Chapter 8
Bats from Azokh Caves

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Abstract Azokh Cave is well-known in the Caucasus not only for its archaeological interest, but also for sheltering large colonies of bats, some of which are rare in the region. During the summer the bat communities in the cave include individuals of at least four different species. Both the Lesser Mouse-eared Bat (*Myotis blythii*) and Schreiber's Long-fingered Bats (*Miniopterus schreibersii*) form large breeding colonies, but abandon the cave during the winter. Another two species, Mehely's Horseshoe Bat (*Rhinolophus mehelyi*) and the Greater Horseshoe Bat (*Rhinolophus ferrumequinum*), can be found roosting in the cave all year round. During the active season, the colonies of *R. mehelyi* reach several thousand individuals, being the largest grouping of this species known in the Caucasus. Excavations in the sediments preserved in the cave, dating from the late middle Pleistocene to Recent, contain evidence that the same four species have been roosting in Azokh Cave for at least the past 300 kyr, accompanied by several other species. However, species richness and relative abundances have varied during this time interval as shown by the thanatocoenosis preserved in the different layers of Azokh 1. The species represented in these assemblages differ in their habitat preferences, and have been used as a means of interpreting the changes that took place in the surrounding environment during this time, mainly concerning vegetation and forest development.

Резюме Азохская пещера хорошо известна на Кавказе не только как археологический памятник, но и по причине проживания в ней больших колоний различных видов летучих мышей, некоторые из которых являются редкими в регионе. Согласно сведениям из доступных источников, колонии из примерно 4000 особей подковоноса Мегели (*Rhinolophus mehelyi*) постоянно ночуют в пещере, а количество летучих мышей увеличивается от весны к осени за счет около 10 тыс. особей длиннопалой ночницы (*Miniopterus schreibersii*). Большая ночница (*Myotis blythii*) и меньшее количество большого подковоноса (*Rhinolophus ferrumequinum*) проживают в пещере вместе с этими двумя видами и другими формами, некоторые из которых также считаются редкими на Кавказе. Такое изобилие особей и богатство видов указывает на то, что летучие мыши региона нашли в пещере и его окружении благоприятные условия для своего проживания.

Данная обстановка имеет, по крайней мере, 280-тысячелетнюю историю – возраст наиболее древнего материала, раскопанного до сих пор в пещере, где останки летучих мышей оказались наиболее часто встречающимися формами в отложениях. К настоящему времени идентифицировано 13 видов в различных горизонтах наиболее тщательно раскопанных седиментов. Хотя основные виды, представленные в коллекции из подразделений *V–I*, относятся к гнездящимся в настоящее время в пещере, между ними все же наблюдаются различия в видовом разнообразии и относительной численности. Так, подразделения *V* и *IV* содержат большее число видов летучих мышей, которое резко уменьшается в подразделении *III*, практически стерильным для окаменелостей этих животных; в подразделениях *II* и *I* разнообразие видов умеренное, не достигая значений для наиболее древних горизонтов.

Несмотря на то, что в отложениях есть свидетельства проживания человека, наблюдаемые различия в видовом разнообразии и количестве летучих мышей, вероятнее всего, связаны с изменениями среды, имея в виду климат и окружающий пещеру ландшафт, а не с антропогенным фактором. Так, с учетом технологии собирательства, географического распределения и температурных характеристик мест гнездования видов, зарегистрированных в каждом подразделении, мы попытались объяснить эти изменения в экологических терминах. Удалось выяснить, что

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незначительное похолодание в регионе с превалированием открытых ландшафтов способствовало относительно бурному развитию лесов, что могло стать причиной большего видового разнообразия летучих мышей, наблюдаемого в подразделении *V*.

Keywords Lesser Caucasus • Upper Pleistocene • Holocene • Chiroptera • Rhinolophidae

Introduction

Azokh Cave is well known as one of the largest caves in the Caucasus. A good part of it remains unexplored, and it consists of several chambers, large and small, connected by galleries that offer a good choice of roosts for cave-dwelling bats. Azokh Cave provides shelter and roosting sites for large colonies of bats, and references to this cave are common in the literature dealing with the bats from the Caucasus (see Rakhmatulina 1989, 1995a, b, 1996a, b).

Two species of horseshoe bats, *Rhinolophus mehelyi* and *R. ferrumequinum*, permanently occupy the cave at present (Fig. 8.1a, b). The colonies of the former are the largest known in the region, with numbers reaching several thousand individuals. From spring to autumn the number of bats in Azokh Cave exceeds 20,000 individuals, as *M. schreibersii* (Fig. 8.1c) and *M. blythii* settle in the cave during the breeding season. The colonies of Schreiber's Bent-winged Bats can reach close to 10,000 individuals and those of *M. blythii* are equally numerous (Rakhmatulina 1996a). Since these species build their colonies at well-exposed roosting sites, they are easily observed (Fig. 8.2). Several other species have been reported in Azokh, but they are either less numerous or roost at less conspicuous places, so that they are more difficult to observe.

A greater number of species have been roosting in Azokh Cave during the last three hundred thousand years. Reports on the excavations conducted in the cave during the 1980s already referred to the finding of fossil bones of five different species in the cave, *R. mehelyi*, *R. ferrumequinum*, *M. blythii*, *M. nattereri* and *M. schreibersii* (Rakhmatulina 1995a). With the new excavations this number has increased to 13 different

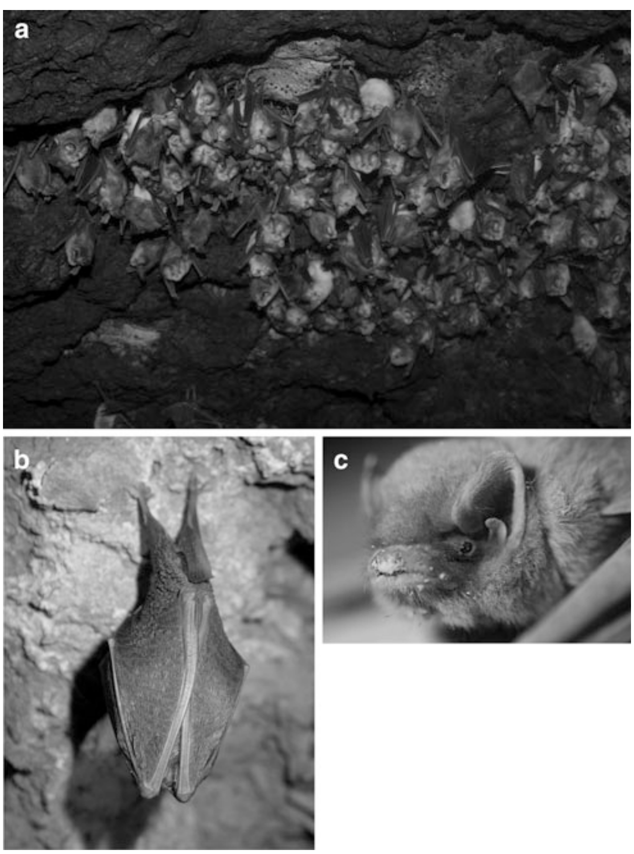

Fig. 8.1 Bats of Azokh Cave. **a** A colony of *Rhinolophus mehelyi*. **b** An isolated specimen of *Rhinolophus ferrumequinum*. **c** Detail of the head of a specimen of *Miniopterus schreibersii* found roosting near the entrance to Azokh 1 (Photographs by P. Domínguez 2004, 2005)

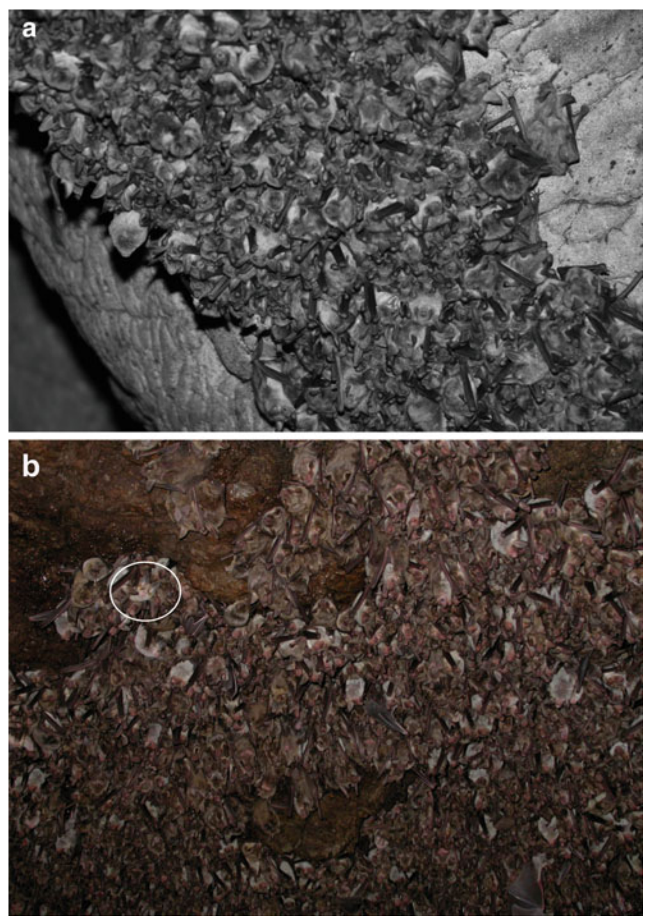

Fig. 8.2 Bats of Azokh Cave. **a** A colony of *Myotis blythii*. **b** A colony of *M. blythii* with an individual of *R. mehelyi* (circle) (Photographs by P. Domínguez 2004, 2005)

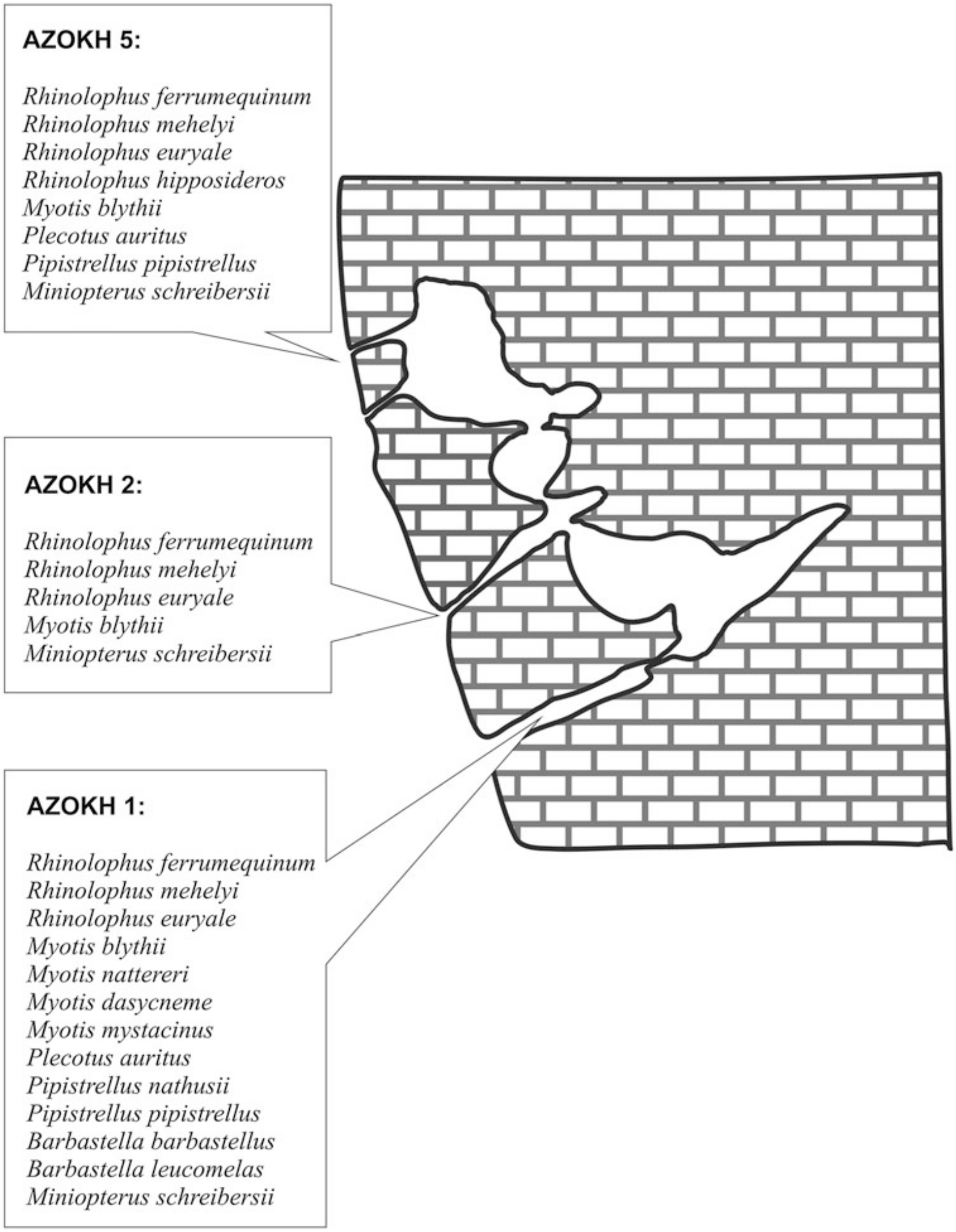

Fig. 8.3 Bat species recorded in the new excavations (2002–2009) in Azokh Cave

bat species in Azokh 1 (Fig. 8.3), and this number might increase with further excavations in other parts of the cave.

In this chapter, the numerous bat fossils found in the new excavations of Azokh Cave are described. The faunal assemblages preserved in each of the units in Azokh 1 have yielded bat bones and teeth of several different species, some of which have not been reported as roosting presently in the cave. Both the abundance of bats and the species represented in each assemblage show that the bat community roosting in Azokh Cave has varied in the last 300 kyr, according to changes that took place both within and outside the cave. Since some of the species found in Azokh Cave are considered rare or vulnerable, the study of these variations and their possible causes may be important to understand the long term dynamics of their populations.

Materials and Methods

The material studied here comes mainly from Azokh 1 (Main Entrance), Unit I (top unit in the stratigraphic succession) to Unit V (bottom unit as presently excavated). Fossil material from Azokh 2 and Azokh 5 passageways have also been examined briefly, but results from these sites are not included in this paper. Most of the bat fossils collected in the recent excavations at Azokh 1, Azokh 2 and Azokh 5 were fragments, mainly isolated teeth, sometimes covered with a dark mineral coating (manganese oxides) that makes taxonomic determination tasks more difficult.

Fossils described here were recovered from the eight excavation seasons carried out from 2002 to 2009 (Fernández-Jalvo et al. 2010). Sediments were labelled by square and vertical coordinate (Z), and wet-sieved in the river using superimposed sieves of 2, 1 and 0.5 mm meshes. Sorting was partially done at the field laboratory, as well as at the laboratory under light microscopes.

Though some cases of exceptional preservation in bats are known, with complete skeletons and bones preserved in articulation, fossilization of bats usually implies a certain degree of disarticulation and loss of the smaller and most delicate bones. The hardest parts of a bat skeleton, such as teeth, mandibles, maxillae and humeri, are the most common anatomical elements in the fossil assemblages. Other parts of the skeleton may also be common, such as scapulae, pelves, femora, cochlea and fragments of phalanges. If preservation is good, and collecting methods are adequate, even deciduous teeth and poorly ossified bones of newly born bats can be collected, as in the case for the bat fossils in Azokh Cave.

Taxonomic determination was focused on the mandibles and maxillae, humeri (if the distal articulation is preserved) and certain teeth, mainly the molars, since these skeletal elements enable species determination. The nomenclature used in the description of the material, and the criteria for taxonomic determination, follow Menu and Sigé (1971), Felten et al. (1973), Sevilla (1986, 1988) and Menu and Popelard (1987). Wear stages to establish age of death are based on Sevilla (1986). Traits of digestion have also been analysed on cranial and/or postcranial anatomical elements according to criteria and stages set up by Andrews (1990).

Species representation was quantified using both numbers of remains and minimum numbers of individuals (MNI). To interpret the environmental conditions implied by the bat assemblage, the known ecology of the extant representatives of each species was considered. The main sources for this information were several papers from the National Bat Reports of Armenia and Azerbaijan, available at eurobats.org/documents/national reports, and the information about habitat and geographic distributions found in Campester Field Researcher's Union site and at the IUCN (2009) Red lists site. The biogeographic character of each species was considered according to Horaček et al. (2000).

Table 8.1 Differences in the representation of bat fossils in Azokh 1. (NR: number of identified remains; MNI: minimum number of individuals)

Distribution of bat remains in Azokh 1						
Azokh 1 (2002–2009)		UNIT I	UNIT II	UNIT III	UNIT Vu	UNIT Vm
Rhinolophus ferrumequinum	NR	3	3		93	14
	MNI	2	2		14	5
Rhinolophus mehelyi	NR	16		1	37	5
	MNI	6		1	6	2
Rhinolophus euryale	NR				3	1
	MNI				3	1
Myotis blythii	NR	271	23	2	2067	22
	MNI	26	7	1	123	5
Myotis nattereri/schaubi	NR				1	1
	MNI				1	1
Myotis mystacinus	NR	2			6	1
	MNI	1			2	1
Myotis dasycneme	NR		1			
	MNI		1			
Plecotus auritus/macrobullaris	NR	3			6	
	MNI	1			1	
Barbastella barbastellus	NR				2	
	MNI				1	
Barbastella leucomelas	NR				2	2
	MNI				1	1
Pipistrellus nathusii	NR					4
	MNI					2
Pipistrellus pipistrellus	NR		1		3	3
	MNI		1		2	2
Miniopterus schreibersii	NR	15	16		94	80
	MNI	6	7		18	23
Total NR		298	43	3	2314	133

Results

Table 8.1 shows the record of bats in Azokh 1, indicating the number of fossil specimens that have been identified for each species, and the minimum number of individuals (MNI) these fossils represent. Skeletal elements are relatively scarce, particularly in the upper units. This is especially evident in Unit II, where destruction of bone has been caused by heavy guano deposition which has destroyed much of the bone. The reduced fossil representation from Unit III may be a consequence of the heavily cemented sediment that hampered the sieving work, and because the only excavation performed in unit III has been restricted to a test pit of no more than 2 square metres near the cave wall.

Two families of bats are represented, the Vespertilionidae and the Rhinolophidae (Fig. 8.4). Five different genera of vespertilionids were identified, *Myotis*, *Pipistrellus*, *Barbastella*, *Plecotus* and *Miniopterus* with ten different species in the assemblages of Azokh 1. The Rhinolophidae are represented since the Quaternary by a single genus, *Rhinolophus*, with five extant species distributed in the Caucasus. Thus, a total number of 13 species of bats are represented in the material, with important differences in their relative abundances along the sequence, the meaning of which will be commented later in the discussion.

The genus *Myotis* is the most diverse in the region, with eight species distributed in the Caucasus (Fig. 8.2), and many of these are frequently found roosting in caves. Their remains are distinctive (Fig. 8.5): the humeri have distal epiphyses with a short styloid process and a shallow depression between the trochlea and the condylus; three premolars are retained in both the upper and lower tooth rows; the upper molars are robust, without a talon; the lower molars are myotodont, with a thick and well-developed labial cingulum; the third molars present an important distal reduction. The anatomical elements of the different species within the genus differ in size and in the development of particular structures in the teeth, mainly of the upper molars.

Myotis blythii, the Lesser Mouse-eared Bat is not only the best represented species of this genus in Azokh 1, but it is also more numerous than all the remaining species of the other genera, except in Unit V. Isolated teeth, mandibles, maxillae, cochlea, humeri and other bones of this species were collected in all of the five units; and even poorly ossified bones, deciduous teeth and a few mandibles with erupting permanent molars were found at certain levels. The skeletal elements of this species stand out for their large size (Fig. 8.5a–d) and are particularly abundant at Unit Vu. Even Unit III, with few bat fossils, yielded a couple of lesser Mouse-eared Bat fossils. *Myotis blythii* is a widely spread species in the Caucasus; and it is found in a variety of habitats, from humid forests to semi-desertic areas, except for alpine meadows. From a biogeographic point of view, it is a "temperate arid" species, linked to warm and dry habitats (Horaček et al. 2000). Its roosts are varied, including large and relatively warm caves. Large nursery colonies of the Lesser Mouse-eared Bat are observed today in Azokh

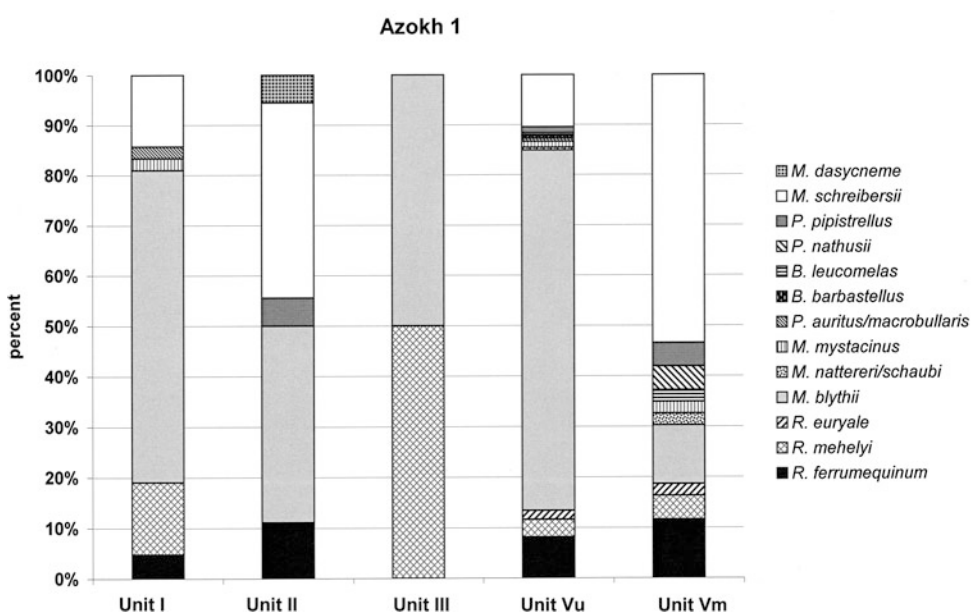

Fig. 8.4 Variation in the relative abundances of bat species in Azokh 1

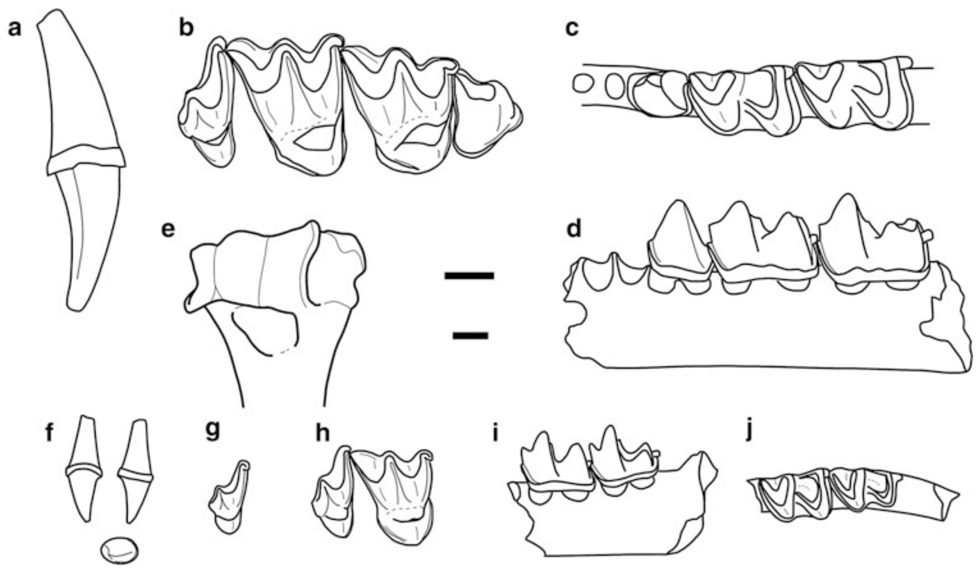

Fig. 8.5 *Myotis blythii*. **a** Right upper canine; **b** right $P^4M^1M^2M^3$; **c**, **d** fragment of left mandible with $P_4M_1M_2$. **e** Distal epiphysis of left humerus. *Myotis mystacinus*. **f** Right upper canine; **g** right M^3. *Myotis nattereri*. **h** Right M^2M^3. *Myotis dasycneme*. **i**, **j** Fragment of left mandible with M_2M_3. Scale = 1 mm. (The short bar is only for **e**)

Cave from spring to autumn, occupying exposed places on the ceiling and in wide fissures, but this species moves to another cave for hibernation. *M. blythii* is common in Quaternary fossil assemblages.

The representation of the other species of the genus *Myotis* may be considered occasional, their fossils restricted to certain units and represented by few individuals. A few teeth and a humeri of *Myotis mystacinus,* commonly known as the Whiskered Myotis, were found in Units I, Vu and Vm (Fig. 8.5f, g). It is the smallest species of the genus in the Caucasus and is considered rare. The morphology of these fossils agrees with the general morphology observed in the species within the genus *Myotis*, but its humeri are half the size of the same bone in *M. blythii*. The two first upper molars are more rectangular in outline than in the Lesser Mouse-eared Bat, and the third molar is less reduced in its distal region. It is a western Palaearctic species with a “temperate humid” pattern of distribution. It occurs in a variety of habitats and hunts exclusively near inland waters. Winter roosts may be located in caves, where they congregate in small groups.

Myotis nattereri, Natterer’s Bat, was reported by Huseinov (according to Rakhmatulina 1995a) as one of the species represented in the bat assemblages from the old excavations, but only two fossils of this species were found in the recent excavations. These are maxillary teeth that were collected at Units Vm and Vu. The teeth and bones of this species are similar in morphology to, but smaller than, those of *M. blythii*, and they are distinctly larger than the Whiskered Myotis (Fig. 8.5h). *Myotis nattereri* is a western Palaearctic species, with an extensive distribution, frequent in Pleistocene fossil assemblages with bats but becoming less common in Holocene assemblages, probably due to a reduction of favourable habitats. This species is currently rare in the Caucasus. It is known to forage mainly in woodland, sometimes over water, and although it occurs both in humid and in dry areas, it depends on the presence of water bodies. Like *M. mystacinus*, it is a species with a temperate humid pattern of distribution. Summer roosts are occasionally located in underground sites, but hibernation takes place preferably in caves and in underground habitats. Its sibling species, *M. schaubi* Kormos 1934, is also distributed in the region, but poorly known. It was described first with Pleistocene fossil material from eastern Europe. It closely resembles *M. nattereri*, though it is slightly more robust, and according to the original description, differences are observed in the lower molars, which have a very weak hypoconulid. With only two fossils in our material, we cannot establish to which of the two species it might belong. New collections of *M. nattereri/schaubi* group fossils in future excavations in Azokh might help to clarify this point.

A single fossil, consisting of a fragment of a lower mandible with two molars of *Myotis dasycneme*, known as the Pond Bat, was found at Unit II (Fig. 8.5i, j). Both the morphology and the size agree with that of extant specimens of this species. It has a wide distribution that extends from

Fig. 8.6 Recent distribution of *Myotis dasycneme* (after Hutson et al. 2008) shown in in dark grey. The approximate position of Azokh Cave is marked by the symbol (*). Note the distance between the cave and the nearest areas at which *M. dasycneme* is known to live at the present time

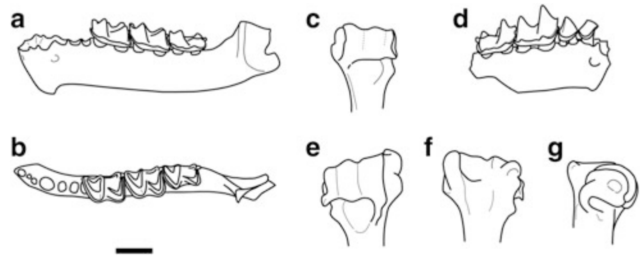

Fig. 8.7 *Pipistrellus pipistrellus*. **a**, **b** Fragment of left mandible with $M_1M_2M_3$; **c** distal epiphysis of right humerus. *Pipistrellus nathusii*. **d** Fragment of right mandible with $P_2P_4M_1M_2$; **e**, **f**, **g** distal epiphysis of left humerus. Scale: 1 mm

north-west Europe to central Russia, (Fig. 8.6), with its southernmost limits at latitude 44º N, well to the north from Azokh Cave. The Pond Bat is known to be a partial migrant; fossils of this species are known in several Holocene localities that are beyond its present range of distribution, though never reaching distances as great as Azokh Cave. It is a species linked to water habitats since it feeds mainly over open calm water, preferring water bodies with banks of open rough vegetation and no trees. It frequently hibernates in natural caves forming small colonies of a few hundred individuals.

Two species of the genus *Pipistrellus* were found in Azokh 1. A few fossils of *Pipistrellus pipistrellus*, known as the Common Pipistrelle, were collected at Units Vm and Vu and II. In Unit V fossils of another species of the genus, *Pipistrellus nathusii* were also found. The pipistrelles are small-sized bats, with a very small skeleton. Their humeri are characterized by the relatively deep fossa for the elbow joint and the hood-like styloid process. The teeth of these bats are slender, with pointed cusps; the lower molars are nyctalodont, with narrow trigonids and relatively large hypoconulids (Fig. 8.7). *P. pispistrellus* is smaller than *P. nathusii*. It is a widespread and abundant species and one of the most common bats in the Palearctic, frequent both in Mediterranean and in temperate humid regions. It forages in a wide variety of habitats including open woodland and woodland edges, Mediterranean shrubland, semi-desert, as well as anthropogenic landscapes, feeding mainly on small moths and flies. Roosts are varied, including tree holes, rock fissures and caves. Fossils of this species are known from several upper Pleistocene and Holocene localities, but never in large numbers. The other pipistrelle species found in Azokh, *P. nathusii*, is rare in the Caucasus, but widespread and abundant in other areas within its range of distribution, probably because of its preference for temperate humid regions. It is a species mainly linked to forest habitats, foraging in woodland edges, wetlands, and open parkland. It is a migratory species, sometimes covering close to 2,000 km during migration. Winter roosts include the entrance of caves, often in relatively cold, dry, and exposed sites. However, signs of digestion were observed on humeri both of *P. pipistrellus* and of *P. nathusii*, and since pipistrelles are occasional prey to owls, it seems reasonable to consider these fossils as coming from pellets from some bird of prey.

A few fossils of the two Barbastelles distributed in the Causasus were found in the lower levels of Azokh 1. A mandible and a broken humerus from Unit Vm and another two fragments of humeri from Unit Vu were identified as belonging to the Eastern Barbastelle, *Barbastella leucomelas,* while a smaller mandible with similar morphology, as well as a humerus from Unit Vu, were determined as fossils of the European barbastelle, *Barbastella barbastellus* (Fig. 8.8). The distal epiphyses of the barbastelles are very characteristic mainly for the triangular shape of the styloid process that projects inwards; the ramus in the mandibles has a relatively high and narrow coronoid process, a low articular process, and long and robust angular process, commonly broken in the fossil material. The molars are nyctalodont, elongate, with wide trigonids. The Eastern Barbastelle is somewhat larger than the European species. It extends its distribution from the Caucasus, through southern Asia to China, where it is found in forest habitats, both in moist temperate and in dry coniferous forests. It is a widespread, but infrequent, temperate arid species. It roosts in small groups both in caves and in tree hollows, or beneath the bark. The European Barbastelle on the other hand, is a temperate humid species, distributed mainly through Europe and part of the Caucasus, absent in the drier areas of its distribution. It is found linked to mountain and lowland forests; the abundance of this species depends on the

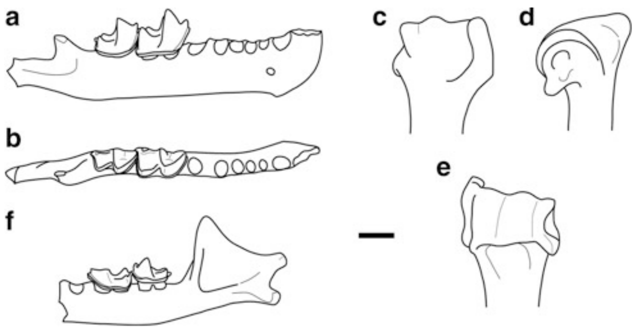

Fig. 8.8 *Barbastella leucomelas*. **a**, **b** Fragment of right mandible with M_2M_3. *Barbastella barbastellus*. **c**, **d**, **e** Distal epiphysis of right humerus; **f** fragment of left mandible with M_2M_3. Scale: 1 mm

presence of old and dead trees with hollows that provide the roosts used during the active season. In winter, the European Barbastelle is commonly found roosting in cold and dry caves, grottos, underground sites, and tree hollows. Though mainly a solitary species, it is sometimes found forming small groups, but a few large wintering colonies have been described. *B. barbastellus* feeds on insects with soft cuticles; it finds its prey mainly in the borders of forests or among separate groups of trees.

The Long-eared bats, genus *Plecotus*, are represented at Azokh 1 by a few teeth collected in Units Vu and I. The isolated upper molars of the species of the Long-eared bats have rounded lingual margins and low protocones with the anterior and posterior cristas evenly curved and without cuspules. The lower molars are myotodont with a clear notch in the preprotocrista. The talonid of the third lower molar is narrow but long (Fig. 8.9). Because of their similarity and the fact that they are found in similar habitats, the alpine long-eared bat, (*P. macrobullaris*) was commonly taken for *P.auritus* Linnaeus, 1758. Both species are distributed in the Caucasus, but *P. macrobullaris* is poorly known, and since no differences between them have been described, either in the dentition or the skeleton, the fossils form Azokh are referred to as *P. auritus*/*P. macrobullaris*. Both of them are linked to forest habitats, though a certain degree of habitat partitioning seems to take place where both species occur, *P. macrobullaris* being more abundant at higher altitudes. *P. auritus* has a temperate humid pattern of distribution, rather common in central Europe, but rare in the Mediterranean. It forages in forest landscapes, gleaning soft bodied insects from the foliage. It forms small colonies during the summer, located mainly in tree holes. During the winter, it is generally solitary and can be found roosting in caves, underground sites as well as in trees.

Fig. 8.9 *Plecotus auritus/macrobullaris*. **a** Fragment of left maxilla with P^4M^1. **b**, **c** Right M_1. Scale: 1 mm

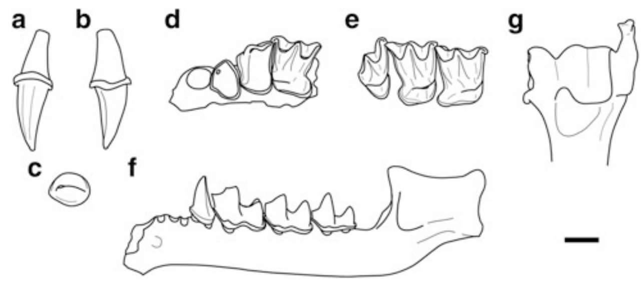

Fig. 8.10 *Miniopterus schreibersii*. **a**, **b**, **c** right upper canine. **d** fragment of left maxilla with $P^3P^4M^1$; **e** right $M^1M^2M^3$. **f** Left mandible with damage in the anterior region, broken angular process and $P^4M^1M^2M^3$ retained in alveoli. **g** Distal epiphysis of left humerus. Scale: 1 mm

Schreiber's Long-fingered Bat, *Miniopterus schreibersii* (Fig. 8.10) have been found in all units of Azokh 1 except Unit III, perhaps due to the sampling bias previously mentioned. It is the most common bat in Unit Vm, where it outnumbers the Lesser Mouse-eared Bat, *M. blythii,* which is the dominant bat species in the other units of Azokh 1. The bones and teeth of *M. schreibersii* are distinctive, even when broken. The humerus has a long, well-developed and flattened styloid process in its distal epiphysis; and the condylus and epicondylus are connected by a deep groove. The mandibles have a marked ventral bend at the connection between the body and the ramus; the coronoid and the articular process are of similar height; the lower third premolar has two roots, and the lower molars are nyctalodont, with narrow and high cusps. The upper canines are long and slender, with deep longitudinal grooves on both the lingual and labial side. The third and fourth upper premolars are large with a lingual talon, both teeth with three roots; the two first upper molars are rectangular in outline, the disto-lingual margin strong, but without a talon; the parastyle is strong and hook-like. Though previously considered the most widespread species of bat in the world, recent studies restrict the distribution of *M. schreibersii* to Northern Africa, European regions adjacent to the Mediterranean, Asia Minor, extending to the east as far as the Caucasus. The remaining distribution is now considered to correspond to several sibling species. Schreiber's Long-fingered Bat is found in a wide variety of landscapes in the Caucasus: steppes, semi-steppes and xerophytes zones, as well as in mountain and humid forests. These bats hunt in open arid landscapes and over woods, preferring mosaic habitats where there is variety and abundance of prey. They are strict cave dwellers, usually choosing cool and highly humid roosting places. Large colonies are common among these bats, sometimes even reaching numbers of several thousands of individuals, and occasionally these colonies are mixed with other species.

Four Rhinolophid species are recorded at Azokh 1. The bones and teeth of Horse-shoe bats have the following charaters: the humerus has a distal epiphysis with a relatively long and slender styloid process; the epitrochlea is wide; a deep and wide groove separates the trochlea from the condylus and epicondylus, which projects laterally; the upper canines are strong, with a narrow crown and a sinuous, well-developed cingulum; in labial view the crown and the root of the canine form an angle; the fourth upper premolar is slender, with a well-developed talon; the first and second upper molars have a talon without a hypocone; no additional cuspules are observed in the cristas of the protocone. The third upper molar is less reduced than in other bats, the premetacrista complete or only slightly reduced. The lower dentition is also slender, and the molars present a nyctalodont pattern (Fig. 8.11).

Two species, *R. ferrumequinum* and *R. mehelyi*, are constant elements in the assemblages of Azokh 1, though numbers of specimens never exceed 20% of the bat material identified in any of the different units. The first of these species, commonly known as the Greater Horse-shoe Bat, is present in all units except for Unit III. It has a wide geographic range in temperate arid environments, extending through the South Palaearctic region from Portugal to China, including all of the Caucasus. It forages in pastures, deciduous temperate woodland, Mediterranean and sub-mediterranean shrubland and woodland. It shelters typically in large caves and underground cavities, choosing warm sites for nursery colonies and cold sites for hibernation. Colonies consist of several dozens to a few hundred individuals, often mixed with other Horse-shoe bats, Schreiber's Bent-Winged bats or the Lesser Mouse-eared Bats.

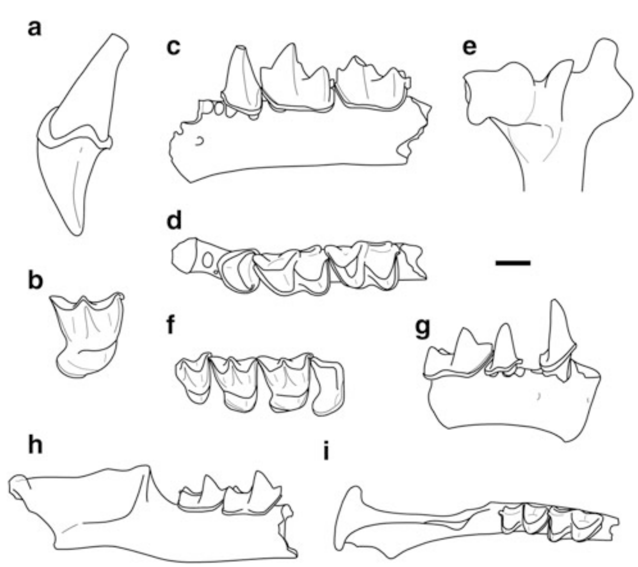

Fig. 8.11 *Rhinolophus ferrumequinum*. **a** Left upper canine. **b** Right M^1. **c**, **d** Fragment of left mandible with $P_4M_1M_2$. **e** Distal epiphysis of left humerus. *Rhinolophus mehelyi*. **f** Right $P^4M^1M^2M^3$. **g** Fragment of right mandible with canine, P_4M_1. **h**, **i** Fragment of right mandible with M_2M_3. Scale: 1 mm

The fossils of *R. mehelyi*, Mehely's Horse-shoe Bat, are similar to those of the Greater Horse-shoe Bat but distinctly smaller. They were collected in all the units of Azokh 1 except Unit II. The species has a Mediterranean distribution and forages mainly in dry shrubland and woodland, and in steppe landscapes. It is found roosting in caves and underground cavities, where it chooses colder conditions for hibernation and warmer sites for its summer roosts, but invariably in places with high humidity. Where Mehely's Horse-shoe Bat finds adequate conditions in the Caucasus region, it is found forming large colonies; this is just the case of Azokh Cave, well known in the Caucasus for sheltering the largest colonies of *R. mehelyi* in the region (Rakhmatulina 1989). Mehely's Horseshoe Bats roost in Azokh Cave the year-round; their nursery colonies are frequently mixed with other species, mainly other Horse-shoe bats, the Lesser Mouse-Eared Bat (*Myotis blythii*) and the Schreiber's Long-fingered Bat (*Miniopterus schreibersii*).

A few fossils found at Units Vm and Vu, agree with the morphology and size of a third rhinolophid species, *Rhinolophus euryale* Blasius, 1853, known as the Mediterranean Horse-shoe bat. Though practically distributed throughout the whole of Transcaucasia, it is considered a rare component of its bat fauna. It forages in Mediterranean and sub-Mediterranean shrubland and woodland. The geographic range of *R. euryale* is relatively wide, it covers forests in karst areas of North-East Africa, Southern Europe, the Caucasus, Middle East and Central Asia. It mainly roosts in caves, frequently sharing its roosts with other species. Nursery colonies comprising up to several dozens or rarely hundreds of individuals, are located in warm places.

Discussion

Caves are perhaps the most favourable environments for the preservation of fossil bats. The delicate bones of these mammals are rapidly destroyed as a result of weathering and other processes, and they are rarely found as fossils in localities even where other small vertebrates may be abundant. Additionally, since predation on bats is opportunistic, their remains are equally rare in fossil assemblages caused by predatory activity. For this reason, it is generally assumed that bones of bats preserved in cave fossil localities belong to animals that died within the cave. In caves where conditions are suitable, bats are common inhabitants, sometimes in extremely high numbers, and natural death occasionally overcomes individuals while roosting. In this case, the possibilities that their bones may be preserved are much higher. These bones usually belong to adult and sub-adult animals that died in winter during hibernation (Kowalski 1995; Zahn et al. 2007); during the summer, the floors of the caves is covered by guano in which bone remains become totally dissolved. However, opportunistic predation on bats cannot be totally excluded as the origin of a fossil bat assemblage, especially when dealing with a mixed assemblage that includes both cave bats and other non cave dwellers such as rodents or insectivores. The signs of digestion observed in some of the teeth and bones of *Pipistrellus pipistrellus*, *Miniopterus schreibersii* and *Myotis blythii* in Azokh 1 indicates a mixed origin for the assemblages collected at Units Vm and Vu. No digestion was observed in the fossils of the Horse-shoe bats, agreeing with observations that Rhinolophidae are the bats least represented in scats and pellets (Krzanowski 1973; Chaline 1974; Aulagnier 1989). In Unit V, the abundance of unworn teeth (stage “0” in Sevilla 1986), the presence of poorly ossified bones from very young specimens of several species, and the preservation of deciduous teeth of *Myotis blythii,* all indicate that young individuals were present in the cave and support the presence of breeding colonies in it.

Fossil bats are poor biostratigraphic indicators. Since their first appearance in the fossil record, only minor changes have taken place in their morphology. In Europe, extant genera such as *Rhinolophus* or *Hipposideros* are known as fossils since the Late Eocene (more than 40 Ma) and some of the recent European species are as old as four million years (Sigé and Legendre 1983). Bats are also considered poor paleoecological indicators, since adaptations such as hibernation, flight or echolocation makes them less restricted by local conditions that otherwise control the abundance and diversity of small mammals (Feldehamer et al. 2007). It is the case, however, that some bat species are restrictive concerning their choice of roosts or of foraging grounds. For instance, the presence of strictly tree roosting bats in a fossil assemblage indicates the presence of forested landscapes, sometimes even the type of forest (deciduous, mixed, mature, etc.). Other species have clear foraging habitat preferences, hunting their prey over open landscapes, or by river banks, etc. This too can be used to infer past environments. Additionally, the recent patterns of distribution of a species can also indicate the degree of tolerance to certain environmental parameters; thus, “Mediterranean” species are restricted in their distribution to areas with short and warm winters, whereas “boreal” species have more northern distributions where the climate is cooler. Occasionally a species may be found in a fossil assemblage located beyond its recent range of distribution; this might indicate either different environmental conditions in the past, or the reduction of a previously wider range of distribution due to landscape degradation.

The density and diversity of bats roosting in a particular cave depends mainly on both temperature and humidity values within the cavity. However, the surrounding landscapes must provide adequate hunting places, and this also influences in the presence or absence of bats in a cave. Within small caves changes in temperatures and humidity may take place in response to changes in the weather and season, and where this is the case bat communities are more unstable. Contrary to this, larger caves such as Azokh Cave, shelter more stable bat communities and the long-term changes in the bats have more to do with changes outside the cave, mainly in the characteristics of the surrounding habitats used as foraging grounds.

Fossil localities with deposits in which bat fossils are well represented may be analysed in these terms to reconstruct past environments. Changes in bat abundance and composition along the fossil sequence may be used to infer past environmental changes in a similar way as rodents and insectivores are used for this purpose. Moreover, since human presence in a cave interferes with cave-roosting bats, having an influence on the communities occupying the cave regularly, intensity of human use of a cave may also be inferred from its consequences on the fossil bat assemblage (Postawa 2004; Rossina 2006; Rossina et al. 2006).

Species richness in the Caucasus is strongly linked to vegetation and availability of roosts (Rakhmatulina 1998). The richest habitats in bat species are the mountain steppes, closely followed by mountain forest habitats. The lowest values are observed in mountain grasslands, due to harder climatic conditions and the fewer available roosts in these habitats. The Karabagh uplands, where Azokh Cave is located, is characterised by arid landscapes; the development of karsts provide abundant and varied roosts that favour an important diversity of bats. Ten species are common or numerous in this part of the Caucasus, including five *Rhinolophus* species, *Myotis blythii*, *Miniopterus schreibersii*, *Pipistrellus pipistrellus*, *P. kuhlii* and *Eptesicus serotinus*. Additionally another 13 less common species are also to be found here. Eight of the ten cave-dwelling species distributed in the region have been identified in the fossil assemblages from Azokh 1: the exceptions are *R. blasii* and *R. hipposideros* (Table 8.2). The possible explanation for their absence in Azokh 1 is that these two species are both rare in the region and do not group in large colonies. (However, we have a few fossils of the latter species in Azokh 5). Occasional cave-dwellers are also represented in the material.

According to the information obtained from the bat assemblages preserved at Units I to V, a paleoecological interpretation has been carried out for each bed (Figs. 8.12 and 8.13).

Table 8.2 Roosts and faunal status of the bats in the Lesser Caucasus at the present time compared with the species recorded in Azokh 1. Roost preferences follow Rakhmatulina (1995b); Faunal status is extracted from the National Reports of Armenia (2006): numerous (++); common (+); rare (−)

Choice of roosts and status of the bat species of Azokh 1						
Bat species in the Lesser Caucasus	Caves, underground spaces	Rock fissures	Buildings or other human constructions	Trees	Faunal status	Recorded in Azokh 1
Rhinolophus ferrumequinum	+		+		+	+
Rhinolophus mehelyi	+				−	+
Rhinolophus euryale	+				−	+
Rhinolophus blasii	+				−	
Rhinolophus hipposideros	+		+		−	
Myotis blythii	+	+	+		+	+
Myotis nattereri/schaubi		+	+		−	+
Myotis mystacinus/aurascens	+		+		−	+
Plecotus auritus/macrobullaris	+	+	+		+	+
Barbastella barbastellus		+	+		−	+
Nyctalus noctula			+	+	−	
Nyctalus leisleri				+	++	
Pipistrellus pipistrellus		+	+	+	+	+
Pipistrellus kuhlii			+		+	
Hypsugo savii		+	+		−	
Eptesicus serotinus			+	+	−	
Miniopterus schreibersii	+				−	+
Tadarida teniotis		+			−	

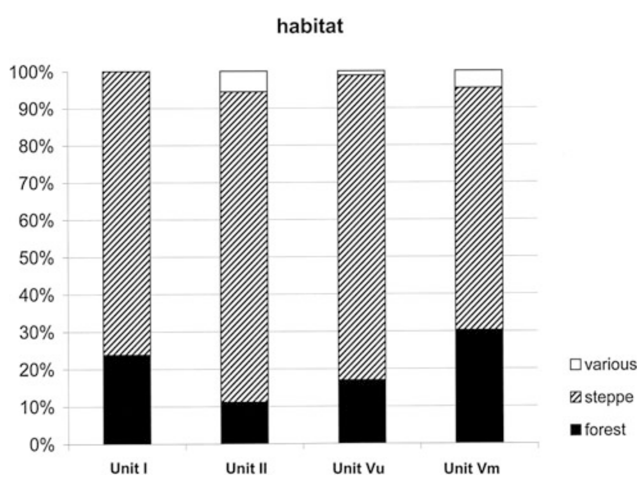

Fig. 8.12 Variation in the proportion of bat species in Azokh 1 grouped according to foraging preferences in different landscapes

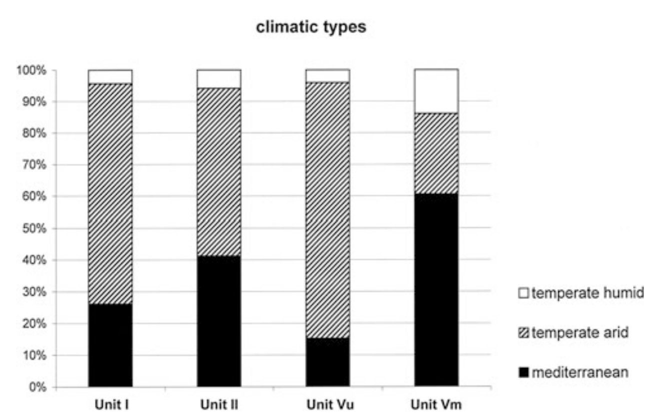

Fig. 8.13 Variation in the proportion of bat species in Azokh 1 grouped according to climatic type (after Horacek et al. 2000)

- Unit Vm is characterised by the presence of six occasional species, all of them frequently foraging in forest areas. This is the only unit where *M. schreibersii* outnumbers *M. blythii* both in number of fossils and in MNI. A dominance of Mediterranean species is observed; this unit has the highest representation of temperate humid species in the series.
- Unit Vu is the richest both in number of bat remains and species of the whole sequence of Azokh 1. The assemblage has a strong temperate arid character, as interpreted from the high predominance of *M. blythii* and the increase in the representation of the species of the genus *Rhinolophus*. A greater extent of open-steppe habitat seems most probable, with the occasional presence of trees.

Warmer temperatures and more arid conditions agree with these changes. It is also the case that this unit has by far the greatest number of small mammals (Parfitt 2016).

- Unit III can be considered practically sterile in bat fossils. The restricted area of excavation and heavily cemented sediment (see methods) might influence such a reduced record. Rodents (Parfitt 2016), for instance, also have a lower species representation at Unit III, but amphibians (Blain 2016), do not. Only the persistence in the cave of *R. mehelyi* and *M. blythii* can be ascertained. This lack of material makes an interpretation difficult, and it might hide a change in the bat community due to an environmental change or to a more permanent presence of humans in the cave.
- Unit II has slightly more bat fossils compared to Unit III. The upper part of this unit is practically sterile due to the influence of guano; this might indicate the settlement of large summer colonies of bats in the cave. The sediment is acidic because of the guano accumulation and this destroys the bones and the evidence of the species that formed these colonies. Nevertheless, the few fossil remains show the presence of three of the four constant species, with *R. mehelyi* missing. On the other hand, the pond bat, *M. dasycneme,* is present as the single occasional species of this unit. The Caucasus is well beyond the recent range of distribution of the pond bat, which has a northern distribution, and the presence of this species might be considered as indicating colder climatic conditions. The absence of *R. mehelyi,* of strict mediterranean distribution, could support this interpretation.
- Unit I has a "modern" sample of the recent community of bats roosting permanently or occasionally in the cave. The four constant species are represented in proportions that are comparable to their present abundance in the cave; two of the three additional species found at this unit are common in the region, and the third (*M. mystacinus*) is considered rare.

Since the four constant species (*M. blythii*, *R. ferrumequinum*, *R. mehelyi* and *M. schreibersii*) seem to be relatively independent of the environmental conditions, the variations in habitat were interpreted focusing attention mainly on the changes observed in the occasional species representation within each assemblage. Figures 8.12 and 8.13 show these variations based on MNI values; the species are grouped according to foraging landscape preferences and climatic type, and the variations in their relative proportions were used as the basis to interpret changes in the environment from one unit to another.

Thus, a picture of a changing landscape may be drawn from the bat fossil assemblages of Azokh 1. During the late middle Pleistocene, though open steppe habitats were common in the surroundings of the cave, a more "Mediterranean" character is inferred, with significant presence of trees and shrubs, probably favoured by a combination of slightly less arid conditions and lower temperatures. During the formation of the upper part of Unit V, these conditions changed towards an increase in open habitats with steppe vegetation, probably accompanied by an increase in temperatures favouring the presence of a higher diversity of species. The changes that might have taken place during the formation of Unit III are hidden because of the few available specimens; however a real decrease in bat abundance may have occurred due to a more intensive occupation of the cave by humans, as indicated by other remains preserved in this unit and perhaps a change in environmental conditions. The slight increase in bat representation in Unit II shows low values of diversity and hints at change towards colder conditions than at Unit V. Finally, environmental conditions similar to those of today are inferred from the assemblage preserved in Unit I.

Conclusions

1. The bat fossils preserved in the Pleistocene and Holocene sediments in Azokh Cave provide good evidence of a long-term occupation of the cave by bats for at least the last 300 kyr.
2. No major change is observed in the main components of the bat communities established in the cave during this time; *Myotis blythii*, *Miniopterus schreibersii*, *Rhinolophus mehelyi* and *Rhinolophus ferrumequinum* all occur through the sequence of Azokh 1, and are represented in all the units that contained a significant number of bat fossils. These four species constitute the main elements of the bat community presently roosting in Azokh Cave.
3. There is evidence in the lowermost units that the Lesser Mouse-eared bat (*Myotis blythii*) both wintered and bred in Azokh 1. At present, the colonies of this species move to another cave during the winter.
4. Variations in the abundance of fossil species and in the relative proportions of the species represented at each unit in Azokh 1 may be linked to changes in the vegetation in the area surrounding the cave, and more particularly to the degree of forest development.
5. There is no evidence of human occupation of the cave having a significant influence on the bat communities, except perhaps in Unit III, where practically no bat fossils are preserved.
6. The bat assemblages represented at Azokh 1 indicate that an open-ground landscape with steppe vegetation

prevailed in the region since the late middle Pleistocene. Slightly less arid conditions, favouring greater development of trees in the area might explain the higher species richness observed at the time of the Unit V faunas.

7. A shift towards a treeless, arid and cold environment could have taken place during the formation of Units III and II, slowly recovering towards more favourable conditions up through Unit II, when large amounts of bat guano accumulated.
8. The Holocene assemblage of Unit I indicates a situation similar to the present, in which mountain steppe species are well represented and dominating in the community of bats, accompanied by a few occasional species.

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