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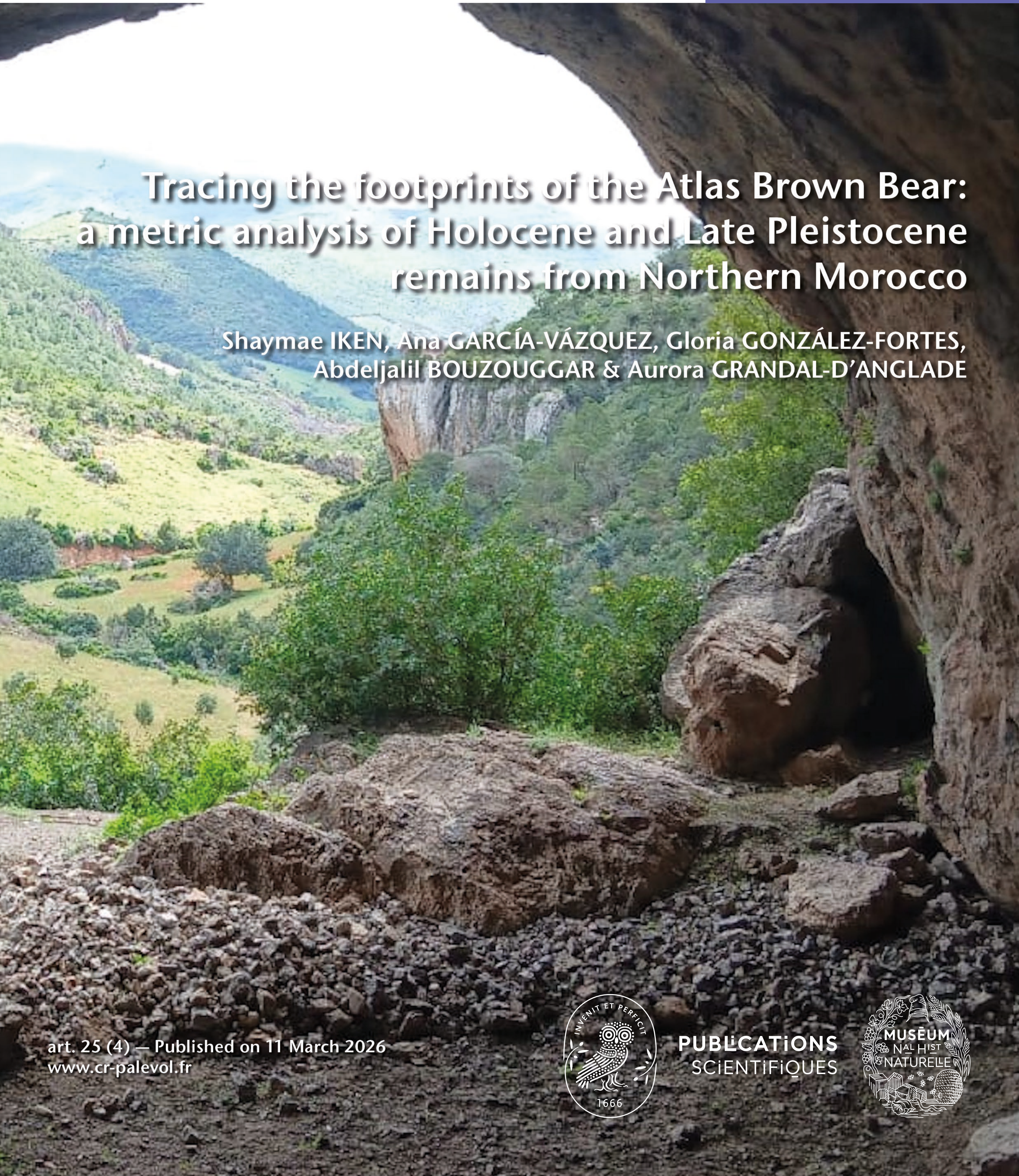

Tracing the footprints of the Atlas Brown Bear: a metric analysis of Holocene and Late Pleistocene remains from Northern Morocco

Shaymae IKEN, Ana GARCÍA-VÁZQUEZ, Gloria GONZÁLEZ-FORTES, Abdeljalil BOUZOUGGAR & Aurora GRANDAL-D'ANGLADE

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A view from the entrance of the Kehf el-Hammar cave, Northwestern Rif of Morocco. Credits: Dr. A. Bouzouggar.

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Tracing the footprints of the Atlas Brown Bear: a metric analysis of Holocene and Late Pleistocene remains from Northern Morocco

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ABSTRACT

The brown bear (*Ursus arctos* Linnaeus, 1758) once inhabited the Atlas Mountains in North Africa. Based on a traveler's description, H. Schinz, 19th-century naturalists described a new species, *Ursus crowtheri* Schinz, 1844, whose existence was soon questioned. This study presents a metric characterization of the fossil Atlas brown bear using both published and new data from Moroccan archaeological sites. The analysis focuses on phalanges and metapodials, which are more frequently preserved, and compares them with Holocene specimens from the Cantabrian Mountains (Spain) and the Zagros Mountains (Iran). Results suggest that the Atlas bear had relatively short and robust paws, partially supporting historical descriptions. No significant size difference was found between Late Pleistocene specimens and Holocene ones, although the number of Pleistocene elements is too low to draw any firm conclusions. New direct radiocarbon dating of remains from Kehf el-Hammar and Hattab II confirms a temporal range spanning the Late Pleistocene to the Holocene. Osteological evidence shows that brown bears were present in North Africa until at least the early Middle Ages. Although some aspects of Crowther's testimony remain unverifiable, his description is fairly consistent with osteological and ecological data. This suggests that the last brown bears of the Maghreb may have survived longer and been better known to local populations than previously assumed.

KEY WORDS
Ursus arctos crowtheri, Maghreb, Late Pleistocene, Holocene, radiocarbon dating, metric analysis, metapodial bones, phalanges.

RÉSUMÉ

Sur les traces de l'ours brun de l'Atlas : une analyse métrique des vestiges de l'Holocène et du Pléistocène tardif du nord du Maroc.

L'ours brun (*Ursus arctos* Linnaeus, 1758) habitait autrefois les montagnes de l'Atlas en Afrique du Nord. Sur la base de la description d'un voyageur, certains naturalistes du XIXe siècle ont décrit une nouvelle espèce, *Ursus crowtheri* Schinz, 1844, dont l'existence a rapidement été remise en question. Cette étude présente une caractérisation métrique de l'ours brun fossile de l'Atlas en utilisant à la fois des données publiées et de nouvelles données provenant de sites archéologiques marocains. L'analyse se concentre sur les phalanges et les métapodes, qui sont plus fréquemment conservés, et les compare avec des spécimens holocènes des monts Cantabriques (Espagne) et des monts Zagros (Iran). Les résultats suggèrent que l'ours de l'Atlas avait des pattes relativement courtes et robustes, ce qui confirme en partie les descriptions historiques. Aucune différence de taille significative n'a été constatée entre les spécimens du Pléistocène supérieur et ceux de l'Holocène, bien que le nombre d'éléments pléistocènes soit trop faible pour tirer des conclusions solides. De nouvelles datations directes au radiocarbone de restes provenant de Kehf el-Hammar et de Hattab II confirment une fourchette temporelle allant du Pléistocène tardif à l'Holocène. Les preuves fossiles montrent que les ours bruns étaient présents en Afrique du Nord au moins jusqu'au début du Moyen Âge. Bien que certains aspects du témoignage de Crowther restent invérifiables, sa description est globalement cohérente avec les données ostéologiques et écologiques. Ceci suggère que les derniers ours bruns du Maghreb ont pu survivre plus longtemps et être mieux connus des populations locales qu'on ne le pensait jusqu'à présent.

MOTS CLÉS
Ursus arctos crowtheri, Maghreb, Pléistocène tardif, Holocène, datation au radiocarbone, analyse métrique, os méthapodes, phalanges.

INTRODUCTION

The Atlas brown bear in the scientific literature

During the Victorian era, the exploration of distant territories and the collection of animal specimens were closely associated with prestige and recognition in the scientific world. In the 19th century, many naturalists, driven by the established Linnaean classification system and a fervent desire to discover new species, dedicated their lives to documenting the fauna of remote regions. Scientific societies actively promoted this expansion of zoological knowledge through institutional support and publication of findings.

Among these naturalists was Edward Blyth, born in England in 1810. He was deeply committed to the description of new species, which he regularly presented to the Zoological Society of London. In 1841, he was commissioned by the East India Company to curate the collections housed in the Asiatic Society of Bengal Museum, in Kolkata (Calcutta). Although his position was poorly remunerated, Blyth diligently collected specimens and submitted detailed annual reports that were published in the Society's journals and various monographs. One of his most notable contributions was in the classification and nomenclature of birds, a field that had long been plagued by inconsistencies. Blyth was among the first naturalists to recognize that species can exhibit significant variation in size and appearance across different parts of their geographical range. He maintained regular correspondence with Charles Darwin, particularly regarding the variation in domestic species, and was familiar with Alfred Russel Wallace's early work on the theory of evolution (Beddall 1972; Brandon-Jones 1997).

It is easy to imagine Blyth continuing his scientific inquiries even while travelling. In a letter sent to the Zoological Society of London in 1841, he recounts an encounter during his voyage to India with Mr. Crowther of the Queen's 65th Regiment.

Seizing the opportunity, Blyth questioned Crowther about North African wildlife, as the latter had reportedly spent time in the region. He was particularly interested in the Atlas bear and, based on Crowther's account, provided the first written description of the animal:

> "Upon questioning Mr. Crowther respecting the Bear of Mount Atlas, which has been suspected to be the Syriacus, he knew it well, and it proves to be a very different animal. An adult female was inferior in size to the American black bear, but more robustly formed, the face much shorter and broader, though the muzzle was pointed, and both its toes and claws were remarkably short (for a Bear), the latter being also particularly stout. Hair black, or rather of a brownish black, and shaggy, about four or five inches long; but, on the under parts, of an orange rufous colour: the muzzle black. This individual was killed at the foot of the Tetuan mountains, about twenty-five miles from that of the Atlas. It is considered a rare species in that part, and feed on roots, acorns, and fruits. Does not climb with facility; and is stated to be very different-looking from any other Bear." (Blyth 1841: 65)

Possibly due to the limited data available, Blyth refrained from formally describing the Atlas bear as a distinct species. This was somewhat unusual, as he was the author of numerous taxonomic entries, not only of birds but also of mammals and other taxa, based on highly detailed comparisons. Just a year earlier (Blyth 1840a, b), he had published a significant work on ovine mammals, including the description of several taxa such as the Atlas goat (*Ammotragus* Blyth, 1840), also native to the North African mountains. It is plausible that the Atlas bear intrigued him, but he did not return to the subject in his later work.

Despite the scant evidence, the Swiss zoologist Heinrich Rudolf Schinz soon included the Atlas bear in first volume of his comprehensive work *Systematisches Verzeichniß aller bis jetzt bekannten Säugethiere oder Synopsis Mammalium nach dem Cuvier'schen System* (1844). Schinz (1777-1861) was an active member of the Zurich Society for Natural Sciences and specialized in vertebrates, particularly mammals and birds. In 1833, he became Professor of Natural History at the University of Zurich. By then, he had already published several important works, including *Naturgeschichte und Abbildungen der Säugethiere. Nach den neuesten Systemen zum gemeinnützigen Gebrauche entworfen, und mit Berücksichtigungen für den Unterricht der Jugend bearbeitet* (Schinz 1824), a richly illustrated monograph featuring lithographs by the famous artist Karl Joseph Brodtmann. This work included descriptions of various bear species such as the Siberian bear, European brown bear, Tibetan bear, American black bear, Malayan bear, grey American bear, and the Cordilleran bear, but not the Atlas bear. In his later publication *Naturgeschichte und Abbildungen der Menschen und der Säugethiere, nach den neuesten Systemen und vorzüglichen Originalien bearbeitet* (1834), Schinz already hinted at the existence of African bears, albeit with skepticism:

> "There are also said to be bears in Africa in the Atlas Mountains, but even if there are, which is very doubtful, the species is certainly just as different as the East Indian bears. [translated from German by M. Resinger]" (Schinz 1824: 97).

In his later monograph on the systematics of known mammals, Schinz went further by naming a new species based on Blyth's account, although curiously, he did not credit Blyth directly. Instead, he copied the 1841 description almost verbatim, added no original observations, and named the species in honour of Mr. Crowther. Thus was born *Ursus crowtheri* Schinz, 1844 (sometimes erroneously cited as 1845), although the name is not recognized as valid today. Schinz's Latin description, clearly inspired by Blyth's text, reads:

> "Bear that is black or dark brown, long shaggy coat, red underneath, short claws, pointed black muzzle.
> Syn. Proceed. 1841, page 65.
> length?
> It lives in the mountains near Tetouan. [translated from Latin by M. Resinger]" (Schinz 1844: 302)

He also included a slightly more detailed description in German, still abridged from Blyth's original English:

> "Black or brown-black; the hair is shaggy, 4-5 inches long, the lower parts are rusty red, tending to orange, the claws are small and blunt, the face is broad, but the muzzle is pointed, black. Smaller than the black American bear. An old female was shot at the foot of the Tetouan Mountains, about 25 English miles from Atlas. This bear is rare there, feeds on roots, acorns and fruits, climbs poorly. Inhabits the Tetouan mountains. [translated from German by M. Resinger]" (Schinz 1844: 302)

However, the existence of the Atlas bear was soon called into question by other naturalists. Several explorers and scholars who had travelled through North Africa, such as Aucapitaine (1860), Lataste (1885), and Grevé (1892), reported never having encountered a bear or any similar animal. Ultimately, Ángel Cabrera, in his influential monograph on Moroccan mammals, categorically denied the bear's existence in modern times, although he did concede the possibility that bears may have inhabited the region during the Pleistocene (Cabrera 1932). This suggests that the Atlas bear had already become extremely rare, or even extinct, by the latter half of the 19th century.

Comments on the fossil record of the Atlas brown bear

Despite early zoological skepticism regarding the presence of brown bears in the Atlas Mountains, Jules René Bourguignat's 1867 exploration of the Djurdjura Mountains (Algeria) led to the discovery of brown bear remains in the Great Mosque cave at Djebel-Thaya (Bourguignat 1867, 1868, 1870). The morphological and metrical variability of these scarce remains prompted Bourguignat to describe multiple species, suggesting a progressive reduction in size and robustness. He distinguished several species: *Ursus lartetianus* (8 000-3 500 BC), large like the cave bear; *Ursus letourneuxianus* (around 3 500 BC), stocky but slightly smaller; *Ursus rouvieri*, smaller and more slender; and finally, *Ursus faidherbianus*, recent, very small and delicate.

Later, Arambourg revised these classifications, downgrading the taxonomic status of Bourguignat's species to "mutations" (Arambourg 1933). It is worth to mention that he collapsed the four types into two: the older and larger *lartetianus* and the recent and smaller *faidherbianus*. This concept influenced the following considerations about the North African brown bear taxonomy. However, it should be noted that none of these "subspecies" or "morphotypes" or "forms" are currently considered to be taxonomically valid. Later on, Ennouchi (1957) described a new subspecies, *Ursus arctos bibersoni*, based on isolated remains of a very large bear from the Sidi-Abderrahman cave in Casablanca, Morocco. Ennouchi reported metric data indicating the bear's enormous size, with a femur measuring 500 mm. Subsequent finds in the same coastal region, such as those at the Grotte des Rhinocéros and El Harhoura 2, also yielded large bear remains, dating from the Middle Pleistocene to the Middle and Late Stone Age (Geraads *et al.* 2010; Geraads & Bernoussi 2016). In fact, Geraads considers it to be a species independent from the brown bear, calling it *Ursus bibersoni* (Geraads 2008).

Despite these findings, the terminology introduced by Bourguignat persists in later works, such as in the study of bear remains from Takouatz, Algeria (Auboire & Gillon 1995) or in a review of all the Maghreb bears (Michaux & Thevenot 2007). However, modern research generally considers these bears to be *Ursus arctos*, with two primary morphotypes: the large "lartetianus" and the smaller Holocene "faidherbianus".

If we focus specifically on Northwest Africa, fossil remains of Holocene or End-Pleistocene brown bears have been identified at several Moroccan sites, including El Ksiba and Toulkine (Ennouchi 1957), Kaf Taht el-Ghar (Ouchaou & Amani 1997; Ouchaou & Hossini 2008), Ghar-Khal (Ouchaou 1999, 2021), Bou-Saria (Ouchaou 2000), Kehf el-Hammar (Slaoui 1995; Ouchaou 2008; Iken 2012; Iken *et al.* 2021), Hattab II (Iken 2012; Iken *et al.* 2021), and Ifri Oussaïd (Benabdelhadi *et al.* 2005; Ouchaou 2008) (Fig. 1). The presence of brown bears is also mentioned in two caves on the Atlantic coast of Morocco, Jbel Lahdid and Ifri N'Amr ou Moussa, although no published results are available yet (Ouchaou 2008).

Most of these sites are anthropogenic in origin, with a broad faunal spectrum, in which brown bears make up a minority. According to Ouchaou & Amani (2002), carnivore remains account for around 2% of the large mammal fauna at most of these Moroccan caves, up to around 4% in Ghar-Khal (Ouchaou 2021). Furthermore, carnivores are better represented in the oldest levels, from the Epipaleolithic and the transition to the Neolithic. For instance, several ^{14}C dates available on charcoal and other material from Kaf-That-el-Ghar cave (Daugas *et al.* 1998, 2008) place most of the brown bear remains at levels in the first half of the Holocene (Ouchaou & Hossini 2008). At Ghar-Khal, ^{14}C dating on charcoal places the levels with the most brown bear remains in the Upper Pleistocene-Holocene transition (around 13 000 cal BP, Bouzouggar *et al.* 2005).

Direct dating are scarce for the bear remains from Morocco, with only two dates up to now: an almost complete bear skeleton from the Ifri Oussaïd cave, dated to 7 300 ± 40 years ^{14}C BP (8 180-8 019 cal BP) (Fontugne *et al.* 2012). Another dating, from a femur fragment found at El Ksiba, places the bear in the historical period, with an age of 1 285 ± 30 years BP (cal 662-778 AD), confirming the presence of brown bears in Morocco into historical times (Calvignac *et al.* 2008).

Objectives of this study

This study aims to metrically characterize the Atlas brown bear, especially in Morocco. However, the limited available data present a challenge for conducting a comprehensive metric analysis or determining whether the bear's size was smaller than that of other contemporary bears, as Crowther described to Blyth. In this work, we conduct a metric comparison of new metric data of brown bears from North African sites, and other from published sources, with the Holocene brown bear from sites in the Cantabrian Mountains in northern Iberia (García Vázquez 2015), and with the Syrian brown bear from Wehzmez Cave in Iran (Monchot *et al.* 2020). A review of the literature has revealed that certain anatomical segments, such as the phalanges and, to a lesser extent, the metapodials, are generally better preserved, allowing for the extraction of their main dimensions. In this work, we have gathered metric data from these elements.

The aim is to determine whether the proportionally small paw, as described by Blyth (1841), is indeed a characteristic of the Atlas brown bear. Additionally, we seek to assess whether Crowther's account was based on real observations or whether the description of the Atlas bear was a result of an error, or even a fabrication, as suggested by some zoologists, such as Lataste (1885) and Cabrera (1932). Given the paucity of data, this paper is a qualitative rather than quantitative approximation of the size and shape of the paws of the Atlas brown bear.

Finally, we contribute to the chronology of the brown bear in the Atlas through four new direct ^{14}C dating of brown bear skeletal remains from two caves in Morocco.

MATERIAL AND METHODOLOGY

For this metric study, we included new data from two caves in northern Morocco, near the city of Tetouan: Kehf el-Hammar and Hattab II.

Kehf el-Hammar

Kehf el-Hammar is in the Chefchaouen region of northwestern Morocco, about ten kilometers from the Mediterranean coast, at an altitude of 97 m a.s.l. (Barton *et al.* 2005). The site's chronology is based on several ^{14}C charcoal dates along the stratigraphic profile (Barton *et al.* 2005), placing its infill at the end of the Pleistocene. The first excavation, conducted

Fig. 1. — Map showing the Moroccan sites (North Africa) that yielded brown bear remains from the Late Pleistocene and Holocene. It also shows the Cantabrian Mountains where the Iberian sites of the same period, used as a comparison in the metric study, are located. It is noteworthy that many of the sites are on the Tingitan peninsula, near the city of Tetouan, where the bear that Crowther described to Blyth in 1841 (Blyth 1841) came from.

in 1992, yielded a few brown bear bones (Ouchaou 2000). Subsequent excavations in 2001, 2002, and 2003, led by Prof. Abdeljalil Bouzouggar (National Institute of Archaeological Sciences and Heritage, INSAP, Morocco) and Prof. Nick Barton (School of Archaeology, University of Oxford), uncovered additional faunal material.

In a preliminary study that included taxonomic identification and metric analysis, Iken (2012) identified 46 brown bear skeletal remains throughout the 2.2 m-deep sedimentary sequence: 28 phalanges, seven metapodials, three vertebrae, one proximal radius fragment, two distal humerus fragments, one jaw fragment, one patella, one pisiform, and two isolated first upper molars. Ouchaou (2000) also reported the presence of a lower canine, a proximal ulna fragment, a proximal radius fragment, and three phalanges from the 1992 excavation.

Brown bear remains are primarily found in the upper levels (1 to 3) and even on the surface. According to charcoal dating (Barton *et al.* 2005), Level 3 dates to 13354 ± 50 BP. Ouchaou (2000) also described two phalanges from Level 4, dated to 13805 ± 55 BP. Only two remains originate from Level 7, which has been dated to 15940 ± 80 BP. For this study, we selected a brown bear bone from the surface of the infill for ^{14}C dating.

Hattab II Cave

Hattab II Cave is located approximately 45 km east of Tetouan, in the Ouled Ali Mansour valley, about 12 km from the Mediterranean coast. Excavations were carried out in 2002 and 2003 by Prof. A. Bouzouggar and Prof. N. Barton. The stratigraphic sequence consists of five levels (5 to 9) attributed to the Late Stone Age, based on the lithic industries identified, and a more recent level (Level 3) assigned to the Neolithic. Levels 2 and 4 consist of stalagmitic flows, although only the upper one is thick and continuous. Level 1 contains a mix of reworked materials, including some bones (Bouzouggar *et al.* 2008).

TABLE 1. — Direct ^{14}C dating of brown bear remains from several stratigraphic levels in Hattab II and of surface remains in Keft el-Hammar, and their 2σ calibration (95.4%) using software OxCal 4.4 (Bronk Ramsey 2009) and the IntCal20 calibration curve from Reimer *et al.* (2020).

Cave	Level	Bone code	Bone type	Dating lab code	AMS ^{14}C y BP	Cal y BP from	Cal y BP to
Keft el-Hammar	surface	HST-1	humerus	Beta-614566	9080 ± 30	10281	10189
Hattab II	Level 3	HAT-212	radius	Beta-614563	9400 ± 30	10716	10512
Hattab II	Level 8	HAT2-674	3rd phalanx	Beta-614564	9480 ± 30	11065	10584
Hattab II	Level 9	HAT2-1213	radius	Beta-614565	8850 ± 30	10155	9763

The faunal material from this site is currently under study (Iken, personnal communication). Among the recovered remains, 16 bones or bone fragments were morphologically identified as brown bear, including one skull fragment, 11 phalanges, four radius fragments, and one vertebra. No metapodials have been found so far.

The remains were recovered from Levels 3, 5/6, 6, 7, 8, and 9. The only chronological reference available for this site is an OSL (optically stimulated luminescence) date from a lithic piece recovered in Level 8, near a human burial, which yielded an age of 8 000 years BP (Barton *et al.* 2008). For this study, we selected three brown bear bone remains from different depths (Levels 3, 8, and 9) for ^{14}C dating.

Furthermore, we compiled published data on brown bear metrics from Moroccan sites, primarily Ifri Oussaïd (Ouchaou 2008) and Kaf-Taht-el Ghar (Ouchaou 2000). Additionally, limited data were sourced from the caves of Ghar-Khal, Kehf el-Baroud, and Bou-Saria (Ouchaou 2000). To contextualize our study, we compared the Atlas bear remains with well-characterized metrically and genetically brown bear data from several sites in the Cantabrian Mountains (northern Iberian Peninsula), where the species was abundant during the Holocene (García Vázquez 2015; García-Vázquez *et al.* 2019). Additionally, we gathered metric data on the Syrian brown bear from Wezmeh Cave in the Zagros Mountains, Iran (Monchot *et al.* 2020). The number of each of the elements included in this study can be found in Appendix 1.

Metric data were collected using a digital caliper. For the first and second phalanges, we measured the total length, transverse and anteroposterior width of the proximal epiphysis, as well as the transverse width of the diaphysis and distal epiphysis. For the third phalanx, we measured total length, proximal breadth, and proximal height. Appendix 2 shows the position of the measurements taken, based on those proposed by Tsoukala & Grandal-d'Anglade (2002) for Ursidae.

Metric data for metapodials are scarce in the literature. At Ifri Oussaïd, complete measurements were available, including length, transverse width, and anteroposterior width of the epiphyses and diaphysis (Ouchaou 2008). In all other cases, only total length and a robustness index, calculated from the transverse width of the diaphysis and total length, were available. Since the width of the diaphysis can be derived from this index, we used only these two measurements for metric comparisons. The calculation of the width of the diaphysis from the index of robustness is shown in Appendix 3.

Due to the small sample size and the incomplete nature of published metric data from some sites, extensive statistical analyses were not feasible. Therefore, for our comparative study, we employed violin and box-and-whisker plots as well as bivariate plots, made with PAST (Hammer *et al.* 2001). Only in the specific case of the first and second phalanges were simple statistical tests (t-test and Mann-Whitney U test) performed to test the differences in length between the Atlas bears and the Cantabrian bears.

For ^{14}C dating, we selected fragments of compact bone weighing between 1 and 4 g from brown bear skeletal remains recognisable by their morphology. The samples were sent to the Beta Analytic Inc. laboratory (Miami, United States) where they underwent a classic organic matter extraction treatment (acid-alkali-acid) prior to graphitisation and dating by Accelerator Mass Spectrometry (AMS).

The materials and originating from Kef el Hammar and Hattab II used in this work are kept at the National Institute of Archaeological Sciences and Heritage (INSAP) in Rabat, Morocco.

RESULTS

RESULTS OF THE ^{14}C DATING

The results of the ^{14}C dating are shown in Table 1. At Keft el-Hammar, the bone dated on the surface of the sedimentary fill is markedly more modern than the dates obtained on the charcoals in the stratigraphic sequence. At Hattab II, on the other hand, the age is very similar for all bones, regardless of their stratigraphic level. In all cases, the new dates fall within the Holocene, at a time after the Younger Dryas, but before the short cold pulse of 8.2 Ky BP.

METRIC DATA OF THE ATLAS BROWN BEAR PHALANGES AND METAPODIALS

A total of 45 first phalanges, 23 second phalanges and 30 third phalanges of the Atlas bear were included in the study (see details in Appendix 1). Metapodials are very rare in the Atlas sites, and not all of them are measurable. We have been able to collect measurements of 24 metacarpals and 30 metatarsals. For most of them, we only have the total length and the width of the diaphysis (calculated in many cases based on the robustness index, see Appendix 3). The statistical summary of the measurements is shown in Table 2. Detailed measurements as shown in Appendix 2 are in Appendix 4.

TABLE 2. — Summary of the dimensions of the metapodials and phalanges of the Atlas brown bear, both from the literature and new ones provided in this work Abbreviations: **APW prox**, proximal anteroposterior width; **H prox**, proximal height; **TL**, total length; **TW dia**, transverse width of diaphysis; **TW dis**, distal transverse width; **TW prox**, proximal transverse width. Detailed measurements are given in Appendix 4.

1st phalanx	**TL**	**TW prox**	**APW prox**	**TW dia**	**TW dis**
mean	36.9	18.2	14.6	11.4	13.3
desv. st.	4.3	2.0	1.4	1.6	1.0
min	30.7	15.8	12.0	9.2	11.8
max	51.0	24.0	18.3	17.3	16.4
n	47	48	46	48	44
2nd phalanx	**TL**	**TW prox**	**APW prox**	**TW dia**	**TW dis**
mean	25.4	15.8	14.4	11.7	13.8
desv. st.	4.7	1.7	2.3	1.4	1.2
min	17.9	13.1	11.2	9.8	12.1
max	34.0	19.5	20.2	14.3	16.0
n	23	22	22	23	23
3rd phalanx	**TL**	**TW prox**	**H prox**		
mean	40.1	25.3	13.6		
desv. st.	9.3	3.0	1.5		
min	28.0	21.0	11.0		
max	56.3	33.0	16.7		
n	30	30	33		
1st metacarpal (MC I)	**TL**	**TW dia**	**1st metatarsal (MT I)**	**TL**	**TW dia**
mean	60.7	9.5	mean	61.2	9.2
desv. st.	2.2	0.8	desv. st.	4.3	0.6
min	57.0	8.9	min	55.6	8.3
max	63.5	10.8	max	66.4	10.0
n	7	7	n	9	9
2nd metacarpal (MC II)	**TL**	**TW dia**	**2nd metatarsal (MT II)**	**TL**	**TW dia**
mean	68.9	10.8	mean	51.8	10.8
desv. st.	1.6	1.5	desv. st.	28.7	1.6
min	66.6	9.8	min	9.0	9.0
max	69.9	13.0	max	70.0	12.8
n	4	4	n	4	4
3rd metacarpal (MC III)	**TL**	**TW dia**	**3rd metatarsal (MT III)**	**TL**	**TW dia**
mean	73.3	10.8	mean	72.0	11.3
desv. st.	1.5	0.4	desv. st.	2.2	0.5
min	71.8	10.5	min	70.0	11.0
max	75.0	11.4	max	74.5	12.2
n	4	4	n	5	5
4th metacarpal (MC IV)	**TL**	**TW dia**	**4th metatarsal (MT IV)**	**TL**	**TW dia**
mean	75.4	13.2	mean	75.4	12.6
desv. st.	5.1	1.7	desv. st.	4.1	1.0
min	710	12.0	min	72.0	11.5
max	84.2	16.1	max	86.0	14.7
n	5	5	n	9	9
5th metacarpal (MC V)	**TL**	**TW dia**	**5th metatarsal (MT V)**	**TL**	**TW dia**
mean	72.0	12.7	mean	77.6	10.9
desv. st.	1.5	1.2	desv. st.	1.8	0.6
min	70.2	11.5	min	76.0	10.3
max	73.4	14.3	max	79.8	11.7
n	4	4	n	4	4

DISCUSSION

METRIC COMPARISON

The description of the Atlas bear provided by Crowther and reported by Blyth (1841) states of the specimen – a female – that: "Both its toes and claws were remarkably short (for a Bear), the latter being also particularly stout." With the data obtained so far, it is possible to compare the dimensions of the metapodials and phalanges of the Atlas brown bear with those of Holocene brown bears from the Cantabrian Mountains in the Iberian Peninsula, and, to a lesser extent, with the Syrian brown bear (*Ursus arctos syriacus*), for which data are more limited.

Considering only the total length of the metapodials, both the metacarpals and metatarsals of the Atlas bears are shorter than those of the Cantabrian brown bears (Fig. 2).

In brown bears, the metatarsals increase in size progressively from the first to the fifth, as described by Torres Pérez-Hidalgo (1988a) in a large sample from the Iberian Peninsula.

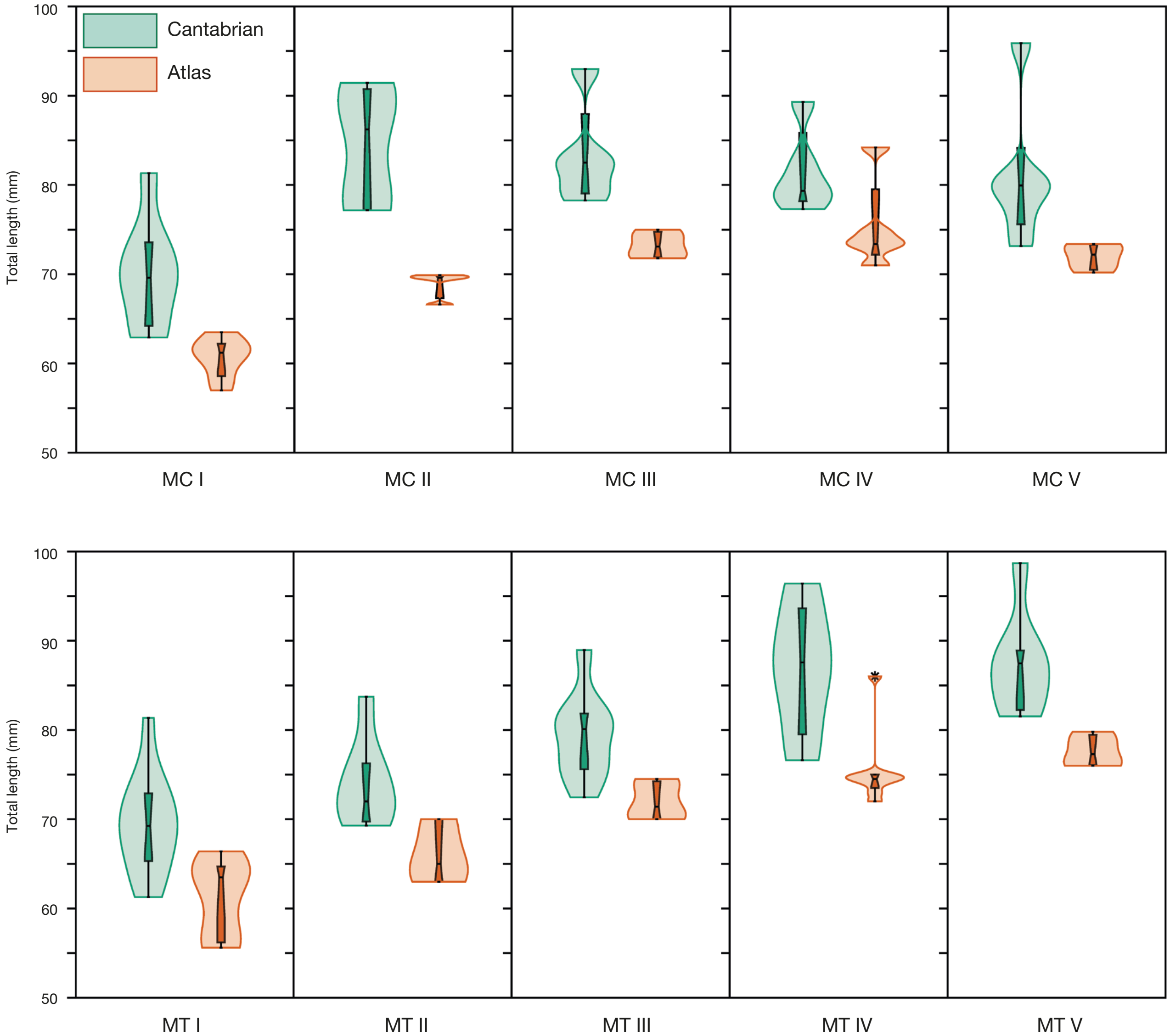

Fig. 2. — Violin plots of Atlas bear metapodial lengths compared with those of Holocene Cantabrian brown bears (García Vázquez 2015). The violin outline represents a kernel density estimation of the data distribution. Embedded box plots indicate the median and the 25-75% interquartile range. Whiskers extend to values within 1.5 times the interquartile range, while outliers are shown as circles, and extreme values exceeding three times the interquartile range are marked with **stars**.

This pattern is mirrored in both the Atlas and Cantabrian bears, suggesting that, despite the small number of elements available, the expected trend is maintained. In contrast, the metacarpals of the forelimb do not follow the same pattern of progressive increase in length. While the first metacarpal is clearly shorter, the lengths of the remaining metacarpals are more uniform (Torres Pérez-Hidalgo 1988b). This trend is also evident in the comparison between the Atlas and Cantabrian bears.

The figure also reveals a certain bimodal tendency in the length of some metapodials, which may reflect sexual size dimorphism. Sexual dimorphism is a well-documented trait in brown bears. At present, in Europe, males weigh approximately twice as much as females in the spring and around 1.7 times as much in the fall (Swenson *et al.* 2023). Although it does not affect the entire skeleton equally, sexual dimorphism can also be expressed in the metapodials, as observed in the Pleistocene cave bear *Ursus spelaeus* (see for instance Grandal-d'Anglade 1993; Baryshnikov & Puzachenko 2017).

In some cases, outliers are observed in the dataset, as in as in the fourth metacarpal and fourth metatarsal of the Atlas bears, or in the third, fourth, and fifth metatarsals of the Cantabrian bears. Whether these outliers are due to exceptionally large individuals within each population, or to a higher representation of females compared to males, cannot be determined based solely on length. The bivariate plots of total length and transverse shaft width (Fig. 3) provide greater detail regarding size and proportions.

We could hypothesize that the Atlas bear sample is composed primarily of females, and that the individuals whose lengths appear as outliers are males. Even so, their overall size remains smaller than that of the Cantabrian bears, although they appear equally robust, or possibly even more so.

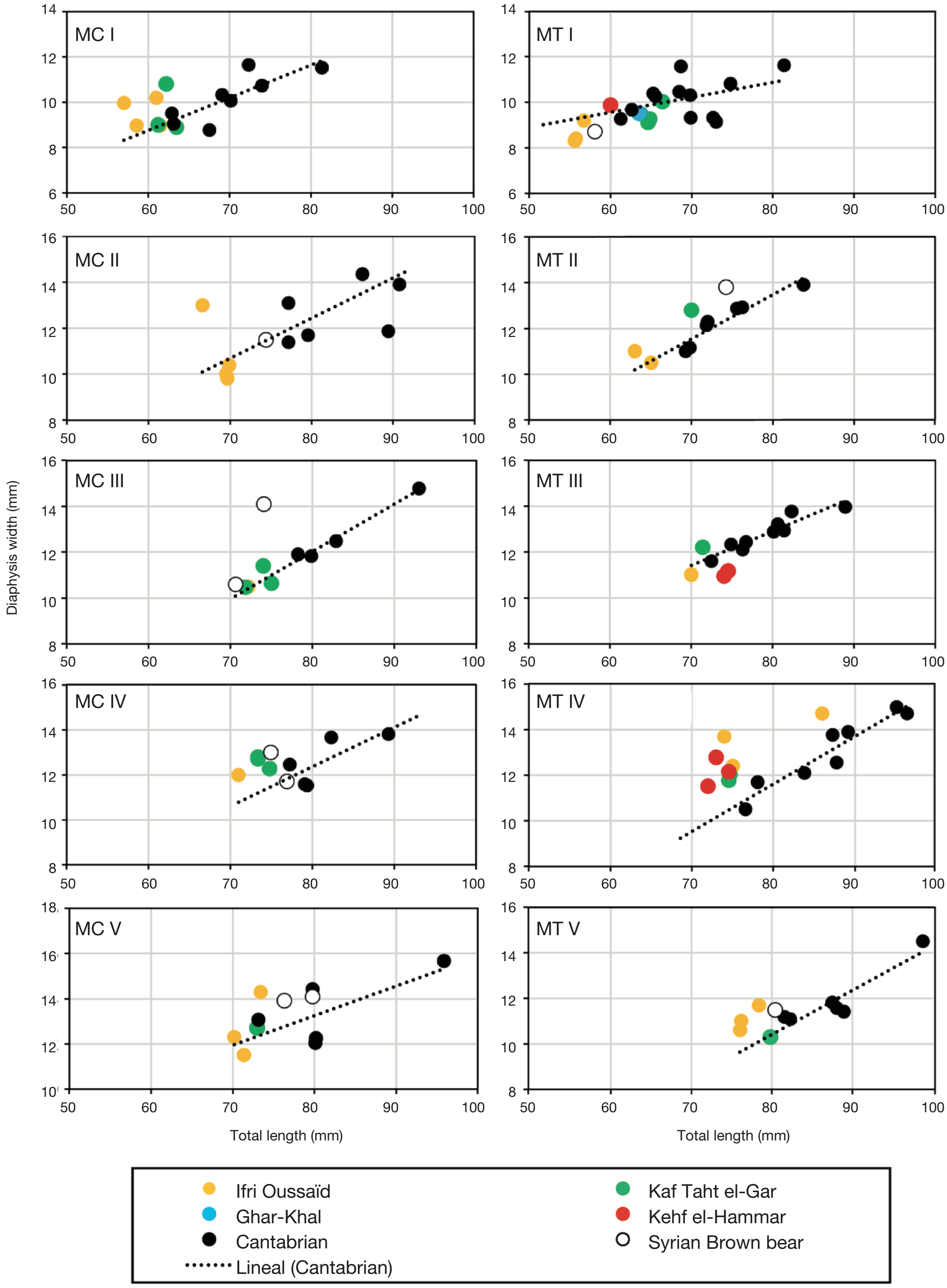

Fig. 3. — Bivariate plots of metapodial dimensions (total length against diaphysis transversal width) of Atlas bears compared with those of Cantabrian brown bears (García Vázquez 2015). The trend line of the latter is represented for comparative purposes. Data from Syrian brown bear from Iran (Monchot *et al.* 2020) are added.

Although the number of cases is small, we see this trend towards greater robustness of the Atlas bears in the first and fourth metacarpals, in the fifth metatarsal and especially in the fourth metatarsal, of which there are also more elements in the analysis.

Therefore, although the number of elements analyzed is limited, and although we only have two dimensions for comparison, we can see that the metapodials of the Atlas bear are shorter and, in some cases, clearly more robust, proportionally, than those of the Cantabrian brown bear. This could explain why the Atlas bear's paws seemed so short, as Crowther mentioned.

As for the phalanges, several caveats complicate their metric characterization. First, the phalanges of each digit differ in size and robustness. According to Koby & Fritz (1950), among

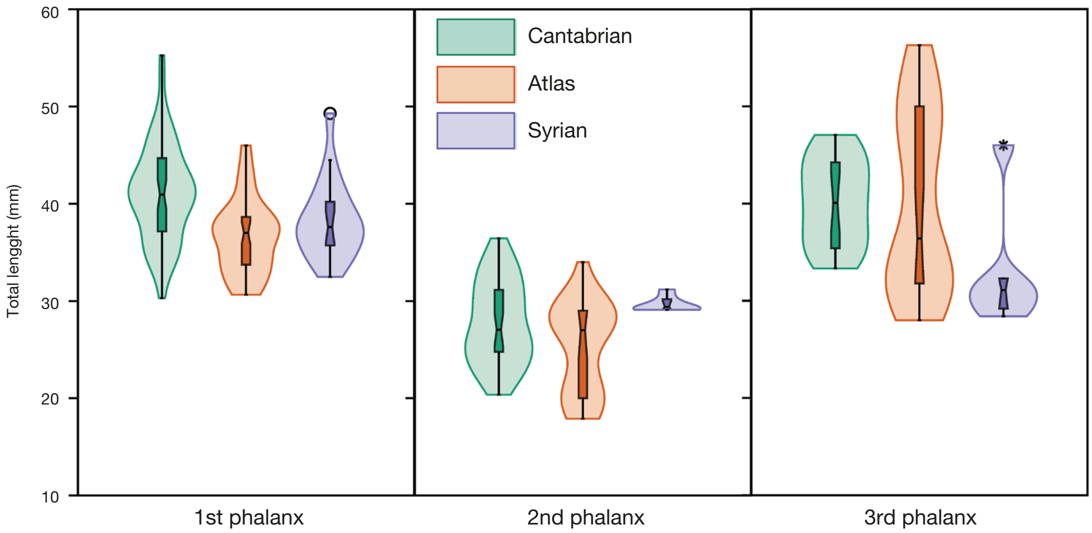

Fig. 4. — Violin plots of Atlas bear phalanges lengths compared with those of Cantabrian brown bears (García Vázquez 2015). Data from Syrian brown bear from Iran (Monchot *et al.* 2020) are added. Extreme values exceeding three times the interquartile range are marked with **star**.

the first phalanges of brown bears, that of digit I is always the longest. In a small sample like the one under study, it is likely that the phalanges of each digit are not equally represented. Moreover, front and hind phalanges are not the same size. This is especially evident in the third phalanges, which support the claws; in brown bears, the forelimb phalanges are significantly longer than those of the hindlimbs. Since it is not possible to confidently distinguish the phalanges by digit or by limb, each dataset necessarily represents a heterogeneous mix. Finally, it must be remembered that sexual dimorphism may also affect phalangeal size.

Nevertheless, Figure 4 shows that the first and second phalanges of the Atlas bear tend to be shorter than those of the Cantabrian brown bear, and also slightly shorter than the Syrian bear. A t-test for the length of the first phalanges shows significant differences in the mean (p same mean = 2.90E-03), and the same is true for a Mann-Whitney test for equal medians (p same median = 4.9102E-06), when comparing the Atlas and the Cantabrian groups. In the second phalanges, on the other hand, the differences are close to the significance threshold, without quite reaching it. In contrast, the distribution of the third phalanges is markedly different. The bimodality is especially pronounced in the Atlas bear compared to the Cantabrians. The Syrian bear may also follow this bimodal trend, but the available data are insufficient to confirm it.

Additionally, Atlas bears show the most extreme lengths. In this case, we might suggest that the size difference between front and hind claws is even greater in the Atlas bear than in the Cantabrian one. This observation seems to contradict Blyth's account, "Both its toes and claws were remarkably short", but it is important to recall that the described specimen was a female, and its dimensions were likely less pronounced than those of the males.

When examining the bivariate plots of the phalanges, comparing proximal widths to total lengths (Fig. 5), a significant difference emerges in the third phalanges. These show not only extreme lengths – both shorter and longer than those of the Cantabrian bears – but also a much greater proximal height, especially in the longer (presumably forelimb) phalanges. The increased height in this proximal area would result in particularly robust claws, which aligns perfectly with Crowther's observations as described by Blyth. The most robust are those of the Kaf Taht el-Gar cave, but in general, all the Atlas sites show this trend.

In summary, the metric comparison highlights differences in size and proportions between the Atlas bears and Cantabrian brown bears, with the former generally showing shorter but equally or more robust skeletal elements.

Chronology and body size

The four new direct radiocarbon dates presented in this study, together with one already available (Fontugne *et al.* 2012) do not cover all the sites included in the analysis, but only three of them: Ifri Oussaïd, Kehf el-Hammar, and Hattab II. None of them go beyond the Holocene. Thus, we do not have any bear remain directly dating to the Pleistocene.

However, there are two cases where the stratigraphic chronology points to slightly older ages. At Kehf el-Hammar the carbon dating of the levels from which the bear remains were recovered are from the very end of the Late Pleistocene. The oldest level with bear remains (Barton *et al.* 2005) is around 19 500-19 000 y cal BP. At Kaf-That-el-Gar, ^{14}C dating of charcoals from the archaeological sequence (Daugas *et al.* 1998, 2008; Martínez Sánchez *et al.* 2021) shows that the lower level also has an End-Pleistocene date, around 15 000-16 500 y cal BP.

This is probably not a long enough time span to assess whether there was a decrease in bear size over time, as suggested by Bourguignat (1870) and endorsed by Arambourg (1933). In fact, based primarily on the dimensions of the molars – of which there is a larger number of remains – Ouchaou (2000, 2008) concludes that bears from the

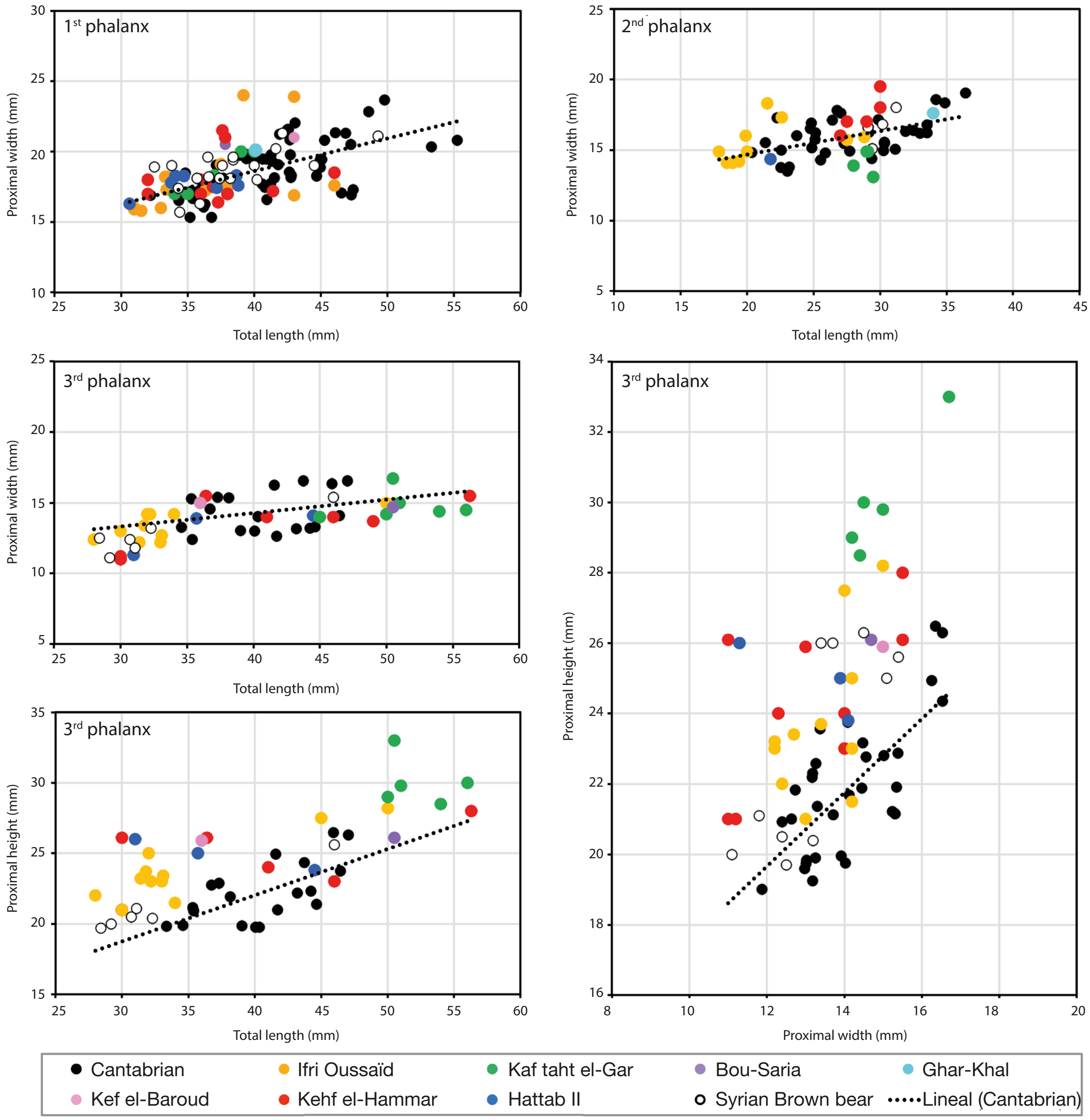

Fig. 5. — Bivariate plots of phalanges dimensions (Length against proximal breadth and proximal height) of Atlas bears, taken from the literature and unpublished, compared with those of Cantabrian brown bears (García Vázquez 2015). The trend line of the latter is represented for comparative purposes. Data from Syrian brown bear from Iran (Monchot *et al.* 2020) are added.

Neolithic and Protohistoric periods are smaller than those from the Paleolithic and Epipalaeolithic. Comparing the scarce End-Pleistocene materials with the Holocene ones (Fig. 6) there does appear to be a decrease in the length of Holocene second phalanges and second, third and fifth metatarsals with respect to the Pleistocene ones. However, very few brown bear elements come from the oldest levels, and in the metatarsals, only one or two elements: clearly, an insufficient number of data to draw a conclusion.

The key issue, however, remains the accurate determination of the chronological context of the materials under analysis. At Hattab II, our dating results yield similar ages regardless of the stratigraphic level from which the samples were taken (see Table 1). This strongly suggests that the sequence is disturbed, as noted by Barton *et al.* (2008), who attribute some of the mixing to animal burrowing. A similar issue has been observed at other sites, such as Ghar-Khal, where recent excavations have revealed signs of disturbance (Ouchaou 2021). Likewise, bioturbation likely contributed to the mixing of Neolithic and older Epipalaeolithic materials at Kaf Taht el-Ghar (Daugas *et al.* 1998). However, in this case, a combination of radiocarbon dating, and ceramic decorative styles supports the integrity of the stratigraphic sequence (Martínez Sánchez *et al.* 2021). In contrast, the Keft el-Hammar sequence shows a good correlation between the depth of the levels and the radiocarbon ages of the carbon samples, despite the presence of some

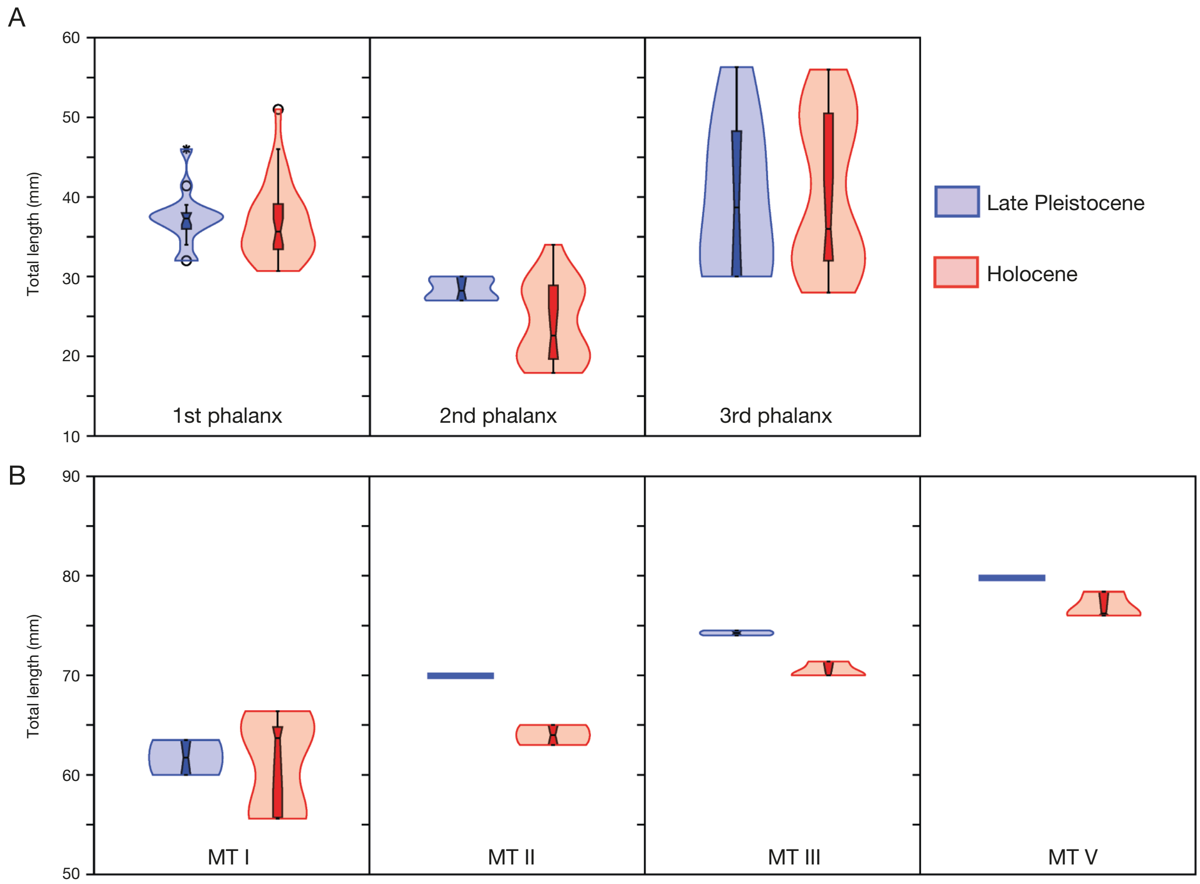

Fig. 6. — Box-and-whisker representation of the total length of phalanges (**A**) and metatarsals (**B**), comparing the End-Pleistocene elements from Kehf el-Hammar, Ghar-Khal and some from Kaf Taht el-Gar with the Holocene ones (from Ifri Oussaïd, Hattab II, Bou-Saria, Kef el-Baroud and Kaf Taht el-Gar).

burrows along the two-metre stratigraphic profile (Barton *et al.* 2008; Bouzouggar *et al.* 2008). Altogether, these findings underscore the importance of obtaining a substantial number of direct radiocarbon dates when attempting to compare size or other attributes over time.

Details on historiography

The main doubts regarding the accuracy of Crowther's account, as transcribed by Blyth, revolve around two key issues. First, the apparent absence of knowledge among the local population about the presence of bears. As Aucapitaine noted just twenty years later, the inhabitants of the region did not even seem to know the animal's name (Aucapitaine 1860). This would suggest that the extinction of the Atlas bear in North Africa may have occurred within that short time frame.

Second, Cabrera (1932) almost jokingly suggested that what Crowther actually saw might have been no more than the skin of another animal, perhaps a large wild boar. Blyth indeed comments that it was not possible to preserve the skin of the specimen. However, Crowther's account gives the impression that he saw the freshly killed body of a hunted animal rather than just its hide. In addition to describing the fur, he comments on characteristics such as overall size and robustness, the short and broad face, and the pointed shape of the muzzle, all of which are difficult to infer from a loose skin alone.

Regarding the size, Crowther claimed that the specimen he observed was "smaller than an American black bear". This comparison is intriguing, as it implies that Crowther was familiar with the American species, an animal from a different continent. It is possible he encountered one during military service abroad, or perhaps he had seen one at the Zoological Gardens in London, where a juvenile black bear had been on display since 1829 (Zoological Society of London 1829). Access to the Gardens, however, was limited to Society members until 1847. Another possibility for seeing a black bear was the Tower of London Royal Menagerie, a collection of exotic wild animals that existed from 1 200 to 1835, which housed at least one yellow American black bear or "cinnamon bear" in 1821 (Griffith 1821: 236), to which another American black bear, probably with common fur, was added in 1824 (Bennet *et al.* 1829: 120).

In any case, it's difficult to determine how Crowther was able to make a reliable comparative assessment of the Atlas bear's size, just as it remains difficult today to estimate the overall dimensions of the Holocene North African population due to the fragmentary nature of the fossil record. No available measurements allow us to reconstruct the width of the face or the exact shape of the muzzle. However, we have seen that the toes of Atlas bears are generally shorter than those of coeval Cantabrian bears, and their claws, if not shorter, are certainly more robust, details that are consistent with Crowther's description.

As for behavioral traits, the metric analysis offers limited information. According to Crowther, the Atlas bear "feeds on roots, acorns, and fruits. Does not climb with facility." This information likely came from local informants, as such details cannot be gleaned from observing a dead animal. Alternatively, Crowther may have inferred the diet based on what was already known about European brown bears at the time. Schinz, for example, offered a detailed description:

> "The bear's diet is chosen from the plant and animal kingdoms, and among all the carnivores it is least restricted to meat, as evidenced by its fine molars, which are adept at chewing and grinding. […] Despite feeding on plants, it is a true predator and its strength allows it to attack large animals" (Schinz 1824: 97).

In contrast, the Atlas bear's diet, as inferred from both Crowther's report, seems to have been more plant-based. Notably, there is no mention of animal prey. This suggests a possibly more herbivorous lifestyle compared to its European relatives.

To approach the diet of fossil bears with greater objectivity, stable isotope analysis of bone collagen can be used. This technique has already been applied to fossil Cantabrian brown bears, revealing a strong plant-based component in their diet (García-Vázquez *et al.* 2018). For Atlas bears, only one such analysis is currently available: a specimen from Ifri Oussaïd (García-Vázquez *et al.* 2024), which, although limited in scope, similarly suggests a low-carnivorous dietary pattern.

In short, although the nineteenth-century accounts of the Atlas bear must be read with caution, the partial alignment with current data suggests that it was not a mere confusion, but a real population, poorly understood and already absent by the time scientific interest began to grow.

CONCLUSIONS

The metric analysis presented in this study supports the idea that the paws of the Atlas brown bear were shorter and proportionally more robust than in the Holocene Cantabrian population. The reduced paw size described by Blyth (1841) based on Crowther's account, is partially supported by the shortness and relative proportions of the metapodial bones and first phalanges, although the available data remain limited and fragmentary. Notably, however, the third phalanx in the Atlas sample is comparatively more robust, which would have facilitated particularly strong claws. The only clear departure from Crowther's description concerns the length of the third phalanx: in one assemblage these elements are conspicuously longer than those of Cantabrian bears, whereas in others they are shorter. This variability may reflect sexual dimorphism – if Crowther's specimen was female, its claws may indeed have been relatively short – or, more simply, differences between the anterior and posterior digits.

In summary, the metapodial and proximal phalanx morphology of the Atlas bear broadly corroborates Crowther's observations of short and robust toes and claws, although some site-specific variation in the terminal phalanges indicates that the full extent of this trait may not have been uniform across populations.

The fossil record reviewed here confirms the presence of brown bears in the Atlas Mountains well into the Holocene, with remains from both Late Pleistocene and Holocene contexts. However, there is no clear evidence of a progressive reduction in body size over time, as hypothesized by Bourguignat in the 19th century. We did not manage to collect enough metric data, and the data that we have is not old enough to allow us to make a reliable comparison of sizes.

Finally, although Crowther's testimony cannot be confirmed with certainty, it is not inconsistent with the known morphology of the Atlas bear. His detailed description – often questioned by later zoologists – aligns in several aspects with osteological gathered from Moroccan sites, suggesting that his account, while anecdotal, may reflect a real encounter with a now-extinct population of *Ursus arctos* in North Africa.

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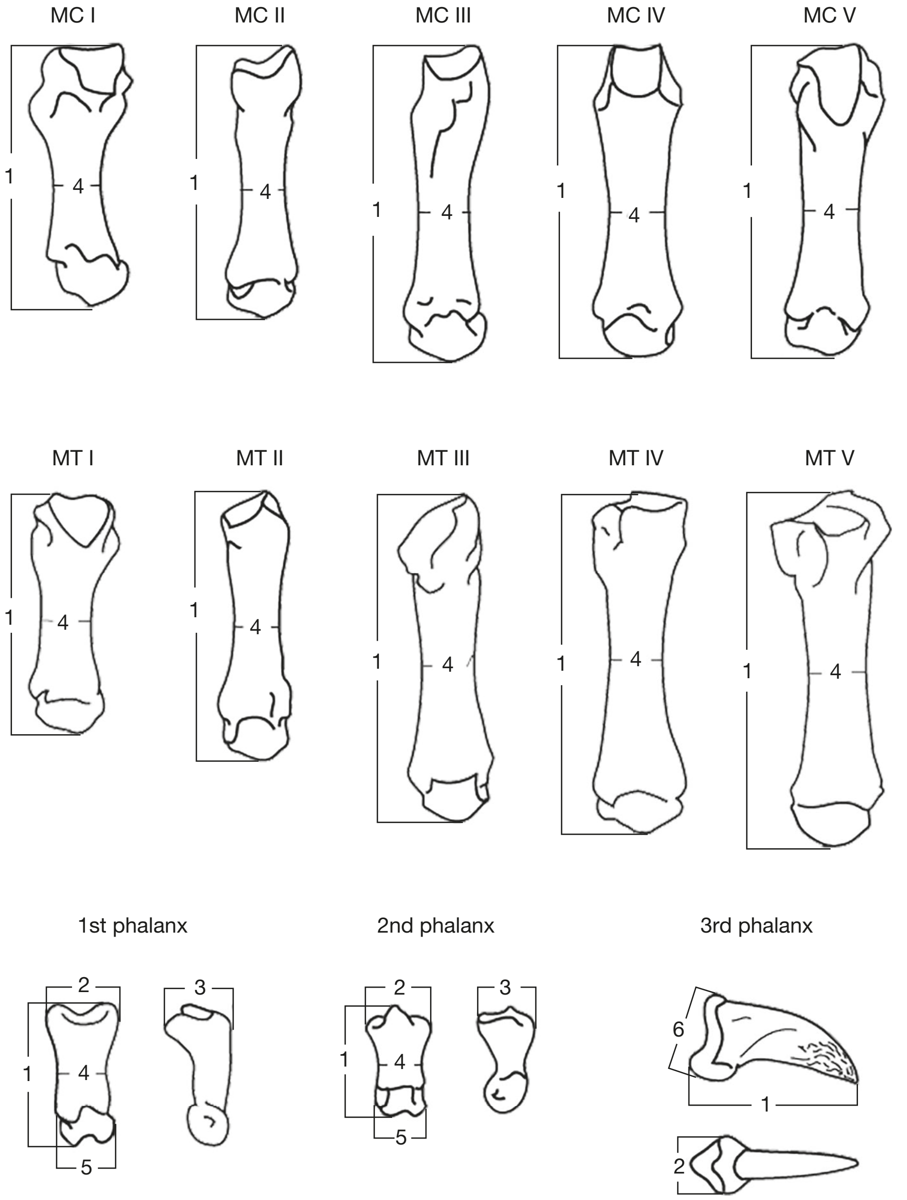
APPENDICES

Appendix 1. — Number of elements of each anatomical segment studied in this work, and the source of the data.

	Phalanges			Metacarpals					Metatarsal					
Cave	**1st**	**2nd**	**3rd**	**I**	**II**	**III**	**IV**	**V**	**I**	**II**	**III**	**IV**	**V**	**Source**
Hattab II	7	1	3	–	–	–	–	–	–	–	–	–	–	This work
Keft el Hammar	13	7	9	–	–	–	–	–	1	–	2	3	–	Iken 2012
Ifri Oussaïd	16	11	11	3	4	1	2	3	3	2	2	4	3	Ouchaou 2008
Kaf-taht-el Ghar	6	4	7	4	–	3	3	1	4	1	1	2	1	Ouchaou 2000
Ghar Khal	1	1	–	–	–	–	–	–	1	–	–	–	–	Ouchaou 2000
Bou-Saria	1	–	1	–	–	–	–	–	–	–	–	–	–	Ouchaou 2000
Kehf el Baroud	1	–	1	–	–	–	–	–	–	–	–	–	–	Ouchaou 2000
Total Atlas bear	45	23	30	7	4	4	5	4	9	3	5	9	4	–
Cantabrian	60	35	35	8	8	5	6	5	12	7	9	8	6	García-Vázquez 2015
Syrian Brown bear	19	7	6	–	1	2	2	2	1	1	–	–	1	Monchot *et al.* 2020

Appendix 2. — Diagram of the measurements used on the metapodials and those taken on the phalanges of brown bears, based in Tsoukala & Grandal-d'Anglade (2002). Abbreviations: **APW prox**, proximal anteroposterior width; **H prox**, proximal height; **TW dia**, transverse width of diaphysis; **TL**, total length; **TW dis**, distal transverse width; **TW prox**, proximal transverse width.



Appendix 3. — Calculation of the diaphysis transversal width (**TW dia**) of metapodials, based on the robustness index (RI = TW dia * 100/TL) reported in the literature (Ouchaou 2000; Iken 2012). Measures in mm. Abbreviations: **GKH**, Ghar-Khal; **KEH**, Khef-el-Hammar; **KTG**, Kaf-that-el Ghar.

Cave	Bone	TL	RI	TW dia	Source
KTG	MC I	58.6	15.3	9.0	Ouchaou 2000
KTG	MC I	61.0	16.7	10.2	Ouchaou 2000
KTG	MC I	57.0	17.5	10.0	Ouchaou 2000
KTG	MC I	61.5	14.6	9.0	Ouchaou 2000
KTG	MC III	75.0	14.2	10.6	Ouchaou 2000
KTG	MC III	74.0	15.4	11.4	Ouchaou 2000
KTG	MC III	71.8	14.6	10.5	Ouchaou 2000
KTG	MC IV	73.4	17.4	12.8	Ouchaou 2000
KTG	MC IV	73.4	17.3	12.7	Ouchaou 2000
KTG	MC IV	74.8	16.4	12.3	Ouchaou 2000
KTG	MC V	73.0	17.4	12.7	Ouchaou 2000
KTG	MT I	64.8	14.3	9.3	Ouchaou 2000
KTG	MT I	64.6	14.1	9.1	Ouchaou 2000
KTG	MT I	66.4	15.1	10.0	Ouchaou 2000
KTG	MT I	63.7	14.9	9.5	Ouchaou 2000
GKH	MT I	63.5	15.0	9.5	Ouchaou 2000
KEH	MT I	60.0	16.5	9.9	Iken 2012
KTG	MT II	70.0	18.3	12.8	Iken 2012
KTG	MT III	71.4	17.1	12.2	Ouchaou 2000
KEH	MT III	74.0	14.8	11.0	Iken 2012
KEH	MT III	74.5	15.0	11.2	Iken 2012
KTG	MT IV	74.7	16.1	12.0	Ouchaou 2000
KTG	MT IV	74.5	15.8	11.8	Ouchaou 2000
KEH	MT IV	72.0	16.0	11.5	Iken 2012
KEH	MT IV	73.0	17.5	12.8	Iken 2012
KEH	MT IV	74.5	16.3	12.1	Iken 2012
KTG	MT V	79.8	12.9	10.3	Ouchaou 2000

APPENDIX 4. — Main measurements (in mm) of brown bear phalanges from the sites of Keft-el-Hammar (**KEH**) and Hattab II (**HAT II**). Abbreviations: **APW prox**, proximal anteroposterior width; **H prox**, proximal height; **n/n**, no number; **TL**, total length; **TW dia**, transversal width of diaphysis; **TW dist**, distal transversal width; **TW prox**, proximal transversal width. The asterisk (*) indicates elements that were published previously (Ouchaou 2000).

First phalanx								
Site	**Level**	**Number**	**TL**	**TW prox**	**APW prox**	**TW dia**	**TW dist**	**Source**
HAT II	7	558	30.7	16.3	15.6	11.4	12.2	1
HAT II	3	115	33.8	17.8	14.8	11.1	13.0	1
HAT II	3	245	34.1	18.3	13.8	10.6	13.3	1
HAT II	6	557	34.7	18.3	13.3	10.8	11.8	1
HAT II	6	360	37.2	17.5	14.8	11.8	13.8	1
HAT II	6	372	38.7	18.3	14.5	12.0	13.7	1
HAT II	3	259	38.8	17.6	15.4	11.7	13.8	1
KEH	1	9	37.3	16.4	15.0	9.5	14.1	2
KEH	1	F7/27	37.6	21.5	12.3	10.5	12.3	2
KEH	1	HST8	37.8	21.0	16.3	13.2	13.4	2
KEH	1	I9/4	38.0	17.0	16.4	17.3	14.0	2
KEH	1	J29	46.0	18.5	15.0	11.5	14.0	2
KEH	2	27/A	32.0	18.0	12.0	11.0	13.0	2
KEH	2	89	32.0	17.0	12.0	11.0	14.0	2
KEH	2	58	34.0	17.0	14.0	11.0	13.0	2
KEH	2	n/n	36.0	17.0	16.0	12.0	14.0	2
KEH	2	n/n	36.0	18.0	15.0	12.0	14.0	2
KEH	2	n/n	37.2	17. 8	–	12.3	13.4	2
KEH	2	n/n	38.0	17.0	15.0	12.0	14.0	2
KEH	2	n/n	41.4	17.2	13.0	12.0	12.3	2
KEH	4	–	36.9	17.5	14.8	11.4	13.8	3
KTG	C	–	35.0	17.0	12.5	9.8	12.8	3
KTG	D	–	34.0	17.0	13.4	10.3	12.4	3
KTG	F	–	35.0	17.0	13.0	9.5	12.5	3
KTG	F	–	37.0	18.3	14.9	11.2	13.3	3
KTG	F	–	40.0	20.0	15.8	13.0	14.9	3
KTG	G	–	39.0	20.0	14.0	12.0	–	3
KBS	3c	–	37.8	20.5	15.5	12.0	13.5	3
GKH	IIIb	–	40.0	20.0	16.0	13.5	13.9	3
KEB	salle	–	43.0	21.0	17.4	14.6	15.7	3
IOS	–	05/21	51.0	23.0	–	13.2	–	4
IOS	–	05/36	43.0	16.9	14.5	9.2	–	4
IOS	–	05/37	–	19.4	14.5	11.3	–	4
IOS	–	06/I6/21	43.0	23.9	18.3	14.9	16.4	4
IOS	–	06/I8/2	38.0	17.5	14.4	11.4	13.9	4
IOS	–	06/I10/8	46.0	17.6	15.0	9.6	14.0	4
IOS	–	06/I10/19	36.3	17.2	15.0	11.5	13.8	4
IOS	–	06/I10/20	37.5	19.1	15.0	11.9	14.0	4
IOS	–	06/I10/28	31.0	16.0	13.0	9.3	12.1	4
IOS	–	06/I10/29	33.0	16.0	13.0	9.3	12.1	4
IOS	–	06/I11/17	31.0	15.9	13.3	9.4	12.2	4
IOS	–	06/I11/18	31.5	15.8	13.5	9.9	12.1	4
IOS	–	06/I11/21	33.5	18.2	14.4	10.4	12.0	4
IOS	–	06/I11/24	31.0	16.0	13.3	10.1	12.2	4
IOS	–	06/I11/25	33.4	17.3	14.1	10.4	12.8	4
IOS	–	06/I11/27	33.3	18.2	14.3	10.5	12.2	4
IOS	–	06/I11/29	34.0	17.3	14.4	10.9	12.9	4
IOS	–	06/J4/1	39.2	24.0	17.7	13.4	15.2	4
Second phalanx								
Site	**Level**	**Number**	**TL**	**TW prox**	**APW prox**	**TW dia**	**TW dist**	**Source**
HAT II	6	430	21.8	14.4	13.3	11.2	12.3	1
KEH	2	n/n	27.0	16.0	15.0	11.0	14.0	2
KEH	2	n/n	27.0	16.0	13.0	11.0	14.0	2
KEH	2	n/n	29.0	17.0	16.2	14.0	15.0	2
KEH	2	n/n	30.0	19.5	15.3	13.0	14.0	2
KEH	2	n/n	30.0	18.0	17.0	13.8	16.0	2
KEH	4	283	27.5	17.0	15.3	13.0	14.1	2
KTG	E	–	28.8	15.9	13.4	11.1	14.0	3
KTG	F	–	26.2	–	–	10.5	13.0	3
KTG	F	–	27.5	15.7	13.1	10.2	14.1	3
KTG	F	–	22.6	17.3	13.9	12.3	14.9	3
GKH	V	–	19.9	16.0	12.9	11.1	13.0	3
IOS	–	05/9	28.8	15.9	13.4	11.1	14.0	4
IOS	–	05/38	26.2	–	–	10.5	13.0	4
IOS	–	06/I10/6	27.5	15.7	13.1	10.2	14.1	4

APPENDIX 4. — Continuation.

Site	Level	Number	TL	TW prox	APW prox	TW dia	TW dist	Source
				Second phalanx				
IOS	–	06/I5/2	22.6	17.3	13.9	12.3	14.9	4
IOS	–	06/I6/17	19.9	16.0	12.9	11.1	13.0	4
IOS	–	06/I10/21	20.0	14.9	11.2	9.8	12.9	4
IOS	–	06/I10/31	18.9	14.1	12.1	10.7	12.1	4
IOS	–	06/I11/10	19.4	14.2	11.5	9.8	12.2	4
IOS	–	06/I11/16	18.5	14.1	12.1	10.5	12.3	4
IOS	–	06/I11/20	17.9	14.9	11.3	10.4	12.3	4
IOS	–	06/J4/10	21.5	18.3	15.6	14.3	15.8	4

Site	Level	Number	TL	H prox	TW prox	Source
				Third phalanx		
HAT II	6	1041	44.5	23.8	14.1	1
HAT II	6	674	35.7	25.0	13.9	1
HAT II	6	879	31.0	26.0	11.3	1
KEH	surface	n/n	–	–	11.0	2
KEH	surface	HST7	–	26.0	13.0	2
KEH	1	1	30.0	21.0	11.2	2
KEH	2	52	46.0	23.0	14.0	2
KEH	2	n/n	36.4	26.0	15.5	2
KEH	2	n/n	30.0	21.0	11.0	2
KEH	3	n/n	30.0	26.0	11.0	2
KEH	3	n/n	41.0	24.0	14.0	2
KEH	3	n/n	49.0	–	13.7	3
KEH	4	n/n	56.3	28.0	15.5	3
KEH	7	n/n	–	24.0	12.3	2
KTG	D	–	50.5	33.0	16.7	3
KTG	E	–	56.0	30.0	14.5	3
KTG	F	–	54.0	28.5	14.4	3
KTG	F	–	50.0	29.0	14.2	3
KTG	F	–	51.0	29.8	15.0	3
KTG	F	–	45.0	–	14.0	3
KBS	3c	–	50.5	26.0	14.7	3
KEB	salle	–	36.0	26.0	15.0	3
IOS	–	05/13	45.0	27.5	14.0	4
IOS	–	06/I10/9	50.0	28.2	15.0	4
IOS	–	06/I10/11	33.0	23.0	12.2	4
IOS	–	06/I10/30	28.0	22.0	12.4	4
IOS	–	06/I10/32	31.4	23.2	12.2	4
IOS	–	06/I11/9	33.1	23.4	12.7	4
IOS	–	06/I11/15	30.0	21.0	13.0	4
IOS	–	06/I12/1	32.2	23.0	14.2	4
IOS	–	06/I13/5	34.0	21.5	14.2	4
IOS	–	06/I10/10	32.0	25.0	14.2	4
IOS	–	06/J5/6	31.8	23.7	13.4	4