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New materials of the white rhinoceros *Ceratotherium simum* and auerochs *Bos primigenius* from a Late Pleistocene terrace of the Oued el Haï (NE Morocco) - two elements of the Maghrebi Palearctic fauna

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ABSTRACT

Most biogeographers considered the Maghreb to be part of the Palearctic biogeographic region, though it is relatively recently that the proportion of Palearctic species increased there. How and when exactly these biogeographic changes occurred is not well understood, but they are probably the result of the increasing aridification of the Sahara and decreasing global temperatures. Fossils of *Bos primigenius* and *Ceratotherium simum* from a new fossil locality in a terrace of the Oued el Haï (NE Morocco) contribute to our understanding of some of these biogeographic processes and their timing. They also suggest an age between ~57 and ~100 ka for the terrace. The same evolutionary change in *Bos* in Europe and the Maghreb suggests gene flow as the most parsimonious explanation, though parallel evolution is an alternative possibility. Oued el Haï has the oldest well-documented record of *C. simum* in the Maghreb. The dispersal of this species to North Africa, where it replaced *C. mauritanicum*, may have occurred during a 'Green Sahara Period' between 80–85 or 100–105 ka, when the Maghreb had acquired already a Palearctic character. The study of the biogeography and requirements of the large mammals of the Maghreb may provide information to calibrate the region's climate modelling.

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Introduction

Despite the fact that the Maghreb is isolated from Eurasia by the Mediterranean, it forms part of the Palearctic biogeographic region (Sclater 1858; Wallace 1876) or Holarctic region (Lydekker 1896, 1897; Matthew 1915, 1939) and not of the Ethiopian region. Even though Holt et al. (2013) proposed an adjustment of the biogeographic regions, the Palearctic affinities of the Maghreb are evident in the mammals which live there: *Sus scrofa*, *Cervus elaphus*, *Vulpes vulpes*, *Macaca sylvanus*, *Mustela nivalis*, *Lutra lutra*, *Canis aureus*, *Ammotragus lervia* as well as micro mammals (Aulagnier et al. 2009). However, a high proportion of Eurasian mammals in the Maghreb is a recent phenomenon on geological time scale.


During the Mio-, Plio- and Pleistocene, the biogeographic borders between the Palearctic and Ethiopian regions seem to have changed position several times (Van der Made 1999a, 2011, 2014). During the Middle Miocene Climatic Optimum, the situation was opposite to the present situation and many mammals of Ethiopian or Oriental affinities, such as primitive Hominoidea, as well as ectothermic

vertebrates expanded into Europe, but they disappeared when the global climate became cooler (Andrews et al. 1996; Suc et al. 1999; Lear et al. 2000; Böhme 2003). During the Messinian, primitive hippopotamuses reached Europe and lived for a limited time in Spain, Italy, and the very south of France (Joleaud 1920; Van der Made 1999b). Not later than the Pliocene, the balance shifted and species with European or Eurasian affinities extended their ranges into North Africa, such as the rhinoceros '*Dicerorhinus africanus*', known from Lake (Lac) Ichkeul (Arambourg 1970), and the bear *Ursus etruscus*, known from Ahl al Oughlam (Geraads 1997). By the Late Pleistocene, the proportion of Eurasian species in the Maghreb had increased markedly. This is probably related to the observed decreasing global temperatures (Lear et al. 2000) and progressive isolation by the increasingly drier Sahara (Trauth et al. 2009; Zhang et al. 2014). Most of this faunal change is outside the range of C¹⁴ dating and the timing of the individual events is poorly known.

Some of the species of Eurasian origin that spread into North Africa seem to have evolved rapidly quite differently from their Eurasian ancestors, but others not. The deer *Megacerooides algericus* became so

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different that there is no consensus on its ancestor: *Praemegaceros*/*Megaceroides* or *Megaloceros giganteus* from western Eurasia or *Sinomegaceros* from China (Joleaud 1914; Arambourg 1938; Ambrosetti 1967; Abbazzi 2004). By contrast, European fossils of Early Pliocene to Late Pleistocene age are assigned to *Macaca sylvanus*, while the species lives in North Africa and its fossil record may go back there as far as the Late Pliocene (Szalay and Delson 1979), suggesting that the European and African populations did not become genetically isolated during a period of some 3 Myr. If the same evolution is observed in the Maghreb and in Eurasia, it seems likely that there was gene flow. Fossils from Oued el Haï provide information on whether this may have been the case with the aurochs *Bos primigenius*, one of the most common Late Pleistocene large mammals in the Maghreb.

Although the 'Palaerctisation' process of the Maghreb approached its present state, there were still new immigrants from the South. One of these is the white rhinoceros *Ceratotherium simum*. According to Geraads (2005, 2010), *Ceratotherium mauritanicum* was replaced in North Africa by *C. simum*, which arrived by dispersal from the South. Geraads (2005) indicated the temporal range of *C. simum* in North Africa as Late Pleistocene, but did not provide a list of localities. Geraads (2010 table 34.1) lists occurrences of the different rhinoceros species, on the basis of which the replacement of *C. mauritanicum* by *C. simum* occurred between 500 and 43.5 ka. Fossils from Oued el Haï and a literature study significantly reduce this interval of uncertainty.

This paper aims to present a new fossil locality in a terrace of the Oued el Haï (NE Morocco) and describe its most relevant fossils of *Ceratotherium simum* and *Bos primigenius*. These remains contribute to our understanding of the formation of the Late Pleistocene to Holocene Palearctic fauna of the Maghreb.

Geology

The Oued el Haï is a tributary of the upper Moulouya catchment, which drains the High Plateaus basin (Muratet 1991; Wengler and Vernet 1992; Wengler 1993). It is located south of the Oujda Mountains in eastern Morocco (Figure 1) and is bordered by Palaeozoic and Mesozoic rocks. Mesozoic formations deposited in marine environments of fluctuating depth form the basement. Tectonic phases of Late Eocene, Tortonian, and Pliocene-early Pleistocene age built up the Atlas system, causing differential subsidence and forming the basin (Frizon de Lamotte et al. 2000; Laville et al. 2007). The Neogene and Pliocene-early Quaternary basin fill rests unconformably on the Jurassic and consists of alluvial, palustrine, and lacustrine deposits. Subsequent Quaternary incision of the Oued el Haï renewed the relief and alternated with depositional phases, creating a sequence of five fluvial terraces, situated from +20-22 m to the modern river, and probably formed from the Middle Pleistocene to the Holocene (Figure 2) (Benito-Calvo et al. 2020).

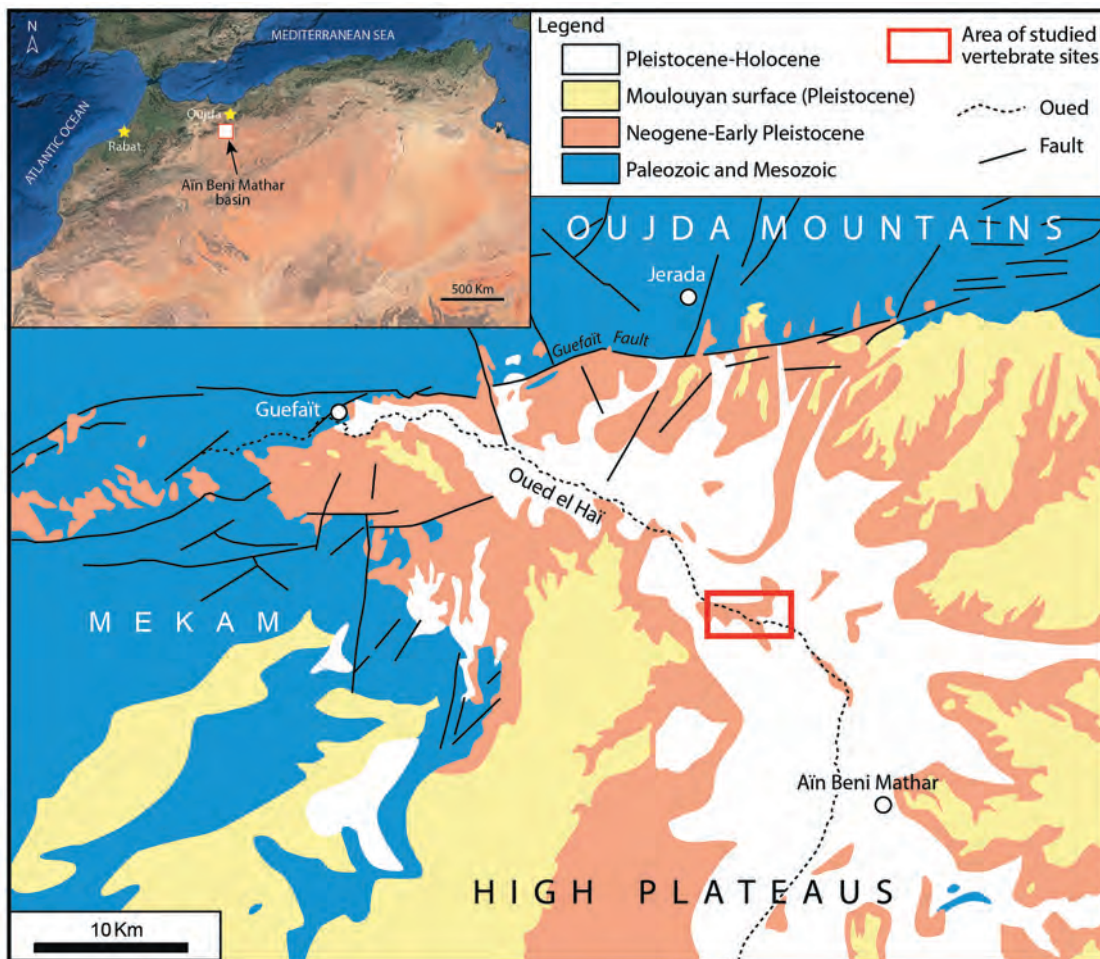


Figure 1. Position and geological map of the Ain Beni Mathar basin (modified after Muratet 1991). The red square indicates the position of the Google Earth view of Figure 4. The position of the study area, shown on the geological map of the Ain Beni Mathar basin.

Wengler and Vernet (1992) proposed a Holocene age for three lower terraces based on C^{14} dates, while Depreux et al. (2021) described the alluvial architecture in the lowest terrace as nested and cut and fill alluvial formations ranging from the Early to Late Holocene (11,350–4450 cal BP, C^{14}). Other works indicate the presence of older terraces (Benito-Calvo et al. 2020), in a catchment with low incision rates (Bartz et al. 2019), and low gradient longitudinal profiles (Pastor et al. 2015). The terraces are mainly composed of sandy sediments, including muds and hydromorphic palustrine deposits, as well as rare loose gravel layers (Benito-Calvo et al. 2020). Several newly discovered fossiliferous sites occur in these terrace sediments (Figure 3). Here we describe fossils from a low terrace (T4), lying at 8–12 m above the present river bed of the Oued el Haï (Figures 2 and 4). The coordinates of the rhinoceros skull are $34^{\circ} 7' 13.01''$ N/ $2^{\circ} 6' 31.53''$ W. Those of the *Bos* skull+horn core and *Bos* horn core are $34^{\circ} 7' 16.68''$ N/ $2^{\circ} 6' 24.39''$ W and $34^{\circ} 7' 15.05''$ N/ $2^{\circ} 6' 26.29''$ W, respectively. These fossils suggest a Late Pleistocene age for the terrace, older than the Holocene as suggested by previous data.

Material and methods

The fossils from Oued el Haï are kept in the Faculty of Sciences (Geology Department) of the Mohamed I University at Oujda (Morocco). Comparisons are made with fossils and recent bones, as indicated in Tables S1 and S2 (Supplementary Information). Where an acronym of a collection is given, material from that collection was studied. If only a reference is given, the data are taken from the literature. For biostratigraphy, the ages of the localities with which we compare are important, and these ages are listed in Table S3, with the corresponding references.

The methods for the study of the fossils are common and follow Guérin (1980a) and Van der Made (2010a) for the Rhinocerotidae, and the way of measuring *Bos* is indicated in the section where the fossils are described.

Statistical comparisons of different metrics among sites or site groups (Table S4 in the Supplementary Information) were attained using U-Mann Whitney tests. This non-parametric test is appropriate when the sample size of at least one of the groups is small. We did not use Bonferroni correction because the variance was homogenous in all instances (Levene test; $p > 0.05$). All analyses were carried out in PAST statistical software v.4.0.3 (Hammer et al. 2001).

Description of the new materials

The white rhinoceros

There is a rhinoceros skull and various other bones, including axis, radius, humerus, fibula, and a second metacarpal, which could be of the same individual. The skull has the retroarticular and paroccipital processes widely separated (Figure 5(a3)), as is common in *Ceratotherium* and *Diceros*, whereas these are much closer together in *Stephanorhinus* (Toula 1902; Loose 1975; Van der Made 2010a). The post tympanic process reaches the retroarticular process, which is like in *Ceratotherium*, while in *Diceros* there remains a space between the two processes. Metrically, the skull from Oued el Haï is within the ranges of *C. simum* as given by Guérin (1980a).

The upper teeth have the crochet and crista completely separating the middle fossa from the lingual valley (Figure 5(a1)), which occurs in *Ceratotherium*, but not in *Diceros* and *Stephanorhinus*, where the postfossa remains connected to the lingual valley. Compared to *C. mauritanicum* from its type locality Tighennif and the recent *C. simum*, the teeth are large (Table 1; Figure 6). The two species have much overlap in size and this does not seem a good feature to separate them.

Various metapodials of *C. mauritanicum* from type locality Tighennif are as gracile as those of most species of *Stephanorhinus*, while those of *C. simum* are much more robust (see MtIII in Figure 7). It should be noted that *S. hemitoechus* had initially very gracile metapodials, but that these evolved to more robust ones, in a way similar to what happened in *Ceratotherium*. The second metacarpal from Oued el Haï

Table 1. Measurements (in mm) of the cheek teeth of *Ceratotherium simum* from Oued el Haï (UMPO OeH-3-2015).

Tooth	s/d	DAPo	DAPb	DTa	DTp	
P ²	s	34.0	33.0	36.4	32.7	Hbu>>20
M ¹	s	55.5	48.1	74.3	67.1	
M ²	s	69.0	64.4	74.0	63.2	
M ³	s		33.9			
P ⁴	d	55.7	49.9	62.4	54.6	Hci = 38.8 (?)
M ¹	d	55.6	48.1	74.2	67.9	Hbu>53.2
M ²	d	71.3	60.9	74.4	66.6	Hbu>85
M ³	d		39.0	≈54.7		Hbu>90

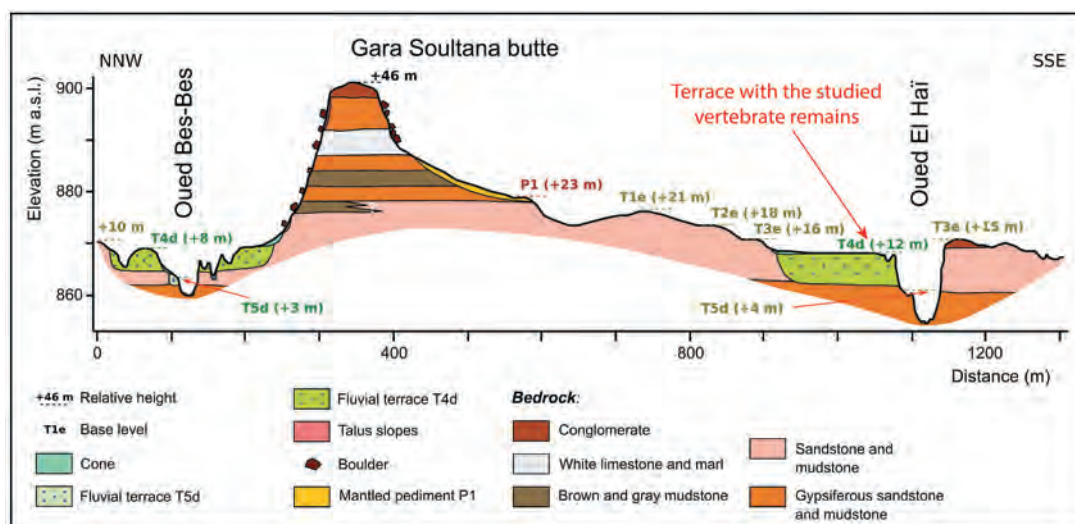


Figure 2. Geological cross-section of the study area with the terrace from which the fossils come. Cross-section showing the bedrock formations, the river valleys cut into them, and river terrace where the fossils were found.

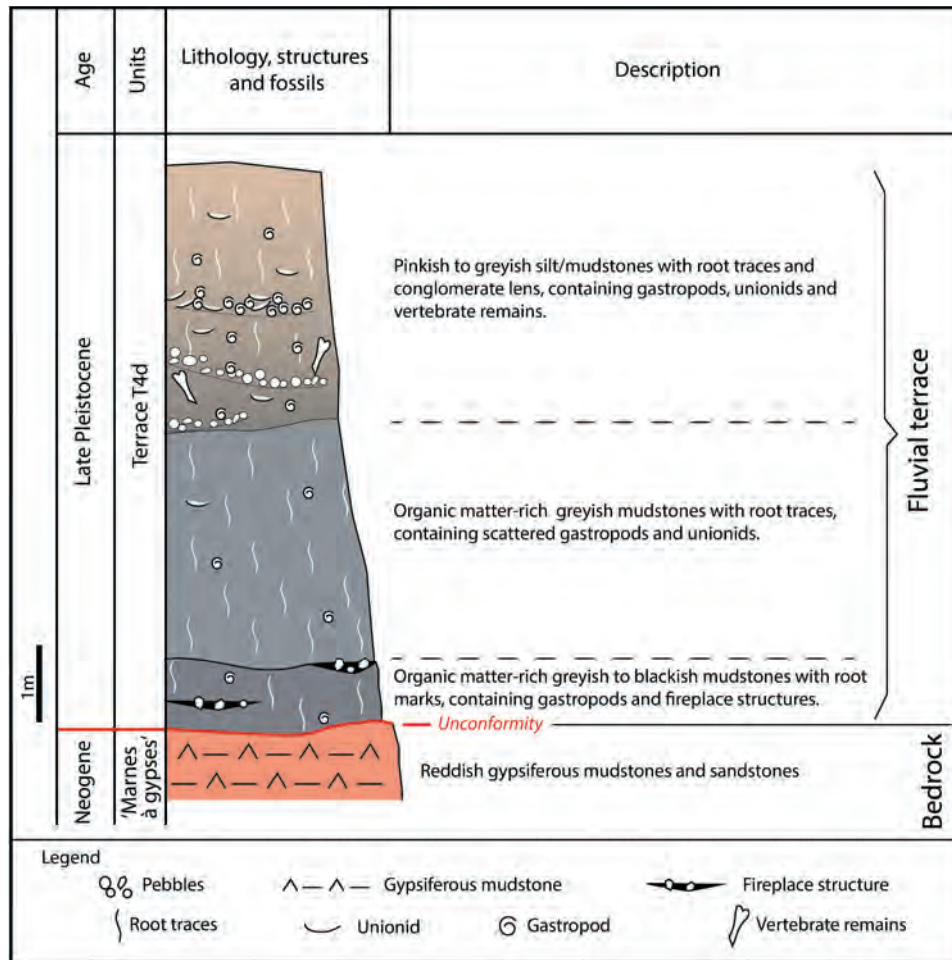


Figure 3. Stratigraphic column of the fossiliferous deposits. Scheme showing the position of the fossils in the sediment layers which make up the river terrace.

Table 2. Measurements (in mm) of the fourth metacarpal of *Ceratotherium simum* from Oued el Haï (UMPO OeH-10-2018).

L	I	DAPp	Dp	DAPmini	DTmini	DAPd	DTd	DTdf
160	151.1	53.2	41.7	22.2	36.6	43.7	48.5	42.2

(Figure 7(a)) is robust like in the living species *C. simum* (Table 2; Figure 7). We assign the fossils from Oued el Haï to that species.

The auerochs

The material includes a partial skull (Figure 5(b)), a second skull and associated bones of the skeleton, probably of the same individual, as well as some isolated finds (Figure 5(c)). The frontals reach the back of the skull, so that the parietals cannot be seen in dorsal view, and the horn cores originate far back, are directed outwards and then curve forwards and upwards. This is the very typical morphology of *Bos*. The upper molars have interlobular columns, pronounced buccal styles and cementum (Figure 5(c)), as is common in the Bovini.

The limb bones include a complete metacarpal (Figure 8(a); Table 3). In order to distinguish between metapodials of *Bos* and *Bison*, Gee (1993) made a comparison with wine bottles. In anterior view, the lateral and medial sides of the metacarpals of *Bos* widen from the middle of the bone towards the distal end, which recalled Gee the 'Burgundy bottle'. The metacarpals of *Bison* have a 'shoulder' at the transition from the diaphysis to the epiphysis and recall the shape of a 'claret (or Bordeaux) bottle'. In this the metapodials of *Syncerus* resemble those of *Bison* and the feature is of use here. Another feature used to separate *Bos* and *Bison* is the shape of the proximal articulations. The antero-abaxial sides of the facets for the magnum and unciform curve from the middle towards the sides of the bone and are more convex in *Bos* than in *Bison* and *Syncerus*. Where these sides reach the posterior sides of these facets, in *Bos* they do so at about a straight angle, while in *Syncerus* (and *Bison*), this is at a somewhat sharper angle. In these features, the metacarpal from Oued el Haï resembles those of *Bos*. The metacarpal from Oued el Haï is also much less robust than that of the living *Syncerus* and the fossil species *Syncerus antiquus*, but is comparable to that of *Bos primigenius* from Europe and North Africa (Figure 8).

Table 3. Measurements (in mm) of the left metacarpal (McIII-IV) of *Bos primigenius* from Oued el Haï (UMPO OeH-5-2015).

L	Lmed	Llat	DAPp	DTp	DAPpf	DTpf	DAPmini	DTmini	DTd	DTdf	DAPd-III	DTd-III	DAPd-IV	DTd-IV
275.3	261.2	262.5	62.6	101.2	53.8	98.2	34.9	59.1	90.4	98.9	48.6	43.7	48.8	46.9

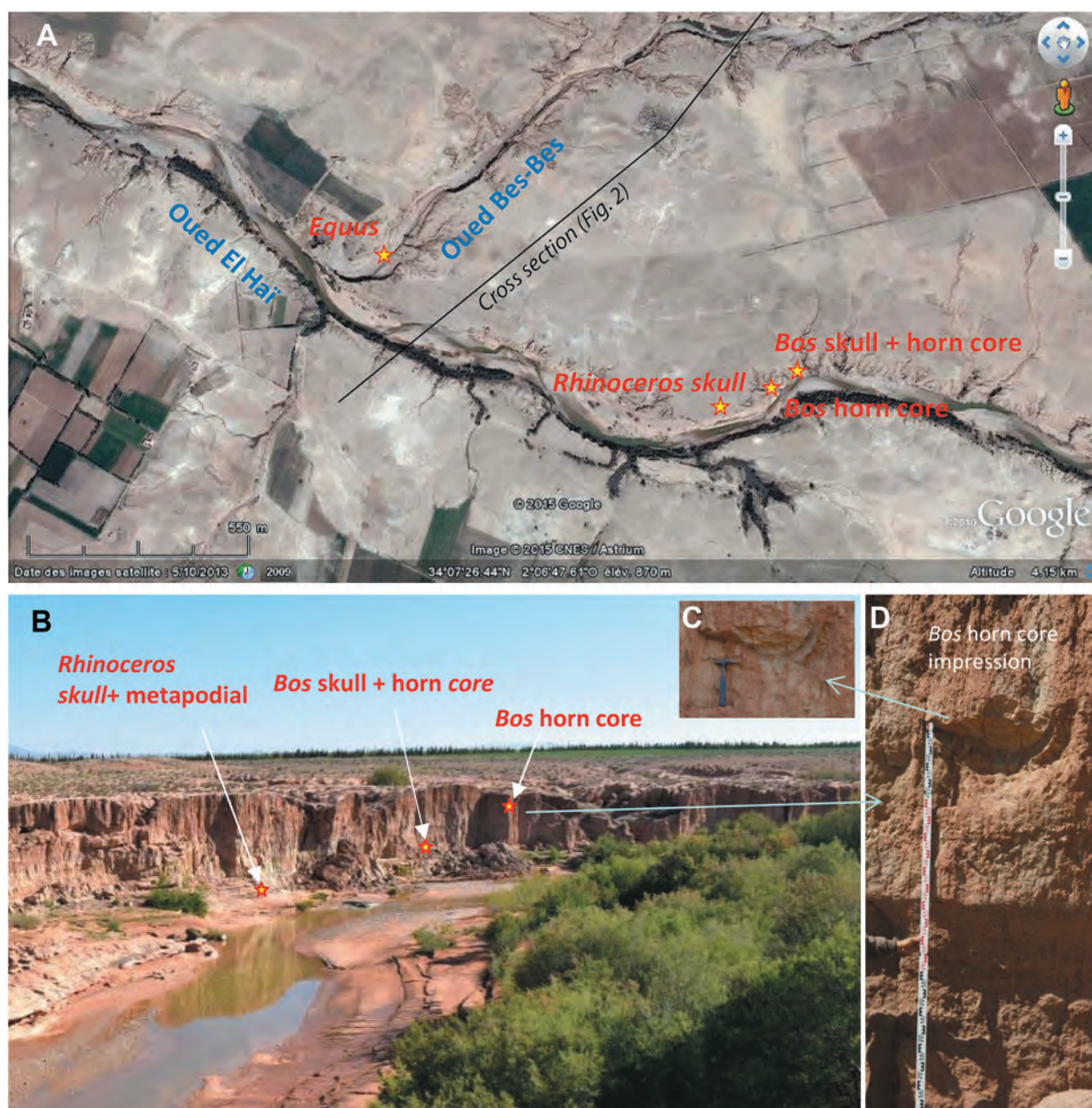


Figure 4. Google Earth view of the Oued el Haï with the position of some of the major finds indicated (a). Panorama of the Oued el Haï (b) and impression of a *Bos primigenius* horn core (c, d). The position of the fossiliferous sites indicated on an aerial photograph and a panorama view of the Oued el Haï.

We assign the bovine fossils from Oued el Haï to *Bos primigenius*. The metacarpal is the widest of all metacarpals in Figure 8, and probably this individual was the heaviest of all.

Discussion

The auerochs – Palaeartic or Ethiopian?

There was a general consensus that the auerochs was a species of Eurasian origins that spread into the North of Africa. It was widely accepted that *Bos* is of Asian or even Indian origin, closely related to *Bison* and some species of *Leptobos* and that it dispersed into Europe during the Middle Pleistocene and into Africa during the Middle or Late Pleistocene (Rütimeyer 1877-1878; Lydekker 1878; Von Zittel 1918; Pilgrim 1938, 1939; Kurtén 1968; Thenius 1972, 1979; Groves 1980; Müller 1989; Geraads 1992; Van Vuure 2003;

Gentry 2010). *Bos primigenius* became the most common large mammal in the North African faunas until it went extinct there in the Holocene. It is often associated with species of Palearctic affinities, such as *Sus scrofa*, *Cervus elaphus*, *Megacerooides algericus*, *Stephanorhinus hemitoechus*, *Vulpes vulpes*, and *Canis aureus*. The North African populations previously assigned to the latter species are currently considered to be more closely related to the grey wolf than to the golden jackal and placed in *Canis lupaster* (Castelló 2011; Knispel Rueness et al. 2020). These species are commonly seen as Late Pleistocene migrants, though they also occur in localities, such as Bouknadel and Ain Bahya, with estimated ages of 0.1 and 0.2 Ma (Geraads 2010). *Bos primigenius* is also present in Tihodaïne in a level that is older than 250 ka (Arambourg and Balout 1952; Thomas 1977). It is also tentatively cited from Jebel Irhoud (Amani and Geraads 1993), which is now dated to 315 or 286 ka (Richter et al. 2017). Still older sites like the ones from

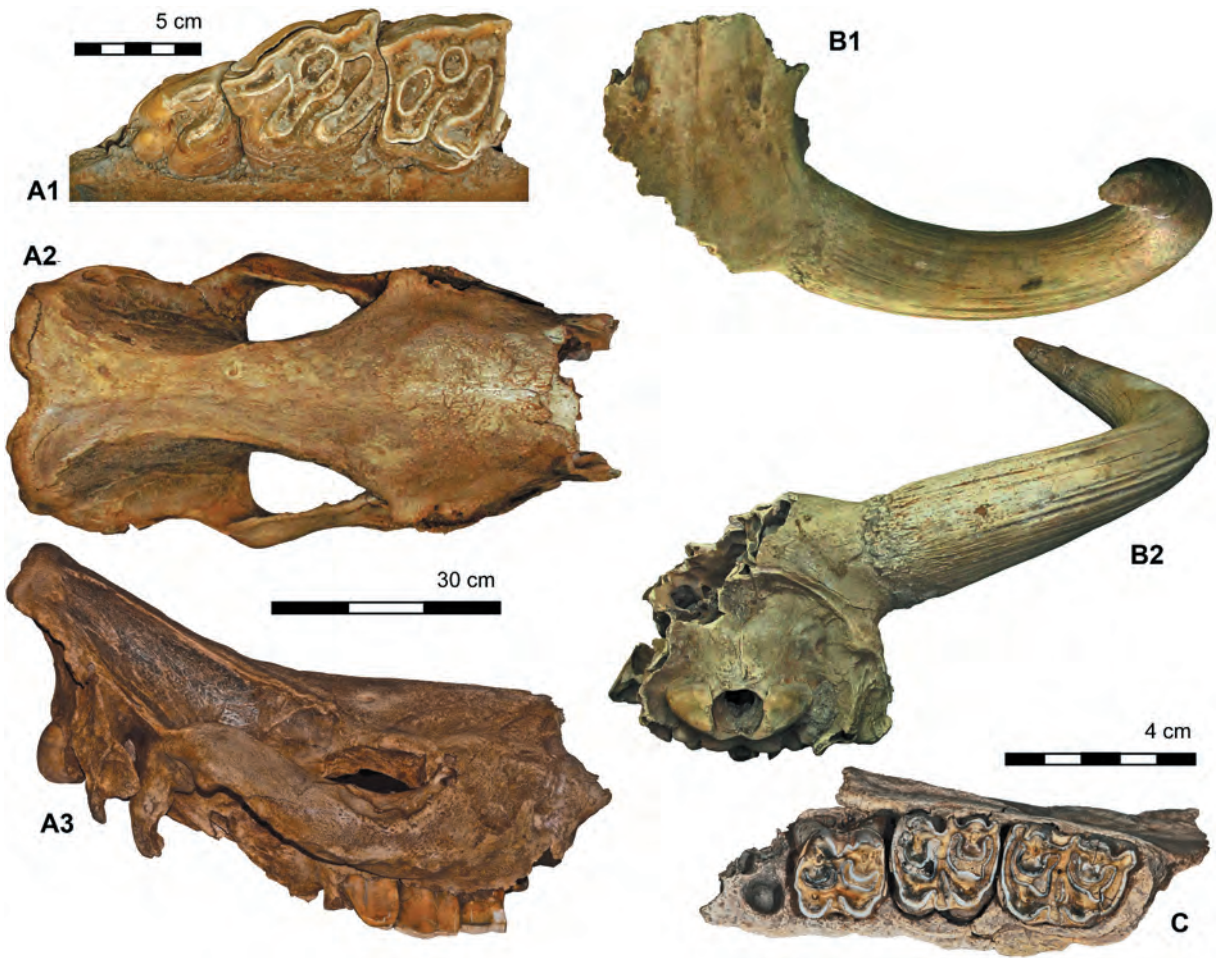


Figure 5. Fossils from Oued el Haï. a) UMPO OeH-3-2015 - *Ceratotherium simum* skull: 1) occlusal view of right M^{1-3} , 2) dorsal view, 3) right lateral view. b) UMPO OeH-11-2018 - *Bos primigenius* skull: 1) dorsal view, 2) posterior view. c) UMPO OeH-4-2015, *Bos primigenius* left maxillary with M^{1-3} . The *Bos* skull is not to scale because of perspective of the protruding horn core.

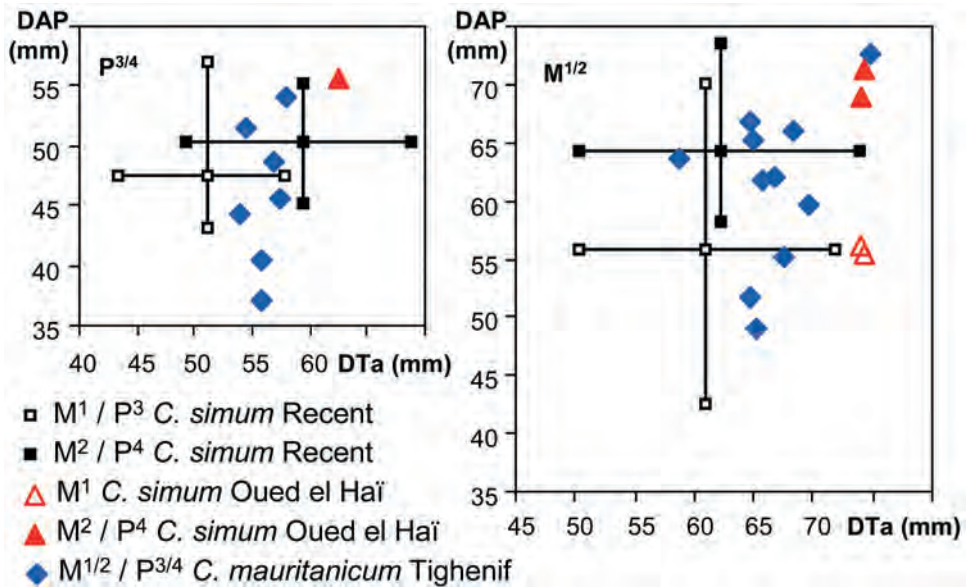


Figure 6. The size of the upper cheek teeth in *Ceratotherium*. The specimens from Tighennif, type locality of *C. mauritanicum*, are isolated specimens and no intent was done to separate M^1 from M^2 and P^3 from P^4 . For the living species, average and extremes are indicated. The provenance of the data is indicated in Table S1.

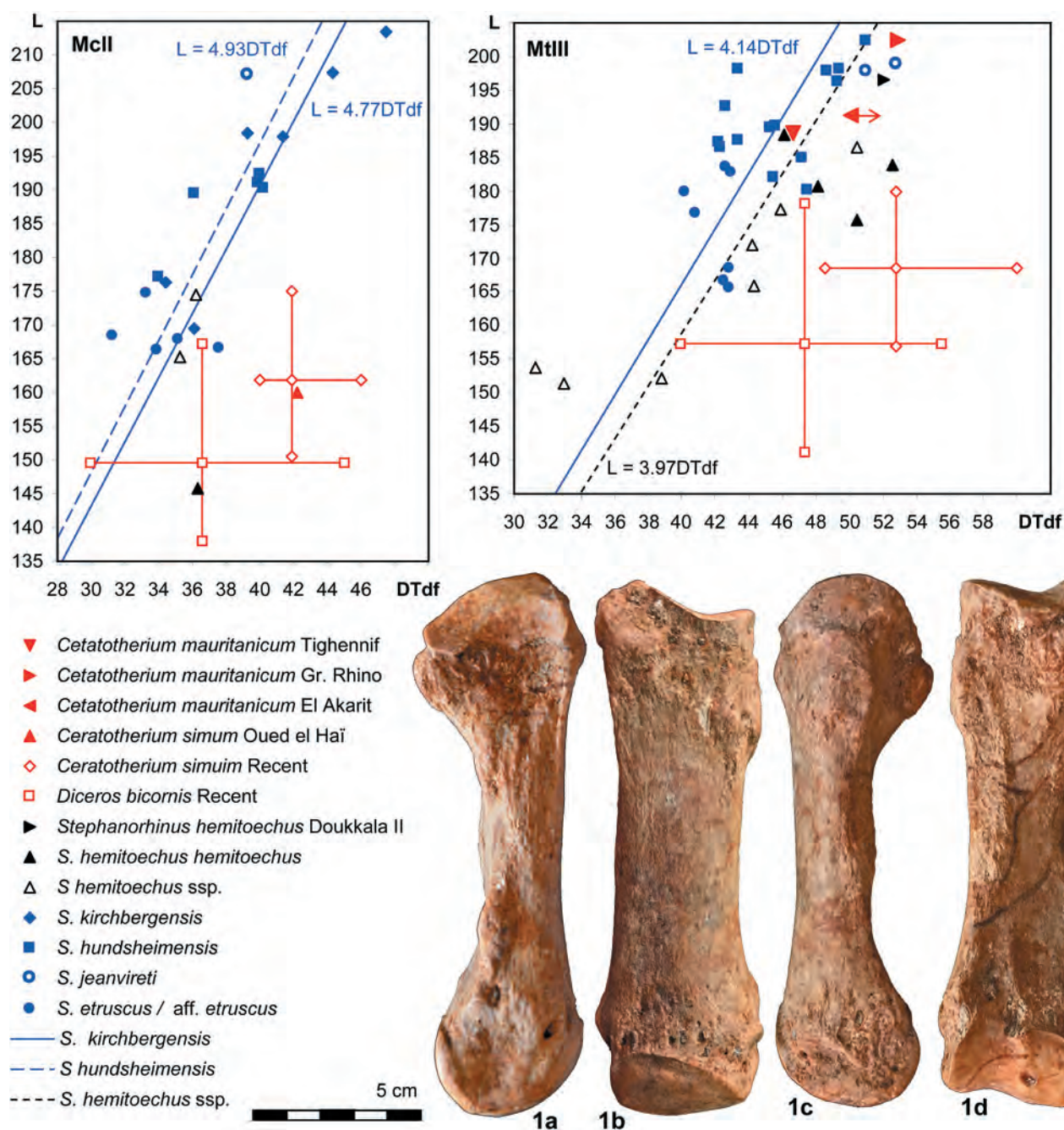


Figure 7. *Ceratotherium simum* from Oued el Hai metacarpal MclIV UMPO OeH-10-2018: 1a) axial, 1b) anterior, 1c) abaxial, and 1d) posterior views. Bivariate diagrams of the distal articular width (DTdf) and length (L) of the second metacarpal (MclII) and third metatarsal (MtIII) comparing various species of *Ceratotherium* and *Stephanorhinus*. Provenance of data as indicated in Table 1. Lines indicate average proportions.

Thomas Quarry and Oulad Hamida, Lac Karâr and Ain Marouf, typically lack *Bos primigenius*, but Wadi Sarrat yielded an aurochs skull, and its age was estimated as 0.7 Ma on the basis of biochronology (Martínez-Navarro et al. 2014). Another skull assigned to *Bos* is from Asbole (Ethiopia), and its age was estimated to be between 0.6 and 0.8 Ma (Geraads et al. 2004). The latter site is the southernmost African occurrence, but *Bos primigenius* has also been reported from various sites at Kom Ombo, Egypt, with ages between 15 and 10.5 ka (Churcher 1974).

Martínez-Navarro et al. (2007, 2010) presented an alternative view on the origin of *Bos primigenius*: that it is the end of a lineage *Pelorovis turkanensis* – *P. oldowayensis* – *Bos buiaensis* – *B. primigenius* and that it originated in Africa in the Ethiopian

biogeographic region. These authors did not adequately discuss previous literature on the evolution and systematics of *Bos*. This model has been criticised by Bibi (2009) for two contemporaneous *Pelorovis* species to be presented as consecutive chronospecies and because arguments for a *Pelorovis*-*Bos* link have not well been documented and moreover do not support the connection, while more relevant features have not been taken into account. Gentry (2010) noted that the model is problematic because it distances *B. primigenius* from other known recent and fossil species of *Bos* and putative relatives such as *Adjiderebos* and *Bison palaeosinensis* and that comparisons with still more relevant species like *Bos acutifrons* are lacking. In addition, there is a paradox between the supposed sub-Saharan origin of *Bos*, where it is known from one locality, and

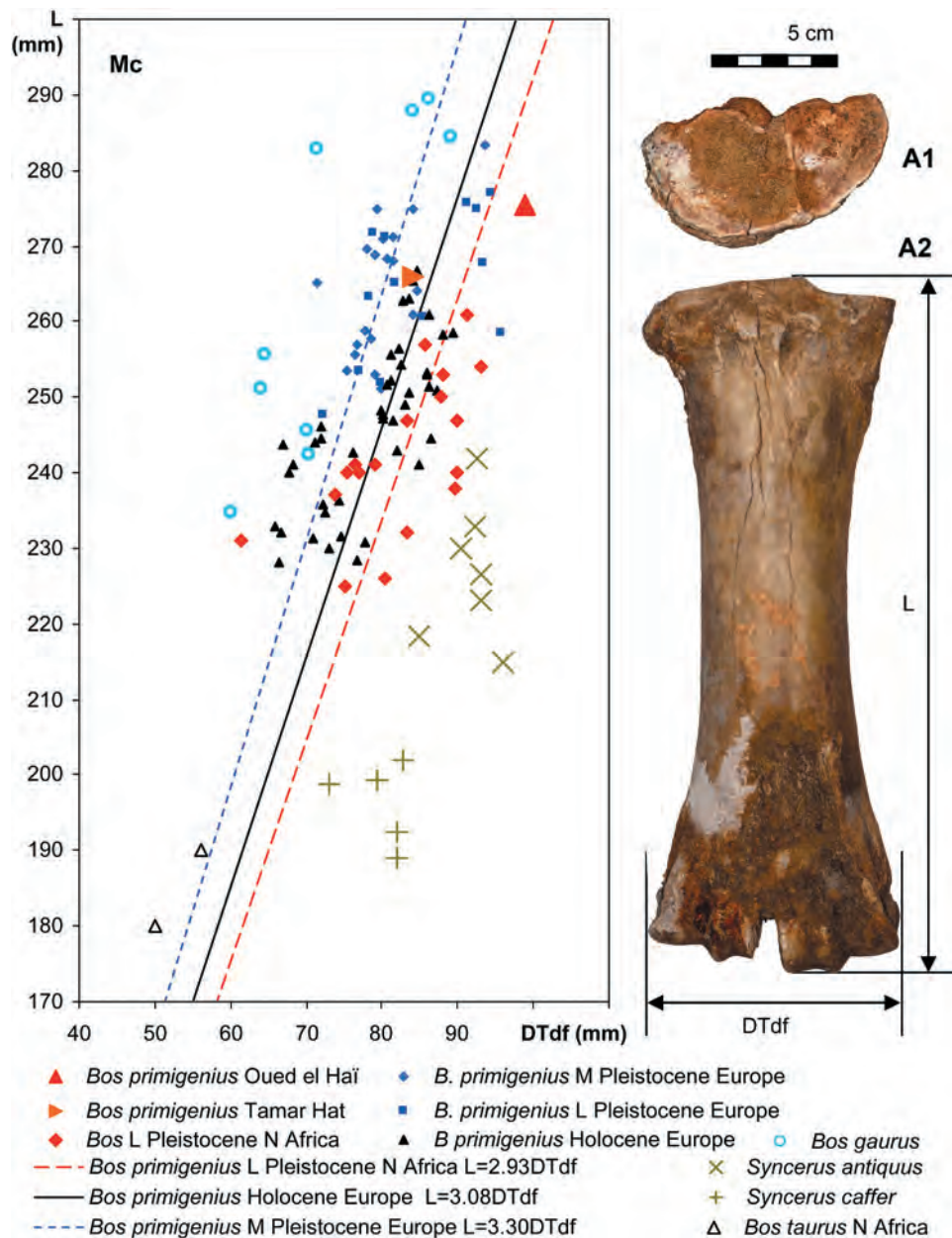


Figure 8. *Bos primigenius* from Oued el Hai UMPO OeH-5-2015 left metacarpal (McIII-IV): 1a) proximal and 1b) anterior views. Bivariate diagram of distal articular width (DTdf) and length (L) of the McIII-IV of selected Bovidae. Provenance of data indicated in Table 1. Lines indicate average proportions.

the extreme abundance of *Bos* fossils in Eurasia. Gentry (2010) also noted a problem in that similarities in the long face and horn core insertion appear to be too advanced in *Pelorovis*, for this genus to be ancestral to *B. primigenius*.

The morphology of the horn core insertion, briefly mentioned by Gentry, merits a more detailed examination. In *Pelorovis*, the horn cores are directed backwards at their base, curve outwards and then forwards, in *P. turkanensis* the distal part of the horn core curves also upwards, while in *P. oldowayensis* it curves downwards. In *Bos? buiaensis*, the horn cores are directed outwards at their bases and more distally they curve upwards, while in *B. primigenius*, they are directed initially outwards and more distally upwards and usually forwards. If these four species would form a lineage, the middle part of the horn cores would be directed forward, forward, outward, and forward, respectively, and the tips would be directed upward, downward, upward, and upward, respectively. This would be an apparently inconsistent 'to and fro evolution'.

The features related to the origin of the horn cores, mentioned by Gentry (2010), combine with other data. In *Pelorovis oldowayensis* and *P. turkanensis* the horn cores originate above the occipital and are directed backwards at their origin. In none of the species of *Bos*, the horn cores are initially directed backwards and in some fossil *Bos* from Trinil (Java, Indonesia, NBC 2774), the horn cores do not even originate at the back of the skull, but leave the occiput visible in frontal view. This is a more primitive state than in *Pelorovis* and a resemblance to *Bison*. In all species of *Bos*, the horn cores curve clearly upwards, but only in some species also forwards. This is a more primitive state, shared with *Bison* and *Leptobos*, and very different from *Pelorovis*. A particularly close relationship between *Bos* and *Bison* was demonstrated on the basis of DNA and it has even been proposed that *Bison bonasus* is a species that originated from interbreeding of *Bos primigenius* and *Bison priscus* in Eurasia (Soubrier et al. 2016). *Bison* is not known from Africa and has a fossil record in Eurasia going back more than the date of the

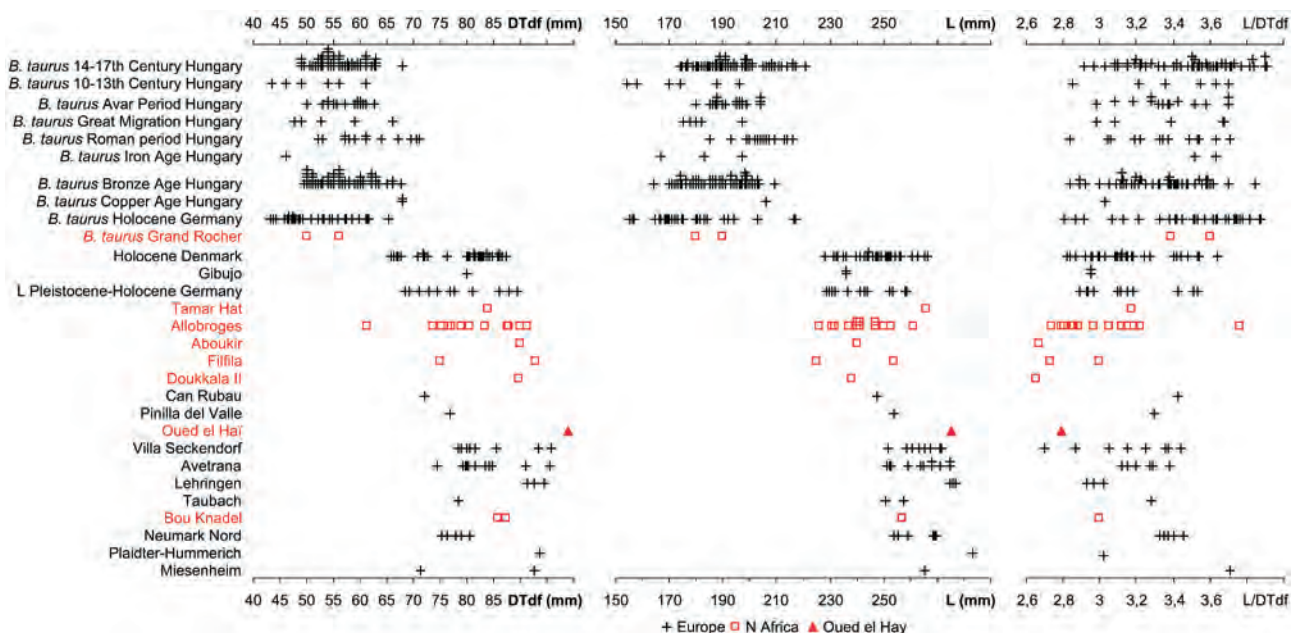


Figure 9. The variation in the distal articular width (DTdf), length (L) and robusticity (L/DTdf) of the metacarpals of *Bos*. The localities are ordered in approximate order from old (bottom) to young (top).

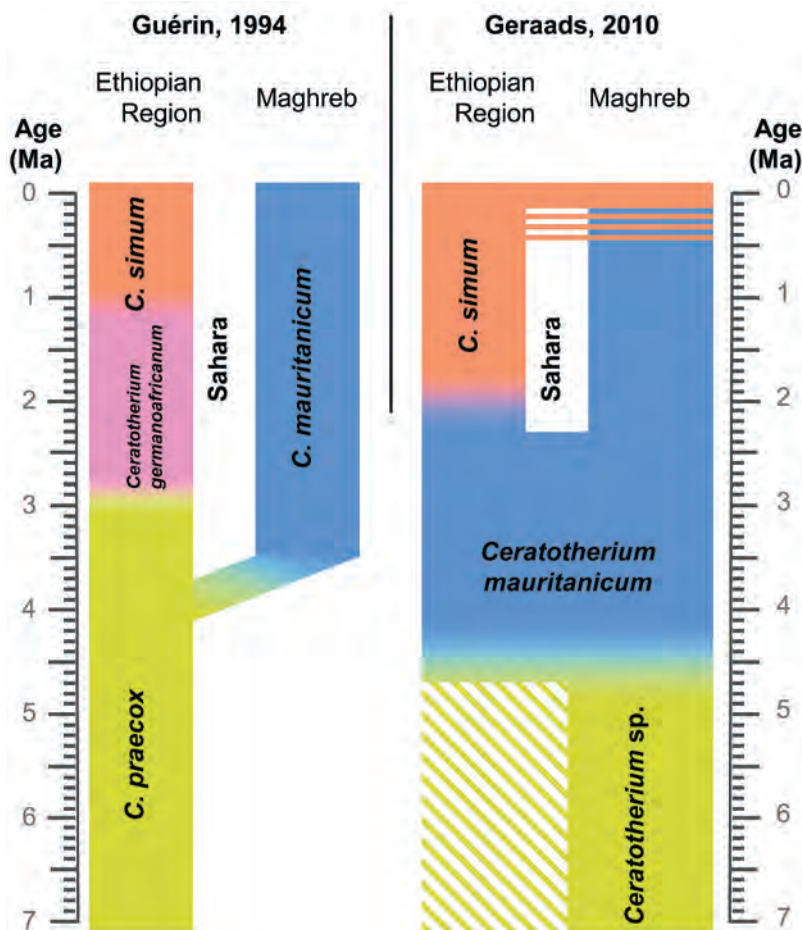


Figure 10. The evolution, biogeography and classification of *Ceratotherium* according to Guérin (1994) and Geraads (2010).

supposed transition of *Pelorovis* to '*Bos*' *buiaensis* in Martínez-Navarro et al.'s (2010) model. *Bison* originated in Asia, while the greatest diversity of fossil and living *Bos* species is in the Oriental Region, suggesting that the split between the two occurred in Asia.

The foregoing suggests that the resemblances between *Bos* and *Pelorovis* are due to convergence and that the genus *Bos* more likely originated in SE Asia (as traditionally believed), that *Bos primigenius* may have originated in an area that includes Northern India and Pakistan, near the boundary of the Oriental and Palearctic regions, and expanded from there into western Eurasia, where it became widespread, and into North Africa. Given its known distribution, it is here considered to be essentially a Palearctic element.

The auerochs – evolution, gene flow and biostratigraphy

In the Bovini, the increase in robustness of the metapodials and particularly of the metacarpals is an important evolutionary feature. In the genus *Bos*, there is an increase in robustness of the metacarpals from *B. gaurus* to *B. primigenius* and within the latter species from the Middle to the Late Pleistocene and Holocene (Figure 8). There is also some decrease in size from the Middle and early Late Pleistocene to the Holocene. The width (DTdf) reflects bodyweight, the index L/DTdf reflects locomotory adaptation and the length (L) a mixture of both. Though some African specimens are particularly small and robust, they seem to follow the same trend as the European ones.

In order to see these trends more in detail, the width (DTdf), length (L) and robustness (L/DTdf) were plotted against age (Figure 9). The ages of the sites are given in Table S3. In Figure 9, it can be seen that in *Bos primigenius* there is a trend in decreasing values for L. The metacarpals from early Late Pleistocene sites like Villa Seckendorf, Avetrana, as well as the combined samples from Miesenheim to Leheringen are significantly longer than those of the Holocene from Denmark (U-Mann Whitney test; $p < 0.001$)

and the Holocene and Late Pleistocene of Germany (U-Mann Whitney test; $p < 0.001$) (see Tables S4–6; Figures S1–3). A single specimen from Can Rubau (MIS4, 71–57 ka) is shorter than all specimens up to Villa Seckendorf. The metacarpals of the combined samples from Doukkala II to Tamar Hat are younger and shorter than the combined European samples from Miesenheim to Villa Seckendorf (U-Mann Whitney test; $p < 0.001$). Bouknadel is supposed to be an older site, and its metacarpal fits the size of the older European samples. This suggests a trend in metacarpal length reduction, which happened in both Europe and Africa and may have started in the period 71–57 ka.

The older European localities (up to Avetrana) have relatively gracile metapodials, while there are specimens from the somewhat younger site Villa Seckendorf which are more robust (lower values for L/DTdf), though the differences between the samples are not statistically significant (U-Mann Whitney test, $p = 0.381$) (see Tables S4–6; Figures S1–3). However, the specimens from the still younger African sites from Doukkala II to Tamar Hat are significantly more robust than those from the European samples from Miesenheim to Avetrana (U-Mann Whitney test; $p < 0.001$). A metapodial from the older African site Bou Knadel has a robustness in the ranges of the earliest European sites. This suggests an increase in robusticity in both Europe and Africa, which may have occurred after Avetrana (about 100–80 ka). The Holocene *Bos primigenius* and domestic *Bos taurus* lack very robust specimens, which suggests a Holocene reversal of the trend.

The decrease in length and the increase in robusticity in both Europe and North Africa, which occurred broadly at the same time, could be explained by geneflow between both areas. This is the most parsimonious explanation, but an alternative explanation is parallel evolution due to climatic changes acting in the whole area of distribution. A combination of both is also possible: environmental change favored survival and mating opportunities of the more evolved individuals.

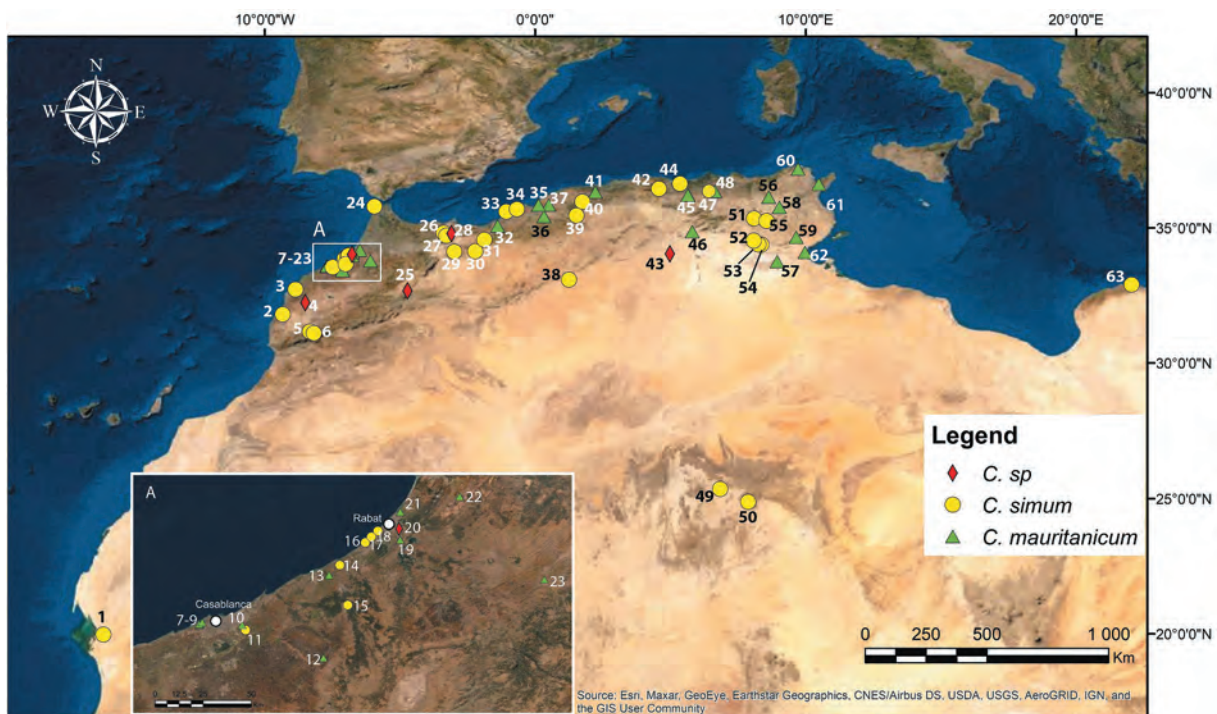


Figure 11. The North African localities with *Ceratotherium*. The key to numbers of the sites is given in Table 4.

Table 4. North African Plio-Pleistocene localities from which *Ceratotherium* has been described or mentioned.

Locality ¹	Map	Material metapodials? ²	Description or mention	Age (Ma)	Reference to age
Hamada Damous	61	Humerus fragment	Coppens (1972)	E Villafranchian 3–3.5 Ma	Coppens (1972) and Guérin (1980b)
Ain Brimba	57	P _{3/4} , M ^{1/2} , 3 x M ³	Arambourg (1970)	Villafranchian? 34 Ma	this paper
Ichkeul	60	P _{3/4}	Arambourg (1970)	Early Villafranchian	Arambourg (1970)
Fouarat	22	?	Arambourg (1979)	Earliest Pleistocene	Arambourg (1970)
				Calabrian	
				Villafranchian	
Oued el Akrech	19	Fragment	Arambourg (1970)	Early Villafranchian	Arambourg (1970)
Miliana ³	41	?	Arambourg (1938)	Sicilian	Arambourg (1938)
Ahl al Oughlam	10	Milk teeth, distal limb elements, metapodials	Geraads (2005)	~2.5 Ma	Geraads (2002)
Ain Boucherit	45	M ³	Arambourg (1970)	2.44 Ma	Sahnouni et al. (2018)
Ain Hanech	45	Skull, mandible, about 20 teeth, bones, Mc III	Arambourg (1970)	~1.7 Ma	Parés et al. (2014)
Mansourah	47	Tooth fragments	Thomas (1884)	Similar to Ain Hanech	Sahnouni and Van der Made (2009)
Bel Hacel	37	P _{3/4}	Arambourg (1970)	Piacenzian, Late Villafranchian	Arambourg (1970)
Tighennif	36	Metapodials, numerous teeth, bones	Pomel (1888, 1895)	Jaramillo?	Sahnouni and Van der Made (2009)
Lac Karâr	32	Upper and lower cheek teeth	Boule (1900)	M Pleistocene/Acheulian	Guérin (1980b)
Wadi Sarrat	58	M _{1/2}	Martinez-Navarro et al. (2014)	0.7 Ma	Martinez-Navarro et al. (2014)
Oulad Hamida	12	Skulls, teeth, bones, Mc III, Mt II, Mt III	Geraads and Bernoussi (2016)	0.5 Ma	Geraads (2010), Rhodes et al. (2006) and Daujeard et al. (2020)
Grotte des Rhinocéros				435 ± 85–737 ± 129 ka lower unit 720–690 ka, upper unit 548–522 ka	
Oulad Hamida <i>H. erectus</i> Cave (= Thomas Quarry III)	7	Radius, calcaneum, cuboid	Geraads (2002)	0.6	Geraads (2002)
Thomas Quarry I hominid level	7	Teeth, metapodials, MC II	Ennouchi (1956) and Geraads (1980)	0.6	Geraads (2002)
Khemisset, 6 m terrace	23	Teeth	Arambourg (1938) and Balout (1955)	M Pleistocene/Acheulian	Guérin (1980b) and Balout (1955)
Chetma	46	M ^{1/2}	Thomas (1884) and Gaudry (1879)	Quaternaire récent Acheulian	Thomas (1884), Balout (1955) and Guérin (1980b)
				M Pleistocene/Acheuléen	
				Acheulian	
Aboukir	35	Mandible ‘éléments abondants’	Pomel (1895) and Balout (1955)		Balout (1955)
Sidi Zin	56	2 molars, and molar fragments	Guérin (1980b)	M Pleistocene/Acheulian	Guérin (1980b)
Carrière STIC, (Sidi Abd er-Ramane) Casablanca	8	5 x M ^k	Ennouchi (1956)	Acheulian	Balout (1955)
Sidi Abderrahman couche D and G	9	Molar fragments	Ennouchi (1956) and Guérin (1980b)	M Pleistocene	Guérin (1980b)
Ain Bahya R2	13	P ⁴ , D ⁴ , M ³ , tibia	Michel (1990, 1992)	0.2 Ma	Geraads (2010)
Bouknadel	21	Of 2 x M ^{1/2} , M ₂ , mandible, humerus, astragalus, at least one M ^{1/2}	Michel (1990) and Ennouchi (1956)	0.1 Ma	Geraads (2010)
Carrière Ouest de Sidi Bouknadel -Dune	21	Mandible fragment, Mt III	Michel (1992)	‘Amirien ou, à la limite Tensiftien’	Michel (1992)
Ifri n’Ammar levels 28 and 45–57	28	Fragmented bones and teeth	Hutterer (2010)	83 ± 6–171 ± 12 ka	Richter et al. (2010)
Ifri N’Ammar	28		Ouchaou et al. (2019)	Holocene	Ouchaou et al. (2019)
El Akarit	62	Skull fragment, teeth, bones, Mt II, Mt III, Mt IV	Guérin and Faure (2007)	100–130 ka	Reyss et al. (2007)
Ain el Guettar	59	6 remains	Aouadi et al. (2014)	Mousterian	Aouadi et al. (2014)
El Harhoura 2 Layer 10	16	Molar fragment	Stoetzel et al. (2012)	118.3 ± 7.1 ka	Campmas (2012)
?Louis Gentil (Youssofiya)	4	Carpal and tarsal bones, vertebrae, pelvis	Ennouchi (1956)	Pleistocene	Guérin (1980b)
Sidi Moussa near Salé	20	p ³⁻⁴	Ennouchi (1956)	Pleistocene	Guérin (1980b)
Fort Bourdonneau	43	Fragment P ^x , foot bones	Depéret et al. (1928)	Pleistocene	Guérin (1980b)
Environs Midelt	25	1 M ^{1/2}	Michel, 990		
Khebibat	18	Palate	Arambourg (1938)	Mousterian	Arambourg (1938) and Guérin (1980b)
				Mousterio-Aterian	
Ain Rorh	3	Fragment of M _x	Ennouchi (1949)	Mousterio-Aterian	Guérin (1980b)
Ain Meterchem	55		Guérin (1980b)	Mousterio-Aterian	Guérin (1980b)
Grotte des Ours	48	A molar	Pallary (1909)	Late Pleistocene/Mousterio-Aterian	Guérin (1980b)
Oued el Haï	30	Skull, bones, Mc IV	This paper	100–57 ka	This paper
Haua Fteah	63	One remain	Klein and Scott (1986)	73.3–43.5 ka	Douka et al. (2014)
‘Levallois-Mousterian unit’					

(Continued)

Table 4. (Continued).

Locality ¹	Map	Material metapodials? ²	Description or mention	Age (Ma)	Reference to age
Mugharet el Aliya (bed 5, bed 9)	24	?	Howe and Movius (1947) and Campmas (2012)	Aterian 35–60 ka	Wrinn and Rink (2003)
El Harhoura 2, layer 4b	16	Tooth fragment	Stoetzel et al. (2012)	44 ± 3 ka	Campmas (2012)
Grès Rabbat, Carrière Marie Feuillet	18	Teeth, mandible	Arambourg (1938)	Würm (Late Pleistocene)	Arambourg (1938)
Carrière 9, région de Rabat	4	M ^{1/2} fragment, foot bones, metacarpal	Ennouchi (1956)	Late Würmian	Ennouchi (1956)
Carrière 8, région de Rabat	4	Molar, calcaneum, metacarpal fragment	Ennouchi (1956)		
Polygone	34		Guérin (1980b)	Late Pleistocene Moustérien- Monastérien	Guérin (1980b)
Ain Tit Mellil	11	D ³⁻⁴ , P ⁴ -M ³	Arambourg (1938)	Mousterian Ibero-Maurusian	Arambourg (1938) and Guérin (1980b)
Columnata	39		Guérin (1980b)	L Pleistocene/Ibero- Maurusian	Guérin (1980b) and Balout (1955)
La Mouilha	40		Guérin (1980b)	L Pleistocene/Ibero- Maurusian	Guérin (1980b)
Tamar Hat	44		Ouchaou et al. (2017b)	10,350 ± 375 to 20,600 ± 500 ka	Fernandez et al. (2015)
Oued Tensift, Talmeste	2	P ²⁻³ and P ³⁻⁴	Ennouchi (1948)	Pleistocene Holocene	Guérin (1980b) and Ouchaou and Bougariane (2015)
Fedj en Nahla	52		Guérin (1980b)	Latest Pleistocene?/ Capsian	Guérin (1980b)
Damous el-Ahmar	51		Ouchaou et al. (2017b)	Latest Pleistocene/ Holocene Capsian	Ouchaou et al. (2017b)
Bir Hmairiya	54		Ouchaou et al. (2017b)	Latest Pleistocene/ Holocene	Ouchaou et al. (2017b)
Grottes de Brézina Brézina El-Arouia	38		Guérin (1980b) and Ouchaou et al. (2017b)	Latest Pleistocene/ Holocene	Ouchaou et al. (2017b)
Chami	1	'restes', no further indication	Elouard (1976) and Guérin (1980b)	Latest Pleistocene/ Neolithic	Guérin (1980b)
Dar es Soltan Bed B, Beds G-I?	17	?	Ruhlman (1951), Balout (1955) and Guérin (1980b)	Neolithic latest Pleistocene/ Neolithic Holocene	Balout (1955), Guérin (1980b) and Ouchaou and Bougariane (2015)
Toulkine	5	Only mention of the presence	Ennouchi (1954)	Holocene	Ennouchi (1954)
Dou ben Adam	6	Only mention of the presence	Ennouchi (1954)	Holocene	Ennouchi (1954)
Ain Fritissa	29		Ouchaou and Bougariane (2015)	Holocene	Ouchaou and Bougariane (2015)
Kehf-el-Baroud	15		Ouchaou and Bougariane (2015)	Holocene	Ouchaou and Bougariane (2015)
Taghit Haddouch	26		Ouchaou et al. (2003)	Neolithic/Protohistoric	Ouchaou et al. (2003)
Hassi Ouenzega	27		Ouchaou and Bougariane (2015)	Holocene	Ouchaou and Bougariane (2015)
Grotte des Troglodytes	34	One molar fragment	Pallary and Tommasini (1892)	Neolithic	Pallary and Tommasini (1892)
Redeyef	53	Patella	Arambourg (1931) and Thomas (1977)	Neolithic	Arambourg (1931) and Thomas (1977)
La Guethna	33	Phalanx 3	Arambourg (1931) and Thomas (1977)	Neolithic	Thomas (1977) and Guérin (1980b)
Adrar Gueldaman near Akbou	42	Mt IV, juvenile Mc III	Arambourg (1931, 1938) and Thomas (1977)	Neolithic	Arambourg (1931, 1938) and Thomas 1977
Tiouririne	50	Mandible, maxilla	Arambourg and Balout (1952) and Thomas (1977)	Neolithic	Arambourg and Balout (1952) and Thomas (1977)
Harhoura 2, layer 1	16	2 tooth fragments	Ouchaou et al. (2011)	Neolithic	Ouchaou et al. (2011)
Rhafas, beds 1, 2, 4, 6	31		Michel (1992)	Bed 1: Holocene, 5.2 ka BP	Michel (1990, 1992)
Tihodaïne	49	6 foot bones (no metapodials)	Thomas (1977)	Holocene, 4,9 ± 0,3 ka	Thomas (1977)
Rouazi-Skhirat	14		Daugas et al. (1989)	4480 ± 190 BP	Daugas et al. (1989)

¹The localities are ordered according to approximate age, but a group of localities of unknown or imprecisely known age is inserted between El Akarit, still with *C. mauritanicum*, and Oued el Hai, with *C. simum*. If one species replaced the other, then all sites older than El Akarit should have *C. mauritanicum* and all sites younger than Oued el Hai should have *C. simum*.

²The presence of metapodials or complete metapodials is highlighted because of their diagnostic importance.

³Arambourg (1938) cited Thomas (1884) for Miliana, but we did not find this back in the publication.

⁴These sites are near Rabat, but we do not know their exact position.

These changes can be used in biostratigraphy. The metacarpal from Oued el Hai is larger (both longer and wider) than the ones from Doukkala II (Würmian/Soltanian) and Can Rubau (about 71–57 ka) and therefore, it is probably older than 57 ka and possibly even older than 71 ka. It is also robust like the samples from Avetrana (100–80 ka) and older sites. Bearing in mind the uncertainty caused by the small sample sizes, and the geographic distance, this suggests that the age of Oued el Hai could be in the range 100 to 57 ka and perhaps even between 80 and 71 ka. This suggests a Late Pleistocene age for these sediments of terrace T4 (+8–12 m) (Benito-Calvo et al. 2020), which is older than previous Holocene ages provided by Wengler and Vernet (1992). Following the cut and fill alluvial architecture proposed by Depreux et al. (2021), Late Pleistocene deposits could form the base of the fluvial terrace, before the incision-aggradation phases described for the Holocene. The succession of different incision-aggradation phases without significant bedrock incision would agree with the low incision rates described in the Moulouya catchment (Bartz et al. 2019), and the low gradient longitudinal profiles described in the study area (Pastor et al. 2015). These new data would imply bedrock incision rates between 0.08–0.2 m/ka since the Late Pleistocene, similar to the incision rates proposed for other locations in the upper Moulouya catchment, estimated at 0.3 m/ka since the Middle Pleistocene (Bartz et al. 2019).

Two species of *Ceratotherium* in the Maghreb – how to distinguish them?

Shortly after Pomel (1888) named the species *Rhinoceros mauritanicus* based on material from Tighennif (= Ternifine, Palikao), Boule (1899) suggested that it is synonymous with the living species *Rh. simus* (= *Ceratotherium simum*). Later authors did not mention the species at all (e.g. Arambourg 1938; Hooijer 1978), or at most recognised it as a subspecies restricted to North Africa (e.g. Arambourg 1970; Guérin 1979, 1980b). In Hooijer and Patterson's (1972) phylogeny, *Ceratotherium praecox* is an offshoot of the *Dicerorhinus* lineage and gave rise to the chronosubspecies *C. simum germanoaffricanum* and *C. simum simum*. Rehabilitation of the species started with Guérin (1994), who proposed a more complex phylogeny, raised the two subspecies to species rank and proposed that *C. mauritanicum* in North Africa was a geographic side branch of the afore mentioned lineage (Figure 10). He indicated that *C. praecox* and *C. mauritanicum* had gracile limb bones and the other two species more robust ones, and that *C. germanoaffricanum* was of very large size.

While Geraads (2002) still assigned Early and Middle Pleistocene North African fossils to *C. simum*, Geraads (2005, 2010) proposed that *C. simum* originated around 2.6 Ma in sub-Saharan Africa from *C. mauritanicum*, while the latter species continued to live in North Africa (Figure 10). Guérin (2011) commented on Geraads' (2005) classification, disagreed and confirmed his own previous classification. Also, Hernesniemi et al. (2011) differed from Geraads and coincided largely with Guérin (1994), but used the name *C. effifax* in stead of *C. praecox*.

Besides a different classification, Geraads (2005, 2010) proposed another new idea. Guérin (1994) listed the localities with *C. mauritanicum*, including some Neolithic ones and Guérin and Faure (2007) stated that there are only two species of rhinoceros in the Late Pleistocene of North Africa: *Ceratotherium mauritanicum* and *Dicerorhinus hemitoechus inermis* (= *Stephanorhinus hemitoechus*). By contrast, Geraads (2005, 2010) proposed that *C. simum* dispersed to North Africa, replacing there *C. mauritanicum*, which implies that there are two North African species of *Ceratotherium* (Figure 10)

The timing of this replacement was not documented. Geraads (2005) stated that the temporal range of *C. simum* in North Africa was the Late Pleistocene, but did not give the localities. In Geraads' (2010) table 34.1 the last record of *C. mauritanicum* is from Grotte des Rhinocéros (0.5 Ma), the rhinos from Doukkala II and Ain Bahya (supposed to date to 0.2 Ma) are not identified with certainty and the oldest record of *C. simum* is from Haua Fteah (0.1 Ma). The latter record is based on Klein and Scott (1986), who reported, but did not describe, a single specimen from a 'Levallois-Mousterian' level. So, we cannot check the identification. Besides, this level is younger than 0.1 Ma. It was previously estimated to date to 65–40 ka and more recently to 73.3–43.5 ka (Douka et al. 2014). The Grotte des Rhinocéros was recently re-dated (Daujeard et al. 2020) giving dates of 720–690 ka for the lower unit and 548–522 ka for the upper unit. We do not know from which level the relevant rhinoceros fossils come. Based on this, the replacement of *C. mauritanicum* by *C. simum* occurred between some 720–522 and 43.5 ka.

Since there is no gradual evolution from *C. mauritanicum* to *C. simum* in North Africa, but a sharp break when one species replaced the other, it might be expected to be easy to assign material to one of the two species and to establish objectively the first appearance of *C. simum*. However, this turns out to be more complicated. The main differences between *C. mauritanicum* and *C. simum* indicated by Guérin (1994) concerned skull and postcranial features. The skull features as presented by Guérin (1994, Figure 2) are difficult to evaluate for practical reasons and concern relatively minor differences in proportions. Guérin (1980a) and Geraads and Bernoussi (2016) gave measurements of the skulls of recent *C. simum* and *C. mauritanicum* from Grotte des Rhinocéros. Most of the measurements of the fossil species are within the ranges of the recent sample and are not diagnostic. However, measurements 25–28 (of Guérin 1980a) tend to be small in the fossil species, pointing to different proportions. These are the height of the skull at various places above the tooth row. The width of the tooth row (28–29) is also small. Measurements 4 and 9 (length of the nasal-incisive notch, distance the orbita to the nasal-incisive notch) tend to be large in the fossil species and even outside the ranges of the recent sample, as well as 5 (minimal width of the brain case behind the orbita). Skulls are rare, and samples with skulls can in some cases be identified better by other means. Most Late Pleistocene and Holocene North African fossils of *Ceratotherium* are teeth and Guérin (1994) assigned them all to *C. mauritanicum*. If teeth would provide good features to separate *C. mauritanicum* and *C. simum*, Guérin (1980b, 1994) and Guérin and Faure (2007) would have detected the replacement of the former by the latter species. The best feature to separate the two species seems to be the more gracile limb bones of *C. mauritanicum*, but they are not common either.

Geraads (2010) gave diagnoses for *C. mauritanicum* and *C. simum*, which should serve to differentiate between the species. His diagnosis for *C. mauritanicum* has five characters, apparently mostly aimed to distinguish the species from *C. neumayri*, and a diagnosis for *C. simum* with some fifteen characters. One character appears in both diagnoses and has the same state for both (premolar row shortened). All other characters appear in only one of the two diagnoses. The P² is said to be small in *C. simum*, but no measurements were given to demonstrate the difference. We do not have data on that tooth from Tighennif, the type locality of *C. mauritanicum*, but the P₂ from Tighennif (n = 7–9) are on average smaller than those of the living species (n = 9–13), raising doubt about this feature. *Ceratotherium simum* is said to have hypsodont upper cheek teeth, but this is also the case in *C. mauritanicum*. Geraads (1980) assigned teeth and bones from Thomas Quarry I and III, assumed to be of similar age, to *C. simum* because of crown height,

while Geraads and Bernoussi (2016) assigned part of this material to *C. mauritanicum*. So, the criterion of crown height is apparently not unequivocal. Still more distinguishing features have been cited, but many are of difficult application, as is the case with the time of shedding the DPI, or have not been sufficiently documented.

In the end, the most precise diagnostic feature to differentiate the two species seems to be the length and robustness of the metapodials (Figure 7; Guérin 1994; Geraads 2005).

The dispersal of *Ceratotherium simum* across the Sahara to the Maghreb

The dispersal of *C. simum* to the Maghreb occurred between some 720–522 and 43.5 ka, but it should be possible to date the event more precisely. According to Geraads (2010, table 34.1), possible records of *C. mauritanicum* are from Doukkala II and Aïn Bahya (0.2 Ma). Identifying these specimens as one of the two species would diminish the uncertainty about the timing of the replacement. The rhinoceros fossils from Doukkala II come from the middle level of the locality, which was assigned a Würmian, Soltanian or Late Pleistocene age (Michel and Wengler 1993), not 0.2 Ma as by Geraads (2010), who did not give an argument for the much older age. These fossils were described by Michel (1989, 1990), who assigned them all to *S. hemitoechus*. There is a $M^{1/2}$ with the crochet and crista not meeting and not forming a medifossette and a $P^{3/4}$ without a medifossette. The teeth do not have a well-marked fold of the paracone on the buccal side, but this might be because of wear. These and other morphological features confirm Michel's identification. A MtIII is long and elongate, this might fit *C. mauritanicum*, but its size might fit a late and large *S. hemitoechus*, while the older populations of the latter species are still more gracile (Figure 7). Such identification would agree with the age as indicated by Michel and Wengler (1993). Michel (1990) described three teeth and a tibia fragment from Aïn Bahya as *C. simum*. The minor size difference between the two species of *Ceratotherium* is too little to reliably assign the material from Aïn Bahya to one of them.

The earliest (and only) record of *C. simum* in North Africa, mentioned by Geraads (2010, table 34.1) is from Haua Fteah, but we cannot check the identification, which is based on a single tooth. Papers published after the rehabilitation of *C. mauritanicus* continued to cite *C. simum*, but did not state diagnostic features. Martínez-Navarro et al. (2014) identified a fossil from Wadi Sarrat as *Ceratotherium simum* and estimated its age to be about 0.7 Ma. This would be by far the oldest fossil of this species in North Africa. The age of the site is based mainly on the size (length x width) of two M_1 of *Paraethomys*. Using the product of two measurements augments the differences between the means of the samples, but also augments the range of variation of the value (in some of the samples the higher value is 150% of the lower value) and this essential information was not given. More important is that the rhinoceros specimen is a much-worn $M_{1/2}$ and that because of its wear, it is not diagnostic.

We reviewed the literature and found over 70 North African sites (Figure 11) with *Ceratotherium*, which are given in approximate chronological order in Table 4. The youngest site with gracile metapodials appears to be El Akarit. Guérin and Faure (2007) described a skull fragment, some teeth and bones as *C. mauritanicum*. The bones include three complete metapodials, which are long and gracile (Figure 7) and confirm the identification. Thermoluminescence dating is problematic but might suggest an age of 80–190 or more likely 80–120 ka. A Th/U age of 71 ka for the peats overlying the deposit is probably too young for technical reasons, but these peats could have been formed between 150 and

130 ka or between 100 and 90 ka (Reyss et al. 2007). Given these data, the most likely age for the fossils from El Akarit seems to be 80–120 ka.

The new fossils from Oued el Haï confirm that *C. simum* indeed dispersed to the Maghreb and provide a minimum age for the event. *Bos primigenius* suggested that bearing in mind the uncertainties caused by small sample sizes and geographic distance, Oued el Haï could date to 100–57 ka. The localities Adrar Gueldaman (Neolithic) and Carrière 9 Region de Rabat (late Würmian) (Table 4) have metapodials, which may belong to *C. simum*; however, we do not have the measurements and cannot confirm such an identification. These localities are younger than Oued el Haï.

The timing of the northward dispersal of *C. simum* is thus between 120 and 57 ka, but this is a long time range, and within this period, there were several times slices that dispersal was more likely. It probably needed one of the periods which have been dubbed Green Sahara (Drake et al. 2011). Sapropels in marine sediments are indicative for such periods and are precisely dated, while continental sediments indicative of humid conditions show a wider spread in the dates. The period which may have allowed *C. simum* to spread northward might correspond to sapropels S3 (~80–85 ka) and S4 (~100–105 ka) (Larrasoña et al. 2013).

Traditionally, the white rhinoceros has been considered to have two subspecies, with *C. s. simum* with a historical distribution from Namibia to Mozambique and *C. s. cottoni* with a historical distribution from northern Zaire to southern Chad. However, Groves et al. (2010) argued that these are two separate species because of metrical differences (which in fact show little difference, but much overlap) and because, based on DNA, the populations are separated since 0.75–1.4 Ma. A more recent study of the DNA broadly confirms an old divergence time of the populations around 972 ka (between 510 and 1523 ka), but treats both as a single species (Moodley et al. 2018). These dates fit paleontological evidence on the origin of this species, which occurred around 1 Ma (Guérin 1994) or 2.5 Ma (Geraads 2005, 2010) (Figure 10) and is well before the dispersal of *C. simum* to the north. The population in the Maghreb is likely to have originated from *C. s. cottoni*.

The two species in the geographic and climatic context

The Maghreb is isolated from most of the Palearctic by the Mediterranean and from the Ethiopian biogeographic region by the Sahara. Morocco and northern Algeria and Tunisia, as well as a small area near Benghazi have a Mediterranean climate, like the Levant, but are disconnected because the Sahara reaches the coasts of Libya and Egypt. The evolution of the biogeographic affinities of the Maghreb reflects climatic changes. The progressive decrease in global temperatures (Lear et al. 2000; Van de Wal et al. 2011) led to an increasing proportion of Palearctic species.

The age and formation of the Sahara is much debated, but it seems that it started to form in the Late Miocene (Zhang et al. 2014), that aridity fluctuated, but increased (deMenocal 1995; Trauth et al. 2009), that there were periods when extensive lakes and river systems existed in this area (Drake et al. 2011; Coulthard et al. 2013; Skonieczny et al. 2015), while Holocene fossils and rock art testify that a rich fauna lived there (Le Quellec 1999). The more humid stages have been called 'Green Sahara' (Drake et al. 2011). Larrasoña et al. (2013) identified 230 Green Sahara Periods over the past 8 Ma, which are related to the eccentricity modulation of the precession of the earth. Wooded grasslands were reconstructed for most of the Eemian Sahara and assumed for the earlier humid periods. However, were all those 'green periods' equally green?

In general, 200–300 mm annual precipitation is considered to be a threshold passing from desert to steppe, but this may have been considerably higher due to the lower pCO₂ of the pre-industrial Holocene and Pleistocene atmospheres (Hopcroft et al. 2017). This means that, even if a variety of geological records as well as modelling indicate increased precipitation in the past, this may not be reflected in significant environmental change, and the Maghreb would still remain isolated by dry environments. At this point, the study of the ecology and geographic distribution of mammals may contribute relevant information.

The two divergent lineages of *Ceratotherium* lived for possibly as much as 3 Myr in different geographic areas, separated by the Sahara, but when *C. simum* spread to the North, it replaced *C. mauritanicum*. That this did not happen during an earlier Green Sahara Period suggests that during many of these periods, there may have been increased precipitation, but not necessarily that the Sahara was ‘greener’, and that it continued to act as a barrier for these rhinoceroses. The white rhinoceros is a strict grazer, lives in grassland and savannah and is found in the highest densities in areas with 700–800 mm annual precipitation (Wilson and Mittermeier 2011). If possible, it drinks twice a day, but, if necessary, it may resist 2–4 days without drinking (Estes 1992). The northward dispersal of *C. simum*, after a long period of isolation, suggests that grasslands did not extend all the way across the Sahara until ~80–85 ka or ~100–105 ka.

It also took other taxa a long time to cross the Sahara. *Giraffa camelopardalis* is present in the latest Pleistocene and Holocene of the Maghreb (Ouchaou et al. 2017a), whereas it originated much earlier in the South. This suggests that another threshold was met after the dispersal of *C. simum*. This could be the continuous presence of dispersed trees, not just grasslands. The living species of hippopotamus originated about 2 Ma, but did not reach the Maghreb until the later Middle Pleistocene (Van der Made et al. 2017). In this case, the constraints may have been more related to the distribution of large water bodies.

While some mammals, which dispersed into the Maghreb became isolated and evolved into endemic species, the populations of *Bos primigenius* in Europe and the Maghreb seem to have maintained gene flow. Most likely, this occurred through the Middle East and suggests a suitable environment for the species in northern Libya and Egypt in the time between the fossil associations from Oued el Hai and Allobroges. The species *Bos gaurus*, *B. javanicus* and *B. sauveli* live in a variety of habitats, including grasslands, savannah, forest and swamps, with annual precipitation in excess of 1000 mm and with available drinking water (Wilson and Mittermeier 2011). *Bos primigenius* is extinct, but its habitat has been reconstructed as swamps and meadows on the floodplains of rivers in an otherwise forested landscape (Van Vuure 2003). If, after the north-ward dispersal of *C. simum*, geneflow occurred in *Bos primigenius* across northern Libya and Egypt, this suggests the existence of a continuous grassland or savannah landscape along the coasts of these countries at that time.

The environmental requirements of the species which lived in the Maghreb while maintaining geneflow with other populations (as *Bos primigenius*), or not (as *Megacerooides algericus*), and those for which the Sahara was a barrier, until there was an opportunity to disperse (as *Ceratotherium simum* and *Giraffa camelopardalis*) may serve to calibrate models on the Green Sahara environments. In this way, the documentation of the dispersals of large mammals to the Maghreb, the dating of these events and the study of their requirements may lead to a better understanding of the impact of climatic change on the environments of the Maghreb and areas around it.

Conclusions

We report on fossil skulls and associated limb bones from a terrace of the Oued el Hai in NE Morocco and assign them to the white rhinoceros *Ceratotherium simum* and the aurochs *Bos primigenius*. Our study led to the following conclusions:

During the Pleistocene, the proportion of Palearctic mammals in the Maghreb increased, and *Bos primigenius* was one of them.

The European *Bos primigenius* evolved shorter and more robust metapodials, and the available data indicate that the same happened at about the same time in the Maghreb, which suggests gene flow between these areas, though we cannot rule out parallel evolution, possibly as a reaction to climatic change in the whole area of distribution of the species.

Bearing in mind the limitations of small sample size and the uncertainty caused by geographic distance, the stages of evolution of the two species from Oued el Hai suggest the presence of Late Pleistocene age sediments in the terrace, possibly between 57–100 ka.

The arrival of *C. simum* in North Africa was not later than 57 ka and may have been during wetter climatic circumstances between 80–85 or 100–105 ka, when the Sahara was no effective barrier to the dispersal of the white rhinoceros.

We reviewed the literature and found over 70 Plio-, Pleisto- and Holocene North African localities with *Ceratotherium*. Fossils that are diagnostic at the species level are rare, but about 27 localities date from before and over 40 from after the likely arrival datum of *C. simum*.

The late arrival of *Ceratotherium simum* in the Maghreb suggests that during earlier Green Sahara Periods the Sahara still acted as a barrier to this species. Some parameter of the environment, possibly related to humidity, did probably not meet the requirements of this species.

The documentation of evolution, biostratigraphy, biogeography and ecology of the Quaternary fauna of the Maghreb may help to understand the environmental changes in the Sahara and the Middle East.

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Supplementary Information:

New materials of the white rhinoceros *Ceratotherium simum* and aurochs *Bos primigenius* from a Late Pleistocene terrace of the Oued el Haï (NE Morocco) - two elements of the Maghrebi Palearctic fauna

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Table S1

Provenance of the data used for comparison in Figures 6-9.

species	locality	Collection ¹	literature
<i>Ceratotherium mauritanicum</i>	Tighennif	MNHN	Arambourg 1970
<i>Ceratotherium mauritanicum</i>	Grotte des Rhinocéros		Geraads and Bernoussi 2016
<i>Ceratotherium mauritanicum</i>	El Akarit		Guérin and Faure 2007
<i>Ceratotherium simum</i>	Recent		Guérin 1980a
<i>Ceratotherium simum</i>	Oued el Haï	UMPO	this paper
<i>Ceratotherium</i> and/or <i>S. hemitoechus</i>	Doukkala II		Michel 1989, 1990
<i>Diceros bicornis</i>	Recent		Guérin 1980a
<i>Stephanorhinus hemitoechus hemitoechus</i>	Doukkala II		Michel 1989, 1990
<i>Stephanorhinus hemitoechus hemitoechus</i>	Azokh V	MUB	Van der Made et al. 2016
<i>Stephanorhinus hemitoechus hemitoechus</i>	La Masque	MRA	
<i>Stephanorhinus hemitoechus hemitoechus</i>	Arenero González (Madrid)	MNCN	
<i>Stephanorhinus hemitoechus</i> ssp.	Megalopolis	NCUA	Sickenberg 1976
<i>Stephanorhinus hemitoechus</i> ssp.	Maastricht-Belvédère	NMMaa	Fortelius et al. 1993
<i>Stephanorhinus hemitoechus</i> ssp.	Orgnac 3	EPCC-CERPT	Guérin 1980 and Aouraghe 1992
<i>Stephanorhinus hemitoechus</i> ssp.	Atapuerca TD10	IPHES / CENIEH	
<i>Stephanorhinus kirchbergensis</i>	Zoukoudian	ZSM	
<i>Stephanorhinus kirchbergensis</i>	Bilzingsleben	FBFSUJ	Van der Made 2000
<i>Stephanorhinus jeanvireti</i>	Camp dels Ninots	IPHES	Gómez de Soler et al 2012
<i>Stephanorhinus etruscus</i>	Upper Valdarno	IGF	Mazza 1988
<i>Stephanorhinus</i> aff. <i>etruscus</i>	Atapuerca TD7	IPHES / CENIEH	

<i>Stephanorhinus hundsheimensis</i>	Untermassfeld	IQW	Kahlke 2001
<i>Stephanorhinus hundsheimensis</i>	Deutsch-Altenburg	NMW	
<i>Stephanorhinus hundsheimensis</i>	Mauer	SMNK	Schreiber 2005
<i>Stephanorhinus hundsheimensis</i>	Soleilhac	MCP	Lacombat 2005
<i>Stephanorhinus hundsheimensis</i>	Hundsheim	NMW and IPUW	Toula 1902
<i>Bos primigenius</i>	Miesenheim	FASMN	Turner 1990
<i>Bos primigenius</i>	Plaidter Hummerich	FASMN	Turner 1990
<i>Bos primigenius</i>	Neumark Nord	FBFSUJ	Döhle 1990
<i>Bos primigenius</i>	Taubach	IQW	
<i>Bos primigenius</i>	Lehringen	HMV	Sickenberg 1969
<i>Bos primigenius</i>	Avetrana		Pandolfi et al. 2011
<i>Bos primigenius</i>	Villa Seckendorf	SMNS	Ziegler 1996
<i>Bos primigenius</i>	Oued el Haï	UMPO	this paper
<i>Bos primigenius</i>	Tamar Hat		Thomas 1977
<i>Bos primigenius</i>	Pinilla del Valle - Camino	UCM, presently MAR	Álvarez Lao et al. 2013
<i>Bos primigenius</i>	Can Rubau	CIAG	
<i>Bos primigenius</i>	Allobroges		Hadjouis 1985
<i>Bos primigenius</i>	Aboukir		Pomel 1894
<i>Bos primigenius</i>	Fifila		Michel 1990
<i>Bos primigenius</i>	Bou Knadel		Michel 1990
<i>Bos primigenius</i>	Doukkala II		Michel 1990
<i>Bos primigenius</i>	Holocene Denmark	NHMD	Degerbøl and Fredskild 1970
<i>Bos primigenius</i>	Late Pleistocene-Holocene Germany	MNB	
<i>Bos primigenius</i>	Gibujo		Altuna 1974
<i>Bos taurus</i>	Grand Rocher		Pomel 1894
<i>Bos taurus</i>	Copper Age Hungary		Bökönyi 1974
<i>Bos taurus</i>	Bronze Age Hungary		Bökönyi 1974
<i>Bos taurus</i>	Iron Age Hungary		Bökönyi 1974
<i>Bos taurus</i>	Roman Period Hungary		Bökönyi 1974
<i>Bos taurus</i>	Great Migration Hungary		Bökönyi 1974
<i>Bos taurus</i>	Avar Period Hungary		Bökönyi 1974
<i>Bos taurus</i>	10-13th Century Hungary		Bökönyi 1974
<i>Bos taurus</i>	14-17th Century Hungary		Bökönyi 1974
<i>Bos gaurus</i>	Yenchingkou / Wan Hsien	AMNH	Colbert and Hooijer 1953
<i>Bos gaurus</i>	Recent	SAPM, MNCN	

<i>Syncerus cf. caffer</i>	Lake Nyasa	MNB	
<i>Syncerus</i>	Recent	SAPM, NBC, MNB	
<i>Syncerus antiquus</i>	Allobroges		Hadjouis 1985
<i>Syncerus antiquus</i>	Bou Knadel		Michel 1990
<i>Syncerus antiquus</i>	Navaisha		Thomas 1977
<i>Syncerus antiquus</i>	Broken Hill	NHM	
<i>Syncerus antiquus</i>	Djelfa		Pomel 1893

¹ If an acronym of a collection is indicated, the material was studied by us, if only a reference is given, the data used come from the publication.

Table S2
Acronyms used to indicate collections.

AMNH	American Museum of Natural History, New York
CENIEH	Centro Nacional de Investigación sobre la Evolución Humana, Burgos
CIAG	Centre d'Investigacions Arquelògiques de Girona
FASMN	Römisch-Germanisches Zentralmuseum, Forschungsinstitut für Vor- und Frühgeschichte, Forschungsbereich Altsteinzeit Schloss Monrepos, Neuwied
FBFSUJ	Forschungsstelle Bilzingsleben, Friedrich Schiller Universität, Jena
HMV	Historisches Museum, Verden
IGF	Istituto di Geologia, now Museo di Storia Naturale, Firenze
IPHES	Institut Català de Paleoecologia Humana i Evolució Social, Tarragona
NSAP	Institut National des sciences d'Archéologie et du Patrimoine, Rabat
IPH	Institut de Paléontologie humaine, Paris
IPUW	Institut für Paläontologie der Universität, Wien (Vienna)
IQW	Institut für Quartärpaläontologie, Weimar. Presently named: Forschungsstation für Quartärpaläontologie of the Senckenberg Forschungsinstitut und Naturmuseum Frankfurt, Weimar
EPCC - CERPT	EPCC-CERPT - Centre Européen de Recherches Préhistoriques de Tautavel.
MAR	Museo Arqueológico Regional, Alcalá de Henares
MCP	Musée Crozatier, Le Puy-en-Velay
MNB	Museum für Naturkunde, Berlin
MNCN	Museo Nacional de Ciencias Naturales, Madrid
MRA	Museum Requier, Avignon
MUB	Medical University, Baku
NBC	Naturalis Biodiversity Center, Leiden
NCUA	National and Capodistrian University of Athens
NHM	Natural History Museum, London
NHMD	Natural History Museum of Denmark, Copenhagen
NMM	Natuurhistorisch Museum, Maastricht
NMW	Naturhistorisches Museum, Wien (Vienna)
SAPM	Staatssammlung für Anthropologie und Paläoanatomie, München
SMNK	Staatliches Museum für Naturkunde, Karlsruhe
SMNS	Staatliches Museum für Naturkunde, Stuttgart
UCM	Universidad Complutense de Madrid
UMPO	Université Mohamed Premier, Oujda
UM5R	Université Mohamed V, Rabat
ZSM	Zhoukoudian Site Museum, Fangshian

Table S3
Ages of the localities with *Bos*.

Locality	Age	Method	Reference
Wadi Sarrat	0.7 Ma (?)	biostratigraphy (magnetostratigraphy)	Martínez Navarro et al. 2014
Grotte des Rhinocéros	0.6 Ma 435±85 ka - 737 ± 129 ka	biostratigraphy ESR	Geraads 2002 Rhodes et al. 2006
Miesenheim	>452 ka	radiometric date in nearby profile	Von Koenigswald and Heinrich 1999
Plaidter Hummerich	Saalian	lithostratigraphy biostratigraphy	Von Koenigswald and Heinrich 1999
Neumark Nord 1	intra-Saale Warmzeit intra-Saale Warmzeit MIS7 late Middle Pleistocene different from Eemian	various methods Biostratigraphy small mammals Biostratigraphy large mammals Amino Acid Racemisation Pollen	Mania 2010 Heinrich 2010 Van der Made 2010b Penkman 2010 Seifert-Eulen 2010
	Eemian Eemian, 117 ka	Pollen ESR	Litt 1994 Schüler 2010
Taubach	Eemian		Von Koenigswald and Heinrich 1999
Lehringen	Eemian - Linden-Ulmen-Hazel-Zeit		Von Koenigswald and Heinrich 1999
Avetrana	80-100 ka	biostratigraphy	Petronio et al. 2008
Villa Seckendorf	early Würmian	biostratigraphy	Ziegler 1996
Oued el Hai	early Late Pleistocene about 100-57 ka	biostratigraphy	this paper
Pinilla del Valle - Camino	90.961±7881 ka	thermoluminescence	Pérez-González et al. 2010
Can Rubau	90-40 ka MIS4? (71-54 ka)	biostratigraphy presence of <i>Ovibos</i> and <i>Rangifer</i>	Álvarez Lao 2007, fig. IV.3.3 this paper
Tamar Hat	10,350 ± 375 to 20,600±500 ka	¹⁴ C	Fernandez et al. 2015
Aboukir	Acheulian	archeology	Balout 1955
Allobroges	Aterian (150-20 ka)		
Filfila			
Bou Knadel	0.2 Ma	biostratigraphy	Geraads 2010
Doukkala II	niveau inférieur	late Middle-early Late Pleistocene	Michel and Wengler 1993
	niveau moyen	Würm / Soltanien 0.2 Ma	Michel and Wengler 1993 Geraads 2010
	niveau supérieur	Soltanien terminal	Michel and Wengler 1993
Holocene Denmark (several localities)	Holocene	¹⁴ C	Gravlund et al. 2012
Holocene / Late Pleistocene Germany (several localities)			
Gibujo	7.380 ±150 ka	¹⁴ C	Altuna 1974

Tihodaine upper Tihodaine middel Tihodaine lower	late Middle Pleistocene, >250 ka Late Pleistocene Holocene, 4.9±0.3 ka	230Th/234U ¹⁴ C	Thomas 1977
Grand Rocher	after domestication <i>Bos</i>	biostratigraphy	Pomel 1894
Holocene Germany (<i>B. taurus</i>)	after domestication <i>Bos</i>	biostratigraphy	
various sites Hungary	Copper Age / Bronze Age / Iron Age / Roman Period / Great Migration / Avar Period / 10-13th Century / 14-17th Century		Bökönyi 1974

Table S4Site groups for statistical comparisons of *Bos primigenius* metacarpals.

Tamar Hat-Doukkala	Tamar Hat Tihodaine Doukkala II Allobroges Aboukir Filfila
Denmark	Holocene sites
Germany	Holocene-Pleistocene sites
Villa Seckendorf	Villa Seckendorf
Avetrana	Avetrana
Miesenheim-Lehringen	Miesenheim Ariendorf Plaidter-Hummerich Neumark Nord Taubach Lehringen
Miesenheim-Avetrana	Miesenheim Ariendorf Plaidter-Hummerich Neumark Nord Taubach Lehringen Avetrana
Miesenheim-Villa Seckendorf	Miesenheim Ariendorf Plaidter-Hummerich Neumark Nord Taubach Lehringen Avetrana Villa Seckendorf

Table S5

Results of U-Mann Whitney comparative tests of width (DTdf), length (L) and robusticity (L/DTdf) of *Bos primigenius* metacarpals. The site groups are explained in Table S4.

Comparisons		DTdf		L		L/DTdf	
		U	p	U	p	U	p
Villa Seckendorf	Denmark	105	0.383	25	<0.001	122	0.852
Villa Seckendorf	Germany	22	0.049	4	<0.001	47	0.969
Villa Seckendorf	Avetrana	44	0.787	48	0.939	21	0.452
Villa Seckendorf	Miesenheim – Lehringen	39	0.365	51	0.616	38	0.464
Villa Seckendorf	Tamar Hata- Doukkala	31	0.665	8	0.008	13	0.052
Denmark	Germany	178	0.617	147	0.154	179	0.742
Denmark	Avetrana	168	0.449	40	<0.001	65	0.089
Denmark	Miesenheim – Lehringen	179	0.386	40	<0.001	147	0.241
Denmark	Tamar Hat-Doukkala	64	0.010	116	0.532	44	0.005
Germany	Avetrana	39	0.0567	11	<0.001	24	0.139
Germany	Miesenheim – Lehringen	41	0.047	10	<0.001	53	0.285
Germany	Tamar Hat-Doukkala	25	0.039	46	0.908	21	0.041
Avetrana	Miesenheim – Lehringen	67	0.568	59	0.487	41	0.966
Avetrana	Tamar Hat-Doukkala	38	0.271	12	0.009	2	0.003
Miesenheim – Lehringen	Tamar Hat-Doukkala	56	0.894	11	0.003	9	0.003
Miesenheim – Avetrana	Villa Seckendorf	83	0.488	99	0.716	59	0.381
Miesenheim –Avetrana	Denmark	347	0.304	79	<0.001	212	0.075
Miesenheim – Avetrana	Germany	80	0.023	21	<0.001	77	0.139
Miesenheim – Avetrana	Tamar Hat-Doukkala	94	0.482	23	0.002	11	<0.001
Miesenheim – Villa Seckendorf	Denmark	452	0.235	104	<0.001	334	0.138
Miesenheim – Villa Seckendorf	Germany	102	0.014	25	<0.001	124	0.254
Miesenheim – Villa Seckendorf	Tamar Hat-Doukkala	125	0.481	31	<0.001	24	0.001

Table S6

Summary metric statistics of *Bos primigenius* metacarpals. The measurement abbreviations are shown in Table S5 and the site groups are explained in Table S4.

	Villa Seckendorf	Denmark	Germany	Avetrana	Miesenheim- Lehringen	Tamar Hat- Doukkala
DTdf						
n	8	33	12	12	13	9
Min	78.4	65.9	68.3	74.6	71.4	73
Max	95.7	87.4	89.4	95.4	94.5	93
Mean	84.2	78.8	77.5	82.8	83.2	84.9
Std.	6.7	6.9	7.2	5.6	8.3	6.7
L						
n	9	34	12	11	13	8
Min	251.8	228.2	228.4	251	250.8	215
Max	271.6	266.6	258.4	275	283.3	266
Mean	263.9	247.7	242.2	263.7	266.1	242.8
Std.	6.3	9.8	11.1	8.8	10.1	16.9
L/DTdf						
n	8	32	12	7	12	8
Min	2.7	2.8	2.9	3.1	2.9	2.7
Max	3.4	3.6	3.5	3.5	3.7	3.2
Mean	3.1	3.2	3.1	3.3	3.3	2.9
Std.	0.3	0.2	0.2	0.1	0.2	0.2

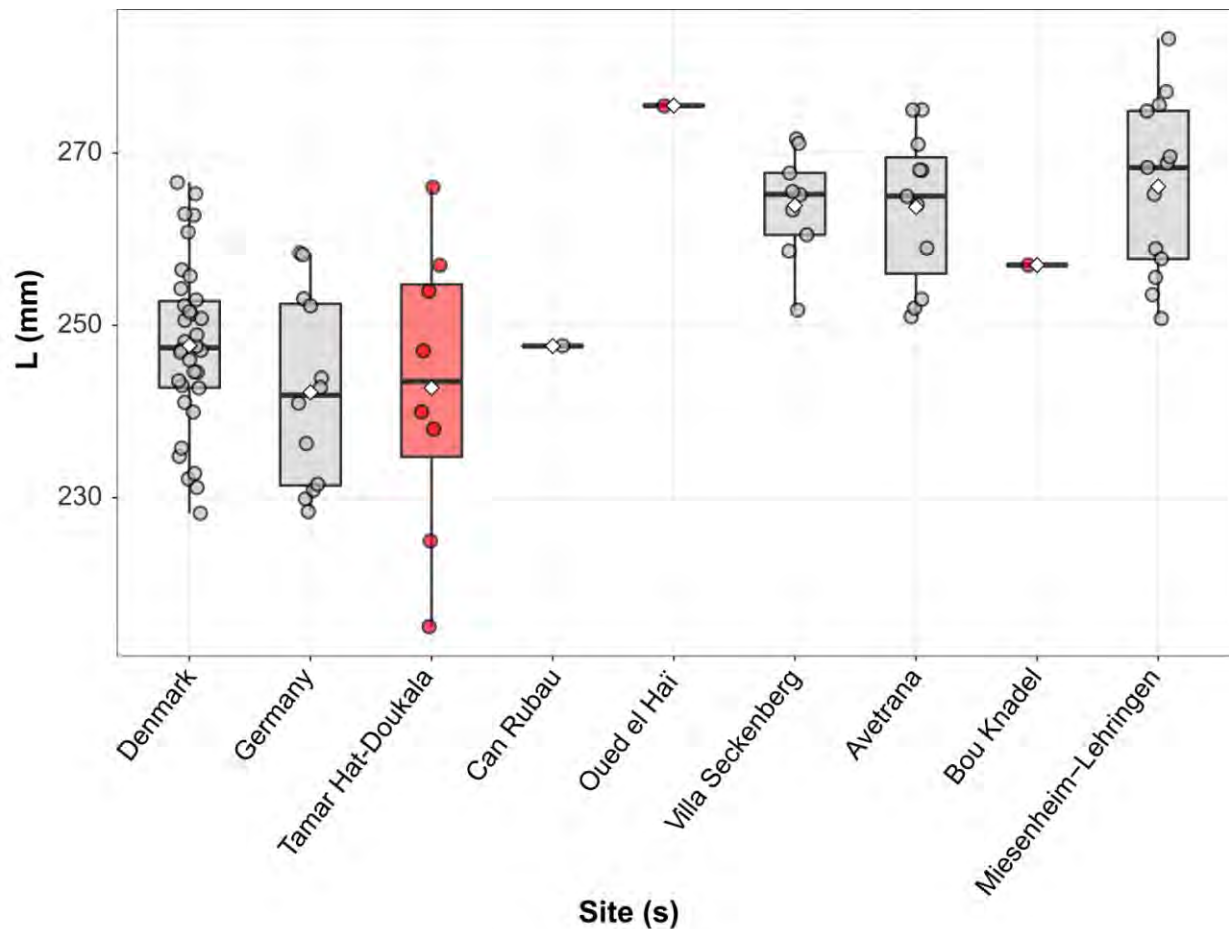


Fig. S1

Boxplots showing the central tendencies and dispersion of the raw values in length (L) of *Bos primigenius* metacarpals, for each site group. The localities are ordered in approximate order from young (left) to old (right). The circles represent each raw data point. The boxes represent the interquartile range (IQR), which accounts from the 25th percentile to the 75th percentile of the data. The median is represented by the horizontal line separating the boxes in two portions. The mean is represented by the white rhombus symbol. The ends of the lines extending from the IQR are the extreme values (within 1.5 times of the IQR from the upper or lower quartile). African localities are colored in red. Note that the distinctive pattern of metacarpal shortening in Can Rubau (71-57 ka) and younger sites in both African and Europe.

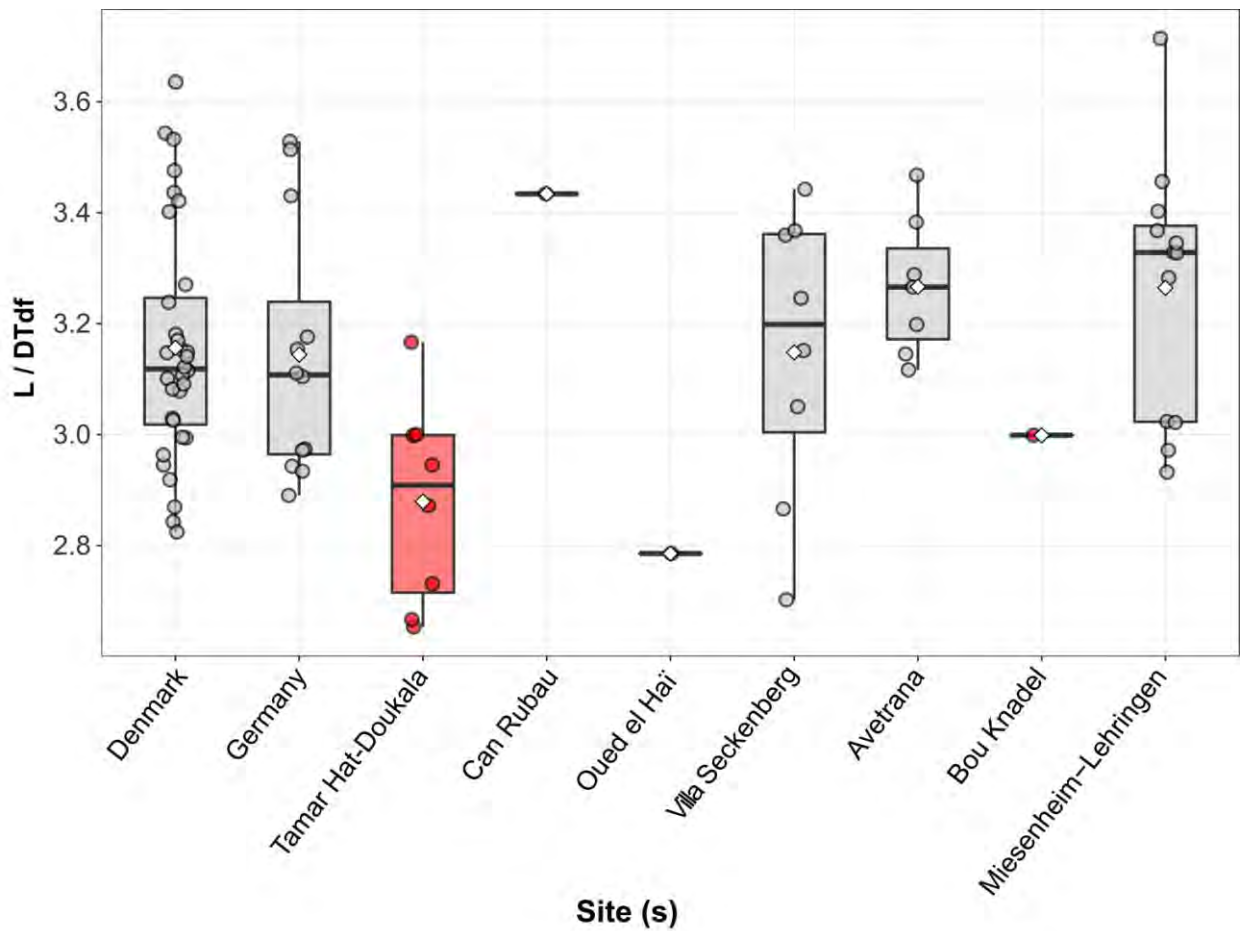


Fig. S2

Boxplots showing the central tendencies and dispersion of the raw values of robusticity ($L/DTdf$) of *Bos primigenius* metacarpals, for each site group. Configuration of boxplots as in Fig. S1.

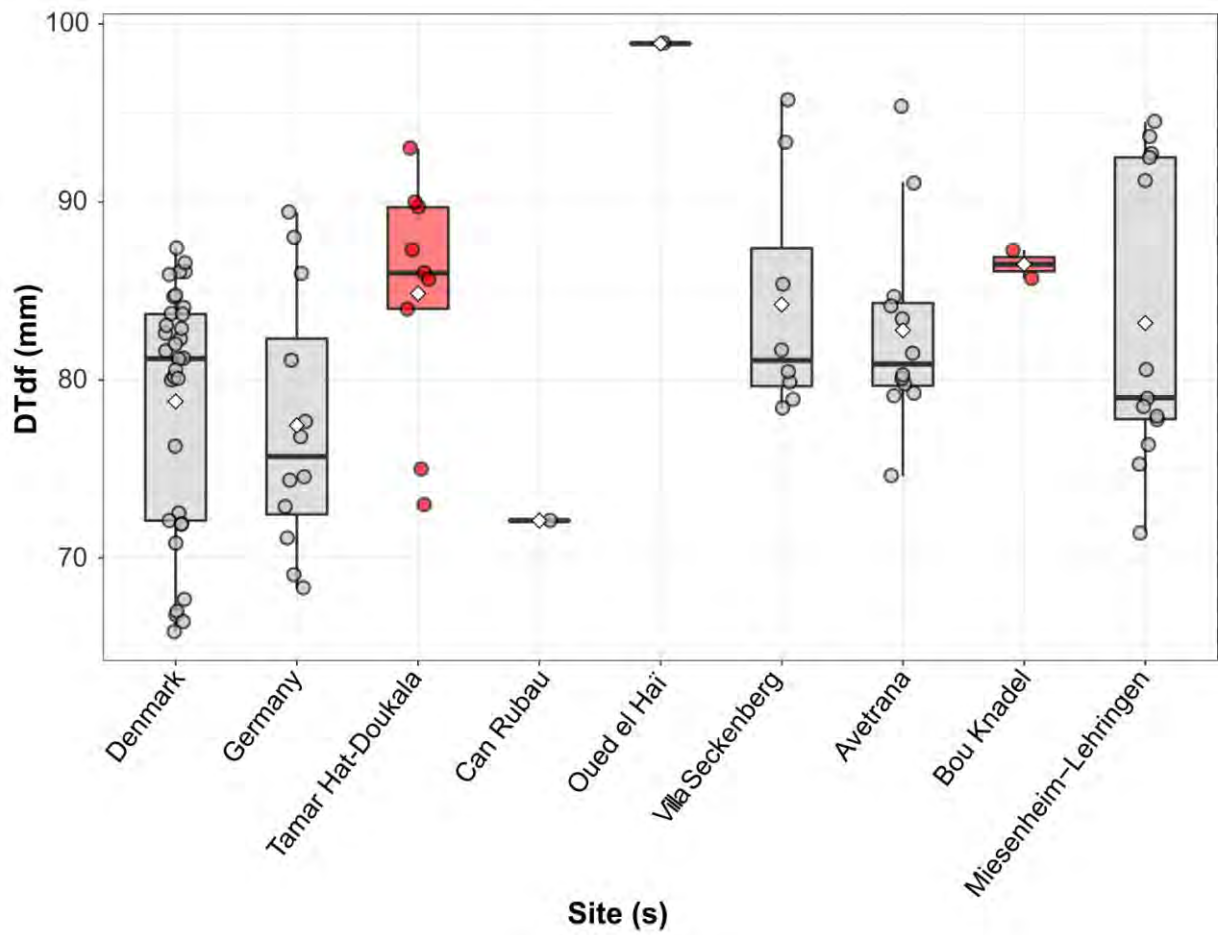


Fig. S3

Boxplots showing the central tendencies and dispersion of the raw values in in distal articular width (DTdf) of *Bos primigenius* metacarpals for each site group. Configuration of boxplots as in Fig. S1.