Historical Biology
Publication details, including instructions for authors and subscription information:
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To cite this Article Stoetzel, E. , Bailon, S. , Nespoulet, R. , El Hajraoui, M.A. and Denys, C.(2010) 'Pleistocene and holocene small vertebrates of El Harhoura 2 cave (Rabat-Témara, Morocco): an annotated preliminary taxonomic list', Historical Biology, 22: 1, 303 — 319, First published on: 29 March 2010 (iFirst)

To link to this Article: DOI: 10.1080/08912960903461288

URL: http://dx.doi.org/10.1080/08912960903461288

Historical Biology
Vol. 22, Nos. 1–3, March–June–September 2010, 303–319

Pleistocene and holocene small vertebrates of El Harhoura 2 cave (Rabat–Témara, Morocco): an annotated preliminary taxonomic list

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(*Received 29 August 2009; final version received 3 November 2009*)

Small vertebrates found in archaeological context can provide important information on the evolution of biodiversity and paleoenvironments of a precise geographical region and sometimes on a large interval of time. However, very few studies are specifically dedicated to small fossil vertebrates in north Africa, especially for the end of the Quaternary period. The Late Pleistocene to Middle Holocene succession of El Harhoura 2 cave, situated in the region of Témara (Morocco), has revealed an exceptional richness of small vertebrates' remains, as well as in bones abundance than in species diversity (rodents, shrews, hedgehogs, amphibians, chelonians and squamates). We present here an annotated preliminary taxonomic list of this material.

Keywords: small mammals; amphibians; reptiles; taxonomy; Morocco; Late Quaternary

Introduction

Morocco is an interesting geographical zone for understanding the evolution of north African biodiversity during the Quaternary. Indeed, this country is located at the extreme north west of the African continent, opening both on the Atlantic Ocean and on the Mediterranean Sea, and in the close vicinity of Europe and the Saharan barrier. Morocco is probably the most studied of the countries of north Africa, including the most numerous and the longest sequence of fossil sites. Morocco has also a major interest in understanding the prehistory of north Africa, the presence of *Homo sapiens* in this country being certified since 160,000 years (Smith et al. 2007).

The region of Témara is located in the north Atlantic part of Morocco and belongs to the coastal Meseta (Figure 1) characterised by a succession of paleodunes, oriented parallel to the coast and consist mainly of sandstone. The caves of the region were formed during the Isotopic Stage 6, resulting from sea erosion in these consolidated paleodunes, and they were occupied by prehistoric populations during the Late Pleistocene and the Holocene (Texier et al. 1985; Niftah et al. 2005; Nespoulet et al. 2008). The oldest human remains attributable to *H. sapiens* in an Aterian[1] archaeological context in Morocco have been found in this region, thus, these sites are of considerable importance for understanding the installation and evolution of the anatomically modern hominids in this region (Debénath 2000; Debénath and El Hajraoui 2007; Nespoulet et al. 2008, 2009).

The El Harhoura 2 site belongs to the Témara caves complex. Discovered in 1977, and after preliminary excavations in 1996, El Harhoura 2 is being excavated since 2001 by the *Mission archéologique El Harhoura-Témara* (French–Moroccan team directed by Nespoulet and El Hajraoui). The entrance of the cave faces west, towards the ocean, around 300 m away from the current shoreline and 18.64 m above the sea level. Deposits of El Harhoura 2 have yielded abundant archaeological material attributed to Middle Paleolithic, Upper Paleolithic and Neolithic cultures (Nespoulet et al. 2008, 2009). The stratigraphy has currently 11 levels (Figure 2), numbered from top to bottom: level 1, Early Neolithic (Cardial, 5800 BP); level 2, Upper Paleolithic (Iberomaurusian, 10–20 ky) and levels 3–11, Middle Paleolithic (Aterian/Mousterian, 20–120 ky). The bedrock was not yet attained, and OSL, ESR and thermoluminescence datings are in progress to refine the chronological context (Jacobs et al. forthcoming; Janati et al. forthcoming).

The El Harhoura 2 cave has also yielded an abundant and diversified microfaunal material, which is currently studied within the framework of a PhD thesis by one of us (Stoetzel). Few north African small vertebrates are still studied in archaeological contexts, especially for the end of the Quaternary period. This is the first time that such a

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ISSN 0891-2963 print/ISSN 1029-2381 online

DOI: 10.1080/08912960903461288
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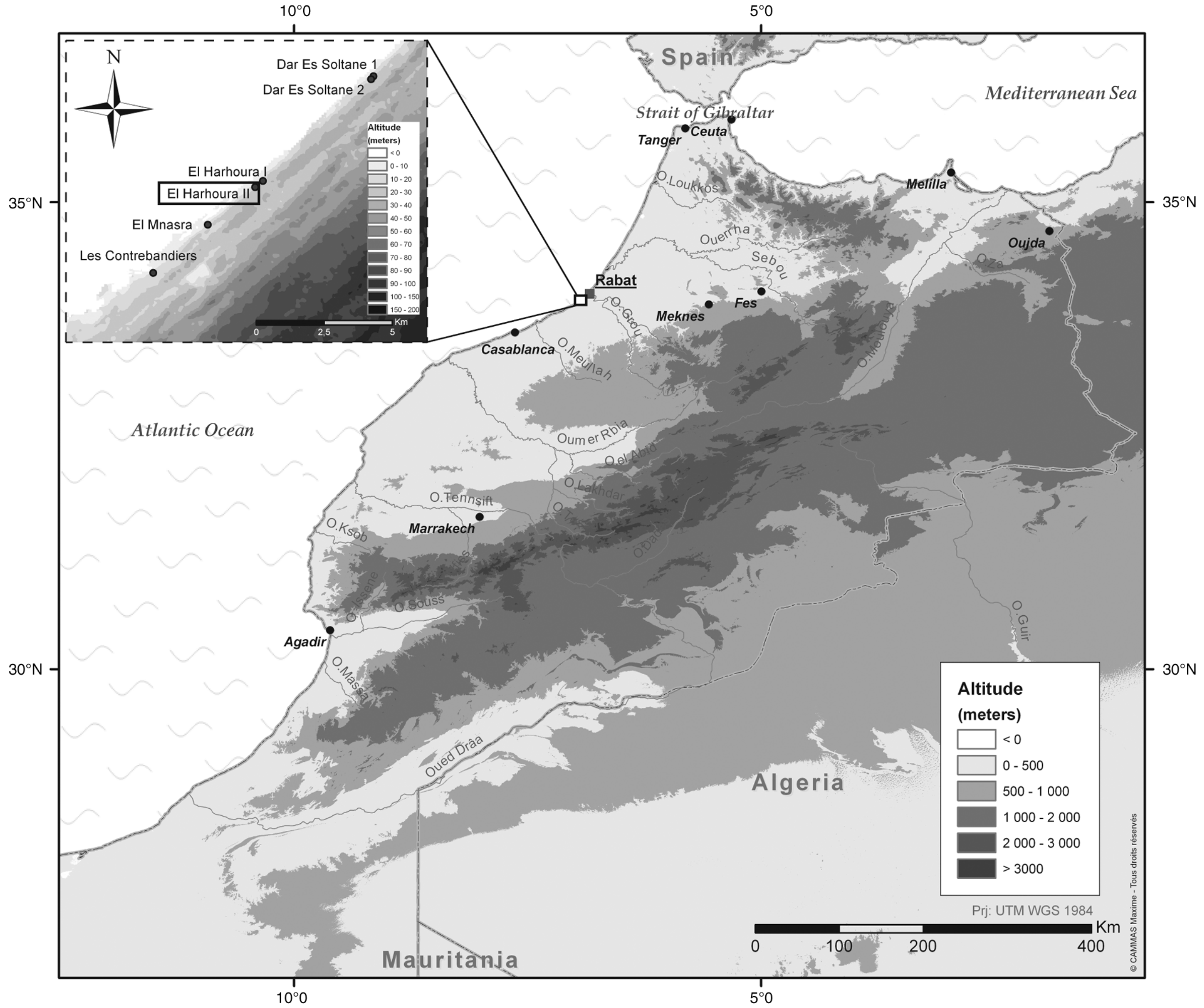

Figure 1. Location of the region of Témara and representation of the main archaeological sites.

study, considering at the same time small mammals, amphibians and reptiles, with a systematic, taphonomic and paleoecological approach is realised for a Maghrebian site. Thus, the study of the microvertebrates from El Harhoura 2 can provide important information on the evolution of biodiversity and paleoenvironments of Morocco, particularly in the absence of palynological data. The taphonomic analysis brought information on the origin of the small vertebrate accumulations (Stoetzel et al. forthcoming). No transport by water seems to have occurred, thus, deposits perturbations due to water action should be low and faunal remains were not imported from another place. In addition, some information (like traces of digestion) indicates that small vertebrate assemblages of El Harhoura 2 result mainly from predators' accumulations, which vary in the different levels (owls, diurnal raptors and/or small carnivores). Amphibians and reptiles could also have frequented the site and died naturally inside the cave. The bias of predation seems to be weak and allows the reliability of the paleocological reconstructions. Several paleoenvironmental variations seem to have occurred during Late Pleistocene and Holocene, with an alternation of dry and wet periods (Stoetzel et al. 2007, 2008, forthcoming).

This article presents an annotated taxonomic list of the small vertebrates of El Harhoura 2, with some remarks on paleobiodiversity and paleobiogeographic implications.

Material and methods

We consider here terrestrial small vertebrate species belonging to mammals, amphibians and reptiles. The studied material comes from levels 1 (Neolithic, 5800 BP) to 8 (Middle Paleolithic, dating in progress) of El Harhoura 2, from the entrance of the cave. During excavations, every bucket of sediment has been precisely located in space before removal. Then sediments were washed on two superposed sieves of 3 and 1 mm mesh,

Figure 2. Stratigraphy of El Harhoura 2 such as known in 2009 (Nespoulet and El Hajraoui 2008). Level 1, Neolithic, 5800 BP; level 2, Upper Paleolithic (Iberomaurusian); levels 3–11, Middle Paleolithic (Aterian). The Bedrock, formed at the end of the Isotopic stage 6, is not yet attained.

and after drying, bones were sorted manually and then investigated under microscope.

In front of the large quantity of material (approximately 1800 determinable elements per square meter of sediment in level 1 to more than 250,000 in levels 7 and 8), several samples were chosen randomly for the present study in a proportional quantity to the excavated volume and the bone concentration. Small vertebrate identifiable remains taken into account represent more than 35,200 elements: 30,818 attributed to small mammals, 496 to amphibians and 3945 to reptiles (Table 1).

The taxonomic identifications have been made by comparison with Maghrebian specimens from the modern collections of rodents, amphibians and reptiles of the *Museum National d'Histoire Naturelle* (MNHN) of Paris, with several Moroccan *Mus* from the collection of the *Institut des Sciences de l'Evolution* of Montpellier, and with some specimens trapped in 2007 in Morocco in collaboration with the *Institut Scientifique* of Rabat. We also used identification keys found in the literature [especially Jaeger (1975), Darviche (1978), Chaline and Mein (1979), Orsini (1982), Poitevin (1984), Aulagnier and Thévenot (1986), Poitevin et al. (1986), Tong (1989) and Barreau et al. (1991) for small mammals; Szyndlar (1984), Bailon (1991, 1999, 2000), Ould Sabar and Michel (1996), Hossini (2001) and Bailon and Aouraghe (2002) for herpetofauna]. Concerning small mammals, determinations were based on dental morphology [cusps nomenclature after Michaux (1971) and Tong (1989)], and the classification follows Wilson and Reeder (2005). This implies some nomenclatural changes for some Gerbillinae such as notably the use of *Dipodillus* instead of *Gerbillus* for the species *campestris*. Consequently, for the fossil material, we decided to use the terminology '*Dipodillus*/*Gerbillus*' in order to make correspondences between the 'new' denomination *Dipodillus* and the

Table 1. Taxonomic list of the small vertebrates of El Harhoura 2, in number of remains.

Class	Order	Species	L.1	L.2	L.3	L.4	L.5	L.6	L.7	L.8
Mammalia	Rodentia	*Apodemus sylvaticus*	7							
		Lemniscomys barbarus	10							
		Mus cf. *spretus*	129	72	95	70	122	119	302	301
		Dipodillus campestris	89	6	4	7	15	17	4	17
		Meriones cf. *shawii*	76	264	325	214	585	785	923	731
		Jaculus cf. *orientalis*					2		1	
		Eliomys sp.					2			3
		Indet. (cranial + post-cranial elements)	1255	1437	1835	1183	2683	4117	5609	5599
	Soricomorpha	*Crocidura* spp. (*C. whitaker*/*C. russula*)	70	154	151	78	171	303	430	429
	Erina ceomorpha	*Atelerix algirus*	7	11	6	9	9	5		
	Chiroptera	Indet.	X	X	X	X	X	X	X	X
Amphibia	Urodela	*Pleurodeles* sp.	1		4	2	5	5		3
	Anura	*Bufo bufo*	2		6	4		9		2
		Bufo mauritanicus	38		7	6	25	17	19	8
		Bufo indet.	26	12	15	12	35	25	13	9
		Hyla meridionalis	5	4	9	3	4	4		1
		Discoglossus pictus	8		3	1			1	
		Pelobates cf. *varaldii*					1			1
		Anura indet.	44	15	24	20	7	18	9	1
Reptilia	Chelonia	*Mauremys leprosa*	3							
		Testudo graeca	1							
		Indet. (cf. *Testudo*)	3		1	1	4		1	13
	Amphisbaenia	*Trogonophis wiegmanni*	64	16	23	12	46	80	31	14
	Sauria	*Ophisaurus koellikeri*	1							
		Gekkonidae	9		2	1	1	2	1	
		Lacertidae (*Acanthodactylus*, other genera)	16	38	95	35	95	128	69	14
		Scincidae (*Eumeces algeriensis*, *Chalcides* spp.)	94	11	40	47	74	187	100	21
		Sauria indet.	35	40	109	34	233	561	449	69
	Serpentes	*Coronella gorondica*	7	14	18	11	53	76	5	6
		Malpolon monspessulanus	53	16	30	30	89	64	4	7
		Natrix maura	2	2	4	2	12	4		2
		Macrovipera mauritanica	3							
		Colubridae indet.	43	11	29	22	40	49	6	15
		Serpentes indet.	158	15	23	11	40	28	6	11
Birds	Indet.	Indet.	X	X	X	X	X	X	X	X
Fishes	Indet.	Indet.	X	X	X	X	X		X	

Notes: Non terrestrial species (chiroptera, birds, fishes) were not included to this study, and their presence is only represented by X; L., archaeological levels; Indet., indeterminated species; in grey, absence.

previous denomination *Gerbillus* that we find in the literature for the other fossil sites. For amphibians and reptiles, determinations were based on a large variety of skeletal elements, and we used the classification from Bons and Geniez (1996) and Schleich et al. (1996). Whenever possible, we compare with morphological and/or biometric data from the literature concerning other Quaternary Maghrebian sites:

- Algeria: El Melah (Early Pleistocene; Tong 1989), Oued Kremia (Early Pleistocene; Tong 1989), Aïn Mefta (Middle Pleistocene; Jaeger 1975; Tong 1989), Tighenif (Middle Pleistocene; Jaeger 1969, 1975; Tong 1986, 1989);
- Morocco: Irhoud Ocre (Early Pleistocene; Jaeger 1975; Tong 1989; Hossini 2001), Ahl-al-Oughlam (Plio–Pleistocene; Geraads 1995, 2006; Bailon 2000), Sidi Abdallah (Early–Middle Pleistocene; Jaeger 1975; Tong 1989), Irhoud Derbala Virage (Middle Pleistocene; Jaeger 1975; Tong 1989), Irhoud Lanz 3 (Middle Pleistocene; Jaeger 1975), Thomas 1 (Middle Pleistocene; Geraads 1980, 2002; Tong 1989), Oulad Hamida 1 (Middle Pleistocene; Geraads 1994, 2002), Salé (Middle Pleistocene; Jaeger 1975; Tong 1989), Aïn Bahya (Middle Pleistocene; Cheddadi 1986), Irhoud Neanderthal (Middle–Late Pleistocene; Jaeger 1975; Tong 1989; Amani and Geraads 1993, 1998), Sidi Abderrahmane 1 and 2 (Middle–Late Pleistocene; Jaeger 1975; Tong 1989), Oulad Hamida 2 (Late Pleistocene; Tong 1989; Raynal et al. 2008), Doukkala 2 (Late Pleistocene; Michel 1992; Ould Sabar and Michel 1996; Darviche et al. 2006), El Harhoura 1 (Late Pleistocene; Aouraghe and Abbassi 2002; Bailon and Aouraghe 2002).

Our aim was not to make an exhaustive list of all works made on Maghrebian microvertebrates, only references used for biometric and/or morphological comparisons or for occurrences of some taxa are cited here (however, an updated bibliographical synthesis is currently in preparation).

Specimens were examined through a binocular microscope (taxonomic identifications and taphonomic analysis). Measurements were performed on digitalised photographies with the use of picture analysers (Optimas® for *Mus* and TpsDig2® for the other species). Some rodent elements were photographed using a scanning electron microscope (JEOL JSM-840A) from the Service Commun de Microscopie Electronique du Laboratoire des Sciences de la Vie of the MNHN.

Results

At present, around 30 taxa have been identified for the whole levels of El Harhoura 2 (at least 10 small mammals, 6 amphibians and 13 reptiles; Table 1). Small mammals, especially rodents, are clearly the dominant group. We detail here by taxa the faunal list of El Harhoura 2.

Small mammals

The small mammals are represented by at least ten species including seven rodents, two Soricomorpha and one Erinaceomorpha. In number of remains (NR) as well as in minimum number of individuals (MNI), the most abundant small mammals are jirds (*Meriones*), followed by shrews (*Crocidura*) and mice (*Mus*; Figure 3). The other species represent less than 5% of the material. *Meriones shawii*, *Dipodillus campestris*, *Mus* cf. *spretus* and *Crocidura* spp. are present all along the stratigraphy. *Apodemus* and *Lemniscomys* are present only in the first level of El Harhoura 2, *Eliomys* in levels 5 and 8 and *Jaculus* in levels 5 and 7.

Among rodents, several remains of El Hahroura 2 were attributed to the striped grass mouse (*Lemniscomys barbarus*), thanks to the molar morphology. The M^1 is large, t9 is well individualised from t8, t7 is absent and t1 and t4 are not much shifted back. On the M_1, the anterior cusps tE–tF and tC–tD are fused, tE has approximately the same size compared to tF, tC and tD, there exists a small tma (median anterior cusp), and a c1. The scatterplot of $M^1/_1$ dimensions indicates they fit well within the range of variability of modern *L. barbarus* as well as the Irhoud

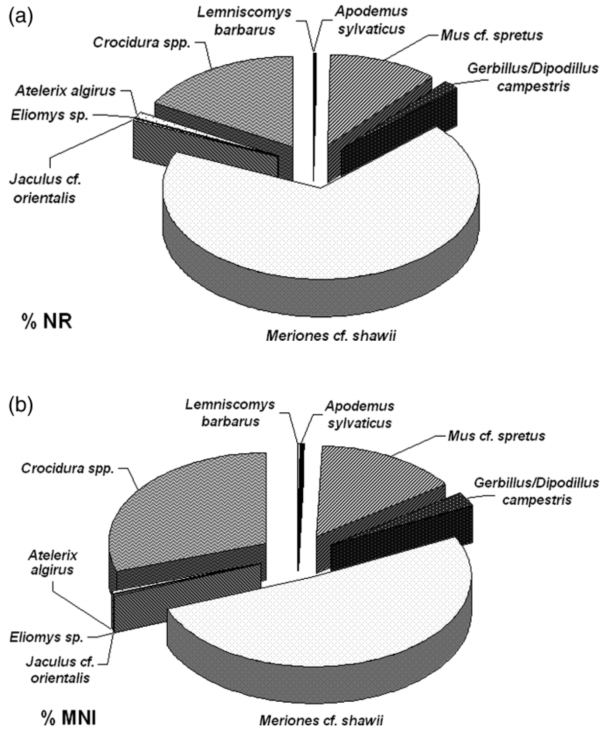

Figure 3. Relative proportion of the species of small mammals of El Harhoura 2 in percentage of total NR and of MNI.

Neanderthal and Lanz 3 specimens attributed to *L. barbarus* (Jaeger 1975; Figure 4). This species is also present in Holocene sites (Ez Zarka; Ouahbi et al. 2003) but without elaborating neither morphological description nor biometric data. Today, *L. barbarus* is the only representative of its genus in Morocco and has a recent tropical origin, having probably derived from the sub-Saharan forms around the Plio–Pleistocene boundary (Jaeger 1975; Carleton and Van der Straeten 1997).

The M_1 of El Hahroura 2 attributed to the wood mouse (*Apodemus sylvaticus*) in level 1 presents a morphology characteristic of this species: six well-fused cusps, the existence of a longitudinal link between the prelobe and the first lobe, a tma, a large labial cingular margin and a strong posterior cingulum. These teeth are well included in the size variability of modern Moroccan populations (Figure 5). No other biometric data on Maghrebian fossils are available for this species. Other species of *Apodemus* were discovered in Miocene sites (*A. jeanteti*, Aïn Guettara, Morocco, Brändy and Jaeger 1980; *A. gudrunae*, Argoub Kemellal 1, Algeria, Coiffait-Martin 1991), but it seems that the modern species *A. sylvaticus* came recently in Maghreb from Europe (through the Strait of Gibraltar or along the Mediterranean coast), probably during the Holocene (Jaeger 1975; Aulagnier 1991, 1992b; Dobson and Wright 2000; Libois et al. 2001; Michaux et al. 2003; Ouahbi et al. 2003).

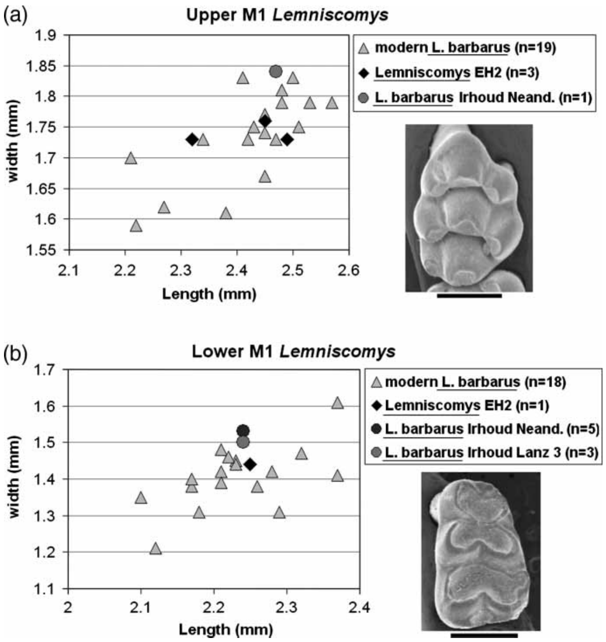

Figure 4. Measurements (length × width in mm) of upper and lower first molars of fossil and modern Maghrebian *Lemniscomys* (EH2, El Harhoura 2; Irhoud Neanderthal and Lanz 3, mean values from Jaeger 1975; modern *L. barbarus* come from Morocco and Algeria. Scale, 1 mm).

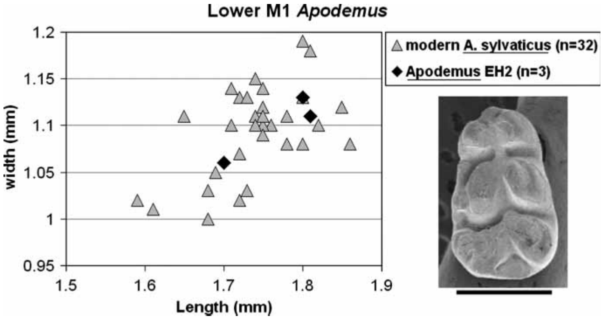

Figure 5. Measurements (length × width in mm) of upper and lower first molars of *Apodemus* (EH2, El Harhoura 2; modern *A. sylvaticus* come from Morocco. Scale, 1 mm).

Compared with measurements on other fossil mice, *Mus* from El Harhoura 2 are close to the '*Mus musculus*' and *M. spretus* from Middle–Late Pleistocene Maghrebian sites (Aïn Mefta, Jaeger 1975; Irhoud Neanderthal, Jaeger 1975; Salé, Jaeger 1975; Doukkala 2, Darviche et al. 2006; Figure 6). We must recall here that the previous fossil attributions to *M. musculus* were realised before the knowledge of the distinction between *Mus musculus domesticus* and *M. spretus*. Consequently, a revision of all fossils of this group is necessary to better understand *Mus* evolution in Maghreb. Today, two species of *Mus* are represented in north Africa (*M. spretus* and *M. m. domesticus*), and our specimens display a larger size (for all levels) compared with the two modern *Mus* species (Figures 6 and 7). In addition, all *Mus* specimens from El Harhoura 2 display a wide morphological variability, but they show in majority the clear pattern of *M. spretus* on the prelobe of the M_1. Indeed, the anterior part of the M_1 has a tetralobed form for *M. spretus* (tE well individualised), while it is trilobed for *M. musculus* (Darviche 1978; Darviche and Orsini 1982; Orsini 1982). In addition, some M^1 present supplementary anterior cingular margin, internal or external accessory cusps, and many M_1 present an external cingular margin with a c1, and sometimes present accessory cusplets on the lingual side. All these characters could be considered as primitive characters (Darviche et al. 2006). It is possible that *Mus* of El Harhoura 2 belong to a new species, close to the modern *M. spretus* and probably at the origin of this one. However, we provisionally retain the attribution to *M.* cf. *spretus* pending refined morphometric analyses of the El Harhoura 2 populations.

Numerous species of gerbils are today present in Morocco (Aulagnier and Thévenot 1986; Aulagnier et al. 2008). According to Tong (1989), remains of *Dipodillus*/*Gerbillus* of El Harhoura 2 correspond well to the modern *D. campestris*: on the M^1, the protocone is lightly shifted anteriorly and mesially compared to the paracone, and these two cusps are always linked by a short crest. Two other alternate and well-developed longitudinal crests

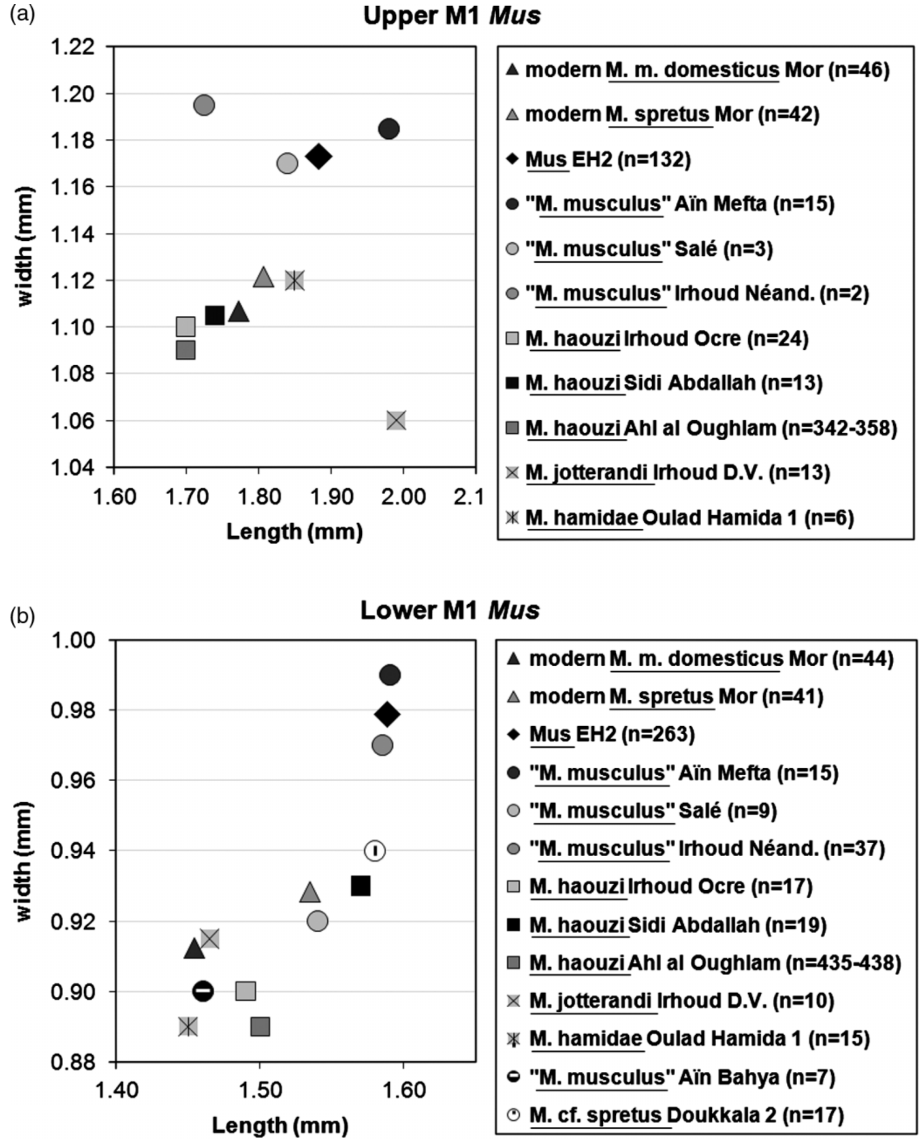

Figure 6. Comparison of mean size of upper and lower first molars of different fossil and modern *Mus* species (EH2, El Harhoura 2; Irhoud D.V., Irhoud Derbala Virage; Irhoud Neand., Irhoud Neanderthal; Mor, Morocco. Fossil data: Jaeger 1975; Cheddadi 1986; Geraads 1994, 2002; Darviche et al. 2006).

are seen between the anterocone–protocone and the paracone–metacone. On the M_1, the anterolophulide links the anteroconide to the protoconide with a labial or more median position, the protoconide and the metaconide are not well individualised, and the neolophide L links the protoconide to the hypoconide. Some M_1 show anterior or posterior cingulum, which represent primitive characters (Tong 1989). The specimens of El Harhoura 2 are in average smaller than fossil and modern Maghrebian *Dipodillus/Gerbillus campestris* (Figure 8). Their size is intermediate between the fossil species *G. minutus* and *G. jebileti*, but in a morphological point of view, there is no or few similitude (Tong 1989): *G. jebileti* is close to the group '*campestris*', but the M_1 is characterised by longitudinal crests much less developed than *D. campestris* and by an anterolophulide linking alternately the anteroconide and the metaconide (as it can be seen on modern *G. gerbillus* and *G. pyramidum/tarabuli*); on the M^1 and M_1 of *G. minutus*, the longitudinal crests are absent or very little developed, and the protocone and the paracone are isolated (*G. minutus* is close to the modern species *G. nanus* and *G. henleyi* by its small size and its morphology). Moreover, the El Harhoura 2 teeth globally fit within the size variability of those of modern *D. campestris* (Figure 9). Therefore, in conclusion, we can attribute the material of El Harhoura 2 to the species *D. campestris*, according to morphology and morphometry. There is no evidence of the presence of *D. maghrebi* at

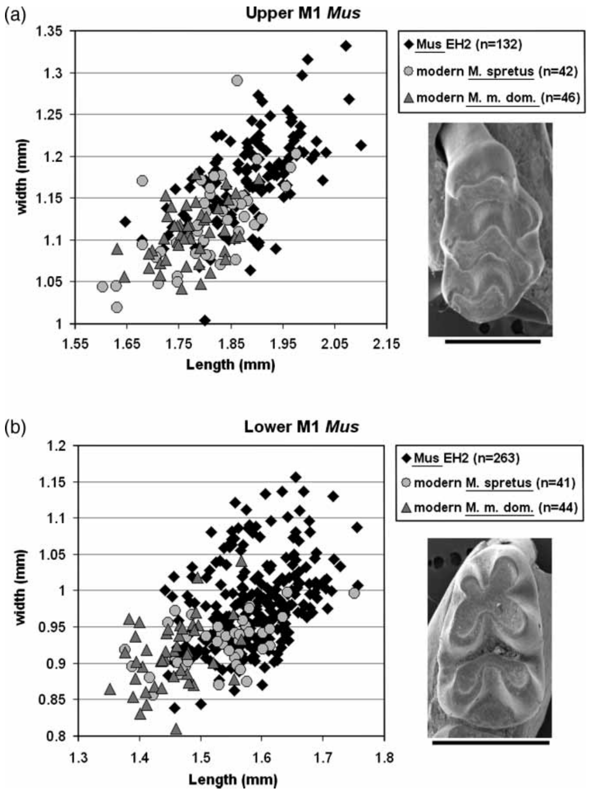

Figure 7. Measurements (length × width in mm) of upper and lower first molars of fossil and modern *Mus* (EH2, El Harhoura 2; modern *M. spretus* and *M. m. domesticus* come from Morocco. Scale: 1 mm).

El Harhoura 2 on the basis of the morphological criteria of Barreau et al. (1991) and Aulagnier et al. (1993).

Jirds (*Meriones*) are the most abundant taxa at El Harhoura 2. Today, four species of *Meriones* are present in Morocco: *M. shawii*, *M. grandis*, *M. crassus* and *M. libycus*. For a long time, *M. grandis* was considered as a sub-species of *M. shawii* (Aulagnier and Thévenot 1986), but *M. grandis* is now recognised as a species on the basis of external morphology/measurements and skull measurements (Pavlinov et al. 1990; Pavlinov 2000). However, their molar morphology and their respective geographic distribution are still little known. The scatterplot of $M^1/_1$ dimensions indicates that the *Meriones* of El Harhoura 2 are close to modern and fossil *M. shawii*, to modern *M. grandis* and to some fossil *M. maghrebianus*. The fossil species *Meriones maximus* appears clearly larger than the other species, while *M. crassus* and *M. libycus* are much smaller (Figures 10 and 11). From a morphological point of view, it is very difficult to distinguish *M. shawii* and *M. maghrebianus*, but the size can be discriminant (Tong 1989). *M. maghrebianus* presents a wide variability of size (including the modern *M. shawii*) due to the fact that this fossil species presents an increase in size through time, but on average *M. maghrebianus* is larger than fossil and modern *M. shawii*. In addition, according to Tong (1989), *M. maghrebianus* is known only in Early–Middle Pleistocene sites from Maghreb and is replaced by *M. shawii* from the end of the Middle Pleistocene until today. So, it is unlikely that our material belongs to *M. maghrebianus*, because if this species had subsisted during Late Pleistocene, measurements should be much larger than those observed at El Harhoura 2. We also noticed that in the El Harhoura 2 material, some M^1 present an anterior cingulum and some M_1 present a posterior cingulum and/or an anterior sinus. These characters could be interpreted as primitive characters (Tong 1989), but similar observations in similar proportions have been made on modern *M. shawii* material. In conclusion, in absence of precise criterion of differentiation between *M. shawii* and *M. grandis*, we decided to attribute the *Meriones* of El Harhoura 2 to the 'group' *Meriones* cf. *shawii*.

Two species of jerboa are present today in Maghreb: *Jaculus orientalis* and *J. jaculus*. They are difficult to distinguish based on dental morphology, but the only size is discriminant: *J. orientalis* is clearly larger than *J. jaculus*. The specimens of El Harhoura 2 are included within the size range of modern *J. orientalis* (Figure 12). The first occurrence of *Jaculus* in Maghreb was observed at Aïn Brimba (Early Pleistocene, Tunisia; Jaeger 1975; Mein and Pickford 1992) and this genus was also found in several Early and Middle Pleistocene sites of Morocco (Irhoud Ocre, Sidi Abdallah, Irhoud Derbala Virage; Jaeger 1975; Aulagnier 1992a). Today, this genus is absent in the north Atlantic coast of Morocco but was already mentioned in the Late Pleistocene site of Oulad Hamida 2 (near Casablanca; Raynal et al. 2008; Geraads et al. 2009); however, as far as we know, neither detailed description nor biometric data are yet available for Maghrebian fossil material.

The two modern north African species of dormice (*Eliomys munbyanus* and *E. melanurus*) are still poorly known, and due to the recent distinction of these two species from the European species *E. quercinus* (Wilson and Reeder 2005), there is still a lot of confusion under the name '*E. quercinus*' in museum collections. The modern specimens from MNHN Moroccan collection taken into account for this study have been checked carefully and, thanks to external morphology characters, have been attributed successfully to *E. munbyanus* (Moroccan specimens) and *E. melanurus* (Tunisian specimens). Remains of '*E. quercinus*' have been discovered at Chrafate (Late Pleistocene) and Ez Zarka (Holocene), but without elaborating neither morphological description nor biometric data (Ouahbi et al. 2003). The scatterplot of $M^1/_1$ dimensions (Figure 13) indicates that the fossil species *E. darelbeidae* is clearly larger than the others, the modern *E. melanurus* is on average larger than the modern *E. munbyanus*, and *Eliomys* of El Harhoura 2 are included in the size variability of

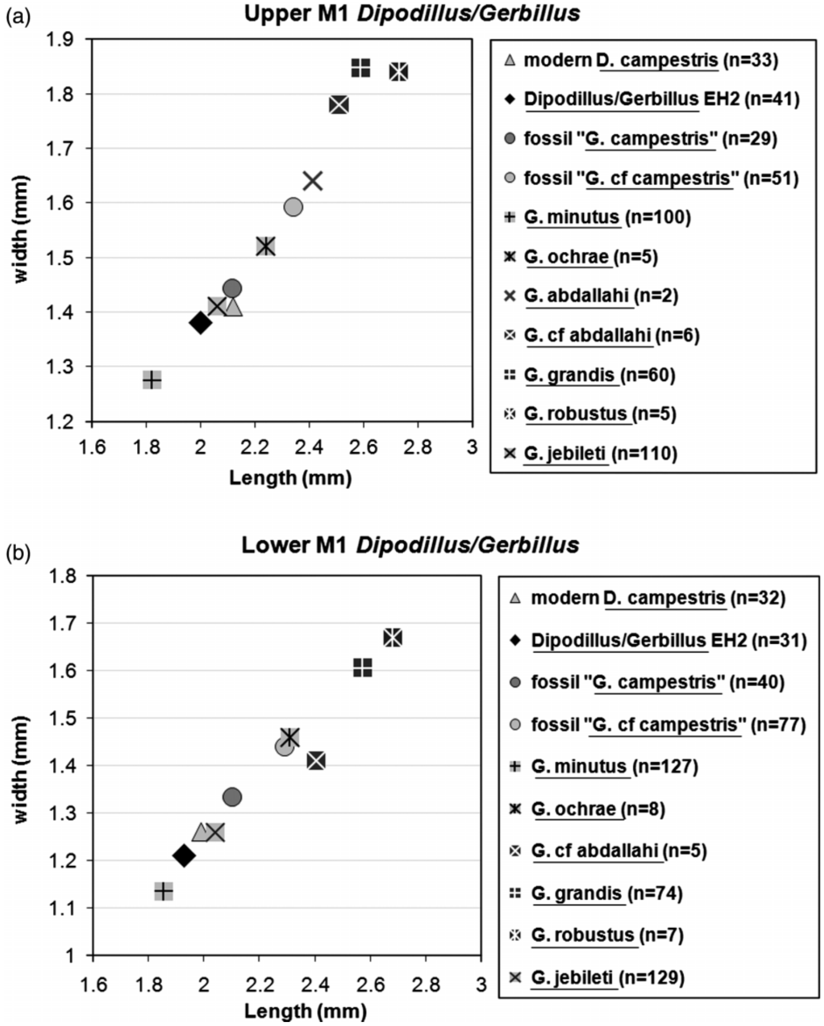

Figure 8. Comparison of mean size of upper and lower first molars of different fossil and modern *Dipodillus* and *Gerbillus* species (EH2, El Harhoura 2. Fossil data, Tong 1989).

modern *E. munbyanus* from Morocco. Thus, the teeth of El Harhoura 2 seem closer to the species *E. munbyanus*, but in the absence of taxonomically valid osteological collections and pending further morphometric analyses of a larger sample, we provisionally retain the attribution to *Eliomys* sp.

Erinaceidae of El Harhoura 2 were attributed to *Atelerix* cf. *algirus* on the basis of comparison with a modern skeleton from Morocco and literature data, but the material for comparison at our disposal for this genus was limited. According to paleontological data, *Erinaceidae* are present in Maghreb since the Miocene, represented by the genera *Protechinus* (Beni Mellal, Miocene, Morocco, Jaeger 1977; Aït Kandoula, Miocene, Morocco, Benammi 2006), *Schizogalerix* (Bou Hanifa 5, Amama 1 and 2, Miocene, Algeria, Coiffait-Martin 1991) and *Galerix* (Pataniak 6 and Oued Zra, Miocene, Morocco, Jaeger 1975, 1977; Amama 3, Pliocene, Algeria, Jaeger 1975). But these taxa do not seem to be the ancestors of the modern species. It is probably during a more recent migration that the first *Erinaceus*/*Atelerix* arrived in north Africa from the northeast (Plio–Pleistocene, Ahl-al-Oughlam, Geraads 1995), the modern species *A. algirus* being known in north Africa only since the Late Pleistocene (Gilman 1975; Kowalski and Rzebik-Kowalska 1991; Aulagnier 1992b).

North African *Soricidae* are also still poorly known from their systematics. Five species of *Crocidura* are today recognised in Morocco: *C. tarfayensis*, *C. lusitania*, *C. viaria*, *C. russula* and *C. whitakeri* (Hutterer 1986). Only the last two species are present today in the region of Témara (Aulagnier and Thévenot 1986; Aulagnier 1987). Considering mandibular/maxillary morphology (Poitevin 1984; Hutterer 1986; Poitevin et al. 1986; Aulagnier 1987), we found clearly at El Harhoura 2 the ‘*russula*’ and the ‘*whitakeri*’ morphotypes (Hutterer pers.

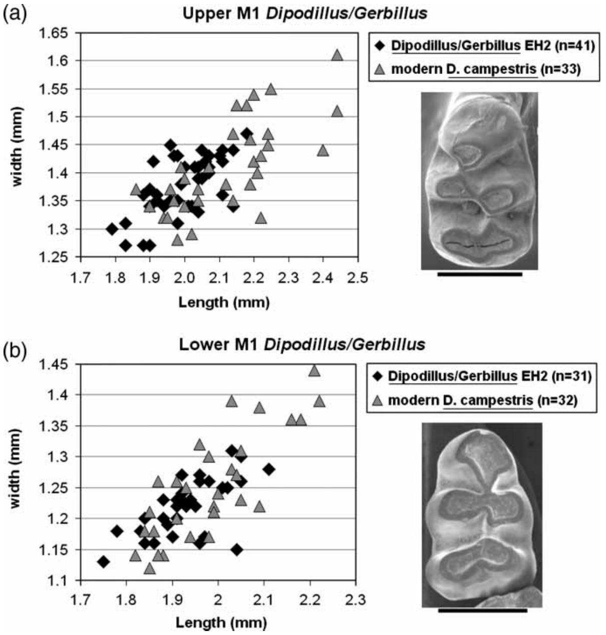

Figure 9. Measurements (length × width in mm) of upper and lower first molars of fossil and modern *Dipodillus*/*Gerbillus* (EH2, El Harhoura 2; modern *D. campestris* come from Morocco. Scale: 1 mm).

comm.), and also many 'intermediate' morphotypes that make identifications very difficult and could indicate a larger diversity among this genus at El Harhoura 2. The first occurrence of *Crocidura* in Morocco is attested in the Early Pleistocene site of Irhoud Ocre (*C. jaegeri*; Jaeger 1975; Rzebik-Kowalska 1988). For the Middle Pleistocene, three species are described at Irhoud Derbala Virage: *C. marocana* (probably the ancestor of *C. whitakeri*, and maybe of *C. tarfayensis* and *C. canariensis*), *C.* cf. *russula* and *C.* cf. *viaria* (Rzebik-Kowalska 1988). During Late Pleistocene, *C. russula* and *C. whitakeri* are definitively differentiated (Rzebik-Kowalska 1988). Recent studies assume that *Crocidura russula* would have a north African origin and would have recently populated Spain, France and nearby countries from the Maghreb during Late Pleistocene, maybe due to human dispersal across the Strait of Gibraltar (Cosson et al. 2005). Further measurements and morphometrical analyses are in progress on the El Harhoura 2 material to improve knowledge of fossil Crocidurinae diversity and evolution in Morocco, so we provisionally retain the identifications to *Crocidura* spp.

Amphibians

A preliminary study of the herpetofauna of level 1 of El Harhoura 2 (Stoetzel et al. 2008) revealed the presence of four Anura species (*Bufo mauritanicus*, *Bufo bufo*, *Hyla meridionalis* and *D. pictus*). A posterior study on new data on the other levels of El Harhoura 2 has shown the presence of two new taxa: *Pleurodeles* sp. and *Pelobates* cf. *varaldii*. Two genera of Urodela are today represented in Morocco, *Salamandra* and *Pleurodeles*, but they are well distinguishable by their vertebral morphology: vertebras of *Pleurodeles* are characterised by a weaker dorso-ventral flattening (the neural arc is arched), a neural spine more developed and an anterior zygapophyseal lamina (crest) most often connected with the ventral costal process or between the ventral and dorsal process (while for *Salamandra*, it is connected with the dorsal costal process). See Bailon (1999) and Rocek (1981) for osteology of *Pelobates*.

Thus, amphibians of El Harhoura 2 are represented by one species of Urodela and five species of Anura (Table 1). In percentage of NR and of MNI, toads (*Bufo* spp.) are always dominant, especially *B. mauritanicus*, followed by *H. meridionalis* (Figure 14). Only *B. mauritanicus* is found in the whole levels.

Amphibian remains found at El Harhoura 2 are very similar to those of modern corresponding species and also to fossil material found in several other Moroccan Plio–Pleistocene sites (Ahl-al-Oughlam, Bailon 2000; Oulad Hamida 1, Hossini 2001; Doukkala, Ould Sabar and Michel 1996; El Harhoura 1, Bailon and Aouraghe 2002). For some taxa (*Pleurodeles* sp., *Pelobates varaldii*), very few osteological references are available for comparison purposes. It is also interesting to note that the European common toad (*B. bufo*) is today absent in the region of Témara. No measurements have yet been made on amphibian remains of El Harhoura 2, but we have planned to do so.

Reptiles

The preliminary study of the material of level 1 (Stoetzel et al. 2008) and the posterior study of the other levels have shown the presence of at least 13 species of reptiles at El Harhoura 2 (two turtles, one Amphisbaenia, at least five lizards and five snakes; Table 1). For snakes, we only considered NR to calculate abundances, because the high number of vertebra per individual biases the MNI in this group (we obtained approximately the same result for all species at all levels). It is *Malpolon monspessulanus* that dominates the material, followed by *Coronella girondica* (Figure 15). Concerning Sauria, the most abundant taxa are Scincidae (*Eumeces algeriensis*, *Chalcides* spp.) and Lacertidae (*Acanthodactylus* sp., other indeterminate genera), which represent more than 90% of the material (%NR and %MNI; Figure 16).

Trogonophis, Lacertidae, Scincidae, *Coronella* and *Malpolon* are present all along the stratigraphy, whereas *Mauremys*, *Ophisaurus* and *Macrovipera* are only present in level 1.

Some other Moroccan Plio–Pleistocene sites have yielded some species we also found at El Harhoura 2 (Ahl-al-Oughlam, Bailon 2000; El Harhoura 1, Bailon and

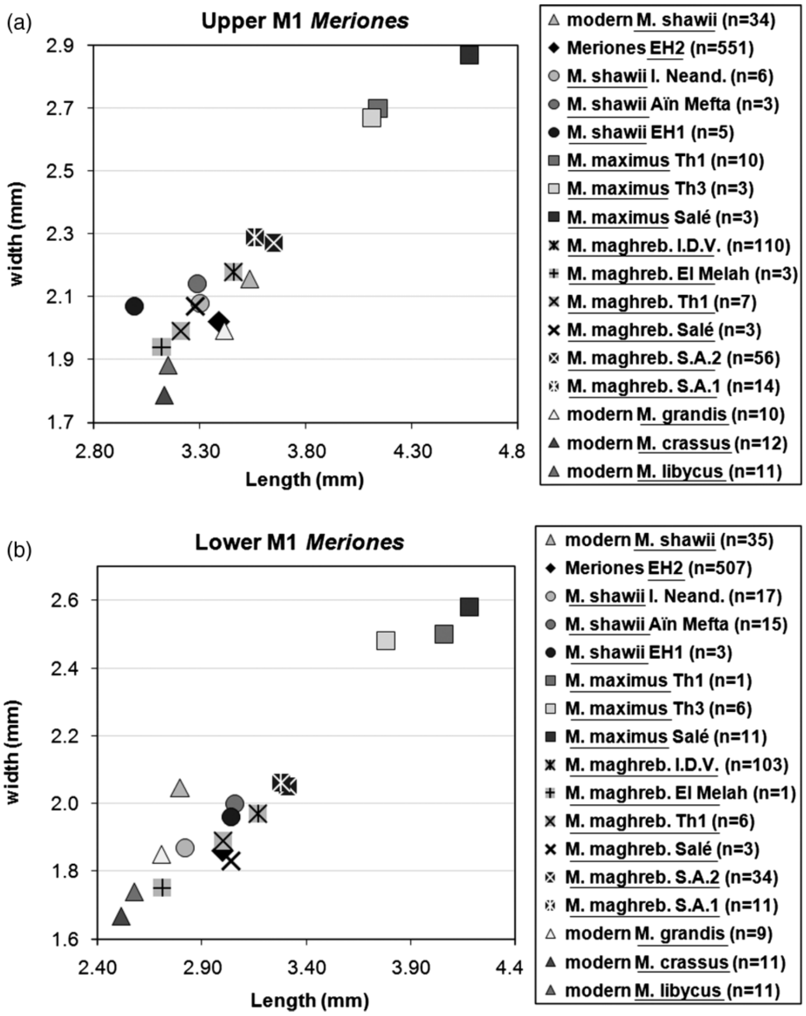

Figure 10. Comparison of mean size of upper and lower first molars of different fossil and modern *Meriones* species (M. maghreb, *Meriones maghrebianus*; EH2, El Harhoura 2; EH1, El Harhoura 1; Th1, Thomas 1; Th3, Thomas 3; S.A.1, Sidi Abderrahmane 1; S.A.2, Sidi Abderrahmane 2; I.D.V., Irhoud Derbala Virage; I. Neand., Irhoud Neanderthal. Fossil data: Tong 1989; Aouraghe and Abbassi 2002).

Aouraghe 2002). In addition, all reptile species found in the fossil assemblage of El Harhoura 2 are also present today in the region of Témara, and most of them have a morphology similar to their modern counterpart. However, in front of the high morphological similitude within some groups and the lack of complete osteological references and of biometrical data for north Africa, it is difficult to make exact identifications (especially for Sauria and 'Colubrinae'). No measurements have yet been made on reptile remains of El Harhoura 2, but we have planned to do so.

Discussion

Problems of taxonomy

The small mammals of El Harhoura 2 have a global morphology very close to modern species living in Morocco. However, some species present a morphological variability (*Mus*, *Dipodillus*/*Gerbillus*, *Meriones*, *Crocidura*) and there are 'primitive' characters on some molars of rodents, but most of these characters are not distinctive and sometimes occur in modern populations. Concerning shrews, at least two species were recognised (*C. whitakeri* and *C. russula*). But most of the material presents intermediate characters, which makes discrimination difficult, but which can be due to a recent speciation of these species in north Africa.

The upper and lower molars of *L. barbarus*, *A. sylvaticus*, *J.* cf. *orientalis* and *Eliomys* sp. are included in the range of size variability of modern Maghrebian populations. But some other rodent species present biometric differences between El Harhoura 2 specimens and the modern ones. *M.* cf. *spretus* are longer and larger at El Harhoura 2 than today. Jaeger (1975) noticed that the Middle and Late Pleistocene were characterised by large specimens of '*Mus musculus*', which he distinguished from '*M. m. spretus*'. Darviche et al. (2006) attributed the

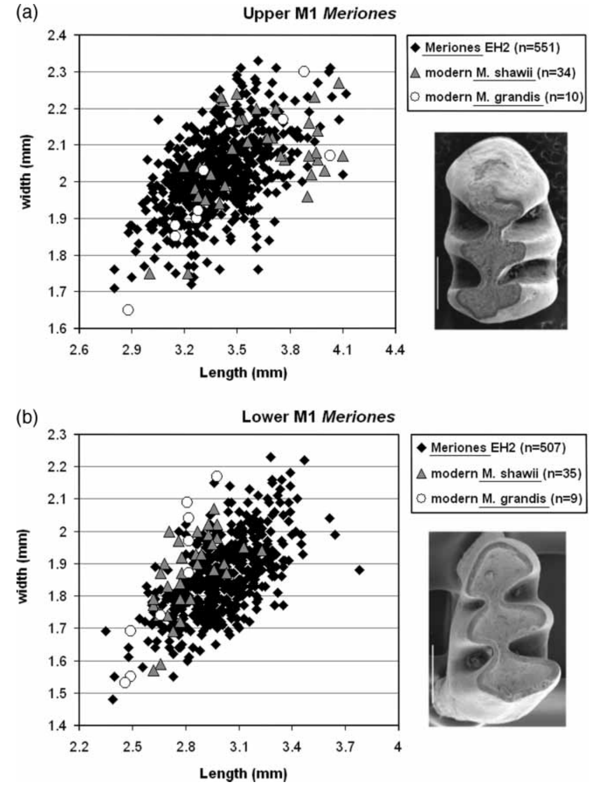

Figure 11. Measurements (length × width in mm) of upper and lower first molars of fossil and modern *Meriones* (EH2, El Harhoura 2; modern *M. shawii* and *M. grandis* come from Morocco. Scale: 1 mm).

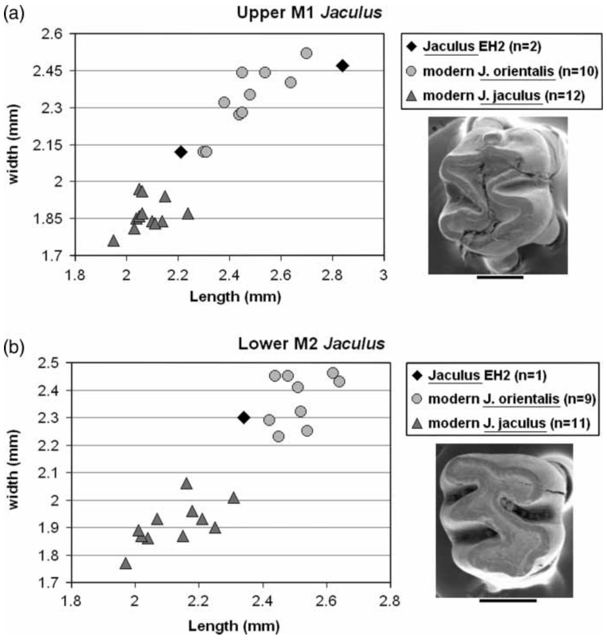

Figure 12. Measurements (length × width in mm) of upper and lower first molars of fossil and modern *Jaculus* (EH2, El Harhoura 2; modern *J. orientalis* and *J. jaculus* come from Morocco, Algeria and Tunisia. Scale: 1 mm).

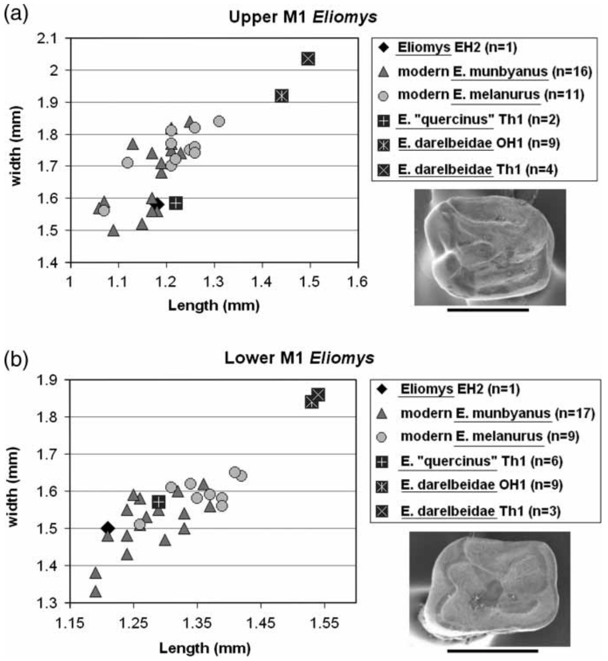

Figure 13. Measurements (length × width in mm) of upper and lower first molars of fossil and modern *Eliomys* [EH2, El Harhoura 2; OH1, Oulad Hamida 1, mean values from Geraads (1994, 2002); Th1, Thomas 1, mean values from Geraads (2002); modern *E.* '*quercinus*' cf. *munbyanus* come from Morocco. Scale: 1 mm].

material of Doukkala 2 (Late Pleistocene, Morocco) to a *M.* cf. *spretus* larger than modern *M. spretus*. All these observations are in agreement with our results. Concerning Gerbillinae, *Dipodillus*/*Gerbillus campestris* is smaller than today and *M. shawii* presents smaller M^1 but larger M_1 than modern populations. According to Tong (1989), *Dipodillus*/*Gerbillus campestris* is present in Maghreb since the Early Pleistocene (El Melah, Algeria) and presents a high morphological stability. Fossil specimens tend to be larger than modern ones, while we observed the opposite trend at El Harhoura 2. Among *Meriones*, Tong (1989) observed an increase in the molar size of *M. maghrebianus* through time, but no trend was put in evidence for *M. shawii*. If we consider Figure 10, we can see that all fossil specimens of *M. shawii* (including El Harhoura 2) have smaller M_1 than modern population, but the M_1 presents a lower width and a bigger length.

Avery (1982) observed rodent size fluctuations through times in the South African caves and was able to correlate them with climatic trends. Further works on the size and morphology evolution by levels will allow verifying if the El Harhoura 2 rodents are also susceptible to vary their size in function of the climate. For example, several questions can be raised concerning the particular case of *Mus*: is the size reduction of *Mus* due to increase of aridity? What were the effects of the arrival of the

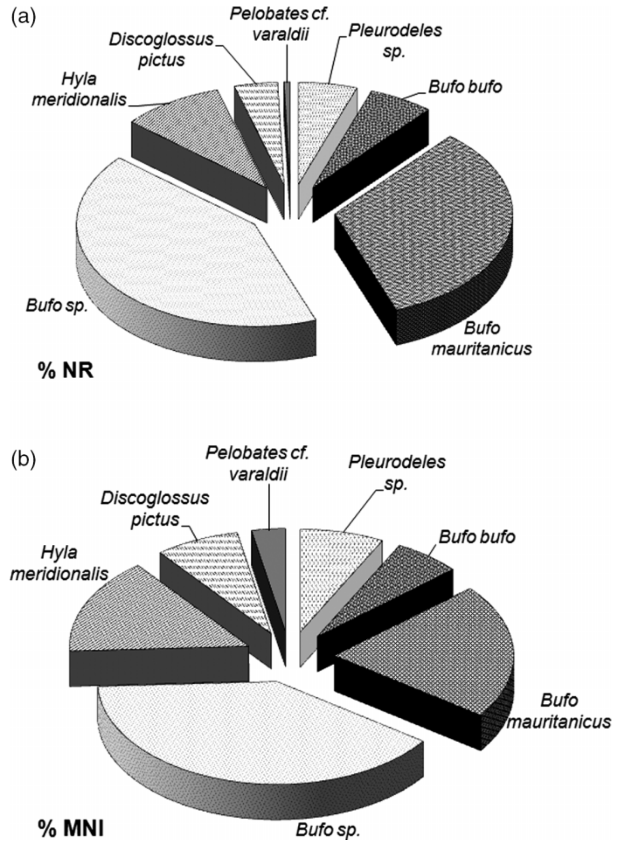

Figure 14. Relative proportion of the species of amphibians of El Harhoura 2 in percentage of total NR and of MNI.

commensal *M. m. domesticus* on the local *M. spretus* (competition, morphological variability)?

The overall fossil diversity of El Harhoura 2 may be underestimated because of the difficulties in identifying some species, high fragmentation of bones and by the lack of reference collections and of associated biometric data.

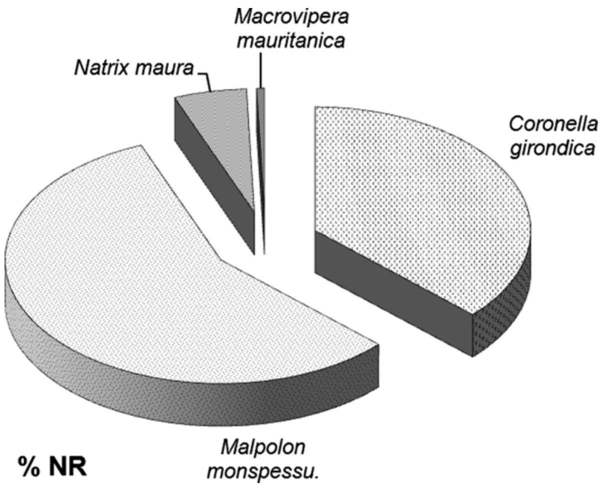

Figure 15. Relative proportion of the species of snakes of El Harhoura 2 in percentage of total NR.

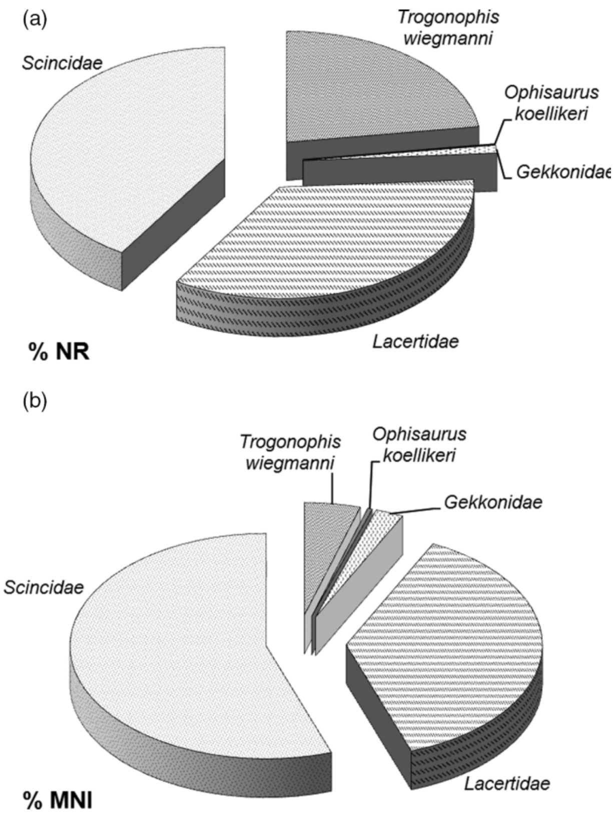

Figure 16. Relative proportion of the species of Sauria of El Harhoura 2 in percentage of total NR and of MNI.

Moreover, it is recognised that many small mammal species in Africa are cryptic ones (see, for example, Benazzou and Genest-Villard 1980; Granjon et al. 1999, 2002; Taylor 2000; Dobigny et al. 2003; Lecompte et al. 2005). Further investigations using genetically typed specimens and morphometric tools are in progress to allow to refine the identifications (Stoetzel et al. forthcoming), especially to solve the question of the eventual presence of the house mouse (*M. m domesticus*) in Morocco before historical times, because its arrival is still not documented in north Africa (Cucchi et al. 2005; Cucchi and Vigne 2006). In addition, very few data are available on the origin and evolution of the local species *M. spretus*.

In the case of amphibians and reptiles, the lack of modern collections and biometrical data prevents some species' assignation and comparisons like in the case of the endemic *Pleurodeles* and *Pelobates.*

First occurrences

El Hahroura 2 presents the first occurrences of modern taxa of different groups.

Concerning amphibians, El Harhoura 2 displays the first occurrences of *Pleurodeles* and *Pelobates* for Morocco and more globally for Africa. The only

Maghrebian fossil remains of Urodela was mentioned in the Early Pleistocene site of Irhoud Ocre, but no description was made and its attribution was limited to an indeterminated Salamandridae (Jaeger 1975). However, a current study on the herpetofauna of some Moroccan sites revealed the presence of remains of *Pleurodeles* in other Quaternary sites (Bailon and Rage forthcoming). The origin of the unique species of *Pleurodeles* in Morocco (*P. waltl*) is still unknown, but several hypotheses were made: anthropogenic introduction (Carranza and Arnold 2004) or natural colonisation (Batista et al. 2004), both in a very recent time frame. But the presence of a *Pleurodeles* species was attested in relatively old levels of El Harhoura 2 (up to 100 ky): is it a relictual form of another north African *Pleurodeles* (*P. poireti* or *P. nebulosus*)? Is the presence of the species *P. waltl* in Morocco older than expected? More detailed studies on archaeological and recent remains of *Pleurodeles* should allow us to answer these questions. According to Jaeger (1975), a *Pelobates* was mentioned – but not described – at Irhoud Ocre (Early Pleistocene, Morocco), but according to Hossini (2001), it was rather a *Pelodytes*. Today, the only Moroccan species is an endemic one (*P. varaldii*), which could have affinities with Western European *Pelobates cultripes*. This may indicate an old presence of this genus in Morocco, having to then undergo a local speciation (Bons and Geniez 1996; Schleich et al. 1996; Garcia-Paris et al. 2003).

Moreover, this is the older occurrence of *Trogonophis wiegmanni, C. girondica* and *Natrix maura* for the Moroccan Quaternary (Late Pleistocene). Today three species of Amphisbaenia are present in Morocco: *T. wiegmanni*, *Blanus mettetali* and *B. tingitanus*. Two species were described in the Plio–Pleistocene site of Ahl-al-Oughlam: *Trogonophis darelbeidae* and *Blanus* sp. (Bailon 2000). This is the unique mention of *T. darelbeidae*, which seems strongly similar to the modern species *T. wiegmanni* (endemic of Maghreb). Only some remains attributed to *T. wiegmanni* were discovered at Guenfouda (Holocene; Aouraghe et al. 2009). Until today, the snakes *C. girondica* and *N. maura* were only mentioned in the Holocene of Guenfouda (Aouraghe et al. 2009). These two species seem to have European origins, having evolved in north Africa since the Pliocene towards different clads (Szyndlar 1984; Schleich et al. 1996; Santos and Pleguezuelos 2003; Guicking et al. 2008).

Biogeography–Paleoecology

In this paragraph, we only consider species whose past distribution is different from the present one.

The great majority of small mammal species represented at El Harhoura 2 are still living today in the region of Témara, except *Jaculus*, whose presence in some levels of El Harhoura 2 (5 and 7) represents an advance northwest of around 80 km from the closer province of occurrence, which is important on a paleoecological point of view (Stoetzel et al. forthcoming). Indeed, Jerboas are adapted to open and arid environments, such as steppic or rocky habitats. However, *J. orientalis* is less adapted to arid and Saharan biotopes compared with *J. jaculus*, and *J. orientalis* also occurs in coastal dunes, grasslands, cultivated areas and open forests (Aulagnier and Thévenot 1986; Aulagnier 1992a, 1992b; Aulagnier et al. 2008). *Jaculus* of El Harhoura 2 is, after those of the Upper Pleistocene sites of Casablanca (Raynal et al. 2008; Geraads et al. 2009), the second described occurrence of the genus in the north Atlantic coast of Morocco. Datings of the archaeological levels of El Harhoura 2 are in progress, thus, we cannot say for the moment how old these remains are, and if they are contemporaneous with those of Casablanca. Dipodidae probably have an Asian origin, because *Protalactaga*, present during Miocene in Morocco (Pataniak 6, Jaeger 1975; Jebel Rhassoul, Bennami 1997), are also known in China. This species quickly disappeared without leaving local descent. The genus *Jaculus* appears around the Plio–Pleistocene boundary in Tunisia (Aïn Brimba; Jaeger 1975; Mein and Pickford 1992), but the lack of data in dry and desert environment prevents the precise location of its origin and the age of arrival in Maghreb (Kowalski and Rzebik-Kowalska 1991; Aulagnier 1992a, 1992b). However, an African origin is unlikely, because in East Africa (Olduvai, the most southern actual distribution), it seems to make only a punctual occurrence during Middle Pleistocene (Denys and Coppens 1989).

Similarly, all the reptile and amphibian species represented at El Harhoura 2 are still living today in the region of Témara, except *B. bufo*. The presence of this species in some levels of El Harhoura 2 (1, 3, 4a, 6, 8) represents an advance westwards of around 60 km from the closer province of occurrence. This species, very common in Europe, lives today in the more humid and temperate area of Morocco (Bons and Geniez 1996) and should indicate a more humid climate than today in some levels of El Harhoura 2 (Stoetzel et al. 2008). The species *B. bufo* was already described in other Middle and Late Pleistocene sites of the north Atlantic coast of Morocco, such as Oulad Hamida 1 (Hossini 2001), Doukkala (Ould Sabar and Michel 1996) and El Harhoura 1 (Bailon and Aouraghe 2002).

We did not find any alternative hypothesis to climate change for explaining the presence of these two species at El Harhoura 2, the distances (60–80 km) being too high for only a ‘taphonomic’ origin (water action, predation; particularly in the absence of digestion on *Jaculus* remains).

Conclusion

Small vertebrates of El Harhoura 2 present an exceptional richness in quantity (more than 35,200 identifiable remains) as well as in diversity (at least 30 species). We noticed variations in the distribution area of some small vertebrate species during Late Pleistocene and Holocene (*Jaculus* cf. *orientalis*, *B. bufo*), and we mentioned first occurrences (*Pleurodeles* sp., *Pelobates* cf. *varaldii*) and older occurrences (*T. wiegmanni*, *C. girondica, N. maura*) of several taxa in Morocco.

We chose to present here a global taxonomic view of the small vertebrates of El Harhoura 2, but a study level by level will be necessary to observe variations in the faunal composition and evolution of species size and/or morphology along the stratigraphy. Comparisons with genetically typed specimens will be necessary to refine the taxonomy of the small mammals and to examine precisely their origins as well as their size and morphology evolution during Late Pleistocene and Holocene in Morocco. Indeed, small vertebrates must be examined precisely along the stratigraphic levels in order to correlate their evolutionary trends with local and global paleoenvironmental changes (Stoetzel et al. forthcoming).

It would also be interesting to make regional comparisons with small vertebrates from nearby caves [for example, El Mnasra, currently studied by Stoetzel; Contrebandiers, currently studied by Reed] and from more remote caves (for example, Guenfouda, Aouraghe et al. 2009).

In conclusion, microvertebrates represent an important paleontological patrimony for north Africa, allowing further knowledge on past biodiversity and environments of this region, but still underestimated. The El Harhoura 2 cave yielded an exceptional material, representing an important contribution for Moroccan small vertebrates' history. But new morphometric tools and an increase of modern references are required to better understand intra-specific variability and species delimitations.

Acknowledgements

We thank the *Mission Archéologique El Harhoura-Témara* (dir. R. Nespoulet and M.A. El Hajraoui) for having procured the material and the *Institut National des Sciences de l'Archéologie et du Patrimoine* (Rabat) for having permitted to export it for this study in France.

A collaboration with the *Institut Scientifique* (Rabat) in 2007 allowed to realise modern small vertebrates trapping and osteological preparations for comparison purposes. We thank all the researchers and technicians for their help, and particularly M. El Agbani.

We thank the NSF-RHOI program (T. White and Late Clarck Howell) for its financial help for the participation of some authors to the First International Congress on North African Vertebrate Paleontology (NAVEP 1), 25–27 May 2009, Marrakech, Morocco.

We also take this opportunity to thank the scientific committee and the committee of organisation of the NAVEP 1 for their reception and their effectiveness.

We greatly thank H. Aouraghe, S. Aulagnier and G. Dyke for their constructive comments, revisions and corrections.

This doctoral work (E. Stoetzel) was supported by grants from Region Ile-de-France.

Note

1. The Aterian is a culture specific to north Africa and Sahara, belonging to Middle Paleolithic, and extending from 20,000 to more than 100,000 years BP (Debénath et al. 1982; Barton et al. 2009; Jacobs et al. forthcoming).

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