridge ca. 3 km E of the Kato Preveli Monastery [53], 30 May 2008: det. & rec. 1 ind.; – Melidoni, Gerontospilios cave [54], 23 February 2006: obs. 3 inds.; – Myloi, abandoned village [55], 12 June 2008: det. & rec. several inds.; – Petradolakia (Idi Mts.), scrubland [56], 3 June 2007: det. & rec. several inds.; – Prinos, Prinou cave [57], 21 May 2005: det. & rec. 3 inds., 1 March 2006: obs. 1 ind., 18 November 2006: det. & rec. 1 ind., 11 October 2007: net. 1 fa, 19 June 2008: net. 2 fa; – Rethymno, pine grove, mine [58], 30 November 2005: obs. 2 inds.; – Rizikas, old village [59], 24 August 2007: obs. 3 inds.; – Roumeli, Geropotamos river [60], 18 April 2007: det. & rec. 1 ind.; – Zoniana, at the Sfentoni cave [61], 23 June 2008: det. & rec. 1 ind. – **Published data:** road between Agya [= Agia] and Kirtomado [= Kyrtomados], cellar of a ruined house [62], 23 April 1958: 1 f (Kahmann 1959); – Azogyres bei Paläochora [= Palaiochora], cave [= Zoure cave] [63], 13 March 1965: 1 ind. (Martens 1967); – hills south of Khania [= Chania], cave [64], March 1904: 1 ind. (Bate 1905); – Katholiko monastery, caves [65], 13 March 1965: 2 inds. (Martens 1967); – Mouri (Kourmass [= Kourna]) [66], chapel, 14 April 1958: 1 f (Kahmann 1959); – Omalos-Katavothron [= Omalos Plateau, Tzani cave] [67], 7 April 1965: 2 inds. (Martens 1967); Omalos, cave [= Omalos Plateau, Tzani cave], 13 July 1995: skeleton (Hanák et al. 2001); – Topolia, Aghia Sophia [= Agias Sofias cave] [68], 16–17 March 1965: 1 ind. (Martens 1967); – Vafes, Krionerida [= Kryonerida] cave [19], 15 January 1968 (Beron 1970); – Bryses [= Vryses Apokoronou], 33 km SW of Chania [69], 1 ind. (Pohle 1953). – I r a k l e i o: Arkalochori [70], 1958 (Kahmann 1959); – Sarchos [71], 1973–1975: 1 ind. (from owl pellets) (Pieper 1977). – L a s i t h i: Mesa Mouliana [72], 1958 (Kahmann 1959); – spilaion Milatou [= Milatou cave] [43], 5 inds. (Iliopoulou-Georgudaki 1977); Milatos Spilia [= Milatou cave], 28 April 2004: det. 1 ind. (Skiba 2007); – Sitia [73], 1958: obs. (Kahmann 1959). – R e t h y m n o: Melidoni Andro [= Melidoni, Gerontospilios cave] [54], 30 April 2003: det. 3–6 inds. (Skiba 2007); – Rethymnon [= Rethymno] [74], 1 ind. (Felten et al. 1977). – Crete (undef.) (Andersen 1907).

COMMENTS. Similarly as the previous species, *Rhinolophus hipposideros* also ranks among the most common bats in Crete; it was evidenced from the whole island (Fig. 11). With 74 record sites it is the third most frequently recorded bat of the island (Table 1). However, in comparison with *R. ferrumequinum*, *R. hipposideros* inhabits a wider range of altitudes (Table 2) – in the summer season it prefers more elevated sites than the former species (mean 365.6 m, median 260.0 m, n=48) while in winter it occurs in slightly lower situated sites (mean 322.6 m, median 277.0 m, n=27), though in a wider altitude range exceeding 1500 m a. s. l.

Majority of records of *R. hipposideros* in Crete are associated with underground spaces (46 sites, i.e. 62.2%), both natural caves (41) and mines (5), they include both findings of bats in their roosts (59 evidences) and nettings/recordings of emerging and/or swarming individuals (33). Additionally, 11 record sites (14.9%) are man-made overground shelters (stone houses or concrete buildings). Out of three horseshoe bats of Crete, this species thus shows the most intensive tendency to synanthropy in its roost preference. Only 10 records (13.5%) refer to foraging bats, mostly recorded by an ultrasound detector in the areas not directly related with their roosts. However, the presence of *R. hipposideros* and possibly other rhinolophids in foraging grounds

considered the single examined Cretan bat to belong to *R. h. minimus* together with numerous samples from the whole Mediterranean Basin. However, Felten et al. (1977), as a result of their broad scale analysis, assigned the single examined Cretan bat to *R. h. minimus* along with the type specimen from Eritrea (only these two among several tens of examined bats). In fact, although identical in the name assignment, the two conceptions clearly differ in geographic classification of Cretan populations; while Andersen (1907) and later also Pohle (1953), Kahmann (1959) and Ondrias (1965) regarded them as a part of European Mediterranean populations of *R. hipposideros*, Felten et al. (1977) recognised *R. h. hipposideros* in the whole continental Europe and considered Cretan bats to be a part of NE African populations. Both these opinions sound theoretically plausible, since Cretan bat populations are related both to Europe/Eurasia and Africa, see e.g. Taxonomy chapters under *Rhinolophus ferrumequinum*, *Pipistrellus hanaki* and *Plecotus macrobullaris*, as well as Discussion.

Since both morphological evaluations by Andersen (1907) and Felten et al. (1977) were based on a single specimen, we examined a series of bats newly collected in different parts of Crete to define the condition of morphological characters of the respective population. External and cranial dimensions (Table 5) of Cretan specimens more or less conform to dimensions taken in representatives of other Mediterranean populations, and their values are slightly lower than those from Central Europe, eastern Turkey and Afghanistan (comp. the data by Felten et al. 1977, Benda et al. 2003, 2006), but much higher than in the specimen examined by Felten et al. (1977) (LAt 34.5 mm, LCc 12.8 mm, CM³ 5.0 mm). However, Felten et al. (1977) in their analysis suggested to register phenetic cranial characters rather than the body and skull size to describe geographic variation in *R. hipposideros* (based on Andersen 1918); viz. the massiveness of the bridge between orbita and infraorbital foramen ('infraorbital bridge' sensu Andersen) and the presence and position of small lower premolars (P₃).

Table 5. Basic biometric data [in mm] on examined Cretan samples of *Rhinolophus hipposideros* (Borkhausen, 1797), *R. blasii* Peters, 1866, and *Myotis blythii* (Tomes, 1857); for abbreviations see p. 110

	<i>Rhinolophus hipposideros</i>					<i>Rhinolophus blasii</i>					<i>Myotis blythii</i>				
	n	M	min	max	SD	n	M	min	max	SD	n	M	min	max	SD
LC	13	42.8	40	46	1.878	9	59.2	56	62	2.167	6	76.3	71	83	4.131
LCd	13	27.9	26	30	1.038	9	29.6	26	37	3.321	6	66.0	61	71	3.347
LAt	13	37.17	35.5	39.1	0.884	10	46.74	45.3	47.9	0.928	12	59.57	56.5	62.2	1.757
LA	13	17.49	17.0	18.4	0.395	9	20.90	19.5	23.0	1.039	6	27.43	26.2	28.5	0.753
LaFE	13	6.97	6.7	7.3	0.202	9	8.60	8.4	9.1	0.229	6	–	–	–	–
LTr	–	–	–	–	–	–	–	–	–	–	6	10.57	10.3	11.3	0.378
LCr	10	15.79	15.25	16.02	0.209	8	19.65	19.33	19.96	0.183	14	22.08	20.70	22.93	0.547
LCc/Cb	9	13.34	13.08	13.57	0.142	8	16.67	16.46	16.84	0.128	14	21.03	19.93	21.67	0.461
LaZ	10	7.54	7.43	7.66	0.073	8	9.21	9.02	9.34	0.110	14	14.22	13.72	15.04	0.359
LaI	10	1.48	1.34	1.76	0.118	8	2.31	2.13	2.51	0.121	14	5.08	4.87	5.29	0.120
LaN	10	6.45	6.21	6.72	0.147	8	8.39	8.18	8.54	0.126	14	9.74	9.42	10.19	0.242
LaM	9	7.32	7.13	8.18	0.325	7	9.17	9.00	9.28	0.094	14	10.29	10.02	10.81	0.201
ANc	9	4.61	4.52	4.68	0.053	8	6.09	5.89	6.34	0.164	14	7.81	7.32	8.19	0.229
CC	9	3.39	3.34	3.54	0.061	8	4.51	4.28	4.67	0.145	14	5.77	5.33	6.10	0.198
M ³ M ³	10	5.35	5.21	5.53	0.098	8	6.53	6.32	6.73	0.120	14	8.97	8.58	9.36	0.192
CM ³	10	5.23	5.14	5.39	0.080	8	6.78	6.62	6.92	0.097	14	9.08	8.58	9.34	0.186
LMd	10	9.42	9.25	9.54	0.098	8	11.91	11.73	12.16	0.137	14	16.81	16.14	17.48	0.410
ACo	10	2.01	1.91	2.15	0.081	8	2.68	2.60	2.75	0.050	14	5.45	5.17	5.81	0.217
CM ³	10	5.46	5.33	5.62	0.071	8	7.13	6.93	7.27	0.128	14	9.78	9.40	10.02	0.175

In the Cretan bat examined by Felten et al. (1977), the infraorbital bridge was found thin and the premolars present, localised labially from the large premolars (P₂, P₄). Concerning the series of ten bats examined by us, the infraorbital bridge was wide in six skulls (according to Abb. 5 by Felten et al. 1977), rather wide in two skulls, rather thin in one skull and very thin in one skull. In eight skulls both small lower premolars were present, localised out of the tooth-row and large premolars were in contact, in two skulls the large lower premolars were in contact but small premolars were missing (one from the latter pair had a wide bridge, the other one thin). The prevailing state of massiveness of the infraorbital bridge was thus different in our series of Cretan bats than in the specimen examined by Felten et al. (1977), being wide in most of cases (>60%), while the position of small lower premolars was similar as in the Felten's et al. (1977) specimen. Our examination thus gave very distinct results from those by Felten et al. (1977). According to the taxonomic division by the latter authors, our Cretan specimens conform to the bats from Sicily, Malta, Pantelleria, and western Anatolia (Felten et al. 1977: 15, 'Gruppe IV'), differing from other Mediterranean populations, including the Balkan ones. Anyway, such a division gives a mosaic-like geographical arrangement of the intraspecific variation in the Mediterranean, which seems to reflect an actual phylogenetic population web rather unclearly. The preliminary results of genetic analyses (Kûs 2007, Benda et al. in press) showed the limited number of examined Cretan bats to be a part of the European lineage of the species and thus suggested the Andersen's (1918) and Felten's et al. (1977) character matrix to be rather hardly useful for tracing up the phylogenetic relationship within the species rank of *R. hipposideros*. However, a profound analysis based on a larger number of evaluated traits is needed to assess intraspecific relations in this species properly (see also the review by Benda et al. 2006).

Rhinolophus blasii Peters, 1866

RECORDS. **Original data:** C h a n i a: Alikampos, Skala cave [1], 7 February 2008: obs. 1 ind.; – Anopoli, Porolagos, pine forest [2], 19 September 2002: det. & rec. 1 ind.; – Fylaki, Psimaki cave [3], 29 January 2006: obs. 3 inds., 21 March 2008: obs. several inds. (exam. 1 fa, 1 fs); – Gouverneto monastery, Koumarospilios cave [4], 22 March 2008: obs. & exam. 2 f; – Katholiko monastery (Fig. 12), Agiou Ioanni cave [5], 28 April 2008: trap. 2 ma, 2 fa, 1 fs, 27 May 2008: net. 2 ma, 1 ms (NMP 92325, 92326 [S+A], 92327 [A]), det. & rec. 1 ind.; – Myloniana, Koulieri cave [6], 2 May 2005: det. & rec. 1 ind., 24 July 2007: net. 1 m, 1 faL; – Omalos Plateau, Tzani cave [7], 1 October 2006: net. 1 fa (NMP 91179 [S+A]), det. 1 ind., 17 August 2008: net. 2 fa; – Palaiochora, gallery [8], 25 April 2008: obs. ca. 30 inds. (exam. 7 ma, 1 faG, 1 fa, 1 fs); – Papadiana, ford [9], 19 July 2008: net. 1 fa; – Perivolia, Mamaloukou cave [10], 9 July 2005: obs. several inds. (obs. K. Paragamian), 2 May 2008: net. 1 ma, 6 faG, 2 fa, 1 fs, 30 April 2008: obs. several inds.; – Samaria, gorge [11], 5 July 2008: net. 1 ma, 1 faL; – Sfinari, Neraidospilia cave [12], 16 September 2005: obs. 10 inds., coll. bones (NHMC FC8084), 5 November 2006: obs. 19 inds.; – Sougia, gypsum mine [13], 14 March 2006: obs. ca. 70 inds., 23 March 2008: obs. 11 inds., exam. 7 ma, 1 fa, 2 fs (coll. 1 fa, NHMC FC11132 [F]); – Stavros, at the Lera cave [14], 26 December 2005: det. & rec. several inds.; – Theriso, Sarakinas cave [15], 8 October 2007: net. 1 fs (NMP 92301 [S+A]). – I r a k l e i o: Alithini, at the Meires cave [16], 25 May 2007: det. & rec. several inds.; – Amnisos, Eileithyas cave [17], 4 October 2006: net. 1 ma (NMP 91190 [S+A]), det. several inds.; – Ano Asites, Nykteridospilios cave [18], 7 October 2005: obs. 1 ind., 25 October 2005: obs. 1 ind., 16 January 2006: obs. 1 ind., 24 February 2006: obs. 1 ind.; – Giouchtas hill, Stravomythi cave [19], 16 September 2007: det. & rec. several inds., 18 May 2008: det. & rec. several inds., 7 June 2008: net. 1 faG, 3 faL, 1 fs, 22 June 2008: det. & rec. several inds.; – Kamaraki, Chainospilios cave [20], 9 October 2006: obs. several inds.; – Linoperamata, Almyros river [21], 5 April 2006: det. & rec. 1 ind.; – Rouva forest, Agiou Ioanni chapel [22], pasture [24], 26 May 2008: net. 2 ma (NMP 92347 [A], 92348 [S+A]), det. & rec. 1 ind.; – Sarchos, Chonos cave [23], 16 January 2005: obs. 1 ind., 20 May 2005: net. 1 m, 26 November 2005: obs. several inds., 1 December 2005: net. 3 ma, 3 ms, 21 December 2005: obs. 5 inds., 19 March 2006: obs. 1 ind., 9 September 2006: net. 2 m, 17 November 2006: obs. 15 inds., 14 February 2008: det. & rec. several inds.; – Spilia, Agia Eirini chapel, 2 km S of Knossos, above a brook [24], 26 May 2008: det. & rec. 1 ind.; – Tylisos, Kamilari cave [25], 3 February 2006: net. 2 ma, 3 ms, 23 March 2006: det. & rec. ca. 10 inds., 7 April 2006: det. & rec. 2 inds., 6 November 2006: obs. ca. 80 inds., 9 November 2006: net. 2 ma, 4 fa, 23 March 2007: net. 2 m, 23 October 2007: net. 1 fs. – L a s i t h i: Agia Fotia, Koufota cave [26], 20 July 2006: obs. ca. 20 inds.; – Agios Georgios, at the Megalo Katofygi cave [27], 5 September 2004: det. & rec. several inds.; – Pefki, Vreiko cave [28], 12 October 2007: net. 1 fs (NMP 92312 [S+A]). – R e t h y m n o: Doxaro, Mougri cave [29],

24 January 2003: obs. 8 inds., 11 November 2004: net. 2 m, 4 fs, 9 November 2007: det. & rec. 1 ind.; – Doxaro, oak grove [30], 9 November 2007: det. & rec. 1 ind.; – Erfoi, at a cave [31], 28 December 2006: det. & rec. several inds.; – Prinós, Prinou cave [32], 21 May 2005: det. & rec. several inds., 18 November 2006: det. & rec. several inds., 1 March 2006: obs. several inds., 11 October 2007: net. 3 ma, 9 ms, 2 fa, 6 fs, 19 June 2008: net. 1 m, 8 faL, 5 fs; – Ski resort (Idi Mts.), scrubland [33], 27 May 2007: det. & rec. 2 inds.; – Zoniana, at the Sfentoni cave [34], 23 June 2008: det. & rec. several inds., 12 August 2008: obs. 4 inds. (exam. 2 fs). – **Published data:** C h a n i a: Aghios Ioannis, cave [= Katholiko monastery, Agiou Ioanni cave] [5], 13–14 March 1965: 5 inds. (Martens 1967); Katholiko monastery, cave [= Agiou Ioanni cave], 11 September 1986: net. 1 m [NMW 36149 (S+B)] (Hanák et al. 2001, Benda et al. 2006); Agios St. Ioannis [= Katholiko monastery, Agiou Ioanni cave], 4 May 2003: det. 15–20 inds. (Skiba 2007); – Paläochora [= Palaiohora], gallery [8], 19 March 1965: 25 inds. (Martens 1967). – I r a k l e i o: Ano Viannos [35], 1973–1975: 2 inds. (from owl pellets) (Pieper 1977); – Katofigi [36], cave, 9 May 1959: skull (Hanák et al. 2001); – Sarhos, cave [= Chonos cave] [23], 10 April 1955: 1 m, 3 f (Hanák et al. 2001). – L a s i t h i: Milo [= Milatos] [37] (Doria 1887); – Piskokefalo, cave [38], 22–23 March 1958: big colony (exam. 3 f) (Kahmann 1959); – Sitia [39], 1 ind. (Felten et al. 1977). – R e t h y m n o: Melidoni Andro [= Melidoni, Gerontospilios cave] [40], 30 April 2003: det. 7–10 inds. (Skiba 2007).

COMMENTS. *Rhinolophus blasii* is one of the earliest known bats from Crete, it was reported as the third one after *M. blythii* and *M. schreibersii*; a record from Milatos was published by Doria (1887). Although this species is not a common bat in Crete, it belongs to those rather abundant. *R. blasii* was recorded at 40 sites situated in a wide range of altitudes, reaching up to 1500 m a. s. l. (Table 2) and covering the whole island (Fig. 13). Similarly as *R. hipposideros*, *R. blasii* prefers higher altitudes in the summer season (mean 376.8 m, median 312.5 m, n=28), while significantly lower situated sites during winter (mean 194.6 m, median 193.5 m, n=16).

An absolute majority of Cretan records of *R. blasii* is associated with underground spaces (31 sites, i.e. 77.5%), mainly natural caves (29) and also two mines. These records represent both



Fig. 12. Ruins of the Katholiko monastery in the Akrotiri peninsula (photo by Z. Bendová). Note the entrance to the Agiou Ioanni cave in the left upper part of the picture. The ruins and the cave are roosting and/or swarming site of *Rhinolophus ferrumequinum*, *R. hipposideros*, *R. blasii*, *Myotis blythii*, *M. emarginatus*, *M. aurascens*, *Pipistrellus kuhlii*, *Plecotus kolombatovici*, *Miniopterus schreibersii*, and *Tadarida teniotis*, one of the richest bat community evidenced at one site in Crete.

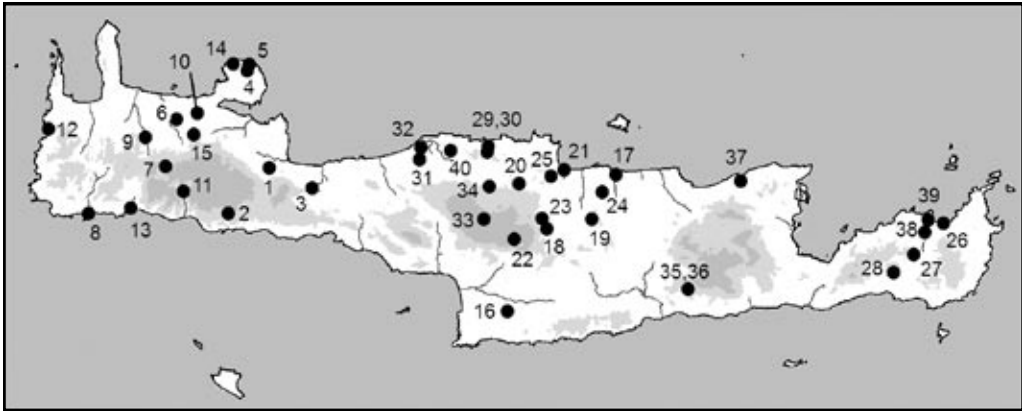


Fig. 13. Records of *Rhinolophus blasii* Peters, 1866 in Crete.

findings of bats in their roosts (29 evidences) and nettings/recordings of emerging and/or swarming individuals (37). No records were made in anthropogenic overground shelters like houses or ruins. At eight sites (20.0%) foraging bats were recorded by an ultrasound detector (6 evidences) and/or netted (3) in areas not directly connected with their roosts. However, as noted in *R. hipposideros*, bat detector records of rhinolophids including *R. blasii* certainly underestimate their real distribution. Pieper (1977) reported findings of two individuals of this bat in owl pellets from one site, Ano Viannos (2.5%). External and cranial dimensions of examined specimens of *R. blasii* from Crete are shown in Table 5.

Records related to nursery colonies of *R. blasii* (both directly observed and indirectly assumed) were made in four sites only, all in underground spaces (three caves and one gallery). The only directly observed nursery colony included ca. 30 individuals. Winter records were made at 11 sites, in natural caves (9) and mines (2). Wintering aggregations were found relatively often, being composed on average of 24.1 bats (range 3–80 bats, $n=10$), solitary individuals were found torpid only five times at three sites. However, true hibernation of *R. blasii* was not documented in Crete.

In Europe, *R. blasii* is distributed only in its southeastern part and Crete thus represents a large portion of the European range of this species. Concerning the area of Crete, occurrence of this species in the island belongs to the most frequent within the Mediterranean (comp. Benda & Horáček 1998, Hanák et al. 2001, Benda et al. 2003, 2007), with an extraordinary density of one record site per ca. 200 km². *R. blasii* is the only medium-sized horseshoe bat commonly inhabiting smaller Mediterranean islands. Of Greek islands, Hanák et al. (2001) reviewed records from Thasos, Lesbos, Euboea, Ikaria, Milos, Rhodes, Karpathos, Crete, Kythira and Petalas, von Helvesen (in Mitchell-Jones et al. 1999) gave an additional unspecified record from Saronic islands (Aigina?). Besides Greek islands, *R. blasii* is known only from the Dalmatian islands of Lastovo (Dulić & Tvrković 1970) and Cres (Tschapka in Dietz et al. 2007) and from Cyprus (Benda et al. 2007). In the latter island, *R. blasii* belongs to rather more abundant bat species and is a summer inhabitant of areas situated on average around 380 m a. s. l., the situation being very similar in both points to that known from Crete.

Myotis blythii (Tomes, 1857)

RECORDS. **Original data:** C h a n i a: Agia Eirini, old chapel [1], 24 April 2008: obs. & exam. 3 ma; – Agia Eirini, stream [2], 18 August 2008: net. 1 ma; – Champatha, Vennidon cave [3], 4 April 2007: net. 11 fa, 12 May 2007: net. 2 ma, 8 ms, 5 faG, 5 fa, 5 fs; – Fylaki, Psimaki cave [4], 8 July 2006: obs. several hundreds inds., 21 September 2006: obs. 5 inds., 6 July 2008: obs. some hundreds inds., 16 August 2008: obs. 2 inds. (exam. 1 ma); – Fylaki, Skoteini cave [5], 1 October 2001: obs. 30 inds.; – Katholiko monastery (Fig. 12), Agiou Ioanni cave [6], 28 April 2008: net. 1 m, 27 May 2008: net. 5 ma (coll. 2 inds., NMP 92328 [S+A], 92329 [A]), in the monastery, net. 2 ma; – Omalos Plateau, Tzani cave [7], 17 August 2008: net. 9 ma, 1 ms; – Samaria, gorge [8], 5 July 2008: net. 3 faL; – Sougia, gypsum mine [9], 6 August 2007: obs. 3 inds.; – Stavros, Lera cave [10], 1 May 2008: net. 12 ma, 6 ms, 1 fs. – I r a k l e i o: Alithini, Meiras cave [11], 11 January 2006: coll. bones (NHMC FC8639), 15 July 2006: obs. several hundreds inds., 25 May 2007: obs. several hundreds inds.; – Ampelouzou, gorge, mine [12], 19 May 2007: obs. ca. 30 inds.; – Ano Asites, Nykteridospilios cave [13], 27 July 2004: obs. 12 inds., net. 2 ma, 20 April 2005: obs. 1 ind., 30 May 2005: net. 6 ma, 26 June 2005: net. 3 ma, 1 ms, 1 faL, 4 July 2005: obs. 3 inds., 27 July 2005: obs. 8 inds., 29 July 2005: net. 2 ma, 1 fs, 9 August 2005: obs. 2 inds., 23 May 2008: obs. & exam. 1 m; – Ano Fortetsa, gallery under a school [14], 10 August 2004: obs. 1 ind., 16 July 2008: obs. & exam. 1 ma (leg. G. Alexandrakis); – Avdou, Agias Foteinis cave [15], 10 October 2007: det. 2 inds.; – Giouchtas hill, Stravomyti cave [16], 28 August 2007: obs. 3 inds. (exam. 1 m), 18 May 2008: obs. 2 inds., 7 June 2008: net. 15 ma; – Gonies, Tsakalou pothole [17], 27 July 2005: obs. 2 inds.; – Irakleion T.E.I. Crete campus [18], 27 August 2003: coll. 1 fa (NHMC FC4940 [F]; leg. D. Kolaros) – Kamaraki, Chainospilios cave [19], 4 August 2006: obs. 5 inds., 10 August 2007: net. 5 ma, 2 fs; – Kamares, Kamaron cave [20], 20 April 2005: obs. 5 torpid inds., coll. bones (NHMC FC10520), 26 February 2006: obs. several torpid inds., 2 April 2007: obs. 65 torpid inds., 25 October 2006: obs. 32 torpid inds.; – Plouti, Mikro Lavyrinthaki mine [21] (Fig. 45), 24 May 2007: obs. 1 ind.; – Rouva forest, Agiou Ioanni chapel, pasture [22], 4 June 2008: det. & rec. 1 ind.; – Sarchos, Chonos cave [23], 20 May 2005: net. 11 ma, 6 ms, 10 June 2005: obs. several inds., 14 May 2006: obs. several inds., 29 May 2006: obs. several inds., 14 June 2006: obs. 3 inds., 1 July 2006: obs. 10 inds., 19 August 2006: obs. several inds., 22 August 2006: net. 33 ma, 2 fs, 9 September 2006: net. 2 ma, 3 ms, 2 fs, 30 June 2007: obs. 10 inds.; – Skinakas (Idi Mts.), pothole [24], 21 October 2006: obs. 5 torpid inds., 26 November 2006: obs. 4 torpid inds., 18 July 2007: obs. 2 torpid inds.; – Tylisos, Kamilari cave [25], 7 April 2006: net. 23 fa, 1 fs, 16 May 2006: net. 17 ma, 8 ms, 16 faG, 4 fa, 14 fs, 12 June 2006: net. 16 ma, 5 ms, 3 mj, 5 faG, 28 faL, 3 fa, 9 fs, 2 fj, 13 June 2006: obs. ca. 500 inds. (ad.+juv.), 4 July 2006: obs. ca. 250 inds., 12 July 2006: net. 26 ma, 18 mj, 2 faG, 9 faL, 11 fa, 7 fs, 10 fj, 23 March 2007: net. 3 fa, 20 April 2007: net. 5 ma, 1 ms, 31 fa, 8 fs, 28 July 2007: net. 24 ma, 3 ms, 2 faL, 2 fa, 11 fs, 2 fj, 13 April 2008: net. 3 ma, 2 ms, 1 faG, 18 fa, 9 fs. – L a s i t h i: Agia Fotia, Koufota cave [26], 20 July 2006: obs. ca. 200 inds., 3 July 2007: obs. several hundreds inds.; – Chochlakies, Karoumes bay, Voreino cave [27], 8 March 2008: obs. & coll. 1 fa (NHMC FC10899 [A]; leg. A. Kardamaki); – Kritsa, Gaidourotrypa cave [28] (Fig. 2), 31 May 2008: det. & rec. 1 ind.; – Milatos, Milatou cave [29], 7 October 2006: net. 1 ms (NMP 91108 [S+A]), 12 August 2007: obs. 6 inds.; – Milatos bay, Agiou Konstantinou chapel, ca. 4 km to E, sea cave [30], 26 July 2003: obs. ca. 50 inds., 8 June 2007: obs. 4 inds. – R e t h y m n o: Lefkoogia, at a Venetian bridge ca. 3 km E of the Kato Preveli Monastery [31], 30 May 2008: net. 1 ma, 2 faL, 1 ind. (coll. 3 inds., NMP 92333–92335 [S+A]); – Petradolakia (Idi Mts.), Agios Fanourios chapel, pothole [32], 1 April 2006: obs. 1 ind., 20 August 2008: net. 2 ma; – Prinios, Prinou cave [33], 19 June 2008: net. 2 ma, 1 fs, 1 fj; – Varsamo (Idi Mts.), Peristerospilios cave [34], 26 March 2006: obs. ca. 50 torpid inds., 8 November 2006: obs. 15 torpid inds., 20 December 2006: obs. 43 torpid inds., 29 March 2007: obs. ca. 90 torpid inds., 30 May 2007: coll. bones (NHMC FC10388, FC10494, FC10519). – **Published data:** C h a n i a: Grottes de Katholiko [= Katholiko monastery, Agiou Ioanni cave] [6], 31 May 1845 (Raulin 1869a, b); – Omalos, water cave [= Omalos Plateau, Tzani cave] [7], 5 August 1971: 5 ma, 1 fa (Hanák et al. 2001); Omalos, cave [= Omalos Plateau, Tzani cave], 12 July 1995: net. 1 ma, 1 faL, 2 inds. (Hanák et al. 2001); – Stavros, cave [= Lera cave] [10], 10 July 1995: net. 6 ma, 2 fa (Hanák et al. 2001); – Topolia [35], 1973–1975: 21 inds. (from owl pellets) (Pieper 1977); – Vafes [36], 1 m (Lanza 1952). – I r a k l e i o: Ag. [= Agio] Pnevma [37], 1973–1975: 5 inds. (from owl pellets) (Pieper 1977); – Ano Viannos [38], 1973–1975: 25 inds. (from owl pellets) (Pieper 1977); Ano Viannos, Mt. Kato cave, August 1999: 4 fa [MHNG 1807.005, 006, 068, 069 (S+A)] (Hanák et al. 2001, Benda et al. 2006); – Gortys [= Gortyna] [39], August and October 1942: 4 inds. (from owl pellets) (Uttendörfer 1952), Gortys, 1 ind. (from owl pellets) (Pohle 1953); – Labyrinth [= Plouti, Gortynas Labyrinth mine] [40], 15 August 1845 (Raulin 1869a, b); Haghia Dekka [= Agioi Dekka], Labyrinth [= Plouti, Gortynas Labyrinth mine], hundreds inds., 1904: coll. 4 inds. (Bate 1905), 3 m, 1 f (Miller 1912); Aji [= Agioi] Dekka, Labyrinth [= Plouti, Gortynas Labyrinth mine], 22 inds. (Pohle 1953); Gortis, labyrinth [= Plouti, Gortynas Labyrinth mine], 4 inds. (Hanák et al. 2001, cf. Strelkov 1972); – spilalion Mikro Lavyrinthaki (resp. Mikro labyrinthi and Mikro Lavyrinthaki) [= Plouti, Mikro Lavyrinthaki mine] [21], 33 inds. (Iliopoulou-Georgudaki 1977), 8 August 1973: 15 m, 18 f (Iliopoulou-Georgudaki 1979, 1984); – Sarchos [41], 1973–1975: 5 inds. (from owl pellets) (Pieper 1977); – Skotino, cave [= Skoteino, Agias Paraskevis cave] [42], 5 inds. (from owl pellets) (Pieper 1977); – Aloni [= Tylisos, Voulismeno Aloni doline] [43], 1973–1975: 5 inds. (from owl pellets) (Pieper 1977). – L a s i t h i: ‘Stausee’ 4 km NW of Ierapetra [= Gra Lygia, Mpramianos river dam] [44], 30 April 2004: det. 1 ind. (Skiba 2007); – Milatos [45], 28 April 2004: 3 inds. (Skiba

up to several tens of bats, the largest observed number in a single site was 90 individuals, the average size of a wintering group was 38.3 bats (n=7). A long lasting hibernation of *M. blythii* takes place probably only in caves above 1450 m a. s. l., characterised by low ambient temperature (ca. 8 °C) and presence of snow at their surroundings at the time of the check. In any case, *M. blythii* is the only species that was confirmed as a true hibernant in Crete so far.

According to the number and distribution of records, *M. blythii* is the second most widespread bat in Greece (Hanák et al. 2001); it was recorded in all geographical parts of the country, including all mainland regions, but in several islands only. Hanák et al. (2001) reviewed records from Samothrace, Lesbos, Ikaria, Karpathos, Crete, Petalas, and Corfu. Mitchell-Jones et al. (1999) showed this bat to be widely distributed in the European Mediterranean and sub-Mediterranean, however, it absents from large western Mediterranean islands (except for Sicily), being substituted by *Myotis myotis* (Balears) or *M. punicus* (Corsica, Sardinia, Malta). Besides some Greek islands incl. Crete, *M. blythii* is known only from Sicily, Ustica, Lipari, Dalmatian islands and Cyprus (see Mitchell-Jones et al. 1999 and Topál & Ruedi 2001). However in Cyprus, *M. blythii* was found only in four sites (Benda et al. 2007), thus representing a rather rare element of its fauna, but similarly as in Crete, it seems to prefer higher situated sites there.

TAXONOMY. Some recent authors suggested to attribute the Mediterranean populations of *Myotis blythii* to a separate species, *M. oxygnathus* (Monticelli, 1885) (see e.g. Simmons 2005, Dietz et al. 2007 and/or Mayer et al. 2007). The main argument for the separation of *oxygnathus* from *blythii* consists in a simple interpretation of results of mitochondrial gene comparisons (cf. Castella et al. 2000, Ruedi & Mayer 2001). However, the Mediterranean populations of *M. blythii* were found hybridizing with *M. myotis* and the mtDNA of the latter species dominating in the populations of both species (Berthier et al. 2006). Therefore, we regard such a type of evidence to be inconvenient for a resolution of intraspecific relations within *M. blythii* and thus, here we follow the traditional broad concept of *M. blythii* as the taxon distributed from the European Mediterranean to the Indomalayan Region (cf. Strelkov 1972, Koopman 1994, Benda & Horáček 1995, Hanák et al. 2001, Benda et al. 2006, etc.), which is also suggested by the recent results of a geometric morphometric analysis (Evin et al. 2008). Anyway, no matter whether the European populations of *oxygnathus* lie within or out of the species rank of *M. blythii*, they always remain distinct from its two west-Palaeartic siblings, partially sympatric *M. myotis* (Borkhausen, 1797) and allopatric *M. punicus* Felten, 1977 (Castella et al. 2000, Evin et al. 2008).

M. blythii has been distinguished as a separate species in Europe (originally as *M. oxygnathus*) since Miller (1912). Therefore, the earlier authors (Raulin 1869b, Bate 1905) considered Cretan populations to be a part of the European *M. myotis* (mentioned also under its synonym *M. murinus*). Miller (1912) evaluated Cretan samples collected by Bate (1905) as *M. oxygnathus* (i.e. *M. blythii* in the contemporary sense). Similarly, von Wettstein (1942) suggested the Bate's (1905) bats to belong to *M. oxygnathus*. On the other hand, Pohle (1953) and Kahmann (1959) considered Cretan mouse-eared bats to be a part of the large European species under the name *Myotis myotis oxygnathus*. Lanza (1959) evaluated one Cretan specimen to be in size intermediate between (Italian) representatives of *M. myotis* and *M. oxygnathus*. Ondrias (1965) listed the Cretan records under *M. oxygnathus*.

Kusjakin (1935) and Harrison & Lewis (1962) showed close similarities of large mouse-eared bats assigned to the names *oxygnathus* (Europe), *omari* (Middle East) and *blythii* (Central Asia) and suggested to regard them as a single species with three subspecies. Topál (1971) and Strelkov (1972), who accepted such an arrangement, included four bats from Crete in their analyses of the group. They evaluated them to be very similar to the Middle Eastern samples of *M. blythii omari* Thomas, 1905, described from central Iran. Therefore, Topál (1971), Strelkov (1972) and Iliopou-

Table 6. Biometric data on comparative sample sets of *Myotis blythii* (Tomes, 1857) from Lesbos (cf. *lesviacus* Iliopoulou, 1984), *M. blythii omari* Thomas, 1905 from the Middle East (between Cyprus to SE Iran, incl.) and Caucasus Region, *M. blythii oxygnathus* (Monticelli, 1885) from southern and central Europe, and *M. punicus* Felten, 1977 from the Maghreb

	Lesbos					<i>Myotis blythii omari</i>				
	n	M	min	max	SD	n	M	min	max	SD
LAt	2	59.10	58.2	60.0	1.273	58	59.58	56.0	66.7	1.975
LCr	7	21.84	21.08	22.65	0.508	98	22.24	21.27	23.20	0.385
LCb	7	20.78	20.10	21.44	0.486	95	21.24	20.27	22.20	0.407
LaZ	7	14.01	13.55	14.41	0.333	89	14.27	13.55	15.23	0.322
LaI	7	5.07	4.74	5.39	0.195	99	5.21	4.86	5.67	0.151
LaN	7	9.68	9.52	10.12	0.212	100	9.85	9.23	10.42	0.237
LaM	7	10.24	9.83	10.53	0.269	49	10.31	9.76	10.76	0.217
ANc	7	7.58	7.38	7.85	0.156	98	7.74	7.27	8.27	0.208
CC	6	5.66	5.33	5.89	0.185	96	5.93	5.32	6.43	0.215
M ³ M ³	7	9.01	8.73	9.48	0.238	101	9.21	8.43	9.88	0.244
CM ³	7	9.00	8.65	9.22	0.188	102	9.30	8.85	9.75	0.199
LMd	7	16.67	15.93	17.12	0.440	102	17.04	16.32	17.83	0.314
ACo	7	5.38	5.08	5.65	0.221	102	5.51	5.02	5.89	0.207
CM ₃	7	9.60	9.21	9.82	0.201	102	10.01	9.50	10.59	0.213
	<i>Myotis blythii oxygnathus</i>					<i>Myotis punicus</i>				
	n	M	min	max	SD	n	M	min	max	SD
LAt	98	57.58	51.4	63.6	2.269	69	59.18	31.5	63.5	3.718
LCr	175	21.35	20.15	22.42	0.467	70	22.05	21.20	22.92	0.410
LCb	169	20.26	18.82	21.78	0.443	69	20.98	19.88	21.71	0.397
LaZ	138	13.66	12.87	14.36	0.332	63	14.14	13.40	14.98	0.296
LaI	177	5.09	4.65	5.62	0.180	70	5.15	4.82	5.51	0.160
LaN	176	9.62	8.88	10.22	0.216	70	9.76	9.33	10.24	0.201
LaM	172	9.97	7.27	10.57	0.319	70	10.44	10.05	10.76	0.178
ANc	169	7.53	7.05	8.07	0.227	70	7.60	5.98	8.05	0.272
CC	167	5.67	4.85	6.22	0.195	67	5.62	5.37	5.97	0.159
M ³ M ³	176	8.83	7.54	9.45	0.278	70	9.06	8.47	9.92	0.256
CM ³	173	8.78	8.06	9.37	0.228	70	9.22	8.80	9.62	0.211
LMd	177	16.18	15.07	17.72	0.412	70	16.64	15.77	17.37	0.318
ACo	172	5.17	4.53	6.02	0.220	70	5.71	5.21	6.12	0.205
CM ₃	177	9.47	8.60	10.02	0.215	69	9.93	9.35	10.42	0.238

lou-Georgudaki (1979, 1984) considered the Cretan populations of large mouse-eared bats to belong to *M. blythii omari*. This conclusion was accepted by most of the subsequent authors (e.g. Topál in Mitchell-Jones et al. 1999, Hanák et al. 2001, Topál & Ruedi 2001, Dietz et al. 2007).

In addition, Iliopoulou-Georgudaki (1984) described another subspecies from the Aegean island of Lesbos, *M. blythii lesviacus* Iliopoulou, 1984, to be intermediate in size between the large-sized *omari* of Crete and small-sized *oxygnathus* of continental Greece. However, the justification of the new subspecies was doubted by Benda & Horáček (1995), Arlettaz et al. (1997), and Dietz et al. (2007) contra some compendia authors (Koopman 1994, Simmons 2005).

Moreover, Arlettaz et al. (1997) suggested to assign all the eastern Mediterranean populations of large mouse-eared bats to *M. myotis* including the populations considered as *omari*, despite their sympatric occurrence with *M. myotis macrocephalicus* in the Levant. Based on this not well understandable suggestion and on the new recognition of *M. punicus* in the Maghreb and some

Table 7. Results of statistic comparison (ANOVA) of Cretan set of *Myotis blythii* (Tomes, 1857) samples and of comparative sample sets (see text); for abbreviations see p. 110

	Crete vs. Lesbos		Crete vs. <i>omari</i>		Lesbos vs. <i>omari</i>		Crete vs. <i>oxygnathus</i>		Crete vs. <i>punicus</i>	
	df	F p	df	F p	df	F p	df	F p	df	F p
LA _t	12	0.126	68	0.000	58	0.113	109	3.592	79	0.126
LC _r	19	0.923	110	1.797	103	6.550 *	187	31.234 ***	82	0.044
LC _b	19	1.282	107	3.081	100	7.909 *	181	38.778 ***	81	0.171
LaZ	19	1.559	101	0.348	94	4.167 *	150	34.722 ***	75	0.682
LaI	19	0.039	111	9.425 *	104	5.652 *	189	0.009	82	2.580
LaN	19	0.324	112	2.790	105	3.594	188	4.061 *	82	0.122
LaM	19	0.251	61	0.089	54	0.629	184	13.748 ***	82	7.734 *
LaN _c	19	5.903 *	110	1.252	103	4.374 *	181	20.584 ***	82	7.475 *
CC	18	1.444	108	6.749 *	100	9.202 *	179	3.380	79	9.651 **
M ³ M ³	19	0.167	113	12.384 **	106	4.416 *	188	3.252	82	1.642
CM ³	19	0.740	114	15.579 ***	107	14.636 ***	185	21.897 ***	82	5.965 *
LM _d	19	0.508	114	6.344 **	107	8.764 **	189	30.209 ***	82	2.969
AC _o	19	0.471	114	0.963	107	2.463	184	21.192 ***	82	17.631 ***
CM ₃	19	4.206	114	15.694 ***	107	24.481 ***	189	27.479 ***	81	5.367 *

western Mediterranean islands instead of *M. blythii* (Castella et al. 2000), Güttinger et al. (2001) suggested possible occurrence of *M. myotis* or *M. punicus* in Crete instead of *M. blythii*. Since the occurrence and morphometric pattern of *M. myotis* populations in the eastern Mediterranean was

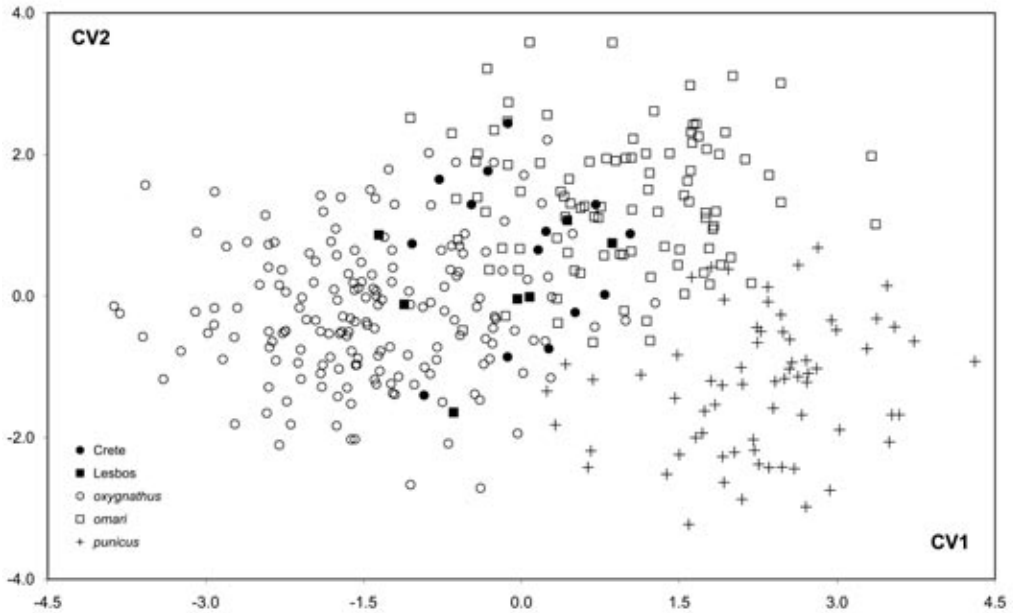


Fig. 15. Bivariate plot of examined Cretan and comparative samples of *Myotis blythii* (Tomes, 1857): results of the discriminant analysis of selected seven most variable skull dimensions (LaZ, LaM, CC, CM³, LM_d, AC_o, CM₃; CV1=71.57% of variance, CV2=26.55%).

reviewed several times (Strelkov 1972, Benda & Horáček 1995, Spitzenberger 1996, Benda et al. 2006) and its more or less clear morphological difference from *M. blythii* was satisfactorily proved, we compared a set of museum specimens of *M. blythii* from Crete (15 bats from four sites at least, incl. the newly collected, see Records above) with a series of specimens from Lesbos (7 bats) and an extensive series of samples from continental Europe (nominally of *M. b. oxygnathus*), from the Middle East (from Cyprus to Azerbaijan and SE Iran, i.e. nominally of *M. b. omari*), and from the Maghreb (i.e. *M. punicus*). The Cretan samples were generally found to conform in their dimensions to the specimens from Lesbos (Tables 5, 6) and a simple statistical test almost did not find any significant difference in forearm length and cranial dimensions (Table 7). On the other hand, the Cretan and Lesbian samples on average differ from both the small-sized European and large-sized Middle Eastern and Maghrebian specimens (Tables 5–7). Samples of *M. punicus* differ from the Cretan bats also by their neurocranium shape, which is indicated by significant differences in the respective dimensions (LaM, ANc, ACo) and by the relative width of rostrum; therefore the canonical discriminant analysis (CDA) of skull dimension clearly separated samples of *M. punicus* from those of *M. blythii* s.l. (Fig. 15). Anyway, most of the dimensional ranges of Cretan and Lesbian samples overlap with those of the European and Middle Eastern bats (Table 6) and the results of CDA conform with them (Fig. 15).

To be summarised, the Cretan and Lesbian samples (1) are dimensionally very similar and hardly can be considered as two distinct taxa, also due the fact that they originate in relatively close areas at the opposite sides of the Aegean Sea; (2) overlap in dimensional ranges with *M. punicus* samples but differ from them by their skull shape; (3) although overlapping, are dimensionally intermediate between the continental European representatives of *M. blythii oxygnathus* and the Middle Eastern individuals of *M. blythii omari*, and create dimensional as well as geographical transitions between these two broadly distributed east-Mediterranean forms; and (4) can be hardly simply attributed to one of the three compared taxa as their dimensional overlap is present in a very similar degree.

While the population from Lesbos was described to belong to the endemic subspecies *M. blythii lesviacus*, the Cretan population can be simply attributed to this form too. On the other hand, although both the European and Middle Eastern subspecies, smaller *M. b. oxygnathus* and larger *M. b. omari*, live in large areas, a considerable zone of transition is found between their ranges covering a belt of ca. 800–1000 km (as well as between the Asian subspecies *M. b. omari* and *M. b. blythii* at the Irani-Turkmenistani border, see the review by Benda et al. 2006). This dimensional transition runs along a cline (Benda & Horáček 1995), and thus, several taxa could be theoretically identified along such a cline from Crete to central Anatolia based on their average dimensions (see also the results by Felten et al. 1977 and Spitzenberger 1996).

Unfortunately, still it seems beyond real chances (due to insufficient sample sizes) to test properly these hypotheses against the hypothesis (mentioned already by Iliopoulou-Georgudaki 1986) that the smaller body size in the Lesbian and Cretan forms are due to the island effect. Even less is possible to answer whether the same trend evolved in different islands is parallel or whether it rather refers to common ancestry of them.

Despite that and possible local variations in the region, we consider Cretan as well as east-Aegean (incl. the Lesbian) and west-Anatolian populations of *M. blythii* to represent a ‘taxonomic transition’ between the two named continental forms, creating a wide margin of ranges of the two clearly metrically defined subspecies. However, if we regard any taxon to represent a natural unit of the classification of the nature and its organisms, we should consider such statement as a very tentative conclusion only. The further information from different sources (e.g. geometric morphometry, microsatellites, nuclear markers, etc.) on relationship of the Cretan bats to European or Asian phylogenetic groups is urgently needed.

Myotis emarginatus (Geoffroy, 1806)

RECORDS. Original data: C h a n i a: Agia Eirini, stream [1], 18 August 2008: net. 1 ma; – Champatha, Vennidon cave [2], 12 May 2007: net. 1 fa; – Palaiochora, gallery [3], 25 April 2008: obs. ca. 50 inds. (exam. 3 fa), 27 April 2008: obs. ca. 25 inds., det. & rec. several inds.; – Perivolia, Mamaloukou cave [4], 30 April 2008: obs. several inds., 2 May 2008: obs. & exam. 2 fa; – Tavronitis [5], highway, 24 April 2008: coll. 1 m (NHMC FC11140 [A]). – I r a k l e i o: Ampelouzoz, gorge, mines [6], 17 May 2008: obs. several inds. (exam. 4 fa); – Ano Asites, Nykteridospilios cave [7], 23 April 2005: obs. & coll. 1 fs (NHMC FC7730 [F]), 30 May 2005: net. 5 faG, 14 June 2005: obs. several adults and 10 juv. inds., 26 June 2005: net. 4 mj, 4 fL, 1 fs, 4 fj, 1 ind., 14 July 2005: obs. several inds., 31 May 2006: obs. ca. 50 inds., 5 July 2007: obs. ca. 80 juv. inds., 23 May 2008: obs. ca. 10 inds. (exam. 3 faG, 1 faL, 1 fs); – Astrakoi, gorge [8], 14 August 2008: net. 1 fs; – Giouchtas hill, Stravomyti cave [9], 7 June 2008: net. 34 faL, 8 fs; – Sarchos, Chonos cave [10], 20 May 2005: net. 5 fa, 1 fs, 14 June 2006: obs. 15 juv. inds.; – Tyllisos, Kamilari cave [11], 16 June 2005: obs. ca. 50 inds. (ad.+juv.), 7 April 2006: net. 2 fa, 16 May 2006: net. 2 fs, 12 June 2006: net. 6 mj, 2 faL, 1 fs, 3 fj, 12 July 2006: net. 1 fj, 4 April 2007: obs. ca. 30 inds., 20 April 2007: net. 4 ma, 1 fs, 13 April 2008: net. 5 fa, 2 fs. – R e t h y m n o: Argyroupoli, Mouselas river [12], 16 August 2008: net. 1 ms, 1 fs, 2 inds.; – Prinos, Prinou cave [13], 19 June 2008: net. 1 faL, 1 fj. – **Published data:** C h a n i a: Hania [= Chania] [14], 12 August 1971: 1 fa (Hanák et al. 2001); – Moni Katholiko, Agios Ioannis cave [= Katholiko monastery, Agiou Ioanni cave] [15], 4 May 2003: det. 3 inds. (Skiba 2007); – Topolia [16], 1973–1975: 6 inds. (from owl pellets) (Pieper 1977). – I r a k l e i o: Amoudara, canyon [= Linoperamata, rocky canyon] [17], 1 ind. (from owl pellets) (Hanák et al. 2001); – Sarchos [18], 1973–1975: 2 inds. (from owl pellets) (Pieper 1977); – Skotino, cave [= Skoteino, Agias Paraskevis cave] [19], 1973–1975: 1 ind. (from owl pellets) (Pieper 1977). – L a s i t h i: Kroustas [20], 1 May 2004: det. 2 inds. (Skiba 2007); – Milatos Spilia [= Milatos, Milatou cave] [21], 28 April 2004: det. 2 inds. (Skiba 2007). – R e t h y m n o: Melidoni Andro [= Melidoni, Gerontospilios cave] [22], 30 April 2003: det. 5–8 inds. (Skiba 2007).

COMMENTS. *Myotis emarginatus* is a relatively uncommon bat in Crete, it was recorded at 22 sites situated in a limited range of 5–600 m a. s. l. but covering almost whole the island (Fig. 16). This bat favours rather low altitudes (Table 2); the real findings of bats are available only from the summer season when this preference is even remarkable (mean 200.6 m, median 150.0 m, n=18).

Most of the Cretan records of *M. emarginatus* are associated with underground spaces (10 sites, i.e. 45.5%), mainly natural caves (8) and also two mines. These records represent both findings of bats in their roosts (13 evidences) and nettings/recordings of emerging and/or swarming individuals (13). Foraging bats were evidenced at seven sites (31.9%) in areas not directly related to their roosts, recorded by an ultrasound detector (3 evidences) and/or netted (3); one finding represents a foraging bat killed by a car (PG). Pieper (1977) reported findings of this bat in the

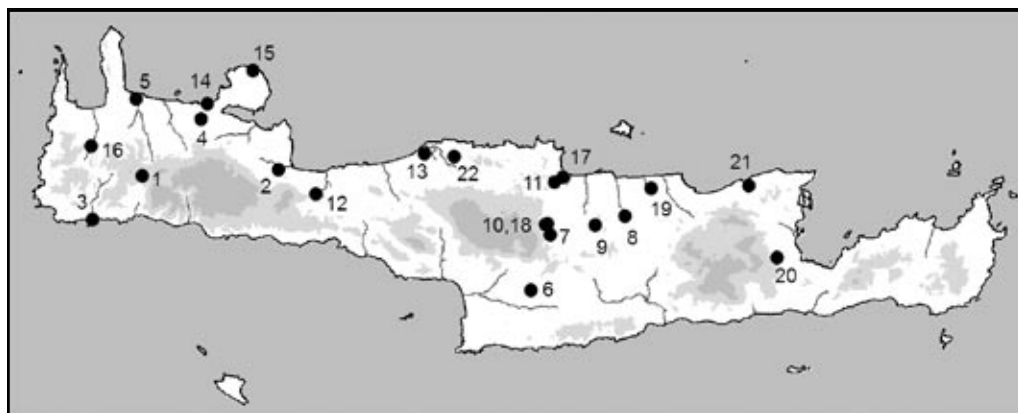


Fig. 16. Records of *Myotis emarginatus* (Geoffroy, 1806) in Crete.

barn owl pellets from three sites and these records represented the only published evidence of *M. emarginatus* from Crete for almost 25 years; another pellet record was mentioned by Hanák et al. (2001) from a canyon at Linoperamata. These four sites with owl pellet records represent 18.2% of the recorded localities.

Evidences representing nursery colonies of *M. emarginatus* (both directly observed and indirectly assumed) were made at least at five sites, four in natural caves and one in a mine. The nursery colonies were composed of several individuals up to several tens of individuals (maximum of 80 juvenile bats was observed in one aggregation). Neither wintering groups nor solitary hibernating individuals of *M. emarginatus* have been found in Crete so far.

Although not rare in southern Europe, including mainland Greece (see Hanák et al. 2001), in the Mediterranean islands the records of *M. emarginatus* are rather exceptional. In the western part of the Mediterranean Basin, Mitchell-Jones et al. (1999) showed its occurrence only in Menorca, Corsica, Sardinia, and in the Dalmatian islands. From Greek islands, Hanák et al. (2001) reported it only from Ikaria, Karpathos, and Crete; Niethammer (1962) suggested occurrence of the species in Corfu based on bone remnants found in the barn owl pellets (but possibly coming from *Myotis nattereri*, see also Hanák et al. 2001). In the eastern Mediterranean region, *M. emarginatus* occurs in the Mediterranean habitats along the Levantine Sea shore, including Cyprus (see the review by Benda et al. 2006). In that island, however, this bat was found only at two sites, both in the mountains and in lowland, and thus represents one of the rarest Cypriot bats (Benda et al. 2007).

Myotis aurascens Kusjakin, 1935

RECORDS. **Original data:** Chania: Agia Eirini, stream [1], 18 August 2008: net. 1 ma; – Katholiko monastery (Fig. 12), Agiou Ioanni cave [2], 28 April 2008: net. 3 fa, 27 May 2008: net. 1 faG (NMP 92330 [S+A]); – Meskla, above a creek [3], 5 October 2006: net. 1 ma (NMP 91191 [S+A]); – Omalos Plateau, Tzani cave [4], 17 August 2008: net. 1 ma (CDIS 1107 [S+A]). – Iraklio: Laloumas, Koutsoulitis river [5], 16 April 2008: coll. 1 ms (NHMC FC11838 [F]); – Pompia, sewage installation [6], 19 March 2008: coll. 1 mummy (NHMC FC11127; leg. G. Alexandrakis). – Rethymno: Lefkogeia, wall fissure of an old bridge ca. 4 km E of the Kato Preveli Monastery [7] (Figs. 17, 18), 16 August 2008: obs. 6 inds. (exam. 3 fa, 1 fs; coll. 1 fa, CDIS 1106 [S+A]); – Petradolakia (Idi Mts.), Agios Fanourios chapel, pothole [8], 20 August 2008: net. 4 ma. – **Published data:** Chania: Stavros, cave [= Lera cave] [9], 10 July 1995: net. 1 ma (NMP 48345 [S+A]) (Benda & Tsytsulina 2000, Hanák et al. 2001, Benda & Karataş 2005, Benda et al. 2006). – Lasiathi: Milatos [10], 28 April 2004: 3 inds. (Skiba 2007 [as *M. mystacinus*]); – Tholos/Kavousi [11], 27 April 2004: obs. 1 ind. (“mit starkem Licht bestimmt”) (Skiba 2007 [as *M. mystacinus*]).

COMMENTS. In accordance with results of the morphological analysis by Benda & Karataş (2005) covering also a specimen from Crete, we regard systematic affiliation of the Cretan populations of the *Myotis mystacinus* complex tentatively to *M. aurascens*, though several authors doubted specific status of this form (Mayer & von Helversen 2001a, Simmons 2005, Mayer et al. 2007). It should be remembered here, of course, that the question of real taxonomic diversity of *M. mystacinus* group in the Mediterranean region is far of being satisfactorily resolved. Hence, it seems to be well substantiated to classify it provisionally in terms of the phenotypically distinct units as suggested in diagnosis of *M. aurascens* by Benda & Tsytsulina (2000) and we follow that scheme also in the present paper.

Myotis aurascens is a rather rare bat species in Crete, only 11 records are known from throughout the island (Fig. 19). Although these records come from a wide range of altitudes 5–1464 m a. s. l., most of them are situated in medium altitudes (mean 342.2 m, median 96.0 m). More than one third of the *M. aurascens* records (4 sites, i.e. 36.4%) is associated with underground spaces, natural caves and a pothole (nettings of emerging and/or swarming individuals). Records of foraging bats in the areas probably not directly related to their roosts were obtained from five



Figs. 17, 18. Habitat of *Myotis aurascens* Kujakin, 1935 in Crete; bridge above the Kourtaliotis river near Lefkogeia (both photos by C. Dietz). 17 (above) – six bats were found roosting in a fissure of a small stone bridge. 18 – foraging habitat above the Kourtaliotis river.

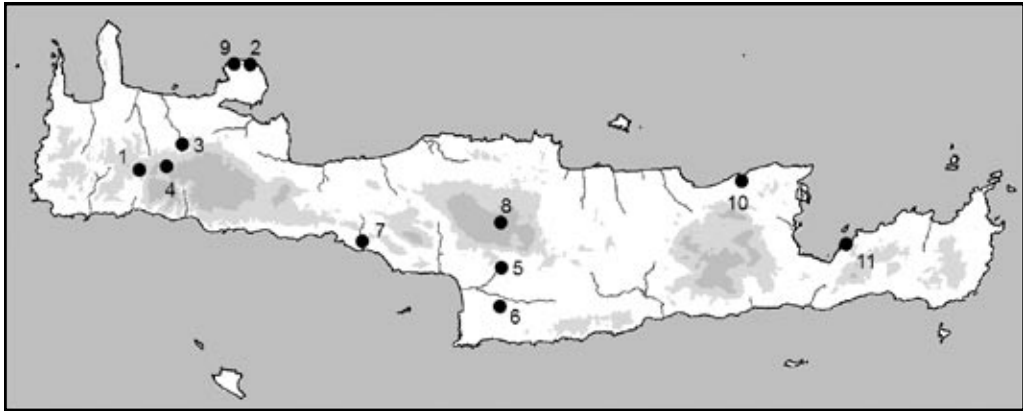


Fig. 19. Records of *Myotis aurascens* Kuszakin, 1935 in Crete.

sites (45.5%); the bats were netted or recorded by an ultrasound detector (Skiba 2007). One roost of a colony was discovered in August 2008; a group of six individuals representing probably a remnant of a nursery colony occupied a fissure in an old bridge at the Kato Preveli monastery (Fig. 17). No hibernation roost of *M. aurascens* was found in Crete and no bone remain was discovered in owl pellets. External and cranial dimensions of examined specimens of *M. aurascens* from Crete are shown in Table 8.

Table 8. Basic biometric data [in mm] on examined Cretan samples of *Myotis aurascens* Kuszakin, 1935 and *M. capaccinii* (Bonaparte, 1837); for abbreviations see p. 110

	<i>Myotis aurascens</i>					<i>Myotis capaccinii</i>				
	n	M	min	max	SD	n	M	min	max	SD
LC	2	41.5	41	42	0.707	3	54.0	54	54	0.000
LCd	2	45.5	44	47	2.121	3	47.0	45	49	2.000
LA _t	5	33.98	33.7	34.8	0.460	3	41.03	40.2	41.5	0.723
LA	2	15.90	15.3	16.5	0.849	3	16.10	15.8	16.5	0.361
LTr	2	7.15	7.0	7.3	0.212	3	6.63	6.3	7.2	0.493
LCr	5	13.70	13.56	13.83	0.120	3	15.10	14.87	15.27	0.207
LCb	5	13.06	12.92	13.28	0.135	3	14.22	14.16	14.28	0.060
LaZ	5	8.15	7.97	8.42	0.175	1	9.32			
LaI	5	3.22	2.97	3.40	0.162	3	3.56	3.54	3.61	0.040
LaN	5	6.55	6.36	6.76	0.153	3	7.76	7.73	7.81	0.042
LaM	4	6.95	6.87	7.03	0.068	3	7.99	7.85	8.06	0.118
ANc	5	4.68	4.51	4.77	0.115	3	5.57	5.42	5.76	0.172
CC	5	3.36	3.15	3.52	0.139	3	3.90	3.88	3.93	0.029
M ³ M ³	5	5.28	5.13	5.38	0.107	3	5.97	5.96	5.98	0.012
CM ³	5	5.21	5.06	5.32	0.103	3	5.69	5.61	5.79	0.092
LMd	5	9.68	9.34	9.92	0.214	3	10.69	10.64	10.75	0.055
ACo	5	2.76	2.63	2.83	0.080	3	2.90	2.81	2.98	0.086
CM ₃	5	5.50	5.31	5.57	0.108	3	5.95	5.91	5.98	0.038

The large-sized bats of the *Myotis mystacinus* complex with rather lightly built teeth, attributed to *M. aurascens* by Benda & Tsytsulina (2000), are distributed in southeastern Europe from Italy, Dalmatia, and the Balkans to southern Ukraine and Caucasus and in the western part of the Middle East (Benda & Karataş 2005). Crete is the only larger island where this bat was found, and its area represents one of the southernmost marginal points of the species distribution range. Concerning its presence in islands, *M. aurascens* is known – besides Crete – only from offshore islands of Dalmatia (Šolta, Brač, Hvar, Korčula, Lastovo, Mljet; Dulić & Tvrtković 1970 [under *M. mystacinus*]) and possibly also from Corfu (cf. Niethammer 1962). On the other hand, in the Balkans and along the south-Anatolian coast this form is not a rare faunal element (von Helversen 1989, Hanák et al. 2001, Benda et al. 2003, own unpubl. data).

Myotis capaccinii (Bonaparte, 1837)

RECORDS. Original data: C h a n i a: Champatha, Vennidon cave [1], 4 April 2007: net. 2 ma, 4 ms, 11 fa, 5 fs, 12 May 2007: net. 4 ma, 11 faG; – Fylaki, Psimaki cave [2], 29 January 2006: obs. 4 inds., 8 July 2006: obs. several inds. (exam. 1 faL), 21 March 2008: obs. several inds., 6 July 2008: obs. 5 inds. (exam. 1 fj), 16 August 2008: obs. ca. 50 inds. (exam. 13 ma, 10 ms, 11 fa, 12 fs); – Kalami, Kiliaris river at the highway bridge [3], 9 October 2007: obs. & det. 1 ind.; – Kavalos, NW shore of the Kourna lake [4], 1 June 2008: det. 3 inds.; – Myloniana, Koulieri cave [5], 24 July 2007: net. 1 faL, 1 fs; – Omalos Plateau, Tzani cave [6], 17 August 2008: obs. several inds. – I r a k l e i o: Linoperamata, Almyros river [7], 5 June 2008: det. & rec. 4 inds.; – Spilia, Agia Eirini chapel, 2 km S of Knossos, above a brook [8], 26 May 2008: det. 2–3 inds.; – Tylisos, Kamilaris cave [9], 3 February 2006: net. 3 ma, 1 m, 16 May 2006: net. 1 ma, 1 faG, 1 fs, 12 June 2006: net. 2 fj, 9 November 2006: net. 1 ind., 23 March 2007: net. 2 m, 28 July 2007: net. 1 mj; – Zaros, Votomos lake [10], 25 May 2008: det. & rec. 1–2 foraging inds. – R e t h y m n o: Argyroupoli, Mouselas river [11], 3 June 2008: net. 2 faL (NMP 92345, 92346 [S+A]), det. & rec. 1 ind., 16 August 2008: net. 2 ms, 2 ma, 2 fs; – Dramia, Petres river bridge [12], 6 October 2006: net. 1 fa (NMP 91196 [S+A]); cf. Benda et al. 2007); – Lefkogeia, at a Venetian bridge ca. 3 km E of the Kato Preveli Monastery [13], 30 May 2008: det. & rec. several foraging inds.; – Monastiraki, Genianos stream [14], 2 June 2008: det. & rec. 6 inds.; – Prinou, Prinou cave [15], 19 June 2008: net. 1 fj, 1 fs. – **Published data:** C h a n i a: Limni Kourna [= Mouri, Kourna lake] [16], 2 May 2003: det. 10–15 inds., 3 May 2003: det. 15–20 inds. (Skiba 2007). – L a s i t h i: Amoudara [= Ammoudara] [17], 29 April 2004: det. 5–7 inds. (Skiba 2007); – Elounda [18], 24 April 2004: det. 10–15 inds. (Skiba 2007); – ‘Stausee’ 4 km NW of Ierapetra [= Gra Lygia, Mpramianos river dam] [19], 30 April 2004: det. 8–10 inds. (Skiba 2007); – Piskokefalo [20], 21 May 1960: 2 inds. (Kock 1974b, cf. Kahmann & Çağlar 1960).

COMMENTS. For a long time, *Myotis capaccinii* has been known from Crete from a single record from Piskokefalo, somewhat enigmatically published by Kahmann & Çağlar (1960); the record

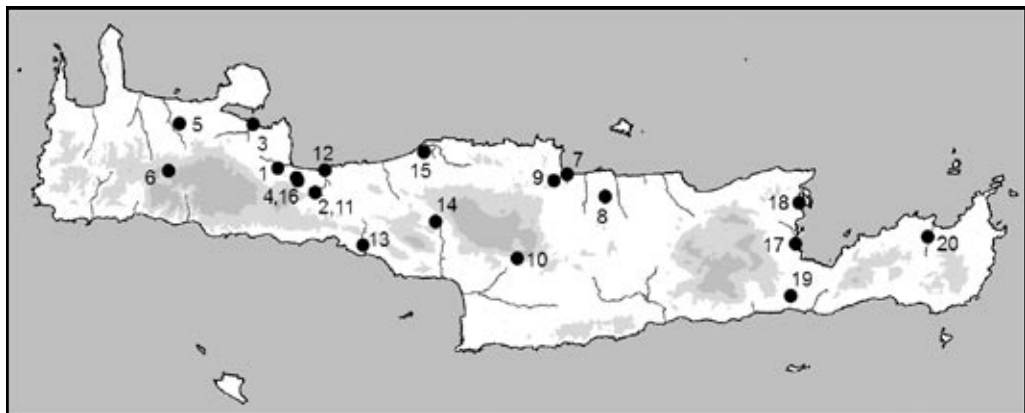


Fig. 20. Records of *Myotis capaccinii* (Bonaparte, 1837) in Crete.

was later specified by Kock (1974b) in a parasitological paper. Several bat detector records were added by Skiba (2007). Here we present 20 record localities covering nearly the whole island, the pattern suggesting a 'patchy' distribution and relative rarity of this bat in Crete (Fig. 20). The sites are situated in a relatively wide range of altitudes, exceeding 1000 m a. s. l. (Table 2). However, *M. capaccinii* prefers sites at lower altitudes (Table 2); this preference is especially apparent in the data on the summer season (mean 159.4 m, median 93.0 m, n=20). Also the two available winter records come from rather low situated sites, 116 m and 260 m a. s. l.

With the exception of one site, the Tsani cave (1025 m a. s. l.), all localities of *M. capaccinii* in Crete lie below 410 m a. s. l. In the Tsani cave, the bats probably formed a transition colony, as it was evidenced in late summer. The bats probably hibernate in the cave, but it is unlikely that they occupy the site in late spring or early summer (perhaps except for males). Thus, the presence of the species in higher altitudes seems to be related to hibernation (as in *M. blythii*).

Majority of Cretan records of *M. capaccinii* (13 sites, i.e. 65.0%) refers to foraging bats in the areas not directly connected with their roosts, mainly with the use of ultrasound detectors (12 evidences) but also by netting (3). With two exceptions of sites of undefined habitats reported by Skiba (2007), these records represent typical foraging habitats of *M. capaccinii* – water bodies including streams, rivers and three large reservoirs (Kourna, Mpramianos and Votomos lakes). Six records (30.0% of sites) are associated with underground spaces, solely natural caves. These records include both findings of bats in their roosts (6 evidences) and nettings/recordings of emerging and/or swarming individuals (10). No records were made in overground shelters and also no remains of *M. capaccinii* are available from owl pellets. External and cranial dimensions of examined specimens of *M. capaccinii* from Crete are shown in Table 8.

Evidence of a possible nursery colony of *M. capaccinii* was obtained in one site, in the Psimaki cave near Fylaki, however, composed of several bats only (and with as much as 50 individuals observed in August). In addition, this cave is the only known winter roost of the species in Crete; the twice evidenced wintering groups were also composed of several bats only. Anyhow, even a mid-winter check of the site on 29 January 2006 found the bats active and mating; the cave seems to be too warm for true hibernation.

M. capaccinii is a typical bat of the Mediterranean Basin, occurring mostly in a narrow belt along the coast of the Mediterranean Sea from eastern parts of Spain and Morocco to the Levant and Mesopotamia, with the exception of arid sections in northeastern Africa. It is more widespread in the Balkans including Greece; it was recorded in all geographical parts of this country (Hanák et al. 2001). Numerous records are known also from western Mediterranean islands; Mitchell-Jones et al. (1999) showed presence of *M. capaccinii* in Mallorca, Menorca, Corsica, Sardinia, Sicily, and in Dalmatian islands. In the east-Mediterranean islands this bat is a rather exceptional faunal element, until now it was recorded only in Thasos, Samos, Crete, and Petalas (Hanák et al. 2001). Kahmann & Çağlar (1960) suggested its occurrence in Cyprus; however, it was not confirmed by subsequent studies (Benda et al. 2007, Georgiakakis & Nicolaou, unpubl. data).

***Eptesicus serotinus* (Schreber, 1774)**

RECORDS. **Original data:** C h a n i a: Agia Eirini, stream [1], 18 August 2008: net. 1 ma; – Kolymvari, cave above the village [2], 13 July 2008: a humerus in *Tyto alba* pellet; – Meskla, above a creek [3], 5 October 2006: net. 1 ma (NMP 91087 [S+A]); – Papadiana, ford [4], 17 July 2008: net. 3 ma, 1 fj, 21 July 2008: net. 1 ma; – Vryses Apokoronou, above river [5], 2 October 2006: det. 1 ind. – I r a k l e i o: Irakleio, city fortification walls [6], 8 July 2007: found 1 mj (leg. G. Alexandrakis), 21 July 2009: net. 1 fj; – Laloumas, Koutsoulitis river, at a Venetian bridge [7], 29 May 2008: det. & rec. 2 inds.; – Linoperamata, Almyros river spring [8], 5 June 2008: det. 1–2 inds.; – Rouva forest, Agiou Ioanni chapel, pasture [9], 4 June 2008: det. 1–2 inds.; – Zaros, Votomos lake [10], 25 May 2008: det. & rec. 2 foraging inds. – R e t h y m n o:

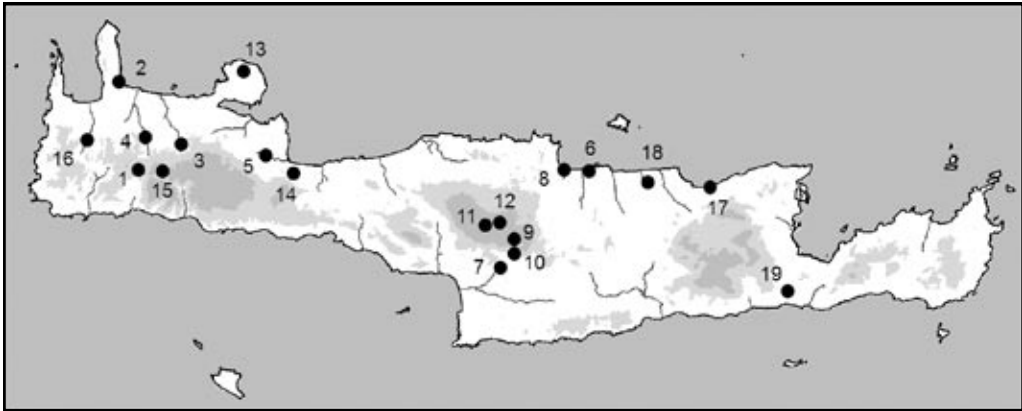


Fig. 21. Records of *Eptesicus serotinus* (Schreber, 1774) in Crete.

Nida Plateau (Idi Mts.), Ideo Andro cave [11], 30 September 2006: obs. & det. 2–3 inds.; – Petradolakia (Idi Mts.), Agios Fanourios chapel, pothole [12], 20 August 2008: net. 1 fa. – **Published data:** Chania: road from Moni Gouvernetou to Moni Agia Triada [= Gouvernetou monastery to Agias Triadas monastery] [13], 4 May 2003: det. 1 ind. (Skiba 2007); – Limni Kourna [= Kourna lake] [14], 2 May 2003: det. 2 inds. (Skiba 2007); – spring in a valley above Samaria, road to Omalos [15], 16 June 1942: 1 ind. (Pohle 1953); – Topolia [16], 1973–1975: 2 inds. (from owl pellets) (Pieper 1977). – Irakleio: Ag. [= Agio] Pnevma [17], 1973–1975: 2 inds. (from owl pellets) (Pieper 1977); – Skotino, cave [= Skotino, Agias Paraskevis cave] [18], 1973–1975: 1 ind. (from owl pellets) (Pieper 1977). – Lassithi: ‘Stausee’ 4 km NW of Ierapetra [= Gra Lygia, Mpramianos river dam] [19], 30 April 2004: det. 1 ind. (Skiba 2007).

COMMENTS. *Eptesicus serotinus* is a rather uncommon bat in Crete, it was recorded only at 19 sites, however, in almost all parts of the island (Fig. 21). The localities are situated in a wide range of altitudes, reaching up to 1500 m a. s. l. (Table 2), the species prefers rather medium elevated sites (mean 362.9 m, median 207.5 m).

At the majority of record sites (12, i.e. 63.2%), foraging individuals of *E. serotinus* were evidenced by an ultrasound detector (8 evidences) and/or netted (3) in the areas not directly connected with their roosts. Two record sites (10.5%) were underground spaces, a natural cave and a pothole. Perhaps both these findings were related to roosts; at the Ideo Andro cave the bats were observed to emerge from fissures in the rocky wall above a huge entrance of the cave just before sunset. Only two records were made in an anthropogenic habitat, a juvenile male and a juvenile female were found at the city walls of Irakleio on 8 July 2007 and 21 July 2009, respectively, representing indirect evidences of maternity colonies in the city. Findings of *E. serotinus* in owl pellets are known from four sites (21.0%); Pieper (1977) reported them from three sites, one additional record has been made recently, in a cave above Kolymvari. External and cranial dimensions of the examined specimen of *E. serotinus* from Crete are shown in Table 9.

The occurrence of *E. serotinus* in Crete more or less continues its distribution range in the Balkans (Mitchell-Jones et al. 1999) as well as Turkey (Benda & Horáček 1998). In the eastern Mediterranean region it belongs to rather frequently recorded bats, known from all geographical parts of Bulgaria (Benda et al. 2003) and Greece (Hanák et al. 2001). The species is known from a lot of Greek islands; Hanák et al. (2001) reviewed records from Samothrace, Lesbos, Skyros, Euboea, Samos, Crete, and Corfu, additionally it was found in Rhodes (von Helvesen 1998) and Thasos (Lane & Alivizatos 2006).

Table 9. Basic biometric data [in mm] on examined Cretan samples of *Eptesicus serotinus* (Schreber, 1774), *Hypsugo savii* (Bonaparte, 1837), *Pipistrellus kuhlii* (Kuhl, 1817), and *P. nathusii* (Keyserling et Blasius, 1839); for abbreviations see p. 110

	<i>Hypsugo savii</i>				<i>Pipistrellus kuhlii</i>				<i>Eptesicus serotinus</i>	<i>Pipistrellus nathusii</i>		
	n	M	min	max	SD	n	M	min			max	SD
LC	12	49.2	45	53	2.329	17	47.9	45	51	2.106	75	–
LCd	12	41.2	37	45	2.406	17	40.6	38	43	1.583	62	–
LAAt	12	33.67	31.2	36.1	1.418	18	33.42	31.0	35.1	1.038	52.7	33.9
LA	12	14.33	13.2	15.5	0.610	17	14.05	13.4	15.2	0.542	22.3	–
LTr	12	4.97	4.4	5.8	0.368	17	5.86	5.10	6.50	0.357	8.1	–
LCr	10	13.43	12.71	13.83	0.356	15	13.25	12.76	13.61	0.239	21.39	13.33
LCb	10	13.07	12.38	13.68	0.431	15	12.81	12.39	13.20	0.243	20.58	12.67
LaZ	10	8.73	8.49	8.93	0.139	11	8.51	8.24	8.85	0.173	14.08	8.06
LaI	10	3.37	3.17	3.61	0.118	15	3.21	3.12	3.43	0.084	4.44	3.48
LaN	10	6.55	6.21	6.74	0.143	15	6.59	6.40	6.78	0.117	9.61	6.83
LaM	10	7.32	7.07	7.64	0.185	14	7.44	7.01	7.71	0.203	11.07	7.28
ANc	10	4.44	4.28	4.61	0.104	15	4.71	4.53	4.88	0.099	6.46	4.58
CC	10	4.38	4.19	4.75	0.179	15	4.19	4.01	4.34	0.114	6.87	3.96
M ³ M ³	10	5.79	5.61	6.03	0.148	15	5.53	5.29	5.73	0.128	8.91	5.26
CM ³	10	4.65	4.43	4.88	0.125	15	4.98	4.81	5.15	0.091	8.28	4.49
LMd	10	9.56	9.08	9.97	0.275	15	9.58	9.34	9.88	0.179	15.59	9.18
ACo	10	3.08	2.67	4.83	0.631	15	3.04	2.85	3.21	0.111	5.87	2.25
CM ₃	10	4.96	4.74	5.11	0.118	15	5.35	5.18	5.49	0.085	9.15	4.75

Hypsugo savii (Bonaparte, 1837)

RECORDS. **Original data:** Chani: Afrata, rocky cliff above sea [1], 14 July 2008: det. 1 ind.; – Agia Eirini, above stream [2], 18 August 2008: net. 5 ma, 2 ms, 1 fa, 4 fs; – Kavalos, NW shore of the Kourna lake [3], 1 June 2008: det. & rec. 3 inds.; – Kolymvari, old agricultural co-op facilities [4], 14 and 20 July 2008: det. & obs. swarming of 4–6 inds.; – Limni, pond [5] (Fig. 51), 19 August 2008: net. 2 ma, 2 fa, 3 fs; – Meskla, above a creek [6], 5 October 2006: net. 2 ma (NMP 91088, 91089 [S+A]; cf. Benda et al. 2006), det. several inds.; – Omalos Plateau, Tzani cave [7], 17 August 2008: net. 1 ma; – Papadiana, ford [8], 19 July 2008: net. 1 fa, 21 July 2008: net. 2 mj, 1 fa, 1 fj; – Platyvola, Athymolakos

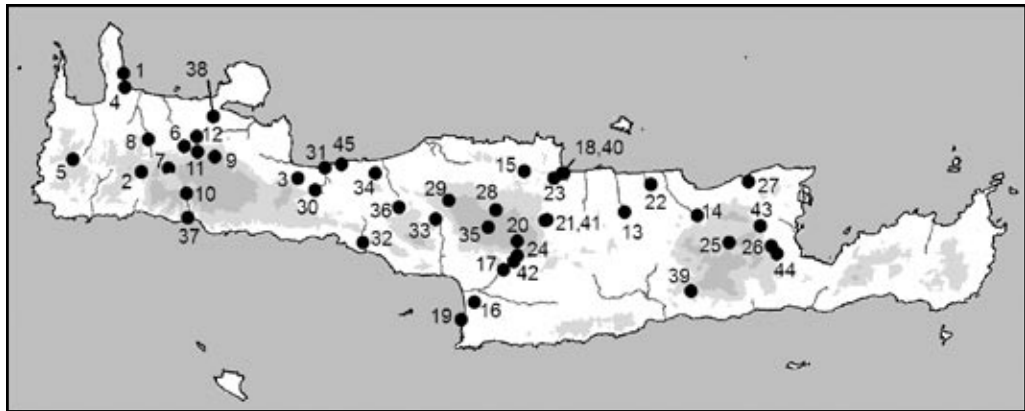


Fig. 23. Records of *Hypsugo savii* (Bonaparte, 1837) in Crete.



Fig. 22. Water sources are rare in the karstic mountains of Crete and usually attract many bats for drinking. At this site near Archaia Eleftherna in the Aravanes oak forest 36 individuals of *Hypsugo savii* and 8 individuals of *Pipistrellus hanaki* were captured in one evening (photo by C. Dietz).

Plateau [9], 22 July 2008: net. 5 ma, 4 mj, det. several inds.; – Samaria, gorge [10], 5 July 2008: net. 1 ma; – Theriso, Aliakes Plateau [11], 2 November 2008: net. 1 ms; – Theriso, Sarakinas cave [12], 8 October 2007: obs. & det. several inds. – I r a k l e i o: Astrakoi, gorge [13], 14 August 2008: net. 1 ma, 2 fs; – Avdou, at the Agias Foteinis cave [14], 10 October 2007: det. several inds.; – Damasta, scrubland [15], 5 June 2008: det. & rec. several inds.; – Kamilari, village [16], 10 August 2008: obs. & exam. 1 fa; – Laloumas, Koutsoulitis river, under a Venetian bridge [17], 29 May 2008: det. & rec. 1 ind.; – Linoperamata, Almyros river spring [18], 5 June 2008: det. & rec. 3 inds.; – Matala, sea shore [19], 8 October 2006: det. several inds.; – Rouva forest, Agiou Ioanni chapel, pasture [20], 4 June 2008: det. & rec. 2 inds.; – Sarchos, Chonos cave [21], 20 May 2005: coll. 1 f (NHMC FC7732 [F]), 1 December 2005: net. 2 ma, 22 August 2006: net. 2 ma, 1 fs, 9 September 2006: net. 1 ma; – Skoteino, Agias Paraskevis cave [22], 4 October 2006: det. plenty inds.; – Tylisos, Kamilari cave [23], 16 May 2006: net. 1 m, 1 fs; – Zaros, Votomos lake [24], 25 May 2008: det. & rec. several foraging inds. – L a s i t h i: Agios Konstantinos, pools of a brook near the Chonos sinkhole [25], 28 May 2008: det. & rec. 3 inds.; – Kritsa, Gaidourotrypa cave [26] (Fig. 2), 31 May 2008: det. & rec. 2 inds.; – Milatos, Milatou cave [27], 7 October 2006: net. 2 ma, 1 fa (NMP 91109–91111 [S+A]; cf. Benda et al. 2006). – R e t h y m n o: Agios Yakinthos (Idi Mts.), water dam [28], 13 July 2008: net. 3 ma, 2 fa, 1 faL, 11 August 2008: net. 1 ma; – Archaia Eleftherna, Aravanes oak forest [29] (Figs. 3, 22), 13 August 2008: net. 17 ma, 9 ms, 5 fa, 2 fs, 1 fj; – Argyroupoli, Mouselas river [30], 16 August 2008: net. 2 ma, 1 ms, 2 fa, 1 fs; – Dramia, Petres river bridge [31], 6 October 2006: net. 2 ma, 1 fs (NMP 91094, 91095 [S+A], 91096 [A]; cf. Benda et al. 2006); – Lefkogeia, at a Venetian bridge ca. 3 km E of Kato Preveli Monastery [32], 11 October 2007: net. 1 ma, 1 ms (NMP 92309, 92310 [S+A]), 30 May 2008: det. & rec. 1 ind.; – Monastiraki, Genianos stream [33], 2 June 2008: det. & rec. 3 inds.; – Myloi, abandoned village [34], 12 June 2008: exam. 1 ma; – Nida Plateau (Idi Mts.), Ideo Andro cave [35], 30 September 2006: net. 1 ind., det. several inds.; – Patsos, Agiou Antoniou cave [36], 3 October 2006: net. 1 ms, 1 fs (NMP 91082 [A], 91083 [S+A]; cf. Benda et al. 2006). – **Published data:** C h a n i a: Agia Roumeli, a rocky cliff [37], 14 July 1995: det. 1 ind. (Hanák et al. 2001); – Koma [= Kourna] lake [3], SW shore, 1 ind. (Hanák et al. 2001); – spilaion Nerokourou [= Nerokouros, Nerokouros cave] [38], 1 m, 2 f (Iliopoulou-Georgudaki 1977); – Xyloskalo n. Omalos, cave [= Omalos Plateau, Tzani cave] [7], 13 July 1995: det. 1 ind. (Hanák et al. 2001).

– I r a k l e i o: Ano Viannos [39], 1973–1975: 1 ind. (from owl pellets) (Pieper 1977); – Amoudara, cave [= Linopetramata, Almyros river spring, cave] [40], 8 July 1995: det. 1 ind., rocky canyon, 7 July 1995: det. 1 ind. (Hanák et al. 2001); – Sarchos [41], 1973–1975: 5 inds. (from owl pellets) (Pieper 1977); – Zaros [42], 5 May 1975: 1 m (Iliopoulou-Georgudaki 1985). – L a s i t h i: Adrianou, Atzigkanospelos [= Atziganospilios cave] [43], 1 f (Iliopoulou-Georgudaki 1977), 10 September 1974: 1 f (Iliopoulou-Georgudaki 1985); – Kroustas [44], 1 May 2004: det. 2 inds. (Skiba 2007). – R e t h y m n o: Gerani, rocky canyon [45], 16 July 1995: det. 1 ind. (Hanák et al. 2001).

COMMENTS. As in other Mediterranean regions, *Hypsugo savii* ranks among rather common bat species in Crete, 45 records are available from nearly the whole island (Fig. 23). The only exception is the easternmost part of Crete where this bat has not been recorded, however, this situation is most probably caused by low survey effort there. The record sites are situated in a wide range of altitudes, reaching up to 1500 m a. s. l. (Table 2), most of them are concentrated to medium to higher altitudes in both summer and winter seasons (mean 414.1 m, median 250.0 m).

Majority of the Cretan findings of *H. savii* (25 sites, i.e. 55.6%) are related to foraging bats recorded in the areas not directly connected with their possible roosts, either netted (14 evidences) and recorded with aid of ultrasound detectors (13). One third of *H. savii* records (15 sites, i.e. 33.3%) are associated with rocky habitats and thus, presumably with possible roosts. Most of these sites are entrances of underground spaces (solely natural caves), however, some of them are represented by open rocks of cliffs, gorges and canyons. *H. savii* was found three times in a village, in Kamilari, Kolymvari and Myloi, pursuant to its tendency to synathropy, known from other parts of its distribution range. In all three sites it was found in abandoned buildings or in buildings under construction, typically visited during night and used as swarming places. Bat detector data suggest *H. savii* may forage in settlements, but it is there far less abundant than *Pipistrellus kuhlii*.

H. savii was found roosting in/at a cave three times, however, most of the cave netting/bat detector records are associated rather with swarming behaviour. Among the relatively numerous records of *H. savii* from Crete, no even indirect finding of a nursery colony or hibernation record are available, obviously due to roosting preferences in this species – it inhabits almost strictly the inaccessible rocky fissures (Horáček & Benda 2004). Pieper (1977) reported findings of this bat in the barn owl pellets from two sites. External and cranial dimensions of examined specimens of *H. savii* from Crete are shown in Table 9.

H. savii is one of the most widespread and the fifth most frequently found bat in Greece (Hanák et al. 2001), it was recorded in all geographical parts of the country with the exception of the Ionian islands; besides Crete, Hanák et al. (2001) reviewed records from the Aegean islands of Thasos, Samothrace, Euboea, Santorini, Amorgos, Rhodes, and Karpathos. Von Helversen (in Mitchell-Jones et al. 1999) showed another unspecified record from Cyclades (Naxos/Ios). Mitchell-Jones et al. (1999) showed this bat to be widely distributed in the European Mediterranean, including numerous islands (Mallorca, Menorca, Corsica, Sardinia, Elba, Sicily, Ustica, Lipari, Tremiti, many Dalmatian islands). In Cyprus, *H. savii* was found to be a rather frequent bat (Benda et al. 2007), though occurring in areas situated on average even higher than it was showed for Crete.

Pipistrellus hanaki Hulva et Benda, 2004

RECORDS. **Original data:** C h a n i a: Agia Eirini, stream [1], 18 August 2008: net. 3 ma, 3 fs; – Elos, chestnut and walnut grove ca. 1 km NE [2], 29 September 2006: det. 2–3 inds.; – Kandanos, chestnut grove with a creek [3], 3 November 2008: det. & rec. 1 ind.; – Limni, pond [4] (Fig. 51), 19 August 2008: net. 1 ma, 1 ms, 3 fa, 1 fs; – Omalos Plateau, Tzani cave [5], 1 October 2006: net. 1 ma (NMP 91180 [S+A]; cf. Hulva et al. 2007), obs. & det. swarming of ca. 5 inds., 17 August 2008: net. 1 ma; – Papadiana, ford [6], 17 July 2008: net. 2 mj, 1 fa, 19 July 2008: net. 1 mj, 1 fa; – Samaria, gorge [7], 4 June 2005: det. & rec. 1 ind., 5 July 2008: det. & rec. several inds.; – Theriso, Aliakes Plateau [8], 2 November 2008: det. & rec. 1 ind. – I r a k l e i o: Faistos, Geropotamos river [9], 28 February 2008: det. & rec. 1 ind.; – Kato Fortetsa [10], 22 April 2008: det. & rec. 1 ind.; – Laloumas, Koutsoulitis river, under a Venetian bridge [11], 29 May 2008: det. &

rec. 1 ind.; – Rouva forest, Agiou Ioanni chapel, pasture [12] (Figs. 24, 25), 1 November 2006: det. & rec. several inds., 4 June 2008: net. 6 ma (coll. 5 inds, NMP 92349–92351, 92353 [S+A], 92352 [A]), det. many foraging inds.; – Zaros, a brook ca. 1 km to N [13], 4 March 2006: det. & rec. 3 inds., 25 May 2008: net. 1 ma (NMP 92323 [S+A]); – Zaros, Votomos lake [14], 25 May 2008: det. & rec. 1+ foraging ind. – R e t h y m n o: Amnatos, village [15], 9 August 2008: det. & rec. 1 ind.; – Archaia Eleftherna, Aravanes oak forest [16] (Figs. 3, 22), 10 June 2008: det. & rec. several inds., 12 August 2008: net. 1 fa, 13 August 2008: net. 4 ma, 1 ms, 1 fa; – Argyroupoli, Mouselas river [17], 16 August 2008: net. 1 fs; – Klisidi, olive grove [18], 9 August 2008: det. & rec. several inds.; – Monastiraki, Genianos stream [19], 2 June 2008: net. 1 ma, 1 faG (coll. 1 m, NMP 92344 [S+A]), det. & rec. many foraging inds.; – Myrthios, Patsianos river [20], 24 August 2007: det. & rec. several inds., 8 January 2008: det. & rec. several inds.; – Roumeli, Geropotamos river [21], 18 April 2007: det. & rec. several inds., 26 June 2008: det. & rec. several inds. – **Published data** (all the data were published under *P. pipistrellus*): C h a n i a: Agia Roumeli, village [22], 14 July 1995: det. ca. 20 inds. (Hanák et al. 2001); – Elos [23], det., ?rec. (Mayer & von Helvesen 2001b); – Kisamo Kastelli, Korfalona [= Kissamos, Korfalona] [24], 20 April 1958: 1 m (Kahmann 1959); – Limni Kourna [= Mouri, Kourna lake] [25], 2 May 2003: det. 2 inds. (Skiba 2007). – L a s i t h i: Amoudara [= Ammoudara] [26], 29 April 2004: det. 2 inds. (Skiba 2007); – ‘Stausee’ 4 km NW of Ierapetra [= Gra Lygia, Mpramianos river dam] [27], 30 April 2004: det. 15–20 inds., perhaps a colony (Skiba 2007); – Kalamafka [28], 30 April 2004: det. 6 inds. (Skiba 2007); – Kroustas [29], 1 May 2004: det. 20–25 inds., probably a colony (Skiba 2007); – Psihro [= Psichro], village [30], 19 July 1995: det. 1 ind. (Hanák et al. 2001). – R e t h y m n o: Adele [31], 30 April 2003: det. 2 inds. (Skiba 2007); – Moni Arkadi [= Arkadiou monastery] and Amnatos, Kiriana and Adele [32], 28 April 2003: det. 4 inds. (Skiba 2007).

COMMENTS. *Pipistrellus hanaki* has been defined within the *P. pipistrellus* complex just recently (Hulva et al. 2004). Originally, it was described from Cyrenaica, Libya, and was considered endemic to this ‘island’ of Mediterranean habitats in northeastern Africa (Benda et al. 2004a). However, an individual belonging to the *P. hanaki* lineage has been very recently discovered in Crete (Hulva et al. 2007). The island represents the only European territory inhabited by this species, and moreover, no other member of the complex was found there (see below). Therefore, *P. hanaki* can be regarded as the most exotic European bat species (perhaps even more than *Myotis punicus* and/or *Eptesicus isabellinus* which are widespread NW African bats besides their European distribution).

P. hanaki belongs to moderately abundant bat species in Crete, 32 records are known from throughout the island (Fig. 26, Table 1). It occurs in a wide range of altitudes, from the sea level up to over 1000 m a. s. l. (mean 380.2 m, median 356.5 m). Both in summer and winter seasons, *P. hanaki* prefers sites at medium to higher altitudes (Table 2), dominated by forest habitats. Almost

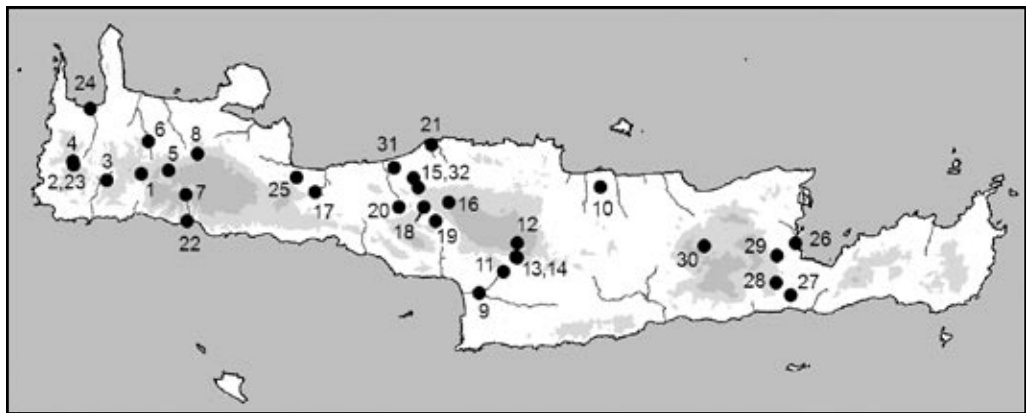


Fig. 26. Records of *Pipistrellus hanaki* Hulva et Benda, 2004 in Crete.



Figs. 24, 25. Two looks at the Rouva oak forest with pasture and creek, the foraging site and type locality of *Pipistrellus hanaki creticus* subsp. nov. (photo by Z. Bendová).

no roosts of *P. hanaki* were discovered in Crete, majority of the records was made at its foraging sites; at nine localities (28.1% of all sites) it was netted (altogether 36 individuals were recorded) and at 24 localities (75%) detected by an ultrasound detector (Hanák et al. 2001, Skiba et al. 2007, present data). Based on bat detector data, Skiba (2007) suggested presence of a colony at Kroustas (518 m a. s. l.). The only roost was described by Kahmann (1959); he found an individual roosting in a wooden box installed in the window of a solitary house at Korfalona in westernmost Crete. Thus, 37 individuals of *P. hanaki* were documented in Crete, a comparable number to those known from Cyrenaica, where 33 bats were caught in an area of comparable size, according to the available data (Qumsiyeh & Schlitter 1982, Hanák & Elgadi 1984, Benda et al. 2004a).

Bats of the *P. pipistrellus* complex are known to occur in the whole Mediterranean region with the only exceptions of arid areas of North Africa and the Middle East. Geographically and ecologically the occurrence spot in Crete is a part of a mosaic of islands almost completely covered by records of bats of the complex. They were found in all larger islands of the western Mediterranean (Ibiza, Mallorca, Menorca, Corsica, Sardinia, Elba, Sicily, Ustica, Malta, see Mitchell-Jones et al. 1999) as well as in a number of Aegean islands (Thasos, Samothrace, Lesbos, Chios, Skiathos, Euboea, Andros, Kithnos, Sifnos, Kimolos, Icaria, Samos, Kos, Rhodes, Karpathos, see Hanák et al. 2001). Bats of the *pipistrellus* lineage (i.e. *P. pipistrellus* s.str.) were confirmed in three eastern Mediterranean islands; with the exception of a single individual in Cyprus, being probably an accidental stray (see Benda et al. 2007), only in offshore Aegean islands of Samos and Rhodes (Mayer & von Helversen 2001b). However, bats of the *pygmaeus* lineage – to which *P. pygmaeus* and *P. hanaki* belong – are known at least from five islands of that region: from Lesbos and Rhodes (Hanák et al. 2001), Crete (Hulva et al. 2007), Kefalonia (Gaisler et al. 2006), and from Cyprus (Benda et al. 2007). While the Lesbian, Rhodian and Kefalonian populations were not investigated properly as only call recordings are available, those from the larger sea islands, Crete and Cyprus, were found to differ markedly from the mainland populations. Endemic forms live in the two islands; in Cyprus *P. pygmaeus cyprius* Benda, 2007, and in Crete an isolated population of a species known from the more distant African continent (see Taxonomy below). In the eastern Mediterranean, pipistrelles of the *pygmaeus* lineage seem to represent a more ancestral element than those of the *pipistrellus* lineage, the former being more diversified and distributed in more extreme and relic occurrence spots (large sea islands and Cyrenaica). However, more detailed investigation including broader geographical sampling is needed for a relevant comprehension to the history and evolution of this group in the respective region and the whole Mediterranean.

ECHOLOCAION. *P. hanaki* from Crete exhibits an echolocation behaviour being typical for the genus and especially very similar to *P. pipistrellus* (Fig. 27). The echolocation calls consist very close or within the vegetation of a short (<2 ms) and nearly pure FM-sweep, the greater the distance to background clutter, the longer the calls become and the more prominent gets the QCF-part of the call (Fig. 28). At distances of more than 10 m from background clutter nearly pure QCF-calls of more than 7 ms length are emitted (Fig. 29).

SF was in the mean (min–max; \pm SD; n) at 59.5 kHz (46.2–101.1; 10.0; 300); EF at 48.8 kHz (43.6–55.2; 2.0; 300); PDUR 4.3 ms (1.5–8.6; 1.6; 300); IPI 145.8 ms (62.0–266.0; 60.5; 254). The relation of end frequency and pulse duration is shown in Fig. 29. The quite long IPI given above can be best explained by the analysis of echolocation sequences recorded in free flight mostly, a situation where quite often less than one call per wingbeat were emitted.

P. hanaki can be well separated by its echolocation repertoire from all other bats of the island, with a small overlap with *Miniopterus schreibersii* in all call parameters (Georgiakakis unpubl. data). EF is much higher than in sympatric *Pipistrellus kuhlii* and *Hypsugo savii* (Fig. 30). However, echolocation calls are quite similar to and only slightly higher in their mean end frequency than

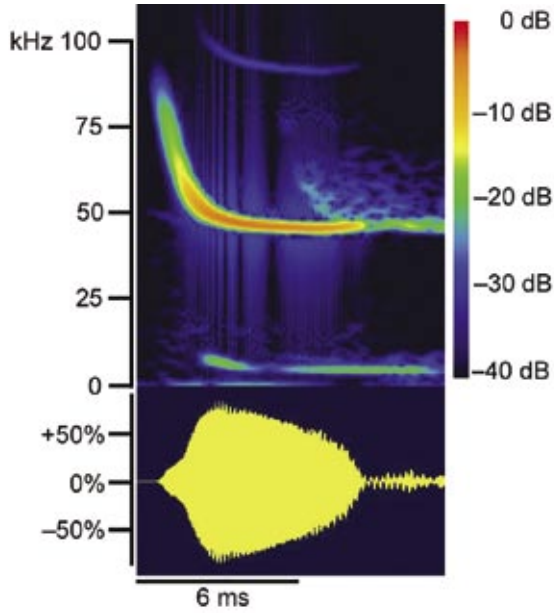


Fig. 27. Sonogram of a single echolocation call of *Pipistrellus hanaki* Hulva et Benda, 2004 from Crete. The typical QCF-call was emitted in open space situation when foraging at late dusk above a *Quercus coccifera* forest in 10 m distance from the next obstacle.

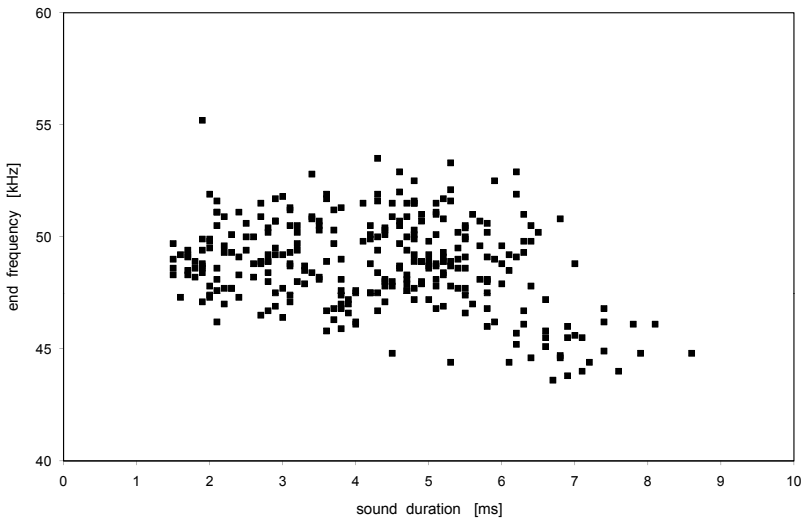


Fig. 29. End frequencies of 300 echolocation calls of *Pipistrellus hanaki* Hulva et Benda, 2004 from Crete recorded from bats flying in open space. The plot shows the relationship between call duration and the end frequency. Statistical parameters of the frequency distribution are given in the text.

those of *P. pipistrellus* from the Greek mainland (EF 46.2 ± 1.9 kHz, $n=351$, Mayer & von Helversen 2001b). Furthermore, in Thrace and in Greek islands EF of the quite small *P. pipistrellus* is in a similar range to Cretan *P. hanaki* (47.5 ± 1.43 kHz, $n=47$, Papadatou et al. 2008, von Helversen, pers. comm., own unpubl. data). As a consequence, echolocation calls of *P. hanaki* differ markedly from those of *P. pygmaeus* from mainland Greece (EF 55.9 ± 1.7 kHz, $n=168$, Mayer & von Helversen 2001b; 56.2 ± 2.03 kHz, $n=45$, Papadatou et al. 2008). In summary, the Cretan *P. hanaki* belongs to a group of pipistrelle-like bats (genera *Pipistrellus* and *Hypsugo*) using QCF calls and mostly preferring a frequency range between 45 and 50 kHz. It can be speculated that this frequency range occupied by *P. pipistrellus*, *P. maderensis*, *P. hanaki*, *P. deserti* and *H. ariel* (own unpubl. data) is perfect for the pipistrelle-like bats being the best compromise between size resolution for detecting prey (the higher the frequency, the better the size resolution) and atmospheric attenuation (the higher the frequency the less is the distance the sound can travel). Hence, the taxonomic value of end frequency distributions seems to be limited to sympatric distributions of species groups of pipistrelle-like bats (e.g. *P. pipistrellus* and *P. pygmaeus*; see Jones & von Parijs 1993, Russo & Jones 2000, Mayer & von Helversen 2001b), while in allopatric distributions pipistrelle-like bat species seem to shift to the 45–50 kHz range even though they can be expected to call at higher (or at deeper) frequencies according to their phylogenetic origin (see also Hulva et al. 2004). This could explain, why the small *P. hanaki* from Crete calls at lower frequencies than its close related congener *P. pygmaeus* from Europe (Mayer & von Helversen 2001b). Unfortunately *P. hanaki* from Cyrenaica can not be compared in respects to echolocation, since no recordings are available at present (Benda et al. 2004a).

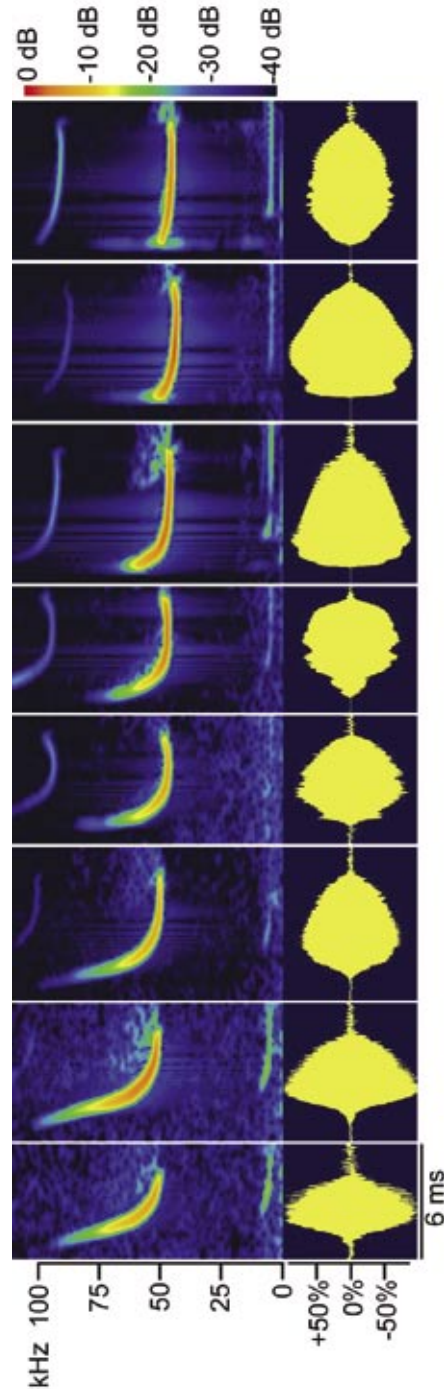


Fig. 28. Composed sonogram of eight typical calls of *Pipistrellus hanaki* from Crete showing the adaption of echolocation behaviour from close to vegetation (left) to clutter-free open space (right). The more open foraging situation the FM-part in beginning of the call is being reduced and the longer the calls get.

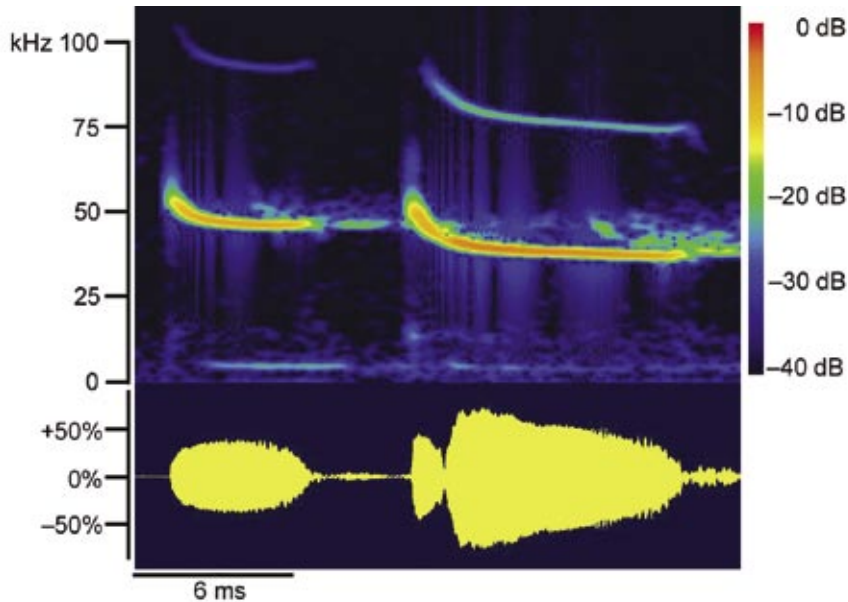


Fig. 30. One call of *Pipistrellus hanaki* Hulva et Benda, 2004 (left) and *Hypsugo savii* (Bonaparte, 1837) (right) recorded near Aravanes. The two sympatric pipistrelle-like species can be easily distinguished by their end frequencies of echolocation calls since the distributions do not overlap.

TAXONOMY. The first bat of the *Pipistrellus pipistrellus* group was discovered in Crete by Kahmann (1959), who reported a single specimen from Kissamos, northwestern Crete. This record, under affiliation to *P. pipistrellus* [s.l.], remained the only report of the species/species group from the island for more than forty years, see von Helversen (in Mitchell-Jones et al. 1999).

When the cryptic diversity in the *P. pipistrellus* group was discovered in Europe by the end of the twentieth century (see Mayer & von Helversen 2001b for a review), two species started to be recognised in the field according to echolocation call frequencies; the 55 kHz phonic type as *P. pygmaeus* (Leach, 1825) and the 45 kHz phonic type as *P. pipistrellus* (Schreber, 1774) s.str. Based on recordings of echolocation calls of the 45 kHz phonic type, Hanák et al. (2001), Mayer & von Helversen (2001b) and Skiba (2007) attributed new 10 records of pipistrelles from Crete to *P. pipistrellus* s.str. However, Hulva et al. (2004) according to the results of their molecular analysis suggested the 45 kHz phonic type to be ancestral within the species group and present in more populations than in *P. pipistrellus* s.str. only, including *P. hanaki* newly identified from Libyan Cyrenaica. Using molecular markers, the latter species was later confirmed also from Crete, the European island closest to Cyrenaica (Hulva et al. 2007).

A question arose, whether only pipistrelles of the Cyrenaican lineage occur in Crete or whether there live more species of the complex, similarly as in European or Asian mainlands. Hence, we selected a marker with high mutation rate (mtDNA control region) for screening of genetic classification of Cretan pipistrelles, both the collection ones and from biopsy samples of released bats (see Records). Phylogenetic relationships of the samples were investigated via tree building methods based on 164 sequences, representing whole range of *P. pipistrellus* complex (Hulva et al., unpubl.). We found only one lineage among the examined samples, *P. hanaki*, congruously

Table 10. Polymorphic sites identified in the partial sequence of mtDNA control region (303 bp) sequenced in *Pipistrellus hanaki* Hulva et Benda, 2004. Dot indicates a same nucleotide compared to the first reference sequence. For haplotype indications see Fig. 31. Haplotypes F and F' differ in insertions of 22 bp (not shown)

taxon	haplotype	position
		111111111222222222222222
		122234599112222345566788
		603678938561259623715467
<i>P. hanaki hanaki</i>	A	TATTGTCCCTTCAGCGGCAGACT
<i>P. hanaki hanaki</i>	BG....
<i>P. hanaki hanaki</i>	CC.....G..
<i>P. hanaki creticus</i> subsp. nov.	D	C..CAC..AG.TG.TAAAT..GTC
<i>P. hanaki creticus</i> subsp. nov.	E	C.C.ACT.AG.TGATAAA..AGTC
<i>P. hanaki creticus</i> subsp. nov.	F	C.C.ACT.GGCTGATAAA..AGTC
<i>P. hanaki creticus</i> subsp. nov.	F'	C.C.ACT.GGCTGATAAA..AGTC
<i>P. hanaki creticus</i> subsp. nov.	G	C.C.ACT.GGCTGATAAA..AGT.
<i>P. hanaki creticus</i> subsp. nov.	H	CG..ACTTAG.TGATA.A..AGTC
<i>P. hanaki creticus</i> subsp. nov.	I	CG..ACTTGG.TGATA.A..AGTC

with the results by Hulva et al. (2007). The Cretan population of *P. hanaki* shows moderate level of genetic variation (Fig. 31); among 18 Cretan samples sequenced, we identified seven haplotypes (Table 10). All individuals clustered to one clade with high statistical support. However, this branch formed a sister group to *P. hanaki* from Cyrenaica, separated by genetic distance about 3.8%. Two specimens (haplotype F') were characterised by a synapomorphic insertion of 22 nucleotides. This pattern suggests, that Crete was colonised by *P. hanaki* by a single event.

The Cretan individuals of *P. hanaki* markedly differ from those examined and described by Benda et al. (2004a) from Cyrenaica also in morphological traits. While the Cyrenaican *P. hanaki* is the largest form among all examined populations of the *P. pipistrellus* group and it shows almost

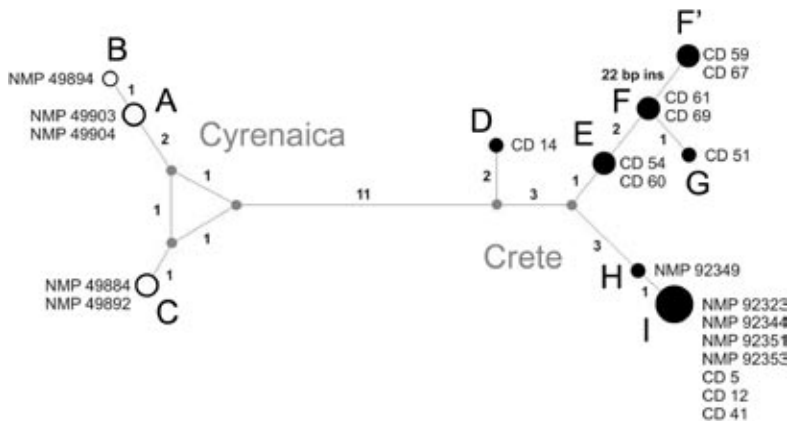


Fig. 31. Median joining network showing relationships among mtDNA (303 bp control region) haplotypes of bats from the *Pipistrellus hanaki* complex. White and black circles denote haplotypes (size of a circle is proportional to the number of individuals with respective haplotype), gray dots missing haplotypes. Numbers at link bars indicate number of mutational steps between haplotypes, numbers at the circles indicate specimens (NMP) or biopsy punches (CD) sequenced.

Table 11. Biometric data [in mm] on examined Cretan and Cyrenaican samples of *Pipistrellus hanaki* Hulva et Benda, 2004 and *P. pygmaeus cyprius* Benda, 2007; for abbreviations see p. 110

	<i>Pipistrellus hanaki</i> Crete					<i>Pipistrellus hanaki</i> Cyrenaica					<i>Pipistrellus pygmaeus</i> Cyprus				
	n	M	min	max	SD	n	M	min	max	SD	n	M	min	max	SD
LC	8	41.0	37	43	1.927	13	44.5	41	49	2.106	11	41.4	39	45	1.963
LCd	8	34.9	34	37	1.126	13	36.5	32	39	1.984	11	34.6	33	36	1.120
LAt	8	29.64	29.0	30.3	0.389	13	32.38	31.2	33.4	0.732	13	29.99	28.5	31.3	0.870
LA	8	12.04	11.3	12.7	0.466	13	11.62	9.5	13.0	1.039	13	11.81	7.8	13.3	1.769
LTr	8	5.01	4.6	5.6	0.356	13	5.24	4.8	5.9	0.310	11	5.05	4.2	5.5	0.437
LCr	7	11.75	11.55	11.99	0.144	12	12.43	12.14	12.69	0.161	13	11.80	11.42	12.43	0.284
LCb	7	11.28	11.09	11.64	0.194	12	11.95	11.64	12.18	0.151	13	11.36	10.90	11.85	0.263
LaZ	5	7.37	7.26	7.45	0.074	12	7.88	7.74	8.12	0.126	11	7.48	7.27	7.82	0.170
LaI	7	3.12	3.02	3.24	0.075	12	3.15	2.98	3.35	0.116	13	3.02	2.88	3.18	0.089
LaInf	7	3.48	3.34	3.59	0.077	12	3.70	3.50	3.90	0.134	13	3.51	3.38	3.63	0.074
LaN	7	6.13	5.91	6.28	0.131	12	6.32	6.12	6.51	0.100	13	6.07	5.81	6.26	0.137
LaM	7	6.65	6.48	6.79	0.110	12	7.17	7.02	7.39	0.132	13	6.61	6.39	6.84	0.105
ANc	7	4.32	4.13	4.48	0.107	12	4.45	4.36	4.63	0.072	13	4.21	3.96	4.33	0.094
ACr	7	5.58	5.37	5.74	0.122	12	5.75	5.58	5.86	0.089	13	5.64	5.41	5.94	0.146
I ¹ I ¹	7	1.67	1.56	1.93	0.145	12	1.87	1.80	1.94	0.047	13	1.74	1.63	1.91	0.085
CC	7	3.55	3.38	3.65	0.085	12	3.91	3.82	4.08	0.069	13	3.62	3.52	3.83	0.093
P ⁴ P ⁴	7	4.16	4.02	4.27	0.096	12	4.50	4.42	4.62	0.073	13	4.24	4.12	4.42	0.104
M ³ M ³	7	4.89	4.74	5.04	0.106	12	5.14	4.98	5.31	0.091	13	4.92	4.73	5.12	0.115
I ¹ M ³	7	4.90	4.74	5.02	0.095	12	5.27	5.20	5.38	0.058	12	4.91	4.73	5.18	0.105
CM ³	7	4.13	4.05	4.21	0.065	12	4.46	4.35	4.53	0.060	13	4.22	4.04	4.41	0.101
M ¹ M ³	7	2.84	2.77	2.91	0.048	12	2.88	2.79	2.96	0.058	12	2.85	2.65	3.02	0.116
CP ⁴	7	1.90	1.84	1.99	0.052	12	1.86	1.76	1.94	0.047	13	1.89	1.77	2.07	0.096
LI ¹	7	0.49	0.46	0.53	0.028	12	0.47	0.43	0.51	0.023	13	0.46	0.41	0.53	0.035
LI ²	7	0.40	0.36	0.45	0.037	12	0.39	0.37	0.46	0.025	13	0.35	0.28	0.41	0.038
LC ¹	7	0.91	0.86	0.96	0.040	12	0.99	0.95	1.04	0.027	13	0.93	0.87	1.01	0.051
LaC ¹	7	0.66	0.58	0.69	0.041	12	0.82	0.74	0.91	0.045	13	0.74	0.68	0.80	0.031
LP ³	7	0.42	0.40	0.45	0.020	12	0.41	0.34	0.47	0.037	13	0.37	0.34	0.41	0.023
LP ⁴	7	0.88	0.83	0.92	0.032	12	0.86	0.81	0.92	0.036	13	0.86	0.79	0.97	0.060
LaP ⁴	7	1.14	1.07	1.18	0.037	12	1.11	1.03	1.16	0.045	13	1.15	1.01	1.29	0.073
ACin	7	0.17	0.10	0.22	0.036	12	0.15	0.02	0.21	0.046	13	0.18	0.10	0.24	0.038
LM ¹	7	1.16	1.10	1.23	0.046	12	1.18	1.13	1.26	0.040	13	1.15	1.01	1.24	0.063
LaM ¹	7	1.35	1.30	1.41	0.040	12	1.38	1.34	1.42	0.031	13	1.38	1.28	1.48	0.049
LM ³	7	0.69	0.67	0.72	0.022	12	0.69	0.56	0.73	0.049	12	0.68	0.64	0.71	0.025
LaM ³	7	1.33	1.27	1.38	0.039	12	1.38	1.34	1.42	0.029	12	1.38	1.30	1.50	0.058
LMd	7	8.07	7.95	8.28	0.123	11	8.72	8.62	8.82	0.064	13	8.30	8.07	8.87	0.227
ACo	7	2.32	2.24	2.41	0.054	11	2.57	2.47	2.76	0.082	13	2.47	2.34	2.61	0.092
IM ₃	7	5.10	5.05	5.19	0.045	11	5.53	5.48	5.59	0.042	12	5.21	5.04	5.36	0.094
CM ₃	7	4.38	4.30	4.48	0.065	11	4.73	4.62	4.83	0.072	12	4.45	4.28	4.75	0.129
M ₁ M ₃	7	3.08	3.00	3.16	0.063	11	3.09	2.99	3.16	0.055	12	3.09	2.86	3.31	0.132
CP ₄	7	1.50	1.46	1.55	0.037	11	1.60	1.56	1.64	0.026	13	1.53	1.43	1.65	0.071
LI ₁	7	0.39	0.35	0.42	0.025	11	0.43	0.41	0.46	0.019	13	0.40	0.35	0.47	0.033
LI ₃	7	0.36	0.34	0.37	0.014	11	0.37	0.30	0.41	0.029	13	0.36	0.35	0.39	0.016
LC ₁	7	0.64	0.60	0.67	0.026	11	0.69	0.65	0.73	0.024	13	0.64	0.58	0.71	0.035
LP ₃	7	0.48	0.45	0.50	0.020	11	0.45	0.41	0.50	0.028	13	0.46	0.41	0.60	0.052
LaN/LCr	7	0.521	0.506	0.530	0.009	12	0.508	0.494	0.522	0.008	13	0.514	0.494	0.535	0.012
ANc/LCr	7	0.368	0.358	0.374	0.006	12	0.358	0.352	0.368	0.006	13	0.357	0.340	0.368	0.008
CC/LCr	7	0.302	0.289	0.310	0.007	12	0.315	0.305	0.327	0.006	13	0.307	0.295	0.321	0.007
CM ³ /LCr	7	0.352	0.345	0.356	0.004	12	0.359	0.349	0.373	0.007	13	0.358	0.342	0.369	0.007
LC ¹ /LaC ¹	7	1.393	1.262	1.545	0.086	12	1.208	1.057	1.380	0.087	13	1.250	1.167	1.377	0.056

no overlap with them in most dimensions, the Cretan samples are similar in size to other compared bats of the group, mainly to the European *P. pygmaeus* or *P. pipistrellus* from the Middle East. Concerning their external dimensions, Cretan samples belong to the smallest representatives of the compared set with the forearm length range of 29.0–30.3 mm only, i.e. rather in the lower part of the dimensional range of the whole group. The skull size of the Cretan bats has a similar range as that of *P. pipistrellus* and *P. pygmaeus* specimens from various parts of their distribution, but it lies deeply below the dimensional range of *P. hanaki* from Cyrenaica (Fig. 32). Similarly, in the skull shape the Cretan samples rather resemble the European samples of *P. pygmaeus* and *P. pipistrellus*, their rostrum being relatively short and narrow (in *P. hanaki* from Cyrenaica relatively the rostrum is long and broad; see Benda et al. 2004a). On the other hand, in the size of selected teeth (canines, molars) the Cretan bats rather resemble their conspecifics from Cyrenaica. The absolute size of molars and molar-rows is similar in the Cretan and Cyrenaican samples of *P. hanaki* (as well as in the Cypriot *P. pygmaeus*; Fig. 33); in that respect the Cretan bats differ in their mean values from the European *P. pygmaeus* and *P. pipistrellus*. Upper canines of the Cretan *P. hanaki* resemble those of *P. p. cyprius* in absolute size (mesiodistal length), however, are much narrower (Fig. 34). While the relative width of upper canine crown is similar in Cyrenaican *P. hanaki*, in European and Cypriot *P. pygmaeus* as well as in *P. pipistrellus* (LaC^1/LC^1 0.68–0.95), it is very narrow in the Cretan *P. hanaki* (LaC^1/LC^1 0.65–0.86). The upper unicuspidal tooth-rows in the Cretan *P. hanaki* are on average longer than in the European *P. pygmaeus* and *P. pipistrellus*, in absolute values in some cases as long as in *P. h. hanaki* and *P. p. cyprius* (CP^4 1.8–2.0 mm). The lower unicuspidal tooth-rows in the Cretan bats are both absolutely and relatively similar in their length to those in the Cypriot *P. pygmaeus* (CP_4 1.4–1.6 mm).

To be summarised, in most morphological characters the Cretan *P. hanaki* resembles *P. pygmaeus cyprius* from Cyprus rather than the conspecific form from Cyrenaica or members of the species

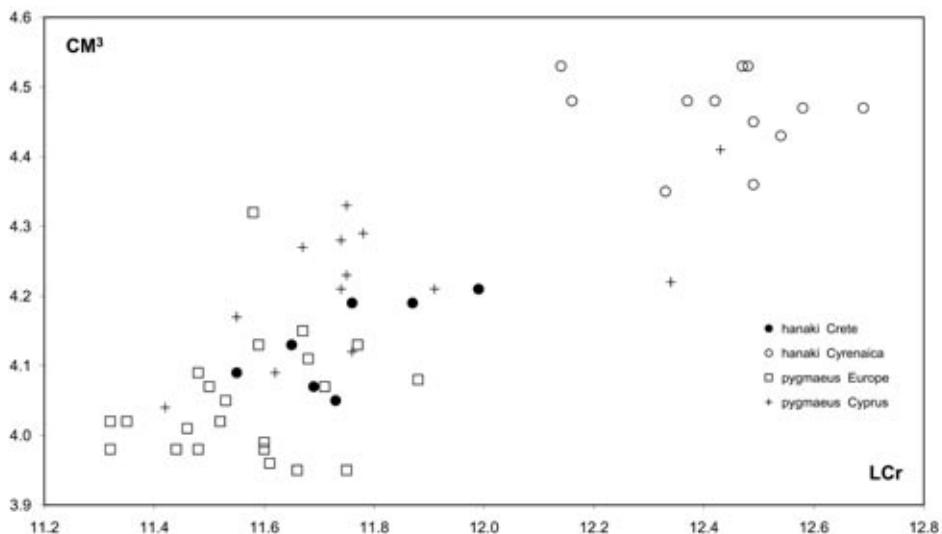


Fig. 32. Bivariate plot of examined Cretan and comparative samples of *Pipistrellus* Kaup, 1829 (*P. pygmaeus* lineage): greatest length of skull (LCr) against length of the upper tooth-row (CM^3).

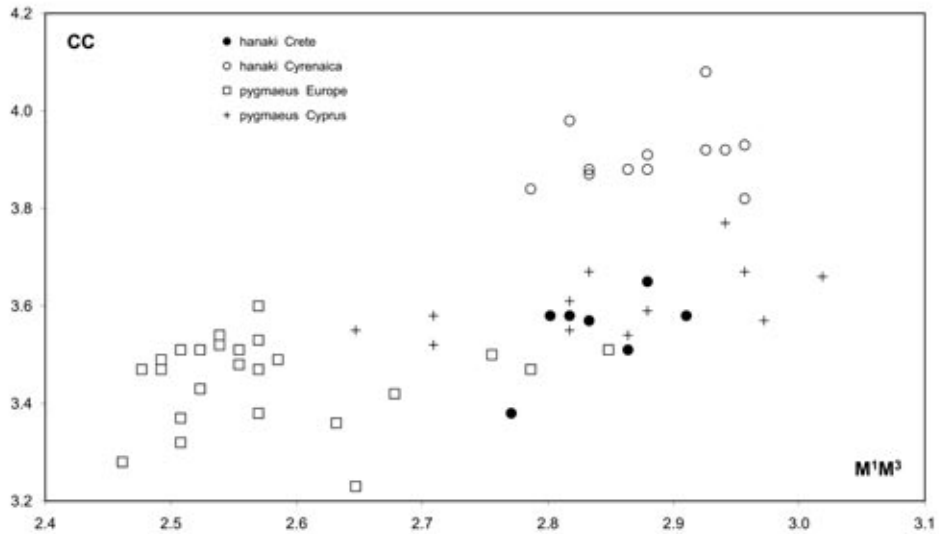


Fig. 33. Bivariate plot of examined Cretan and comparative samples of *Pipistrellus* Kaup, 1829 (*P. pygmaeus* lineage): length of the upper molar-row (M^1M^2) against the rostral width across upper canines (CC).

group from the European or Asian mainlands. However, the Cypriot and Cretan representatives of the *pygmaeus* lineage differ significantly in genetic characters, see above. In the context of the *Pipistrellus pipistrellus* group in the Mediterranean, *P. hanaki* from Crete represents a unique

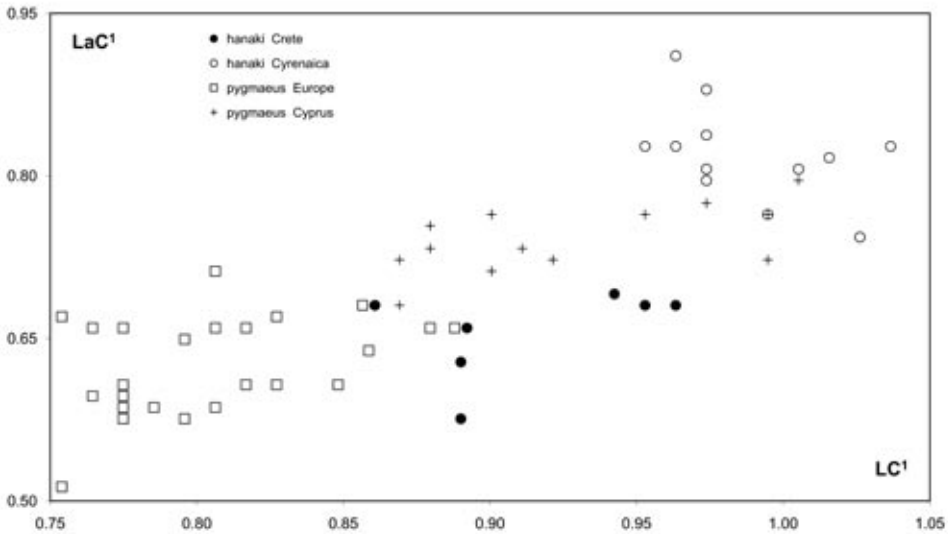


Fig. 34. Bivariate plot of examined Cretan and comparative samples of *Pipistrellus* Kaup, 1829 (*P. pygmaeus* lineage): mesiodistal length of the upper canine (LC¹) against palatolabial width of the upper canine (LaC¹).

morphological, genetic and also geographical unit, showing a sufficient combination of distinctive characters to be here designated as a separate subspecies:

***Pipistrellus hanaki creticus* Benda, subsp. nov.**

TYPE MATERIAL. **Holotype:** adult male (NMP 92350 [S+A]), Rouva forest at Agiou Ioanni chapel, 4 June 2008, leg. P. Benda, P. Georgiakakis & V. Hanák. **Paratypes** (7): 3 ma, 1 ms (NMP 92349, 92351, 92353 [S+A], 92352 [A]), site, date and collectors as in the holotype; – 1 ma (NMP 91180 [S+A]), Omalos plateau, Tzani cave, 1 October 2006, leg. P. Benda, V. Hanák & P. Hulva; – 1 ma (NMP 92323 [S+A]), at a brook ca. 1 km N of Zaros, 25 May 2008, leg. P. Benda & V. Hanák; – 1 ma (NMP 92344 [S+A]), above the Genianos river at Monastiraki, 2 June 2008, leg. P. Benda, P. Georgiakakis & V. Hanák.

COMPARATIVE MATERIAL. See the Appendix 1 by Benda et al. (2004a), Appendix II by Benda et al. (2006) and Appendix III by Benda et al. (2007).

TYPE LOCALITY. Greece, Crete, Rouva oak forest; a pasture with creek at the Agiou Ioanni chapel, Prefecture of Irakleio; 35° 11' N, 24° 55' E, 940 m a. s. l. (Figs. 24, 25).

DESCRIPTION AND DIAGNOSIS. *Pipistrellus hanaki creticus* subsp. nov. is a small bat belonging to the *Pipistrellus pipistrellus* complex, in most of its morphological and genetic characters conforming to the nominotypical subspecies of *P. hanaki* from Cyrenaica. *P. h. creticus* subsp. nov. differs from *P. h. hanaki* Hulva et Benda, 2004, by its significantly smaller body and skull size (see Table 11); ranges of wing and skull dimensions only marginally overlap in the two subspecies, while tooth dimensions overlap largely or are of similar ranges. Within the species, the skull of *P. h. creticus* subsp. nov. is absolutely very small (LCr 11.5–12.0 mm), the braincase is relatively rather broad (LaN 5.9–6.3 mm; LaN/LCr 0.51–0.53) and high (ANc 4.1–4.5 mm; ANc/LCr 0.36–0.37), in absolute size ranges similar to the European *P. p. pygmaeus* and to *P. pipistrellus* from the Middle East (see Benda et al. 2007: 99). The rostral part of the skull is on average rather short

Table 12. Basic biometric data [in mm] on the holotype specimen and type series *Pipistrellus hanaki creticus* subsp. nov.; for abbreviations see p. 110. Data on the holotype are bold-typed

coll. No. NMP	91180	92323	92344	92349	92350	92351	92352	92353
LC	43	40	43	42	37	41	41	41
LCd	34	36	34	35	34	34	35	37
LAt	30.3	29.4	29.9	29.8	29.7	29.6	29.0	29.4
LA	11.3	11.8	11.7	12.1	11.9	12.6	12.7	12.2
LTr	5.0	4.9	4.6	5.5	4.9	4.9	4.7	5.6
G	3.9	3.5	3.3	3.6	3.5	3.6	3.3	3.4
LCr	11.99	11.65	11.55	11.87	11.73	11.76	–	11.70
LCb	11.64	11.16	11.09	11.44	11.17	11.28	–	11.19
LaZ	7.45	7.41	7.26	–	7.40	–	–	7.34
LaI	3.24	3.19	3.02	3.07	3.13	3.11	–	3.08
LaN	6.28	6.09	5.91	6.01	6.21	6.23	–	6.15
LaM	6.79	6.55	6.48	6.74	6.69	6.68	–	6.59
ANc	4.48	4.28	4.13	4.32	4.32	4.39	–	4.33
CC	3.58	3.58	3.51	3.58	3.57	3.65	–	3.38
M ³ M ³	4.88	4.94	4.76	5.04	4.94	4.92	–	4.74
CM ³	4.21	4.13	4.09	4.19	4.05	4.19	–	4.07
LMd	8.28	8.05	7.95	8.13	8.16	7.98	–	7.96
ACo	2.33	2.36	2.24	2.41	2.33	2.28	–	2.32
CM ₃	4.48	4.32	4.39	4.42	4.33	4.41	–	4.30



Fig. 35. Composed table showing some characters of *Pipistrellus hanaki creticus* subsp. nov. (left column), *P. pygmaeus* (Leach, 1825) from Thrace (column in the middle) and *P. pipistrellus* (Schreber, 1774) from Thrace (right column). In the first row face in frontal view, in the second row right ear in lateral view and in the third row penis in antero-dorsal view (all photos by C. Dietz).



Figs. 36, 37. Coloration in *Pipistrellus hanaki creticus* subsp. nov. (both photos by C. Dietz). 36 – from a distance *P. h. creticus* subsp. nov. resembles a small individual of *Pipistrellus nathusii* (Keyserling et Blasius, 1839), especially females and young males, since they are uniformly coloured. 37 – older adult male of *P. hanaki creticus* subsp. nov. in full reproductive condition have a more ‘colourful’ appearance since the fur on the head and behind the ears has an

and narrow (CM^3/LCr 0.35–0.36; CC/LCr 0.29–0.31). Tooth-rows are short (CM^3 4.1–4.2 mm; CM_3 4.3–4.5 mm; CP^4 1.8–2.0 mm; CP_4 1.5–1.6 mm), almost without overlap with the dimensions in *P. h. hanaki*. Crowns of the upper canines are mesiodistally absolutely and relatively long and narrow (LC^1 0.86–0.96 mm; LaC^1 0.58–0.69 mm); the upper canines are in their mesiodistal lengths as long as in *P. pygmaeus cyprius* but rather shorter than in *P. h. hanaki*, palatolabially are very narrow, on average narrower than in any other compared population (LaC^1/LC^1 0.65–0.86; mean 0.72). Unicuspidal tooth-rows are long, on average longer than in *P. p. pygmaeus* and *P. pipistrellus*, in absolute values in some cases as long as in *P. h. hanaki* and *P. p. cyprius* (CP^4 1.8–2.0 mm; CP_4 1.4–1.6 mm); the second upper premolar (P^4) crown is on average as large as in *P. h. hanaki*, significantly larger than in *P. p. pygmaeus* and reaching the size of this tooth in *P. p. cyprius* (LP^4 0.83–0.92 mm, mean 0.88; LaP^4 1.07–1.18 mm, mean 1.14). Molars are absolutely and relatively very large, the first upper molar (M^1) is extremely wide (M^1 mesiodistal length 1.10–1.23 mm, mean 1.16; palatolabial width 1.30–1.41 mm, mean 1.35); molar-rows are on average similarly long as in *P. h. hanaki* and *P. p. cyprius* and significantly longer than in *P. p. pygmaeus* and on average also than in *P. pipistrellus*. For other dimensional points of the differential diagnosis see Table 11 and Figs. 32–38, for dimensions of the examined specimens of *P. h. creticus* subsp. nov. (i.e. the type series) see Table 12.



Fig. 38. Open mouth of an adult male *Pipistrellus hanaki creticus* subsp. nov. showing the teeth and the colour of the gular pads (photo by C. Dietz).

The venation of wing membrane in *P. h. creticus* subsp. nov. is of the *P. pipistrellus* type according to von Helversen & Holderied (2003: 424, Abb. 4 B). Based on fixed specimens examination, the glans penis in *P. h. creticus* subsp. nov. has more or less obvious pale medial stripe on dorsal side of praeputium that is covered by greyish-brown hairs. In several examined specimens it resembles the *P. pipistrellus* type and in others the *P. mediterraneus/pygmaeus* type as described by von Helversen & Holderied (2003). For an example of coloration in living individual see Fig. 35.

Echolocation calls of *P. h. creticus* subsp. nov. have a start frequency in the mean (min–max; \pm SD; n) at 59.5 kHz (46.2–101.1; 10.0; 300), an end frequency at 48.8 kHz (43.6–55.2; 2.0; 300) and a pulse duration of 4.3 ms (1.5–8.6; 1.6; 300). All frequency parameters (including the maximum energy of the terminal frequency) are by their mean slightly higher than in *P. pipistrellus* but widely overlapping. According to the present knowledge, *P. h. creticus* subsp. nov. is geographically limited to Crete where it represent the only representative of the species group.

Partial sequence of the mitochondrial gene for cytochrome *b* of a paratype (NMP 91180; 402 bp, NCBI Accession Number EF370417; after Hulva et al. 2007, haplotype CRE1):

```
atg aca aac att cga aaa tca cat ccc cta att aaa att atc aac agc tca ttc att gac cta cca gcc cca tca aac att tca gca tga tga aac
ttt gga tcc tta tta ggc atc tgt cta gga cta cag atc cta aca ggc cta ttt ctt gct ata cat tat aca tca gac aca gca acc gcc ttc agc tct
gtc acc cac atc tgc cga gat gta aat tat gga tga gtc cta cga tat cta cat gca aac gga gcc tca ata ttt ttt att tgc cta tat cta cac gta
gga cgg ggc ctt tac tat gga tcc tac cta ttt aaa gaa acc tga aat att ggg gtt att tta cta ttc gct gta ata gca acg gcc ttc ata ggc tat
gtc tta cca.
```

According to the haplotypes published by Hulva et al. (2007) and Benda et al. (2004a), partial sequence of the mitochondrial gene for cytochrome *b* (402 bp, 5' end, haplotype CRE1) of the examined Cretan specimen of *P. h. creticus* subsp. nov. (NMP 91180) has unique mutations within the *P. hanaki* haplotype group at 16 positions (132, 348, 378: A→G; 21, 345: A→T; 33, 39, 57, 162, 165, 306, 355: C→T; 96, 127, 186, 322: T→C), at one position it shares an identical mutation with the *P. h. hanaki* haplotype LIB1 and differs from the other one from Cyrenaica, LIB2 (304: C→A). Hence, the uncorrected genetic p distances between the examined haplotypes of *P. h. creticus* subsp. nov. and *P. h. hanaki* from Cyrenaica are 3.98% and 4.23%, respectively. For the substitutions within the examined part of the control region of mtDNA typical for *P. h. creticus* subsp. nov. see Table 10.

DERIVATIO NOMINIS. The name *creticus* (meaning Cretan in Latin) refers to the island of Crete, the only known area of distribution of *P. h. creticus* subsp. nov.

Pipistrellus nathusii (Keyserling et Blasius, 1839)

RECORDS. **Original data:** L a s i t h i: Gra Lygia, Mpramianos river dam [1], 19 May 2003: coll. 1 ma (NHMC FC4816 [S+A]; leg. M. Ivović). – **Published data:** C h a n i a: Limni Kourna [= Mouri, Kourna lake] [2] (Fig. 39), 2 May 2003: det. 1–3 inds., incl. a repeated mating call (Skiba 2007).

COMMENTS. *Pipistrellus nathusii* has been discovered in Crete only recently; Skiba (2007) reported recordings of its calls made at the Kourna Lake in northwestern Crete in May 2003. Although the recorded social calls clearly pointed toward *P. nathusii*, they were of rather poor recording quality. The echolocation calls of *P. nathusii* can be easily confused with the calls of *P. kuhlii* (Zingg 1990). Thus, the Skiba's evidence remained slightly uncertain, being the only available record of a rather isolated occurrence of *P. nathusii* in the island. However, our revision of a NHMC specimen collected at the Mpramianos river dam in southeastern Crete, also in May 2003, confirmed clearly the presence of *P. nathusii* in the island. Dimensions of the examined specimen of *P. nathusii* from Crete are shown in Table 9. Nevertheless, as only two records are available now, this species is the rarest bat in Crete (Figs. 40, 54). Both records come from the same spring

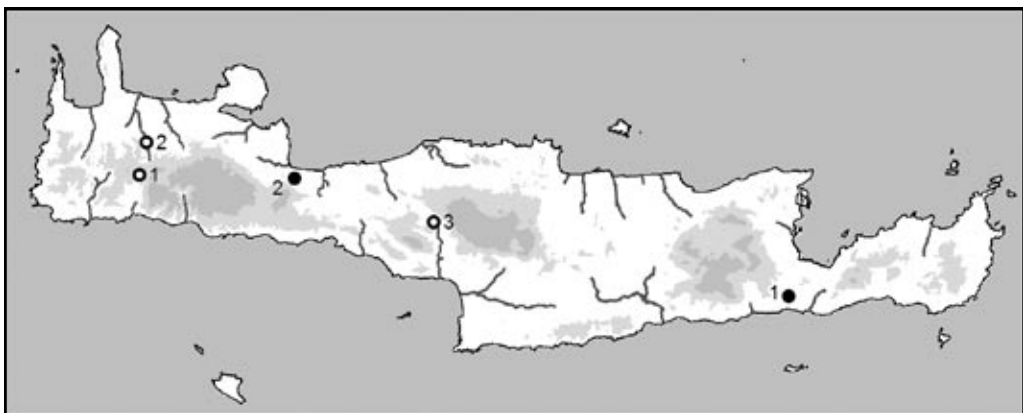


Fig. 40. Records of *Pipistrellus nathusii* (Keyserling et Blasius, 1839) (closed symbols) and *Nyctalus leisleri* (Kuhl, 1817) (open symbols) in Crete.



Fig. 39. The Kourna Lake, close to northwestern sea shore of Crete (photo by Z. Bendová). An area of the first Cretan record of *Pipistrellus nathusii* (Skiba 2007) and the second record of *P. kuhlii* (Kahmann 1959). At the lake bank or in its surroundings a number of bat species was recorded, viz. *Myotis capaccinii*, *Hypsugo savii*, and *Pipistrellus kuhlii* (present review) and *Rhinolophus ferrumequinum*, *Myotis capaccinii*, *Eptesicus serotinus*, *Pipistrellus hanaki*, *P. kuhlii*, and *Tadarida teniotis* (Skiba 2007).

season (2 and 19 May 2003) from similar habitats – a lowland landscape with a large water body – though in distant parts of the island.

P. nathusii is a typical long-distance migratory bat, its main breeding area in Europe lies north of 50° N (Strelkov 2000, Vierhaus 2004). Hence the newly evidenced bats from Crete most probably represent migrating individuals from mainland Greece and a resident population of *P. nathusii* is unlikely to occur there. The closest locality of *P. nathusii* to the Cretan findings was reported from the northwestern Peloponnese (Pieper 1978, von Helversen & Weid 1990) and the nearest possible breeding subpopulation is supposed to exist in northern Greece (Hanák et al. 2001), though most of the Balkan records are presumably related to migrants from far north as assumed from the record seasons (Strelkov 2000, Hanák et al. 2001, Benda et al. 2003).

Although *P. nathusii* was found in Calabria, southern Italy (Miller 1912) and more abundantly in southern Spain (Palomo & Gisbert 2002), its occurrence spot in Crete represents the southernmost margin of the whole distribution range (Hanák & Gaisler 1976, Vierhaus 2004). Besides Crete, *P. nathusii* was found in a few other Mediterranean islands only; in the western Mediterranean there are known records from much more northwards situated Corsica, Elba and Sardinia (Vierhaus 2004) and in the eastern Mediterranean region from Greek island of Lesbos (Hanák et

al. 2001). All the respective islands lie relatively close to the mainland regions where density of *P. nathusii* during time of migrations (and supposedly in winter) can be quite a high. For instance, in northwestern Anatolia and/or in Turkish Thrace this species may in autumn months present even one of the commonest species according to detectoring data (Benda & Horáček 1998). In comparison to this, the Cretan records seem to be quite isolated and it does not seem too probable that the island belongs to a regular migration or wintering range of this species.

Pipistrellus kuhlii (Kuhl, 1817)

RECORDS. Original data: C h a n i a: Agia Marina [1], village, 27 September 2006: det. 1 ind.; – Kalami, Kiliaris river at the highway bridge [2], 9 October 2007: net. 1 fs (NMP 92302 [S+A]), det. several inds.; – Kandanos, chestnut grove with a creek [3], 3 November 2008: net. 1 fs; – Katholiko monastery (Fig. 12), at the Agiou Ioanni cave [4], 27 May 2008: det. 2 foraging inds.; – Kavalos, NW shore of the Kourna lake [5], 1 June 2008: det. & rec. 4 inds.; – Kolymvari, at a mine above the village [6], 9 October 2006: det. & rec. several inds.; – Krya Vrissi, village [7], 10 September 2006: coll. 1 ma (NHMC FC94444 [A]); – Limni, pond [8] (Fig. 51), 19 August 2008: net. 2 ms, 2 fa; – Nopigeia, Tyflos river estuary [9], 5 November 2008: det. & rec. 1 ind.; – Nteres, at a bridge near the village [10], 16 July 2008: net. 1 fj, det. & obs. ca. 8 inds.; – Papadiana, ford [11], 17 July 2008: net. 1 fa, 19 July 2008: net. 3 fa, 21 July 2008: net. 2 mj, 4 fa; – Platania, above the Xekollomenos river [12], 29 September 2006: det. several inds.; – Rapaniana, village [13], 12–22 July 2008: regularly foraged ca. 5 inds., 23 July 2008: 1 fj in a hotel room; – Vryses Apokoronou, above river [14], 2 October 2006: net. 1 ma, 2 fa (NMP 91185, 91186 [S+A], 91187 [A]), obs. & det. ca. 15 inds. – I r a k l e i o: Ano Asites, village [15], November 2006: coll. 1 ms (NHMC FC10246 [F]; leg. S. Liapakis); – Irakleio, Agios Ioannis vicinity [16], 23 September 2008: coll. 1 m (NHMC FC11461 [A]; leg. S. Liapakis); – Irakleio, old university campus [17], 10 July 2005: obs. & exam. 1 faL; – Kato Fortetsa, storehouse [18], 22 April 2008: obs. 5 inds. emerg., 14 June 2008: obs. & exam. 5 faL; – Kato Gouves, H.C.M.R. facilities [19], 5 August 2007: coll. 1 mj (NHMC FC10529 [A]; leg. Ch. Doxa); – Kavrochori, Gazanos river [20], 3 July 2008: rec. several inds., 12 July 2008: net. 2 ma, 6 mj, 5 faL, 8 fj; – Laloumas, Koutsoulitis river, under a Venetian bridge [21], 29 May 2008: det. & rec. several inds.; – Linoperamata, Almyros river [22], 5 June 2008: det. & rec. many foraging inds.; – Linoperamata, Almyros river spring [23], 20 October 2006: rec. few inds., 5 June 2008: det. & rec. 2 inds.; – Patsides, village [24], 28 January 2006: coll. 1 m (NHMC FC8832 [A]; leg. S. Liapakis); – Spilia, Agia Eirini chapel, 2 km S of Knossos, above a brook [25], 26 May 2008: net. 1 ma, 4 fG (coll. 1 m, NMP 92324 [S+A]), det. & rec. several inds.; – Venerato, Agios Fanourios chapel, at a creek [26], 31 August 2008: net. 2 ma, 2 ms, 1 fa, 1 fs; – Zaros, Votomos lake [27], 25 May 2008: det. & rec. several foraging inds. – L a s i t h i: Agios Konstantinos, pools of a brook near the Chonos sinkhole [28], 28 May 2008: det. & rec. 1 ind.; – Gra Lygia, Mpramianos river dam [29], 11 May 2000: coll. 1 f (NHMC FC4680 [F]; leg. M. Dretakis); – Kritsa, Gaidourotrypa cave [30] (Fig. 2), 31 May 2008: det. & rec. 1 ind.; – Sisi, village [31], 7 September 2004: coll. 1 m (NHMC FC5879 [F]). – R e t h y m n o: Ano Viran Episkopi, a valley below the village [32], 16 October 2007: det. several foraging inds.; – Anogia, storehouse [33], 15 June 2008: exam. & rec. 2 faL; – Argyroupoli, Mouselas river [34], 3 June 2008: det. & rec. many foraging inds., 16 August 2008: net. 1 ma, 1 ms, 1 fa; – Lefkogeia, at a Venetian bridge ca. 3 km E of Kato Preveli Monastery [35], 11 October 2007: net. 1 ma, 1 ms, 3 fa (NMP 92304, 92305, 92307, 92308 [S+A], 92306 [A]), 3 inds., det. many foraging inds., 14 October 2007: net. 1 ma (NMP 92321 [S+A]), det. many inds., 30 May 2008: net. 3 ma, 5 faG (coll. 6 inds., NMP 92337–92341 [S+A], 92336 [A]), det. & rec. many foraging inds.; – Monastiraki, Genianos stream [36], 2 June 2008: det. & rec. 3 inds.; – Plakias, around the street lamps in the village [37], 17 October 2007: det. 1–2 inds.; – Roumeli, Geropotamos river [38], 18 April 2007: det. & rec. several inds. – **Published data:** C h a n i a: a reservoir at Agya [= Agia] [39], 6 April 1943: 1 ind. (Pohle 1953); – Agia Roumeli [40], 14 July 1995: det. ca. 30 inds. (Hanák et al. 2001); – Chania [41], 21 May 1942: 1 ind., 24 May 1942: 1 ind. (Pohle 1953); – Hania [= Chania], castle [= fortress] [42], 9 July 1995: obs. ca. 20 inds. (Hanák et al. 2001); – Moni Katholiko – Agios St. Ioannis [= Katholiko monastery, Agios Ioannis] [4], 4 May 2003: det. 15–20 inds. (Skiba 2007); – Kisamo Kastelli [= Kissamos, town] [43], 22 April 1942: 1 ind., 26 April 1942: 1 ind. (Pohle 1953); – Kourna-See bei Mouri [= Kourna Lake near Mouri] [44], 15 April 1958: 1 f [SMF 28220] (Kahmann 1959, Felten & Storch 1970, Kock et al. 1972, Benda et al. 2006); Limni Kourna [= Mouri, Kourna lake], 2 May 2003: det. 5 inds., 3 May 2003: det. 5 inds. (Skiba 2007); – Topolia [45], 1973–1975: 4 inds. (from owl pellets) (Pieper 1977). – I r a k l e i o: Sarchos [46], 1973–1975: 3 inds. (from owl pellets) (Pieper 1977). – L a s i t h i: Amoudara [= Ammoudara] [47], 29 April 2004: det. 3 inds. (Skiba 2007); – Elounda and its vicinity [48], 21 April 2004: det. 12 inds. (Skiba 2007); – ‘Stausee’ and Agios Georgios, 4 km NW of Ierapetra [= Gra Lygia, Mpramianos river dam] [29], 30 April 2004: det. 1 ind. (Skiba 2007); – Istro [49], 27 April 2004: det. 1 ind. (Skiba 2007); – Kalamafka [50], 30 April 2004: det. 6 inds. (Skiba 2007); – Kroustas [51], 1 May 2004: det. 8–12 inds. (Skiba 2007); – Paralia [= Paralia Milatou] [52], 7 and 12 July 1996: det. min. 5 inds. (Hanák et al. 2001); – Prina, Kalo Horio [= Kalo Chorio] and Istro [53], 30 April 2004: det. 6 inds. (Skiba 2007). – R e t h y m n o: Adele and its vicinity [54], 30 April 2003: det. 8–10 inds. (Skiba 2007); – Gerani [55], 29 April

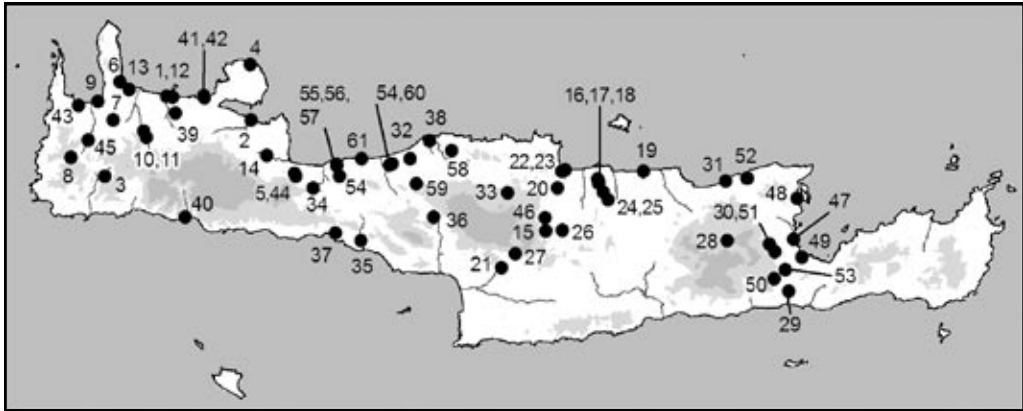


Fig. 41. Records of *Pipistrellus kuhlii* (Kuhl, 1817) in Crete.

2003: det. 2 inds. (Skiba 2007); – Gerani, rocky canyon [56], 16 July 1995: det. 1 ind. (Hanák et al. 2001); – Metochia [= Frantzeskiana Metochia] [57], 29 April 2003: det. 2 inds. (Skiba 2007); – Melidoni Andro [= Melidoni, Gerontospilios cave] [58], 30 April 2003: det. 7–10 inds. (Skiba 2007); – Moni Arkadi [= Arkadiou monastery] and Amnatos, Kiriana and Adele [59], 28 April 2003: det. 35–40 inds. (Skiba 2007); – Platania and its vicinity [60], 24 April 2003: det. 4–6 inds., 27 April 2003: det. 7–9 inds. (Skiba 2007); – Rethymno [61], 19 April 1974: 1 m, 1 f (Iliopoulou-Georgudaki 1985). – Kreta [= Crete], six closely unidentified records mapped (Kahmann 1959).

COMMENTS. *Pipistrellus kuhlii* is a rather common bat in Crete, with 67 records it is the fourth most frequently recorded bat (Table 1). Its occurrence was evidenced from the whole island (Fig. 41), however, the records come predominantly from lower situated areas, the highest known locality lies at 815 m a. s. l. In the summer season *P. kuhlii* clearly prefers low situated sites (mean 166.1 m, median 70.0 m, n=51), while the very limited number of its winter records comes on average from slightly higher altitudes (mean 282.0 m, median 317.5 m, n=4). However, as two of the winter findings are records of foraging bats and only two remaining are real findings of individuals, the selection of hibernation roosts and their preferred altitude remains rather unclear.

An absolute majority of the Cretan records of *P. kuhlii* (46 sites, i.e. 75.4%) is related to foraging bats, recorded by an ultrasound detector (39 evidences) and/or netted (14). At least 33 of these sites were habitats probably not directly connected with possible roosts, while nine of them were human settlements and four were cave entrances; the two latter types may represent potential roosts. The occasional finds of either live or dead individuals (13 sites) come solely from settlements, so altogether at least 21 record sites (34.4%) are represented by anthropogenic habitats. The only discovered roosts of *P. kuhlii* were two storehouses used as shelters by nursery colonies, in Anogia (800 m a. s. l.) and Kato Fortetsa (126 m a. s. l.). Pieper (1977) reported findings of this bat in owl pellets from two sites (3.3%). External and cranial dimensions of examined specimens of *P. kuhlii* from Crete are shown in Table 9.

P. kuhlii is one of the most abundant and widespread bats of the Mediterranean. In Greece it was recorded as the third most common bat distributed in all geographical parts of the country (Hanák et al. 2001), although its occurrence in mainland regions is rather scattered to several spots. On the other hand, the species was evidenced in many Greek islands; Hanák et al. (2001) reviewed records from Skiathos, Euboea, Mykonos, Santorini, Rhodes, Crete, Zakynthos, Kefalonia, Lefkada, and Corfu, further unpublished records are available from Karpathos (own data).

Besides Greece, *P. kuhlii* was found in 39 islands within the Mediterranean Basin (see a review by Bogdanowicz 2004), thus representing a typical island bat of the region together with *Tadarida teniotis*. In Cyprus, *P. kuhlii* was reported as the second most common bat species (Benda et al. 2007), occurring in very similarly situated sites as in Crete.

Nyctalus leisleri (Kuhl, 1817)

RECORDS. **Original data:** C h a n i a: Agia Eirini, stream [1] (Fig. 42), 18 August 2008: net. 2 ma; – Papadiana, ford [2], 19 July 2008: net. 1 ma. – R e t h y m n o: Monastiraki, Genianos stream [3], 2 June 2008: det. & rec. 1 ind.

COMMENTS. *Nyctalus leisleri* is a bat species reported here from Crete for the first time; three males were netted and calls of one individual were recorded in the summer 2008. All three record sites are situated in a forested landscape of medium to higher altitudes (mean 381.7 m, median 305.0 m, range 240–600 m a. s. l.) (Fig. 40)

Considering the well known migratory behaviour of *N. leisleri* (e.g. Strelkov 1969, Hutterer et al. 2005), a question arises whether there is a resident population of *N. leisleri* in Crete, or whether the bats represent (accidental?) migrants from the European mainland. Since the three netted individuals were adult males and all were recorded during the same season within one month, the possibility of strays which arrived during one migration wave cannot be excluded. In any case, even if an alternative interpretation is valid and a resident population of this species



Fig. 42. Portrait of an adult male of *Nyctalus leisleri* (Kuhl, 1817) captured within a chestnut grove above the Agia Eirini stream (photo by C. Dietz).

occurs in Crete, it is clear that its distribution there must be very limited. Even the present records are restricted to the patches of dense high stand (mostly *Platanus orientalis*) woodland in a humid mountain valleys, the habitat quite rare in the island.

Besides Crete, *N. leisleri* was found only in two eastern Mediterranean islands, Rhodes (Hanák et al. 2001) and Cyprus (Benda et al. 2007). In Rhodes, an offshore neighbour of Anatolia, the record is well interpretable as of a possible stray from the mainland population. In Cyprus, where the occurrence of *N. leisleri* has been discovered just recently, a resident population is supposed to exist (Benda et al. 2007). In support of a resident occurrence, the following facts are to be mentioned; (1) the bats were recorded repeatedly at the same site in two years and in different parts of the season, (2) adults of both sexes were recorded, (3) the Cypriot occurrence spot is isolated, and no sufficiently abundant population is known in the neighbouring mainland to be a source (though one record is known from southwestern Anatolia; von Helversen 1989), and (4) a resident population of another *Nyctalus* species was discovered in the island, *N. lasiopterus* (see Benda et al. 2007). In Crete, none of such supporting arguments is available. Moreover, as the abundance of the species in forested mountainous parts of Greek mainland and Peloponnese can be seasonally even very high (von Helversen & Weid 1990, von Helversen in Mitchell-Jones et al. 1999, Hanák et al. 2001), a probability of incidental extension of migratory range in Crete is much more higher than in Cyprus. Moreover, *N. leisleri* was found in Cyrenaica, Libya (Hanák & Gaisler 1983) and this single record could be also connected with a (irregular?) migration wave from Europe passing via the peninsular Greece and Crete.

Anyhow, the distant marginal records suggesting isolated local populations seem to be quite characteristic for *Nyctalus leisleri* and its metapopulation dynamics, and undoubtedly present an exciting topics worthy of a detailed study. In most instances just single records are available from the southern Mediterranean and as no further information on actual abundance and structure of the local population is available as a rule, the vast majority of the references concerning reproductive status of these populations and their natural history are necessarily based just on speculations. The situation in Crete opens a chance to investigate that topics in details. We expect that repeated controls of the respective habitat patches in Crete and standardised monitoring of these sites with aid of bat detectors could elucidate the question quite satisfactorily.

Plecotus macrobullaris Kuzjakin, 1965

RECORDS. **Original data:** Chania: Omalos Plateau, Tzani cave [1], 1 October 2006: net. 3 ma (NMP 91181 [A], 91182, 91183 [S+A]). – Rethymno: Nida Plateau (Idi Mts.), Ideo Andro cave [2], 30 September 2006: net. 1 ma (NMP 91052 [S+A]); – Petradolakia (Idi Mts.) (Fig. 43), Agios Fanourios chapel, pothole [3], 20 August 2008: net. 1 ma (Fig. 44). – **Published data:** Topolia [4], 1973–1975: 1–10 inds. (from owl pellets) (Pieper 1977 [as *P. auritus*]). – Iraklio: Mires, old mine (Microlavirynth) [= Plouti, Mikro Lavyrinthaki mine] [5] (Fig. 45), 2 April 1999: net. 1 ma (Hanák et al. 2001 [as *P. kolombatovici*], cf. Kiefer & von Helversen 2004a) = Roufas, 1 ind. (Juste et al. 2004).

COMMENTS. *Plecotus macrobullaris* is one of the rarest bats of Crete, only five records are known from mountainous areas (Fig. 46). Besides the skeletal remains in the barn owl pellets reported from Topolia (265 m a. s. l.) by Pieper (1977), all records come from high altitudes in the range 385–1490 m a. s. l. (mean 1091.0 m, median 1244.5 m), where the bats were netted at entrances to underground spaces (two caves, a pothole and a mine) during the summer season (April and from August to October). Three sites are situated in rather open pastures on subalpine plateaus of central and western parts of Crete, at altitudes above 1000 m a. s. l. (Fig. 43); the only netting site situated at a lower altitude is entrance to a mine surrounded by agricultural landscape at the southern foot of the Idi Mts.



Fig. 43. Foraging habitat of *Plecotus macrobullaris* Kuzjakin, 1965 in the Idi Mountains. Due to heavy grazing most of the karstic surface is free of vegetation or covered by small scrub-like vegetation (photo by C. Dietz).



Fig. 44. Portrait of an adult male of *Plecotus macrobullaris* Kuzjakin, 1965 caught above a deep pothole near Petradolakia in the Idi Mountains (photo by C. Dietz).



Fig. 45. A look out of the Mikro Labyrinthaki mine at Plouti to the north, at the agriculture landscape below the southern slopes of the Psiloreitis Mts on the background (photo by Z. Bendová). The mine is a roost and/or netting site of *Rhinolophus ferrumequinum*, *R. hipposideros*, *Myotis blythii*, and *Plecotus macrobullaris*.

P. macrobullaris is apparently the ‘most mountain’ bat of Crete (Table 2), although the available records are rather scarce to be able to make any relevant ecological conclusion. However, this species is a mountain faunal element throughout its distribution range; in continental Europe

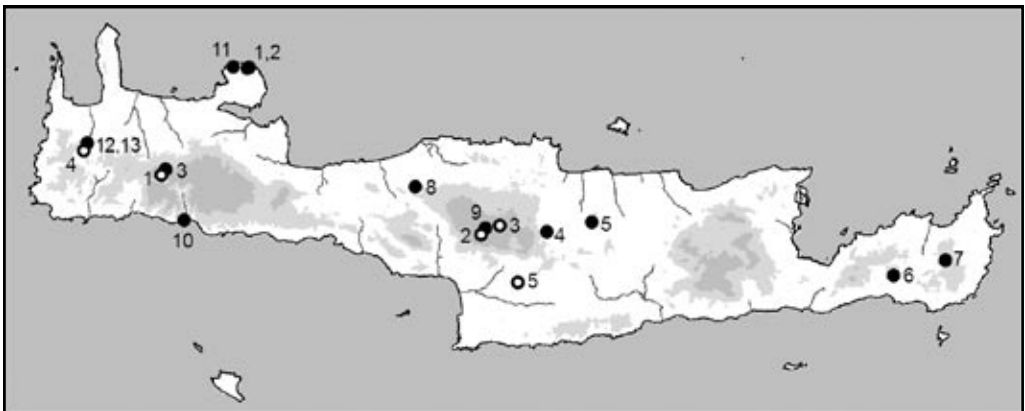


Fig. 46. Records of *Plecotus macrobullaris* Kuzjakin, 1965 (open symbols) and *P. kolombatovici* Đulić, 1980 (closed symbols) in Crete.

it is found almost solely in mountains (Kiefer & von Helversen 2004a) and a limited number of its records from southwestern Asia come from higher altitudes too (Benda et al. 2006, Karataş & Sözen 2006, Spitzenberger et al. 2006). In Croatia *P. macrobullaris* occupies the highest altitudes and the widest altitudinal range of sites among four continental European species of the genus *Plecotus* (Pavlinić & Tvrtković 2004). Besides Crete *P. macrobullaris* was discovered only in one Mediterranean island, Corsica (Kiefer & von Helversen 2004a). However, no information is available on its ecological characteristics in the latter island.

Unlike other Cretan bat species which all extend their Peloponnese distribution in Crete (with the exception of *Pipistrellus hanaki* known only from Libya), *P. macrobullaris* has a slightly isolated spot of occurrence in Crete; its closest records are known from Sterea Ellada, central Greece (Kiefer & von Helversen 2004a). However, such seeming isolation may be caused by the lack of reliable records rather than by real absence of the species in the Peloponnese.

TAXONOMY. Considering all relevant reports of bats from Crete, altogether four species of *Plecotus* were mentioned from the island; *P. auritus* (Linnaeus, 1758) (Pieper 1977), *P. austriacus* (Fischer, 1829) (Martens 1967, Pieper 1977, Hanák et al. 2001), *P. kolombatovici* Đulić, 1980 (Hanák et al. 2001, Kiefer & von Helversen 2004b), and *P. macrobullaris* Kuzjakin, 1965 (Juste et al. 2004, Kiefer & von Helversen 2004a, Spitzenberger et al. 2006). Nevertheless, some of these reports were based on currently abandoned taxonomic conceptions and/or on misinterpretations. According to the available evidence, only two species of the genus live on the island.

The first bat of the genus *Plecotus* was reported from Crete by Martens (1967) under the name *P. austriacus* from the Agias Sofias cave near Topolia; it was the second record of this form from Greece (the first record for Greece was reported by Niethammer [1962] from Corfu, the first one for the Greek mainland by Kock [1969] from Meteora). The respective specimen bore the typical

Table 13. Basic biometric data [in mm] on examined Cretan samples of *Plecotus macrobullaris* Kuzjakin, 1965, *P. kolombatovici* Đulić, 1980, and *Miniopterus schreibersii* (Kuhl, 1817); for abbreviations see p. 110

	<i>Plecotus macrobullaris</i>					<i>Plecotus kolombatovici</i>					<i>Miniopterus schreibersii</i>				
	n	M	min	max	SD	n	M	min	max	SD	n	M	min	max	SD
LC	4	51.0	49	55	2.708	11	50.9	47	53	1.640	25	56.8	52	62	2.718
LCd	4	53.8	53	55	0.957	11	49.4	47	52	1.804	25	61.2	58	65	1.786
LAt	4	41.20	40.3	42.1	0.775	11	37.48	35.9	39.8	1.308	25	44.90	44.0	46.0	0.528
LPol	4	7.13	6.9	7.3	0.171	11	5.75	5.5	6.1	0.170	–	–	–	–	–
LA	4	40.35	39.1	41.3	0.947	11	35.90	34.7	36.8	0.707	25	12.69	11.8	13.4	0.453
LTr	4	19.40	18.6	19.9	0.560	11	16.22	15.5	16.9	0.387	25	5.44	4.9	6.1	0.361
LCr	3	17.33	16.93	17.56	0.345	9	16.14	15.75	16.53	0.227	19	14.85	14.49	15.13	0.184
LCb	3	16.16	15.88	16.49	0.308	9	14.95	14.65	15.39	0.225	19	14.44	14.11	14.67	0.132
LaZ	2	9.13	9.12	9.14	0.014	9	8.38	8.23	8.53	0.107	19	8.52	8.22	8.77	0.130
LaI	3	3.58	3.52	3.64	0.060	9	3.21	3.07	3.31	0.069	19	3.55	3.38	3.73	0.100
LaN	3	8.77	8.61	9.02	0.217	9	8.10	7.91	8.48	0.225	19	7.83	7.68	7.96	0.080
LaM	3	9.47	9.38	9.53	0.078	9	8.74	8.58	8.90	0.117	19	8.57	8.42	8.71	0.084
ANc	3	5.46	5.42	5.48	0.032	9	5.35	5.24	5.44	0.072	19	6.24	6.02	6.44	0.099
LBT	3	4.77	4.71	4.87	0.085	9	4.25	4.14	4.36	0.075	–	–	–	–	–
CC	3	3.68	3.62	3.75	0.065	9	3.56	3.48	3.70	0.071	19	4.53	4.39	4.74	0.085
M ³ M ³	3	6.15	6.12	6.19	0.035	9	5.82	5.58	5.93	0.116	19	6.28	6.09	6.42	0.087
CM ³	3	5.81	5.72	5.97	0.137	9	5.35	5.26	5.52	0.077	19	5.86	5.62	5.98	0.086
LMd	3	10.96	10.73	11.19	0.230	9	10.19	9.93	10.60	0.211	19	10.55	10.27	10.77	0.116
ACo	3	3.17	3.02	3.31	0.145	9	2.95	2.82	3.06	0.070	19	2.57	2.42	2.66	0.060
CM ₃	3	6.31	6.16	6.44	0.142	9	5.78	5.66	5.96	0.090	19	6.24	6.02	6.34	0.068

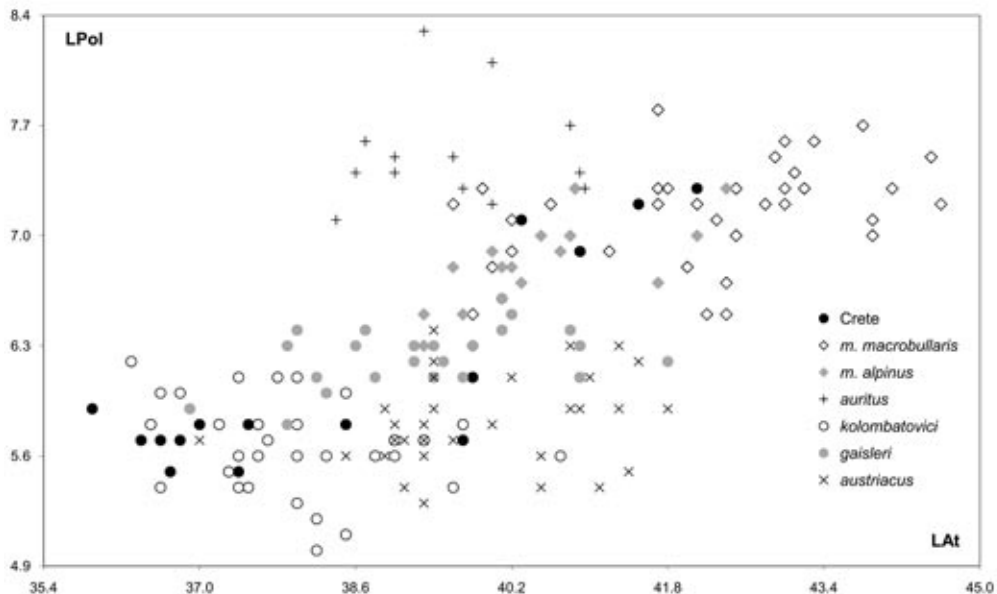


Fig. 47. Bivariate plot of examined Cretan and comparative samples of *Plecotus* Geoffroy, 1818: forearm length (LAT) against thumb length (LPol).

austriacus characters, such as short thumb and thumb claw, long upper canine and relatively large tympanic bullae, however, was markedly smaller than *P. austriacus* representatives from Central Europe (Martens 1967: 253). Pieper (1977) found bone remnants of 11 individuals of *Plecotus* bats in barn owl pellets collected at Topolia, close to the previous site; among them he identified two morphotypes, a smaller one bearing the *austriacus* characters and a larger one, with the *auritus* characters. The evidence of the latter morphotype was evaluated as a record of *P. auritus* in the island (Pieper 1977, von Helversen & Weid 1990, von Helversen in Mitchell-Jones et al. 1999). Von Helversen & Weid (1990) suggested that the small *austriacus* representatives could belong to the form described from the Adriatic islands, *P. austriacus kolombatovici* Đulić, 1980 or to the form of North Africa, *P. a. christii* Gray, 1838, though the two forms may be even identical under the latter synonym.

Spitzenberger et al. (2001) were the first to evidence in detail and explain a hidden variation within the European *Plecotus* populations. They suggested existence of a third species in central and southeastern Europe, living in sympatry with *P. auritus* and *P. austriacus*, and they identified this new species with the Adriatic form *P. kolombatovici*. In accordance with the analysis by Spitzenberger et al. (2001), Hanák et al. (2001) assigned the records of *Plecotus* bats from Greece to three species, *P. auritus*, *P. austriacus* and *P. kolombatovici*, and four available records from Crete to *P. kolombatovici* (i.e. *P. macrobullaris* and *P. kolombatovici* in their modern sense) and to *P. austriacus* s.l. and *P. cf. kolombatovici* (= *P. kolombatovici*, *P. macrobullaris* or *P. austriacus* in their modern sense). Such an arrangement is rather confusing with respect to the present knowledge.

Nevertheless, in several subsequent studies (Kiefer & Veith 2002, Kiefer et al. 2002, Spitzenberger et al. 2002, 2003, Juste et al. 2004) the situation in systematics of *Plecotus* populations

in southeastern Europe was shown to be more complex because at least four species do occur there, viz. the above mentioned three plus *P. macrobullaris*. The latter form is the only species confirmed from Crete with the aid of genetic methods published as yet (Juste et al. 2004, see Spitzenberger et al. 2006). An insufficiently fixed tissue collected from the specimen reported by Martens (1967) was sequenced only partially but the analysis of the fragment confirmed its affiliation to *P. kolombatovici* s.str. (A. Kiefer in litt.).

A simple morphological comparison of the newly collected material of 15 specimens of *Plecotus* bats from Crete with the samples of congeners from the surrounding Mediterranean regions (SE Europe, NE Africa, Middle East) showed only two morphotypes among Cretan bats (Figs. 47, 48, Table 13). Comparison of two external dimensions, forearm length and thumb length, arranged the Cretan bats to two clusters with no overlap (Fig. 47); (1) a cluster of four bats with long thumbs (6.9–7.3 mm) (*P. auritus* species-group sensu Spitzenberger et al. 2006) and rather longer forearms (40.3–42.1 mm), fitting the clusters of *P. macrobullaris* from different parts of its range and slightly overlapping and/or oversizing the cluster of *P. auritus* from the Balkans, and (2) a cluster of eleven bats with short thumbs (5.5–6.1 mm) (*P. austriacus* species-group) and short forearms (35.9–39.8 mm), fitting the cluster of *P. kolombatovici* and largely overlapping with the clusters of *P. gaisleri* from Libya and *P. austriacus* from the Balkans. Comparison of two basic skull dimensions, the greatest length of skull and length of the upper tooth-row, also arranged Cretan *Plecotus* bats to two distinct clusters (Fig. 48); the bats of the above defined cluster (1) have large skulls (LCr 16.9–17.6 mm, CM³ 5.7–6.0 mm) and the cluster of their skull dimensions fits the clusters of *P. macrobullaris* from the Middle East and *P. gaisleri* from Libya, by skull length but not by tooth-row length it also corresponds to the cluster of *P. austriacus* from the Balkans. The bats of the above defined cluster (2) have much smaller skulls (LCr 15.7–16.5 mm,

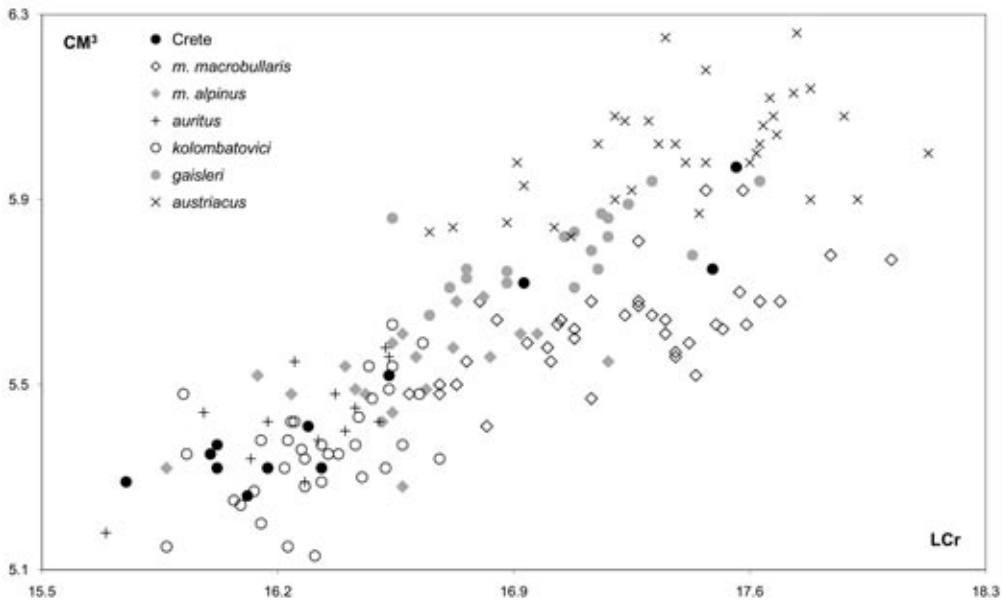


Fig. 48. Bivariate plot of examined Cretan and comparative samples of *Plecotus* Geoffroy, 1818: greatest length of skull (LCr) against length of the upper tooth-row (CM³).

CM³ 5.2–5.5 mm) and their cluster of skull dimensions corresponds to the clusters of *P. auritus* from the Balkans and of *P. kolombatovici* from all parts of its range, and partly overlaps with the cluster of *P. macrobullaris* from Europe. In both comparisons the Cretan bats of the cluster (1) correspond to *P. macrobullaris* and bats of the cluster (2) to *P. kolombatovici*. The clusters of other compared *Plecotus* species (*P. auritus*, *P. austriacus*, *P. gaisleri*) fit in the above two comparisons differently to the clusters of Cretan bats (Figs. 47, 48) and hence, these species should be excluded as possible inhabitants of the island considering the limited available material.

Two subspecies differing in skull size and genetic traits are recognised within *P. macrobullaris* (Spitzenberger et al. 2006); viz. smaller *P. m. alpinus* Kiefer et Veith, 2002 in Europe and larger *P. m. macrobullaris* Kuzjakin, 1965 in the Middle East and Caucasus. A border between the ranges of these two forms is expected to be found in different regions depending upon the character system in study (Spitzenberger et al. 2006); the genetic analyses indicate the border between two genetic lineages to the region of eastern Alps, while morphological data suggest the border to be situated in the region of Euro-Asian transition, an area where also the island of Crete lies. However, the examined Cretan specimens of *P. macrobullaris* clearly correspond in their skull dimensions to dimensional ranges of *P. m. macrobullaris* from the Middle East (Fig. 48). Considering morphological characters (skull size), the Cretan population of *P. macrobullaris* belongs to the nominotypical subspecies and the border between the two forms of this species seems to be located west and north of Crete.

To be concluded, both morphological comparison and casual genetic analyses showed presence of only two species in Crete, *P. macrobullaris* and *P. kolombatovici*. This conclusion well corresponds to the morphological evidence mentioned already by Martens (1967) and Pieper (1977). On the other hand, evidence of any other species of the genus *Plecotus* known from Mediterranean habitats of the surrounding regions can be hardly expected in Crete considering their known distribution and ecological characteristics (see Benda et al. 2004b and Spitzenberger et al. 2006).

Plecotus kolombatovici Đulić, 1980

RECORDS. Original data: Chania: Katholiko monastery (Fig. 12), monastery ruins [1], 27 May 2008: net. 1 ma (NMP 92331 [S+A]); – Koumares, 4 km NE, Panagias Arkoudiotissas cave [2], 28 September 2006: net. 1 ma, 2 fa (NMP 91049 [A], 91050, 91051 [S+A]); – Omalos Plateau, Tzani cave [3], 1 October 2006: net. 1 ma (NMP 91184 [S+A]), 17 August 2008: net. 2 fa (Fig. 49). – Irakleio: Ano Asites, Nykteridospilios cave [4], 28 February 2005: coll. 1 ma (NHMC FC7726 [F]); – Giouchtas hill, Stravomyti cave [5], 7 June 2008: net. 1 m. – Lassithi: Pefkoi, Vreiko cave [6], 12 October 2007: net. 1 ma, 1 ms, 1 fs (NMP 92314, 92315 [S+A], 92313 [A]); – Sitanos, Exo Latsidi cave [7], 13 October 2007: net. 1 fa (NMP 92318 [S+A]), obs. 2 flying *Plecotus* inds., perhaps of the same species. – Rethymno: Arkadiou monastery, vault of a monastery corridor [8], 16 October 2007: obs. & coll. 1 ma (NMP 92322 [S+A]); – Nida Plateau (Idi Mts.), Ideo Andro cave [9], 30 September 2006: net. 1 fa (NMP 91160 [S+A]). – **Published data:** Chania: Agia Roumeli, village [10], 14 July 1995: obs. 5 inds. (Hanák et al. 2001 [as *P. austriacus*]); – Stavros, small cave [= Lera cave] [11], 10 July 1995: net. 1 faL (Hanák et al. 2001 [as *P. austriacus*]); – Topolia [12], 1973–1975: 1–10 inds. (from owl pellets) (Pieper 1977 [as *P. austriacus*]); – Topolia, cave Aghia Sophia [= Agias Sofias cave] [13], 16–17 March 1965: 1 f (Martens 1967 [as *P. austriacus*]), Kiefer & von Helversen 2004b).

COMMENTS. *Plecotus kolombatovici* is a rather rare bat species in Crete, only 13 records are known from throughout the island (Fig. 46). Several records were published under *P. austriacus* affiliation, however, we consider *P. kolombatovici* as the only species of the *P. austriacus* species-group to occur in Crete (see also Taxonomy under *P. macrobullaris*).

Although the records of *P. kolombatovici* come from a wide range of altitudes, this bat clearly prefers more elevated sites (mean 478.8 m, median 396.0 m), even in the summer season (mean 515.0 m, median 440.5 m, n=10). Majority of records of *P. kolombatovici* (10 sites, i.e. 76.9%) are related to underground spaces, in all cases natural caves (incl. the ruined Katholiko monastery,

associated with the Agiou Ioanni cave and several other caves), they include netting records of emerging and/or swarming individuals (8 cases) and findings of torpid bats in their roosts (2). No records are related to foraging individuals in areas not directly connected with a potential roost, similarly, no nursery colony nor winter aggregation of *P. kolombatovici* were found. Pieper (1977) reported findings of this bat (although under assignment to ‘smaller Mediterranean representatives’ of *P. austriacus*) in owl pellets from one site (7.7% of the record sites); remnants of an uncertain number of individuals (up to 10) were found in Topolia in western Crete. External and cranial dimensions of examined specimens of *P. kolombatovici* from Crete are shown in Table 13.

The distribution range of *P. kolombatovici* sensu stricto (after Mayer et al. 2007) lies in a narrow belt of Mediterranean habitats along the northeastern margin of the Mediterranean Basin from Dalmatia over peninsular Greece, Cyprus, central and southern Anatolia to Hatay (Kiefer & von Helversen 2004b, Tvrtković et al. 2005, Benda et al. 2004b, 2007, Spitzenberger et al. 2001, 2006). Thus, the territory of Crete creates a geographical centre of the *P. kolombatovici* distribution range (in longitudinal sense), but also represents its southernmost fringe (the single record from the African offshore island of Pantelleria needs to be confirmed by field sampling; cf. Benda et al. 2004b).

Besides the latter questionable record from Pantelleria (Italy), *P. kolombatovici* was recorded in the Mediterranean islands of Cyprus (Benda et al. 2007), Rhodes (Spitzenberger et al. 2001, 2006, Kiefer & von Helversen 2004b), Thasos (Kiefer & von Helversen 2004b), Chios (Benda et al. 2004b, Kiefer & von Helversen 2004b, cf. Kock 1974a), Karpathos (own unpubl. data), Corfu



Fig. 49. Portrait of an adult female of *Plecotus kolombatovici* Đulić, 1980 from the Tzani cave on the Omalos Plateau (photo by C. Dietz).

(Kiefer & von Helversen 2004b, cf. Niethammer 1962) as well as in many Dalmatian islands (Sveti Andrija, Šolta, Brač, Hvar, Sušac, Korčula, Mrčara, Lastovo, Mljet, Lopud; Dulić & Tvrković 1970 [under *P. auritus*], Tvrković et al. 2005). Most probably also the historic finding of '*P. auritus*' from Santorini belongs to this species (Douglass 1892, cf. Kiefer & von Helversen 2004b) and perhaps also the record of '*P. austriacus*' from Samothrace (Hanák et al. 2001). *P. kolombatovici* seems to represent the most typical eastern Mediterranean island form among *Plecotus* species (cf. Spitzenberger et al. 2006) and its occurrence in Crete is thus well understandable.

In mainland Europe (Dalmatia, Greece), *P. kolombatovici* occurs in rather lower situated habitats (Hanák et al. 2001, Benda et al. 2004b, Pavlinić & Tvrković 2004), in Croatia it is the most 'lowland dweller' among four *Plecotus* species, it was evidenced from the sea level up to 400 m a. s. l. only (Pavlinić & Tvrković 2004). In Asia Minor, the species occurs both in the areas along the Mediterranean Sea coast at the sea level (Benda et al. 2004b) and in central Anatolia (Karataş & Sözen 2006), at sites situated between 1200 and 1900 m a. s. l. In Cyprus *P. kolombatovici* was found at sites lying between 300 and 1700 m a. s. l. (Benda et al. 2007). Hence, the occurrence pattern in Crete resembles rather the situation in the eastern part of the species distribution range.

Miniopterus schreibersii (Kuhl, 1817)

RECORDS. Original data: C h a n i a: Agia Eirini, stream [1], 18 August 2008: net. 1 ma, 1 fs; – Champatha, Vennidon cave [2], 2 July 2005: net. 1 ma, 12 May 2007: net. 2 fs; – Fylaki, Psimaki cave [3], 8 July 2006: obs. several hundreds inds. (exam. 1 m, 1 faL), 21 March 2008: obs. several inds., 6 July 2008: obs. several hundreds inds. (exam. 2 m, 2 faL), 16 August 2008: obs. ca. 50 inds. (exam. 2 ma, 1 ms); – Katholiko monastery (Fig. 12), Agiou Ioanni cave [4], 28 April 2008: net. 1 ma, 4 ms, 20 fa, 2 fs; – Omalos Plateau, Tzani cave [5], 1 October 2006: obs. & coll. 1 ma inside the cave, net. ca. 40 inds., exam. & coll. 13 ma, 2 fs (NMP 91161–91171, 91176 [S+A], 91172–91175 [A]), 17 August 2008: obs. several inds., net. 12 ma, 4 ms, 2 fa, 2 fs, 1 ind.; – Papadiana, ford [6], 17 July 2008: net. 2 fa, 19 July 2008: net. 1 fa, 21 July 2008: net. 1 fa. – I r a k l e i o: Alithini, Meires cave [7], 25 May 2007: obs. several hundreds inds.; – Ampelouzos, gorge, mines [8], 6 April 2008: obs. 1 ind.; – Ano Asites, Nykteridospilios cave [9], 26 June 2005: net. 1 m, 20 November 2005: obs. 1 ind., 24 November 2005: obs. 1 ind., 24 March 2006: obs. 1 ind.; – Tylisos, Kamilari cave [10], 23 March 2006: net. 1 ms, 6 fs, 7 April 2006: net. 8 m, 3 fa, 14 fs, 16 May 2006: net. 7 m, 13 faG, 1 fa, 1 fs, 12 June 2006: net. 2 m, 1 faL, 1 fs, 12 July 2006: net. 1 ma, 6 November 2006: det. several ind., 23 March 2007: net. 1 m, 5 fs, 20 April 2007: net. 7 m, 14 fa, 1 fs, 28 July 2007: net. 1 ma, 8 ms, 23 October 2007: net. 4 m, 2 fs, 9 April 2008: det. several inds., 13 April

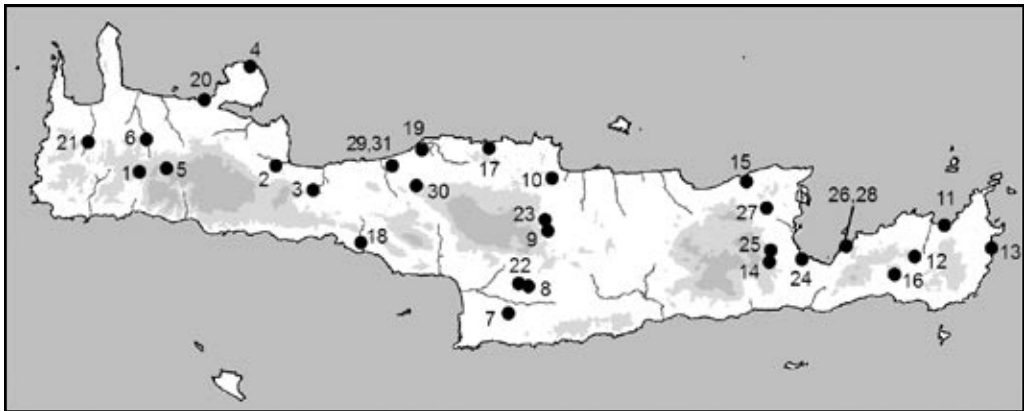


Fig. 50. Records of *Miniopterus schreibersii* (Kuhl, 1817) in Crete.

2008: net. 7 m, 6 fa, 7 fs. – *L a s i t h i*: Agia Fotia, Koufota cave [11], 20 July 2006: obs. ca. 1000 inds., 3 July 2007: obs. several hundreds inds.; – Agios Georgios, at the Megalo Katofygi cave [12], 5 September 2004: det. & rec. several inds.; – Chochlakies, Karoumes bay, Voreino cave [13], 6 September 2007: obs. ca. 20 inds.; – Kroustas, at the Tafos cave [14], 23 November 2007: det. & rec. several inds.; – Milatos, Milatou cave [15], 2 November 2004: net. 1 ma, 1 fa, 7 October 2006: net. 3 ma, 1 fa, 2 fs, 1 ms (NMP 91112–91115, 91118 [S+A], 91116, 91117 [A]), 9 October 2006: obs. ca. 50 inds. (obs. K. Paragamian), 12 August 2007: obs. 1 ind.; – Pefkoi, Vreiko cave [16], 12 October 2007: net. 1 fs (NMP 92316 [S+A]), 1 ind., 23 November 2007: obs. 5 inds., net. 1 m, 1 fa. – *R e t h y m n o*: Doxaro, Mougri cave [17], 11 November 2004: net. 16 m, 3 fs, 9 November 2007: det. & rec. several inds.; – Lefkogeia, at a Venetian bridge ca. 3 km E of the Kato Preveli Monastery [18], 11 October 2007: net. 1 ma (NMP 92311 [S+A]); – Prinost, at the Prinou cave [19], 21 May 2005: det. & rec. several inds., 18 November 2006: det. & rec. several inds., 11 October 2007: net. 1 fs, 19 June 2008: net. 9 faL. – **Published data**: *C h a n i a*: Chania [20], before 1886: 1 ind. (Kock 1974b); – Moni Katholiko, Agios Ioannis cave [= Katholiko monastery, Agiou Ioanni cave] [4], 4 May 2003: det. 1 ind. (social call), 5–7 inds. (Skiba 2007); – Omalos, cave [= Omalos Plateau, Tzani cave] [5], 12 July 1995: net. 1 ma (Hanák et al. 2001); – Topolia [21], 1973–1975: 10 inds. (from owl pellets) (Pieper 1977). – *I r a k l e i o*: Labyrinth [= Plouti, Gortynas Labyrinth mine] [22], 15 August 1845 (Raulin 1869a, b); Haghia Dekka [= Agioi Dekai], Labyrinth [= Plouti, Gortynas Labyrinth mine], obs. individuals, 1904: coll. 2 inds. (Bate 1905), 1 m (Miller 1912); Labyrinth [= Plouti, Gortynas Labyrinth mine], 11 June 1925: 1 fa (Pohle 1953); Gortis, Labyrinth [= Plouti, Gortynas Labyrinth mine], 3 inds. (Hanák et al. 2001); – Sarchos [23], 1973–1975: 1 ind. (from owl pellets) (Pieper 1977). – *L a s i t h i*: Istro [24], 30 April 2004: det. 2 inds. (Skiba 2007); – Kroustas/Kritza [= Kroustas/Kritsa] [25], 1 May 2004: det. 2 inds. (Skiba 2007); – Kavousi and Tholos [26], 27 April 2004: det. 1 ind. (Skiba 2007); – Limnes [27] (Theodor 1967); – Milatos Spilia [= Milatos, Milatou cave] [15], 28 April 2004: det. 15–20 inds. (Skiba 2007); – Tholos/Kavousi [28], 27 April 2004: det. 3 inds. (Skiba 2007). – *R e t h y m n o*: Adele [29], 30 April 2003: det. 5 inds. (Skiba 2007); – Arkadiou monastery [30], 28 April 2003: det. 2 inds. (Skiba 2007); – Platania – Adele [31], 27 April 2003: det. 5 inds. (Skiba 2007). – Kreta [= Crete] (no exact. loc.), 1 ma (Pohle 1953).

COMMENTS. *Miniopterus schreibersii* ranks among moderately abundant bat species in Crete, 31 records are known from throughout the island (Fig. 50, Table 1). Moreover, this species belongs to the earliest known bats of Crete; a record from the Gortynas Labyrinth was published by Raulin (1869b). The occurrence of *M. schreibersii* was evidenced in all parts of the island, from the sea level up to medium elevated regions slightly exceeding 1000 m a. s. l. Although *M. schreibersii* inhabits a wide range of sites of Crete, it prefers rather lower altitudes (mean 275.5 m, median 221.5 m). Despite a relatively low number of records, in the breeding period *M. schreibersii* forms colonies of a few tens to several hundreds of individuals, and thus it seems to be one of the most abundant species of Crete. In the winter period it occurs in slightly higher situated sites (mean 341.5 m, median 268.5 m, n=8), though the total range of the known winter sites lies lower than in summer, between 116 and 782 m a. s. l. only (Table 2). However, true hibernation has not yet been confirmed from the island. In a higher situated and colder winter roost at 782 m a. s. l. (Tafos cave), the bats emerged to feed at warmer evenings. Being observed in the cave the bats are irritable by a minor disturbance even when the weather is quite cold.

Majority of Cretan records of *M. schreibersii* (17 sites, i.e. 54.8%) are associated with underground spaces, both natural caves (15) and mines (2), these include both findings of bats in their roosts (15 evidences) and nettings/recordings of emerging and/or swarming individuals (34). No man-made overground shelters of *M. schreibersii* were found. Eleven records (35.5%) are related to foraging bats recorded in the areas not directly connected with their roosts, mostly by an ultrasound detector (8 cases/sites, see Skiba 2007). Pieper (1977) reported findings of *M. schreibersii* in owl pellets from two sites (6.5%). External and cranial dimensions of examined specimens of *M. schreibersii* from Crete are shown in Table 13.

Most of the roost records of *M. schreibersii* are findings of individuals, aggregations representing nursery colonies (both directly observed and indirectly assumed) were found in eight caves only, in three of them agglomerations of several hundreds to one thousand individuals were present. Wintering bats were recorded rather occasionally (in three caves) and only single bats were found; true hibernation has not been confirmed in Crete. Torpid but irritable bats were found only at two sites (the Tafos cave at Kroustas and the Vreiko cave at Pefkoi) during a winter check.

M. schreibersii is a widespread bat in Greece, it was recorded in all geographical parts of the country (Hanák et al. 2001), including some islands; Hanák et al. (2001) reviewed records from Skiathos, Lesbos, Kos, Rhodes, Crete, Zakynthos, Corfu, von Helversen (in Mitchell-Jones et al. 1999) gave an additional record from Karpathos. Mitchell-Jones et al. (1999) showed this bat to be widely distributed in the European Mediterranean and sub-Mediterranean, including the largest islands (Mallorca, Menorca, Corsica, Sardinia, Sicily, Dalmatian islands). In Cyprus, *M. schreibersii* is a relatively frequently recorded bat (Benda et al. 2007) occurring at a similar altitude range as in Crete.

Tadarida teniotis (Rafinesque, 1814)

RECORDS. **Original data:** C h a n i a: Agia, dam [1], 22 December 2007: rec. few inds.; – Agia Eirini, gorge [2], 24 April 2008: det. & rec. several inds.; – Agia Marina, village [3], 27 September 2006: det. 1–2 inds.; – Anopoli, Agathopi Plateau, scrubland [4], 14 September 2002: det. & rec. 2 inds.; – Anopoli, village [5], 17 September 2002: det. & rec. several inds.; – Anopoli, Argidolagos, cypress forest [6], 16 September 2002: det. & rec. 11 inds.; – Anopoli, Dragou, scrubland [7], 15 September 2002: det. & rec. several inds.; – Anopoli, Porolagos, cypress forest [8], 18 September 2002: det. & rec. several inds.; – Anopoli, Porolagos, pine forest [9], 19 September 2002: det. & rec. several inds.; – Kolymvari, at a mine above the village [10], 13 July 2008: det. 1 ind.; – Koumares, 4 km NE, at the Panagias Arkoudiotissas cave [11], 28 September 2006: det. several inds.; – Krya Vrisi, village [12], 26 April 2008: det. & rec. several inds.; – Limni, pond [13] (Fig. 51), 19 August 2008: net. 1 fa (Fig. 52); – Madaro, scrubland (Volikas Mts. refuge) [14], 27 October 2002: det. & rec. several inds.; – Myloniana, around the Koulieri cave [15], 24 July 2007: det. & rec. 1 ind.; – Papadiana, ford [16], 17 July 2008: net. 1 ma; – Platyvola, Athymolakos Plateau [17], 22 July 2008: det. & rec. several inds.; – Lefka Ori Mts., Poria, scrubland above the Samaria gorge [18], 5 October 2002: det. several inds.; – Samaria, gorge [19], 4 June 2005: det. & rec. 1 ind.; 5 July 2008: det. & rec. several inds.; – Sougia, stream [20], 14 March 2006: det. & rec. 1 ind.; – Stavros, at the Lera cave [21], 26 December 2005: det. & rec. 1 ind., 1 May 2008: det. & rec. 1 ind.; – Theriso, Aliakes Plateau [22], 2 November 2008: det. & rec. 1 ind.; – Theriso, around the Sarakinas cave [23], 8 October 2007: det. 3 inds.; – Theriso, scrubland (close to Panagia) [24], 4 October 2002: det. & rec. several inds.; – Theriso, village [25], 27 September 2002: det. & rec. several inds.; – Zourva, cypress forest [26], 26 October 2002: det. & rec. several inds. – I r a k l e i o: Agia Varvara, village [27], 18 July 2008: det. & rec. several inds.; – Alithini, around the Meires cave [28], 25 May 2007: det. & rec. several inds.; – Amnisos, at the Eileithyias cave [29], 4 October 2006: det. 1 ind.; – Ano Asites, Agiou Charalampou gorge [30], 22 May 2008: obs. a colony of 5 inds.; – Ano Asites, at the Nykteridospilios cave [31], 5 July 2007: det. & rec. several inds.; – Astrakoi, gorge [32], 3 June 2008: det. & rec. several inds.; – Avdou, at the Agias Foteinis cave [33], 10 October 2007: det. several inds.; – Damasta, scrubland [34], 5 June 2008: det. & rec. 1 ind.; – Demati, Anapodaris river bridge [35], 24 May 2008: det. & rec. several inds.; – Faistos, Geropotamos river [36], 28 February 2008: det. & rec. several inds.; – Giouchtas hill, at the Stravomyti cave [37], 7 June 2008: det. & rec. 1 ind.; – Gonia, village [38], 16 October 2002: det. & rec. 3 inds.; – Gonia, scrubland [39], 25 June 2008: det. & rec. several inds.; – Irakleio, city fortification walls [40], 27 November 2007: det. & rec. 1 ind.; – Irakleio, city center [41], 22 May 2001: found & coll. 1 fa (NHMC FC3705 [F]); – Irakleio, old university campus [42], 7 April 2008: det. & rec. several inds.; – Kamaraki, stream [43], 9 October 2006: det. & rec. several inds.; – Keratokampos, Kerato hill, at the Vigla cave [44], 12 March 2007: det. & rec. 1 ind.; – Keri hill, scrubland [45], 15 July 2008: det. & rec. several inds.; – Laloumas, Koutsoulitis river [46], 26 August 2007: det. & rec. several inds., 31 August 2007: det. & rec. several inds.; – Linoperamata, rocky canyon [47], 20 October 2006: det. & rec. several inds.; – Linoperamata, Almyros river [48], 19 March 2007: det. & rec. several inds.; – Linoperamata, Almyros river spring [49], 20 October 2006: det. & rec. several inds.; – Marathitis [50], 9 August 2008: det. & rec. 1 ind.; – Matala, sea shore [51], 8 October 2006: det. 1 ind.; – Rouva forest, Agiou Ioanni chapel, pasture [52], 4 June 2008: det. 1–2 inds.; – Sarchos, at the Chonos cave [53], 17 November 2006: det. & rec. several inds.; – Stroumboulas Plateau, scrubland [54], 11 October 2002: det. & rec. 9 inds.; – Zaros, a brook ca. 1 km to N [55], 4 March 2006: det. & rec. several inds.; – Zaros, Votomos Lake [56], 4 March 2006: det. & rec. several inds., 12 April 2008: det. & rec. several inds., 25 May 2008: det. & rec. 2 foraging inds. – L a s i t h i: Kritsa, Gaidourotrypa cave [57] (Fig. 2), 31 May 2008: det. & rec. 2 inds.; – Milatos, at the Milatou cave [58], 7 October 2006: det. several inds.; – Sitanos, at the Exo Latsidi cave [59], 13 October 2007: det. 2 inds. – R e t h y m n o: Agios Ioannis, Platis river [60], 26 May 2007: det. & rec. several inds.; – Agios Yakinthos (Idi Mts.), scrubland [61], 2 November 2002: det. & rec. 1 ind.; – Amnatos, village [62], 9 August 2008: det. & rec. 1 ind.; – Archaia Eleftherna, Aravanes oak forest [63] (Figs. 3, 22), 11 July 2008: det. & rec. several inds.; – Nida Plateau (Idi Mts.) [64], 18 October 2002: det. several inds.; – Klisidi, olive grove [65], 9 August 2008: det. & rec. several inds.; – Melissourgaki, Kouroupi oak forest [66], 23 October 2002: det. & rec. 2 inds.; – Monastiraki, Genianos stream [67], 2 June 2008: det. 1 ind.; – Myrthios, Patsianos river [68], 24 August 2007: det. & rec. several inds.; – Panormo, Geropotamos river estuary [69], 2 September 2007: det. & rec. several inds.; – Patsos, at the



Fig. 51. A small pond near Limni is a drinking and foraging site for at least five bat species: *Rhinolophus ferrumequinum*, *Hypsugo savii*, *Pipistrellus hanaki*, *P. kuhlii*, and *Tadarida teniotis* (photo by C. Dietz). Fig. 52. Adult female of *Tadarida teniotis* (Rafinesque, 1814) captured at a small pond near Limni (photo by C. Dietz).

Agiou Antoniou cave [70], 3 October 2006: det. 1 ind.; – Petradolakia (Idi Mts.), Agios Fanourios chapel [71], 17 October 2008: det. & rec. 1 ind.; – Prinos, at the Prinou cave [72], 11 October 2007: det. & rec. 1 ind., 18 November 2006: det. & rec. several inds.; – Roumeli, Geropotamos river [73], 16 April 2006: det. & rec. several inds., 18 April 2007: det. & rec. several inds., 26 June 2008: det. & rec. several inds.; – Ski resort (Idi Mts.), scrubland [74], 27 May 2007: det. & rec. 1 ind., 19 October 2007: det. & rec. several inds.; – Varsamo (Idi Mts.), at the Peristerospilios cave [75], 8 November 2006: det. & rec. 1 ind.; – Viran Episkopi, olive grove [76], 9 August 2008: det. & rec. several inds. – **Published data:** C h a n i a: Agia Roumeli, a rocky cliff [77], 14 July 1995: det. 1 ind. (Hanák et al. 2001); – Azogyres bei Paläochora [= Palaiochora] [78], 19 March 1965: obs. (Martens 1967); – Kalives [= Kalyves], E of Chania [79], 22 March 1965: obs. (Martens 1967); – Katholiko, monastery ruins [= Katholiko monastery ruins] [80], 13 March 1965: obs. (Martens 1967); Moni Katholiko [= Katholiko monastery] and its vicinity, 4 May 2003: det. 2 inds. (Skiba 2007); – Weiße Berge oberhalb Lakki [= Lefka Ori Mts. above Lakkoi] [81], 6 April 1965: obs. (Martens 1967); – Limni Kourna [= Mouri, Kourna lake] [82], 2 May 2003: det. 3 inds., 3 May 2003: det. 4–5 inds. (Skiba 2007); – Omalos [= Omalos Plateau], above the valley [83], 12 July 1995: det. 1 ind. (Hanák et al. 2001); – Paläochora [= Palaiochora] [84], 21 March 1965: obs. (Martens 1967); – Stavros [85], 10 July 1995: det. 1 ind. (Hanák et al. 2001); – Topolia [86], 17 March 1965: obs. (Martens 1967), Topolia, 1973–1975: 1 ind. (from owl pellets) (Pieper 1977); – Xyloskalo near Omalos [= Omalos Plateau], at a small cave [87], 13 July 1995: det. 1 ind. (Hanák et al. 2001). – I r a k l e i o: Ano Viannos [88], 1973–1975: 2 inds. (from owl pellets) (Pieper 1977); – Dia Island [89] (Kahmann 1959); – Amoudara, cave [= Linoperamata, Almyros river springs, cave] [90], 8 & 10 July 1995: det. 2 inds., 10 July 1995: det. 1 ind. (Hanák et al. 2001); – Amoudara rocky canyon [=

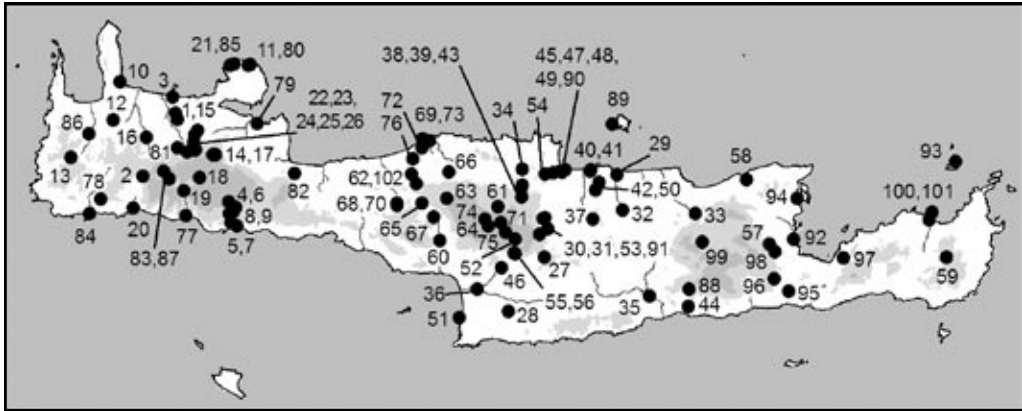


Fig. 53. Records of *Tadarida teniotis* (Rafinesque, 1814) in Crete.

Linoperamata, rocky canyon] [48], 7 July 1995: det. 1 ind. (Hanák et al. 2001); – Sarchos [91], 1973–1975: 1 ind. (from owl pellets) (Pieper 1977). – L a s i t h i: Amoudara [= Ammoudara] [92], 29 April 2004: det. 2 inds. (Skiba 2007); – Dragonada Island [93] (Kahmann 1959); – Elounda and its vicinity [94], 21 April 2004: det. 3 inds., 24 April 2004: det. 3 inds. (Skiba 2007); – ‘Stausee’ 4 km NW of Ierapetra [= Gra Lygia, Mpramianos river dam] [95], 30 April 2004: det. 4 inds. (Skiba 2007); – Kalamafka [96], 30 April 2004: det. 2 inds. (Skiba 2007); – Kavousi and Tholos [97], 27 April 2004: det. 2–3 inds. (Skiba 2007); Tholos, 27 April 2004: det. 1 ind. (Skiba 2007); – Kroustas [98], 1 May 2004: det. 6 inds. (Skiba 2007); – Milatos Spilia [= Milatos, Milatou cave] [58], 28 April 2004: det. 1 ind. (Skiba 2007); – Psihro [= Psychro], village [99], 19 July 1995: det. 1 ind. (Hanák et al. 2001); – Sitia, Kap Sitia [= Sitia, cape], rocky crevice [100], 22 March 1958: 1 ind. (Kahmann 1959, Kock 1969); – Sitia [101], 23 March 1965: obs. (Martens 1967). – R e t h y m n o: Moni Arkadi [= Arkadiou monastery] and its vicinity [102], 28 April 2003: det. 3 inds. (Skiba 2007).

COMMENTS. According to the number of records, *Tadarida teniotis* is the most common bat species of Crete (Table 1). Its records come from all parts and altitudes of the island (Fig. 53, Table 2), it is the only bat recorded also in small islets off the northern shore of Crete, Dia and Dragonada (Kahmann 1959). Record sites of *T. teniotis* in Crete lie in a wide range of altitudes from the sea level up to 1600 m a. s. l. During the summer season, the species prefers higher situated localities of the island (mean 455.6 m, median 400.0 m, n=79), while in winter it is found at rather lowland sites (mean 319.6 m, median 140.0 m, n=19), although the altitudinal range is comparable in the two seasons (Table 2).

However, the picture of *T. teniotis* as the most widespread bat in Crete should be corrected by the fact that vast majority of the records – 88 (87.1%) regards to acoustic indentifications (Hanák et al. 2001, Skiba 2007, present data), either with or without ultrasonic detectors. *T. teniotis* produces very strong, low frequency echolocation calls, quite well audible at large distances and a trained ear registers them at each instance. In comparison to that, the abundances of any other species are much underestimated and the number of records can hardly be compared. Only five records of *T. teniotis* (5.0%) refer to findings of individuals – either netted (three bats at three sites, at 44 m, 240 m and 582 m a. s. l.) and incidentally found in urban habitats (two individuals in two towns close to sea shore). Only one roost was identified for sure; a group (colony?) of five individuals was observed in the Agiou Charalampou gorge at Ano Asites in the second half of May 2008. Pieper (1977) reported findings of this bat in owl pellets from three sites (3.0%).

T. teniotis seems to be a common species in the European thermo-Mediterranean zone (Ibáñez & Pérez-Jordá 2004), including most of the Balkan Peninsula and Mediterranean islands. In

Greece, it was recorded in all geographical parts of the country (Hanák et al. 2001), but mainly in coastal areas of the mainland and in many islands. Hanák et al. (2001) reviewed records from Lesbos, Euboea, Chios, Kos, Santorini, Rhodes, Karpathos, Crete, and Kythira; von Helversen (in Mitchell-Jones et al. 1999) gave an additional record from Lefkada and possibly also from Thasos and Leros and/or Patmos. However, *T. teniotis* was found in many other Mediterranean islands and in the Canary Islands (Mitchell-Jones et al. 1999, Ibáñez & Pérez-Jordá 2004), thus it represents a typical island bat of the region together with *Pipistrellus kuhlii*; viz. Teneriffa, Gomera, Hierro, La Palma, Gran Canaria, Ibiza, Mallorca, Cabrera, Menorca, Corsica, Cerbicales, Sardinia, San Pietro, Toro, Giglio, Giannutri, Sicily, Ustica, Scoglio, Lipari, Vulcano, Malta, Šolta, Brač, and Korčula.

Recently the occurrence of *T. teniotis* has been confirmed in Cyprus (Benda et al. 2007), however, its distribution pattern in this island markedly differs from that found in Crete. While in Crete *T. teniotis* is the most frequently recorded bat species, its records in Cyprus as well as in the Mediterranean Levant (s.str.) are rather scarce (Benda et al. 2006, 2007, Horáček et al. 2008), despite the wide availability of suitable habitats similar to Crete or mainland Greece. Obviously, there is no simple ecological and/or biogeographical explanation for such a striking difference and the phenomenon certainly deserves a closer attention.

DISCUSSION

The present review summarises 622 records of 17 bat species available from the island of Crete (Table 1). Comparing to the most recent review of Cretan bat fauna published by Hanák et al. (2001), the number of known species increased by two species, *Pipistrellus nathusii* and *Nyctalus leisleri*. *P. nathusii* was first reported on the basis of sound recordings (Skiba 2007), here we mention the first specimen collected and thus confirm the presence of the species in Crete. *N. leisleri* is here reported from Crete for the first time. Both species newly proved to occur in Crete belong to typical European migratory bats and thus a question arose whether their Cretan records (1) document a regular part of their migration routes or of their summer occurrence range, or whether they rather (2) document an incidental or at least irregular arrival of stray individuals. Since individuals of the two species were recorded in the island in very limited time periods only (17 days in *P. nathusii*, 77 days in *N. leisleri*), their evidence rather indicate the latter possibility. However as stated in the Comments on *N. leisleri* records above, such a conclusion remains rather speculative until sufficient long-time research in Crete is carried out.

Due to intensive bat research in the last few years, the total number of bat records in Crete increased more than five times in comparison with the data by Hanák et al. (2001), from 120 to 622. On average the number of records per species increased 6.6 times, ranging from 3.7 to 20 times. The highest increase in the number of records appeared in *Myotis capaccinii*, for which only one record was available for a long time (Kock 1974b) while 20 records are available now. However, a significant increase occurred both in the numbers of records of common bat species, such as *Tadarida teniotis* (5.9 times), *Rhinolophus ferrumequinum* (4.4), *R. hipposideros* (4.6), or *Pipistrellus kuhlii* (6.1), as well as those of the previously rarely found bat species, such as *Myotis emarginatus* (4.4), *M. aurascens* (11.0), *Eptesicus serotinus* (4.8), *Plecotus kolombatovici* (4.3), or *Miniopterus schreibersii* (5.2). Moreover, presence of *Rhinolophus* and *Plecotus* bats at their foraging grounds was, in contrast to other species, certainly not distinguished at more sites studied with aid of ultrasound detectors, since their echolocation calls are extremely difficult to detect (Waters & Jones 1995, Vaughan et al. 1997).

According to the total number of records (Table 1, Fig. 54), the Cretan bat fauna can be subdivided into six abundance classes; (1) very abundant and common species, known from

>65 records in the island, including four species (*Tadarida teniotis*, *Rhinolophus ferrumequinum*, *R. hipposideros*, and *Pipistrellus kuhlii*); (2) rather abundant species with the number of available records between 40 and 50, including three species (*Myotis blythii*, *Hypsugo savii* and *Rhinolophus blasii*); (3) two species can be considered moderately abundant, in which 30–33 records are known (*Pipistrellus hanaki* and *Miniopterus schreibersii*); (4) moderately abundant to uncommon species, with 19–22 known records, including three species (*Myotis emarginatus*, *M. capaccinii* and *Eptesicus serotinus*); (5) two species are rather rare in Crete, with 13 and 11 records (*Plecotus kolombatovici* and *Myotis aurascens*), respectively; and (6) three bat species are extremely rare in Crete (*Plecotus macrobullaris*, *Nyctalus leisleri* and *Pipistrellus nathusii*), known from less than six records. This classification of the bat fauna is generally similar to that known from another large eastern Mediterranean island, Cyprus (Fig. 54), where, however, a much lower number of records is available (195; Benda et al. 2007). In the latter island, *Rhinolophus ferrumequinum*, *R. hipposideros* and *Pipistrellus kuhlii* are the most abundant species, but *Tadarida teniotis* and *Myotis blythii* belong to rather moderately abundant to uncommon, and *Plecotus kolombatovici* is not quite rare there. In other species inhabiting the two islands, general pattern of their occurrence is similar.

According to altitudinal distribution (Table 2), several bat species can be considered mountain faunal elements in Crete, while some others rather lowland dwellers. The ‘most mountain’ bat of Crete is *Plecotus macrobullaris*, in the previous paragraph noted as one of the rarest Cretan bats, with mean and median values of its altitudinal range above 1000 m a. s. l. When compared with the mean and median values for all known Cretan record sites (Table 2), the dwellers of rather elevated areas in Crete include also *Plecotus kolombatovici* (mean 478.8 m, median 396.0 m a. s. l.), *Tadarida teniotis* (425.5, 333.5), *Myotis blythii* (423.5, 262.5), *Hypsugo savii* (414.1, 250.0), *Nyctalus leisleri* (381.7, 305.0), and *Pipistrellus hanaki* (380.2, 356.5). *Myotis blythii* is a bat preferring mountain habitats most noticeably during the hibernation period. On the other hand, *Myotis capaccinii* (mean 159.4 m, median 93.0 m), *Pipistrellus kuhlii* (176.0, 80.0), *Myotis emarginatus* (213.9, 204.5), *Rhinolophus ferrumequinum* (262.1, 210.0), and *Miniopterus schreibersii* (275.5, 221.5) are regular inhabitants of rather low situated areas in Crete, this group possibly includes also *Pipistrellus nathusii* in which only two records are available though. For most Cretan species these patterns are typical for both the summer and winter seasons. However, according to the available data three species, *Rhinolophus hipposideros*, *R. blasii* and *Tadarida teniotis*, prefer rather more elevated sites in summer and rather lower situated sites in winter; an opposite pattern was found in the seasonal distribution of *Miniopterus schreibersii* (Table 2). However, with the exception of *Myotis blythii* that was found in true hibernation in a few mountain caves, no species was evidenced to hibernate in Crete. In comparison to the situation in the mainland Mediterranean where the cave dwelling species like *Rhinolophus* spp., *Miniopterus* or *Myotis capaccinii* form quite large winter colonies, the absence of any recorded one suggesting a similar situation in Crete, is worthy of a special attention. The winter biology of Mediterranean bats is unfortunately still only poorly known; the question to which degree the seasonal biology of the Cretan bats differs from that in their mainland populations and which are sources of these differences presents undoubtedly one of the most exciting tasks for future research.

The bat fauna of Crete includes almost all elements expected to occur in the island (Table 14). With one exception (*Pipistrellus hanaki* – the species otherwise known only from African Cyrenaica), the Cretan bat fauna resembles that of the southern Balkans and of Cyprus, respectively. The similarity of Cretan and Cypriot faunas is well understandable as both islands are very similar in size and in the distance from the closest continental shore. Out of 19 species composing the bat fauna of Cyprus, almost all were found in Crete as well – except five species (Table 14). One of them can be excluded of the faunal list of Crete almost for sure; *Rousettus aegyptiacus* (Geoffroy,

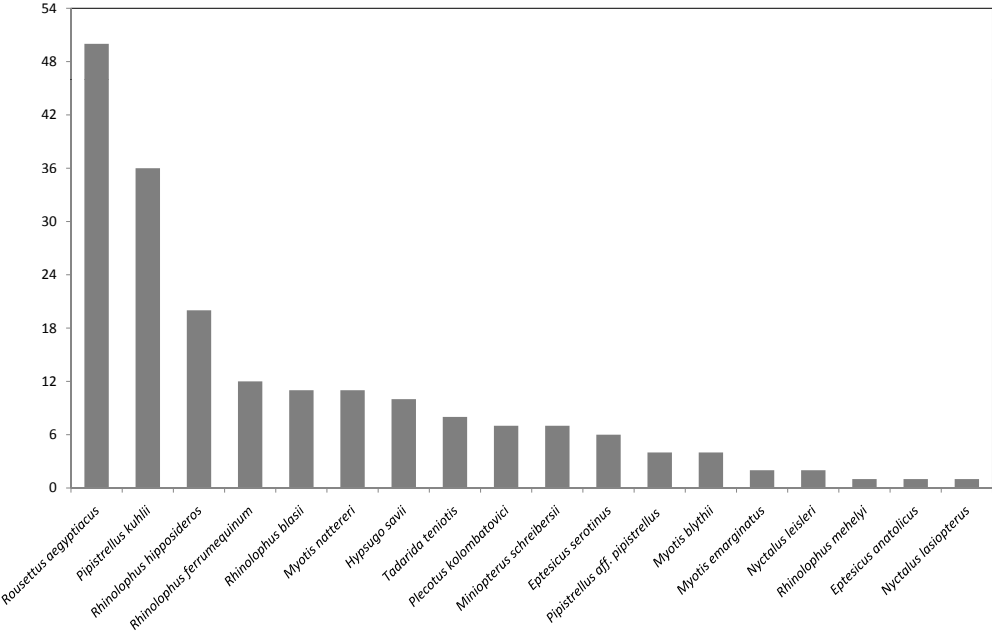
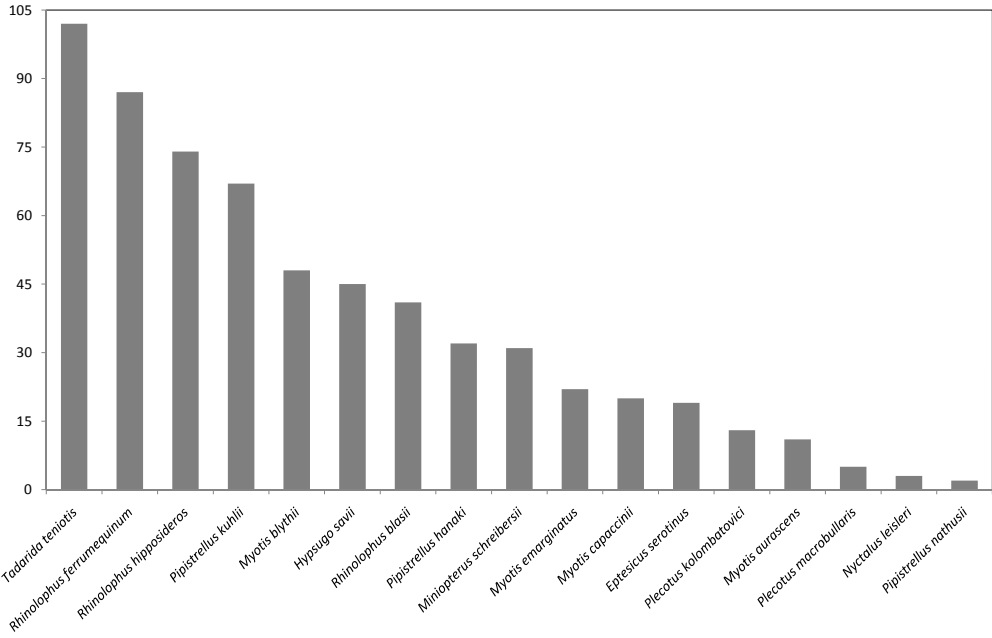


Fig. 54. Comparison of bat fauna compositions and bat record numbers in Crete (above) and in Cyprus (below, after Benda et al. 2007).

Table 14. List of bat species per individual regions of the Eastern Mediterranean with marked faunal status (+ = occurrence confirmed; – = occurrence unconfirmed). Based on the data by Hanák & Elgadi (1984), Benda & Horáček (1998), Hanák et al. (2001), Benda et al. (2004a, b, 2007) and unpublished data. The status in parentheses is considered doubtful

species	Crete	Peloponnese	S Aegean islands	other Greek islands	SW Anatolia	Cyprus	Cyrenaica ¹
<i>Rousettus aegyptiacus</i>	–	–	–	–	+	+	–
<i>Rhinolophus ferrumequinum</i>	+	+	+	+	+	+	–
<i>Rhinolophus clivosus</i>	–	–	–	–	–	–	+
<i>Rhinolophus hipposideros</i>	+	+	+	+	+	+	–
<i>Rhinolophus euryale</i>	–	+	–	+	+	(+)	–
<i>Rhinolophus mehelyi</i>	–	+	–	+	+	+	+
<i>Rhinolophus blasii</i>	+	+	+	+	+	+	–
<i>Myotis myotis</i>	–	+	+	+	+	–	–
<i>Myotis blythii</i>	+	+	–	+	+	+	–
<i>Myotis bechsteinii</i>	–	+	–	–	+	–	–
<i>Myotis nattereri</i>	–	+	–	+	+	+	–
<i>Myotis emarginatus</i>	+	+	+	(–)	+	+	–
<i>Myotis aurascens</i>	+	+	–	–	+	–	–
<i>Myotis capaccinii</i>	+	+	–	+	+	(+)	–
<i>Vespertilio murinus</i>	–	–	–	+	–	–	–
<i>Eptesicus serotinus</i>	+	+	+	+	+	+	–
<i>Eptesicus anatolicus</i>	–	–	+	–	+	+	–
<i>Hypsugo savii</i>	+	+	+	+	+	+	–
<i>Pipistrellus pipistrellus</i> ²	–	+	–	–	(–)	+	–
<i>Pipistrellus pygmaeus</i>	–	+	+	+	–	+	–
<i>Pipistrellus hanaki</i>	+	–	–	–	–	–	+
<i>Pipistrellus nathusii</i>	+	+	–	+	–	–	–
<i>Pipistrellus kuhlii</i>	+	+	+	+	+	+	+
<i>Nyctalus noctula</i>	–	+	–	+	–	(+)	–
<i>Nyctalus leisleri</i>	+	+	+	–	+	+	+
<i>Nyctalus lasiopterus</i>	–	–	–	–	+	+	+
<i>Plecotus auritus</i>	–	+	–	–	–	–	–
<i>Plecotus macrobullaris</i>	+	–	–	–	–	–	–
<i>Plecotus kolombatovici</i>	+	+	+	+	+	+	–
<i>Plecotus gaisleri</i>	–	–	–	–	–	–	+
<i>Miniopterus schreibersii</i>	+	+	+	+	+	+	+
<i>Tadarida teniotis</i>	+	+	+	+	+	+	+
No. of species	17	24	16	19	23	19	9

¹ only its Mediterranean portion, without southern desert parts

² confirmed records of *P. pipistrellus* s.str.

1810) is strictly endemic to the Levantine part of the eastern Mediterranean (in its Palaearctic part of distribution range) and, moreover, it is a species which presence is well marked as a rule and can be hardly overlooked. However, the other species of that group, i.e. *Rhinolophus mehelyi* Matschie, 1901, *Myotis nattereri* (Kuhl, 1817), *Eptesicus anatolicus* Felten, 1971, and *Nyctalus lasiopterus* (Schreber, 1780), deserve close attention.

Rhinolophus mehelyi is a horseshoe bat which occurs in southern Europe including a wide area of the Balkans, in several Greek islands, in the Middle East including Anatolia, Cyprus, Levant, and in the Mediterranean parts of North Africa (Gaisler 2001b); its absence from Crete presents a surprising gap in its range that is more or less continuous throughout whole the eastern Mediterranean. On the other hand, *R. mehelyi* is a rare bat in general and its presence both in Peloponnese and Cyprus is evidenced by single records only (Hanák et al. 2001, Benda et al. 2007). This spe-

cies can be theoretically found in Crete too, when a considerable number of individuals of both *Rhinolophus blasii* and *R. ferrumequinum*, two horseshoe bat species close in size to *R. mehelyi*, is carefully examined.

Myotis nattereri inhabits Mediterranean habitats of the whole eastern Mediterranean with the exceptions of Cyrenaica and Crete. In Cyprus, southern Anatolia, Levant and Peloponnese it is not a rare species (Benda & Horáček 1998, Hanák et al. 2001, Benda et al. 2006, 2007, Horáček et al. 2008). However, its occurrence in Crete is highly improbable, considering the intensive research performed in Crete in the last few years. In all areas of its Mediterranean range, this bat is easy to find by nettings at cave entrances or by checks of natural and artificial underground spaces, as it was carried out in all the above mentioned regions. Despite intensive survey effort in Crete, the species was not found. Why *M. nattereri* did not colonise Crete but successfully colonised Cyprus, remains one of enigmas of historical biogeography of the eastern Mediterranean.

Nyctalus lasiopterus is (most probably) a migratory bat occurring in southern and eastern Europe as well as in Cyrenaica and Morocco, from the Middle East there are three available records from Anatolia, one from Cyprus and one from northern Iran (Ibáñez et al. 2004, Benda et al. 2007). Its records in the whole eastern Mediterranean region are rather scarce and irregular and a lack of a record in Crete is thus not too surprising. The island of Crete lies on a crossroads of its potential migration routes between Europe, Cyrenaica and Asia Minor; if such a migration really exists, the finding of *N. lasiopterus* in Crete remains only a question of time.

Another species present in Cyprus and missing in Crete is *Eptesicus anatolicus*. This species, endemic to the Middle East, is known to occur in the belt of Mediterranean habitats from Rhodes, southern Anatolia, Levant to northern Iraq and southeastern Iran (Benda et al. 2006, 2007). In the Dodecanese island of Rhodes it was found not to be rare (von Helversen 1998). Its potential occurrence in eastern Crete as well as in other Dodecanese islands of Kassos and Karpathos cannot be excluded, since Rhodes lies at the distance of ca. 140 km east from Crete only.

On the other hand, three bat species living in Crete have not yet been proved convincingly in Cyprus, viz., *Myotis capaccinii*, *Plecotus macbullaris*, and *Pipistrellus hanaki*. While the latter species is an endemic of Cyrenaica and Crete and is vicariantly substituted by *Pipistrellus pygmaeus* in the Cypriot fauna, the former two species are distributed in Anatolia near to the shore adjacent to Cyprus and their absence from that island is surprising in respect to their ability to colonise Crete, an island slightly more distant from the continental shore than Cyprus.

Although close to the Balkans, in composition of its bat fauna, Crete resembles rather Cyprus than the closest area of the Balkan region, the Peloponnese (Table 14). This peninsula is inhabited by several bat species which do not live in Crete (Hanák et al. 2001), viz. *Rhinolophus euryale* Blasius, 1853, *Myotis myotis* (Borkhausen, 1797), *Myotis bechsteini* (Kuhl, 1817), *Nyctalus noctula* (Schreber, 1774), and *Plecotus auritus* (Linnaeus, 1758). However, these species are also absent in Cyprus (the published records of *R. euryale* and *N. noctula* are rather doubtful, see Benda et al. 2007) as well as from other east Mediterranean islands other than the offshore ones (Mitchell-Jones et al. 1999).

Pieper (1977) suggested two possible new members of the Cretan bat fauna, *Nyctalus noctula* and a medium-sized species of the genus *Rhinolophus* other than *R. blasii*, i.e. *R. euryale* and/or *R. mehelyi*. Until now, the focused bat research has not proved occurrence of these bats in Crete, although in the case of *R. mehelyi* we cannot exclude its evidence in the future, see above. *N. noctula* ranks among migratory bat species and its possible stray could also be expected to appear in Crete, although its regular range lies more to the north and even in the mainland Greece it occurs rather in the northern areas.

The Cretan bat fauna shows the most apparent and also understandable biogeographical affinity to that of the Balkans. All bat species occurring in Crete live also in southern Greece, with the

only exception of *Pipistrellus hanaki*. The latter species occurs (besides Crete) in Cyrenaica only and documents an extremely exceptional historical contact of Cretan and African faunas, which certainly deserves close attention during the next research. However, some Cretan bat populations also show close similarities with those of the Middle East, in morphological characters the Cretan *Myotis blythii* and *Plecotus macrobullaris* resemble rather Asian than European representatives of these species. In summary, by its composition and taxonomic affinities the Cretan bat fauna well conforms to the geographical position of the island of Crete on the crossroad among Europe, Africa and Asia, a phenomenon not visible in such extent in other terrestrial vertebrate groups.

Acknowledgements

We are thankful to Isabel Dietz (Horb), Frieder Mayer (Berlin), Wolfram Schulze (Erlangen) and Elena Papadatou (Athens) for joining us in the field in August 2008; we also thank Zdeňka Bendová and Eva Veselá (Praha) for their help in the field in 2007 and 2008. We are grateful to George Alexandrakis, George Iliopoulos and many other colleagues and friends for joining us in the field and/or providing information and voucher specimens. Special thanks go to Manolis Nikolakakis for his assistance in preparation of this paper and production of the maps, to Radek Lučan for his help with evaluation of some bat call recordings, and Andreas Kiefer for his kind sequencing of the Martens' (1967) specimen of *Plecotus kolombatovici*.

The activities of Panagiotis Georgiakakis were partially funded by the 03ED375 research project, implemented within the framework of the "Reinforcement Programme of Human Research Manpower" (PENED) and co-financed by the National and Community Funds (25% from the Greek Ministry of Development, General Secretariat of Research and Technology and 75% from the European Social Fund). Petr Benda, Vladimír Hanák, Ivan Horáček and Pavel Hulva were supported by grants of the Czech Science Foundation (# 206/05/2334, 206/09/0888), Petr Benda by grants of the Ministry of Culture of the Czech Republic (CR) (# DE06P04OMG008, MK00002327201), and Pavel Hulva and Adéla Chudárková by grants of the Grant Agency of the Academy of Sciences CR (KJB601110807) and of the Ministry of Education CR (MSMT 0021620828). Field works of the authors in Crete were permitted by the Hellenic Ministry of Rural Development and Food (# 92702/2220).

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GAZETTEER

Original localities

Prefecture of Chania

Afrata [Αφράτα], rocky cliff	35° 34' N, 23° 47' E	5 m
Agia [Αγιά], dam	35° 29' N, 23° 56' E	35 m
Agia [Αγιά], old building	35° 28' N, 23° 56' E	35 m
Agia Eirini [Αγία Ειρήνη], gorge	35° 20' N, 23° 50' E	550 m
Agia Eirini [Αγία Ειρήνη], stream	35° 21' N, 23° 50' E	600 m
Agia Eirini [Αγία Ειρήνη], old chapel	35° 20' N, 23° 50' E	590 m
Agia Marina [Αγία Μαρίνα]	35° 31' N, 23° 55' E	10 m
Alikampos [Αλικάμπος], Skala cave	35° 21' N, 24° 12' E	350 m
Anopoli [Ανώπολη], Agathopi Plateau, scrubland	35° 16' N, 24° 05' E	1600 m
Anopoli [Ανώπολη], village	35° 13' N, 24° 06' E	600 m
Anopoli [Ανώπολη], Argidolagos, cypress forest	35° 15' N, 24° 06' E	1200 m
Anopoli [Ανώπολη], Dragou, scrubland	35° 13' N, 24° 07' E	500 m
Anopoli [Ανώπολη], Porolagos, cypress forest	35° 15' N, 24° 06' E	800 m

Anoroli [Ανόπολη], Porolagos, pine forest	35° 14' N, 24° 05' E	600 m
Argyroupoli [Αργυρούπολη], Mouselas river, old building	35° 19' N, 24° 20' E	105 m
Azogryes [Αζογυρές], Zoure cave	35° 16' N, 23° 43' E	585 m
Champatha [Χάμπαθα], Vennidon cave	35° 21' N, 24° 13' E	210 m
Elos [Έλος], a grove ca. 1 km N	35° 22' N, 23° 38' E	468 m
Episkopi [Επισκοπή], pumping station	35° 28' N, 23° 55' E	45 m
Fylaki [Φυλακή], Psimaki cave	35° 18' N, 24° 20' E	116 m
Fylaki [Φυλακή], Skoteini cave	35° 18' N, 24° 20' E	150 m
Gouverneto Monastery [Μονή Γουβερνέτου], Koumarospilios cave	35° 35' N, 24° 09' E	283 m
Kalami [Καλάμι], Kiliaris river	35° 28' N, 24° 09' E	5 m
Kandanos [Κάνδανος], chapel	35° 20' N, 23° 44' E	365 m
Kandanos [Κάνδανος], a grove	35° 20' N, 23° 44' E	365 m
Kastelos [Κάστελος], cave	35° 19' N, 24° 18' E	220 m
Katholiko Monastery [Μονή Καθολικού], Achyrosopilios cave	35° 35' N, 24° 09' E	50 m
Katholiko Monastery [Μονή Καθολικού], Agiou Ioanni cave	35° 35' N, 24° 09' E	80 m
Kavalos [Καβάλος], Kourna lake, NW shore	35° 20' N, 24° 17' E	20 m
Kolymvari [Κολυμβάρι], old agricultural co-op facilities	35° 32' N, 23° 47' E	15 m
Kolymvari [Κολυμβάρι], mine	35° 33' N, 23° 46' E	44 m
Koumares [Κουμάρες], Panagias Arkoudiotissas cave	35° 35' N, 24° 09' E	198 m
Krya Vrissi [Κρύα Βρύση]	35° 28' N, 23° 45' E	250 m
Lefka Ori Mts [Λευκά Όρη], Samaria gorge, Poria	35° 19' N, 24° 00' E	1500 m
Limni [Λίμνη], pond	35° 22' N, 23° 38' E	582 m
Madaro [Μαδαρό], scrubland	35° 23' N, 24° 03' E	1236 m
Meskla [Μεσκλά], creek	35° 24' N, 23° 57' E	206 m
Myloniana [Μυλωνιανά], Koulieri cave	35° 28' N, 23° 56' E	155 m
Norigeia [Νοπήγεια], German tunnel	35° 30' N, 23° 43' E	10 m
Norigeia [Νοπήγεια], Tyflos river estuary	35° 30' N, 23° 43' E	3 m
Nteres [Ντερές]	35° 26' N, 23° 50' E	200 m
Omalos Plateau [Οροπέδιο Ομαλού], Tzani cave	35° 21' N, 23° 54' E	1025 m
Palaiochora [Παλαιόχωρα], gallery	35° 14' N, 23° 41' E	20 m
Papadiana [Παπαδιανά], ford	35° 25' N, 23° 51' E	240 m
Perivolias [Περβόλια], Mamaloukou cave	35° 29' N, 24° 00' E	150 m
Platanias [Πλατανιάς], Xekollomenos river	35° 31' N, 23° 54' E	5 m
Platyvola [Πλατυβόλα], Athymolakos Plateau	35° 23' N, 24° 02' E	1350 m
Rapaniana [Ραπανιανά], village	35° 32' N, 23° 48' E	5 m
Rodopos peninsula [Χερσόνησος Ροδόπου], cave	35° 36' N, 23° 43' E	5 m
Samaria [Σαμαριά], Agiou Georgiou chapel	35° 17' N, 23° 58' E	380 m
Samaria [Σαμαριά], pond	35° 17' N, 23° 58' E	340 m
Samaria [Σαμαριά], old village	35° 17' N, 23° 58' E	350 m
Samaria [Σαμαριά], gorge	35° 18' N, 23° 57' E	400 m
Sfinari [Σφηνάρι], Neraidospilias cave	35° 26' N, 23° 34' E	10 m
Sougia [Σούγια], gypsum mine	35° 15' N, 23° 49' E	50 m
Sougia [Σούγια], stream	35° 15' N, 23° 49' E	10 m
Stavros [Σταυρός], Lera cave	35° 36' N, 24° 06' E	235 m
Tavronitis [Ταυρωνίτης], village	35° 31' N, 23° 49' E	18 m
Theriso [Θέρισο], Aliakes Plateau	35° 23' N, 23° 59' E	860 m
Theriso [Θέρισο], cave	35° 23' N, 23° 59' E	
Theriso [Θέρισο], Sarakinas cave	35° 25' N, 23° 59' E	480 m
Theriso [Θέρισο], scrubland (to Panagia)	35° 26' N, 23° 60' E	400 m
Theriso [Θέρισο], village	35° 24' N, 23° 59' E	580 m
Vafes [Βαφές], Kalamato cave	35° 22' N, 24° 10' E	280 m
Vafes [Βαφές], Kryoneridas cave	35° 22' N, 24° 10' E	280 m
Voukolies [Βουκολιές], mine	35° 25' N, 23° 49' E	
Vryses Arokoroitou [Βρύσες Αποκορώνου], river	35° 23' N, 24° 12' E	50 m
Vryses Kydonias [Βρύσες Κυδωνιάς], Keras Spiliotissas cave	35° 29' N, 23° 53' E	
Zourva [Ζούρβα], cypress forest	35° 23' N, 23° 58' E	584 m
<i>Prefecture of Irakleion</i>		
Agia Varvara [Αγία Βαρβάρα], village	35° 08' N, 24° 60' E	600 m

Alithini [Αληθινή], Meires cave	35° 00' N, 24° 53' E	365 m
Amnisos [Αμνισός], Eileithyias cave	35° 19' N, 25° 12' E	62 m
Ampelouzos [Αμπελούζος], gorge	35° 04' N, 24° 57' E	200 m
Ano Asites [Άνω Ασίτες], Agiou Charalampou gorge	35° 11' N, 24° 59' E	580 m
Ano Asites [Άνω Ασίτες], Ano Asites	35° 12' N, 24° 60' E	490 m
Ano Asites [Άνω Ασίτες], Nykteridospilios cave	35° 12' N, 25° 00' E	480 m
Ano Fortetsa [Άνω Φορτέτσα], gallery under school	35° 18' N, 25° 09' E	165 m
Astrakoi [Αστρακοί], gorge	35° 14' N, 25° 13' E	146 m
Avdou [Αβδού], Agias Foteinis cave	35° 14' N, 25° 26' E	713 m
Damasta [Δαμάστα], scrubland	35° 20' N, 24° 56' E	500 m
Demati [Δεμάτι], Anapodaris river bridge	35° 02' N, 25° 18' E	208 m
Faistos [Φαιστός], Geropotamos river	35° 03' N, 24° 48' E	26 m
Giouhtas hill [Λόφος Γιούχτα], Stravomyti cave	35° 13' N, 25° 08' E	396 m
Gonies [Γωνιές], village	35° 18' N, 24° 56' E	628 m
Gonies [Γωνιές], scrubland	35° 02' N, 25° 18' E	1000 m
Gonies [Γωνιές], Tsakalou pothole	35° 17' N, 24° 57' E	750 m
Irakleion [Ηράκλειο], Agios Ioannis	35° 19' N, 25° 09' E	100 m
Irakleion [Ηράκλειο], city fortification walls	35° 20' N, 25° 08' E	46 m
Irakleion [Ηράκλειο], city center	35° 20' N, 25° 08' E	30 m
Irakleion [Ηράκλειο], old university campus	35° 18' N, 25° 09' E	117 m
Irakleion [Ηράκλειο], T.E.I. Crete campus	35° 19' N, 25° 06' E	58 m
Kamaraki [Καμαράκι], Chainospilios cave	35° 18' N, 24° 56' E	545 m
Kamaraki [Καμαράκι], stream	35° 18' N, 24° 56' E	482 m
Kamares [Καμάρες], Kamaron cave	35° 11' N, 24° 50' E	1650 m
Kamilari [Καμηλάρι], gallery	35° 02' N, 24° 47' E	130 m
Kamilari [Καμηλάρι], village	35° 02' N, 24° 47' E	95 m
Kato Fortetsa [Κάτω Φορτέτσα], storehouse	35° 18' N, 25° 09' E	126 m
Kato Gouves [Κάτω Γούβες], H.C.M.R. facilities	35° 20' N, 25° 17' E	10 m
Kavrochori [Καβροχώρι], Gazanos river	35° 18' N, 25° 02' E	48 m
Keri hill [Λόφος Κέρης], pothole	35° 20' N, 25° 02' E	500 m
Keri hill [Λόφος Κέρης], scrubland	35° 20' N, 25° 01' E	500 m
Laloumas [Λαλουμάς]	35° 06' N, 24° 52' E	170 m
Linoperamata [Λινοπεράματα], Almyros river	35° 20' N, 25° 03' E	10 m
Linoperamata [Λινοπεράματα], Almyros river spring	35° 20' N, 25° 03' E	43 m
Marathitis [Μαραθίτης]	35° 17' N, 25° 09' E	237 m
Marathos [Μάραθος], Arcalospilios cave	35° 21' N, 24° 58' E	547 m
Marathos [Μάραθος], Doxas cave	35° 21' N, 24° 60' E	458 m
Matala [Μάταλα], sea shore	34° 59' N, 24° 45' E	0 m
Patsides [Πατσιδες], village	35° 16' N, 25° 11' E	270 m
Plouti [Πλουτή], Gortynas Labyrinth mine	35° 05' N, 24° 55' E	390 m
Plouti [Πλουτή], Mikro Lavyrinthaki mine	35° 05' N, 24° 55' E	385 m
Pompia [Πόμπια], sewage installation	35° 01' N, 24° 52' E	96 m
Rouva forest [Δάσος Ρούβα], Agiou Ioanni chapel	35° 11' N, 24° 55' E	940 m
Sarchos [Σάρχος], Chonos cave	35° 13' N, 24° 59' E	233 m
Skinakas (Idi Mts.) [Σκίνακας (Ιδη)], pothole	35° 12' N, 24° 53' E	1550 m
Spilia [Σπήλια], Agias Eirinis chapel, aquaduct	35° 17' N, 25° 10' E	
Stroumboulas Plateau [Οροπέδιο Στρούμπουλα], scrubland	35° 20' N, 24° 60' E	500 m
Tylisos [Τύλισος], Kamilari cave	35° 19' N, 25° 01' E	260 m
Venerato [Βενεράτο], Agiou Fanouriou chapel	35° 12' N, 25° 03' E	210 m
Keratokampos [Κερατόκαμπος], Vigla cave	35° 01' N, 25° 24' E	550 m
Vorizia [Βοριζία], olive grove	35° 08' N, 24° 53' E	370 m
Zaros [Ζαρός], a brook ca. 1 km to N	35° 09' N, 24° 54' E	348 m
Zaros [Ζαρός], Votomos Lake	35° 08' N, 24° 55' E	410 m
<i>Prefecture of Lasithi</i>		
Agia Fotia [Άγια Φωτιά], Koufota cave	35° 12' N, 26° 09' E	10 m
Agios Georgios [Άγιος Γεώργιος], Megalo Katofygi cave	35° 07' N, 26° 03' E	450 m
Agios Konstantinos [Άγιος Κωνσταντίνος], Chonos sinkhole	35° 10' N, 25° 31' E	815 m
Chochlakies [Χοχλακιές], Karoumes bay, Voreino cave	35° 08' N, 26° 17' E	30 m

Gra Lygia [Γρα Λυγιά], Mpramianos river dam	35° 03' N, 25° 42' E	65 m
Kritsa [Κριτσά], Gaidourotrypa cave	35° 09' N, 25° 39' E	725 m
Kroustas [Κρούστας], Tafos cave	35° 07' N, 25° 38' E	782 m
Lithines [Λιθίνες], Agiou Antoniou cave	35° 04' N, 26° 03' E	
Milatos [Μίλατος], Milatou cave	35° 18' N, 25° 35' E	129 m
Milatos bay [Μίλατος, παραλία], sea cave ca. 4 km to E of Agiou Konstantinou chapel	35° 20' N, 25° 35' E	0 m
Pefkoi [Πεύκοι], Vreiko cave	35° 05' N, 25° 60' E	548 m
Riza [Ρίζα], Krygiospilios cave	35° 02' N, 25° 33' E	
Sisi [Σίσσι]	35° 18' N, 25° 31' E	10 m
Sitanos [Σίτανος], Exo Latsidi cave	35° 07' N, 26° 09' E	678 m
Vrahasi [Βραχάσι], Peristeras cave	35° 16' N, 25° 34' E	300 m
<i>Prefecture of Rethymno</i>		
Agios Ioannis [Άγιος Ιωάννης], Platis river	35° 10' N, 24° 42' E	190 m
Agios Yakinthos (Idi Mts.) [Άγιος Υάκινθος (Ιδη)], Agiou Yakinthou chapel	35° 15' N, 24° 52' E	1000 m
Agios Yakinthos (Idi Mts.) [Άγιος Υάκινθος (Ιδη)], scrubland	35° 15' N, 24° 52' E	1200 m
Agios Yakinthos (Idi Mts.) [Άγιος Υάκινθος (Ιδη)], dam	35° 15' N, 24° 51' E	1000 m
Agridia [Αγρίδια], cave	35° 20' N, 24° 51' E	430 m
Amnatos [Αμνατός]	35° 20' N, 24° 37' E	319 m
Ano Viran Episkopi [Άνω Βιράν Επισκοπή], valley	35° 22' N, 24° 37' E	70 m
Anogia [Ανώγεια], storehouse	35° 17' N, 24° 53' E	800 m
Archaia Eleftherna [Αρχαία Ελευθέρνα], Aravanes forest	35° 16' N, 24° 43' E	1000 m
Argyroupoli [Αργουρούπολη], Mouselas river	35° 18' N, 24° 20' E	125 m
Arkadiou monastery [Μονή Αρκαδίου]	35° 18' N, 24° 38' E	495 m
Doxaro [Δοξάρó], Mougri cave	35° 24' N, 24° 50' E	277 m
Doxaro [Δοξάρó], oak grove	35° 23' N, 24° 50' E	380 m
Dramia [Δράμια], Petre river bridge	35° 21' N, 24° 21' E	2 m
Erfoi [Ερφοι], Erfoi cave	35° 22' N, 24° 38' E	154 m
Fourfouras [Φουρφουράς], water reservoir	35° 13' N, 24° 45' E	1510 m
Gallos river gorge [Φαράγγι Γάλλου], old watermill	35° 21' N, 24° 28' E	220 m
Gerani [Γεράνι], Geraniou cave	35° 22' N, 24° 24' E	21 m
Klisidi [Κλησιδί], olive grove	35° 16' N, 24° 39' E	485 m
Lefkogeia [Λευκόγεια], Venetian bridge ca. 3 km E of the Kato Preveli Monastery	35° 10' N, 24° 28' E	45 m
Melissourgaki [Μελισσουργάκι], Kouroupi oak forest	35° 20' N, 24° 43' E	
Monastiraki [Μοναστηράκι], Genianos stream	35° 14' N, 24° 41' E	305 m
Myloi [Μύλοι], old village	35° 20' N, 24° 30' E	260 m
Myrthios [Μύρθιος], Patsianos river	35° 16' N, 24° 34' E	180 m
Nida Plateau (Idi Mts.) [Οροπέδιο Νίδας (Ιδη)], Ideo Andro cave	35° 12' N, 24° 50' E	1490 m
Panormo [Πάνορμο], Geropotamos estuary	35° 25' N, 24° 39' E	5 m
Patsos [Πατσός], Agiou Antoniou cave	35° 15' N, 24° 34' E	200 m
Petradolakia (Idi Mts.) [Πετραδολάκια (Ιδη)], scrubland	35° 13' N, 24° 52' E	1500 m
Petradolakia (Idi Mts.) [Πετραδολάκια (Ιδη)], Agiou Fanouriou chapel, pothole	35° 13' N, 24° 52' E	1464 m
Plakias [Πλακιάς]	35° 11' N, 24° 24' E	10 m
Prinos [Πρίνος], Prinou cave	35° 24' N, 24° 39' E	140 m
Rethymnon [Ρέθυμνο], pine grove, mine	35° 21' N, 24° 29' E	104 m
Rizikas [Ριζικάς], old village	35° 08' N, 24° 44' E	223 m
Roumeli [Ρουμελή], Geropotamos river	35° 25' N, 24° 40' E	40 m
Siripidiana [Σιριπιδιανά], olive grove	35° 24' N, 24° 43' E	40 m
Ski resort (Idi Mts.) [Χιονοδρομικό κέντρο (Ιδη)], scrubland	35° 13' N, 24° 49' E	1500 m
Varsamo (Idi Mts.) [Βάρσαμο (Ιδη)], Peristerospilios cave	35° 11' N, 24° 53' E	1450 m
Viran Episkopi [Βιράν Επισκοπή], olive grove	35° 22' N, 24° 37' E	60 m
Zoniana [Ζωνιανά], Sfentoni cave	35° 18' N, 24° 50' E	664 m

Published localities

Prefecture of Chania

Agia [Αγιά], way from Agia to Kyrtomados	35° 28' N, 23° 55' E	35 m
Agia Roumeli [Αγία Ρουμέλη], rocky cliff	35° 14' N, 23° 58' E	40 m

Agia Roumeli [Αγία Ρουμέλη], village	35° 14' N, 23° 58' E	15 m
Agias Triadas monastery [Μονή Αγίας Τριάδας]	35° 34' N, 24° 08' E	85 m
Azogryes [Αζογυρές]	35° 16' N, 23° 43' E	380 m
Chania [Χανιά], fortress	35° 31' N, 24° 01' E	5 m
Elos [Έλος]	35° 22' N, 23° 38' E	540 m
Hills south of Chania [Λόφοι νότια των Χανίων], cave	35° 28' N, 24° 01' E	
Kalyves [Καλύβες]	35° 27' N, 24° 10' E	5 m
Katholiko monastery [Μονή Καθολικού]	35° 35' N, 24° 09' E	80 m
Kissamos [Κίσσαμος]	35° 30' N, 23° 39' E	10 m
Kolymvari [Κολυμβάρι], Gonias Monastery	35° 33' N, 23° 47' E	10 m
Kissamos [Κίσσαμος], Korfalona	35° 30' N, 23° 41' E	2 m
Lakkoι [Λάκκοι], Lefka Ori Mts.	35° 24' N, 23° 56' E	500 m
Moni Gouvernetou to Moni Agias Triadas [Μονή Γουβερνέτου προς Μονή Αγίας Τριάδας]	35° 34' N, 24° 08' E	180 m
Mouri [Μουρί], Kourna lake	35° 20' N, 24° 17' E	40 m
Mouri [Μουρί]	35° 20' N, 24° 17' E	42 m
Nerokouros [Νεροκούρου], cave	35° 28' N, 24° 02' E	160 m
Omalos Plateau [Οροπέδιο Ομαλού]	35° 20' N, 23° 54' E	1050 m
Palaiochora [Παλαιόχωρα]	35° 14' N, 23° 41' E	15 m
Stavros [Σταυρός]	35° 35' N, 24° 05' E	5 m
Topolia [Τοπόλια], Agias Sofias cave	35° 25' N, 23° 41' E	350 m
Topolia [Τοπόλια]	35° 26' N, 23° 41' E	265 m
Vryses Apokorionou [Βρύσες Αποκορώνου]	35° 23' N, 24° 12' E	50 m
<i>Prefecture of Irakleion</i>		
Agio Pnevma [Αγιο Πνεύμα]	35° 18' N, 25° 29' E	10 m
Agioi Deka [Άγιοι Δέκα]	35° 03' N, 24° 57' E	150 m
Ano Viannos [Άνω Βιάννος]	35° 03' N, 25° 25' E	550 m
Arcalochori [Αρκαλοχώρι]	35° 09' N, 25° 16' E	386 m
Dia Island [Νήσος Ντία]	35° 27' N, 25° 12' E	100 m
Gortys [Γόρτυνα]	35° 04' N, 24° 57' E	167 m
Linoperamata [Λινοπεράματα], Almyros river gorge	35° 20' N, 25° 03' E	70 m
Linoperamata [Λινοπεράματα], Almyros river spring, small cave	35° 20' N, 25° 03' E	43 m
Sarchos [Σάρχος]	35° 13' N, 24° 60' E	233 m
Skoteino [Σκοτεινό], Agias Paraskevis cave	35° 18' N, 25° 18' E	209 m
Tylisos [Τύλισος], Voulismeno Aloni doline	35° 20' N, 25° 01' E	327 m
Zaros [Ζαρός]	35° 08' N, 24° 54' E	327 m
<i>Prefecture of Lasithi</i>		
Adrianos [Αδριανός], Atziganospilios cave	35° 12' N, 25° 37' E	650 m
Ammoudara [Αμμουδάρα]	35° 10' N, 25° 43' E	20 m
Dragonada Island [Νήσος Δραγονάδα]	35° 21' N, 26° 11' E	50 m
Elounda [Ελούντα]	35° 16' N, 25° 43' E	70 m
Gra Lygia [Γρα Λυγιά], Mpramianos river dam	35° 03' N, 25° 42' E	65 m
Istro [Ιστρο]	35° 07' N, 25° 44' E	25 m
Kalamafka [Καλαμαύκα]	35° 04' N, 25° 39' E	493 m
Kalo Chorio [Καλό Χωριό]	35° 07' N, 25° 43' E	56 m
Kavousi [Καβούσι]	35° 07' N, 25° 51' E	95 m
Kroustas [Κρούστας]	35° 08' N, 25° 39' E	518 m
Kritsa [Κριτσά]	35° 09' N, 25° 39' E	400 m
Limnes [Λίμνες]	35° 15' N, 25° 38' E	179 m
Mesa Mouliaana [Μέσα Μουλιανά]	35° 09' N, 25° 58' E	407 m
Milatos [Μίλατος]	35° 18' N, 25° 34' E	43 m
Piskokefalo [Πισκοκέφαλο]	35° 11' N, 26° 06' E	45 m
Prina [Πρίνα]	35° 06' N, 25° 41' E	350 m
Psihro [Ψυχρό]	35° 10' N, 25° 27' E	853 m
Sitia [Σητεία]	35° 12' N, 26° 06' E	40 m
Stavrohoiri [Σταυροχώρι]	35° 05' N, 25° 56' E	323 m
Tholos [Θόλος]	35° 09' N, 25° 52' E	26 m

Tzermiado [Τζερμιάδο]	35° 12' N, 25° 29' E	844 m
<i>Prefecture of Rethymno</i>		
Adele [Άδελε]	35° 21' N, 24° 33' E	110 m
Gerani [Γεράνι]	35° 21' N, 24° 24' E	85 m
Kiriana [Κυριανά]	35° 20' N, 24° 36' E	223 m
Melidoni [Μελιδόνι], Gerontospilios cave	35° 23' N, 24° 44' E	218 m
Fratzeskiana Metohia [Φρατζεσκιανά Μετόχια]	35° 20' N, 24° 24' E	200 m
Arkadiou monastery [Μονή Αρκαδίου]	35° 18' N, 24° 38' E	500 m
Platania [Πλατάνια]	35° 14' N, 24° 42' E	405 m
Platanias [Πλατανιάς]	35° 21' N, 24° 33' E	10 m
Rethymno [Ρέθυμνο]	35° 22' N, 24° 28' E	21 m