Appendix 1 Continued

Habitat	Geographic situation	Bibliography	Bird community
Inland salty lake in a meadow	Pétrola. Mesomediterranean stage. **(9)**	Cirujano (1986*a*)	Wintering
Inland salty lake	Nava Grande (Malagón). Mesomediterranean stage. Max. depth 30 cm. **(10)**	Cirujano (1986*b*)	Wintering (predominant species only)
Riparian grove	Pyrenees. Supramediterranean stage. (4)	Pedrocchi-Renault (1987)	All seasons
Lake and surroundings	Pyrenees. Supramediterranean stage. (4)	Pedrocchi-Renault (1987)	All seasons
Meadow	Gibraltar. Humid thermomed. stage. 600–1000 masl. (3)	Arroyo & Tellería (1984)	Wintering, wintering (predominant species only)
Meadows with cliffs	Pyrenees. Subalpine stage. Alpine stage. (4)	Pedrocchi-Renault (1987)	All seasons
Rocky outcrops	Pyrenees. Mesomediterranean stage. (4)	Pedrocchi-Renault (1987)	All seasons
Rocky outcrops in bushland	Pyrenees. Dry supramediterranean stage. (4)	Pedrocchi-Renault (1987)	All seasons
Rocky outcrops in pinewood	Pyrenees. Dry supramediterranean stage. (4)	Pedrocchi-Renault (1987)	All seasons
Shrub steppe	Masa. Supramediterranean stage. 1100 masl. **(11)**	Tellería *et al.* (1988)	Wintering, breeding, wintering+breeding
	Segovia province. Supramediterranean stage. 1000 masl. (2)	Santos & Tellería (1987)	Wintering, wintering (predominant species only). Breeding, breeding (predominant species only). Wintering+breeding, wintering+breeding (predominant species only)
Semidesert	Los Monegros. Mesomediterranean stage. 380 masl. **(12)**	Tellería *et al.* (1988)	Wintering, wintering (predominant species only). Breeding, wintering+breeding, wintering+breeding (predominant species only)
	Guadix depression. Meso-thermomedit. stage. 750 masl. **(13)**	Tellería *et al.* (1988)	Wintering, wintering (predominant species only). Breeding, wintering+breeding, wintering+breeding (predominant species only)
Shrub steppe	Alcarria. Supramediterranean stage. 1200 masl. **(14)**	Tellería *et al.* (1988)	Wintering, breeding
	Sepúlveda. Supramediterranean stage. 1000 masl. **(15)**	Tellería *et al.* (1988)	Wintering, breeding, wintering+breeding
Semidesert	Almería coast. Thermomediterranean stage. 10 masl. **(16)**	Tellería *et al.* (1988)	Wintering, wintering (predominant species only). Breeding, breeding (predominant species only). Wintering+breeding, wintering+breeding (predominant species only)
	Níjar. Thermomediterranean stage. 120 masl. (17)	Tellería *et al.* (1988)	Wintering, wintering (predominant species only). Breeding, breeding (predominant species only). Wintering+breeding, wintering+breeding (predominant species only)

Jan van der Made
Museo Nacional de Ciencias Naturales, c. José Gutiérrez Abascal 2, 28006 Madrid, Spain. E-mail: mcnvd1a@pinar1.csic.es

Received 19 November 1997
Revision received 7 May 1999
and accepted 9 September 1999

Keywords: Atapuerca, ungulates, Equidae, Rhinocerotidae, Suidae, Cervidae, Bovidae, Early Pleistocene.

Ungulates from Atapuerca TD6

The ungulates from unit 6 of Gran Dolina (TD6) in the Sierra de Atapuerca (northern Spain) are studied. They include *Stephanorhinus etruscus*, *Equus* cf. *altidens*, *Sus scrofa*, *Dama nestii? vallonetensis*, *Cervus elaphus*, *Eucladoceros giulii*, Cervidae indet. and Bovini cf. "*Bison voigtstedtensis*." The taxonomy and stratigraphical distribution of most of these taxa are not universally accepted. *S. etruscus*, *D. n.? vallonetensis*, *E. giulii* and "*B. voigtstedtensis*" are late Early and early Middle Pleistocene elements. *S. scrofa* and *C. elaphus* range from the late Early Pleistocene to Recent. The fauna indicates a late Early or earliest Middle Pleistocene age, which fits the latest Early Pleistocene age suggested by palaeomagnetism. The faunal assemblage does not indicate extreme climatic conditions. The virtual absence of "glacial" taxa from the Spanish Early and Middle Pleistocene suggests that glaciations did not have a great impact on the fauna, suggesting that climate was no impediment to a continuous human occupation of Spain from the late Early Pleistocene onwards.

Journal of Human Evolution (1999) **37**, 389–413
Article No. jhev.1998.0264
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Introduction

The Sierra de Atapuerca, near Burgos (Spain), has several fissure fillings that have yielded fossils and artefacts (Aguirre *et al.*, 1990). The best known sites are Sima de los Huesos (SH), Galeria (TG) and Gran Dolina (TD). The TD sequence has some 17 m of sediment exposed that are divided into 11 units, named from bottom to top TD1 to TD11. A palaeomagnetic reversal in the top of TD7 was interpreted as the Matuyama–Brunhes boundary, placing the lower part of the sequence in the interval between the Jaramillo Event and the Brunhes Epoch, between 0·78 and 0·99 m.y.a. (Parés & Perez González, 1995). The type material of the recently described species *Homo antecessor* is from TD6 (Bermúdez de Castro *et al.*, 1997). From the same unit, 105 ungulate fossils were recovered that are assigned to eight taxa. The study of these ungulates helps to place the early humans in their stratigraphical and palaeoecological context.

Materials and methods

Material, measurements and their abbreviations and additional information are listed in Appendix 1. Since 1982, a standardized geographical and stratigraphical nomenclature has been used, and labels include detailed provenance information. The labels include the prefix of Atapuerca and the year of excavation (e.g., ATA94), the site and level (e.g., TD6), the square (e.g., G-16), the number of the fossil within this square (e.g., 22) and additional information, for instance on depth (e.g., talla 39=level 39 of excavated sediment, or depth in cm: z=506). The year is the key to the catalogue; there is one for each campaign. The full label is given as: ATA94, TD6, G-16, talla 39, 33. The fossils are temporarily stored in the Museo Nacional de Ciencias Naturales, Madrid and the Laboratori de Arqeologia de la Universitat Rovira i Virgili, Tarragona, and will be stored permanently in the Museo de Burgos.

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Nomenclature of dental morphology follows van der Made (1996). Right/left in phalanges, distal metapodials, sesamoids etc., refers to the position relative to the axis of the foot. A "right phalanx" is a phalanx of the fourth toe in a right foot or phalanx of the third toe in a left foot. These phalanges cannot be separated in Artiodactyla. Measurements are generally taken as indicated by van der Made (1996). Measurements of *Equus* are according to Eisenmann *et al.* (1988). DAP of teeth of *Stephanorhinus* are taken at the base, buccally in upper molars and lingually in the lower. All measurements are given in millimetres, unless otherwise indicated.

When comparisons are made with material from other localities, either a bibliographical reference is given or the abbreviation of the institute where that material was studied (Appendix 2). The stratigraphical position of these localities is indicated in Table 1.

Systematics

Order Perissodactyla Owen, 1848
Family Equidae Gray, 1821
Equus cf. *altidens* Von Reichenau, 1915

Description and comparison

Lower cheek teeth with V-shaped linguaflexids (Figure 1). Upper cheek teeth with small protocones. The molars have slightly larger protocones than the premolar, but this is normal in molars. The number of plications is generally low in all cheek teeth.

A series of three lower premolars is relatively large and moreover has the enamel of the fossils slightly more plicated (Figure 1). Plications are variable and the size of all teeth from TD6 are within the range of Spanish material assigned to *Equus stenonis* and *E. altidens* (Figure 2). At present there are insufficient grounds to assume the presence of more than one equid species in TD6.

Table 1 The localities mentioned in the text and their stratigraphical and geographical positions

	Biozone MN unit	Localities
Upper Pleistocene		Paglicci (Italy)
Middle Pleistocene		Pinilla del Valle (Spain)
		Weimar-Ehringsdorf (Germany)
		Steinheim (Germany)
		Atapuerca TG & TZ (Spain)
		'Mundesley' (UK)
		'Sidestrand' (UK)
		'Trimingham' (UK)
		Loreto (Italy)
		Süssenborn (Germany)
		Cullar de Baza 1 (Spain)
		Petralona (Greece)
		Isernia la Pineta (Italy)
		Mosbach 2 (Germany)
		Voigtstedt (Germany)
	0.78 Ma	Westerhoven (Netherlands)
Lower Pleistocene	MmQ 3b	Atapuerca TD4-6 (Spain)
		Huescar 1 (Spain)
	MmQ 3a	Le Vallonet (France)
		Soleilhac (France)
		?Blanzac (France)
		Untermassfeld (Germany)
	1.07 Ma	Mosbach 1 (Germany)
	MmQ 2	Apollona-1 (Greece)
		Pietrafitta (Italy)
		Pirro Nord (Italy)
		Venta Micena (Spain)
	1.4 Ma	Selvella (Italy)
		?Láchar (Spain)
	MmQ 1	Il Tasso (Italy)
		Casa Frata (Italy)
	1.77 Ma	'Upper Valdarno' (Italy)
Upper Pliocene	MN 17	Matasino (Italy)
		Olivola (Italy)
		Tegelen (Netherlands)
		Senèze (France)
	MN 16	Huélago (Spain)
		Ponte a Elsa (Italy)
		Montopoli (Italy)

Stratigraphy mainly after Agustí *et al.* (1987), approximate ages of the lower limits of the units updated. Question marks in front of a locality indicates uncertainty about the position. Locality names between quotation marks indicate that the material comes from more than one stratigraphical level

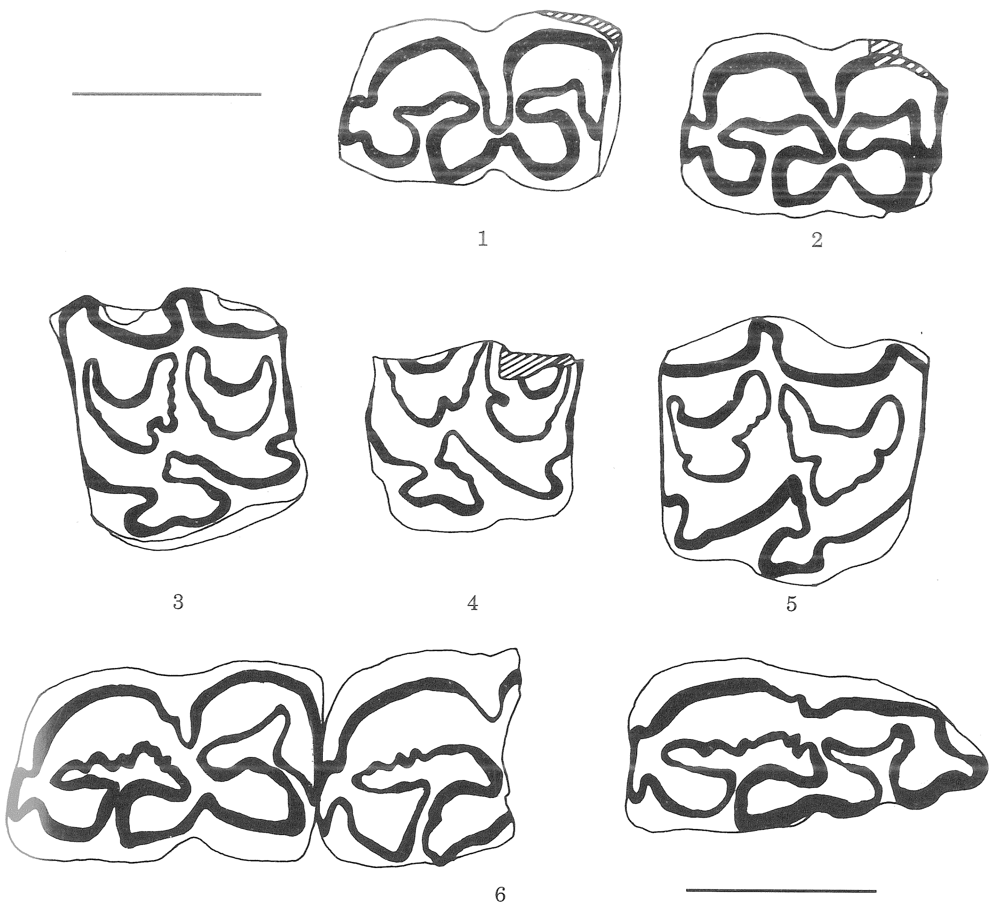

Figure 1. *Equus* cf. *altidens* from Atapuerca TD6, occlusal view of cheek teeth. (1) ATA96, TD6, I-16, talla 53, 298—left $M_{1/2}$. (2) ATA96, TD6, I-18, talla 48, 82—left $M_{1/2}$. (3) ATA96, TD6, H-17, 302, talla 50—left $M^{1/2}$. (4) ATA96, TD6, G-16, 239, talla 40-41—lingual side to left upper P or M. (5) ATA96, TD6, H-18, 150—right $P^{3/4}$. (6) ATA95, TD6, talla 53, I-16, 300—left P_{2-4}. The bar represents 2 cm.

Discussion

V-shaped linguaflexids, as in the TD6 teeth, are typical for stenonid horses, whereas U-shaped linguaflexids are typical for caballoid horses (Forsten, 1992). The large *Equus suessenbornensis* is placed either in the caballoid group (Alberdi *et al.*, 1995*a*), or in the stenonid group (Forsten, 1988). *Equus bressanus* is large, and the remaining European stenonid horses are of small size.

Alberdi & Ruiz-Bustos (1989) and Alberdi *et al.* (1995*a*,*b*, 1998) proposed, in different taxonomical variants, a long lineage comprising *E. stenonis–E. altidens*. The subspecies "*granatensis*" (type material from Venta Micena), was first included in *E. stenonis* and later in *E. altidens*. Azzaroli (1990) suggested that the horse from Venta Micena is *E. altidens*. Guerero-Alba *et al.* (1997) included the material from Venta Micena in *E. altidens*, which they considered an immigrant that replaced *E. stenonis*. Both species are similar in size (Figure 2), in plication formulae (van der Made, 1999) and in protoconal indices. A consensus seems to be growing that *E. altidens* is the

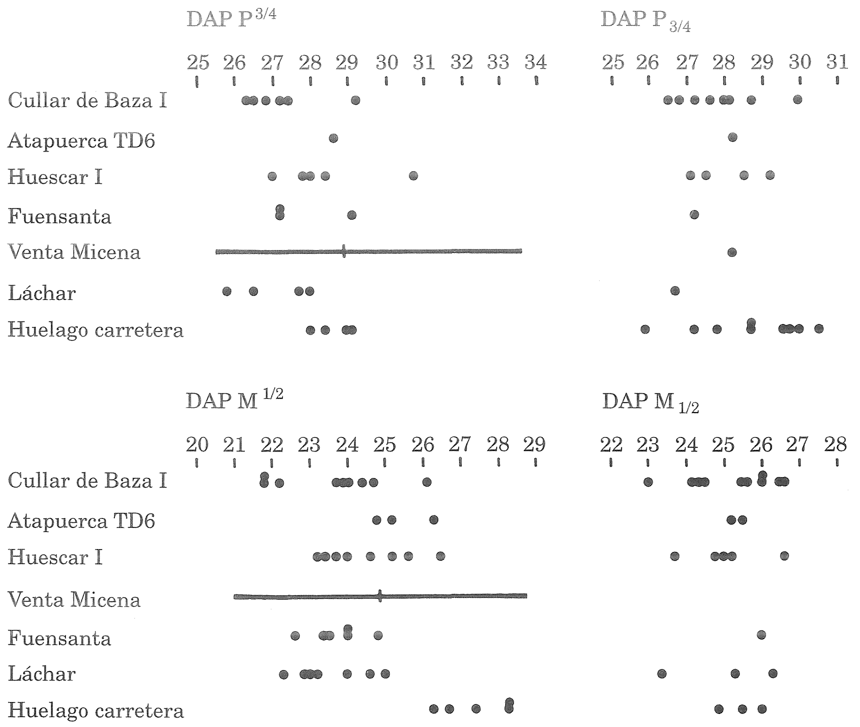

Figure 2. Length (measured 2 cm above the base) of the molars and premolars of stenonid horses. Huelago Carretera=*E. s. livenzovensis*; Láchar, Fuensanta & Venta Micena (all Spain, Lower Pleistocene)=*E. s. granatensis*; Huescar I (Spain, lower Middle Pleistocene)=*E. s. stenonis* intermedio *granatensis-altidens*; Cullar de Baza I=*E. altidens*. Data and taxonomy from Marín (1987; average and range of upper teeth from Venta Micena) and Alberdi & Ruiz-Bustos (1989; remaining data).

only small stenonid horse present in Europe between 1 and 0·5 m.y.a.

In view of the difficulty in separating *E. altidens* from *E. stenonis* and other small stenonid horses, the equid from TD6 is assigned to *E.* cf. *altidens*.

During the early Middle Pleistocene caballoid horses became dominant and stenonid horses declined in Europe, but did not disappear (Forsten, 1988). The presence of stenonid horses in TD6 is thus not a good biostratigraphical indicator.

Family Rhinocerotidae Owen, 1845
Stephanorhinus etruscus (Falconer, 1868)

Description and comparison

Rhino bones and teeth from TD6 have a morphology that is common in *Stephanorhinus* (Figure 3). The astragalus is small (Figure 4) and has a narrow width compared to its height; *S. hundsheimensis* and *S. kirchbergensis* have larger and relatively wider astragali.

Discussion

Guérin (1980, p. 803) placed Atapuerca in his zone 24 and assigned fossils (including specimens from TD), shown to him by Soto, to *Dicerorhinus hemitoechus*. Soto (1987) described rhino remains, which he stated are from TD3, as *D. hemitoechus*. Cerdeño & Sanchez (1988) described largely the same material and, after a comparison with the species of zone 24, assigned it to *D. hemitoechus*. Cerdeño (1990) updated the generic attribution, and suggested that the material

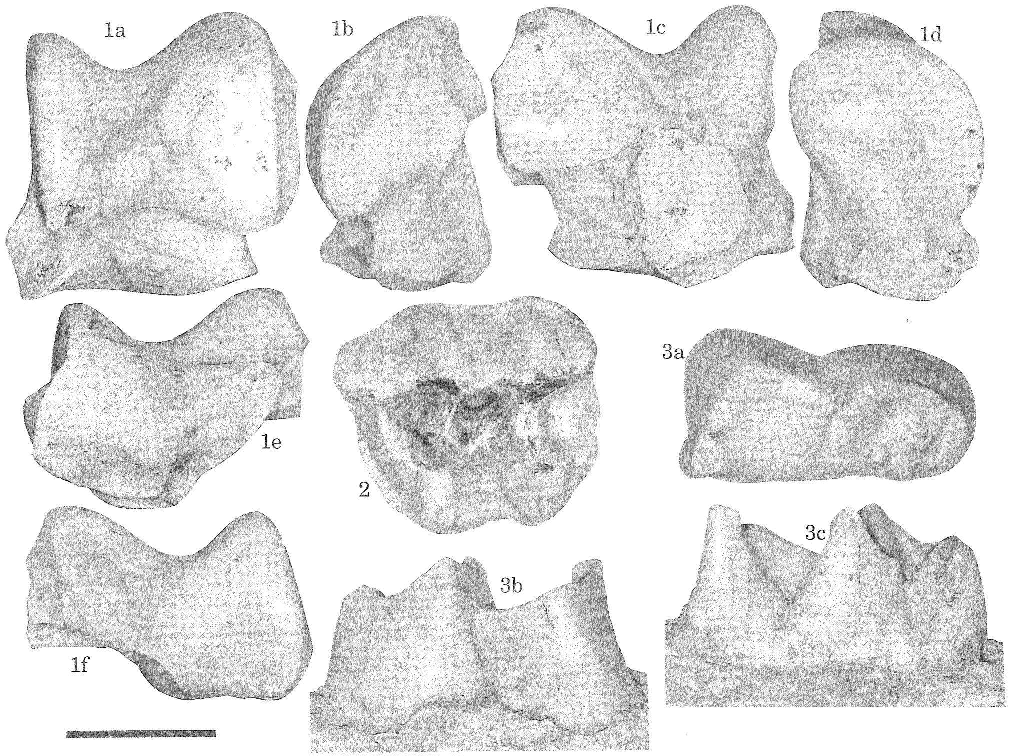

Figure 3. *Stephanorhinus etruscus* from Atapuerca TD6. (1) ATA96, TD6, G-18, talla 52, 445—left astragalus, anterior (a), external (b), posterior (c), internal (d), distal (e) and proximal (f) views. (2) ATA95, TD6, G-16, talla 40–41, 132—left D^2, occlusal view. (3) ATA95, TD6, H-16, talla 40–41, 195—left D_3, occlusal (a), buccal (b) and lingual (c) views. The bar represents 4 cm for (1) and 2 cm for (2) and (3).

of *Stephanorhinus hemitoechus* comes from TG-TZ (other localities at Atapuerca) and the upper levels of TD, while Cerdeño (1993) assigned rhino remains from TD4 to *S. etruscus*. Fortelius *et al.* (1993) doubted Cerdeño & Sanchez's (1988) determination as *S. hemitoechus* and assigned the material to *S. hundsheimensis*, but also noted resemblances to *S. etruscus*. *D. hemitoechus* played a role in discussions of the age of TD6, both before (Aguirre, 1989) and after the recovery of *Homo* in TD6 (Raposo & Santonja, 1995).

Recently collected material from TD4-6 is small like *S. etruscus* and early *S. hemitoechus* (Figure 4; younger *S. hemitoechus* seems to be larger) and a mandible from TD4 has relatively large premolars and a small M3 (Figure 5), like the former and unlike the latter species. It is assumed here that there is little time difference between TD4 and TD6, and the material from both levels is believed to represent the same species.

S. etruscus of the Early Pleistocene was replaced by *S. hemitoechus* of the late Middle Pleistocene. The transition is not well documented, but may have been anagenetic. The presence of *S. etruscus* in the lower part of the TD sequence is suggestive of an Early or early Middle Pleistocene age.

Order Artiodactyla Owen, 1848
Family Suidae Gray, 1821
Sus scrofa Linnaeus, 1758

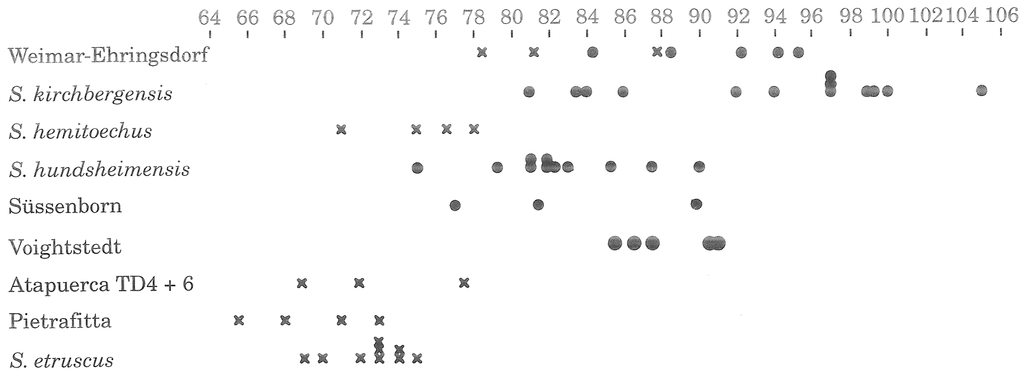

Figure 4. Length of the astragalus of *Stephanorhinus*. Data on *S. etruscus*, *S. hundsheimensis* and *S. hemitoechus* from Fortelius *et al.* (1993), *S. hundsheimensis* from Hundsheim (crosses; IPUW) data on Pietrafitta from Mazza *et al.* (1993), Voigtstedt from Kahlke (1965), Süssenborn from Kahlke (1966) and Weimar-Ehringsdorf from Kahlke (1975). The latter locality has both *S. hemitoechus* (crosses) and *S. kirchbergensis* (dots).

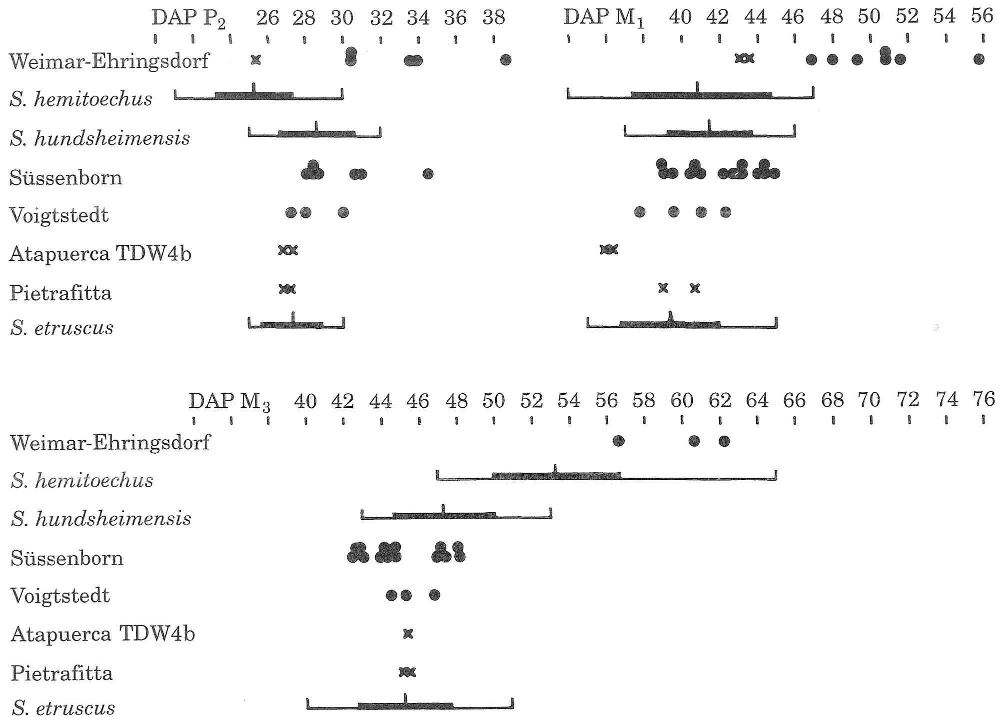

Figure 5. Basal length (DAP) of P_2, M_1 and M_3 of *Stephanorhinus*. Provenance data and symbols as in Figure 1. Averages, standard deviations and extremes indicated for the three species.

Description and comparison

The P_3 (Figure 6) has a length/width index of 185. *Sus strozzii* (Figure 7) has wide premolars and *Sus scrofa* has narrower premolars, with higher values for this index.

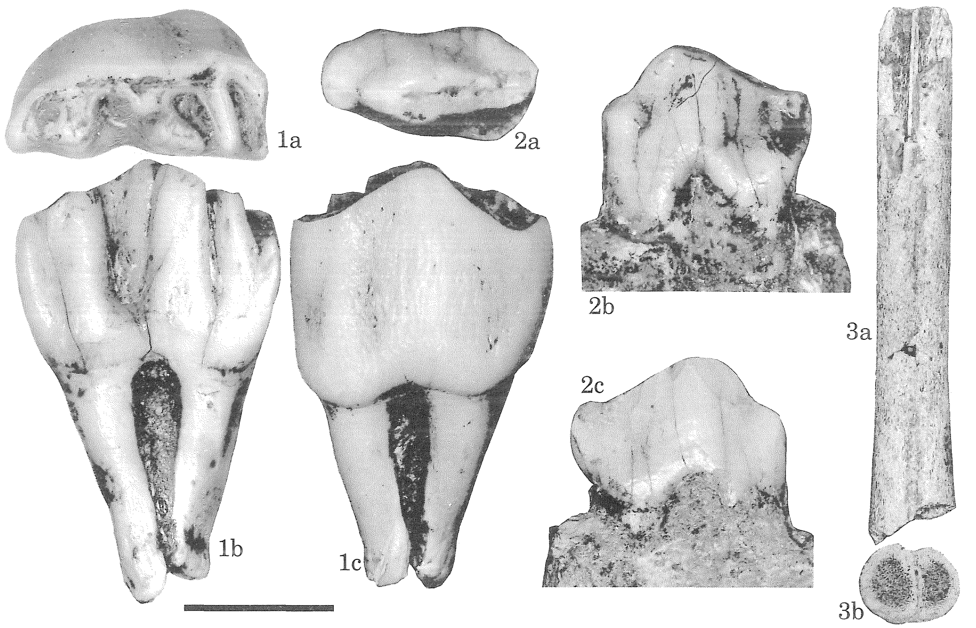

Figure 6. *Cervus elaphus* from Atapuerca TD6. (1) ATA94, TD6, G-17, talla 38, 41—right P_3, occlusal (a), lingual (b) and buccal (c) views. *Sus scrofa* from Atapuerca TD6. (2) ATA94, TD6, G-16, talla 39, 22—left P_3, occlusal (a), buccal (b) and lingual (c) views. *Dama nestii? vallonetensis* (*Capreolus?*) from Atapuerca TD6. (3) ATA94, TD6, J-18, talla 37, 3—shaft of metatarsal, anterior (a) and distal (b) views. The bar represents 1 cm for (1), 2 cm for (2) and (3).

Discussion

In the Pleistocene of Europe, two species of suids are known: *Sus strozzii* is replaced near the end of the Early Pleistocene by *Sus scrofa* (van der Made & Moyà-Solà, 1989). The index suggests that the TD6 tooth belongs to *S. scrofa*.

Family Cervidae Gray, 1821
Dama nestii? vallonetensis De Lumley, Kahlke, Moigne & Moullé, 1988

Description and comparison

The remains differ from *Cervus* and resemble recent *Dama* (Figures 8 and 9); the P_2 has a low and "inflated" shape, the antlers have rather smooth surfaces and burrs, and lack bez tines. The bifurcation of brow tine and main beam in the antlers from TD6, as well as in those from TD4, is relatively high above the burr (Figures 10 and 11).

The last three specimens in the list of material (Appendix 1) have been attributed to *Capreolus* sp. (Carbonell *et al.*, 1995). The fragment of the shaft of a metatarsal (Figure 6) of cervid morphology from TD6 is slightly smaller than the metatarsal of a recent *Capreolsu*. The bone surface suggests that the bone belonged to a juvenile individual. The magnum and scapula from TD6 are slightly larger than recent *Capreolus*. This material is here considered insufficient proof of the presence of the roe deer, and is only tentatively assigned to the present taxon.

Discussion

Antlers described and figured as *Dama* cf. *clactoniana* (Atapuerca oc = old collections in Figure 11) are said to be from TD3 (Soto, 1987, Pl. 16, Figures 1–4). Azanza & Sánchez (1990) assigned this, and older

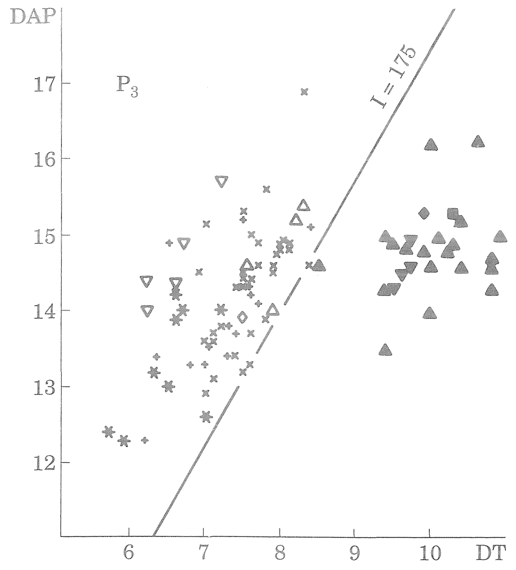

Figure 7. Bivariate plot of length (DAP) versus width (DT) of the P_3 of *Sus*. Solid symbols represent *Sus strozzii* from different localities: square=Senèze (cast in UCBL), triangles pointing down=Olivola (IGF), triangles pointing up=upper Valdarno (IGF, AVP). Open symbols represent *Sus scrofa*: diamond=Atapuerca TD6, triangles pointing down=Mosbach 2 (NMM), triangles pointing up=Pinilla del Valle (UCM), asterisks=recent Spain (MNCN, UCM), crosses=Recent Netherlands and Germany (ZMA, HUJ), oblique crosses=recent Israel (HUJ). The line indicates index I=100 DAp/DT=175.

material from Láchar, to *Dama* cf. *clactoniana*. Raposo & Santonja (1995) used the presence of *D. clactoniana* (without "cf.") in their discussion of the age of TD6.

There are *Dama*-like deer throughout the European late Pliocene and Pleistocene. The older populations include antlers with more vertically oriented beams and brow tines, a smaller angle between brow tine and main beam, a longer distance of the bifurcation of the brow tine and main beam to the burr (Figure 11, measurements as in Figure 10), and simpler distal morphology of the antler. With decreasing age, the opposite character states gradually appear. In the youngest samples (*Dama d. dama*), palmation occurs. Geologically older samples, such as from Tegelen, show more variation in antler morphology. However, biometrics of bones and teeth suggest that there is but one species at Tegelen (Spaan, 1992). There are few morphological differences in bone or teeth between the different samples of *Dama*-like deer. For example, a P_4 without a metaprecristid may occur in the older samples, but is rare or absent in the younger samples, and the size shows some fluctuation (Figure 12). Altogether, the available morphological and metrical data do not support the idea of more than one lineage (*contra* Azzaroli, 1992), and there seems to be a continuity between the older *Dama*-like deer and the samples that everyone places in *Dama*. Azzaroli named the genus *Pseudodama* for the samples that are listed below Atapuerca in Figures 11 and 12, but the proposal was rejected by Kahlke (1997). From the age of about 1 Ma, samples are increasingly assigned to "*Cervus*" or *Pseudodama* instead of to *Dama* or *Dama clactoniana* in particular, although morphological criteria seem to vary from author to author.

Kahlke (1997) included in "*Cervus*" *nestii vallonetensis* material from the Early Pleistocene localities Le Vallonet, Untermassfeld, Selvella, Casa Frata and Pirro Nord. Data given by de Lumley *et al.* (1988) and Kahlke (1997), compared with my own data from Casa Frata and Selvella, suggest a size increase in the younger samples. The deer from Pinilla del Valle was assigned to *D. clactoniana* (Alférez *et al.*, 1982), a subspecies of *Dama dama*, in the opinion of others (Lister, 1986). The samples from TD4 and TD6 have the first bifurcation higher than in Pinilla (Figure 11) and in undescribed material from Bilzingsleben, assigned to the same taxon. The TD4 and TD6 remains show closer affinities with "*C.*" *n. vallonetensis*.

The material from TD6 and TD4 is here assigned to the genus *Dama* and to the subspecies *vallonetensis*. Whether or not designation to the species *nestii* is more

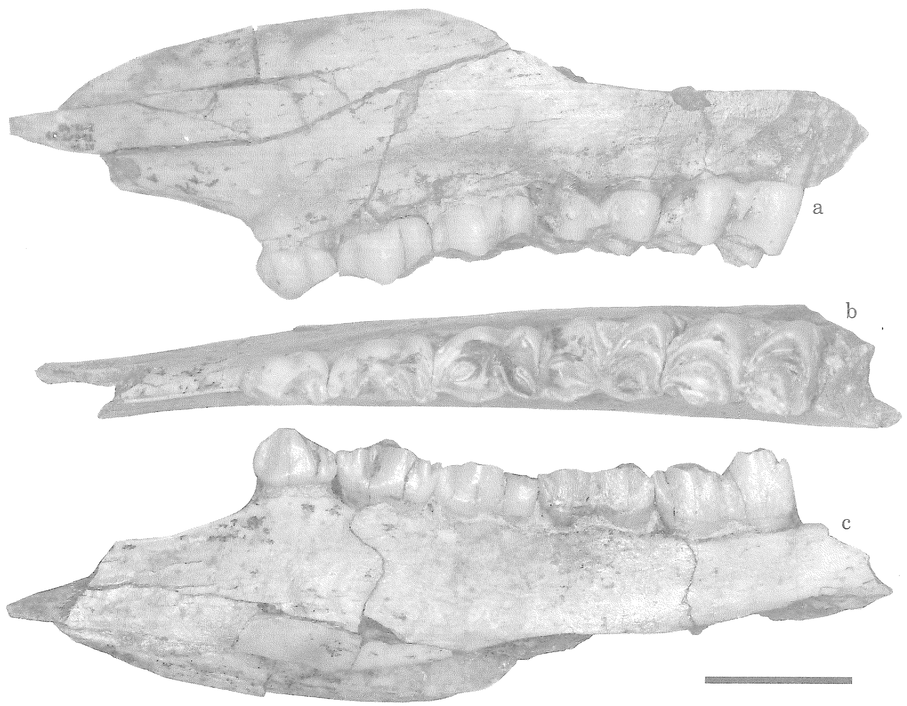

Figure 8. *Dama nestii? vallonetensis* from Atapuerca TD6. ATA94, TD6, I-18, talla 37, 40—right mandible with P_2–M_2, buccal (a), occlusal (b) and lingual (c) views. The bar represents 2 cm.

appropriate needs further consideration, but in the meantime, the TD6 and TD4 material is assigned to *Dama nestii? vallonetensis*. *D. n.? vallonetensis* suggests a late Early Pleistocene age for TD4 and TD6.

Eucladoceros giulii Kahlke, 1997

Description and comparison

A large antler has a cylindrical anterior tine that originates high above the burr and is directed anteriorly (Figure 13). This is interpreted as the brow tine. The main beam curves backwards at the place of the bifurcation. In these characters the specimen resembles an antler from TD4 (Azanza & Sánchez, 1990; Pl. 1, Figure 1), the antler of *E. giulii* from Untermassfeld (Kahlke, 1997; Pl. 41, Figure 2) and the antlers from Apollonia-1 assigned to *Megaloceros* sp. (Kostopoulos, 1997) in general size, and in having a fairly high to high origin of the brow tine with the initial part of the brow tine having a subcylindrical cross-section.

The D^2 (Figure 13) is similar to that of *E. giulii* (Kahlke, 1997; Pl. 42, Figures 4–6), except that it lacks the small crista in the posterior fossid. Their morphology is probably common in all large Cervinae. Metrically, the TD6 tooth falls just within the upper ranges of *E. giulii* from Untermassfeld (Kahlke, 1997) and Venta Micena (Menéndez, 1987).

A first phalanx is wider than 13 specimens of *C. elaphus* and narrower than 12 specimens of *Megaloceros* from Voigtstedt (IQW). A third phalanx is also intermediate in size. The phalanges from TD6 resemble those from TD4 in proportions. The other limb bones from TD4 are all long and slender compared to those of *Megaloceros*.

Figure 9. *Dama nestii? vallonetensis* from Atapuerca TD6. ATA95, TD6, talla 42, I-17, 74—right shed antler, internal (a) and external (b) views. The bar represents 2 cm.

Discussion
The remains from TD6 and TD4 suggest a deer the size of the Pliocene–Early Pleistocene *Eucladoceros* or the predominantly Middle–Late Pleistocene *Megaloceros* (=*Megaceroides*=*Praemegaceros*; Lister, 1993).

Megaloceros antlers with flattened brow tines are assigned to the "*M. giganteus* group" and those with cylindrical brow tines to the "*M. verticornis* group" (Azzaroli, 1953). Most of the European species of the former group are now considered to be subspecies of *M. giganteus*, except *M. savini*. The latter species is a primitive member of this group and is smaller in size. *M. giganteus* has large and robust metapodials (Figure 14). Limb bone proportions and the lack of a flattened brow tine indicate that the TD4 and TD6 remains belong to a different kind of cervid.

The forms from mainland Europe assigned to the "*M. verticornis* group" include *M. solilhacus* (a possible senior synonym of *M. verticornis*), *M. dawkinsi* and a number of forms that are currently considered to be synonyms or subspecies. *M. dawkinsi* frequently lacks a brow tine, a character that Azzaroli (1953) believed to be a secondary reduction. In Soleilhac (MCP) antlers with and without a brow tine occur, suggesting that *M. dawkinsi* is no separate species, but a variant of *M. solilhacus*. East Anglian specimens assigned to *M. dawkinsi* (including the type material) might belong to a later grade of evolution of the *M. solilhacus* lineage. Observations by the author suggest that pachyostosis might be stronger in the younger samples. No dental or postcranial evidence for more than one European lineage in the "*M. verticornis* group" has been published and the variation in antler morphology can be explained as grades in a single lineage. All metapodials assigned to this group are robust (Figure 14). The relation to the small Early

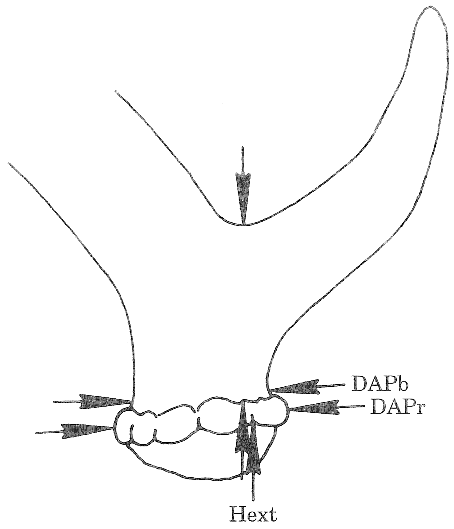

Figure 10. The way of measuring H (distance lower side of the burr—first bifurcation) and DAp (anteroposterior diameter above the burr) in deer antlers. H_{ext} is measured at the external side.

Pleistocene "*M. boldrini*" described by Azzaroli & Mazza (1992) is not quite clear. The metapodial from TD4 and the phalanges from TD4 and TD6 are more slender than in this group and much longer than in "*M. boldrini*".

De Vos *et al.* (1995) and Kahlke (1997) recognized three species of *Eucladoceros* from a group of localities correlated with MN 17 and MmQ 1 by Agustí *et al.* (1987), and which are presumably older than 1·4 Ma. All these forms have small and slender metapodials. The metapodial from TD4 is much longer than those of these species (Figure 11).

Kahlke (1997) described the species *Eucladoceros giulii* from Untermassfeld and assigned material to this species from other late Early Pleistocene localities, including Venta Micena, Würzburg-Schalksberg and Akhalkalaki. Doubtless, the large deer from Apollonia-1, assigned by Kostopoulos (1997) to "*Megaloceros* sp.", belongs to the same lineage. The deer from these localities have generally been assigned to species of the "*M. verticornis* group" or to *Megaceroides*. However, they differ from that group in having long and slender metapodials (Figure 14). The antlers assigned to this species are variable, but seem to share a brow tine with a high origin and with a basal subcylindrical section. The antlers and metapodials from TD4 and TD6 resemble their homologues in *E. giulii*.

E. giulii has been recognized as a distinct species only recently, but already a large amount of material from localities in Germany, Spain, Greece and Georgia can be assigned to this species. All these localities are late Early Pleistocene, suggesting a similar age for TD4 and TD6.

Cervus elaphus Linnaeus, 1758

Description
The P_3, M^3 (Figure 6), incisor and limb bones belong to a species intermediate in size between *Dama* and most *Megaloceros* species. In TD4 an antler with a bez tine typical of *Cervus elaphus* was found.

Discussion
Pleistocene deer that are larger than *Dama* and smaller than most of the *Megaloceros* species include *Cervus*, *Megaloceros savini* and *Eucladoceros*. *M. savini* from Cullar de Baza and Süssenborn and *Eucladoceros* have a large P_3 relative to the other cheek teeth. The specimen from TD6 is too small for *M. savini* and *Eucladoceros*, but is within the ranges for *Cervus elaphus*.

In early samples of *Cervus*, the distal part of the antler is simply bifurcated instead of having a "crown" of several tines. This form was named *C. acoronatus*. Nowadays, it is considered by most authors to be a chronosubspecies, *C. elaphus acoronatus* (Lister, 1990; Di Stefano & Petronio, 1995). Distal parts of antlers are not known from Atapuerca, so an attribution to subspecies is not possible. Probably one of the oldest records

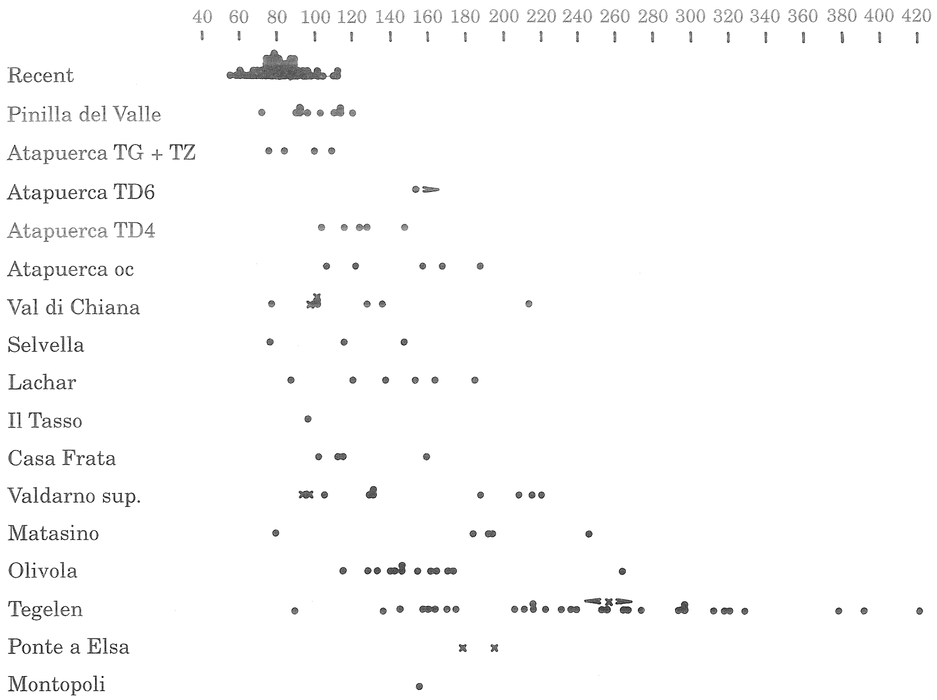

Figure 11. The position of the first bifurcation in antlers of *Dama*-like deer. The values indicated in the figure represent the index 100 H_{ext}/DAP, where H_{ext} is the distance from below the burr to the bifurcation. The localities are in approximate stratigraphical order from old (below) to young (above): Montopoli (IGF), Ponte a Elsa (IGF), Tegelen (NNML, TMH), Olivola (IGF), Matasino (IGF), Valdarno (IGF), Casa Frata (IGF), Il Tasso (IGF), Lachar (MNCN), Selvella (IGF), Val di Chiana (IGF), Atapuerca, Pinailla del Valle (UCM), "Recent" (includes mainly individuals from the Doñana reserve, Spain [EBDS], as well as specimens from other localities in Spain [MNCN] and Austria [NMW]). The upper Valdarno sample includes specimens from several levels which lack exact provenance data. Types indicated as crosses (Tegelen, type of *Cervus rhenanus*, Ponte a Elsa, type of *Pseudodama lyra*, Valdarno, type of *Dama nestii* and Val di Chiana type of *P. farnetensis*). Approximate values indicated with arrows.

of an acoronate cervid is from Mosbach 1, a locality within or below the Jaramillo Event (Von Koenigswald & Tobien, 1987). *Cervus* indicates that TD6 should be dated from late Early Pleistocene to Recent.

Cervidae indet.

Description and comparison

Remains of heavily worn P^4–M^3 may belong to a single individual. The morphology of the M^2 shows that the teeth are cervid: the lower limit of the crown does not undulate much, unlike in Bovinae. The lower part of the buccal wall of the paracone has an inflated shape and its upper part curves much lingually; the paracone was very low, lower than in the deer of the *Megaloceros*/*Eucladoceros* group. What remains of the styles along the paracones of the cheek teeth is not pronounced, unlike in *Alces*.

The teeth are much larger than the homologues of *E. giulii* and *M. soleilhacus*/*verticornis* and are even large compared to specimens of *M. giganteus*, especially the P^4.

Discussion

Large Pleistocene cervids include the *Megaloceros*/*Eucladoceros* group and *Alces*.

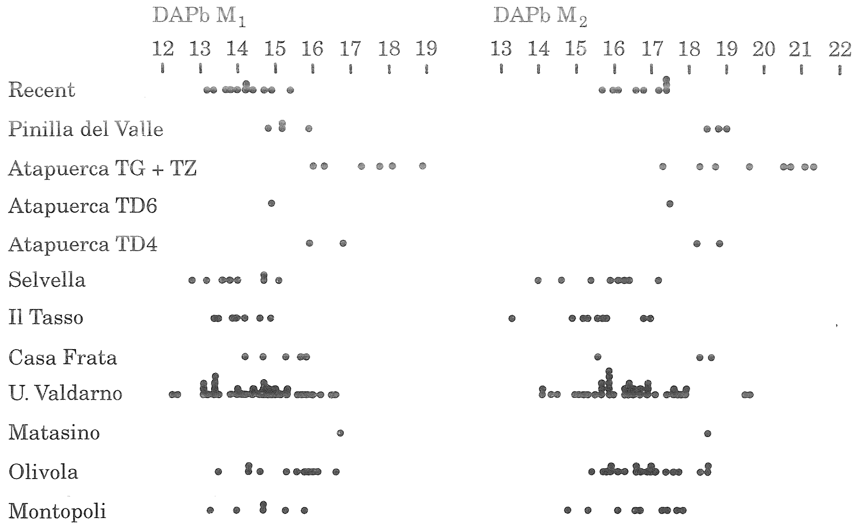

Figure 12. Variation in size of the M_1 and M_2 in the *Dama*-like deer. Sizes in mm. DAP_b is the length (measured at the base of the crown). Localities in approximate stratigraphical order from old (below) to young (above). Provenance of the data as in Figure 11. The Valdarno sample might include some specimens of the smaller *Croizetocerus ramosus*, a species that is also present in Montopoli. Material from Montopoli, Olivola, Matasino, Valdarno, Il Tasso, Casa Frata and Selvella in IGF, from Pinilla del Valle in the UCM, from Atapuerca in MB or temporarily in the MNCN, and recent material from Spain in MNCN.

The large size makes it unlikely that the TD6 specimens belong to any cervid of the first group, save for *M. giganteus*. However, the teeth seem to have lower crowns. What is left of the morphology differs from *Alces*. At present this material cannot be assigned to a species.

Family Bovidae Gray, 1821
Bovini cf. "*Bison voigtstedtensis*" Fischer, 1965

Description and comparison

The horn core has a strong curvature and ends in a blunt tip (Figure 15). The deep furrows and the lack of torsion recall *Bison*, rather than *Bos*.

The lower cheek teeth have a bovine morphology (Figure 16). The P_4 is larger than those of the bovines from Venta Micena. Both P_3 and P_4 are larger than those of *Leptobos* (specimens in the IGF, not indicated in Figure 17) and *Bison* from Pirro Nord and Soleilhac-Blanzac, smaller than those of *Bison* from Mosbach and Isernia and are close in size to the premolars of *Bison menneri* from Untermassfeld (Sher, 1997), "*Bison voigtstedtensis*" from Voigtstedt (Figure 17) and *Dmanisibos* from Dmanisi (Vekua, 1997).

The distal width (DTd) of the metacarpals from TD6 is in the upper limit of the sample from Venta Micena, is between Pirro Nord on the one hand and Blanzac and Mosbach on the other (Figure 18), and is close in size to the metacarpal of *Dmanisibos* from Dmanisi (Vekua, 1997). Two unciforms and an ulnar are tentatively assigned to this species.

The TD6 dental and postcranial remains are smaller than those of *Bos primigenius* from Gesher Benot Ya'akov (HUJ), Lunel Viel (Brugal, 1985), Torralba (MNCN) and Pinilla del Valle (UCM) and Paglicci (Figure 17; Sala, 1987).