Taphonomic approach to Fonelas P-1 site (late Upper Pliocene, Guadix basin, Granada): descriptive taphonomic characters related to hyaenid activity

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The Guadix Basin

Geological general features

The Guadix Basin (Fig. 1) is located in the central sector of the Betic Cordillera and occupies some 4600 km^2 on the contact between the Internal and External Zones. The basin's sedimentary filling has been divided into six genetic units (Fernández *et alii*, 1996a) whose boundary unconformities are related to both tectonic events and eustatic changes (Soria *et alii*, 1998, 1999*)*. The two lower units (Units I and II) are Late Tortonian, corresponding to a stage of marine sedimentation, the third (Unit III) includes sediments deposited during sea retreat from the central sector of the Betic Cordillera at the end of the Tortonian and the three most modern (Units IV, V and VI) cover the Late Turolian to the Late Pleistocene, which was a period of exclusively continental sedimentation in an endorheic (a basin with internal drainage, where no surface drainage reaching the ocean can be detected) basin context (Fernández *et alii*, 1993; Viseras and Fernández, 1994, 1995; Viseras *et alii*, 1998).

This sedimentary stage was interrupted in the Late Pleistocene, when a geomorphological inversion of the basin took place and it was captured in its entirety by the drainage network of the Guadalquivir River, becoming an exorheic domain mainly subjected to erosion (Viseras and Fernández, 1992; Calvache and Viseras, 1997). The Fonelas P-1 large mammals site is dated to 2,000,000 year B.P. (Pla *et alii*, 2008) and forms part of the continental sediments of Unit V (Upper Pliocene).

Palaeogeography and local sedimentary context

Using both the origin of the sediment supply and analysis of sedimentary facies during the continental filling of the basin, two sectors with different depositional characteristics have

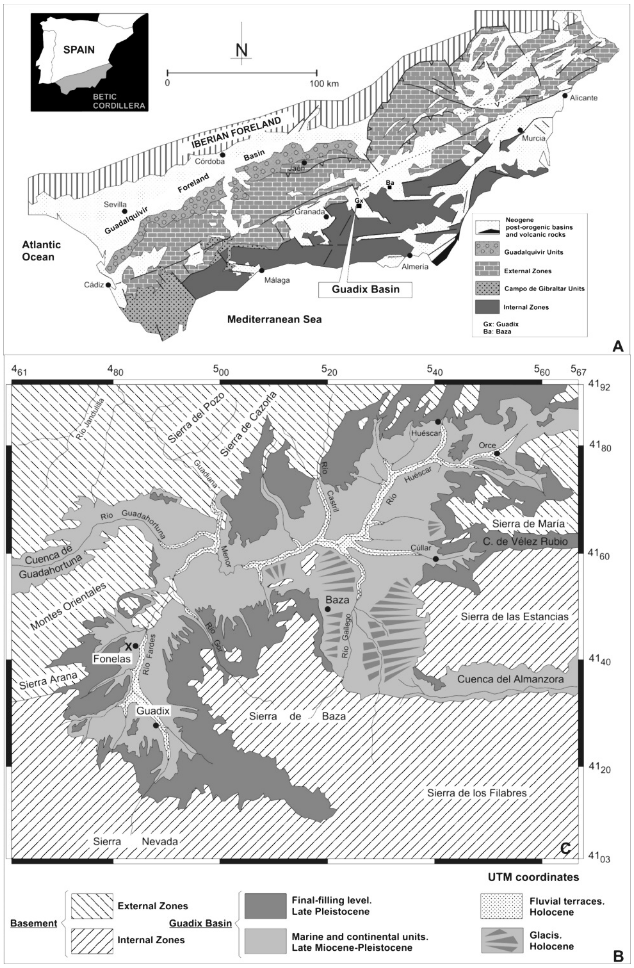

Fig. 1. Geological maps of the Betic Cordillera and Guadix Basin. The location of Fonelas P-1 large mammals site, close to the Fonelas village, is indicated in the lower map (from Viseras *et alli*, 2006).

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been differentiated (Vera, 1970): the eastern sector, mostly occupied by a large shallow lake acting as base level for the whole basin, and the western sector, dominated by alluvial fans and fluvial plains, draining towards the eastern lake (Fig. 2). Three main drainage systems have been distinguished in this western sector, where the Fonelas P-1 site is located.

Lying approximately parallel to the axis of the basin, the Axial System (Fernández *et alii*, 1993; Viseras and Fernández, 1994) is represented by a broad fluvial valley through which the main drainage to the eastern lake took place. In its proximal zone this system connects with alluvial fans lying at the foot of the Sierra Nevada reliefs. The rest of it consists of a flood plain crossed by high sinuosity channels (meandering rivers) and occasionally occupied by shallow ephemeral lakes and palustrine areas (Viseras and Fernández, 1995; Viseras *et alii*, 1998). The Fonelas P-1 site is located palaeogeographically on the flood plain of this Axial System, near the mouth of a channel in one of the shallow lakes (Fig. 2).

The Axial or Longitudinal System was fed transversally by two other drainage systems made up of coalescing alluvial fans and named the Internal and External Transverse Systems (Viseras and Fernández, 1994, 1995), as their source areas were installed on the reliefs of the Internal Zones (Sierra Nevada and Sierra de Baza) to the South, and the External Zones (Sierra Arana, Montes Orientales, Sierra del Pozo and Sierra de Cazorla) to the North (Figs. 1 and 2). In the case of the top of Unit V (Upper Pliocene) and in Unit VI (Lower Pleistocene), the Axial System was located closer to the reliefs of the External Zones. This meant that the fans of the External Transverse System had a short radius (less than 3-4 km) and a wide sweep angle, whereas the fans of the Internal Transverse System had a 10-12 km radius and less sweep angle, coalescing to form a bajada system (Viseras and Fernández, 1992; Calvache and Viseras, 1997).

Progradation of the transverse systems led to local obstruction of axial drainage in the basin, which explains why some sectors of the main valley were temporarily occupied by small shallow lakes. Their shallowness and small size in relation to their alluvial feeder systems affected their ephemeral nature, subjecting them to frequent changes in depth and displacement of coastline (Fernández *et alii*, 1993).

The literature contains numerous examples of vertebrate sites in sediments of the axial system of continental basins with this paleogeographic pattern, such as the Pliocene in the Aswash River basin in Ethiopia (Quade *et alii*, 2004), the Miocene of the Siwalik Group in Pakistan or the Paleogene of the Bighorn Basin in Wyoming (Willis and Behrensmeyer, 1995).

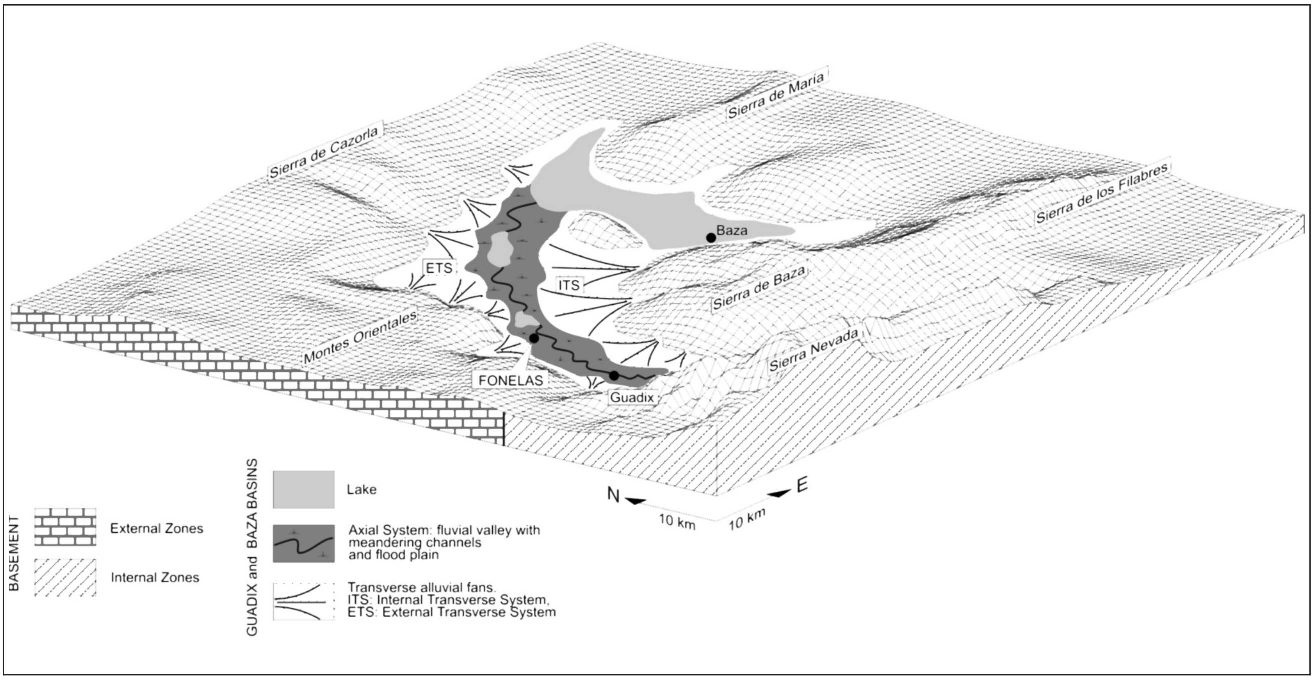

Fig. 2. Palaeogeography of the Guadix Basin during deposition of Units V and VI (Late Pliocene–Late Pleistocene). Notice the location of Fonelas on the Axial System, close both to the External Transverse System and to one of the small ephemeral lakes occupying the axial valley (from Viseras *et alii*, 2006).

The stratigraphic series of Units V and VI at the Fonelas P-1 site is 70 m thick (Fig. 3). There is alternation of detrital and carbonate sediments in fining-upward cycles 2 to 6 m thick. As described in detail in previous studies of this basin (Fernández *et alii*, 1996b; Viseras *et alii*, 1998), this vertical succession of lithofacies with upward decreasing energy characterizes sedimentation of a meandering dominated flood plain (Allen, 1970; Alexander *et alii*, 1994; Dalhoff and Stemmerik, 2000; Heydari and Towsend, 2001; Quade *et alii*, 2004), similar to what occurs in many other examples.

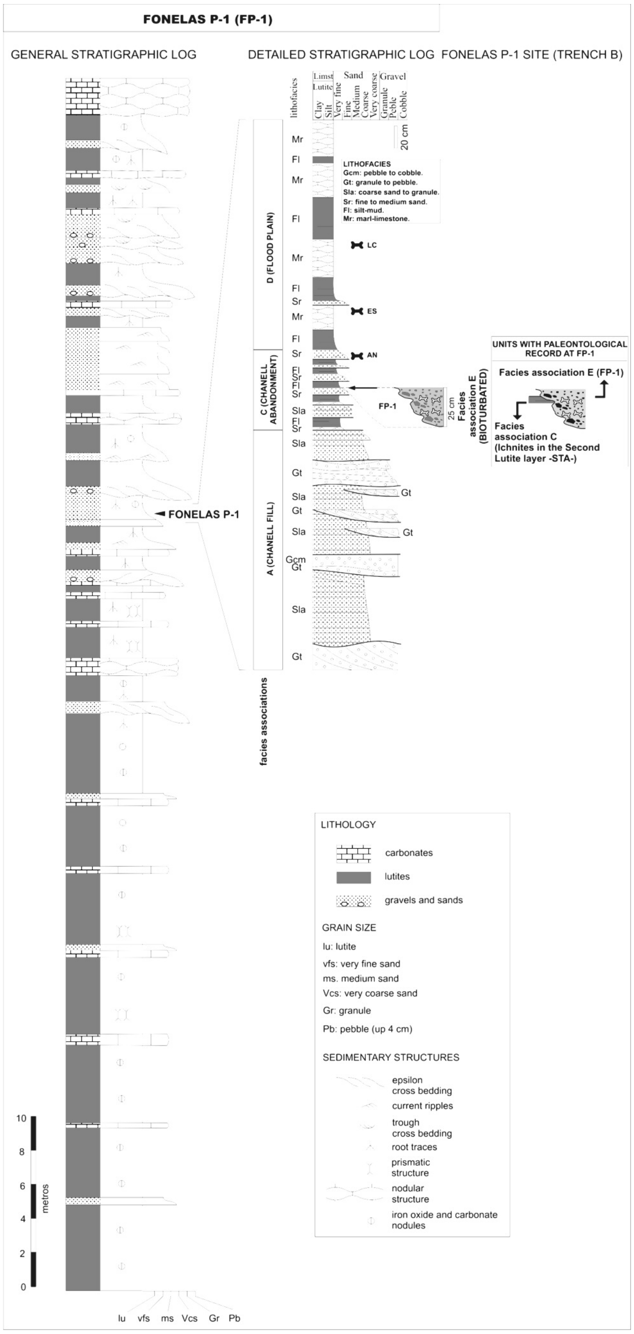

Fig. 3. General stratigraphic log of Units V and VI next to the Fonelas P-1 site (FP-1 is located at the top of Unit V). The column indicates other layers (LC, ES and AN) with a sporadic palaeontological record that are genetically independent of that located in facies E (modified after Viseras *et alii*, 2006).

Fonelas P-1 site

Facies associations related to the Fonelas P-1 site

The Fonelas P-1 site lies on the intermediate part of one of the fining-upward cycles characterizing sedimentation in this sector of the basin (Fig. 3). Palaeontological excavation of the site (Trench B) has identified several sections of different orientation distributed over approximately 30 m^2. It has therefore been possible to draw up several detailed stratigraphic logs lying very close together, establish a direct correlation between them and identify the lithofacies and 3-D geometry of the sedimentary bodies where the accumulation of large mammal fossils is found (Fig. 4).

Five facies associations at the site (A-E) have been described (Viseras *et alii*, 2006), and facies association E contains the bone association (the significance of facies C, D and E are discussed in terms of subenvironments and sedimentary processes).

Facies association C (abandoned channel)

This overlies association A by means of a gradual change (Fig. 4). It consists of alternating layers of sand and lutite from 5 to 25 cm thick and several metres wide, but no bigger than the channel where association A developed. In the sandy layers, grain size is medium and current ripples can be distinguished (lithofacies Sr) indicating flow towards the NNE (Fig. 4) and horizontal lamination (Sh). The lutite intervals present parallel or slightly wavy lamination (lithofacies Fl) with a base adapted to the top of the underlying association A sigmoids and a top tilting less than the bottom, developing a spoon shape in vertical section. Their southeastern part is thicker and base and top are concave upwards. Site excavation has exposed several square metres of the top of one of these lutite layers, showing both current marks indicating northeastwardly flow and ichnites caused by passage of large mammals on a substratum consisting of lutitic mud beneath a shallow layer of water (Fig. 3 and 4). The top of this layer, of which 18 m^2 have been mapped, also shows desiccation cracks at several points.

According to its types of lithofacies and the shapes of the sedimentary bodies they form, facies association C can be interpreted, as in other examples (Kraus and Wells, 1999) as the filling of a channel in a stage of gradual abandonment. During this process, periods of low energy traction flow (development of sandy layers with current ripples) alternated with periods of lack of flow, when fine sediments settled and clay plugs developed that gradually filled and softened the topographical depression of the old channel (Guccione *et alii*, 2001).

Facies association D (flood plain)

This is located in gradual transition above facies association C. It is a series of cycles with two intervals: a lower one of horizontally laminated lutite (lithofacies Fl) and calcium carbonate nodules, occasionally beginning with medium to fine sand with ripples (lithofacies Sr); and an upper interval of nodulous limestone or marly limestone and abundant root traces (lithofacies Mr). These elementary lutite-carbonate cycles recur four times (Figs. 3 and 4) with remarkable (tens of metres) extension. Disperse large mammal fossils are found, although no ichnites can be detected, unlike the case of the lutite layers in facies association C.

Because of the similarity between these sediments and other examples described in the literature (e.g., Guccione *et alii*, 2001; Retallack, 2001; Bridge, 2003), we interpret this facies association as distal flood plain deposits. By comparison with other outcrops in the basin, where this facies association can be traced by direct correlation to the channel whose overflow produced it (Viseras and Fernández, 1995; Viseras *et alii*, 1998), we can estimate a distance of around one hundred metres from the sinuous active channel.

Facies association E (bioturbation)

This occupies the same stratigraphic position as facies association C (abandoned channel) and is separated from it by a highly irregular net surface (Figs. 3-5). Facies association E is a ribbon-shaped body 25 to 40 cm thick and tens of centimetres wide mainly oriented SW-NE. The base has a very irregular morphology, while the top is flat-horizontal. Seen in cross-section, the boundary surface of this body has vertical walls with scalloped morphology (small saw-toothed cavities) tens of centimetres thick (Fig. 4). The

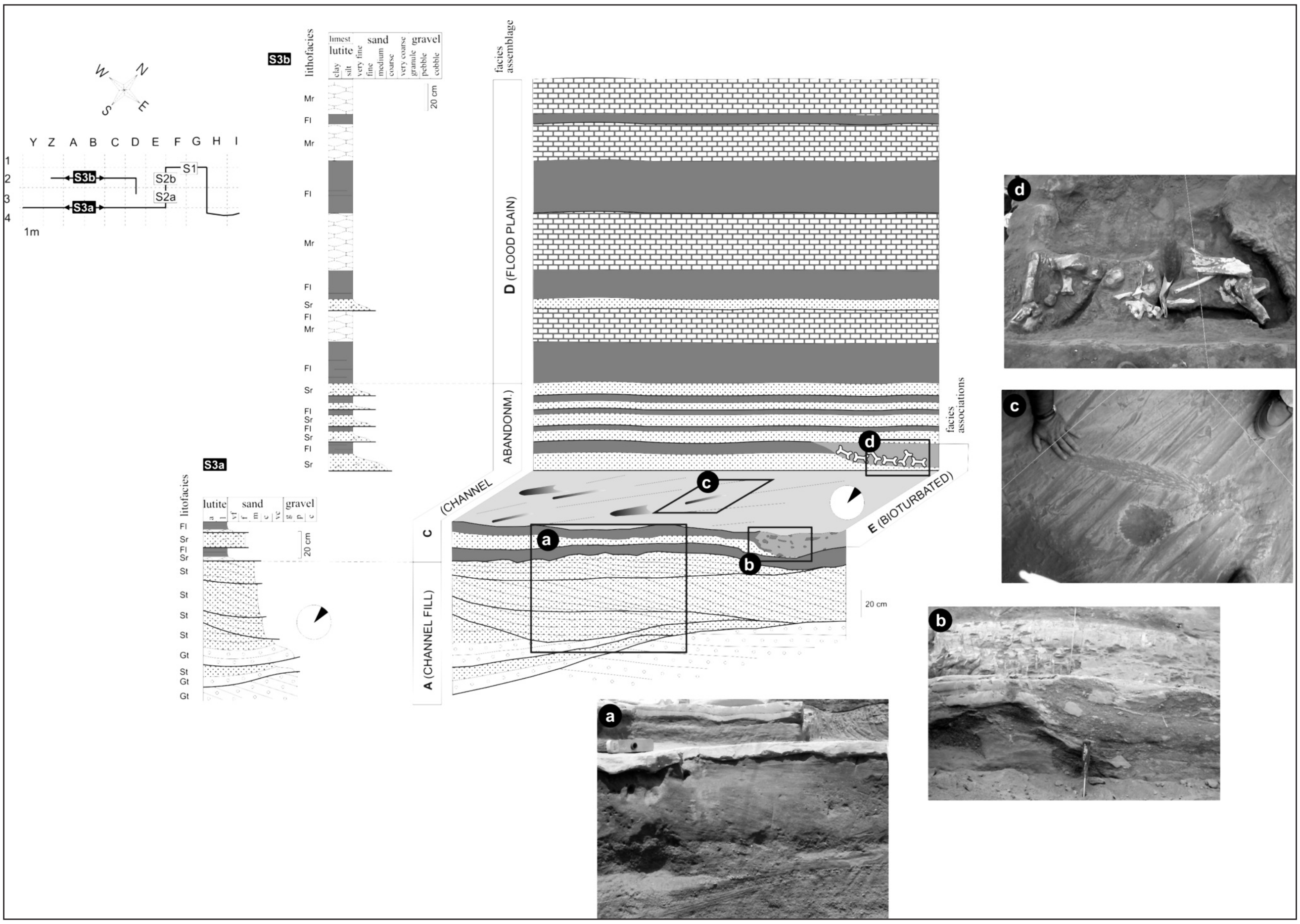

Fig. 4. Detailed stratigraphic logs S_3a and S_3b (see location in the sketch, upper left) and photographs of the facies associations described in the text (from Viseras *et alii*, 2006).

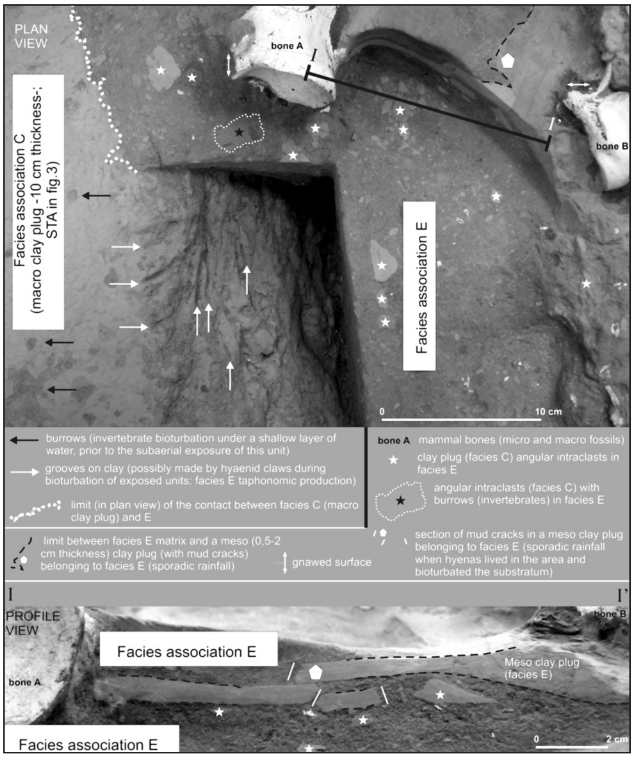

Fig. 5. Spatial relation between facies C (sterile in bones) and facies E, which contains the fossil association at Fonelas P-1 site (Trench B). Sediments of facies E are result of bioturbation (trampling) of the facies C (specially of the macro clay plugs, that contribute intraclasts to facies E). The facies E matrix is composed by a mixture of clay plugs angular intraclasts and sands of medium size grain coming both of them from the facies C. Facies E occasionally presents, in small depressions, meso clay plugs (small water puddles of decimetric extension) that indicate sporadic rains during the occupation of the zone by the hyaenids, during the formation of the site.

most characteristic lithofacies of this body are sub-angular, very irregularly sized fragments of lutite strata from association C held in a matrix of sand, clay and silt (Figs. 4 and 5). It has no internal organization (massive or chaotic structure) and there are some rather narrow levels of sand not more than 3 cm thick with ripples similar to the sandy intervals in facies association C (Sr). It should be pointed out that there is often lateral coincidence between the lutite levels of association C and stratiform lutite fragments in facies association E. The importance of association E is that it contains the large mammal fossil concentration with most elements and highest diversity of species at the Fonelas P-1 site (Trench B; Fig. 6).

We interpret this facies to be the result of animal bioturbation of the sediments of association C (abandoned channel) exposed to weathering and whose original features were completely destroyed by the effects of mammal passage, since we take the site, linked with facies association E, to be a hyena den where these animals were active. The excavating action of these animals' feet on a soft substratum (clay plugs) was the main cause of the massive or chaotic structure of association E (Fig. 5). This interpretation is supported by two main pieces of evidence: 1) the presence of large mammal ichnites in the lutite interval of facies association C, immediately prior to association E and on which the latter lies at several places of the site and 2) the concentration of the most abundant accumulation of bones in the bioturbated lithofacies, as there is a direct relation between this lithofacies and the fossil record (Fig. 6). Similar examples of deformation of soft sediments by passage of large vertebrates have been described in both modern and ancient fluvial and marginal lacustrine flood

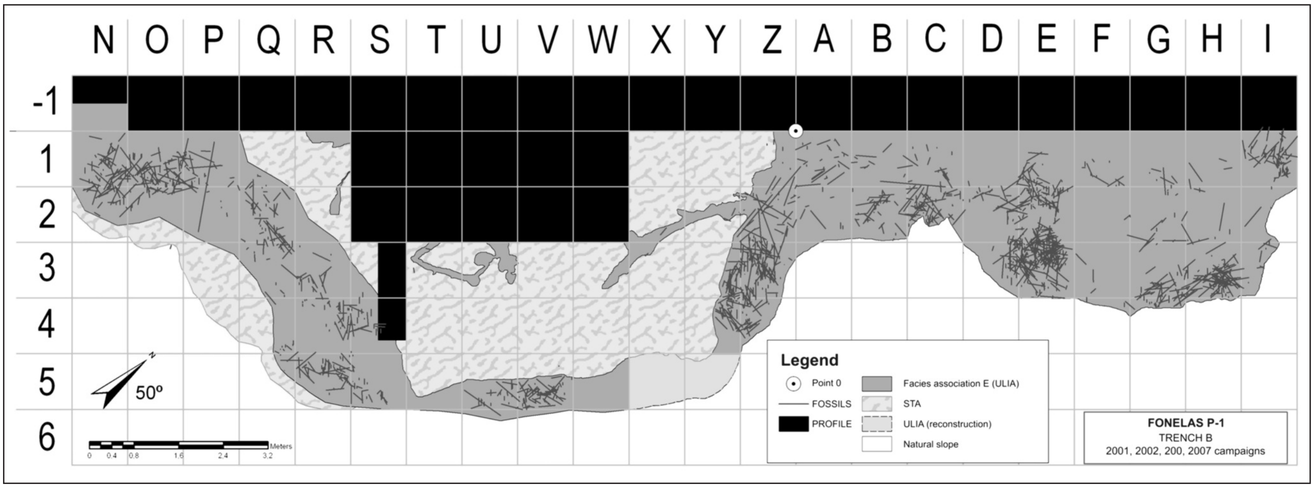

Fig. 6. Excavation grid at the Fonelas P-1 site (Trench B). The fossil-bearing layer (facies E) is not continuous either horizontally or vertically, but wherever it appears it contains a large mammal fossil record. The clay plug or sandy units between which this facies intercalates are void of vertebrate bone remains.

plain environments (Laporte and Behrensmeyer, 1980; Paik *et alii*, 2001).

Sedimentological/taphonomical production of the site

The largest concentrations of bone remains at the Fonelas P-1 site (Trench B) appear in what we have described as facies association E, located in a very specific position in one of the characteristic cycles of the succession in Unit V of this sector of the basin.

The simple lithofacies making up associations A to D, as well as the spatial relation between facies associations were explained in Viseras *et alii* (2006) (Fig. 7). The sedimentological evidence indicates that the area was crossed by a sinuous fluvial channel flowing north-eastwards which at this point made a convex curve towards the East (Fig. 7). The reconstruction of this channel in the area excavated suggests its sinuous nature, as is corroborated by the continuation of the sedimentary body to the North, where, several hundred metres from the site, another curve of the same channel can be reconstructed, in this case convex towards the West.

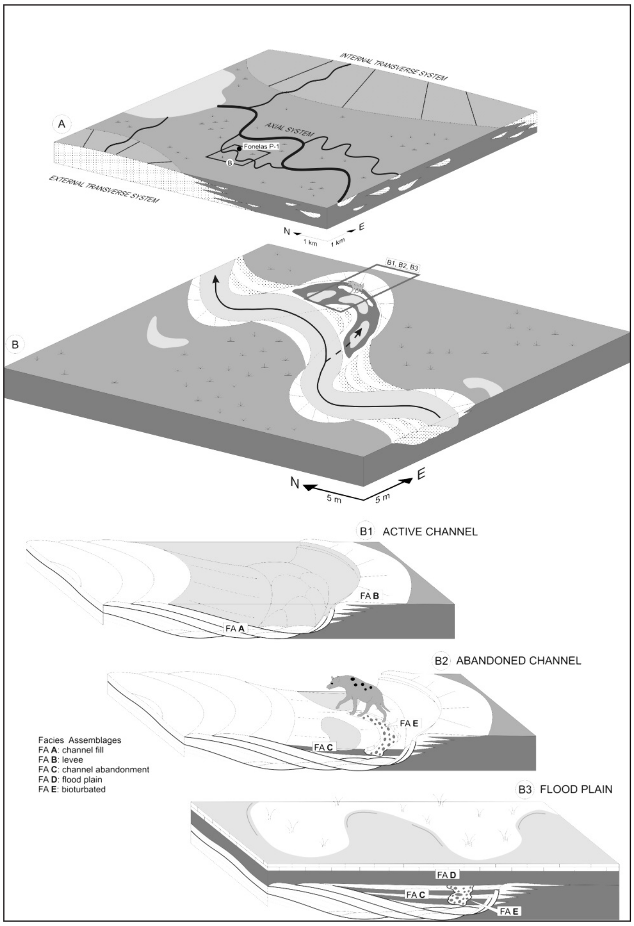

Fig. 7. Reconstruction of the sedimentary environment of the Fonelas P-1 site. A: axial valley with meandering channels (Axial System) between the alluvial fans of the Internal and External Transverse Systems (see palaeogeographic sketch of Fig. 4). B: laterally migrating sinuous channel abandoned in one meander by chute cut-off. This is the place occupied by large mammals. B1, B2 and B3: location of the facies associations throughout three evolutionary stages of the channel, active (B1), abandoned (B2) and establishment of flood plain conditions (B3) (from Viseras *et alii*, 2006).

Unfortunately, neither the base of the channel nor the accretion margin during maximum fluvial activity outcrop sufficiently well for observation. However, the grain size of the sediment and the size of the bars and other bedforms suggest that this was not the main channel of the Axial System, but rather one of the many meandering secondary channels crossing the distal plain of the system and connected to the main channel (Fig. 7). Taking the data available from the outcropping part of this channel and by comparison with other well exposed examples in this sector of the basin (Viseras and Fernández, 1994; Viseras *et alii*, 1998), we can estimate a size for this channel in bankfull state of 6-8 m wide and around 1.5 m deep.

The remarkable facies association E (bioturbated) is clearly unlinked to this evolution of purely fluvial processes (Figs. 3-7). Moreover, it does not appear in the other cycles of the succession. The fact that it is coetaneous with association C (abandoned channel) means we can genetically link the animal bioturbation with the last stages of the channel's evolution. Thus, the slight depression formed by the residual channel in the stage of abandonment (ox-bow lake), occasionally ponded by both rainwater and overflow from the nearby active channel, would have been a relatively protected area, with easy access to water for the animals, probably used by some (carnivorous scavengers) as feeding place and den. This hypothesis of a hyena den is also based on data, which show intensive feeding on bones by scavenging carnivores, as well as the fact that the animals did not die at the site (with the possible exception of *Pachycrocuta brevirostris* cubs). Passage of animals over such a depression with a very soft substratum would have caused a very dense pattern of tracks, creating narrow corridors with an intensely bioturbated bottom, coinciding approximately in orientation with the abandoned channel). After complete filling of this residual channel, the topography would have been homogenized at the level of the flood plain (Fig. 4). This is why the particular location of the site ceased to be a preferential occupation zone for the animals, just at the beginning of the development of facies association D (flood plain). At this point, the main animal occupation must have transferred to another place providing the topographical conditions described above (probably to Fonelas SCC-1 paleontological site, one kilometre to the North; Arribas *et alii*, 2004). The high sedimentation rate in the abandoned channel, resulting from both the local concentration of sediment from rainfall and detrital supply from overflow of the active channel in its new position (about a hundred metres from its previous position), and from chemical precipitation of the flood plain, led to the burial of the fossil accumulations. This genetic context characterizing the site remained outside the erosive influence of fluvial channels, which were displaced tens or hundreds of metres from the abandoned channel. Consequently, the position of this site in the context of the local evolution of an alluvial channel abandoned by avulsion coincides with that of other vertebrate sites described in the literature (Behrensmeyer, 1988; Behrensmeyer *et alii*, 1995; Quade *et alii*, 2004).

The main results of the stratigraphic and sedimentological study are the following (Viseras *et alii*, 2006):

- On the scale of the general palaeogeography of the basin, the Fonelas P-1 site is located on the distal stretch of the axial drainage system of the Guadix Basin, near its connection to a shallow lake, occupying a palaeogeographic situation similar to that of many other vertebrate sites.
- The site is located in a sedimentary cycle typical of a meandering fluvial system. This cycle consists of four facies associations related to fluvial processes: (A) gravel and/or sand in layers with sigmoidal geometry, caused by the lateral accretion natural to the filling of a sinuous channel, (B) sand and lutite in wedge-shaped bodies abutting onto the erosion bank of the channel, interpreted as levee deposits, (C) fine sand and lutite in sigmoidal laminae, gradually overlying the A facies and representing progressive channel abandonment deposits, (D) lutite and carbonate in extensive horizontal layers lying directly on the C facies and recording typical flood plain sedimentation.
- The main accumulation of large mammal fossils (Trench B) is found in a facies genetically independent of those described above, as it is unconnected with purely fluvial processes. This facies (E) consists of very angular fragments of lutite of the C facies (channel abandonment) with no internal organization, held in a matrix of sand, silt and clay (Fig. 5) and is interpreted as the result of bioturbation of a soft substratum by continuous passage of large mammals (carnivorous scavengers, specifically hyaenids) in an occupation space (Figs. 6 and 7).
- The detailed palaeogeographic context inferred for facies E is that of an abandoned meander. This would have described a slight topographic depression that was periodically flooded, either by rainfall or by small overflow from the distant active channel, and occupied by large mammals.
- The type of facies represented by association E has never before been identified and described in continental basin filling. Its sedimentological and palaeobiological importance is due to the fact that these are biogenetic facies characteristic of the biological activity of large scavenging carnivores on fluvial substrata. Whether they present fossil content or not, they are predictive, as they indicate sedimentary interruption, subaerial exposure and biological occupation wherever they may be identified in the geological record. Recognition of this facies association can be used as a sedimentological criterion for prospecting large mammal activity in future palaeontological research (Viseras *et alii*, 2006).

Fossil record at Fonelas P-1 (Trench B)

The Fonelas P-1 site contains a vertebrate fossil assemblage consisting mainly of large mammal fossil remains - as well as small minority of amphibians, reptiles, small mammals and birds - by which it can be dated to the Late Upper Pliocene (in the top of Unit V of the Guadix Basin), near the Pleistocene boundary (Late Villafranchian, ca 2,0 Ma) (Pla *et alii*, 2008).

In four seasons of systematic excavation, almost three thousand bone fragments were recovered. Many are anatomically complete to a high degree (allowing their taxonomic classification), which leads us to consider this as the most important large mammals site from the end of the Pliocene in the entire Iberian Peninsula.

Analysis of first and last appearance data (FAD and LAD) of the species identified to date, and new palaeomagnetic results, corroborates the hypothesis of the time-scale being on the Late Upper Pliocene (2,0 Ma) in zone MNQ18 (Arribas *et alii*, 2008).

The faunal assemblage to date identified at this site consists of 32 species of mammals (Mammalia). Four groups of large mammals have been identified according to their paleobiogeographic origin and the time-scale of their incorporation into the Iberian paleomastocenosis: i) a group of animals typical of the Late Pliocene in Europe, some of which extended from Asia into these ecosystems around 2,6-2,5 Ma; ii) a second mammal association of Asian origin reaching these latitudes during the Late Upper

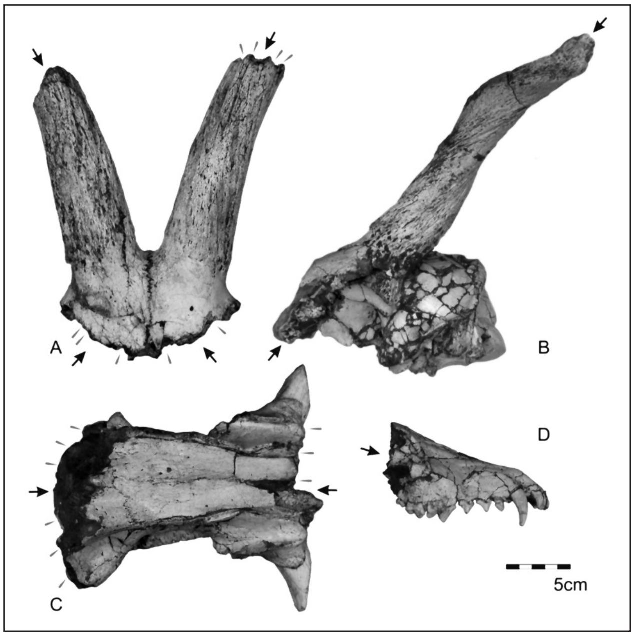

Fig. 8. Hyaenid activity in cranial fragments from Fonelas P-1 (Trench B). A: Neurocranium fragment of *Capra baetica*. B: Neurocranium fragment of *Gazellospira toticornis hispanica*. C: Splacnocranium fragment of *Potamochoerus magnus*. D: Splacnocranium fragment of *Canis etruscus*. Arrows shows the incidence areas for disarticulation and feeding. Black arrows indicate the direction of the activity beginning. Grey arrows the damage produced by hyaenid teeth.

Pliocene; iii) a third group native to Africa which also reached the Iberian Peninsula during the Late Upper Pliocene; iv) a fourth set of endemic taxa (Arribas and Garrido, 2007; Garrido and Arribas, 2008). There is also a fifth group of animals at Fonelas P-1 of uncertain origin (either Asian or African) that reached Atlantic Europe in the same brief interval. Thanks to the quality of the paleontological remains, their extraordinary state of preservation and the abundance of skeletal elements, advanced taxonomic study has led to verification of the presence of new species or subspecies of the genera *Meles*, *Canis*, *Megantereon*, *Gazellospira*, *Croizetoceros,* *Capra* and *Potamochoerus* (see Arribas, 2008).

As this is the only known paleontological record with such a variety of species of such diverse origin, the large mammals assemblage at Fonelas P-1 holds extremely interesting information for the reconstruction of the main migratory routes and the interrelations between African and Eurasian species. In addition, the high scientific interest in this site is due to the fact that, because of the time-scale and combined presence of African and Caucasian species, it is the only site in western Europe similar to the Caucasian site at Dmanisi (Gabunia *et alii*, 2000). Fonelas P-1 is, therefore, the first evidence in Europe to allow definition of the paleoenvironmental framework of the Late Upper Pliocene, when the first humans spread beyond Africa. As such, therefore, attention should be drawn to the enormous similarities between the sedimentary environment of Fonelas P-1 and the recently reconstructed context of the sites of the earliest stone tool makers in the Awash River Basin, Ethiopia.

The provisional assemblage of this site is heterogeneous as regards the palaeobiogeographic significance of the identified taxa and also their biochronological significance. In view of the foregoing, the taxonomic study of Fonelas P-1 will lead to interesting paleontological discov-

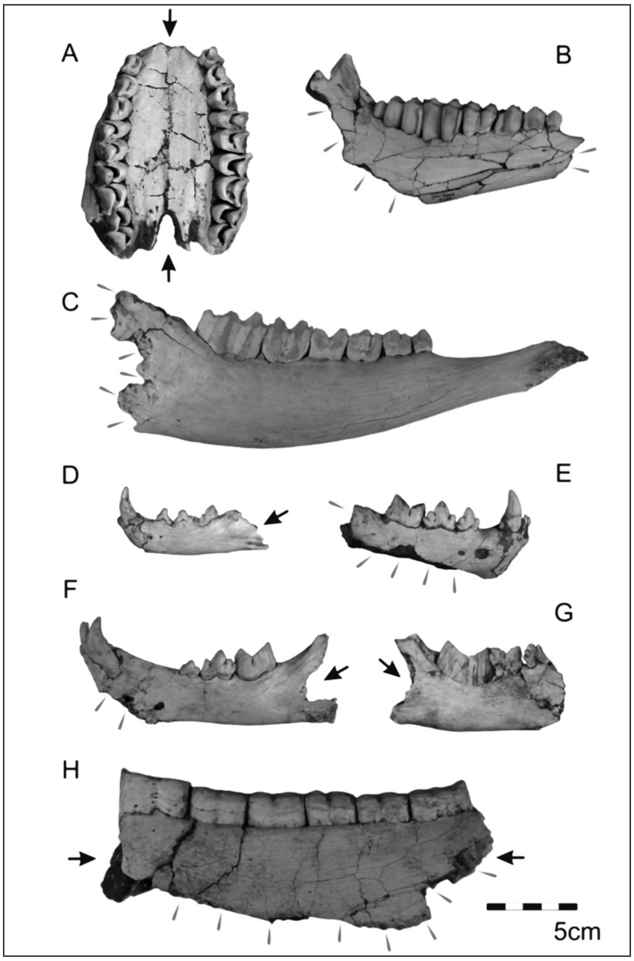

Fig. 9. Hyaenid activity in maxilla and mandibles from Fonelas P-1 (Trench B). A: Maxilla of *Gazellospira torticornis hispanica*. B: Hemimandible fragment of *Gazellospira torticornis hispanica*. C: Hemimandible fragment of *Leptobos etruscus*. D: Hemimandible fragment of *Lynx issiodorensis valdarnensis*. E: Mandible fragment of *Acinonyx pardinensis*. F: Hemimandible fragment of *Megantereon cultridens roderici*. G: Hemimandible fragment of a juvenile *Homotherium latidens*. H: Hemimandible fragment of *Equus* cf. *major*. Arrows shows the incidence areas for disarticulation and feeding. Black arrows indicate the direction of the activity beginning. Grey arrows the damage produced by hyaenid teeth.

eries regarding faunal turnover and distribution in time of different groups across the European Pliocene-Pleistocene boundary.

Out of all the new sites located by our team since 2001 in this area of the Guadix basin (62 locations with large mammal records), the Fonelas P-1 site has proved to be especially rich in number and diversity of large mammal remains. It is significant that most of the taxa identified at this location are represented by both cranial elements (mainly complete crania, half maxillas and half lower jaws) and parts of the postcranial skeleton (bones of the spine and limbs) that in many cases can be identified as belonging to the same individual. Isolated teeth are rare in this record. They represent only 10% of the total sample and often appear either fragmented with traces of gastric dissolution (teeth belonging to grazing animals such as *Equus*, *Gazellospira* or *Leptobos*), or complete, in a site position vertical to the alveolar region of their corresponding crania (belonging to carnivores such as *Canis* and *Hyaena*).

Vertebrate association of Fonelas P-1 (Trench B) (in Arribas *et alii*, 2008).

REPTILIA

Lacertidae gen. indet.
Anguidae gen. indet.
Rhinechis scalaris (Schinz, 1822)
Viperidae gen. indet.

AVES

Aves gen. indet.

MAMMALS (LAGOMORPHA)

Prolagus cf. *calpensis* Major, 1905
** *Oryctolagus* sp.

MAMMALS (INSECTIVORA)

** Erinaceidae gen. indet.

MAMMALS (RODENTIA)

Eliomys sp.
Mimomys sp.
Apodemus cf. *atavus* Heller, 1936
Castillomys sp. gr. *C. crusafonti* Michaux, 1969-*C. rivas* Martín Suárez y Mein, 1991
Stephanomys sp.

MAMMALS (CARNIVORA)

* *Meles iberica* Arribas y Garrido, 2007
Vulpes alopecoides (Forsyth-Major, 1877)
* *Canis accitanus* Garrido y Arribas, 2008
Canis etruscus Forsyth-Major, 1877
Canis cf. *falconeri* Forsyth-Major, 1877
Pachycrocuta brevirostris (Aymard, 1846)
Hyaena brunnea Thunberg, 1820
Lynx issiodorensis valdarnensis Werdelin, 1981
Acinonyx pardinensis (Croizet y Jobert, 1828)
* *Megantereon cultridens roderici* Arribas y Garrido, 2008
Homotherium latidens (Owen, 1846)

MAMMALS (ARTIODACTYLA)

* *Potamochoerus magnus* Arribas y Garrido, 2008
* *Croizetoceros ramosus fonelensis* Garrido, 2008
Metacervoceros rhenanus philisi (Schaub, 1941)
Eucladoceros sp.
** *Mitilanotherium* sp.
* *Gazellospira torticornis hispanica* Garrido, 2008
* *Capra baetica* Arribas y Garrido, 2008
** *Praeovibos* sp.
Leptobos etruscus (Falconer, 1868)

MAMMALS (PERISSODACTYLA)

Equus cf. *major* Depéret, 1893
Stephanorhinus etruscus (Falconer, 1859)

MAMMALS (PROBOSCIDEA)

Mammuthus meridionalis (Nesti, 1825)

(*) singular taxa at Fonelas P-1.
(**) in study.

Other taxa (unpublished):
Eurotestudo sp. (fossils).
Hystrix sp. (taphonomical evidence: toothmarks).
Hominini gen. indet. (taphonomical evidence: cutmarks)

Advance on the taphonomy

Methodology

The fossil-bearing layer (average thickness 20 cm to a maximum of 40 cm) was excavated in 2001, 2002, 2004 and 2007. Systematic paleontological excavation followed the classic methodology for analysis of this type of sites, using a grid of 1m^2 squares (Fig. 6). The field data recorded for each fossil element were: date, sounding, surface/depth, symbol, size in millimetres (length, width and depth), marks [abrasion/polished, weathering stage (0-1, 2-3, 4-5), roots, dissolution, insects], breakage (longitudinal, spiral, fossil diagenetic), trace [rodents (micro, macro), carnivores (canids, felids, hyaenids)], hominids (chop-marks, cut-marks, etc), trampling marks, colour, colour congruence/sediment, anatomical element (tooth, bone, splinter; bone name; complete, proximal, shaft, distal), side (left, right), taxa (48 possibilities), age (infant, young, adult, senile), joint, association, sedimentary filling, filling congruence, cartography (direction, slope, X, Y, Z), remarks and photograph. This set of field variables were verified in the laboratory and, once the fossils were restored and consolidated, completed by descriptive and

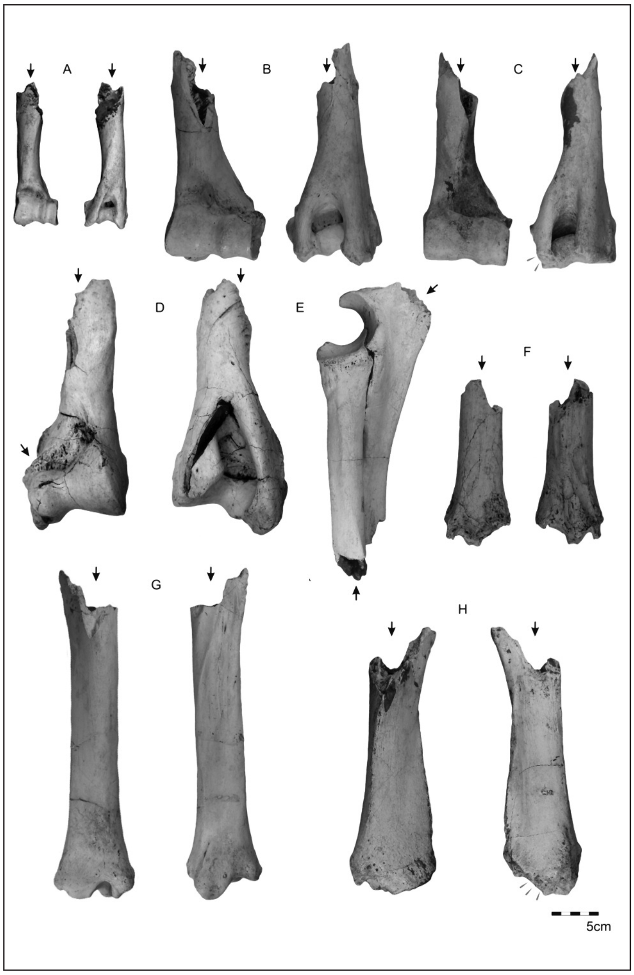

Fig. 10. Hyaenid activity in postcranial bones from Fonelas P-1 (Trench B). A: Letf humerus fragment of *Gazellospira torticornis hispanica*. B: Letf humerus fragment of *Leptobos etruscus*. C: Letf humerus fragment of *Equus* cf. *major*. D: Right humerus fragment of *Stephanorhinus etruscus*. E: Right radio-ulna fragment of *Stephanorhinus etruscus*. F: Left tibia fragment of *Leptobos etruscus*. G: Right tibia fragment of *Equus* cf. *major*. H: Left tibia fragment of *Stephanorhinus etruscus*. Arrows shows the incidence areas for disarticulation and feeding. Black arrows indicate the direction of the activity beginning. Grey arrows the damage produced by hyaenid teeth.

metric characterization of taxonomic and taphonomic features.

The taxonomic study (Garrido, 2006; Arribas, 2008) was carried out using classic paleontological methods, based on direct observation and morphological comparison with other fossil or present-day records, including metrical analysis to bear out or reject the results obtained by the anatomical study of the taxon to be classified. Biometrical results in no case prevail over anatomical results in taxonomic identification. The procedures used in this study do not therefore differ substantially from those generally used by specialists in large mammal palaeontology. Biometrical data were acquired in the same way for all groups, using a Sylvac RS 232 digital gauge with 0.01 mm precision. The dental study was carried out using criteria generally used by specialists in the group in question. For most groups the postcranial skeleton was examined following Driesch (1976).

Biostratinomic advance

Taphonomic analysis is still in progress, following criteria and emphasizing variables applied in research on other Pliocene-Pleistocene sites (Arribas, 1999; Arribas and Palmqvist, 1998, 2001; Palmqvist and Arribas, 2001). The methodology has been widened, mainly as regards descriptive variables and their links with sedimentological aspects of our own research project. However, it is still too early to make very precise palaeoecological interpretations, as the samples recovered from Fonelas P-1, although significant, are not yet sufficient in either number of remains or minimum number of individuals (Arribas and Palmqvist, 1998; Palmqvist *et alii*, 2003). The approximately 30 m^2 excavated in 2001 and 2002, yielding 2000 fossils, 84% of which are anatomically and taxonomically identifiable elements while the other 16% are indeterminate fragments, are only a small part of the minimum extension of the site (800 m^2). Future campaigns are therefore expected to broaden the spectrum of taxonomic diversity, possibly to include *Hystrix*, *Macaca*, *Theropithecus* and *Hippopotamus*, among others. We calculate that palaeoecological research can begin after three more campaigns of systematic excavation.

Taphonomic interpretation of the site is premature, as the sample is still insufficient. However, the data obtained during the 2001 and 2002 campaigns (NISP 1375) allow us to hypothesize that this is an accumulated association (accumulated taphonomic stage) with a very short period of subaerial exposure before burial, in which scavenging carnivore activity was essential during the biostratinomic stage (secondary association collected by scavengers).

As can be deduced from the integration of the provisional values of the descriptive taphonomic variables (Table 1; Figs. 8-11), we can discard predators, as well as physical agents, as concentrators of the bone association, excluding therefore the possibility of a primary association collected by the former. Thus, we postulate that the site is the result of the occupation of this particular section of the territory by a hyaenid clan, probably belonging to *Pachycrocuta brevirostris*, as it is the only eudemic hyaenid in the assemblage (deciduous dentition record; Fig. 11). The site could have been a feeding area or den where the hyenas collected and modified (Figs. 8-10) numerous skeletal remains of the animals they scavenged.

The feeding habits of this extinct hyaenid are well known in the fossil record and their presence and taphonomic identification (see Arribas, 1999) are constant across the Pliocene-Pleistocene boundary and during the beginning of the European Pleistocene.

The provisional values of the taphonomic and stratigraphic variables in the Fonelas P-1 sample differ clearly from the characteristic of other sites in this and other conti-

ASSEMBLAGE DATA (2001-2002)	**NISP (taxonomic identification) (1375)**	Carnivora NISP		9.0 % (1)
		Artiodactyla NISP		40.0 %
		Perissodactyla NISP		13.0 %
		Proboscidea NISP		1.0 %
		Other groups NISP		11.0 %
		Uncertain specimens		26.0 %
	Body weight range	< 0.2 - > 3000 Kg (1,2)		
	Number of species (35)	Micromammal species (rodents in disgregated coprolites)		8
		Macromammal species		24 (1,2)
	Macromammal MNI (84)	Carnivora MNI		23.0 % (1)
		Artiodactyla MNI		58.0 % (*Gazellospira* 30 %)
		Perissodactyla MNI		17.0%
		Proboscidea MNI		2.0 %
	Carnivore/ungulate index [f(MNI)]	29.2 % (1)		
	Macromammal age spectrum	Infant	26.0 % (1) [(Hyaenidae, *Pachycrocuta* 2.4%) (*Gazellospira* 9.5 %)]	
		Juvenile	5.0 % (1)	
		Adult	68.0 % (*Gazellospira* 20.2 %)	
		Senile	1.0 %	
	Bone articulation	4.0 % (1)		
	Grouping	20.0 %		
	Sedimentary infilling	5.0 % (3) (only in broken bones; periosteum sheath present at burial)		
	Sedimentary infilling/ matrix congruence	100.0 %		
	Reworked bones	0.0 %		
	Skeletal parts	Bone size range	1.1-58.3cm (2)	
		Deer antlers	0.3 %	
BONE MODIFICATION DATA (2001-2002)	**Bone completeness**	Bone (1) (including craneal elements) (73.0 %)	Complete (limb+girdle bones)	40.0 %
			Fragment (limb+girdle bones)	60.0 %
			· Proximal epiphyses	39.0 %
			· Shaft	22.0 %
			· Distal epiphyses	39.0 %
		Isolated teeth		10.0 %
		Splinter (spiral and/or longitudinal fractures)		17.0 % (1)
	Marks	Abrasion/ polished		0.0 % (2)
		Weathering stage · 0-1		94.1 % (3)
		· 2-3		5.2 %
		· 4-5		0.6 %
		Fossil root marks		0.0 % (3)
		Modern root marks (fossils associated with the natural slope)		20.0 %
		Digestive corrosion		5.0 % (1)
		Fossil insects		0.6 %
		Modern insects		0.1 %
	Biostratinomic breakage	Longitudinal		14.0 % (1)
		Type II Spiral		26.0 % (1)
	Fossildiagenetic breakage	Ortogonal (manifold features)		57.0 %
	Traces	Gnawing marks (tooth marks) · Micro rodents		0.0 %
		· Macro rodents		0.0 %
		· Canids		0.0 %
		· Felids		0.1 %
		· Hyaenids		37.0 % (1)
		Cut marks (homimids)		0.0 %
		Trampling marks [f(matrix composition)]		0.4 %
QUARRY DATA (2001-2002)	**Size of accumulation**	ca. 800 m^2		
	Excavated surface	ca. 43 m^2		
	Fertile surface (facies association E) (ca. 25 m^2)	Mean thickness	20 cm	
		Density	ca. 70/m^2	
		Orientation	40% with preferred orientation	
		Dip	Assemblage average	Sub-horizontal; 8° (2)
			Isolated bones average	Horizontal; 3° (2)
			Grouping bones average	Sub-horizontal; 15° (2)
			Patchiness	Highly patchy
	Lithology and other stratigraphical aspects in the text			

Table 1. Summary of the provisional taphonomic data of the Fonelas P-1 site (Trench B; samples from 2001 and 2002 campaigns). Overall analysis of the variables suggests that the site represents a secondary association, collected by scavengers, with very rapid burial of the bone remains. (NISP: number of identifiable specimens; MNI: minimal number of individuals) (1: Secondary association, collected by scavengers, 2: No hydraulic sorting, 3: Very short period of subaerial exposure before burial). Note: some fossil bones from the excavations of 2004 and 2007 shows tooth marks of porcupines, and other cut marks.

nental basins, where the principal cause of site genesis is geological (concentration, selection and burial of bone remains by water currents in circum-lake environments, e.g., Huélago, Huéscar-1 and Cúllar de Baza-1; Alberdi *et alii*, 2001). However, the taphonomic features of the Fonelas P-1 sample are similar to the specific attributes of the feeding area or hyena den characteristic of *Pachycrocuta brevirostris*. The taphonomic research in progress will verify this hypothesis and evaluate the existing paleontological bias and its significance.

As presented, taphonomic interpretation of vertebrate fossil sites needs an exhaustive stratigraphical and sedimentological characterization of the fossiliferous and lower and upper units.

The definition of the different facies associations and its integrated interpretation, are basic for the taphonomic analysis. This allows to set out a previous genetic model which should be compatible with the taphonomic interpretation derived from the quantitative and qualitative study of the fossiliferous association. Consequently, the interpretation of the fossil record would be contextualized correctly and as a result of the progressive analysis, the uncertainty would fall and the resolution capacity of the definitive genetic model would increase.

Fonelas P-1, an exceptional site due to its stratigraphical and paleontological characteristics (in a macro, meso and micro scale), will offer a definitive taphonomic model when the fossil number increases the sample in about a thousand of them and it had enough plans and stratigraphic profiles (macro, meso and micro) with highly decisive information about the place of the fluvial plane which the hyaenids occuped for a brief period of time (geological time).

Scientific nuances of the physical configuration of this specific part of a continental basin (800 m^2 aprox.) and the biological use represented by a fossiliferous unit of 20 cm thick (Fonelas P-1, Trench B), are essential for a correct taphonomic interpretation of the fossil record. This studied unit is part of a continental landfill of more than 120 m thick, with a geological record of 2,9 Ma (3,5-0,6 Ma) at least.

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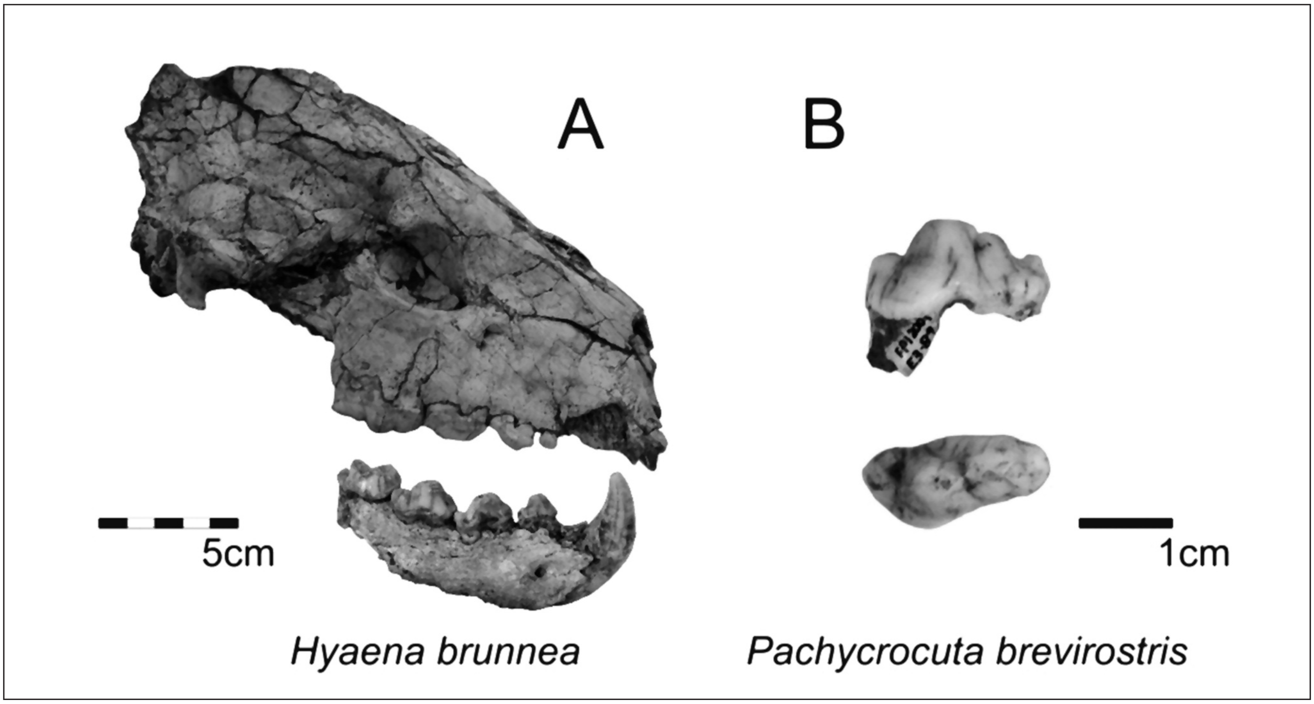

Fig. 11. Scavenger agents located at Fonelas P-1 site (Trench B). A: Skull and hemimandible of *Hyaena brunnea*. B: Decidual tooth (left DP_3) of *Pachycrocuta brevirostris*.

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