

UNGULATES FROM GRAN DOLINA (Atapuerca, Burgos, Spain)

Jan VANDER MADE*

ABSTRACT

The ungulate fauna from the Gran Dolina sequence (Atapuerca, Burgos, Spain) is discussed. Special attention is paid to the fauna from level TD8.

The lower levels of Gran Dolina (TD4, 5, 6, 7, 8a) contain a fauna that is typical of the latest Early or earliest Middle Pleistocene : *Equus* sp. stenorid type, *Stephanorhinus etruscus*, *Sus scrofa*, *Hippopotamus amphibius*, *Dama nestii* ? *vallonetensis*, *Cervus elaphus*, *Eucladoceros giulii*, cf. «*Bison voigtstedtensis*» and *Ovibos/Praeovibos* sp.

The upper levels (TD 10, 11) contain a fauna with a younger aspect : *Equus* sp. caballoid type, *Stephanorhinus* cf. *hemitoechus*, *Dama dama clactoniana*, *Megaloceros giganteus* ?, *Bos/Bison* and *Caprini* indet.

In none of the levels there is a «glacial» fauna (the first ovibovines lacked typical «glacial» adaptations). Mammals that are typical of glacial periods in central Europe, such as *Rangifer*, *Alces*, *Saiga*, *Ovibos moschatus* etc., have not been found in the Lower and Middle Pleistocene of Spain, or only in the north of the Pyrenees and Cantabrian Mountains. Glaciations did not have a great impact on the ungulate fauna. Climate is not likely to have been an impediment to continuous human occupation of Spain from the Early Pleistocene onwards.

Key-words : Atapuerca, Gran Dolina, Pleistocene, Ungulates, *Eucladoceros*, *Dama*.

RÉSUMÉ

LA FAUNE DES ONGULÉS DE LA SÉQUENCE DE GRAN DOLINA (Atapuerca, Burgos, Espagne)

La faune des ongulés de la séquence de Gran Dolina (Atapuerca, Burgos, Espagne) est discutée. L'attention est spécialement donnée à la faune du niveau TD8.

Les niveaux inférieurs de Gran Dolina (TD4, 5, 6, 7, 8a) contiennent une faune typique du Pléistocène Inférieur supérieur ou Moyen inférieur : *Equus* sp. type sténonide, *Stephanorhinus etruscus*, *Sus scrofa*, *Hippopotamus amphibius*, *Dama nestii* ? *vallonetensis*, *Cervus elaphus*, *Eucladoceros giulii*, cf. «*Bison voigtstedtensis*» et *Ovibos/Praeovibos* sp.

Les niveaux supérieurs (TD10, 11) contiennent une faune avec un caractère plus récent : *Equus* sp. type caballoide, *Stephanorhinus* cf. *hemitoechus*, *Dama dama clactoniana*, *Cervus elaphus*, *Megaloceros giganteus* ?, *Bos/Bison* et *Caprini* indet.

Aucun niveau ne présente de faune «glaciaire» (des adaptations typiquement «glaciaires» manquent chez les premiers ovibovins). Des mammifères typiques des époques glaciaires dans le centre de l'Europe, comme *Rangifer*, *Alces*, *Saiga*, *Ovibos moschatus* etc., ne sont pas observés dans le Pléistocène Inférieur et Moyen de l'Espagne, ou seulement dans le nord des Pyrénées et de la Cordillère Cantabre. Les périodes glaciaires n'ont pas eu d'impact important sur la faune des ongulés. Cette donnée supporte l'idée d'une occupation humaine continue de l'Espagne à partir du Pléistocène Inférieur.

Mots-clés : Atapuerca, Gran Dolina, Pléistocène, Ongulés, *Eucladoceros*, *Dama*.

INTRODUCTION

The Sierra de Atapuerca (province of Burgos, Spain) has a series of fissure fillings that contain fossil mammals and lithic industry or other indications of human presence. A railway trench, which is now abandoned, cut through several

fossiliferous fissure fillings. The best known sites are Gran Dolina (code TD = Trinchera Dolina) and the complex of Tres Simas (TS) consisting of Galeria (TG), Zarpazos (TZ) and Trinchera Norte (TN). Sima del Elefante is a locality, where research started recently. The well known locality of Sima de los Huesos (SH) is in a cave nearby.

* Consejo Superior de Investigaciones Científicas, Museo Nacional de Ciencias Naturales, c. José Gutiérrez Abascal 2, 28006 MADRID, Espagne.

Sima de los Huesos is well known for its huge collection (well over 2000 specimens) of *Homo heidelbergensis* of late Middle Pleistocene age (Journal of Human Evolution, 1997, Vol. 33., monographic numbers 2/3 : 105-421). Tres Simas yielded some human remains as well as lithic industry of a similar age. Gran Dolina became well known when late Early Pleistocene human remains were discovered in level TD6 (Carbonell *et al.*, 1995). The approximately 80 human specimens were found in association with lithic industry and bones with cutmarks and represent the species *Homo antecessor*, that is supposed to be ancestral to both our own species and the Neanderthals (Bermúdez de Castro *et al.*, 1997).

The fissure filling of Dolina has a thickness of some 17 m and is divided into 11 stratigraphic units : TD1 (bottom) to TD11 (top). The Brunhes-Matuyama boundary was found in the top of TD7 (Parés & Pérez-González, 1995), which corresponds to the Early - Middle Pleistocene boundary. The study of rodents revealed a hiatus within TD8 (Laplana & Cuenca-Bescós, 1997). TD1 till the lower part of TD7 belongs to the Lower Pleistocene and the upper part of TD7 and TD8a to the lowermost Middle Pleistocene. The upper part of TD8 (TD8b or TD8sup.) till TD11 belongs to the upper Middle Pleistocene.

Ungulate remains, collected in the late seventies, were described from what was claimed to be TD3 (Soto, 1987). Excavations in the nineties did not yield large mammals from TD3. Either the fossil content in TD3 was not homogenous, or the use of the term TD3 may have varied since the seventies. TD1-5 are accessible in the western part of the fissure (TDW) and TDW4-5 have been excavated in the early nineties. A 6 m² test pit in the main fissure reaches presently level TD5 and a 100 m² excavation reaches the top of TD10. It is the test pit that yielded the remains of *Homo antecessor*.

Detailed descriptions of the ungulates from TD6, TDW4 and TD7 are in preparation or planned (Van der Made, in prep.). It is the aim of this paper to give an overview of the ungulates of the TD sequence and describe more in detail those of TD8a.

The fossils bear labels with provenance data. For instance, ATA94 means Atapuerca 1994 (each year has a catalogue), TD8 is level 8 of Dolina, talla 29 refers to a more or less standardized thickness of sediment (the fossil was found in the 29th unit), I-16 is the quadrant and 62 the object number in this quadrant. The complete label is ATA94, TD8, talla 29, I-16, 62.

ABBREVIATIONS OF MEASUREMENTS AND INDICES

Measurements are generally taken as indicated by Van der Made (1989, 1996). All measurements are given in mm, unless indicated otherwise. 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 lowers.

DAP Antero-posterior diameter.
 DAPb DAP at the base of a tooth, or DAP of an antler, measured just above the burr.
 DAPm Minimal DAP of a bone.

DAPd DAP of the distal part of a bone.
 DAPdf DAP of a facet at the distal end of a bone.
 DAPo DAP of a tooth, measured at the occlusal surface.
 DAPp DAP of the proximal part of a bone.
 DLL Linguo-labial diameter of incisors.
 DLLo DLL measured at the occlusal surface.
 DMD Meso-distal diameter of incisors.
 DMDo DMD measured at the occlusal surface.
 DT Transverse diameter («width»)
 DTa DT of anterior lobe of a cheek tooth.
 DTb DT of an antler, measured just above the burr.
 DTd DT of the distal part of a bone.
 DTm DT of the middle lobe in D_4 , or minimal DT of a bone.
 DTp DT of the second lobe of a cheek tooth or transverse width of the proximal part of a bone. DTp in *Equus* is measured at the metastylid.
 H Height of a tooth or a bone.
 Ha H of a molar at the lingual side of the metaconid or at the buccal side of the paracone.
 Hla H at the labial side of an incisor, canine or premolar.
 Hli H at the lingual side of an incisor, canine or premolar.
 Hp H of a molar at the lingual side of the entoconid or at the buccal side of the metacone.
 I Index (DAP / DT) x 100% or (DMD / DLL) x 100%.
 L Length of a bone ; Lext = external length, Lm = length in the middle, Lint = internal length.
 R Diameter of the distal part of a humerus, measured at different places (R1, R2 etc.) (See Van der Made, 1996.)

Occasionally, measurements of teeth are given as DAP x DT, as DAP x DTa - DTp or as DAPo/DAPb x DTa - DTp (for instance 23.5/22.9 x 12.3 - 12.2). For *Equus* measurements are given at the occlusal surface and at half the height of the crown (for instance : 25.3/25.1 x 15.7/15.6 - 15.6/15.4). .. or — in such formulas indicate that measurements could not be taken because of damage or wear (—), or that they were not taken for another reason (.), for instance, the tooth was partially covered by sediment or bone.

COLLECTIONS AND THEIR ABBREVIATIONS

The ungulates from Gran Dolina are at present stored in the Laboratori de Arqueologia de la Universitat Rovira i Virgili, Tarragona (LAUT) and in the Museo Nacional de Ciencias Naturales, Madrid (MNCN), but will finally be stored in the Museo de Burgos (MB). The remains from Atapuerca were compared with fossil and recent bones stored in the following institutes :

DSCGPF Dipartimento di Scienze Geologiche e Paleontologiche, Università di Ferrara, Ferrara.
 EBDS Estación Biológica de la Doñana, Sevilla.
 HUJ Hebrew University of Jerusalem.
 IGF Istituto di Geologia, Firenze.
 IPS Instituto de Paleontología, Sabadell.
 IQW Institut für Geowissenschaften, Bereich Quartärpaläontologie, Weimar.
 MCP Musee Crozatier, Le Puy-en-Velay.

MNCN	Museo Nacional de Ciencias Naturales, Madrid.
NMB	Naturhistorisches Museum, Basel.
NMM	Naturhistorisches Museum, Mainz.
NMW	Naturhistorisches Museum, Wien.
NNML	Nationaal Natuurhistorisch Museum, Leiden.
SMNS	Staatliches Museum für Naturkunde, Stuttgart.
TMH	Teylers Museum, Haarlem.
UCM	Universidad Complutense de Madrid.

SYSTEMATICS

Equus sp. stenonid type

Material from TD8 and description

ATA94, TD8, talla 28, G-17, 10 - Left P^{3/4}. H > 71.4, DAP 31.2/26.7, DT 22.8/26.2, protocone 12.9/10.6. Occlusal surface covered with sediment. Destroyed for analysis.

ATA94, TD8, talla 28, G-16, 44 - Left M^{1/2}. H > 49.7, DAP 26.0/26.6, DT 26.1/26.6, protocone 9.2/9.0. 1-1-1/0. Protocone type 3. No hypoconal constriction. Groove on parastyle, para- and mesostyles not particularly wide. Destroyed for analysis.

ATA94, TD8, talla 29, I-16, 28 - Left P². Hla > 55.2, DMDo 22.9, DLLo 10.3.

ATA94, TD8, talla 27, H-16, 12 - Second phalanx. L ± 54.5, L dorsal 38.2, DTm 53.6, DTp ≥ 62.2, DAPp 36.6, DTd —, DTpf 57.1.

ATA94, TD8, talla 28, G-17, 13 - Right P². Unworn. H > 37.7, DAP 36.5/36.7, DT 25.4/25.6, Protocone ± 8.7/...

ATA94, TD8, talla 28, G-17, 11 - Proximal part of third phalanx. DAPpf 28.3.

ATA94, TD8, G-16, 9 - Left DI₁. DMDo 13.1, DMD 15.2, DLL 7.0.

ATA94, TD8, talla 29, H-16, 45 - Left astragalus. Lext >> 53.6, measurement 2 52.3, measurement 3 28.1, DT ≥ 61.3, DTdf 52.0, DAPdf ..., DAP (measurement 7) 51.0, Lm 48.8, Lint ± 58.7, DTp ± 50.1.

ATA94, TD8, talla 28, G-17, 12 - Left D². H 12.0, DAP —/40.6, DT —/22.7, protocone —/6.0. Surface partially covered by sediment.

ATA94, TD8, talla 29, H-16, 53 - Left third cuneiform. DAP 39.9, DT 47.1.

ATA94, TD8, H-16, 1 - Right I₁. DMDo 13.7, DTo 10.6.

ATA94, TD8, talla 31, I-16, 65 - Right first phalanx. L 86.8, L dorsal 79.7, DTm ..., DTp 49.1, DAPp ≥ 35.1, DTd 42.9, DTdf 40.2, DAPd 25.3, measurement 9 53.6, measurement 10 69.8, measurement 11 69.5, measurement 12 14.0, measurement 13 15.5.

ATA94, TD8, talla 29, I-16, 21 - Left astragalus. Lext 59.2, measurement 2 > 53.2, measurement 3 30.7, DT > 59.0, DTdf 48.2, DAPdf 35.3, Lint 60.2, Lm 45.2, DTp ≥ 45.4.

ATA94, TD8, talla 28, I-16, 14 - Left C². DAP 13.5, DT 9.2.

ATA94, TD8, talla 29, I-16, sc - Left DI¹. DMDo 18.2, DTb 9.7.

ATA94, TD8, talla 28, G-16, 35 - Right trapezoid. DAP 32.7, DT 27.5, H 24.3.

ATA94, TD8, talla 27, H-16, 11 - Sesamoid behind third phalanx. DT 54.0, H 13.9.

ATA94, TD8, talla 28, H-16, sc - Right I₁. DMD ≥ 17.2, DLL ± 10.4.

ATA94, TD8, talla 28, G-17, 14 - Left P². Not worn, no base. H > 28.5, DAP 34.9/—, DT 25.3/—, protocone 7.1/—.

ATA94, TD8, talla 28, H-16, 34 - Right D^{3/4}. Very little wear. H 30.6, DAP 35.9/34.2, DT 21.8/24.3, protocone 10.6/10.5.

ATA94, TD8, talla 29, I-16, 29 - Right trapezoid. DAP 33.9, DT 25.7, H 25.1.

Comparison and discussion

The material represents an *Equus* of small size and is comparable to the equid from TD4 and TD6 (Pl. 1, fig. 2, 9, 10). Lower cheek teeth from those levels have stenonid linguaflexids, typical of stenonid horses (Forsten, 1992).

Several variants of a model for the evolution of the small stenonid horses were proposed by Alberdi *et al.*, (1989, 1995a, 1995b, in prep.). This model supposes a single lineage, but vary between the first variant with six chronosubspecies of *E. stenonis* and the latest variant with four chronospecies with a total of eight chronosubspecies. A preliminary publication by Guerrero-Alba *et al.*, (1997) assigned the small stenonid horses to two species, *E. stenonis* and *E. altidens*, the latter being supposed to be an immigrant. Both models suggest that the stenonids younger than 1.2 Ma belong to *E. altidens*.

Alberdi & Ruiz Bustos (1989) gave common data on samples from a series of localities from the Guadix Baza basin, including samples assigned to early forms of *E. stenonis* and to *E. altidens*. The size of the cheek teeth in these samples do not separate the different forms nor assign the material from Gran Dolina to one of them (Van der Made, submitted, fig. 2). The protoconal index is very variable. On average, it shows a gradual increase in the molars, though there is still overlap between the oldest and youngest samples from the Guadix Baza basin (fig. 1). The commonly counted folds of the enamel show few changes throughout the sequence (fig. 2). Only with huge sample sizes, it might be possible to establish differences in average values of these parameters in the six or eight subspecies.

Alberdi *et al.*, (1995) estimated body weights of horses; the stenonid horses showed a gradual decrease in estimated weight from 563 kg in *E. s. livezovensis* to 223 kg in *E. s. granatensis* and then a rise to 339 kg in *E. altidens*. The best estimators of body weight were antero-posterior diameters of metapodials and phalanges. It seems thus that those measurements are the best ones for recognition of the different stenonid forms. *E. s. livezovensis* from Húelago

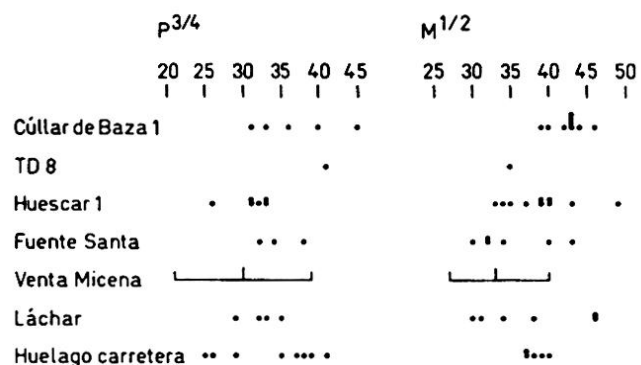


Fig. 1 : Protoconal indices in *Equus* from Húelago carretera, Láchar, Fuentesanta, Huescar 1 and Cúllar de Baza (Alberdi & Ruiz Bustos, 1989) and from Venta Micena (Marín, 1987) compared to those from Atapuerca TD8. Localities in approximate order from old (bottom) to young (top).

Fig. 1 : Les indices protoconiques en *Equus* de Húelago carretera, Láchar, Fuentesanta, Huescar 1 et Cúllar de Baza (Alberdi & Ruiz Bustos, 1989) et de Venta Micena (Marín, 1987) sont comparés avec ceux d'Atapuerca TD8. Les gisements sont arrangés à peu près en ordre stratigraphique de bas en haut.

	P ^{3/4}					M ^{1/2}				
	1	2	3	4	5	1	2	3	4	5
Cúllar de Baza	fs.	fs.	fs.	fs.	fs.	fs.	fs.
TD 8					
Huescar 1	fs.	fs. .	fs.	fs.	fs.	fs.	fs.	fs.
Fuente Santa	fs.	fs.	fs.	. fs.	fs.	fs.	fs.
Venta Micena	fs.
Láchar	fs.	. fs.	fs.	fs.	fs.	. fs.	fs.	fs.	fs.
Huelago carret. fs.	. fs.

Fig. 2 : Plications in the upper cheek teeth of *Equus*. The number of plications is graphically indicated, the sequence is the same as in the conventional plications formula : 1) plis protoloph, 2) plis prefossette, 3) plis postfossette, 4) plis hypostyle, 5) pli caballin (Eisenmann et al., 1988). The marks indicate 0-8 plications. Data from Alberdi & Ruiz Bustos (1989).

Fig. 2 : Les plis des dents jugales d'*Equus*, les numéros des plis sont ceux de la formule conventionnelle : 1) plis protolophe, 2) plis prefossette, 3) plis postfossette, 4) plis hypostyle, 5) pli caballin (Eisenmann et al., 1988). Les marques indiquent 0-8 plications. Origine des données : Alberdi & Ruiz Bustos (1989).

carretera has a first phalanx with a DAPp of 34.0, the form from Huescar has 34.2, 29.5 and 33.7 and *E. altidens* from Cúllar de Baza 32.9 (Alberdi & Ruiz Bustos, 1989) and 14 phalanges of *E. s. granatensis* from Venta Micena range from 31.3 till 38.0 (Marín, 1987). These data show that the range of variation is great and that small samples cannot reliably be assigned to a taxon using this variable. The TD8 phalanx (DAPp ≥ 35.1) is probably within the ranges of «*granatensis*».

The question arises, whether the small and gradual changes in this lineage allow for the recognition of so many chrono(sub)species. The material from TD8a belongs to a small stenorid horse and the combination of its young age and current ideas on the evolution of these horses suggest that it belongs to the later species *E. altidens*. However, a critical revision of this group with full publication of the relevant raw data is needed.

Equus sp. caballoid type

Description and discussion

Material from TD10 includes lower cheek teeth with caballoid linguaflexids, indicating a caballoid horse (Forsten, 1992). The postcranial elements from TD10 suggest a form that is not very large.

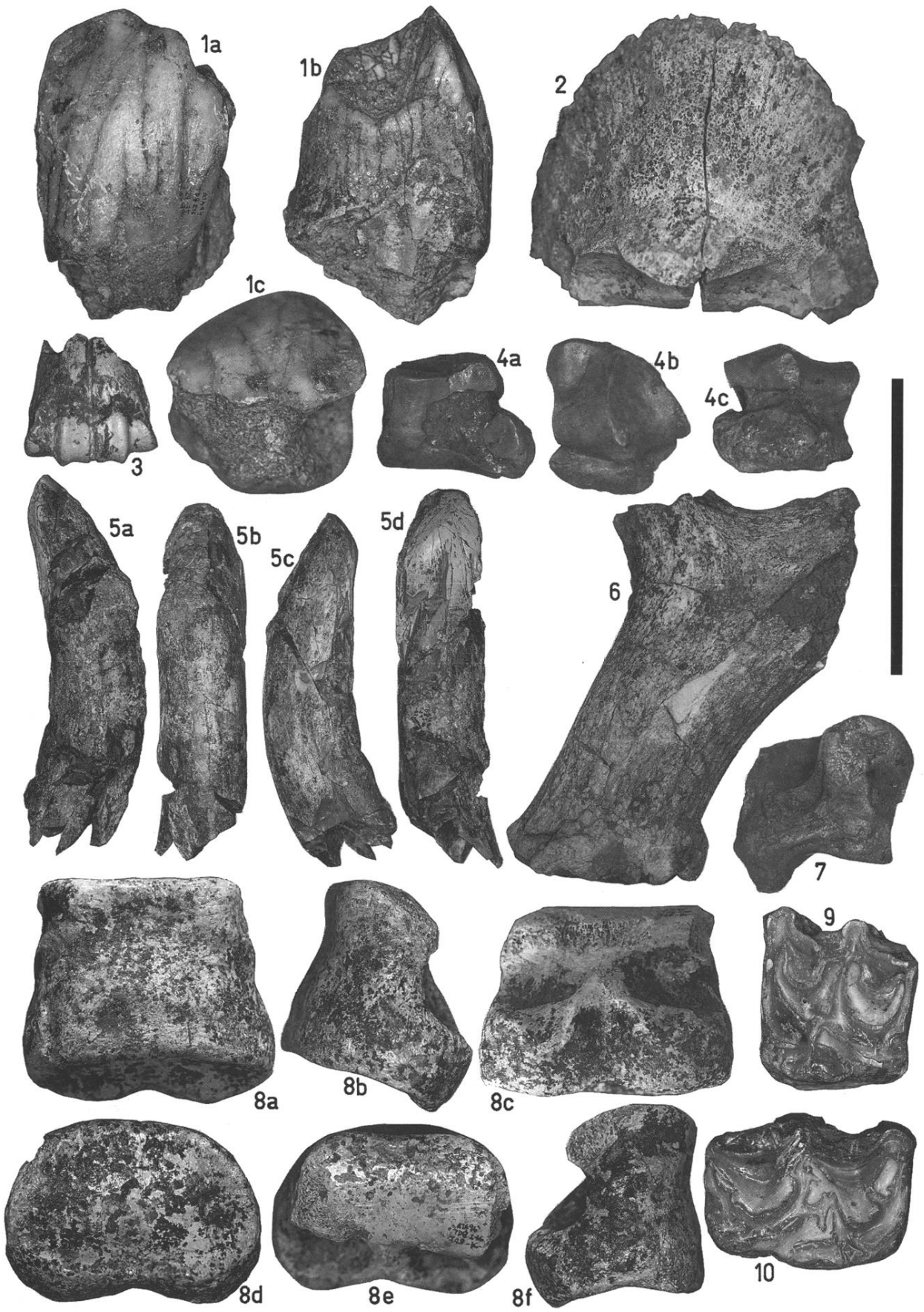
Eisenmann (1991) listed eleven caballoid species for Europe, Alberdi *et al.*, (1995) six and Forsten (1988) tree and others (cited by Forsten) recognize only one species. All agree on a general decrease in size, though the interpretations are different : three groups with a total of eleven species with overall decreasing size, a series of six species with declining body size, or three species the smaller ones appearing later and living together with the larger species. Considering the variability found in other groups, the data cited in favor of several contemporaneous species leave space for some doubts in many cases, nor are the

Pl. 1 :

1. *Stephanorhinus etruscus*, left P² from TD8 (ATA94, TD8, talla 29, I-16, 63), buccal, anterior and occlusal views.
2. *Equus altidens*, third phalanx from TD6 (ATA96, TD6, perfil, G-16, 281), dorsal view.
3. Cf. «*Bison voigtstedtensis*», distal metacarpal from TD6 (ATA94, TD6, G-18, 32), dorsal view.
4. Cf. «*Bison voigtstedtensis*», right unciform from TD6 (ATA95, TD6, talla 40-41, H-17, 111), internal, proximal and posterior views.
5. *Hippopotamus amphibius*, right upper incisor from TD8 (ATA94, TD8, talla 29, I-16, 62), mesial, labial, distal and lingual views.
6. *Eucladoceros giulii*, right antler from TD6 (ATA96, talla 52, H-16, 435), internal view.
7. Cf. «*Bison voigtstedtensis*», right ulnar from TD6 (ATA95, TD6, talla 40-41, H-17, 106), external view.
8. *Stephanorhinus etruscus*, right first central phalanx from TD8 (ATA94, TD8, talla 28, I-16, 16), dorsal, external, plantar, proximal, distal and internal views.
9. *Equus altidens*, left M^{1/2} from TD6 (ATA96, TD6, talla 50, H-17, 302), occlusal view.
10. *Equus altidens*, right D^{3/4} from TD6 (ATA95, TD6, talla 38-39, G-18, 53), occlusal view.

Pl. 1 :

1. *Stephanorhinus etruscus*, P² gauche de TD8 (ATA94, TD8, talla 29, I-16, 63), vues buccale, antérieure et occlusale.
2. *Equus altidens*, troisième phalange de TD6 (ATA96, TD6, perfil, G-16, 281), vue dorsale.
3. Cf. «*Bison voigtstedtensis*», métacarpe distale de TD6 (ATA94, TD6, G-18, 32), vue dorsale.
4. Cf. «*Bison voigtstedtensis*», oncliforme droit de TD6 (ATA95, TD6, talla 40-41, H-17, 111), vues interne, proximale et postérieure.
5. *Hippopotamus amphibius*, incisive supérieure droite de TD8 (ATA94, TD8, talla 29, I-16, 62), vues mésiale, labiale, distale et linguale.
6. *Eucladoceros giulii*, bois droit de TD6 (ATA96, talla 52, H-16, 435), vue interne.
7. Cf. «*Bison voigtstedtensis*», ulnaire droit de TD6 (ATA95, TD6, talla 40-41, H-17, 106), vue externe.
8. *Stephanorhinus etruscus*, première phalange centrale droite de TD8 (ATA94, TD8, talla 28, I-16, 16), vues dorsale, externe, plantar, proximale, distale et interne.
9. *Equus altidens*, M^{1/2} gauche de TD6 (ATA96, TD6, talla 50, H-17, 302), vue occlusale.
10. *Equus altidens*, D^{3/4} droit de TD6 (ATA95, TD6, talla 38-39, G-18, 53), vue occlusale.



morphometrical data very convincing for recognizing a large number of subsequent species.

Stephanorhinus etruscus

Material from TD8

ATA94, TD8, talla 28, I-16, 16 — Right first central phalanx. L 42.0, dorsal length 30.6, DAPp 31.3, DAPpf 27.3, DTp 43.8, DTpf 42.4, DTd \geq 35.9, DAPd 21.0.

ATA94, TD8, talla 29, H-16, 52 — Protocone of a left upper molar. ATA94, TD8, talla 29, H-16, 63 — Buccal fragment of a totally worn upper cheek tooth. DAPb 36.7.

ATA94, TD8, talla 29, I-16, 63 — Left P². DAP 34.6, DAPb 30.5, DTa 31.6, DTp 35.1. Hla = 45.6.

Description and comparison

The P² (Pl. 1, fig. 1), with a *Stephanorhinus* morphology, enters in the range of metrical variation for *S. etruscus*, *S. hundsheimensis* and *S. hemitoechus* (fig. 3). The size of the phalanx (Pl. 1, fig. 8) suggests a small species.

Discussion

S. hundsheimensis has large and *S. kirchbergensis* very large phalanges (Staesche, 1941). The TD8a rhino either represents *S. etruscus* or *S. hemitoechus*, which have smaller postcranials.

There are more remains from TD6 and especially from TD4 and TD5, including many small sized postcranials. These are all assumed to belong to the same species. Figure 3 gives the DAP of teeth of a mandible from TD5 compared with data given by Fortelius *et al.*, (1993). *S. hemitoechus*

has relatively large M₃ and relatively small premolars and probably evolved from *S. etruscus*, with small M₃ and large premolars. The M₃ from TD5 is outside the range for *S. hemitoechus*. The same is the case for the P₂ (Van der Made, in prep. fig. 4). One of the P₃ is outside the ranges for *S. etruscus* from the Valdarno, but inside the ranges for *S. hemitoechus* of the Middle and Late Pleistocene. This is in accordance with the intermediate position of TD4-8a.

Stephanorhinus cf. hemitoechus

Description and discussion

Some remains of rhinos from TD10 and TD11 are too poor for a determination, but considering their age, they might represent *S. hemitoechus*.

Sus scrofa

Description and discussion

A suid P₃ was recovered from TD6. Currently two suid species are recognized from continental Europe : *Sus strozii* and *Sus scrofa* (Faure & Guérin, 1984 ; Van der Made & Moyà Solà, 1989).

The length of the P₃ of *S. strozii* and *S. scrofa* overlaps, but for a given length, the width does not overlap. The length/width index has higher values in *Sus scrofa*. In 18 specimens of *S. strozii* from Olivola and the upper Valdarno these values range from 132 to 171. European *Sus scrofa* has narrow premolars, with values over 171. The P₃ from TD6 has a length/width index I of 185 and is within the ranges for *Sus scrofa*.

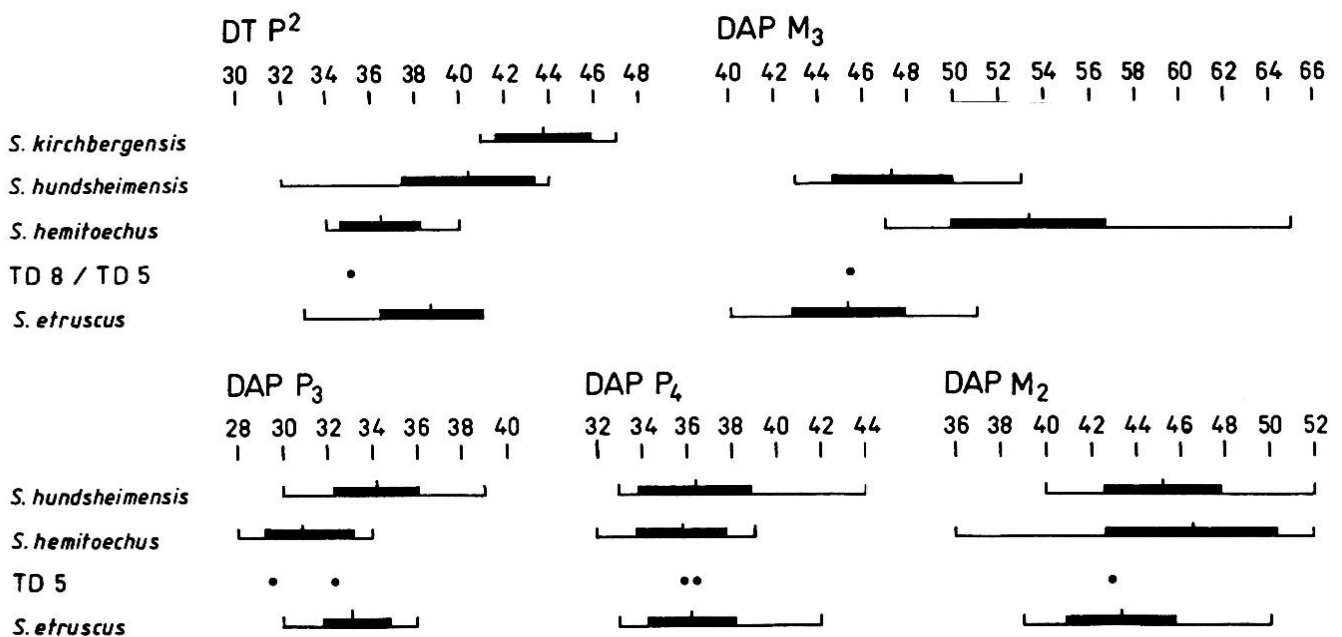


Fig. 3 : The sizes of the cheek teeth of *Stephanorhinus etruscus* from TD8 (P²) and TD5 compared to the averages, standard deviations and ranges of their homologues in other species of *Stephanorhinus* (data from Fortelius *et al.*, 1993).

Fig. 3 : Les dimensions des jugales de *Stephanorhinus etruscus* de TD8 (P²) et de TD5 comparées avec les moyennes, écart-types, maximum et minimum *Stephanorhinus* (données de Fortelius *et al.*, 1993).

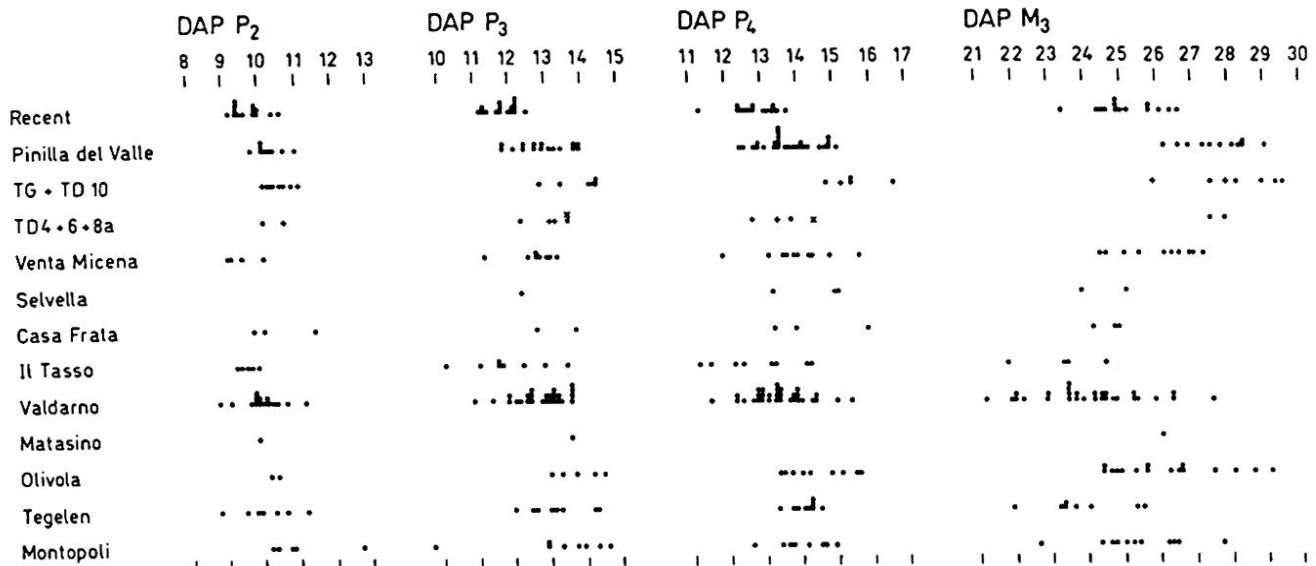


Fig. 4 : The size of the cheek teeth of the *Dama*-like deer. The localities are in approximate order from old (bottom) to young (top) : Montopoli (IGF), Tegelen (type locality of «*Cervus*» *rhenanus* ; NNML, TMH), Olivola (IGF), Matasino (IGF), Upper Valdarno (mostly old collections without exact provenance data ; «type locality» of «*Dama nestii*» ; IGF), Il Tasso (IGF), Casa Frata (IGF), Selvella (IGF), Venta Micena (IPS), TD4 (dots), TD6 (crosses), TD8a (oblique crosses), TG (dots), TD10 (crosses), Pinilla del Valle (UCM) and recent *Dama* from Spain (MNCN, EBDS) and Austria (NMW).

Fig. 4 : Diamètre antéro-postérieur des dents de cervidés semblables à *Dama*. Les gisements sont arrangés à peu près en ordre stratigraphique de bas en haut : Montopoli (IGF), Tegelen (gisement type de «*Cervus*» *rhenanus*; NNML, TMH), Olivola (IGF), Matasino (IGF), Upper Valdarno (surtout des collections vieilles sans indications exactes d'origine ; «gisement type» de «*Dama nestii*»; IGF), Il Tasso (IGF), Casa Frata (IGF), Selvella (IGF), Venta Micena (IPS), TD4 (points), TD6 (croix), TD8a (croix obliques), TG (points), TD10 (croix), Pinilla del Valle (UCM) et *Dama* récent de l'Espagne (MNCN, EBDS) et d'Autriche (NMW).

Hippopotamus amphibius

Material from TD8

ATA94, TD8, talla 29, I-16, 62 — Right upper incisor, probably I². DMD 30.9, DLL 30.9.

Description and comparison

The tooth is curved and has a large linguo-apical facet (Plate 1, fig. 5). The band of enamel at the labial side varies in width between 2.1 and 14.3 mm. The specimen is 13-14 cm long and has a wide pulp cavity.

Discussion

Opposing views exist on the taxonomy of the European Pleistocene hippos (Faure, 1985 ; Alberdi & Ruiz Bustos, 1985 ; Mazo, 1989 ; Kahlke, 1987). One of the views is, that there is a single species, *H. amphibius*, that evolved smaller body size. Since hippo incisors have continuous growth, they are very variable in size and useless in recognizing the subspecies. Therefore the incisor from TD8a is here assigned to *H. amphibius* and not to any of the subspecies.

Dama nestii? *vallonetensis*

Material from TD8

ATA94, base TD8, I-17, sc, z=468 — Right first phalanx. DAPp 23.0, DAPpf 21.7, DTp 16.8.

ATA94, base TD8, I-17, sc, z=468 — Right second phalanx. DAPp 23.4/21.7, DTp 17.5.

ATA94, TD8, talla 29, I-16, 54 — Left M_{1/2} (M₁ on size). 16.1/15.7 x 10.8 - 10.7.

ATA94, TD8, talla 28, G-18, 2 — Right scapula. DAPp —, DAPdf 37.8, DTd 35.0, DAPn 28.2, DTn ≥18.3.

ATA94, TD8, talla 28, G-16, 47 — Antero-distal fragment of right femur.

ATA94, TD8, talla 29, I-16, 34 — Left distal articulation of metapodial. DAPd >21.6, DTd ≥15.5.

ATA94, TD8, talla 28, H-16, 26 — Right distal humerus. DAPd —, DTd >40.0, DTdf 37.6, R1-5: 30.3, 22.3, 25.9, 18.6, 19.9.

ATA94, TD8, talla 29, I-16, sc — Distal metacarpus (right/left?); left roller: DAP 22.7, DT 14.8, right roller: DAP 22.5, DT 14.5.

ATA94, TD8, talla 28, g-16, 39 — Left distal ulna. DAPd 12.6, DTd 11.3.

ATA94, TD8, talla 28, G-16, 38 — Right second phalanx. DAPp 21.0, DAPpf 19.9, DTp 16.1, L 34.6, DAPd 18.8, DTd 12.6.

ATA94, TD8, talla 28, G-16, 34 — Left distal metacarpal. Roller MC III DAP 23.1, DT 15.8.

ATA94, TD8, talla 29, H-16, 47 — Right mandible with P₂-M₁. P₂: 13.6 x 7.2 - 8.3, D ±27.3, P₄: 14.4 x 8.1 - 8.7, D ±28.4, M₁: 16.5 x 10.6 - 11.6, D ±31.1.

ATA94, TD8, talla 16, G-16, sc — Right P². >12 x 10.7/11.4 x -.

ATA94, TD8, talla 29, I-19, 50 — Right M², paracone.

ATA94, TD8, talla 29, I-16, 48 — Much worn left M². 18.8 x 19.0 - 16.8.

ATA94, TD8, talla 29, I-16, 46 — Left humerus. DAPd 42.8, DTd 42.8, DTdf 39.3, R1-5: 30.5, 23.8, 27.0, 19.3, 19.9.

ATA94, TD8, talla 29, I-16, 43 — Right M^{1/2}. 18.8/16.5 x 18.1 - 17.7.

ATA94, TD8, talla 29, I-16, 42 — Left M_{1/2}. 18.1/17.2 x 11.2 - 11.8.

ATA94, TD8, talla 29, H-16, 56 — Proximal part of left metatarsus. DAPp ±34.0, DTp ±27.9, DAPpf ±28.9, DAPm ≤19.3, DTm 18.1.

ATA94, TD8, talla 29, I-17, 2 — Proximal left femur. DAPf 28.9.
 ATA94, TD8, talla 28, G-17, 5 — Distal part of juvenile metatarsal, without articulation facets. DAPm 17.4, DTm 18.5.
 ATA94, TD8, talla 28, G-17, 17 — Left first phalanx. DAP 22.0, DAPf 20.2, DTp 17.7, L 48.8, DAPd 14.3, DTd 14.7.
 ATA94, TD8, talla 28, G-17, 25 — Right second phalanx. DAP 20.6/19.4, DTp 15.8, L 34.1, DAPd 18.6, DTd \geq 12.7.
 ATA94, TD8, talla 28, G-17, 20 — Left P⁴. 12.9/10.3 x 15.5.
 ATA94, TD8, talla ..., G-16, 21 — Right third phalanx. DAP 23.2/20.5, DAPf 16.1, DTp 12.7, L 34.3.
 ATA94, TD8, talla 28, H-16, 36 — Left distal metacarpus. MC III: DAPd —, DTd 15.5. MC IV: DAPd \geq 21.9, DTd 14.6.
 ?ATA94, TD8, G-16, 10 — Posterior lobe of right D⁴ or M⁴. Hp 17.3.
 ?ATA94, TD8, talla 28, G-16, 51 — right M⁴ (M⁴?). \pm 16.4, x — 16.5.

Description and comparison

The bones and teeth have a typical cervine morphology and are small. The P₄ lacks a metaprecristid to the paraconid, thus leaving the protofossid open. The specimens are similar to more abundant material from TD6 and TD4.

Discussion

The material from TD8a represents a small cervine and is morphologically different from *Capreolus* and *Rangifer*, which are odocoilines. The smallest cervines in the European Pleistocene are *Dama*-like deer. A similar deer is present in the TD4 and TD6 collections. Antlers from these levels corroborate this assignment.

Dama-like deer were present already in Europe in the Pliocene and were placed by Azzaroli (1953) in the genus *Dama*, whereas Azzaroli (1992) introduced a new genus name for them, *Pseudodama*, with type species *P. nestii*. In the geologically younger forms of *Dama*-like deer, the bifurcation between brow tine and main beam becomes lower and their angle wider, the main beam is directed more backwards and outwards, the distal part of the antler becomes more complex and finally palmation develops (Van der Made, submitted). These changes seem to be gradual and unidirectional. There are no important morphological changes in the teeth and postcranials. However, there are size changes, but these are not unidirectional, they are fluctuations. Figure 4 gives the size of some cheek teeth. The samples are in approximate order from old (bottom) to young (top). Size seems to drop from Olivola till Selvella, then size increases again towards Atapuerca TG and TD10 and then it drops again. This is best seen in the molars, premolar length seems to be subject to reduction and the P₂ and P₃ of the larger late Early and Middle Pleistocene deer are not much longer than those of the smaller Early Pleistocene deer.

Azzaroli (1992) admitted a relationship between the early Pleistocene *Dama*-like deer and the living fallow deer. However, he introduced the name *Pseudodama* for the former group, because he did not consider a particularly close relationship demonstrated. The necessity for the introduction of a new taxon should be demonstrated, rather than that the absence should be stressed of a study demonstrating the

contrary. The continuum in size and morphology, described above, seems to indicate a direct ancestor-descendant relationship and strongly suggests that *Pseudodama* should be included in *Dama*. «*Pseudodama*» has simple antlers, like some living Asian deer. The retention of primitive characters in the latter deer is no indication of a closer relationship between them and «*Pseudodama*».

The taxon «*Cervus nestii vallonensis*» should be placed in *Dama*. Kahlke (1997) included material from Casa Frata, Selvella, Pirro Nord, Vallonet and Untermassfeld in this taxon. There seems to be a size increase in these localities from old to young, so it is questionable whether all this material should be included in the same subspecies, or even in the same species. The TD 4-8 material is smaller than later material assigned to *D. d. clactoniana*, but it is close to values indicated for Untermassfeld (Kahlke, 1997), a locality of the same age as type locality Vallonet (de Lumley *et al.*, 1988). It is not the intention here to discuss the specific assignment of the subspecies *vallonensis* and the material from the lower levels of Gran Dolina is assigned to *Dama nestii? vallonensis*.

The apparent affinities of the material from TD4, TD6 and TD8a with *D. n.? vallonensis* suggests a late Early Pleistocene or early Middle Pleistocene age.

Dama dama clactoniana

Description and discussion

This form is found in TD10. It is larger than the fallow deer from TD4-8a and it is even slightly larger than the deer from Pinilla del Valle that was believed to represent the Clacton fallow deer (Alferez *et al.*, 1982).

Eucladoceros giulii

Material from TD8

ATA94, TD8, G-16, 19 — Left P₃. 23.3 x 11.2 - 12.9.
 ATA94, TD8, talla 28, I-17, 1 — Right calcaneum. DAPsf \pm 42.8.
 ATA94, TD8, talla 28, G-17, 4 — Left astragalus. Lext >73.3, Lm 60.9, Lint >72.0, DTp 47.8, DTd >41.4.
 ATA94, TD8 base, I-17, sc, z=468 — Left astragalus. Lext 71.7, Lm 58.0, Lint 69.1, DTp 45.8, DTd 45.5.

Description and comparison

The tooth has the typical morphology of the cervid P₃: a low crown with better developed metaconid and paraconid than the P₂, but with smaller metaconid than the P₄.

Compared to the larger cervids from Voigtstedt, the premolar (square in figure 5) and bones are larger than their homologues of *Cervus* (crosses), similar in size to, though slightly more elongate than, those in *Megaloceros solilhacus/verticornis* (open triangles) and much smaller than those of *Alces* (asterisk). The premolar from TD8a shows also morphological differences with the latter. The specimen is close in size to specimens of *Eucladoceros giulii* from Venta Micena (solid triangles) and much larger than the premolars of *Eucladoceros* from the Upper Valdarno (dots).

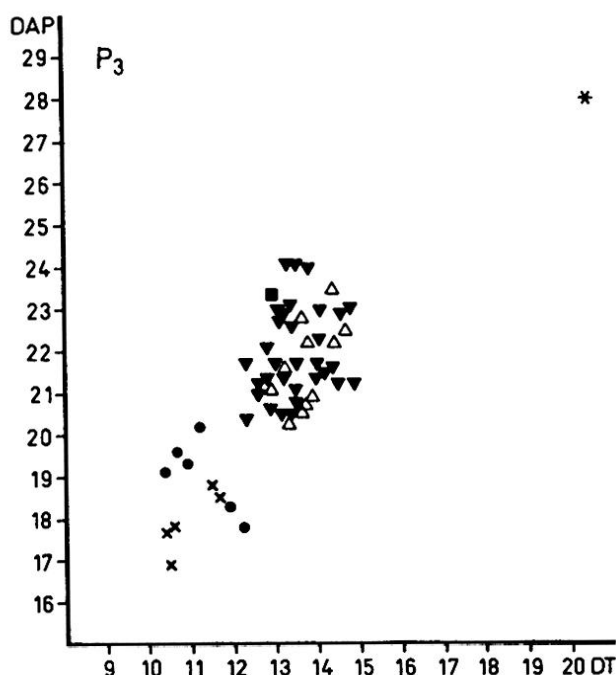


Fig. 5 : Bivariate plot of the P_3 . Crosses = *Cervus elaphus* from Voigtstedt (IQW). Dots = *Eucladoceros* from the Upper Valdarno (IGF). Solid triangles = *Eucladoceros giulii* from Venta Micena (Ménendez, 1987). Solid square = *Eucladoceros giulii* from TD8a. Open triangles = *Megaloceros* from Voigtstedt (IQW). Asterisk = *Alces* from Voigtstedt (IQW).

Fig. 5 : Diagramme de dispersion des P_3 . Croix = *Cervus elaphus* de Voigtstedt (IQW). Points = *Eucladoceros* de Valdarno supérieur (IGF). Triangles noirs = *Eucladoceros giulii* de Venta Micena (Ménendez, 1987). Carré noir = *Eucladoceros giulii* de TD8a. Triangles ouverts = *Megaloceros* de Voigtstedt (IQW). Asterisque = *Alces* de Voigtstedt (IQW).

Discussion

It is assumed here that the specimens from TD8a belong to the same species as the large cervid material from TD4 and TD6. There are antlers from TD4 and TD6 (Pl. 1, fig. 6) and a complete metacarpal from TD4.

Megaloceros is taken here to include : *Megaceros*, *Praemegaceros*, *Praedama*, *Dolichodoryceros* and *Megaceroides* (Lister, 1993 ; Van der Made, in press) as well as *Allocaenelaphus* and possibly *Psekupsoceros*. Some *Megaloceros* have palmated brow tines and others not. This character is variable, especially in the populations from the period when palmated brow tines first evolved. At present the evolution and systematics of *Megaloceros* are not well understood. However, some general trends can be seen.

De Vos *et al.*, (1995) revised the genus *Eucladoceros* and recognized two species (and a dubious third one) in Europe. The transition of *E. ctenoides* (MN17 ; MN units De Bruijn *et al.*, 1992) to *E. dicranios* (MmQ1 ; MmQ zones Agustí *et al.*, 1987) involved an increase in the complexity of the antlers. Kahlke (1997) named a new species, *Eucladoceros giulii* for the large deer from Untermassfeld, Venta Micena and a number of other localities from the later Early Pleistocene (MmQ2-3). The metapodials appear to be of particular interest for the systematics of the large Pleistocene deer and their morphology and size allows for an assignation to four classes.

1) *Eucladoceros* from MN17-MmQ1 has small and slender metapodials (diamonds in fig. 6).

2) The metapodials of *Eucladoceros giulii* from Untermassfeld and Venta Micena and of the deer from TD4 (fig. 6 ; asterisks) are slender, as in the MN17-MmQ1 *Eucladoceros*, but much larger.

Antlers from TD4 and TD6, suggest a simple model, with cylindrical brow tine, originating relatively high above the burr. The parts that are known are similar to the antlers of *E. giulii*.

3) *Megaloceros* with small and robust metapodials (fig. 6 : crosses) are present in Ubeidiya (Geraads, 1986), Sidstrand, Mundesley and Rotbav, as well as in Petralona (Tsoukala, 1989). Material from some of these localities is assigned to *M. dawkinsi*, *M. obscurus* and *Allocaenelaphus arambourgi* (Azzaroli, 1953 ; Radulesco & Samson, 1967 ; Abbazzi, 1995). There may prove to be relations to material from Algeria, that is currently assigned to *Megaceroides algericus* (Hadjouis, 1990). There is, however, much variation in basal antler morphology. Characters that tend to occur in this group are pronounced pachyostosis of the mandible and small size of the cheek teeth and other parts.

4) *Megaloceros* from Soleilhac, Voigtstedt, Süssenborn and Trimmingham have large and robust metacarpals (fig. 6 : squares). The *Megaloceros* of this group are currently assigned to *M. solilhacus* and *M. verticornis*. These deer have antlers with or without brown tine, with or without an extra tine or sprout near the burr, with the latter tines fused into a palmate structure or separate, with palmate distal antlers or not. Frequently several morphotypes occur in one locality, while the dentition and postcranial remains do not indicate more than one species. Thus, antler morphology does not seem to exclude the possibility that all belong to one lineage.

5) The metacarpals in *M. giganteus* (fig. 6 : dots) are also large and robust. The size and robusticity change through time, but do not show a simple trend. Breaks or changes in trends in size or robusticity have not been interpreted as taxonomical breaks at the species level or indications of migrations (Lister, 1993).

Eucladoceros giulii is the only deer that shares metapodial morphometrics and morphology and size of the teeth and antlers with the large deer from TD4 and TD6. In addition to the Early Pleistocene localities mentioned by Kahlke (1987) and TD, *E. giulii* seems to be present also in the late Early Pleistocene of Apollonia-1 («*Megaloceros* sp.» of Kostopoulos, 1997). This suggests a late Early Pleistocene age for TD4 and TD6 and, if the material from TD8 belongs to the same species as that from TD4-6, an earliest Middle Pleistocene age for TD8 (which is above the Matuyama-Brunhes boundary). Alternatively, the poor material from TD8a could belong to *M. solilhacus*.

Megaloceros giganteus?

Description and discussion

The posterior lobe of an upper molar with selodont structure comes from TD10c. The crenulation of the enamel suggests it is a cervid. The DTp of 25.8 suggests a large cervid, a very large *Cervus elaphus* or *Megaloceros*. The

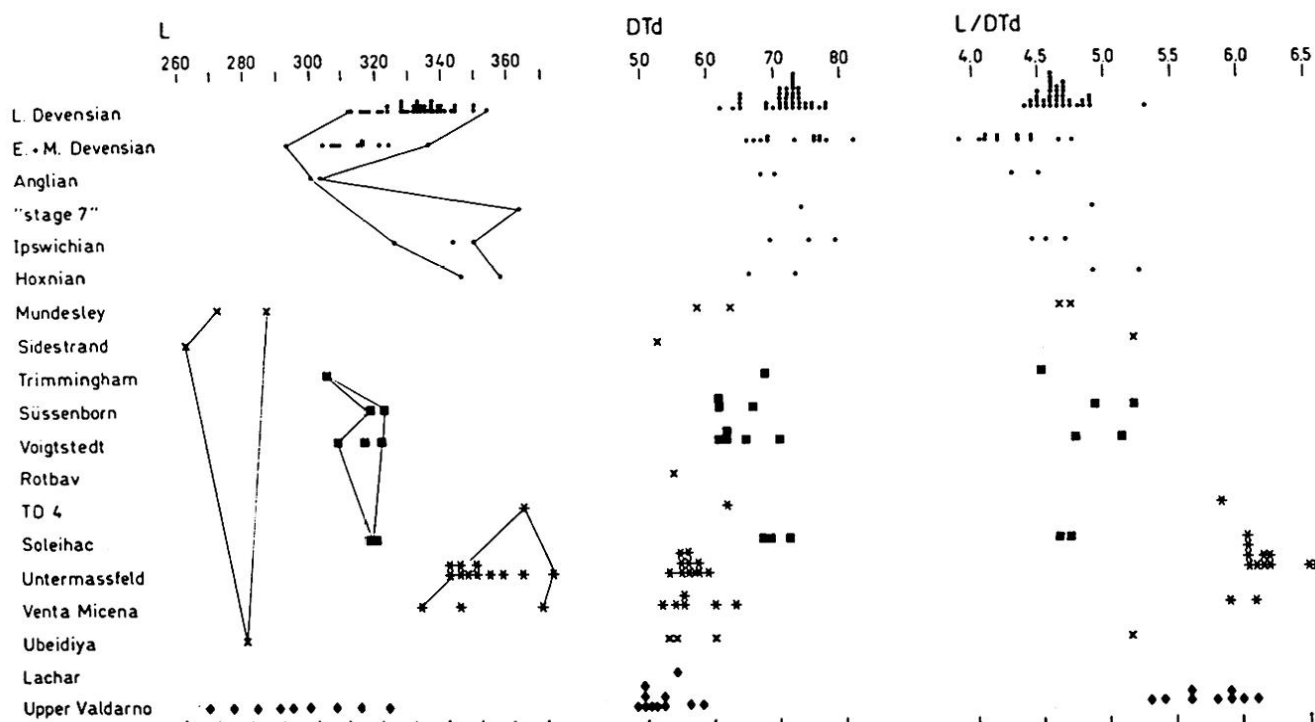


Fig. 6 : Length (L), distal width (DTd) and robusticity (L/DTd) of megalcerine metacarpals. The localities are in approximate order from old to the bottom to young at the top. The position of Rotbav is not secure, and Anglian should be below Hoxnian and « stage 7 » below Ipswichian. *Eucladoceros* from the Upper Valdarno (IGF). *Megaloceros obscurus*-group : Ubeidiya (HUJ ; Geraads, 1986), Rotbav (Radulesco & Samson, 1967), Pietrafitta (Abazzi, 1995), Sidestrand and Mundesley (Azzaroli, 1953). *Eucladoceros giulii* from Venta Micena (Ménendez, 1987) and TD4. *Megaloceros solilhacus/verticornis* from Soleilhac (MCP), Voigtstedt (IQW), Süssenborn (IQW) and Trimmingham (Azzaroli, 1953). *Megaloceros giganteus*, ages and measurements from Lister (1994).

Fig. 6 : Longueur (L), largeur distale (DTd) et robustesse (L/DTd) des métacarpiens des grands cervidés du Pliocène-Pléistocène. Les gisements sont classés en ordre à peu près stratigraphique de bas en haut. La position de Rotbav n'est pas sûre, et l'Anglien est au-dessus de l'Hoxnien et le « stage 7 » au-dessus de l'Ipswichien.

Eucladoceros de Valdarno supérieur (IGF). Groupe de *Megaloceros obscurus* : Ubeidiya (HUJ ; Geraads, 1986), Rotbav (Radulesco & Samson, 1967), Pietrafitta (Abazzi, 1995), Sidestrand et Mundesley (Azzaroli, 1953). *Eucladoceros giulii* de Venta Micena (Ménendez, 1987) et de TD4. *Megaloceros solilhacus/verticornis* de Soleilhac (MCP), Voigtstedt (IQW), Süssenborn (IQW) et Trimmingham (Azzaroli, 1953). *Megaloceros giganteus*, attribution stratigraphique et dimensions selon Lister (1994).

Megaloceros of this age is *M. giganteus*. For a reliable determination, more material is needed.

Cervus elaphus

Material from TD8

ATA94, TD8, talla 29, G-16, 59 — Juvenile right calcaneus. DAPn 31.0, DTn 16.5.

ATA94, TD8, H-16, 19 — Left juvenile first phalanx. DAPd >18.7, DTd >18.4.

ATA94, TD8, talla 28, G-17, 22 — Shaft of a right tibia. DAPd ≥28.1.

ATA94, TD8, talla 28, G-16, 32 — Left juvenile first phalanx. DAPd ±18.3, DTd ±19.5.

ATA94, TD8, talla 28, I-16, 9. Left P³. 17.0/16.9 x 17.5 - 17.6.

ATA94, TD8, talla 29, I-16, 9 — Fragment left M⁴.

ATA94, TD8, talla 29, H-16, 59 — Left juvenile second phalanx, proximal part. DAPp ≥32.7/≥29.9, DTp 24.8.

Description and comparison

The bones and teeth have typical cervid morphologies. The size is close to that of *Cervus elaphus* from Voigtstedt.

Discussion

Cervus elaphus is also found in TD4, TD6, TD10 and TD11. An antler with the bez tine, that is so characteristic of *Cervus*, was found in TD4.

Caprinae indet.

Description and discussion

Some fragmentary bones from TD11 have the morphology of a caprine.

Praeovibos/Ovibos

Description and discussion

The bones of two hind limbs were recovered from TD7. Very likely, they belonged to the same individual. The metatarsals are short compared to the femur and tibia and compared to their own width. The specimens are more robust and shorter than those of *Bos*, *Bison*, *Leptobos* and *Bubalus*. They are larger than those of *Soergelia*, but are in the ranges of material assigned to *Ovibos* and *Praeovibos*.

The evolution of *Ovibos* and *Praeovibos* is not perfectly known, making a classification of the material from TD7 difficult. The metatarsals from Atapuerca are more robust than the one of *Praeovibos* sp. from Venta Micena (Moyà Solà, 1987) and suggest a smaller animal than from Bad Frankenhausen (IQW). The astragali are less shortened than those from Arago (Crégut, 1980). The size and robusticity seem best to correspond to *Ovibos suessenbornensis* (IQW ; Kahlke, 1963). However, more material and/or more and better comparisons and a revision of this group are necessary to confirm this determination.

Cf. «*Bison voigtstedtensis*»

Material from TD8

- ATA94, TD8, talla 29, G-16, 61 — Left juvenile first phalanx. DAPd ±24.0, DTd >24.6.
- ATA94, TD8 — Left M_{1/2}, probably M₁. 22.3/21.9 x 15.9 - 18.7.
- ATA94, TD8, talla 29, I-16, 55 — Left M^{1/2}, probably M¹. 21.2/20.5 x 23.6 - 25.2.
- ATA94, TD8, talla 29, I-16, 39 — Left second phalanx. DAPp 34.3/32.3, DTp 29.1, L 48.8, DAPd 29.4, DTd 25.2.
- ATA94, TD8, talla 29, I-16, 64 — Right juvenile first phalanx. DAPd 21.4, DTd 25.8.
- ATA94, TD8, talla 27, G-17, 1 — Right M_{1/2}. ≥30.5/±26.9 x ±16.2 - ±15.8, Ha >48, Hp >45.
- ATA94, TD8, talla 29, I-16, 23 — Fragment of the first lobe of an

upper cheek tooth.

ATA94, TD8, talla 28, G-16, 45 — Distal metatarsal. Right articulation: DT 31.7.

Description and comparison

The lower molars have large ectostylids and the upper molars have large stylids at the lingual side. This is typical of Bovinae, such as *Bos* and *Bison*. Ovibovini do not have such stylids.

One of the lower molars is probably a M₁, because its first lobe is much narrower than its second lobe. This may also occur in the M₂, but to a lesser extent. The other lower molar is less clear. The M₁ is within the ranges of the Middle Pleistocene bisons (fig. 7).

The upper molar seems to be a M¹ because of the narrow first lobe in comparison to the second lobe. The first lobe is narrower than in teeth from Isernia (DSCGPF) and Mosbach (NMM).

The second phalanx (open triangle pointing up in fig. 8) has a small DTd (distal width) relative to its DAPd (distal antero-posterior diameter) compared to the state in *Bison* (crosses) as indicated by Sala (1987). It is close in size and proportions to the ovibovine from TD7 (asterisks), but it also resembles phalanges from Blanzac (open square) and Voigtstedt (open triangle pointing down), which belong to the Bovinae.

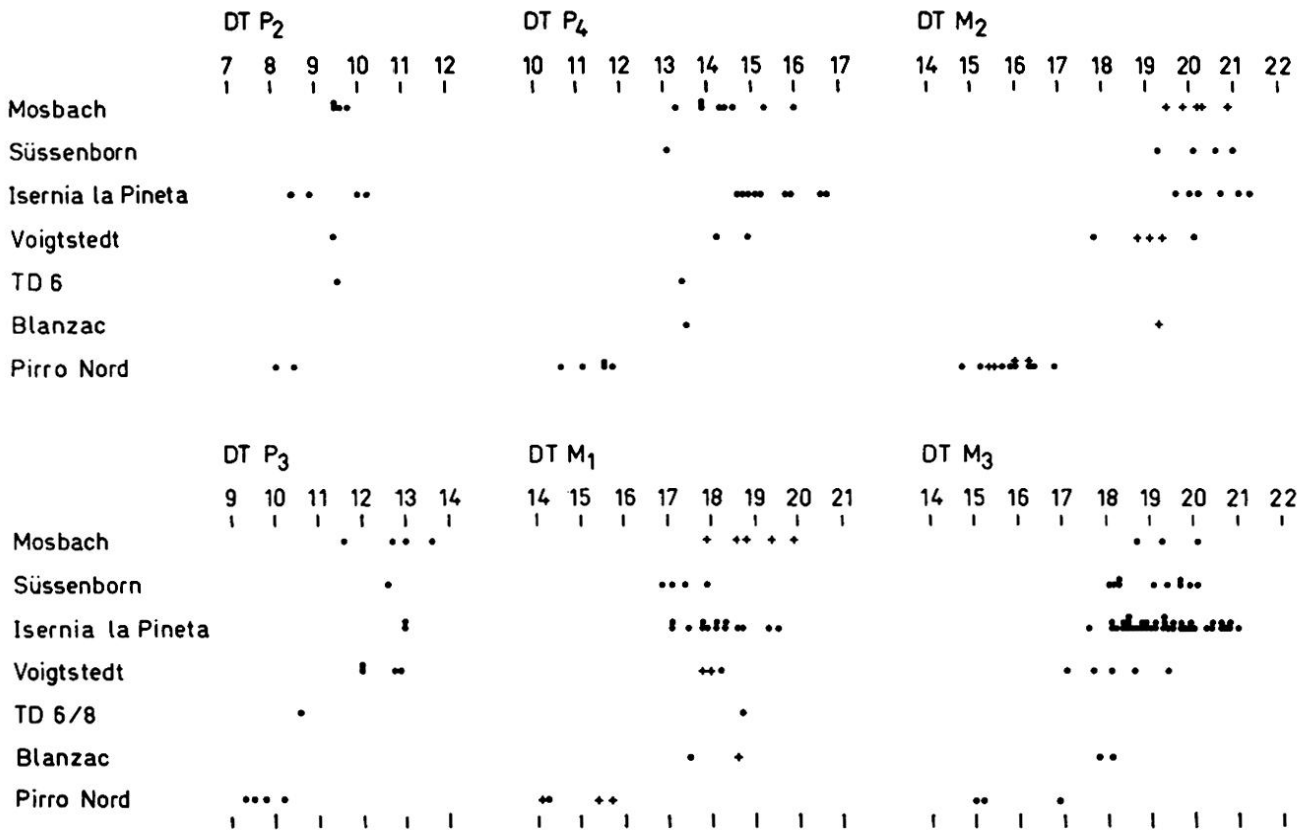


Fig. 7 : Size of the premolars and molars in *Bison*. The localities are in approximate order from old (bottom) to young (top) : Pirro Nord (IGF), Blanzac (NMB), TD6 (premolars) and TD8 (molar), Voigtstedt (IQW), Isernia (DSCGPF), Süssenborn (SMNS) and Mosbach (NMM). The M₁ and M₂ in mandibles are given a different symbol (crosses), since the isolated molars are difficult to separate, and thus introduce a possible error. Fig. 7 : Taille des prémolaires et molaires de *Bison*. Les gisements sont classés en ordre à peu près stratigraphique de bas en haut : Pirro Nord (IGF), Blanzac (NMB), TD6 (prémolaires) and TD8 (molaire), Voigtstedt (IQW), Isernia (DSCGPF), Süssenborn (SMNS) et Mosbach (NMM). M₁ et M₂ isolées (points) et sur mandibules (croix).

Discussion

Levels TD4, TD6 (Pl. 1, fig. 3, 4, 7) and TD8a have yielded remains of a small bovine with more slender phalanges and metapodials than typical *Bison schoetensacki*, *B. priscus* and *Bos primigenius*. There is a skull, said to be from TD3, which was described as *Bison schoetensacki* cf. *voigtstedtensis* (Soto, 1987). The taxon has been given species status : *B. voigtstedtensis* (Sher, 1997).

The earliest bison from Europe is from Pirro Nord (De Giuli *et al.*, 1987). It is a small animal (fig. 7). The skull is relatively wide and has convex frontals and the horn cores seem to be directed outwards and, initially, slightly downwards, just as in the later and larger bisons from Isernia and Mosbach.

The skulls from Atapuerca and Voigtstedt («*Bison voigtstedtensis*») do not have convex frontals, seem a little bit more elongate than the typical bison, and have horn

cores that are directed posteriorly and outwards, not downwards. Some of these characters are shared with the bovid *Dmanisibos* from Dmanisi (Vekua, 1997) and with *Leptobos etruscus*.

Bison schoetensacki and *B. priscus* have wide second phalanges (fig. 8). This seems to be a derived feature: more primitive Bovinae, such as *Leptobos*, and Cervidae have phalanges with a greater DAPd than DTd. The character is not necessarily an adaptation to great weight, since *Alces* has phalanges with a small DTd relative to the DAPd.

The phalanges from TD8a, Voigtstedt and Blanzac have relatively small DTd. In *Bos*, they seem to be slightly wider, but narrow compared to the bison phalanges. Also the bovid metacarpals from TD6 have a small DTd (Van der Made, in press), but greater than in *Leptobos*. The bovine from Dmanisi has a slender metacarpal with a similar estimated distal width (Vekua, 1997).

To explain the observations, there are at least two simple models.

In the first model, all are bisons and there is a gradual increase in size from Pirro Nord to Isernia and Mosbach. Skull morphology is variable and TD6 and Voigtstedt fit in a trend of increasing size of the dentition and increasing robusticity of the postcranial skeleton.

In the second model, there are two groups characterized by different skull morphology : on the one hand the small and large bisons (Pirro Nord, Isernia, Mosbach etc.) and on the other the bovines of intermediate size with relatively slender metapodials and phalanges, narrower skulls and horncores directed posteriorly. The latter group might include the skull from Gran Dolina, TD6, TD8a, Voigtstedt and Dmanisi and may not be closely related to *Bison*. Instead these samples might represent primitive forms of the genus *Bos*, represent progressive forms of *Leptobos*, or constitute the different genus *Dmanisibos*. The recently described *Bison menneri* from Untermassfeld (Sher, 1997) seems to share some characters with this group.

More data are needed to solve the evolution of early Bovini and to determine the material from TD8a, TD6 and TD4. Provisionally the material is assigned to cf. «*Bison voigtstedtensis*», since it resembles the type material of that taxon. However, it is repeated that more research might reveal that «*voigtstedtensis*» is no bison, but a species of a different genus.

Bovinae indet.

Description and discussion

A large bovine is found in TD10. It is much larger than the bovid from TD4-8a. No cranial remains have been found that allow for an unambiguous classification of the material. Pleistocene Bovinae include : *Bos primigenius*, *Bison priscus*, *Bison schoetensacki* and *Bubalus murrensis*. The latter species is only known from cranial fragments, not from teeth or postcranial elements. The cranial fragments suggest that *B. murrensis* is not a very large species.

Figure 8 shows the size of the distal articulation surface of the second phalanx. Crosses represent *Bison priscus*, oblique crosses represent *Bison schoetensacki* and circles represent *Bos primigenius* (data from Sala, 1987). These data suggest

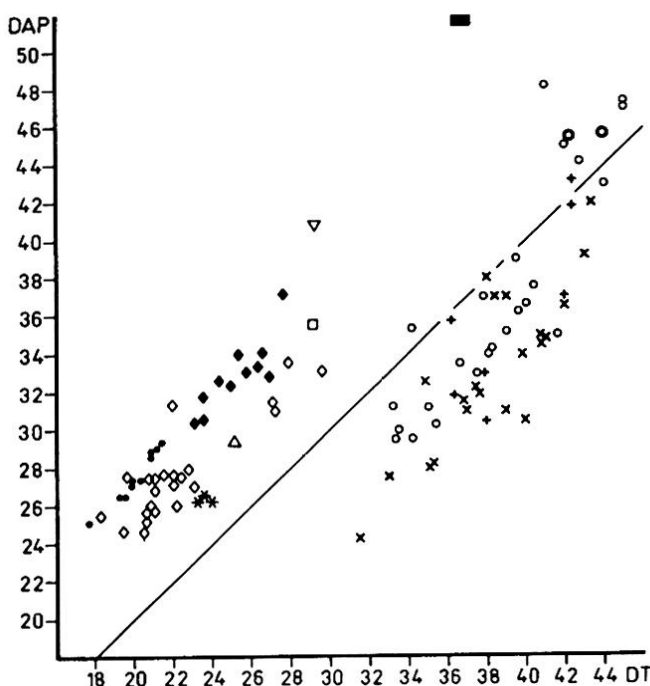


Fig. 8 : The size of the distal articulation (DAPd and DTd) in the second phalanx in selected bovids and cervids.

Open symbols, crosses and asterisks = Bovidae. Asterisks = Ovisovini from TD7. Diamonds = *Leptobos* from Montopoli and Olivola (IGF). Triangle pointing up = cf. «*Bison voigtstedtensis*» from TD8a. Triangle pointing down = «*Bison voigtstedtensis*» from Voigtstedt (IQW). Square = «*Bison*» from Blanzac (NMB). Crosses = *Bison priscus* from Cava Filo (Sala, 1987). Oblique crosses = *Bison schoetensacki* from Isernia la Pineta (Sala, 1987). Circles = *Bos primigenius* from Paglicci (Sala, 1987). Fat circles = *Bos/Bison* from TD10. Solid symbols = Cervidae from Voigtstedt (IQW). Dots = *Cervus elaphus*. Diamonds = *Megaloceros*. Squares = *Alces*.

Fig. 8 : Rapport du diamètre transverse de l'articulation distale (DTd) sur le diamètre antéro-postérieur (DAPd) pour les secondes phalanges d'artiodactyles.

Des symboles ouverts, des croix et des astérisques = Bovidae. Astérisques = Ovisovini de TD7. Rhombes = *Leptobos* de Montopoli et d'Olivola (IGF). Triangle avec le point vers le haut = cf. «*Bison voigtstedtensis*» de TD8a. Triangle avec le point vers le bas = «*Bison voigtstedtensis*» de Voigtstedt (IQW). Carré = «*Bison*» de Blanzac (NMB). Croix = *Bison priscus* de Cava Filo (Sala, 1987). Croix obliques = *Bison schoetensacki* d'Isernia la Pineta (Sala, 1987). Cercles = *Bos primigenius* de Paglicci (Sala, 1987). Des cercles gros = *Bos/Bison* de TD10. Symboles noirs = Cervidae de Voigtstedt (IQW). Points = *Cervus elaphus*. Rhombes = *Megaloceros*. Carrés = *Alces*.

that on average the *Bos* phalanges have greater DAPd compared to the DTD than the bison phalanges. The fat circles represent the bovid from TD10. Their large size and their relatively great DAPd suggests that they might represent *Bos primigenius*. However, more data are needed to confirm this.

DISCUSSION

Figure 9 gives the distribution of the ungulates in the different levels of Gran Dolina. Though Soto (1987) described a rich ungulate fauna from what he stated to be TD3, recent excavations did not yield large mammal remains from TD1-3. TD7 has a very restricted fauna and TD8b-9 have no large mammals at all.

Stephanorhinus etruscus suggests an Early or early Middle Pleistocene age for TD4, TD6 and TD8a. Stenonid horses are found in TD4, TD6 and TD8a, whereas caballoid horses are found in TD10 and TD11. In general caballoid horses replaced stenonid horses as the dominant horses during the Middle Pleistocene, though stenonid horses persisted. This seems to be reflected in the TD sequence. *Dama nestii? vallonensis* suggests an Early or early Middle Pleistocene age for TD4, TD6 and TD8a and *Dama dama clactoniana* indicates a Middle Pleistocene age for TD10. *Eucladoceros giulii* is only known from Lower Pleistocene localities and from TD4, TD6 and TD8a. The evolutionary level of the ovibovine suggests an Early or

early Middle Pleistocene age for TD7. The bovine remains from TD3, TD4, TD6 and TD8a share a number of primitive characters with the bovines from Voigtstedt, Blanzac and Dmanisi, but not from localities younger than Voigtstedt. *Sus scrofa* and *Cervus elaphus* appeared in the late Early Pleistocene (Von Koenigswald & Tobien, 1987). The ungulate fauna indicates a late Early to early Middle Pleistocene age for TD4-8a, which is in accordance with the palaeomagnetic study placing the Brunhes-Matuyama boundary in the upper part of TD7.

The ungulates from TD10-11 are less indicative and agree with a Middle Pleistocene or younger age.

The ovibovine from TD7 has elongate metatarsals and astragali compared with *Ovibos moschatus*. The *Praeovibos* from Venta Micena was found in association with a «warm» fauna, including *Hippopotamus*. The earliest *Praeovibos* and *Ovibos* were probably not yet adapted to polar or glacial environments like the living species. The dominance of *Dama*, *Cervus* and *Equus* throughout the sequence suggests that the environment did not change very much. *Rangifer*, *Alces*, *Saiga*, *Ovibos moschatus*, *Gulo gulo*, *Alopex* and other «glacial» taxa have not been found in Spain, or only in the north of Basque country and Catalonia in deposits contemporary with the last glaciation (Aguirre, 1989). This suggests that the impact of the glaciations on the Spanish fauna was much less than north of the Pyrenees and that an «interglacial» fauna continued to live and evolve here.

Denell & Roebroeks (1996) suggested that human

	Proboscidea indet.	<i>Equus</i> sp. stenonid type	<i>Stephanorhinus etruscus</i>	<i>Hippopotamus amphibius</i>	<i>Dama nestii? vallonensis</i>	<i>Megaloceros</i> sp.	Cf. "Bison voigtstedtensis"	<i>Ovibos/Praeovibos</i>	<i>Sus scrofa</i>	<i>Cervus elaphus</i>	<i>Equus</i> sp. caballoid type	<i>Stephanorhinus</i> cf. <i>hemitoechus</i>	<i>Dama dama clactoniana</i>	<i>Megaloceros giganteus</i> ?	<i>Bos/Bison</i>	Caprini indet.
TD12																
TD11																
TD10																
TD9																
TD8 sup.																
TD8 inf.																
TD7																
TD6																
TDW5																
TDW4																
TD3																
TD2																
TD1																

Fig. 9 : The distribution of the ungulates in the different levels of Gran Dolina.
Fig. 9 : Répartition des ongulés dans les niveaux de Gran Dolina.

occupation of southern Europe may have been late Early Pleistocene, but not continuous. Bermúdez de Castro *et al.*, (1997) supposed a lineage *Homo antecessor* - *H. heidelbergensis* - *H. neanderthalensis*. Continuity in the Spanish ungulate fauna suggests that the Middle Pleistocene climate was no impediment for this model.

ACKNOWLEDGEMENTS

I thank Dr. A.M. Moigne for inviting me to the symposium in Tautavel and for comments on the manuscript. The following persons allowed me to study material in their care, helped me during my stay in their institutions, helped me with comments and discussions or in other ways: Drs. J.M. Bermúdez de Castro, L. Abazzi, M.T. Alberdi, L. Alcalá, P. Anconetani, F. Alférez, J.L. Arsuaga, B. Azanza, A. Buitrago, F. Cabot, E. Carbonell, B. Castillo, G. Daxner Höck, B. Engesser, A. Forsten, E. Heizmann, R.D. Kahlke, H. Lutz, F. Masini, J. Morales, P.E. Moullé, M. Negro, E. Nicolás, G. Rabeder, K. Rauscher, L. Rook, B. Sala, C. Smeenk, E. Tchermov, D. Torre, J. de Vos, R. Ziegler. The DGES (project PB96-1026-C03-02), the «Unidades Asociadas» program of the DGICYT, Ministerio de Educación y Cultura, Consejo Superior de Investigaciones and the Consejería de Cultura y Turismo de la Junta de Castilla y León made this investigation possible.

REFERENCES

- ABBAZZI, L., 1995 - *Megaceroides obscurus* from the Val di Chiana (Cava Liberatori, Tuscany, Central Italy, Farneta f.u., early Pleistocene). Remarks on the early evolution and systematics of *Megaceroides*. *Bolletino della Società Paleontologica Italiana*, 34, (2), 223-234.
- AGUIRRE, E., 1989 - Vertebrados del Pleistoceno continental. In (A. Pérez González, P. Cabra & A. Martín Serrano, eds.) *Mapa del Cuaternario de España*. Escala 1:1000.000, Madrid, ITGE, 47-69.
- AGUSTI, J., MOYÁ-SOLÁ, S. & PONS-MOYÁ, J., 1987 - La sucesión de Mamíferos en el Pleistoceno inferior de Europa: proposición de una nueva escala bioestratigráfica. *Paleontología i Evolución*, memoria especial 1, 287-295.
- ALBERDI, M.T., ORTIZ JAUREGUIZAR, E. & PRADO, J.L., 1995 - Revisión sistemática, paleoecología y evolución de los estenonianos europeos (Perissodactyla, Equidae). *XI Jornadas de Paleontología*, Tremp, 26-29 octubre 1995, resúmenes, 17-18.
- ALBERDI, M.T., ORTIZ JAUREGUIZAR, E. & PRADO, J.L., 1998 - A quantitative review of European stenonid horses. *Journal of Paleontology*, 72 (2), 371-387.
- ALBERDI, M.T., PRADO, J.L. & ORTIZ-JAUREGUIZAR, E., 1995 - Patterns of body size changes in fossil and living Equini (Perissodactyla). *Biological Journal of the Linnean Society*, 54, 349-370.
- ALBERDI, M.T. & RUIZ BUSTOS, A., 1985 - Descripción y significado bioestratigráfico y climático del *Equus* e *Hippopotamus*, en el yacimiento de Venta Micena (Granada). *Estudios geológicos*, 41, 251-261.
- ALBERDI, M.T. & RUIZ-BUSTOS, A., 1989 - Taxonomía y Bioestratigrafía de Equidae (Mammalia, Perissodactyla) en la Cuenca de Guadix-Baza (Granada). *Trabajos sobre el Neogeno-Cuaternario*, 11, 239-270.
- ALFÉREZ, F., MOLERO, G., MALDONADO, E., BUSTOS, V., BREA, P. & BUITRAGO, A.M., 1982 - Descubrimiento del primer yacimiento cuaternario (Riss-Würm) de vertebrados con restos humanos en la provincia de Madrid (Pinilla del Valle). *COL-PA*, 37, 15-32.
- AZANZA, B. & SANCHEZ, B., 1990 - Les Cervidés du Pléistocène Moyen d'Atapuerca (Burgos, Espagne). *Quaternaire*, 3-4, 197-212.
- AZZAROLI, A., 1953 - The deer of the Weybourn Crag and Forest Bed of Norfolk. *Bulletin of the British Museum (Natural History), Geology*, 2 (1), 1-96.
- AZZAROLI, A., 1979 - Critical remarks on some giant deer (genus *Megaceros* Owen) from the Pleistocene of Europe. *Palaeontographia Italica*, 71, 5-16, pls. 1-6.
- AZZAROLI, A., 1992 - The cervid genus *Pseudodama* n. g. in the Villafranchian of Tuscany. *Palaeontographia Italica*, 79, 1-41.
- BERMUDEZ DE CASTRO, J.M., ARSUAGA, J.L., CARBONELL, E., ROSAS, A., MARTINEZ, I. & MOSQUERA, M., 1997 - A hominid from the Lower Pleistocene of Atapuerca, Spain: Possible ancestor to Neandertals and modern humans. *Science*, 276, 1392-1395.
- BRUIJN, H. DE, DAAMS, R., DAXNER-HÖCK, G., FAHLBUSCH, V., GINSBURG, L., MEIN, P., MORALES, J., HEIZMANN, E., MAYHEW, D.F., VAN DER MEULEN, A.J., SCHMIDT-KITTLER, N. & TELLES ANTUNES, M., 1992 - Report of the RCMNS working group on fossil mammals, Reisenburg 1990. *Newsletters on Stratigraphy*, 26(2/3), 65-118.
- CARBONELL, E., BERMUDEZ DE CASTRO, J.M., ARSUAGA, J.L., DIEZ, J.C., ROSAS, A., CUENCA-BESCOS, G., SALA, R., MOSQUERA, M., RODRIGUEZ, X.P., 1995 - Lower Pleistocene Hominids and Artifacts from Atapuerca-TD6 (Spain). *Science*, 269, 826-830.
- CREGUT, E., 1980 - La faune de mammifères du Pléistocène moyen de la Caune de l'Arago à Tautavel, Pyrénées Orientales. *Travaux du Laboratoire de Paléontologie Humaine et de Préhistoire*, 3, (1), 381 p.
- DE GIULI, C., MASINI, F. & TORRE, D., 1987 - The latest Villafranchian faunas in Italy: the Pirro Nord fauna (Apricena, Gargano). *Palaeontographia Italica*, 74, 51-62.
- DENELL, R. & ROEBROEKS, W., 1996 - The earliest colonization of Europe, the short chronology revisited. *Antiquity*, 70, 535-542.
- EISENMANN, V., 1991 - Les chevaux Quaternaires Européens (Mammalia, Perissodactyla). Taille, typologie, biostratigraphie et taxonomie. *Geobios*, 24 (6), 747-759.
- EISENMANN, V., ALBERDI, M.T., DE GIULI, C. & STAESCHE, U., 1988 - Volume 1: Methodology. In (M. Woodburne & P. Sondaar eds.) *Studying Fossil Horses*, Leiden, New York, Kobenhavn, Köln: E.J. Brill., 71 p.
- FAURE, M., 1985 - *Les Hippopotamidae (Mammalia, Artiodactyla) d'Europe occidentale*. Thesis. Lyon, Université Claude Bernard, 233 p.
- FAURE, M. & GUERIN, C., 1984 - *Sus strozzi* et *Sus scrofa*, deux mammifères artiodactyles, marqueurs des paléoenvironnements. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 48, 215-228.
- FORSTEN, A., 1988 - Middle Pleistocene replacement of stenonid horses by caballoid horses - ecological implications. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 65, 23-33.
- FORSTEN, A., 1992 - Early *Equus* dispersal and taxonomy: conflicting opinions. *Courier Forschungsinstitut Senckenberg*, 153, 171-176.
- FORTELIUS, M., MAZZA, P. & SALA, B., 1993 - *Stephanorhinus (Mammalia: Rhinocerotidae)* of the western European Pleistocene, with a revision of *S. etruscus* (Falconer, 1868). *Palaeontographia Italica*, 80, 63-155.
- GERAADS, D., 1986 - Les ruminants du Pléistocène d'Oubeidyeh (Israël). *Mémoires et Travaux de Centre de Recherches français de Jérusalem*, 5, 143-174, pls. 1-4.
- GUERRERO-ALBA, S., PALMQVIST, P., MARTINEZ-NAVARRO, B. & ARRIBAS, A., 1997 - Estudio morfométrico del caballo de Venta Micena (Orce, Granada) y su comparación con los équidos actuales y del Plio-Pleistoceno de Europa y África. *XIII Jornadas de Paleontología*, La Coruña, 16-18/10/1997. Resúmenes, 189-192.
- HADJOUIS, D., 1990 - *Megaceroides algericus* (Lydekker, 1890), du gisement des phacochères (Alger, Algérie). Étude critique de la position systématique de *Megaceroides*. *Quaternaire*, 3-4, 247-258.

- KAHLKE, H.D., 1963 - *Ovibos* aus den Kiesen von Süßenborn. Ein Beitrag zur Systematik und Phylogenie der Ovibovini und zur Stratigraphie des Pleistozäns. *Geologie*, 12,(8), 942-972.
- KAHLKE, H.D., 1997 - Die Cerviden-Reste aus dem Untepleistozän von Untermassfeld. Pp. 181-275, plates 34-44 in R.D. Kahlke (ed.) *Das Pleistozän von Untermassfeld bei Meiningen (Thüringen)*. Dr. Rudolf Habelt GmbH, Bonn.
- KAHLKE, R.D., 1987 - Die unterpleistozänen *Hippopotamus* Reste von Untermassfeld bei Meiningen (Bezirk Suhl, DDR) - Ein Beitrag zur Forschungs-, Entwicklungs- und Verbreitungsgeschichte fossiler Hippopotamiden in Europa. Thesis, Ernst Moritz Arndt Universität, Greifswald: 167 p.
- KOENIGSWALD, W. VON & TOBIEN, H., 1987 - Bemerkungen zur Altersstellung der pleistozänen Mosbach-Sande bei Wiesbaden. *Geologisches Jahrbuch Hessen*, 115, 227-237.
- KOSTOPOULOS, D.S., 1997 - The Plio-Pleistocene artiodactyls (Vertebrata, Mammalia) of Macedonia 1. The fossiliferous site «Apollonia-1», Mygdonia basin of Greece. *Geodiversitas*, 19, (4), 845-875.
- LAPLANA, C. & CUENCA-BESCOS, G., 1997 - Los arvicólidos (Arvicolidae, Rodentia) del límite Pleistoceno Inferior-Medio en el relleno cárstico Trinchera Dolina (Sierra de Atapuerca, Burgos, España). *XIII Jornadas de Paleontología*, La Coruña, 16-18/10/1997. Resúmenes: 192-195.
- LISTER, A.M., 1986 - New Results on Deer from Swanscombe, and the Stratigraphical Significance of Deer in the Middle and Upper Pleistocene of Europe. *Journal of Archaeological Science*, 213, 319-338.
- LISTER, A.M., 1993 - The stratigraphical significance of deer species in the Cromer Forest-bed Formation. *Journal of Quaternary Science*, 8, 95-108.
- LISTER, A.M., 1994 - The evolution of the giant deer, *Megaloceros giganteus* (Blumenbach). *Zoological Journal of the Linnean Society*, 112, 65-100.
- LUMLEY, H. DE, KAHLKE, H.-D., MOIGNE, A.-M., & MOULLE, P.-E., 1988 - Les faunes de grands mammifères de la grotte du Vallonnet Roquebrune-Cap-Martin, Alpes-Maritimes. *L'Anthropologie*, 92, (2), 465-469.
- MADE, J. VAN DER, 1989 - The bovid *Pseudoeotragus seegrabensis* nov. gen. nov. sp. from the Aragonian (Miocene) of Seegraben near Leoben (Austria). *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen*, serie B, 92, (3), 215-240.
- MADE, J. VAN DER, 1996 - Listriodontinae (Suidae, Mammalia), their evolution, systematics and distribution in time and space. *Contributions to Tertiary and Quaternary Geology*, 33, (1-4), 3-254.
- MADE, J. VAN DER, in press - Ungulates from Atapuerca TD6. *Journal of Human Evolution*.
- MADE, J. VAN DER & MOYÁ-SOLÁ, S., 1989 - European Suinae (Artiodactyla) from the Late Miocene onwards. *Bolletino de la Società Paleontologica Italiana*, 28, (2/3), 329-339.
- MARÍN, M., 1987 - *Equus stenonis granatensis* en el Pleistoceno inferior de Venta Micena (Granada, España). *Paleontología i Evolució*, Memoria Especial 1, 255-283.
- MAZO, A., 1989 - Los hipopótamos del Pleistoceno medio de Huéscar-1 (Granada). *Trabajos sobre el Neogeno-Cuaternario*, 11, 317-325.
- MENÉNDEZ, E., 1987 - Cérvidos del yacimiento del Pleistoceno inferior de Venta Micena-2, Orce (Granada, España). *Paleontología i Evolució*, Memoria Especial 1, 129-180.
- MOYÁ-SOLÁ, S., 1987 - Los bóvidos (Artiodactyla, Mammalia) del yacimiento del Pleistoceno inferior de Venta Micena (Orce, Granada, España). *Paleontología i Evolució*, Memoria Especial 1, 181-236.
- PARÉS, J.M., PERÉZ-GONZÁLEZ, A., 1995 - Paleomagnetic Age for Hominid Fossils at Atapuerca Archaeological Site, Spain. *Science*, 269, 830-832.
- RADULESCO, C. & SAMSON, P., 1967 - Sur un nouveau cerf Mégacérin du Pléistocène Moyen de la Dépression de Brasov (Roumanie). *Geol. Rom.*, 6, 317-344.
- SALA, B., 1987 - *Bison schoetensacki* Freud. from Isernia la Pineta (early Mid-Pleistocene - Italy) and revision of the European species of bison. *Palaeontographica Italica*, 74, 113-170.
- SHER, A.V., 1997 - An Early Quaternary bison population from Untermassfeld: *Bison menneri* sp. nov. Pp 101-180, plates 22-33 in R.D. Kahlke (ed.) *Das Pleistozän von Untermassfeld bei Meiningen (Thüringen)*. Dr. Rudolf Habelt GmbH, Bonn.
- SOTO, E., 1987 - Grandes herbívoros del Pleistoceno medio de la Trinchera de Ferrocarril de Atapuerca (Burgos, España). In (E. Aguirre, E. Carbonell & J. M. Bermúdez de Castro eds.) *El hombre fósil de Ibeas y el Pleistoceno de la Sierra de Atapuerca I*, Valladolid: Junta de Castilla Y Leon, 92-112.
- STAESCHE, K., 1941 - Nashörner der Gattung *Dicerorhinus* aus dem Diluvium Württembergs. *Abhandlungen der Reichsstelle für Bodenforschung*, NF 200, 148 p.
- TSOUKALA, E.S., 1989 - Contribution to the study of the Pleistocene fauna of large mammals (Carnivora, Perissodactyla, Artiodactyla) from Petralona Cave, Chalkidiki (N. Greece). *Aristotle University of Thessaloniki, School of Geology - Scientific Annals*, 1, (8), 360 p.
- VEKUA, A., 1997 - Die Wirbeltierfauna des Villafranchium von Dmanisi und ihre biostratigraphische Bedeutung. *Jb. Röm.-Germ. Zentralmuseums Mainz*, 42, 77-180.
- VOS, J. DE, MOL, D. & REUMER, J.W.F., 1995 - Early Pleistocene Cervidae (Mammalia, Artiodactyla) from the Oosterschelde (the Netherlands), with a revision of the cervid genus *Eucladoceros* Falconer, 1868. *Deinsea*, 2, 95-121.