

History of the *Pipistrellus pipistrellus* group in Central Europe in light of its fossil record

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In contrast to proposed paleobiogeographic scenarios based on molecular data, the fossil record suggests that in Central Europe the common pipistrelles, quite rich in the Holocene fossil record, first appeared as late as the present glacial cycle (including the Weichselian interstadials). Bats of this group are completely absent from the rich pre-Weichselian record available from Central Europe but occur in the early Middle Pleistocene record in the Mediterranean (Spain, Malta). Thus, it seems that the European range of common pipistrelles was restricted to the Mediterranean region until their northward spread during the present glacial cycle. The proposed range expansion (supposedly from multiple sources) is explained by climatic specificities of the present glacial cycle, namely with repeated extension of the semiarid, warm open-ground habitats that began in the Mediterranean region by the end of the Eemian.

Key words: *Pipistrellus pipistrellus*, fossil record, paleobiogeography, Central Europe, Weichselian, Holocene, dynamic biogeography, range extension

INTRODUCTION

The aspects of cryptic variation in the *Pipistrellus pipistrellus* group are among the hottest topics of current European bat research. In the early 1990s, the routine application of bat detectors proved that echolocation calls of the European common pipistrelle fall into two distinct frequency bands with terminal frequency at 45 kHz and 55 kHz respectively. Since then the view of that species, traditionally considered monotypic in the western Palearctic realm (Koopman, 1994), changed quite readily. The extensive study by Jones and Parijs (1993) indicated that at least in Britain the two phonic types occur in sympatry

without sharing the same roosts. Differences in songflight calls and social calls between the phonic types were demonstrated by Barlow and Jones (1997), and their separation in time of mating suggested their reproductive isolation (Park *et al.*, 1996). These findings provided convincing evidence to support the conclusion that the phonic types represent separate species, though they do not differ in morphology (Barlow *et al.*, 1997). Barrat *et al.* (1995) showed considerable genetic differences between the phonic types (in a 308 bp fragment of cytochrome *b*). Further mitochondrial DNA analyses undertaken with samples from western Europe revealed four cytochrome *b* haplotypes clustered into two distinct

clades, with divergence among clades exceeding 11% (Barrat *et al.*, 1997). Clade I (with terminal frequency at 55 kHz) was allopatric in Sweden, Denmark and the Iberian peninsula, while most of Europe was colonized exclusively by clade II (45 kHz), except for Britain, where both species occurred in sympatry. Extensive screening in additional regions of Europe and the Middle East using both echolocation and genetic data demonstrated a sympatry of the two species in southern Germany, Switzerland, Hungary and Greece (Mayer and Helversen, 2001a, 2001b; Benda *et al.*, 2003). The two species were almost indistinguishable morphologically (Barlow *et al.*, 1997), but Häussler *et al.* (2000) discovered fine differences in some morphological characters including the characters diagnostic of *P. mediterraneus* proposed by Cabrera (1904), although none were skeletal or dental traits. Discriminative power of some of these characters subsequently was questioned (Sendor *et al.*, 2002) and other morphologic characters were discovered (e.g., wing venation pattern — Helversen and Holdried, 2003). A vivid debate on the proper names for the cryptic species terminated with Opinion 2028 of the International Commission on Zoological Nomenclature (2003) that supported the use of the name *P. pipistrellus* (Schreber, 1774) for the 45 kHz form, and adoption of the name *Pipistrellus pygmaeus* (Leach, 1825) for the 55 kHz form [instead of *P. mediterraneus* (Cabrera, 1904) proposed by Häussler *et al.* (2000) and Helversen *et al.* (2000)]. More recently, the taxonomy of the group was further complicated with the discovery of considerable genetic differences between two allopatric populations of common pipistrelles in northern Africa that may be considered separate species (Hulva *et al.*, 2004). The taxonomic consequences were subsequently established with description of the Libyan form as *P. hanaki*

Hulva and Benda, 2004, by Benda *et al.* (2004).

The latter contributions call into question the model regarding the origin and history of the cryptic pipistrelles presented by Jones (1997) and Barrat *et al.* (1997), who suggested that the European cryptic species originated by sympatric speciation which forced them into competitive release through diverging echolocation frequencies. In contrast, Hulva *et al.* (2004) proposed an allopatric speciation model based on phylogeographic patterns of genetic variation, with a biogeographic scenario that predicts: (a) an afromediterranean range in the ancestor of the clade, (b) a split of the range into western and eastern parts due to the Messinian salinity crisis (MN13, ca. 5 My ago), (c) a long period of allopatry with disparate genotypic diversification in the western *pipistrellus* and eastern *hanaki-pygmaeus* clades, until (d) the eastward extension of the Mediterranean distributional range in the former species during the Early Pleistocene (supported by a considerable amount of genetic variation along the east-west axis of its present range), with (e) character displacement in echolocation frequency (shift to 55 kHz in *pygmaeus*) and establishment of specific mate-recognition systems separating the sympatric species (cf. Park *et al.*, 1996), which subsequently becomes a reproductive isolating mechanism, pre-requisite to (f) later enlargement of the zone of sympatry over most of Europe. Using a molecular clock, the predicted dates for the following events are as follows: split between clade I and clade II, 3.1–4.1 My; split between *pygmaeus* and *hanaki*, 2.1–1.8 My; spread of *P. pipistrellus* into Europe and Asia via the Iberian route, beginning 0.8 My colonization of Europe by *pygmaeus* via the eastern Mediterranean route, after ca. 0.25 My. The last date corresponds to a marked contrast between mid-European *pipistrellus*

and *pygmaeus* in the level of genetic polymorphism in cytochrome *b* that is pronounced in the former but not in the latter species.

In short, two biogeographic hypotheses have been proposed to explain the history of pipistrelles in Europe: (1) a continuous appearance of both species in Europe for at least 5 My, or (2) separate waves of colonization at 0.8 My (*pipistrellus*) and 0.25 My (*pygmaeus*). Unfortunately, support for one or the other of these competing hypotheses requires the determination of whether the observed genetic differences resulted from a reticulate split or a geographic sorting event, and thus require a data set independent of the molecular data. In general, answers to these questions are expected to come from the fossil record. Surprisingly, however, the fossil record of pipistrelles has neither been reviewed nor extensively discussed in that respect. To fill this gap, first we have to answer whether there is any reliable fossil record of the taxa in question, and second, whether the fossil record is complete enough to allow discriminating between the above-mentioned alternative hypotheses. With regard to the first question, the answer is positive: the fossil evidence is surprisingly rich — at least 113 records are reported from Central Europe. Answering the second question is more problematic. Until recently, no odontological or osteological characters were available for the identification of the particular cryptic species. Therefore, it is difficult to discuss what happened within the *P. pipistrellus* species group. Nevertheless, the fossil record is detailed enough to allow a discussion on timing of appearance for this bat group. At least two points important in the above-mentioned context can be addressed: the first appearance datum (FAD) for the group in Central Europe, and the abundance and distributional trends in its fossil record.

SURVEY OF RECORDS

This paper is largely based on original data obtained from the Czech and Slovak Republics, mostly during studies by the senior author in 1970 (partly reviewed, e.g., by Horáček, 1976, 1995; Horáček and Ložek, 1988; Fejfar and Horáček, 1990). Additionally, we checked all major literary sources on fossil bats in Central Europe (about 300 items) for data on *Pipistrellus*, including extensive checklists of mammalian fossil assemblages by Maul (1990), Jánossy (1986), Koenigswald and Heinrich (1999), Wołoszyn (1989), and others. Unfortunately, for the vast majority of literature records I was unable to examine the original material and therefore cannot confirm the validity of the published identifications.

Original Data (Czech and Slovak Republics)

Pipistrellus sp. was found in 60 assemblages from 25 localities in six geographical regions (Fig. 1).

Czech Republic

The North Bohemian Sandstone region: (1) Bezděz, the basal layer of the section, 1 individual (ind.) of *Pipistrellus* in a mesolithic fireplace dated to 7,745 BP (calibrated ^{14}C age — Svoboda, 2003). (2) Nízká Lešnice, sedimentary series in a sandstone overhang, layer 6, mesolithic (1 ind.).

Bohemian karst: (3) Srbsko, Barrandova cave surface deposits, ca. 1,000 items (ca. 100 individuals — Horáček, 1976). (4) Srbsko, U nádraží cave, surface deposits, 3 ind. (Horáček, 1976). (5) Karlštejn, Skalka pod Čihovou, layer 3 (postneolithic) of the sedimentary series, 1 ind. (Horáček and Ložek, 1988). (6) Srbsko, Koda 1504 cave, layers 1 (1 ind.), 7-early Holocene (1 ind.), and 10-Late Weichselian (2 ind.).

Moravian karst: (7) Koňská jáma cave, subsurface horizon in the entrance corridor,

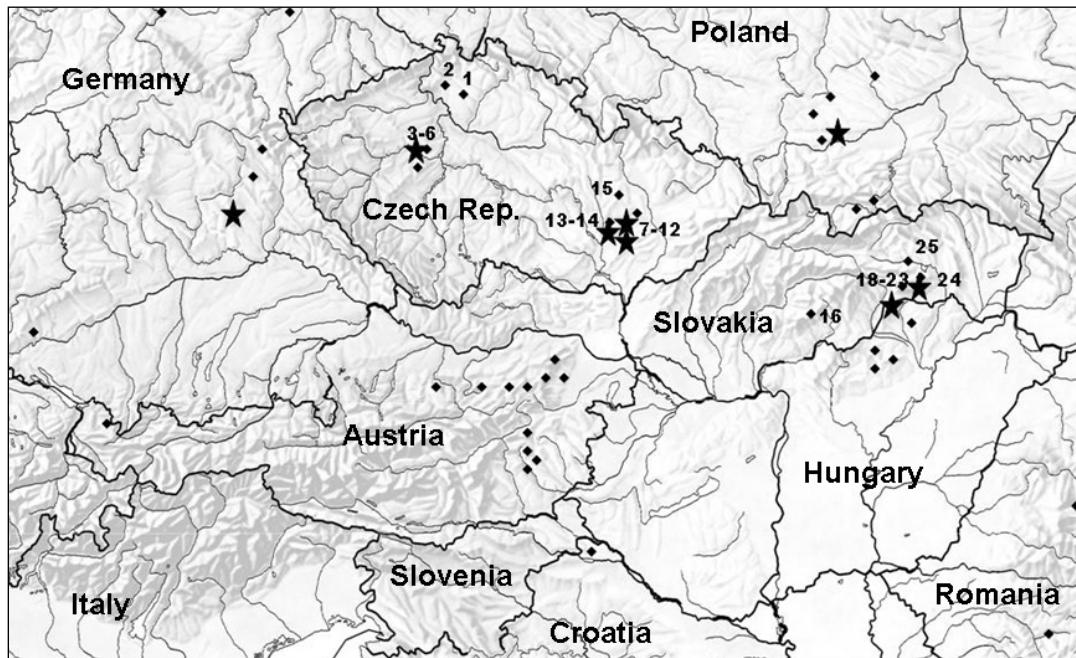


FIG. 1. A map of the fossil sites yielding remains of members of the *P. pipistrellus* group in Central Europe. Large stars refer to records of mass bone assemblages in caves. Numbers correspond to those in the text list of the respective sites

a nearly monospecific mass assemblage of ca. 300 pipistrelle skeletons. (8) Kateřinská cave, massive debris deposit in front of cave entrance (exposed during rearrangement of the cave opening in 1980), numerous pipistrelles and a rich assemblage apparently of early Holocene age. (9) Propast'ovité bludistié cave in Pustý žleb, surface deposits deep in the cave with predominant chiropteran (and particularly pipistrelle) remains. (10) Zazděná cave, ca. 3.5 m deep section in the sequence of scree deposits in front of the cave, situated at the base of a ca. 140 m-high rocky wall, Koňský spád: this site was investigated in 1978–1982 and provided a sequence of vertebrate and mollusc assemblages from the late Weichselian at the base up to the Recent (for further details see Table 1). *Pipistrellus* appeared there continuously from layer 11, i.e., from the Late Weichselian (with assemblage characterized, e.g., by a high percentage of *Microtus*

oeconomus, *M. gregalis* and *M. arvalis*), and with a particular abundance increase from layer 8 (late Boreal). (11) Ostrov n. Macocha, Srnčí cave, a Holocene sedimentary series in cave entrance with a single *Pipistrellus* in layer 4 dated to late Boreal. (12) Rytířská cave, surface layers of the entrance deposits, several ind. supposedly of the Late Holocene age. (13) Barová cave, a sedimentary sequence in front of cave entrance (excavated in 1983–1985) covering a period from the Late Weichselian to Recent and quite rich in both paleontological and archeological records (Svoboda, 2000). Single individuals of *Pipistrellus* occurred in layers 3, 5, 8 (postneolithic), more individuals are in the Boreal horizons (10a: 6 ind., 9: 5 ind.), and the species occurs also in the Preboreal or Late Weichselian layer (10b: 1 ind.). (14) Býčí skála, surface horizons of a thick debris talus in-fill of a side entrance, few skeletal remains together with

TABLE 1. Composition of the samples obtained from particular layers of the sedimentary sequence in the debris deposit in the entrance of Zazděná cave in Moravian karst, particularly rich in *P. pipistrellus* s.l., given as minimum number of individuals

Species	Stratigraphy													
	Late Weichselian				Boreal			Atlantic			Postneolithic			
	13	12	11	10	9	9a	8	7	6	5	4	3	2	1
Chiroptera														
<i>Myotis cf. bechsteinii</i>					1	1			1	1				1
<i>M. cf. nattererii</i>								1	1				1	
<i>M. cf. daubentonii</i>							1	1						
<i>Vespertilio murinus</i>										1	1			
<i>Pipistrellus pipistrellus</i>	1	6	1	14	36	37	51	41	28	19	40	12		
<i>Nyctalus noctula</i>		1	2	1	5	3	2	2	2	1	2	2		
<i>Plecotus auritus</i>					1		1		1		2			
<i>Barbastella barbastellus</i>					1	1					1	1		
Insectivora														
<i>Talpa europaea</i>	2	1	3	1	2	1	1			1	1	1	1	
<i>Sorex araneus</i>	3		3	1	1	1	1						1	
<i>S. minutus</i>				1			1			1				
<i>Neomys fodiens</i>													1	
<i>Crocidura cf. suaveolens</i>										1				
<i>C. cf. leucodon</i>												1		
<i>Erinaceus</i> sp.							1							
Rodentia														
<i>Spermophilus citellus</i>													1	
<i>Sciurus vulgaris</i>								1		1	1	1		
<i>Glis glis</i>							1		1	1	1	2	1	
<i>Muscardinus avellanarius</i>						1								
<i>Apodemus (Sylvaemus) sp.</i>			1	3	1	1	1			3	4	3		
<i>A. cf. agrarius</i>										1	1			
<i>Mus cf. musculus</i>												2		
<i>Micromys minutus</i>												2		
<i>Cricetus cricetus</i>			1					1						
<i>Clethrionomys glareolus</i>	1	1	3	2	4	3	7	5	3	1	2	9	8	3
<i>Arvicola terrestris</i>			1	2	3	1	1		1	1		1	2	
<i>Microtus cf. nivalis</i>								1*		1*				
<i>M. cf. oeconomus</i>			8	3	4	1	2						1*	
<i>M. arvalis-agrestis</i>		3	26	7	20	7	11	3	3	1	2	2	8	6
<i>M. gregalis</i>	2	2	3	2	8	5	6	3*	1*	4*	3*	5*		
<i>M. cf. subterraneus</i>							1							
<i>Lemmus cf. lemmus</i>						1					1*			
<i>Dicrostonyx gulielmi</i>			1	1	2	1	1	1*	1*	1*	1*	1*		1*
Other Mammalia														
<i>Ochotona cf. pusilla</i>			1					1						
<i>Lepus europaeus</i>			1										1	
<i>Mustela cf. nivalis</i>			1		1	1			1					
<i>Sus scrofa</i>											1		1	
<i>Alces alces</i>										1				
Total number of individuals	3	6	52	25	52	39	81	59	67	51	43	41	73	37
Total number of species	2	3	13	10	12	14	17	18	14	14	15	14	13	16

* — possible contamination from fissure infillings in the source area

predominating *Nyctalus noctula*, supposedly of the Late Holocene age.

North-Moravian karst: (15) Javoříčko, Zkameněnlý zámek, section C, layers 1–2 (Late Holocene), 1 and 3 ind., respectively.

Slovakia

Southern Slovakia: (16) Divín, Mara Medvedka n. Lučenec: a Holocene sequence in cave entrance: *Pipistrellus* (1 ind.) was found in a deep layer 8 assumed to be of the Preboreal or Late Weichselian age (with *M. gregalis*, *M. arvalis*, *M. nivalis*). (17) Peskō near Bretka — a 4 m-deep section in an entrance of a small cave, pipistrelles were found in layers 2, 3 (1 and 2 ind.) representing the Late Holocene, and in layer 9b (1 ind.) that is undoubtedly of Weichselian age (Ložek *et al.*, 1989).

Slovak karst: (18) Slavec, Maštalná cave: a 5 m-thick deposit in the cave entrance, extremely rich in fossils; pipistrelles were found continuously from layer 10 (Preboreal) with particularly high abundance (12–18 ind.) in layers 3, 4a, and 4b (Bronze II age). (19) Rožňava, Červeného mnícha cave — an entrance series of a cave in slopes of Silická plateau, *Pipistrellus* in layers 3b (1 ind.), 4a (2 ind.), i.e., Early to Middle Holocene. (20) Silická Brezová, Červená skala I, a Holocene series in scree talus under a rocky wall, layers 3 (1 ind.), 4 (1 ind.), 5 (1 ind.), 6 (3 ind.), Early Holocene to Postneolithic. (21) Silica, Zbojnická skala cave — cemented breccia in main passage of a spacious cave, rich in remains of *N. noctula* and *P. pipistrellus*, apparently of Holocene age. (22) Zadielske Dvorníky, Ernya cave — mass bone assemblages, nearly monospecific, in subsurface horizon in several sections excavated at different points in a giant cave dome. (23) Háj, Slaninová cave, an entrance series with pipistrelles in layers 2 and 4. (24) Čertův most cave near Háj — surface layers of the deposit (several ind.).

North-East Slovakia: (25) Ružín, Ružinská cave (pipistrelles in layers 6 and 7, Early Holocene).

Literary data from Slovakia: The common pipistrelle was the predominant element in 15 bone deposits obtained from rocky fissures in Slovakia (supposedly of subrecent age) by Obuch (1989). It formed nearly one-half of the total sample (1,021 of 2,451 individuals) particularly in the narrow fissures and in the warmer part of Slovakia. Obuch (1995) further reported two records (supposedly subrecent) from cave surface sediments in Drienčanská and Izbica caves.

Structure of the record

Besides sparse records of limited significance because of uncertain stratigraphic context (sites numbered: 4, 8, 12, 14, and 24 above), the remaining records are of real interest. They either come from continuous sedimentary series where a stratigraphical position of the record is fixed by direct superposition and is supplemented with both lithogenetic and further faunal information (sites: 1, 2, 6, 10, 11, 13, 15, 16, 17, 18, 19, 20, 21, 25) or they are remarkable for extremely high abundance of the form in question (sites: 3, 7, 8, 9, 10, 21, 23). Except for (10) Zazděná (cf. Table 1), the last type records came from surface or subsurface layers of interior facies of cave sediments, typically in spacious domes not too distant from the cave entrances. Pipistrelle bone remains from there often form nearly monospecific, dense bone breccia.

As concerns the pipistrelle records from continuous series, the following is worthy of mentioning: (a) bats of this species group appeared in about 26% of the sites having a continuous appearance of vertebrate remains, but only in 3 sites (10, 13, 18) were they detected in more than two layers. The last three sites are situated under high rocky walls. Surprisingly, *Pipistrellus* is completely absent from such series in the

limestone region of southern Moravia (Pálava Mts.) where both *P. pipistrellus* and *P. pygmaeus* are now very common. No pipistrelle was found in the rich Holocene bat assemblages from the high-mountain caves in Slovakia (Belanská, Alabastrová, Dobšinská, Záskočie, Nový hrad, Stratenská) and/or in deposits under the Carpathian high-mountain rock walls (Muráň, Ohniště etc.).

All the surveyed records listed above come from the Holocene and/or late Weichselian. No remains of pipistrelles were found in any of 101 Pleistocene and Late Pliocene (MN17-Q3) sites from the Czech and Slovak republics (some of them represent multilayered sedimentary complexes covering several glacial cycles) including 42 which yielded remains of other species of bats [for lists of sites see Horáček and Ložek (1988) and Fejfar and Horáček (1990) — 21 sites supplementing the list were discovered in recent years].

Situation in Other Regions

Literature data from neighbouring regions of Central Europe show nearly the same picture as described above. There are relatively large numbers of Holocene records of pipistrelles, including those in continuous sedimentary series, at least from Poland and Hungary. In Poland, the majority of records come from the Holocene layers of the cave sedimentary series in Kraków-Częstochowa Upland and/or in piedmont of the Pieniny Mts.: Puchalska Skała cave, Żytnia Skała cave (after Wołoszyn, 1989), Ojców (Madeyska, 1981), Mamutowa cave (Nadachowski, 1976), cave in Sobceński Gully in Pieniny Mts. (Alexandrowicz *et al.*, 1985), Wierzchowska Góra cave near Kraków (Wołoszyn, 1987, 1989), Nad Mosurem Starym Duża Cave near Kraków (Nadachowski *et al.*, 1989), Pod Sokolą Góra cave (Ochman and

Wołoszyn, 2000), Obłazowa cave, layer DVIII (32 ky BP ^{14}C) (Ochman and Wołoszyn, 2003). Postawa (2004) reported *Pipistrellus* from 5 of 17 Holocene bat assemblages in the caves of Kraków-Częstochowa Upland, including one monospecific mass deposit (Wierzchowska cave with 547 ind.) dated to 2,325 y BP (^{14}C). No record older than middle Weichselian is available (Wołoszyn, 1987, 1989). The situation is nearly identical in Hungary. Jánossy and Kordos (1976) reported pipistrelles from the Holocene series of Petényi cave H1–H5 (with maximum 7 ind. in H2), in Felsnische Rejtek layers 2 (1 ind.) and 12 (mesolithic). Jánossy (1986) supplemented it also with Subalyuk cave layer 12 (?late Weichselian) and a side cavity at Felsnische Tarkö in the Bükk Mts. Kordos (1982) summarized the Hungarian records of *P. pipistrellus* (including unpublished data) as a continuous appearance of the species from 10 ky BP. Except for the records in Subalyuk and Tarkö (which could be of the earliest Holocene age), no pipistrelles are reported in about 200 Hungarian Early and Middle Pleistocene assemblages. In Austria, Spitzerberger (2001) reported 16 Holocene records of the *P. pipistrellus* group, including 13 from caves (5 in Steiermark, 7 in Niederösterreich, 1 in Vorarlberg), including the high alpine caves (up to 1,350 m a.s.l., such as Bärenhöhle im Karlech, Schnealpen, Steiermark — Bauer, 1973).

Data from Germany and Switzerland seem to bring a similar picture, though apparently we did not succeed in finding all the literature actually available from there. It is because most of the Holocene faunal records are dispersed in numerous reports on mammalian remains in archeological excavations. At least the following of them reported also a pipistrelle record (usually a single item of '*Pipistrellus sp.*') : Magdalénienstation bei Ettingen in Baselland (Sarasin and Stehlin, 1924), Bildstockfels,

Petersfels (Mandach, 1930), Brillenhöhle-Magdalenen (12–17 ky BP) (Storch, 1973), Falkensteinhöhle, oberen Donautal (Magdalenen — Boessneck, 1978). Further records of Holocene age are, e.g., in Geyerloch cave near Streitberg (Heller, 1980) and Einhornhöhle near Scharzfeld (Scheer, 1987).

Nevertheless, at least three records in Germany are supposedly of critical significance with respect to the FAD of pipistrelles. Historically, the oldest records are from Breitenberghöhle near Gössweinstein in Oberfranken (Brunner, 1958). The rich bone material obtained from that site was considered to come from the early Middle Pleistocene, and Brunner's (1958) record of numerous remains of pipistrelles in Breitenberghöhle was long the only source on the pipistrelle FAD in the Middle Pleistocene, i.e., the information repeatedly appearing in review literature (e.g., Kurtén, 1968). Unfortunately, due to incorrect excavation technique, a considerable part of the material was apparently of Holocene age. For that reason the fauna is considered doubtful and was not included in the otherwise nearly complete list of middle Pleistocene mammalian assemblages compiled by Koenigswald and Heinrich (1999). We examined Brunner's collection in Munich, 1983, and could confirm that impression, at least because the fossilization pattern in *Pipistrellus* did not differ from that in the Holocene mass assemblages mentioned above.

The other German record that may count as the FAD of pipistrelles, is that in Hunas near Nürnberg, a large sedimentary complex infilling a spacious cave, which has been continuously investigated since the 1970s. Pipistrelle remains were reported from layers I and K of the main profile (as *Pipistrellus* aff. *pipistrellus* by Heller *et al.*, 1983). The entire complex including these layers was long believed to be of Middle Pleistocene age (Heller *et al.*, 1983) until

quite recently, when uranium dating of the flowstone underlying the respective sequence (76–79 ky) demonstrated that whole sedimentary sequence is of the Weichselian age, particularly of the Early Weichselian time (B. Kaulich, in litt.). The respective pipistrelle material (if it is actually referable to *P. pipistrellus* group) is to be considered as Early Weichselian, supposedly even MIS3.

Gröbern bei Gräfenhainichen is another pre-Holocene site from which a pipistrelle (*Pipistrellus* sp.) was reported (Benecke *et al.*, 1990). The item was identified in the bone material obtained from the surface layer of Eemian limnic deposits by which it is dated to the early Weichselian, as in the case of Hunas. Nevertheless, here it comes from open-ground deposits, i.e., from the context of a lowland forest, and it seems quite possible that the specimen may belong to the tree-dwelling species *P. nathusii* rather than to the *P. pipistrellus* group.

Data on the Holocene and Weichselian appearance of the *Pipistrellus pipistrellus* group in caves are available also from Romania (Pestera Hotilor — Terzea, 1971, 1986; Pestera lui Climente — Terzea, 1979; Pestera Ursilor in Bihor Mts. — Jurcsák *et al.*, 1981; a cave in Sfinta Helena in Banat — authors' unpubl. data, 1993; Ungurască cave near Turda, layer 3, late Holocene — authors' unpubl. data, 2003), Serbia (e.g., Velika Pecina — Malez, 1974) and Bulgaria (e.g., the Middle Weischselian mass assemblage in Karlukovo 4 cave: 456 ex. — Horáček, 1982; two mandibles in Weichselian deposits of Bacho Kiro cave — Wołoszyn, 1982; Karlukovo, lower layers of cave 16, Middle Weichselian — Popov, 2000; uppermost layers of cave 15, Lower Holocene — Popov and Ivanova, 1995). Nevertheless, to my knowledge there is no pre-Weichselian record from the Eastern Mediterranean. This contrasts with such records in Spain (middle Pleistocene Las

Grajas — Sevilla, 1988, 1989; Sese and Sevilla, 1996); upper Pleistocene: Cueva del Aqua) and Malta (Ghar-Dalam cave, *Leithea cartezi* Stuppe or *Hippopotamus* layer — Storch, 1974).

DISCUSSION

Zoologists often expect from the fossil record a definite answer on presence or absence of a taxon in certain critical time periods, an objective test of paleobiogeographic scenarios generated with the aid of various neontologic techniques. Unfortunately, such high expectations are rarely realized. The fossil record is fragmentary and in many instances the preserved skeletal fragments do not allow a correct species identification. In bats, which are frequently beyond the focus of paleontologists' or zooarcheologists' interest, species identification is often quite provisional and the published species accounts are not always reliable. The fossil record is, of course, incomplete also in geographic and stratigraphical respects. The latter point is particularly important to remember because it is the contextual stratigraphic information that makes a fossil record important. Unfortunately, in any single record, the stratigraphic context can be biased due to factual absence of some stratigraphic information in the fossiliferous deposit (quite typical in many intracave deposits) or misinterpreted due to incorrect sampling techniques (frequent in many historical records) or not recognizing lithogenetic irregularities (postsedimentary redepositions, subrosion, etc.). Thus, a cross-control of the contextual setting is generally required in any single record. Repeated evidence from critical stratigraphic horizons and geographic areas is particularly important. A single isolated record can be taken into account only if its contextual information is extraordinarily reliable. At the same time, the absence of a record in a given

period or area never grants the actual absence of the taxon. In short, to be useful in testing paleobiogeographic scenarios, the fossil record should be rich and provide contrasting pictures such as the predominance of a taxon in one horizon and its absence in the other horizon or region. Fortunately, the fossil record of pipistrelles exhibits these qualities.

The above list clearly confirms previous statements (e.g., Kordos, 1982; Horáček, 1984; Taake and Vierhaus, 2004) that *P. pipistrellus* s.l. is a common element in the Holocene fossil record throughout most of Central Europe. This holds true not only for the number of sites where it was recorded (which is 25 in the Czech Republic and Slovakia what correspond to number of records in wide-spread resident paleochoric mid-European taxa such as *Eptesicus serotinus*, *Myotis nattereri*, or *Nyctalus noctula*), but also for its extraordinary abundance in certain cases. This is pertinent for at least eight sites (of those surveyed above) where abundance of pipistrelle remains clearly dominates everything else in the samples. Mass accumulations of pipistrelles — attaining the form of a compact bone breccia forming a conspicuous subsurface horizon in certain sites — is a very remarkable phenomenon in the mid-European fossil record. It is indeed a very conspicuous phenomenon in cave-interior facies that hardly could be overlooked, and as such the phenomenon undoubtedly does not appear in any deposit older than Holocene. Several questions arise with such a phenomenon that is so unique in the bat fossil record. What was the source of these thanatocenoses and what kind of information do they provide? Except for one, none of the above-mentioned sites is recently inhabited by pipistrelles (either in summer or winter), nor does this species-group use the respective caves during times of swarming. Cave Eryna in Slovakian karst, a giant underground dome

opened to surface with a ceiling hole, is an exception. It is intensively visited by pipistrelles during summer and autumn swarming (hundred ind. per night as a rule), and in winter it hosts clusters of about 30,000 hibernating pipistrelles (corresponding to the largest colony in Sura Mare cave, Romania — Nagy and Szanto, 2003). Per analogiam, it seems quite probable that the major source of the mass bone assemblages were mass winter colonies.

Of course, the critical question is: what is the biological meaning of the discrepancy between vast deposits of pipistrelles during the Holocene and their virtual absence during modern time in regions like the Bohemian or Moravian karst? Could the apparent disappearance of mass colonies from these regions be explained by a recent population decline of pipistrelles in these regions, or is it related to a large-scale metapopulation dynamic of the species in Central Europe? Nevertheless, in discussions on these alternatives one should take into account also some other factors influencing the dynamics of massive bat colonies. Similar to other species of bats (barbastelles, in particular), massive hibernating colonies of pipistrelles are extremely sensitive to disturbances, while at the same time, they are extremely attractive to predators, such as martens which enter deep cave interiors quite regularly. Over time, some predators could succeed in climb to the cluster of hibernating bats, and the colony disappears rapidly. Under the repeated appearance of an experienced predator in several subsequent years, the social tradition of the respective mass hibernaculum is soon lost. We directly observed such cases in a former mass hibernaculum of a mixed colony of *Barbastella barbastellus* (1,112–7,798 ind.) and *Pipistrellus* spp. (940–2,343 ind.) in Dielik, central Slovakia (Uhrin *et al.*, 2002). All this suggests that mass winter colonies may represent a rather temporal phenomenon

that could sooner or later disappear without regard to actual abundance changes. In this respect, the present-day absence of pipistrelles in caves where they were highly abundant in the fossil record need not necessarily indicate much higher abundances of the species in the past. They might simply reflect the episodic abandonment of the respective local roosts. In any case, what is significant with respect to the history of pipistrelles is that all the mass fossil assemblages in Central Europe are apparently of Holocene age (supposedly even the post-neolithic ones). Even more significant is that nearly all of 113 records reported from Central Europe are of Holocene or late Weichselian age. The two records which were reported as Middle Pleistocene were disproved, either for doubtful stratigraphic context (Breitenberghöhle) or for current re-dating the deposit to the Early Weichselian (Hunas). In conclusion, the contrast between the enormously rich record of the *P. pipistrellus* group in the Holocene (including Late Weichselian) and its absence in pre-Weichselian periods suggests convincingly that in Central Europe, this taxon is apochoric to the present cycle, and the Late Weichselian-Holocene stage in particular.

There are more bat species, now widespread in Central Europe which are absent from the fossil record prior to the Holocene and thus are looked upon as the Holocene apochoric elements in Central Europe. In full it holds for *Plecotus austriacus* and *Myotis myotis* (cf., e.g., Güttinger *et al.*, 2001; Horáček *et al.*, 2004). In these species, of course, no record prior to the post-Neolithic period is available from Central Europe. Because both are characterized by a synanthropic roosting strategy, it seems probable that the northward spread of these thermophilous forms from their Mediterranean range began with their roosting in human constructions and/or in dependence upon the postneolithic spread of warm open

country, the cultural steppe. When analyzing the fossil record of pipistrelles twenty years ago (Horáček, 1984), we expected that the same explanation was valid also in the case of *P. pipistrellus*. The few records suggesting the pre-Neolithic age that were available at that time were considered either doubtful or not sufficiently strong for disproving that interpretation. Nevertheless, since that time, remains of *Pipistrellus* sp. have been found not only in the Early Holocene layers in several continuous sedimentary sequences in which post-depositional contamination is largely improbable (Maštálka, Srnčí, Barová, Červená skála, Ružín, Bezděz etc.) but repeatedly also in the horizons dated to the Late Weichselian. A sequence of scree debris sediments under a rocky wall in the entrance of Zazzděná cave in Moravian karst can serve here as an impressive example (Tab. 1). The particularly high abundance of pipistrelles in that section is apparently due to a specific source area of the deposits — a 150 m-high rocky wall rich in fissures providing an excellent roosting possibilities for the lithophilic bats. The first appearance of *Pipistrellus* sp. is here proved in the context of the Late Weichselian assemblages (cf. *M. gregalis*, *M. arvalis*, *Dicrostonyx*) and two further increases in its abundance are demonstrated: one at the beginning of the Holocene (layers 7 to 9a) and the second at the late Atlantic (i.e., Neolithic stage; layer 6).

These results are in agreement with corresponding data from Hungary (see above). Also the first appearance datum in the Carpathian Basin was situated in the Late Weichselian (Jánossy, 1986; Kordos, 1982). The record from Hunas n. Nürnberg (layers I and K, now dated to ca. 50 ky) and that from Subalyuk cave, layer 12, in North Hungary (Jánossy, 1986) suggest that the species may have appeared here even in the interstadials of the Early Weichselian. Unfortunately, this is the period which in

Central Europe is rarely well evidenced by a detailed fossil record. Confirming data from the Early Weichselian are thus urgently needed.

It is worth mentioning that nearly the same pattern of abundance development as in the *P. pipistrellus* group (i.e., a fairly rich Holocene and Late Weichselian record but nearly none in the pre-Weichselian period) appears also in another lithophilous species, *Vesptilio murinus*. This species is known from two Early Pleistocene sites (Chlum 4S, Koněprusy JK, besides of MN17 Vilány 3 — Horáček, 1997), four Q3 sites in Central Europe, while plenty of records are available from the Holocene and Weichselian, mostly in deposits situated under rocky walls (e.g., 14 sites in the Czech Republic, 22 in Slovakia, including a mass assemblage in Muránská cave in the High Tatras — cf. Schaefer, 1974). Also in *V. murinus*, repeated continuous records from the Early Holocene and late Weichselian (Barová, Murán 3) clearly prove that its Holocene spread began prior to the Neolithic deforestation, and the same is the case also with some other Holocene apochoric mammals such as *Crocidura suaveolens* and *C. leucodon*. Hence, the question is: if not the post-Neolithic changes, what else caused the synchronous spread of the inhabitants of warm open country (*P. pipistrellus*, *Vesptilio*, *Crocidura*), and why did it not occur prior to the Weichselian?

In answer to these questions, the following facts must be taken into account: (1) In comparison with previous interglacials, the Holocene is a rather dry period particularly during the first five millenia until its climatic (and precipitation) optimum was achieved (Bradley, 1999). In comparison to the Eemian, the mid-European Holocene is characterized by a long transitional period with persistence of a mosaic of semi-open habitats and with early spread of the apochoric elements that colonized Central

Europe never before, all closely linked to warm open country. (2) The Weichselian climatic dynamic was characterized by highly pronounced millennial oscillations (Dansgaard-Oeschger cyclicity) and, besides of them, by unique large-scale climatic events caused by accidental dislocations of polar ice sheet in the Northern Atlantic (Heinrich events). (3) The millennial climatic oscillations were particularly well pronounced in the Mediterranean region where they repeatedly produced periodic stages of abrupt warming during most of the Weichselian (Martrat *et al.*, 2004). (4) The Eemian interglacial terminated with a long period of repeated dry and warm climatic pulses (MIS 5d-a), which in the temperate zone caused several stages of reappearance of forest habitats (Kukla *et al.*, 2002). Such conditions reappeared also during Early Weichselian what preserved habitat patchiness, and prolonged survival of some demanding (as recorded, e.g., in Hunas). (5) In the Mediterranean, the repeated warm periods at the end of the Eemian and beginning of the Weichselian were not followed by expansion of the closed forest habitats but with expansion of semiarid habitats of warm open or semi-open country (Tzedakis *et al.*, 2004).

Simply said, it seems quite probable that the climatic regime of the late Eemian and Weichselian produced, at least in the Mediterranean, advantageous conditions for population increase in species utilizing warm open ground habitats. Thus it provided for their further spread beyond the limits of the inner Mediterranean. In other words, the biotopes in which the common pipistrelles reach their maximum abundance in the Recent period, grew from the predominant component of the Mediterranean habitats since the end of the Eemian and their repeated expansion throughout the Weichselian, including the late Weichselian warming pulse at 14 ka BP) and in the

Early Holocene. The Weichselian and Holocene spread of pipistrelles is a ‘faunogenetic event’ (as early Holocene spread of *Crocidura*, *Eliomys*, and *Rhinolophus hipposideros*) for which current data on the unique climatic history of the present glacial cycle provide a good explanation. The question is, To what degree is this pertinent also for the cave-dwelling bats of the *P. pipistrellus* group, in particular for the appearance of their mass winter colonies in caves? In the inner Mediterranean, pipistrelles are not true cave-dwellers (in contrast to those in the Carpathians — cf. Nagy and Szanto, 2003) and there is no reported pre-Weichselian record of a mass monospecific assemblage in the Mediterranean corresponding to those in the mid-European Holocene record. Could it mean that mass hibernation in caves developed as an adaptive strategy with the northward spread of the species during the present glacial cycles? Or is it all simply a series of misinterpretations due to incomplete information? It is difficult to answer those question, at least until a sufficiently dense fossil record is available from the Mediterranean. In any case, the paleobiogeography of pipistrelles still represents an interesting topic and a problem that is undoubtedly worthy of additional study.

CONCLUSIONS

With respect to the history of common pipistrelles in Central Europe and/or the two above-mentioned paleobiogeographic scenarios, the information obtained from the fossil record suggests that:

- (a) The common appearance of the *P. pipistrellus* group in Holocene deposits contrasts with its absence in fairly rich Early and Middle Pleistocene fossil records in Central Europe (the doubtful data from Breitenberghöhle being excluded);
- (b) Thus, it seems quite probable that in Central Europe, the common pipistrelles

(both species) are apochoric to the Holocene and their spread started during the Weichselian (at least its latest stage);
 (c) It seems improbable that common pipistrelles colonized Central Europe anytime prior to the Holocene in the same way as in the Holocene (by forming mass winter colonies in caves);
 (d) In contrast to Central Europe, in the Mediterranean repeated records of pipistrelles of early Middle Pleistocene age are available (Spain, Malta), but nowhere do they form mass monospecific cave assemblages characteristic of the Holocene and Weichselian records.

With these results, neither of the two proposed scenarios is directly supported: (1) a continuous appearance of both pipistrelle species in Europe for at least 5 My; or (2) separate waves of colonization at 0.8 My (*P. pipistrellus*) and 0.25 My (*P. pygmaeus*), respectively. Rather it seems that the European range of common pipistrelles was limited to the Mediterranean region until its northward spread during the present glacial cycle supposedly from multiple sources, and perhaps by the beginning of Weichselian.

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