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Hervé Monchot, Marjan Mashkour, Fereidoun Biglari, Kamyar Abdi. The Upper Pleistocene brown bear (Carnivora, Ursidae) in the Zagros: Evidence from Wezmeh Cave, Kermanshah, Iran. *Annales de Paléontologie*, 2019, 106 (2), pp.102381. 10.1016/j.anpal.2019.102381 . hal-02367214

HAL Id: hal-02367214

<https://hal.science/hal-02367214>

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The Upper Pleistocene brown bear (Carnivora, Ursidae) in the Zagros: Evidence from Wezmeh Cave, Kermanshah, Iran

Les Ours brun (Carnivora, Ursidae) du Pléistocène supérieur dans le Zagros : l'exemple de la grotte Wezmeh, Kermanshah, Iran

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article info

Keywords:

Brown bear
Ursus arctos
Skeletal representation
Ageing
Biometry
Zagros Mountain

abstract

While bears (Ursidae) are well represented in Western Europe and the Caucasus during the Pleistocene, bear remains from this period are rare in Southwest Asia. Only a limited number of sites, both natural and archaeological, have yielded evidence of brown bear (*Ursus arctos Linnaeus, 1758*). Skeletal remains for this species are often represented by a limited number of elements. The discovery of 192 remains identified as brown bear in Wezmeh Cave (Kermanshah Province, Iran) is exceptional. This paper presents a detailed description of the Wezmeh osteological assemblage, which confirms that *U. arctos* was already present in Zagros during the Upper Pleistocene.

r é s u m é

Mots clés :

Ours brun
Ursus arctos
Représentation squelettique
Profil de mortalité
Biométrie
Montagnes du Zagros

Si les ours (Ursidae) sont bien représentés en Europe occidentale, y compris dans le Caucase, pendant le Pléistocène, ils sont plus rares en Asie du Sud-Ouest. Seul un nombre limité de sites naturels ou archéologiques ont livré des ossements d'ours brun (*Ursus arctos Linnaeus, 1758*) et généralement les restes squelettiques de cette espèce sont souvent représentés par peu de spécimens. La découverte de 192 restes identifiés comme appartenant à des ours bruns dans la grotte de Wezmeh (province de Kermanshah, Iran) constitue une exception. Cet article a pour but de décrire en détail cet assemblage ostéologique qui confirme la présence déjà d'*Ursus arctos* au Pléistocène supérieur dans le Zagros.

1. Introduction

The brown bear (*Ursus arctos Linnaeus, 1758*) is a terrestrial mammal species with a very broad geographic distribution across Europe, Asia and North America. The Syrian brown bear subspecies (*Ursus arctos syriacus* Hemprich and Ehrenberg, 1928), which is

smaller than the nominate *U. arctos arctos*, is native to Southwest Asia and is found in Turkmenistan, Iran, Iraq and Turkey. It is extinct in Palestine and more recently, in Syria, although a few Syrian brown bears still exist along the border between Lebanon and Syria (e.g. Hatt, 1959; Heptner and Naumov, 1998; Masseti, 2009). The Iranian brown bear is found in the present day in the north and west of Iran, primarily in the Zagros Mountains from the Azerbaijan border to the Shiraz region in Fars, and also in the Alborz Mountains from Astara to eastern Golestan. Generally found in the mountainous areas throughout its home range, the Syrian brown bears appear to den and hibernate in caves and tree hollows in high elevation forests (e.g. Lay, 1967; Etemad, 1985; Ziaie, 2008; Farhadinia and Valizadegan, 2015).

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The majority of the Pleistocene sites in Southwest Asia that contain ursid bones are located along the Levantine coast from northern Palestine to the Lebanese mountains (Table 1; Fig. 1). The earliest evidence of bear was found in the Lower Pleistocene site of Ubeidiya in the Jordan valley where 13 remains of Ursus *etruscus* (Cuvier, 1823) were recovered (Martínez-Navarro et al., 2009). The only sites during the Middle Pleistocene with the presence of ursid remains are Cave Bear in the Upper Galilee (Tchernov and Tsoukala, 1997) and Darband Cave in the Alborz (Biglari and Shidrang, 2006;

Biglari et al., 2007). These comprise large assemblages of teeth and bones identified as *Ursus deningeri* (von Reichenau, 1904) (Argant unpublished report; interested readers may refer in particular to Argant and Philippe (2002) for an overview of the complex phylogeny of Plio-Pleistocene Eurasian Ursidae). Finally, during the Upper Pleistocene only *U. arctos* has been identified, from remains found in Mount Carmel, in northern Levant/Galilee, in the Lebanon Mount (e.g. Kurtén, 1965; Hooijer, 1961; Garrard, 1980) and in Northwest Syria (Griggo, 2004). In the Zagros Mountains

Table 1

List of Pleistocene ursid remains from Southwestern Asia (not exhaustive).

Liste des restes d'ours du Pléistocène du Proche et du Moyen-Orient (liste non exhaustive).

Site (Level)	Country	Species	Age/Culture	NISP (MNI)	Reference
Antelias	Lebanon	<i>Ursus arctos</i>	Upper Palaeolithic	Not counted	Garrard, 1980
Amud (B2)	Israel	<i>Ursus sp.</i>	Upper Pleistocene/Middle Palaeolithic	1	Rabinovich and Hovers, 2004
Abri Bezez (B)	Lebanon	<i>Ursus arctos</i>	Upper Pleistocene/Middle Palaeolithic	3	Garrard, 1983
Abri Zumoffen (9–3)	Lebanon	<i>Ursus arctos</i>	Middle Palaeolithic	3	Garrard, 1983
Abri Zumoffen (21–11)	Lebanon	<i>Ursus arctos</i>	Middle Palaeolithic	1	Garrard, 1983
Azokh cave	Nagorno-Karabakh	<i>Ursus spelaeus</i>	Late Pleistocene	265 (8)	Van der Made et al., 2016
Bear's cave	Israel	<i>Ursus deningeri</i>	Middle Pleistocene (Early Toringian)	63	Tchernov and Tsoukala, 1997
Darband cave	Iran	<i>Ursus deningeri</i>	Middle Pleistocene	62	Biglari et al., 2007
Dederiyeh	Syria	<i>Ursus arctos</i>	Middle Palaeolithic	1	Griggo, 2004
El-Wad (B–C)	Israel	<i>Ursus arctos</i>	Upper Palaeolithic-Epipalaeolithic	Not counted	Garrard, 1980
Emirkaya (2)	Turkey	<i>Ursus deningeri</i>	Middle Pleistocene	Not counted	Sen et al., 1991
Hayonim	Israel	<i>Ursus arctos</i>	Upper Paleolithic/Mousterian-Kebaran	2	Stiner, 2006
Hovk-1	Armenia	<i>Ursus spelaeus</i>	Upper Pleistocene	186 (12)	Bar-Oz et al., 2012
Karin (E)	Turkey	<i>Ursus sp.</i>	Upper Pleistocene/Middle Palaeolithic	73	Otte et al., 1998
Kebara	Israel	<i>Ursus arctos</i>	Upper Pleistocene/Middle Palaeolithic	2	Dayan, 1994
Kéoué	Lebanon	<i>Ursus arctos</i>	Upper Pleistocene/Middle Palaeolithic	Not counted	Garrard, 1980
Ksar Akil	Lebanon	<i>Ursus arctos</i>	Upper Pleistocene/Middle Palaeolithic	Not counted	Hooijer, 1961
Maslouk	Lebanon	<i>Ursus arctos</i>	Upper Pleistocene/Middle Palaeolithic	1	Monchot and Gauthier, unpublished
Nahr Ibrahim	Lebanon	<i>Ursus arctos</i>	Upper Pleistocene/Middle Palaeolithic	31	Monchot and Gauthier, unpublished
Nahr el Joz	Lebanon	<i>Ursus arctos</i>	Middle Palaeolithic	Not counted	Garrard, 1980
Ras-El-Keb	Lebanon	<i>Ursus arctos</i>	Middle Palaeolithic	49 (11)	Garrard, 1998
Shanidar	Iraq	<i>Ursus arctos</i>	Upper Pleistocene/Middle Palaeolithic	5 (3)	Evins, 1982
Tabun	Israel	<i>Ursus arctos</i>	Middle/Early Upper Palaeolithic	Not counted	Garrard, 1980
Ubeidiya	Israel	<i>Ursus etruscus</i>	Early Pleistocene	13	Martínez-Navarro et al., 2009
Wezmeh	Iran	<i>Ursus arctos</i>	Upper Pleistocene	192 (8)	Mashkour et al., 2009 (this study)
Zuttiyah	Israel	<i>Ursus arctos</i>	Acheulo-Yabrudian complex	(3/4)	Bate, 1927
Yarimburgaz	Turkey	<i>U. arctos/deningeri</i>	Middle Pleistocene	3920	Stiner et al., 1998

NISP: number of identified specimens; MNI: minimum number of individuals/ NISP : nombre de restes déterminés ; MNI : nombre minimum d'individus .

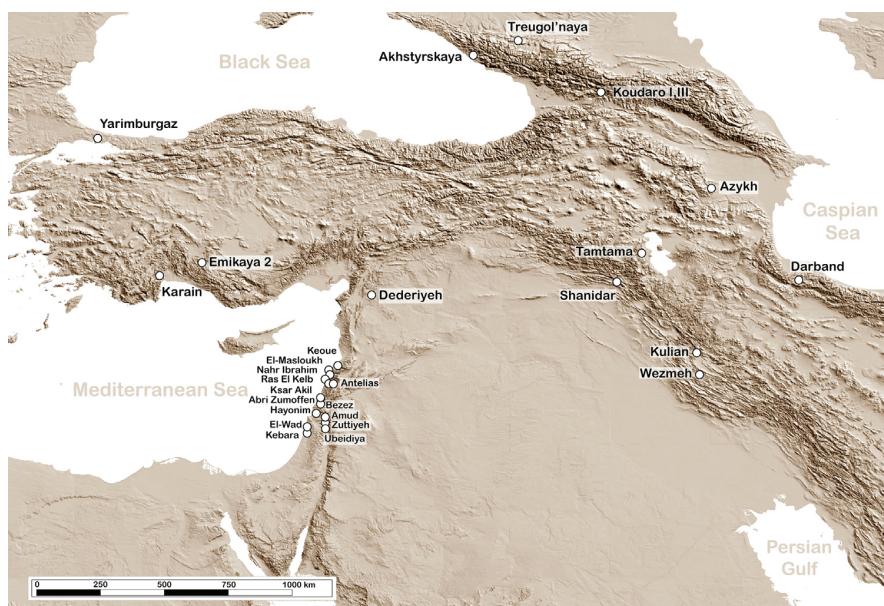


Fig. 1. Map of the main Pleistocene Ursid sites of Southwest Asia (not exhaustive).
Carte des principaux sites à ursidés du Pléistocène en Asie du Sud-Ouest (liste non exhaustive).

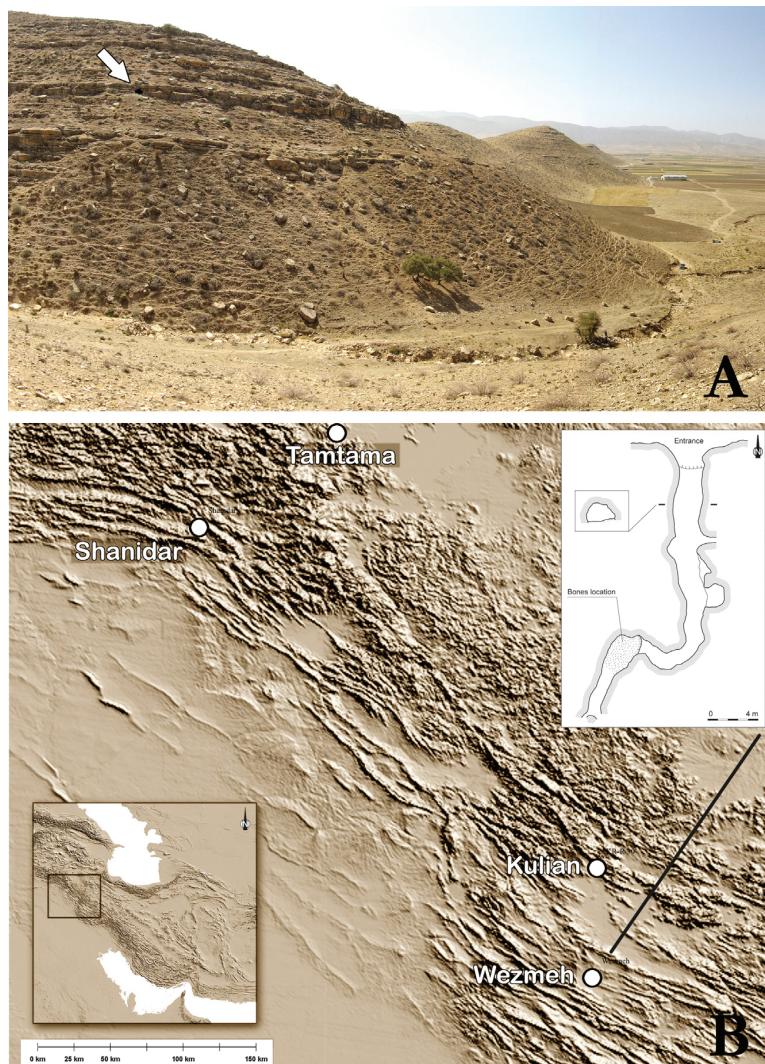


Fig. 2. A. General view of the narrow valley at the Qazivand Mountain where the Wezmeh Cave is located. The site is indicated by an arrow. B. Location of Wezmeh cave and map of the site with bone assemblage location (after Abdi et al., 2002).
A. Vue générale de l'étroite vallée de la montagne Qazivand avec localisation de la grotte Wezmeh (indiquée par une flèche). B. Localisation de la grotte Wezmeh et carte du site avec l'emplacement de l'assemblage osseux (d'après Abdi et al., 2002).

the brown bear has only been identified in Shanidar (Evins, 1982), although a bear tooth was also collected on the surface of the Mar Koulian cave, an Upper Pleistocene/Holocene site near Rawansar (Biglari and Taheri, 2000). To date, no remains of cave bear (*Ursus spelaeus* Rosenmüller, 1794) have been described in Southwest Asia. Although common in the Caucasus (e.g. Baryshnikov, 1998; Bar-Oz et al., 2012; Van der Made et al., 2016), it seems that this species never reached the Zagros-Taurus and Alborz mountain ranges.

Several recent studies have investigated the phylogeny of the Syrian brown bear (Murtskhvaladze et al., 2010; Calvignac et al., 2009). A genetic study on mitochondrial DNA shows that all brown bears occurring in the Caucasus appear to be monophyletic, and are a subspecies of the Eurasian brown bear (*U. arctos arctos*) (Murtskhvaladze et al., 2010; Lortkipanidze, 2010). However, the taxonomic status of the species in this region remains unclear and its distribution and our understanding of its evolution during the Pleistocene in this part of the world remains fragmentary. The

discovery of 192 brown bear bones in Wezmeh cave in the Zagros Mountains is therefore an important contribution to the history of this taxon in Southwest Asia.

2. Wezmeh Cave

This site was discovered in 1999 during an archaeological survey under the direction of Kamyar Abdi in the area of Islamabad-e Gharb (Province of Kermanshah, Iran), a region with numerous Palaeolithic sites (Smith, 1986). The cave is located about 10 km southeast of the city of Islamabad-e Gharb and 3.5 km northeast of the village of Tajar-e Akbar. The cave is at an elevation of 1,430 m a.s.l., approximately 100 m lower than the summit of the Qazivand Mountains, and about 60 m above the valley floor on a steep slope with a 36° dip. The cavity is almost horizontal, formed between geological layers of karstic limestone. Its entrance faces north and is 2 m wide and 1.20 m high. The cave is about 27 m long and about 45 m² (Fig. 2, Abdi et al., 2002). The cave was looted during the 1990s,

resulting in piles of disturbed deposits in front of the cave entrance above the steep slope. After a careful inspection of the site, geoarchaeological studies indicate that the disturbed sediments came from the rear of the cave where sedimentation reaches a maximum of 3 m deep. These disturbed deposits on the exterior slope yielded an abundant faunal assemblage in excellent preservation, particularly rich in carnivore and ungulate remains. An initial faunal list was established, and notably all of the carnivore families known to be present during the Upper Pleistocene in Southwest Asia are present in the Wezmeh assemblage: Hyaenidae (spotted hyena), Canidae (wolf and red fox), Felidae (lion, leopard, lynx/caracal and wild cat), Mustelidae (badger, stone marten and polecat), Herpestidae (mongoose) and of course Ursidae (brown bear). This last taxon represents 11.1% of the total NISP (carnivore and ungulate) and 13.9% of the carnivore remains found in Wezmeh site (Table 2). The first series of palaeontological and taphonomical studies suggest an Upper Pleistocene origin for this assemblage, with a similar skeletal element profile to the Middle Palaeolithic assemblages from the southern Levantine (Mashkour et al., 2009).

Due to the disturbed context of this assemblage, and to the notable diversity of the mammalian species present, it was extremely important to run a direct dating analysis on the principal species present in the cave. Several bones were selected from the carnivore and herbivore remains, including bear, spotted hyena and wild boar. A series of U/Th dates (CNRS, Gif-sur-Yvette) were performed on tooth enamel, providing ages of 63.1 ± 12.6 and 67.3 ± 11.8 Kya for the brown bear, 14.4 ± 1.3 , 23.4 ± 4.9 and 26.6 ± 9.4 Kya for the spotted hyena and finally 13.8 ± 3.4 Kya for the wild boar (Mashkour et al., 2009 : tab. 2). The oldest occupation of the cave may therefore be dated to the Late Pleistocene. Three hyena coprolites were dated by the AMS radiocarbon method, producing calibrated ^{14}C ages of 19228 ± 352 cal BP and 12744 ± 370 cal BP, as well as a Holocene date of 405 ± 59 cal BP (Djamali et al., 2011). Several fragmented human bones and teeth were discovered in the cave among the faunal remains, including the Neanderthal premolar "Wezmeh 1" (Trinkaus et al., 2008; Zanolli et al., 2019). One of the human remains was dated to the early Neolithic, around 9300 cal BP (Broushaki et al., 2016). No

evidence of human activity (e.g. industry, burned bone, cutting traces) was observed.

3. The brown bear assemblage

The species identification of brown bear (*Ursus arctos*) versus cave bear (*Ursus spelaeus* and *Ursus deningeri*) was based on the shape (morphology and size) of certain skeletal elements (e.g. Kurtén, 1955; Stiner, 1998; Stiner et al., 1998; Petronio et al., 2003; Schweizer, 1999, 2005). All the bones (N = 192) present at Wezmeh cave undoubtedly belong to the brown bear (Figs. 3–5).

3.1. The bear bone conservation

The surfaces of the bones are in an excellent state of preservation; in most cases they are smooth without cracks or fissures, characteristic of unweathered bones. Nevertheless, some pieces (n = 9) present very limited surface weathering with a cracking parallel to the fibre structure (longitudinal) (Todisco and Monchot, 2008 : Tab. 2). While the small bones are complete or almost complete, the long bones exhibit recent fragmentation related to the looting activities or post-depositional processes. The fracture characteristics of the long bones clearly indicate a complete shaft circumference, a transverse fracture outline and a smooth fracture edge. All these criteria suggest that these long bones were broken when they were dry, i.e. an indication of post-depositional breakage (Villa and Mahieu, 1991). Finally, the bone surfaces show some traces of manganese (n = 3), concretions (n = 3) and carnivore tooth pits (n = 3).

3.2. The distribution of skeletal elements

Among skeletal elements there is a dominant presence of isolated teeth (20.8%) and extremity elements (45.8%) including carpal, tarsal, phalanges and metapodial; trunk elements, i.e. vertebrae and ribs, contribute a smaller percentage (16.7%) (Table 3, Fig. 6). The long bones are never complete and are very fragmented. Humerus elements are represented by two distal and one proximal fragment, tibia by one distal fragment, femur by four proximal and four distal fragments, the ulna by four proximal and one distal fragments, and the radius by three shafts, one distal and one proximal fragments. There is no marked predominance of a single anatomical region or module (e.g. forelimb vs hindlimb) or in bone laterality ($\chi^2 = 19.09$; df = 22; p = 0.639), which excludes any selective transport (i.e. anthropogenic, carnivore, hydraulic) of brown bear bones within the cave (cf. Quiles, 2003). This type of assemblage, which consists primarily of isolated teeth and extremities of the appendicular skeleton (i.e. carpal, tarsal, metapodial and phalanges), is found in many caves or dens of *Ursus deningeri* (e.g. Château, Scharzfeld, Westbury, Vertesszöllős II, Fosse et al., 2002 : Fig. 3) and *Ursus spelaeus* (e.g. Ekain, Azé 1–3, Divje Babe, Fosse et al., 2002 : Fig. 4) in Europe and in the Caucasus (Hovk-1 cave, Bar-Oz et al., 2012). This type of skeletal representation is also found in the Mesolithic rock shelter of Kostias Klde in the Republic of Georgia where brown bears have been hunted by humans (Bar-Oz et al., 2009), highlighting the differential survivorship of different skeletal elements.

4. Thanatocoenosis structure and mortality profile

Two main methods were utilised in order to estimate the age at the time of death. The first method through the estimation of the stage of tooth eruption, and by analysing dental wear. Following sequential eruption, teeth become progressively more worn and distinctive wear patterns are formed on the different enamel

Table 2
Species distributions of large mammals in NISP (Number of Identified Specimens) and MNI (Minimum Number of Individuals) for Wezmeh cave.
Liste des grands mammifères en NISP (nombre de spécimens identifiés) et MNI (nombre minimal d'individus) pour la grotte de Wezmeh.

		NISP	% NISP	MNI
Carnivora				
<i>Crocuta crocuta spelaea</i>	Spotted Hyena	437	25.2	10
<i>Ursus arctos</i>	Brown Bear	192	11.1	8
<i>Panthera leo</i>	Lion	16	0.9	2
<i>Panthera pardus</i>	Leopard	2	0.1	1
<i>Caracal/Lynx/Felis chaus</i>	Caracal/Lynx/Jungle cat	4	0.2	2
<i>Felis silvestris</i>	Wildcat	8	0.5	2
<i>Canis lupus</i>	Wolf	176	10.1	6
<i>Vulpes vulpes</i>	Red Fox	492	28.4	19
<i>Meles meles</i>	Badger	42	2.4	7
<i>Mustela putorius</i>	Polecat	7	0.4	2
<i>Martes martes (foina?)</i>	Stone marten	2	0.1	1
<i>Herpestes sp.</i>	Mongoose	5	0.3	3
Perissodactyla				
<i>Dicerorhinus</i>	Rhinoceros	2	0.1	1
<i>Equus caballus</i>	Horse	1	0.1	1
<i>Hemionus/E. asinus</i>	Hemione/Donkey	4	0.2	1
Artiodactyla				
<i>Bos primigenius</i>	Aurochs	13	0.8	2
<i>Sus scrofa</i>	Wild boar	97	5.6	4
<i>Cervus elaphus</i>	Red deer	59	3.4	3
<i>Gazella sp.</i>	Gazelle	17	1.0	1
<i>Ovis orientalis</i>	Mouflon	127	7.3	6
<i>Capra aegagrus</i>	Wild goat	31	1.8	2

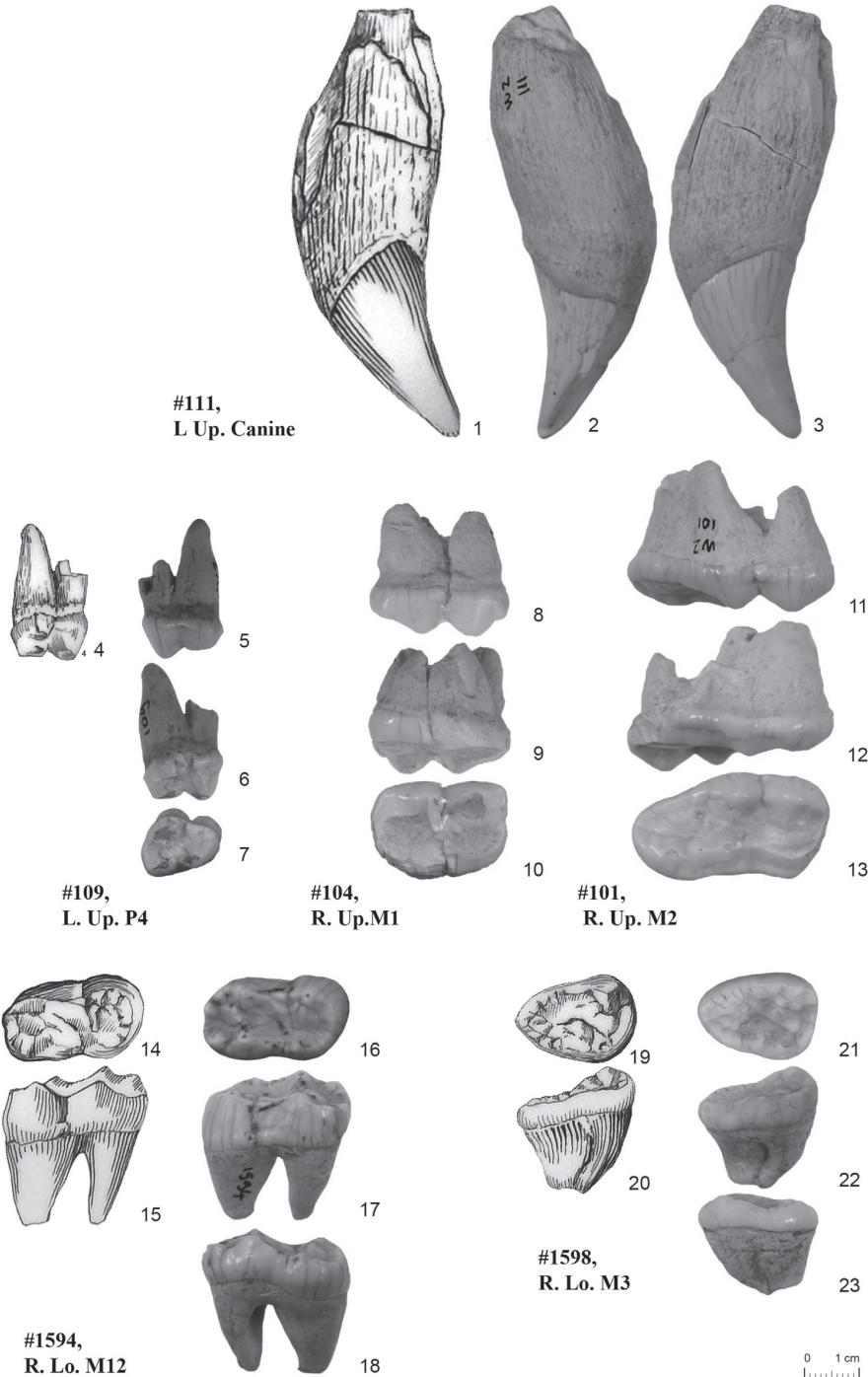


Fig. 3. Teeth of *Ursus arctos* from Wemezh cave. Left upper P4 (WZ 109, 1-2 =lingual view; 3=occlusal view); right upper M1 (WZ 104, 4=lingual view; 5=occlusal view); right upper M2 (WZ 101, 6=lingual view; 7=vestibular view; 8=occlusal view); left upper canine (WZ 111, 9=lingual view; 10-11 =buccal view); right lower M3 (WZ 1598, 12-14 =occlusal view; 13-15 =vestibular view); lower M2 right (WZ 1594, 16-18 =occlusal view; 17-19 =vestibular view).
Dents d'*Ursus arctos* de la grotte de Wemezh. P4 supérieure gauche (WZ 109, 1-2 =vue linguale ; 3 =vue occlusale) ; M1 supérieure droite (WZ 104, 4 =vue linguale ; 5 =vue occlusale) ; M2 supérieure droite (WZ 101, 6 =vue linguale ; 7 =vue vestibulaire ; 8 =vue occlusale) ; canine supérieure gauche (WZ 111, 9 =vue linguale ; 10-11 =vue vestibulaire) ; M3 inférieure droite (WZ 1598, 12-14 =vue occlusale ; 13-15 =vue vestibulaire) ; M2 inférieure droite (WZ 1594, 16-18 =vue occlusale ; 17-19 =vue vestibulaire).

facets. According to the work of Quiles (2003, 2004), age estimation is correlated to nine age groups (see a description of each age group in Quiles, 2004 : tab. 5): infantile, juvenile, sub-adult 1, sub-adult 2, adult 1, adult 2, adult 3, old adult and very adult. These

age-classes have unfortunately not yet been calibrated with real ages known for present day brown bear. The second method is based on the epiphyseal fusion (Weinstock, 2009), and is less reliable as a result of the various taphonomical processes that affect

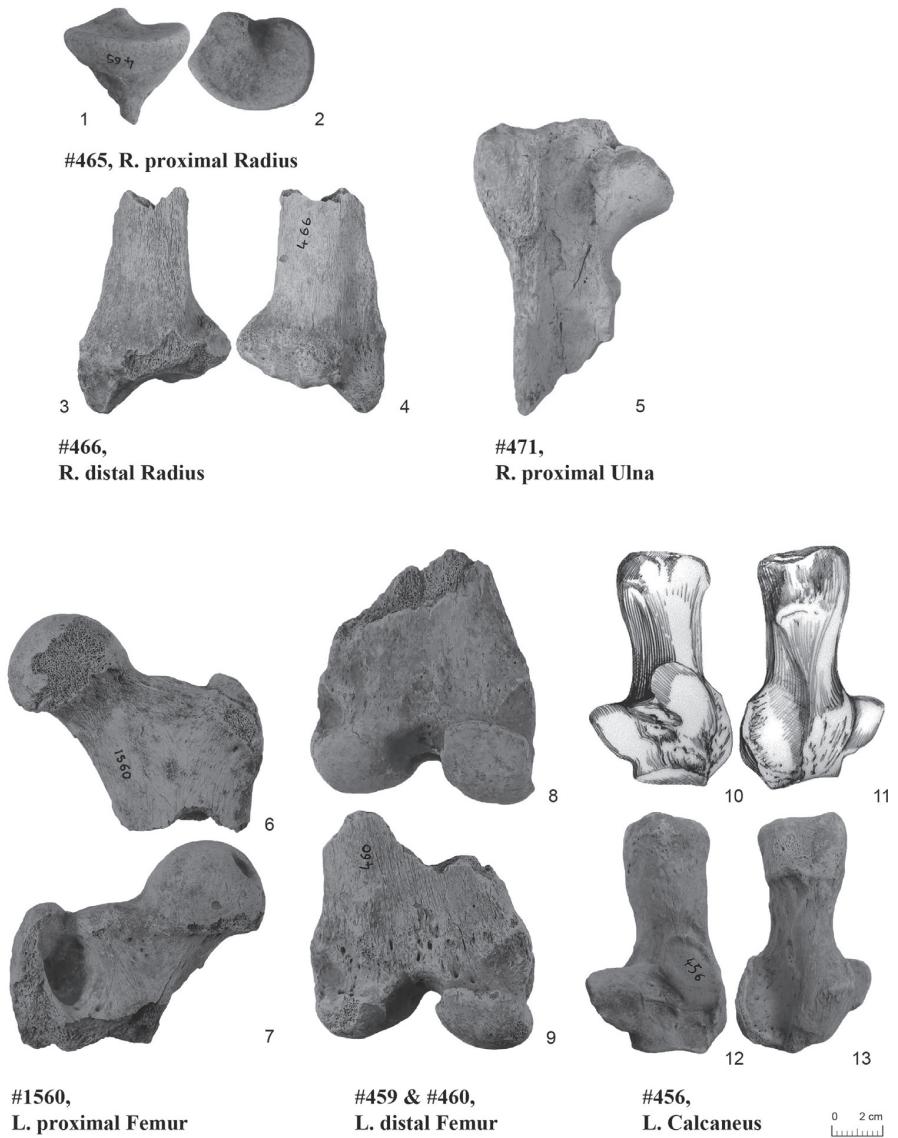


Fig. 4. Post-cranial elements of *Ursus arctos* from Wemezh cave. Right proximal radius (WZ 465, 1 = posterior view, 2 = proximal view); Right distal radius (WZ 466, 3 = posterior view, 4 = anterior view); right proximal ulna (WZ 471, 5 = lateral view); left proximal femur (WZ 1560, 6 = anterior view, 7 = posterior view); left distal femur (WZ 460, 9 = posterior view); left calcaneus (WZ 456, 10-12 = anterior view, 11-13 = posterior view). Éléments post-crâniens d'*Ursus arctos* de la grotte de Wemezh. Radius proximal droit (WZ 465, 1 = vue postérieure ; 2 = vue proximale) ; radius distal droit (WZ 466, 3 = vue postérieure, 4 = vue antérieure) ; ulna proximale droite (WZ 471, 5 = vue latérale) ; fémur proximal gauche (WZ 1560, 6 = vue antérieure, 7 = vue postérieure) ; fémur distal gauche (WZ 459, 8 = vue postérieure) ; fémur distal gauche (WZ 460, 9 = vue postérieure) ; calcaneum gauche (WZ 456, 10-12 = vue antérieure, 11-13 = vue postérieure).

skeletal remains, especially those of immature individuals and the types of skeletal elements with a high marrow and spongiosa content. Only four imprecise age-classes may be defined with the appendicular epiphyseal fusion method: foetus or newborn, juvenile, sub-adult and adult.

Thus, based on 40 identifiable teeth found at Wezmeh, 29 teeth (12 lower and 17 upper teeth) were assigned an age group, and when combined with tooth type a minimum of eight individuals were identified: one juvenile, three sub-adults and four adults (Table 4). The only unfused bones present in the brown bear assemblage are one distal metapodial (an element which fuses around 4–5 years) and one proximal phalanx (which fuse around 2–3 years). This confirms the absence of young and old bears from the assemblage.

5. Osteometry: The Wezmeh brown bear

The Wezmeh brown bear metrical analysis is presented in Table 5 for the teeth and Tables 6–9 for the post-cranial material. The measurements were taken following the procedures outlined by Schweizer (1999). The tooth dimensions of *U. arctos* from the Wezmeh cave were compared with those from other Southwest Asian sites, and the post-cephalic dimensions were compared with material from various European assemblages. However, due to the small sample size and to the lack of published data on brown bears, the dimensions of the Wezmeh brown bear bones appear to fall within the size range of both present day and fossilised European brown bears (Altuna, 1973; Ballesio, 1983). For example, if we calculate the ratio of the length of the first

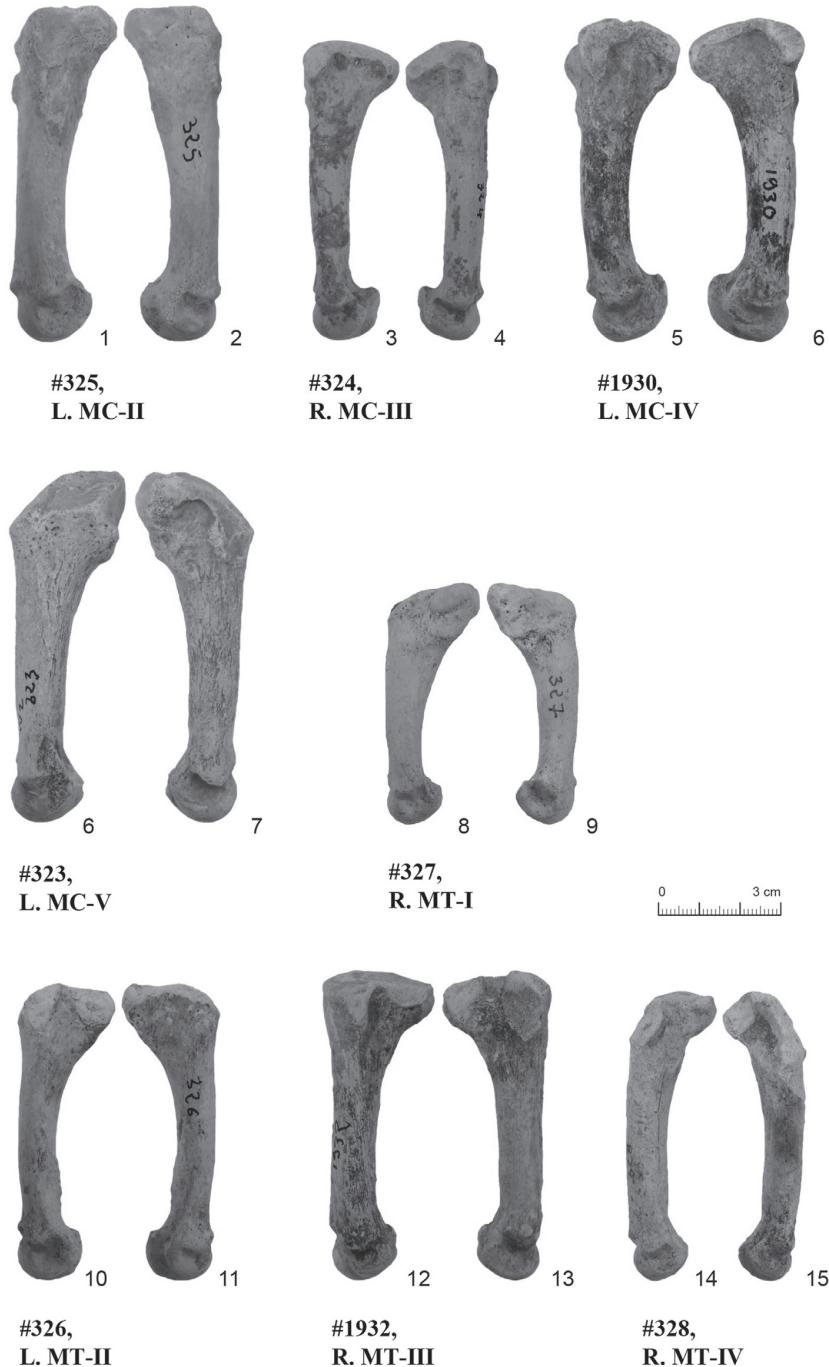


Fig. 5. Metacarpals (MC) and metatarsals (MT) of *Ursus arctos* from Wemezh cave: left MC II (WZ 325, 1 = lateral view; 2 = medial view), right MC III (WZ 324, 3 = medial view, 4 = lateral view), left MC IV (WZ 1930, 5 = lateral view; 6 = medial view), left MC V (WZ 323, 7 = lateral view, 8 = medial view); right MT I (WZ 327, 8 = medial view, 9 = lateral view); left MT II (WZ 326, 10 = lateral view, 11 = medial view); right MT III (WZ 1932, 13 = lateral view, 14 = medial view), right MT IV (WZ 328, 15 = medial view, 16 = lateral view).

Métacarpiens (MC) et métatarsiens (MT) d'*Ursus arctos* de la grotte de Wemezh : MC II gauche (WZ 325, 1 = vue latérale, 2 = vue médiale) ; MC III droit (WZ 324, 3 = vue médiale, 4 = vue latérale), MC IV gauche (WZ 1930, 5 = vue latérale, 6 = vue médiale) ; MC V gauche (WZ 323, 7 = vue latérale, 8 = vue médiane) ; MT I droite (WZ 327, 8 = vue médiale, 9 = vue latérale) ; MT II gauche (WZ 326, 10 = vue latérale, 11 = vue médiale) ; MT III droite (WZ 1932, 13 = vue latérale, 14 = vue médiale) ; MT IV droit (WZ 328, 15 = vue médiale, 16 = vue latérale).

metatarsal as a percentage of the length of the fifth, we obtain 72.3% for the Wezmeh material. This index ranges between 71.1% and 74.2% for *Ursus arctos*, and between 62.3% and 66.9% for *Ursus spelaeus* and *Ursus deningeri* (Ballesio, 1983 : Tab. 19). The

teeth (Fig. 7) of the Wezmeh specimens are larger than those of the present day Syrian brown bear (*U. a. syriacus*) and are similar to those found at Middle Palaeolithic sites such as Ksar'Akil or Tabun C, which are prehistoric sites with later dates than

Table 3

Census of brown bear (*Ursus arctos*) remains on Wezmeh cave in number of identified specimens (NISP) and in minimum number of individual of combination (MNlc)/ inventaires des restes d'ours brun(*Ursus arctos*)de la grotte de Wezmeh en nombre de spécimens identifiés (NISP) et en nombre minimal d'individu de combinaison (MNlc).

Skeletal element	NISP		% NISP	MNlc
	Left	Right		
Mandible	–	1	–	1
Upper isolated teeth	8	9	1	18
Lower isolated teeth	13	8	1	22
Thoracic vertebra	–	–	13	13
Lumbar vertebra	–	–	1	1
Rib	–	–	17	17
Sternebra	–	–	1	1
Humerus	1	2	–	3
Radius	1	2	2	5
Ulna	1	4	–	5
Carpal	3	–	1	4
Metacarpal I	2	1	–	3
Metacarpal III	1	2	–	3
Metacarpal IV	2	1	–	3
Metacarpal V	2	1	–	3
Pelvis	3	3	–	6
Femur	4	4	–	8
Patella	1	–	–	1
Tibia	–	1	–	1
Fibula	2	–	–	2
Tarsal	4	5	2	11
Metatarsal I	1	1	–	2
Metatarsal II	1	1	–	2
Metatarsal III	–	2	–	2
Metatarsal IV	1	3	–	4
Metatarsal V	–	2	–	2
Metapodial	–	1	6	7
Phalange I	–	–	22	22
Phalange II	–	–	9	9
Phalange III	–	–	11	11
TOTAL	51	54	87	192
			100	8

SH: diaphysis; D: distal extremity; P: proximal extremity/ SH : diaphyse ; D : extrémité distale ; P : extrémité proximale .

the Acheuleo-Yabrudian site of Zuttiyeh (Tchernov and Tsoukala, 1997).

Like other ursids, the brown bear displays a strong sexual dimorphism, which is particularly notable in the transverse diameter of the canines (Koby, 1949; Kurtén, 1955). However the overlap

Table 4

Minimum number of individuals according to the 9 classes of age.
Nombre minimum d'individus selon les 9 classes d'âge.

	I	Juv	SA1	SA2	A1	A2	A3	OA	VOA	Total
Lower teeth	0	1	1	1	1	1	0	0	0	5
Upper teeth	0	1	2	1	2	1	1	0	0	8
Total (MNlc)	0	1	2	1	2	1	1	0	0	8

I: infantile; Juv: juvenile; SA1: sub-adult 1; SA2: sub-adult 2; A1: adult 1; A2: adult 2; A3: adult 3; OA: old adult; VOA: very adult/ I : infantile ; Juv : juvénile ; SA1 : sub-adulte 1 ; SA2 : sub-adulte 2 ; A1 : adulte 1 ; A2 : adulte 2 ; A3 : adulte 3 ; OA : adulte âgé ; VOA : adulte très âgé.

between the two sexes is such that it is impossible to separate them only from univariate and bivariate diagrams (Kurtén, 1955; Schweizer, 2004). It is therefore preferable to use more reliable statistical methods, such as mixture analysis (Quiles and Monchat, 2004; Quiles et al., 2005). However the small sample size and the general lack of data on sexual dimorphism in brown bears also prevents the types of analyses that are necessary in order to distinguish male and female remains.

6. Discussion

6.1. Structure of the Wezmeh bear population

The mortality profile indicates that sub-adult and adult males appear to have preferentially occupied the cave. The absence of very young juveniles may be explained by the fact that they do not hibernate and are exclusively nursed by their mother (Nelson et al., 1983). In addition, they are probably underrepresented because of the fragility of the tooth buds and bone remains, which are subject to extensive destruction, exacerbated by the absence of sieving during the excavation. The sub-adult period, which includes the first two hibernations, is critical to individual survival. Foraging by themselves, and still physically immature and inexperienced, young adults have the greatest probability of dying during hibernation (McLoughlin et al., 2003). An abundance of young adult remains is found for instance on the sites of Fate, Basura, Hortus and Arbreda (Quiles, 2003). The presence of adult 1 remains in the Wezmeh assemblage, mostly males (e.g. Badalucco), is probably due to these factors, especially as the dominant older

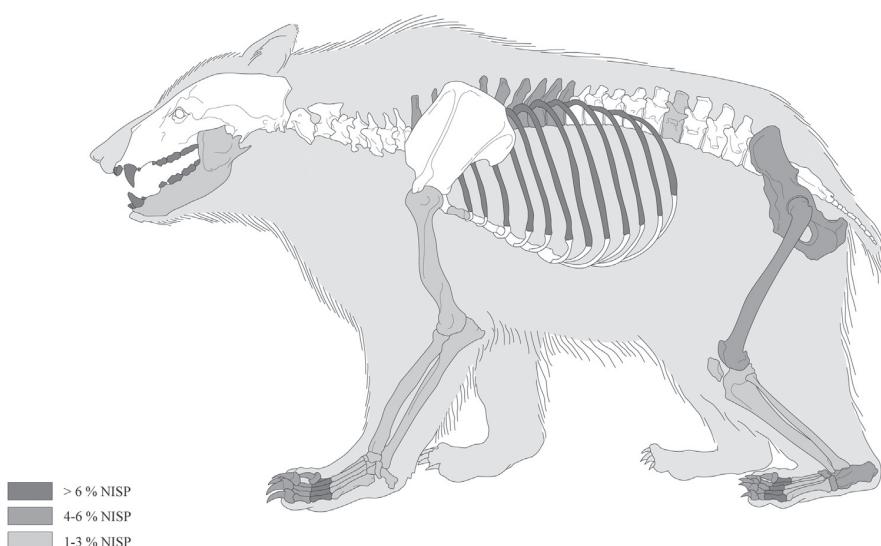


Fig. 6. Anatomical distribution of Wezmeh brown bear remains established as % of the number of identified specimens (NISP).
Profil anatomique de l'ours brun de Wezmeh établi en % du nombre de spécimens identifiés (NISP).

Table 5

Tooth measurements of Ursus arctos from Wezmeh cave.
Mesures des dents d'Ursus arctos de la grotte de Wezmeh.

		L	B	Bpost	HC	Wear stage
WZ 101	Upper M2	35.7	19.4	15.8	8.1	4
WZ 100	Upper M2	39.2	21.1	16.8	9.1	4
WZ 102	Upper M2	38.2	20.7	-	8.5	5
Bant						
WZ 104	Upper M1	24.6	17.1	16.7	9.0	6
WZ 109	Upper P4	15.0	11.6	-	7.7	4
WZ 1596	Upper P4	16.2	12.3	-	8.3	4
WZ 1597	Upper P4	15.5	11.2	-	9.0	2
WZ 116	Upper I3	9.3	10.2	-	-	4
WZ 119	Upper I3	9.8	12.5	-	3.3	5
WZ 118	Upper I3	10.4	13.1	-	7.9	4
WZ 120	Upper I3	11.6	13.1	-	3.3	6
WZ 1592	Upper I3	11.2	12.9	-	3.0	6
WZ 125	Upper I1	7.0	8.1	-	8.1	3
B DT rac						
WZ 110	Upper C	17.1	21	-	-	2
WZ 111	Upper C	16.3	19.1	-	-	3
L Bpost Bant						
WZ 108	Lower M2	23.7	14.4	13.9	8.0	5
WZ 105	Lower M2	26.6	17.0	15.7	7.5	4
WZ 1594	Lower M2	24.7	15.1	14.4	9.3	4
L Bpost						
WZ 102	Lower M3	22.4	16.0	-	5.7	3
WZ 106	Lower M3	20.7	15.7	-	8.7	4
WZ 107	Lower M3	22.4	16.0	-	5.7	3
WZ 1598	Lower M3	21.7	16.0	-	6.5	3
WZ 113	Lower M1	-	-	13.9	-	5
WZ 82	Lower P4	14.2	7.3	-	7.3	3
WZ 1589	Lower P4	13.9	7.1	-	7.1	3
WZ 126	Lower I2	6.6	9.3	-	4.7	3
WZ 124	Lower I2	6.8	9.5	-	2.9	5
WZ 1591	Lower I3	8.6	9.7	-	6.2	5

All measurements are in mm. L: Antero-posterior length near the base of the crown; B: transversal breadth near the base of the crown; HC: height of the crown; Bant: anterior transversal breadth near the base of the crown; Bpost: posterior transversal breadth near the base of the crown/ Toutes les mesures sont en mm. L : longueur antéro-postérieure à la base de la couronne ; B : largeur transversale à la base de la couronne ; HC : hauteur de la couronne ; Bant : largeur transversale antérieure à la base de la couronne ; Bpost : largeur transversale postérieure à la base de la couronne .

males exert a social pressure that results in restricted access to food resources (Stokes et al., 1981; Nelson et al., 1983). Adult 1 males are also typically forced to live in less favourable environments (see the dispersion of sub-adult males, McLellan and Hovey, 2001), as dominant males already occupy the highest quality territories.

Furthermore, it's interesting to note that bear MNI based on teeth is about twice the MNI based on post-cranial bone elements (3 to 8), emphasizing the dramatic loss of bone material in situ in Wezmeh Cave. Relatively speaking, the bones from Wezmeh Cave are in good condition, and the conditions for fossilisation appear to be favorable; the lack of certain skeletal parts therefore cannot be readily explained. The cavity has been used by many carnivores, including the spotted hyena (*Crocuta crocuta spelaea* Goldfuss, 1823), which has the reputation of bone crusher (Monchot, 2008). We may suppose that some of the bear bones were therefore consumed while the tissue was still fresh and edible. There is evidence of gnawing by carnivores on material from the cave, suggesting that some fragile bone elements (such as those that are thin, flat and trabecular) may have been partly or completely destroyed by biological agency soon after death (Mashkour et al., 2009 : 689).

Table 6

Measurements of the calcaneus, patella, femur and radius and ulna of Ursus arctos from Wemeh cave/
Mesures du calcaneum, de la patella, du fémur, du radius et du cubitus d'Ursus arctos de la grotte de Wemeh.

		GL	DT	DAP	L manu	DT facdist	DAP st	DDP st
WZ 456	Calcaneus	76.5	50.9	38.5	42.9	26.5	19.4	15.5
		GL	DT	DAP	DAP art.	L art.		
WZ 458	Patella	49.7	35.8	22.6	20.5	38.9		
		DAP	DT	DT troch	DT fossa	DAP epimed		
WZ 460	Femur distal	(66.2)	81	43.2	15.4	(50.5)		
WZ 459	Femur distal	55.1	80	42.0	15.9	50.3		
		DAP col	DT col	Bcaput	Dcaput			
WZ 463	Femur proximal	21.6	33.9	-	-			
WZ 462	Femur proximal	-	-	49.0	48.1			
WZ 1560	Femur proximal	20.5	32.7	42.7	41.2			
		DAP col	DT ol					
WZ 471	Ulna proximal		69.2		45.1			
WZ 1561	Ulna proximal		63.1		-			
		DTd	DAPd					
WZ 468	Ulna distal		41.4		24.2			
WZ 472	Fibula distal		25.6		15.8			
WZ 1566	Fibula distal		25.9		16.0			
WZ 466	Radius distal		-		58.4			

All measurements are in mm. GL: greatest length; DT: transversal diameter; DAP: antero-posterior diameter; L art.: length of the articulation; DAP art.: articulation antero-posterior diameter; L manu: length of the manubrium ; DT facdist: transversal diameter of the distal articulation; DAP st: antero-posterior diameter of the sustentaculum tali; DDP st: dorso-plantar diameter of the sustentaculum tali ; DT troch: maximum transversal diameter of the trochlea; DT fossa: maximum transversal diameter of the fossa between the two condyles; DAP epimed: antero-posterior diameter of the medial condyle; DAP col: antero-posterior diameter of the diaphysis just under the proximal epiphysis; DT col: transversal diameter of the diaphysis just under the proximal epiphysis; Bcaput: Greatest breadth of the caput femoris; Dcaput: greatest depth of the caput femoris; DT ol: olecranon transversal diameter/Toutes les mesures sont en mm. GL: longueur maximale ; DT : diamètre transversal ; DAP : diamètre antéro-postérieur ; L art: Longueur de l'articulation ; DAP art. : diamètre antéro-postérieur de l'articulation ; L manu : longueur du manubrium ; DT facdist : diamètre transverse de l'articulation distale ; DAP st : diamètre antéro-postérieur du sustentaculum tali ; DDP st : diamètre dorso-plantaire du sustentaculum tali ; DT troch : diamètre transverse maximal de la trochée ; DT fossa : diamètre transverse maximal de la fosse entre les deux condyles ; DAP epimed : diamètre antéro-postérieur du condyle interne ; DAP col : diamètre antéro-postérieur de la diaphyse juste en dessous de l'épiphyse proximale ; DT col : diamètre transverse de la diaphyse juste en dessous de l'épiphyse proximale ; Bcaput : la plus grande largeur du caput femoris ; Dcaput : plus grande profondeur du caput femoris ; DT ol : diamètre transverse de l'olécrane .

6.2. An update on the genetics of brown bears in the Southwest Asia

The genetics of Southwest Asian bears have not yet been studied in detail despite a large number of publications (Taberlet and Bouvet, 1992; Talbot and Shields, 1996 , Miller et al., 2006). Most recently, Calvignac and colleagues have analysed samples from Syria, Lebanon and Iran (Calvignac et al., 2009). The phylogenetic reconstruction based on mtDNA has revealed a high genetic diversity, with the presence of three distinct clades (Miller et al., 2006). The Syrian specimens display a genetic proximity to the east-European bears, whereas the Lebanese specimens are closer to the west-European bears (Talbot and Shields, 1996). Iranian bears form a third unique group that for the moment cannot be grouped with any of the others (Miller et al., 2006; Calvignac et al., 2009). The history of the species in this area is therefore much more complex than previously thought, and it may have involved several

Table 7

Measurements of metacarpal (MC) and metatarsal (MT) bones from Ursus arctos from Wezmeh cave.

Mesures des métacarpiens (MC) et métatarsiens (MT) d'Ursus arctos de la grotte de Wezmeh.

		GL	Bp	Dp	Bdia	Ddia	Bd	Dd
WZ 327	MT I	58.1	20.0	20.1	8.7	9.1	15.9	13.7
WZ 1937	MT I	—	21.2	21.6	—	—	—	—
WZ 326	MT II	68.0	13.8	23.2	12.5	8.8	18.6	15.1
WZ 1276	MT II	—	13.3	20.8	—	—	—	—
WZ 1932	MTT III	74.2	18.1	26.8	13.8	10.4	18.3	15.8
WZ 1932	MTT III	—	16.4	—	12.1	9.1	—	—
WZ 330	MT IV	77.0	18.0	23.6	12.2	11.0	18.4	15.7
WZ 328	MT IV	68.6	—	—	10.7	9.3	16.0	13.2
WZ 331	MT IV	—	16.2	22.3	12.2	9.8	—	—
WZ 1933	MT IV	—	17.1	23.1	—	—	—	—
WZ 1934	MT V	80.4	22.6	20.6	11.4	11.5	20.2	13.5
WZ 325	MC II	74.4	16.3	21.9	11.5	10.9	19.5	16.7
WZ 1931	MC II	—	15.7	22.1	10.8	11.0	—	—
WZ 324	MC III	70.6	15.7	20.3	10.6	9.1	18.8	15.7
WZ 1936	MC III	—	—	—	11.4	10.5	20.4	16.8
WZ 1935	MC III	74.1	—	—	14.1	12.6	20.3	18.2
WZ 321	MC IV	76.9	18.2	25.0	11.7	10.7	19.2	17.6
WZ 1930	MC IV	74.9	18.5	26.0	13.0	11.8	20.8	18.7
WZ 323	MC V	79.8	23.1	25.6	14.1	12.0	22.4(16.5)	
WZ 322	MC V	76.3	24.1	25.8	13.9	11.8	22.3	17.0
WZ1575	MC V	—	25.4	26.7	15.3	10.4	—	—

All measurements are in mm. GL: greatest length; Bp: breadth of the proximal end; Dp: depth of the proximal end; Bdia: greatest breadth of the diaphysis; Dia: smallest breadth of the diaphysis; Bd: breadth of the distal end; Dd: depth of the distal end/Toutes les mesures sont en mm. GL: longueur maximale ; Bp : largeur de l'extrémité proximale ; Dp : hauteur de l'extrémité proximale ; Bdia: plus grande largeur de la diaphyse ; Dia : plus petite largeur de la diaphyse ; Bd : largeur de l'extrémité distale ; Dd : hauteur de l'extrémité distale .

Table 8

Measurements of phalanx I and II of Ursus arctos from Wezmeh cave.

Mesures des phalanges I et II d'Ursus arctos de la grotte de Wezmeh.

		GL	Bp	Dp	Bdia	Ddia	Bd	Dd
WZ 570	Phalanx I	35.7	18.1	16.2	12.7	7.8	14.7	10.1
WZ 563	Phalanx I	41.6	20.2	16.2	13.0	10.2	15.5	10.5
WZ 567	Phalanx I	38.4	19.4	15.9	13.0	8.6	15.4	10.0
WZ 572	Phalanx I	40.2	18.0	15.1	12.0	9.4	14.6	10.5
WZ 576	Phalanx I	—	—	—	—	—	16.4	10.3
WZ 564	Phalanx I	36.6	18.2	15.0	12.4	9.5	15.4	8.6
WZ 575	Phalanx I	34.3	17.4	14.5	11.4	10	13.6	9.1
WZ 569	Phalanx I	42.1	21.3	17.3	13.9	8.9	15.7	10.7
WZ 573	Phalanx I	36.5	19.6	14.4	11.5	8.8	15.0	8.0
WZ 566	Phalanx I	37.4	18.1	15.9	12.6	8.6	13.9	10.0
WZ 571	Phalanx I	37.6	19.0	14.6	12.4	8.8	15.4	8.3
WZ 574	Phalanx I	35.9	16.3	12.6	10.4	8.3	14.7	9.0
WZ 568	Phalanx I	32.5	18.9	14.4	11.7	8.7	12.4	8.2
WZ 565	Phalanx I	34.4	15.7	13.0	10.4	8.1	11.4	8.9
WZ 1576	Phalanx I	40.0	19.0	16.2	13.0	8.5	16.2	10.2
WZ 1577	Phalanx I	49.3	21.1	17.2	14.6	11.2	16.3	12.1
WZ 1578	Phalanx I	38.4	19.6	17.5	13.5	8.8	15.7	10.1
WZ 1579	Phalanx I	38.2	18.1	16.4	12.7	9.6	14.4	10.0
WZ 1580	Phalanx I	33.8	19.0	13.6	11.8	8.3	13.9	8.4
WZ 1581	Phalanx I	44.5	19.0	15.5	14.3	12.2	16.1	11.9
WZ 1582	Phalanx I	—	—	—	13.7	9.5	16.0	11.0
WZ 619	Phalanx II	30.2	16.8	13.7	11.4	8.3	13.6	11.5
WZ 618	Phalanx II	31.2	18.0	14.7	12.3	8.3	15.6	12.5
WZ 621	Phalanx II	29.1	16.6	13.6	11.5	8.0	16.1	11.7
WZ 620	Phalanx II	29.4	15.1	12.5	11.6	7.4	13.4	11.4
WZ 577	Phalanx II	—	—	—	—	—	13.3	11.1
WZ 1585	Phalanx II	29.1	16.6	13.6	11.5	8.0	16.1	11.7
WZ 1586	Phalanx II	29.4	15.1	12.5	11.6	7.4	13.4	11.4
WZ 1587	Phalanx II	—	—	—	—	—	13.3	11.1
WZ 1588	Phalanx II	29.1	16.6	13.6	11.5	8.0	16.1	11.7

All measurements are in mm (Measurement references in Table 7)/Toutes les mesures sont en mm (Références de mesure dans le Tableau 7).

Table 9

Measurements of some carpal, tarsal and phalanx 3 of Ursus arctos from Wezmeh cave.

Mesures de carpes, tarses et phalanges 3 d'Ursus arctos de la grotte de Wezmeh.

		DPD	DT	DDP
WZ 449	Unciform	32.1	26.3	25.4
WZ 1927	Capitatum	30.2	17.4	22.7
WZ 452	Cuneiform I	20.8	11.6	15.7
WZ 453	Cuneiform I	23.9	12.7	17.1
WZ 1168	Cuneiform I	21.9	11.6	16.3
WZ 1567	Cuneiform I	21.4	12.3	18.2
WZ 1456	Cuneiform II	20.9	9.1	14.7
WZ 1507	Cuneiform III	24.1	19.0	13.3
WZ 1928	Cuneiform III	25.3	21.3	15.5
WZ 451	Trapezium	15.8	12.3	21.3
WZ 457	Trapezium	20.9	14.7	24.8
WZ 1921	Cuboid	38.0	27.5	24.5

		GL	Bp	Dp	Barti	Darti
WZ 579	Phalanx III	46.0	15.4	25.6	14.4	15.6
WZ 580	Phalanx III	—	14.5	26.3	13.0	15.0
WZ 581	Phalanx III	—	13.7	26.0	12.5	14.6
WZ 582	Phalanx III	—	13.4	26.0	12.8	14.3
WZ 583	Phalanx III	32.3	13.2	20.4	13.1	14.0
WZ 584	Phalanx III	30.7	12.4	20.5	12.1	12.8
WZ 585	Phalanx III	29.2	11.1	20.0	—	—
WZ 586	Phalanx III	28.4	12.5	19.7	—	—
WZ 587	Phalanx III	—	15.1	25.0	14.3	15.2
WZ 1584	Phalanx III	31.1	11.8	21.1	11.2	13.6

All measurements are in mm. DPD: proximo-distal diameter; DT: transversal diameter; DDP: Dorso-plantar (palmar) diameter; GL: greatest length; Bp: proximal breadth; Dp: proximal depth; Barti: articular breadth; Darti: articular depth/Toutes les mesures sont en mm. DPD : diamètre proximo-distal ; DT : diamètre transverse ; DDP : diamètre dorso-plantaire (palmaire) ; GL : longueur maximale ; Bp : largeur proximale ; Dp : hauteur proximale ; Barti : largeur articulaire ; Darti : profondeur articulaire .

Wezmeh may therefore have an important role in the future understanding of this phenomenon. A recent genetic study has indicated that there was also a coinciding emergence of several haplotypes ([Ho et al., 2008](#)), corresponding with the oldest dates provided by the deposits in Wezmeh. However no viable DNA samples have yet been recovered from the Wezmeh bear remains in order to further investigate this relationship, despite several attempts ([Calvignac et al., 2009](#)).

7. Conclusions

Ursid remains from Wezmeh Cave may be identified as brown bear, based on the metric and morphological characteristics of the skeletal elements present in the assemblage. The size of the Wezmeh specimens fall within the ranges of variation of both Upper Pleistocene and extant brown bears in Southwest Asia and can be attributed to a local species of brown bear (*Ursus arctos*), but cannot be conclusively identified as the Syrian brown bear (*Ursus arctos syriacus*).

In respect to the palaeogenetic research, for the time being the absence of DNA prevents the identification of the brown bear bones of Wezmeh to a specific haplotype. The genetic analyses on modern bears show that Iranian and Syrian bears belong to different haplotypes. Any possible morphological markers of these genetic differences are as of yet unidentified. Unfortunately there are no large bone assemblages to our knowledge that are sufficiently representative of this small-sized subspecies of brown bear in order to provide the material to address this question. Only the re-analysis of the Ksar Akil site in Lebanon ([Hooijer, 1961](#)), which contains ursid remains that are large in size, would allow for a direct morphometric or even geometric morphometric analysis. Unfortunately, to our knowledge this assemblage has been lost.

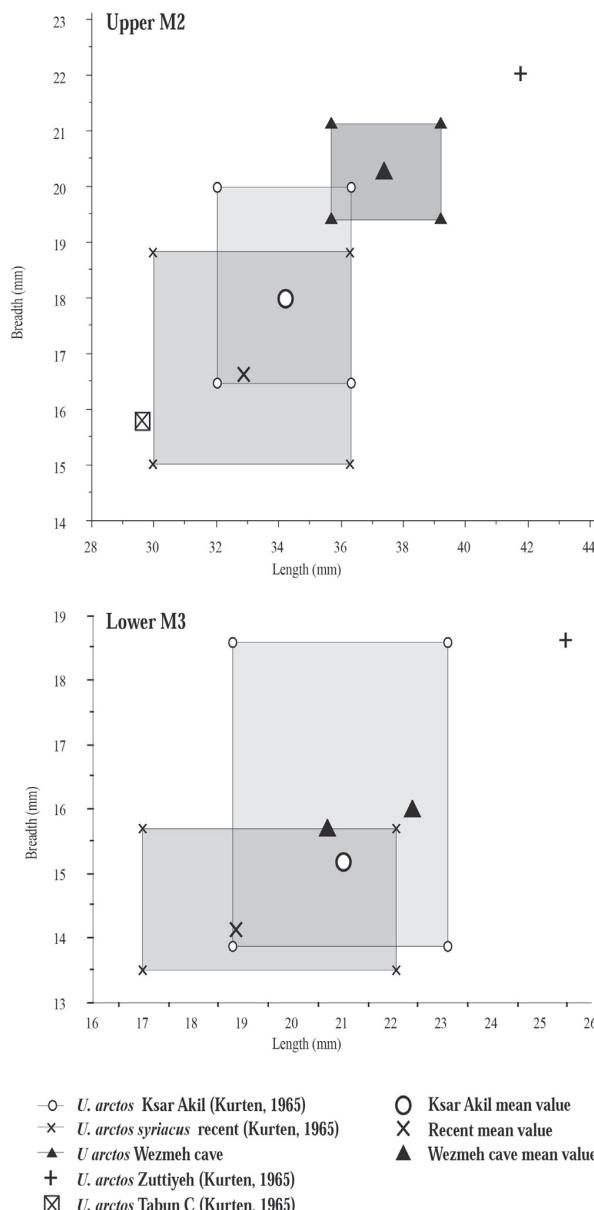


Fig. 7. Comparison of length and breadth of the upper M2 and lower M3 of brown bear (*Ursus arctos*) from Wezmeh Cave and specimens from southern Levantine sites (after Mashkour et al., 2009).

Diagrammes bivariés longueur par largeur (en mm) des M2 supérieures et des M3 inférieures de l'ours brun (*Ursus arctos*) de la grotte de Wezmeh et de différents spécimens provenant de sites du Levant sud (d'après Mashkour et al., 2009).

It is unusual to find older bear remains that display such a distinctively small size, especially across the whole sample of elements. The small dimensions of these remains strongly exclude species identification as *U. spelaeus*. In addition, the dates obtained for the bear remains are notably older than those for *Crocuta crocuta* (Mashkour et al., 2009), despite spotted hyena becoming extinct in this region and brown bears persisting until the present day. However, there are only five dated samples (3 for the hyena and 2 for the bear), which may not be representative of the whole time-range of occupation of bears and hyenas in Wezmeh (Monchot, 2008; Monchot et al., 2019). Based on the present material it is not

possible to fully understand the biogeographic chronology, especially when bearing in mind that very little is known of the evolution of Pleistocene carnivore fauna in the Zagros. Despite the lack of material, differential occupation of carnivores may have existed in the cave over about 65,000 years.

Disclosure of interest

The authors declare that they have no competing interest.

Acknowledgments

We are grateful to Sanaz Beizaee Doust (Bioarchaeology Laboratory, Central Laboratory University of Tehran), for her assistance in the preparation of the figures, and to Michèle Ballinger (CNRS-UMR 7041, Arscan) for the drawings. We also thank Elizabeth Kerr for the English copy editing of the paper.

References

- Abdi, K., Biglari, F., Heydari, S., 2002. Islamabad project 2001: test excavations at Wezmeh cave. *Archäologische Mitteilungen aus Iran und Turan* 34, 171–194.
- Altuna, J., 1973. Hallazgos de oso pardo (*Ursus arctos*, Mammalia) en cuevas del País Vasco. *Munibe* 2-4, pp. 121–170.
- Argant, G., Philippe, M., 2002. Les ours et leur évolution. In: Tillet, T., Binford, L.R. (Eds.), *L'ours et l'homme. Liège : études et recherches de l'université de Liège*, 100, pp. 17–26.
- Ballesio, R., 1983. Le gisement pléistocène de la grotte de Jaurens à Nespolis, Corrèze, France : les carnivores (Mammalia Carnivora). III. Ursidae. *Ursus arctos Linnaeus. Nouvelle Archive du Muséum d'Histoire naturelle de Lyon* 21, 9–43.
- Bar-Oz, G., Belfer-Cohen, A., Meshveliani, T., Jakeli, N., Matskevich, Z., Bar-Yosef, O., 2009. Bear in mind: bear hunting in the Mesolithic of the southern Caucasus. *Archaeology, Ethnology & Anthropology of Eurasia* 37 (1), 15–24.
- Bar-Oz, G., Weissbrod, L., Gasparian, B., Nahapetyan, S., Wilkinson, K., Pinhasi, R., 2012. Taphonomy and zoarchaeology of a high-altitude Upper Pleistocene faunal sequence from Hovik-1 Cave, Armenia. *Journal of Archaeological Science* 39, 2452–2463.
- Baryshnikov, G.F., 1998. Cave bears from the Palaeolithic of the Greater Caucasus. In: Saunders, J.J., Styles, B.W., Baryshnikov, G.F. (Eds.), *Quaternary paleozoology in the Northern Hemisphere*, 27. Illinois State Museum Scientific Papers, Springfield, pp. 69–118.
- Bate, D.M.A., 1927. On the animal remains obtained from the Mugharet-el-Zuttiyeh in 1925 & 1926. In: Turville-Petre, F. (Ed.), *Researches in prehistoric Galilee 1925–1926. The Council of the British School of Archaeology in Jerusalem*, London, pp. 27–51.
- Biglari, F., Taheri, K., 2000. The discovery of Upper Paleolithic remains at Mar Kulian and Mar Dalan caves, Rawansar. In: Taheri, K. (Ed.), *Essays on the archaeology, geology, and culture of Rawansar Area*. Taq-e Bostan Publications, Kermanshah, pp. 7–27 [In Persian].
- Biglari, F., Shidrang, S., 2006. The Lower Paleolithic occupation of Iran. *Near Eastern Archaeology* 69 (4), 160–168.
- Biglari, F., Jahaní, V., Mashkour, M., Argant, A., Shidrang, S., Taheri, K., 2007. Darband cave: new evidence for Lower Paleolithic occupation at Western Alborz Range, Gilan. *Iranian Journal of Archaeology and History* 41, 30–37 [In Persian, with an English abstract].
- Broushaki, F., Thomas, M.G., Link, V., López, S., van Dorp, L., Kirsanow, K., Hofmanová, Z., Diekmann, Y., Cassidy, L.M., Díez-del-Molino, D., Kousathanas, A., Sell, C., Robinson, H., Martiniano, R., Blöcher, J., Scheu, A., Kreutzer, S., Bollongino, R., Bobo, D., Davudí, H., Muñoz, O., Currat, M., Abdi, K., Biglari, F., Craig, O.E., Bradley, D.G., Shennan, S., Veeramah, K.R., Mashkour, M., Wegmann, D., Hellenthal, G., Burger, J., 2016. Early Neolithic genomes from the eastern Fertile Crescent. *Science* 353 (6298), 499–503.
- Calvignac, S., Hughes, S., Hänni, C., 2009. Genetic diversity of endangered brown bear (*Ursus arctos*) populations at the crossroads of Europe, Asia and Africa. *Diversity and Distributions* 15, 742–750.
- Dayan, T., 1994. Carnivore diversity in the late Quaternary of Israel. *Quaternary Research* 41, 343–349.
- Djamali, M., Biglari, F., Abdi, K., Andrieu-Ponel, V., de Beaulieu, J.-L., Mashkour, M., Ponel, P., 2011. Pollen analysis of coprolites from a late Pleistocene-Holocene cave deposit (Wezmeh Cave, west Iran): insights into the late Pleistocene and late Holocene vegetation and flora of the central Zagros Mountains. *Journal of Archaeological Science* 38, 3394–3401.
- Etemad, E., 1985. The mammals of Iran. *Carnivora, Pinnipedia, Perissodactyla, Artiodactyla, Cetacea*, 2. Department of the Environment, Tehran [In Persian].
- Evins, M.A., 1982. The fauna from Shanidar cave: Mousterian wild goat exploitation in Northeastern Iraq. *Paléorient* 8, 37–58.
- Farhadinia, M.S., Valizadegan, N., 2015. A preliminary baseline status of the Syrian Brown Bear *Ursus arctos syriacus* (Mammalia: Carnivora: Ursidae) in Golestanak, Northern Iran. *Journal of Threatened Taxa* 7, 6796–6799.

- Fosse, F., Morel, P., Brugal, J.-P., 2002. Taphonomie et paléoéthologie des Ursidés pléistocènes. In: Tillet, T., Binford, L.R. (Eds.), *L'ours et l'homme*. Liège : études et recherches de l'université de Liège, 100, pp. 79–101.
- Garrard, A.N., 1980. Man-Animal-Plant relationships during the Upper Pleistocene and Early Holocene of the Levant [Unpublished Ph.D. Thesis, University of Cambridge].
- Garrard, A.N., 1983. The Palaeolithic faunal remains from Adlun and their ecological context. In: Roe, D.E. (Ed.), *Adlun in the Stone Age*. British Archaeological Reports, International series 159, Oxford, pp. 397–413.
- Garrard, A.N., 1998. Food procurement by Middle Palaeolithic hominids at Ras el-Kelb Cave, Lebanon. In: Copeland, L., Moloney, N. (Eds.), *The Mousterian Site of Ras el-Kelb, Lebanon*. British Archaeological Reports, International series 706, Oxford, pp. 45–65.
- Griggo, C., 2004. Mousterian fauna from Dederiyeh cave and comparisons with fauna from Umm El Tiel and Douara cave. *Paléorient* 30, 149–162.
- Hatt, R., 1959. The mammals of Iraq. *Museum of Zoology, University of Michigan* 106, Ann Arbor.
- Heptner, V.G., Naumov, N.P., 1998. *Mammals of the Soviet Union*, 2. Science Publishers, Inc., USA [Part 1a: Sirenia and Carnivora].
- Ho, S.Y.W., Saarma, U., Barnett, R., Haile, J., Shapiro, B., 2008. The effect of inappropriate calibration: three case studies in molecular ecology. *PLoS ONE* 3 (2), e1615, <http://dx.doi.org/10.1371/journal.pone.0001615>.
- Hooijer, D.A., 1961. The fossil vertebrates of Ksar'Akil, a palaeolithic rockshelter in the Lebanon. *Zoologische Verhandelingen* 49, 3–67.
- Koby, F.E., 1949. Le dimorphisme sexuel des canines d'*Ursus arctos* et d'*U. spelaeus*. *Revue Suisse de Zoologie* 56, 675–687.
- Kurtén, B., 1955. Sex dimorphism and size trends in the cave bear, *Ursus spelaeus Rosenmüller & Heinroth*. *Acta Zoologica Fennica* 90, 1–48.
- Kurtén, B., 1965. The carnivora of the Palestine caves. *Acta Zoologica Fennica* 107, 3–73.
- Lay, D.M., 1967. A study of the mammals of Iran resulting from the Street expedition of 1962–63. *Zoology, Fieldiana*, pp. 1–282.
- Lortkipanidze, B., 2010. Brown bear distribution and status in the South Caucasus. *Ursus* 21, 97–103.
- Martinez-Navarro, B., Belmaker, M., Bar-Yosef, O., 2009. The large carnivores from Ubeidiya (early Pleistocene, Israel): biochronological and biogeographical implications. *Journal of Human Evolution* 56, 514–524.
- Mashkour, M., Monchot, H., Reys, J.L., Trinkaus, E., Baillon, S., Biglari, F., Heydari, S., Abdi, K., 2009. Carnivores and their prey in the Wezmeh cave (Kermanshah, Iran) – a late Pleistocene refuge in the Zagros. *International Journal of Osteoarchaeology* 19, 678–694.
- Masseti, M., 2009. Carnivores of Syria. In: Neubert, E., Amr, Z., Taiti, S., Gümus, B. (Eds.), *Animal Biodiversity in the Middle East*. Proceedings of the First Middle Eastern Biodiversity Congress, Aqaba, Jordan, 20–23 October 2008, ZooKeys 31, pp. 229–252.
- McLellan, B.N., Hovey, F., 2001. Natal dispersal of grizzly bears. *Canadian Journal of Zoology* 79, 838–844.
- McLoughlin, P.D., Mitchell, K.T., Cluff, H.D., Gau, R.J., Mulders, R., Case, R.L., Boutin, S., Messier, F., 2003. Demography of barren-ground grizzly bears. *Canadian Journal of Zoology* 81, 294–301.
- Miller, C.R., Waits, L.P., Joyce, P., 2006. Phylogeography and mitochondrial diversity of extirpated brown bear (*Ursus arctos*) populations in the contiguous United States and Mexico. *Molecular Ecology* 15, 4477–4485.
- Monchot, H., 2008. Des hyènes tachetées au Pléistocène supérieur dans le Zagros (grotte Wezmeh Iran). *Archaeozoology of the Near East VIII*, TMO 49. Maison de l'Orient et de la Méditerranée, Lyon, pp. 65–78.
- Monchot, H., Mashkour, M., Abdi, K., 2019. The spotted hyena (*Crocuta spelaea*) of the Wezmeh cave, Kermanshah, Central Western Zagros Mountains. In: Biglari, F., Shidrang, S., Mashkour, M. (Eds.), *Pleistocene archaeology of the Iranian Plateau, Iraq and the Caucasus*. [In press. National Museum of Iran Paleolithic Studies Series No. 1].
- Murtskhvaladze, M., Gavashelishvili, A., Tarkhnishvili, D., 2010. Geographic and genetic boundaries of brown bear (*Ursus arctos*) population in the Caucasus. *Molecular Ecology* 19, 1829–1841.
- Nelson, R.A., Folk, G.E., Pfeiffer, E.W., Craighead, J.J., Jonkel, C.J., Steiger, D.I., 1983. Behaviour, biochemistry and hibernation in black, grizzly and polar bears. *Bears: Their Biology and Management* 5, 284–290.
- Otte, M., Yalcinkaya, I., Kozłowski, J., Bar-Yosef, O., López Bayón, I., Taskiran, H., 1998. Long-term technical evolution and human remains in the Anatolian Palaeolithic. *Journal of Human Evolution* 34, 413–431.
- Petronio, C., Di Stefano, G., Di Canzio, E., 2003. Morphological and biometrical differences in the limb bones of *Ursus arctos* and *Ursus spelaeus* and phylogenetic considerations on the two species. *Palaeontographica Abteilung A* Stuttgart 269 (4), 137–152.
- Quiles, J., 2003. Les Ursidae du Pléistocène moyen et supérieur en Midi méditerranéen : apports paléontologiques, biochronologiques et archéozoologiques. *Muséum national d'Histoire naturelle Paris* [Unpublished Ph. D thesis].
- Quiles, J., 2004. Tanières d'ours des cavernes (Carnivora Ursidae) du pourtour méditerranéen : étude taphonomique et paléobiologique de huit assemblages du Pléistocène supérieur. *Paléo* 16, 171–192.
- Quiles, J., Monchot, H., 2004. Sex ratio et analyse des mélanges d'*Ursus spelaeus* (Carnivora, Ursidae) du gisement pléistocène supérieur de Fate (Ligurie Italie). *Implications paléobiologiques*. *Annales de Paléontologie* 90, 115–133.
- Quiles, J., Monchot, H., Pacher, M., 2005. Mixture analysis: a new method for cave bear sex-ratio determination. *Bulletin Société d'Histoire Naturelle de Toulouse* 141, 29–37.
- Rabinovich, R., Hovers, E., 2004. Faunal analysis from Amud cave: preliminary results and interpretations. *International Journal of Osteoarchaeology* 14, 287–306.
- Schweizer, M., 1999. Étude d'une population d'ours des cavernes (*Ursus spelaeus Rosenmüller & Heinroth*, 1794) provenant de la grotte de Vaucluse (Doubs, France). *Travail de diplôme. Département d'anthropologie et d'écologie, université de Genève* [Unpublished].
- Schweizer, M., 2004. Les ours des cavernes (*Ursus spelaeus Rosenmüller & Heinroth*, 1794) de la grotte de Vaucluse (Doubs, France) : détermination du sexe et estimation du sex-ratio. *Cahiers scientifiques Hors-série* 2, 81–86.
- Schweizer, M., 2005. Étude des caractères non-métriques dans une population d'ours des cavernes (*Ursus spelaeus Rosenmüller & Heinroth*, 1794) provenant de la grotte de Vaucluse (Doubs, France). *Revue de Paléobiologie Genève* 10, 3–9.
- Sen, S., de Bonis, L., Dafes, N., Geraads, D., Jaeger, J.-J., Mazin, J.-M., 1991. Première découverte d'un site à mammifères pléistocènes dans une fissure karstique en Anatolie centrale, 313, pp. 127–132 [Compte rendus de l'Académie des sciences série II].
- Smith, P.E., 1986. *Paleolithic archaeology in Iran*. University of Pennsylvania, Philadelphia.
- Stiner, M.C., 1998. Mortality analysis of Pleistocene bears and its paleoanthropological relevance. *Journal of Human Evolution* 34, 303–326.
- Stiner, M.C., 2006. The faunas of Hayonim cave, Israel. A 200,000 years record of Palaeolithic diet, demography and society. *American School of Prehistoric Research*, 48, Peabody Museum of Archaeology and Ethnology Harvard University.
- Stiner, M.C., Achyuthan, H., Arsebük, G., Howell, F.C., Josephson, S.C., Juell, K.E., Pigati, J., Quade, J., 1998. Reconstructing cave bear paleoecology from skeletons: a cross-disciplinary study of middle Pleistocene bears from Yarimburgaz cave, Turkey. *Paleobiology* 24, 74–98.
- Stokes, A.W., Elgert, A., Luque, M.H., 1981. Social behaviour of brown bear at MacNeil River. In: Oehser, P.H., Lea, J.S., Powars, N.L. (Eds.), *National Geographic Society Research reports*. National Geographic Society, Washington, pp. 583–590.
- Taberlet, P., Bouvet, J., 1992. Génétique de l'ours brun des Pyrénées (*Ursus arctos*) : premiers résultats, 314, pp. 15–21 [compte rendus de l'Académie des sciences de paris. Série III].
- Talbot, S.L., Shields, G.F., 1996. Phylogeography of brown bears (*Ursus arctos*) of Alaska and paraphyly within the Ursidae. *Molecular Phylogenetics and Evolution* 5, 477–494.
- Tchernov, E., Tsoukala, E., 1997. Middle Pleistocene (early Toringian) carnivore remains from northern Israel. *Quaternary Research* 48, 122–136.
- Todisco, D., Monchot, H., 2008. Bone weathering in a periglacial context: the Tayara site (Kbfk-7), Qikirtaq Island, Nunavik (Canada). *Arctic* 61, 87–101.
- Trinkaus, E., Biglari, F., Mashkour, M., Monchot, H., Reys, J.-L., Rougier, H., Heydari, S., Abdi, K., 2008. Late Pleistocene human remains from Wezmeh cave, Western Iran. *American Journal of Physical Anthropology* 135, 371–378.
- Van der Made, J., Torres, T., Ortiz, J.E., Moreno-Pérez, L., Fernández-Jalvo, Y., 2016. The new material of large mammals from Azokh and comments on the older Collections. In: Fernández-Jalvo, Y., King, T., Yepiskoposyan, L., Andrews, P. (Eds.), *Azokh cave and the transcaucasian corridor*. Springer Science +Business Media Dordrecht, pp. 117–162.
- Villa, P., Mahieu, E., 1991. Breakage patterns of human long bones. *Journal of Human Evolution* 21, 27–48.
- Weinstock, J., 2009. Epiphyseal fusion in Brown Bears: a population study of Grizzlies (*Ursus arctos horribilis*) from Montana and Wyoming. *International Journal of Osteoarchaeology* 19, 416–423.
- Zanolli, C., Biglari, F., Mashkour, M., Abdi, K., Monchot, H., Debue, K., Mazurier, A., Bayle, P., Le Luyer, M., Rougier, H., Trinkaus, E., Macchiarelli, R., 2019. A Neandertal from the Central Western Zagros, Iran. Structural reassessment of the Wezmeh 1 maxillary premolar. *Journal of Human Evolution* 135, 102643.
- Ziae, H., 2008. *The book of field guide to mammals of Iran*, 2nd ed. Wildlife Center Publication, Tharan, Iran [Persian].