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A new site from the Spanish Middle Pleistocene with cold-resistant faunal elements: La Parte (Asturias, Spain)

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Abstract

The La Parte (Asturias) northern Spain site contains a cold-adapted mammal faunal assemblage that corresponds to a level radiometrically dated to a minimum age of 150 ka. It represents the most ancient site with cold resistant fauna in the Iberian Peninsula.

Among the species recorded in La Parte, *Coelodonta antiquitatis* and *Rangifer tarandus* represent the typical cold-adapted large mammal association.

The presence of the woolly rhino at La Parte provides relevant environmental information about the Mammoth Steppe. This species was not as abundant in the Middle Pleistocene as during the Late Pleistocene, when its cold-adapted features can be studied from an evolutionary perspective. The remains attributed to *R. tarandus* suggest an open steppe ecosystem.

The presence of *Marmota* sp. is also confirmed in La Parte. A first interpretation would suggest an alpine or periglacial ecosystem, but based on recent results which do not support the correlation between phylogeny and climatic tolerance for extant species of *Marmota* (López and Cuenca, 2002. Palaeogeography, Palaeoclimatology, Palaeoecology 186, 311), we propose the presence of this rodent suggests an open landscape with cold conditions.

The rest of the taxa included in the La Parte assemblage (*Crocuta crocuta*, *Panthera leo*, *Cervus elaphus*, *Megaloceros* cf. *giganteus*, *Bison priscus* and *Equus caballus*) are usually associated with typical cold-adapted faunas, but they are also found in woody temperate zones so they do not characterize by themselves a cold period. The faunal association from La Parte suggests a combination of steppic and open woodland ecological conditions.

1. Introduction

The construction of a highway near the city of Oviedo (Asturias) caused the destruction of part of the terrain surface and thus the discovery of a cave filling, with a level containing faunal remains (mostly macromammals) (Fig. 1). The karstic cavity where the site is included is in the Lower Cretaceus Ullaga Formation. There can be distinguished different ossiferous accumulations but the most relevant correspond to the same layer (lower or principal level) (Fig. 2). This ossiferous level is rich in speleothems which surround or fill the fossil bones. U-series analyses of two speleothems, which included several bone fragments coming from the bone accumulation level, yielded dates of 188 ± 11 and 141 ± 8 ka. Following the results obtained by the geochronologist team who worked out the analyses (Institut de Ciencies de la Terra "Jaume Almera", Barcelona), the most likely minimal age for this level is 150 ka. The La Parte faunal association is biochronologically consistent with the end of the Middle Pleistocene, during a time span that could correspond with oxygen isotope stage 6, a glacial interval.

There exists another more reduced fossil accumulation in an uppermost level (upper level) for which

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Fig. 1. Location of the Pleistocene La Parte (Asturias, Spain) paleontological site, within the framework of the Iberian and Cantabrian range, Nalon river and main towns.

materials and fossil taxa indicate not only a younger age but also different environmental conditions than the principal level. Nevertheless this upper level is not analyzed here. This study is focused on the La Parte lower level (level C), which is the layer that has yielded a faunal assemblage with cold-adapted elements (Fig. 2).

2. Material and methods

Because of the construction of the highway, a salvage excavation was undertaken at La Parte with a great time limitation and without adequate methods. The bones could not be treated in situ with chemical preservatives, and became very fragmentary. For this reason, the sample is limited and fragmentary.

The fossil remains recovered are abundant but just a low percentage of the sample ($NISP_{number\ of\ identified\ specimens} = 87$) is useful for study purposes due to the bad state of preservation of the bones (extremely fragile and decalcified). The identifiable fossils were selected from the gross collection, numbered, registered and preserved for taxonomic study. These consisted of the most compact and dense elements: teeth, metapodials and carpal and tarsal bones. The remaining specimens were studied for recording taphonomic information only.

The measurements used for comparative analyses with other specimes are the standard ones from Von den Driesch (1976), Guérin (1980) and Eisenmann et al. (1988). A number of different modern and fossil collections were also included in this study, as indicated in each table. Measurements are given in mm.
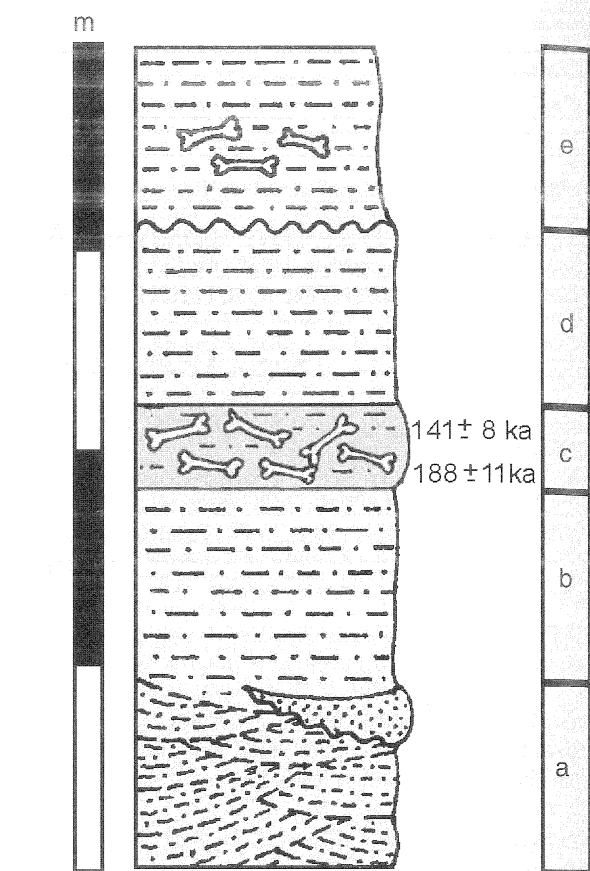

Fig. 2. Stratigraphic column of the La Parte site; (a, b and d) reddish and yellowish sands and silts with black manganese concentrations; (c) lower level (or principal): silts with bones and coprolites accumulations that contain speleothems and calcite. Two samples calcites coming from this level were dated by U-series yielding 188 ± 11 ka and 141 ± 8 ka ages; (e) upper level: clays, silts and black organic material with bones.

3. Taxonomic analysis

Order Rodentia Bowdich, 1821
Family Sciuridae Gray, 1821
Genus *Marmota* Blumenbach, 1779
    Marmota sp.
Material referred: LP-1, a left humerus which lacks the proximal end and with an incomplete distal end is the only fossil recovered of this taxon (Fig. 3a). Measurements that were possible to take are as follows: width of the trochlea = 5 mm; depth of the distal end = 9 mm; smallest width of diaphysis = 8 mm.

Specific assignment of the La Parte marmot to either of the European species (*M. marmota, M. bobac*) is not possible due to the lack of any cranial or dental remains. thus the humerus can only be assigned to a generic level.

This genus is recorded in the early and middle Pleistocene layers of Atapuerca (Cuenca-Bescós et al., 2001). Several Quaternary sites from Asturias including Peñón de Malverde (Lorenzana, 1983) and in the
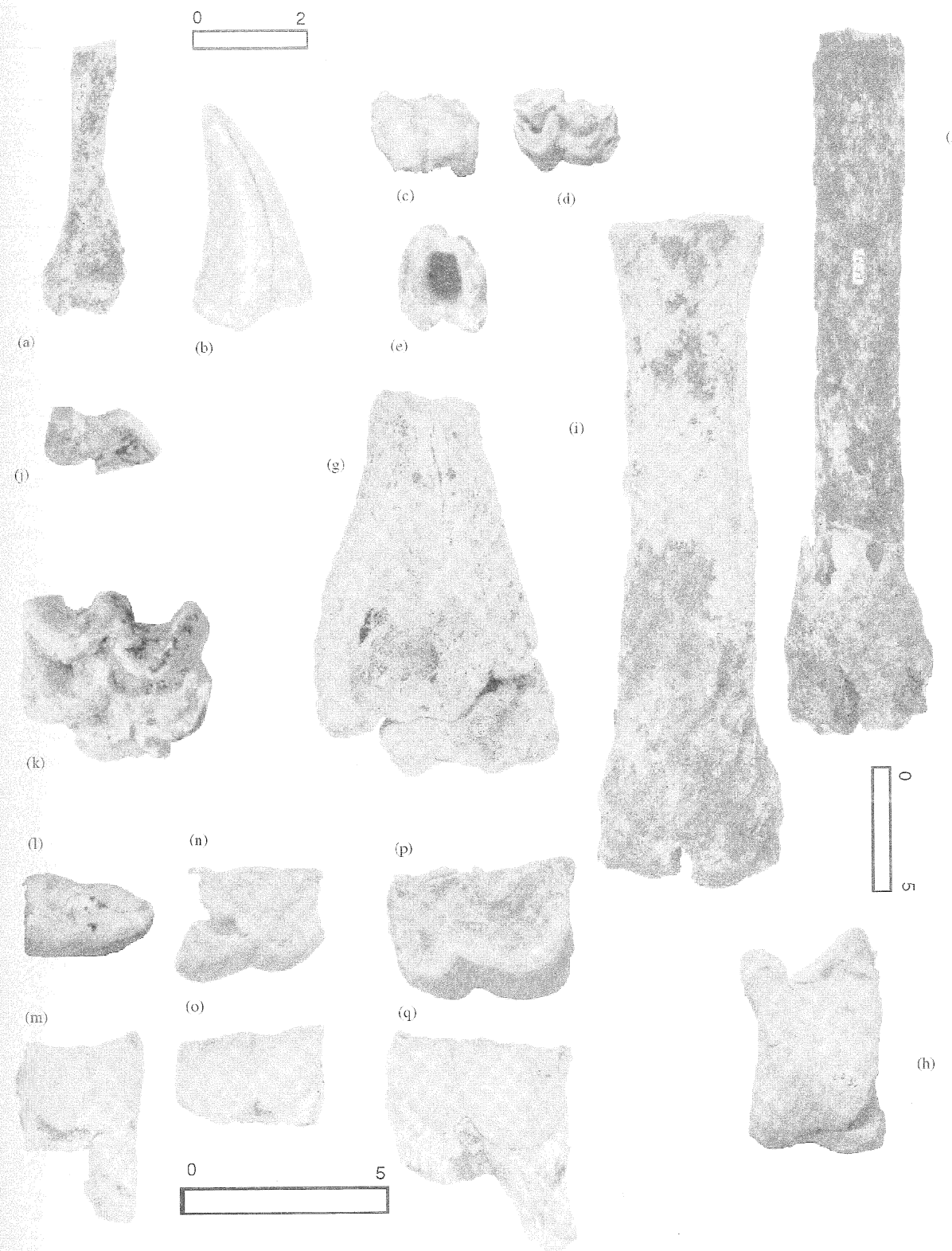

Fig. 3. (a) *Marmota* sp., left humerus in posterior view (b) *Panthera leo* ssp., lower right canine in labial view. (c) *Rangifer tarandus*, M^2 or M^3 in labial view; (d) *Rangifer tarandus*, M^2 or M^3 in occlusal view; (e) *Rangifer tarandus*, metatarsal cross section (scale bar 2 cm); (f) *Megaloceros* cf. *giganteus*, distal end of a metatarsal in anterior view; (g) *Bison priscus*, distal end of a left humerus in posterios view; (h) *Bison priscus*, right astragalus in palmar view; (i) *Bison priscus*, left metatarsal in anterior view (*Megaloceros* and *Bison* elements at same scale bar, 5 cm); (j) *Equus caballus*, fragmented upper right molar in occlusal view; (k) *Equus caballus*, upper right molar in occlusal view (scale bar 2 cm); (l) *Coelodonta antiquitatis*, right P_2 in occlusal view; (m) same in labial view; (n) *Coelodonta antiquitatis*, right P_3 in occlusal view; (o) same in labial view; (p) *Coelodonta antiquitatis*, right P_4 in occlusal view; (q) same in labial view (*Coelodonta* molars at same scale bar, 5 cm).

Cantabrian mountain range have yielded *Marmota* fossil remains.

    Order Carnivora Bowdich, 1821
    Family Hyaenidae Gray, 1821
    Genus *Crocuta* Kaup, 1828
       Crocuta crocuta, Erxleben, 1777

Material referred: LP-3, a cusp of a right second upper premolar of a juvenile spotted hyaena was recovered from La Parte, together with a great number of coprolites attributed to this taxon. The specimen does not show any wear surface or cementum, so this germen was likely in the eruption process in a juvenile individual.

This fossil does not allow any diagnostic measurements to be taken, but the morphology of the piece undoubtedly places it in the *Crocuta* group. Spotted hyaena makes its first appearance in Europe during the late Early Pleistocene, the first undoubted occurrence in level TD4-5 of the Gran Dolina site at Sierra de Atapuerca (Spain) (García and Arsuaga, 1999). The occurrence of this species in the Sierra is almost continuous throughout the TD sequence dating older than 800 ka in the lowermost level TD4–TD8 which is dated to between 563 ± 84 and 653 ± 98 ka (Falguères et al., 1999). Spotted hyaenas spread during the Middle Pleistocene and occupied all Europe with great success until the end of the Upper Pleistocene. Their remains are also common in the Iberian Peninsula: in Las Caldas (Asturias), a site placed very close to La Parte, 160 *C. crocuta* remains of juveniles were recovered (Álvarez Laó, 2002). A number of Middle and Upper Pleistocene sites, i.e. Columbeira (Cardoso, 1993), Cueva del Buho, Zafarraya, Valdegoba, Gorham's Cave, Aizbitarte, Aizkirri, among many others also have yielded remains of this carnivore-scavenger, showing its wide spread in the peninsula.

    Family Felidae Gray, 1821
    Genus *Panthera* Oken, 1826
       Panthera leo ssp. indet.

Material referred: LP-4, a lower right canine of an adult individual was recovered in La Parte site. The remain preserves the crown but not the root (Fig. 3b). The canine measurements (taken at the base of the crown) are: antero-posterior diameter = 28 mm; transversal diameter = 23 mm; height of the crown = 52 mm.

The taxonomic attribution to a large *Panthera* is clear. When we compare the La Parte lower canine dimensions with a modern African sample and several fossil specimens of *P. leo* from a diverse number of Eurasian and American Pleistocene localities, we observe it is large, but it also shows different length/width proportions (Table 1). The La Parte specimen is not the largest canine (antero-posterior diameter = length) in the sample, but relative to its length it is very broad (transverse diameter = width). Two specimens from the Azé (Argant, 1991) late Middle Pleistocene site, and one

from Malarnaud (Dufour, 1989) present a greater length for the same or less width than La Parte. The canine clearly belongs to a large and robust (in terms of length/ width index) lion (*P. leo*). Nevertheless, the subspecific attribution (*P. leo spelaea* Goldfuss, 1810 or *P. leo fossilis* von Reichenau, 1906) is made on the basis of dental and cranial analyses (Schütt, 1969). The large size of the canine does not provide enough evidence, because large animals are included in both subspecies, and only specific identification is suggested. It seems that the Beringian and Yakutian Late Pleistocene lions were smaller than lions that inhabited western and Eastern Europe (Baryshnikov and Boeskorov, 2001).

    Order Artiodactyla Owen, 1848
    Family Cervidae Goldfuss, 1820
    Genus *Cervus* Linnaeus, 1758
       Cervus elaphus Linnaeus, 1758

Material referred: LP-5, a left humerus diaphysis with the distal end; LP-6, a right humerus diaphysis with distal end; LP-7, a right humerus diaphysis; LP-8, a right metatarsal diaphysis).

All the remains are very fragmentary elements which only permit to measure the minimal width of the humeral diaphysis (LP-5 = 30 mm; LP-6 = 27 mm). The scarcity of red deer remains in La Parte lower level (5.15% of the identified remains) is noteworthy, because this is possibly the most common Pleistocene species recovered in this region (de Fraga Torrejón, 1958; Adán, 1997; Álvarez Laó, 2002). Nevertheless the morphology and measurements of the pieces are undoubtedly attributed to *C. elaphus*.

    Genus *Megaloceros* Brookes, 1828
       Megaloceros cf. *giganteus* Blumenbach, 1799

Material referred: LP-13, a distal end of a metatarsal (Fig. 3f); LP-14 a fragment of metatarsal diaphysis.

Only LP-13 can provide some measurements: breadth of the distal end (Bd) = 61 mm; depth of the distal end (Dd) = 42 mm). Both metatarsal fragments show clear cervid morphologies, as the medial sulcus is distally

closed and a longitudinal depression appears in the posterior part of the diaphysis. The dimensions of this metatarsal fragment are much larger than those in *C. elaphus* and are within the *Megaloceros* range. The most diagnostic elements for specific attribution are antlers, which in *M. giganteus* are more widespread and have reached a palmate stage. Unfortunately no antlers have been recovered from La Parte, nevertheless, *M. giganteus* is the only species of giant deer jet described in the Cantabrian mountain range (Altuna, 1972; Altuna and Mariezkurrena, 2000). *Megaloceros savini* chronological range is placed during the Cromerian Complex and up to the early phase of the Elsterian Complex. The *Coelodonta antiquitatis* remains were found at the same level as the giant deer but it seems that the oldest European woolly rhinoceros were recovered from several German Elsterian gravels (Kahlke, 1999). This gap of time between the two species makes more likely the attribution to *M. giganteus*, which occurs since the late Middle Pleistocene and during the Late Pleistocene, a period when *C. antiquitatis* was also present. La Parte represents the first *M. giganteus* find for the Asturias region.

    Genus *Rangifer* H. Smith, 1827
       Rangifer tarandus Linnaeus, 1758

Material referred: LP-9, a right metatarsal diaphysis; LP-10, a left metatarsal (fragment with diaphysis and proximal end); LP-11, an upper right molar; LP-12, a left mandible with deciduous dentition- D_1 and D_2).

The juvenile mandible is a small fragment with two unworn milk teeth. It is attributable to reindeer because of its size (too small for *C. elaphus* and too large for *Capreolus capreolus*) although with some doubts. The morphology of the adult upper molar clearly resembles a reindeer (Fig. 3c and d), because the labial denticulate is very pronounced, and the lingual face not so sloped as observed in *C. elaphus*. It is difficult to distinguish between isolated M^2 and M^3 and both dimensions overlap in different individuals. We have compared our

Table 1
Panthera leo ssp. La Parte

Variable	La Parte	*Panthera leo* modern sample ♀	*Panthera leo* modern sample ♂	Malarnaud[a] Taubach	Somerset[b]	Jaurens[c]	Azé[d]	La Fage[c]	Gissey-Sur-Duche[d]	Russian sites[f]	Yakutia[g] (Late Pleistocene)	Lezetxiki[h]
APD C_i	28	24.3 ± 2.05	16.3 ± 1.48	30.5 29	27.9; 24.9	25.8	29.6 / 28.7	26.3 / 26.5	25.6; 21	23.5; 28 / 29.4; 27	29; 26.4; 29.5 / 23; 24.5	31
TD C_i	23	14 ± 0.98		22.5 22	20.2	18	23.1 21	17.9 17.5	19 ; 14.7	18; 19; 21.7 / 19	20.3 ; 21; 21.2; / 21; 18.9 ; 14.7	22.8

Selected comparative measurements of lower canines. (*Panthera leo* modern sample is $n = 21$ for females and $n = 22$ for males).
Anteroposterior diameter C_i: APD C_i; transversel diameter C_i: TD C_i.
[a]Dufour (1989).
[b]Dawkins and Sandford (1866).
[c]Ballesio (1980).
[d]Argant (1991).
[e]Ballesio (1975).
[f]Vereshchagin (1971) (Eemian or Late Pleistocene sites from Azerbaydjan, Ukraine, Siberia and Don river).
[g]Baryshnikov and Boeskorov (2001).
[h]Altuna (1972).

Table 2
Rangifer tarandus, La Parte (selected comparative measurements of upper molars (in mm))

Site	M^2		M^3	
	L	W	L	W
La Parte (Spain)	19.6	15.9		
Foix (France)[a]	17.0	18.0	18.0	17.0
Villestofte; Strangegaard (Denmark)[a]	19.5; 20.0	16.8	19.5; 18.5	16.0
Irkustk (Siberia)[a]	19.0	19.9		
Modern European sample (Norway, and Greenland)[a] and Sweden[b]	18.4; 18.7; 17.7	14.2; 16.2; 15.7	17.2; 19.0; 16.9	13.5; 16.0; 13.9
Domestic reindeer (Sweden)[a]	17.5	15.0	16.0	12.5
Urtiaga (Spain)[c]	19.5;19.6;20.2			
Modern American sample ($n = 12$) (Alaska and Yukon Territory)[b]	18.2 ± 1.34	15.4 ± 1.07	17.7 ± 1.06	14.7 ± 1.09

[a]Bochud (1967).
[b]Own data.
[c]Altuna (1972).

specimen dimensions with a sample of modern and fossil reindeer, and it can be identified as either of the two molars (Table 2).

The two metatarsals belong to young individuals and the morphology corresponds well with the reindeer type, with a very deep diaphysis section. Reindeer metatarsals present a different width/depth diaphysis relationship than other cervids, showing a larger depth proportionally to its width. The dimensions of the juvenile individual from La Parte are exactly the same as those obtained from an extant juvenile reindeer (width diaphysis = 14 mm; depth diaphysis = 18 mm). The specimen LP-9 clearly presents this deep section morphology typical of reindeer (Fig. 3e). In addition to these reindeer remains there were recovered numerous very fragmentary diaphyses which could belong to the same species, but their classification remains uncertain.

Reindeer finds provide very valuable paleoclimatic information. There is wide evidence of the presence of this taxon during the Quaternary in Asturias at a number of sites, with fossil records and also cave art representations (Blas, 1982; García and Arsuaga, 2003). In the Asturias region, reindeer is also present at Tito Bustillo (Altuna, 1976), La Riera (Altuna, 1986), Cueto de La Mina (Castaños, 1982), La Paloma (Castaños, 1980), El Bufón (Menéndez, 1923), Las Caldas and La Ancenia (Adán, 1997).

Family Bovidae Gray, 1821
Genus *Bos* Linnaeus, 1758 and *Bison* H. Smith, 1827
Bovini cf. *Bison priscus* Bojanus 1827

Material referred: LP-15, a fragment of an upper molar; LP-16: unerupted upper right molar; LP-17: fragment of dorsal vertebra; LP-18: fragment of lumbar vertebra; LP-19: fragment of vertebra indet; LP-20: distal end of left humerus which keeps part of the trochlea; LP-21: fragment of trochlea of a right humerus; LP-22: fragment of trochlea of a left humerus; LP-23: distal end of a right radius; LP-24: distal end fragment of a left radius; LP-25: distal end fragment of a juvenile radius diaphisis; LP-26: proximal end fragment of a left ulna; LP-27: diaphisis fragment of left metacarpal; LP-28: distal end of metacarpal; LP-29: proximal end of right metacarpal; LP-30: left pelvis which keeps acetabulum and part of ischium; LP-31: right pelvis which keeps part of acetabulum and ischium; LP-32: left pelvis which keeps part of acetabulum and ischium; LP-33: capitum femoris; LP-34: distal end of a left tibia. LP-35: right astragalus; LP-36: right astragalus (eroded); LP-37: left astragalus (eroded); LP-38: fragmentary left astragalus; LP-39: left calcaneus (very eroded); LP-40: fragment of left calcaneus; LP-41: right centro-tarsal (eroded); LP-42: right centro-tarsal (eroded); LP-43: left centro-tarsal; LP-44: right centrotarsal; LP-45: left metatarsal; LP-46: proximal end of a left metatarsal; LP-47: proximal end

of a left metatarsal; LP-48: distal end of metapodial; LP-49: fragment of distal end of metapodial; LP-50: proximal phalange; LP-51: proximal phalange (Table 3).

3.1. Humerus

The olecranon fossa morphology of the humerus (LP-20) allows a likely attribution to *Bison*. In *Bos*, the proximal limit of the olecranon fossa is almost horizontal at an almost straight angle to the anterior edge. This trait is also observed in the extant forms of *Bos*. However in *Bison*, the proximal limit of the olecranon fossa is anteriorly sloped at any angle. The humerus fragment LP-20 preserves the olecranon fossa and it clearly displays the morphology of *Bison* (Fig. 3g).

3.2. Ulna

LP-26 preserves the radio-ulnae articulation which is flat, and an apophysis enters into the radius groove at an obtuse angle. This is a diagnostic trait for *Bison*. In *Bos*, the apophysis penetrates deeper into the radius groove at an acute angle.

Table 3
cf. *Bison priscus*, La Parte (measurements of postcranial elements)

Element	Variable				
Humerus	SD	Bd	BT	MDT	
LP-20	92			58	
LP-21				59	
LP-22			118		
Ulna	SDO	BPC			
LP-26	68	46			
Femur	DC				
LP-32	62				
Astragalus	GLl	GLm	Dl	Bd	
LP-35	88	80	47	52	
LP-36	83		46	60	
LP-37		75	42	56	
Calcaneus	GL	Mb			
LP-39	176	56			
Metacarpus	Bd	DD			
LP-28	70	40			
Metatarsus	GL	Bp	SD	Bd	DD
LP-45	273	60	53	72	36
LP-46		88			
LP-47		68			

Bd, breadth of the distal end; Mb, maximum breadth; SD, smallest breadth of diaphyses; BT, maximum breadth of the trochlea; Bp, breadth of the proximal end; BPC, greatest breadth of the proximal articular surface; MDT, medial diameter of the trochlea; DC, depth of the Caput femoris DD, depth of distal end; Dl, depth of the lateral half; SDO, smallest depth of the olecranon; GL, greatest length; GLl, Greatest length of the lateral half; GLm, Greatest length of the medial half.

3.3. Astragalus

Some indexes of width and length taken on its lateral face are proposed to distinguish between *Bos* and *Bison*, but we do not consider that they provide enough confidence given a highly overlapping range (Stampfli, 1963). Nevertheless in plantar view, there is a line on the superior edge, bordering on the articulate surface with the talus, which in *Bison* describes a smooth curve ending on the lateral region, at an open angle (100–110°) with the lateral angle. In *Bos*, this line describes a straight angle instead of an arc, in the medio-plantar area and continues towards the lateral edge reaching it perpendicularly (Stampfli, 1963).

This trait is only observable in one of the La Parte astragali (LP-35) and it resembles the *Bison* morphology (Fig. 3h).

3.4. Metapodials

The articulate surfaces of three out of the eight metapodials recovered in La Parte lower level are very symmetrical and with a similar area, morphology defined for *Bison*. The metatarsal recovered from the lower level (LP-45) presents an inflexion in the diaphysis–epiphysis limit which is not observed in *Bos* (Fig. 3i).

The anatomical arguments described for humerus, astragalus, ulna and metapodials support the *B. priscus* attribution at least for the lower level but we cannot totally deny the presence of *Bos* at La Parte, because both genera were very common during the Quaternary in this area.

Order Perissodactyla Owen, 1848
Family Equidae Gray, 1821
Genus *Equus* Linnaeus, 1758
Equus caballus Linnaeus, 1758

Material referred: LP-56, a fragment of a right upper molar; LP-57: right upper molar; LP-58: fragment of distal end of a left radius; LP-59: juvenile metacarpal; LP-60: distal end of a right tibia; LP-61: right astragalus; LP-62: fragment of right astragalus; LP-63: distal end with diaphysis of metapodial; LP-64: distal end with diaphysis of metapodial; LP-65: distal end of metapodial; LP-66: distal end of metapodial; LP-67: fragmented distal end of metapodial;

The upper right molar is fragmented but preserves the hypocone and clearly shows the *pli caballine* (Fig. 3j). The other upper molar is very large (Fig. 3k; Table 4) but belongs to a young individual and does not present any worn surface.

The radius, metapodials and tibia are eroded and no measurements can be taken.

The tibia allows the following measurements: distal width: 64 mm and distal depth: 38 mm. One of the astragali (LP-61) is well preserved and can be mea-

Table 4
Equus caballus ssp., La Parte

SITE	M¹–M²		
	L	W	LPr
La Parte (Spain)	34	30	17
Equus caballus ssp.			
Huéscar (Spain)[a]	26.1±2	25.7±1.0	10.1±1.2
Equus stenonis (n = 12)			
Cúllar de Baza-1 (Spain)[a]	26.0	27.2	11.2
Equus altidens	26.1	26.9	11.2
Cúllar de Baza-1 (Spain)[a]	27.4	28.4	12.7
Equus sussenbornensis			
Atapuerca-TG (Spain)[b]	24.4; 25.5		13; 14.4
Equus caballus cf. *steinheimensis*	25.3; 27.5		13.4; 11.4
Taubach (Germany)[c]	30.3±1.6	26.9±1.6	15.1±0.8
Equus taubachensis (n = 12)	27.7±2.1	26.5±1.4	14.3±0.8
Labeko Koba (Spain)[d]	25.3±5.7	26.0±3.0	13.81±2.8
Equus sp. (n = 33)			

Selected comparative measurements of upper molars.
[a] Alberdi and Ruiz-Bustos (1989).
[b] Sánchez and Soto (1987).
[c] Musil (1977).
[d] Altuna and Mariezkurrena (2000).

sured: GH (greatest height) = 56 mm; GW (greatest width) = 71 mm; BFd (breadth of the Facies articularis distalis) = 53 mm; GBT (greatest breadth of the Trochlea tali) = 58 mm.

The most diagnostic elements to be able to consider a subspecfic level are the teeth. Tooth morphology cannot be studied in detail in any of the upper molars, in one case because it is only a fragment and in the other because it is not worn enough.

Family Rhinocerotidae Owen, 1845
Genus *Coelodonta* Bronn, 1831
Coelodonta antiqitatis Blumenbach, 1799

Material referred: a number of 15 remains attributed to woolly rhino were identified, likely belonging to the same adult individual. LP-69: right P₂ (Fig. 3l and m); LP-70: right P₃ (Fig. 3n and o); LP-71: left P₄ (Fig. 3p and q); LP-72: right scaphoid; LP-73: fragment of left pelvis with part of acetabulum; LP-72: distal end of a left tibia; LP-75: left calcaneus; LP-76: right fourth metacarpal; LP-77: mandible fragments; LP-78: diaphysis of long bone. Furthermore, some diaphysis fragments are likely attributable to the same specimen, most of them presenting hyaena gnaw marks.

The dental traits, including presence of thick cementum and enamel with abundant ridges, are typical of *C. antiquitatis*. Also the external groove does not clearly reach the base of the crown and is separated from the groove that ascends from the base between the two roots. The worn stage of the molars indicates they belong to an aged animal. Table 5 includes the dental measurements compared with a European sample.

Table 5
Coelodonta antiquitatis, La Parte

SITE		P₂		P₃		P₄	
		L	W	L	W	L	W
La Parte		27	19	33	25	41	31
Cueva de Nando[a]	Left					38.5	26.4
	Right					37.7	26.5
Starunia[b]						35	15
L'aven de Coulon[b]						34	28
Kesslerloch[b]						46.2	29.0
Ordos[b]						44	27
Labeko Koba[c]	Left mandible	27	18.6	32	24	41	27.5
	Left mandible	29.5	18.5	37	24		
	Right mandible			38	24	44	29
	Isolated teeth			34	27	45	28
	Isolated teeth			35.5	26.5	45	28.5
(Guerin, 1980) (several European localities = 94sites)		29	18.68	34.17	24.0	41.53	26.84
	Min–max	23–35.5	16–22	29–39.5	18–29	35–48.5	22–31.5

Selected comparative measurements of lower premolars.
[a]Fuentes and Meijilde (1979).
[b]Bonifay (1961).
[c]Altuna and Mariezkurrena (2000).

Table 6
Coelodonta antiquitatis, La Parte

Variable	La Parte	European sites (Guerin, 1980)	
		~	Min–max
Calcaneus			
APD Tub	64	75.24	60–90
TD Tub	55	55.18	45–66
TD Sust	82.8	80.27	65–93
MTD Post	42.9	44.12	35–59
Scaphoid			
Maximal Breadth	51.2	60	51–71.5
Metacarpal IV			
TDD	33.4	37.58	32–46
APDD	20	24.39	20–30
APDDT	35.9	42.26	34–48

Selected comparative measurements of postcranial elements.
APDTub, anteroposterior diameter of the tuberosity; TDTub, transversal diameter of the tuberosity; TD Sust, transversal diameter tallo sustentaculum; MTD Post, minimal transversal diameter of the posterior border; TDD, transversal diameter of diaphysis; APDD, anteroposterior diameter of diaphysis; APDD, anteroposterior diameter of distal end.
In Guerin (1980), several European localities were analysed, 16 for the escaphoid, 27 for the calcaneus, and 30 for the metacarpus IV.

Table 6 includes the postcranial measurements available, compared with a European sample. The early *Coelodonta* forms are considered less adapted to the cold than the last-glacial, more robust forms (Kahlke, 1999). The postcranial elements from La Parte are within the European range although always closer to the minimum values.

Although the presence of *C. antiquitatis* is confirmed in several localities of the Cantabrian Mountain Range (Altuna, 1972; Altuna and Mariezkurrena, 2000), the remains recovered from La Parte represent the first undoubted woolly rhino recorded in the Asturias region.

4. Origin of the accumulation

The origin of the bone accumulation seems to be related to a hyaena den. This is interpreted from a variety of evidence: almost all the fossil remains represent herbivores, being mainly limb bones, which are the easiest to disarticulate and to transport into a cave; furthermore, a high percentage of the bone assemblage presents puncture marks and gnawing damage produced by the teeth of spotted hyaenas; in addition, several coprolite accumulations attributed to hyaenas were detected at all levels. Furthermore, a fragmentary P² of a juvenile *C. crocuta* was recovered which also evidences its presence.

5. Paleo-landscape reconstruction

Some of the taxa of the La Parte assemblage like *C. crocuta*, *P. leo*, *C. elaphus* and *E. caballus* are considered eurythermic species and related with more or less open forest but can also be present in a number of different paleoecosystems.

M. giganteus is a cold tolerant species, which expanded in open regions of Europe. Giant deer succeeded in wooded steppes or steppe-like biotopes,

reaching its optimum in temperate faunal associations, under relatively mild climatic conditions, such as interstadials (Kahlke, 1999).

Among the bovids, *B. priscus* is always associated with cool areas, while *Megaloceros* is more related to a steppe-like biotope. These species are usually associated with typical cold-adapted faunas, but they are also found in woody temperate zones without cold resistal elements.

Marmots have been classically associated with cold conditions, based on the ecology of their extant European relatives (*Marmota marmota* and *M. bobak*). Their extant geographic range is limited to the Alps, Carpathians, Poland, Rumania and Tatra mountains, with altitudes varying between 750 and 2700 m above or at the edges of forests (Corbet and Ovenden, 1982). The diet of marmots consists largely of green vegetation, specially grass and forbs, and they generally occupy subalpine open habitats, such as steppes, alpine meadows, pastures and forest edges (Nowak, 1999). The presence of marmots in the Iberian peninsula is proved since the Early Pleistocene (Cuenca-Bescós et al., 2001). Remains of *Hystrix vinogradovi* in association with *M. marmota* were recovered at Trinchera Galería (Atapuerca) levels GII and GIII, placed between the Holsteinian Complex and the Saalian by paleontological and radiometric evidence. This raises the question whether *Hystrix* and *Marmota* are valuable climatic indicators themselves (López Antoñanzas and Cuenca Bescós, 2002) at least in the Iberian Middle Pleistocene. During the Late Pleistocene, marmots spread in Western Europe occupying the Cantabrian mountian range. La Parte site altitude is about 250 m and the presence of marmot in the La Parte faunal assemblage makes us consider this was an open landscape with cold and steppic conditions. Another site named Peñón Malverde de Grado, very close to La Parte, also has registered the presence of Marmot at an even lower altitude (Lorenzana, 1983).

The only two species of la Parte that can be considered by themselves as paleoclimatical indicators are the reindeer and the woolly rhinoceros. Reindeer inhabit arctic tundra and surrounding boreal coniferous forest, nevertheless some extant populations are found in mountainous areas farther south (Nowak, 1999) but always associated with very open forest (Corbet and Ovenden, 1982). Tundra reindeer (*tarandus* type) would be restricted to arctic or boreal refugia in northern latitudes during the warmer periods like the interglacials extending its geographic range in glacial periods (Kahlke, 1999). All the sites where reindeer remains were found during the last glacial are associated to more or less cold periods. During the Middle Pleistocene cold periods, reindeer temporarily belonged to the resident fauna in Central Europe occupying wooded or steppe tundra (Kahlke, 1999). The reindeer finds in La Parte indicate an open forest or steppe tundra biotope.

The woolly rhinoceros is the other paleoclimatic indicator species recovered from La Parte. Although it is considered by some authors as slightly more eurythermic than the reindeer (Altuna, 1995), Guérin (1980) mostly found them both associated in around 170 western European sites. The diet of *Coelodonta* based on gastrointestinal tract from a Yakutian site consisted of grasses, cotton grasses and other reeds while other evidences reveal tundra-like habitat with much scrub vegetation, especially dwarf birch (Kahlke, 1999). The presence of *C. antiquitatis* at La Parte would suggest a dry and open-steppe tundra landscape without or only with low snow in winters.

The co-occurrence of reindeer and woolly rhinoceros points to an open, dry and cold steppe tundra landscape for La Parte site. The marmot and *Megaloceros* support the interpretation of an open landscape with cold and steppic conditions and the rest of the species from the assemblage although are eurythermic, are consistent with an open landscape and an open forest in proximity.

6. Chronological framework and biostratigraphic correlations

U-series analyses on speleothems sampled from the studied fossiliferous level, yielded dates ranging between 200 and 133 ka (Fig. 2). These results are biochronologically consistent with the end of the Middle Pleistocene. The La Parte faunal assemblage indicates, specially by several elements, a dry, steppic and cold, open landscape, so it most like would correlate with oxygen isotope stage 6.

Marmots have been recorded in a number of Early and Middle Pleistocene Iberian layers as in several levels of Trinchera Dolina (Atapuerca) (TD4-TD5-TD6 and TD7) (López Antoñanzas and Cuenca Bescós, 2002) and ranging from a period older than 780 ka (but younger than the Jaramillo subchron), to about 600 ka (Falguéres et al., 1999). Remains were also recorded in younger layers from Trinchera Galería (GII and GIII) also in Atapuerca placed between 200 and 350 ka (Falguéres, pers. com.). Nevertheless the *Marmota* distribution area has a larger extent from OIS 6 up to the end of OIS 2. At Würm IV, Marmots were still present in the Cantabrian mountain range (Altuna, 1995).

The first occurrence of *C. crocuta* in Europe is at the lowermost level at Dolina (Atapuerca), at around 900 ka (García and Arsuaga, 1999), so it probably entered into the continent at least in the Jaramillon subchron. Afterward, it spread all over the European continent with great ecological success, displacing (and probably replacing) the giant hyaena (*Pachycrocuta brevirostris*), that was the great bone/meat eater of the European ecosystem at the time of the *Crocuta* arrival. The giant

hyaena seems not to have survived the Holstein Complex, and since the Saalian, *C. crocuta* expanded surviving until the Holocene. Some authors (Klein and Scott, 1989) consider canine size varies extremely in glacial and interglacial periods, but unfortunately this cannot be tested in the La Parte specimen, and biostratigraphic correlation remains unclear.

P. leo presents a similar problem. Its presence in Europe is first recorded at around 600–700 ka in Isernia La Pineta (Italy) Middle Pleistocene site (García and Arsuaga, 1999) and remains expanding with great ecological success in the continent until its extinction close to the Holocene. Nevertheless the La Parte evidence is not enough to distinguish to a subspecific level that allows us to allocate this lion in a more focused biostratigraphic context. A similar problem is pointed for *E. caballus* that without a subspecific attribution (not possible with the available sample), very little can be discussed, since the species is present from the Cromerian Complex to recent times. *C. elaphus* lacks chronostratigraphic interest due to the scarcity of remains and its wide time range from the Middle Pleistocene to recent times.

Early forms of *Rangifer* occur in the Early to early Middle Pleistocene, probably originating in the arctic, and reindeer expanded into north Western Europe in the early Saalian Complex (Kahlke, 1999). Tundra reindeer (as named for the *tarandus* type) are restricted to arctic or boreal refugia in northern latitudes during the warmer periods like the Holstenian Complex and the Eemian Interglacial extending its geographic range in glacial periods especially during the last glacial complex (Kahlke, 1999). There are a number of localities with reindeer remains in the Iberian peninsula, but all limited to the northernmost regions, chronologically related to OIS 4 and OIS 2 (García and Arsuaga, 2003). In the northern East Catalonia, south of the Pyrenees, a few localities from Girona have yielded reindeer remains. The Basque mountains connect the Pyrenees with the Cantabrian mountain range in the west, where the first sierras of the range start to appear. Nevertheless the altitude of Basque peaks is low (Gorbea Peak is the most significant at 1,544 metres) and the northern part of the region has numerous valleys that run parallel with the coast providing an easy access to the French Southernmost Aquitania valleys. Reindeer are more mentioned in sites from the Pyrenees during the Maximum Lower and Upper Pleniglacials, than horses and cervids (Clot and Duranthon, 1990). During the Late glacial, reindeer also occur in art manifestations by the first modern humans in Iberia, including not only north Iberia sites but a southerly range reaching Guadalajara to the south and Salamanca almost on the Portugal frontier (García and Arsuaga, 2003). The Iberian reindeer fossils are among the south-westernmost records and these expansions to the south from their most typical northern latitudes are

usually explained as immigrations during extremely hard winter season (Kahlke, 1999). Nevertheless, although the presence of reindeer in Iberia during OIS 4 and OIS 2 is widely proved, the presence of arctic elements predating the OIS 4 is of special interest. Most researchers today believe that the Iberian glaciers were restricted to the maximum upper pleniglacial and lateglacial (except, of course, in the Pyrenees), including Portugal where seems that no glacial processes nor a cold climate affecting the vegetation was recorded until the maximum upper pleniglacial (Raposo, 1995). However, some authors recognize very degraded moraines in Sierra Nevada (Granada), at a lower altitude, that could be interpreted as an earlier "Riss" glaciation (Rubio Campos et al., 1993).

M. savini is the most likely ancestor of *M. giganteus* (Kahlke, 1999) and was a typical representative of the Cromerian Complex faunas and apparently did not persist beyond the early phase of the Elsterian Complex. Some *C. antiquitatis* remains were recovered from the same giant deer level at La Parte chronologically (radiometrically dated at around 150 ka), nevertheless the oldest European finds indicative of an early form of woolly rhinoceros were recovered from several early Elsterian gravels in Germany (Kahlke, 1999). *M. giganteus* occurs since the late Middle Pleistocene and during the Late Pleistocene, a period when *C. antiquitatis* was also present. La Parte represents the first *M. giganteus* find for the Asturias region.

The Middle Pleistocene woolly rhinoceros did not reach the northeastern Siberian sites, so these early *Coelodonta* forms are considered less adapted to cold conditions than the most robust last glacial specimens (Kahlke, 1999). The postcranial elements from La Parte are on the most slender values of the European range. Although the material recovered is attributable only to one individual, the proportions do not show the typical very robust ones of the Upper Pleistocene forms.

7. Conclusions

The cold-adapted taxa are considered rare in the Iberian Peninsula (when compared with other European regions), so any new faunal discovery is of relevance and provides important information related to the glacial mammalian species. The presence of *C. antiquitatis* and *R. tarandus*, which clearly correspond to a cold-adapted ecosystem is confirmed. No arctic taxa have been reported prior to OIS 4 in the Iberian Peninsula, so it was commonly assumed that very cold conditions never existed before the last glaciation, with the exception of some reindeer remains from a level described as 'Acheulian' that could be placed at the end of the Middle Pleistocene (García and Arsuaga, 2003). The La Parte fauna reinforces the idea of earlier cold conditions

with some cold-adapted taxa that correspond to a level radiometrically dated to a minimun age of 150 ka placing this locality as the most ancient site with cold resistant fauna in the Iberian Peninsula.

Furthermore, La Parte site represents the first occurrence of *C. antiquitatis* and *M. giganteus* in Asturias, a region placed in the most occidental margin of the Cantabrian Mountain Range. These taxa are typically related to arctic to subarctic or inner-continental regions. The presence of the woolly rhinoceros in La Parte makes this site especially relevant for environmental purposes, and from an evolutionary perspective due to the ancient chronology of the site, a period when this species is not as well known in Western Europe. The La Parte paleolandscape suggests from the faunal evidence that this area was an open forest, dry and cold, with steppe elements.

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Arctic Siberia: refuge of the Mammoth fauna in the Holocene

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Abstract

Global climate change at the end of Pleistocene led to extinction in the huge territories of Northern Eurasia of the typical representatives of the Mammoth fauna: mammoth, woolly rhinoceros, wild horse, bison, musk-ox, and cave lion. Undoubtedly the Mammoth fauna underwent pressure from Upper Paleolithic humans, whose hunting activity could also have played a role in decreasing the number of mammoths and other representatives of megafauna. Formerly it was supposed that the megafauna of the "Mammoth complex" had become extinct by the beginning of the Holocene. Nevertheless the latest data indicate that extinction of the Mammoth fauna was significantly delayed in the north of Eastern Siberia. In the 1990s some radiocarbon dates established that mammoths existed in the Holocene on Wrangel Island—from 7700 until 3700 yBP. Radiocarbon data show that wild horses inhabited the north of Eastern Siberia 4600–2000 yBP. Muskoxen lived here about 3000 yBP. Some bison remains from Eastern Siberia belong to the Holocene. The following circumstances could promote the survival of representatives of Mammoth fauna. Cool and dry climate in this region promotes the maintenance of steppe associations—the habitats of those mammals. Late Paleolithic and Mesolithic settlements are not found in the Arctic zone of Eastern Siberia from Taimyr Peninsula to the lower Yana River; they are very rare in basins of the Indigirka and Kolyma Rivers. The small number of Stone Age hunting tribes in the northern part of Eastern Siberia was probably another factor that contributed to the survival of some Mammoth fauna representatives.
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1. Introduction

In the Late Pleistocene (120 000–10 000 years before present) Eastern Siberia, the main part of Northern Eurasia, was inhabited by a late variant of the Mammoth complex (or the Upper Paleolithic complex, after Vangengeim, 1977). The composition of this fauna was due to the prevalence of open landscapes—arctic steppes and "tundra-steppes" (Vangengeim, 1961; Yurtsev, 1981; Sher, 1997). The "mammoth" fauna of Eastern Siberia has been studied for about 200 years and is well known (Chersky, 1891; Vangengeim, 1961, 1977; Russanov, 1968; Sher, 1971; Vereshchagin, 1977, 1979; Lazarev and Tomskaya, 1987; Boeskorov, 1998, and others).

Typical representatives of the Late Pleistocene megafauna of Eastern Siberia, now extinct, were widely distributed: mammoth (*Mammuthus primigenius* Blum.), woolly rhinoceros (*Coelodonta antiquitatis* Blum.), the Lena horse (*Equus lenensis* Russ.), onager (*E. hemionus* Pall.), Pleistocene bison (*Bison priscus* Boj.), Pleistocene saiga antelope (*Saiga tatarica borealis* Tscherski (= *ricei* Frick), Pleistocene musk-ox (*Ovibos pallantis* H.Smith), and cave lion (*Panthera spelaea* Golf.). The fauna also included some modern species of mammals inhabiting the tundra zone (such as: arctic fox *Alopex lagopus* and tundra lemmings *Dicrostonyx* and *Lemmus*) and ecologically plastic species (such as: brown bear *Ursus arctos* L., wolf *Canis lupus* L., red fox *Vulpes vulpes* L., wolverine *Gulo gulo* L., caribou *Rangifer tarandus* L. and Alpine hare *Lepus timidus* L.) that lived in the Late Pleistocene tundra steppes of Eurasia.

Typical representatives of the Mammoth fauna were the main prey of Upper Paleolithic humans and their numerous remains are found in many sites from that period in Eastern Siberia, in the basins of Angara,