Naturwissenschaften (2001) 88:217–223
DOI 10.1007/s001140100225

SHORT COMMUNICATION

O. von Helversen · K.-G. Heller · F. Mayer · A. Nemeth
M. Volleth · P. Gombkötö

Cryptic mammalian species: a new species of whiskered bat (*Myotis alcathoe* n. sp.) in Europe

Received: 22 November 2000 / Accepted in revised form: 17 March 2001 / Published online: 18 May 2001

Abstract The analysis of morphological, behavioural and genetic characters of whiskered bats revealed a new European bat species within the family Vespertilionidae. We describe the morphology, karyology, genetic similarity, ecology and distribution of *Myotis alcathoe* n. sp. It closely resembles *Myotis mystacinus*, *Myotis brandtii* and *Myotis ikonnikovi* in morphology, but all four species show clear genetic differences in two mitochondrial genes (ND1 and 12S rRNA). *Myotis alcathoe* n. sp. is the smallest species among the European whiskered bats and uses the highest-frequency echolocation calls of all the European *Myotis* species. It prefers to hunt in small valleys with deciduous trees and flowing water, which is an endangered habitat. Records from Greece and Hungary indicate a distribution range in south-eastern Europe.

Introduction

Biological species – even those belonging to the most thoroughly investigated taxa in the world, such as the mammals – can resemble one another morphologically to such an extent that the acute gaze of taxonomists has failed to distinguish them even after two centuries of systematic research. Recently, comparisons employing the modern methods of molecular genetics have progressively revealed the existence of cryptic species even among the mammals, mainly in the tropics (see, e.g. nonvolant small mammals in Amazonian Brazil; Patton et al. 1997). In Europe, too, several new bat species have been discovered or confirmed by molecular genetics in recent years: the common pipistrelle, probably the most common species of bat in Europe, has up until now included two newly discovered species which, although similar, are distinct throughout Europe. First, two distinctive groups of echolocation call frequencies were identified (Weid and von Helversen 1987; Zingg 1990). It was then shown that the two groups represent different species (Jones and Parijs 1993), which were also distinguished on molecular genetic grounds (Barratt et al. 1997; F. Mayer and O. von Helversen, unpublished data). Furthermore, it now appears that the genus *Plecotus* is represented by at least four different species in Europe (Kiefer et al. 2000).

A new European species of the genus *Myotis* KAUP 1829 which previously would have been confused with *Myotis mystacinus* (KUHL 1817) is described here, followed by brief characterisations of its chromosomal and molecular genetic features, ecological requirements, hunting behaviour and echo-orientation.

O. von Helversen (✉) · K.-G. Heller · F. Mayer · A. Nemeth
M. Volleth · P. Gombkötö
Institut für Zoologie der Universität Erlangen, Staudtstrasse 5, 91058 Erlangen, Germany
e-mail: helver@biologie.uni-erlangen.de
Tel.: +49-9131-8528051, Fax: +49-9131-8528060

Myotis alcathoe von Helversen & Heller, new species

Derivatio nominis

The new species is native to Greece, inhabiting the brookside groves and remote stream gorges where the nymph Alcathoe, daughter of Minyas, once refused to honour Dionysos and to yield to his importunings, whereupon he responded by turning her into a bat (Ovid, Met. IV, 410).

Holotype

Adult male, skin and skull, Senckenberg Museum (SMF 90249); collected by O. von Helversen, K.G. Heller and M. Volleth on 14 August 1981, netted over a small stream, the Fournikos Potamos, near the village of Kleistos (39°05′N, 21°49′E), Nomos Evritanias, Greece.

Paratypes

Three adult females, skins and skulls, one in the Zoologial Museum of the University of Athens (ZMUA

4001), two in collection of Helversen (nos. 92–1 and 93–2), netted by O. von Helversen on 17 June 1992 at a small stream near the village of Loutropigi (39°07′N, 22° 01′E), Nomos Karditsa, Greece.

Diagnosis

Myotis alcathoe n. sp., on average, has a smaller body size than *M. mystacinus* Kuhl 1817 and *Myotis brandtii* Eversmann 1845. In particular, its thumb, thumb claw and hind feet are shorter, and its ears are shorter and lighter with a tragus that hardly extends beyond the notch at the outer edge of the ear. The species is also distinguishable from *M. mystacinus* by the cingulum cusp on the upper P4 and the protoconuli on the upper molars, discernible at least where the dentition is unworn, and from *Myotis ikonnikovi* Ognev 1912 and *M. brandtii* primarily by the differently shaped baculum (Strelkov 1989).

Above all, however, *M. alcathoe* n. sp. can be distinguished from all related European *Myotis* species and from *M. ikonnikovi* by the sequence differences in mitochondrial genes (12S-rRNA and ND1) as well as the pattern of active nucleolus organiser regions (NORs) (Volleth 1987, *Myotis* sp. B).

The possibility that an older name for *M. alcathoe* n. sp. could be unearthed among the various forms synonymized with *M. mystacinus* (see, for example, Corbet 1978) is extremely unlikely, because all these forms were described from western and central Europe, where the new species does not occur to the best of our current knowledge (see also Benda 1999).

Measurements of external and selected cranial characters

Forearm (without wrist) 31.4±0.5 mm (mean±SD, *n*=13); finger5 40.3±1.3 mm (*n*=12); finger3 51.4±1.0 mm (*n*=10); tibia 13.4±0.6 mm (*n*=8); hindfoot (without claw) 6.1±0.3 mm (*n*=12), thumb (maximum extension, without claw) 4.6±0.3 mm (*n*=9); weight 4.2±0.4 g.

Skull (*n*=7): condylobasal length 12.3±0.27 mm; zygomatic width 8.13±0.16 mm; interorbital width 3.34±0.11 mm; width of skull at crowns of C 3.26±0.08 mm, at M^3 5.16±0.10 mm; upper tooth row C–M^3 (crowns) 4.94±0.09 mm; mandible length (from condylus) 9.5±0.26 mm; height of coronoid process 2.75±0.10 mm; lower tooth row C–M^3 5.27±0.16 mm.

Holotype: FA 30.5; F5 40; F3 50; Ti 13; HF 5.5; thumb 4.0; claw 1.0 mm; CBL 11.7; ZW 7.87; IOW 3.27; width at C 3.17; width at M^3 5.15; C–M^3 4.80; ML 9.01; coronoid height 2.77; C–M^3 5.05 mm.

Description

Myotis alcathoe n. sp. is the smallest of all European bats of the genus *Myotis* (length of forearm <32 mm, weight <5 g). In most specimen, the dorsal pelage is reddish brown, in some (younger?) animals, more greyish brown. Dorsal hairs have an indistinct darker base and brown (not golden) tips; in the middle of the back these are 6–8 mm long. Tips of ventral hairs are only a little paler than their dark base, the underside is therefore brown not white. Wing membranes are uniformly brownish. The plagiopatagium inserts at the base of the 5th toe (Fig. 1B). About 1 mm of the last caudal vertebra is free from the uropatagium. The calcar is slender without a keel, bearing only a narrow (about 0.3 mm wide) border of skin. The notch of the uropatagium, at the tip of the calcar, lies at about 60% of the distance from the foot to the tip of the tail, along the back edge of the uropatagium. Hindfeet and thumbs are very small, compared with those of all other European species of the genus: hindfeet (without claw) <6.5 mm (Fig. 1B); length of the thumb (without claw), when measured as the longest possible extension from the wrist in the living animal, less than 5 mm (Fig. 1C). Claw of the thumb very short (<1.5 mm).

Ears brownish, always a lighter colour inside, about 13 mm long, shape as shown in Fig. 1A, with a sharp notch in the outer edge. Tragus pointed, hardly projects beyond this notch at the outer edge of the ear. Muzzle with glandular swellings, especially in reproductive males, upper lip and facial region in front of the eyes reddish (unpigmented).

Penis narrow (width about 1.3 mm) with no thickening at the end. Baculum (Fig. 1G) about 0.5 mm long, lateral parts well developed, length-to-width ratio about 1.8.

Shape of the skull (Fig. 1D) similar to *M. mystacinus* Kuhl 1817, the frontal part of the brain case comparatively high. The upper P4 in most individuals with a distinct cingulum cusp, of medium height compared to *M. mystacinus* and *brandtii* (Fig. 1E), in other specimen the cusp was smaller). If teeth are unworn, minute but clearly visible protoconuli on all three upper molars (Fig. 1F). The upper premolars P2 and P3 are small and tightly adjusted to one another and to C and P4, both within the line of the tooth row.

Karyology

Chromosomes of two males (holotype and one other male of *M. alcathoe* n. sp. from Skaloti/Rhodopi mountains, Greece) and of three females (paratypes, Loutropigi) have been studied. As with other *Myotis* species, the karyotype of *M. alcathoe* n. sp. consists of 44 chromosomes with a fundamental number of 52. However, the distribution of active NORs, visualised by silver staining, showed a characteristic pattern clearly distinguishable from all other related European *Myotis* species. Data for two specimen of *M. alcathoe* n. sp. (as *Myotis* specimen B) in comparison to other *Myotis* species, especially to *M. mystacinus* and *M. brandtii*, are given by Volleth (1987). The pattern of active NORs in the remaining three specimen was similar to the

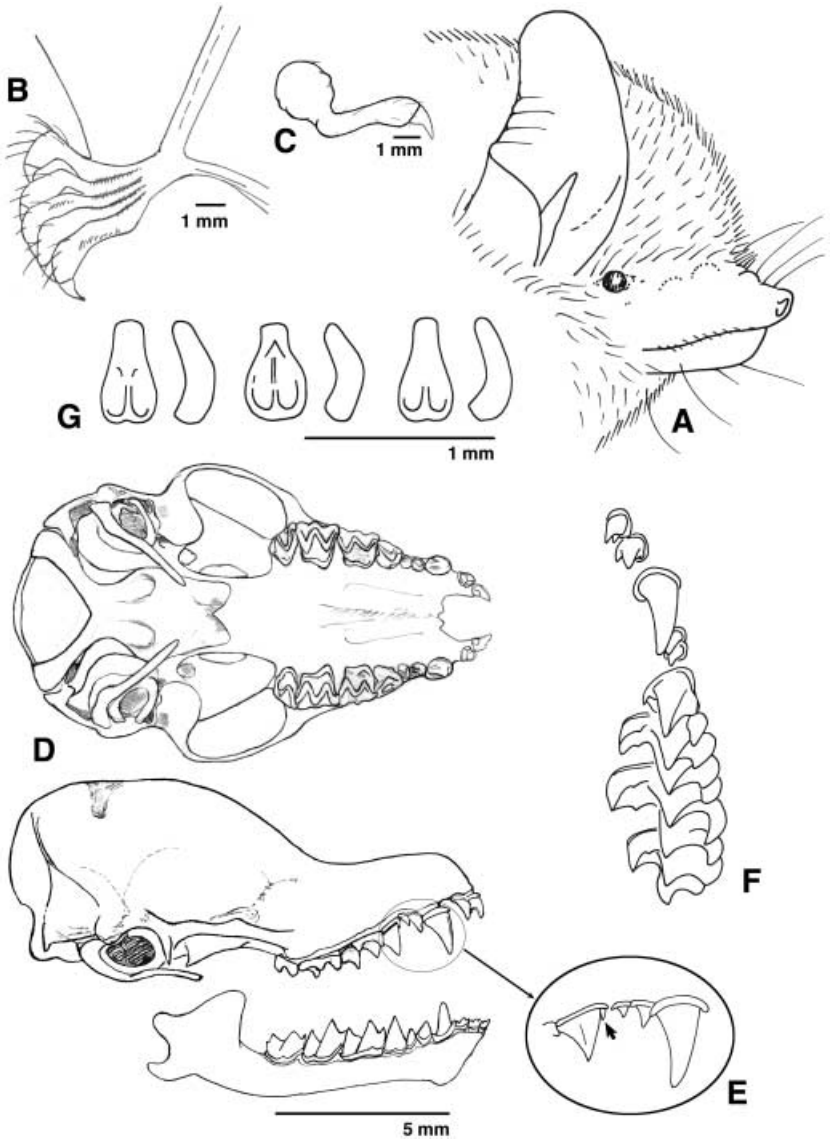

Fig. 1A–G Morphological characteristics of *Myotis alcathoe* n. sp. (drawings from different specimen). **A** Head of a living animal, **B** hind foot, **C** thumb, **D** skull of a female (paratype; 17 June 1992, at Loutropigi) viewed from below and the side; **E** and **F** details of the teeth (**E** upper canine viewed at an angle from the front to make the cingulum cusp visible; **F** view of the left upper row of teeth to show the protoconuli on the upper molars. The cingulum cusp and the protoconuli are not as large as this in all specimen, especially if the teeth are worn down). **G** Bacula of three males: holotype from Kleistos (*left*), specimen from Skaloti/Rhodhopi mountains, and from Loutropigi (*middle and right*)

published pattern, with additional NORs on chromosome 15.

Sequence differences in the mitochondrial DNA

So that comparisons could also be made at the molecular level between the currently known western Palaearctic species of whiskered bats (as well as *M. ikonnikovi* and *Myotis emarginatus*, which may be fairly closely related to them), two mitochondrial gene sections were sequenced: the first 800 bp of the gene coding for subunit one of the NADH dehydrogenase (ND1; for technical details see Petit et al. 1999) and a 385 bp region of the 12S rRNA gene using the two primer pairs l00883/H01214 and L01091/H01478 (Kocher et al. 1989). Among the ND1 sequences, 195 parsimony-informative positions were detected. In the 12S gene four insertions or deletions were found which were always species-specific: a 1 bp deletion in all *M. alcathoe* n. sp., a 7 bp insertion in all *M. brandtii*, a 1 bp insertion in all *M. mystacinus* and a 1 bp insertion in *Nyctalus noctula*. Among the remaining 375 base pairs, 33 were parsimony-informative.

All five species had distinct DNA sequences at both mitochondrial loci (Table 1). Individuals which had been assigned to a certain taxon based on morphology had identical or similar DNA sequences and always formed a monophyletic group, irrespective of the chosen algorithm (Fig. 2). This was true for *M. mystacinus* also, regardless of origin (from Spain, Germany, Greece or Anatolia). A particularly important implication of this finding is that the whiskered bats of the southern Balkans and Anatolia, which Stubbe and Chotolchu (1968) assigned to *Myotis mystacinus przewalskii* Bobrinskoy 1926, do not differ in either mitochondrial gene from *M. mystacinus* of western and central Europe. These animals are larger and have longer feet than the central European animals and their distribution of NORs is differ-

Table 1 List of specimen used for DNA analysis. *Asterisks* refer to the catalogue number of specimen in the Senckenberg Natural History Museum in Frankfurt (SMF, provided by D. Kock), Zoological Museum of Moscow University (MU, provided by P.P. Strelkov) and Natural History Museum of St. Petersburg (NHM-SP, provided by P.P. Strelkov)

Species	DNA sample number	Genebank accession number		Sampling		
		ND1	12S rRNA	Date	Location	By
Myotis alcathoe n. sp.	Mnsp149a	–	AY027824	14.8.1981	Fournikos, Potamos, Greece (holotype)	Heller and Helversen
	Mnsp69a	AY027833	–	16.6.1992	Loutropigi, Greece (paratype)	Helversen
	Mnsp67a	AY027833	–	16.6.1992	Loutropigi, Greece (paratype)	Helversen
	Mnsp65a	AY027834	–	16.6.1992	Loutropigi, Greece (paratype)	Helversen
	Mnsp82a	AY027832	AY027822	5.6.1991	Loutropigi, Greece	Helversen
	Mnsp2199	AY027837	–	2.9.1997	Nestos, Greece	Helversen
	Mnsp158a	–	AY027823	Sept. 1985	Skaloti, Greece	Weid
	Mnsp2315	AY027835	–	12.6.1997	Kacs, Bükk mountains, Hungary	Gombkötö
	Mnsp2313	AY027836	–	8.8.1997	Parad, Matra mountains, Hungary	Gombkötö
Myotis mystacinus	Mmys089a	–	AY027827	20.8.1982	Grammos, Greece	Helversen
	Mmys100a	AY027849	AY027826	21.8.1982	Grammos, Greece	Helversen
	Mmys93a	AY027838	–	30.5.1983	Angiti, Greece	Helversen
	Mmys2030	AY027844	–	18.8.1997	Arkoudoremma, Greece	Helversen
	Mmys2024	AY027845	–	18.8.1997	Arkoudoremma, Greece	Helversen
	Mmys2043	AY027844	–	6.9.1997	Vrosina, Greece	Helversen
	Mmys1863	AY027846	–		Peloponnisos, Greece	Helversen
	Mmys118	–	AY027831	29.6.1986	Manavgat river, Ibradi, Turkey	Helversen
	Mmys2046	AY027842	–	15.8.1994	Lovetch, Bulgaria	Ivanova
	Mmys2045	AY027843	–	15.8.1994	Lovetch, Bulgaria	Ivanova
	Mmys2314	AY027839	–	2.10.1996	Debrecen, Hungary	Gombkötö
	Mmys136a	–	AY027830		Linares de Rio Frio, Spain	SMF 21547 *
	Mmys147a	AY027847	AY027826	9.8.1993	Gredos, Spain	Helversen
	Mmys2298	AY027840	–		Tétouan, Morocco	Ibanez
	Mmys122a	AY027848	AY027827	31.7.1985	Oberkessach, Württemberg, Germany	Mayer
	Mmys113a	–	AY027826	4.7.1988	Effeltrich, Bavaria, Germany	Helversen
	Mmys140a	–	AY027828	1993	Würzburg, Bavaria, Germany	Kerth
	Mmys139a	–	AY027829	1993	Rossbrunn, Bavaria, Germany	Kerth
	Mmys137a	–	AY027827		Vorarlberg, Austria	SMF 73326 *
	Mmys2073	AY027841	–		Krasnoyarsky Kray, Russia	NHM–SP 82432 *
Myotis ikonnikovi	Miko163	–	AY027825	29.5.1985	Krasnoyarsk, Russia	NHM–SP W77192 *
	Miko2179	AY027850	–	7.6.1993	Bikin, Russia	MU S–158583 *
Myotis brandtii	Mbra079	–	AY027820	21.7.1983	Dechsendorf, Bavaria, Germany	Helversen
	Mbra97a	AY027851	AY027819	18.8.1984	Neuhaus, Bavaria, Germany	Helversen
	Mbra78a	AY027852	AY027821	1.8.1988	Weiherhammer, Bavaria, Germany	Helversen
	Mbra2044	AY027856	–	3.8.1994	Stara Planina mountains, Sofia, Bulgaria	Ivanova
	Mbra2048	AY027855	–	1994	Mazata cave, Plovdiv, Bulgaria	Ivanova
	Mbra1911	AY027857	–	16.7.1996	Chernogolovka, Moscow, Russia	Kozhurina
	Mbra1590	AY027858	–	11.4.1996	Tuchkovo, Moscow, Russia	Kozhurina
	Mbra2312	AY027853	–	8.8.1997	Parad, Matra mountains, Hungary	Gombkötö
	Mbra2310	AY027854	–	5.8.1997	Kacs, Bükk mountains, Hungary	Gombkötö
Myotis emarginatus	Mema99a	AY027859	AY027818	1986	Kato Stavros, Chalkidike, Greece	Helversen
Nyctalus noctula	Nnoc519	–	AY027817	1985	Bavaria, Germany	Helversen
	Nnoc80e	AY027860	–	4.7.1995	Aubeterre, La Poterie, France	Petit

ent (*Myotis* sp. A in Volleth 1987); this form might possibly be another distinct species if it turns out to be syntopic with *M. mystacinus*, as Benda (1999) suggests. Strelkov (1983) described this form as *Myotis mystacinus popovi*, but it is most likely that if *M. mystacinus przewalskii* is not the most appropriate name, then *Myotis mystacinus bulgaricus* Heinrich 1936 (Heinrich 1936) or *Myotis mystacinus aurascens* Kuzyakin 1935 would have priority (Benda 1999). In any case, however, genetically this form closely resembles the nominate form.

The interspecific divergence of DNA sequences between *M. alcathoe* n. sp. and all other species was at least 5% for the 12S region and 13% for the ND1 gene. Phylogenetic relations above species level could not be resolved, but *M. alcathoe* n. sp. is definitely not the sister species of *M. mystacinus*; *M. ikonnikovi* was always placed nearer to *M. mystacinus* than all the other investigated species (Fig. 2).

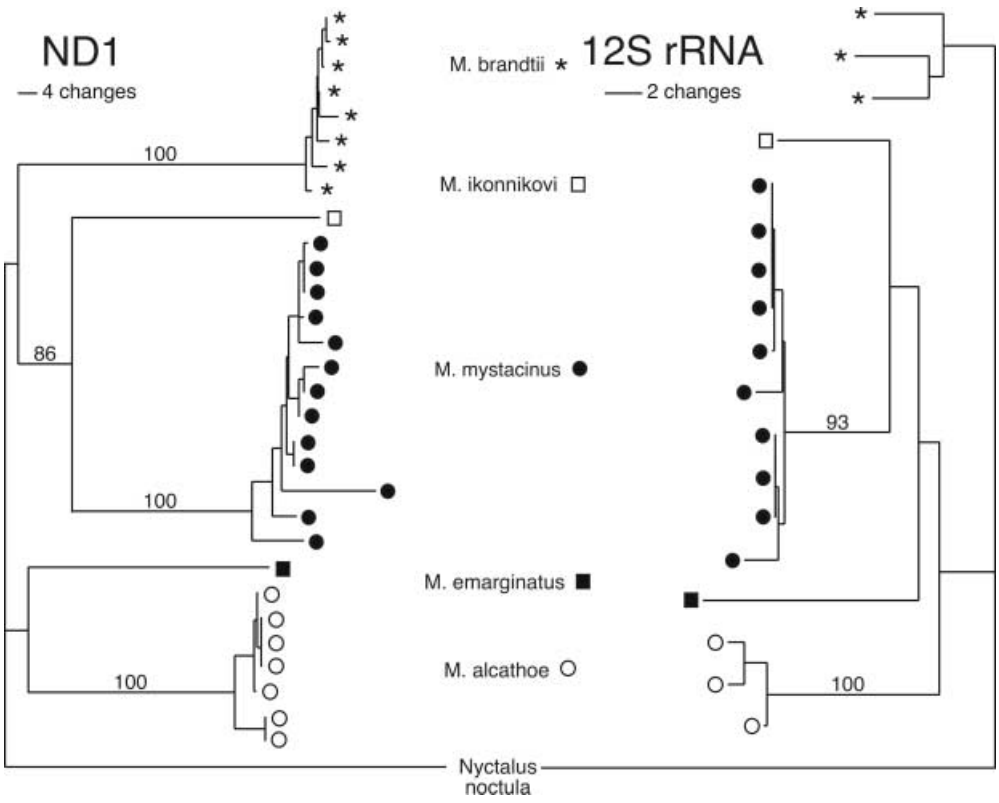

Fig. 2 Neighbour-joining trees for mitochondrial ND1 (*left*) and 12S rRNA (*right*) sequences of five *Myotis* species and *Nyctalus noctula*, which was used as an outgroup. Ten positions with insertions or deletions were removed from the 12S sequences. The remaining 375 bp of the 12S gene and the first 800 bp of the ND1 gene were equally weighted. Bootstrap values over 70% under the parsimony criterion are given (100 replicates). The software package PAUP* 4.0b was used for all phylogenetic analysis (Swofford 2000). Sampling locations and GenBank accession numbers of DNA sequences (ND1: AY027832–AY027860; 12S rRNA: AY027817–AY027831) are listed in a table at http://www.biologie.uni-erlangen.de/zoo2/mayer.html

Distribution

All our records stem from two mountainous areas in Greece: from the southern Pindus (Nomoi Evritania and Karditsa) and from the Rhodopi mountains (Nomos Drama). In recent years, the species has also been detected in north-eastern Hungary (P. Gombkötö, personal observation). The possibility cannot be ruled out that at least in some cases, the *M. ''ikonnikovi''* reported from Bulgaria (Kwartirnikov 1957), Romania (Dumitrescu et al. 1962) and the Ukraine (Abelencev et al. 1956) is in fact *M. alcathoe* (but see Hanak 1965).

Habitat, ecological requirements and behaviour

Myotis alcathoe n. sp. prefers to hunt in dense stands of deciduous trees near bodies of water, and in Greece it is found mostly in dense groves of plane trees or the alder woods in ravines bordering small streams. The bats tend to fly close to the vegetation, within the stands of trees (where they are often syntopic with *Rhinolophus hipposideros* Bechstein 1800 and also *M. mystacinus*). In the case of *M. mystacinus* these appear to be marginal habitats, given that this species is widely distributed in Greece and generally hunts near larger bodies of standing and flowing water; in contrast, *M. alcathoe* n. sp. is specialized for small valleys through which brooks flow. We found only one maternity colony of *M. alcathoe*: a finger-wide fissure in the trunk of a plane tree, about 1.5 m long at a height of about 8 m (containing three females and two babies, at Loutropigi, 17.6.1992). Animals kept in an aviary often rested during the day in narrow crevices in the rocks near the ground.

The habitat of the species is endangered by reservoir construction projects. Two of the localities where we found these bats (near Loutropigi in the Nomos Karditsa and near Loutra Thermia in the Nomos Drama) have already been destroyed.

Echo-orientation

Myotis alcathoe n. sp. has the highest-frequency echolocation calls of all the European *Myotis* species, in particular with respect to the frequency at the (lower) end of the calls. When the species is hunting in more or less open terrain, the calls are up to about 4 ms long. At the beginning, the frequency falls sharply, after which the frequency modulation first flattens out somewhat and finally becomes steeper again, so that a slightly sigmoid curve results (Fig. 3); the “inflection point” was at 51.5±3.7 kHz, which is approximately the same as the frequency with the greatest amplitude (52.5±9.6 kHz). These calls ended at 43±2.4 kHz and their average duration was 2.5±0.7 ms. When the bats are flying close to obstacles, their calls – like those of all vespertilionids – are shorter and the frequency falls still more steeply; then they end somewhat sooner, at around 46±1.1 kHz. The starting frequency (the measured value of which naturally depends greatly on the recording conditions) was about 120 kHz. The interval between the calls (first peak

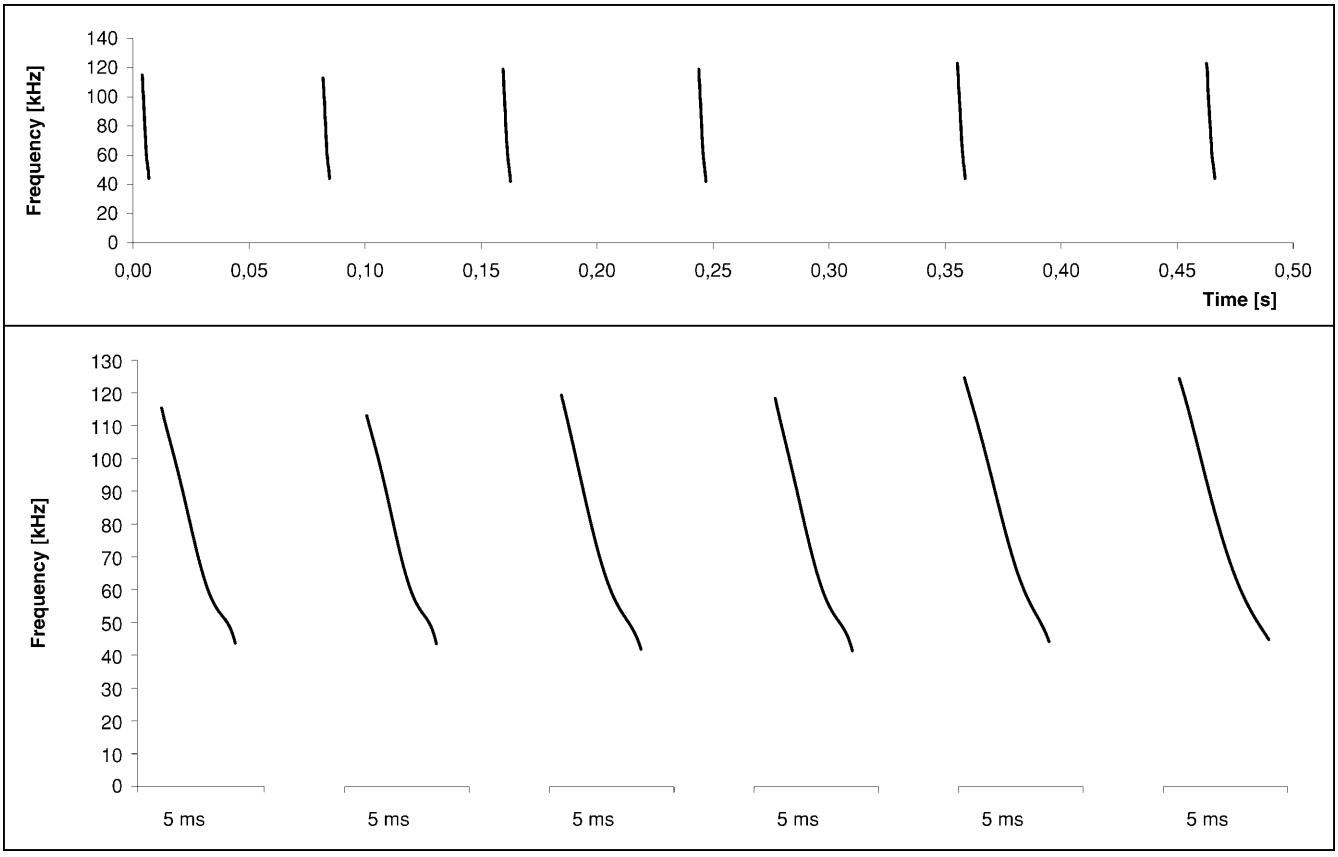

Fig. 3 Echolocation calls of *Myotis alcathoe* n. sp. when hunting over a small stream between trees, after releasing the animal at dusk. Echolocation calls were recorded either with a time expansion ultrasound detector (350 kHz sampling rate, model D980, Pettersson Elektronic), a digital ultrasound recorder (500 kHz sampling rate, Institute of Technical Electronics, University of Erlangen) or a modified video recorder (response flat up to 300 kHz). *Above*: calls at the natural intervals; *below*: individual calls on an expanded timescale (frequency maximum as a function of time; Avisoft analysis program, R. Specht)

in the distribution) is correlated with the wingbeat, and was 85±14 ms in the first situation and 66±19 ms in the second. Further tests will be needed to determine whether these characteristics of the echolocation calls are sufficient to identify the species by its calls.

Conclusion

The methods of molecular genetics make it possible to detect cryptic species that would otherwise be likely to escape the biologist's attention, although once they have thus been discovered, they can often also be differentiated morphologically. These species not uncommonly also differ from sibling species in ecology and behaviour, but this aspect cannot be investigated until clear criteria for their identification are available. It appears that the diversity of even the mammalian fauna of Europe is by no means completely understood.

Acknowledgements We thank Dr. P. Strelkov of Leningrad and Dr. D. Kock of Frankfurt am Main for critical discussion and advice. Roland Weid, Felix Matt and Marc Holderied assisted during the field observations and evaluation of the findings. We thank Dr. A. Legakis and Dr. G. Chandrinos (Zoological Museum, University of Athens) for help in obtaining the collecting permits (Nos. 71600/1556 and 61848/248) from the Ministry of Agriculture of the Greek Democracy, Directorate of Aesthetic Forests, Parks and Hunting.

References

Abelencev VI, Pidoplitschko IG, Popov BM (1956) Ukrainian fauna (in Russian). Ssavci, Kiev

Barratt EM, Deaville R, Burland TM, Bruford MW, Jones G, Racey PA, Wayne RK (1997) DNA answers the call of pipistrelle bat species. Nature 387:138–139

Benda P (1999) Three notes on the taxonomy of *Myotis brandtii* (Chiroptera, Vespertilionidae) and on the history of its recognition in the western part of Europe. Lynx Praha 30: 5–26

Corbet GB (1978) The mammals of the Palearctic region: a taxonomic review. British Museum and Cornell University Press, London and Ithaca

Dumitrescu M, Tanasachi J, Orghidan T (1962) The distribution of bats in the R.P. Romania (in Romanian). Lucr Inst Speol "Emil Racovita" 1–2:509–574

Hanak V (1965) Zur Systematik der Bartfledermaus *Myotis mystacinus* Kuhl 1819 und über das Vorkommen von *Myotis ikonnikovi* Ognev 1912 in Europa. Vestn Cesk Spol Zool 29: 353–367

Heinrich G (1936) Über die von mir im Jahre 1935 in Bulgarien gesammelten Säugetiere. Mitt Königl Wiss Inst Sofia 9:33–48, Sofia

Jones G, Parijs SM van (1993) Bimodal echolocation in pipistrelle bats: are cryptic species present? Proc R Soc Lond B 251:119–125

Kiefer A, Kosuch J, Veith M, Mayer F, Helversen O von (2000) Kryptische Diversität unter europäischen Langohr-Fledermäusen. Z Säugetierkd 65:23–24

Kocher TD, Thomas WK, Meyer A, Edwards SV, Pääbo S, Villablanca FX, Wilson AC (1989) Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. Proc Natl Acad Sci USA 86:6196–6200

Kwartirnikov M (1957) Bats in Bulgaria: two new species for our fauna (Bulg.) Priroda Sofia 6:63–64

Patton JL, Silva MNF da, Lara MC, Mustrangi MA (1997) Diversity, differentiation, and the historical biogeography of nonvolant small mammals of the Neotropical forests. in: Laurance WF, Bierregaard RO Jr (eds) Tropical forest remnants: ecology, management and conservation of fragmented communities. University of Chicago Press, Chicago, pp 455–465

Petit E, Excoffier L, Mayer F (1999) No evidence of bottleneck in the postglacial recolonization of Europe by the noctule bat (*Nyctalus noctula*). Evolution 53:1247–1258

Strelkov P (1983) The whiskered bat (*Myotis mystacinus*) and Brandt's bat (*Myotis brandtii*) in the USSR and the relationships of these species (in Russian). Zool Zh 61:1227–1241

Strelkov P (1989) New data on the structure of baculum in Palaearctic bats. I. The genera *Myotis*, *Plecotus*, and *Barbastella*. In: Hanak V, Horacek I, Gaisler J (eds) European bat research 1987. Charles University Press, Prague, pp 87–94

Stubbe M, Chotolchu N (1968) Zur Säugetierfauna der Mongolei. Mitt Zool Mus Berlin 44:5–121

Swofford DL (1998) PAUP*: phylogenetic analysis using parsimony (* and other methods), version 4. Sinauer, Sunderland, Mass.

Volleth M (1987) Differences in the location of nucleolus organizer regions in European vespertilionid bats. Cytogenet Cell Genet 44:186–197

Weid R, Helversen O von (1987) Ortungsrufe europäischer Fledermäuse beim Jagdflug im Freiland. Myotis 25:5–27

Zingg P (1990) Akustische Artidentifikation von Fledermäusen (Mammalia: Chiroptera) in der Schweiz. Rev Suisse Zool 97: 263–294