



## Biochronological, taphonomical, and paleoenvironmental background of the fossil great ape *Pierolapithecus catalaunicus* (Primates, Hominidae)

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### ABSTRACT

The Late Aragonian (late middle Miocene) stratigraphic sequence of Abocador de Can Mata (ACM) from Els Hostalets de Pierola (Vallès-Penedès Basin, Catalonia, Spain), rich in fossil vertebrate localities, provides a unique opportunity to study the evolution of western Eurasian hominoids. Among these sites, Barranc de Can Vila 1 (BCV1) recently delivered a well-preserved hominoid partial skeleton of a new genus and species, *Pierolapithecus catalaunicus*. On the basis of the small-mammal fauna recovered at BCV1, we infer an early MN 7+8 age, between 12.5 and 12 Ma, for this site. The spatial distribution of macromammal fossils, the relative abundances of skeletal elements, and their state of preservation suggest that different agents were involved in the accumulation of the *P. catalaunicus* individual and the remaining taxa. Carnivore marks occur on some bones of the *P. catalaunicus* skeleton, documenting the action of predators and/or scavengers in this case. In contrast, carnivore marks are extremely rare on other macromammal remains, which seem to be derived from adjacent alluvial-fan plain areas. The small-mammal fauna from BCV1 and the large-mammal fauna from the ACM series, indicate the presence of considerably humid and warm forest environments. The compositions of the small-mammal fauna from BCV1 and from other Late Aragonian sites from the Vallès-Penedès area are similar to those from France and central Europe. The former are clearly distinct from those of Iberian inner basins, where the environment appears to have been drier, thus precluding the dispersal of hominoids into that area.

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### Introduction

This paper concerns the chronological and paleoenvironmental background of the recently discovered *Pierolapithecus catalaunicus* partial skeleton from the Late Aragonian (middle Miocene) locality of Barranc de Can Vila 1 (BCV1) near Els Hostalets de Pierola (Catalonia, Spain) (Moyà-Solà et al., 2004). The postcranial morphology demonstrates that *Pierolapithecus* is a crown hominoid, while the

cranial morphology indicates that this taxon is a stem hominid (i.e., an early member of the clade comprising great apes and humans), which must have branched off after the hylobatid-hominid split, but before the pongine-hominine divergence (Moyà-Solà et al., 2004). As such, *Pierolapithecus* best fits the ancestral morphotype for great apes and humans and, at least for the moment, it cannot be attributed to any of the two extant subfamilies (contra Begun and Ward, 2005), but is best considered a plesion within the Hominidae. It is currently uncertain whether *Pierolapithecus* migrated from Africa or evolved locally in Eurasia from a more primitive form. This taxon, in any case, provides the oldest unambiguous evidence of an orthograde body plan in the hominoid fossil record (Moyà-Solà et al., 2004, 2005).

A better understanding of these and other questions requires an accurate contextualization of the *Pierolapithecus* remains from

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BCV1. The aim of this paper is to provide this context by reporting updated information regarding the geological setting and taphonomy of the site and the associated fauna, with special emphasis on biochronology, paleobiogeography, and paleoenvironmental reconstruction.

### Geological setting and historical background

The type locality of *P. catalaunicus*, BCV1, is located near Els Hostalets de Pierola at the northwestern margin of the Vallès-Penedès Basin (Fig. 1). This basin is a NNE–SSW Neogene half-graben, which was generated in relation to the rifting of the northwestern Mediterranean, and stretches between two parallel mountain ranges (the Pre-littoral and Littoral ranges). The sedimentary sequences of the basin cover most of the Miocene (Cabrera and Calvet, 1990; Bartrina et al., 1992; Roca and Desegaulx, 1992; Roca and Guimerà, 1992; Cabrera et al., 2004) and consist mainly of proximal to distal-marginal alluvial-fan sediments (Cabrera and Calvet, 1990, 1996; Cabrera et al., 2004; De Gibert and Robles, 2005). The area of Els Hostalets de Pierola is characterized by thick middle-to-late Miocene sedimentary sequences that resulted from high-rate accumulation, most likely controlled by its proximity to the actively subsiding northwestern margin of the basin. The sediments were deposited in the distal-to-marginal, inter-fan zones of two major coalescing alluvial-fan systems: a short-radius alluvial-fan system (Els Hostalets de Pierola System) sourced from the northwest Pre-littoral range by local catchments, and a radially extensive alluvial-fan system (Olesa System), sourced from the northeast by more extensive catchments in the Pre-littoral Range (Fig. 1).

The fossiliferous potential of the area of Els Hostalets de Pierola was discovered by M. Guérin. During the 1920s, Guérin collected an isolated right  $M^2$  of a great ape. This tooth, however, was mistaken for a suid and not “rediscovered” until much later (Van der Made and Ribot, 1999). In 1941, paleontologist Miquel Crusafont found a left mandibular fragment with  $M_2$  and  $M_3$  at a locality called Can

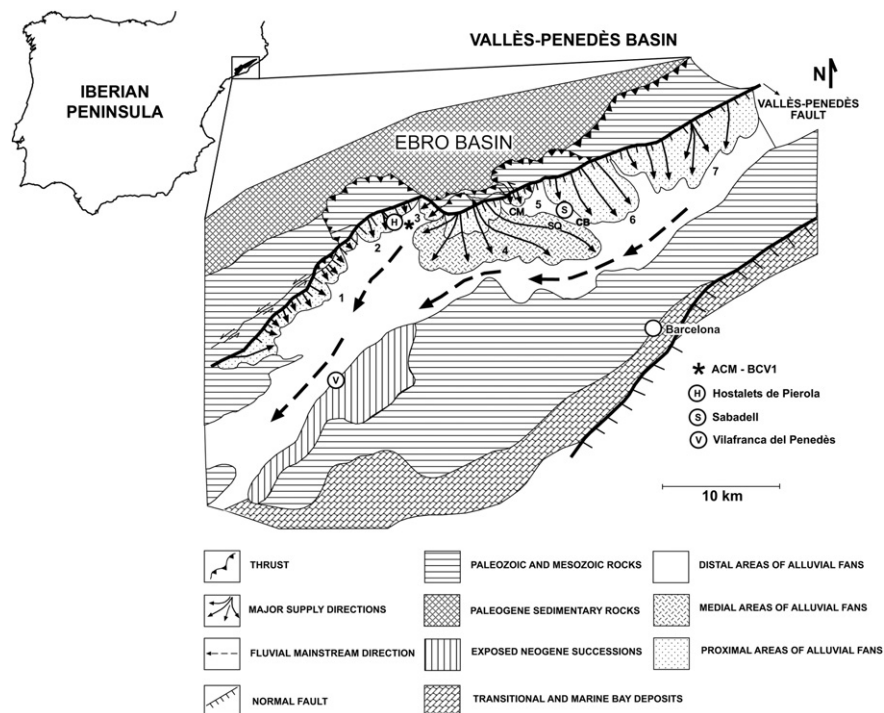
Vila. This specimen was initially attributed to *Dryopithecus fontani* Lartet, 1856, by Villalta Comella and Crusafont Pairó (1941), but Villalta Comella and Crusafont Pairó (1944) used the specimen to erect a new species, *Sivapithecus occidentalis*. Much later, Crusafont and Hürzeler (1961) attributed the Can Vila remains to *Hispanopithecus laietanus* Villalta Comella and Crusafont Pairó, 1944. The justification for the inclusion of the latter remains in the hypodigm of *H. laietanus* is, however, far from clear, since the remains from Can Vila are too fragmentary to permit a secure taxonomic assignment.

From the 1950s to the 1970s, many hominoid fossils were recovered in the Vallès-Penedès Basin by Crusafont and coworkers, although most of the new material discovered came from localities in the Vallès area. Simultaneously, the rubbish dump of Abocador de Can Mata (ACM) was built in the area of Els Hostalets de Pierola. Since November 2002, the paleontological control of the removal of Miocene sediments by excavators at ACM has provided thousands of large- and small-mammal remains, and about 90 fossiliferous localities have been sampled. In 2002, the works marginally affected a ravine situated near Can Vila. Some postcranial remains and a splanchnocranium belonging to a fossil great ape were unearthed by an excavator. Systematic paleontological excavations of the site were undertaken during May and June 2003.

### Material and methods

#### Sampling and taphonomic analysis

The fauna recovered from BCV1 includes 19 species of small mammals and eight of larger mammals, besides some fragmentary bird and reptile remains (Table 1). The material examined for the taphonomic analysis came from the excavation at BCV1 in 2003. A surface of about 50 m<sup>2</sup> was excavated, resulting in the recovery of nearly 300 macrovertebrate remains, including 83 identifiable primate bones or bone fragments. In 2004, a new field campaign



**Fig. 1.** Paleogeographical map of the Vallès-Penedès Basin during the latest Serravalian (i.e., Late Aragonian, MN 7 + 8), indicating the position and extent of the main alluvial-fan systems and their source area. Alluvial-fan systems are numbered as follows: 1 = Torrelles de Foix; 2 = Els Hostalets de Pierola; 3 = Collbató; 4 = Olesa de Montserrat; 5 = Terrassa; 6 = Castellar del Vallès; 7 = Granollers. The position of the BCV1 site is indicated by an asterisk (\*); other sites: Sant Quirze (SQ), Castell de Barberà (CB), and Can Missert (CM).

**Table 1**  
Synthetic list of the mammal fauna from the BCV1 and the ACM sites

Order Insectivora	<i>Albanensia albanensis quiricensis</i>
<b>Soricidae indet.</b>	<i>Miopetaurista neogrivensis</i>
<b>Crocidosoricidae indet.</b>	<b><i>Miopetaurista cf. crusafonti</i></b>
<b><i>Talpa minuta</i></b>	<i>Heteroxerus</i> sp.
<b>cf. <i>Proscapanus</i> sp.</b>	<b><i>Spermophilinus bredai</i></b>
<b><i>Parasorex socialis</i></b>	<i>Chalicomys</i> n. sp.
<b>Erinaceidae indet.</b>	Order Proboscidea
Erinaceinae indet.	<b><i>Deinotherium giganteum</i></b>
<b><i>Dinosorex sansaniensis</i></b>	<i>Gomphotherium longustidens</i>
<i>Plesiodimylus chantrei</i>	cf. <i>Tetralophodon longirostris</i>
Order Chiroptera	Order Perissodactyla
Gen. et sp. indet.	<i>Chalicotherium grande</i>
Order Lagomorpha	<i>Anchitherium</i> sp.
<b><i>Prolagus oeningensis</i></b>	<i>Alicornops simorrensis</i>
<i>Eurolagus fontannesi</i>	cf. <i>Hoploacatherium tetradactylum</i>
Order Rodentia	Order Artiodactyla
<b><i>Eumyarion leemani</i></b>	<b><i>Listriodon splendens</i></b>
<i>Hispanomys decedens</i>	<i>Conohyus steinheimensis</i>
<i>Hispanomys daamsi</i>	<i>Korynochoerus palaeochoerus</i>
<i>Hispanomys</i> cf. <i>lavocati</i>	<i>Albanohyus pygmaeus</i>
<b><i>Hispanomys</i> sp.</b>	cf. <i>Taucanamo</i> sp.
<b><i>Democricetodon brevis brevis</i></b>	<i>Dorcatherium naui</i>
<i>Democricetodon brevis nemoralis</i>	<i>Miotragocerus</i> cf. <i>monacensis</i>
<b><i>Democricetodon larteti</i></b>	cf. <i>Eotragus</i> sp.
<i>Democricetodon crusafonti</i>	<b><i>Micromeryx flourensianus</i></b>
<b><i>Megacricetodon minor minor</i></b>	<b><i>Euprox furcatus</i></b>
<i>Megacricetodon minor debruijini</i>	Order Carnivora
<i>Megacricetodon</i> cf. <i>crusafonti</i>	<i>Martes munki</i>
<i>Megacricetodon ibericus</i>	<i>Ischyriictis mustelinus</i>
<i>Anomalomys gaudryi</i>	<i>Trocharion albanense</i>
<i>Keramidomys carpathicus</i>	<i>Sansanosmilus jourdani</i>
<i>Eomyops</i> cf. <i>oppligeri</i>	<b><i>Leptoplesictis cf. aurelianus</i></b>
<b><i>Glirudinus undosus</i></b>	<i>Pseudaelurus</i> sp.
<b><i>Muscardinus sansaniensis</i></b>	<b><i>Thalassictis montadai</i></b>
<i>Muscardinus hispanicus</i>	<i>Protictitherium crassum</i>
<i>Myoglis meini</i>	cf. <i>Protictitherium</i> sp.
<b><i>Microdyromys complicatus</i></b>	Order Primates
<i>Microdyromys koenigswaldi</i>	Pliopithecidae indet.
<i>Paraglirulus werenfelsi</i>	<b><i>Pierolapithecus catalaunicus</i></b>
<b><i>Brsatoglis astaracensis</i></b>	<i>Dryopithecus</i> sp.
<i>Albanensia</i> cf. <i>albanensis albanensis</i>	Hominidae gen. et sp. nov.

The taxa that have been recovered from BCV1 are in bold. Besides these taxa, BCV1 has also delivered a canine of Mustelidae indet., multiple bone fragments of megaherbivores, and a few turtle-shell fragments.

was carried out at BCV1, but no further primate remains appeared, and fewer (less than 100) macrovertebrate fossils were recovered, which have not yet been prepared. Therefore, these remains are only considered as far as their spatial distribution and orientation are concerned, but they are not included in the study of their state of preservation.

The three-dimensional position and orientation (when a clear major axis existed) of each bone were recorded in the field. The dip angle was recorded in very few cases, since most of the bones appeared to be subparallel to the plane of stratification. For the study of the state of preservation, the bones were examined by two observers (ICV and DMA) before deciding what to record. The preservation was compared between different taxa to investigate the possibility of different taphonomic histories. We distinguished up to three groupings: *P. catalaunicus*, megaherbivores (including *Deinotherium giganteum*), and other remains (including some carnivore and artiodactyl remains, turtle-shell fragments, and mostly indeterminate small- to medium-sized bone fragments).

About ten tons of the sediment were screen-washed in order to recover the remains of microvertebrates and small macrovertebrates. Screen-washing may imply some degree of destruction of the material. Most of the teeth were not affected, but a large percentage of bones were broken. This resulted from the action of water during washing and from the fact that some bones were already broken by pressure while buried. In the latter case, the sediment that joined the broken parts was removed during

washing, so that further separation of the fragments occurred. Due to these methodological limitations, it is not possible to apply many of the taphonomic criteria based on bone breakage (see Andrews, 1990). The fossil collection includes about 100 postcranial bones, 43 isolated incisors, a few mandibles, and 414 isolated cheek teeth. These remains were examined under a stereomicroscope at a variable magnification (8–40 $\times$ ), while photomicrographs (see Fig. 7) were taken using a scanning electron microscope (SEM).

#### Paleoecology and paleobiogeography

Micro- and macromammals were analyzed separately since the collecting methods in each case were different. The excavated surface at BCV1 (ca. 50 m<sup>2</sup>) is relatively large compared to other localities from ACM. The richness of the BCV1 fossiliferous level, however, was not exceedingly high, with bone concentration per surface unit being five to ten times lower than the richest localities in ACM. This difference means that macromammal paleodiversity is relatively undersampled at BCV1, especially regarding carnivores and certain ungulate families. Accordingly, information on macromammals from BCV1 is complemented with data from the stratigraphic series of ACM (see taxonomic list in Table 1). Together, they condense information from a time interval of about 1.5 million years, from the latest MN 6 to the boundary between MN 7 + 8 and MN 9 (Alba et al., 2006).

The large-mammal fauna was analyzed by means of a discriminant (canonical variate) analysis, based on the relative contribution of several selected taxonomic groups to the large-mammal sample (after Hernández Fernández et al., 2003). Fossil localities were classified on the basis of the discriminant functions according to the composition of several Recent localities from four different biomes (Hernández Fernández et al., 2003; see also Hernández Fernández, 2001): temperate evergreen forests, savanna, tropical deciduous forests, and evergreen tropical rain forests. This classification defines temperate evergreen forests as mainly evergreen forests with some deciduous species, which are characteristic of warm-temperate (subtropical) climates with high levels of humidity. Savannas correspond to mainly herbaceous vegetation, and are characterized by tropical to subtropical temperatures and semiarid conditions (very marked hydric seasonality). Tropical deciduous forests are characterized by tropical temperatures and a summer rain season. Finally, evergreen tropical rain forests are diverse, dense, and highly stratified forests, characteristic of equatorial climates, with high humidity throughout the year and only a slight termic seasonality. Other biomes, such as the sclerophyllous Mediterranean forests and broad-leaf deciduous forests were not included in the analysis. Besides ACM, other MN7 + 8 localities were included in the analysis for comparison: Hostaletes Inferior, Castell de Barberà, and Sant Quirze (also from the Vallès-Penedès Basin); Toril 3A (Spain); Steinheim (Germany); and La Grive (France). Data from these localities were taken from the NOW database (available at <http://www.helsinki.fi/science/now/data.html>), except for La Grive (data taken from Mein and Ginsburg, 2002) and Toril 3A (Azanza et al., 2004); data for extant biomes were taken from Hernández Fernández et al. (2003: Appendix 2, p. 280). When compiling these data, we noticed that the latter authors had mixed the definition of variables 7 and 8 (% Proboscidea and % Primates, according to their Table 4) with regard to the extant biomes listed in their Appendix 2, whereas fossil sites are correctly listed. The results provided by Hernández Fernández et al. (2003) are, however, correct (i.e., they do not mix primate and proboscidean data), but this caveat should be taken into account by any investigator trying to replicate their results.

Unlike the case of macromammals, the generally larger micro-mammal samples permit adequate sampling of paleodiversity at a single site. The small-mammal fauna from BCV1 is compared to

those of other European sites of similar age. Therefore, we have compiled a database including up to 28 sites dated to MN 7 + 8 and covering a geographical range from central Spain to Turkey. In the case of the several sites for which magnetostratigraphic data are not available, it is impossible to judge their age more precisely. Raw data for the analysis included a presence/absence matrix recording all the rodent and insectivore genera confidently identified in these sites. Uncertain determinations were not taken into account. Lagomorphs were excluded from the calculations since they have not been studied in many of the sites considered. We chose to use qualitative instead of quantitative data for two reasons: first, sample sizes are not always comparable; second, quantitative data are usually not available in the case of insectivores. The data sources are indicated in [Supplementary Table S1](#) (see online Supplementary material).

On the basis of our raw data matrix, we performed a correspondence analysis (CA), a multivariate ordination technique used to search for underlying patterns. The algorithm used was taken from [Davis \(1986\)](#). Such ordination methods order samples and taxa in multivariate space, so that their disposition may be related to some underlying biogeographical or ecological attributes. Additional information on the environment associated with particular sites and/or the ecology of particular taxa must be used to interpret the meaning of the results. Ordination assumes continuity, but still reveals grouping structure where it exists ([Shi, 1993, 2001](#)). Since the raw data set contains a large number of variables (more than 70 micromammal genera) it is unlikely that the results of CA will adequately summarize this variation. Therefore, CA results were used to perform a cluster analysis, with the aim of reducing dimensionality by creating new, uncorrelated variables, and subsequently group localities according to their similarity using ordination scores ([Everitt, 1977](#)).

## Biochronology

An important number of micromammal species (such as *Democricetodon larteti*, *Democricetodon brevis brevis*, *Megacricetodon minor minor*, and *Glirudinus undosus*) are shared between BCV1 and La Grive M, the reference site for the MN 7 + 8 biozone ([De Bruijn et al., 1992](#)). [Mein and Ginsburg \(2002\)](#) recently subdivided this biozone on the basis of several fissure infillings of La Grive, placing some of them in MN 7 and others in MN 8. La Grive M was proposed by these authors as the MN 7 reference locality, being characterized by the presence of *Democricetodon larteti*, among other species, and by the absence of some inferred MN 8 immigrants (such as *Megacricetodon* aff. *M. ibericus*, *Muscardinus hispanicus*, *Crusafontina endemica*, and *Dryopithecus fontani*). In contrast,

La Grive L3 was chosen by these authors as the reference site for MN 8. Interestingly, in La Grive L3, *Democricetodon crusafonti* is found instead of its inferred ancestor, *Democricetodon larteti*.

This subdivision of the MN 7 + 8 into two different biozones can also be recognized in the ACM series ([Alba et al., 2006](#); [Casanovas-Vilar, 2007](#)), where the lower biozone is named the *Megacricetodon ibericus* + *Democricetodon larteti* Zone, while the upper is referred to as the *Megacricetodon ibericus* + *Democricetodon crusafonti* Zone ([Table 2](#)). Locality BCV1 is placed within the first one of these local biozones, which roughly corresponds to MN 7 sensu [Mein and Ginsburg \(2002\)](#). Therefore, BCV1 is older than other late Aragonian sites of the same basin that have produced primate remains, such as Sant Quirze and Castell de Barberà, which are correlated to the *Megacricetodon ibericus* + *Democricetodon crusafonti* Zone [i.e., MN 8 sensu [Mein and Ginsburg \(2002\)](#)]. Locality BCV1 thus far represents the earliest known occurrence of the great apes in the Vallès-Penedès Basin. Unfortunately, the age of the lower boundary of MN 7 is not well constrained, although it is thought to be close to 12.5–13.0 Ma, while its upper boundary would be at about 11 Ma, marking the beginning of the late Miocene ([Agustí et al., 2001](#); [Garcés et al., 2003](#)). An age close to 12.0–12.5 Ma seems a reasonable estimate for BCV1 in the context of the ACM series. Ongoing magnetostratigraphic studies in the new sections of Els Hostalets de Pierola will refine the dating of this and other macromammal sites.

## Taphonomy

We divided the taphonomic analysis into three parts: the first and second are devoted to the macro- and micromammal taphonomy, respectively; the third evaluates the taphonomic biases that may affect paleoenvironmental interpretations.

### Macromammal taphonomy

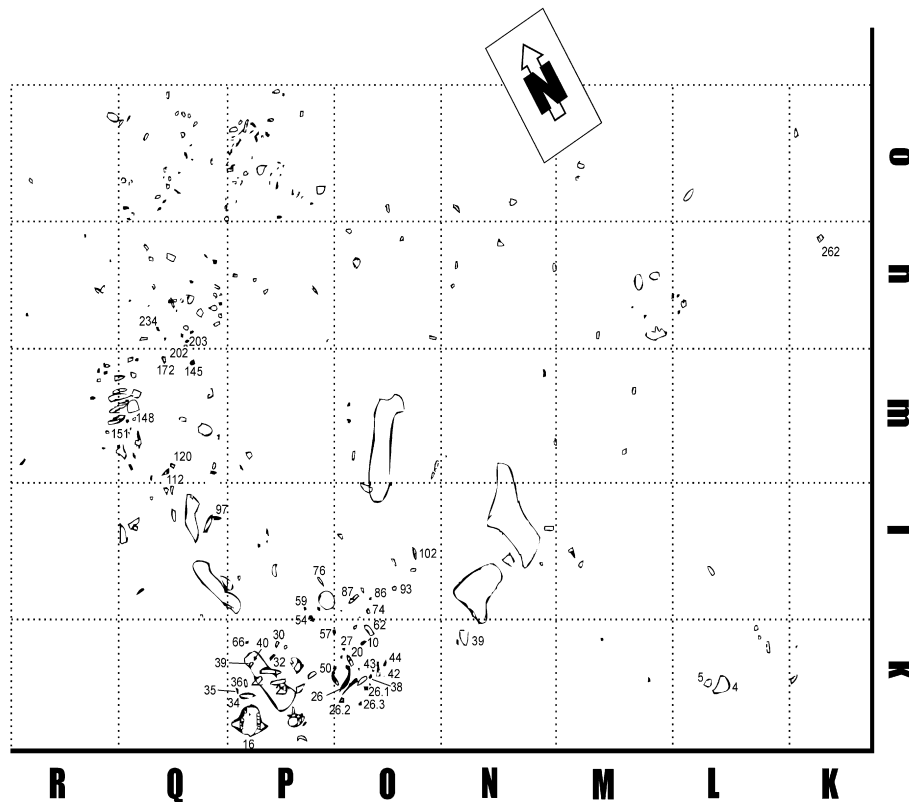
There is evidence of at least two different accumulation processes. The first one was responsible for the deposition of the megaherbivore, carnivore, artiodactyl, and most other remains; the second accumulation process affected the *P. catalaunicus* individual. Evidence for these different taphonomic histories is apparent from analysis of the spatial distribution of the bones and the preservational state in each case.

The remains clearly cluster in a semicircular front with an approximate northeast-southwest trace ([Fig. 2](#)) surrounded by relatively poor zones. There is no apparent pattern in bone distribution related to depth.

**Table 2**  
Local biozonation for the middle and late Miocene of the Vallès-Penedès Basin

Mammal ages	MN zones	Local biozones	ACM series sites	Other sites
Vallesian	MN 9	<i>Cricetulodon</i> Zone		<b>Can Llobateres 1</b> <b>Can Ponsic</b> Creu Conill 22 Creu Conill 20
		<i>Megacricetodon ibericus</i> + <i>Hipparion</i> s.l. Zone	Can Mata III	
Aragonian	MN 7 + 8	<i>Megacricetodon ibericus</i> + <i>Democricetodon crusafonti</i> Zone	<b>Can Mata I</b> CCV1 C4-A1 C3-A2 <b>BCV1</b> C3-B2 C2-B2 C1-E9	Can Feliu Can Missert <b>Castell de Barberà</b> <b>Sant Quirze A</b>
		<i>Megacricetodon ibericus</i> + <i>Democricetodon larteti</i> Zone		
		Unnamed zone	BDL1	
	MN 6	Unnamed zone		

Local biozones for the Vallesian are after [Agustí et al. \(1997\)](#), while the Late Aragonian ones are after [Alba et al. \(2006\)](#) and [Casanovas-Vilar \(2007\)](#). Some of the ACM series sites and other sites of the Vallès-Penedès Basin are correlated to these biozones. Bold indicates the presence of great apes.



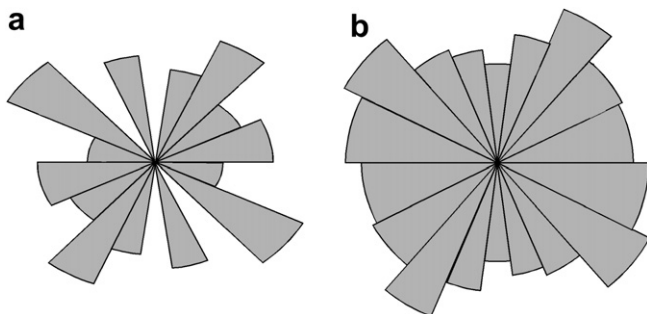
**Fig. 2.** Map of the area excavated at BCV1 during the 2003 field campaign, indicating the position of the recovered material. The sides of each square of the grid measure 1 m. Small bone fragments are not represented. The numbered specimens correspond to elements of the *Pierolapithecus catalaunicus* individual (see Supplementary Table S2 for identification of these skeletal elements). Note the concentration of the primate elements in Pk, Ok, Ol, Qm, and Qn.

Most of the remains of the *P. catalaunicus* individual are concentrated in five squares: Pk, Ok, Ol, Qm, and Qn; only two pelvic fragments have been recovered from Lk (Fig. 2 and Supplementary Table S2). Despite anatomical disassociation of elements, the bones belonging to different parts of the primate skeleton are spatially associated, phalanges being close to associated metapodials and podials. This pattern suggests that the primate skeleton was little affected by transport. The orientations of the long bones in the case of the *P. catalaunicus* individual appear to be random (Fig. 3a), suggesting either little transport or transport in a non-unidirectional flow. The different anatomical elements were classified according to their susceptibility to hydraulic transport (after Voorhies, 1969; as modified by Beherensmeyer, 1975; Hunt, 1978). The recovered elements of the primate skeleton are a mixture of easily transportable bones (such as ribs and vertebrae; Voorhies category I)

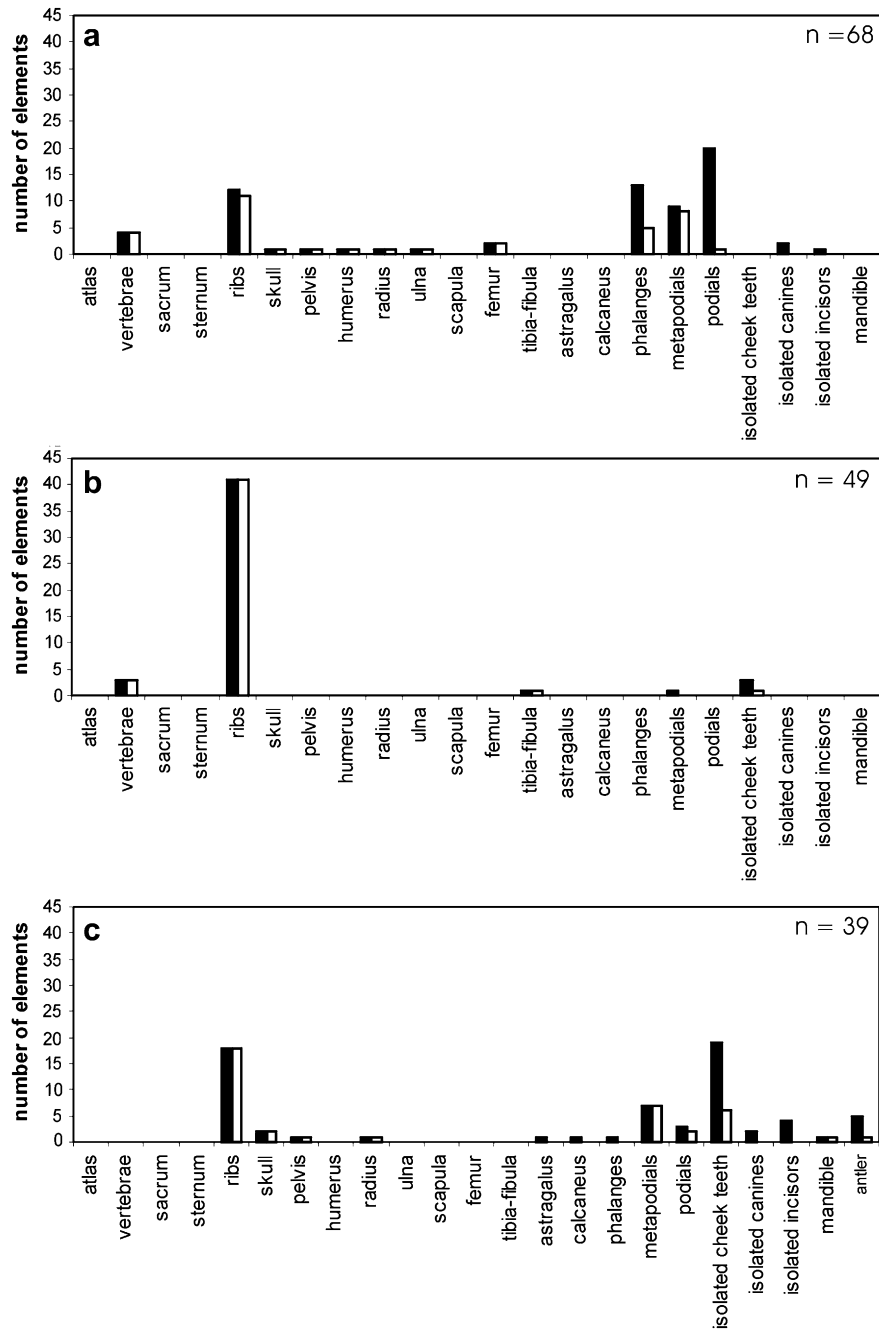
and denser ones (such as the skull and podials; category III), so that selection by density can be rejected (Fig. 4a).

Highly compact bones, such as podials, are mostly complete, while metapodials and phalanges are mostly fragmented. With regard to the long bones of the arms and legs, only blade-like cortical fragments of diaphyses have been recovered. The preferential removal and destruction of these long bones is attributable to the action of carnivores, which is confirmed by the presence of carnivore marks on a total of 27 (out of 83) primate bones (see Fig. 5 for an example). Punctures and pits are observed on 14 bones, while scratches and grooves are present on 13. These marks are predominantly found on diaphyseal fragments. Accordingly, carnivore activity seems to have played the dominant role in the accumulation of the *P. catalaunicus* individual.

The rest of the fossils seem to derive from a different source, since neither partial skeletons nor spatial association of bones belonging to any other single taxon or individual are observed among the remaining taxa. Orientations of the long bones also appear to be random in this case (Fig. 3b), which again suggests little transport or transport in a non-unidirectional flow. This is congruent with the sedimentary environment (distal to marginal facies of alluvial fans), with the bones being transported and buried by a low-energy, muddy current flow. The anatomical elements highly susceptible to hydraulic transport are very common, particularly for the megaherbivores, which are nearly exclusively represented by rib fragments (Fig. 4b). Given the fact that ribs are among the least dense elements (Voorhies category I) of the skeleton and can be easily transported, we conclude that the megaherbivore remains were removed and driven to the place of burial by water currents. Artiodactyls and carnivores are mostly represented by dental remains, although in the case of the cervid *Euprox furcatus*, two shed antlers have also been recovered. Rib fragments



**Fig. 3.** Rose plots showing the orientations of the macromammal remains from BCV1. Area of the segments is proportional to frequency. (a) *Pierolapithecus catalaunicus* long bones; (b) all other bones that can be oriented.

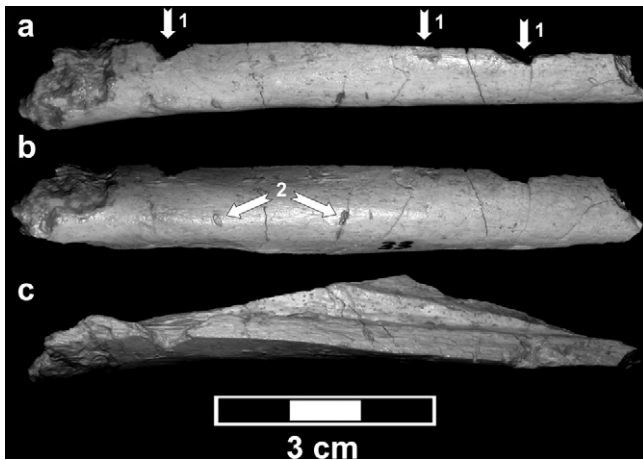


**Fig. 4.** Number and kind of macromammal anatomical elements recovered from BCV1. The black bar represents the total number of elements recovered of each kind, while the white bar shows the proportion of those that are fragmented. Data shown include: (a) *Pierolapithecus catalaunicus*; (b) megaherbivores; (c) other remains.

of undetermined small- to medium-sized mammals are the second most common elements within this group. Unlike ribs, isolated cheek teeth are very dense (category III) and can define lag deposits. This also points towards the existence of hydraulic sorting in the case of these groups, although a mixture of transported and locally derived lag elements defines the assemblage. Abrasion is very uncommon in the case of the *P. catalaunicus* individual, while it affects more than half of the rest of the fossils. These commonly display variable degrees of rounding, and more rarely heavy polishing of the bone—even leading to the loss of its original morphology. Heavy polishing is more common in the megaherbivore bones. Although wind and minor sediment movement during diagenesis may also cause abrasion, the high degree of abrasion and its common occurrence among these remains is, in all probability,

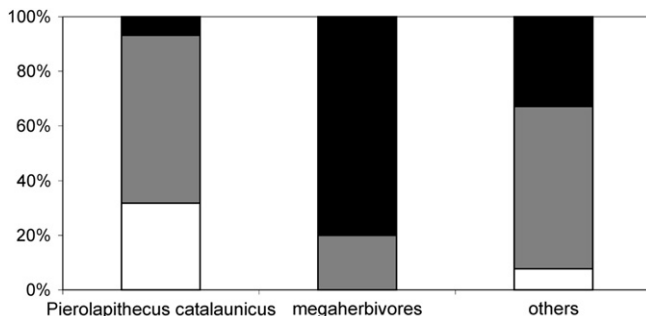
the product of hydraulic transport. The very light degree of abrasion observed in a few bones of *P. catalaunicus* may be related to minor sediment movement (compaction or slight slippage), which would be sufficient to produce slight abrasion without transport.

Variable degrees of weathering were recognized in all groups (*P. catalaunicus*, megaherbivores, and the rest of the fossils). However, the relative abundance of each weathering stage (after Beherensmeyer, 1978; as modified by Alcalá, 1994) varies according to group. In the case of *P. catalaunicus*, most of the elements show only superficial weathering, and a relatively large proportion (more than 30%) show no weathering at all; weathering stage 3 (after Alcalá, 1994) is very rare (Fig. 6). In contrast, the megaherbivore remains are heavily weathered (about 75% of them belong to stage 3), and there are no fresh bones. The third group (mainly artiodactyl



**Fig. 5.** Carnivore marks on a diaphyseal cortical fragment of the ulna of *Pierolapithecus catalaunicus* (IPS 21350-78). Two scratches can be seen on the bone surface (2), while pits appear on the margin of the shaft (1). Two of these pits completely perforate the cortical bone.

and carnivore remains) includes a minor proportion of fresh bones (<10%) and abundant superficially or heavily weathered bones (Fig. 6). Weathering has been generally used to estimate the time elapsed between the loss of the soft parts and the definitive burial of the bones (Beherensmeyer, 1978). Recent studies, however, suggest that the rate of weathering varies depending on the habitat (Tappen, 1994; Andrews and Armour-Chelu, 1998) and therefore cannot be directly related to the burial time. Nevertheless, the low degrees of weathering observed in the bones of *P. catalaunicus* may be indicative of rapid burial, while the rest of the fossils, particularly the megaherbivore bones, seem to have been exposed for a longer time. These remains, except for the *P. catalaunicus* individual, were probably scattered around the alluvial plain next to the burial area. This would account for the differences in weathering and the preservation stages described, since the bones exposed at the floodplain may have remained there for variable lengths of time. In the megaherbivores, abrasion is intense in some bones, and there seems to have been hydraulic selection of the bones with lower density (mainly ribs). Among other remains, the recovered elements represent a mixture of easily transportable and lag deposits. Only a minor proportion of the megaherbivore and other nonhominoid remains (11 out of 203) show carnivore marks. Therefore, carnivores were probably a secondary agent of accumulation in this case.



**Fig. 6.** Weathering stages recorded in the macromammal remains from BCV1. White indicates stage 1 (intact bone), gray indicates stage 2 (weathering of superficial bone tissues), while black indicates stage 3 (weathering of the whole bone tissue). In order to compare the occurrence of the different weathering stages, the remains are classified in three groups as follows: *Pierolapithecus catalaunicus*, megaherbivores, and the remaining bones.

All of the remains would have been buried by a low-energy, muddy current flow and soon afterwards underwent some early diagenetic modifications related to their shallow burial in the alluvial deposits. These include the relatively common development of hard, thin, gray carbonate crusts that affect the remains of all taxa. In a significant portion of the larger bones (20% in the case of megaherbivore ones), this crust is more developed, sometimes associated with the growth of calcite crystals on the surface of the bone and inside the bone cavities. Encrustation and crystal development occur preferentially in the zone of oscillation of the ground-water table, near the interface between the vadose and phreatic zones (Polonio and López-Martínez, 2000). The widespread occurrence, among others, of Mesozoic carbonates and Paleogene carbonate conglomerates in the Pre-littoral Range catchments of the alluvial fans could account for the high groundwater calcium-bicarbonate content. This high carbonate-solute content could also have triggered incipient carbonate cementation of the coarse-grained alluvial facies, as well as the development of widespread nodular pedogenic and lenticular groundwater calcretes. The infilling of the inner cavities of the bones with a limonitic matrix that includes the crumbled cancellous bone is observed in 20% of the material. A significant proportion of unidentified bone fragments, as well as some of the megaherbivore bones, possess a fragile and dusty texture that blurs the original bone shape and complicates their separation from the surrounding matrix. Both kinds of alterations are related to the burial of the bones in water-saturated, slightly acid conditions (Polonio and López-Martínez, 2000), which might have resulted either from the direct influence of meteoric waters in the upper vadose zone, or from the action of acid waters related to soils rich in organic matter.

#### *Micromammal taphonomy*

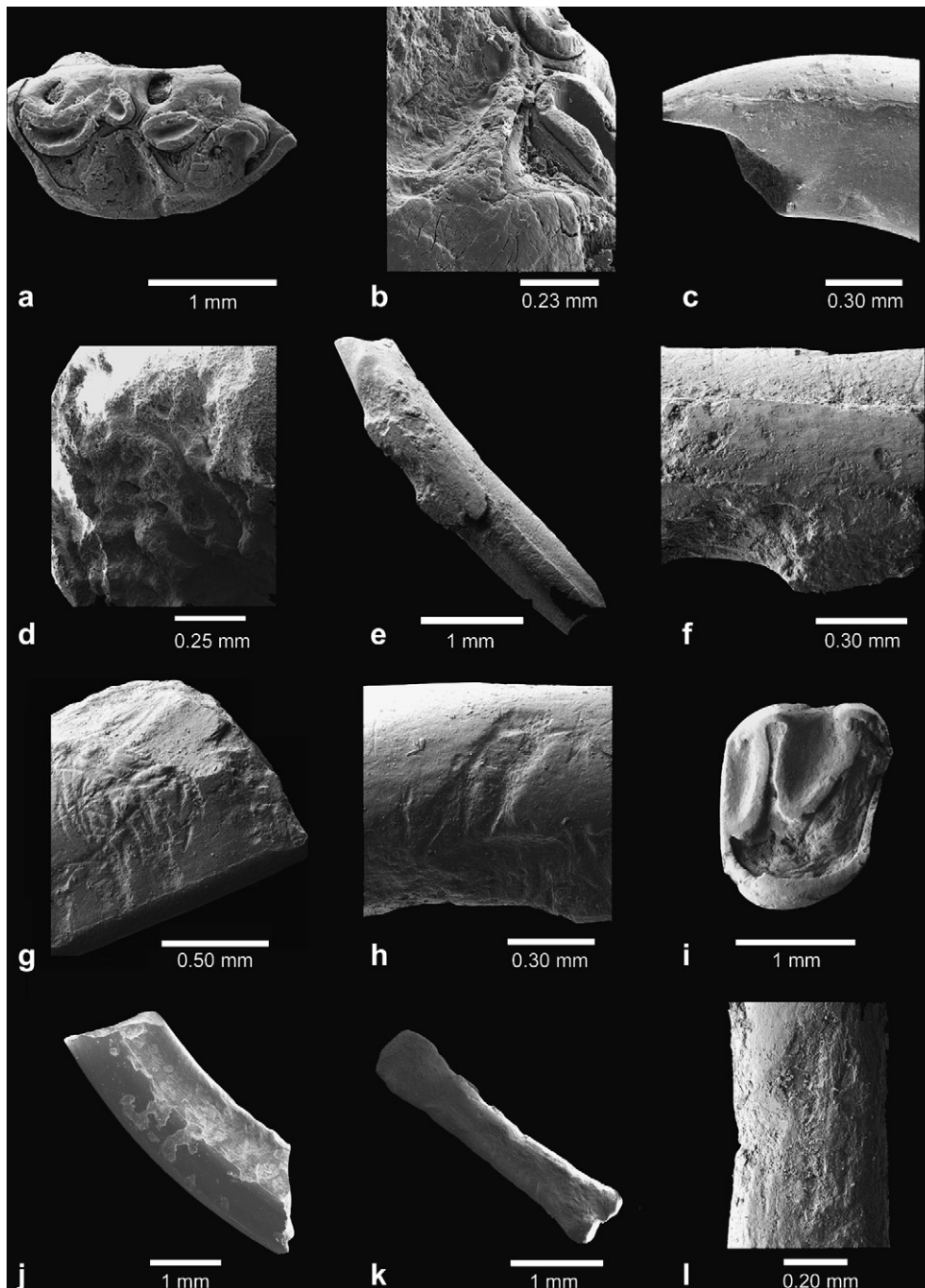
Predation has been proposed as the most important process involved in the origin of small-mammal fossil assemblages (Mellet, 1974; Korth, 1979; Andrews and Evans, 1983; Andrews, 1990). Since the hunting habits of the predators involved in the accumulation may introduce biases in paleoecological interpretation, considerable effort has been devoted to identifying them by recognizing characteristic patterns of bone breakage and modifications on teeth and bones (Andrews, 1990). This procedure is based on the comparison with extant small-mammal prey assemblages, and has been successfully applied to many Pleistocene sites (Andrews, 1990; Fernández-Jalvo and Andrews, 1992; Fernández-Jalvo et al., 1998). Since many of the recent small-mammal predators already existed in the Pleistocene, the correction of the bias introduced by them in these cases seems justified. However, only a few genera of these predators have been found in Miocene deposits, and the identification of the predators involved in accumulations older than the Pleistocene is therefore controversial. In pre-Pleistocene predator-derived accumulations, the identity of the predator is unknown, and no correction of the bias introduced by the predator can be applied on the basis of the behavior of living species.

Because of the considerable postrecovery breakage of the bones in the case of BCV1, we have only focused on the degree of digestion of both bones and teeth (after Andrews, 1990). Most of the remains (>90%) do not show any trace of digestion. In the case of the cheek teeth, moderate to heavy digestion, consisting of pitting on the surface of the teeth and partial removal of the enamel along the edge of wear facets, was observed in some cricetid and insectivore cheek teeth (22 out of 425 teeth). This category of digestion has been identified in some cricetids (*Eumyarion lemani*, *Democricetodon larteti*, *Hispanomys* sp., and *Democricetodon brevis brevis*), the ground squirrel *Spermophilus bredai*, and the erinaceid *Parasorex socialis*. Extreme digestion is

very rare, being observed only in *Eumyarion leemani* (six teeth) and *Democricetodon larteti* (two teeth) (Fig. 7a,b). Digestion seems to affect particularly *Hispanomys* sp., since half of the molars recovered ( $n = 4$ ) show heavy digestion. Digestion of rodent incisors is also uncommon, but two different categories can be distinguished: light digestion concentrated at the tips of the

incisors (3 out of 42 incisors) (Fig. 7c); and moderate to heavy digestion reducing the enamel to islands on the surface of the dentine, which is also affected (one incisor; Fig. 7e). Signs of light to moderate digestion were observed on a few bones (Fig. 7d).

The degree of concentration of micromammal remains is approximately 10 teeth per square meter, which is rather low



**Fig. 7.** Photomicrographs of small-mammal remains from BCV1 showing traces of digestion and other surface alterations. (a) Right  $M^1$  of *Democricetodon larteti*, very heavily digested. The mesial end of the tooth is broken. The whole surface is heavily cracked and pitted. Note that digestion is greater at the buccal margin—enamel has been nearly removed and the dentine has also been affected, resulting in polishing and rounding of the buccal cusps. (b) Detail of the protocone of the same specimen showing the collapse of dentine inside this cusp, as well as extensive cracking and splitting of the enamel. (c) Very light digestion of the tip of a rodent lower incisor. Note the slight pitting of the enamel and digestion of the dentine resulting in a polished occlusal surface. (d) Femoral head of a juvenile specimen showing moderate digestion. (e) Very heavy to extreme digestion of a rodent lower incisor. Note that most of the enamel has been removed and that the dentine has also been affected, producing a wavy outline. (f) Detail of the same specimen showing extensive pitting and removal of incisor enamel. (g) Broken rodent incisor showing some small irregular scratches that may be attributable to insect damage. (h) Root mark on a diaphyseal fragment of a long bone of a small mammal. The same fragment shows small scratches and surface corrosion. (i) Left  $M^{1/2}$  of *Spermophilinus bredai* showing preferential dissolution of dentine in worn areas, especially on the protocone. (j) Fragment of a lower incisor of a rodent showing postdepositional corrosion of both enamel and dentine. (k) Small-mammal metapodial with postdepositional corrosion of the whole surface. (l) Detail of the same specimen showing the loss of some bone layers.



compared to predator-accumulated assemblages (see Andrews, 1990). In light of this evidence, predators do not seem to be the primary agent responsible for the origin of the small-mammal assemblage of BCV1. However, the category 1 predators of Andrews (1990) have minimal effects on their prey, consisting of superficial pitting of enamel on incisors and microtine molars, but no noticeable effects on insectivore teeth or those of rodents having bunodont teeth. Since the recovered rodent species possess bunodont teeth, the role of these kinds of predators can only be evaluated in the case of the incisors. Evidence of digestion is mostly absent on incisors, and the few teeth that present some indication of digestion exhibit category 2 digestion or higher. Unfortunately, the action of category 1 predators cannot be evaluated on the cheek teeth, so the possibility that part of the assemblage may derive from a category 1 predator cannot be excluded.

Other preburial alterations include abrasion, which is very uncommon in the sample. Only a light degree of rounding has been recognized on a small proportion of the postcranial bones. Weathering, which would indicate the exposure of remains on the ground surface, affects approximately 20% of the postcranial bones. Splitting and, in advanced stages, flaking are present on the bones. Concerning the teeth, weathering produces cracking and splitting of the dentine and, in more advanced stages, may result in the loss of parts of the crown. Since enamel is more resistant to weathering than bones, this may account for the very rare occurrence of weathering in teeth, although cracking of the dentine was observed on a few of the molars. Microscopic grooves are common, especially on the bone diaphyses (17%) but also on a few incisors, where they may affect the dentine (Fig. 7g). These kinds of marks are often attributed to insect damage (Fernández-Jalvo et al., 1998). Possible rodent gnawing marks have also been identified in a small-mammal incisor. All these alterations show that a high proportion of the remains were exposed for some time, while the low occurrence of abrasion also indicates that they experienced little transport.

Once buried, the micromammal remains persisted for some time in a biologically and chemically active environment. Root marks are present on a few of the bones and incisors (Fig. 7h). In contrast, chemical corrosion, with the removal of parts of the surface of bones and teeth, is common, particularly in the case of incisors (more than 30% are affected) and postcranial bones (close to 22%), while the cheek teeth are rarely affected (5%). In some of the affected cheek teeth and incisors, the effects of corrosion are more evident on the dentine than on the enamel (Fig. 7i). In these cheek teeth, the dentine has been partially removed from the main cusps and, in some extreme cases, small holes are present. In cave environments, similar alterations have been related to the existence of highly alkaline soils (Fernández-Jalvo and Andrews, 1992). The high carbonate solute contribution related to the groundwater could account for these alkaline conditions. In the rest of the material affected by chemical corrosion, dentine and enamel are equally damaged (Fig. 7j). On the postcranial bones, extensive pitting is observed on the whole surface of the bone, and it may be accompanied by the loss of some bone layers (Fig. 7k, l).

#### Evaluation of the taphonomical biases and conclusions

Since the BCV1 macromammal assemblage cannot adequately reflect paleodiversity, paleoenvironmental inferences must be drawn from the whole ACM fauna, and therefore reflect the varied environmental conditions in that area from latest MN6 throughout MN7 + 8. In contrast, the abundant small-mammal sample provides a more adequate estimate of the existing paleodiversity. The small-mammal remains do not seem to have experienced extensive transport. Since the role of category 1 predators (see Andrews, 1990) could not be evaluated in much of the material, the relative

abundance data of the recovered micromammal species were not used in the paleoecological analyses, which are based on presence/absence data.

#### Paleoecology and paleobiogeography

##### *The evidence provided by large mammals*

When the large-mammal composition of ACM is taken into account (see Table 1), the most informative taxon regarding environmental conditions is the tragulid *Dorcatherium*. It is usually compared with the extant genus *Hyemoschus* (Köhler, 1993), a forest inhabitant that is an excellent swimmer and diver. As such, the presence of *Dorcatherium* is a good indicator of more or less permanent water streams, though only on a local scale. At ACM, however, this taxon is much rarer than the moschid *Micromeryx* or the cervid *Euprox*, being securely documented only in the lower part of the ACM stratigraphic series. The higher frequencies of the *Micromeryx* and *Euprox* indicate the presence of a relatively closed and humid forest environment, while the presence of the bovid *Miotragocerus* further confirms the presence of water streams, since it is interpreted as a semiaquatic animal (Köhler, 1993). Suoids are usually not very informative, although small Miocene suoids such as *Albanohyus* are generally interpreted as forest dwellers, and the same can be asserted about the considerably larger hard-object feeder *Conohyus* (Fortelius et al., 1996a). Larger-bodied suids (the omnivorous *Korynochoerus* and the more folivorous *Listriodon*) could have exploited more open habitats (Fortelius et al., 1996a), but this would not necessarily preclude the exploitation of forested biomes.

Regarding perissodactyls, the presence of *Anchitherium* is very remarkable, representing the last occurrence of this taxon in the Vallès-Penedès Basin. Anchitheriine horses, characterized by low-crowned and lophodont cheek teeth, were browser inhabitants of tropical and warm-temperate forest environments (Hernández Fernández et al., 2003). The small size of the *Anchitherium* fossils from ACM suggests either small body size and/or a small relative tooth size, both of which are compatible with a densely forested habitat. This taxon was progressively replaced during MN 6 and MN 7 + 8 by the relatively small and brachyodont rhinocerotid *Alicornops* (Cerdeño and Nieto, 1995). The latter taxon, which is much more frequent than *Anchitherium* at ACM, has been interpreted as a cursorial browser that was better adapted than was *Anchitherium* to the increasingly humid conditions of this period (Hernández Fernández et al., 2003). The presence of several primate taxa (especially great apes) also strongly supports the existence of a closed and humid forest at ACM, and probably a dense and continuous canopy, as inferred from the adaptations to arboreal climbing documented in *Pierolapithecus*.

In summary, the large-mammal composition of ACM is consistent with the presence of a warm to tropical, relatively humid, dense evergreen forest, which hosted a considerable diversity of mammals during the Late Aragonian. This inference strongly contrasts with previous studies based on the classical collections of Hostalets Inferior. “Hostalets Inferior” represents an aggregate of material recovered from a more or less restricted stratigraphic interval that corresponds to the late MN 7 + 8 (Agustí, 1981; Alba et al., 2006; Casanovas-Vilar, 2007). This material is frequently treated as if it had been recovered from a single site (Agustí et al., 1984; Morales et al., 1999). Crusafont Pairó (1950) first made some tentative inferences on the paleoenvironmental conditions of the classical Hostalets assemblage from sedimentological and faunal data, suggesting less humid conditions than for Sant Quirze, the other then-known Vallès-Penedès locality from the Late Aragonian. Recently, Hernández Fernández et al. (2003) concluded that Hostalets Inferior should be interpreted as a savanna environment.

Certainly, the presence of some taxa such as tragulids and castorids at ACM but not in Hostalets Inferior, together with the higher diversity of primates at ACM, suggests more humid and densely forested conditions in ACM. This could be attributable to the different time intervals represented by these two sets of localities: while many of the remains from Hostalets Inferior come from locality Can Mata I, attributed to late MN 7 + 8, most of the ACM remains range from latest MN 6 to early MN 7 + 8 (Alba et al., 2006; Casanovas-Vilar, 2007). However, the faunal composition of both sets of localities is not so strikingly different as to suggest open and semiarid conditions for Hostalets Inferior.

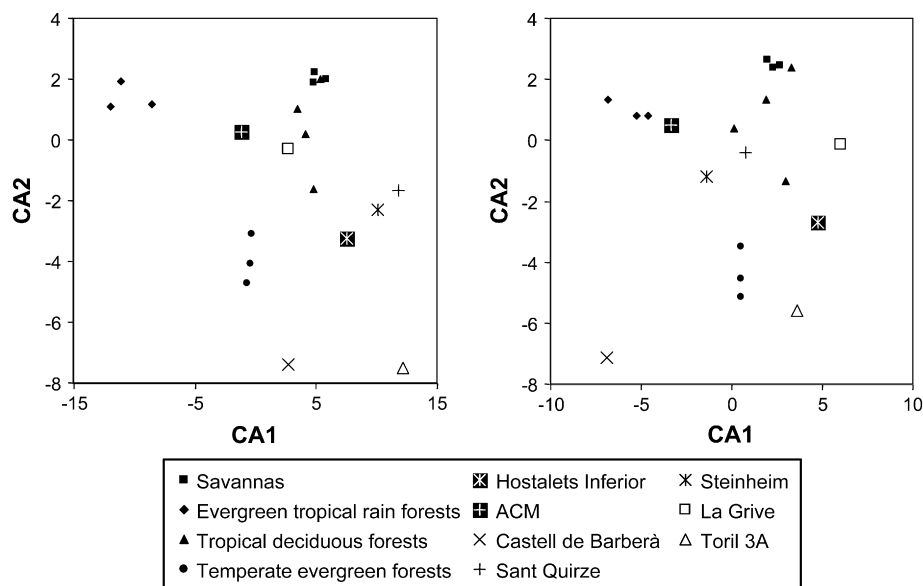
Close inspection of the data employed by Hernández Fernández et al. (2003) reveals that the authors omitted the suiform and primate species from Hostalets Inferior. Data were taken from Morales et al. (1999: Table 6.1), who inadvertently omitted some of the taxa (suids, primates, rhinocerotids, and chalicotheriids) from Hostalets Inferior, and these omissions were only partially emended by Hernández Fernández et al. (2003). We replicated the discriminant analysis in order to correctly classify Hostalets Inferior (on the basis of emended data), as well as ACM and other MN 7 + 8 sites. The analysis (Fig. 8, left) classifies MN 7 + 8 localities as tropical deciduous forests, which are characterized by tropical temperatures and a summer rain season. The only exception is Castell de Barberà, which is classified as a temperate evergreen forest. Locality ACM is very close to La Grive; however, while the latter is next to tropical deciduous forests, ACM is somewhat intermediate with respect to evergreen tropical rain forests. Hernández Fernández et al. (2003) omitted carnivores from their analysis in order to avoid the bias introduced by their usual underrepresentation. It is reasonable to assume that primates, which require an even greater sampling effort, might introduce a comparable, if not greater, taphonomical bias. When our analysis was repeated excluding primate taxa, a similar discrimination was attained (see Fig. 8, right), and most fossil localities are still classified as tropical deciduous forests. Castell de Barberà and ACM, however, are classified as evergreen tropical rain forests, which are characterized by higher levels of humidity throughout the year. This contrasts with Hostalets

Inferior, which displays an intermediate position between tropical deciduous forests and temperate evergreen forests.

This kind of paleoenvironmental characterization of fossil localities should be viewed with great caution because it is based on a small number of recent localities and a simplistic classification that, judging from the dispersion of fossil localities in Fig. 8, do not accurately reflect the diversity of environments in western Europe during the Miocene. In fact, paleobotanical data are not consistent with the existence of tropical forests in western Europe during the latest middle Miocene, indicating instead the presence of warm-temperate forests with a high proportion of deciduous taxa (see below). Be that as it may, the analysis permits rejection of the depiction of Hostalets Inferior as a savanna, but still suggests that ACM records a different interval of time and corresponds to a more forested and humid environment.

#### The evidence provided by the small mammals

The small-mammal fauna from BCV1 includes up to 19 different taxa (11 rodents, seven insectivores, and one lagomorph; see Table 1). The presence of several arboreal taxa (the dormice and the flying squirrels; for a discussion on the ecology of these fossil rodents, see Casanovas-Vilar and Agustí, 2007), albeit rare, indicates the existence of forested environments in the area of Els Hostalets de Pierola. As in the case of macromammals, this contrasts with previous paleoenvironmental interpretations based on the rodents of Hostalets Inferior, which is probably younger than BCV1. The small-mammal fauna of Hostalets Inferior is dominated by cricetids, with the most abundant genera being *Cricetodon* and *Hispanomys*, while *Eumyarion*, which is the most abundant taxon from BCV1, is completely absent (see Alba et al., 2006). The dormice are also absent from Hostalets Inferior, while the insectivores are rather diverse. This faunal composition has been interpreted as indicative of an open environment, markedly different from other Late Aragonian sites from the Vallès area (such as Sant Quirze or Castell de Barberà), which are located slightly to the northeast (Crusafont Pairó, 1950; Agustí et al., 1984).



**Fig. 8.** Discriminant analysis of selected Late Aragonian fossil localities on the basis of four extant biomes (after Hernández Fernández et al., 2003). Plot of second (CA2) versus first (CA1) canonical axes: (left) replication of the original analysis by including ACM and emended Hostalets Inferior data; (right) analysis excluding primates (in order to remove the potential taphonomical bias introduced by the great sampling effort necessary to adequately sample their paleodiversity). The CA1 explains 87% (left) and 58% (right) of variance, respectively, and mainly separates evergreen tropical rain forests from other biomes. The CA2 explains 12% (left) and 38% (right) of variance, respectively, and further separates temperate evergreen forests from tropical deciduous forests and savannas. The two latter biomes are quite close to one another on the plot, but they can be further discriminated on the basis of the CA3.

In order to outline an environmental scenario that would account not only for the habitat difference observed between the sites of the Vallès-Penedès Basin, but also between other Spanish and European localities, we compiled a presence/absence database that was analyzed using correspondence analysis (CA). The scatter of points along the first two axes is shown in Fig. 9a. The first axis explains 18% of the inertia (eigenvalue = 0.63; total inertia = 3.56), while the second explains 11% (eigenvalue = 0.38) for a sum of 29%. The third and fourth axes each account for about 7% of the inertia. The original data include up to 71 genera (i.e., 71 dimensions). Therefore, capturing 29% of the total inertia in only two axes must be regarded as a good result given the high number of dimensions. The first axis (Fig. 9a) reflects differences between the sites of Turkey and Greece, which take positive values, from all the others, which are grouped in the negative half of this axis. The second axis discriminates between the sites of the inner Iberian basins, which take high positive values, and the rest of the localities. Many of the Vallès-Penedès sites, including BCV1, are mixed with the central European and French sites. Other Vallès-Penedès sites (Hostalets Inferior, HI; Can Missert, CM; Can Feliu, CAF) appear to be closer to the sites of the inner Iberian basins. A cluster analysis based on the results of the CA clarifies these patterns (Fig. 10). The eastern

Mediterranean and Turkish sites are set apart from the rest of the sites and cluster together, although they are not very similar to each other. The sites from the inner Iberian basins appear to be different from the remaining localities, which cluster together and include the Vallès-Penedès localities. However, not all of the latter cluster together, since BCV1, Castell de Barberà (CB), and Sant Quirze A (SQA) appear to be closer to French and Swiss localities.

Figure 9b represents the ordination of the genera present in the sites considered in the same multivariate space. As a general rule, the genera characteristic of an association will plot in the vicinity of this association. Greek and Turkish sites are characterized by a few genera that are not recorded in other areas (such as *Myocricetodon*, *Schizogalerix*, *Pliospalax*, *Hystrix*, and *Byzantinia*; see also Supplementary Table S3). The terrestrial dormouse *Myomimus* is also characteristic of these localities, although it occurs in Spain as well (Solera, SOL). The highest diversity of genera is seen at the negative half of both the first and second axes, a quadrant that is occupied by several central European, French, and Vallès-Penedès sites (SQA, CB, and BCV1). Most of the insectivores, arboreal/scanorial dormice, all of the flying squirrels and eomyids, and all of the beavers plot near these sites. These genera are not recorded in the sites of the inner Iberian basins, which present a few endemic taxa

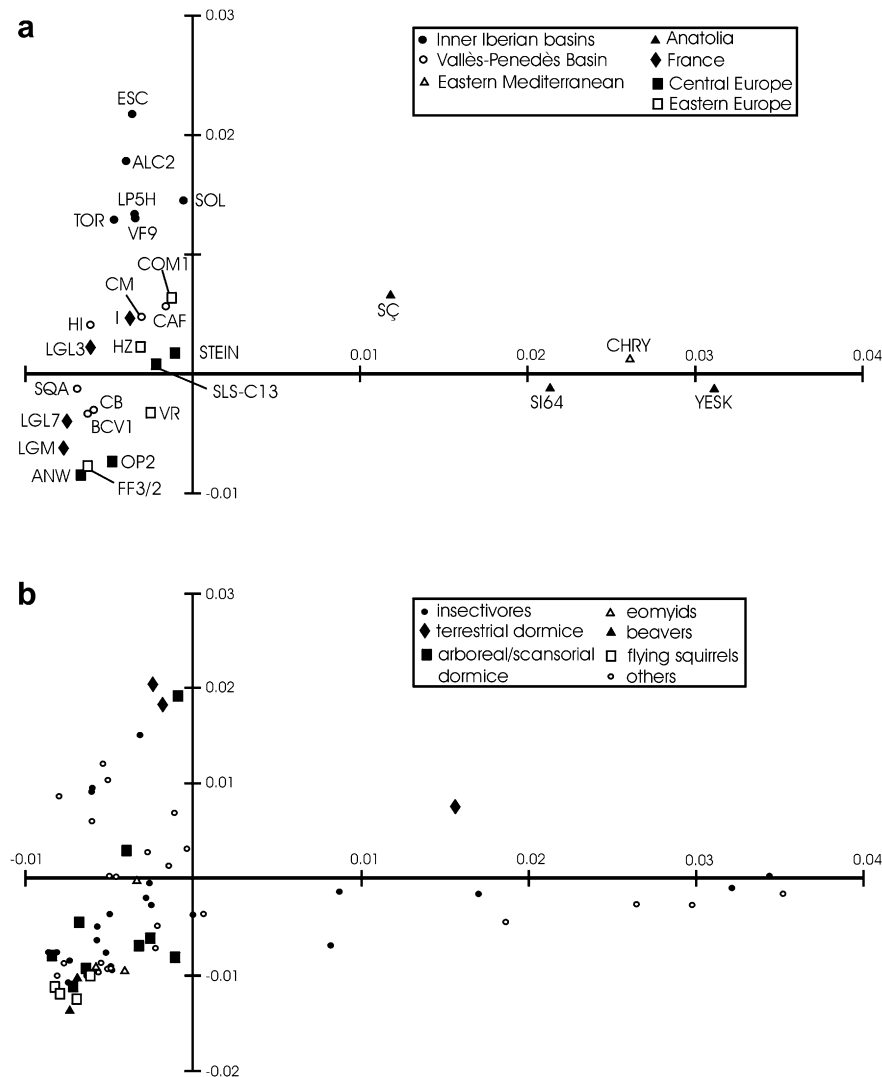
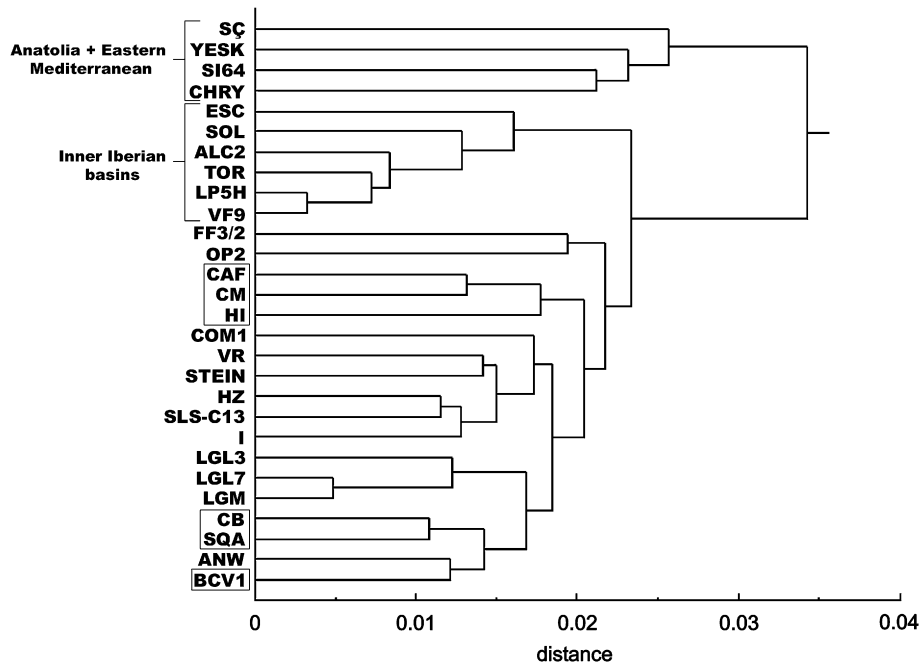


Fig. 9. The first two axes of the correspondence analysis: (a) position of the localities considered (see Supplementary Table S1 for locality acronyms and sources of the presence/absence data); (b) plotting of the genera present at the sites considered. We distinguished between small- and medium-sized *Megacricetodon* and *Democricetodon* species since distinct ecological preferences have been suggested for them (Daams et al., 1988). The scale of the axes is the same in both plots.



**Fig. 10.** Cluster analysis based on the results of the CA (see Fig. 9). Localities are grouped according to their similarity space. The localities from the Vallès-Penedès Basin are boxed. For locality acronyms, see Supplementary Table S1.

such as the high-crowned terrestrial dormouse *Armantomys*. The insectivore fauna of these sites is very poor and only includes two genera: the soricid *Miosorex* and the erinaceid *Galerix*. It is very unlikely that these differences result from differences in sampling or collecting effort, which has been intensive in certain areas of central Spain such as the Calatayud-Daroca Basin. Small-mammal generic richness seems to increase with latitude in western Europe (see Supplementary Table S3), so the number of genera present in inner Spain is about half of the number present in France or central Europe. Some of the Vallès-Penedès sites share an important number of taxa with France/central Europe, although their faunas are not as diverse. The shared genera include the eomyids, beavers, several dormice and insectivore genera, the flying squirrels *Miopetaurista* and *Albanensia*, the anomalomyid *Anomalomys*, and the cricetid *Eumyarion*, which are not recorded in inner Spain by the Late Aragonian (see Supplementary Table S3). Other genera characteristic of higher latitudes—such as the flying squirrels *Blackia*, *Hylometes*, and *Forsythia*; the spiny-dormouse *Neocometes*; and the cricetids *Deperetomys* and *Collimys*—are not recorded in the Vallès-Penedès (see Supplementary Table S3). The Vallès-Penedès sites of CAF, CM, and HI show a poorer rodent fauna in comparison to BCV1, SQA, and CB, although samples sizes are roughly similar (see Casanovas-Vilar and Agustí, 2007). Many forest-dwelling taxa are absent and the fauna is more similar to those of the sites of the inner Iberian basins. Sites CAF, CM, and HI have been correlated to the latest MN 7 + 8, being younger than BCV1 and probably younger than SQA and CB (Agustí et al., 2001; Alba et al., 2006; Casanovas-Vilar, 2007).

On the basis of the small-mammal fauna, three different bioprovinces may be distinguished: the eastern Mediterranean (including Greece and Turkey), the inner Iberian Peninsula, and the rest of Europe from the northeastern margin of the Iberian Peninsula (Catalonia) to Poland and Romania. The existence of two main bioprovinces during the Miocene was first recognized by Tobien (1967) and has been confirmed by subsequent studies (see Bernor, 1984; de Bonis et al., 1992; Fortelius et al., 1996b; Casanovas-Vilar et al., 2005). The eastern province is known as the “sub-Parathethyan” (Bernor, 1984) or the “Greek-Iranian” province (de

Bonis et al., 1992). Other authors (Agustí et al., 1984; Sesé, 1988; Agustí, 1990; Casanovas-Vilar et al., 2005; Casanovas-Vilar and Agustí, 2007) have stressed the differences between the eastern coastal basins of the Iberian Peninsula and the inner ones, particularly during the late Miocene. The paleoenvironment in the Vallès-Penedès Basin appears to have been more humid and forested than in the inner areas of Spain.

#### Discussion

The faunal similarity observed between some of the Vallès-Penedès localities and those from France and central Europe indicates that similar environments existed in those areas during the late middle Miocene. Taken as a whole, the mammal fauna from these sites indicates the presence of humid forest environments. The occurrence of a high diversity of taxa with arboreal feeding and/or locomotor adaptations (great apes, pliopithecids, flying squirrels, arboreal dormice) is dependent upon the productivity and complexity of the vegetation. The high diversity of insectivores at these localities is also consistent with this environmental picture, since insectivorous mammals benefit from the abundance of insects and small invertebrates in moist environments such as forests and humid soils (Van Dam, 2006). These taxa are mostly absent from the Greek-Iranian province and the inner Iberian basins, while their maximum generic richness is recorded in central Europe (see Supplementary Table S3), thus suggesting that different environments existed in those areas by this time.

Fortelius et al. (2002) calculated mean hypsodonty for several Eurasian macromammal sites and used it as a proxy for mean annual precipitation. Independently, present-day relations between small-mammal community structure and rainfall were applied to small-mammal fossil assemblages by Van Dam (2006) to reconstruct the late Neogene precipitation patterns in Europe. Their maps for the middle Miocene (MN 7 + 8) show the existence of lower paleoprecipitation levels in the area occupied by the Greek-Iranian province. In the inner Iberian Peninsula, paleoprecipitation was slightly lower than in both France and central Europe, which are referred to as the European Temperate Wet Zone (ETWZ) by Van

Dam (2006). The Vallès-Penedès Basin would also belong to the ETWZ, and thus would have been characterized by higher precipitation levels than inner Spain, resulting in denser forest environments in this area.

Paleobotanical data further support these interpretations. During the late middle Miocene, a large part of central Europe was covered by mixed mesophytic forests, including a significant proportion of deciduous forms but also with a core of evergreen forms (i.e., temperate evergreen forests of Hernández Fernández, 2001), while broad-leaved deciduous forests occupied more northern regions (Kovar-Eder, 2003; Utescher et al., 2007). On the basis of phytolith evidence, Strömberg et al. (2007) suggested that the landscape in Turkey was dominated by pooid open-habitat grasses from the early Miocene. Forest-indicator phytoliths are also present, although they become progressively rarer towards the late Miocene. These forested areas included many sclerophyllous taxa together with some relict evergreen genera already present in central Europe in preceding periods (Kovar-Eder, 2003). Unfortunately, there is no direct paleobotanical evidence in the Vallès-Penedès Basin for the same time span. The macrofloral remains from the site of Montjuïc in Barcelona next to the Vallès-Penedès Basin may provide a glimpse of the environments that would have existed in the area. This flora, which has been assigned to the Serravallian (Sanz de Siria, 1994; Gómez Gras et al., 2001) and would be approximately equivalent to MN 6 or MN 7 + 8, records the occurrence of warm-temperate evergreen forests close to the coastal areas. The paleofloral assemblage includes some taxa indicating a warm climate (*Cinnamomum*, *Daphnogene*, *Laurus*) and an important proportion of deciduous trees (*Acer*, *Populus*, *Juglans*, *Salix*). This forest assemblage appears to have been similar to that existing in northern latitudes, although mean annual temperatures were probably higher in the Vallès-Penedès (Sanz de Siria, 1994). In contrast, the palynological data from the Torremormojón section (Late Aragonian of the Duero Basin, west-central Spain) revealed the existence of a temperate, open *Quercus* forest in that area (Rivas Carballo and Valle, 1986; the age estimation for the locality of Torremormojón 9 is taken from García Moreno, 1987). On the basis of the limited available paleobotanical information, inner Spain is hence also interpreted as a warm but drier area, which was probably not suitable for some macromammal taxa such as primates. Accordingly, the Vallès-Penedès Basin may well represent the southernmost limit of the biogeographic range of this mammal group in western Europe during the middle Miocene. The fact that the rodent fauna of some Vallès-Penedès sites (CAF, CM, and HI) appears closer to those of the sites of inner Spain may indicate that these sites had less forested environments. All of these localities are correlated to the latest MN 7 + 8, and this may indicate that paleoenvironmental conditions in the Vallès-Penedès Basin were relatively drier by this time than in the early MN 7 + 8.

## Conclusions

The site of BCV1 has produced remains of eight species of macromammals and an abundant sample of micromammal cheek teeth distributed among 19 species. The small-mammal fauna indicates an early MN 7 + 8 age for the site (between 12.5 and 12.0 Ma), which represents the earliest occurrence of hominoids in the Vallès-Penedès Basin.

Predation/scavenging is proposed as the main agent responsible for the presence of the *Pierolapithecus catalaunicus* individual in the assemblage. In contrast, the remaining macromammal fossils seem to derive from isolated bones scattered around the alluvial plain, near to the burial area. Concerning the micromammals, the rare occurrence of alterations produced by digestion is quite remarkable, as predation has been proposed as the main accumulation agent for small-mammal remains in many sites. Nevertheless,

category 1 predators such as barn owls may have played a role in the genesis of the small-mammal accumulation. Hence, presence/absence data were used for paleoecological reconstruction instead of the relative abundances of the recovered small-mammal taxa. The large-mammal fauna from BCV1 does not provide an adequate estimate of paleodiversity, so the whole macromammal fauna recovered at ACM was considered as a whole.

In contrast with previous paleoenvironmental reconstructions, the large-mammal fauna from ACM indicates the presence of a relatively humid, warm forest environment. Concerning the composition of the small-mammal fauna from BCV1, correspondence analysis shows that BCV1 and many of the remaining small-mammal localities from the Late Aragonian of the Vallès-Penedès Basin are closer to those from France and central Europe than to other Spanish localities. The higher diversity of insectivores and arboreal dormice, plus the presence of flying squirrels, confirms that the environment was more humid in the Vallès-Penedès than in the inner Iberian basins. The latest Aragonian sites of the Vallès-Penedès Basin, such as Can Missert or Can Feliu, appear to have been characterized by more open environments, closer to those of central Spain. Paleobotanical data suggest that the humid, warm-temperate forests present at higher latitudes extended to the Vallès-Penedès Basin during the Late Aragonian, whereas open woodland environments seem to have existed in inner Spain, precluding the spread of hominoid primates into that area.

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## Appendix. Supplementary materials

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.jhevol.2008.05.004.

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