Restored group of bones scavenged by hyenids, from the paleontological excavation of Fonelas P-1 (photo by A. Arribas).
The fossil vertebrate remains of the Spanish Pliocene and Pleistocene are of the highest European and even world international relevance, thanks to the abundance of deposits and the good preservation of their fossil record, corresponding to the last two and half million years, and with a great faunal diversity. Of particular interest is the unquestionable presence of remains of the oldest human populations of the continent, which have even enabled the definition of a new human species (García Cortés et al., 2000 and 2001; Jordá Pardo, 2006).

All the deposits are located in the most favourable geological environments for the accumulation and preservation of fossil remains (Arribas and Jordá, 1999): the karst system, the fluvial system and the limnic system (lacustrine and paludal environments). More than 80% of the deposits belong to accumulations in karst systems, mainly those from the Middle and Upper Pleistocene. The Pliocene deposits mostly correspond to vertebrate accumulations originated by physical and biological processes, whereas in the Pleistocene deposits another accumulating agent is human activity, of which there are remains of several species: Homo antecessor, H. heidelbergensis, H. neanderthalensis and H. sapiens (Aguirre, 1996).

The main deposits are spread through all the Spanish peninsular territory, and in very diverse geomorphological positions of the following geological units: Cantabrian Mountain Range and Pyrenees, Central System, Iberian and Catalonian-Coastal Mountain Ranges, Betic Mountain Range, Tajo river and Guadiana river basins (including the inner sub-basin of Campo de Calatrava) and Guadix-Baza Basin (Figure 1).

In the Cantabrian Mountain Range and the Pyrenees there are several caves with fossil remains of Middle Pleistocene vertebrates, and predominantly of the Upper Pleistocene. The most remarkable are:

Galicia: Eirós Cave, A Valiña

Asturias: El Sidrón, El Conde, La Güelga, La Viña, Llonín, Cueto de la Mina, La Paloma, Las Caldas, Cova Rosa, Tito Bustillo, La Riera, El Buxu, Los Azules

Cantabria: El Esquilleu, Covalejos, El Castillo, Altamira, El Pendo, El Juyo, El Mirón, Morín, Rascacho, La Garmá, Salitre, El Otero

Castilla-León: Ojo Guareña, Valdegoba.

Navarra: Zatoya, Abarantz, Berrobería and Amutxate.


Cataluña: Banyoles, La Rocal dels Bous, Estret de Tragó, Cova Gran, Les Ermitons, Bora Gran, Arbreda, Mollet, Recalú Viver, Balma Guilanyà, El Parco.

The time recorded in most of these deposits is usually short. It is only in the case of El Castillo (Puente Viesgo, Cantabria) where it is possible to find a long sequence including the end of the Middle Pleistocene and the whole Upper Pleistocene.

These deposits mostly correspond to accumulations of bones and technology remains made by man in the Middle Paleolithic (Homo neanderthalensis) and Upper Paleolithic (Homo sapiens), and to a lesser extent to accumulations generated by other species (prey birds, carnivore mammals and scavengers). The information gathered so far, allows for a good knowledge of biodiversity in vertebrate communities, and of their evolution from the end of the Middle Pleistocene until the end of the Upper Pleistocene and beginning of the Holocene.

Figure 1. Location of the geosites herein described:

1) El Sidrón.
2) El Castillo.
3) Pinilla del Valle.
4) Jarama VI.
5) Atapuerca;
6) Torralba y Ambrona.
7) Cova Negra.
8) Cueva de Nerja.
9) Áridos.
10) Fonelas.
11) Amutxate.
Among the aforementioned deposits, the caves of El Sidrón in Asturias, and of El Castillo in Cantabria, deserve to be highlighted due to their special relevance.

The **Cave of El Sidrón** (Borines, Piloña, Asturias) is located in the Asturian Central Depression and was developed on Paleogene calcareous sandstones and conglomerates. It is a karst deposit originated by the action of an underground fluvial system and by collapse processes (Fortea et al., 2003) (Figure 2).

The findings have provided the biggest collection of remains of *Homo neanderthalensis* for the whole paleontological record of the Iberian Peninsula. This cave offers an important record of the Upper Pleistocene, which in this case is almost exclusively paleoanthropological (Figure 3). It has to be noted that among the human remains there is a very well preserved left humerus which is one of the best six examples in the world. With regard to the chronology, the dates obtained through different methods do not offer definite results, although the ones obtained by aminoacid racemization date the deposit between 40,000 and 30,000 years ago.

Figure 2, above left. *El Sidrón, cave access (photo by M. Navazo).*

Figure 3. *El Sidrón, stratigraphic section of the Galería del Osario (photo by F.J. Fortea).*

Figure 4, below. *Panoramic view of Valle del Pas in the area of Puente Viesgo, with Monte Castillo in the background (photo by F. Bernaldo de Quirós).*
The Cave of El Castillo, located in Puente Viesgo (Cantabria) (Figure 4), has the longest chronological sequence among all the deposits in the Cantabrian Mountain Range and the Pyrenees, from the end of the Middle Pleistocene to almost all of the Upper Pleistocene, comprising since 150,000 years ago to the beginning of the Holocene (Cabrera Valdés and Bernaldo de Quirós, 2003).

The long time duration of its record (Figure 5) gives this deposit a great relevance when it comes to study the evolution of Prehistoric human populations in the Cantabrian Mountain Range (Montes, 2003). Its remains of technological and subsistence activities of the Middle Paleolithic include paleoanthropological remains and are attributed to Neanderthal populations. The Late Paleolithic cultures produced by modern man are also represented here, from their early stages (Aurignatian and Gravetian) to their late stages (Solutrian, Magdalenian and Azillian), including Homo sapiens remains. Apart from having abundant remains of vertebrates all along its record, El Castillo is extraordinarily rich in archaeologic remains such as lithic and bone technology elements, as well as exceptionally interesting rock art objects.

In the cave of El Castillo there is significant evidence for the coexistence of Neanderthal and modern human populations between 40,000 and 28,000 years ago, a topic which used to be object of debate. It also gathers the oldest testimonies of art manifestations of the Peninsula, dated as older than 38,500 years. These are splendid art manifestations (carvings and paintings) from the Upper Paleolithic, decorating the cave walls and forming one of the most important Upper Paleolithic wall arts in the Iberian Peninsula.

The cave of Amutxate, in Navarra, must be mentioned, set in highly karstified limestones of Urgonian facies of Sierra de Aralar. It is especially interesting for its important deposits of cave bears (Ursus spelaeus Ros.-Hen.), discovered by the speleological group Satorrak from Pamplona, and studied in five excavation campaigns by the School of Mines of Madrid (Torres et al., 2007) with the collaboration of the aforementioned speleological group, and financed by the Regional Government of Navarra (Figure 6).

The main heritage value of Amutxate cave is linked to the perfect preservation of its taphonomy which has not been affected by furtive excavations, so what has been obtained from it faithfully reflects the real distribution of remains within the deposit. Thousands of cave bear bones and teeth, including the remains of dead at birth animals as well as cubs, juveniles and very old bears, have been extracted from this cave, not yet fully excavated. The study of the relative death age reveals the high death rate among young specimens, which is much lower in the new born animals. Thousands of milk teeth have been recovered. Human presence may explain the twenty bones of herbivores recovered. Several thousands of micromammal teeth proof that big size predators lived for long periods of time in this cave. The deposit age is of 45,000 years, and its occupation lasted at least 10,000 years.

In the northern and southern flanks of the Central System, there are large exposures of Cretaceous carbonate rocks, inside of which more than 180 karstic caves have been inventoried, twenty of them include vertebrate deposits covering a time interval between the Lower-Middle Pleistocene and the Upper Pleistocene-Holocene. The main cavities with vertebrates deposits are:

- Segovia: Villacastín, Cueva de la Griega, Cueva del Búho, Pinarillo I, Murcielaguinos, and La Peña de Estebanvela.
- Madrid: Pinilla del Valle, Cueva del Reguerillo, Cueva de los Huesos, and Cueva de las Pinturas.
- Guadalajara: Jarama I, Jarama II, Jarama VI, Cueva de los Torrejones, Abrigo de los Enebrales, Cueva del Congosto, and Cueva de las Figuras.

The karst deposit of El Calvero de la Higuera, better known by the name of the village where it is located, Pinilla del Valle (Madrid), is developed on Cretaceous dolostones (Figure 7) of Conian-Santonian age in the Lozoya graben (Guadarrama Mountain Range). It is a, redeposited accumulation of bone remains, dated between 150,000 and 250,000 years old, at the end...
of the Middle Pleistocene (Alférez et al., 1982). It was occupied by hyenas and also includes sporadic human activity near the entrance area of an old cave currently dismantled –known as Camino sector- (Figure 8) which is part of the surrounding exokarst.

The fauna recovered consists of insectivores, chiropters, rodents, primates, mustelids, canids, felids, hyenids, ursids, cervids, bovids, suids, echids and rhynocerids remains. Outstanding within its record is the presence of a few human remains, including two molars of Homo heidelbergensis. The fact that these fossil accumulations are related to hyenas’ activities, and that from humans, points to a change in the use of the caves between these two groups of vertebrates, as it has been proven in several deposits. Two newly discovered sites in this area (Abrigo de Navalmillolo and Cueva de la Pinta) dated as late Middle Pleistocene-Late Pleistocene, have provided evidence of human activity such as combustion structures, fauna remains, and lithic industry, as well as human remains.

Abrigo del Jarama VI is a karstic deposit located in Valdesotos (Guadalajara), developed on Santonian-Campanian (Upper Cretaceous) dolostones and limestones (Figure 9). It has evidence for human occupation dated by 14C between 33,000 and 30,000 years old, placing it in the Late Pleistocene. Its biggest inter-

Figure 6, above. Chamber of the Amutxate cave deposit. The accumulation of skulls is found in the middle.

Below. Cave-bear skull accumulation in the big chamber of Amutxate cave (photos by Satorrak Speleological Group).
Figure 7, above. Pinilla del Valle: general view of the Lozoya Valley, indicating the location of the deposit (photo by E. Baquedano).

Figure 8. Pinilla del Valle: view of the N section of the Camino Sector deposit (photo by B. Márquez).

Figure 9, below. Jarama VI: location of the rocky shelter on the left side of the Jarama canyon (photo by J.F. Jordá).
est lies on the abundant remains of human activity of Neanderthals in very recent times and in an area with very scarce evidence of this species. The deposit is organized in several levels (Figure 10), where the Neanderthal populations carried out their technological and survival activities (Middle Paleolithic or Musterian), leaving plenty of vertebrate remains, as well as those generated by other accumulating agents (birds). The recovered fauna includes 6 macromammal taxaons, 9 micromammals, 10 birds, 1 reptile and 2 amphibians. In addition, a phalanx of Homo sp. was also recovered. The human occupation levels correspond to cold weather stages separated by a deposit caused by a great paleoflood of the Jarama river (Jordá Pardo, 2007).

The Iberian Mountain Range and the Coastal Catalonian Mountain Range display a great development of Mesozoic carbonate sediments, which in some cases and due to karst processes, create caves with excellent Pleistocene paleontological records. Among the remarkable caves and outdoor sites with Pleistocene paleontological records in both ranges the following are worth mentioning:

**Burgos:** Karst complex of Sierra de Atapuerca, La Mina, La Ermita and Cueva Millán.

**Soria:** Torralba and Ambrona, Cueva del Polvorista.

**La Rioja:** Peña Miel.

**Guadalajara:** Los Casares, La Hoz.

**Cuenca:** Verdelpino and Buendía.

**Teruel:** Eudoviges and Los Toros.

**Valencia:** Bolomor, Mallaetes, Parpalló and Volcán del Faro.

**Castellón:** Cova dels Blaus, Fuente San Luis and Matutano.

**Cataluña:** El Filador, Sant Gregori, Abric Romani and Abric Agut.

Broadly speaking, apart from the exceptional site of Atapuerca, all these deposits include mostly bones and technological accumulations created by men in the Middle Paleolithic (Homo neanderthalensis) and in the Upper Paleolithic (Homo sapiens), and to a lesser extent generated by other species of birds and mammals.

The karstic caves in Sierra de Atapuerca (Burgos) (Figure 11) have provided a paleontological and paleoanthropological record unique worldwide for the quantity and quality of recovered fossil vertebrate remains, including those from three species of the genus Homo: H. antecessor, H. heidelbergensis, and H. sapiens (Bermúdez de Castro et al., 1999; Arsuaga, 2003). The main caves providing fossil remains are Gran Dolina, Galería, Sima del Elefante in Trinchera del Ferrocarril, and Sima de los Huesos in Cueva Mayor.

The deposit of Gran Dolina corresponds to the filling of a sinkhole open to the outside, with a bone accumulation originated by humans whose approximate age is of 800,000 years, it is formed by a list of taxaons including insectivores, chiropters, rodents, mustelids, canids, felids, ursids, cervids, bovids, suids, echids, rhynocerids and proboscids. In the level TD6 (Aurora Bed) stands out the presence of a large collection of human fossils (Figure 12) which has enabled the definition of the species Homo antecessor, the oldest direct evidence of men in the Iberian Peninsula, and the last common ancestor of the lines leading to the H. sapiens and H. neanderthalensis. This fact,
worldwide relevant to know human evolution, adds to another discovery of great relevance: human remains consumed by other humans (cannibalism). The long and extraordinary stratigraphical record of this deposit has allowed the paleoclimate reconstruction for the Middle Pleistocene (Hoyos and Aguirre, 1995).

Sima de los Huesos holds the biggest fossil accumulation of *Homo heidelbergensis* of the whole world record, and includes 14 skulls and 28 individuals identified so far, which additionally represent a great variety of growth stages, to which it should be added a unique biface, a man made lithic piece (Arsuaga, 2003). It also contains an important accumulation of ursid remains, such as *Ursus deningeri*, ancestor of the cave bear, together with other species of fossil vertebrates. It is an endokarstic deposit with redeposited remains which might have been a natural trap, or it may have received intentional anthropic contributions of human bodies. Its age is comprised between 200,000 to 300,000 BP.

Excavated at the beginning of the XX century by Marqués de Cerralbo (Figure 13), the paleontological deposit of *Torralba*, located in Loma de Saúco (Torralba, Medinaceli, Soria), near the margin of the Iberian Mountain Range, is of late Middle Pleistocene age, slightly more modern than the deposit of *Ambrona* (Miño de Medinaceli, Soria) of early Middle Pleistocene age. The quality of their paleontological record, with abundant well preserved remains of elephants (Figure 14), the presence of evidence for human activity, the geomorphologic features of the Conquezuela polje where
they are found, and their geographical location along a transit area between two big river basins (Duero and Ebro), give a great relevance to these deposits (Aguirre, 1989).

With regard to their origin, recent investigations reject human intervention in the origin of these deposits, even if both of them include late Achelian lithic artifacts and intentional marks on bones attributed to human groups. There are no evidences of organized hunting, and it all seems to point out to the remarkable similarities between the bone accumulations of Torralba and Ambrona to the present models of accumulation of elephant and bovid remains in areas of the south of Africa with pools and small lagoons used during long draught periods.

The existence of big thicknesses of karstified carbonate rocks (limestones, dolostones and marbles) is common in the Betic Mountain Ranges. Some of the cavities hold important Pleistocene paleontological records, mainly generated by human activity. The main deposits are:

- **Málaga:** Bajondillo, Boquete de Zafarraya, Complex of Humo, La Araña, Hoyo de la Mina, Tajo de Jorox, La Pileta, and Cueva de Nerja.

- **Granada:** Cueva del Agua, Cueva de Horá, and La Carihuela.

- **Almería:** Cueva de Ambrosio.

- **Murcia:** Cueva Victoria.

- **Alicante:** El Salt, Cova Beneito, Cova Foradada, Cova de les Cendres, Tossal de la Roca, Coves de Santa Maira, and Ratlla del Bubo.

- **Valencia:** Bolomor, Cova Negra, Cova de la Pechina, Parpilloló, and Malladetes.

**Cova Negra** (Figure 15) is located at the base of the El Paller mount (Xátiva, Valencia), in Campanian (Upper Cretaceous) limestones, and contains a thick Upper Pleistocene sedimentary sequence. It is an anthropic deposit located at the entrance of a big rocky shelter, with Musterian (Neanderthal) human occupation (Middle Paleolithic) which has provided abundant remains of insectivores, rodents, primates, canids, felids, hyenids, ursids, bovids and echids (Vilaverde, 2001).

Here, the presence of *Homo neanderthalensis* stands out, represented by abundant fragments of at least eight individuals (five children, a teenager, a young adult and an aged adult). Together with the Asturian cave of El Sidrón, this is one of the biggest amounts of Neanderthal remains in the Iberian Peninsula.

**Cueva de Nerja** is located on the edge of the Almijara massif (Figure 16), Alpujárride Complex of the Betic Mountain Ranges (Málaga), and is developed on Triassic dolomitic marbles. The deposit, which partially fills the area of the old entrance (chambers of La Torca, La Mina and El Vestibulo), has a chronology between 30,000 and 4,500 years, comprising the lat-
est Pleistocene and most of the Holocene. It displays
important evidence of human activity all along its
record, as well as abundant remains of plants and ani-
mals. These paleobiological remains include thirty vege-
table taxa from conifers and angiosperms, almost
a hundred species of abundant marine and continen-
tal invertebrate classes (Gastropoda, Scaphopoda,
Bivalvia, Cephalopoda, Crustacea, Echinoidea) and
more than one hundred vertebrate species of reptiles,
birds and mammals, including marine mammals. The
anthracological remains exceed 13,000 years, while
those from vertebrates are around 30,000 and the
invertebrates reach 200,000 years. The presence of
remains from Homo sapiens in different chronological
moments of the record is of relevance (Aura et al.,
2002; Jordá Pardo et al., 2003).

Cueva de Nerja, apart from the fact that man is the
main accumulating agent, can be considered as the
cave with the most important Upper Pleistocene-
Holocene fossil record (paleobotanical, paleontologi-
cal, paleoanthropological and archeological) in the
western Mediterranean. It is represented by a long
stratigraphic sequence including the Pleistocene-
Holocene boundary (Figure 17). In addition, it is one
of the best examples of Spanish karst geomorphology,
with stalagmite features and size development unique
in the world.

The Tajo and Guadiana river Basins are depres-
sions on the Iberian Massif filled by Cenozoic sedi-
ments. The Sierra de Altomira divides the Tajo in three
subbasins: Madrid basin, Intermediate depression
or Loranca basin, and La Mancha plain, which con-
nects to the Guadiana basin through the subbasin of
Campo de Calatrava.

The Pleistocene fluvial terrace systems developed
by the Manzanares, Jarama, Henares and Tajo rivers
stand out in the Madrid Basin, with abundant pale-
ontological and archeological deposits whose chro-
nologies cover almost all the Pleistocene (Baena et
al., 2002). The main deposits were found at gravel
and sand extraction activities, particularly at Áridos,
Arriaga, Orcasitas, San Isidro, Transfesa, Las Delicias,
El Sotillo, La Gavia, Perales del Río and Vaciamadrid.
Several Pliocene vertebrate deposits should also be
mentioned in Campo de Calatrava subbasin (Pozo de
Valverde, Cantera de Valverde, Finca Galiana and El
Jaralejo). In particular, Las Higueruelas (Alcolea de
Calatrava, Ciudad Real) stands out due to the quality
of its record and abundance of mastodont remains
(Mazo, 1999).

The Áridos deposit (Arganda, Madrid) is remarkable
for its record, as well as for the monography compil-
ing its study (Santonja et al., 1980), which meant
the beginning of a new period in the investigations
about Spanish Pleistocene deposits. This deposit is
found on the left bank of the Jarama river, on the
+15/20 m terrace (Pérez-González, 1980), and the
research has individualized two locations: Áridos I
and Áridos II.
Áridos I is an anthropic accumulation corresponding to a butchering area of big mammals (Figure 18) and to a temporary camping site developed on fine flood plain sediments. The mammal fauna includes remains of insectivores, chiropters, rodents, lagomorphs, canids, cervids, bovids, suids and proboscids. Besides, 20 bird species, 4 reptile, 6 amphibian and 7 fish taxa have been identified.

Áridos II corresponds to a quartering area where remains of *Elephas antiquus* have been recovered (Figure 19). In both locations, human occupation provided middle Achelian lithic artifacts (lower Paleolithic, technology mode 2) with an approximate chronology of 350,000 years, in the middle Pleistocene.

Finally, the Guadix-Baza Basin, a postorogenic Neogene basin located inside the Betic Ranges, displays a good sedimentary Pliocene-Pleistocene record where several vertebrate deposits have been identified in river and lacustrine-paludal environments, as well as in karstic ones. Almost all the lower, middle and upper Pliocene record is represented (Alberdi et al., 1989), and some of these deposits have human remains or show clear evidence of human activity.

Several late Pliocene mammal fossil deposits are known in this area (Fonelas P-1, Huélago-1, Fuente Nueva-1, Barranco de los Conejos, and Orce-2), as well as early Pleistocene (Venta Micena, Fuente Nueva-3, Barranco León-5, Huéscar-1, Barranco de los Zagales, Cortijo de F. Alcón, Cortijo de D. Alfonso, Cortijo de D. Diego, Cortijo de Dª Milagros, and Barranco del Paso), and middle Pleistocene (Cúllar de Baza-1, and Solana del Zamborino).

The importance of the Fonelas P-1 deposits must be highlighted (Figure 20), as it corresponds to the Pliocene-Pleistocene boundary and has been used to cover the information gap there was for big mammals from the end of the Pliocene and the beginning of the Quaternary (Arribas and Garrido, 2004). It is a recently discovered deposit (year 2000) located in the Pocico Ravine (Fonelas, Granada) and originated by the accumulating activity of hyenids. It is found within the flood plain deposits of an abandoned meander and the preservation stage of its remains are excellent (Figure 21). Up to now, 35 vertebrate taxa have been identified, 32 of which are mammals, and with 24 species of big mammals. The faunal association registered in Fonelas P-1 shows a wide range of continental paleobiological diversity, including hyenids, giraffids, canids, bovids and ovibovids. Of particular interest is the diversity in carnivores and artiodactiles, the first record in the Iberian Peninsula and only Spanish record of *Canis etruscus*, the first mention of several species outside Africa, and new species of eight genii of carnivores and artiodactils.
The importance of this deposit, presently under excavation, lies on the information that the remains found (hyenids, giraffids, canids, bovids and ovibovids) can provide about the big Pliocene-Pleistocene mammals. The research on this deposit will have remarkable consequences on the biostratigraphy and paleobiography of the Pliocene-Pleistocene transit in Europe, as well as on the paleoecological configuration of the continental environment.

From all the aforementioned geosites, the relevance of the Spanish Pliocene and Pleistocene vertebrates deposits is characterized by the following aspects:

- The long continuity in the paleontological record shown by the selected deposits, which almost covers the last three million years, and with particular precision for the last two million years.

- The great taxonomical diversity of Pliocene, Plio-Pleistocene and Pleistocene vertebrate associations present in the selected deposits.

Figure 21. Bone remains of elephantids and giraffids excavated in Fonelas P-1 (photo by A. Arribas).

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● The oldest presence of human population in the Iberian Peninsula, whether through direct evidence (human fossils) or indirect (anthropic technological remains and evidence for animal consumption), which shows a continuity all along the record of the different deposits up to modern man.

● The special importance of the contributions made by the study of the selected deposits to the paleoenvironmental, paleoclimatic and paleogeographical knowledge of the upper Pliocene and the Pleistocene of the represented geographical areas.

● The wide geographical and geological distribution of the elements making up this geological framework, since it is developed in three main depositional environments and the vertebrate deposits are found in most of the geological units in Spain.

● The scientific importance of the selected deposits to solve certain problems or to determine new vertebrate species, including the different species of the genus Homo.