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First description of the large mammals from the locality of Penal, and updated faunal lists for the Atapuerca ungulates – *Equus altidens*, *Bison* and human dispersal into Western Europe

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ABSTRACT

The Sierra de Atapuerca is well known for the human remains that have been collected from the different localities, but these localities also yielded abundant fossils of other vertebrates, particularly ungulates. The large mammals from a locality called Penal are described and the updated faunal lists of the ungulates and cercopithecids from four localities at Atapuerca are presented. *Equus altidens* and an early West European *Bison* occur at Atapuerca.

The oldest human remains from Western Europe are from Atapuerca TE9. Human dispersal into Western Europe was probably related to environmental change as detected in the fossil record of large mammals. The dispersal of various species of large mammals, including bison and possibly *E. altidens*, suggests a temporal extension of open habitats towards the West, which may have allowed humans to spread into the open environments of southwestern Europe.

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1. Introduction

The sites of the Sierra de Atapuerca are well known for the human remains that were found at Gran Dolina, Sima de los Huesos, Sima del Elefante, and Galería. However, there are many more archaeological and paleontological sites in the Sierra de Atapuerca. There are numerous open air sites that yield lithic industry, but no fauna, possibly because of acidity of the soils. Sima de los Huesos is a site in a cave and is well known for the thousands of remains of nearly thirty individuals of *Homo heidelbergensis* (eg. Arsuaga et al., 1993; Journal of Human Evolution, 33(2–3), 1997). It yielded also fossils of carnivores and micro vertebrates (Cuenca-Bescos et al., 1997; García et al., 1997), but no ungulates. The sites of El Mirador and El Portalón are Holocene to Late Pleistocene and are not considered here.

The remaining excavated localities have all ungulate fossils of Early and Middle Pleistocene age and are all in the Trincheras del Ferrocarril, an abandoned railway trench which was cut during the late 19th century, and are all exposed with vertical sections in the walls of the trench. There have been excavations in these localities before the 1970s and some of this material is preserved in the paleontological museum in Sabadell, but the exact provenance is

not known. The excavations in the 1970s directed by Trino Torres were shortly afterwards followed by those directed by Aguirre and later by Arsuaga, Bermúdez de Castro and Carbonell. This material is treated here as well as the scarce remains of *Macaca*, which have been found in several levels. General information on the earlier phases of excavation is to be found in a monograph (Aguirre et al., 1987). Monographs deal with geology, stratigraphy, paleontology, paleoanthropology and archaeology of these localities, as will be indicated below. Updated lists of the ungulates of the different sites and levels are presented here and a small collection of large mammals from the locality of Penal are described for the first time.

The faunal record of Atapuerca has a special interest for the study of the European Pleistocene: it provides information on the environment of the earliest Europeans, fossil collections are increasing and for some species there are very abundant samples, there is a good stratigraphic control and there many samples in superposition, which are often dated by multiple methods. Atapuerca has in some cases the earliest records of species in Western Europe, and in other cases there are exceptionally well preserved remains or very abundant samples.

As Atapuerca has the oldest European human fossils, this invites discussion of the circumstances or reasons of human dispersals into Europe. Recently, a model has been proposed that relates human dispersal to environmental change as detected in the fauna. This model is refined here.

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2. Materials and methods

Material is described in the section on Penal. Measurements on the fossils of *Panthera* are taken in the same way as by Van der Made (1996), those on rhinoceros fossils are after Van der Made (2010a), those on deer fossils are after Van der Made (1989) and Van der Made and Tong (2008), while those on *Equus* are largely after Eisenmann et al. (1988), with the following modifications: width measured at the anterior and posterior lobes (DTa and DTp); measurements at occlusal surface/half of estimated crown height/2 cm above crown basis. The measurements are indicated with the following acronyms:

DAP = antero-posterior diameter
 DAPb = DAP at the base of the crown of a tooth
 DAPp = DAP of the proximal part of a bone or posterior or second lobe of a tooth
 DTpp = DT of third lobe of a third lower molar
 DAPd = DAP of the distal part of a bone
 DT = transverse diameter
 DTa = DT of the anterior lobe of a tooth or anterior part of a bone
 DTd = DT of the distal part of a bone
 H = height
 Hu = height of upper part of a bone
 max/mini = maximal or minimal diameters (DAPmini, DTmax, etc.)

The material from TP is presently kept at the University of Tarragona, but its permanent storage will be in the Centro de Investigación sobre la Evolución Humana (Burgos, Spain). Where comparisons are made with material from other localities, either literature is cited or the institute where the material was studied is indicated in the text and Fig. 5.

3. Updated faunal lists

Fig. 1 gives the different localities and levels with ungulates and Cercopithecidae in the Trinchera del Ferrocarril (Railway Trench). The localities and levels are ordered in approximate order from old (bottom) to young (top) largely following Rodríguez et al. (2011). However, the levels TG8-TG11, TN3-8 and TZ are used, rather than the synthetic GII and GIII units (which appear in brackets). This is because the more precise indications of stratigraphic provenance are favored here, because this information forms part of the collection numbers that are written on the fossils and because these collection numbers appear in the papers where the material was described. These units will be discussed below. The determinations of the taxa in Fig. 1 result from ongoing research, which will be cited in the corresponding sections below. Fig. 1 gives the most complete and detailed faunal lists for the Atapuerca ungulates to date.

3.1. Galeria – TG/TZ/TN

The first locality to have been excavated extensively is Galería. It is a complex that consists of three areas, each with their own stratigraphy, the units being numbered from bottom to top. The interfingering fossiliferous units are: La Covacha de los Zarpazos (TZ), Galería (the central part; TG8-11) and Trinchera Norte (TN3-8). The latter name is confusing and does not refer to its position relative to Galería (south), but it refers to the fact that it is the northernmost of three fissures before Galería was exposed. The locality yielded but few human remains (Rosas and Bermúdez de Castro, 1999; Arsuaga et al., 1999). A monograph and a general paper treat the different aspects of the locality (Rosas et al., 1998; Carbonell Roura et al., 1999). After this monograph, excavations

continued in the area of La Covacha and are now starting again in the central area.

The Carnivora were described by Morales et al. (1987), Torres (1987), García and Arsuaga (1998, 2001a), Cervera et al. (1999) and García García (2003), the Perissodactyla were described by Sánchez Chillón and Soto Rodríguez (1987), Sánchez and Cerdeño (1999), a caprine was described by Sánchez Chillón (1997), the Cervidae by Azanza and Sánchez (1990) and the Artiodactyla in general were described by Van der Made (1999b). Since that time no new material has been described, but the assignment of some of the material has been revised in subsequent faunal lists (Van der Made, 2001; Van der Made et al., 2003; Cuenca Bescós and García, 2007; Rodríguez et al., 2011).

3.2. Gran Dolina – TD

Gran Dolina is widely known because for some time it held the record of the oldest human remains known from Europe (Carbonell et al., 1995), which Bermúdez de Castro et al. (1997) subsequently described as the new species *Homo antecessor*. The locality is large and more complex than Galería.

T. Torres directed excavations in the lower and also upper part of Gran Dolina in 1976, 1978 and 1982. In the early 1990s the lower part of Gran Dolina was excavated again and subsequently a test pit of about six square meters was excavated from the top to the bottom, and still later the top of the locality was cleared and a surface of about 80 square meters is being excavated. An area in which the upper levels protrude into the Trinchera (like a balcony) was excavated faster for safety reasons and at present reached the top of TD5.

A monograph was dedicated to this locality (Journal of Human Evolution, 37(3–4), 1999). The stratigraphic units are numbered from bottom to top, starting with TD1. The lower part of the locality is divided in two parts leading to a separation in TDE and TDW. The herbivores described by Soto (1987) come from the excavations by T. Torres and are said to come from TD3. This unit cannot be recognized now; it may have wedged out or there may be another reason. The lowermost levels with fossils and lithic industry are TD3+4 and fossils are found till TD8. TD6 has *Homo antecessor* and lithic industry, while in TD7 and TD8 there are no signs of human presence. In the test pit TD7 was a thin unit with little fauna, but now a thick wedge has been excavated that is not present in the test pit and a richer fauna was collected. A unit formerly called TD8b and now called TD8-9 has only remains of small mammals (many Lagomorpha). TD9 is sterile. TD10 has abundant fossils and lithic industry. The limits between TD10 and TD11 have been redefined and fossils labelled as from TD11 and previously published as from TD11, are now included in TD10A. There is a palaeomagnetic change within TD7, which is interpreted as the Brunhes-Matuyama boundary (Parés and Pérez-González, 1995). Various other dating techniques have been applied confirming a late Early Pleistocene age for the lower units (e.g. Berger et al., 2008).

The Carnivora were described by Torres (1978, 1987), Morales et al. (1987), García and Arsuaga (1999, 2001a,b), García García (2003). The herbivores of TD3 were described by Soto (1987). A proboscidean from TD6 was described by Aguirre (1999). Soto (1987) described, as mentioned above, the herbivores from TD3. The Perissodactyla were described by Sánchez Chillón and Soto Rodríguez (1987), Cerdeño and Sánchez (1988) and Sánchez and Cerdeño (1999), while Cerdeño (1993) referred to the rhinoceroses from Gran Dolina. The Cervidae were described by Azanza and Sánchez (1990). The ungulates of TD8 were described (Van der Made, 1998), while all large mammals from TD8 from the latest excavations were reviewed by Rosell et al. (2010). The ungulates from TD6 and the whole sequence were described or discussed

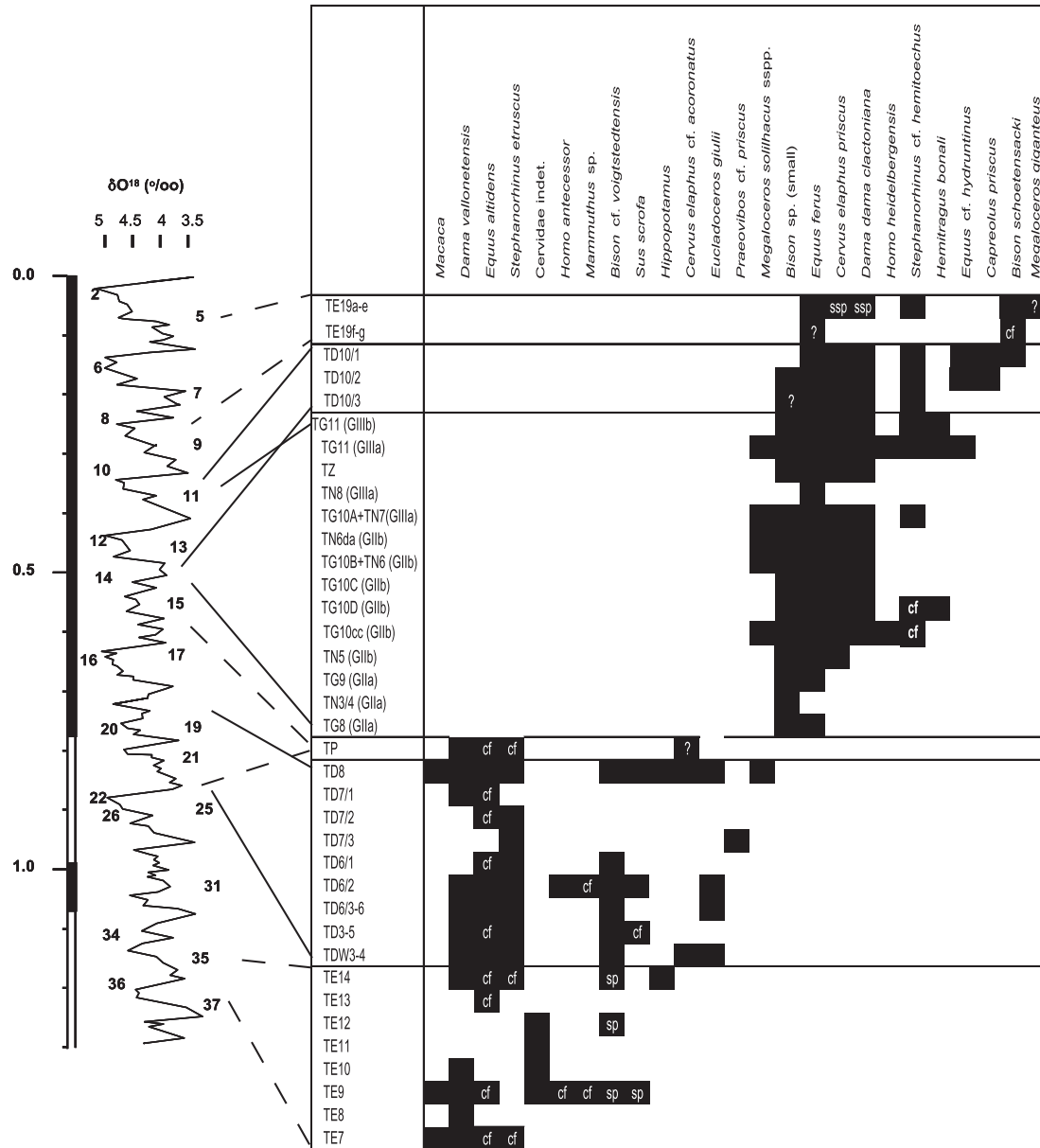


Fig. 1. The ungulates and Cercopithecidae from Atapuerca. The different localities and sedimentary units and subunits at Atapuerca on the left in approximate stratigraphic and chronologic order from lower/older at the bottom to upper/later at the top and their approximate correlation to the oxygen isotope stages. Sima del Elefante = TE; Gran Dolina = TD; Penal = TP; complex of Galería = TG, la Covacha de los Zarpazos = TZ, and Trincheras Norte = TN. Presence of a taxon in a unit is indicated with a black square, if there is some uncertainty about the presence this is indicated by “cf.” or “?” and if the species or subspecies is not known this is indicated by “sp.” and “ssp.”.

(Van der Made, 1999a, 2001). Ungulate fossils were briefly discussed and figured by Bermúdez de Castro et al. (1999). Updated faunal lists were provided by Rosas et al. (1997), Van der Made (2001), Van der Made et al. (2003), Cuenca Bescós et al. (2004), Cuenca Bescós and García (2007) and Rodríguez et al. (2011).

3.3. Sima del Elefante – TE

This locality became well known because of the recovery of the oldest human remains in Europe (Carbonell et al., 2008). It is a large and complex locality. Some work has been done on the locality before 1995, but since the study of the stratigraphy and sampling for micromammals started in that year, the effort has been continuous and gradually increased to a full scale excavation. An introduction to the locality is given by Rosas et al. (2001, 2004, 2006), who also mentioned but not described the large mammals

recovered. At present, the lowest level excavated is TE7 and the levels are numbered upwards. TE19 is the highest level in the central part of the locality. The lower units have reversed palaeomagnetism. A change towards normal was detected between TE16 and TE17. Dating with cosmogenic nuclides suggest ages around 1.1–1.2 Ma for levels TE7 and TE9 (Carbonell et al., 2008).

The older units (TE7–14) are fossiliferous and have broadly similar faunas. Up to now, no fossils or lithic industry have been recovered from TE15–17, although some fauna and lithic industry was collected from TE18 and more abundantly from TE19. In the lower levels, the carnivores tend to be better preserved, with skulls and even an articulated skeleton, than the ungulates, which mostly are represented by isolated and broken bones. Ungulates are more abundant and better preserved in the upper levels, but there they are covered by concretion and have not yet been prepared. Carnivore remains were described by García and Arsuaga (2001a,b),

García and Howell (2008) and García et al. (2008). Faunal lists including the ungulates were given by Rosas et al. (2001, 2004, 2006), Van der Made et al. (2003), Cuenca Bescós and García (2007), and Rodríguez et al. (2011). In recent years, well-preserved fossils of a large bovine appear in TE9, which most probably represent an early bison: the remains are bigger than any *Leptobos* and dental morphology is as in *Bison*. Scanty remains of an equid from TE9, are indeterminate, but might belong to *Equus altidens*, which is recorded from younger levels. These remains are still under study, but the species will be briefly discussed below.

3.4. Penal – Tp

The small locality of Penal has received relatively little attention. A section of the locality can be seen in the upper part of the wall of Trinchera opposite Gran Dolina. It is horizontally and vertically restricted, at least in what can be seen at the surface. Before excavation it was believed to have been connected to Gran Dolina, and it was suspected that it might have been one of the entrances of the cave. However, the beds dip away from Gran Dolina and have different taphonomical features (Fernández-Jalvo, 1995). The units recognized are numbered Tb1 to Tb4 and TP3 to TP9 from bottom to top and faunal lists of small mammals elaborated by G. Cuenca and A. van der Meulen include *Mimomys* in virtually all levels (Fernández-Jalvo, 1995). The presence of this rodent suggests that these levels are time equivalent to some of the units of the lower part of Gran Dolina (TD3–8). The locality has few fossils of large mammals. These remains are described below.

3.4.1. cf. *Panthera gombaszoegensis*

3.4.1.1. *Material*. ATA92, TP9, T-49, 2. Two fragments of left ulna. Anterior part of the head: $Hu \geq 42$; DT facet humerus (upper part) = 20.5. Area of articulation with radius: DT facet humerus (lower part) = 20.0.

3.4.1.2. *Description*. The facet of the ulna for articulation with the radius allows rotation of these bones with respect to each other (Fig. 2), whereas in most ungulates this movement is usually impeded by the shape of this facet. The ulna has the size for a large carnivore and is slightly smaller than in a lion.

3.4.1.3. *Discussion*. The European Early and Middle Pleistocene carnivores of large size include various species of Ursidae, *Megantereon*, *Homotherium*, *Panthera gombaszoegensis* (or *Panthera onca gombaszoegensis*) and *Panthera leo*. Most Ursidae and *Panthera leo* tend to be larger. *Panthera gombaszoegensis* has been described from the lower units of Gran Dolina (García and Arsuaga, 1999, 2001b; García García, 2003). Possibly the ulna represents that species.

3.4.2. *Equus cf. altidens*

3.4.2.1. *Material*. ATA92, TP1, X-50, 2. Left M₃, $H > 40.4$; DAP = –/–/34.2; DTa = 12.3/12.3/12.4; DTp = 10.9/10.1/10.1; Double buckle = 13.8/13.8/13.8; fossid 1 = 7.6; fossid 2 = 8.7.

3.4.2.2. *Description*. Part of the area of the double buckle is damaged, but slightly below the occlusal surface, the linguaflexid can be seen to be V-shaped (Fig. 3), as in stenorid horses, whereas caballoid horses tend to have a U-shaped linguaflexid. The fossids are small and their shape is simple. The ectoflexid is wide and deep and reaches between the fossids. There is no caballinid fold or antecaballinid fold.

3.4.2.3. *Discussion*. There are many different opinions on the classification, phylogenetic relationships and stratigraphic distribution of the European stenorid horses (e.g. Azzaroli, 1990; Eisenmann,

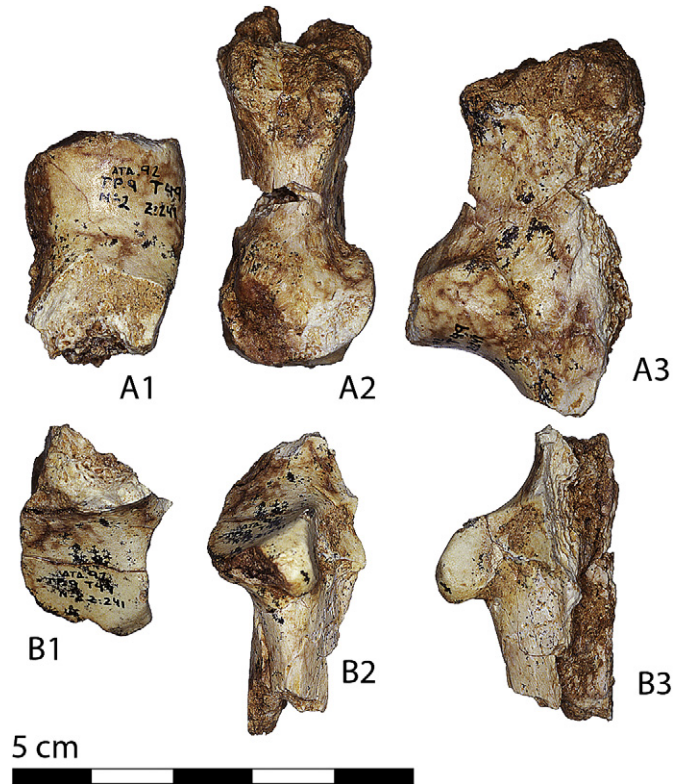


Fig. 2. cf. *Panthera gombaszoegensis* from Atapuerca – Penal, level TP9. ATA92, TP9, T-49, 2 – two fragments of left ulna, A) proximal part, B) a slightly more distal part, articulating with the proximal radius: A1) distal view of proximal part, A2) anterior view of proximal part, A3) lateral view of proximal part, B1) proximal view of distal part, B2) anterior view of distal part, B3) lateral view of distal part.

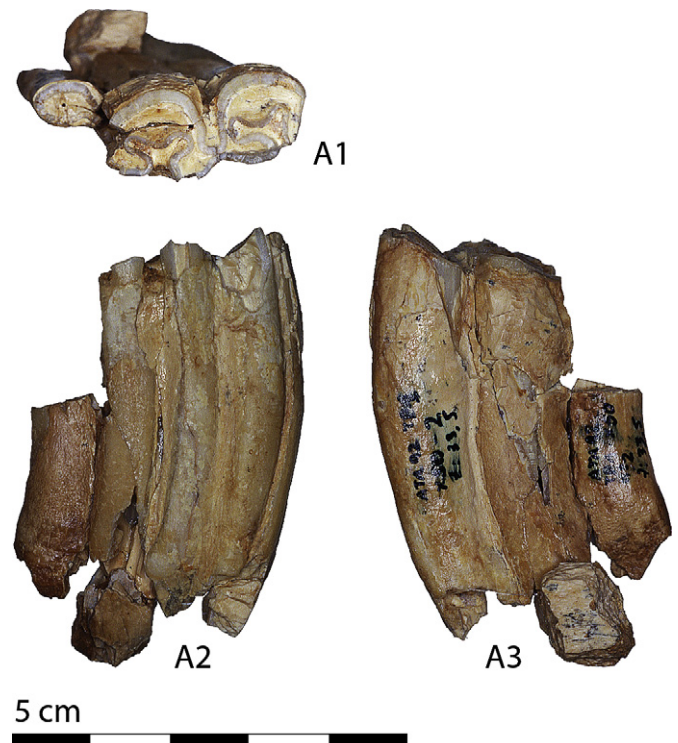


Fig. 3. *Equus cf. altidens* from Atapuerca – Penal, level TP1. ATA92, TP1, X-50, 2 – left lower third molar: A1) occlusal view, A2) lingual view, A3) buccal view.

1991; Alberdi et al., 1998; Forstén, 1999; Musil, 2001). There are large stenorid horses, variously assigned to *Equus livenzovensis*, *E. major*, *E. bressanus* and *E. suessenbornensis*, but these tend to have cheek teeth that are larger than the specimen from Penal. Smaller species, but with a relatively robust skeleton include *E. stenonis*, while from the late Early Pleistocene onward there is a group or lineage of gracile and mostly small forms including *E. altidens*, *E. wuesti* and *E. hydruntinus*. *Equus wuesti* is the largest, while *E. hydruntinus* is very small and restricted to the late Middle and Late Pleistocene. *E. altidens* was reported from Atapuerca (Van der Made, 1998, 1999a; Rodríguez et al., 2011). Probably the material from Penal belongs to that species.

3.4.3. *Stephanorhinus cf. etruscus*

3.4.3.1. *Material*. ATA92, TP9, V-49, 6 ($Z = 280$) – right metapodial III, distal part: DAPd = 40.9; DTdmax = 56.2; DTdf \geq 46.7. ATA92, TP9, W-49, 6 ($Z = 280$) – right metacarpal III, proximal part: DAPP \geq 43.4; DTp = 51.8.

3.4.3.2. *Description*. Both fragments were probably once part of the same bone, a right Mc III. The morphology is of a rhinoceros (Fig. 4). The specimen is very small (Fig. 5).

3.4.3.3. *Discussion*. The European Pleistocene rhinoceroses belong to *Stephanorhinus* and *Coelodonta*, while there is also the very rare giant *Elasmotherium*. A small rhinoceros of the late Early and earliest Middle Pleistocene has been considered to be *Stephanorhinus etruscus* (Cerdeño, 1993; Van der Made, 1998, 1999a, 2001; Van der Made et al., 2003), *Stephanorhinus aff. hundsheimensis* (Mazza et al., 1993) or related to *S. jeanvireti* (Lacombat, 2006). This rhinoceros has teeth that are comparable to those of *S. etruscus*, but postcranials that are relatively small (Giles Pacheco et al., 2011). This rhinoceros is present in the lower part of the sequence of Gran Dolina. Most probably the material from Penal belongs to this species.

3.4.4. *Dama vallonnetensis*

3.4.4.1. *Material*. ATA92, TP9, W-49, 7 ($Z = 322$) – left M_3 : DAP = 26.1, DAPb = 26.3, DTa \geq 11.6, DTp = 11.6, DTpp = 6.1. ATA92,

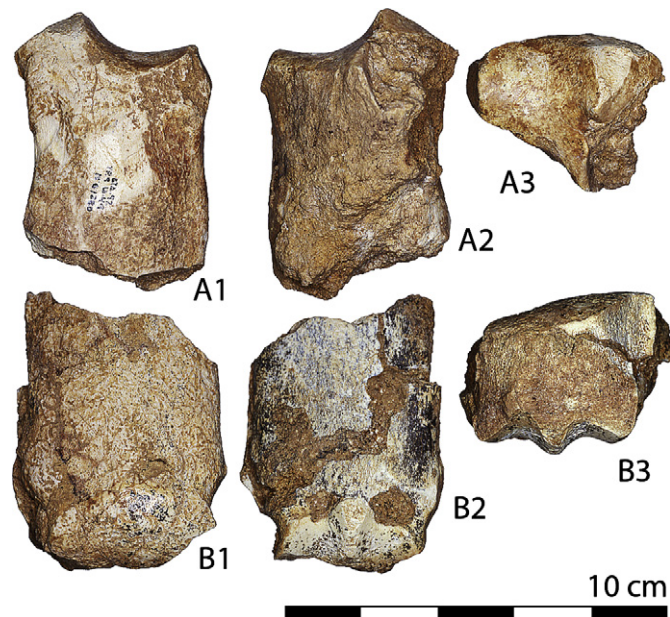


Fig. 4. *Stephanorhinus cf. etruscus* from Atapuerca – Penal, level TP9. A) ATA92, TP9, V-49, 6 – right metacarpal III, proximal part: 1) anterior, 2) posterior, and 3) proximal views. B) ATA92, TP9, W-49, 6 – right metacarpal III, distal part: 1) anterior, 2) posterior, and 3) distal views.

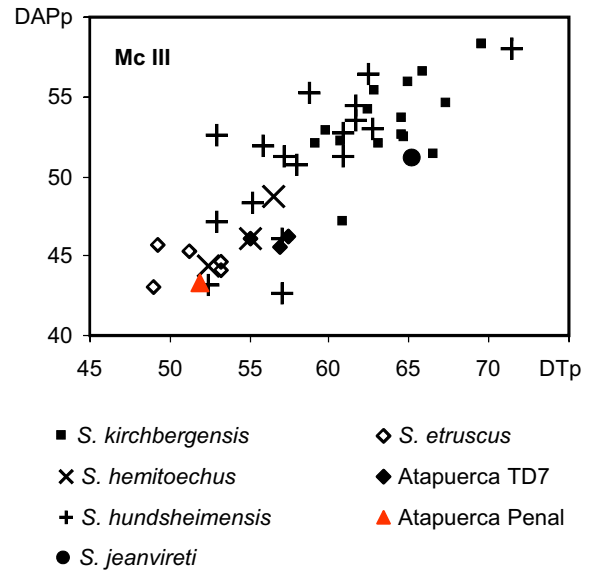


Fig. 5. Bivariate diagram of the proximal width (DTp) against proximal antero-posterior diameter (DAPP) of the third metacarpal of selected Rhinocerotidae: *Stephanorhinus kirchbergensis* and *S. hemitoechus* from Bilzingsleben (measured at the Forschungsstelle Bilzingsleben, Friedrich Schiller-Universität Jena, Bilzingsleben), *S. hemitoechus* from Azokh V (Medical University, Baku), *S. hundsheimensis* from Untermassfeld (Forschungsinstitut und Naturmuseum Senckenberg, Forschungsstation für Quartärpaläontologie, Weimar), Soleilhac (Musée Crozatier, Le Puy-en-Velay), Hundsheim (Institut für Paläontologie der Universität, Wien), and Mauer (Staatliches Museum für Naturkunde, Karlsruhe), *S. jeanvireti* from Montopoli (Istituto di Geologia, Firenze = IGF), *S. etruscus* from Olivola and Valdarno (IGF) and from El Rincón (Museo Nacional de Ciencias Naturales, Madrid), Atapuerca Gran Dolina TD7 and Atapuerca Penal TP9.

TP9, W-49, 5 ($Z = 317$) – left metatarsal, shaft and proximal part: DAPmini = 18.5; DTmini = \sim 17.9. ATA92, TP9, V-49, 9 ($Z = 293$) – left third phalanx: DTp $>$ 13.8. ATA92, TP8, W-49, 4 ($Z = 305$) – remains of a molar in sediment.

3.4.4.2. *Description*. The molar shows a number of characters that are typical of *Dama* and different from *Cervus* (Lister, 1996), for instance the lingual side shows a “step” from the third lobe to the second lobe (Fig. 6A), whereas in *Cervus* this area is usually nearly flat. Other Pleistocene deer are much larger, save for *Capreolus*, which is much smaller and also morphologically different. This tooth and the other fossils (like the metatarsal, Fig. 6B) are of the size of the *Dama*-like deer and fit well late Early and early Middle Pleistocene forms (compare Van der Made, 2010b, fig. 2).

3.4.4.3. *Discussion*. The opinions on the evolution, phylogenetic relationships and classification of the late Early Pleistocene European *Dama*-like deer differ widely: at the generic level they have been classified as *Cervus*, *Dama*, *Pseudodama*, *Euraxis*, *Axis*, *Rusa*, and *Metacervoceros*, while at the species level a frequently applied name is *Cervus* (s.l.) *nestii vallonnetensis*, *Dama* “*nestii*” *vallonnetensis* or *Dama vallonnetensis* (e.g. Kahlke, 1997; Van der Made, 1999a; Croitor, 2006; Rodríguez et al., 2011). Material from the lower part of Gran Dolina was assigned to the latter taxon (Van der Made, 1998, 1999a, 2001; Van der Made et al., 2003; Rosell et al., 2010; Rodríguez et al., 2011). Here the suggestion that the taxon should be considered as an independent species is followed.

3.4.5. *Cervidae cf. Cervus elaphus acoronatus/Megaloceros savini*

3.4.5.1. *Material*. ATA92, TP4, M-49, 2 ($Z = 107$) – shaft of right metatarsus: DAP of this fragment of the shaft 38.3, DTm \sim 27.9.

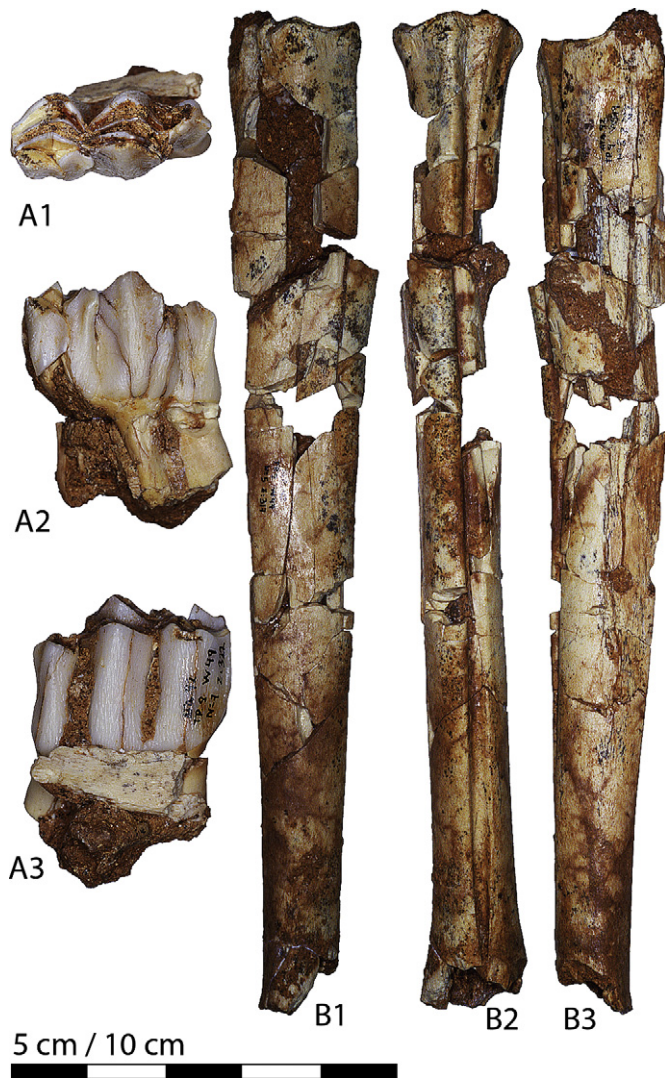


Fig. 6. *Dama vallonnetensis* from Atapuerca – Penal, level TP9. A – ATA92, TP9, W-49, 7 – left M₃: 1) occlusal, 2) lingual, and 3) buccal views. B – ATA92, TP9, W-49, 5 – left metatarsal, shaft and proximal part: 1) medial, 2) anterior, and 3) lateral views. The scale bar represents 5 cm for figure A and 10 cm for figure B.

3.4.5.2. Description. The shaft of the metatarsal does not show remarkable morphological features (Fig. 7). The DAP given above is of the fragment, it is not one of the standard measurements, but the DTm can be measured. With about 27.9 mm, the minimal transverse diameter (DTm) is smaller than in *Eucladoceros giulii* from Atapuerca, lower part of Gran Dolina (≤ 31.5 ; specimen measured in the Museo de Burgos), Akhalkalaki (32.6, 30.1, 29.4, 33.4, 33.0, 32.5, 28.4, 28.9 specimens in Georgian State Museum), and Apollonia 1 (33.9, 33.1, 31.2; Aristotle University of Thessaloniki = AUT), all localities of about the same age as Penal. The DTm of *Megaloceros solilhacus* (or *Megaceroides solilhacus*) is much larger in Voigtstedt (34.6, 35.4, 33.7, 34.4, 35.7; Forschungsinstitut und Naturmuseum Senckenberg, Forschungsstation für Quartärpaläontologie, Weimar), Soleilhac (≤ 37.3 ; Musée Crozatier, Le Puy en Velay), Mosbach (33.9, 37.3; Naturkunde Museum, Mainz) and Petralona (~ 34.5 , 39.4, 33.7, 34.9; AUT). A species of *Megaloceros* from Libakos is close to *Megaloceros savini*, but larger (26.0, 27.0, 25.6; Technische Universität Clausthal, Institut für Geologie und Paläontologie). The metatarsus from *M. savini* is expected to be about the same size of a large *Cervus elaphus*, maybe a specimen from West Runton (28.2;



Fig. 7. Cf. *Cervus elaphus* from Atapuerca – Penal, level TP9. ATA92, TP4, M-49, 2 – shaft of right metatarsus: A1) proximal, A2) lateral, A3) anterior, and A4) medial views.

Natural History Museum, London) belongs to that species. European *Cervus elaphus* shows fluctuations in size; the representatives around the Early–Middle Pleistocene transition are large, but can be confused with *M. savini*. However, a good sample of *Cervus elaphus* from Neumark Nord is dentally as large as those from around the Early–Middle Pleistocene transition, but occur with *Megaloceros giganteus*, a much larger species, with much more robust metapodials. With ~ 27.9 mm, the metapodial from Penal is well within the ranges of *Cervus elaphus* from Neumark Nord (26.6, 25.7, < 23.3 , 22.8, 27.6, 27.2, 24.4, 24.7, 28.0, 24.5, 28.6; studied in Bilzingsleben, presently kept in the Landmuseum für Vorgeschichte, Halle).

3.4.5.3. Discussion. Most species of European Pleistocene deer were large and include species assigned to *Eucladoceros* and *Megaloceros*, while some species are variously assigned to *Megaloceros*, *Megaceroides* or *Praemegaceros*. Middle size species were *Cervus elaphus* and *Megaloceros savini*. The *Dama*-like deer and *Cervus perolensis* were small, and *Capreolus* even smaller. The metatarsal from Penal belongs to a middle sized species. Remains of *Cervus elaphus*, including an antler, were found at level TD4 just across Trinchera (Bermúdez de Castro et al., 1999), while fragmentary basal antlers of *Megaloceros savini* were described from TD3 (Soto, 1987). The latter remains are from the earliest excavations, and since that time no fossils of that species have been found in Atapuerca. Most probably the metatarsal from Penal belongs to *Cervus elaphus*, but it cannot be excluded that it belonged to *M. savini*.

3.4.6. *Hystrix/Castor*

3.4.6.1. *Material*. ATA92, X-49, TP1 ($Z = 27$). Two cheek teeth in sediment. First cheek tooth $DAP > 6.5$; second cheek tooth $DAP 7.5$, $H > 14.5$.

3.4.6.2. *Description*. These teeth show the presence of a large rodent. They are in sediment and have not been prepared. Earlier studies of the rodents of from Penal did not detect the presence of a large rodent species (Fernández-Jalvo, 1995, Table 1b).

4. Discussion

4.1. Faunal lists from Atapuerca

The small collection of large mammals from Penal has been described. The large mammals from Penal belong probably to the same species as those known already from the lower part of Gran Dolina and they fit an age around the Early–Middle Pleistocene transition. This material is included in the updated faunal lists for the ungulates and cercopithecids of the different sites and levels of Gran Dolina, Galeria and Sima del Elefante in the Sierra de Atapuerca. The ungulate record from the different sites and levels in the Sierra de Atapuerca, is of interest for the study of the evolution, biogeography and biostratigraphy of the European ungulates.

The Atapuerca deposits contain the oldest record in Europe of several ungulate species. *Sus scrofa* and *Cervus elaphus* are first recorded in Atapuerca TD5 or TD6, and TDW3–4, respectively and in Dorn Dürkheim (Germany; Franzen et al., 2000) in sediments with reversed polarisation below the Brunhes–Matuyama boundary. A large bovine from TE9 is probably one of the oldest bison from Europe. A small bison from TG and TD10/2 differs from *Bison schoetensacki*, shares characters with *Bison priscus*, and might be an early representative of that lineage in Western Europe. Fossil dentition and articulated limb bones of *Praeovibos* cf. *priscus* from TD7/3 are possibly the oldest West European record of that species. Remains of other species from the Atapuerca sequence do not represent the oldest record of a species, but are close in age to the oldest record. In other occasions, the collections from Atapuerca include particularly abundant or well preserved remains that complete knowledge of these species. The precise dating of new arrivals of large mammals in Europe is of interest for the studies on biogeography and human dispersal into Europe.

4.2. Existing models on the link between faunal and human dispersal to Europe

Faunal dispersal is often studied in relation to human dispersal. However, often this does not go much further than noting a coincidence in time between human and faunal dispersal. There are few models that try to explain human dispersal in terms of cause and effect. The possible ways how human and faunal dispersal could be related are:

- 1) Animals that disperse modify the environment in such a way that it allows for human dispersal into an area that previously could not maintain viable human populations. It can be imagined that this could be by providing a suitable prey species for human hunters, by megaherbivores modifying the landscape, etc. In these cases, the cause is faunal change itself.
- 2) The same or contemporaneous changes in geography, global climate or local environment allow for the dispersal of both humans and other fauna. This may occur in complex ways as the following examples will show. Sea level changes may allow contemporaneous dispersals in different parts of the world. Environmental change in an area that acts as a barrier may

allow for faunal exchange: human dispersal out of Africa might be coincident with some species of large mammal dispersing into Africa. Global climatic amelioration may allow for the northward dispersal of different species in Western and Eastern Eurasia. If there is a common cause for human and faunal dispersal, faunal dispersal may help to detect and understand that cause.

A model that has been published repeatedly during the past twenty years tries to link human dispersal to the dispersal of *Megantereon whitei* (e.g. Martínez Navarro and Palmqvist, 1995). In this model it is assumed that the sabretooth cat *M. whitei* dispersed across the strait of Gibraltar from Africa to Europe, where it replaced an ancestral species. *Megantereon whitei* is believed to have less capacity to break bones than the species it replaced, and that by dispersing into Europe it modified the environment in such a way that human populations, specialized on scavenging these bones for marrow, now could survive in Europe. Evidently, the marrow had to contribute significantly to the diet of the whole group of humans and they had to arrive at the kill site before hyenas did so. This must have been a difficult task, since home ranges of leopards are reported to vary between 9 and 63 km² (Estes, 1992) and the home ranges of a top predator like *Megantereon* may have been even larger. The same authors relate the dispersal of *Pachycrocuta*, *Canis falconeri* and *Hippopotamus* from Africa to Europe to the same human dispersal event. Guerrero-Alba and Palmqvist (1997) and Martínez Navarro (2010) also suggested that a dispersal of *E. altidens* from Africa to Europe formed part of this event. It remained obscure how these dispersals are related to human dispersal. There are serious doubts as to whether these dispersals were contemporaneous, whether they were across the Strait of Gibraltar, the directions in which they occurred, systematics of *Megantereon*, and whether it is feasible that *Megantereon* leftovers significantly contributed to human diet.

In a later publication, Martínez Navarro (2010, p. 216) offered a link between the dispersals of *Hippopotamus antiquus* and humans from Africa to Europe: “Aquatic large megaherbivores that probably never or only sporadically go outside water, such *Hippopotamus antiquus*, are not dangerous for hominins – who live on land – and they are easier to hunt using big stones when they are in swamps close to the riverine margins than are other terrestrial large mammals that can run and also be very aggressive, such as bison, rhinos, elephants, horses, etc.” In this model humans are seen as active hunters, but the hippos may have been depicted as too defenceless.

Carbonell et al. (1999) offered a different model, in which competition between humans with Mode 1 and others with Mode 2 lithic industry forced the ones with the more primitive technology to disperse out of Africa and subsequently into Europe. The latter dispersal was assumed to have been possible during climatic change caused by the increasing effect of the 100 ka Milankovich cycle and seen in the dispersal of large mammals towards Europe. In this context, the possible link was discussed between human dispersal through Asia and that of *Bison* and *Soergelia* from Asia to Europe. In this model human dispersal is not caused or allowed for by faunal dispersal, instead both were made possible by the same agent (climatic change).

4.3. A new model on human dispersal out of Africa and into Europe

The latter aspect of this model was further developed (Van der Made, 2011, in press) and from 2008 onward was presented at a number of meetings, including the workshop in Shanghai on “International Meeting First Human Settlements in Eurasia”, where the possible relationship between human dispersal and that of bison was further stressed. In this newer model, possible

competition between humans with different types of lithic industry moved to the background, while the effect of environmental change as seen in faunal dispersal moved to the foreground. A two-step dispersal out of Africa and into Europe was proposed.

The dispersal out of Africa was controlled by the degree of aridity of the area stretching from the Sahara across the Middle East to Central Asia. In this area, the aridity increased with time, but is overprinted with fluctuations due to the different Milankovich cycles (deMenocal and Bloemendal, 1996). Assuming that early humans were adapted to open, but not to really arid, landscapes, the dispersals of large mammals into and out of Africa are used as a proxy for the “permeability” of the North of Africa and the Middle East, or the possibility of humans to disperse across this area into Asia. Human dispersal into Asia occurred before aridity increased and faunal exchange between Eurasia and Africa nearly ceased. This may have happened once or twice: around 2 Ma, or even as early as shortly after 2.5 Ma (Van der Made, in press).

The dispersal into Europe is a separate event in this model. There is an important biogeographical transition in SE Europe, reflecting the difference between closed environments in central Europe and the open and dry landscapes of the Middle East. This boundary has existed for possibly as much as 20 Ma and numerous species lived for millions of years limited by this boundary before spreading into Europe (Van der Made and Mateos, 2010). As far as the present universally accepted data go, this is also the case for humans, since they were present at Dmanisi some 1.8 Ma ago (Lordkipanidze et al., 2005), but arrived only around 1.2 Ma ago in Western Europe (e.g. Carbonell et al., 2008). Starting from about 1.2 Ma ago, the 100 ka eccentricity Milankovich cycles started to become increasingly important leading to the well-known glacial cycles. During interglacials, the tundra, taiga and steppe extend as parallel bands across Eurasia, but during glacials, the increasing cold causes the taiga to disappear and tundra and steppe fuse into a habitat that has been called the “mammoth steppe” (Guthrie, 1990). In the following interglacial, temperatures rise and herbs followed by different tree species spread with different speeds out of their refugia to the North, causing a series of vegetation types that follow each other in time (Lang, 1994; Reille et al., 2000). It is possible that rising temperatures and the lagging northward spread of trees created short-lived extensive open habitats with moderate

temperatures, which during a short time slice allowed fauna adapted to more or less open landscapes, including humans, to disperse into the more open landscapes of SW Europe. The mechanism of such East–West (and West–East) dispersals resembles a little that of the North–South and South–North dispersals in the Traffic Light Model of Vrba (1996). In a similar, but not exactly the same, way it could explain the enigmatic dispersals into Western Europe of earliest Pleistocene, Pliocene and Miocene large mammals (e.g. Van der Made and Morales, 2011).

4.4. Large mammals dispersing through open habitats into western Europe

In order to test the hypothesis of dispersal through open landscapes, the fauna that dispersed into Europe is here separated according to its likely origin (Fig. 8). If human dispersal coincided with the dispersal of species adapted to open environments, this supports the hypothesis, if the dispersal coincided with that of species adapted to closed environments, it is rejected. Fig. 8 does not include all large mammal dispersals towards Western Eurasia, because some species reached Eastern or central Europe, but not Western Europe, or reached it during a later climatic cycle. For example, Steensma (1988) described *Eucladoceros* aff. *boulei* from Greece, a species which is well known from China.

As stated above, human presence is established around 1.2 Ma in Western Europe. Dispersals around this age include *Megantereon whitei* (if Martinez Navarro and Palmqvist’s, 1995, taxonomy is accepted), *Hippopotamus* (if it did not disperse earlier around 1.4 Ma), *Praeovibos mediterraneus* (which is also claimed to have dispersed earlier), *Soergelia minor*, *Capra? alba*, *Bison degiulii* and possibly a large bison and *E. altidens*. The last six taxa suggest open or more or less dry environments. *Hippopotamus* is a grazer, and thus needs extensive open spaces where abundant grass grows. *Megantereon* may have been a stalker and suggests a more closed environment. The bison are of interest here and also the equid needs some clarification.

4.5. Bison

When they arrived in Europe, bison may have replaced two lineages of *Leptobos*, one lineage with posteriorly directed horn

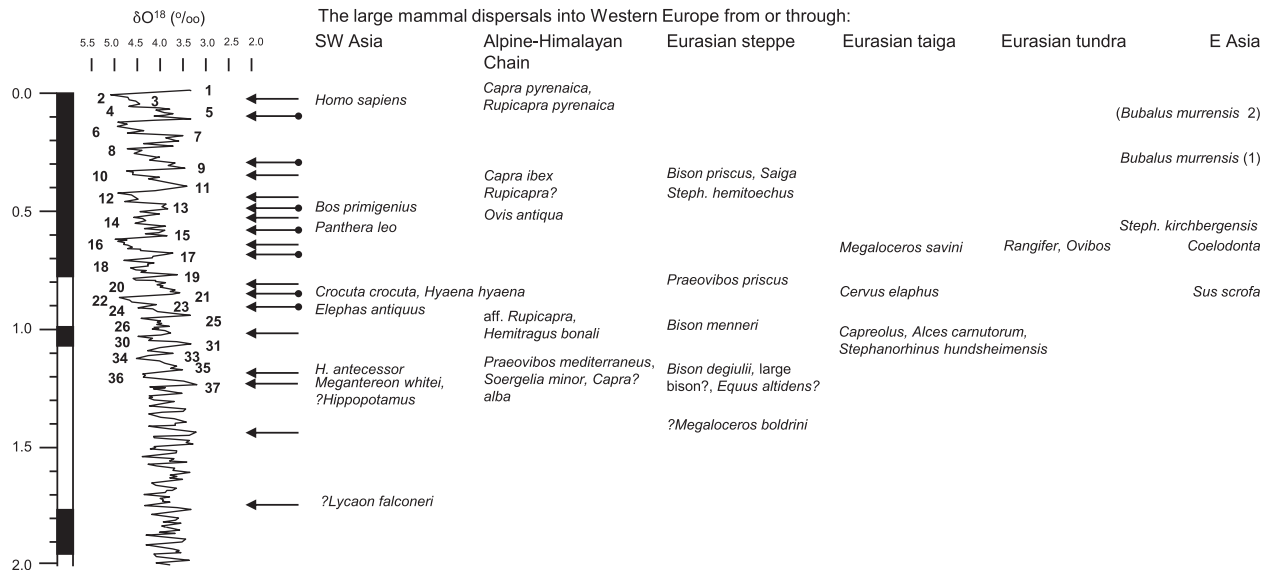


Fig. 8. Dispersals of large mammals into western Europe (west of the eastern borders of Germany and Italy). Based on Fig. 3 of Van der Made (2011), but with the provenance indicated according to different tentative areas or environments. Question marks in front of a species or genus indicate doubts about the exact date of dispersal; question marks behind the name indicate doubts as to whether this dispersal really occurred.

cores (the *Leptobos etruscus* lineage) and the other with outward directed and upward curving horn cores (the *Leptobos elatus* lineage). The first European bison is *Bison degiulii*, notably present in Pirro Nord, with an age of probably around 1.2 Ma. It was a small species with wide frontals and relatively robust metapodials (De Giuli et al., 1987). Probably it evolved into the larger, but similar *Bison schoetensacki*, which is known from Vallonnet (Jaramillo Subchron; Van der Made, 2001). *Bison menneri* is a large species, that is primitive in its more gracile metapodials (Sher, 1997), narrow skull and the orientation of its horn cores. It is known from Untermassfeld (Jaramillo Subchron). *Bison voigtstedtensis* might be a somewhat smaller descendant. A large bovine is found at Sima del Elefante TE9. Good fossils come out gradually and are presently under study. This bovine is larger than *Bison degiulii* and any *Leptobos* and most likely belongs to *Bison*. If an age of 1.2 Ma for this level is accepted (Carbonell et al., 2008) and

the material from TE9 does belong to a large bison, there are two bison dispersals at 1.2 Ma: one of *Bison degiulii* and another one of this large bison.

As common in bovid species that live in herds in open habitats, the females of the living species of bison have horns. This may have been also the case with the Pleistocene species, since no hornless fossil bison skulls are known. Hornless *Leptobos* skulls are known and this may be an indication that these animals had a different social structure and that they possibly did not live in large herds and may have been less adapted to open landscapes. The replacement in Western Europe of *Leptobos* by *Bison* is an important event, reflecting major environmental change, most probably the spread of open environments. The likely origin of *Bison*, the Asian steppe, supports the idea that humans may have dispersed through open environments into Western Europe.

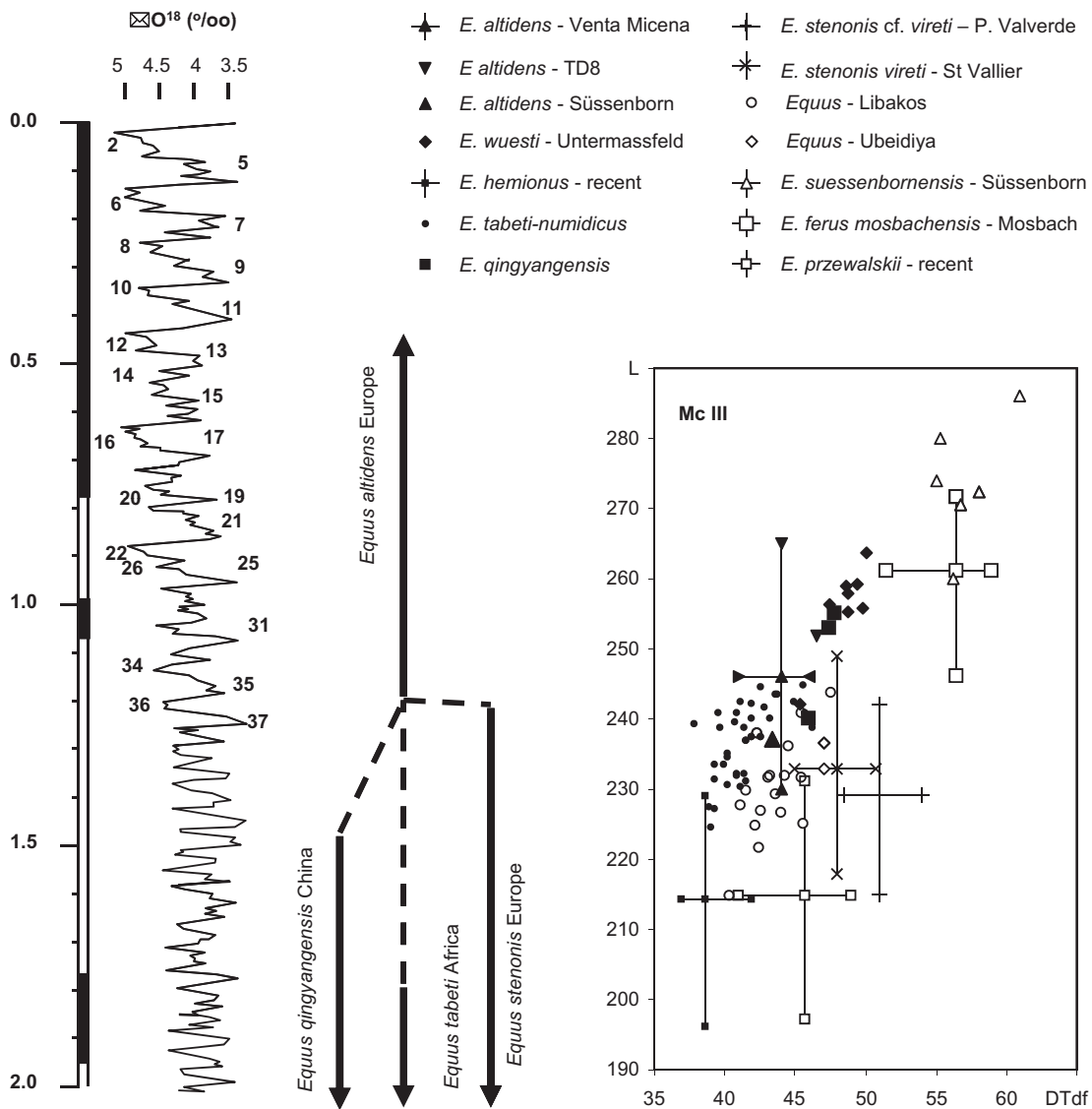


Fig. 9. Three competing models of the origin of *Equus altidens*: *Equus stenonensis*, the African *Equus tabeti*, the Chinese *Equus qingyangensis*. Timescale and isotope stages on the left. Possible relationships indicated by dashed lines. Solid lines give the known chronologic distribution of the species, while arrows indicate that this distribution continues (but how much is irrelevant here). On the right bivariate diagram of the width of the distal articular (DTdf) against length (L) of the metacarpals of selected species or samples of *Equus*: *E. tabeti* and *E. numidicus* from Ain Hanech and Ain Boucherit (Muséum National d'Histoire Naturelle, Paris = MNHN) and from El Kherba and Puit des Rahmani 2 (Sahnouni et al., 2011); *E. stenonensis* from St. Vallier and Puebla de Valverde, *E. mosbachensis* from Mosbach, *E. przewalski* and *E. hemionus* (Eisenmann, 1979); *E. altidens* from Venta Micena (Marín, 1987); *E. wuesti* from Untermassfeld (Musil, 2001); *E. suessenbornensis* and *E. altidens* from Süßenborn (Musil, 1969); *E. qingyangensis* (Deng and Xue, 1999); *E. altidens* from Atapuerca TD8 (Rosell et al., 2010); and *Equus* from Libakos (Technische Universität Clausthal, Institut für Geologie und Paläontologie) and from Ubeidiya (Eisenmann, 1986). In some case individual specimens are indicated, in others minimum, mean and maximum of a sample.

4.6. *Equus altidens*

Equus altidens is included with some doubt in Fig. 8. It is generally seen as closely related or ancestral to *E. hydruntinus* and the living *E. hemionus*. Though it has been suggested that the *E. altidens* lineage (including *E. granatensis*) goes back in Europe to Huélago (close to 2.5 Ma) (Eisenmann, 1999; Forstén, 1999), more likely the first record is considerably later from localities like Venta Micena (Guerrero-Alba and Palmqvist, 1997), here believed to have an age close to 1.2 Ma. Horses can be fairly well separated into species with slender metapodials, including *Equus numidicus*, *E. tabeti*, *E. wuesti*, *E. hydruntinus*, and *E. hemionus*, and species with robust metapodials, including *Equus ferus*, *E. suessenbornensis*, and *E. stenonis* (Fig. 9). There seem to be but few intermediate forms. The species *Equus hemionus* lives in xeric steppes of central Asia.

Guerrero-Alba and Palmqvist (1997) suggested that slender limbed horses dispersed about 2.5 Ma from America into the Old World, reaching Africa, where the lineage *E. numidicus* – *tabetti* – *grevyi* originated and gave rise to *E. altidens*, which dispersed some 1.8 Ma ago to Europe in the company of *Pachycrocuta*, *Megantereon whitei*, *Hippopotamus antiquus* and *Homo*.

Alternatively, the species has been related to the stenooid horses *Equus stenonis* or *Equus senezensis* (Alberdi et al., 1995, 1998), while the material from Huélago, mentioned before, has been assigned to *E. livenzovensensis* (Alberdi et al., 1998). *Equus stenonis* has more robust metapodials, but different samples (e.g. Puebla de Valverde and Saint Vallier) might be interpreted as reflecting an evolution towards more slender metapodials (Fig. 9). In addition material from Libakos described as *Equus stenonis* cf. *senezensis* (Steensma, 1988), is intermediate between those samples and *E. altidens* (Fig. 9). These four samples could be four stages of evolution from *E. stenonis* to *E. altidens*. Material from Ubeidiya was assigned to *Equus* cf. *tabeti* (Eisenmann, 1986), but is more robust than that species and in fact it is in this respect similar to the material from Libakos (Fig. 9).

Deng and Xue (1999) described material from China as *Equus qinyangensis*, that is gracile (Fig. 9). This species was indicated to have a temporal range from 2.5 to 1.2 Ma. Eisenmann and Deng (2005) interpreted this species as a proof for the early existence of a lineage or group of slender equids (in which they included *E. altidens*) that co-existed with *Equus stenonis*.

Considering metacarpal morphology, there are thus at least three possible scenarios of the origin of *E. altidens*: it may have evolved within Europe, or it may have dispersed from Africa or China. Obviously, this question cannot be solved with metapodial morphology only, but good skulls are rare, and dentitions not very informative. In future studies, the possibility of dispersal from China has to be taken into account, especially as there is no temporal gap between the last Chinese and first European record, while the temporal gap in the African scenario is considerable. A dispersal largely along the same latitude is more easy for the species (and thus more likely to happen) than from the tropics to a temperate climate with marked seasonality.

A dispersal of bison and *E. altidens* into Western Europe, either from or through Asia, would support the model that open landscapes extended temporarily to the west, allowing large mammals, including early humans, to disperse. Bison and *E. altidens* are probably present in the lower part of Sima del Elefante, where also the oldest human remains were found.

5. Conclusions

The following conclusions are drawn:

- Inedited material from the locality Penal has been described and assigned to cf. *Panthera gombaszoegensis*, *Equus* cf. *altidens*, *Stephanorhinus* cf. *etruscus*, *Dama vallonnetensis*, and Cervidae cf. *Cervus elaphus acoronatus/Megaloceros savini*.
- Updated faunal lists for the ungulates and Cercopithecidae from Atapuerca are presented. The Atapuerca sequence has many well-dated levels and the fossil record includes many first appearances of large mammals.
- Fossils of a bovine from Sima del Elefante level TE9 most probably belong to *Bison* and, with a date of around 1.2 Ma, are among the oldest remains of this genus in Europe.
- *E. altidens* is present at Atapuerca, possibly even at TE9. The origin of this species is discussed. There are three possible scenarios for the origin of that species, but a particularly interesting possibility is that it dispersed to Europe from China around 1.2 Ma.
- Human dispersal into Europe occurred in a context of major climatic change, when glacial cycles became increasingly better developed. Human arrival in Europe may have coincided with that of species adapted to open environments, such as bison. During glacial periods such environments became widespread in Europe and during the subsequent interglacials were not immediately replaced by closed environments. Human dispersal may have occurred shortly after one of the first really cold climatic cycles.

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