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Faunas from Atapuerca at the Early–Middle Pleistocene limit: The ungulates from level TD8 in the context of climatic change



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ABSTRACT

An extraordinary sequence of fossiliferous levels at the locality of Gran Dolina in the Atapuerca Hills (Burgos, Spain) records the Early–Middle Pleistocene transition. These levels are well dated by a variety of methods, including palaeomagnetism, which locates Lower–Middle Pleistocene boundary at the top of level TD7. Level TD6 is the type site of the species *Homo antecessor* and yielded over 90% of the European Early Pleistocene human record, while other levels have an archaeological record. The present paper deals with the earliest Middle Pleistocene ungulates of TD8, but we plan to describe the faunas, or at least the ungulates, of levels TD4 to TD8 in the context of the faunal changes that took place around the Early–Middle Pleistocene transition.

About 600 fossils could be assigned to a taxon and on this basis the following ungulates are described from TD8: horse *Equus altidens*, rhinoceros *Stephanorhinus* aff. *etruscus*, wild boar *Sus scrofa*, hippopotamus *Hippopotamus* sp., red deer *Cervus elaphus*, giant deer *Eucladoceros* aff. *giulii*, giant deer *Megaceroides solilhacus*, fallow deer *Dama vallonnetensis*, and bison *Bison voigtstedtensis*. The evolution of these taxa is discussed. The fauna from level TD8 dates to the earliest Middle Pleistocene (stage 19) and differs from later faunas in the retention of a small rhinoceros (*Stephanorhinus* aff. *etruscus*) and the latest representative of the genus *Eucladoceros*. It differs from earlier faunas in having the striped hyaena. Together with the fauna from TD7, in which the Brunhes–Matuyama boundary is recorded, TD8 will provide the most precise criteria for correlation of the Early–Middle Pleistocene boundary on the basis of fossils of large mammals.

Profound changes in the global climate system started to take place during the late Early Pleistocene, leading to intensive environmental and faunal change and to human dispersal into Europe. These events mark the beginning of a new time and the Early–Middle Pleistocene boundary is taken somewhere in the middle of this drawn out process. It is taken at a palaeomagnetic change, which is convenient, but this does not appear to be close to an important climatic or faunal change. Ten faunal events are recognized in the period from about 1.2 to 0.5 Ma. The event closest to the Early–Middle Pleistocene boundary is one of the minor events and up to now it is recorded in only few localities, principally in TD8.

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1. Introduction

The sequence of Gran Dolina covers the uppermost part of the Lower Pleistocene, records the Lower–Middle Pleistocene limit and

covers the lowermost part of the Middle Pleistocene (Figs. 1 and 2). These rock units correspond to a very interesting time.

It has been known since long that towards the end of the Early Pleistocene great changes in the fauna took place, but what, when, where, how and why is not exactly known. Azzaroli (1983) believed this to be a single event, which happened between 1.0 and 0.9 Ma in all Eurasia, and called it the “End-Villafranchian Dispersal Event”. This name or variants of it are still often applied. However, there is not a single dispersal event, but an increase in the frequency of dispersals into Europe, which was maintained during the whole

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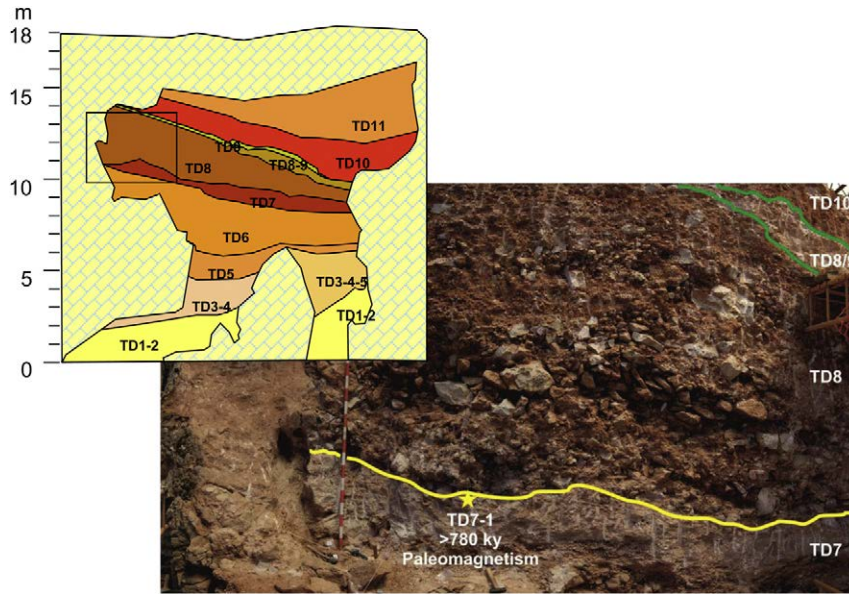


Fig. 1. Schematic section of Gran Dolina and photograph of TD8 and the top of TD7, indicating the approximate level of the Brunhes–Matuyama Boundary.

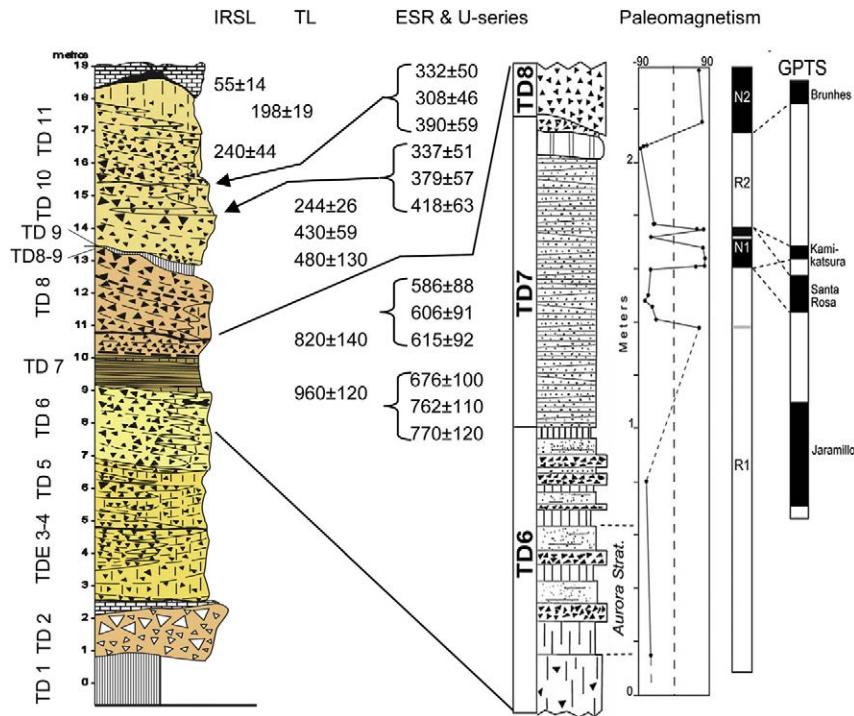


Fig. 2. Lithostratigraphic section of Gran Dolina with amplification of TD6–8 to show the Brunhes–Matuyama boundary and normal events within TD7, as well as the IRSL, TL and ESR and U-series dates. After Berger et al. (2008) and Parés et al. (2013).

Middle Pleistocene (e.g. Van der Made, 2011a). Also many extinctions occurred and species evolved into other species. A biogeographic novelty of major importance was that after 1–0.9 Ma there was a cyclic alternation in mid-latitude Europe and Asia of glacial and interglacial faunas. On a large scale, European species longevity decreased and the rates of evolution increased markedly as well as turnover corrected for species richness, while this did not happen the same way in Africa (Van der Made, 2014). This pattern of increasing change happened probably the same all over northern

Eurasia, but probably not in low-latitude Asia. It is reflected in the transition of the continental stage Villafranchian to the Galerian or Cromerian, the transition period also being called “Epi-Villafranchian” (R.D. Kahlke, 2007; Bellucci et al., 2014-on line). Part of all these events, is the dispersal of the genus *Homo* to Europe.

This faunal turnover was caused by environmental change, induced by modifications in the global climatic system, which in turn resulted from astronomic changes. The different Milankovich cycles, with durations of about 20, 40 and 100 ky have a major

impact on global climate. Before about 1.2–0.9 Ma, the 40 ky obliquity cycle was the one that had most influence on global climate, but in this time lapse, the 100 ky eccentricity cycle became more prominent, leading to the well known alternation of glacial and interglacial periods (Shackleton, 1995; deMenocal, 1995). The period after these changes occurred is markedly different in climate, flora and fauna. More or less this difference is reflected in the subdivision of the Pleistocene into Early and Middle + Late Pleistocene. However, the Early–Middle Pleistocene boundary was conveniently chosen to coincide with the Brunhes–Matuyama boundary, which objectively can be recognized around the globe, but does not coincide exactly with the most important climatic or biotic events.

The different archaeological and paleontological localities and levels in the Atapuerca Hills (Sierra de Atapuerca) range in age from about 1.2 Ma till recent, with an important concentration between about 1.2 and 0.75 Ma. The locality of Sima del Elefante has fossiliferous levels TE7 to TE14 with ages between 1.2 and 1.07 Ma, Gran Dolina has fossiliferous levels TD4 to TD8 with ages between 0.99 and about 0.75 Ma, and the locality of Penal is in approximately the same time range (Rodríguez et al., 2011). For the study of the late Early Pleistocene faunal events, such a paleontological sequence is unique in Europe. It is also unique for another reason.

As stated above, human dispersal to Europe formed part of these late Early Pleistocene events. Nearly all these levels in the sites in the Atapuerca Hills have also an archaeological record and some have human fossils. With at present 160 human fossils recovered, level TD6 has over 90% of the European Early Pleistocene human record, while the remaining specimens are from Sima del Elefante TE9, Cueva Negra, and Barranco León, while there are also remains from Cueva Victoria and Venta Micena, which are disputed (Gibert et al., 1998, 1999, 2008; Walker et al., 2006; Carbonell et al., 2008; Toro-Moyano et al., 2013). The human species *Homo antecessor* was defined on the basis of fossils from TD6 (Bermúdez de Castro et al., 1997). The human fossils and archaeological record of Atapuerca played a decisive role in the debate on early human occupation of Europe. In addition, Gran Dolina, Sima del Elefante, Galería and Sima de los Huesos have also middle Middle Pleistocene younger levels with an important paleontological, archaeological and paleoanthropological record.

The karstic locality of Gran Dolina is situated in an abandoned railway trench that was cut through the hill. This trench exposes nearly 20 m of its sediments, while there are still many more metres below the bottom of the trench. The exposed stratigraphic units are numbered from bottom till top from TD1 to TD12. In TD, T stands for Trinchera (=trench) and D for Dolina. In a similar way TE = Sima del Elefante, TP = Penal, and TG = Galería. Due to the shape of the cavity and the position of the railway trench, level TD4 is exposed at two sides of a rock, one side is called TDW4 and the other TDE4; the precise stratigraphic relationship between both sides is not yet exactly clear. Unit TD2 is said to have yielded some and TD3 many fossils (Soto, 1987). These units have been excavated in the nineteen seventies, and at present they cannot well be recognized. In the present situation fossils come from levels TD4 to TD8 and from TD10. In the early nineteen nineties, there have been excavations in TDW4. A test pit of about 6 m² was excavated through all levels, reaching TD8 in 1994. The front of the locality was very irregular and was subsequently straightened, to avoid collapse. Material from TD8 was recovered from 2002 till 2006. The concept of TD8 has changed. Originally, it was considered to consist of two subunits: TD8a, with fossils of small and large mammals, which is overlain by TD8b, with only small mammals. Now TD8b is considered a separate unit, called TD8-9 and TD8a is called simply TD8 (Rodríguez et al., 2011, table 2). In the near future, excavations

are planned in a relatively extensive area of TD4 at the base of the locality.

It is the aim of this paper to describe the fauna from TD8, or at least the ungulates, within the context of the faunal change around the Early – Middle Pleistocene transition. It is also an aim, to do the same in future papers for the faunas from levels TD7 to TD4. In this paper, a scheme of late Early and early Middle Pleistocene faunal change is presented. The same scheme will be used and improved in the future papers.

2. Material and methods

The fossils described here are presently kept in the IPHES, but the final repository will be the CENIEH (see acronyms below). The labels of the specimens indicate first “Ata” for Atapuerca and the year, then the locality (TD for Gran Dolina) and the level and in some cases the sublevel, the square (a letter and a number), and finally the specimen number. Specimen numbers are within a square and level and start each year again from 1. In the test pit, spit numbers were recorded as t (=talla = spit). A complete number is: Ata06, TD8B, G-4, 145.

In about 600 specimens from Atapuerca TD8 relevant morphology could be observed or standard measurements could be taken. The specimens studied are indicated under each species or in the tables of measurements in the supplemental information. When these fossils are compared to fossils and bones and teeth of recent animals, either a bibliographic reference or an acronym is given for the institute where the material was studied or where it is presently kept:

AHAPMR	Azov Historical, Archeological and Paleontological Museum-Reserve, Azov.
AUT	Aristotle University of Thessaloniki.
AVP	Accademia Valdarnese del Poggio, Montevarchi.
CENIEH	Centro Nacional de Investigación sobre la Evolución Humana, Burgos.
CIAG	Centre d'Investigacions Arquelògiques de Girona.
DGFSUPV	Departamento de Geología, Facultad de Ciencias, Universidad del País Vasco, Bilbao.
DSTUSR	Dipartimento di Scienze della Terra, Università “La Sapienza”, Roma.
EBD	Estación Biológica de la Doñana, Sevilla.
ETSI	Escuela Técnica Superior de Ingenieros de Minas y Energía de la Universidad Politécnica de Madrid.
FBFSUJ	Forschungstelle Bilzingsleben, Friedrich Schiller-Universität Jena, Bilzingsleben.
FISF	Forschungsinstitut Senckenberg, Frankfurt.
GIN	Geological Institute, Moscow.
GSM	Georgian State Museum, Tbilisi.
HGSB	Hungarian Geological Survey, Budapest.
HMV	Historisches Museum, Verden.
HUJ	Hebrew University, Jerusalem.
IGF	Istituto di Geologia, now Museo di Storia Naturale, Firenze.
IPH	Institut de Paléontologie Humaine, Paris.
IPHES	Institut Català de Paleocologia Humana i Evolució Social, Tarragona.
IPRFWUB	Institut für Paläontologie der Rheinischen Friedrich-Wilhelms Universität Bonn.
IPUW	Institut für Paläontologie der Universität, Wien (Vienna).
IQW	Institut für Quartärpaläontologie, Weimar.
LPTUP	Laboratoire de Préhistoire de Tautavel, Université de Perpignan.
L VH	Landesmuseum für Vorgeschichte, Halle.
MAC	Museo de Arqueología de Cartagena.
MAN	Museo Arqueológico Nacional, Madrid.
MAR	Museo Arqueológico Regional, Alcalá de Henares.
MB	Museo de Burgos, Burgos.
MCP	Musée Crozatier, Le Puy-en-Velay.
MH MV	Museo Histórico Municipal de Villamartin.
MNB	Museum für Naturkunde der Humboldt-Universität, Berlin.

(continued)

MNCN	Museo Nacional de Ciencias Naturales, Madrid.
Monrepos	Römisch-Germanisches Zentralmuseum, Forschungsinstitut für Vor- und Frühgeschichte, Forschungsbereich Altsteinzeit Schloss Monrepos, Neuwied.
MSI	Museo de San Isidro, Madrid.
MUB	Medical University, Baku.
NBC	Naturalis Biodiversity Center, Leiden (previously Nationaal Natuurhistorisch Museum).
NCM	Norwich Castle Museum, Norwich.
NCUA	National and Capodistrian University of Athens.
NHM	Natural History Museum, London.
NMM	Naturhistorisches Museum, Mainz.
NMMaa	Natuurhistorisch Museum, Maastricht.
NMP	National Museum, Prague.
NMW	Naturhistorisches Museum, Wien (Vienna).
MPRM	Musée de Préhistoire Régionale, Menton.
PIMUZ	Paläontologisches Institut und Museum der Universität, Zürich.
PIN	Palaeontological Institute, Moscow.
SIAP	Servei d'Investigacions Arqueològiques I Prehistòriques, Castellón.
SMNK	Staatliches Museum für Naturkunde, Karlsruhe.
SMNS	Staatliches Museum für Naturkunde, Stuttgart.
SMS	Spengler Museum, Sangershausen.
TMH	Teylers Museum, Haarlem.
TUC	Technische Universität Clausthal, Insitut für Geologie und Paläontologie.
UCBL	Université Claude Bernard, Lyon.
UCM	Universidad Complutense, Madrid.
VMM	Vernadzki Museum, Moscow.
ZMA	Zoologisch Museum, Amsterdam; presently transferred to NBC.
ZPALUWr	Division of Palaeozoology, Department of Evolutionary Biology and Ecology, University of Wrocław.

The way of measuring and nomenclature for the Equidae are after Eisenmann et al. (1988). These authors number the measurements; in addition to these numbers also the acronyms are given which are generally applied here. The nomenclature and way of measuring for the Rhinocerotidae is after Van der Made (2010). Tooth nomenclature for the Artiodactyla is after Van der Made (1996). The way of measuring the teeth of the Suiformes and the bones of the Artiodactyla is generally after Van der Made (1996). Bovid and cervid metapodials and teeth are measured after Van der Made and Tong (2008) and Van der Made (1989, 2012).

The following acronyms and names are used for the measurements in the figures and tables:

buckle	DAP of the “double knot” or buckle in the lower molar of <i>Equus</i>
DAP	Antero-posterior diameter
DLL	Labio-lingual diameter
DMD	Mesio-distal diameter in incisors
DT	Transverse diameter, width
fossid 1/2	DAP of the first and second fossid in the lower cheek teeth of <i>Equus</i>
H	Height
h	An alternative measurement for the height
L	Length
l	An alternative measurement of length
protocone	DAP of the protocone in an upper cheek tooth of <i>Equus</i>
P index	Protoconal index = $100 \times \text{protocone}/\text{DAP}$
plis	Folds of the enamel in the upper cheek tooth of <i>Equus</i>
R	A diameter (as in R1, R2, ... of the humerus)
T	Enamel thickness
The position of these measurements is indicated by lower case letters, as in DTa or DTp:	
a	of the anterior lobe of a tooth, at the anterior side of a bone
b	at the crown base
bu	at the buccal side of a tooth
d	at the distal or dorsal side
dors	at the dorsal side

(continued)

ext	at the lateral side
f	of the facet (as in DTdf = DT of the distal facet)
fa, fast	of the facet for the astragalus
fp	of the articular facet for the patella (in the femur)
h	of the head of a bone
int	at the medial side
l	of the lower part of a bone
la	at the labial side of a tooth
li	at the lingual side of a tooth
m	in the middle
maxi/max	maximal
mini	minimal
n	of the “neck” of a bone
o	at the occlusal surface
p	of the posterior lobe of a tooth, of the proximal part of a bone
pp	of the third lobe of an M ₃
root	of the root of a tooth
sf	at the level of the sustentacular facet in a calcaneum
u	of the upper part of a bone
III	of the third digit, “anatomical length” at the medial side of a canon bone
IV	of the fourth digit, “anatomical length” at the lateral side of a canon bone
*	an alternative measurement

Phalanges, isolated distal articulations of metapodials and sesamoids of artiodactyls are similar in the third and fourth digit, and cannot be separated. In the tables, these are indicated as left or right (“l” or “r”), with reference to the axis of the manus or pes. Other bones are indicated as being “s” or “d” (sinistralis, dextralis).

A third metacarpal of *Equus* is broken at the distal end and length (L), medial length (Lm), distal width above the articulation (DTd), nor distal articular width (DTdf) could be measured. These are the standard measurements 1, 2, 10 and 11 of Eisenmann et al. (1988). However, this is an important bone for equid systematics. In order to be able to make the relevant metric comparisons, the length and distal articular width were estimated, using regressions of lateral length ($LI = 244.9$ in the specimen from TD8) and length ($LI = 0.9978L + 7.4477$, $R^2 = 0.9829$, $n = 50$) and proximal width (DTp) against DTdf ($DTdf = 0.8976DTp - 0.1155$, $R^2 = 0.8784$, $n = 66$), using data of several other species, giving the following results: $L = 251.8$ and $DTdf = 46.6$. These values have been used in the metric comparisons and are indicated in Table 3. A similar procedure was followed to estimate the distal articular width (DTdf) from the width from the articulation with the fourth digit (DT_{IV}) of a metacarpal of *Dama* ($DTdf = 2.1936 DT_{IV} - 0.1862$; $R^2 = 0.9959$, $n = 255$). The result $DTdf = 32.9$ is indicated in Table 21.

3. Systematics

3.1. Horse

Order Perissodactyla Owen, 1848
 Family Equidae Gray, 1821
 Genus *Equus* Linnaeus, 1758
Equus altidens Von Reichenau, 1915

3.1.1. Material

All material studied here is indicated in Tables 1–5. Numbers Ata94, TD8, t28, G16, 44 and Ata94, TD8, t28, G17, 10 were used (destroyed) for dating (Falgüères et al., 1999). A taphonomic study assigned 125 fossils to the horse, representing a minimum of 6 individuals (Rosell et al., 2010).

Table 3 (continued)

Ata03, TD8A, H-6, sc	d	–	–	–	–	–	47.9	..	26.8	–	–	–	–	–
Ata06, TD8B, G-4, 110	?	–	–	–	–	–	–	–	–	–	–	–	–	–

Table 4

Measurements of the carpals and tarsals of *Equus altidens* from Atapuerca TD8 (in mm).

Scaphoid		DAP	DT	Ha	
Ata03, TD8B, G-5, 14	s	–	≥22.0	26.7	
Ata06, TD8B G-4, 111	d	37.3	25.3	28.1	
Lunar		DAP	DTp	DTd	Ha
?Ata06, TD8b, H-3, 42	s	38.0	30.5	23.5	16.0
Ata95, TD8, H-16, t27, 6		46.0	34.4	≥25.9	30.6
Ata94, TD8, t27, H-16, 6	s	46.5	34.2	>6.1	30.4
Ulnar		DAP	DT	H	
Ata2002, TD8B, F-12, 47	s	32.2	16.3	21.3	
Trapezoid		DAP	DT	H	
Ata94, TD8, t28, G-16, 35	s	32.7	27.5	24.3	
Ata94, TD8, t29, I-16, 29	s	33.9	25.7	25.1	
Magnum		DAP	DT	H	
Ata2002, TD8B, G-8, 81	d	39.0	44.5	≥20.3	
Ata04, TD8B, G-5, 45	s	–	43.7	–	
Navicular		DAP	DT		
Ata03, TD8B, G-6, 41	d	36.3	49.6		
Ata2002, TD8B, G-8, 54	d	46.3	56.3		
Ata2002, TD8B, G-8, 79	s	40.9	52.3		
Cuboid		DAP	DT	H	
Ata2002, TD8B, G-8, 83	d	38.4	25.4	28.8	
Ata03, TD8B, G-5, 14	s	–	≥22.0	>26.7	
Cuneiform III		DAP	DT		
Ata94, TD8, t29, H-16, 53	s	39.9	47.1		
Ata2002, TD8B, G-8, 71	s	41.7	50.2		
Ata2002, TD8B, F-11, 59	d	43.8	54.5		
Ata03, TD8B, G-6, 23	d	42.3	55.6		

Table 5

Measurements of the lateral metapodials, phalanges and sesamoids of *Equus altidens* from Atapuerca TD8 (in mm). If one or several measurements could not be taken because a bone belonged to a juvenile, this is indicated in this and following tables by the indication juv. or juvenile.

Mc II, Mc IV, Mt II, Mt IV		DAPp	DTp	L				
Ata 2002, TD8B, G-10, 55	d	Mc II	>21.9	15.8				
Ata2002, TD8B, G-10, 36	s	Mc IV	19.7	14.4				
Ata2002, TD8B, F-11, 65	?	?	–	–				
Ata03, TD8B, G-5, 51	s	Mc IV	19.2	13.6				
Ata03, TD8B, G-15, 5	s	Mc IV	18.6	13.5				
				distal frag.				
Phalanx 2		1 (L)	2	3 (DTmini)	4 (DTp)	5 (DAPp)	6 (DTdf)	DAPd
Ata2002, TD8B, G-7, 95	s	43.2	32.9	43.5	45.8	29.2	43.5	25.6
Ata94, TD8, t27, H-16, 12	..	≈54.5	≈38.3	53.6	≥62.0	36.6	–	–
Ata2002, TD8B, G-7, 32	d?	≥44.4	40.3	28.6	38.6	–
Ata2002, TD8B, G-13, 9	d	51.9	–	48.4	54.5	–	49.6	27.6
Ata03, TD8B, G-5, 29	s	≥51.9	40.8	..	–	34.2	≥48.0	28.2
Ata03, TD8B, G-5, 42	s	44.4	32.4	38.1	≥46.3	29.6	42.1	26.5
Phalanx 3		1 (Lb)	2(Ld)	3 (DT)	4 (DTpf)	5 (DAPpf)	DAP (H)	6
Ata94, TD8, t28, G-17, 11	?	–	–	–	–	28.3	–	–
Ata03, TD8B, H-15, 7	?	juvenile	≈30	–	–	–	–	–
Ata03, TD8B, G-6, 15	s	>55.4	>56.9	–	51.6	26.3	44.1	48
Ata03, TD8B, G-15, 12	d?	55.6	53.5	≥63.1	44.8	27.9	≈41.5	53
Sesamoid behind phalanx 1		DAP	DAP'	DT	L			
Ata03, TD8B, G-4, 21	r	29.9	27.8	27.9	36.0			
Sesamoid-3		DAP	DT	L				
Ata2002, TD8B, F-10, 13	s?	15.8	46.0	12.9				

3.1.2. Description and comparison

The **lower molars, premolars and deciduous molars** have V-shaped linguaflexids, as is typical of the “stenoid” species of *Equus*, while the “caballoid” species have U-shaped linguaflexids. Two lower molars fit together and apparently are the M₁ and M₂ of the same individual (Fig. 3/2 and 3/3). The ectoflexid in the molars may or not enter the “isthmus” between the pre- and postflexid (fossid). There is no clear pli-caballinid, but the hypocones are angled at that place.

The M^{1/2} and P^{3/4} (Fig. 3/1) have small protocones that are roughly triangular with slightly convex lingual sides. There is a slight constriction anterior to the hypocone. The para- and meso-styles are rounded and do not have a groove.

Metric comparisons have been made for the upper cheek teeth. The protoconal indices have relatively low values (PI in the upper diagrams in Fig. 3), as is common in most fossil non caballoid species, while the values are higher in fossil and recent caballoid horses and in the recent hemiones. *Equus hydruntinus* seems to be intermediate in this respect. The sizes of the cheek teeth vary relatively little between the different species and the sizes from TD8 are compatible with most, save for the largest and smallest species.

The **third metacarpal** (Mc III; Fig. 4) is slender. Fig. 4 (left graph) shows that caballoid species tend to have robust metacarpals, while a group of species, including *E. wuesti*, *E. nalaikhensis*, *E. altidens*, *E. petraloniensis*, *E. hydruntinus* and *E. hemionus*, have slender metacarpals. The specimen from TD8 clusters with the latter group. *Equus suessenbornensis* is intermediate, but is much larger. The specimen from TD8 is close to those of *E. altidens*, *E. wuesti* and *E. nalaikhensis*, and is larger than those of the other slender species. Fig. 4 (right graph) shows another comparison, with various subspecies or samples of *Equus stenonis* and of a

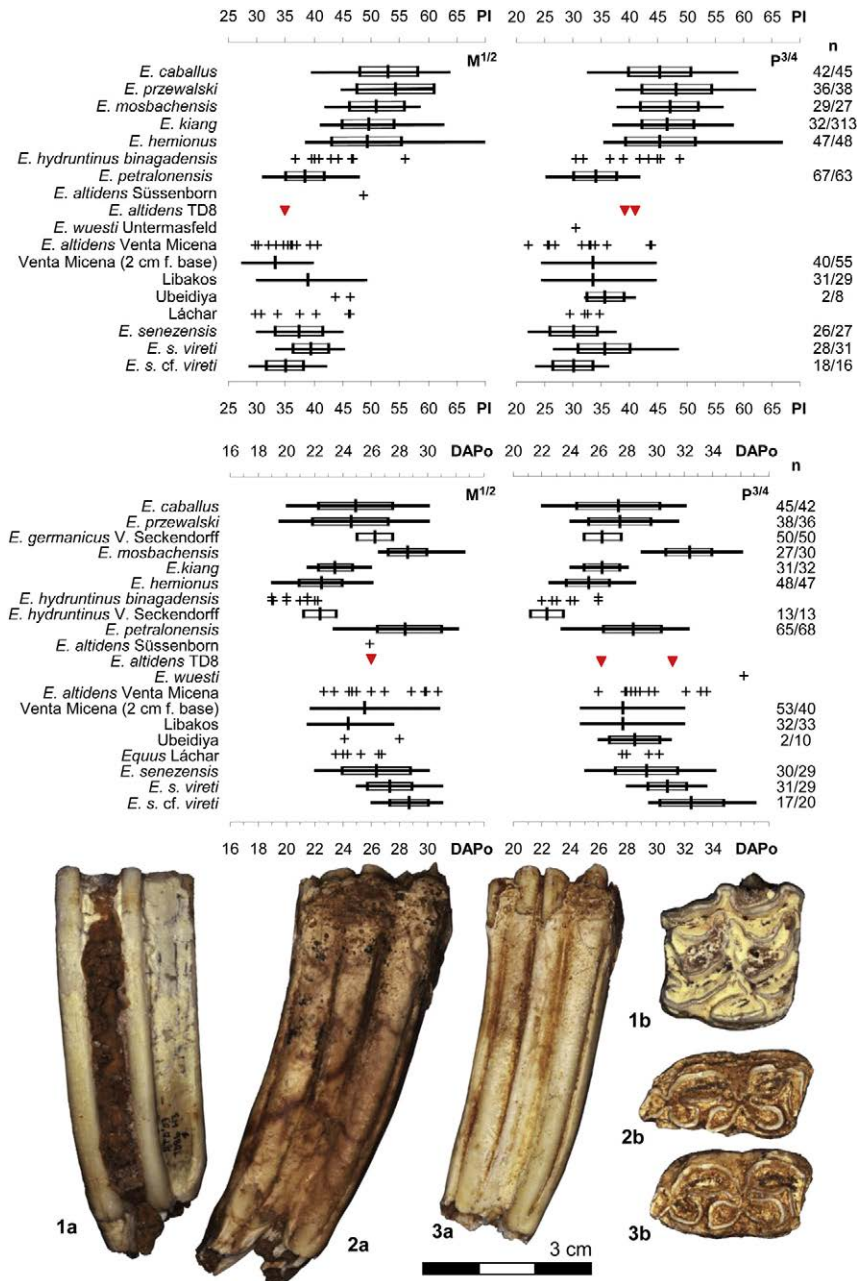


Fig. 3. *Equus altidens* from Atapuerca TD8: 1) Ata03, TD8B, H3, 1 – right P^{3/4}. a) buccal, and b) occlusal views. 2) Ata03, TD8B, G-6, 18 – left M₁: a) lingual, and b) occlusal views. Ata03, TD8B, G-6, 17 – left M₁: a) lingual, and b) occlusal views. Diagrams showing the occlusal length (DAPo) and protoconal index (PI) of the M^{1/2} and P^{3/4} of *Equus altidens* from Atapuerca TD8 compared to selected samples and species of *Equus*. Provenience of data: *E. caballus*, *E. przewalskii*, *E. mosbachensis*, *E. kiang*, *E. hemionus*, *E. stenonensis senezensis*, *E. stenonensis vireti*, *E. stenonensis cf. vireti* (all from Eisenmann, 1979), *E. germanicus* and *E. hydruntinus* from Villa Seckendorff (Forsten and Ziegler, 1995), *E. hydruntinus binagadiensis* from Binagady (Eisenmann and Kuznetsova, 2004), *E. petraloniensis* from Petralona (Tsoukala, 1989), *E. wuesti* from Untermassfeld (Musil, 2001), *Equus altidens* from Venta Micena (Marín, 1987; also the larger sample measured near the crown base is included), *Equus* sp. from Libakos (Steenma, 1988), Ubeidiya (Eisenmann, 1986), and *Equus* sp. from Láchar (Alberdi and Ruiz-Bustos, 1987).

group of samples, most of which have either been attributed to *E. stenonensis*, *E. altidens* or *E. cf. tabeti* (Eisenmann, 1986; Steensma, 1988; Alberdi and Palombo, 2013), and which is intermediate between *E. altidens* and *E. stenonensis*. The specimen from TD8 is much more slender than those of *E. stenonensis*, but is close to the largest and most slender specimens of the intermediate group, and it is close to *E. altidens*.

The first phalanx (Fig. 6) is relatively gracile. It is to be expected that the differences in proportions, which are noted in the metacarpals, are also seen to some extent in the phalanx. Similar comparisons have been made as in the metacarpal (Fig. 5), and

indeed the same patterns of gracile and robust forms is seen, but the separation is somewhat less clear. In part, this is possibly due to the mixing of anterior and posterior phalanges. However, separating phalanges in anterior or posterior, is likely to use robustness as a criterion, with some danger of circle reasoning, if later the results are used for intraspecific comparisons. In any case, for *Equus altidens* the anterior and posterior specimens are given separately. The specimen from TD8 is more gracile than the phalanges of the caballoid horses, *E. stenonensis* and *E. suessenbornensis*, it is close to those of *E. nailakhensis* and *E. wuesti*, it is in the upper ranges of the intermediate species and is in the range of *E. altidens*.

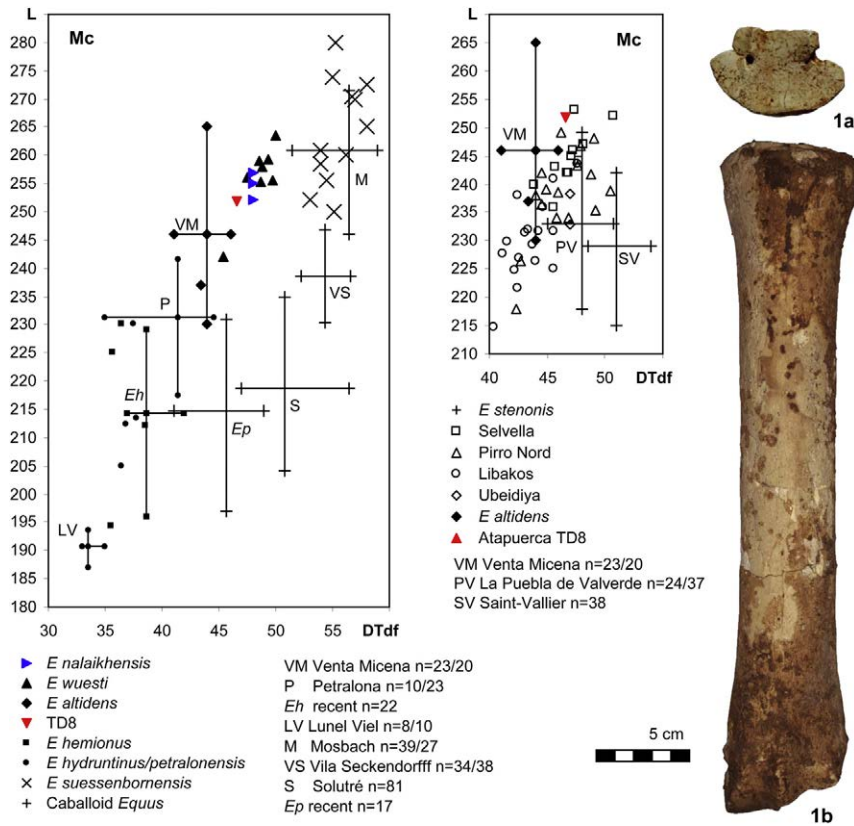


Fig. 4. The third metacarpal (Mc III) of *Equus altidens* from Atapuerca TD8: Ata2002, TD8B, G-10, 35 – right third metacarpal from TD8: 1a) proximal, and 1b) anterior views. Bivariate diagrams of the distal articular width (DTdf) and length (L) of the third metacarpal comparing a specimen from Atapuerca TD8 to those of selected Equidae. The upper diagram shows the presence of two well defined groups with robust and gracile metapodials. Provenance of data: robust cabaloid *Equus* from Villa Seckendorff (Forsten and Ziegler, 1995), Solutré (Prat, 1980), and Mosbach and *E. przewalskii* (Eisenmann, 1979); gracile *E. wuesti* from Untermassfeld (Musil, 2001), *E. nalakhensis* from Nalaikha (Eisenmann and Kuznetsova, 2004), *E. altidens* from Venta Micena (Marín, 1987) and Süssenborn (isolated specimen; Musil, 1969), *E. petraloniensis* from Petralona (Tsoukala, 1989), *E. minor* from Lunel Viel (LV) and *E. hydruntinus* from Lunel Viel and Binagady (isolated specimens) (both Eisenmann and Mashkour, 1999); and the intermediate *E. suessenbornensis* from Süssenborn (Musil, 1969), Ceyssaguet (Prat, 1980), Nalaikha (Eisenmann and Kuznetsova, 2004) and Semibalki (AHAPMR). The right diagram shows a series of samples that show a transition from robust to gracile: *E. stenonis vireti* from Saint Vallier and *E. s. cf. vireti* from La Puebla de Valverde (Eisenmann, 1979), *Equus* sp. from Ubeidiya (Eisenmann, 1986), Pirro Nord and Selvella (Alberdi and Palombo, 2013), and Libakos (TUC), and *E. altidens* from Venta Micena (Marín, 1987).

Other specimens, less important for the systematics of *Equus*, are not described here, but are listed in Tables 1–5.

3.1.3. Remarks on context and taxonomy

There are no very recent comprehensive reviews on European Pleistocene Equidae, but the published opinions (Azzaroli, 1990; Eisenmann, 1991; Guérin, 1996d; Alberdi et al., 1998; Forsten, 1999) differ markedly in the species recognized and their chronological distribution. It seems to be accepted that there are but few morphological features of taxonomical value and there is a long-standing consensus that the size and proportions of the metapodials and phalanges are of prime importance (Sickenberg, 1962; Forsten, 1973, 1999; Eisenmann, 1979, 1991; Alberdi et al., 1995), even though these are used in different ways. Forsten (1999) used mainly size and proportions of the phalanges and metapodials, but did not use indices because she assumed allometry to interfere with the skeletal proportions. However, the differences in size between these species are very modest and allometry is not likely to cause important differences in proportions.

The range chart in Fig. 5 uses the most commonly accepted names and/or those used by Forsten (1999) and in addition some more recently published names. Different interpretations of the ages of the localities and some different assignments of specimens or samples explain differences in temporal ranges with Forsten's Fig. 16.

The smaller stenonid species (right part of the range chart), are of relevance here. These species differ in robusticity of the metapodials and phalanges with *E. stenonis* on the robust end of variation and the geologically younger *E. altidens* and *E. hydruntinus* on the gracile end. Samples of intermediate age and intermediate degree of robustness have either been included in *E. stenonis* or in *E. altidens*. There are three proposals for the origin of *Equus altidens* (Van der Made, 2013):

- 1) Alberdi et al. (1995) proposed that it evolved from *E. stenonis* and the overall trend from robust to gracile, to some extent, supports the proposal of Alberdi et al. (1995). This is the case with the metacarpals and phalanges (Figs. 4–6), but also with the metatarsals. There is a problem here that the earliest samples with an intermediate degree of robusticity (as Gerakarou) are not after, but contemporaneous with robust *E. stenonis*, suggesting, that the two lineages overlapped in time. Gerakarou is the type locality of *Equus mygdoniense* and if the species with an intermediate degree of robusticity are all the same species, this would be an available name for them. In addition, there is also a smaller species with metapodials of intermediate robustness, which is either called *E. senzensis* or *E. stehlini*. The transition of the larger intermediate form (as present in Selvella, Libakos and Pirro Nord) to the gracile *E. altidens* (as in Venta Micena) may well have been conform Alberdi's model.

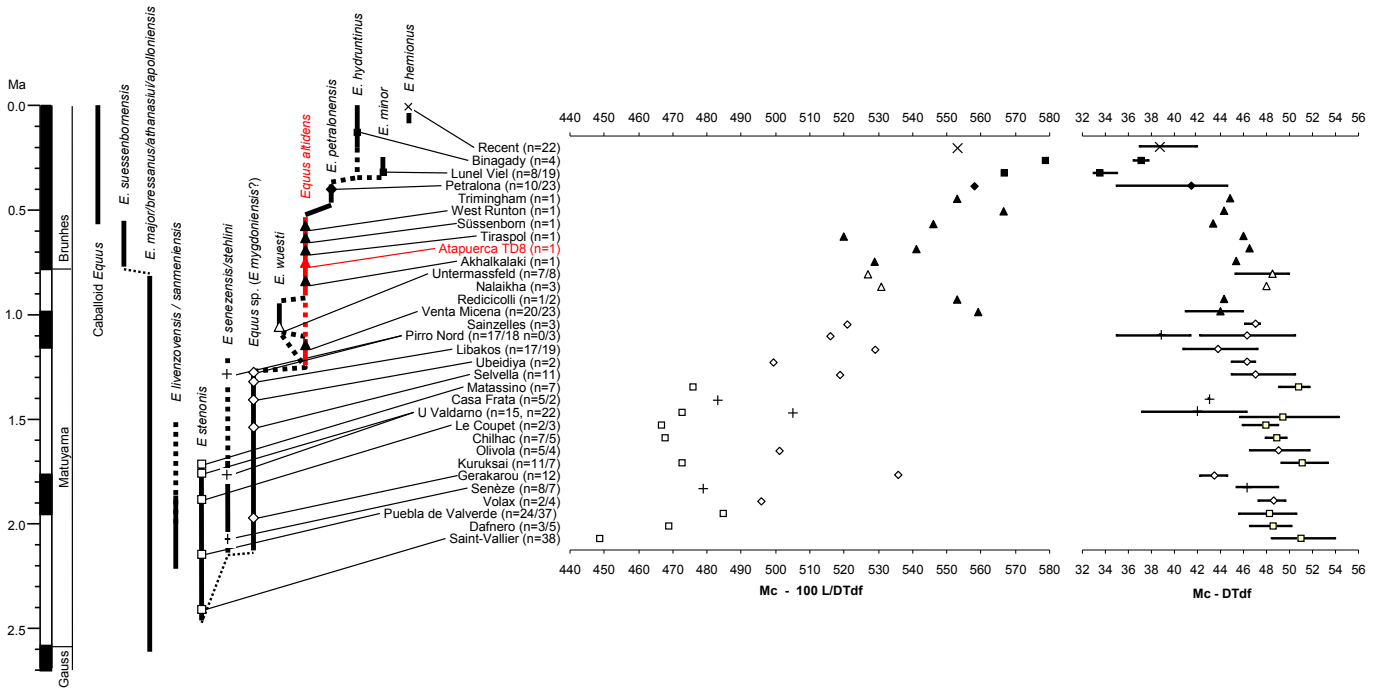


Fig. 5. The robusticity (100 L/DTdf; average values only) and distal width of the articular surface (DTdf; average and range) of the third metacarpal (Mc III) in the smaller stenonid horses. Provenance of data as in the previous figure and, in addition, from Forsten (1999) and Steensma (1988). The chronologic distribution of the European Pleistocene Equidae; systematics largely after Forsten (1999).

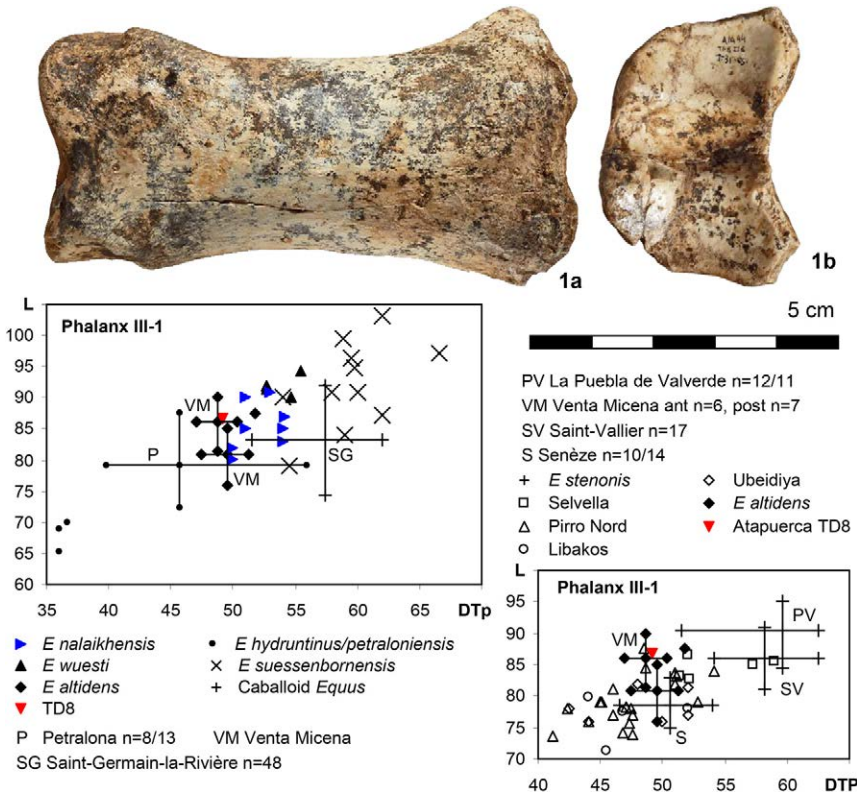


Fig. 6. The right first phalanx (III-1) of *Equus altidens* from Atapuerca TD8 – Ata94, TD8, t31, I-16, 65: 1a) dorsal, and 1b) proximal views. Bivariate diagrams of the proximal width (DTP) and length (L) of the first phalanx, comparing a specimen from Atapuerca TD8 to those of selected Equidae. The difference between robust and gracile equids is also noted, though not as clear as in the Mc (left upper diagram). Provenance of data: robust cabaloid *Equus* from Saint-Germain-la-Rivière (Prat, 1980), gracile *E. wuesti* from Untermaassfeld (Musil, 2001), *E. nalakhensis* from Nalakhka (Eisenmann & Kuznetsova, 2004), *E. altidens* from Venta Micena (Marín, 1987), *E. petraloniensis* from Petralona (Tsoukala, 1989), *E. hydruntinus* from Lunel Viel (Eisenmann & Mashkour 1999) and Arenero Santa Catalina (Madrid; MAN) and the intermediate *E. suessenbornensis* from Süssenborn (Musil, 1969), Soleilhac (Prat, 1980) and Tiraspol (Gromova & Dubrovo 1975). The right lower diagram shows the tentative transition of robust *E. stenonis* vireti from La Puebla de Valverde (Alberdi et al., 1997) and Saint Vallier (Prat, 1980), to more gracile *E. stenonis* senezensis from Senèze (Prat, 1980), to intermediate *Equus* from Ubeidiya (Eisenmann, 1986), Selvella (Alberdi & Palombo, 2013), Pirro Nord (Alberdi & Palombo, 2013), and Libakos (TUC), and to gracile *E. altidens* from Venta Micena (Marín, 1987).

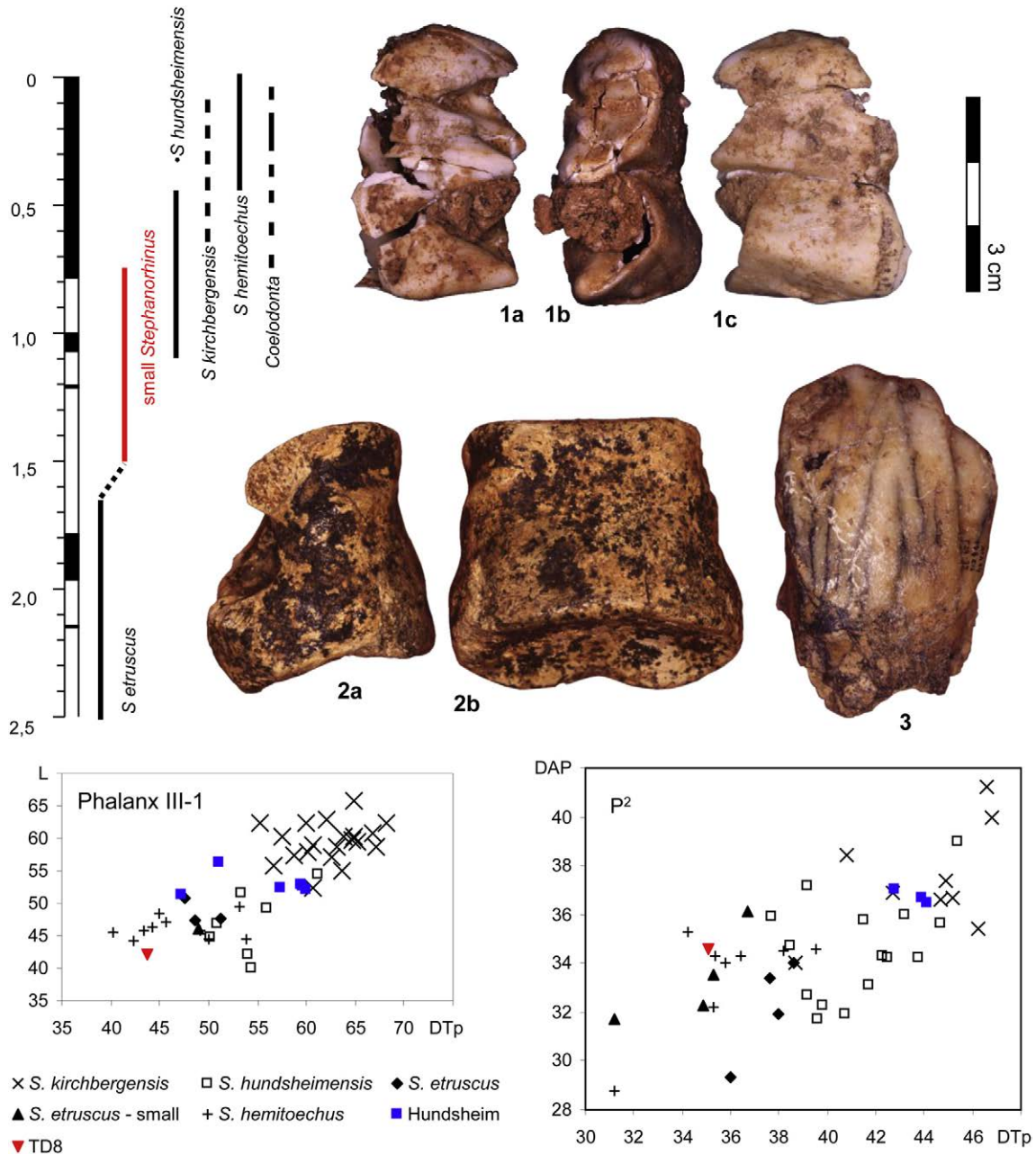


Fig. 7. *Stephanorhinus* aff. *etruscus* from Atapuerca TD8: 1) Ata2002, TD8B, F-12, 50 – D₃ dext.: a) lingual, b) occlusal, and c) buccal views. 2) Ata94, TD8, t28, I-16, 16 – Phalanx III-1 sin.: a) lateral, and b) dorsal views. 3) Ata94, TD8, t29, I-16, 35 – P² sin.: buccal view. The chronologic distribution of the European Pleistocene Rhinocerotidae (after Van der Made and Grube, 2010). *Coelodonta* is present mainly in glacials and *S. kirchbergensis* only in interglacials, these are not “dashed lines” but indicate discontinuous presence in Europe. Bivariate diagram of the proximal width (DTp) against length (L) of the first phalanx comparing the *Stephanorhinus* from TD8 to *Stephanorhinus* aff. *etruscus* from Atapuerca TD7/2 (IPHES), *S. etruscus* from the Upper Valdarno (IGF); *S. hundsheimensis* from Untermassfeld (IQW) and Mauer (SMNK); and from Hundsheim (NMW); *S. hemitoechus* from Arago (LPTUP), Bilzingsleben (FBFSUJ), Atapuerca TD10 (IPHES), and Azokh 1-V (MUB); *S. kirchbergensis* from Bilzingsleben (FBFSUJ). Bivariate diagram of the proximal width (DTp) against length (L) of the first phalanx comparing the *Stephanorhinus* from TD8 to *Stephanorhinus* aff. *etruscus* from Libakos (TUC), Huéscar 1 (MNCN), Atapuerca TDW4 (MB), and Cueva Victoria (MAC); *S. etruscus* from the Upper Valdarno (IGF); *S. hundsheimensis* from Vallonnet (MPRM), Dorn Dürkheim (FISF), Voigtstedt (IQW), Süßenborn (IQW), Mosbach (NMM), Soleilhac (MCP), Mauer (SMNK), Mosbach (NMM), and from Hundsheim (NMW); *S. hemitoechus* from Bilzingsleben (FBFSUJ), Murr (SMNS), Ehringsdorf (IQW), and the Rheinebene (NMM); *S. kirchbergensis* from Bilzingsleben (FBFSUJ), Ehringsdorf (IQW), Neumark Nord (FBFSUJ), and Gimbshelm (Rheinebene; NMM).

2) It has been proposed that *E. altidens* evolved from the African species *E. tabeti*, and that it dispersed shortly after 1.8 Ma to Europe (e.g. Guerrero-Alba and Palmqvist, 1997). In this view, the material from Ubeidiya (described by Eisenmann, 1986) also belongs to *E. tabeti* and fills the temporal gap between the last African representative of that species and the first European *E. altidens*. However, the horse from Ubeidiya is more robust than either *E. tabeti* or *E. altidens* and is similar to that of Pirro Nord, Selvella and Libakos. As a consequence, deriving *E. altidens* from

the population from Ubeidiya is in fact arguing for Alberdi's model. This also leaves a long time gap, of about 600 ky, between the African *E. tabeti* and the appearance of *E. altidens* in Europe. 3) A third alternative, is that *E. altidens* dispersed from Asia, where it evolved from *E. qingyangensis*, which is reported there to have ranged from 2.5 to about 1.2 Ma (Deng and Xue, 1999). In fact, this species is very similar to *E. nalaikhensis* and *E. wuesti* and all are as gracile but a little larger than *E. altidens*. It is not clear, whether *E. altidens* had size fluctuations in time, and whether *E.*

wuesti and *E. nalaikhensis* are large subspecies of *E. altidens* or contemporary larger species.

- 4) Yet another scenario would be deriving *E. altidens* from *E. livenzovensis*, which is much larger, but also relatively gracile. However, the latter is an earliest Early Pleistocene species and the scenario would imply a ghost lineage of nearly 1 My.

Given the apparent gradual transition within western Eurasia, a local origin of *E. altidens* by evolution seems most likely.

Most of the samples of *E. altidens*, included in Fig. 5, are of single specimens and therefore there is more apparent variation in the values, than in the means of large samples. *E. petraloniensis* and *E. hydruntinus* are still more gracile and are smaller than *E. altidens*. *Equus hydruntinus* is a possible descendant of *E. altidens* (Musil, 1969; Forsten, 1990) and *Equus petraloniensis* is intermediate between the two in metacarpal and phalanx biometrics (Figs. 3 and 4), as well as in age. *Equus altidens* became rare towards the end of its temporal range and it is possible that samples of insufficient size are assigned to this species, while they fit better *E. petraloniensis*, a species which is less widely known and cited. This might be the case with the material from Cúllar de Baza (Alberdi and Ruiz-Bustos, 1987). A gradual evolution from one to the other species is possible. A very small equid from Lunel Viel was described as *E. hydruntinus minor*, but is so much smaller that it could be a different species. *Equus hydruntinus* seems to be closely related to the living *E. hemionus* (Orlando et al., 2006), though it retains shorter protocones (Fig. 3).

Material from the lower levels of Gran Dolina has previously been assigned to “*Equus stenonis* aff. *granatensis*” “*Equus* sp. *stenonid* type”, “*Equus* cf. *altidens*” and finally “*Equus altidens*” (Maldonado Diaz, 1996; Van der Made, 1998a, 1999a; Rosell et al., 2010). The latter more precise classification is based on material from the more recent excavations, including the metacarpal figured here (Fig. 4), phalanx (Fig. 6) and dental material (Fig. 3/1–3). The linguaflexids of the lower cheek teeth indicate that this is a *stenonid* species (Fig. 3/2–3), which is supported by the short protocone (Fig. 3 upper diagrams). The metacarpal and phalanx (Figs. 4–6) indicates that it belongs to one of the gracile *stenonid* species, the size of the metacarpal indicates it is larger than *E. hydruntinus* and *E. petraloniensis*, and the size of the third phalanx that it is more likely *E. altidens* than *E. wuesti* or *E. nalaikhensis*. The material belongs to *E. altidens*.

If an evolution from *E. stenonis*, or at least from the equid from Libakos and Pirro Nord to *E. altidens* and, then to *E. petraloniensis* and *E. hydruntinus* is assumed, this has various implications. The first one concerns the temporal range of *E. altidens* and its application in biochronology. The localities with metapodials with an intermediate degree of robustness include Selvella, Libakos and Pirro Nord and the first with a really gracile *Equus*, that is widely accepted to belong to *E. altidens*, is Venta Micena (a large sample described as *E. granatensis* by Alberdi and Ruiz Bustos (1985) and Marín (1987)). Material from the nearby locality of Fuente Nueva 3 is assigned to the same species (Alberdi, 2010). If the model of evolution of *E. altidens* is correct, these localities in the Orce area are thus younger than Selvella, Ubeidiya, Libakos and Pirro Nord. Human presence in the Orce area at Venta Micena is disputed, but at Fuente Nueva 3 and Barranco León it is firmly established (Toro-Moyano et al., 2013). These localities are geographically and stratigraphically close and may be younger than Pirro Nord, where lithic industry confirms human presence (Arzarello et al., 2007, 2012) and Ubeidiya, where human presence has since long been recognized.

The type locality of *E. altidens* is Süssenborn, with an age of about 650 ka, based on biochronology, and in Elsterian sediments (stage 16). If material from Cúllar de Baza, already belongs to *Equus petraloniensis*, the transition to this species should be after 650 ka

(age of Süssenborn) and before 476 ± 24 ka (date for Cúllar de Baza; Ortiz et al., 2000). The temporal range of *E. altidens* is from about 1.2 Ma to some 0.55 Ma. The age of TD8 is slightly younger than 780 ka and fits in this range.

The remaining implication is that, if *Equus altidens* evolved in Europe from an equid with moderately gracile metapodials, present in Selvella, Libakos, Pirro Nord, and also Ubeidiya, it did not originate in Africa from the very gracile *E. tabeti*. The scenario, that around 1.8 Ma ago, *E. altidens* dispersed from Africa to Europe, together with *Homo* and other large mammals, including *Hippopotamus*, *Megantereon whitei* and *Pachycrocuta*, (e.g. Guerrero-Alba and Palmqvist, 1997), seems less likely.

3.2. Rhinoceros

Family Rhinocerotidae Gray, 1821

Genus *Stephanorhinus* Kretzoi, 1942

Stephanorhinus aff. *etruscus* (Falconer, 1868)

3.2.1. Material

Ata94, TD8, t28, I-16, 16 – Phalanx III-1 sin.

Ata94, TD8, t29, H-16, 52 – protocone of M^x.

Ata94, TD8, t29, H-16, 63 – buccal wall of right upper cheek tooth.

Ata94, TD8, t29, I-16, 35 – P² sin.

TD8 (A) – Fragment of phalanx III-3.

Ata2002, TD8B, F-12, 50 – D₃ dext.

Ata06, TD8B, H-4, 8 – D² dext.

The measurements of this material are given in Table 6. A taphonomic study assigned 9 fossils to the rhinoceros, representing a minimum of 2 individuals (Rosell et al., 2010).

Table 6

Measurements of the teeth and bones of *Stephanorhinus* aff. *etruscus* from Atapuerca TD8.

Upper cheek teeth	element	DAP	DAPb	DTa	DTp	H
Ata06, TD8b, H-4, 8	d D ²	>>38.6	–	–	–	–
Ata94, TD8, t29, I-16, 35	s P ²	34.6	30.5	31.6	35.1	45.6
Ata94, TD8, t29, H-16, 52	.. M ^x	–	–	–	–	–
Ata94, TD8, t29, H-16, 63	d D ^{3/4?}	36.7	–	–	–	–
Lower cheek teeth	element	DAP	DAPb	DTa	DTp	H
Ata2002, TD8B, F-12, 50	d D ₂	42.8	40.6	19.7	22.0	–
Phalanx III-1	DAPp	DTp	L	Ldors	DAPd	DTd
Ata94, TD8, t28, I-16, 16	s 31.3	43.8	42.0	30.6	21.0	≥35.9
Phalanx III-3	DApp	DAPpf	DTpf	DTp	L	
TD8 (A)	.. –	20.0	–	–	–	

3.2.2. Description and comparison

The teeth have the typical structure of rhinoceros teeth and the enamel is relatively smooth as in most species of *Stephanorhinus*. Of the European Pleistocene rhinoceroses (Fig. 7), the enamel in the cheek teeth of *Stephanorhinus hemitoechus* is clearly more and of *Coelodonta* much more crenellated.

The general size of the **teeth** is smaller than in *S. kirchbergensis* and the size of the **P²** (Figs. 7–3) in particular is smaller than in *S. hundsheimensis* and comparable to that of *S. etruscus*, *S. hemitoechus* and a small rhinoceros indicated here as *S. aff. etruscus* (Fig. 7 bivariate diagram).

A lower decidual molar has the paraconid and parastyloid separated (Fig. 7–1), which would suggest the tooth to be a D₂, but the tooth is far too large, so it is probably a D₃. Both valleys are V-shaped, if seen from the lingual side.

A **first central phalanx** (Phalanx III-1; Fig. 7-2) has the common rhinoceros morphology, and is smaller than the few specimens of *S. etruscus* and *S. aff. etruscus*, and is clearly smaller than *S. hundsheimensis*, which is represented by a better sample (Fig. 7 bivariate diagram).

3.2.3. Remarks on context and taxonomy

The material from TD8 is relatively small and as appears from the comparisons made above, its resemblances are in particular with *S. etruscus* and *S. aff. etruscus*, and in fact, material from the lower levels of Gran Dolina has been assigned previously to *S. etruscus* (Cerdeño, 1993; Van der Made, 1998a, 1999b, etc.). Barring nomenclatorial and other differences of minor importance, there are presently three opinions on the evolution and affinities of these rhinoceroses:

- 1) *S. etruscus* evolved into a small *S. aff. hundsheimensis* and then into *S. hundsheimensis* (Guérin, 1980, 1996c; Cerdeño, 1993; Mazza et al., 1993; Kahlke, H.D. 2001b; partially Fortelius et al., 1993).
- 2) *S. jeanvireti* evolved into the small rhinoceros, which is already *S. hundsheimensis*, while *S. etruscus* is a lineage that went extinct in western Europe (Lacombat, 2005, 2006, 2009; partially Fortelius et al., 1993).
- 3) *S. etruscus* evolved into the small rhinoceros, either called *S. etruscus* or *S. aff. etruscus*, while *S. hundsheimensis* is a different lineage (Van der Made, 2010; Van der Made and Grube, 2010; Giles Pacheco et al., 2011).

These three models have been discussed, and the species were found to differ in proportions in the tooth row and of the limb bones, but the relationships between them is still an open question (Van der Made, 2015b). The P² and first phalanx from TD8 are small and cluster best with *S. aff. etruscus* and *S. etruscus* whereas *S. hundsheimensis* has these elements large. However, in the size of other elements (not represented in TD8), there are also differences between *S. aff. etruscus* and *S. etruscus*. Whereas the scant material from TD8 is not resolving the relationship between these different rhinoceroses, its assignation to *S. aff. etruscus* is justified.

3.3. Pig

Order Artiodactyla.
Family Suidae.
Genus *Sus* Linnaeus, 1758
Sus scrofa Linnaeus, 1758

3.3.1. Material

Ata06, TD8B, G-4, 145 – left M¹.

A taphonomic study assigned 2 fossils to a suid, representing a minimum of 1 individual (Rosell et al., 2010).

3.3.2. Description and comparison

The M¹ (Fig. 8/3) is bunodont with four cusps, as is common in the D⁴ and M1-2 of the Suidae. One of the anterior cusps has three posterior lobes, these are the protopostcrista and the internal and external protoendocrista (terminology of Van der Made, 1996). Such a morphology occurs in the D⁴ and M¹⁻³ of nearly all Suidoidea, but not in other groups. The anterior cingulum is perpendicular to the long axis of the tooth, while it is oblique in the D⁴. Like in the genus *Sus*, the M¹⁻² is a little more elongate and the crests are more marked than in primitive Suidoidea. With a length of 18.2 mm and anterior and posterior width of 16.4 and 16.7 mm, the specimen is

within the metrical ranges of *Sus scrofa* and outside those of *Sus strozzi* (Fig. 5).

3.3.3. Remarks on context and taxonomy

At present two species of *Sus* are recognized in the Pleistocene of Europe: *Sus strozzi* and *Sus scrofa*. From the literature there appear to be two different views on their temporal distribution.

- 1) Faure and Guérin (1984, 1992) and Guérin (1996a) considered *Sus strozzi* to be present already at the beginning of the Pleistocene and to reach the beginning of the Middle Pleistocene, when it was replaced by *Sus scrofa*; both species were indicated to be present in zone MNQ 20. It should be noted that their Middle Pleistocene starts earlier than the present definition at 780 ka.

Faure and Guérin (1984) listed Ubeidiya and Tegelen as the youngest localities with *Sus strozzi*. The occurrence of *Sus strozzi* at Ubeidiya (Geraads et al., 1996; zone MNQ19) seems to be universally accepted, but is not in Europe. The record from Tegelen was indicated to be from zone MNQ 20, but rodents collected from a channel cut into in the sediments that yielded the large mammals, indicate that this is a much older locality (Freudenthal et al., 1976). As a result, the last European record of *Sus strozzi* listed by Faure and Guérin (1984) is in Mugello (Farneta Unit, about 1.5 Ma; Sardella et al., 1998).

Guérin and Faure (1997) and Guérin (1980) described and mentioned material from Untermassfeld, Vallonnet and Ceysaguet (all zone MNQ 20 or MmQ3) as *Sus scrofa*, though the sample from Vallonnet has been assigned to *Sus strozzi* (Moullé, 1998). The male lower canines in these samples are of the “verrucose type” as in *Sus strozzi* and unlike in *Sus scrofa*.

- 2) Van der Made and Moyà Solà (1989) and Van der Made (1990a, 1990b, 1997) gave range charts, where there is a gap in the available data between the last record of *Sus strozzi* and the first record of *Sus scrofa*. This gap corresponds to zone MmQ2 of Agustí et al. (1987) and Guérin's (1980) zones MNQ 18-19, which have a low density of fossil localities (see Van der Made, 2011a, fig. 1, and corresponding text). Nevertheless, suids are cited from Atapuerca TE9 (Rodríguez et al., 2011), Ceysaguet (Guérin and Faure, 1997), Pirro Nord (De Giuli et al., 1987), Selvella (De Giuli, 1987), and Mugello (Faure and Guérin, 1984) and are present in Peyrolles (fossils in NHM). These localities cover the whole range from the well known records of *Sus strozzi* from the Upper Valdarno (Olduvai subchron) till Untermassfeld and Vallonnet (Jaramillo subchron).

The living species, *Sus scrofa*, is first documented with certainty in Atapuerca TD6 (Van der Made, 1997, 1999a). Atapuerca TD6 is in sediments with inverse polarisation below the Santa Rosa palaeomagnetic event in level TD7 and therefore its age should be between 0.936 and 0.98 Ma (Parés et al., 2013). The ranges of the different species are indicated in Fig. 8. Though it is clear that there is a period with a poor suid record, the youngest samples with “verrucose” canines approach the oldest record *Sus scrofa*. The replacement of one species by the other must have been around the end of the Jaramillo Event and very fast, with no temporal hiatus in between. At present, there is no evidence of a period without Suidae in the Early Pleistocene of Europe.

In size and morphology, the specimen from TD8 fits best an M¹ of *Sus scrofa* and the age of the specimen fits the known temporal range of this species. This is one of the oldest records of the species.

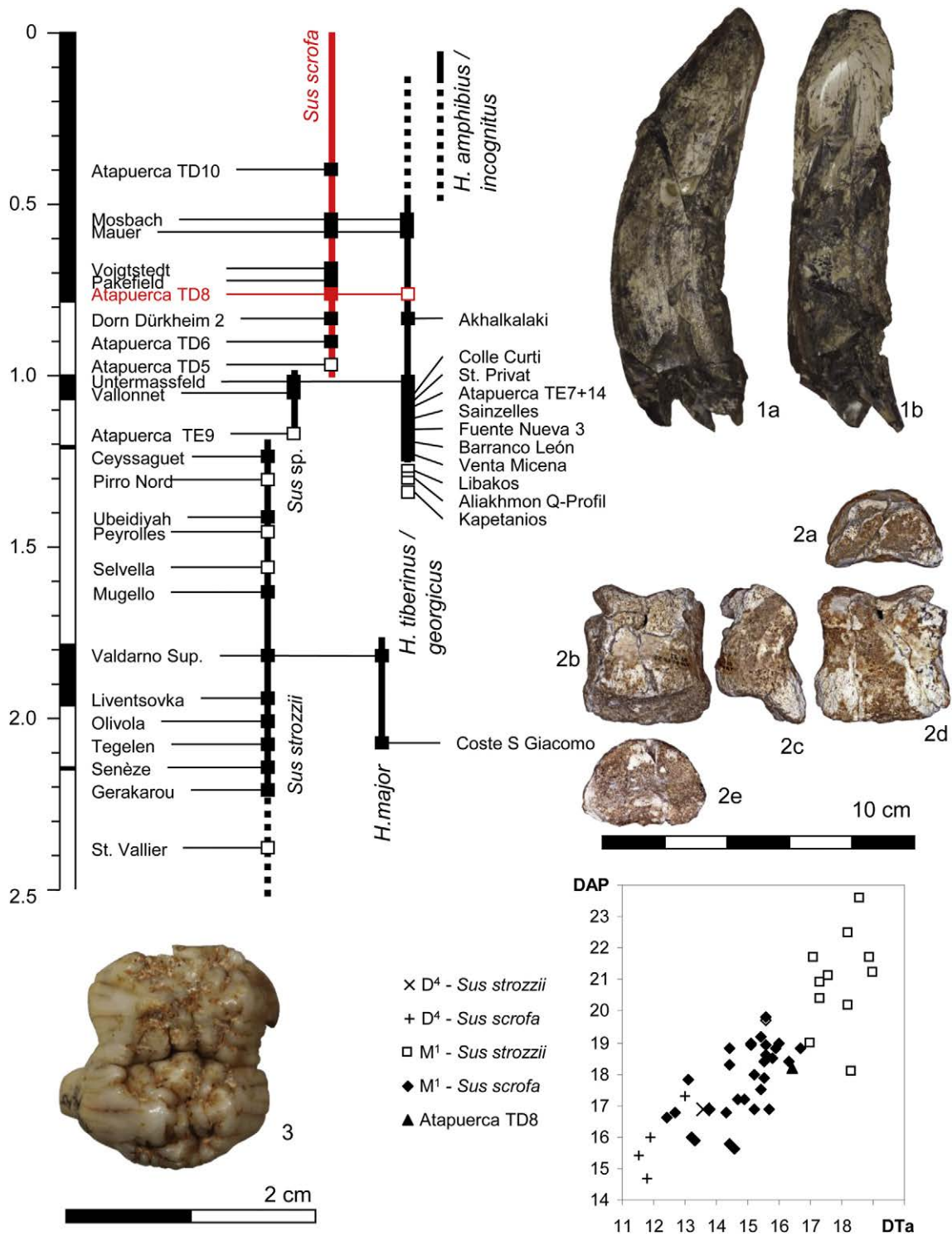


Fig. 8. The Suiformes from Atapuerca TD8: 1) Ata94, TD8, t29, I-16, 62 – right I²⁷ of *Hippopotamus* sp. from TD8: a) mesial, b) lingual, and c) labial views. 2) Ata2002, TD8b, G-7, 32 – right second central phalanx (phalanx III/IV-2) of *Hippopotamus* sp. from TD8: a) distal, b) dorsal, c) abaxial, d) plantar, and e) proximal views. *Sus scrofa* from TD8: Ata06, TD8B, G-4, 145 – left M¹ occlusal view (photograph). The chronologic distribution of the Pleistocene European species of *Sus* and *Hippopotamus*. Localities according to their approximate age, the presence of a species in a locality is indicated with a solid square, while tentative or possible (cf., aff., sp., ?) presence is indicated with an open square. Bivariate diagram of the width of the anterior lobe (DTa) against length (DAP): *Sus strozii* from: Gerakarou (AUT), Senèze (UCBL), Tegelen (NBC, MNB), Olivola (IGF), Valdarno (IGF, AVP), Il Tasso (IGF); and *Sus scrofa* from: Atapuerca TD8 & TD10 (IPHES), Koneprusy (PIMUZ, cast), Mosbach (NMM), Mauer (SMNK), Trimmingham (NHM), Megalopolis (AUT), Taubach (IQW), Pinilla del Valle (UCM), Kafzeh (IPH), Can Rubau (CIAG), Sakazia (GSM), Cueva de Saldarañao (ETSI), Némét Bogdan (HGSB), and recent *Sus scrofa* from Spain, the Netherlands and Germany (MNCN, ZMA, NBC, DGFSPV).

3.4. Hippopotamus

Family Hippopotamidae Gray, 1821
Genus *Hippopotamus* Linnaeus, 1758
Hippopotamus sp.

3.4.1. Material

Ata94, TD8, t29, I-16, 62 – right I^{2?}.

Ata2002, TD8b, G-7, 32 – right second central phalanx (phalanx III-2).

A taphonomic analysis assigned a single fossil to the hippopotamus, representing a minimum of one individual (Rosell et al., 2010).

3.4.2. Description and comparison

The **upper incisor** (Fig. 8/1) has a height of about 13–14 cm and a linguo-labial diameter of 34.2 and a meso-distal diameter of 30.9 mm. It is curved with the inner and outer radius of curvature of 7.5 and 11 cm, respectively. There is a labial enamel band with a width of about 14.3 mm near the tip and 2.1 mm near the base. The pulp cavity is open. It has a large apico-lingual facet, caused by occlusion with the lower incisor, which seems to be more typical of the second than of the first upper incisors of the hippopotami (which tend to have a medially oriented facet).

A **phalanx** (Fig. 8/2) is close in size and proportions to the first phalanx of *Stephanorhinus*, which is also present in the locality (Fig. 7/2). Its dimensions are: DAPp = 27.3, DTp = 40.2, L = 44.9, DAPd = –, DTd = 38.4. However it differs from the rhinoceros phalanx in a number of features. In side view, the proximal facet is more concave. In proximal view, the proximal facet is more square at the plantar side. In dorsal view, the proximal edge of the dorsal surface is convex towards proximal. In dorsal view, the distal articulation is not straight, but has a groove in the middle. In distal view, the plantar edge of the distal facet is not straight, but is elevated in the middle. The specimen is much more elongate and has other morphological differences with the rhinoceros second phalanx. Proboscidean phalanges are much larger. The first phalanx of a hippopotamus may be much more elongate, and the second shorter (R.D. Kahlke, 1997b, plate 56, figs. 15–24). However, the specimen is close in size and proportions to a phalanx IV-2 of the hand of a recent *Hippopotamus* in the MNCN. The plantar edge of the proximal side is a little more straight in the fossil, but otherwise the morphology fits.

3.4.3. Remarks on taxonomy and evolution

For a long time, the first appearance of *Hippopotamus* in Europe has been a point of discussion. Faure (1985) reviewed the West European hippos and noted that it is present in various localities of the Upper Valdarno, and that outside Italy, it is present in Sainzelles and other localities, believed then to be Middle Pleistocene in age. Presently Sainzelles is believed to be late Early Pleistocene. Since they would be so much older, Faure had doubts about the exact provenance (and age) of the Valdarno specimens.

Subsequently, other localities close in age to Sainzelles have also yielded hippos: Untermassfeld, Libakos, Aliakmon, Atapuerca TE7 and TE14, Venta Micena, Barranco León (Alberdi and Ruiz Bustos, 1985; Steensma, 1988; Gibert et al., 1992; R.D. Kahlke, 1997b, 2001b, 2006; Rodríguez et al., 2011). Rook and Martínez-Navarro (2010) considered the entry of *Hippopotamus* typical of the Colle Curti faunal unit (which correlates to the Jaramillo Event), but remained silent about the material from the Upper Valdarno (e.g. Blandamura and Azzaroli, 1977).

Bellucci et al. (2012, 2014a) reported on a hippo specimen from Coste San Giacomo. This would strengthen the case for *Hippopotamus* in Italy between some 2.1 and 1.8 Ma. However, the problem remains that all other European localities seem to be much younger. This

recalls the situation around the Mio-Pliocene transition, when a more primitive hippopotamus reached Italy, Spain and the South of France, but did not disperse further north, and went extinct after a relatively short time (Van der Made, 1999b). It is not impossible, that *Hippopotamus* reached Italy around 2–1.8 Ma, went extinct, and later, around 1.2 Ma, dispersed again into Italy and other parts of Europe.

There are different opinions on the taxonomy of the European species of *Hippopotamus*. They are seen as two species, the large early Middle Pleistocene *Hippopotamus major* (= *H. antiquus*) and the smaller early Middle to Late Pleistocene *H. incognitus* (Faure, 1985; Guérin, 1996b), or as two subspecies of the living *H. amphibius* (R.D. Kahlke, 1997b, 2001b, 2006). Alternatively, *H. antiquus* is believed to have given rise to *H. tiberinus*, the two coexisting for a while, while later the latter species coexisted with *H. amphibius* (Mazza, 1991).

Mazza (1991) believed the European hippos to have originated from *Hippopotamus gorgops*, which is known from Olduvai. Interesting in Mazza's model is that the early Middle Pleistocene *H. tiberinus* has a short brain case, and elevated orbits and occiput, in which it resembles the African *H. gorgops*. However, *H. major* from the Upper Valdarno does not have such an occiput. Since Mazza's paper, the age of the Upper Valdarno deposits is known to be older than previously believed and older than Olduvai Bed 1. A possible scenario is that *H. antiquus* originated from an African form that did not yet have the typical orbita and occipital morphology of *H. gorgops*, while later, *H. tiberinus* originated later from *H. gorgops* and dispersed into Europe. Skull morphology from Untermassfeld would support this scenario (R.D. Kahlke, 2001b, fig. 5, pls. 77–78; 2006, fig. 12). Again according to Mazza (1991), late Middle or Late Pleistocene European hippos do not have this morphology of the orbits and occiput, but resemble in these features the living species *H. amphibius*. They are also smaller. This would then represent another dispersal event from Africa to Europe in the late Middle or early Late Pleistocene.

Hippopotamus georgicus is known from Akhalkalaki by some limb bones Vekua (1986). It is a large hippo, like *H. tiberinus* and it is of the same age. In case of a synonymy, the name with priority is *H. georgicus*. However, considering that *H. amphibius* had a range stretching from Africa to mid-latitude Europe, it could be questioned, whether the European *H. tiberinus* is not a variety or subspecies of *H. gorgops*. The European hippos arose most probably from North African populations. The species *H. sirensis* has been defined on the basis of material from Tighenif (Ternifine, Palikao; see Pomel, 1896) and might be another name that has priority over *H. tiberinus*, *H. georgiensis* or *H. gorgops*. An extensive taxonomical study is necessary to solve this problem.

These species mainly differ in size, the elevation of the orbits and the position and morphology of the occiput. Incisors tend to increase their diameter from the tip to the base, and tend to continue growing. There are very few published data on phalanx size. For these reasons, the material from TD8 cannot be assigned to one of the European species or subspecies. Because of their age, these specimens are expected to belong to *H. tiberinus*, but more material is needed to confirm this.

3.5. Red deer

Family Cervidae Goldfuss, 1820
Genus *Cervus* Linnaeus, 1758
Cervus elaphus Linnaeus, 1758

3.5.1. Material

Ata94, TD8, t28, I-16, 9 – left P³ and fragment of left M^x.

Ata94, TD8, t28, G-17, 22 – shaft of right tibia.

Ata04, TD8b, G-5, 4 – distal part of the right scapula.

Ata94, TD8, t29, H-16, 59 – proximal epiphysis of the second phalanx, left of the axis of the foot, juvenile.

Ata94, TD8, t29, I/H-16, sc – distal part of the second phalanx, left of the axis of the foot.

Ata03, TD8b, I-9, 72 – first phalanx, right of the axis of the manus/pes, distal part.

Ata04, TD8b, G-14, 4 – proximal epiphysis of the second phalanx, left of the axis of the foot, juvenile.

Ata05, TD8b, F-13, 2 – second phalanx, right of the axis of the foot.

? Ata02, TD8b, H-8, 14 – tine of an antler.

? Ata94, TD8, t29, G-16, 59 – right calcaneum, juvenile.

? Ata94, TD8, H-16, 19 – left first central phalanx (phalanx III/IV-1), juvenile.

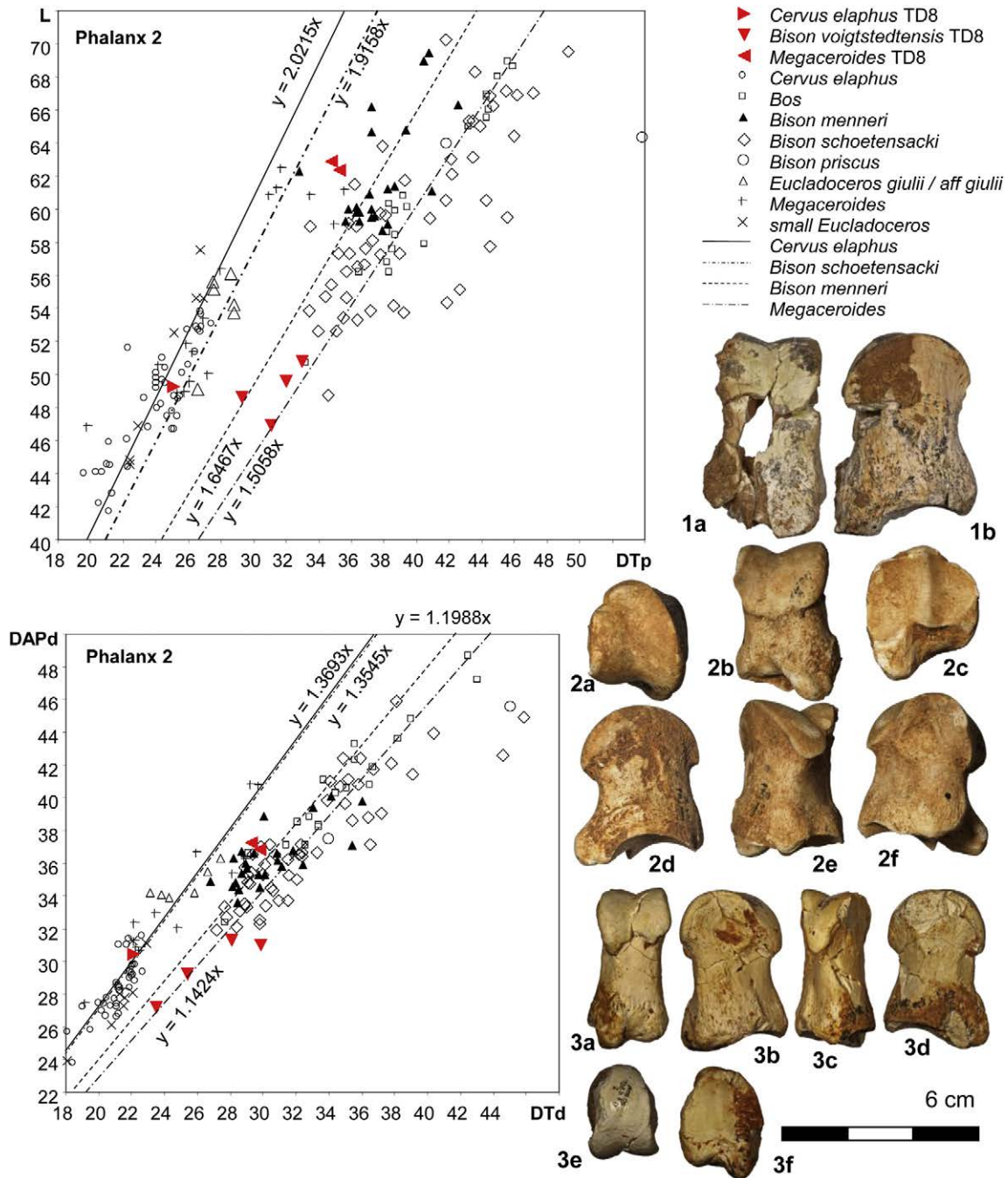


Fig. 9. The second phalanx of the larger ruminants from Atapuerca TD8: 1) Ata06, TD8b, G-3, 71 – left second phalanx of *Megaceroides solilhacus*: a) plantar, and b) abaxial views. 2) ATA06, TD8b, G-4, 38 – left second phalanx of *Bison voigtstedtensis*: a) distal, b) plantar, c) proximal, d) abaxial, e) dorsal, and f) axial views. 3) Ata05, TD8b, F-13, 2 – right second phalanx of *Cervus elaphus*: a) plantar, b) axial, c) dorsal, d) abaxial, e) distal, and f) proximal views. Bivariate diagrams comparing the length (L), proximal width (DTp), distal antero-posterior diameter (DAPd) and distal width (DTd) of the second phalanx of *Cervus*, *Megaceroides* and *Bison* from Atapuerca TD8 to: *Cervus elaphus* from Azokh V & VI (MUB) and Neumark Nord (FBFSUJ); *Bos primigenius* from Miesenheim (Monrepos), Torralba (MNCN), Neumark Nord (FBFSUJ), and Lehringen (HMV); *Bison menneri* from Untermassfeld (IQW); *Bison schoetensacki* from Akhalkalaki (IQW), Apollonia 2 (AUT), Konéprusy (NMP), Süßenborn (IQW), West Runton (NHM), Soleilhac (MCP), Blanzac-Soleilhac (NMB), Tsona (GSM), Mauer (SMNK), Bacton (NHM), Mundesley (NHM), Vértesszölös (HGSB), Bilzingsleben (FBFSUJ), and Azokh V (MUB); *Bison priscus* from Unkelstein (IPRFWUB) and Ortvala Klde (GSM); *Eucladoceros giulii* and *E. aff. giulii* from Untermassfeld (IQW) and Akhalkalaki (GSM); *Megaceroides* from Ubediya (HUJ), Cesi (IGF), Voigtstedt (IQW), Süßenborn (IQW), and Soleilhac (MCP); and small *Eucladoceros* from Tegelen (NBC), Olivola (IGF), and Il Tasso (IGF).

? Ata94, TD8, t28, G-16, 32 – left first central phalanx (phalanx III/IV-1), juvenile.

The measurements of this material are given in Table 7. A taphonomic study assigned 94 fossils to Cervidae indet., representing a minimum of 5 individuals (Rosell et al., 2010); part of this material is here assigned or tentatively assigned to the red deer.

3.5.2. Description and comparison

If seen from anterior, the P³ has the lingual side convex, as is the case in *Cervus* and unlike in *Dama*, *Megaceroides* or *Eucladoceros*. It is a little smaller than the *Megaceroides* P³ with which it has been compared and it is much smaller than the P³ of the large *Eucladoceros* from around the E-M Pleistocene transition (Akhalkalaki, Apollonia 1, Lakhuti, Dursunlu; GSM, AUT, PIN, MTA).

The scapula has the tuberosity slightly down turned as in *Cervus elaphus*, but not distinctly hooked (feature 1 of Lister, 1996). Metrically, the specimen is in the range of large *Cervus elaphus* as from Neumark Nord (FBFSUJ) and it is much smaller than in *Eucladoceros giulii* (H.D. Kahlke, 1997, table 61) and *Megaceroides* from Voigtstedt (IQW).

The shaft of a tibia is not very informative, but it indicates an animal the size of *Cervus elaphus*. Other bones are of juveniles (or a juvenile), their morphology and final size is not yet well established and as a consequence their assignment to this taxon is tentative.

Of four second phalanges, one is complete (Fig. 9/3). Lister (1996) gave one feature to discriminate between red and fallow deer phalanges: the emargination on the axial side of the dorsal edge of the proximal facet, which is present in *Dama* and absent in *Cervus*. It is absent here. This emargination is also faintly present in a specimen assigned to *Eucladoceros* aff. *giulii* from TD6. The complete specimen is narrow (Fig. 9 DTd–DAPd diagram) and elongate (Fig. 9 DTp–L diagram) and is in the metrical ranges of a large *Cervus elaphus* as from Neumark Nord, and in some of its measurements is slightly smaller than the specimens assigned to *Megaceroides* and *Eucladoceros* aff. *giulii*, and the fragmentary specimens are still smaller. Even the latter specimens are still clearly larger than those of *Dama* from TD8 (Tables 7 and 25).

A tine of an antler with part of the main beam, might represent the tine above the bez-tine. In *Cervus elaphus* this is the third tine (after the brow and bez tine), if it were *Dama*, it might be the homologous time, which in this case is the second tine (since no bez tine is developed). The latter option seems less likely, in view of the morphology of an antler from TE7, which is assigned to *Dama*.

3.5.3. Remarks on context and taxonomy

Cervus elaphus is well known from the Middle Pleistocene of western Europe, but it is cited or described from a few late Early Pleistocene localities, which would make its appearance nearly 300 ky older.

Cervus elaphus is cited from Mosbach 1 (Koenigswald and Tobien, 1987), which is correlated to the Jaramillo Subchron. The locality is in a sand pit, which has three fossiliferous levels. The oldest, Mosbach 1, is in a discontinuous unit, called Grobes Mosbach (grob = coarse, referring to the grain size of the sands). This unit is overlain discomformably by the Graues Mosbach (grau = grey, referring to the colour of the sands), which contains fossiliferous levels 2 and 3. The richest fauna is from Mosbach 2 and is mainly composed of “interglacial” species, with a possible age of 500–600 ka. In the younger Mosbach 3, “glacial” species are more prominent. Most fossils of the historic collections from Mosbach lack precise provenance data. Koenigswald and Tobien (1987) provided faunal lists for these three levels, but did not indicate on which fossils the lists are based. Material from Trlica in Montenegro has been assigned to *Cervus elaphus* and is probably

pre-Jaramillo in age (Bogićević & Nenadić, 2008; Derevjanko et al., 2012; Van der Made & Dimitrijević, in press).

At present, the oldest unambiguous West European records of *Cervus elaphus* are from Dorn Dürkheim (Franzen et al., 2000), Atapuerca TDW4, where an antler with bez tine was recovered (Bermúdez de Castro et al., 1999; figure on p. 90) and Happsburgh HSB3 (Parfitt et al., 2010). Dorn Dürkheim is below the Brunhes–Matuyama boundary. Happsburgh HSB3 is correlated to stage 21 or 25. Atapuerca TDW4 is well below the Santa Rosa palaeomagnetic event in level TD7, but still above the Jaramillo Event, and therefore its age should be between 0.936 and 0.98 Ma (Parés et al., 2013).

There have been marked size changes in European *Cervus elaphus* (Van der Made, 1998b, 2001, 2011b; Van der Made et al., 2014). The earliest representatives of this species were large and a large size is to be expected in TD8.

Cervus elaphus is relatively easy to recognize, since it differs in numerous morphological features from *Dama dama* (Di Stefano, 1995b; Lister, 1996). Several of the Early Pleistocene species of fallow deer size have been assigned to *Cervus*, by one author or another, but they tend to have *Dama* morphologies and in any case are clearly smaller. Asian deer like *Axis* and *Rusa* share some dental morphologies with *Cervus elaphus*. Also the early Pleistocene European *Cervus perolensis* has similarities to the red deer, but is clearly smaller; whether it belongs to this genus is not solved.

The giant deer tend to share many morphological features with *Dama*, rather than with *Cervus*. This is also the case with the shape of the lingual wall of the upper premolars. In this feature, the specimen from TD8 differs from the giant deer, it is also smaller than the P³ from *Megaceroides* and the large *Eucladoceros* from around the E-M Pleistocene transition. It is larger than the P³ of *Cervus perolensis*. The premolar and bones fit the red deer. The *Cervus elaphus* from TD8 is among the oldest from western Europe.

3.6. Giant deer I

Genus *Eucladoceros* Falconer, 1868.

Eucladoceros aff. *giulii* Kahlke, 1997.

3.6.1. Material

Ata2002, TD8b, G-12, 26 – right M₃.

Ata2002, TD8b, G-12, 10 – left P⁴.

Ata03, TD8b, G-5, 40 – right calcaneum.

? Ata06, TD8b, G-4, 115 – left P².

? Ata94, TD8, G-16, 19 – left P₃.

The measurements of this material are given in Tables 8 and 9, along with material of *Megaceroides* and with material which belongs to one of the two taxa. A taphonomic study assigned 31 fossils to a giant deer, representing a minimum of 2 individuals (Rosell et al., 2010); part of this material is included here in *Eucladoceros* and represents at least one individual.

3.6.2. Description and comparison

The M₃ (Fig. 10/1) has relatively smooth stylids on the lingual side, a wide overlap of the metapost- and entopreocrisid, there is no ridge connecting these crests (metaendocrisid), a clear “step” between the lingual sides of the second and third lobes. These are all features described by Lister (1996) as typical for *Dama* and different from *Cervus*, while some other features could not be observed. Such features are also common in *Eucladoceros*, *Megaceroides* and *Megaloceros*. The buccal interlobular column is well developed. The specimen from TD8 is very large and is larger than any M₃ of *Megaceroides*, and the majority of *Eucladoceros* and *Megaloceros* species, save for *M. giganteus*, and is similar in size to material

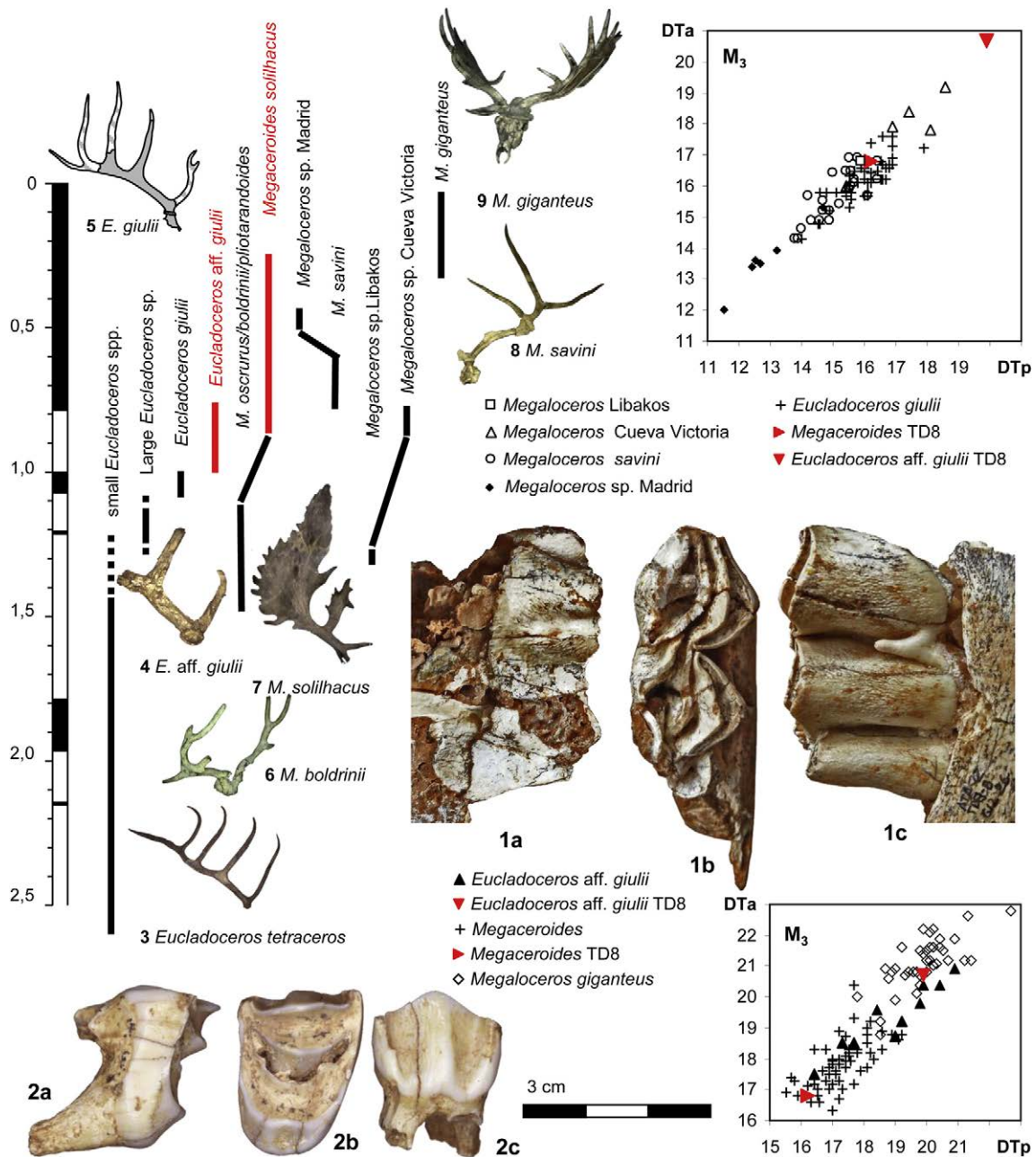


Fig. 10. Giant deer from Atapuerca TD8 and other localities: 1) Ata2002, TD8b, G-12, 26 – right M_3 of *Eucladoceros* aff. *giulii* from TD8: a) lingual, b) occlusal, and c) buccal views. 2) Ata2002, TD8b, G-12, 10 – Left P^4 of ?*Eucladoceros* aff. *giulii* from TD8: a) posterior, b) occlusal, and c) buccal views. 3) *Eucladoceros tetraceros* from Peyrolles: NHM 34409 left shed antler, lectotype, medial view. 4) *Eucladoceros* aff. *giulii* from Atapuerca Gran Dolina: ATA90, TD4 left shed antler, lateral view. 5) *Eucladoceros giulii* from Untermassfeld: reconstruction after H.D. Kahlke (1997). 6) *Megacerooides boldrinii* from Aliakmon, NCUA no number, oblique right-anterior view. 7) *Megacerooides solilhacus* from Soleilhac: MCP no number, left antler, medial view. 8) *Megaloceros savini* from Süßenborn: IQW 1964/1937, Süs 7075 skull fragment with left antler oblique lateral/inferior view. 9) *Megaloceros giganteus* from Steinheim: SMNS 15795 skull with antlers (oblique frontal view). The teeth are to scale, the antlers not. The temporal distribution of the giant deer of the European main land. Bivariate diagrams comparing width of the anterior (DTa) and posterior (DTp) lobes of the M_3 of the giant deer from TD8 to: *Megaloceros* sp. from Libakos (TUC), Cueva Victoria (MAC), and localities in the Madrid area (MSI, MAN, MNCN), *Megaloceros savini* from Voigtstedt (IQW), Süßenborn (IQW) and Mundesley (NHM); *Megaloceros giganteus* from Ireland (NHM) and the Rheinschotter (NMM); *Megacerooides* from Tiraspol (GIN), Voigtstedt (IQW, SMS), Süßenborn (IQW), Soleilhac (MCP), West Runton (NHM), and Mosbach (NMM); *Eucladoceros giulii* from Untermassfeld (IQW); and *Eucladoceros* aff. *giulii* from Akhalkalaki (GSM), Apollonia 1 (AUT), and Lakhuti II (PIN).

assigned here to *Eucladoceros* aff. *giulii* from other levels at Gran Dolina, Akhalkalaki, Apollonia 1 and Lakhuti (Fig. 10).

The P^4 (Fig. 10/2) has a weak postero-lingual cingulum and the lingual wall, if seen from anterior or posterior, is sinuous: near to the base of the crown it is convex and higher up it is concave. These features have been mentioned by Lister (1996) as typical of *Dama*, and different from *Cervus*. The tooth is large, close to the upper ranges of *Megacerooides*, but well within the range of *Eucladoceros* aff. *giulii*.

The P^2 has a lingual wall with a morphology similar to that described under the P^4 and metrically it is also in a similar position.

The P^3 has a small and backward placed metaconid, which is not really separated from the protoendocristid. The paraconid and parastylid are well separated in the upper part of the crown. There is no well individualized entoconid, but the crest at this place is transversely oriented and not fused to the metaconid. In some of these features the state is as in the fallow deer in others as in the red deer. In *Megacerooides* and *Eucladoceros*, the predominant states are

transversely oriented entoconids, that are not connected to the metaconid, but exceptions occur, while well separated paraconids and parastylids are not uncommon (depending on the species). In size, the specimen is large as in *Megaceroides* and *Eucladoceros* aff. *giulii*; it is relatively long for its width, especially compared to *Megaceroides*.

A **calcaneum** is large. It is longer than 17 specimens of *Megaceroides* from Voigtstedt, Süssenborn and Petralona, but is in the range of 13 specimens from Akhalkalaki (AUT) and Apollonia 1 (AUT).

3.6.3. Remarks on context and taxonomy

Fig. 10 gives the temporal distribution of the giant deer species of the main land of Europe (after Van der Made and Tong, 2008; Van der Made & Dimitrijević, in press). Insular species are not considered here. What is indicated here as “small *Eucladoceros* spp.”, includes *E. tegulensis*, *E. senezensis*, *E. tetraceros* and *E. dicranios*. H.D. Kahlke (1997) named the much younger species *Eucladoceros giulii* and included in it material from type locality Untermassfeld, and from Würzburg-Schalksberg, Selvella, Pirro Nord, Sainzelles and Venta Micena. Later material from the lower units of Atapuerca Gran Dolina, and Akhalkalaki, Apollonia 1 and Vallonnet was also assigned to this form (Van der Made, 1998a, 1999a; Van der Made, et al., 2003). Whereas bones or teeth of these samples are clearly larger than those of the older and “smaller *Eucladoceros*”, these samples are not homogenous and many have teeth that are larger than the teeth of *E. giulii* (Fig. 10), while this is not necessarily true for the bones (eg. Fig. 11). This points to different proportions, not just size differences. It seems that *E. giulii* is from the Jaramillo event (Untermassfeld, Vallonnet), while there is a large form that seems to be older (Venta Micena, Trlica) and another large form that is younger (Atapuerca, Würzburg-Schalksberg, Akhalkalaki, Apollonia 1, and possibly Lakhuti). These three forms share slender metapodials and a generally a large size, the first has an antler with a very high first bifurcation (Van der Made & Dimitrijević, in press) and the latter species has by far the biggest teeth.

Initially, the material from the lower part of the sequence at Gran Dolina was assigned to *Eucladoceros giulii* (Van der Made, 1998a, 1999a). This was mainly based on a metacarpal from TD4. In fact there is a similar metacarpal from this or an even older level from an older excavation. The material from TD8 is but few. It has a morphology that is typical of the giant deer in general. The M_3 is clearly larger than the majority of the giant deer; it is in the upper range of the large *Eucladoceros* aff. *giulii* and well within the ranges of *M. giganteus*, the largest of all. Though with the few specimens available, it is difficult to formally exclude the latter species, but because of its much younger age, it is unlikely to be present in TD8. The record from the lowermost Middle Pleistocene of TD8 represents the youngest well dated record of *Eucladoceros*.

According to metacarpal length, the species of TD8 is the tallest species of *Eucladoceros* (Van der Made & Dimitrijević, in press, fig. 14). *Eucladoceros giulii*, of which the skeleton is relatively well known (Kahlke, 1997), is only a little less tall. *Megaloceros giganteus* had shorter but wider metapodials, while the radius was much longer (Martin, 1987), it must have been taller than any *Eucladoceros* species and certainly more heavy. The metapodials of *Sinomegaceros yabei* were nearly as long and robust as those of the species from TD8 (Van der Made and Tong, 2008, fig. 22). Most species of elk were still larger. In any case, the *Eucladoceros* species of TD8, was one of the tallest species of deer that ever lived.

3.7. Giant deer II

Genus *Megaceroides* Joleaud, 1914
Megaceroides solilhacus.

3.7.1. Material

Ata2002, TD8b, G-7, 93 – right mandible with P_2 - M_3 .

Ata2002, TD8b, G-7, 91 – first phalanx, left of the axis of the manus/pes.

Ata06, TD8b, G-04, 113 – first phalanx, left of the axis of the manus/pes.

Ata06, TD8b, G-3, 48 – second phalanx, left of the axis of the manus/pes.

Ata04, TD8b, G-3, 71 – second phalanx, left of the axis of the manus/pes.

? Ata94, TD8, I-17, sc – left astragalus.

? Ata94, TD8, t28, G-17, 4 – left astragalus.

? Ata03, TD8b, G-12, 9 – metacarpal (s/d?), distal part.

? Ata03, TD8b, G-16, 16 – first phalanx, right of the axis of the manus/pes.

? Ata04, TD8b, F-14, 10 – first phalanx, left of the axis of the manus/pes.

? Ata04, TD8b, G-5, removed – metacarpal (s/d?), distal part.

? Ata05, TD8b, H-3, 34 – distal articulation of metapodial (juvenile), right of the axis of the manus/pes.

? Ata05, TD8b, H-3, 49 – distal articulation of metapodial (juvenile), left of the axis of the manus/pes.

The measurements of this material are given in Tables 8 and 9, along with material of *Eucladoceros* and with material which belongs to one of the two taxa. A taphonomic study assigned 31 fossils to a giant deer, representing a minimum of 2 individuals (Rosell et al., 2010); part of this material is included or tentatively included here in *Megaceroides* and represents at least one, tentatively at least two individuals.

3.7.2. Description and comparison

The **mandible** (Fig. 12) is badly damaged and its degree of pachyostosis cannot be established; however, all cheek teeth are in place.

The M_3 (Fig. 12) has lingual stylids that are not very strongly developed, no connecting ridge between the ends of the metapost- and entopreocrisid (not even near the base of the metaconid, what can be seen very well because this cusp is broken off), there is a faint ridge on the lingual side (feature 12), but no cuspule or cingulum on the lingual side of the third lobe. These are features given by Lister (1996) to separate teeth of *Dama* and *Cervus*. In most features, the state is as in *Dama*, but not in feature 12. The latter feature occurs also in *Megaceroides* and *Megaloceros*, but is not common (or does not occur at all) in *Eucladoceros*. The size of the M_3 from TD8 is much smaller than that of the one assigned to *E. aff. giulii* (Fig. 7), but it is in the range of *E. giulii*. It is close to the lower range of *Megaceroides* and the upper of *M. savini*.

The M_1 is in a bad state, but the M_2 (Fig. 12) has a morphology similar to that of the M_3 . Whereas the M_3 was damaged, here it can be observed that there is only moderate overlap of the metapost- and entopreocrisid and there is a “pouch” between the ends of the metapost- and entopreocrisid (feature 10), both more typical of *Cervus*. These two features are a difference with the isolated M_3 , which is here assigned to *Eucladoceros* aff. *giulii* (Fig. 10/1).

The P_4 (Fig. 12) has the entoconid well connected to the hypoconid and oriented more transversely, the lingual opening of the fossid between the entoconid and hypopostocrisid is very shallow, no anterior cingulum. These are again Lister's (1996) features and some of them are like in *Cervus*. The metaconid of the P_4 does not have any trace of a metapreocrisid and the anterior fossid is wide open lingually; the P_4 is not “molarized”. A “molarized” P_4 has a metapreocrisid, which reaches the paraconid and which closes the anterior fossid. The hypoconid sticks out buccally and there is a relatively well developed vertical groove on the buccal side where the protopostocrisid reaches the hypoconid.

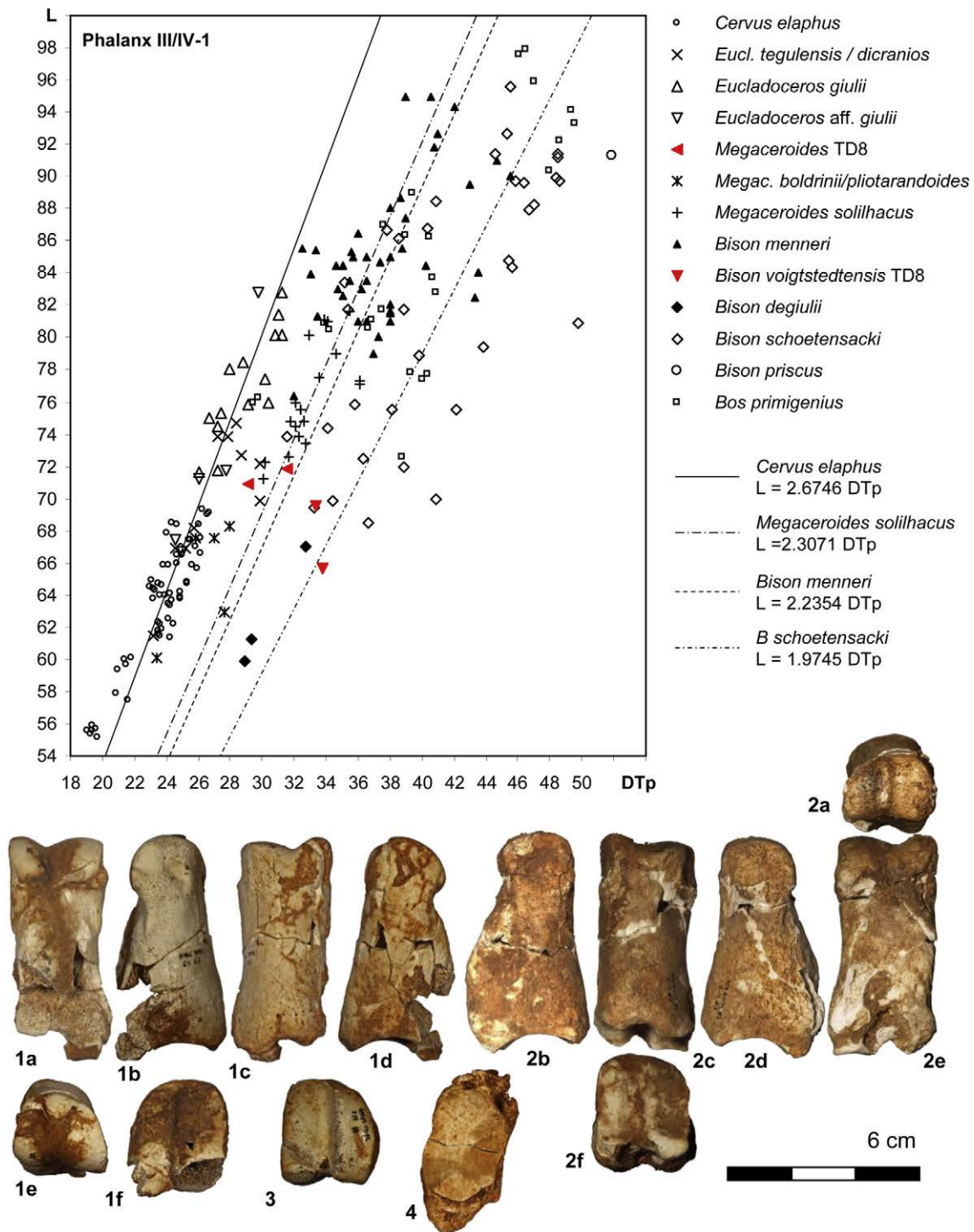


Fig. 11. The first and third phalanx of the larger ruminants from Atapuerca TD8: 1) Ata06, TD8b, G-04, 113 – left first phalanx of *Megaceroides*: a) plantar, b) abaxial, c) dorsal, d) axial, e) distal, and f) proximal views; 2) right first phalanx of *Bison*: a) distal, b) axial, c) dorsal, d) abaxial, e) plantar, and f) proximal views; 3) Ata04, TD8b, F-14, 10 – right first phalanx of *Megaceroides*, proximal view; 4) Ata06, TD8b, G-4, 41 – left third phalanx of *Bison*, proximal view. Bivariate diagrams comparing the length (L) and proximal width (DTp) of the first phalanges from Atapuerca TD8 with: *Cervus elaphus* from Neumark Nord (FBFSUJ); *Eucladoceros tegulensis* from Tegelen (NMMaa) and *E. dicranios* from Il Tasso (IGF); *Eucladoceros giulii* from Untermassfeld (H.D. Kahlke, 1997), *Eucladoceros aff. giulii* from Atapuerca TD4 and TD7 (MB, IPHES) and Apollonia 1 (AUT); *Megaceroides boldrinii* from Ubeidiya (HUJ); *Megaceroides solilhacus* from Voigtstedt (IQW), Süssenborn (IQW), Soleilhac (MCP) and West Runton (NHM); *Bison menneri* from Untermassfeld (Sher, 1997), *Bison degiulii* from Pirro Nord (IGF); *Bison schoetensacki* from Akhalkalaki (GSM), Apollonia 1 (AUT), Süssenborn (IQW), Soleilhac (MCP), Mauer (SMNK), Vérteszölös (HGSB), and Bilzingsleben (FBFSUJ); *Bison priscus* from Unkelstein (IPRFWUB); and *Bos primigenius* from Miesenheim (Monrepos), Neumark Nord (FBFSUJ), Lehringen (HMV), and Can Rubau (CIAG).



Fig. 12. The right lower cheek teeth of *Megaceroides solilhacus* from Atapuerca TD8 (Ata2002, TD8b, G-7, 93): a) lingual, b) occlusal, and c) buccal views.

In the *Eucladoceros* species that were checked, the entoconid connection and the alignment of the entoconid in the P_4 tends to be different from the TD8 premolar and more like in *Dama*. In *Eucladoceros* the molarization is variable, but in *E. giulii*, the non-molarized type is by far the most common, while in the large *E. aff. giulii* (also present in TD8), this is the other way around. In *Eucladoceros*, there is a well developed groove on the buccal wall and the hypocone sticks out buccally as in TD8. Overall, the specimen from TD8 differs from its homologue in *Eucladoceros*.

Most *Megaloceros* species have P_4 that are not molarized, but *M. giganteus* has nearly always a molarized P_4 . *Megaloceros giganteus* has a groove on the buccal wall and a prominent hypoconid, like in TD8, but in the older species of this genus, the hypoconid is less prominent and the groove is absent. In one way or another the P_4 of the *Megaloceros* species differ from the one from TD8.

In the *Megaceroides* samples checked, the entoconid morphology of the P_4 is variable and sometimes is more “*Dama*-like” than in the specimen from TD8. The hypoconid and its preceding vertical groove on the buccal wall are well developed. In the *Megaceroides* sample from Süssenborn, which is only slightly younger than TD8, the P_4 is predominantly non-molarized, but the younger samples tend to have molarized premolars. The P_4 from TD8 fits thus best the somewhat older samples of this genus.

The P_3 (Fig. 12) has the entoconid fused to the hypoconid and transversely oriented. The paraconid and parastyloid are not well separated. The lingual opening of the posterior fossid is shallow. These morphologies predominate in the giant deer.

The P_2 (Fig. 12) has a moderately high crown, but its buccal wall is not as flat as in *Cervus*. The parastyloid is very well developed, but

there is no trace of a paraconid. In *Eucladoceros giulii*, often a small paraconid is developed and this also tends to be the case in *Megaloceros*.

Some **first phalanges** (Fig. 11/1 and 11/3) are robust and similar in size to some phalanges from TD8, that are assigned here to *Bison* (Fig. 11/2 and bivariate diagram). These phalanges have the following features described by Heintz (1970) for separating Bovidae and Cervidae: a rectangular facet for the abaxial sesamoid (feature a), in proximal view no deep fossa in the middle below the proximal articular surface (feature b), no clear proximo-axial tuberosity on the dorsal surface (feature d), while it is not clear what was meant with feature c. Features a and d are as in Bovidae and b is as in Cervidae. However, other features might serve to separate these phalanges from those of the Bovini (including *Bison*). The first phalanges from TD8 have a distal articular surface that is relatively high and narrow. If seen from distal, the lower edge of this surface slopes from the furrow in the middle downwards towards the axial and abaxial borders. In the Bovini, this surface is lower and its lower edge frequently curves up near the axial and abaxial edges. The furrow in the middle of the distal facet is sharp, while in the Bovini it appears more wide (open V-shaped against U-shaped). Where preserved, the facets for the sesamoids are well developed. In the Bovini, these tend to be low and may be very badly developed. At the axial side of the plantar surface, there is a relatively well developed crest. Such a crest is usually more prominent in the Bovini than in the Cervidae. There is much variation in the proportions and size of the bison phalanges. In general, *Bison menneri* has phalanges that are larger and on average more robust than in the giant deer, and those of *Bison degiulii* and *Bison schoetensacki* and especially those of *Bison priscus* are still more robust. In all, the morphology looks more cervid.

The first phalanges, in which length could be measured, are more robust than in *Eucladoceros*, but correspond to the proportions and size in *Megaceroides solilhacus* (Fig. 9).

Even the best preserved **second phalanx** (Fig. 9/1) is in a bad state, but what is left of the proximal articular surface is high. If seen from the proximal side, the plantar-axial process is not reduced as in bovids and there is no clear gully in the middle of the post articular plateau (features of Heintz, 1970). In general, the post articular plateau projects more proximally. This morphology is more like in Cervidae than in Bovidae. For a cervid, the two more complete second phalanges look very stout and this is confirmed by the measurements. The distal articular surface is wide and both specimens are in the overlap of *Bison menneri*, the most gracile bison, and *Megaceroides*, one of the most robust deer (Fig. 9). Compared to the length, again the width is great. Especially length and distal width are much larger than the specimens of *Eucladoceros*, with which they are compared here. The sample of *Bison menneri* forms two clusters, which could be interpreted as phalanges of the pes and manus. Similarly, the specimens from TD8, assigned here to a giant deer, could be interpreted as phalanges of the pes of *Bison*, while four other specimens from TD8, assigned to *Bison*, could be interpreted as being from the manus. However, if this were the case, the range of variation of the length of the phalanges from TD8 would be much greater than that of *B. menneri*. All this points to the larger phalanges from TD8 to belong to *Megaceroides*.

The **astragalus** is represented by two specimens. They are tentatively included in this species, because they are in the lower metrical range of twelve specimens of the large *Eucladoceros aff. giulii* from Akhalkalaki (GSM) and Apollonia (AUT) and in the ranges of over thirty specimens of *Megaceroides* from Süssenborn (IQW) and Petralona (AUT).

3.7.3. Remarks on taxonomy and evolution

Different opinions have been published on the systematics of *Megaceroides*. Such deer have been placed in *Megaloceros* (e.g. Azzaroli, 1953; Lister, 1993; Van der Made, 2001), in *Praemegaceros* (e.g. Kahlke, 1965b; Vislobokova, 1990) or in *Megaceroides* (Azzaroli and Mazza, 1992; Abbazzi et al., 1999), but after Hadjiouis (1990) argued that type species of *Megaceroides algericus* is not related to the European species, these have been placed predominantly in *Praemegaceros* (e.g. Pfeiffer, 1999; Abbazzi and Lacombat, 2005; Croitor, 2006). It is not the intention to discuss this issue here, but the widened pedicle is a synapomorphy of *M. algericus* and the European species of this genus and separates the genus from other giant deer.

The number of species in this genus from the European mainland is another issue. Possibly most species are recognized by Croitor and Kostopoulos (2004) and Croitor (2006): three subgenera with five continental species, having overlapping temporal and geographic ranges. Croitor (2011) presented a model in which initial vicariant speciation occurred and in which later differences in antler morphology account for different ecologies causing reproductive isolation of three different lineages, so that three species could co-exist in the same locality. Generally several species are recognized (Vislobokova, 1990; Lister, 1993; Abbazzi, 1995; Delpech and Guérin, 1996). See also the discussion on synonymies by Vislobokova (2012).

Excluding the insular endemics, *Megaceroides* is the genus that shows least morphological and metrical variation of all the giant deer. The main differences are found in: 1) the progressive reduction of the brow tine, from large to a little knob and completely absent; 2) a later reduction of the second tine; 3) the distal part of the antler is branching in the older samples and palmate in the geologically younger samples (Azzaroli, 1953; Azzaroli and Mazza, 1993; Abbazzi, 1995; Croitor, 2006). The reduction of the second tine lags behind the reduction of the brow tine (when the brow tine is small or completely gone, the second tine still tends to be relatively large), and the appearance of the distal palmation is very imprecisely documented, but is always found in antlers with very small or no brow tines. There are few or no publications comparing the postcranials of the different forms, but maybe the earliest representatives of the genus were smaller. *Megaceroides* is taken here as having a primitive species with a large brow tine and a branching antler (known under the names: *M. pliotarandoides*, *M. obscurus*, *M. boldrinii*), and a more evolved species with a browtine that is reduced to a small knob or that is lacking all together, and with a distal palmation (for which *M. solilhacus* is the oldest name) (Van der Made, 2015a,b).

Material from the lower part of the Gran Dolina sequence has been previously assigned to *Praemegaceros* sp. by Azanza and Sánchez (1990) and to *Megaloceros solilhacus* (Rodríguez et al., 2011). The latter identification is based in part on the tooth row, which is described here. As appears from the description and comparison, the cheek teeth show morphological and metrical differences with the species of *Megaloceros* and *Eucladoceros*. The first and second phalanges are robust as in *Megaceroides* and differ in this from *Eucladoceros*. As far as known, the earlier *Megaloceros* species had gracile metapodials (Van der Made and Tong, 2008) and first phalanges. The bones and teeth described in this section belong to a large deer, but differ in size from the smaller *Eucladoceros* species and from *Megaloceros* spp. from Madrid and from Cueva Victoria. The material from TD8 is assigned here to *Megaceroides*.

Material from a not specified level of the sequence at Gran Dolina has lost the brow tine completely by reduction (Azanza and Sánchez, 1990, Pl. 1, fig. 1). This specimen is likely to have come from the lower part of the section, units TD3/4 to TD8, being collected in the 1980's, most probably from TD3/4. This morphology is typical

of the evolved *Megaceroides*, here all included in *M. solilhacus*. This antler fragment allows to assign the material from TD8 to that species, even though antler material is lacking so far from TD8.

3.8. Fallow deer

Genus *Dama* Frisch, 1775

Dama vallonnetensis (De Lumley, Kahlke, Moigne & Moullé, 1988)

3.8.1. Material

Ata03, TD8b, G-5, 44 – the basal part of a left antler. The antler is shed.

All other bones and teeth studied here, about 400 fossils, are listed in Tables 10–27. A taphonomic study assigned 615 fossils to the fallow deer, representing a minimum of 16 individuals (Rosell et al., 2010).

3.8.2. Description and comparison

Of the antler (Fig. 13/1), only the base is preserved. The antero-posterior diameter of the burr (DAPr) is 35.0 mm, the same diameter just above the burr (DAPb) is ≥ 43.8 mm and the height of the bifurcation is 33.7 mm measured from below the burr and 29.3 mm from the upper surface of the burr (Hext and Hext'; measured at the lateral side). There is a large angle between the brow tine and main beam. The bifurcation between the brow tine and main beam is low in absolute terms and expressed as the index $100 \times \text{Hext}/\text{DAPb} = 96$. This value is lower than those of the antlers from TD4-6 and is comparable to those from Vallonnet, Untermassfeld, and Atapuerca TE7 (Fig. 13). In general, this value decreased in the *Dama*-like deer, but the samples from Atapuerca TD4-6 and Ponte Galeria, have high values for their age. It seems that in the samples with high values, it is the ontogenetically younger individuals that have the highest values.

The M_3 (Figs. 14/1-2, 14/4 and 15/1-2) has the lingual styliids moderately developed, the anterior fossid usually opens lingually and is not blocked by a little crest (metaendocrisid), there is no very pronounced depression on the lingual wall between the bases of the entoecostyloid and metapoststyloid, there is a clear step in the lingual wall between the second and third lobes, there is no cingulum on the lingual side of the third lobe. These are all features described by Lister (1996) and they are all developed as in *Dama* and not as in *Cervus*.

Another feature mentioned by Lister (1996) is a vertical crest on the lingual wall of the third lobe, which is often clear in *Cervus* and weak or absent in *Dama*. In the fossils from TD8, this feature is as in *Dama*. The feature might be related to the pattern of the occlusal surface (Fig. 15/3-7). There are marked differences in the way the crests at the junction of the second and third lobes connect to each other. With progressive wear, more crests become connected, but there are differences in the order in which the connections are formed. A little cusp, called hexaconid (Fig. 15/3), is usually present, but becomes connected to one of the main crests early (usually to the forwards curving pentaendocrisid) and from then onwards it is not seen as a distinct cusp. Bovidae often lack such a cusp, but there is also a rare example from TD8 of a cervid lacking this cusp (Fig. 14/4). In the Capreolinae (*Capreolus*, *Alces*, *Rangifer*), the hexaconid tends to be well developed and may connect early to the entopostcrisid, while the hypoendocrisid does not reach far lingually, but may connect to the pentaprecrisid. As a result the fossids of the second and third lobes may be connected (Fig. 15/5). In the Cervinae this does not occur and the hypoendocrisid connects first to the entopostcrisid (Fig. 15/4) or pentaendocrisid (which curves forward and incorporates the hexaconid) (Fig. 15/7). There is variation in the length and orientation of the hypoendocrisid,

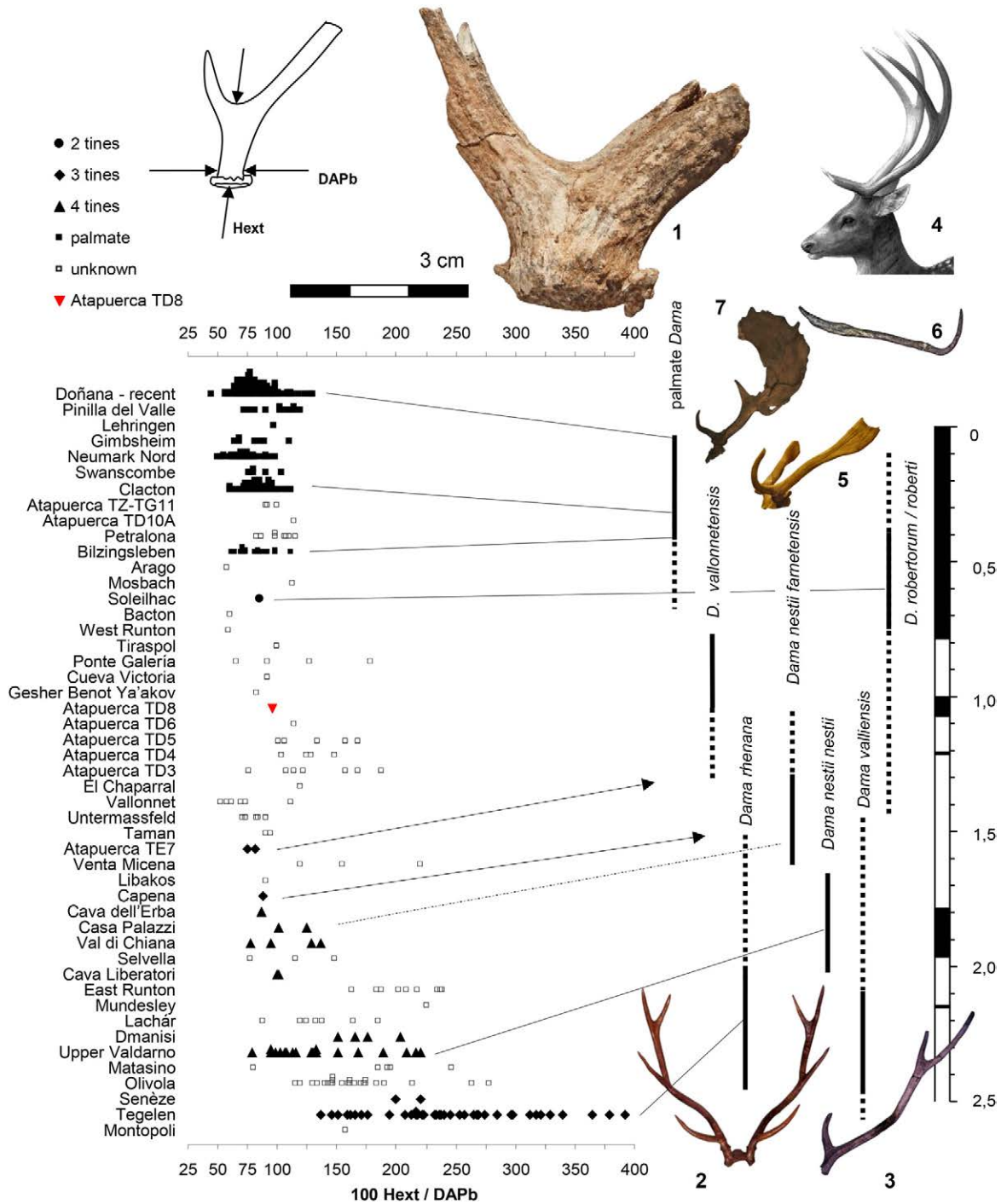


Fig. 13. The antlers of the *Dama*-like deer. 1) Ata03, TD8b, G-5, 44 – the basal part of a left shed antler of *Dama vallonnetensis* from Atapuerca TD8. 2) IGF363 – skull fragment with two antlers of *Dama nestii*, type from the upper Valdarno: frontal view. 3) NBC St28148 – left antler of *Dama rhenana* from Tegelen: lateral view. 4) Reconstruction of *Dama* from Atapuerca TE9 by Eduardo Saíz. 5) NCM 2004.831.13/14 – skull fragment with both antlers, holotype of *Dama robertorum*, from Pakefield: oblique left view. 6) MCP Sol 2003-4-390 right antler of *Dama* from Soleilhac: lateral view. 7) FBFSUJ 27/6/89-13 – right antler and skull fragment of *Dama dama geiselana* from Neumark Nord: medial view. Figures 2–7 not to scale. The temporal distributions of the different west European species of *Dama*-like deer, indicated as thick lines, dashed in the case of tentative distributions. The scale applies to photograph 1; other photographs not to scale. The position of the bifurcation of brow tine and main beam above the burr, indicated as the index 100 Hext/DAPb in the following samples: Montopoli (IGF), Tegelen (NBC, NMMA, TMH), Senèze (IQW), Olivola (IGF), Matassino (IGF), Upper Valdarno (IGF), Dmanisi (GSM), Láchar (MNCN), Mundesley (NHM), East Runton (NHM), Cava Liberatori (IGF), Selvella (IGF), Val di Chiana (IGF), Casa Palazzi (IGF), Cava dell'Erba (IGF), Capena (DSTUSR), Libakos (TUC), Venta Micena (IPS), Atapuerca TE7, TDW3-4, TDE5, TD6, TZ, TG11, TD10 (MB, CENIEH, IPHES), Taman (PIN), Untermassfeld (IQW), Vallonnet (MPRM), El Chaparral (MHMV), Geshar Benot Ya'akov (HUJ), Cueva Victoria (MAC), Ponte Galeria (DSTUSR), Tiraspol (GIN), West Runton (NHM), Bacton (NHM), Soleilhac (MCP), Mosbach (IQW), Arago (LPTUP), Bilzingsleben (FBFSUJ), Petralona (AUT), Clacton (NHM), Swanscombe (NHM), Neumark Nord (FBFSUJ, now in LVH), Gimbshheim (NMM), Lehringen (HNV), Pinilla del Valle (UCM, presently MAR), recent *Dama dama* from the Doñana national park (EBD).



Fig. 14. The dentition of *Dama vallonnetensis* from Atapuerca TD8. 1) Ata06, TD8b, G3, 62 – right mandible with P₂–M₃: a) lingual, b) occlusal, and c) buccal views. 2) Ata06, TD8b, G4, 126 – left mandible with P₂–M₃: a) buccal, b) occlusal, and c) lingual views. 3) Ata02, TD8b, G10, 26 – left M₂: a) lingual, b) occlusal, and c) buccal views. 4) Ata02, TD8b, G11, 14 – left M₂–3: a) buccal, b) occlusal, and c) lingual views. 5) Ata02, TD8b, G8, 44 – left P₄: a) lingual, b) occlusal, and c) buccal views. 6) Ata02, TD8b, G7, 12 – right M₃: a) buccal, and b) occlusal views. 7) Ata05, TD8b, H3, 33 – right P₃–4: a) lingual, and b) occlusal views. 8) Ata02, TD8b, G8, 16 – left P₃: a) lingual, b) occlusal, and c) buccal views. 9) Ata02, TD8b, G13, 18 – right M₃: a) occlusal, b) buccal, and c) anterior views. Upper scale: figure 1; left lower scale: figures 3, 5 & 8; right lower scale: figures 2, 4, 6, 7 & 9.

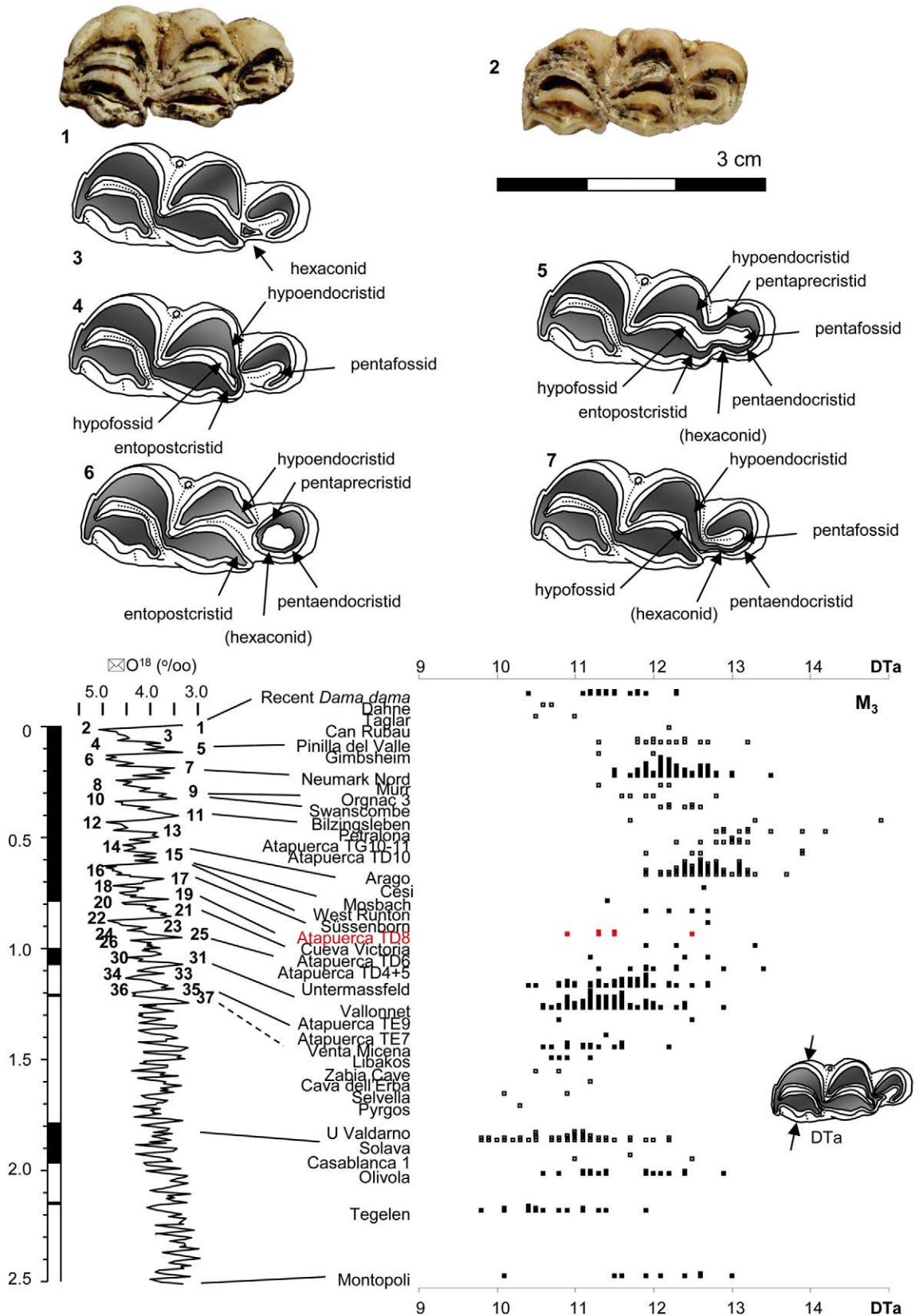


Fig. 15. The M₃ of *Dama vallonnetensis*: 1) Ata05-TD8b-F13-15 – right M₃, occlusal view; 2) Ata05-TD8b-F13-17 – right M₃, occlusal view. Schematic representation of different morphologies of the third lobe of the M₃, occlusal view: 3–7. The width of the first lobe (DTa) of the M₃ of the *Dama*-like deer, as indicative of general size from: Montopoli (IGF), Olivola (IGF), Tegelen (NNML, TMH, NMMaa), Casablanca 1 (SIAP), Solava (IGF), Upper Valdarno (incl. Il Tasso & Casa Frata; IGF), Pyrgos (IVAU, presently NCUA), Selvella (IGF), Cava dell'Erba (IGF), Zabia Cave (ZPALUWr), Libakos (TUC), Venta Micena (Menéndez, 1987), Atapuerca TE7 & TE9 (CENIEH, IPHES), Vallonnet (MPRM), Untermassfeld (IQW), Atapuerca TD4 + 5, TD6 & TD8 (CENIEH, MB, IPHES), Cueva Victoria (MAC), Süssenborn (IQW), West Runton (NHM), Cesi (IGF), Mosbach (NMM), Arago (LPTUP), Atapuerca TD10 & TG10-11 (MB, IPHES), Petralona (AUT), Bilzingsleben (FSBFSUJ), Swanscombe (NHM), Orgnac 3 (LPTUP), Murr (SMNS), Neumark Nord (FSBFSUJ, presently LVH), Gimbshheim (NMM), Pinilla del Valle (UCM, presently MAR), Can Rubau (CIAG), Taglar (MUB), Dahne (MNB), Spain recent (MNCN).

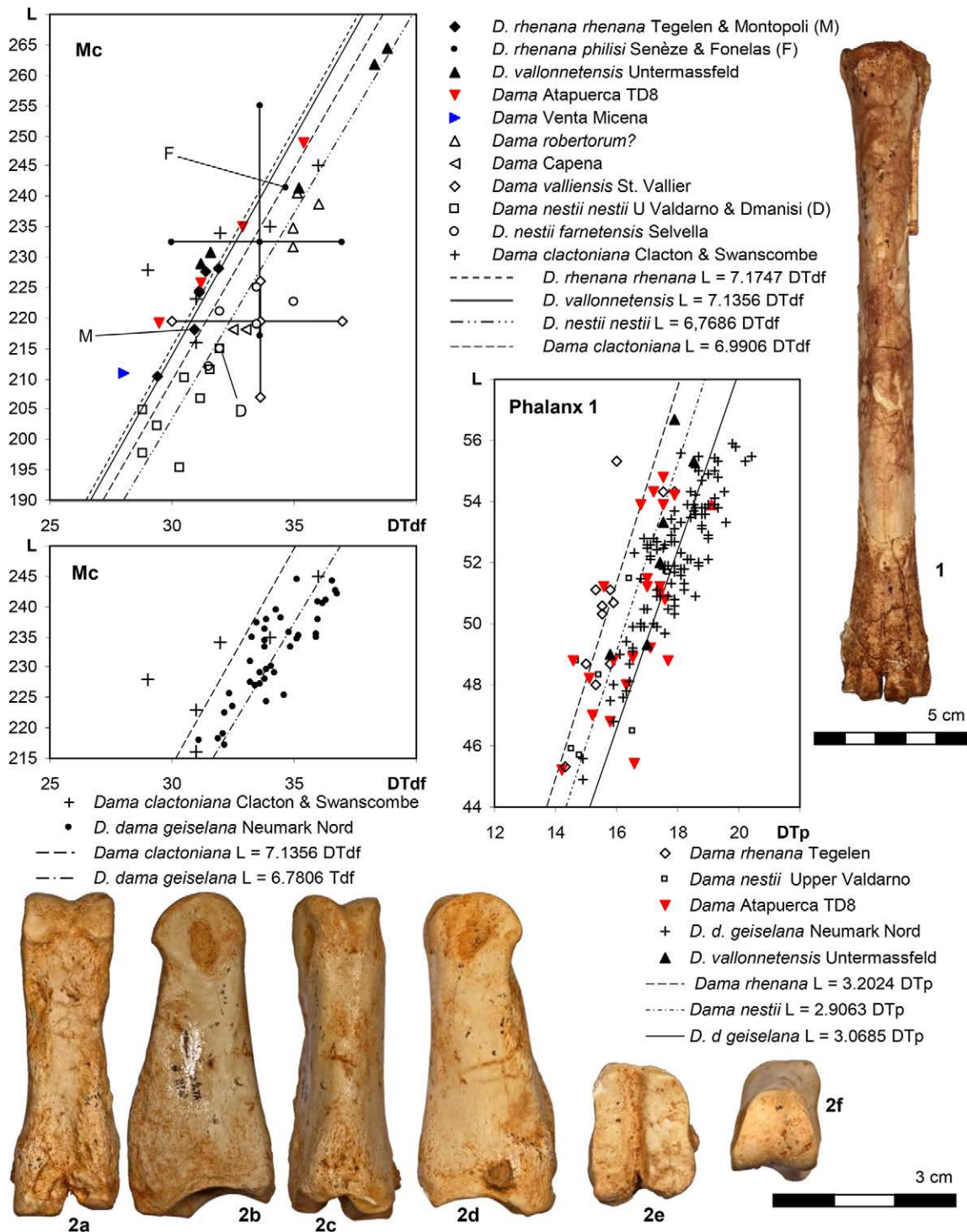


Fig. 16. The metacarpal and first phalanx of *Dama vallonnetensis* from Atapuerca TD8: 1) Ata02, TD8b, G-8, 55 + 39 – left metacarpal, anterior view. 2) Ata03, TD8b, G-15, 6 – first phalanx, right of the axis of the foot, a) plantar, b) axial, c) dorsal, d) abaxial, e) proximal, and f) distal views. Bivariate diagram comparing the distal width (DTdf) and length (L) of the metacarpals of *Dama vallonnetensis* from Atapuerca TD8 to those of *Dama rhenana rhenana* from Tegelen (NMMaa, NBC) and Montopoli (IGF); *Dama rhenana philisi* from Senèze (Heintz, 1970) and Fonelas (Garrido, 2008a); *Dama vallonnetensis* from Untermassfeld (H.D. Kahlke, 1997); *Dama robertorum?* from Isernia la Pineta and Valdemino (Breda et al., 2015) and from Overstrand and Trimmingham (Azzaroli, 1953); *Dama* from Venta Micena (Menéndez, 1987); *Dama* from Capena (Petronio, 1979); *Dama valliensis* from Saint Vallier (Heintz, 1970); *Dama nestii nestii* from the Upper Valdarno (IGF) and Dmanisi (GSM); *Dama nestii farnetensis* from Selvella (Azzaroli, 1992); and *Dama clactoniana* from Clacton, Swanscombe and Jaywick (all Leonardi and Petronio, 1976). As an indication for the expected variability of a population, a diagram is given with the large sample of *Dama dama geiselana* from Neumark Nord (Halle). Bivariate diagram comparing the proximal width (DTp) and length (L) of the first phalanges of *Dama rhenana* from Tegelen (NBC, NMMaa); *Dama nestii* from the Upper Valdarno (IGF); *Dama vallonnetensis* from Untermassfeld (H.D. Kahlke, 1997); *Dama dama geiselana* from Neumark Nord (Halle).

Table 7
Measurements of the teeth and bones from Atapuerca TD8 assigned to *Cervus elaphus*.

			DAP	DAPb	DTa	DTp	DTpp	Ha (Hbu)	Ta	Taxon	
Ata94, TD8, t28, I-16, 9	s	p ³	17.0	16.9	17.5	17.6				C	
Incisor			DT	DMd	DLL	DTroot	DLLroot				
Ata2002, TD8b, F-13, 2	s	I _{3?}	–	6.7	7.4	4.4	5.4				
Ata03, TD8b, G-6, bn	d	I ₃	–	6.6	6.1	–	–			C?	
Scapula			DAPd	DAPpf	DTd	DAPn	DTn				
Ata04, TD8b, G-5, 4	d		64.6	47.4	–	43.8	21.1			C?	
tibia			DAPd								
Ata94, TD8, t28, G-17, 22	d		≥28.1							C	
Calcaneum			DAPh	DTTh	DAPn	DTn	DAPsf	DTfs	DAPm	L	
Ata94, TD8, t29, G-16, 59	d		juv	–	31.0	16.5	–	–	–	–	C?
Ata94, TD8, t28, I-17, 1	s		–	–	–	–	≈42.8	–	–	–	C?
Ata06, TD8b, G-4, 125	d		29.0	23.3	juv	–	–	–	–	–	C?
Metacarpal			DTd	left DAP_{III/IV}	left DT_{III/IV}	right DAP_{III/IV}	right DT_{III/IV}				
Ata04, TD8b, G.5, remofido	?		≈58	31.7	25.7	32.3	27.7				
Phalanx		type	DAPp	DAPpf	DTp	L	DAPd	DTd			
Ata94, TD8, H-16, 19	l	III/IV 1	juv	–	–	–	>18.7	>18.4		C?	
Ata94, TD8, t28, G-16, 32	l	III/IV 1	juv	–	–	–	≈18.3	≈19.5		C?	
Ata03, TD8b, I-9, 72	r	III/IV 1	–	–	–	–	16.9	18.7		C	
Ata94, TD8, t29, H-16, 59	l	III/IV 2	≥32.7	–	24.8	–	juv	–		C?	
Ata94, TD8, t29, I/H-16, sc	l	III/IV 2	–	–	–	–	–	21.9		C?	
Ata04, Td8b, G-14, 4	l	III/IV 2	26.1	–	24.2	–	juv	–		C?	
Ata05, TD8b, F-13, 2	r	III/IV 2	33.2	–	24.9	49.5	30.4	22.1		C	

which may be directed towards the hexaconid or anteriorly curved pentaendocristid and connect first to this structure (Fig. 15/7 and 15/2) or be long and reach the lingual wall (Fig. 15/4) or be long and reach the lingual wall, fusing to the entopostcrisid (Figs. 15/4 and 14/4). The situation in which the hypoendocrisid is short and directed posteriorly (Fig. 15/1), as is more common in the Capreolinae, is less common. In this specimen also the pentaendocrisid fuses to the hexaconid and thus to the pentaprecrisid, closing the pentafossid, and remaining isolated from the hypoendocrisid (Fig. 15/1 and 15/6). A long hypoendocrisid directed towards the anterior end of the pentaendocrisid and reaching the lingual wall might be related to Lister's (1996) vertical crest on the lingual wall (feature 12) and be more typical of *Cervus* and related taxa. In this case the vertical crest is an expression of the hypoendocrisid reaching the lingual wall posterior of the end of the entopostcrisid or of a more posteriorly positioned hexaconid, which connects the hypoendocrisid and pentaendocrisid. Though there is variability in the different samples, the predominant way these crests connect to each other might be different in the different Cervinae. More work on this feature is needed.

The size of the M₃ in the different samples of *Dama* is compared in Fig. 15. This is probably the most common fossil and since there are no very important differences in proportions in the tooth row, it can be taken as an indication of gross size. It can be seen that the

earliest samples indicate a relatively large average body size, then size decreased towards 1.8 Ma, followed by an increase towards 0.4 Ma, followed again by a size decrease. The sample from TD8 fits within the ranges of Vallonnet and Untermassfeld, but is on average a little smaller than those from TD6 and TD4 + 5, and those of the samples commonly assigned to *Dama clactoniana*.

The M₁ and M₂ (Fig. 14/1–14/4) have morphologies that are similar to those described under the M₃ (save for that they lack a third lobe). The anterior fossid usually opens lingually and is not blocked by a little crest (metaendocrisid), but occasionally the entoprecrisid is longer than usual and reaches the metapostcrisid, closing the anterior fossid (Fig. 14/3b).

The P₄ has an entoconid that may be aligned transversely and be connected with the hypoconid (Fig. 14/1, 14/2, 14/5) or be aligned antero-posteriorly and be disconnected from the hypoconid, but fused to the metaconid (Fig. 14/7). The posterior fossid (hypofossid) is not closed on the lingual side, but has a deep opening there. Each time, the latter state is common in *Dama*, but rare or absent in *Cervus* (Lister, 1996). The tooth may have a well developed meta-precristid closing the anterior fossid (protofossid) on the lingual side (Fig. 14/1, 14/2 and 14/7), or may completely lack this structure (Fig. 14/5). These states are called “molarized” and “non-molarized” respectively. The latter state is primitive. In many species this feature is variable; in *Cervus elaphus* from Ehringsdorf (IQW) the

Table 8
Measurements of the teeth from Atapuerca TD8 assigned to *Eucladoceros* (*E*) and *Megaceroides* (*M*).

			DAP	DAPb	DTa	DTp	DTpp	H (Hbu)	Ta	Taxon
Ata2002, TD8b, G-12, 10	P ⁴	s	19.3	18.7	–	26.6	–	–	–	E?
Ata2002, TD8b, G-12, 26	M ₃	d	44.3	42.8	20.7	19.9	11.4	–	–	E
Ata06, Td8b, G-4, 115	P ²	s	20.7	20.0	18.5	19.8	–	>21.7	–	E?
Ata94, TD8, G-16, 19	P ₃	s	23.3	–	11.2	12.9	–	>20.1	–	E?
Ata2002, TD8b, G-7, G-3	M ₃	d	38.3	37.4	15.5	11.8	9.9	–	–	M
	M ₂		30.8	27.6	18.1	17.4	–	–	0.7	
	M ₁		≈24.4	–	–	–	–	–	–	
	P ₄		22.6	21.2	12.6	13.8	–	–	–	
	P ₃		22.3	20.5	11.3	12.4	–	–	–	
	P ₂		17.9	16.2	8.5	9.8	–	–	–	

Table 9Measurements of the bones from Atapuerca TD8 assigned to *Eucladoceros* (*E*) and *Megaceroides* (*M*) (* = juvenile).

Scaphoid		DAP	DT	Ha									
Ata03, TD8b, G-5, 58	d	45.8	28.9	≥32.0									
Goes with lunar no. 59													
Lunar		DAP	DTp	DTd	Ha								
Ata03, TD8b, G-5, 56	s	38.7	27.7	17.9	28.7								
Ata03, TD8b, G-5, 59	d	37.8	28.7	20.6	30.1								
Calcaneum		DAPh	DTTh	DAPn	DTn	DAPsf	DTfs	DAPm	L	Lu	LI	<i>E</i>	
Ata03, TD8b, G-5, 40	d	49.7	41.2	43.4	25.4	58.5	52.0	62.2	165	108.0	65.0	<i>E</i>	
Astragalus		Lext	Lm	Lint	DTp	DTp							
Ata94, TD8, I-17, sc	s	71.7	58	69.1	45.8	45.5							
Ata94, TD8, t28, G-17, 4	s	>73.3	60.9	>72.0	47.8	>41.4							
Metapodial		type	DTd	left DAP_{III/IV}	left DT_{III/IV}	right DAP_{III/IV}	right DT_{III/IV}						
Ata04, TD8b, G-5, removido	?	Mc	≈ 58	31.7	25.7	32.3	27.7						
Ata03, TD8b, G-12, 9	?	Mc	56.0	36.1	25.3	35.3	25.5						
Ata05, TD8b, H-3, 49*	?	?	–	–	>26.8	–	–						
Ata05, TD8b, H-3, 34*	?	?	–	–	–	–	–						
Phalanx 1		type	DAPp	DAPpf	DTp	L	DAPd	DTd					
Ata2002, TD8b, G-7, 91	l	III/IV 1	34.5	31.7	31.6	71.9	24.8	32.0					
Ata03, TD8b, G-16, 16	l	III/IV 1	33.3	–	28.1	–	juv	–					
Ata04, TD8b, F-14, 10	r	III/IV 1	≥33.1	31.7	30.3	–	–	–					
Ata06, TD8b, G-04, 113	l	III/IV 1	–	>31.3	>29.1	70.9	23.6	30.2					
Phalanx		type	DAPp	DAPp'	DTp	L	DAPd	DTd	L				
Ata06, TD8b, G-3, 48	l	III/IV 2	>41.7	≈ 40.2	35.1	62.5	37.0	29.6	–				
Ata06, TD8b, G-3, 71	l	III/IV 2	>42.7	34.6	63.1	37.3	29.2	–	21.9				
Ata06, TD8b, G-4, 48		II/V 2	18.9	–	8.1	20.2	14.5	10.3	–				

Table 10Measurements of the isolated upper cheek teeth of *Dama vallonnetensis* from Atapuerca TD8.

Number	Tooth	s/d	DAP	DAPb	DTa	DTp	Ha	(Hbu)
Ata94, TD8, t28, G-16, 51	M ³	d	≈ 16.4	–	–	16.5	–	–
Ata94, TD8, t29, I-19, 48	M ³	s	18.8	18.8	19.0	16.8	–	–
Ata2002, TD8b, G-13, 18	M ³	d	18.7	17.1	18.1	17.1	18.3	–
Ata03, TD8b, G-5, bn	M ³	s	–	–	–	16.2	–	–
Ata03, TD8b, H-4, bn	M ³	d	18.1	16.5	17.9	16.3	–	–
Ata06, TD8b, G-3, 45	M ³	d	19.8	17.9	19.9	17.6	–	–
Ata2002, Tdb, G-12, 36	M ^x	s	–	–	–	≥ 17.1	–	–
Ata06, TD8b, G-4, 13	M ^x	–	–	–	–	–	–	–
Ata94, TD8, t29, I-19, 50	M ^x	d	–	–	–	–	–	–
Ata2002, TD8b, F-13, 17	M ^x	d	–	–	–	–	17.0	–
Ata94, TD8, t29, I-16, 50	M ^x	d	–	–	–	–	–	–
Ata06, Td8b, G-3, 10	M ²	s	19.3	18.0	20.1	19.0	–	–
Ata06, TD8b, G-3, 86	M ²	s	–	–	–	20.1	–	–
Ata06, Td8b, H-4, 13	M ²	s	20.3	18.2	19.7	–	–	–
Ata94, TD8, t29, I-16, 43	M ¹	d	18.8	16.5	18.1	17.7	–	–
Ata06, TD8b, G-3, 2	M ^x	d	18.7	18.7	–	–	–	–
Ata03, TD8b, G-6, 22	M ²	s	17.9	16.8	–	–	–	–
Ata03, TD8b, G-4, 10	M ^x	s	–	–	18.8	–	–	–
Ata06, TD8b, G-3, 11	M ^{1/2}	–	–	–	–	≥ 17.2	–	–
Ata2002, TD8b, G-15, 2	M ¹	s	17.2	15.1	16.6	17.4	–	–
Ata06, TD8b, G-4, 87	M ¹	s	18.2	14.9	–	–	–	–
Ata06, TD8b, G-4, 140	M ¹	d	–	–	–	16.9	–	–
Ata06, TD8b, H-3, 23	M ¹	s	19.2	16.5	18.1	17.7	–	–
Ata94, TD8, G-16, 10	D ^x /M ^x	d	–	–	–	–	–	–
Ata94, TD8, t28, G-17, 20	P ⁴	s	12.9	10.3	–	15.5	>13.9	–
Ata2002, TD8b, G-7, 85	P ⁴	d	11.3	10.9	–	15.0	–	–
Ata06, TD8b, G-3, 44	P ⁴	d	12.7	11.3	–	16.3	15.8	–
Ata06, TD8b, H-3, 10	P ³	s	14.0	13.2	–	13.6	–	–
Ata94, TD8, t16, G-16, sc	P ²	d	>12	>12	11.4	–	–	–
Ata05, TD8b, G-13, 4	P ²	s	12.8	11.8	10.4	11.6	–	–
Ata06, TD8b, H-4, 6	P ²	d	12.7	12.3	11.0	12.3	–	–
Ata2002, TD8b, F-12, 21	D ⁴	d	–	–	–	–	–	–
Ata2002, TD8b, G-8, 22	D ⁴	s	14.4	13.7	14.6	14.4	–	–

proportion not molarized/molarized is 6/21 and in Bilzingsleben it is 7/70 (FBFSUJ). In the old and primitive *Dama rhenana* from Tegelen this is 12/0 (NBC, NMMaa, TMH), while in *Dama nestii* from the Upper Valdarno (IGF) this is 7/24, in *Dama* from Venta Micena it is 10/3 (IPS) and in *Dama vallonnetensis* from Vallonnet and Untermassfeld this is 2/12 (MPRM) and 7/47 (IQW), respectively, and in the still younger and “more progressive” *Dama clactoniana* from Arago (LPTUP) and Swanscombe (NHM) this is 10/45 and 5/7, respectively, while in *Dama dama* from Neumark Nord and Pinilla del Valle-Camino, this is 30/30 and 10/16 (FBFSUJ, presently LVH; UCM, presently MAR). In TD8 this is 8/7, which is thus clearly less than in the red deer, the deer from the Upper Valdarno and all younger *Dama*-like deer, but more than in *Dama rhenana* and the deer from Venta Micena.

The P₃ (Fig. 14/1, 14/2, 14/7 and 14/8) has the paraconid and parastylid well separated as in *Dama*, while in *Cervus* this is often not the case (Lister, 1996). The entoconid tends to be oriented transversely and be connected to the hypoconid. The hypofossid is wide open lingually.

The P₂ (Fig. 14/1 and 14/2) has a relatively low crown, a convex buccal wall and the lingual wall at the place of the protoconid recedes clearly. This is as in *Dama*, while in *Cervus*, *Rusa* and *Axis*, the crown is higher with flatter lingual and buccal walls. The protoconid curves lingually in its distal part, forming what is usually called the parastylid and paraconid, which is as in *Dama*, while in *Cervus*, *Rusa* and *Axis*, this lingual curvature is less marked and not bifurcated in its distal part.

The M^{1/2} and M³ (Fig. 14/6 and 14/9) have relatively weak buccal styles, especially the metaecto- and metapoststyles, as in *Dama*, while in *Cervus*, but also in *Rusa* and *Axis*, these styles tend to be much stronger. These features are as in *Dama* and differ from the state in *Cervus* (Lister, 1996). Like in *Dama*, the lingual interlobular column and associated cingulum are weakly developed, whereas

Table 11
Measurements of the articulated upper cheek teeth of *Dama vallonnetensis* from Atapuerca TD8.

Number	Tooth	s/d	DAP	DAPb	DTa	DTp
Ata2002, TD8b, G-7, 12	M ³	s	19.4	17.2	17.7	15.6
	M ²		>15.8	>15.8	–	18.5
Ata2002, TD8b, G-11, 14	M ³	d	20.6	17.9	20.4	≈ 19.0
	M ²		–	–	–	–
	M ¹		18.4	15.8	17.5	18.3
	P ³		13.4	11.6	–	–
	D ⁴		15.0	12.7	14.3	14.7
	D ³		–	–	9.1	–
Ata03, TD8b, G-3, 6	D ²		13.0	12.2	–	–
	M ²	d	>20.5	18.7	20.6	19.2
	M ¹		18.6	17.0	–	–
	P ⁴		–	–	–	–
Ata03, TD8b, G-5, 38	P ⁴	s	–	–	–	–
	P ³		12.9	11.7	12.9	13.0
	P ²		12.2	11.2	10.7	11.4
Ata03, TD8b, G-5, 45	M ³	s	19.9	18.6	18.6	15.6
	M ²		–	..
	M ¹		≈ 16.6	≈ 16.6	≈ 16.2	–
Ata06, TD8b, G-3, 110	M ¹	d	17.0	17.0	18.9	18.4
	P ⁴		11.9	11.4	–	15.6
	P ⁴	s	10.7	9.5	–	–
Ata06, TD8b, G-4, 22	P ²		–	–	–	–
	M ³	s	–	–	18.7	≈ 16.7
Ata06, TD8b, G-4, 100	M ²		19.4	17.3	19.5	18.3
	M ²		≈ 19.2	≈ 16.2
	M ¹		18.9	17.3	17.9	–
Ata06, TD8b, G-4, 138	P ⁴		13.1	11.6	–	15.2
	P ³		12.4	11.5	–	–
	M ¹	s	19.4	17.9	17.9	17.7
Ata2002, TD8b, G-7, 75	D ⁴		15.5	14.0	15.2	15.2

these are better developed in *Axis* and much better in *Rusa* and *Cervus* (features of Lister, 1996).

The P⁴, P³ and P² have, in anterior or posterior view, the profile of the lingual wall convex in the lower part and concave in the

upper part, as is common in the *Dama*-like deer, while in *Cervus* it is more straight or slightly convex (feature 3 of Lister, 1996).

The metacarpal (Fig. 16/1) is an interesting bone for its proportions. Some species have robust and others have gracile

Table 12
Measurements of the isolated lower cheek teeth of *Dama vallonnetensis* from Atapuerca TD8.

Number	Tooth	s/d	DAP	DAPb	DTa	DTp	DTpp	H (Ha)	Ta
Ata05, TD8b, F-13, 17	M ₃	d	26.9	26.6	12.5	11.9	7.6		0.9
Ata02, TD8b, F-12, 43	M ₃	s	–	–	11.9	11.6	–		
Ata05, TD8b, F-13, 15	M ₃	d	25.2	24.7	11.3	10.8	6.9		
Ata06, TD8b, H-4, 21	M ₃	d	≥ 24.2		
Ata94, TD8, t29, I-16, 42	M ₂	s	18.1	17.2	11.2	11.8	–		
Ata2002, TD8b, G-7, 11	M ₂	d	–	–	≥ 11.5	–	–		
Ata2002, TD8b, G-10, 26	M ₂	d	20.1	19.2	12.4	12.3	–		
Ata06, TD8b, G-4, 25	M ₂	s	20.4	18.6	11.5	–	–		
Ata2002, TD8b, G-9, 59	M ₂₇	s	–	–	12.8	–	–		
Ata94, TD8, t29, I-1, 54	M ₁	s	16.1	15.7	10.8	10.7	–		
Ata2002, TD8b, G-8, 11	M ₁	s	13.7	>13.7	10.9	10.9	–		
Ata2002, TD8b, G-8, 43	M ₁	s	18.6	16.9	10.6	10.7	–		
Ata06, TD8b, G-3, 51	M ₁	d	16.1	16.1	10.6	11.0	–		0.5
Ata06, TD8b, H-4, 2	M ₁	d	21.3	17.8	11.0	10.9	–	17.5	
Ata03, TD8b, G-6, 27	P ₄	s	12.3	12.3	9.2	8.0	–		
Ata03, TD8b, G-6, bn	P ₄	d	14.7	13.4	9.0	8.6	–		
Ata05, TD8b, H-3, 6	P ₄	d	13.9	12.5	8.0	8.9	–		
Ata06, TD8b, G-4, 49	P ₄	d	13.0	11.9	6.9	7.7	–		
Ata06, TD8b, H-3, 12	P ₄	s	13.5	12.1	7.6	7.4	–		
Ata06, TD8b, G-4, 84	P ₄	d	12.5	11.3	6.4	7.4	–		
Ata2002, TD8b, G-8, 44	P ₄	s	13.7	12.6	8.0	7.8	–		
Ata2002, TD8b, G-8, 16	P ₃	s	12.9	11.6	8.0	8.5	–		
Ata2002, TD8b, G-8, 42	P ₃	s	12.2	11.4	≥ 6.6	–	–		
Ata2002, TD8b, G-8, 47	P ₂	s	10.9	9.5	6.3	7.1	–		
Ata06, TD8b, G-4, 1	P ₂	s	9.8	8.5	5.8	6.5	–		
Ata06, TD8b, G-4, 12	D ₄	s	–	–	7.9	9.0	–		
Ata06, TD8b, H-4, 4	D ₃	d	13.8	13.5	5.6	7.8	–		
Ata03, TD8b, G-5, bn	D ₂	s	8.9	8.9	3.9	5.0	–		

Table 13Measurements of the associated lower cheek teeth and mandibles of *Dama vallonnetensis* from Atapuerca TD8.

Number			DAP	DAPb	DTa	DTp	DTpp	Ha	Ta	D	W	DT condyle
Ata94, TD8, t29, H-16, 47	M ₁	d	16.5		10.6	11.6				≈31.1		
	P ₄		14.4		8.1	8.7				≈28.4		
	P ₃		13.6		7.2	8.3				≈27.3		
Ata2002, TD8b, G-11, 4	M ₃	d	27.4	26.7	11.5	10.8	5.7					
	M ₂		20.0	19.0	12.2	11.3						
Ata2002, TD8b, F-12, 14	M ₂	d	21.5	19.4	12.9	11.8						
	M ₁		17.3	16.6	11.3	10.9						
Ata03, TD8b, G-5, 50	M ₃	s	26.3	24.7	11.5	11.3	6.9					
	M ₂		20.3	17.9	11.9	11.7						
	M ₁		12.5	15.3	10.5	11.2						
	P ₄		14.9	13.3	8.2	9.2						
	P ₃		13.9	11.9	6.3	8.2						
	P ₂		10.6	10.0	6.0	6.7						
Ata03, TD8b, H-15, 8	M ₃	s	27.0	26.0	..	10.6	6.7					
	M ₂		18.7	17.6						
Ata03, TD8b, G-6, 28	M ₁		–	–	10.8	–						
	M ₃	s	27.0	26.0	..	10.6	6.7					
	M ₂		18.7	17.6						
Ata03, TD8b, H-5, nc	M ₁		–	–	10.8	–						
	P ₄	d	14.2	>14.2	–	–						
Ata05, TD8b, G-3, 1	P ₃		–	–	7.3	9.0						
	M ₂	s	18.1	17.7	12.2	12.1		0.6				
	M ₁		17.5	11.1	10.1	10.9		0.5				
Ata05, TD8b, H-3, 33	P ₄		13.9	12.3	8.4	8.5						
	P ₄	s	13.2	12.4	8.7	8.4						
	P ₃		12.9	11.8	7.3	7.8						
Ata06, TD8b, G-3, 62	M ₃	d	≈25	≈23	10.9	10.7				25.9	17.6	
	M ₂		19.9	18.2	11.3	11.3				27.0	10.8	
	M ₁		18.0	16.5	10.2	10.3				24.9	13.3	
	P ₄		13.9	12.6	8.3	8.2				21.9	13.0	
	P ₃		13.4	12.0	6.5	7.4				22.1	12.2	
	P ₂		10.9	9.4	5.2	6.6				22.8	9.8	
Ata06, TD8b, G-4, 57	M ₃	d	26.5	26.1	11.3	10.9	6.9	19.1				
	M ₂		21.1	18.7	11.6	11.3		19.0				
	M ₁		18.7	16.8	10.6	10.6			0.5			
	P ₄		14.4	13.5	8.8	8.3						
	P ₃		13.5	12.0	7.7	7.8						
	P ₂		10.7	9.5	6.4	7.1						
Ata06, TD8b, G-4, 22	M ₃	d	26.1	≈26.1	≈12	–	6.8					
	P ₄		13.3	11.9	–	8.6						
	P ₃		11.7	10.4	7.0	8.2						
Ata06, TD8b, H-3, colada inf., bn	P ₂		10.0	9.0	5.7	6.7						
	P ₄	d	13.9	12.7	–	–						
Ata06, TD8b, H-3, 21	P ₃		13.1	12.0	6.8	7.4						
	M ₂	d	–	–	11.6	–						
Ata06, TD8b, G-4, 126	M ₁		17.1	15.5	9.7	10.1						
	M ₃	s	23.6	22.2	10.6	11.0	6.6					
	M ₂		19.6	17.9	11.4	11.6						
	M ₁		18.6	16.9	10.4	10.7						
	P ₄		13.5	12.0	8.0	8.3						
	P ₃		13.2	11.2	6.7	7.5						
Ata2002, TD8b, G-7, 62	P ₂	s	10.9	9.8	5.4	–						20.0

Table 14Measurements of the incisors and canines of *Dama vallonnetensis* from Atapuerca TD8.

Number	Tooth	s/d	DT	DMD	DLL	DTroot	DLLroot	Hli
Ata2002, TD8b, G-13, 12	I ₁	d	–	–	5.5	5.7	4.8	
Ata2002, TD8b, F-13, 22	I ₁	s	–	8.8	6.2	–	–	
Ata03, TD8b, G-3, 10	I ₁	d	11.4	8.4	6.1	5.0	4.4	
Ata03, TD8b, H-5, nc	I ₁	d	9.5	7.9	6.5	5.3	4.8	
Ata05, TD8b, F-13, 1	I ₁	d	10.3	8.8	–	–	–	
Ata06, TD8b, G-3, 74	I ₁	s	8.0	7.3	5.8	5.2	4.4	
Ata06, TD8b, G-4, 65	I ₁	s	10.7	9.3	6.8	5.7	4.8	
Ata2002, TD8b, G-10, 58	I ₂	s	6.7	5.1	5.3	3.3	4.2	
Ata03, TD8b, G-5, 24	I ₂	s	5.4	5.1	5.5	4.1	4.5	
Ata05, TD8b, H-3, 19	I ₂	d	8.1	6.3	5.5	4.0	4.9	
Ata05, TD8b, H-3, 414	I ₂	d	9.5	6.6	5.3	3.6	5.0	
Ata06, TD8b, G-3, 3	I ₂	s	8.3	5.8	6.1	4.6	3.8	
Ata06, TD8b, G-4, 40	I ₂	s	8.2	5.5	5.4	4.0	4.4	
Ata2002, TD8b, G-10, 49	C _x	s	4.5	3.8	4.8	2.6	4.0	
Ata2002, TD8b, G-12, 17	C _x	d	4.2	3.4	4.5	2.6	3.8	

Table 15Measurements of the vertebrae of *Dama vallonnetensis* from Atapuerca TD8.

Number	Vertebra	DT tooth	DTa	DTforamen ant.	DTmin				
Ata2002, TD8b, G-7, 16	axis	24.2	53.5	20.7	36.9				
Ata94, TD8, t28, G-17, 16	axis	24.6	56.0	≥18.7					
Ata94, TD8, t29, I-16, 27	axis	25.2	59.7	≈17					
Number	Vertebra		4	13	15	19	20	Remarks	
Ata05, TD8b, G-13, 3	C2/4/5	s d	24.8	18.9	18.8	8.0 11.4	9.1 9.4		
Ata05, TD8b, E-13, 3	Lumbar							2 specimens in sediment	
Ata06, TD8b, G-3, 84	Thoracic								
Ata06, TD8b, G-3, 97	Thoracic								
Ata06, TD8b, G-3, 104	Thoracic								

Table 16Measurements of the scapula and humerus of *Dama vallonnetensis* from Atapuerca TD8.

Scapula		DAPd	DAPdf	DTd	DAPn	DTn			
Ata94, TD8, t28, G-18, 2	d	–	37.8	35.0	28.2	≥18.3			
Ata2002, TD8b, G-9, 31	s	–	–	–	–	–			
Ata2002, TD8b, G-9, 45	s	49.9	38.8	35.5	26.6	17.7			
Ata2002, TD8b, G-9, 49	d	–	–	–	–	–			
Ata04, TD8b, G-5, 3	d	–	≥30.8	–	22.8	..			
Ata06, TD8b, G-4, 95	s	47.4	38.4	33.0	–	≥16.8			
Ata06, TD8b, H-4, 14	d	46.8	37.5	32.3	25.7	16.4			
Ata06, TD8b, G-3, 42	d	44.1	35.4	32.8	23.8	17.2			
Ata06, TD8b, G-3, 100	s	–	40.2	37.4	29.8	20.6			
Ata06, TD8b, H-2, 22	d?	>28.4			
Humerus		DAPd	DTd	DTdf	R1	R2	R3	R4	R5
Ata94, TD8, t28, H-16, 26	d	–	>40.0	37.6	30.3	22.3	25.9	18.6	19.9
Ata94, TD8, t29, I-16, 46	s	42.8	42.8	39.3	30.5	23.8	27.0	19.3	19.9
Ata2002, TD8b, H-8, 16	d	42.1	45.0	–	30.9	22.8	26.5	18.2	–
Ata2002, TD8b, G9, 27	d	–	–	–	–	21.4	25.7	19.1	19.1
Ata2002, TD8b, F-11, 12	d	–	–	–	32.6	24.0	27.2	–	–
Ata2002, TD8b, G-14, 9	d	46.8	45.0	42.7	32.7	24.4	28.7	21.7	–
Ata2002, TD8b, G-7, 64	s	42.9	42.9	37.4	29.8	22.8	26.7	18.6	19.9
Ata2002, TD8b, G-8, 59	s	43.9	–	39.9	31.6	23.4	27.9	20.1	≥20.6
Ata2002, TD8b, G-10, 45	s	42.0	30.9
Ata2002, TD8b, G-7, 84	d	–	35.8	35.4	26.7	20.7	24.4	17.2	17.5
Ata03, TD8b, G-5, 41	s	43.9	42.6	40.3	33.6	24.5	28.8	21.4	21.9
Ata06, TD8b, H-4, 10	d	42.9	42.1	39.5	30.9	22.6	25.6	20.6	20.0
Ata2002, TD8b, F-9, 3	s	40.8	43.0	38.5	31.3	22.5	26.1	18.3	20.1

Table 17Measurements of the radius, ulna, femur and tibia of *D. vallonnetensis* from Atapuerca TD8.

Radius		DAPP	DAPPf	DTp	DTpf	L	I	DAPd	DAPdf	DTd	DTdf	
Ata2002, TD8b, G-12, 27	d	–	–	–	–	–	–	27.0	23.4	37.6	35.7	
Ata2002, TD8b, G-7, 31	d	21.7	21.0	>41.7	41.1	>207	–	juv	–	–	–	
Ata2002, TD8b, G-8, 3	d	–	–	juv	–	–	–	≥26.1	20.4	≥37.5	33.7	
Ata2002, TD8b, G-8, 25	d	–	–	47.1	41.0	240.4	230.2	29.4	23.2	45.0	37.7	
Ata2002, TD8b, G-12, 34	d	22.8	20.8	41.0	37.9	–	–	–	–	–	–	
Ata04, TD8b, G-5, 20	s	–	–	–	–	juv	–	–	–	38.1	35.0	
Ata03, TD8b, G-5, 57	s	≈20.3	–	–	–	–	–	–	–	–	–	
Ata05, TD8b, E-13, 5	s	–	–	–	–	–	–	24.9	22.7	–	–	
Ulna – prox		DAPH	DTh	DAPn	DTn	DAPma	DTfu	DTmax	DAPmini	Lu	DAPd	DTd
Ata2002, TD8b, F-10	d	–	–	–	–	45.3	12.9	23.3	27.1	–	–	–
Ata2002, TD8b, H-8, 22	s	–	–	–	–	40.1	13.9	21.5	25.3	–	–	–
Ata2002, TD8b, F-10, 5	d	–	–	–	–	43.8	13.3	23.7	26.8	–	–	–
Ata04, TD8b, G-14, 22	s	–	–	–	–	≈40.7	12.2	21.6	24.8	–	–	–
Ata06, TD8b, H-3, 1	d	–	–	–	–	–	12.0	23.2	–	–	–	–
Ata06, TD8b, H-4, 5	d	–	–	≥25.9	7.9	32.0	11.6	19.4	–	–	–	–
Ata06, TD8b, H-4, 23	–	–	–	–	–	–	14.1	–	–	–	–	–
Ata06, TD8b, G-3, 27	d	–	–	–	–	–	14.4	–	–	–	–	–
Ata94, TD8, t28, G-16, 39	s	–	–	juv	–	–	–	–	–	–	–	–
Ata2002, TD8b, G-12, 27	d	–	–	–	–	–	–	–	–	–	–	12.6
Ata2002, TD8b, H-8, 19	d	–	–	juv	–	–	–	–	–	–	–	10.4
Ata04, TD8b, G-5, 23	d	–	–	juv	–	–	–	–	–	–	–	11.1
				juv	–	–	–	–	–	–	–	10.6
				juv	–	–	–	–	–	–	–	9.7

(continued on next page)

Table 17 (continued)

Femur		DAPpf	DTp	L	I	DAPd	DAPd'	DTd	DTdfp	
Ata94, TD8, t29, I-17, 2	s	28.9								
Ata04, TD8b, G-5, 13		≥28.8								
Ata03, TD8b, G-5, 22			juv							
Ata94, TD8, t28, G-16, 47	d	–	–							
Tibia		DAPp	DAPp'	DTp	DTpf	L	I	DAPd	DTd	DTdfa
Ata94, TD8, t28, G-17, 5	d	–	–	–	–	–	–	29.6	–	–
Ata2002, TD8b, G-12, 22	s	–	–	–	–	–	–	27.2	≥35.6	–
Ata2002, TD8b, G-9, 34	s	–	–	juv	–	–	–	27.9	≥34.7	27.4
Ata2002, TD8b, G-7, 21	s	–	–	>59.4	–	juv	–	–	–	–
Ata2002, TD8b, G-7, 34	d	–	–	–	–	–	–	29.1	≥35.4	27.4
Ata2002, TD8b, G-7, 50	s	–	–	–	–	juv	–	32.3	40.0	30.0
Ata2002, TD8b, G-13, 17	s	–	–	–	–	–	–	33.0	40.1	22.3
Ata2002, TD8b, F-10, 14	d	–	–	≈305.3	287.6	36.4	37.6	26.8
Ata2002, TD8b, G-7, 39	d	–	–	–	–	–	–	31.1	40.0	29.9
Ata94, TD8, t28, G-17, 22	s	–	–	–	–	–	–	≥28.1	–	–
Ata05, TD8b, E-12, 11	d	–	–	–	–	–	–	30.9	38.8	26.4
Ata06, TD8b, H-3, 32	s	–	–	–	–	–	–	29.6	38.2	24.3
Ata06, TD8b, H-3, 40	s	–	–	–	–	–	–	–	–	–

metapodials. Fig. 16 compares the size and proportions of the metacarpals of the earlier species and gives the large sample of *Dama dama geiselana* from Neumark Nord as an example for the variability. The lines indicate the average proportions of the different species. The deer from TD8 has gracile metapodials, like those of *Dama vallonnetensis* and un-like those assigned to *Dama robertorum* (= *D. roberti* Breda and Lister, 2013 – see end of Section 3.8.3.) and those of *Dama nestii*.

Table 18
Measurements of the carpals of *Dama vallonnetensis* from Atapuerca TD8.

Scaphoid		DAP	DT	Ha	
Ata2002, TD8b, G-7, 47	d	26.3	14.9	19.5	
Ata2002, TD8b, G-8, 9	d	23.4	12.5	17.2	
Ata2002, TD8b, F-10, 10	s	≥25.6	13.5	≥19.8	
Ata2002, TD8b, G-5, 40	d	26.9	14.9	20.0	
Ata05, TD8b, F-13, 14	s	>26.1	13.8	–	
Ata05, TD8b, F-13, 16	s	26.9	14.2	19.3	
Lunar		DAP	Ha	DTp	DTd
Ata05, TD8b, F-12, 17	d	24.9	18.4	16.8	13.0
Ata06, TD8b, H-3, 26		24.9	17.7	17.4	12.4
Ata06, TD8b, G-3, 105		22.6	17.2	>15.1	11.7
Ata06, TD8b, G-3, 16	d	>20.5	16.6	15.8	11.9
Ulnar		DAP	DT	H	Ha
Ata2002, TD8b, H-8, 20	d	19.0	9.8	25.3	17.6
Ata05, TD8b, G-4, 47	d	17.8	9.7	>20.0	15.8
Ata2002, TD8b, F-11, 77	s	>19.9	14.6	–	–
Pisiform		DAP	DTf	H	Hf
Ata06, TD8b, G-3, 69	s	18.0	8.1	14.2	11.6
Magnum		DAP	DT	H	h
Ata2002, TD8b, G-7, 42		21.8	18.9	–	–
Ata2002, TD8b, F-10, 11	d	22.4	18.5	14.2	11.5
Ata2002, TD8b, G-5, 2	s	19.4	18.0	12.9	9.8
Ata05, TD8b, H-3, 5	s	22.9	21.5	14.4	11.4
Ata05, TD8b, F-12, 7	s	≥19.9	17.9	14.1	10.8
Ata05, TD8b, E-12, 2	s	21.3	17.2	14.5	11.2
Ata06, TD8b, G-3, 40	d	20.0	17.4	13.3	10.1
Unciform		DAP	DT	H	
Ata2002, TD8b, G-5, 37	d	20.9	16.9	14.8	
Ata2002, TD8b, G-13, 5	d	–	15.0	–	
Metacarpal II		DAPp	DTp	L	
Ata04, TD8b, G-5, 38	s	6.4	3.9	–	

The first phalanx (Fig. 16/2) is represented by many specimens (Table 24). Lister (1996) indicated one feature to separate red and fallow deer phalanges. In the middle of the proximal side and plantar of the central furrow, there is a proximally facing area of bone in *Cervus*, while in *Dama* it is lacking. The latter morphology is found in TD8. The differences in proportions of the metacarpals, suggests, that similar differences could be found also in the phalanges. On average, there are some differences, but they are not so clear (Fig. 16). This might be due to the fact that posterior phalanges tend to be more elongate than the anterior ones, and they have not been separated. The anterior and posterior phalanges tend to differ in proportions and morphological features, but there is a continuum of morphologies and a reliable separation is not possible, or difficult at least.

The astragalus has, in anterior view, the medial edge of the proximal articular surface projecting further medially at its distal part than at its proximal part and a not very pronounced bulge at the medio-distal end of this facet (feature 4 and 5 of Lister, 1996), as

Table 19
Measurements of the maleolar, navicuboid and cuneiform of *Dama vallonnetensis* from Atapuerca TD8.

Maleolar		DAP	DT	H
Ata2002, TD8b, G-13, 12	s	22.0	14.3	18.4
Ata2002, TD8b, G-7, 51	s	21.9	11.8	18.7
Ata05, TD8b, H-3, 9	s	21.2	10.4	>16.5
Ata06, TD8b, H-3, 29	s	21.4	10.9	20.2
Ata06, TD8b, G-3, 115	s	>23	>17.5	..
Navico-cuboid		DAP	DT	DTfast
Ata2002, TD8b, G-7, 42	d	32.6	36.2	29.2
Ata2002, TD8b, G-9, 16	d	≥36.3	36.7	30.1
Ata2002, TD8b, H-8, 5		juv		
Ata2002, TD8b, G-8, 14	d	32.3	34.0	27.9
Ata2002, TD8b, G-7, 22	d	32.4	36.2	29.3
Ata2002, TD8b, G-12, 46	d	–	33.3	27.7
Ata92, TD8, limpieza corte	d	28.6	31.6	25.3
Ata2002, TD8b, F-13, 2	d	31.8	28.1	34.5
Ata05, TD8b, G-4, 3	d	28.1	31.7	26.1
Ata05, TD8b, E-12, 9		25.8	30.0	24.4
Ata06, TD8b, G-4, 130		≈32.2	–	–
Cuneiform II + III		DAP	DT	
Ata2002, TD8b, G-12, 45	s	21.8	14.1	
Ata06, TD8b, G-4, 79	d	23.1	15.0	
Ata06, TD8b, G-13, 6	d	23.4	≥15.0	
Ata06, TD8b, H-3, 7	s	20.6	14.0	

Table 20
Measurements of the calcaneum and astragalus of *Dama vallonnetensis* from Atapuerca TD8.

Calcaneum		DAPh	DTh	DAPn	DTn	DAPsf	DTfs	DAPm	L	Lu	LI
Ata2002, TD8b, G-8, 80	d	26.8	21.1	25.8	11.4	30.2	24.5	32.2	–	66.8	–
Ata2002, TD8b, G-8, 35	s	–	–	–	10.7	27.0	23.8	–	91.5	61.8	34.5
Ata2002, TD8b, G-7, 92	s	–	–	25.2	10.6	27.4	–	30.5	–	–	34.1
Ata04, TD8b, G-6, 10		juv	–	16.2	10.6	21.7	21.6	–	–	–	–
Ata04, TD8b, G-6, removido		>22.5	20.0	juv	–	–	–	–	–	–	–
Ata04, TD8b, G-5, 22	s	22.8	18.7	21.1	12.5	26.2	24.3	30.4	–	57.3	–
Ata05, TD8b, G-3, 8	d	–	–	–	13.0	–	–	–	>93.4	>63.0	34.8
Ata05, TD8b, G-3, 2	s	25.4	20.9	juv	–	–	–	–	–	–	–
Ata05, TD8b, F-12, 22	d	–	19.8	–	–	–	–	–	–	–	–
Ata05, TD8b, F-12, 5	s	26.9	22.1	26.6	11.7	31.4	–	36.6	92.6	63.4	34.1
Ata06, TD8b, H-3, 11	s	≈25.9	–	22.9	10.8	28.0	24.2	32.9	>87.7	>58.4	33.1
Ata02, TD8b, G-7, 75	d	>22.8	≥20.5	22.9	11.0	–	–	>29.6	89.0	–	–
Astragalus		Lext	Lm	Lint	DTp	DTp'	DTd				
Ata2002, TD8b, G-9, 39	s	39.4	33.0	42.3	27.0	24.0	27.6				
Ata2002, TD8b, G-7, 103	s	36.6	29.1	34.4	23.9	21.7	23.0				
Ata2002, TD8b, G-9, 17	s	41.5	..	38.7	26.6	23.8	26.0				
Ata94, TD8, t28, H-16, 39	d	39.2	<33.4	–	25.7	22.8	24.9				
Ata94, TD8, t28, H-16, 39	d	39.3	32.2	–	25.7	24.5	≥24.9				
Ata2002, TD8b, F-12, 59	s	>44.3	35.2	>40.7	28.2	25.5	–				
Ata03, TD8b, G-5, 27	s	44.2	36.3	40.9	28.0	24.9	27.7				
Ata05, TD8b, H-3, 18	d	41.6	32.5	38.2	25.6	22.8	24.4				
Ata06, TD8b, G-4, 128	s	–	36.9	42.9	29.1	26.2	29.9				
Ata06, TD8b, H-4, 9	d	41.9	..	39.6	27.2	24.4	26.6				
Ata06, TD8b, G-3, 5	s	41.7	33.2	37.9	27.6	25.2	26.7				
Ata02, TD8b, G-17, 97	s	–	–	–	24.7	22.2	–				

Table 21
Measurements of the metacarpals of *Dama vallonnetensis* from Atapuerca TD8. ** estimated value.

Metacarpal (Mc III + IV)	DAPp	DTp	DAPpf	DTpf	DAPmini	DTmini	DTdf	DAPIII	DTIII	DAPIV	DTIV	L	LIII	LIV
Ata94, TD8, t28, G-16, 34	s	–	–	–	–	–	–	23.1	15.8	–	–	–	–	–
Ata94, TD8, t28, H-16, 36	s	–	–	–	–	–	–	–	15.5	≥21.9	14.6	–	–	–
Ata2002, TD8b, G-10, 39	?	–	–	–	–	–	–	22.5	15.0	23.7	–	–	–	–
Ata2002, TD8b, G-9, 39	s	24.5	34.9	22.2	31.3	18.5	20.5	juv	–	–	–	–	–	–
Ata2002, TD8b, G-9, 29	s	≈23	≈31.8	–	–	–	–	–	–	–	–	–
Ata2002, TD8b, G-9, 33	d	–	–	–	–	–	–	32.4	21.5	14.8	21.5	14.6	–	–
Ata2002, TD8b, G-10, 3	d	≈24.1	32.3	≈20.8	29.1	–	–	–	–	–	–	–	–	–
Ata2002, TD8bG-8, 39 + 55	s	23.0	30.6	14.6	28.2	14.1	<20.9	29.5	21.2	13.2	21.3	14.2	219.1	212.7
Ata2002, TD8bG10, 51 + 52	d	24.6	33.5	22.4	30.0	<19.3	20.0	–	–	–	–	–	–	–
Ata2002, TD8b, G-10, 57	?	–	–	–	–	–	–	33.5	23.0	15.5	22.8	15.6	–	–
Ata2002, TD8b, G-9, 39	s	24.3	37.7	21.8	34.4	18.0	20.4	–	–	–	–	–	–	–
Ata2002, TD8b, G-8, 62	d	–	–	–	15.8	–	–	32.9**	–	–	23.9	15.1	235	≈228
Ata04, TD8b, F-13, 3	s	23.1	20.7	32.8	28.9	–	–	–	–	–	–	–	–	–
Ata04, TD8b, G-4, 2	d	–	–	–	14.0	–	–	31.1	21.8	15.0	22.0	14.4	–	–
Ata04, TD8b, G-6, 27	s	≥19.6	28.1	19.6	27.1	–	–	–	–	–	–	–	–	–
Ata04, TD8b, G-5, 99	s	..	36.4	..	35.4	..	22.6	35.4	248.9	244.3
Ata03, TD8b, G-3, 18	d	22.9	31.7	20.3	29.8	–	–	–	–	–	–	–	–	–
Ata2002, TD8b, G-8, 89	s	–	29.0	–	–	15.2	17.7	31.2	≥21.6	–	>21.2	14.6	225.7	223.0
Ata03, TD8b, G-6, 31	s?	–	–	–	–	–	–	32.7	21.8	15.5	21.8	15.7	–	–
Ata05, TD8b, H-2, 3	..	–	–	–	–	<20.6	–	–	–	–	–	–	–	–
Ata06, TD8b, G-4, 82	s	–	–	–	–	16.3	19.5	31.5	21.7	14.7	21.9	14.8	>227	–
Ata06, TD8b, H-3, 43	d	juv	–	–	15.3	–	–	32.5	22.2	15.0	21.7	≈14.2	–	–
Ata06, TD8b, G-3, 115	..	–	–	–	–	–	–	29.1	20.4	13.3	20.7	13.2	–	–
Ata06, TD8b, G-3, 113	d	–	–	–	–	15.2	19.3	31.9	32.8	15.2	–	≥15.2	–	–
Ata2002, TD8b, G-10, 4	d	–	–	–	–	15.2	–	>32	22.1	15.1	–	–	–	–

Table 22
Measurements of the metatarsals of *Dama vallonnetensis* from Atapuerca TD8.

Metatarsal (Mt III + IV)	DAPp	DTp	DAPpf	DTpf	DAPmini	DTmini	DTdf	DAPIII	DTIII	DAPIV	DTIV	L	LIII	LIV
Ata94, TD8, t29, H-16, 56	s	≈34.0	≈27.9	≈28.9	–	≤19.3	18.1	–	–	–	–	–	–	–
Ata94, t28, G-17, 5	s	–	–	–	–	17.4	18.5	–	juv	–	juv	–	–	–
Ata94, TD8, t28, G-17, 5	..	–	–	–	–	–	–	–	–	–	–	–	–	–
Ata2002, TD8b, H-8, 7	d	–	–	–	–	–	–	33.3	22.7	15.4	22.5	15.4	–	–
Ata2002, TD8b, G-9, 8	s	–	–	–	–	–	–	–	juv	–	juv	–	–	–
Ata2002, TD8b, G-10, 3	s	–	–	–	–	≤17.7	≤18.6	–	–	–	–	–	–	–
Ata2002, TD8b, G-8, 29	d	31.9	29.2	27.6	26.9	–	–	–	–	–	–	–	–	–
Ata2002, TD8b, G-8, 37	d	–	–	–	–	–	–	–	–	15.4	20.1	15.7	–	–
Ata06, TD8b, G-4, 144	..	–	–	–	–	–	–	36.0	25.3	16.2	24.9	17.1	–	–
Ata06, TD8b, G-13, 1	d	–	–	–	–	≤17.3	18.3	–	–	–	–	–	–	–
Ata06, TD8b, G-3, 109	s	33.6	28.8	29.3	26.6	16.8	18.3	–	juv	–	juv	–	–	–

Table 23

Measurements of the distal articulations of the metapodials of *Dama vallonnetensis* from Atapuerca TD8 (* = juvenile).

Metapodial (Mc/MT)		DAP _{III/IV}	DT _{III/IV}
Ata94, TD8, t29, I-16, 34	l	>21.6	≥15.5
Ata94, TD8, t29, I-16, sc	l	22.7	14.8
Ata94, TD8, t29, I-16, sc	r	22.5	14.5
Ata2002, TD8b, G-9, 7	r	≥20.9	14.2
Ata2002, TD8b, G-9, 5	l	20.8	14.8
Ata2002, TD8b, G-8, 40*	l	22.8	15.6
Ata2002, TD8b, G-8, 40*	r	22.8	15.2
Ata94, TD8, t29, I-16, sc	l	22.7	14.8
Ata94, TD8, t29, I-16, sc	r	22.5	14.4
Ata03, TD8b, G-5, 28*	r	23.1	15.2
Ata06, TD8b, H-3, 31*	r	20.5	14.1

Table 24

Measurements of the first phalanges of *Dama vallonnetensis* from Atapuerca TD8.

Phalanx III/IV-1		DAPp	DAPpf	DTp	L	DAPd	DTd
Ata94, TD8 base, I-17, sc	r	23.0	21.7	16.8	—	—	—
Ata94, TD8, t28, G-17, 17	l	22.0	20.2	17.7	48.8	14.3	14.7
Ata2002, TD8b, G-7, 78	l	23.9	21.6	17.2	≥54.3	—	—
Ata2002, TD8b, G-8, 61	r	23.7	23.5	16.8	53.9	15.6	15.4
Ata2002, TD8b, G-8, 38	r	22.2	22.2	16.4	—	—	14.9
Ata2002, TD8b, G-8, 61	r	23.6	22.0	19.1	53.9	15.8	15.4
Ata2002, TD8b, H-8, 21	l	20.3	18.7	14.6	48.8	13.6	14.1
Ata2002, TD8b, G-7, 27	r	20.6	19.3	16.3	—	—	—
Ata2002, TD8b, F-13, 23	r	—	—	>>15	>52.1	≥14.7	—
Ata94, TD8, t29, H-16, 58A	l	18.9	18.6	15.1	48.2	13.6	13.6
Ata04, TD8b, G-14, 21	l	23.9	22.9	17.9	54.2	15.2	15.1
Ata04, TD8b, G-5, 47	l	23.3	22.3	17.0	51.2	15.4	15.3
Ata04, TD8b, G-5, 12	r	23.4	22.8	17.5	54.8	14.7	15.8
Ata04, TD8b, G-14, 25	..	—	—	—	—	—	—
Ata04, TD8b, G-5, 43	l	19.5	17.6	14.2	45.2	12.5	12.9
Ata04, TD8b, G-5, 16	r	22.3	20.5	17.1	49.2	>14.4	>15.2
Ata04, TD8b, G-5, 70	l	≥19.8	≥17.1	15.8	46.8	13.2	13.9
Ata04, TD8b, G-14, 15	r	—	—	16.3	>48.4	—	14.3
Ata03, TD8b, G-3, 14	l	—	—	—	—	13.6	14.4
Ata03, TD8b, G-5, 52	r	23.9	21.8	17.6	50.8	15.0	15.5
Ata03, TD8b, G-6, 52	l	—	≈20.1	17.1	—	—	—
Ata03, TD8b, G-15, 3	l	21.9	20.3	17.4	51.2	14.0	15.1
Ata03, TD8b, G15, 6	l	23.7	22.9	17.5	53.9	15.1	15.1
Ata03, TD8b, G-5, bn	l	—	—	—	—	14.6	15.7
Ata05, TD8b, H-3, 15	r	21.5	19.0	15.6	51.2	13.9	14.9
Ata05, TD8b, H-3, 24	l	—	—	—	>46.5	13.9	14.4
Ata05, TD8b, G-3, 10	r	19.9	19.2	15.2	47.0	13.9	14.2
Ata05, TD8b, G-4, 2	l	19.7	18.6	15.9	48.8	13.6	14.0
Ata05, TD8b, H-3, 36	r	≥22.0	≥19.4	16.3	48.0	13.6	14.4
Ata06, TD8b, G-4, 116	l	—	—	—	—	≈17	≥12.7
Ata06, TD8b, G-3, 34	r	21.9	20.6	16.5	48.9?	14.1	14.7
Ata06, TD8b, H-3, 19	r	21.6	20.3	12.4	51.0	15.0	15.4
Ata06, TD8b, H-3, colada inf., bn	l	—	—	—	—	14.9	15.2
Ata06, TD8b, H-4, 3	r	21.6	21.1	16.6	45.4	14.0	13.9
Ata06, TD8b, H-4, 15	r	20.7	18.5	17.0	51.5	14.9	15.1
Ata06, TD8b, H-4, 11	l	21.5	19.5	16.3	—	13.6	14.1

Table 25

Measurements of the second phalanges of *Dama vallonnetensis* from Atapuerca TD8.

Phalanx III/IV-2		DAPp	DTp	L	DAPd	DTd
Ata94, TD8, t28, G-18, 2	r	23.4	17.5	—	—	—
Ata94, TD8, t28, G-16, 38	r	21.0	16.1	34.6	18.8	12.6
Ata94, TD8, t28, G-17, 25	r	20.6	15.8	34.1	18.6	≥12.7
Ata2002, TD8b, G-12, 39	l	20.7	—	37.9	19.2	14.2
Ata2002, TD8b, G-7, 45	r	21.1	16.2	—	—	>12.3
Ata2002, TD8b, H-8, 1	r	22.4	17.1	37.9	18.5	13.3
Ata2002, TD8b, F-12, 58	l	22.2	16.6	37.1	18.1	13.1
Ata2002, TD8b, G-7, 45	r	20.6	16.2	—	—	12.9
Ata2002, TD8b, G-7, 96	r	—	≈15.7	33.6	19.9	13.2
Ata04, TD8b, G-5, 67	l	22.0	16.7	37.3	18.6	13.5
Ata04, TD8b, G-5, 32	l	19.9	14.4	34.4	16.6	11.3
Ata04, TD8b, G-14, 13	r	21.5	16.3	36.1	≥16.9	≥12.3

Table 25 (continued)

Ata04, TD8b, G-5, 68	r	>21.0	17.2	33.8	18.9	12.8
Ata03, TD8b, G-4, 23	r	19.0	14.9	31.8	17.4	11.8
Ata03, TD8b, G-6, 24	r	—	≥16.7	—	17.9	12.9
Ata03, TD8b, G-5, 34	r	22.6	16.9	38.7	18.1	17.9
Ata03, TD8b, G-5, bn	r	—	—	—	18.7	≥12.4
Ata05, TD8b, F-13, 2	r	33.2	24.9	49.5	30.4	22.1
Ata05, TD8b, H-3, 7	r	≥22.1	16.5	34.2	17.2	12.3
Ata05, TD8b, H-3, 8	r	21.9	17.2	34.5	17.5	12.3
Ata05, TD8b, H-3, 4	r	21.6	16.1	34.8	17.1	12.2
Ata05, TD8b, E-12, 13	r	—	14.9	≥28.9	≈17	—
Ata06, TD8b, G-4, 2	l	22.0	17.0	36.5	19.0	13.3
Ata06, TD8b, G-4, 86	l	18.4	14.9	30.7	18.0	12.0
Ata06, TD8b, G-4, 23	r	20.7	16.2	≥33.4	19.6	≥12.8
Ata06, TD8b, G-4, 143	r	—	16.7	37.2	—	—
Ata06, TD8b, G-4, 28	l	19.7	15.2	>34.0	17.1	12.4
Ata06, TD8b, G-4, 30	r	19.6	16.0	33.4	18.2	12.1
Ata06, TD8b, G-4, 46	l	—	—	—	≈17	≥12.7
Ata06, TD8b, G-3, 6	r	22.2	17.6	37.6	17.9	>13.3
Ata06, TD8b, G-3, 107	r	>23.4	19.3	≥39.4	19.7	14.2
Ata06, TD8b, G-3, 91	l	—	—	—	—	—

Phalanx II/IV-2		DAPp	DTp	L	DAPd	DTd
Ata06, TD8b, G-3, 99	l	7.8	4.0	9.2	7.3	3.5

Table 26

Measurements of the third phalanges of *Dama vallonnetensis* from Atapuerca TD8.

Phalanx III/IV-3		DAPp	DAPp'	DTp	L
Ata94, TD8, t28, H-16, 36	r	23.2	20.5	12.7	34.3
Ata2002, TD8b, G-12, 39	l	20.8	18.8	12.5	37.5
Ata2002, TD8b, G-8, 82	..	—	—	≥13.3	39.1
Ata2002, TD8b, G-9, 58	l	22.4	19.9	13.9	36.5
Ata2002, TD8b, G-8, 26	l	23.2	18.9	15.0	—
Ata04, TD8b, G-14, 27	r	—	—	>11.6	>34.9
Ata04, TD8b, G-6, 13	l	22.6	21.9	17.3	>35.5
Ata04, TD8b, F-14, 22	r	21.4	19.6	13.1	36.1
Ata03, TD8b, G-5, 12	l	21.6	19.9	13.2	37.1
Ata05, TD8b, H-3, 16	r	—	—	14.1	35.1
Ata05, TD8b, H-3, 37	l	22.5	18.9	15.1	38.2
Ata05, TD8b, H-3, 21	r	22.3	18.8	13.7	37.4
Ata05, TD8b, G-13, 1	r	22.8	20.8	13.6	33.2
Ata05, TD8b, F-13, 9	r	22.7	19.5	12.6	—
Ata06, TD8b, G-4, 101	r	22.4	19.8	12.9	35.4
Ata06, TD8b, G-4, 132	l	23.2	21.7	13.9	34.2
Ata06, TD8b, H-3, 6	l	21.7	18.8	12.2	35.7
Ata06, TD8b, H-3, 4	r	23.1	21.7	14.3	39.4
Ata06, TD8b, H-3, 25	r	24.9	22.7	14.4	—
Ata06, TD8b, H-3, 36	r	25.0	21.1	14.0	39.6
Ata06, TD8b, G-3, 46	l	23.3	20.2	13.3	38.9
Ata06, TD8b, G-3, 22	l	23.1	21.0	14.7	38.9

Table 27

Measurements of the sesamoids of *Dama vallonnetensis* from Atapuerca TD8.

Sesamoid behind phalanx 1		L	DT	DAP	DAP'
Ata04, Td8b, G-5, 58	l axial	17.0	7.4	9.6	8.0
Ata04, TD8b, G-5, 87	l axial	18.7	8.7	11.0	8.5
Ata04, TD8b, G-6, removido	l axial	15.8	7.6	8.9	7.7
Ata04, Td8b, G-5, 34	l axial	15.6	17.4	8.4	6.6
Ata04, TD8b, G-5, 35	r abaxial	14.4	7.0	11.2	10.8
Ata05, TD8b, G-13, 9	l axial	18.2	9.0	10.8	8.4
Ata05, TD8b, F-13, 13	r axial	16.1	6.8	8.9	7.8
Ata05, TD8b, F-12, 11	l axial	>16.6	8.0	>9.7	>8.6
Ata06, TD8b, G-4, 129	l abaxial	—	7.1	>11.9	..
Ata06, TD8b, G-4, 11	r axial	17.9	7.9	9.4	7.8
Ata06, TD8b, G-4, 108	l axial	16.4	7.8	9.0	7.7
Ata06, TD8b, G-4, 133	l axial	17.9	8.5	9.3	8.0
Ata06, TD8b, H-4, 7	r abaxial	13.7	6.9	11.3	10.5
Ata04, TD8b, G-5, 36	l abaxial	14.2	6.5	11.5	11.1

Sesamoid behind Phalanx 3		L	DT	DAP
Ata06, Td8b, G-3, 25	l	5.6	10.8	4.5

Table 28Measurements of the teeth of *Bison voigtstedtensis* from Atapuerca TD8.

Upper cheek teeth			DAP	DAPb	DTa	DTp	DTpp	Ha	Ta
Ata2002, TD8b, G-9, 42	M ³	s	31.5	–	–	–	–		
Ata2002, TD8b, G-7, 90	M ³	d	31.9	29.6	26.1	23.9		>54.8	
Ata2002, TD8b, F-11, 69	M ²	s	≥32.8	≥31.0	28.4	28.0			
Ata94, TD8, t29, I-16, 55	M ^{1/2}	s	21.2	20.5	23.6	25.2			
Ata94, TD8, t29, I-16, 24	M ^{1/2}	..	–	–	–	–			
Ata06, TD8b, G-3, 4	M ^{1/2}	s	30.4	26.4	27.0	26.6			
Ata94, TD8, t29, I-16, 23	M/D ^x	d	–	–	–	–			
Ata2002, TD8b, B-8, 21	M ^{1/2}	d	34.3	30.3	28.0	28.0		>>56	
Ata2002, TD8b, F-12, 31	M ²	s	29.6	27.9	27.4	27.8			
	M ¹		22.0	21.4	24.0	26.1			
	P ⁴		18.9	16.5		20.4			
Ata2002, TD8b, G-8, 28	P ⁴	d	18.8	15.8		20.3			
Ata2002, TD8b, G-8, 72	P ²	d	18.3	17.8	14.1	–			
Ata06, TD8b, H-3, 27	D ^{3/4}	s	28.6	23.4	–	–			
Ata04, TD8b, H-6, 6	D ³	d	–	–	13.4	–			
Ata2002, TD8b, F-11, 23	D ³	d	28.6	22.3	14.6	18.3			
Ata2002, TD8b, G-9, 20	D ³	s	–	–	–	17.5			
Ata2002, TD8b, F-12, 13	D ²	d	15.9	≥15.0	–	12.4			
Lower cheek teeth			DAP	DAPb	DTa	DTp	DTpp	Ha	Ta
Ata2002, TD8b, G-14, 2	M ₃	d	44.1	42.8	18.0	16.1	10.3		0.9
Ata94, TD8, t2	M _{1/2}	s	22.3	21.9	15.9	18.7			1.0
Ata94, TD8, t27, G-17, 1	M _{1/2}	d	≥30.5	≈26.9	≈16.2	≈15.8			
Ata2002, TD8b, F-12, 16	M _{1/2}	d	29.9	26.0	16.6	17.8			1.0
Ata2002, TD8b, G-14, 2	M _x	d	–	–	–	–			
Ata02, TD8b, F-12, 55	M _{1/2}	s	30.6	–	–	–			
Ata2002, TD8b, F-12, 28	P ₃	d	20.6	18.5	9.9	11.8			
Ata05, TD8b, G-8, 1	P ₂	s	11.8	10.7	8.2	9.2			
Ata2002, TD8b, G-11, 23	D ₄ ?	?	–	–	–	–	–		
Incisors			DT	DMD	DLL	Hli	DTroot	DLLroot	
Ata04, TD8b, G-5, 9	I ₁	s	15.7	15.0	10.4	21.1			
Ata2002, TD8b, G-9, 1	I ₂	d	13.0	11.7	10.3		7.8	8.8	
Ata2002, TD8b, G-8, 4	DI ₂	d	7.2	6.9	5.4		4.8	4.5	

Table 29Measurements of the bones of *Bison voigtstedtensis* from Atapuerca TD8.

Rib		DAPhf	DThf	DHF					
Ata06, TD8b, H-3, 13	d	19.7	30.2	>15					
Humerus		DAPd	DTd	DTdf	R1	R2	R3	R4	R5
Ata94, TD8, t35, G-18, 1	d	–	–	–	–	–	–	–	–
Ata2002, TD8b, F-9, 10	d	–	84.4	82.7	52.1	43.3	47.5	36.3	37.5
Ata05, TD8b, G-3, 12	s	–	–	≥73.7	≈48	–	45.7	33.3	35.3
Radius		DAPdf							
Ata06, TD8b, G-3, 114	d	37.8							
Ulnar		DAP	DT	H	Ha				
Ata04, TD8b, H-6, 8	s	36.9	21.8	44.1	31.7				
Ata06, TD8b, G-3, 77	s	≥41.3	22.5	>36.6	32.2				
Pisiform		DAP	DTf	H	Hf				
Ata06, TD8b, G-3, 59		28.8	13.1	25.4	19.0				
Magnum		DAP	DT	H	h				
Ata03, TD8, H-4, 1	s	46.7	49.0	27.9	24.4				
Metacarpal V		DAPp	DTp	L					
Ata06, TD8b, G-3, 85	s	14.4	11.7	>47.6					
Cuneiform II + III		DAP	DT						
Ata06, TD8b, G-4, 14	d	37.6	22.8						
Metapodial		DTd	left DAP_{III/IV}	left DT_{III/IV}	right DAP_{III/IV}	right DT_{III/IV}			
Ata94, TD8, t28, G-16, 45	?			32.0	>38	32.0			
Ata06, TD8b, G-3, 29	?		>33.7	29.5				juv.	

in *Dama* and unlike in *Cervus*. This is so in, for instance, Ata02, TD8b, G-17, 103, but occasionally this is the other way around in a specimen (Ata06, TD8b, G-3, 5), which has the same size as the other specimens and is far too small for *Cervus* (Table 20).

The **scapula** tends to have the tuberosity hook-shaped as in *Dama*, but this is variable.

Other teeth and bones are indicated in the tables, but are not described here in detail.

3.8.3. Remarks on taxonomy and evolution

The European Pleistocene deer with a size between the roe and red deer include the living fallow deer and many other species, which share many morphological features besides the modest size. All agree that the name *Dama* applies to the species with palmate antlers (*Dama dama*, *D. mesopotamica* and *D. clactoniana*), while the non-palmate species are under discussion and the different authors include them in different genera, such as: *Dama* (e.g. Azzaroli, 1948, 1953; Pfeiffer, 1999; Van der Made, 1998b, 1999a, 2001, etc.; Croitor, 2006; Breda and Lister, 2013), the living genera *Axis*, *Rusa* or *Cervus* (e.g. Spaan, 1992; H.D. Kahlke, 1997, 2001a; De Lumley et al., 1998; Croitor, 2006), or in a genus based on a fossil species, like *Metacervoceros*, *Pseudodama*, and *Euraxis* (Azzaroli, 1992; Di Stefano, 1995a; Di Stefano and Petronio, 1998, 2002; Croitor, 2006).

Lister (1996) described many morphological differences between *Dama* and *Cervus*. The non-palmate *Dama*-like deer tend to have the morphologies that are typical of *Dama* and differ in these from *Cervus*, *Rusa* and *Axis*. A cladistic analysis groups several of these species with *Dama* (Pfeiffer, 1999). These species have antlers with three or four points, but the recently described species *Dama robertorum* includes an apparently adult antler from Soleilhac (Fig. 13/6) with only two points and a skull cap with a pair of antlers from Pakefield, which are not totally complete, but which both widen towards, what could have been the split between two tines (Fig. 13/5). If this were indeed the case, it would have had three tines. The fossils of a small deer from Atapuerca TE9 were assigned to *D. vallonnetensis* and include a complete antler with three points, that is very similar to the material from Pakefield.

The new data mentioned above, suggest the existence of two divergent evolutionary trends within the *Dama*-like deer: one with increasing antler complexity, leading to the palmate *Dama*, and another one, which went un-noticed until recently, with decreasing antler complexity, leading to the two pointed *Dama robertorum*.

Fig. 16 includes a bivariate diagram that shows that the *Dama*-like deer are divided in two groups according to the robusticity of their metacarpals. Species with gracile metapodials (length around 7 times distal width; $L \approx 7$ DTdf) include *Dama rhenana rhenana* and *Dama rhenana philisi* with three points, and *Dama vallonnetensis*, of which the number of points is not known from the type material. Species with robust metapodials ($L \approx 6.5$ DTdf) include the three pointed “*Cervus philisi*” *valliensis* Heintz, 1970 and the four pointed *Dama nestii*. Metapodials recently assigned to *Dama roberti* (Breda et al., 2015) are robust and others previously described by Azzaroli (1953) are very similar in size and proportions (Fig. 16). The deer from Capena (Petronio, 1979) has an antler with three points and robust metapodials (Fig. 16).

These differences in robusticity of the metapodials seem small, but there are similar and consistent differences between the living species of deer, which probably reflect different ecologies. Though it is not the intention here to discuss the ecology of these species, it should be noted that functional morphology suggests that longer metapodials mean a longer stride length and probably a greater maximum speed, beneficial in open landscapes, while shorter metapodials might allow faster acceleration, favourable when cover is near.

The taxa in the range chart in Fig. 13 can be characterized using a limited number of features:

- *Dama valliensis* has robust metapodials (Fig. 16), three pointed antlers and probably a bifurcation of the main beam and brow tine that is situated far from the burr. Heintz (1970) named the taxon as a subspecies of “*Cervus philisi*”, but it differs clearly from that species in having more robust metapodials.
- *Dama robertorum* has robust metapodials (Fig. 16) and may have reduced the points in the antler from three to two (Fig. 13/5 and 13/6); it is a larger species than the previous one (Fig. 16). The deer from Capena seems to belong to either *D. robertorum* or *D. valliensis*.
- *Dama nestii nestii* has robust metapodials (Fig. 16), four pointed antlers (Fig. 13/2) and a bifurcation of the main beam and brow tine that is far above the burr (Fig. 13).
- *Dama nestii eurygonos* has a wider angle between the brow tine and main beam (Azzaroli, 1992) and is a little larger than *D. n. nestii*, if the metapodials from Selvella indeed belong to this subspecies (Fig. 16), while dentally, there does not seem to be size difference (Fig. 15).
- *Dama rhenana* has gracile metapodials (Fig. 16), three pointed antlers (Fig. 13/3) and a very high first bifurcation of the antler (Fig. 13/diagram). It is a small species (Fig. 15/diagram). Spaan (1992) considered “*Cervus philisi*” synonymous with “*Cervus rhenanus*”. However, they are not exactly identical: what is here considered the subspecies *D. r. philisi* is a little larger than *D. r. rhenana* (Fig. 16).
- *Dama vallonnetensis* has gracile metapodials (Fig. 16) and a first bifurcation that is much lower than in *D. rhenana* (Fig. 13).
- The later *Dama* had palmate antlers (Fig. 13/7) and low bifurcations (Fig. 13/diagram).

These different species have to belong to different lineages, but the lowering of the bifurcation seems to be a general trend, occurring in all of them (Fig. 13). If there are parallel lineages, it would be expected that there are differences in size between the contemporary species. Nevertheless, the size of the M_3 of the different samples do not suggest species of different size at the same time, but rather a large scale general size fluctuation over 2.5 Ma for all species.

The material from the lower part of the Atapuerca Gran Dolina sequence has previously been assigned to *Dama* cf. *clactoniana*, *Dama nestii?* *vallonnetensis*, *Dama “nestii” vallonnetensis* and *Dama vallonnetensis* (Soto, 1987; Azaña and Sánchez, 1990; Van der Made, 1998a, 1999a, 2013; Rodríguez et al., 2011). Now there are large collections from the different levels of Gran Dolina, which permit to discuss the affinities of the deer of each level individually. The deer from TD8 shares gracile metapodials with *Dama rhenana*, *D. vallonnetensis* and the earliest palmate *Dama*, *D. clactoniana* (Fig. 16). The bifurcation between brow tine and main beam is low, as in *D. vallonnetensis* and unlike in *D. rhenana*, where it is high (Fig. 13). The distal part of the antler is not known from TD8, so the number of tines or the possible presence of a palmation is not known in this level. The size, as indicated by the M_3 size, is in the range of *Dama vallonnetensis* and is smaller than in *D. clactoniana* from Swanscombe or Bilzingsleben (Fig. 15). These features allow to attribute the material from TD8 to *Dama vallonnetensis*.

The species *Dama roberti* was mentioned above. Pomel (1853, p. 103) named a *Cervus roberti* and gave in the synonymy “*Cervus dama polignacus* F. Robert”. Azzaroli (1953, p. 83) indicated that “the name *Cervus dama polignacus* was given by Robert (1829) to two incomplete skeletons from Solilhac: one of them is identical with his *Cervus solilhacus* (now *Megaceros solilhacus*) from the same locality. The second is a small red deer with abnormal characters;

Pomel (1853) named it *Cervus roberti*." Breda and Lister (2013, p. 157) wrote "Robert (1829) described the small cervid remains from Soleilhac, here the paratype of *D. roberti*, immediately after his description of a much larger deer species from the same area that he named *Cervus Dama polignacus*". The combination of all this information suggests, that the holotype of *Cervus roberti* Pomel, 1853 is the paratype of *Dama roberti* Breda and Lister, 2013. If this indeed is the case, the two species could be synonymous and homonymous at the same time. However, the situation is more complicated. Since Breda and Lister (2013) named the species in honour of two men, Robert Mutch and Félix Robert, this is an inadvertent error and should be corrected (ICZN, 1999, article 32.5.1) to *Dama robertorum* Breda and Lister, 2013. With this correction, there is no homonymy anymore. There is still another complication. The holotype of *Dama robertorum* is from Pakefield and the main beams of the antlers become distally markedly flattened, suggesting a split into two tines, so that the antler has three points. The geologically younger paratype from Solilhac has two points. If these differences would reflect an evolutionary reduction of the number of tines, the two names would apply to the two different forms.

3.9. *Bison*

Family Bovidae.

Genus *Bison*.

Bison voigtstedtensis Fischer, 1965.

3.9.1. *Material*

All material studied here is listed in Tables 28–30. A taphonomic study assigned 60 fossils to a bovine, representing a minimum of 4 individuals (Rosell et al., 2010).

3.9.2. *Description and comparison*

The **upper molars** (Fig. 17/1-2) have marked styles on the buccal side and interlobular columns on the lingual side. They have high crowns. This morphology is typical of the Bovini.

The **lower molars** (Fig. 17/3) have marked stylids on the lingual side and interlobular columns on the buccal side. The third lobe of the M₃ has no fossid, but is a single crest formed by the pentatonid and its pre- and endocristid. Again, these morphologies are typical of the Bovini. The size of the M₃ from TD8 is in the lower ranges of *Bison schoetensacki* from its type locality Mauer, *B. schoetensacki lagenocornis* from its type locality Süssenborn and *B. menneri* from its type locality Untermassfeld (Fig. 14). It is slightly bigger than the few specimens of *B. degiulii* from its type locality Pirro Nord and in the ranges of *B. voigtstedtensis* from its type locality Voigtstedt and of the material from Süssenborn, which might belong to the latter species.

The upper and lower premolars, deciduous molars and incisors have also bovine morphologies.

The **first phalanx** (Fig. 11/2) has a very low and wide facet for the abaxial sesamoid (feature a), a marked fossa in the middle below the proximal articulation (feature b), no indication of an proximo-axial tuberosity on the dorsal side (feature d of Heintz, 1970). Features a, b, and d are as in Bovidae and unlike in Cervidae, while Heintz' description of feature c is less clear. In addition, it has a distal articular surface with a longitudinal groove that is U-shaped, while in the giant deer it is more open V-shaped. The proximal articular surface is wide and low and its dorso-abaxial corner sticks out making the contour of the facet square. The facets for the sesamoids are low. Though the phalanges are small for a bison, these are all morphological differences with the phalanges of the giant deer and similarities to *Bison*. There is a well developed ridge on the axial edge of the plantar surface. The specimens from TD8 are more robust than those of the giant deer and are similar to those of *B. schoetensacki*, but are not more robust than the most

Table 30
Measurements of the phalanges and sesamoids of *Bison voigtstedtensis* from Atapuerca TD8.

Phalanx 1		DAPp	DAPpf	DTp	L	DAPd	DTd
Ata94, TD8, t29, G16, 61	l	juv				≈24.0	>24.6
Ata94, TD8, t29, I-16, 64	r	juv				21.4	25.8
Ata2002, TD8b, G-14, 9	r						
Ata06, TD8b, G-3, 58	r	juv				≥21.3	≥24.0
Ata06, TD8b, G-04, 36	l	36.6	34.9	33.8	65.7	24.0	28.8
Ata06, TD8b, G-04, 62	r	37.8	32.4	33.4	69.5	22.8	31.0
Ata06, TD8b, G-04, 119	l	–	≥31.3	≥29.1	70.9	23.6	30.2
Phalanx 2		DAPp	DAPp'	DTp	L	DAPd	DTd
Ata94, TD8, t29, I-16, 39	l	34.3	32.3	29.1	48.8	29.4	25.2
Ata2002, TD8b, F-11, 58	r	31.8	30.9	30.9	47.1	≥27.4	≥23.3
Ata06, TD8b, G-04, 38	l	37.3	32.2	31.8	49.8	31.5	27.9
Ata06, TD8b, G-04, 61	r	36.5	32.7	32.8	51.0	31.2	29.7
Ata06, TD8b, G-04, 114	r	–	–	33.0	–	–	–
Phalanx 3		DAPp	DAPp'	DTp	L		
Ata04, TD8b, G-6, 4	r	–	–	26.6	>76.7		
Ata06, TD8b, G-3, 48	l	45.4	39.3	24.0	71.1		
Ata06, TD8b, G-04, 41	l	46.5	38.6	26.8	81.2		
Ata06, TD8b, G-04, 59	r	43.1	35.3	26.2	74.3		
Sesamoid behind Phalanx 1			L	DT	DAP	DAP'	
Ata06, TD8b, G-4, 72	l	abaxial	20.6	14.5	21.1	20.2	
Ata06, TD8b, G-4, 63	l	axial	23.8	14.6	14.9	12.9	
Ata06, TD8b, G-4, 74	r	axial	23.5	15.6	15.1	13.4	
Ata06, TD8b, G-4, 76	r	abaxial	20.5	15.0	19.7	17.9	
Ata06, TD8b, G-3, 119	l	abaxial	≥20.6	10.5	>18.2	18.2	
Sesamoid behind Phalanx 3		L	DT	DAP			
Ata06, TD8b, G-4, 37	l	14.4	24.9	12.9			
Ata06, TD8b, G-4, 60	r	14.7	23.9	13.6			

robust *B. menneri*. For a bison, they are small, as is the case in *B. giulii*. A comparison with *Leptobos* was made, but not included in Fig. 11 for keeping the figure simple. The phalanges of TD8 are as long as those of *Leptobos*, but wider and more robust.

The **second phalanx** (Fig. 9/2) is stout and has a wide and low proximal articular surface. The plantar edge of this surface is situated much more proximally, than the “post-articular surface” below it, especially at the axial side. The ridge in the middle of the articular surface forms a little protruding point at the plantar edge of this surface. These morphologies are common in Bovini, but not in deer. The phalanges from TD8 are very small compared to those of *Bison menneri*, *B. schoetensacki*, *B. priscus* and *Bos primigenius* (Fig. 9). No comparisons with the second phalanx of the very small species *Bison degiulii* could be made, nor with *Bison voigtstedtensis*. The phalanges are robust compared to those of *Leptobos* and one of them is distinctly more robust. In a previous study (Van der Made, 1998a, fig. 8), a bison phalanx from TD8 and one from Voigtstedt taken as typical for *B. voigtstedtensis* were compared to data on *Bison schoetensacki*, *B. priscus* and *Bos primigenius* taken from Sala (1987) and were found to be much narrower. This would imply, that *B. voigtstedtensis* does not only have more slender metapodials than *B. schoetensacki*, but also more slender second phalanges, making identification of such bones very easy. However, Sala's measurements for the three species have nearly all DAPd < DTd and differ from the measurements one of us (JvdM) took on these species. The most plausible explanation is that Sala (1987) measured the specimens in a different way. Also the more extensive comparisons suggest that the phalanx from Voigtstedt seems more likely to be *Megaceroides*. Here the measurements are taken as indicated by Van der Made (1996, fig. 20) and the four specimens from TD8 are not narrower than those of *Bison schoetensacki* and *Bos primigenius* (Fig. 9).

The **third phalanx** differs from the phalanx of the large Cervidae, which are also present in TD8, in having two well developed foramina on the proximal part of the dorsal side (Fig. 11/4), an axial and an abaxial one, and a small one on the proximo-plantar part of the axial side. The abaxial dorsal foramen does not occur in the Cervidae, and usually (but not always) the axial proximo-plantar foramen is lacking in the Bovidae (Heintz, 1970).

There are several other bones, which have relatively small sizes, but their morphologies suggest they belong to the bison, rather than to the giant deer. The sesamoids are low and rounded, and the carpals low and wide, like in the Bovinae and unlike in Cervidae. The humerus as a distal articulation, that is low and wide.

3.9.3. Remarks on taxonomy and evolution

Bisons appeared in western Europe during the later part of the Early Pleistocene, probably close to 1.2 Ma (Van der Made, 2013), replacing the more primitive bovine *Leptobos*. Around the middle of the Middle Pleistocene, the aurochs *Bos primigenius* appeared. Commonly recognized species of bison in western Europe include *Bison voigtstedtensis*, *Bison priscus*, the living species *Bison bonasus*, as well as *Bison degiulii* and *Bison menneri* (Flerov, 1975; Masini, 1989; Crégut-Bonnoure and Guérin, 1996; Sher, 1997). A small bovine from Atapuerca TG (Van der Made, 1999c) and also TD10 is now believed to be a form close to *Bison priscus*. The temporal distribution of these species is indicated in Fig. 14.

The different species of *Bison* differ in the morphology of the skull, which is relatively narrow in *Bison menneri* and *B. voigtstedtensis* (Fischer, 1965; Soto, 1987; R.D. Kahlke, 2006), and wide in *B. degiulii*, *B. schoetensacki* and *B. priscus* and *B. bonasus* (Flerov, 1975; De Giuli et al., 1987; Sala, 1987). They differ also in orientation, shape and size of the horn cores. Sher (1992, 1997) documented major differences in size and robusticity of the metacarpals: *Bison menneri* has gracile metacarpals, *B. schoetensacki* and *B. giulii*

have more robust, the ones of *B. giulii* being clearly smaller, and *B. priscus* has still more robust metacarpals.

Sher (1997) noted the presence of different types of metacarpals in Süssenborn. In a much increased data set, the *B. schoetensacki* clusters are much wider than Sher's and include his “*Bison priscus*”, while it becomes apparent that Sher's Roterberg sample is more likely to be *Bison priscus*. Most of the Süssenborn metacarpals cluster with *B. schoetensacki*, while one clusters indeed with *B. menneri*. It has a great length, but it is slender and has a small width, suggesting it belonged to a small individual or species and this is most probably *Bison voigtstedtensis*, which shares also skull and horn core morphology with *B. menneri*. The teeth of *B. voigtstedtensis* are also on average smaller than those of *B. menneri* and *B. schoetensacki* (Fig. 17). There are a number of teeth from Süssenborn, which are too small for *Bison schoetensacki*, the dominant species in this locality, and which more likely belong also to *B. voigtstedtensis*.

Remains from the lower part of the Gran Dolina sequence have previously been tentatively assigned to *Bison voigtstedtensis* (Soto, 1987; Van der Made, 1998a, 1999a, etc.). This was largely based on a skull from TD4 or a lower level and a metapodial from TD4, but now there is more material from TD8.

The phalanges from TD8 have a series of morphologies typical of Bovidae or Bovini and are more robust than those of *Leptobos*, and smaller than those of *Bos primigenius* (Figs. 9 and 11). Compared to the different species of *Bison*, they are smaller than those of *B. menneri* and *B. schoetensacki* and smaller and more gracile than those of *B. priscus*. In addition, the first phalanges are close to those of *B. degiulii*. No second phalanges of that species could be studied and also no phalanges, that were reliably assigned to *Bison voigtstedtensis*, were included in Figs. 9 and 11. Since the teeth of *B. voigtstedtensis* are smaller than those of *B. menneri* (Fig. 14), the same might be expected for the phalanges. The material from TD8 seems thus to be most similar to *B. voigtstedtensis* or *B. giulii*. The latter, is a much older species and may have evolved into *B. schoetensacki* long before the fossil association of TD8 was formed. These data support the earlier tentative assignation to *Bison voigtstedtensis*. *Bison voigtstedtensis* is a relatively rare species and much of its skeleton is not well known, but the continuing excavations in the lower part of Gran Dolina may solve this.

4. The context: faunal changes around the E-M Pleistocene transition

The lower part of the Gran Dolina sequence, including TD8, is situated chronologically in the middle of the climatic and faunal changes, which occurred from the end of the Early to the beginning of the Middle Pleistocene. This can be seen in Fig. 18, which includes around 50 localities, covering ages from around 1.2 Ma to 0.5 Ma, and their large mammal species or genera. The date of about 1.2 Ma is chosen, because that is when the faunal change (which “grosso modo” is associated to the E-M Pleistocene transition) started, and the date of 0.5 Ma is chosen because it is sufficiently after that transition.

The localities in Fig. 18 were selected on the basis of their associations being varied and representative of a particular time, the recording of first or last appearances, and the availability of independent means of dating. Table 31 gives the references to the published faunal lists of the localities and the different dates of the localities, dating techniques and references. Even though there is on average about one locality per 15 ky, the faunal associations of some times or climatic cycles are not well represented and more localities are needed. However, many localities, even well-known ones, with a varied faunal list cannot be precisely assigned to faunal associations of a particular time, because they lack the important taxa.

Table 31

The localities discussed in Section 4 on faunal change and in Fig. 18, their ages and references. Bibliographic references to the faunas, and, in case material from a locality has been studied by one of us, the acronym of the museum or university where it has been studied. An indication on the age is given, either in ka (kilo annum), Ma (mega annum), or palaeomagnetic chron or subchron, a guide fossil, etc. The method of “dating” is given: AAR = amino acid racemization, BC = biochronology, CN = cosmogenic nuclides, ESR = electron spin resonance, IRSL = infrared stimulated luminescence, K/Ar = potassium / argon, PM = palaeomagnetism, IR-RF = infrared radiofluorescence, OSL = optically stimulated luminescence, TL = thermoluminescence, US = Uranium Series.

Locality	Reference fauna	Age	Reference age
Vértészölös Mosbach 2	Jánossy (1986), HGSB Koenigswald and Heinrich, (1999), NMM	BC: <i>Arvicola</i>	Koenigswald and Heinrich (1999)
Hundsheim	Koenigswald and Heinrich, (1999), NMW IPUW	BC: <i>Arvicola</i>	Koenigswald and Heinrich (1999)
Mauer	Koenigswald and Heinrich (1999), SMNK, GPIRKUH	IR-RF: 420±23 to 607±55 ka; ESR-US: 388±29 to 627 + 73/-71 ka (for the whole sequence)	Wagner et al. (2010)
Westburry B3-8 Pontón de Oliva Soleilhac	Bishop (1982), Lister et al. (2010), Breda et al. (2010) Sesé and Soto (2000), MNCN Lacombat, (2005), MCP	BC: <i>Arvicola</i>	Stuart and Lister (2001)
Isernia la Pineta	Sala (1996), IGUF	>602±2 ka; 610±10 ka; BC: <i>Arvicola</i>	Roebroeks and Van Kolfschoten, (1995) Coltorti et al. (2005), Sala (1996)
Bad Frankenhausen	R.D. Kahlke, (1995), Koenigswald and Heinrich, (1999), IQW	in lower Elsterian sediments	R.D. Kahlke, (1995), Koenigswald and Heinrich (1999)
Süssenborn	H.D., Kahlke, (1969b), IQW	BC: <i>Mimomys</i> ; in lower Elsterian sediments	H.D. Kahlke (1969b)
Stránská Skála Bed 13 Prezletice Konéprusy C718	Musil, (1995a,b), MMB Fejfar, 1995 Koenigswald and Heinrich, (1999), NMP	BC: <i>Mimomys</i> , “cold” association BC: <i>Mimomys</i> , “cold” association BC: <i>Mimomys</i> , “cold” association	Musil, (1995b) Koenigswald and Heinrich (1999)
West Runton Tiraspol Pakefield Voigtstedt Gombaszög (Gombasek) Stránská Skála Bed C Würzburg-Schalksberg Atapuerca TD8	Stuart (1982), Lister et al. (2010), NHM Nikiforova et al. (1971), VMM, GIN Stuart and Lister (2001), Lister et al. (2010), Breda et al. (2010), NHM H.D. Kahlke, (1965a), IQW, SMS Kretzoi (1938) Musil (1995a,b), HGSB Mäuser (1987) Rodríguez et al. (2011), Van der Made (2001), Van der Made (2001), García and Arsuaga (2001), MNCN, IPHES	BC: <i>Mimomys</i> BC: <i>Mimomys</i> BC: <i>Mimomys</i> , OIS 17 BC: <i>Mimomys</i> BC: OIS17 / OIS19 BC: <i>Mimomys</i> PM: <780 ka; 820±140 ka; 602±52 ka	Stuart (1982) Nikiforova et al. (1971) Parfitt et al. (2005) H.D. Kahlke (1965a) Wagner and Gasparik (2015) Musil (1995b) Parés et al. (2013), Falguères et al. (1999), Berger et al. (2008)
Atapuerca TD7	Rodríguez et al. (2011), Van der Made (2001), García and Arsuaga (2001), IPHES	PM: 780 ka in top of unit	Parés et al. (2013)
Cueva Victoria Lakhuti 2 Dorn Dürkheim 3	Carbonell et al. (1981), IPS, MAC Vangengeim et al. (1988), PIN Franzen et al. (2000), FISF	PM: >780 ka PM: >780 ka PM: >780 ka; BC: latest Early Pleistocene PM: >780 ka	Franzen et al. (2000) Parfitt et al. (2010)
Happisburgh HB3 Akhalkalaki Apollonia 1	Parfitt et al. (2010) Vekua (1986), GSM Koufos and Kostopoulos (1997), Kostopoulos, (1997), AUT	BC: 0.6–0.9 Ma	Koufos and Kostopoulos (1997, fig. 2)
St. Prest Atapuerca TD6	Guérin et al. (2003) Rodríguez et al. (2011), Van der Made (1999), García and Arsuaga, (1999), IPHES	PM: >780 ka; BC: 0.1 Ma PM: 0.936–0.98 Ma	Guérin et al. (2003) Parés et al. (2013)
St. Privat Atapuerca TD4-5	Lacombat (2005) Rodríguez et al. (2011), Van der Made (2001), García and Arsuaga, 2001, IPHES, MB	BC: 1.8–1 Ma PM: 0.936–0.98 Ma	Lacombat (2005) Parés et al. (2013)
Huércar 1	Alberdi and Bonadonna (1989), MNCN	PM: normal (Brunhes/Jaramillo); OSL: ~420–570 ka BC	Scott and Gibert (2009), Demuro et al. (2015) Giles Pacheco et al. (2011), López-García et al. (2012)
El Chaparral	Giles Pacheco et al. (2011), MHMV	BC	Koenigswald and Tobien (1987)
Mosbach 1	Koenigswald and Tobien (1987), Koenigswald and Heinrich (1999), NMM	PM: Jaramillo	Koenigswald and Tobien (1987)
Vallonnet Untermassfeld Colle Curti Atapuerca TE9	Moullé et al. (2006), MPRM R.D. Kahlke, (1997a, 2001a, 2006), IQW Coltorti et al., 1998 Rodríguez et al. (2011), Van der Made (2001), García and Arsuaga, (2001), IPHES	PM: Jaramillo PM: Jaramillo PM: earliest Jaramillo CN: 1220±140 ka	De Lumley et al. (1988) Wiegank (1997) Coltorti et al. (1998) Carbonell et al. (2008)
Atapuerca TE7	Rodríguez et al. (2011), Van der Made (2001), García and Arsuaga (2001), IPHES	CN: 1130±180 ka	Carbonell et al. (2008)
Atapuerca TE7-14	Rodríguez et al., 2011; Van der Made, 2001; García and Arsuaga, 2001; IPHES	PM: reversed, Matuyama	Carbonell et al. (2008)
Ceyssaguet Trlica	Lacombat, (2005), Guérin and Faure (1997) Crégut-Bonnouere and Dimitrijević (2006), Forsten and Dimitrijević, (2003), DPFMGB, Van der Made and Dimitrijević (in press)	K/Ar: <1.3 Ma	Kaiser and Croitor (2004)
Sainzelles Quibas Fuente Nueva 3 Barranco León 5 Venta Micena	Lacombat (2005) Montoya et al. (1999), MNCN Toro et al. (2010) Toro et al. (2010) Agustí (1987), IPS, MNCN	BC: 1.3 Ma BC: 1.3–1 Ma US/ESR: 1.19±0.21 Ma BC: 1.2 Ma BC: 1.2 Ma;	Agustí et al. (1987) Montoya et al. (1999) Duval et al. (2012) Agustí et al. (1987) Agustí et al. (1987)

(continued on next page)

Table 31 (continued)

Locality	Reference fauna	Age	Reference age
Pirro Nord	De Giuli et al. (1987), IGF	AAR: 1095±55 ka;	Ortiz et al. (200)
Aliakhmon q Profil	Steensma (1988), TUC	US/ESR: 1.37 Ma	Duval et al. (2012)
Kapetianos	Steensma (1988), TUC	BC: 1.3 Ma	Sardella et al. (1998)
Libakos	Steensma (1988), TUC	BC: -1.15 Ma/Farneta Unit	Steensma (1998)

The large mammals included in Fig. 18 are about 70 species or genera of Proboscidea, Perissodactyla, Artiodactyla, Carnivora and Primates, but do not include *Homo*, nor Mustelidae, which generally are small. Though literature is cited for the faunal lists (Table 31), classifications may have been changed on the basis of specialised literature (dedicated to a taxon and not to a fossil locality), the discussions in the previous section, or on own observations. If there is an established, or likely, ancestor–descendant relationship between species, the thick lines indicating their temporal range are connected. Probably not all cases are indicated. The taxa are ordered by appearance and disappearance, save for the cases of evolution from a previously present species.

At the first sight, Fig. 18 shows gradual change, but in detail, there appear to be many discrete events. At the right side, the appearance of 36 taxa can be seen, concentrated in approximately 10 events. At the left side the disappearances are not that prominent. In part this is an impression due to the ordering of the taxa, which favours the pattern of appearance, but it is also real. There are about 22 disappearances, so the diversity increased. Due to the cyclic appearance of the glacial fauna, the disappearances are not always clear: for instance, *Praeovibos priscus* re-appeared, *Soergelia elisabethae* probably did not and *Ovibos pallantis* re-appeared much later (in a time not covered by the figure). The different events are discussed below. It should be understood, that these events are described on the basis of the data in Fig. 18, but that new dates for the localities, new fossils, systematic revisions or the inclusion of new localities may change the grouping of individual dispersals in events and the dates of these events.

4.1. The dispersals of hippopotamus and two species of large deer

The first faunal event in Fig. 18 is the arrival of *Hippopotamus tiberinus* (= ? *H. georgicus* = ? *H. gorgops*; Section 3.4.), a large deer indicated as *Megaloceros* sp. L, a large deer called *Eucladoceros* sp. T and possibly one of the *Dama*-like deer. *Megaloceros* sp. L from Libakos has been discussed by Van der Made and Tong (2008). *Eucladoceros* sp. T includes material from Trlica (Van der Made & Dimitrijević, in press) and probably material from Kapetianos, described originally as *Eucladoceros* aff. *boulei* (Steensma, 1988), which shares the morphology of the antler base.

These taxa appear first in three Greek localities, of which Libakos has a varied faunal list and the other two poor faunal lists. Two of the localities still have *Leptobos*. These three localities are geographically close and probably also chronologically, though there might be minor age differences. Libakos was “dated” biochronologically to 1.2 Ma (Steensma, 1988).

Hippopotamus gorgops, present in the North of Africa dispersed northward, reaching Israel, where it is known from Ubeidiya (about 1.4 Ma), and apparently reaching Greece a little later. The *Eucladoceros* probably came from East Asia and the *Megaloceros* from Asia or eastern Europe. None of these species are cold or arid adapted and if their arrival is related to climatic or environmental change, this may have been during the very warm stage 37, or alternatively the warm stages 47/49, close to 1.4 Ma.

4.2. Events possibly related to stage 36: the dispersal of the first bison

A second event seems to be the arrival of *Bison degiulii*, *Soergelia minor*, “*Capra*” *alba*, *Praeovibos* and maybe *Bison menneri*.

The bison have been discussed in Section 3.9. *Bison degiulii* appears first in Pirro Nord, Sainzelles, Capena and Redicicoli (De Giuli et al., 1987; Masini, 1989). They replaced *Leptobos*, but may have co-existed for a short time. Material from Venta Micena was initially assigned to *Bison* sp. (Moyà-Solà, 1987), later to *Bubalus* sp. (Martínez-Navarro, 1992) and more recently out of 938 specimens one was assigned to *Hemibos* sp. aff. *H. gracilis* and one to *Bison* sp. (Martínez Navarro et al., 2011). Each of these two identifications is based on about one promille of the available material, and is therefore preliminar. The first specimen, assigned to *Hemibos*, is a skull fragment, which has similarities to *Leptobos brevicornis*, defined on the basis of material from Gongwangling and present also in Yunxian (Hu and Qi, 1978; Echassoux et al., 2008), rather than to *Hemibos gracilis*, defined in the much older locality Longdan (Qiu et al., 2004). Both are bovines with backward directed horn cores. In any case, it seems that *Leptobos* survived for a short time after the arrival of bison. Material from Barranco León 5 and Fuente Nueva 3 (Martínez-Navarro et al., 2010) either represents primitive bison or *Leptobos*. A large bison identical to *B. menneri* appears first in Atapuerca TE9.

Soergelia and *Praeovibos* are present in Venta Micena and Pirro Nord (De Giuli et al., 1987; Moyà Solà, 1987). *Soergelia* is also cited from Monte Argentario, which is possibly close in age to Pirro Nord (Siori et al., 2014). This marks the first occurrence of *Soergelia* in western Europe, but its origin is known: there is a much older record from Dmanisi (Vekua, 1995), with a morphology that is similar to the one from Venta Micena. Citations of possible still older *Praeovibos* are from Casa Frata (De Giuli and Masini, 1983; Sher, 1992) and Fonelas (Garrido, 2008b), with ages in the range 2.1 to 1.7 Ma. However, these do not include horn cores (the most significant element). A metapodial from Casa Frata, that has been cited as *Praeovibos*, is a little more robust than the few ones known of *Megalovis*, the more common ovibovine of this time, but still could fit this taxon.

“*Capra*” *alba* was first described from Venta Micena, but is also present in Quibas and Huéscar and seems to be present in Barranco León 5 (Moyà Solà, 1987; Montoya et al., 1999, 2001; Van der Made et al., 2008; Martínez-Navarro et al., 2010). It is different from *Capra baetica*, described from Fonelas (Arribas and Garrido, 2008), situated below the Olduvai.

Most of the aforementioned localities have similar faunas, including Venta Micena, Barranco León, Fuente Nueva 3, Quibas, and Sainzelles, but several of these have *Equus altidens*, while Pirro Nord has a more primitive *Equus* (see Section 3.1.) and therefore is probably a little older. Based on biochronology, Pirro Nord was placed between 1.2 and 1.3 Ma (Sardella et al., 1998), but later, after lithic industry was found, older ages were mentioned, based on rodents and correlations to Venta Micena (Arzarello et al., 2007). Fuente Nueva 3 has been dated close to 1.19 ± 0.21 Ma (Duval et al.,

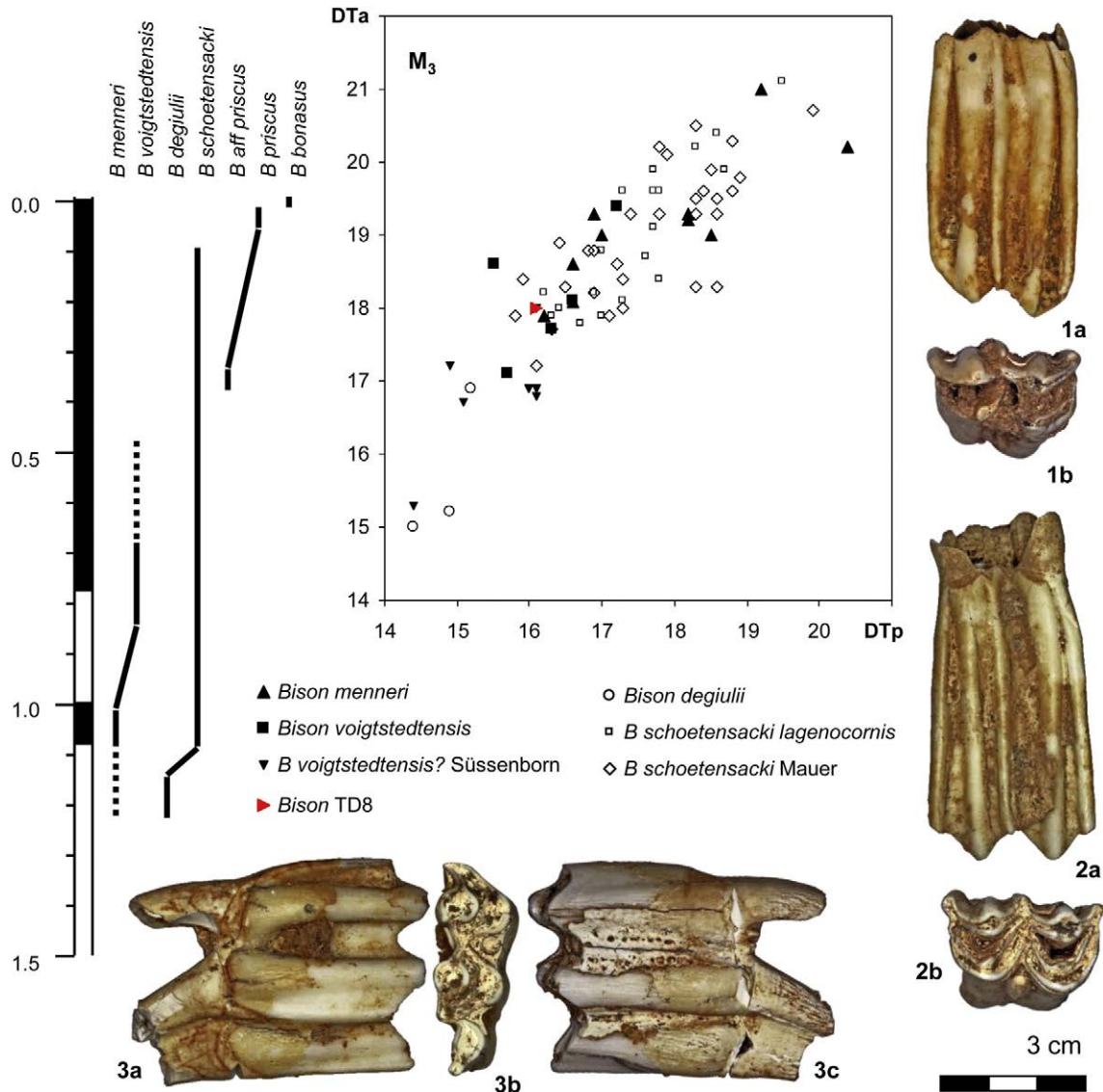


Fig. 17. *Bison voigtstedtensis* from Atapuerca TD8: 1) Ata02, TD8b, G7, 90 – right M²: a) buccal, b) occlusal view; 2) Ata02, TD8b, G8, 21 – right M²: a) buccal, b) occlusal view; 3) Ata02, TD8b, G12, 26 – right M₃: a) lingual, b) occlusal, c) buccal view. The temporal distribution of the European bison. Bivariate diagram of the width of the anterior (DTa) and posterior lobe (DTp) of the M₃, comparing *Bison voigtstedtensis* from Atapuerca TD8 with: *B. menneri* from Untermassfeld (IQW); *B. voigtstedtensis* from Voigtstedt (IQW); *B. voigtstedtensis?* from Süssenborn (IQW), *B. degiullii* from Pirro Nord (IGF); *B. schoetensacki lagenocornis* from Süssenborn (IQW); *B. schoetensacki* from Mauer (SMNK).

2012). Venta Micena was dated by amino acid racemisation to 1095 ± 55 ka (Ortiz et al., 2000). Duval et al. (2012) analysed five samples for combined U-series/ESR dating: two very young samples were discarded for technical reasons and the remaining three gave an average of 1.37 Ma (Duval et al., 2011). However, a value of 1.79 Ma is much older than the other two dates used; if it would be considered as an outlier, the remaining values would give as an average 1.105 Ma, close to the date by Ortiz et al. (2000).

Soergelia and *Praeovibos* are generally considered to be cold adapted taxa, and, at least in the Middle Pleistocene, they tend to be present in glacial faunas (Sections 4.5. and 4.8). However, in Venta Micena, the more primitive species of these genera occur along with *Hippopotamus*, usually seen as an interglacial taxon. It is possible, that in the Early Pleistocene, these Ovibovini were not yet so much adapted to cold as well as to open environments. In any case, it seems likely, that these taxa were adapted to open or dry landscapes. The dispersal of Ovibovini, “*Capra*” *alba* and bison, adapted to open or arid environments into western Europe may have occurred during a cold period, when open environments

prevailed; once in open and dry landscapes in the SW of Europe, they could have survived into the following warm periods. Stage 36 is colder and longer than previous isotope stages and marks the beginning of the shift towards the 100 ka climatic cycles, culminating in the well known Middle and Late Pleistocene glaciations. During these well studied glaciations, the northern limit of distribution of trees moved southward and, as result, the taiga disappeared and the tundra and steppe fused into, what is called, the “Mammoth steppe” (e.g. Guthrie, 1990). The open landscape could have permitted dispersals into western Europe of species adapted to open landscapes, which then could reach Spain, which probably always had a more open landscape than Europe north of the Pyrenees. This could have happened during stage 36, allowing bison to reach western Europe. The restauration of the Taiga during the following warm period may have been a gradual process. This is well studied for the later interglacials: temperatures rise, pollen diagrams show predominance of herbs (open landscapes), subsequently one tree type after the other arrives and becomes abundant. It has been proposed, that this process, permitted humans to

reach western Europe at the end of stage 36 (Van der Made, 2011a, 2013).

4.3. Events before or around the beginning of the Jaramillo

Various taxa appeared and disappeared shortly before or around the beginning of the Jaramillo.

Bison schoetensacki is very similar to *B. degiulii*, but is a little larger (Section 3.9.) and its appearance is probably by evolution from that species.

Stephanorhinus hundsheimensis is cited from several pre-Jaramillo localities. The taxonomic problems regarding this taxon have been discussed above (Section 3.2.) and in some cases it seems very likely, that the rhinoceros present in these localities is the small form, assigned here to *S. etruscus*. If this is the case, *S. hundsheimensis* may have appeared within the Jaramillo.

Eucladoceros giulii is present in Untermassfeld (H.D. Kahlke, 1997), but also in Vallonnet (Section 3.6). The fossils of large deer from TE9 fit *E. giulii*. This is a large deer with slender metapodials and antlers with tines originating at the front of the main beam, and with little indication of these tines being bifurcated, save for the brow tine (Fig. 10). The earliest *Eucladoceros* had antlers with many simple tines, but by the Olduvai, these tines bifurcated, resulting in very complex antlers. Still later, the smaller *E. tetraceros* appeared, which had again simple, non-bifurcating tines. A large deer from Ceysaguet with antlers with tines that do not or nearly not bifurcate was assigned to *E. ctenoides* (Croitor and Bonifay, 2001). For various reasons, it seems more likely, that this material belongs *E. tetraceros* or *E. giulii*. The appearance of the latter could be related to the demise of *Eucladoceros* sp. T.

Hemitragus bonali is first recorded in Vallonnet (Moullé, 1998; Moullé et al., 2006).

Untermassfeld and Vallonnet have *Sus* sp., which resembles *Sus strozii* in the section of its canine, but which differ in other features. The same form could be present in Atapuerca TE9.

The name *Ursus etruscus* used to be applied to late Early Pleistocene bears, but now *Ursus rodei* has been defined in Untermassfeld (Musil, 2001) and *Ursus dolinensis* in Atapuerca TDW4 (García and Arsuaga, 2001). The cladogram by the latter authors is compatible with a model in which *U. etruscus* gave rise to the brown bear *U. arctos* on the one hand and the cave bear lineage with *U. savini*, *U. deningeri* and *U. spelaeus* on the other. It is not clear in how far this affects the attributions of bear material slightly older than the Jaramillo, that were traditionally assigned to *U. etruscus*.

The equid *Equus altidens* became rare or absent and a larger, but otherwise similar horse appeared, to which the names *Equus wuesti*, *E. nalaikhensis* and *E. hipparionoides* have been applied, while later *E. altidens* reappeared. It is not clear whether this is a fluctuation in size, or whether these are different lineages (see Section 3.1; Fig. 4). *Equus wuesti* is present in Untermassfeld and *E. hipparionoides* in Akhalkalaki (Vekua, 1986; Musil, 2001).

The oldest locality in which these changes have been recorded may be Ceysaguet, if *E. giulii* is indeed present there. This locality is in a maar, and the underlying rock has been dated to 1.3 Ma, and the fossils have been estimated to date to 1.2 Ma (Kaiser and Croitor, 2004). The next locality that records these changes is Atapuerca TE9, dated to 1220 ± 140 ka, and the underlying TE7, dated to 1130 ± 180 ka (Carbonell et al., 2008), resulting in a likely age of a little less than 1.2 Ma. Given the differences in fauna, these localities are probably younger than Fuente Nueva 3, which has been dated to 1.19 ± 0.21 Ma (Duval et al., 2012). The next oldest localities are Jaramillo in age. Since the taxa which dispersed are mostly probably adapted to warm or more or less closed environments, these events may have occurred during stages 33 or 31.

4.4. Events around the end of the Jaramillo

Crocota crocuta, is first recorded in Atapuerca TD4-8 and Akhalkalaki and somewhat later in Casal Selce near Rome and has a previous record in Ubeidiya and in Africa (García and Arsuaga, 2001; Sardella and Petrucci, 2012).

Eucladoceros aff. *giulii* is first recorded in Atapuerca TD4-6, Akhalkalaki and Apollonia 1 and replaced *E. giulii*, present in Untermassfeld and Vallonnet (Section 3.6.).

Sus scrofa is first recorded in Atapuerca TD6 (Van der Made, 1999a) and a bone from TD5 may belong to the same species (Section 3.3.). It replaced a species with verrucose canines, present in Untermassfeld and Vallonnet.

Unequivocal antlers of *Cervus elaphus* have been recovered from Atapuerca TDW4, while dental remains attest its presence in Dorn Dürkheim. The species has been cited from Mosbach 1, but it is not clear on which material this is based. Further to the east, it is described from Trlica in Montenegro (Section 3.5).

The evolution of *Megaceroides* with large brow tines and branching antlers to *M. solilhacus* with reduced brow tines and palmate antlers seems to have occurred around the end of the Jaramillo (Section 3.7).

The latest record of “*Capra*” *alba* and possibly of primitive *Soergelia* are in Huéscar and this age. However, the locality has recently been dated (Demuro et al. 2015), but that very young date is incompatible with the microfauna. There might be a hiatus in the presence of *Soergelia*, starting at this time, but this is problematic, since most samples of this bovid (including Huéscar and Vallonnet) do not have enough systematically relevant elements.

Crocota, *Sus scrofa*, and *Eucladoceros* aff. *giulii* are first recorded in Atapuerca TD4-6 and this is also the case for the first certain *Cervus elaphus* in western Europe. These levels are situated below the Santa Rosa event and above the Jaramillo (Parés et al., 2013), bracketing these dispersals between 0.99 and 0.936 Ma. *Crocota crocuta* came from SW Asia and favoured open landscapes, while the other species are temperate and came from mid latitudes in Asia or eastern Europe. At least the latter events occurred probably during a temperate stage, probably 27 or 25.

4.5. The appearance of the giant elk

In mid-latitude Europe, the elk *Alces carnutorum* was replaced by the giant elk *Alces latifrons*. The former is last recorded from a unit below the main site at Voigtstedt and at St. Prest, and the latter is first recorded from Happisburgh and Dorn Dürkheim. For discussions on this event see Breda and Marchetti (2005), Ravazzi et al. (2005), as well as Parfitt et al. (2010). Here the entry of *A. latifrons* is taken at the moment when very large forms replace much smaller ones (Van der Made et al., 2014).

Praeovibos re-appeared after a period of absence and is known from Apollonia, where the material is rather poor. In Atapuerca TD7, below the Brunhes–Matuyama boundary, there is good material suggesting that this is *Praeovibos priscus*, the species known from the Middle Pleistocene.

Soergelia has in Europe a total temporal range of just some 0.6 Ma, but there are six species names for them or very similar forms: *S. minor*, *S. intermedia*, *Megalovis balcanicus*, *Ammotragus europaeus*, *S. brigittae*, *S. elisabethae* (Schaub, 1951; Moyà Solà, 1987; Kostopoulos, 1997; Moulé et al., 2004; Crégut-Bonnoure & Dimitrijević, 2006). Probably there are more names than real species.

The geologically oldest and second named species, is *Soergelia minor* from Venta Micena, which has slender horn cores, that are oriented more upwards and which curve forwards in a pronounced way. *Megalovis balcanicus* from Trlica has similar horn cores, save for that these are very flattened. Its horn cores are very different

from those of the typical *Megalovis*. *Soergelia intermedia* is defined on poorer material from Trlica. Moullé et al. (2004) named the species *Ammotragus europaeus* on the basis of material from Vallonnet and used the supposed replacement of *Soergelia minor/brigitiae* by *A. europaeus* to assign localities like Fuente Nueva 3, Apollonia 1 and Venta Micena to certain ages. Crégut-Bonnoure (2007) considered *A. europaeus* a synonym of *S. elisabethae*. It certainly looks like *Soergelia*, but since no horn cores and no complete metapodials are known, it is not possible to know what kind of *Soergelia* it is. The *Soergelia* from Apollonia 1 has been described as *S. brigittae*, but its horn cores are not known (Kostopoulos, 1997). A metacarpal from Apollonia is robust and indicates an animal larger than *S. minor*; it approaches those of *S. elisabethae*. The geologically youngest (Süssenborn and Rastenberg) and first named species is *S. elisabethae*, which is also the largest (though differences are small) and which has massive horn cores, which taper rapidly towards the tip, and which are directed outwards and a little upwards and then curve forwards (Schaub, 1951; H.D. Kahlke, 1969a). The orientation, curvature and shape of the horn cores of *S. elisabethae* are closer to the older and more primitive ovibovine *Megalovis*, while the horn cores *S. minor* seem to be more evolved. As a consequence, *Soergelia elisabethae* does not seem to be a descendant of *S. minor*, but rather a parallel lineage that retained a primitive morphology. The first record of this lineage or group in Europe may have been in Apollonia 1 (or else in Vallonnet).

Ovis occurs in Cueva Victoria and in Apollonia 1 (Crégut Bonnoure, 2007). After this there is no record until about 500 ka.

The localities that record these events are Dorn Dürkheim, Happisburgh, and Apollonia 1. Dorn Dürkheim is below the Brunhes–Matuyama boundary, but has no more precise dating (Franzen et al., 2000). Happisburgh HSB3 is also below the Brunhes–Matuyama boundary, has a “warm” fauna and has been correlated to either stage 21 or 25 (Parfitt et al., 2010). These localities, with *Alces latifrons*, might be stage 21 and St. Prest, with *Alces carnutorum*, from before the cold peak of stage 22. Apollonia 1 has no other dating than by biochronology and was initially believed to be between 0.6 and 1.0 Ma old (Koufos and Kostopoulos, 1997), later older dates have been proposed. *Eucladoceros* aff. *giulii* increased in size and is larger in Apollonia 1 and Akhalkalaki than in Atapuerca TD4–6. *Equus major* is believed to have given rise to *E. suessenbornensis* (Forsten, 1999). Various names have been applied to horses of this type: *E. major*, *E. athanasiui* and *E. apolloniensis* share metapodial size and proportions, as well as stenonid dental features. The latter was defined on the basis of fossils from Apollonia, while the apparently oldest record of *E. suessenbornensis* at Akhalkalaki. This might be an indication that Akhalkalaki is a little younger than Apollonia. Apollonia 1 records *Praeovibos* and *Soergelia*, which are suggestive of cold conditions. Apollonia 1 might date to stage 22 and the dispersal of the four taxa treated in this section, might be related to this cold stage.

4.6. Striped hyaena and baboon

The baboon *Theropithecus* was known from a single tooth from Cueva Victoria (Gibert et al., 1995), while a phalanx was either attributed to *Homo* (e.g. Gibert and Pérez-Pérez, 1989; Gibert et al., 2008) or to *Theropithecus* (Marínez-Navarro et al. 2005). There is also a record from India (Delson, 1993) and material from Ubeidiya has been tentatively assigned to this genus (Belmaker, 2010). Material from Pirro Nord was assigned to this genus (Rook et al., 2004), but seems now more probably to belong to *Hystrix* (Alba et al., 2014). Recently some new dental material was described from Cueva Victoria (Ferrández-Cañadell et al., 2014), which thus remains the only European locality with this genus.

Hyaena striata (= *H. hyaena*), *Pliocrocota perrieri* and *Hyaena prisca* are cited from numerous localities from the middle Middle Pleistocene onwards, such as Mosbach, Mauer, Hundsheim, L'Escaie, Ponte Galeria 3, Lunel Viel, etc. (Bonifay, 1971; Crégut-Bonnoure, 1996; Koenigswald and Heinrich, 1999; Milli and Palombo, 2005). These hyaenas have massive lower carnassials with a metaconid, as opposed to *Pachycrocota*, which has massive carnassials without a metaconid and *Crocota* which has slender carnassials without a metaconid. *Pliocrocota perrieri* or *Hyaena perrieri* was present in Europe till about 2 or 1.8 Ma, when it was replaced by *Pachycrocota brevirostris*. Today, *Hyaena hyaena* lives not only in Africa, but also in an area extending from Turkey to India. It seems likely that the Middle Pleistocene European hyaena is one species. It seems also more likely that it is more closely related to, or identical with, the living species, rather than with a species that lived in Europe before 1.8 Ma. The oldest European record after 1.8 Ma seems to be from Atapuerca TD8 (Rosell et al., 2010; Rodríguez et al., 2011). This is shortly after the appearance of *Crocota* in Europe and it appears to be long before the demise of *Pachycrocota*. So it seems that there was a long time that three hyaena species coexisted in Europe, though *Hyaena hyaena* does not seem to have been very common during the first 200–300 ky of its presence in Europe.

The appearance of the baboon is in Cueva Victoria, just below a palaeomagnetic reversal, that is either interpreted as the lower limit of the Brunhes or the Jaramillo (Ferrández-Cañadell et al., 2014). Cueva Victoria has a *Dama*-like deer, that is comparable in size to the Middle Pleistocene species/samples and larger than the Early Pleistocene ones. If the locality is placed below the Jaramillo, this would extend the range (towards older) of a number of species that are cited from there, whereas if it is placed just below the Brunhes, this does not extend the range of any species (towards younger). Other questions are, whether all specific determinations as used here are correct, or whether much value should be given to the known temporal range of rare species. A monograph with detailed descriptions is in press and this can be checked in the near future. For the time being, the locality is placed just below the Brunhes.

Atapuerca TD8 is placed just above the lower limit of the Brunhes (Parés et al., 2013). ESR and U–Th dating gave a mean age of 602 ± 52 ka (Falguères et al., 1999) and luminescence dating gave an age of 820 ± 140 ka (Berger et al., 2008). The fauna has various hold-overs from the Early Pleistocene, such as the small rhinoceros, here classified as *Stephanorhinus etruscus*, and *Eucladoceros*. Faunas that are correlated to stage 17 or even 19, such as Pakefield, Voigtstedt, West Runton and Tiraspol, have the large *S. hundsheimensis* and the giant deer *Megaloceros savini* and/or *Megacerooides*. The most likely correlation is of TD8 to stage 19 and the other faunas to stage 17 or the warm peak within stage 18.

Both *Hyaena* and *Theropithecus* came probably from or through SE Europe and SW Asia. Their dispersals may have been favoured by the same environments: relatively warm and open environments at the transition from stage 20 to 19. Alternatively, Cueva Victoria could be older than the Jaramillo, and in that case, the dispersal of the *Theropithecus* would coincide more or less with the appearance of a suid, a species of *Eucladoceros* and a new bear, which all are expected to have originated from different areas and environments.

4.7. Steppe mammoth, straight tusked elephant, caballoid horses and lion

The classic view on *Mammuthus* is that *M. meridionalis* evolved into the steppe mammoth *M. trogontherii*, acquiring more and

thinner plates or lamellas in the molars, the transition of one species to the other occurring between the localities of Voigtstedt and Süssenborn. However, Franzen et al. (2000) described an older sample from Dorn Dürkheim 3 as *M. trogontherii*, which would not fit the model. Lister et al. (2005) presented a different model, in which *M. trogontherii* originated in East Asia and gradually spread towards Europe in a complex process of dispersal, hybridisation and gene flow. They recognized samples with bimodal distribution of the features, suggesting the presence of the two species. This is the case with Sinyaya Balka, Dorn Dürkheim and Voigtstedt. In this scenario, the latest *M. meridionalis* is also in Voigtstedt, but *M. trogontherii* appears earlier.

Elephas antiquus or *Palaeoloxodon antiquus* was described from Huéscar (Mazo, 1989), a site that has been considered to be latest Early Pleistocene in age. Nevertheless, Lister (2004) considered the first straight tusked elephant of Europe to be the one from Pakefield. If *M. meridionalis* and *M. trogontherii* have coexisted in Europe as different species, and if the last record of the latter species is in Voigtstedt, the demise of this species may have been related to the appearance of *E. antiquus*.

Caballoid horses differ from stenonid horses, such as *E. suessenbornensis*, in having U-shaped instead of V-shaped linguaflexids in the lower cheek teeth and in having longer protocones in the upper teeth.

Eurasian caballoid horses include the domestic *Equus caballus* and its wild ancestor *Equus ferus*. Many fossil species have been named, which some include all in the living species (e.g. Azzaroli, 1990), while others recognize two or several separate species (respectively Eisenmann, 1991; Forsten, 1999). *Equus mosbachensis* is a very large species with robust metapodials. The living *Equus ferus przewalskii* is much smaller. There are also forms with less robust metapodials.

In a broad sense, caballoid horses replaced *Equus suessenbornensis*, but various opinions on how this occurred have been published. Forsten (1988, 1992) and Azzaroli (1990) were of the opinion that caballoid horses originated in North America and dispersed from there into Eurasia, where they occurred along with the large stenonid *E. suessenbornensis*. Eisenmann (1992) was of the opinion, that it is not possible to say where caballoids originated. Alberdi et al. (1995) included *E. suessenbornensis* in the caballoid group, which implies an older presence of caballoid species in Europe. In the latter scenario, the citation of both caballoid horses and *E. suessenbornensis* from the same locality, might be interpreted as variability in samples of an intermediate state of evolution. On the basis of DNA, Orlando et al. (2009) grouped caballoid horses with the new World Horses, separate from the Old World horses, including “sussemiones”. This would argue for an origin in the New World and dispersal into Eurasia. The localities where both types of horse are cited indicate then temporal overlap and, as a consequence, the dispersal of the former and the extinction of the latter are two events that are separated in time.

There is some discussion on some very old samples, such as Beresti, but Forsten (1992) cited the oldest European caballoid horses to be from Soleilhac, Tiraspol and Süssenborn. However, they are also present in Prezletice (Fejfar, 1995), Koneprusy (Koenigswald and Heinrich, 1999), Westbury and possibly in West Runton (Lister et al., 2010). These are *E. mosbachensis* or similar. The different *E. cf. germanicus* is cited from Bad Frankenhausen (Koenigswald and Heinrich, 1999). *Equus mosbachensis* and *E. suessenbornensis* are both large with robust limb bones and could be confused if the material is not good. They are occasionally cited from the same localities, but the co-occurrence of two so similar species raises the question how this functioned ecologically.

The oldest record of the lion *Panthera leo* is in Pakefield and Tiraspol (Nikiforova et al., 1971; Sala, 1996; Stuart and Lister, 2001).

Most of the localities that record these events are of early Middle Pleistocene age, though Sinyaya Balka and Dorn Dürkheim are below the Brunhes–Matuyama boundary (Franzen et al., 2000; Shchelinski et al., 2010). These are the localities, with, in the model of Lister et al. (2005), the earliest European *Mammuthus meridionalis*. Voigtstedt, Gombaszög, Prezletice, Pakefield and Tiraspol, are Middle Pleistocene, retain *Miomys*, but not the small *Stephanorhinus* and large *Eucladoceros*, which are still present in Atapuerca TD8. The large *Eucladoceros* is probably also still present in Würzburg-Schalksberg, for which no rodents are known. If Atapuerca TD8 and Würzburg-Schalksberg are correlated to stage 19, Voigtstedt and Gombaszög could be correlated to younger warm period in stage 18 and Pakefield and Tiraspol, where the first caballoid horses and lion are recorded in stage 17. Alternatively, the correlations could be respectively to stage 17 and the first warm peak of stage 15. A correlation of Pakefield to stage 17 or 19 has been proposed previously (Parfitt et al., 2005). The transition of *Mammuthus meridionalis* to *M. trogontherii*, whatever its nature (evolution, replacement by dispersal, or a more complex process), could have been a relatively short process comprised between stages 20 (Sinyaya Balka and Dorn Dürkheim) and 17 (Pakefield and Tiraspol?) or 16 (Süssenborn).

4.8. Reindeer, woolly rhinoceros, musk ox

The first European record of the reindeer *Rangifer*, is from Süssenborn, Bad Frankenhausen and Bornhausen (H.D. Kahlke, 1969b; R.D. Kahlke, 1995; Koenigswald and Heinrich, 1999).

The first record in Europe of the woolly rhinoceros *Coelodonta* is in Bad Frankenhausen and Bornhausen (Koenigswald and Heinrich, 1999; Kahlke and Lacombat, 2008), but there is also one tooth from Süssenborn (IQW).

The oldest European record of the musk ox *Ovibos* is also in Süssenborn: originally described as *O. suessenbornensis*, but presently included in *O. pallantis* (H.D. Kahlke, 1963; Crégut-Bonnoure, 2007).

All of these taxa appear to be adapted to cold conditions or open environments. They all occur first in Süssenborn. This locality and Rastenberg have *Soergelia elisabethae* (Schaub, 1951; R.D. Kahlke, 1995) and Bad Frankenhausen has also *Praeovibos priscus*, again “glacial” elements. These localities, with these “cold” faunas, are in the area where the Elsterian has been defined and are said to be from Elsterian sediments (R.D. Kahlke, 1995; Koenigswald and Heinrich, 1999). The Elsterian was an important glacial and its correlation to stage 16 seems likely. This is a long stage, and this would also explain, why there are relatively many localities with large mammals of this time, while the faunas of other glacials are known by fewer localities. The appearance of these taxa in Europe is probably by dispersal from Asia and due to the Elsterian glacial or cold conditions.

4.9. Leopard and black bear

The first *Ursus thibetanus* and the leopard *Panthera pardus* might be from Koneprusy C718 (Koenigswald and Heinrich, 1999). For the leopard this is perhaps also Voigtstedt, but the material is poor and the assignation uncertain (Thenius, 1965). The oldest records of black bears were reviewed by Wagner et al. (2011) and none of the old records could with certainty be assigned to *U. thibetanus*.

Koneprusy C718 still has *Miomys* and has an association that includes “cold” elements such as *Praeovibos* and *Soergelia*. It seems

likely that the locality is to be correlated to stage 16. However, it does not seem likely that the leopard and black bear dispersed into Europe during such cold conditions as the musk oxen and reindeer and possibly this happened early or late in stage 16, but not during the maximum, if indeed Koneprusy is the locality that first records these species.

4.10. Forest rhinoceros and dhole

The forest rhinoceros *Stephanorhinus kirchbergensis* is known from Mosbach 2 by a huge amount of fossils and it is well known from younger localities. It is also recorded from the Frankenbacher Sande (Döppes and Rosendahl, 2008). Some specimens of the large rhinoceros collection from Mauer were also assigned to this species (Schreiber, 2005). Like in Mauer, most rhinoceros material from Soleilhac belongs to *S. hundsheimensis*, but a single calcaneum was assigned to *S. kirchbergensis* (Lacombat, 2005). The species *S. kirchbergensis* is well represented in Tiraspol (Beliajeva and David, 1971).

The last record of *Xenocyon lycaonoides* and the first record of the dhole *Cuon* are both in Mosbach 2 (Koenigswald and Tobien, 1987). *Cuon* is also known from Hundsheim (Koenigswald and Heinrich, 1999). Mosbach is a complex locality, in which the fauna from the lower part of the lithostratigraphic unit “Graues Mosbach” is called Mosbach 2 and the fauna from the upper part Mosbach 3 (Koenigswald and Tobien, 1987; see also Section 3.5.3.). The former has predominantly “interglacial” species and the latter “glacial”. Possibly, this is an artificial division of a gradually changing fauna and possibly *Xenocyon* is from the lower part of the sequence and *Cuon* from somewhat higher.

Tiraspol still has the vole *Mimomys*, while Mosbach 2, Mauer and Soleilhac have *Arvicola*. Mauer has been dated: ten dates indicate ages from over 600 ka to over 400 ka (Wagner et al., 2010). Most dates are concentrated in or near stages 15 and 13. The fauna has mostly “warm” elements, including *Hippopotamus*, *Sus scrofa* and *Elephas antiquus*. Hundsheim and Mosbach 2 still have *Stephanorhinus hundsheimensis*, a species that was replaced by *S. hemitoechus* in faunas that are assigned to stages 12 and 11 (e.g. Arago sol G and Bilzingsleben; Lacombat, 2006; Van der Made, 2000, 2010). While Koenigswald and Tobien (1987) did not cite *S. hemitoechus* at all from Mosbach, Koenigswald and Heinrich, 1999 cite it from Mosbach 2, and indeed this species does occur in Mosbach (NMM). Possibly, *S. hundsheimensis* is replaced by *S. hemitoechus* within the sequence. The ages of Mosbach 2 and 3 are not known precisely, but could correspond to stages 13 and 12. Hundsheim is predominantly a warm fauna, which could correspond to stage 13. The first representatives of *Cervus elaphus* were large, and they are still large in Süssenborn (stage 16), but in Mosbach and Mauer the a-cornate deer are already as small as the earliest coronate *Cervus* (Van der Made et al., 2014). Soleilhac might be stage 15 or 13, but not older because of the presence of *Arvicola*.

The extinction of *Xenocyon* and the dispersal of *Cuon* seem to have occurred within stage 13. The dhole, has a long previous record in China, where *Cuon dubius* is cited from early Early Pleistocene (Xue and Zhang, 1991). Material described from Yunxian was assigned to “*Xenocyon dubius*” (Échassoux et al., 2008), but is very similar to the first European *Cuon*. If *S. kirchbergensis* is present in Mauer, it may well come from the upper part of the section (stage 13). The single calcaneum from Soleilhac might be older. *Stephanorhinus kirchbergensis* dispersed probably each interglacial from the east into Europe, and may have arrived further west in subsequent interglacials, reaching first Moldavia (Tiraspol), in a later

glacial Germany and France (stage 13 or 15) and if it reached Spain, this was much later and only in the very North.

5. Discussion: TD8 in the context of faunal change

Fig. 18 and the review in Section 4 show that the period around the Early–Middle Pleistocene transition was one of intense faunal change. The period from stage 37 till stage 13 has 12 climatic cycles, some of them minor ones. Ten discrete events could be documented; on average one event per 80 ky and one event for each major climatic cycle, though some of the major cycles had two events and some of the minor ones none. Thirty six appearances of new taxa (by dispersal), 22 extinctions and ten cases of the evolution of one species into the other, are on average nearly four dispersals, over two extinctions and one new species by evolution per event. Future work may modify details of this scheme, and the planned descriptions of the other faunas from Gran Dolina may do so, but the general picture is not likely to change much.

This intensive faunal change occurred when the influence of the 100 ky eccentricity cycles on global climate increased, and when glacial cycles of this duration were established, reaching progressively colder temperatures (Shackleton, 1995; deMenocal, 1995). The faunal events were tentatively correlated to the isotope stages, by: 1) using information from localities dated by a variety of methods, 2) correlating dispersals of presumably cold adapted species to cold stages and warm adapted species to warm stages, 3) correlating faunal events to the most important of the chronologically close climatic events, 4) correlating preferentially subsequent events to subsequent stages and not to two moments in the same stage.

Some of the most important faunal events are correlated to the most significant climatic events (cold stages 36 and 16), but others not (warm stages 31/33, stage 27). Given the overall trend of decreasing temperatures, which is overprinted by the 100 ky cycles, resulting subsequent cycles reaching lower temperatures, it might be expected that, faunal change was noted especially during cold stages in the appearance of new cold adapted (“glacial”) species. Surprisingly, this is not that clear: three of the four first events concern the appearance of species adapted to warm or moderate climates. Either the cold stages before stage 16 did not lead to the spread into mid-latitude Europe of species that we recognize as “glacial”, or these periods are poorly represented in the fossil record.

While the first dispersals of cold adapted species can be explained by colder or longer cold periods, it is less clear, why new species adapted to temperate or warm climates did not survive in the refugia in southern Europe (e.g. *Stephanorhinus etruscus*), or why new species adapted to such climates appeared (e.g. *Cervus elaphus*). In nine cases, an extinction of a lineage may have been related to the dispersal of a similar taxon, though there may have been a short overlap. This is the case with the following couples: *Leptobos* – *Bison*, *Sus strozzi* – *Sus* sp., *Alces carnutorum* – *A. latifrons*, *Mammuthus meridionalis* – *M. trogontherii* & *Elephas antiquus*, *Xenocyon* – *Cuon*, *Eucladoceros* sp. T – *E. giulii*, *E. giulii* – *E. aff. giulii*, *Sus* sp. – *Sus scrofa*. Such related dispersals and extinctions are sometimes called “replacements”. In elephants one species was replaced by a cold adapted and a warm adapted species. In other cases, there is no clear replacement and similar animals have a long overlap, as in the case of *Pachycrocuta*, which survived long after the appearance of *Crocuta* and *Hyaena*. During a million of years the European ecosystems supported only one species of hyaena and then for half a million it supported three. This could be related to the general increase in biodiversity. Faunal change was the result of

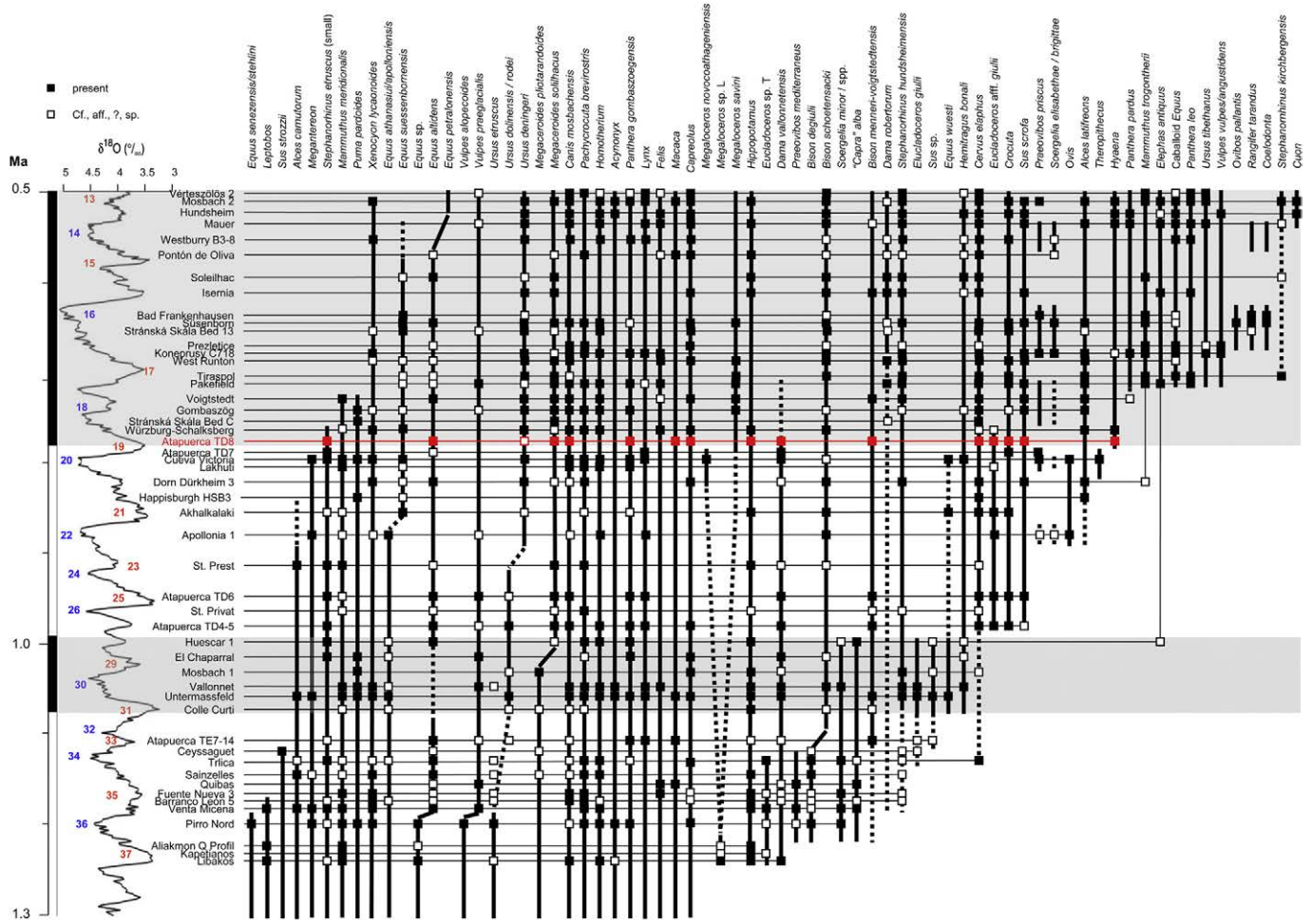


Fig. 18. The fauna from Atapuerca TD8 in the context of faunal change around the Early Middle Pleistocene transition. From left to right: age in millions of years (Ma), paleomagnetism, isotope stages, the localities in their tentative chronologic positions, the fauna. Thick lines indicate assumed temporal distribution, dashed lines indicate uncertainty, oblique lines connecting vertical lines indicate tentative ancestor–descendant relationships. Solid squares indicate presence of a taxon in a locality, open squares indicate tentative or possible presence of a taxon (usually indicated as: cf., aff., ?, sp.).

complex processes and not the simple cyclical appearance of cold adapted species in mid-latitude Europe.

The Early Middle Pleistocene transition is situated in the middle of these climatic, environmental and faunal changes. It is conveniently defined by the Brunhes–Matuyama boundary. However, this is not at a moment of major faunal change. The fossil association from Atapuerca TD8 is situated directly above the Lower–Middle Pleistocene boundary, which is palaeomagnetically recorded in the underlying level TD7. The combination of the two levels documents the fauna exactly at this boundary. This may well be the only place in all of Europe, where this is the case. The lowermost Middle Pleistocene fossil association of TD8 is characterized by the youngest records of the small rhinoceros (which we assume to be closely related to or a small variant of *S. etruscus*) and the otherwise exclusively Early Pleistocene genus *Eucladoceros*. It is also characterized by the first record of *Hyaena*. In future papers, the faunas from TD7 and lower levels will be described, documenting the latest Early Pleistocene of the Gran Dolina sequence.

6. Conclusions

The even and odd toed ungulates (Artiodactyla and Perissodactyla) from TD8 have been described and their evolution,

systematics and the stratigraphic and biogeographic context have been discussed, leading to the following conclusions:

- Nine species of six families of ungulates are present: *Equus altidens* (Equidae) *Stephanorhinus* aff. *etruscus* (Rhinocerotidae), *Sus scrofa* (Suidae), *Hippopotamus* sp. (cf. *tiberinus/georgicus*) (Hippopotamidae), *Bison voigtstedtensis* (Bovidae) and *Cervus elaphus*, *Eucladoceros* aff. *giulii*, *Megaceroides solilhacus*, and *Dama vallonnetensis* (Cervidae).
- *Equus altidens* is a very slender equid, which may have evolved in Europe from a slightly less gracile species. If this is indeed the case, the transition is of stratigraphic interest and places Pirro Nord below Venta Micena. Since *Equus altidens* originated in Europe, it did not disperse from Africa to Europe and is not related to human dispersal from there, as has been suggested.
- The affinities of the small *Stephanorhinus* are still under discussion, but the record from TD8 is the latest well dated record of this small rhinoceros.
- There is a not very dense, but continuous record of *Sus* in Europe covering the period between the Olduvai and Jaramillo subchrons. *Sus scrofa* replaced a different species with verrucose canines around the end of the Jaramillo Subchron and the record of *Sus scrofa* from TD8 is one of the oldest known of this species.

- *Hippopotamus* may have dispersed three times to Europe during the Pleistocene: *H. antiquus* did so around 2 Ma, *H. tiberinus/georgicus* did so shortly before 1.2 Ma, and *H. amphibius/incognitus* did so during the later part of the Middle Pleistocene. The material from TD8 belongs probably to the second species.
- The *Cervus elaphus* from TD8 is one of the oldest records of this species in western Europe.
- The *Eucladoceros* from TD8 is the latest well dated record of this genus and one of the largest deer that ever lived.
- *Megaceroides* coexisted in TD8 with *Eucladoceros*. This is also the case in other levels of Gran Dolina, but this is uncommon: in Middle Pleistocene localities where *Megaceroides* coexists with another giant deer, it is with *M. savini*.
- *Dama vallonnetensis* is a fallow deer with gracile metapodials and a relatively low bifurcation between the brow tine and main beam. Until recently, fallow deer with antlers with three or just two tines and with robust metapodials were not recognized as a different group or lineage.
- A very small bovine from TD8 is identified as *Bison voigtstedtensis*, a species that is still not well known.
- The fauna of TD8 has been studied in the context of the faunal change at the end of the Early and beginning of the Middle Pleistocene. Ten faunal events are recognized, with 36 appearances by dispersal, 25 extinctions and ten species originating by evolution. These faunal events are tentatively correlated to isotope stages 37, 36, 33/31, 27, 22, 19, 18, 16, 16–15 and 13.
- The Lower–Middle Pleistocene boundary is conveniently taken at the palaeomagnetic Brunhes–Matuyama boundary. However, this is not the position of the major faunal events.
- TD8 is probably one of very few localities recording the earliest Middle Pleistocene fauna. It is right above the Brunhes–Matuyama boundary and is correlated to stage 19. It records the latest small *Stephanorhinus etruscus*, the latest *Eucladoceros*, and the earliest *Hyaena*.

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