

Short Paper

The Olduvai buffalo *Pelorovis* and the origin of *Bos*

Bienvenido Martínez-Navarro^{a,*}, Juan Antonio Pérez-Claros^b, Maria Rita Palombo^c,
Lorenzo Rook^d, Paul Palmqvist^b

^a ICREA, Area de Prehistòria-IPHES, Universitat Rovira i Virgili, Plaça Imperial Tàrraco, 1. 43005 Tarragona, Spain

^b Departamento de Geología y Ecología (Área de Paleontología), Facultad de Ciencias, Campus Universitario de Teatinos. 29071 Málaga, Spain

^c Department of Earth Sciences, University of Roma “La Sapienza”, and CNR Istituto di Geologia Ambientale e Geoingegneria,
Piazzale Aldo Moro 5, 00185 Roma, Italy

^d Dipartimento di Scienze della Terra, Università di Firenze, via G. La Pira 4, 50121 Firenze, Italy

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Abstract

The origin of the genus *Bos* is a debated issue. From ~0.5 Ma until historic times, the genus is well known in the Eurasian large mammal assemblages, where it is represented by *Bos primigenius*. This species has a highly derived cranial anatomy that shows important morphological differences from other Plio-Pleistocene Eurasian genera of the tribe Bovini such as *Leptobos*, *Bison*, *Proamphibos-Hemibos*, and *Bubalus*. The oldest clear evidence of *Bos* is the skull fragment ASB-198-1 from the middle Pleistocene (~0.6–0.8 Ma) site of Asbole (Lower Awash Valley, Ethiopia). The first appearance of *Bos* in Europe is at the site of Venosa-Notarchirico, Italy (~0.5–0.6 Ma). Although the origin of *Bos* has traditionally been connected with *Leptobos* and *Bison*, after a detailed anatomical and morphometric study we propose here a different origin, connecting the middle Pleistocene Eurasian forms of *B. primigenius* with the African Late Pliocene and early Pleistocene large size member of the tribe Bovini *Pelorovis sensu stricto*. The dispersal of the *Bos* lineage in Western Europe during middle Pleistocene times seems to coincide with the arrival of the Acheulean tool technology in this continent.

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Keywords: Bovini; *Pelorovis*; *Bos*; African origin

Introduction

Bos is a common member of the Eurasian middle Pleistocene–Holocene assemblages, but the oldest clear record of this genus comes from Africa: the skull fragment ASB-198-1 from Asbole, Ethiopia (~0.8–0.6 Ma) (Geraads et al., 2004a). In Europe, the oldest evidence of *Bos* is at the site of Venosa-Notarchirico, Italy (~0.5–0.6 Ma), where it has been found associated with the oldest Acheulean tools in Europe (Cassoli et al., 1999). It is worth mentioning that an older record for this genus was proposed with *Bos galerianus* from the site of Ponte Galeria, Central Italy (~0.7–0.8 Ma) (Petronio and Sardella,

1998), but this species was later reassigned to *Hemibos*, a genus of Indian origin, as *Hemibos galerianus* (Martínez-Navarro and Palombo, 2004).

The genus *Bos* is characterized by a robust postcranial skeleton and a highly derived cranial anatomy. The middle–late Pleistocene and Holocene species *B. primigenius* has a robust skull with elongated and hollowed frontals covering the parietal bones and the nuchal crest. There is no preorbital fossa. The premaxilla has a short contact with the nasal bones. The occipital is low and wide. A marked neck is present at the base of the horn-cores, which are large, posterolaterally inserted and dorsoventrally compressed, with an oval cross-section that lacks keels, going a little backward, outward, forward and slightly upward. Both sexes bear horn-cores but show an important degree of sexual dimorphism. The largest *B. primigenius* specimens are from the late middle Pleistocene and probably attained individual body masses around 1500 kg, a figure close to the upper size limit

* Corresponding author.

E-mail addresses: bienvenido@icrea.es (B. Martínez-Navarro), Johnny@uma.es (J. Antonio Pérez-Claros), mariarita.palombo@uniroma1.it (M.R. Palombo), lorenzo.rook@unifi.it (L. Rook), ppb@uma.es (P. Palmqvist).

of ruminants: above that size there is no advantage to foregut fermentation in terms of digestive efficiency (Clauss et al., 2003).

The phylogeny of the tribe Bovini, based on the sequence of nucleotides for the mitochondrial *b* gene, groups *Bos* with *Bison* and separates both genera from other Asian and African buffaloes such as *Bubalus* and *Syncerus*, respectively (Hassanin and Douzery, 1999). However, although *Bos* and *Bison* show important differences in the anatomy of the skull and postcranium, their hybridization is possible (Polziehn et al., 1995). The phylogeny of bovine species based on amplified fragment length polymorphisms (AFPL) (Buntjer et al., 2002) also shows a tree in which Bison and yak species (*Bison bison*, *Bison bonasus* and *Poephagus*) and oxen (*Bos taurus*, *Bos indicus* and *Bos gaurus*) are grouped separately, and also from both *Bubalus* and *Syncerus*. In previous systematic classifications, however, some authors (e.g., Gentry, 1978; Groves, 1981) considered *Bos*, *Bibos*, *Bison* and *Poephagus* as subgenera of the genus *Bos*. Similarly, other researchers also included in this group the Late Pliocene genus *Leptobos*, considering it also as a subgenus (e.g., Brugal, 1985; Moyà-Solà, 1987).

The *Bison* lineage (including the extinct forms *Bison paleosinensis*, *Bison sivalensis*, *Dmanisibos georgicus*, *Eobison*, *Bison meneri*, *Bison schoetensacki*, *Bison priscus* and the extant forms *B. bison* and *B. bonasus*) (Bukhsianidze, 2005), based on skull anatomy, can be interpreted as resulting from anagenetic evolution of the Late Pliocene forms of *Leptobos* across the Plio-Pleistocene transition (~2.0–1.7 Ma) (Fig. 1). After Duvernois (1990) there are two lineages of *Leptobos*, the

group of *Leptobos elatus*—ascribed to the subgenus *Leptobos*, which is characterized by curved horn-cores that go backward, outward and upward—and the group of *Leptobos etruscus*—which she ascribed to a subgenus named *Smertiobos*, with mostly elongated horn-cores going backward, a little outward and finally a little inward. The cranial anatomy and the base of the horn-cores are situated forward at the same point, however, in both groups of *Leptobos* (see Fig. 1). Duvernois (1990) proposes that a form of *Leptobos* (*Leptobos*) or *Leptobos falconeri* from the Siwaliks (Pilgrim, 1939), which is in connection with *L. (Leptobos)*, is the ancestor of the Pleistocene genera *Bison*, *Bos* and *Bibos*. The cranial anatomy of *Bos*, however, is highly derived as to be considered the result of a direct anagenetic evolution from any form of *Leptobos*.

Phylogeny of *Bos*

The African genus *Pelorovis sensu stricto* (considering the Late Pliocene and early Pleistocene forms) is a taxon that has never been considered within the framework of the evolutionary history of *Bos*, although some cladistic studies included it within the same group (e.g., Geraads, 1992). *Pelorovis*, evolved from the Early Pliocene African form *Simatherium* (Gentry, 1967; Vrba, 1987), is known as the Olduvai buffalo because the type species of this genus, *Pelorovis oldowayensis* (Reck, 1927) was discovered at Olduvai (Tanzania) and redescribed by Gentry (1967). *Pelorovis* is recorded in Late Pliocene and early Pleistocene large mammal assemblages of Africa, and also in

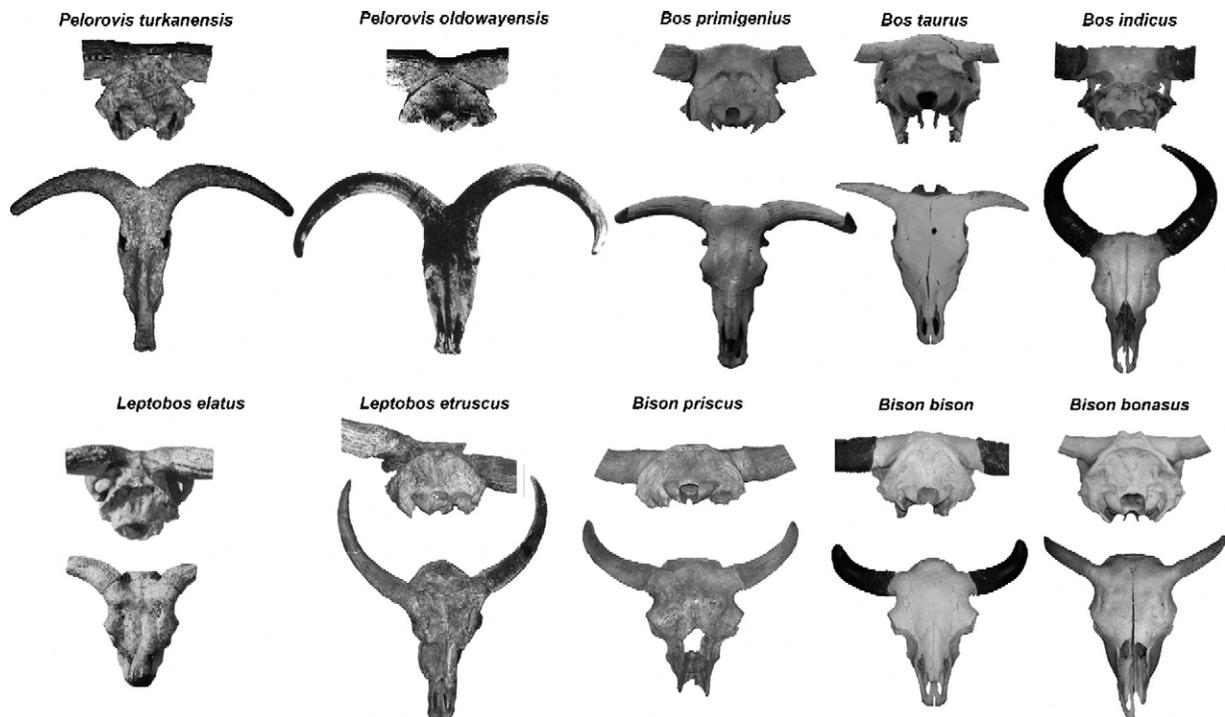


Figure 1. Posterior and superior views of *Pelorovis turkanensis* (KNM ER 524); *Pelorovis oldowayensis* (Pel II, posterior view, and Pel I, upper view, Olduvai Bed II, from Gentry, 1967, Pl. 3 Fig. 1 and Pl. 1 Fig. 2, respectively); *Bos primigenius* (MP 60037); *Bos taurus* (THK-0453S MCPA2); *Bos indicus* (MZB 82-7702); *Leptobos elatus* (Cast MB FP 18, Dusino, from Duvernois, 1990, Pl. 5 and 4, respectively); *Leptobos etruscus* (IGF-612); *Bison priscus* (IGF-1024); *Bison bison* (MZB 94-0843); and *Bison bonasus* (MZB 94-0960). *Bos* and *Pelorovis* have the bases of the horn-cores situated posteriorly, showing an elongation of the frontal bones and overhanging the parietooccipital area. This morphology is not present in *Bison* and *Leptobos*.

some early Pleistocene localities from the Middle East. A revised diagnosis of the genus *Pelorovis* closely resembles that of *Bos* (Gentry and Gentry, 1978).

For this analysis, we include the Eastern African Late Pliocene species *Pelorovis turkanensis* from eastern Africa (Harris, 1991) and *P. oldowayensis*, recorded in the early Pleistocene of Eastern Africa and the Levantine corridor.

The African genus *Syncerus* and the Eurasian genus *Bubalus* are not included in this analysis because they show a very different cranial anatomy from that of *Bos*—but also from *Bison*—with flattened and keeled horn-cores that are situated in a forward position of the frontal bones.

The species *Pelorovis kaisensis*, created by Geraads and Thomas (1994) from Kaiso (Uganda), has been excluded from this study because its adscription to *Pelorovis* is questioned, and its morphology is close to *Syncerus* (Hadjouis and Sahnouni, 2006). The same decision was taken with the late Pleistocene giant African buffalo, named *Bubalus antiquus* (Duvernoy, 1851), *Bubalus nilssoni* (Lönnberg, 1933), *Homoioceras antiquus* (Bate, 1949), *Pelorovis antiquus* (Gentry and Gentry, 1978) and *Bubalus/Homoioceras/Pelorovis antiquus* (Gautier and Muzzolini, 1991). Although this species has been included in the group of *Pelorovis sensu lato*, it was excluded from the diagnosis because it has a different anatomy in the skull—with the occipital crest situated backward and the base of the horn-cores placed forward, going directly outward, downward and upward—and in the postcranial skeleton from that of genuine *Pelorovis s.s.* Given that the anatomy of this giant buffalo has important similarities with the genus *Syncerus*, as described by Klein (1994), it has been included within this genus and named *Syncerus antiquus* (see Peters et al., 1994; Hadjouis, 2002; Hadjouis and Sahnouni, 2006, and references therein).

Bos primigenius is anatomically similar to *Pelorovis* and the only remarkable difference between the two forms relates to the robustness of the skeleton, especially when the skull of the Eurasian form is compared to that of the African genus. According to the results obtained in the morphometric study developed here, the anatomical transformation of the cranium of the Late Pliocene African species *P. turkanensis* (Harris, 1991) to the cranium of *B. primigenius* can be described with a few landmark displacements, which involve only a slight increase in the degree of robustness of the skull of *P. turkanensis* into *P. oldowayensis* and finally into *B. primigenius* (Fig. 1). The form *P. turkanensis brachyceras* from Melka Kunture, Ethiopia (Geraads et al., 2004b), was created on the base of a cranial fragment, which preserves part of the frontal and parietal/occipital region with a dorsoventrally compressed horn-core. Although this specimen clearly belongs to *Pelorovis*, it is very incomplete and fragmented to be included in the present analysis. The same problem was found with the species *Pelorovis howelli*, recently described in the North African early Pleistocene site of Aïn Hanech, Algeria (Hadjouis and Sahnouni, 2006), although it was not included in this analysis because it has a very incomplete cranium—only the neurocranium and the horn-cores—and although we can affirm that it is very close to *P. oldowayensis*, it looks to be a more evolved form with the horn-cores more separated at the base.

Geraads et al. (2004a) indicate the overall resemblance of skull fragment ASB-198-1 from Asbole to *P. oldowayensis*, and also to its relative *P. turkanensis*. However, they interpret this anatomical similarity as a convergence to the African genus *Pelorovis*, suggesting that the Asbole finding corresponds to the arrival of an Asian immigrant in Africa.

In addition, the dentition of *Pelorovis* is characterized by a high degree of hypsodonty (i.e., relative tooth crown height), which among ungulates indicates a diet in open habitat based on abrasive grasses with high silicophytolith contents and airborne grit (Mendoza et al., 2002) and by the presence of an enamel fold in the distolingual face of the upper cheek teeth, which is very marked in *P. turkanensis* (Fig. 2). The latter feature is still present, although drastically reduced, in the early Pleistocene form *P. oldowayensis*, recorded in different localities of Africa—Olduvai, Tanzania; Ain Hanech and Ternifine, Algeria, where it was named *Bos bubaloides* (Arambourg, 1979; Geraads, 1981); Buia, Eritrea (Martínez-Navarro et al., 2004); and the Levantine Corridor 'Ubeidiya and Gesher Benot Ya'aqov, Israel (Geraads, 1986; Martínez-Navarro et al., 2000). The European species, *B. primigenius*, shows a

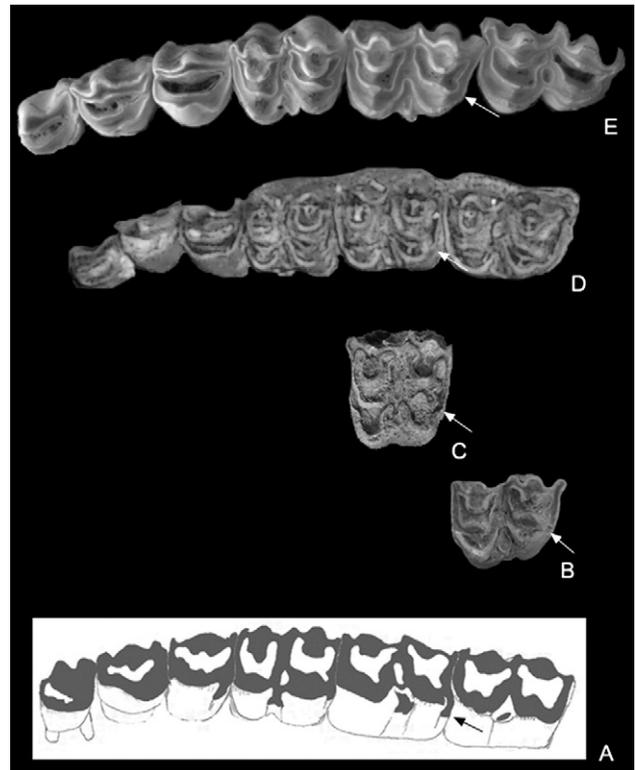


Figure 2. Occlusal view of the upper molar series of (A) *Pelorovis turkanensis* from Koobi Fora, Kenya (KNM ER-524, holotype); (B) *Pelorovis oldowayensis* from 'Ubeidiya, Israel (UB-438, M³); (C) *Pelorovis* from Buia, Eritrea (DAN-63, M²); (D) *Bos primigenius* from the middle–late Pleistocene–Holocene of Europe (MP 60037); and (E) the extant *Bos taurus* (IPHES-1, Tarragona). *P. turkanensis* shows a pronounced enamel fold in the distolingual face. This feature is still present, although drastically reduced, in the early Pleistocene form *P. oldowayensis*. The European species, *B. primigenius*, shows a similar anatomical condition to that of *P. oldowayensis*, preserving the small distolingual fold in the upper dentition. In the extant forms of *Bos*, this feature is usually less marked. All of these forms have a high degree of hypsodonty, which is much more developed than in the Eurasian specimens of *Bison*.

similar anatomical condition in the cheek teeth to that of *P. oldowayensis*, preserving the small distolingual fold in the upper dentition and the high degree of hypsodonty, which is much more developed than in the Eurasian specimens of *Bison*.

These anatomical and biostratigraphical arguments are supported by a morphometric analysis of these genera. Given the scope of this study, which is focused exclusively on the anatomical differences among genera, only a low number of specimens and species per genus were analyzed [*B. primigenius*: 1; *B. taurus*: 4; *B. indicus*: 2; *Bison bison*: 3; *B. bonasus*: 2; *B. priscus*: 1; *P. turkanensis*: 1; *P. oldowayensis*: 1; *L. elatus*: 1; and *L. etruscus*: 1]. Consequently, the following conclusions assume that intraspecific differences are not as important as interspecific or intergeneric ones. A set of 22 landmarks were recorded on the lateral view of the cranium (for their anatomical description, see the legend of Figure 3). These landmarks correspond either to homologous points where three structures meet (i.e., type I landmarks *sensu* Bookstein, 1991), to points of maximum curvature (type II landmarks) or to extreme points (type III landmarks, in our case basically the intersection of interlandmark segments). Once digitized, the Cartesian coordi-

nates of these landmarks were transformed into shape coordinates (see Bookstein, 1986), which are simply the original coordinates after translation, rotation and scaling with respect to two of these points, which define a baseline of unit length from [0,0] to [1,0]. The landmarks selected for the baseline were the infraorbital foramen and the external auditory meatus. Both are type I landmarks, are relatively distant from each other and can be easily identified on the specimens compared.

On the whole, the results obtained in the morphometric analyses corroborate the conclusions obtained in the anatomically based comparisons and are easily interpretable in morphological terms. A principal components analysis of the shape coordinates, performed using the free-downloaded program PAST implemented by Hammer et al. (2001, 2005), yields two first principal components that jointly account for more than 85% of the original variance in terms of landmarks positions, allowing us to characterize the cranial morphospace of the bovid genera compared (Fig. 3).

The first component is defined almost exclusively by the forward movement of the landmarks positioned in the orbital and frontal region. Both *Pelorovis* and *Bos*, which show a compa-

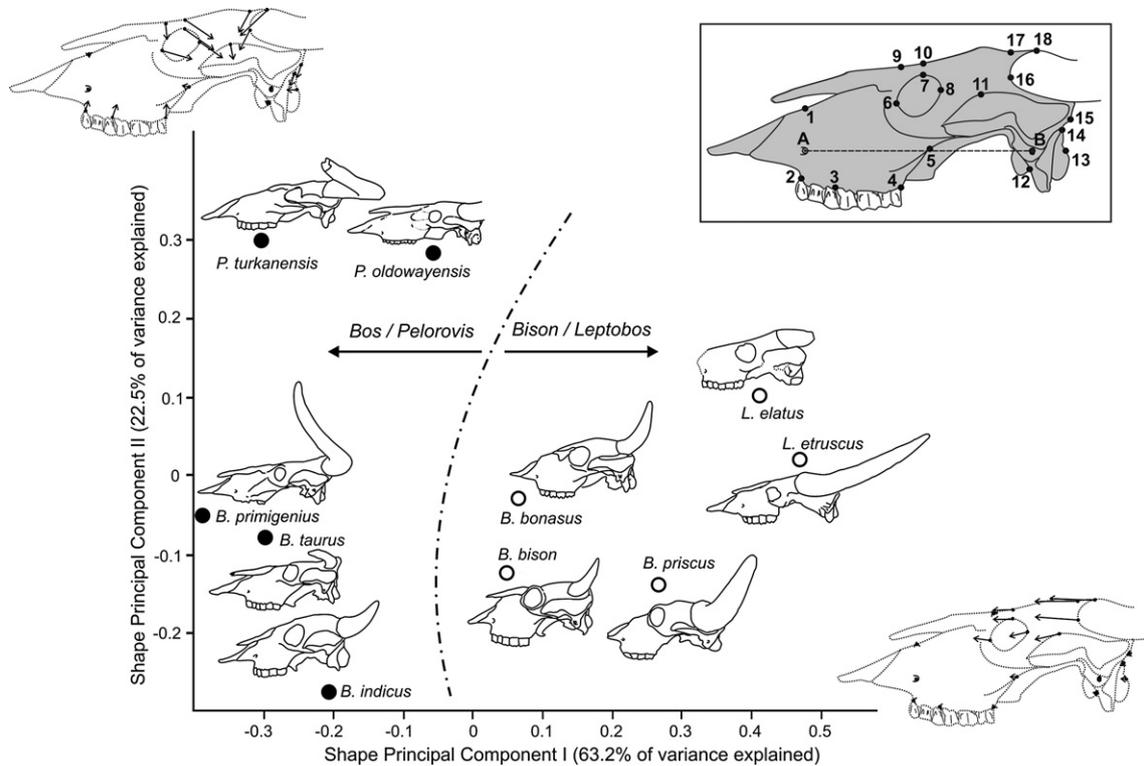


Figure 3. Lateral view projection of the species analyzed on the first two principal components of shape coordinates. The geometrical interpretation of each component is represented as vector displacements from the mean shape. The first principal component, which accounts for more than 63% of the variance of landmark positions, segregates clearly *Bison* and *Leptobos* from *Pelorovis s.s.* and *Bos*, respectively. Landmarks used in this morphometric study are shown with small circles (1: maximum height of the maxilla at the level of point A; 2 and 4: points more anteriorly and more posteriorly positioned for the intersection between the upper cheek teeth and the maxilla, respectively; 3: idem for the limit between the upper premolars and molars; 5: intersection between the maxilla and the zygomatic arch; 6, 7 and 8: most anterior, most superior and most posterior points of the ocular orbit, respectively; 9 and 10: maximum height of the cranial vault at the level of points 6 and 7, respectively; 11: point of maximum curvature of the lateral projection of the frontal bone outline; 12: tip of the outline of the jugular process in lateral view; 13: intersection between the base line and the occipital condyle; 14: tip of the occipital condyle in lateral view; 15: point of maximum curvature of the posterior part of the occipital; 16 and 18: most anterior and most superior points of the horn base, respectively; 17: maximum height of the skull vault measured at the level of landmark 16). Landmarks A (point of maximum curvature of the infraorbital foramen) and B (center of the external auditory meatus) were used for defining the baseline used for estimating shape coordinates. Points A, B, 2, 3, 4, 5, 12, 14 and 18 are type I landmarks; points 11 and 15 are type II landmarks; and points 1, 6, 7, 8, 9, 10, 13, 16 and 17 are type III landmarks (see Bookstein, 1991).

ratively longer splanchnocrania, are clearly segregated on this component from *Bison* and *Leptobos*, which have a more anteriorly positioned orbital and frontal region (Fig. 3). The second component is characterized by an anteroposterior contraction and a downward displacement of the posterior upper part of the skull cap, which reflects a shortening of the neurocranium, while the tooth baseline describes an upward motion, which would result in a decrease of hypsodonty for the upper cheek teeth in those forms that score positively on this component (Fig. 3). The two *Pelorovis* species and, to a lesser extent, *L. elatus* have higher scores than other forms with more stoutly built crania such as the *Bison* species or *B. indicus*. Equivalent results are obtained using other methods for optimal superposition of landmarks, such as the analysis of generalized procrustes and the technique of relative warp analysis. It is worth noting, however, that given the amount of variation usually found in biological shape data, the different landmark methods lead to similar statistical conclusions (see Rohlf, 2000).

Figure 4 shows the phenogram derived from a cluster analysis computed on the specimen's procrustes residuals, obtained using Ward's method. The morphologic affinities of the extant representatives of *Bos* and *Bison* are consistent with

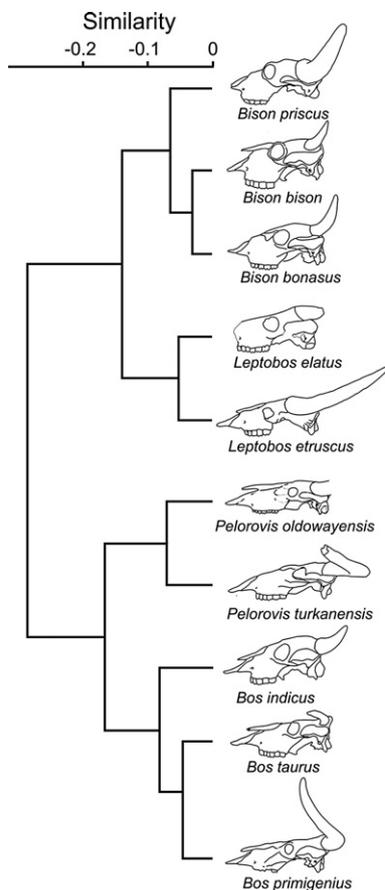


Figure 4. Hierarchical cluster (Ward's method) for the bovid species analyzed, obtained using as variables the procrustes residuals of the 20 landmarks selected. Two major groups are distinguished within this dendrogram, which correspond to the specimens of the genera *Pelorovis s.s./Bos* and *Leptobos/Bison*, respectively. Note that the species of *Bos* and *Bison* are consistently grouped. Scale: Euclidean distance converted to similarity by changing the sign.

their purported monophyly based on molecular genetics (Polzheim et al., 1995; Hassanin and Douzery, 1999; Buntjer et al., 2002), which adds robustness to these morphometrically based conclusions.

Discussion and conclusions

According to the evidence discussed above, we propose a reclassification of the Late Pliocene and early Pleistocene African members of the tribe Bovini ascribed to *Pelorovis* and the middle Pleistocene–Holocene African and Eurasian specimens ascribed to *Bos*, including all of them in the genus *Bos*. The evolutionary transition from the oldest form of *Pelorovis* from eastern Africa to Eurasian *B. primigenius* seems to have been gradual. A similar evolutionary pattern has been described in other large mammal lineages such as the woolly mammoth (Lister and Sher, 2001) and the African hunting dog (Martínez-Navarro and Rook, 2003). Under this new interpretation, we recognize here three chronospecies: (1) *Bos turkanensis* for the Late Pliocene African form; (2) *Bos oldowayensis* for the early Pleistocene form of Africa and the Middle East; and (3) *B. primigenius* for the Eurasian middle Pleistocene to Holocene form. The inclusion of the African and Israeli late early and early middle Pleistocene specimens from Buia, Asbole, Gesher Benot Ya'akov or other possible sites in one or another species remains unclear until new and more complete material is found.

In addition, we can say that the dispersal of this lineage in Western Europe, and probably to Asia, seems to have been contemporaneous with the arrival in this continent of human populations carrying with them the Acheulean tool technology. In fact, the dispersals of the *Bos* lineage are coincidental with the age of the oldest Acheulean localities outside Africa: from 1.4 Ma in the Middle East at the site of 'Ubeidiya, Israel (Bar-Yosef and Goren-Inbar, 1993), to the early/middle Pleistocene transition recorded at the site of Gesher Benot Yaakov, Israel (Goren-Inbar et al., 2000) and finally into Europe at around 0.6–0.5 Ma at Venosa-Notarchirico, Italy (Piperno, 1999). In this context, it is worth noting that statistical analyses of haplotype trees for mitochondrial DNA, Y-chromosomal DNA, two X-linked regions and six autosomal regions of human populations have revealed a major expansion event out of Africa at 0.84–0.42 Ma, characterized by interbreeding and not replacement of earlier populations (Templeton, 2002). This inference is consistent with the time frame of the archaeological record of cultural expansions during middle Pleistocene times, as it broadly overlaps the arrival in Europe of the Acheulean tool technology.

The extant representatives of the genus *Bos* are common animals in human settlements, but now we can suggest that they have been part of the human ecological scenario since the beginning of the genus *Homo*, during the African Late Pliocene.

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References

- Arambourg, C., 1979. *Vertèbres Villafranchiens d'Afrique du Nord (Artiodactyles, Carnivores, Primates, Reptiles, Oiseaux)*. Singer-Polignac, pp. 1–141 + 61 pl., Paris.
- Bar-Yosef, O., Goren-Inbar, N., 1993. The lithic assemblage of 'Ubeidiya. A Lower Paleolithic site in the Jordan Valley. Qadem. Monographs of the Institute of Archaeology. The Hebrew University of Jerusalem, vol. 34, pp. 1–266.
- Bate, D.M.A., 1949. A new African fossil long-horned Buffalo. *Annals and Magazine of Natural History*, London 2, 396–398.
- Bookstein, F.L., 1986. Size and shape spaces for landmark data in two dimensions (with discussion and rejoinder). *Statistical Science* 1, 181–242.
- Bookstein, F.L., 1991. *Morphometric Tools for Landmark Data. Geometry and Biology*. Cambridge Univ. Press, New York. 435 pp.
- Brugal, J.P., 1985. *Le Bos primigenius* BOJ. 1827 du Pleistocene Moyen des grottes de Lunel Viel (Herault). *Bulletin Museum Anthropologie Préhistorique Monaco* 28, 7–62.
- Bukhsianidze, M., 2005. The Fossil Bovidae of Dmanisi. PhD International Doctorate "Environmental, Humans and Compartmental Dynamics" XVI cycle 2001–2004 at the University of Ferrara (Italy), 192 pp.
- Buntjer, J.B., Otsen, M., Nijman, I.J., Kuiper, M.T.R., Lenstra, J.A., 2002. Phylogeny of bovine species based on AFLP fingerprinting. *Heredity* 88, 46–51.
- Cassoli, F., Di Stefano, G., Tagliacozzo, A., 1999. I Vertebrati dei livelli superiori (Alfa ed A) della serie stratigrafica di Notarchirico. In: Piperno, M. (Ed.), *Notarchirico: Un sito del Pleistocene medio iniziale nel bacino di Venosa*, Edizioni Osanna, Venosa, Italia, pp. 361–438.
- Clauss, M., Frey, R., Kiefer, B., Lechner-Doll, M., Loehlein, W., Polster, C., Rössner, G.E., Streich, W.J., 2003. The maximum attainable body size of herbivorous mammals: morphophysiological constraints on foregut, and adaptations of hindgut fermenters. *Oecologia* 136, 14–27.
- Duvernois, M.-P., 1990. Les *Leptobos* (Mammalia, Artiodactyla) du Villafranchien d'Europe occidentale. Systématique, évolution, biostratigraphie, paléocologie. *Documents Lyon* 113, 1–213.
- Duvernoy, G.L., 1851. Note sur une espèce fossile de Buffle fossile (*Bubalus (Arni) antiquus*) découverte en Algérie. *Compte rendu hebdomadaire des séances de l'Académie des Sciences de Paris* 33, 595–597.
- Gautier, A., Muzzolini, A., 1991. The life and times of the giant buffalo alias *Bubalus/Homioceras/Pelorovis antiquus* in North Africa. *Archaeozoologia* IV, 39–92.
- Gentry, A.W., 1967. *Pelorovis oldowayensis* Reck, an extinct bovid from East Africa. *Bulletin of the British Museum (Natural History)*. *Geology* 14, 245–299.
- Gentry, A.W., 1978. Bovidae. In: Maglio, J.V., Cooke, H.B.S. (Eds.), *Evolution of African Mammals*. Harvard Univ. Press, pp. 264–278.
- Gentry, A.W., Gentry, A., 1978. Fossil Bovidae (Mammalia) of Olduvai Gorge, Tanzania. Part II: *Bulletin of the British Museum (Natural History)*. *Geology* 30, 1–83.
- Geraads, D., 1981. Bovidae et Giraffidae (Artiodactyla, Mammalia) du Pléistocène de Ternifine (Algérie). *Bulletin Museum National d'Histoire Naturelle*, Paris 3, 47–86.
- Geraads, D., 1986. Les ruminants du Pléistocène d'Oubeidiyeh (Israël). In: Tchernov, E. (Ed.), *Les Mammifères du Pléistocène inférieur de la Vallée du Jordain a Oubeidiyeh*, Mémoires et Travaux du Centre de Recherche Français de Jerusalem, vol. 5, pp. 1143–1181.
- Geraads, D., 1992. Phylogenetic analysis of the tribe Bovini (Mammalia Artiodactyla). *Zoological Journal of the Linnean Society* 104, 193–207.
- Geraads, D., Thomas, H., 1994. Bovidae du Plio-Pléistocène d'Ouganda. In: Senut, B., Pickford, M. (Eds.), *The Geology and Palaeobiology of the Albertine Rift Valley, Uganda-Zaire*. Publication 1994/29, vol. 2. Orléans CIFEG, pp. 383–407.
- Geraads, D., Alemseged, Z., Reed, D., Wynn, J., Roman, D.C., 2004a. The Pleistocene fauna (other than Primates) from Asbole, lower Awash Valley, Ethiopia, and its environmental and biochronological implications. *Geobios* 37, 697–718.
- Geraads, D., Eisenmann, V., Petter, G., 2004b. The large mammal fauna of the Oldowan site of Melka Kunture. In: Chavaillon, J., Piperno, M. (Eds.), *Studies on the early Paleolithic Site of Melka Kunture, Ethiopia*. Istituto Italiano di Preistoria e Protostoria, Florence, pp. 169–192.
- Goren-Inbar, N., Feibel, C.S., Verosub, K.L., Melamed, Y., Kislev, M.E., Tchernov, E., Saragusti, I., 2000. Pleistocene milestones on the Out-of-Africa corridor at Gesher Benot Ya'avaq, Israel. *Science* 289, 944–947.
- Groves, G.B., 1981. Systematic relationship of the Bovini (Artiodactyla, Bovidae). *Zeitschrift für die Zoologische und systematische Evolutionsforschung* 4, 264–278.
- Hadjouis, D., 2002. A new Bovini in the Upper Pleistocene fauna of Algeria. *L'Anthropologie* 106, 377–386.
- Hadjouis, D., Sahnouni, M., 2006. *Pelorovis howelli* nov. sp. (Mammalia, Artiodactyla): a new bovine from the Lower Pleistocene site of Aïn Hanech (El-Kherba locus), Northeastern Algeria. *Geobios* 39, 673–678.
- Hammer, O., Harper, D.A.T., Ryan, P.D., 2001. PAST: paleontological statistics software package for education and data analysis. *Palaeontologia* 4 (http://palaeo-electronica.org/2001_1/past/issue1_0.htm).
- Hammer, O., Harper, D.A.T., Ryan, P.D., 2005. PAST. *Palaeontological Statistics* 1.34, pp. 1–83 (<http://folk.uio.no/ohammer/past/past.pdf>).
- Harris, J.M., 1991. Family Bovidae. In: Harris, J.M. (Ed.), *Koobi Fora Research Project. The Fossil Ungulates: Geology, Fossil Artiodactyls and Palaeoenvironments*, vol. 3. Clarendon Press, Oxford, pp. 139–320.
- Hassanin, A., Douzery, E.J.P., 1999. The tribal radiation of the family Bovidae (Artiodactyla) and the evolution of the mitochondrial cytochrome *b* gene. *Molecular Phylogenetics and Evolution* 13, 227–243.
- Klein, R., 1994. The long-horned African buffalo (*Pelorovis antiquus*) is an extinct species. *Journal of Archaeological Science* 21, 725–733.
- Lister, A., Sher, A., 2001. The origin of the woolly mammoth. *Science* 294, 1094–1097.
- Lönnberg, T., 1933. Description of a fossil buffalo from East Africa. *Arkiv för Zoology* 25A (17), 1–32.

- Martínez-Navarro, B., Rook, L., 2003. Gradual Evolution in the African hunting dog lineage. Systematic implications. *C.R. Palevol* 2, 695–702.
- Martínez-Navarro, B., Palombo, M.R., 2004. Occurrence of the Indian genus *Hemibos* (Bovini, Bovidae, Mammalia) at the early-Middle Pleistocene Transition in Italy. *Quaternary Research* 61, 314–317.
- Martínez-Navarro, B., Rabinovich, R., Goren-Inbar, N., 2000. Preliminary study of the fossil Bovidae assemblage from the late Lower Pleistocene archaeological site of Gesher Benot Ya'aqov (northern Israel). Abstracts of the 2000 SEQS Meeting “The Plio-Pleistocene Boundary and the Lower/Middle Pleistocene Transition: Type Areas and Sections”. Bari (Italy).
- Martínez-Navarro, B., Rook, L., Segid, A., Yosief, D., Ferretti, M.P., Shoshani, J., Teclé, T.M., Libsekal, Y., 2004. The large fossil mammals from Buia (Eritrea): systematics, biochronology and paleoenvironments. *Rivista Italiana di Paleontologia e Stratigrafia* 110, 61–88.
- Mendoza, M., Janis, C.M., Palmqvist, P., 2002. Characterizing complex craniodental patterns related to feeding behaviour in ungulates: a multivariate approach. *Journal of Zoology (London)* 258, 223–246.
- Moyà-Solà, S., 1987. Los bóvidos (Artiodactyla, Mammalia) del yacimiento del Pleistoceno inferior de Venta Micena (Orce Granada, España). *Paleontologia i Evolució, Memoria Especial* 1, 181–236.
- Peters, J., Gautier, A., Brink, J.S., Haenen, W., 1994. Late Quaternary extinction of ungulates in sub-Saharan Africa: a reductionist's approach. *Journal of Archaeological Science* 21, 17–28.
- Petronio, C., Sardella, R., 1998. *Bos galerianus* n. sp. (Bovidae, Mammalia) from the Ponte Galeria Formation (Rome Italy). *Neues Jahrbuch für Geologie und Paläontologie* 5, 269–284.
- Pilgrim, G.E., 1939. The fossil Bovidae of India. *Memoirs of the geological survey of India. Palaeontologia Indica* 26, 1–356.
- Piperno, M. (Ed.), 1999. *Notarchirico: Un sito del Pleistocene medio iniziale nel bacino di Venosa*. Edizioni Osanna, pp. 1–621 + 15 pl., Venosa.
- Polzehl, R.O., Strobeck, C., Sheraton, J., 1995. Bovine mtDNA discovered in North American Bison populations. *Conservation Biology* 9, 1638–1643.
- Reck, H., 1927. *Pelorovis oldowayensis* nov. gen. nov. sp. *Wissenschaft. Ergebnisse der Oldoway-Expedition 1913, N.F.*, 3, 56–67.
- Rohlf, F.J., 2000. Statistical power comparisons among alternative morphometric methods. *American Journal of Physical Anthropology* 111, 463–478.
- Templeton, A.R., 2002. Out of Africa again and again. *Nature* 416, 45–51.
- Vrba, E.S., 1987. A revision of the Bovini (Bovidae) and a preliminary revised checklist of Bovidae from Makapansgat. *Palaeontologia Africana* 26, 33–46.