

Figure 13. *Eucladoceros giulii* from Atapuerca TD6. (1) ATA96, TD6, talla 52, H-16, 505—right antler, external view. (2) ATA94, TD6, talla 39, H-18, 53—left D<sup>2</sup>, lingual (a), occlusal (b) and buccal (c) views. Cervidae indet. from Atapuerca TD6. (3) ATA96, TD6, talla 45, I-18, b<sub>n</sub>—left P<sup>4</sup>, occlusal view. (4) ATA96, TD6, talla 47, H-18—left M<sup>2</sup>, occlusal view. The bar represents 4 cm for (1), 1 cm for (2) and 2 cm for (3) and (4).

#### Discussion

The remains from TD6 cannot be attributed to *Leptobos*, the bovine species from Venta Micena or *Bos primigenius*. The morphology of the horn core resembles *Bison*. *Bison schoetensacki* and *Bison priscus* are too large and *Bison* from Piro Nord too small. General dimensions of teeth and bones resemble “*Bison voigtstedtensis*” and *Dmanisibos*.

A skull from the old excavations, claimed to be either from TD2 (Aguirre, 1995) or TD3 (Soto, 1987) was assigned to *Bison schoetensacki* cf. *voigtstedtensis*, although “*voigtstedtensis*” was already given species status (see Sher, 1997).

Sher (1997) discussed the direction of the horn cores in *Bison* and noted that those from Untermaßfeld and Voigtstedt are directed much more posteriorly. The horncores of *Dmanisibos* and the

skull from Atapuerca are also directed posteriorly.

The frontals between the horn cores have a convex transverse profile in *Bison* as early as in Pirro Nord. A concave transverse profile is present in material from Voigtstedt, Untermaßfeld and Atapuerca assigned to *Bison*, and in *Dmanisibos*.

*Bison* from Pirro Nord, Isernia, Mosbach and other localities have relatively wide skulls. The skulls from Voigtstedt, Atapuerca and Dmanisi are relatively narrow.

Sher (1997) discussed in detail the robusticity of the metapodials; they are very robust in *B. priscus*, robust in *B. schoetensacki* and *Bison* from Pirro Nord and more slender in *B. menneri*. Robust metapodials are derived. *Dmanisibos* has small and slender metapodials (Vekua, 1997). Material from

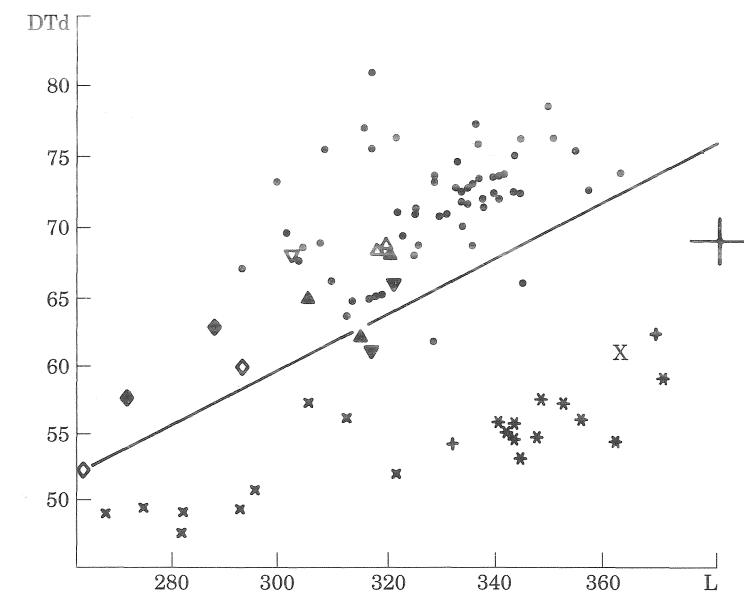


Figure 14. Bivariate plot of length (L) versus distal width (DT<sub>p</sub>) in metacarpals of *Megaloceros* and *Eucladoceros*. The line indicates L=5 DT<sub>p</sub>. *Eucladoceros*. Oblique crosses= *Eucladoceros* from Upper Valdarno (IGF). Asterisks= *E. giulii* from Untermaßfeld (Kahlke, 1997). Crosses= *E. giulii* from Venta Micena (“*Praemegaceros solihacus*” of Menéndez, 1987). Letter “X”= *E. giulii* from Atapuerca TD4. The average and ranges (n=3) for Apollonia-1 are indicated (“*Megaloceros* sp.” of Kostopoulos, 1997). *Megaloceros verticornis* and (=? *M. solihacus* from Trimingham (open triangle pointing downwards, Azzaroli, 1953), Voigtstedt (solid triangles pointing upwards, IQW), Süssenborn (solid triangles pointing downwards, IQW) and Soleilhac (open triangle pointing upwards, MCP). Diamonds= *Megaloceros dawkinsi* (?) from Mundesley (solid diamonds) and Sidestrand (open diamonds); data from Azzaroli (1953). Dots= *Megaloceros giganteus* from Europe (data from Lister, 1994).

the latest Late Pleistocene of Apollonia-1, assigned to *Bison* sp. (Kostopoulos, 1997), has metapodials of a robusticity comparable to the bison from Pirro Nord and *Bison schoetensacki*, and of a size intermediate between these two taxa, suggesting that these three forms might belong to a single lineage with increasing size but with stasis in the locomotor apparatus. A robusticity index cannot be calculated for the metacarpals from TD6, but their small distal width suggests that the metacarpals were relatively slender. Their distal width is outside the ranges of *B. schoetensacki* and close to the lower limit of *Bison* from Apollonia-1.

Posteriorly directed horncores, concave frontals, narrow skulls, and slender metapodials are primitive characters in the

Bovinae, found long after the derived characters appeared at Pirro Nord and Apollonia-1. This might be explained by variability. However, the fact that these primitive characters occur together in Dmanisi (*Dmanisibos georgicus* Burchak-Abramovich & Vekua, 1992), Untermaßfeld (*Bison menneri* Sher, 1997), Voigtstedt (*Bison voigtstedtensis* Fischer, 1975) and Atapuerca, suggests that these bovines are closely related and different from the *B. schoetensacki* and *B. priscus* lineages. The early evolution of *Bison* and similar forms is still poorly known. Pending a revision of early “*Bison*,” the TD6 material is assigned here provisionally to Bovini cf. “*Bison voigtstedtensis*.”

The morphologies described above (whether representing distinct species or just “primitive morphologies” within

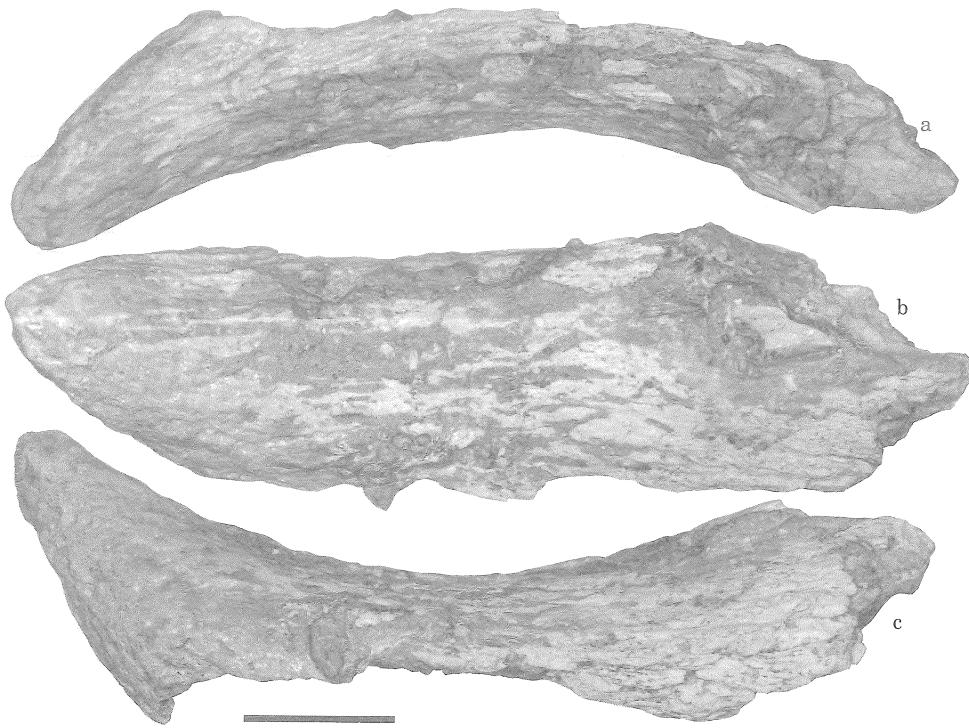


Figure 15. Bovini cf. "Bison voigtstedtensis" from Atapuerca TD6. ATA95, TD6, G-17, 144, z=508—tip of horn core. The bar represents 2 cm.

populations), occur latest in Voigtstedt. Agustí *et al.* (1987) placed Voigtstedt in their biozone MmQ3b, just below the Matuyama–Brunhes boundary. However, the locality seems to be in normally polarized sediments, and is generally placed in the Cromer (Wiegank, 1983). Taking this into account, the small bison-like bovid from TD6 suggests a late Early or an early Middle Pleistocene age.

### Conclusions

The ungulates from Atapuerca TD6 include *Equus* cf. *altidens*, *Stephanorhinus etruscus*, *Sus scrofa*, *Dama nestii?* *vallonetensis*, *Cervus elaphus*, *Eucladoceros giulii*, Cervidae indet. and Bovini cf. "Bison voigtstedtensis."

*S. etruscus*, *D. n.?* *vallonetensis* and "Bison voigtstedtensis" are late Early and/or early Middle Pleistocene elements. *Sus scrofa* and

*Cervus elaphus* seem to have entered Europe during the late Early Pleistocene. *E. giulii* is known from the late Early Pleistocene. The presence of a stenonid *Equus* is probably not very helpful. The fauna fits a late Early Pleistocene age, coinciding with palaeomagnetic findings that situate TD6 between the Jaramillo Event and Brunhes Epoch. Assuming a younger age would extend the known range of *E. giulii* into the Middle Pleistocene. However, this species has been recognized only recently and its full temporal range may not yet be known. Although the ungulates are suggestive of a latest Early Pleistocene age, they do not conclusively rule out an earliest Middle Pleistocene age.

Several of the taxa found in TD6 are considered to be part of the interglacial faunas in central Europe (*Dama*, *Sus*) and

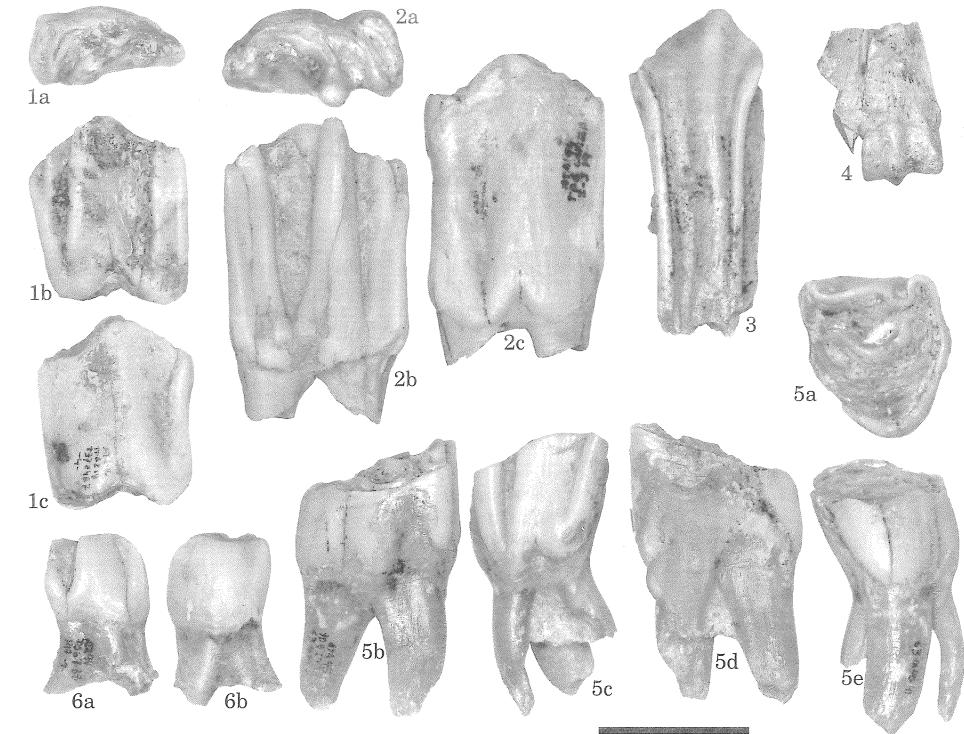


Figure 16. Bovini cf. "Bison voigtstedtensis" from Atapuerca TD6. (1) ATA94, TD6, talla 37, I-18—left  $P_3$ , occlusal (a), lingual (b) and buccal (c) views. (2) ATA94, TD6, I-3 (capilla), 19—right  $P_4$ , occlusal (a), lingual (b) and buccal (c) views. (3) ATA95, TD6, talla 40/41, H-17, 174—right  $M_x$ , first lobe, lingual view. (4) ATA94, TD6, H-18, talla 38, 19—distal metacarpal, anterior view. (5) ATA95, TD6, I-17, talla 40/41, 69—right  $P^4$ , occlusal (a), anterior (b), buccal (c), posterior (d) and lingual (e) views. (6) ATA94, TD6, H-17, talla 38, 19—left  $P_2$ , lingual (a) and buccal (b) views. The bar represents 2 cm for (1–3) and (5–6) and 6 cm for (4).

typical glacial taxa are lacking. The fauna from TD6 does not indicate an extremely cold climate. Typical glacial taxa include *Rangifer* and *Ovibos moschatus*. Others, such as *Alces* and *Saiga*, extended their ranges far to the southwest during glacial periods. Taxa like *Praeovibos* and *Ovibos* probably developed their "glacial" adaptations or life style gradually during the Middle and Late Pleistocene. Both *Praeovibos* and *Hippopotamus* are found in the Early Pleistocene of Venta Micena (Martínez Navarro, 1992); certainly no glacial environment.

"Cold taxa" are not known from Spain, except from the Cantabrian Cordillera and

Pyrenees, and late in the Pleistocene (Aguirre, 1989). *Coelodonta antiquitatis* is known from a number of localities, as well as from cave art (Arsuaga Ferreras & Aguirre Enríquez, 1979). As far as I can judge, all of these localities are from the Late Pleistocene. The same seems to be the case with *M. primigenius* (Aguirre, 1989). The composition of the micromammal faunas suggests that Spain had a milder climate than Europe north of the Pyrenees throughout the Pleistocene (Sesé, 1994). The only record of a lemming from Spain (*Dicrostonyx andaluciensis*) is based on a single tooth from the Late Pleistocene, from an assemblage that otherwise does not indicate cold

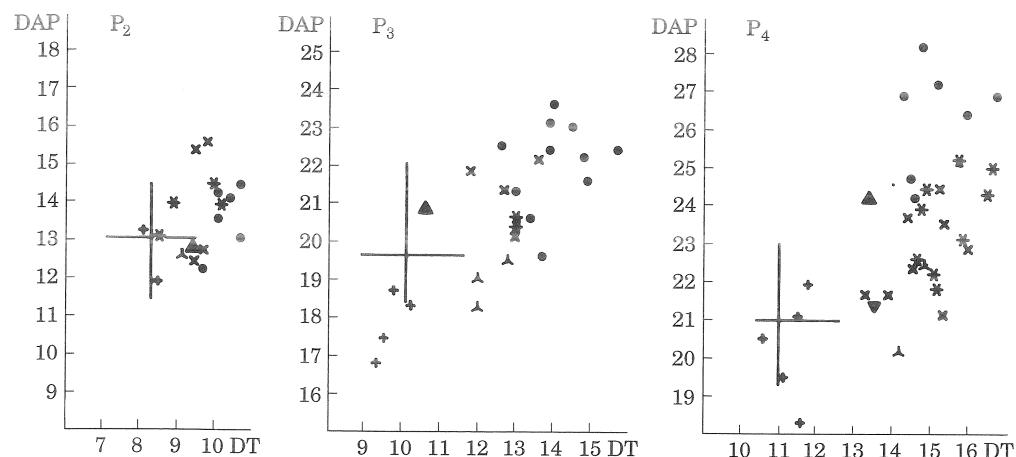


Figure 17. *Bison*, “*Bison*” and *Bos* lower premolars. The upper part of the figure gives maximum length (DAP)-maximum width (DT) bivariate plots. *Bos primigenius* from Paglicci (dots; DSCGP). *Bison* from Pirro Nord (crosses; IGF), Mosbach (oblique crosses; NMM), Isernia (asterisks; DSCGP) and Soleilhac-Blanzac (triangles pointing downwards; NMB). (Bovini cf.) “*Bison voigtstedtensis*” from TD6 (triangles pointing upwards), Voigtstedt (three pointed stars; IQW). Means and ranges of “*Bison*” from Venta Micena (Moya Solà, 1987,  $n=7$  for P<sub>2</sub> and  $n=12-14$  for the other premolars).

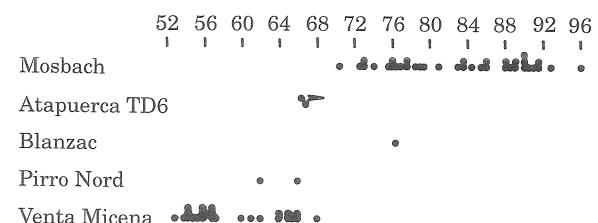


Figure 18. Distal width (DT<sub>d</sub>) of *Bison* and “*Bison*” metacarpals. Provenance of data as in Figure 17.

conditions (Sesé, 1994). All this suggests that glaciations did not have a great impact on the Spanish large mammal community and certainly not in the Early and early Middle Pleistocene. The “interglacial” fauna seems to have had continuity in Spain, uninterrupted by glacial cycles.

Denell & Roebroeks (1996) supposed that humans “might have occasionally moved into southern Europe well before 500,000 years ago, as and when conditions permitted, but without living there ‘continuously’.” If the “interglacial” fauna had continuity in Spain, so might human populations.

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### References

- Aguirre, E. (1989). Vertebrados del Pleistoceno continental. In (A. Pérez-González, P. Cabra & A. Martín-Serrano, Eds) *Mapa del Cuaternario de España. Escala 1:1.000.000*, pp. 47–69. Madrid: Instituto Tecnológico GeoMinero de España.
- Aguirre, E. (1995). Registro faunístico Pleistoceno antiguo de Atapuerca (Burgos). *Trab. Prehist.* 52 (2), 47–60.
- Aguirre, E., Arsuaga, J. L., Bermúdez de Castro, J. M., Carbonell, E., Ceballos, M., Diez, C., Enamorado, J., Fernández-Jalvo, Y., Gil, E., Gracia, A., Martín-Nájera, A., Martínez, I., Morales, J., Ortega, A. I., Rosas, A., Sánchez, A., Sánchez, B., Sesé, C., Soto, E. & Torres, T. J. (1990). The Atapuerca Sites and the Ibeas hominids. *Hum. Evol.* 5(1), 55–73.
- Agustí, J., Moyà-Solà, S. & Pons-Moyà, J. (1987). La sucesión de Mamíferos en el Pleistoceno inferior de Europa: proposición de una nueva escala bioestratigráfica. *Pal. Evol. mem. esp.* 1, 287–295.
- Alberdi, M. T. & Ruiz-Bustos, A. (1989). Taxonomía y bioestratigrafía de Equidae (Mammalia, Perissodactyla) en la cuenca de Guadix-Baza (Granada). *Trab. Neogeno-Cuat.* 11, 239–270.
- Alberdi, M. T., Ortiz Jaureguizar, E. & Prado, J. L. (1995a). Revisión sistemática, paleoecología y evolución de los estenonianos europeos (Perissodactyla, Equidae). XI Jorn. Paleontol. Tremp, 26–29 octubre 1995, resúmenes, 17–18.
- Alberdi, M. T., Prado, J. L. & Ortiz-Jaureguizar, E. (1995b). Patterns of body size changes in fossil and living Equini (Perissodactyla). *Biol. J. Linn. Soc.* 54, 349–370.
- Alberdi, M. T., Ortiz-Jaureguizar, E. & Prado, J. L. (1998). A qualitative review of European stenonid horses. *J. Palaeontol.* 72(2), 371–387.
- Alférrez, 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.
- Arsuaga Ferreras, P. M. & Aguirre Enríquez, E. (1979). Rinocerontes lanudos en la provincia de Madrid (*Coelodonta antiquitatis* Blumenbach). *Bol. R. Soc. Española Hist. Nat.* 77, 23–59.
- Azanza, B. & Sánchez, B. (1990). Les Cervidés du Pléistocène moyen d’Atapuerca (Burgos, Espagne). *Quaternaire* 3–4, 197–212.
- Azzaroli, A. (1953). The deer of the Weybourne Crag and Forest Bed of Norfolk. *Bull. Brit. Mus. nat. Hist. Geol.* 2(1), 1–96.
- Azzaroli, A. (1990). The genus *Equus* in Europe. In (E. H. Lindsay, V. Fahlbusch & P. Meir, Eds) *European Neogene Mammal Chronology*, pp. 339–356. New York: Plenum Press.
- Azzaroli, A. (1992). The cervid genus *Pseudodama* n. g. in the Villafranchian of Tuscany. *Paleont. Ital.* 79, 1–41.
- Azzaroli, A. & Mazza, P. (1992). On the possible origin of the giant deer genus *Megaceroides*. *Rend. Fi. Acc. Lincei, Series 9*, 3, 23–32.
- Bermúdez de Castro, J. M., Arsuaga, J. L., Carbonell, E., Rosas, A., Martínez, I. & Mosquera, M. (1997). A hominid from the Lower Pleistocene of Atapuerca, Spain: Possible ancestor to Neandertals and modern humans. *Science* 276, 1392–1395.
- Brugal, J.-P. (1985). Le *Bos primigenius* Boj., 1827 du Pléistocène moyen des grottes de Lunel-Viel (Hérault). *Bull. Mus. anthr. préh. Monaco* 28, 7–62.
- Carbonell, E., Bermúdez de Castro, J. M., Arsuaga, J. L., Diez, J. C., Rosas, A., Cuenca-Bescós, G., Sala, R., Mosquera, M., Rodríguez, X. P. (1995). Lower Pleistocene hominids and artifacts from Atapuerca-TD6 (Spain). *Science* 269, 826–830.
- Cerdeño, E. (1989). Rhinocerotidae (Mammalia, Perissodactyla) de la cuenca de Guadix-Baza. *Trab. Neogeno-Cuat.* 11, 273–288.
- Cerdeño, E. (1990). *Stephanorhinus hemioechus* (Falc.) (Rhinocerotidae, Mammalia) del Pleistoceno medio y superior de España. *Estud. geol.* 46, 465–479.
- Cerdeño, E. (1993). Remarks on the Spanish Plio-Pleistocene *Stephanorhinus etruscus* (Rhinocerotidae). *C. R. Acad. Sci., Paris* 317, série II, 1363–1367.
- Cerdeño, E. & Sánchez, B. (1988). Le Rhinocéros du Pléistocène moyen d’Atapuerca (Burgos, Espagne). *Gebios* 21(1), 81–99.
- Denell, R. & Roebroeks, W. (1996). The earliest colonization of Europe, the short chronology revisited. *Antiquity* 70, 535–542.
- Di Stefano, G. & Petronio, C. (1992). Nuove osservazioni su *Cervus elaphus acronatus* Beninde del Pleistocene europeo. *Boll. Soc. Palaeontol. Ital.* 31(3), 295–315.
- Eisenmann, V., Alberdi, M. T., de Giuli, C. & Staesche, U. (1988). Methodology. In (M. Woodburne & P. Sondaar, Eds) *Studying Fossil Horses*, Volume 1, pp. 1–71. Leiden: E. J. Brill.
- Forsten, A. (1988). Middle Pleistocene replacement of stenonid horses by caballoid horses—ecological implications. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 65, 23–33.

- Forsten, A. (1992). Early *Equus* dispersal and taxonomy: conflicting opinions. *Courier Forsch.-Inst. 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). *Palaeontol. Ital.* 80, 63–155.
- Guerro-Alba, S., Palmqvist, P., Martínez-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 Jorn. Paleontol. La Coruña*, 16–18/10/1997. Resumenes, 189–192.
- Guérin, C. (1980). Les Rhinocéros (Mammalia, Perisodactyla) au Pléistocène Supérieur en Europe occidentale; comparaison avec les espèces actuelles. *Doc. Lab. Géol. Lyon* 79(1–3), 1–1185.
- Heintz, E. (1970). Les cervidés Villafrançais de France et d'Espagne. *Mém. Mus. natl. d'Hist. nat., nouv. sér., série C, Sci. de la Terre* 22, 1–303.
- Kahlke, H.-D. (1965). Die Rhinocerotiden-Reste aus den Tonen von Voigtsstet in Thüringen. *Paläontol. Abh., A* 2(2/3), 451–520.
- Kahlke, H.-D. (1966). Die Rhinocerotiden-Reste aus den Kiesen von Süßenborn bei Weimar. *Paläontol. Abh., A* 3(3/4), 667–709.
- Kahlke, H.-D. (1969). Die Cerviden-Reste aus den Kiesen von Süßenborn bei Weimar. *Paläontol. Abh., A* 3(3/4), 547–609.
- Kahlke, H.-D. (1975). Die Rhinocerotiden-Reste aus den Travertinen von Weimar-Ehringsdorf. *Paläontol. Abh., A* 23, 337–398.
- Kahlke, H.-D. (1997). Die Cerviden-Reste aus dem Untereleistozän von Untermaßfeld. In (R. D. Kahlke, Ed.) *Das Pleistozän von Untermaßfeld bei Meiningen (Thüringen)*, pp. 181–275. Bonn: Dr Rudolf Habelt GMBH.
- Koenigswald, W. von & Tobien, H. (1987). Bemerkungen zur Alterstellung der pleistozänen Mosbach-Sande bei Wiesbaden. *Geol. Jb. Hesse* 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.
- Lister, A. M. (1986). New results on deer from Swanscombe, and the stratigraphical significance of deer in the Middle and Upper Pleistocene of Europe. *J. Archeol. Sci.* 213, 319–338.
- Lister, A. M. (1990). Critical reappraisal of the middle Pleistocene deer species "*Cervus*" *elaphoides* Kahlke. *Quaternaire* 3–4, 175–192.
- Lister, A. M. (1993). The stratigraphical significance of deer species in the Cromer Forest-bed Formation. *J. Quatern. Sci.* 8, 95–108.
- Lister, A. M. (1994). The evolution of the giant deer, *Megaloceros giganteus* (Blumenbach). *Zool. J. Linn. Soc.* 112, 65–100.
- Lumley, H. de, Kahlke, H.-D., Moigne, A.-M., Mouillé, 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 (1996). Listriodontinae (Suidae, Mammalia), their evolution, systematics and distribution in time and space. *Contrib. Tert. Quatern. Geol.* 33(1–4), 3–254.
- Made, J. van der (1999). Ungulates from Grant Dolina, Atapuerca. *Quaternaria* (in press).
- Made, J. van der & Moyà-Solà, S. (1989). European Suinae (Artiodactyla) from the Late Miocene onwards. *Boll. Soc. Palaeont. It.* 28(2/3), 329–339.
- Marín, M. (1987). *Equus stenonis granatensis* en el Pleistoceno inferior de Venta Micena (Granada, España). *Paleont. Evol. Mem. esp.* 1, 255–283.
- Martínez Navarro, B. (1992). Revisión sistemática de la fauna de macromamíferos del yacimiento de Venta Micena (Orce, Granada, España). In (J. Gibert, Ed.) *Proyecto Orce-Cueva Victoria (1988–1992), Presencia humana en el Pleistoceno inferior de Granada y Murcia*, pp. 21–85. Orce: Museo de Prehistoria Josep Gibert.
- Mazza, P., Sala, B. & Fortelius, M. (1993). A small latest Villafranchian (late Early Pleistocene) rhinoceros from Pietrafitta (Perugia, Umbria, Central Italy), with notes on the Pirro and Westerhoven rhinoceroses. *Palaeontol. Ital.* 80, 25–50.
- Menéndez, E. (1987). Cérvidos del yacimiento del Pleistoceno inferior de Venta Micena-2, Orce (Granada, España). *Pal. Evol. Mem. esp.* 1, 129–180.
- Moyà-Solà, S. (1987). Los bóvidos (Artiodactyla, Mammalia) del yacimiento del Pleistoceno inferior de Venta Micena (Orce, Granada, España). *Pal. Evol. Mem. esp.* 1, 181–236.
- Parés, J. M. & Pérez-González, A. (1995). Paleomagnetic age for hominid fossils at Atapuerca archaeological site, Spain. *Science* 269, 830–832.
- Raposo, L. & Santona, M. (1995). The earliest occupation of Europe: the Iberian peninsula. In (W. Roebroeks & T. van Kolfschoten, Eds) *The Earliest Occupation of Europe*, pp. 7–25. Leiden: University of Leiden.
- Sánchez Chillon, B. & Soto Rodriguez, E. (1987). Los équidos Pleistocenos de la Trinchera de Ferrocarril de Atapuerca (Burgos). In (E. Aguirre, E. Carbonell & J. M. Bermudez de Castro, Eds) *El hombre fósil de Ibeas y el Pleistoceno de la Sierra de Atapuerca I*, pp. 117–129. Valladolid: Junta de Castilla y Leon.
- Sala, B. (1987). *Bison schoetensacki* Freud. from Isernia la Pineta (early Mid-Pleistocene—Italy) and revision of the European species of bison. *Palaeontol. Ital.* 74, 113–170.
- Sesé, C. (1994). Paleoclimatical interpretation of the Quaternary small mammals of Spain. *Geobios* 227(6), 753–767.
- Sher, A. V. (1997). An Early Quaternary bison population from Untermaßfeld: *Bison menneri* sp. nov. In (R. D. Kahlke, Ed.) *Das Pleistozän von Untermaßfeld bei Meiningen (Thüringen)*, pp. 101–180. Bonn: Dr Rudolf Habelt GMBH.
- Soto, E. (1987). Grandes herbívoros del Pleistoceno medio de la Trinchera de Ferrocarril de Atapuerca (Burgos, España). In (E. Aguirre, E. Carbonell & J. M. Bermudez de Castro, Eds) *El hombre fósil de Ibeas y el Pleistoceno de la Sierra de Atapuerca I*, pp. 92–112. Valladolid: Junta de Castilla y Leon.
- Spaan, A. (1992). A revision of the deer from Tegelen (Province of Limburg, The Netherlands). *Scripta Geol.* 98, 1–85.
- Vekua, A. (1997). Die Wirbeltierfauna des Villafranchium von Dmanisi und ihre biostratigraphische Bedeutung. *Jb. Röm.-Germ. Zentralmuseum 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.
- Wiegank, F. (1983). Beitrag zur Chronostrigraphie und Entwicklung der Grosssägerfaunen im jüngeren Känozoikum von Europa auf geochronologischer und magnetostratigraphischer Grundlage. *Schriftenr. geol. Wiss.* 19–20, 355–380.
- Wiegank, F. (1997). Paläomagnetische Charakteristik des Unterpleistozäns von Untermaßfeld. In (R. D. Kahlke, Ed.) *Das Pleistozän von Untermaßfeld bei Meiningen (Thüringen)*, pp. 63–69. Bonn: Dr Rudolf Habelt GMBH.
- I** distance from below the burr is used.
- L** Index (DAP/DT) × 100% or (DMD/DLL) × 100%.
- R** Length of a bone.
- H** Diameter in 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 × DT, as DAP × DT<sub>a</sub> – DT<sub>p</sub>, or as DAP<sub>o</sub>/DAP<sub>b</sub> × DT<sub>a</sub> – DT<sub>p</sub> (for instance 23·5/22·9 × 12·3 – 12·2). For *Equus*, measurements are given at the occlusal surface, at half the height of the crown and 2 cm above the base (for instance: 25·3/25·1/23·4 × 15·7/15·6/14·9 – 15·6/15·4/14·7). In such formula, . . or -- indicates 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.
- Appendix 1 Material and abbreviations of measurements**
- Abbreviations of measurements.**
- DAP** Antero-posterior diameter in teeth or bones. Bones: DAP<sub>p</sub> proximal, DAP<sub>pf</sub> proximal facet, DAP<sub>d</sub> distal, DAP<sub>df</sub> distal facet, DAP<sub>m</sub> minimal. Teeth: DAP<sub>b</sub> basal, DAP<sub>o</sub> occlusal. Antler: DAP<sub>b</sub> DAP measured just above the burr, DAP<sub>r</sub> DAP of burr.
- DLL** Linguo-labial diameter in incisors.
- DMD** Meso-distal diameter in incisors.
- DT** Transverse diameter ("width"). Bones: DT<sub>p</sub> proximal DT<sub>d</sub> distal, DT<sub>df</sub> distal facet, DT<sub>m</sub> minimal. Teeth: DT<sub>a</sub> anterior lobe, DT<sub>p</sub> posterior lobe, DT<sub>pp</sub> third lobe in M3. Antler: DT<sub>b</sub> measured just above burr, DT<sub>r</sub> burr.
- H** Height. Bones: H<sub>a</sub>, anterior, H<sub>ext</sub> external, H<sub>int</sub> internal. Teeth: H<sub>la</sub> labial, H<sub>li</sub> lingual. Antler: distance of the first bifurcation till the burr, H<sub>ext</sub> external, H<sub>int</sub> internal (measured in two ways: from below the burr and from the top of the burr). In the index 100H<sub>ext</sub>/DAP<sub>b</sub>, the
- Material**
- Equus cf. altidens*
- ATA94, TD6, G-16, talla 38, 16. Unworn left D<sup>3/4</sup>. 34·5/33·5/33·5 × . /25·6/25·6, H=29·1, Protocone . /9·2/9·2.
- ATA94, TD6, H-17, talla 38. 9. Three small fragments of a P<sub>x</sub> or M<sub>x</sub>.
- ATA95, TD6, H-16, talla 40–41, 274. Fragment of left D<sup>x</sup>.
- ATA95, TD6, G-17, talla 40/41. Third phalanx forelimb. L basal >48·7, L dorsal --, DT >71·1, width of facet 47·8, DAP<sub>pf</sub>--, DAP<sub>p</sub>--, angle ± 50°.
- ATA95, TD6, G-18, talla 38–39, 53. Right D<sup>3/4</sup>. 33·9/31·2/31·2 × 23·6/25·9/25·9, H>22·9, Protocone 9·1/. ., PI 27, 2-3-1-2/1 protocone type 4, pli caballin, hypoconal constriction, hypoconal islet, wide parastyle, narrow mesostyle.
- ATA95, TD6, H-16, talla 4, 77. Left M<sup>1/2</sup>. 25·5/24·8. . × 25·1/25·7/. ., H>60, Protocone 9·5/9·2/. ., PI 37/37/. ., 1-3-1-1-0/0,

protocone type 4, no hypoconal constriction, nor hypoconal islet, wide parastyle, narrow mesostyle.

ATA95, TD6, I-16, 129. Left  $M^{1/2}$ . 27·1/26·3/.. × 24·9/26·1/., H>70, Protocone 13·2/12·2/., PI 49/46/., 1-4-2-1/0, protocone type 6, no hypoconal constriction, nor hypoconal islet, narrow para- and mesostyle.

ATA95, TD6, I-16, talla 53, 300. Left  $P_{2-4}$  and fragment of the anterior lobe, possibly of the  $M_1$ .  $P_2$ : 37·1/37·1/34·8 × 12·8/14·5/12·6 – 15·8/17·2/15·5, H>58·5, Double knot 16·5/17·1/16·8, Preflexid 9·6, Postflexid 17·3, type 7 linguaflexid, extremely shallow ectoflexid with pli caballinid.  $P_3$ : posterior half, DT<sub>p</sub> 19·0/18·9/17·6, Postflexid 15·5, type 7 ectoflexid.  $P_4$  (partially in mandible): 30·1/29·4/28·2 × 17·1/.. . . – 17·6/.. . ., H>77·2, Double knot 17·7/18·2/17·4, Preflexid 9·0, Postflexid ± 14·0 (partially covered by sediment), type 2 linguaflexid, type 1 ectoflexid, no pli caballinid.

ATA96, TD6, G-16, 239, talla 40–41. Lingual side of the left upper P or M. H>30, DAP ± 24, Protocone 9·7/–/9·7, PI ± 40, 1-1-1-0/0, protocone type 3/4.

ATA96, TD6, H-17, 302, talla 50. Left  $M^{1/2}$ . 24·7/–/25·2 × 26·8/–/28·4, H>34, Protocone 11·7/–/., PI 47/–/., 0-3-2-0/0, protocone type 3/6, no hypoconal constriction, nor hypoconal islet, wide and convex parastyle, wide mesostyle.

ATA96, TD6, I-16, talla 53, 298. Left  $M_{1/2}$  ( $M_2$  of the same individual as ATA96, TD6, I-16, 300?). 27·2/27·6/25·2 × 15·5/18·9/16·4 – 14·0/16·2/14·2, H>64, Double knot 15·4/17·4/15·7, Preflexid 6·9, Postflexid 8·3, type 1 linguaflexid with V-shape until near the bottom (where it nearly touches the ectoflexid and turns convex), deep ectoflexid type 6, no pli caballinid.

ATA96, TD6, I-18, talla 48, 82. Left  $M_{1/2}$ . 27·6/27·8/25·5 × 16·5/16·4/15·0 – 15·9/17·5/15·0, H>53, Double knot 15·7/16·8/

15·3, Preflexid 8·2, Postflexid 11·4, type 2 linguaflexid, type 1 ectoflexid, which does not enter the isthmus, no pli caballinid.

ATA96, TD6, G-16, z=606, perfil, 281. Third phalanx, hind limb. L 50·1, dorsal length 48·6, width –, width of facet 39·2, DAP<sub>pf</sub> 20·9, DAP<sub>p</sub> ± 34, angle 40–45°, circumference ± 125.

ATA96, TD6, H-16, talla 51, 481. Fragment of proximal facet of a third phalanx.

ATA96, TD6, H-18, 150. Right  $P^{3/4}$  29·0/–/28·6 × 28·6/–/27·8, H>42·2, protocone 6·8/–/8·2, PI 23, 1-3-3-1/1, protocone type 4, but short and square, hint of a hypoconal constriction, no hypoconal islet, wide para and mesostyles.

ATA96, TD6, talla 49, G-18, 132. Root of left C<sup>x</sup>.

ATA96, TD6, I-18, talla 44, 65. Right D<sub>x</sub>/P<sub>x</sub>/M<sub>x</sub>, germ, central fragment.

ATA97, TD6, H-16, talla 54, 548. Left  $M_3$ . 30·9/33·2/31·5 × 12·9/12·8/12·7 – 11·3/11·3/11·4, H>61·5, prefexid 8·1, postflexid 8·3, double knot 13·6/15·0/14·3. Type 5 linguaflexid, but reaching the ectoflexid and therefore slightly “deformed”, type 5 ectoflexid, entering the isthmus, no pli caballinid.

ATA97, TD6, G-16, talla 54, 333. Left astragalus. Internal length ≥ 55·3, DT<sub>p</sub> ≥ 42·2, DT<sub>d</sub> 49·0, DAP<sub>d</sub> facet 35·1.

#### *Stephanorhinus etruscus*

ATA95, TD6, H-16, talla 40–41, 165. Left  $P_{3/4}$ , anterior lobe. DT<sub>a</sub> >19·1.

ATA95, TD6, H-16, talla 40–41, 195. Left  $D_3$ . 39·1 × 17·5 – 20·1.

ATA95, TD6, H-17, talla 40–41, 127. Left  $M^{1/2}$ , antero-buccal side damaged. DAP >45·2.

ATA95, TD6, G-16, talla 40–41, 132. Left  $D^2$ . 34·8 × 31·2 – 30·6.

ATA95, TD6, G-16, talla 42, G-16, 154. Fragment of upper cheektooth.

ATA95, TD6, H-16, talla 42, 290. Left  $D^{3/4}$ , antero-buccal fragment.

ATA95, TD6, H-17, talla 42, 203. Fragment of upper cheek tooth.

ATA96, TD6, G-18, talla 52, 445. Left astragalus. DT<sub>p</sub> 68·3, H<sub>int</sub> 68·9, H<sub>m</sub> 57·8, H<sub>ext</sub> 67·9, DT<sub>df</sub> 61·5, DAP facet navicular 37·8.

ATA96, TD6, H-16, perfil. Posterior fragment of a left cheek tooth. DT<sub>p</sub> >22·1.

#### *Sus scrofa*

ATA94, TD6, G-16, talla 39, 22. Left  $P_3$  in a mandible fragment with the alveoli for the  $P_2$ . DAP 13·9, DT<sub>a</sub> 6·4, DT<sub>p</sub> 7·5.

#### *Dama nestii?* *vallonensis*

ATA94, TD6, I-18, talla 37, 40. Right mandible with  $P_2$ – $M_2$ .  $P_2$  10·7 × 6·6;  $P_3$  13·1 × 7·8;  $P_4$  13·4 × 8·8;  $M_1$  14·9 × 10·2 – 10·9;  $M_2$  17·5 × 11·9 – 11·4.

ATA94, TD6, I-16, talla 39, 116. Right distal humerus. DT<sub>d</sub> facet 4·5, R1 33·0, R2 23·1, R3 28·1, R4 21·1.

ATA94, TD6, I-16, talla 38, sc. Left  $M^x$ . 19·1/.. × 19·6 – . ., Hla >18·1.

ATA94, TD6, G-17, talla 38, 6. Left naviculo-boid. DAP 30·9, DT 33·3.

ATA94, TD6, I-16. Right lunar. DAP 26·3, DT<sub>p</sub> 17·1, DT<sub>d</sub> 12·2, H<sub>a</sub> 19·0, Facet magnum 9·0, Facet unciform 4·4.

ATA94, TD6, I-18, talla 37, 8, z=486. Right first phalanx, DAP<sub>p</sub> >34·6, DT<sub>p</sub> 29·6.

ATA94, TD6, H-16, talla 38, 20, z=510. Right third phalanx. DAP 17·0/19·7. DT<sub>p</sub> 14·7, L 36·6.

ATA94, TD6, G-17, talla 39, 70. Juvenile right second phalanx. DAP<sub>d</sub> 11·8, DT<sub>d</sub> 17·8.

ATA94, TD6, I-18, talla 36, 22. Distal metacarpal (left?). DT<sub>d</sub> 32·9. Left pulley DAP 22·8, DT 15·2. Right pulley 22·9, 15·3.

ATA94, TD6, H-18, talla 38, 12. Dorso-proximal part of left first phalanx.

ATA95, TD6, G-17, talla 40–41, 118. Postero-proximo part of left metatarsal.

ATA95, TD6, H-18, talla 40–41, 76. Right proximal radius. DT<sub>p</sub> >39·5.

ATA95, TD6, H-16, talla 40–41, 88. Left scapula. DAP<sub>d</sub> >48·7, DAP<sub>df</sub> 34·4, DT<sub>d</sub> 32·3.

ATA95, TD6, I-17, talla 42, 74. Right shed antler. DAP<sub>r</sub> 44·6, DT<sub>r</sub> 47·7, DAP<sub>b</sub> 35·9, DT<sub>b</sub> 36·9, H<sub>ext</sub> >51·9/ >45·8, 100H<sub>ext</sub>/DAP<sub>b</sub> >145.

ATA95, TD6, G-17, talla 42, 241. Sesamoid from behind the external side of a left first phalanx. L 13·4, DAP 10·7, DT 6·7. ATA95, TD6, G-17, talla 40–41; 207. Right mandible with much worn  $M_{1-2}$ .  $M_1$ : 15·3/15·3 × 10·7 – 11·9.  $M_2$ : 19·4/19·4 × 12·8 – 12·2.

ATA95, TD6, G-17, talla 40–41, 197. Left naviculocuboid. DAP 28·1, DT31·8.

ATA96, TD6, H-16, talla 43, 385. Left  $I_2$ . DT 7·0, DMD 5·2, DLL 5·6, H –, DMD root 3·9, DLL root 4·6.

ATA96, TD6, H-16, talla 43, 739. Proximal part of a left first phalanx. DT<sub>p</sub> 17·1.

?ATA96, TD6, G-17, talla 52, 143. Paracone of right  $M^x$ .

?ATA96, TD6, I-17, talla 45, 109. Tip of the tine of an antler.

?ATA96, TD6, G-17, talla 52, 360. Left  $M^2$ ? 20·9/19·7 × 206 – ≥ 19·9.

ATA96, TD6, H-16, talla 43, 339. Proximal part of left first phalanx. DAP<sub>p</sub> >22·7, DT<sub>p</sub> 17·1.

ATA96, TD6, G-17, talla 44, 288. Distal part of left third phalanx.

ATA96, TD6, talla 48, lavado micro. Left  $P^3$ . 13·9 × 14·8 – 15·0. “Lavado micro” = found while wet screening sediment for micro-mammals.

ATA96, TD6, I-18, 77. Left pedicle and basal part of antler. Pedicle: DAP 40·2, DT 37·5. Antler: DT<sub>b</sub> >36·4.

ATA96, TD6, H-17, talla 43, 215. Fragment of right mandible. Condyle: DT>14·3.

ATA97, TD6, H-16, talla 54, sc. Right  $P_3$ . 13·2 × 6·9 – 7·7.

ATA97, TD6, G-16, talla 54, 323. Left third phalanx. DAP<sub>p</sub> >21·6/ >19·1, DT<sub>p</sub> 14·9, L 41·3.

- ATA97, TD6, H-16, talla 54, 601. Basal fragment of shed antler (*Dama/Cervus?*).  
 ATA97, TD6, H-16, talla 54, 324. Basal fragment of shed antler.  
 ATA97, TD6, H-10, talla 54, 570. Right shed antler, basal part. Rose: DAP >60·7, DT 55·4. Antler: DAP<sub>b</sub> 51·5, DT<sub>b</sub> 43·9, H<sub>ext</sub> 58·7/54·5, 100H<sub>ext</sub>/DAP<sub>b</sub> 114.  
 ATA97, TD6, G-16, talla 54, 349, z=645. Fragment of left shed antler. (*Cervus?*)  
 ?ATA94, TD6, J-18, talla 37, 3. Shaft of left metatarsal. Juvenile. DAP<sub>m</sub> 8·4, DT<sub>m</sub> 9·0.  
 ?ATA94, TD6, J-17/18 (capilla), talla 37. Left magnum. Juvenile.  
 ?ATA94, TD6, I-16, talla 39, 68. Left scapula, distal part. Facet: DAP 29·2, DT 25·3.

*Eucladoceros giulii* Kahlke, 1997

- ATA94, TD6, I-18, talla 37, 8. Right phalanx 1. Proximal fragment. DT<sub>p</sub> 29·6.  
 ATA94, TD6, H-18, talla 39, 42. Left unciform. DAP 29·9, DT 27·6, H 22·6.  
 ATA94, TD6, H-18, talla 39, 53. Left D<sup>2</sup>. 21·9 × 12·6 – 14·6, H<sub>la</sub> 14·9.  
 ?ATA94, TD6, H-18, talla 38, 23. Fragment of the distal pulley of a metapodial.  
 ATA95, TD6, I-17, talla 42, 81. Proximal part of a left third phalanx. DAP<sub>p</sub> >31·2, DT<sub>p</sub> 23·6, L --.  
 ATA95, TD6, G-16, talla 40–41, 69. Dorso-proximal fragment of a right first phalanx.  
 ATA95, TD6, G-18, talla 38/39, 40. Fragment of the shaft of a metatarsal.  
 ATA96, TD6, H-16, talla 52, 505. Right shed antler, including base of the brow tine and base of main beam. Diameters (DAP × DT): below the burr: 57·4 × 52·0, burr: ≥67·2 × 63·6, above the burr: 60·3 × 55·5, brow tine 35·2 × 34·6, main beam: -- × ≥40·4. H<sub>ext</sub> 124·9/119·8, H<sub>int</sub> 127·5/115·7.

*Cervus elaphus*

- ATA94, TD6, G-17, talla 38, 41. Right P<sub>3</sub>. 17·9 × 9·7.

- ?ATA94, TD6, H-16, talla 38, 18, z=510. Right DI<sub>1</sub>. DT 10·6, DLL 5·2, H<sub>li</sub> 9·7, Root: DMD 5·2, DLL 4·9.  
 ATA94, TD6, H-18, talla 38, 20. Naviculocuboid. DAP 36·9, DT 36·1.  
 ATA96, TD6, talla 48. Left M<sup>3</sup>. --/ >25·1 × -- 23·2.  
 ATA96, TD6, H-17, talla 43, 207. Sesamoid from behind the external side of the left first phalanx. L 15·6, DAP 13·0, DT 7·6.  
 Cervidae indet.  
 ATA95, TD6, H-16, talla 45. Paracone of left M<sup>1</sup>.  
 ATA96, TD6, I-18, talla 45. Much worn left P<sup>4</sup> and M<sup>2</sup>. P<sup>4</sup>: --/19·7 × 27·1. M<sup>2</sup>: --/ 30·4 × 32·7 --.  
 ATA96, TD6, H-16, talla 47, 435. Much worn left M<sup>3</sup>. --/28·3 × 30·4 – 27·5.  
 Bovini cf. "Bison voigtstedtensis"  
 ATA94, TD6, G-18, 32. Distal metacarpal. DT<sub>d</sub> >66·7, DAP<sub>m</sub> <33·3, left pulley: DAP 40·1, DT >28·3, right pulley DAP 41·5, DT 33·4.  
 ATA94, TD6, H-17, talla 38, 19. Left P<sub>2</sub>. DAP 12·7, DT 9·5.  
 ATA94, TD6, H-18, talla 38, 19. Distal metacarpal with one pulley. Pulley: DAP 37·1, DT 32·6.  
 ATA94, TD6, H-18, talla 36. --. Distal part of a right first phalanx. DT<sub>d</sub> ≥32·4, DAP<sub>d</sub> ≥24·4.  
 ATA94, TD6, I-17, talla 39, 23. Fragmentary left first phalanx. DT<sub>p</sub> ≥32·7.  
 ATA94, TD6, I-3 (capilla), 19. Right P<sub>4</sub>. 24·2/23·5 × 13·4, H<sub>la</sub> 35·2.  
 ATA94, TD6, I-18, talla 37. Left P<sub>3</sub>. 20·8/ 18·8 × 10·7.  
 ATA94, TD6, G-17, talla 39, 68. Sesamoid from behind the internal side of a left first phalanx. L 19·8, DAP 20·6, DT 17·1.  
 ATA94, TD6, H-17, talla 39, 43. Distal fragment of a right first phalanx.  
 ATA94, TD6, H-18, talla 39. Fragment of (probably) a right parietal.

- ATA94, TD6, I-18, talla 37, 35. Fragment of left P<sup>3</sup>.  
 ATA94, TD6, I-17, talla 39, 28. Fragment of distal pulley of metapodial.  
 ATA95, TD6, H-16, talla 40–41, 235. Sesamoid from behind the external side of a left first phalanx. L 23·1, DT 12·2, DAP 20·1.  
 ATA95, TD6, H-17, talla 40/41, 174. First lobe of right M<sup>x</sup>, upper part, not worn.  
 ATA95, TD6, talla 40–41, 183. Sesamoid from behind the internal side of a left first phalanx. L 20·1, DAP 20·6, DT 16·7.  
 ATA95, TD6, G-16, 69. Distal metacarpal (left?). DT<sub>d</sub> 67·4, DAP<sub>m</sub> 28·9, left pulley DAP 36·9, DT 31·4, right pulley DAP 36·8, DT 37·6.  
 ATA95, TD6, G-17, 144, z=508. Tip of horn core.  
 ATA95, TD6, I-17, talla 40/41, 69. Right P<sup>4</sup>. 18·2/16·0 × 21·7.  
 ATA95, TD6, H-17, talla 40–41, 106. Right ulnar. H 45·3, H<sub>a</sub> 33·5, DAP 38·4, DT 26·8.  
 ATA95, TD6, H-16, talla 40–41, 158. Distal part of a left second phalanx. DAP<sub>d</sub> 30·8, DT<sub>d</sub> >27·5. ATA95, TD6, H-17, talla 40–41, 111. Right unciform. Articulates with ulnar no. 106. DAP 37·0, DT 35·7, H 29·1.  
 ATA96, TD6, G-18, talla 44, 106. Metacone of right M<sup>x</sup> or D<sup>3/4</sup>.

**Appendix 2 Abbreviations of collections**

- AVP=Accademia Valdarnese del Poggio, Montevarchi. 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. IPUW=Institut für Paläontologie der Universität Wien. IQW=Institut für Geowissenschaften, Bereich Quartärpaläontologie, Weimar. MB=Museo de Burgos. MCP=Musée 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. TMH=Teylers Museum, Haarlem. UCBL=Université Claude Bernard, Lyon. UCM=Universidad Complutense de Madrid. ZMA=Zoölogisch Museum, Amsterdam.