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The Gran Dolina site (Lower to Middle Pleistocene, Atapuerca, Burgos, Spain): new palaeoenvironmental data based on the distribution of small mammals

Raquel López Antoñanzas [a,*], Gloria Cuenca Bescós [b]

[a] *Laboratoire de Paléontologie, UMR 8569 CNRS, Muséum national d'Histoire naturelle, 8, rue Buffon, F-75005 Paris, France*
[b] *Área de Paleontología, Dpto. Ciencias de la Tierra, Facultad de Ciencias, Universidad de Zaragoza, E-50009 Zaragoza, Spain*

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Abstract

New palaeoenvironmental data are reported after analysing the distribution of micromammals (orders Rodentia, Insectivora, Chiroptera, and Lagomorpha) in the 11 stratigraphical levels at the Gran Dolina site (TD1–TD11, Early to Middle Pleistocene; Atapuerca, Spain). A continental, dry and cold climate is inferred at the beginning of the succession (TD3 to lower TD5). The fauna in the upper TD5 and in TD6 reflects a complex interglacial period with fluctuations in the degree of relative humidity. In the lower part of TD8, the presence of *Microtus* aff. *ratticepoides* indicates a relatively cold period. Finally, data from upper levels (TD8b, TD10, TD11) reflect another interglacial period with slight oscillations in relative moisture. The different levels at Gran Dolina are also correlated with oxygen isotope stages (OIS): TD3, TD4, and, TD5 may be correlated with OIS 22, TD6 is correlated with OIS 21, lower TD8 (TD8a) is correlated with OIS 18, upper TD8 (TD8b) is correlated with OIS 13 or 15, TD10 and TD11 are correlated with OIS 9 or 11.

Keywords: Gran Dolina; Atapuerca; micromammals; faunal diversity; palaeoenvironment; oxygen isotope stage

1. Introduction

The Atapuerca sites are part of a complex karst system in the Sierra de Atapuerca, a Mesozoic-core hill related with the Iberian Range. Atapuerca is 14 km east of Burgos in northwestern Spain (Fig. 1A).

The Sierra de Atapuerca has two main cave systems, the Cueva Mayor and the Trinchera del Ferrocarril. The latter is exposed in an old railway cut that reveals several fossiliferous cave infillings including the Gran Dolina. Other sites in the Trinchera del Ferrocarril are the Trinchera Penal, the Galería-Tres Simas, and the Elefante (Fig. 1B).

The Gran Dolina site (TD) exposes the longest stratigraphical succession at Atapuerca, with 18 m of cave sediments subdivided into 11 stratigraphical levels (Fig. 2). Almost all of them (TD3–TD11) are rich in fauna and artefacts. The palaeomagnetic Matuyama/Brunhes boundary is at

* Corresponding author. Tel.: +33-1-40-79-30-37.
E-mail address: ralopan@mnhn.fr (R. López Antoñanzas).

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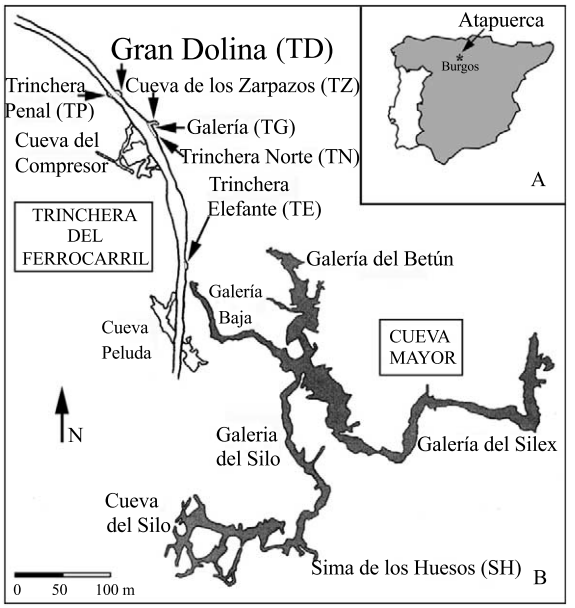

Fig. 1. Geographical situation of the Atapuerca Ibeas site. (A) Iberian Peninsula indicating the situation of Burgos (the nearest important town to the site). (B) Sites of Trinchera del Ferrocarril (showing the location of Gran Dolina in the north) and Cueva Mayor.

TD7 (Parés and Pérez-González, 1999), so lower levels (TD6–TD3/4) are older than 780 ka. Direct dating using ESR and U/Th has shown that large fossil mammals in TD6 range from 780 to 886 ka (Falguères et al., 1999). TD8a (lower TD8) is between 563 ± 84 ka and 653 ± 98 ka and TD10–11 is between 400 and 300 ka (Falguères et al., 1999).

A hiatus in fauna and stratigraphical succession at Gran Dolina was first revealed by the study of small mammals (Cuenca-Bescós et al., 1998), at the limit between TD8a and TD8b (upper TD8), possibly at the beginning of the Middle Pleistocene.

2. Micromammal associations

Approximately 5000 first lower molars (M_1) of micromammals were analysed at Gran Dolina to reconstruct the palaeoenvironment in the Lower and Middle Pleistocene at Atapuerca (López-Antoñanzas, 2000). The number of individuals per archaeological level varies from 9 to 1091 (Tables 1 and 2). The infilling contains 44 taxa (for detailed systematic data see Cuenca-Bescós et al., 1999a).

The micromammal assemblage is listed in Table 3. Taxa from TD3–TD8a are typical of the European late Early Pleistocene while those in TD8b–TD11 are from the European Middle Pleistocene.

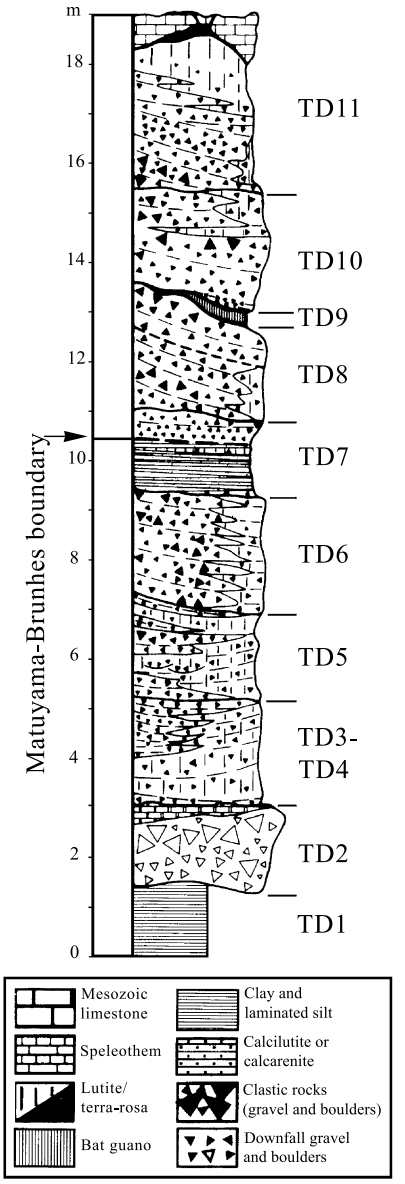

Fig. 2. Stratigraphic section of Gran Dolina (modified from Parés and Pérez-González (1999)).

3. Methods

Fossil micromammals are often useful to interpret palaeoclimates since they were sedentary and very sensitive to environmental changes. The main criterion to establish the ecology and habitat of the species that subsist nowadays was based on their modern counterparts (actualism). For extinct species, phylogenetic relationships and biogeographical criteria were used.

The dominance of some species can be used to predict the climate. However, reconstruction of past environments is an interdisciplinary task that requires support from other fields such as

Table 1
Number of individuals recorded in the lower levels of Gran Dolina (TD8a, Middle Pleistocene and TD6, TD5, TD4, TD3, Lower Pleistocene) included in the analysis

	TD8a	TD7	TD6								TD5					TD4		TD3
	T28	T30–31	T32	T34	T36	T40–41	T45	T48–49	T50	T54	T59	TD5-E5	T60	T61	T68–76	TD4BW	TD4	
ORDER CHIROPTERA																		
Miniopterus schreibersii	3			1			1		1						1		2	1
Myotis sp.	26		1					1	3			1			9		10	1
Rhinolophus sp. 1	5									4							2	1
Rhinolophus sp. 2																	1	
ORDER INSECTIVORA																		
Beremendia fissidens					2	2	2	1				1		10			1	
Crocidura sp.	3					2	2	2	2			1		1	5		10	
Neomys sp.																		
Sorex sp.	4								6						1			1
Sorex minutus		X	1	1	2	1	3	3				2		10	1		3	
Talpidae indet.					1			1						1	2			
Galemys sp.	1			1	1				1									
Talpa sp.	3	X			1										1			
Talpa europaea							1		1			4		5			1	
Erinaceus europaeus	2							1		1		1						
Erinaceus sp.				1			1		1					2			1	
ORDER LAGOMORPHA	X	X	X				X			X							X	
ORDER RODENTIA																		
Allophaiomys chalinei							1	4	22	28		2		1	6	12	2	1
Clethrionomys sp.																		
Iberomys huescarensis	42		2	2	1	3	6	11	10	7	3	16		25	14	132	22	5
Microtus sp.	7																	
Microtus seseae		15	42	64	98	17	24	15	3	3	9	162		84	1	20		1
Mimomys savini	2			1		X	5	2	2	8	3	9		19	1	4	3	
Pliomys episcopalis			1	2	1	2	2	1				6		18	3	10	8	2
Stenocranius gregaloides															12	301	122	23
Terricola arvalidens	2	1	13	30	25	4	14	4			10	116		105	5	29	10	2
Apodemus gr. *flavicollis-sylvaticus*	22	1			3		1	3	6					2	7		8	3
Allocricetus sp.	18	2	2	8	5	1	1	2	3	1	1	6		3	11		7	1
Micromys minutus							1	1							3			
Eliomys quercinus									X								2	
Hystrix refossa						X	X											
Castor fiber						X												
Marmota sp. 2		X			X									1			2	

X: presence of the species based on tooth but no M_1.

taphonomy, palynology, stratigraphy, biogeography, and statistics, in addition to fauna.

3.1. Species ecology at Gran Dolina

The ecological characteristics of modern small mammals are well known but those of fossil mammals are under debate.

Stenocranius gregaloides is an extinct species that gave way during the Middle Pleistocene to the extant *Stenocranius gregalis*, namely the Siberian vole (Chaline, 1990; Conroy and Cook, 2000). The latter is typical of the Siberian tundra, but occupies steppe areas in eastern and central Asia as well. *Stenocranius gregaloides* disappeared from the Gran Dolina site in the Early Pleistocene but remained in the Middle Pleistocene across northern and eastern Europe (Sutcliffe and Kowalski, 1976; Fejfar and Horácék, 1990; Horácék, 1990). This local disappearance will be discussed below.

Stenocranius gregaloides (Fig. 3) is associated

Table 2
Number of individuals recorded in the upper levels of Gran Dolina (TD8b, TD10 and TD11, Middle Pleistocene) included in the analysis

	TD11		TD10											TD8b
	250–270	270–290	T1	T2	T3	T4	T5	T11	T14	T15	T17	T18	T22	T24
ORDER CHIROPTERA														
Miniopterus schreibersii												1	1	1
Myotis sp.			1					2	20	1	7	6	6	
Myotis myotis	1													
Rhinolophus sp. 1							1		1					
ORDER INSECTIVORA														
Crocidura sp.	1						1						2	
Neomys sp.				2			1		2		1	2		
Sorex sp.	2	2	1	2	4		4	1	22		20	36	4	
Sorex minutus	2	1	2						11		2			
Talpidae indet.			2	3			1		2			4	1	
Galemys sp.	1			1					2		1			
Talpa europaea			1		1	1	2	1	3	1	2	3	1	
Talpa sp.														
Erinaceus europaeus			1	1	1	1	1	1	1	1		1	1	
ORDER LAGOMORPHA	X	X					X							
ORDER RODENTIA														
Arvicola sp.	2	2	X	1	1		1		4			4		
Clethrionomys sp.						1	1							
Iberomys brecciensis			2	17	2	1	9		2	2	2	0	14	3
Microtus agrestis	16	11	7	13	2	2	29	6	13		5	5	4	
Microtus arvalis	38	14	16	43	14	5	61	13	33	3	24	33	10	1
Pliomys lenki	9	4	3	4	2		8		1				5	
Terricola atapuerquensis	151	87	61	182	114	22	337	203	890	48	455	576	177	4
Apodemus gr. *flavicollis-sylvaticus*	2	1	5	4	2		4		4		2	1	1	
Allocricetus bursae	96	25	19	7	26	21	65	10	78	1	30	56	19	
Eliomys quercinus	1	1							2			3		
Castor fiber														
Marmota sp. 1									X					

X: presence of the species based on tooth but no M_1.

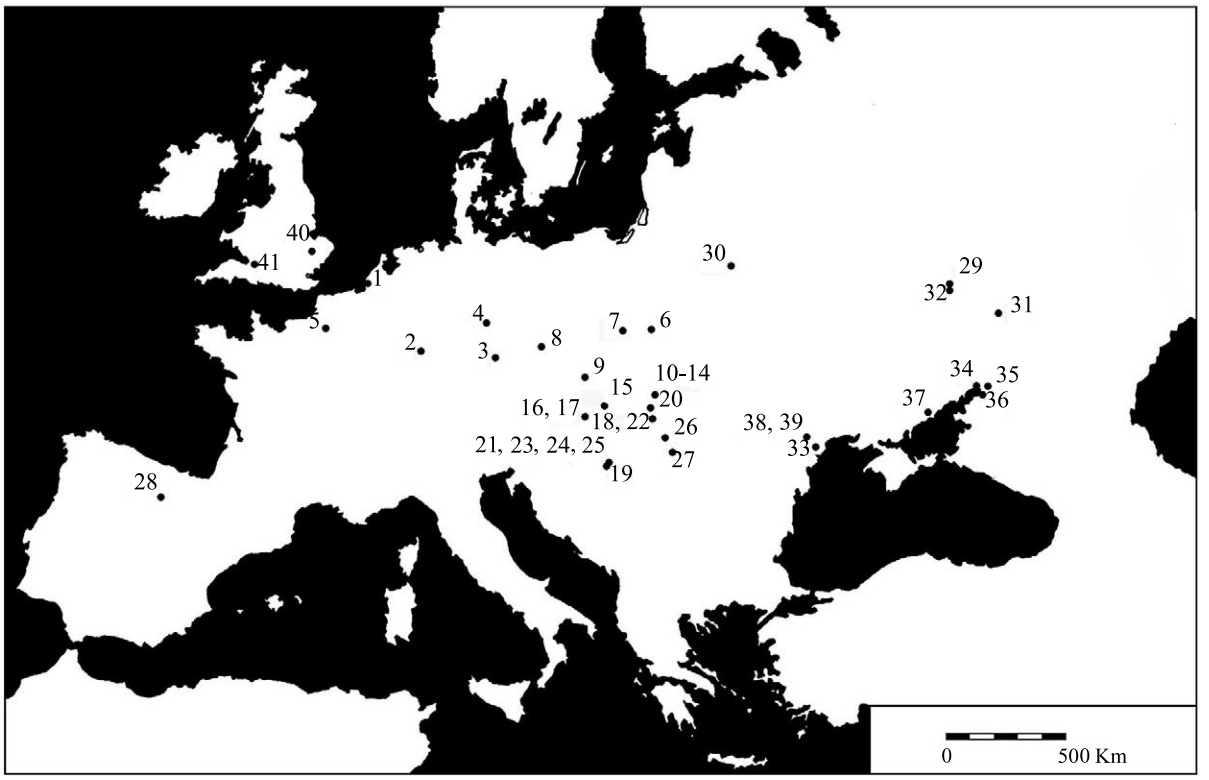

Fig. 3. Geographical distribution of Lower and Middle Pleistocene *Stenocranius gregaloides* in association with cold faunas. The Netherlands (1: Brielle 2), Germany (2: Hohensülzen, 3: Sackdilling, 4: Süssenborn), France (5: Grâce), Poland (6: Kozi Grzbiet, 7: Zalesiaki 1/A), Czech Republic (8: Chlum 4, 10: Holstejn, 11: Koneprusy C718, 12: Koneprusy JK 1–3, 14: Prezletice, 15: Stránská skála), Slovak Republic (9: Gombasek 1, 13: Plesivec 1, 16: Vceláre 1, 17: Zirany), Hungary (18: Kovesvárad, 19: Nagyhársányhegy 4, 20: Osztramos 12, 21: Somssich-hegy, 22: Tarko/Schicht 16, 23: Villány 6, 24: Villány 8/9–11, 25: Villány 8/12), Romania (26: Betfia 5, 27: Chiscan), Spain (28: Atapuerca), former USSR (29: Bogdanovka, 30: Korchevo, 31: Petropavlovka 2, 32: Uryv 3, 33: Bol'shevik, 34: Platovo 1, 35: Platovo 2, 36: Semibalka, 37: Tikhonovka 2, 38: Tiraspol 1, 39: Tiraspol 2), UK (40: West Runton, 41: Westbury).

with cold faunas in many Lower and Middle Pleistocene European sites (Chaline, 1974a; Clot et al., 1978; Maul, 1990; Nadachowski, 1991), including the arvicoline species *Dicrostonyx torquatus*, *Dicrostonyx simplicior*, *Dicrostonyx* sp., *Lemmus lemmus*, *Lemmus* sp., *Microtus nivalinus* (supposed ancestor of the extant *Microtus oeconomus*), which are typical of cold and even boreal climates. Some authors, such as Horácék (1990), also relate the numerical decrease of *Stenocranius gregaloides* with an increase of *Mimomys savini* and *Microtus arvaloides*. The latter has a similar morphology to *Microtus seseae* and *Terricola arvalidens* and, therefore, possibly similar ecological preferences. On the other hand, the decrease of the *Stenocranius* lineage from the Early Pleistocene to modern day is quite remarkable. Towards the end of the Pleistocene and during the Holocene, *Stenocranius gregalis* went extinct across most of Europe, only persisting in isolated nuclei in the northernmost areas of the Urals and western Siberia (Dupal, 1998). *Stenocranius gregaloides* most probably reached more southern areas during glacial periods, where the climate was cold enough but not too harsh. During the interglacials it would have withdrawn northwards in search of lower temperatures. Therefore, its presence in the Iberian Peninsula might indicate a period of harsh climate.

The biotope of *Iberomys brecciensis* can be in-

ferred from its descendant *Iberomys cabrerae*, viz. the Mediterranean vole (López-Martínez, 1980), both endemic rodents of the Iberoccitana province. This hypothesis is supported because the morphology of the occlusal surface of M_1 is similar in both species. *Iberomys huescarensis* was the first representative of the *Iberomys* lineage to evolve in the Iberian Peninsula from a population of *Allophaiomys hintoni*, which were widespread in the later part of the Early Pleistocene. The *Iberomys* lineage appeared towards the end of the Early Pleistocene when *Iberomys huescarensis*

Table 3
Micromammal assemblage of Gran Dolina

	TD3	TD4	TD5	TD6	TD7	TD8a	TD8b	TD10	TD11
ORDER CHIROPTERA									
Miniopterus schreibersii	♦	♦	♦	♦		♦	♦	♦	
Myotis sp.	♦	♦	♦	♦		♦		♦	
Myotis myotis									♦
Rhinolophus sp. 1	♦	♦		♦		♦		♦	
Rhinolophus sp. 2		♦							
ORDER INSECTIVORA									
Beremendia fissidens		♦	♦	♦					
Crocidura sp.		♦	♦	♦		♦		♦	♦
Neomys sp.								♦	
Sorex sp.	♦		♦	♦		♦		♦	♦
Sorex minutus		♦	♦	♦	♦			♦	♦
Talpidae indet.			♦	♦				♦	
Galemys sp.				♦		♦		♦	♦
Talpa sp.			♦	♦	♦	♦			
Talpa europaea		♦	♦	♦				♦	
Erinaceus europaeus			♦	♦		♦		♦	
Erinaceus sp.		♦	♦	♦					
ORDER LAGOMORPHA		♦		♦	♦	♦		♦	♦
ORDER RODENTIA									
Terricola arvalidens	♦	♦	♦	♦	♦	♦			
Allophaiomys chalinei	♦	♦	♦	♦					
Iberomys huescarensis	♦	♦	♦	♦		♦			
Microtus aff. *M. ratticepoides*						♦			
Microtus seseae	♦	♦	♦	♦	♦				
Mimomys savini		♦	♦	♦		♦			
Pliomys episcopalis	♦	♦	♦	♦					
Stenocranius gregaloides	♦	♦	♦						
Terricola atapuerquensis							♦	♦	♦
Arvicola sp.								♦	♦
Clethrionomys sp.								♦	
Pliomys lenki								♦	♦
Iberomys brecciensis							♦	♦	
Microtus agrestis								♦	♦
Microtus arvalis							♦	♦	♦
Apodemus gr. *flavicollis-sylvaticus*	♦	♦	♦	♦	♦	♦		♦	♦
Allocricetus bursae								♦	♦
Allocricetus sp.	♦	♦	♦	♦	♦	♦			
Micromys minutus			♦	♦					
Eliomys quercinus		♦		♦		♦		♦	♦
Hystrix refossa				♦					
Castor fiber				♦					
Marmota sp. 1								♦	
Marmota sp. 2		♦	♦	♦	♦				

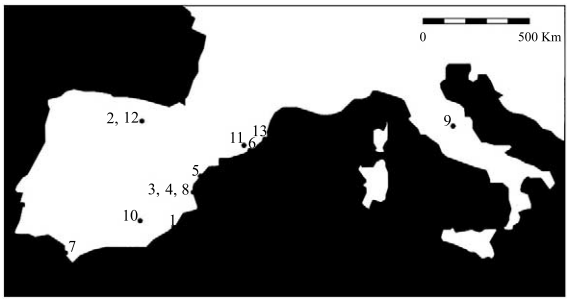

Fig. 4. Geographical distribution of *Allophaiomys chalinei*. 1: Cueva Victoria (Murcia); 2: Gran Dolina (Sierra de Atapuerca, Burgos); 3, 4: Muntanyeta dels Sants y El Castell (Valencia); 5: Almenara-3 (Castellón); 6: Castelldefels (Barcelona); 7: La Cabezas (Cádiz); 8: Autopista A-7, Km 585 (Valencia); 9: Pietrafitta (Italy); 10: Fuente Nueva-3 (Granada); 11: Cal Guardiola (Barcelona); 12: Sima del Elefante (Sierra de Atapuerca, Burgos); 13: Bagur-2 (Girona) (after Laplana, 1999).

was in southern regions of western Europe, i.e. southern France and Spain (Laplana et al., 2000). *Allophaiomys hintoni* has been found in northern sites (Untermassfeld and Neuleiningen: Germany), where it is mentioned as *Microtus thenii* (Maul, 1996) and in the south. The southernmost record is at Podumci 1, Croatia (Malez and Rabeder, 1984). Its widespread distribution implies ecological preferences that were not strongly influenced by climate. The Mediterranean adaptations of the *Iberomys* lineage were probably not complete until the early Middle Pleistocene when the direction of some evolutionary trends suffered reversions including a shift to more asymmetric molars. Therefore, *Iberomys huescarensis* would be more similar to its ancestor *Allophaiomys hintoni* than to its descendant, *Iberomys brecciensis*. Hence, the habitat of *Iberomys huescarensis* should not be extrapolated from the modern *Iberomys cabrerae*.

Iberomys cabrerae has very strict habitat requirements and is always associated with conditions of certain moisture in the ground (San Miguel, 1994).

The extinct *Terricola arvalidens* is the oldest representative of the recent *Terricola subterraneus-multiplex* group (Brunet-Lecomte, 1988, 1990; Brunet-Lecomte and Chaline, 1991).

Microtus seseae is a fossil species with unknown affinities within the genus *Microtus*. On the basis of its morphological similarities to *Terricola arvalidens*, it may have had similar ecological preferences.

According to Cuenca-Bescós et al. (1999b), *Terricola atapuerquensis* is morphologically close to *Terricola vaufreyi*, which belongs to the *subterraneus-multiplex* group (Brunet-Lecomte, 1990). For this reason, the ecological preferences of *Terricola atapuerquensis* were probably similar to living representatives of this group of ground voles in central Europe.

Allophaiomys chalinei (Fig. 4) has only been found in the Iberian Peninsula and Italy (Pietrafitta) (Laplana, 1999), especially on the Mediterranean coast. This suggests that this species is typical of a Mediterranean climate without important contrasts.

According to Fejfar and Horácék (1990), *Pliomys episcopalis* is found within dry associations whereas *Pliomys lenki* lived in wooded areas or during moister periods. Other authors, such as Marquet (1989), place *Pliomys lenki* in open environments that were neither too dry nor wet. It was probably typical of open spaces and common in rather dry Mediterranean areas with scrub (cf. Chaline, 1974b; Chaline et al., 1995). In fact, as shown below, the distribution of both species appears random.

Mimomys savini is the ancestor of *Arvicola mosbachensis*, itself the ancestor of the aquatic species *Arvicola terrestris* and *Arvicola sapidus*. Most species in the genus *Arvicola* are swimmers so the ecological requirements of *Mimomys savini* may have been very similar to the extant species of *Arvicola*, i.e. it was probably a swimmer species.

Allocricetus bursae is closely related to the genus *Cricetulus*, especially with respect to odontological characteristics (Marquet, 1989). Moreover, Chaline (1974b) suggests that *Cricetulus migratorius* is a descendant of *Allocricetus bursae*. Therefore, it is likely that *Allocricetus bursae* had a similar diet and, consequently, similar habitat to the *Cricetulus* species, i.e. steppes under dry conditions, as already suggested by several authors (Chaline, 1974b; López-Martínez, 1980; Marquet, 1989; Sesé, 1991; Desclaux, 1992).

Based on the current geographical distribution of *Hystrix cristata* (porcupine), representatives of the family Hystricidae are sometimes used to indicate hot climates. Nevertheless, *Hystrix* remains have been found with cold faunas in the Lower Pleistocene. Thus, in Osztramos 8 (northeastern Hungary), *Hystrix major* and *Hystrix vinogradovi* are found together with *Lemmus* sp. (Jánossy, 1986). In historic times, a rigorous climate did not hamper the expansion of *Hystrix* in Great Britain. At Gran Dolina (TD6T43 and TD5T53), *Hystrix refossa* coexisted with *Marmota marmota*, a species traditionally considered an indicator of cold climates. In the Galería site, remains of *Hystrix vinogradovi* have been found in association with *Marmota marmota*. Based on this evidence, Cuenca-Bescós et al. (1999b) question whether *Hystrix* and *Marmota* are valuable climatic indicators. Furthermore, recent results do not support the correlation between phylogeny and climatic tolerance for extant species of *Marmota* (Davis, 2001). For all these reasons, *Hystrix* and *Marmota* were not used as climatic indicators in the present study.

Traditionally, species of the order Insectivora have been considered indicators of wet environments. However, for some species (*Talpa europaea*, *Galemys pyrenaicus*) the edaphological characteristics and the presence of water currents are more limiting than the climate. Other species, including *Crocidura* spp. (Crocidurinae), are occasionally considered steppe inhabitants (Rabeder, 1972; Reumer, 1984) but their climate preferences remain unclear. Rabeder (1972) considers that *Crocidura* indicates hot climates whereas Reumer (1984) concludes that it can endure low temperatures, based on its distribution in Europe. Because species of *Crocidura* have adapted to diverse environments (Kotsakis, 1984) and the identification of *Crocidura* species at Gran Dolina remains doubtful, this taxon is excluded from the following analysis.

3.2. Relative abundance of soricines and cricetines as indicators of humidity–dryness

Soricinae are unambiguous indicators of humidity (Wolf-Dieter and Janossy, 1978). On the contrary, as mentioned above, *Allocricetus bursae* (Cricetinae) probably lived in open and dry environments. Wet/dry oscillations at Gran Dolina can, therefore, be appreciated by comparing the percentages of soricines and cricetines (only represented by the genus *Allocricetus*).

Even though most samples are very rich in fossil micromammals, insectivores (and therefore soricines) are quite scarce. Therefore, to make the analysis more reliable, adjacent samples with similar fauna are joined.

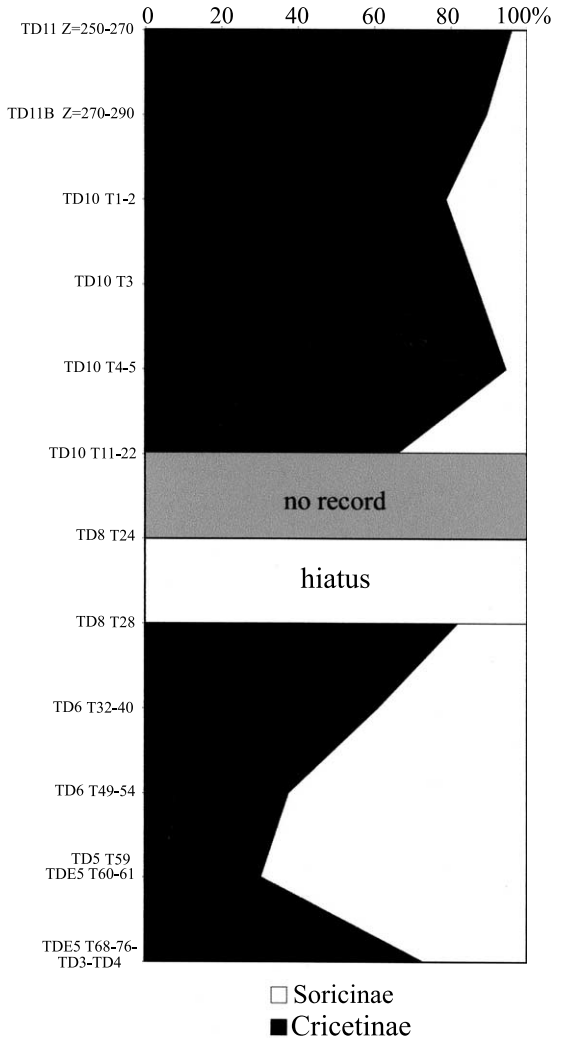

Fig. 5. Variation in the Cricetinae–Soricinae ratio along the Gran Dolina sequence as indicators of relative moisture.

An analysis of the most striking changes in Fig. 5 is presented below.

3.2.1. TD3, TD4, TD5bcd T68–76

The environment was probably dry since cricetines (73%) are more abundant than soricines (27%). According to Chaline (1974c), *Crocidura* would be typical of dry environments. Its relative abundance (15 specimens) in these levels lends support to this hypothesis.

3.2.2. TD5 T61–59

In this part of level TD5, soricines increase dramatically (70%), cricetines decrease (30%), and crocidurines disappear, implying a considerable climatic change, probably towards moister conditions. The acme of *Beremendia fissidens* (11 specimens) occurs here.

3.2.3. TD6

TD6 T54–49 (lower part of TD6): Soricines decrease slightly (62%) and, consequently, cricetines increase (38%), implying a drier environment than the previous level.

TD6 T40–32: The structure of the association of micromammals changes again with respect to the lower level. Soricines decrease (39%) implying drier conditions.

3.2.4. TD7

Not enough material was available at this level to make inferences about humidity (only two M_1 of *Allocricetus bursae* and no soricine remains).

3.2.5. TD8

Lower TD8 (TD8a): Cricetines are abundant (82%) implying dry conditions but, when the global community is considered (especially the high percentage of murines and glirids), it appears that the degree of dryness was not extreme. In addition, this is the only level with *Hippopotamus amphibius*, although the identification is based on an isolated incisive (Van der Made, 1998).

Upper TD8 (TD8b): No inferences are made since no soricines or cricetines have been found.

3.2.6. TD10

In the lower archaeological sublevels (T22–T11), the high relative proportion of cricetines (66%) reflects a dry environment. Conditions may have been even drier at sublevels T5 and T4, in which the proportion of cricetines increases (94.5%). It decreases in T3 (87%) and T1–T2

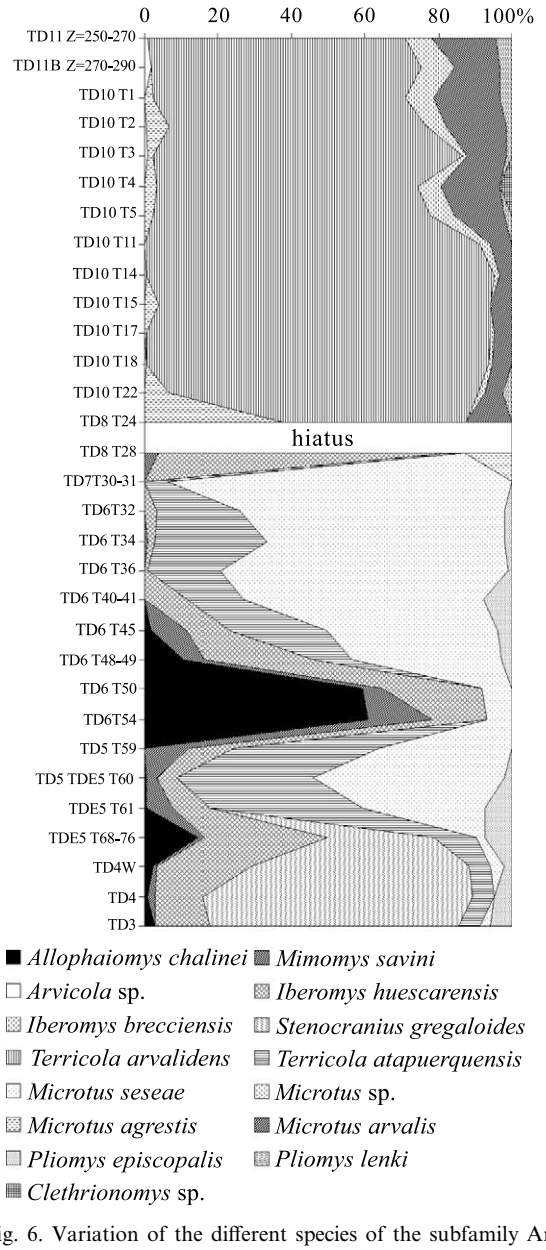

Fig. 6. Variation of the different species of the subfamily Arvicolinae along the Gran Dolina sequence. Percentages are expressed in Tables 4 and 5.

(79%), but the climate was probably still quite dry.

3.2.7. TD11

Samples at TD11 Z 270–290 and TD11 Z 250–270 are very rich in cricetines (94.5%), so the climate may have been even drier than that inferred for the upper part of TD10 (T1–T3). At the top of TD11 (TD11 Z 250–270), the aridity was similar to TD10 T5–T4 (i.e. the maximum for TD10 globally).

In general, oscillations across the upper section of Gran Dolina (Middle Pleistocene) are not as clear as in the Lower Pleistocene part. This might be the consequence of a faster rate of sedimentation, which results in a more homogeneous fauna.

3.3. Relative abundance of the different species pertaining to the subfamily Arvicolinae

This section analyses the fluctuations within the subfamily Arvicolinae (Rodentia). A particular study of arvicolines is essential since they are the best recorded subfamily at Gran Dolina and represent at least 50% of all the material (Fig. 7). The changes they underwent were probably the result of climatic oscillations that led some to migrate. Their ecological niches were subsequently occupied by other species, which expanded rapidly.

Fig. 6 shows the relative abundance of arvicoline species throughout the succession. Percentages are expressed in Tables 4 and 5 and details are provided below.

3.3.1. TD3, TD4, TD4W

Stenocranius gregaloides, which may indicate low temperatures, is clearly dominant followed by *Iberomys huescarensis* and minor percentages of *Microtus seseae*, *Terricola arvalidens*, *Allophaiomys chalinei*, and *Pliomys episcopalis*. Possibly, the Iberian Peninsula was undergoing a glacial period.

3.3.2. TD5

In the lower part of this level (TD5 T68–76), there is an important expansion of *Iberomys huescarensis* (one of the most important of the Gran Dolina succession) and *Allophaiomys chalinei* increases by about 10%. The development of both species correlates with a decrease of *Stenocranius gregaloides*, indicating slightly warmer temperatures. However, the climate would still have been cold.

Important changes occur upward (TD5 T61). *Iberomys huescarensis* decreases and *Stenocranius gregaloides* and *Allophaiomys chalinei* are replaced by *Microtus seseae* and *Terricola arvalidens*. The nearly complete colonisation by the latter two species coincides with wetter conditions (Fig. 5). This could suggest, keeping in mind the ecological preferences of the extant *Terricola subterraneus* (wet meadow), that these species might have found a more favourable environment under these

Table 4
Percentages of the different species pertaining to the Arvicolinae subfamily recorded in the lower levels of Gran Dolina (TD8a, Middle Pleistocene and TD6, TD5, TD4, TD3, Lower Pleistocene)

	TD8	TD7	TD6								TD5				TD4		TD3
	T28a	T30–31	T32	T34	T36	T40–41	T45	T48–49	T50	T54	T59	T60	T61	T68–76	TD4BW	TD4	
Allophaiomys chalinei							1.92	10.81	59.46	60.87	0.00	0.64	0.40	14.29	2.36	1.20	2.94
Clethrionomys sp.	0.00		0.00	0.00	0.00	0.00	0.00		0.00		0.00	0.00	0.00		0.00		
Iberomys huescarensis	79.25		3.45	2.02	0.80	11.54	11.54	29.73	27.03	15.22	12.00	5.14	9.92	33.33	25.98	13.17	14.71
Mimomys savini	3.77		0.00	1.01	0.00		9.62	5.41	5.41	17.39	12.00	2.89	7.54	2.38	0.79	1.80	
Microtus sp.	13.2		0.00	0.00	0.00	0.00	0.00		0.00		0.00	0.00	0.00		0.00		
Microtus seseae	0.00	93.75	72.41	64.65	78.40	65.38	46.15	40.54	8.11	6.52	36.00	52.09	33.33	2.38	3.94		2.94
Pliomys episcopalis	0.00		1.72	2.02	0.80	7.69	3.85	2.70	0.00		0.00	1.93	7.14	7.14	1.97	4.79	5.88
Stenocranius gregaloides	0.00		0.00	0.00	0.00	0.00	0.00		0.00		0.00	0.00	0.00	28.57	59.25	73.05	67.65
Terricola arvalidens	3.77	6.25	22.41	30.30	20.00	15.38	26.92	10.81	0.00		40.00	37.30	41.67	11.90	5.71	5.99	5.88

conditions of humidity. However, as shown below, the expansion of *Microtus seseae* and *Terricola arvalidens* in the upper part of TD6 (T40–T32) coincides with increasing dryness (Fig. 5), implying that their increase was more related to temperature than humidity. In any case, the faunal association is characteristic of an interglacial climate and persists throughout the upper TD5 (TD5–TDE5 T60 and TD5 T59).

3.3.3. TD6

Lower TD6 (T54–T50): The population of arvicolines underwent another drastic change in the lower part of this level. The decrease of *Terricola arvalidens* and *Microtus seseae* concurs with the expansion of *Allophaiomys chalinei* (a species not very abundant to date) and *Iberomys huescarensis*. This is probably because of a new climatic oscillation. According to Agusti (1991), *Allophaiomys chalinei* would have preferred dry environments because it was found only in karstic fillings. However, it is now known in marshy deposits like Pietrafitta (Gentilli et al., 1996) and Fuente Nueva 3 (Martínez-Navarro et al., 1997). The great increase of *Allophaiomys chalinei* in the lower part of TD6 (T54–T49) coincides with drier conditions (Fig. 5). Nevertheless, it disappears in the upper part of TD6 (T40–T32), where *Microtus seseae* and *Terricola arvalidens* expand concurrently, under increasing dryness (Fig. 5). Therefore, as shown above, the successive replacement of *Microtus seseae* and *Terricola arvalidens* by *Allophaiomys chalinei* (and vice versa) was probably more related to changes in temperature than humidity. Since *Allophaiomys chalinei* has only been found in southern Europe, especially along the Mediterranean coasts (Fig. 4), its expansion in the lower part of TD6 (T54–49) was probably more related with an increase in temperature than with a drop in humidity.

At sublevel T48–49, *Terricola arvalidens* and *Microtus seseae* increase again along with a drastic decrease in *Allophaiomys chalinei* (10% vs. 60% in previous sublevels). This indicates another climate change but the interglacial conditions probably persisted since no species indicates a clear temperature drop.

Upper TD6: T45 is the last archaeological sublevel with *Allophaiomys chalinei*. As mentioned above, in TD6 T45–32, a progressive decrease of *Iberomys huescarensis* and an expansion of *Terricola arvalidens* and *Microtus seseae* is observed. The association of arvicolines is similar to the previous sublevel described (T48–49), implying stable climatic conditions.

3.3.4. TD7

The arvicolines identified in this level are *Terricola arvalidens* and *Microtus seseae*, but the fossil content of the sample is rather scarce.

3.3.5. TD8

Lower TD8 (TD8a): Even though this horizon is already in the Brunhes magnetozone and therefore in the Middle Pleistocene, its fauna is still typical of the Lower Pleistocene. Typical Middle Pleistocene fauna starts to occur from the upper part of TD8 (TD8b).

Several remarkable events occurred in TD8a including the disappearance of *Microtus seseae* and *Terricola arvalidens*, the great abundance of *Iberomys huescarensis* and, especially, the appearance of *Microtus* aff. *ratticepoides*. The latter is usually associated with cold faunas (Laplana, in preparation) such as *Lemmus* sp. at Hohensülzen, Germany (Storch et al., 1973), *Lemmus* sp. and *Dicrostonyx* sp. at Grâce, France (Chaline, 1974a), and *Lemmus* sp. and *Predicrostonyx compitalis* in level 1A/13 of Zalesiaki, Poland (Nadachowski, 1991). Therefore, its ecological affinities were possibly similar to lemmings, indicating a cold climate. Probably, the lower part of this level deposited during a glacial period.

The record of one isolated incisor of *Hippopotamus amphibius* (Van der Made, 1998) seems to be inconsistent with a cold climate. Alberdi and Ruiz-Bustos (1985, p. 256) question the traditional opinion according to which this animal is unequivocally related with a warm climate. The fact that this species has been recorded in TD8a does not contradict the assumption that this sublevel corresponds to a cold climate because the glacial periods in southern Europe would not have been as harsh as in northern areas.

Upper TD8 (TD8b): No inferences are made for this section because the fossil record is poor.

The arvicolines are *Iberomys brecciensis*, *Terricola atapuerquensis*, and *Microtus arvalis*, all typical of the Middle Pleistocene. The acme of *Iberomys brecciensis* occurred here at 40% of all arvicolines. The dominant species is *Terricola atapuerquensis* (50%) while the least common is *Microtus arvalis*.

3.3.6. TD10, TD11

Both levels have a very homogeneous fauna, which is probably the result of a rapid rate of sedimentation.

Terricola atapuerquensis is the dominant species followed by *Microtus arvalis*, which never exceeds 20% of the total. The upper part of TD10 (TD10 T5–T1) and TD11 have the highest proportions of *Microtus arvalis* at Gran Dolina. According to Pokines (1998), the extant representatives of this species prefer open and dry environments. This agrees with the proportion of cricetines (Fig. 5) that suggest an increased aridity in the upper part of TD10 and in TD11.

Chaline et al. (1995) note that the respective abundances of *Microtus arvalis* and *Microtus agrestis* vary inversely, but in this study both species tend to increase in the same sublevels.

The appearance of *Arvicola* sp. is discontinuous and only represented by a few individuals. This might be the result of a taphonomic bias since this taxon was not within the size range of the preys of avian predators that were responsible for the micromammal accumulation in TD10 and TD11. These birds include *Falco tinnunculus* (kestrel) in TD10 and *Asio otus* (long-eared owl) in TD10 and TD11 (Fernández-Jalvo, 1995a,b). The presence of *Arvicola* sp. indicates the presence of a nearby river (nowadays known as Arlanzón) because it was adapted to water environments.

Two lower molars of *Clethrionomys* sp. are found in TD10 T4 and TD10 T5, indicating a dense forest (Chaline et al., 1995).

Iberomys brecciensis and *Pliomys lenki* are also present, but intermittently and never above 10% of all arvicolines. The biology of *Pliomys lenki* is controversial. Some authors (Chaline, 1974b; Marquet, 1989) consider that it inhabited open environments that were neither very dry nor wet (i.e. a typical dweller of Mediterranean areas with scrub) while others (Fejfar and Horácék, 1990) place it in humid periods or woody areas. For Chaline (1974b), the variation in the number of individuals of *Pliomys lenki* coincides with those of *Microtus arvalis* and *Allocricetus bursae*. At Gran Dolina, the distribution of *Pliomys lenki* is quite random, so neither opinion is supported.

The association of arvicolines in both levels is typical of an interglacial climate.

3.4. Relative abundance of Arvicolinae, Murinae and Cricetinae and Insectivora

This section considers the abundance of the most representative groups (Arvicolinae, Murinae, Cricetinae and Insectivora) in the entire faunal succession of Gran Dolina (Fig. 7).

Arvicolines always constitute the dominant subfamily. This is probably not a taphonomic bias because most predators identified at Gran Dolina were opportunistic (Fernández-Jalvo, 1995a,

Table 5
Percentages of the different species pertaining to the Arvicolinae subfamily recorded in the upper levels of Gran Dolina (TD8b, TD10 and TD11, Middle Pleistocene)

	TD11		TD10											TD8b
	250–270	270–290	T1	T2	T3	T4	T5	T11	T14	T15	T17	T18	T22	T24
Arvicola sp.	0.93	1.69		0.38	0.74	0.00	0.22	0.00	0.42	0.00	0.00	0.65	0.00	
Clethrionomys sp.						3.23	0.22	0.00	0.00	0.00	0.00	0.00	0.00	
Iberomys brecciensis			2.25	6.54	1.48	3.23	2.02	0.00	0.21	3.77	0.41	0.00	6.67	37.5
Microtus sp.						0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
Microtus agrestis	7.41	9.32	7.87	5.00	1.48	6.45	6.50	2.70	1.38	0.00	1.03	0.81	1.90	
Microtus arvalis	17.59	11.86	17.98	16.54	10.37	16.13	13.68	5.86	3.50	5.66	4.94	5.34	4.76	12.5
Pliomys lenki	4.17	3.39	3.37	1.54	1.48	0.00	1.79	0.00	0.11	0.00	0.00	0.00	2.38	
Terricola atapuerquensis	69.91	73.73	68.54	70.00	84.44	70.97	75.56	91.44	94.38	90.57	93.62	93.20	84.29	50

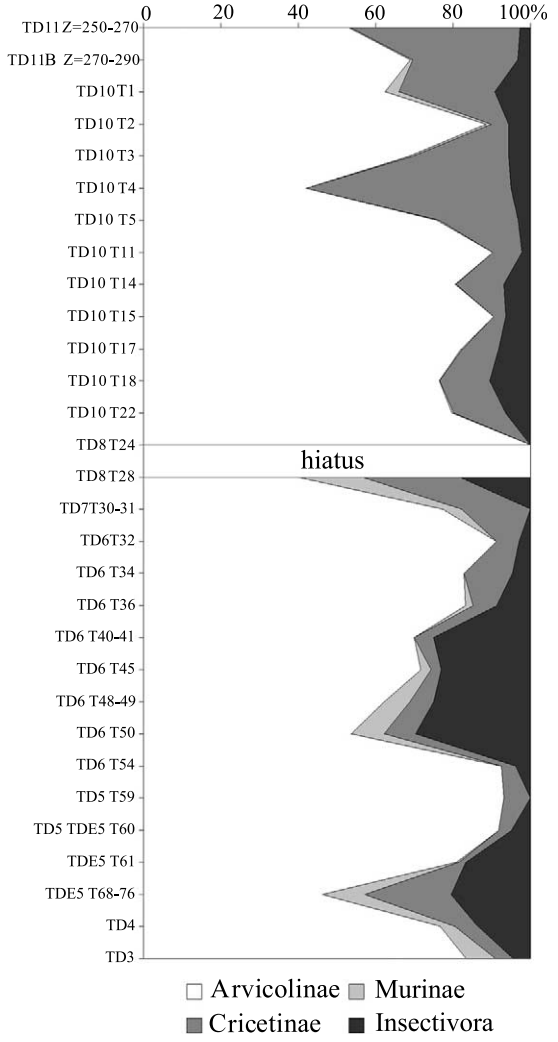

Fig. 7. Relative abundances of the representatives of the order Insectivora, the subfamilies Arvicolinae, Cricetinae and Murinae at Gran Dolina.

1998). However, the proportion of insectivores may be biased because the feeding preferences of *Asio otus* did not include species of this group (Corral et al., 1979; Delgado et al., 1986).

In the lower part of the succession (Lower Pleistocene), three points of minimum abundance of arvicolines are noteworthy. These coincide with important changes within this subfamily such as migration, substitution and disappearance of species and also with an increase in the abundance of cricetines, murines and insectivores. Since these groups are characteristic of different biotopes, the changes probably reveal a shift from a simple, monotonous ecosystem in the Atapuerca area to a more varied one. Considerable climatic changes can then be inferred. The complex populations of steppe species (such as *Allocricetus bursae* and, possibly, *Stenocranius gregaloides*) and species typical of wooded warm areas (such as *Apodemus* gr. *sylvaticus-flavicollis*, *Eliomys quercinus*, and several species of insectivores) suggests a transition between phases of distinct climates (cf. Chaline, 1974b and Chaline and Brochet, 1989). As shown below, the three points of minimum abundance of arvicolines also coincide with climatic transitions highlighted by the diversity indices of Shannon–Wiener and Simpson (Figs. 8 and 9).

3.4.1. TD3, TD4

Arvicolines predominate (85% of the global population) followed by murines (4.5%), cricetines (3.5%), and insectivores (7%). These proportions reflect a rather open environment, although the presence of Murinae (*Apodemus* gr. *sylvaticus-flavicollis*), Gliridae (*Eliomys quercinus*), and Insectivora (*Erinaceus europaeus*) also indicates the presence of forests.

3.4.2. TD5

Cricetines great increase in the lower part of TD5 (TD5 T68–76) from 3.8% to 21.15%, as well as insectivores (from 2.76% to 8.76%) and murines (from 4.4% to 19.2%) with a subsequent decrease in arvicolines. The record of *Apodemus* gr. *sylvaticus-flavicollis* confirms the presence of forest patches, although glirids are not found. This archaeological sublevel coincides with the first of the three points marking a climatic change. The complex population of steppe micromammals (*Allocricetus bursae*, *Stenocranius gregaloides*) and species typical of warm wooded areas (e.g. *Apodemus* gr. *sylvaticus-flavicollis*, *Eliomys quercinus*, and several insectivore species) suggests that there was a transition from a cold phase to a warmer one. At the transition, the population of *Stenocranius gregaloides* may have been significantly reduced, prior to its complete disappearance from the Iberian Peninsula.

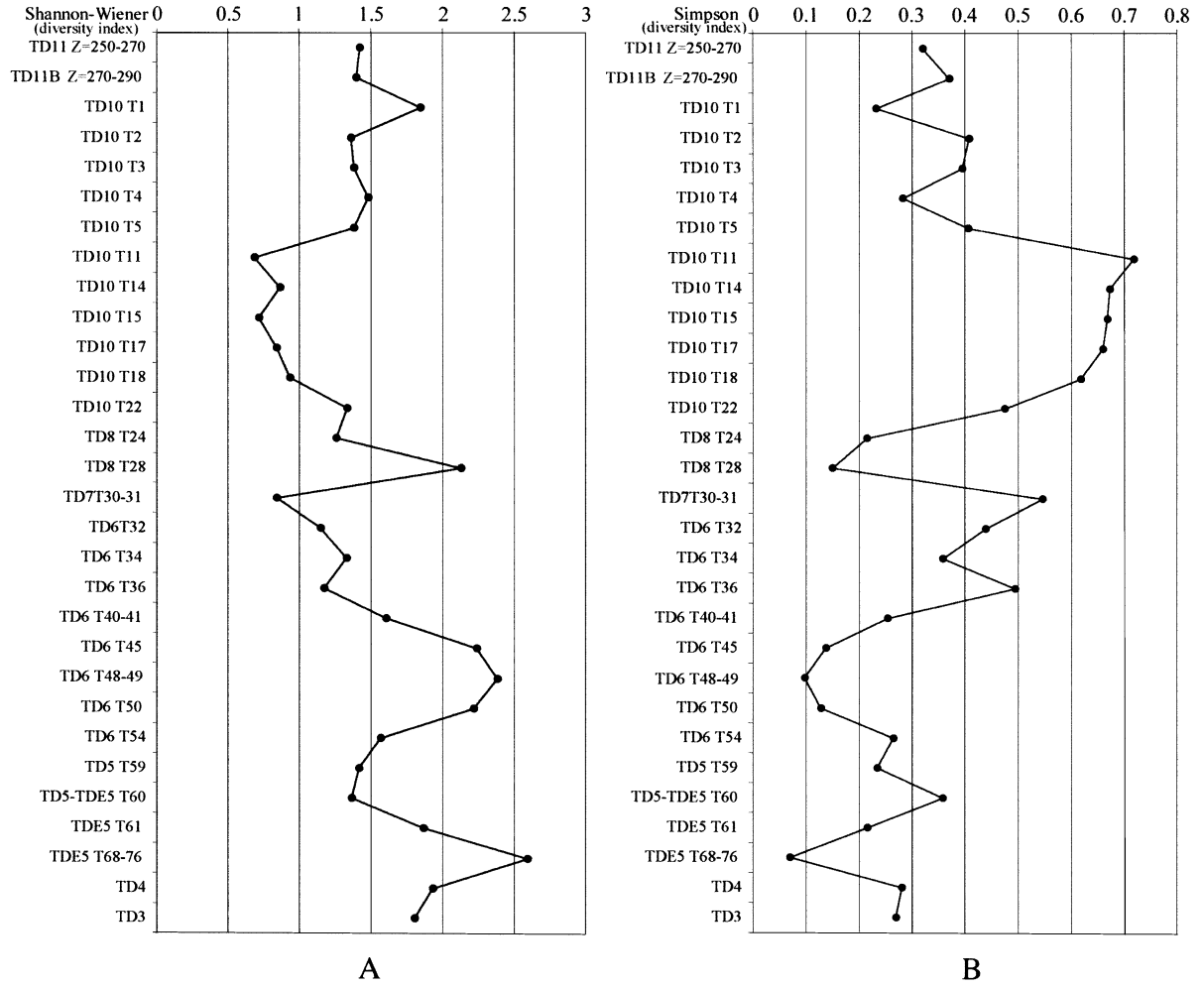

Fig. 8. Representation of faunal diversity. (A) Shannon–Wiener index obtained from the minimum number of individuals. (B) Simpson index obtained from the minimum number of individuals.

Higher up, at sublevel 61, there is an important decrease in the number of cricetines (from 21.15% to 1.07%) and murines (from 19.23% to 0.71%). The insectivores also decrease significantly, but to a lesser degree, while arvicolines increase to almost 80%. The increase in arvicolines and the large decrease in murines and cricetines coincide with the expansion of *Microtus seseae* and *Terricola arvalidens*. Hence, these species were probably involved in a competition for habitat that caused their significant retreat. The presence of *Erinaceus europaeus* still indicates the existence of forests, although *Eliomys quercinus* is not found at this horizon. *Marmota marmota* (Sciuridae), an extant high-mountain dweller, is also present.

The decrease of insectivores in the upper part of TD5 (TD5–TDE5 T60 and TD5 T59 and in TD6 T54) implies an increase of dryness. Although no representatives of *Apodemus* gr. *sylvaticus-flavicollis* are found, the appearance of the hedgehog *Erinaceus europaeus* still indicates the presence of forest patches. The environment would be slightly more open than at the lower part of this level.

3.4.3. TD6

Lower TD6 (TD6 T50 and T48–49): The second important climatic change occurs at this part of the level. The proportion of arvicolines decreases again whereas murines, insectivores and cricetines expand once more. Species adapted to warm climates and wooded habitats, such as *Erinaceus europaeus* and *Eliomys quercinus*, are also common.

Upper TD6: In TD6 T45 and T40–41 the decrease of murines and cricetines, which favours the expansion of arvicolines, is observed once more. The percentage of Insectivora remains nearly constant. The record of *Erinaceus europaeus* and *Apodemus* gr. *sylvaticus-flavicollis* implies the presence of forest patches.

In the uppermost part of this level (archaeological sublevels 36–32), the insectivores decrease progressively. The environment was probably open and rather dry.

3.4.4. TD7

Fig. 7 shows an expansion of the cricetines. This might suggest that the dry conditions characteristic of upper TD6 were maintained when this level was deposited. Nevertheless, these results should be taken cautiously because the sample is quite poor.

3.4.5. TD8

Lower TD8 (TD8a): TD8 T28 marks the third regression of arvicolines and expansion of cricetines and murines that reflects the third climatic change at Gran Dolina. The prevailing conditions might have corresponded to a glacial period. It is noteworthy that *Allocricetus* dominates over *Apodemus* at all levels of the succession except TD8a. The high number of murines (*Apodemus* gr. *flavicollis sylvaticus*), along with the presence of *Eliomys quercinus* and insectivores (Erinaceinae), indicates the existence of forest areas.

The large number of bats suggests that the cave was quite closed at this time.

Upper TD8 (TD8b): The sample from the upper section of this level is not analysed since it is quite poor and only contains arvicolines.

3.4.6. TD10, TD11

Arvicolines are the best represented group, although the percentage of the cricetine *Allocricetus bursae* is also important. The latter reaches its acme in the upper part of the succession (TD10 T4, T1 and in TD11), which coincides with the maximum expansion of *Microtus arvalis*. This event is related to an increase in aridity (Fig. 5). The *Apodemus* gr. *sylvaticus-flavicollis* is scarce or absent, although the record of *Erinaceus europaeus* and *Eliomys quercinus* indicate forest areas. The insectivores are not very abundant but their presence remains constant throughout the unit. *Marmota marmota* is found in archaeological sublevel T14.

The remaining archaeological sublevels have an exceptionally rich fossil content except for TD10 T15 and T4.

TD10 lacks species that would indicate a cold climate so an interglacial period can be inferred for this level. An arid steppe species (*Allocricetus bursae*) coexists with a humid meadow species (*Terricola atapuerquensis*), probably reflecting a landscape where high areas were more arid and steppe-like, and the valleys maintained a higher level of humidity.

3.5. Diversity analyses

One way to measure the development of an ecosystem is to study the distribution of the number of individuals in relation to the number of species. This distribution is the specific diversity, which is more informative than a mere estimation of the number of species, viz. the specific richness (López-Martínez and Truyols, 1994, p. 155).

Specific diversity is normally measured using the Simpson, Shannon–Wiener or Whittaker indices (Andrews et al., 1979; De Bonis et al., 1992). The Shannon–Wiener index was chosen here since it is the most widely used to measure ecological diversity and is reasonably independent of sample size and misidentification of poorly sampled species (López-Martínez and Truyols, 1994). The results from this index coincide with the Simpson index (Figs. 8 and 9).

The Shannon–Wiener index is usually designated by the symbol H' and responds to the fol-

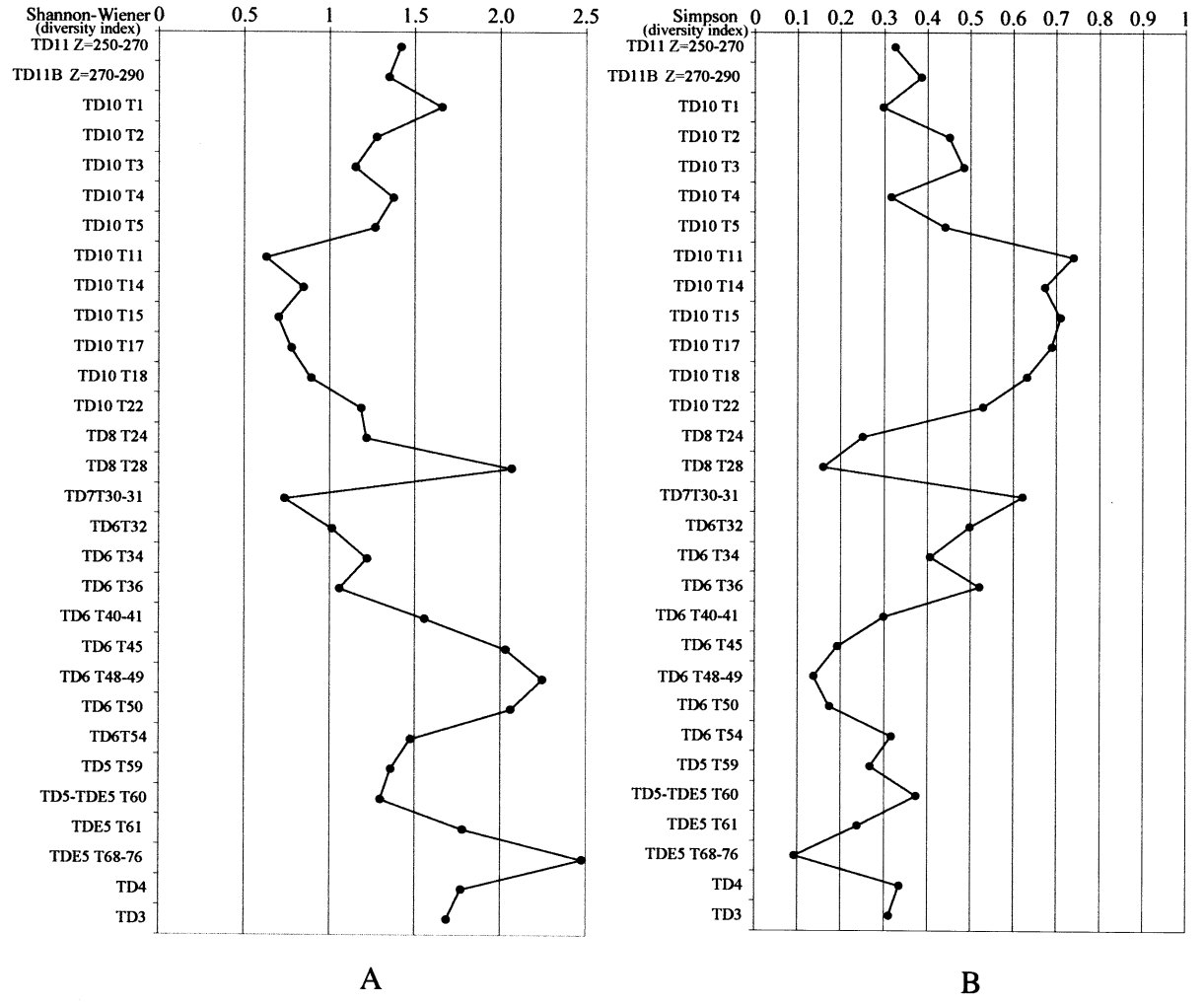

Fig. 9. Representation of faunal diversity. (A) Variation of the Shannon–Wiener index at Gran Dolina from the total number of individuals. (B) Variation of the Simpson index at Gran Dolina from the total number of individuals.

lowing mathematical formula:

$$H' = \sum_{i=1}^{s} (n_i/N) \ln (n_i/N)$$

where n_i corresponds to the minimum number of individuals of the ith species, N is the total number of individuals, and S is the number of species.

Two graphs have been plotted for each index (Figs. 8 and 9). In the first (Fig. 8), n_i is assigned to the minimal number of individuals of the ith species. In the second (Fig. 9), n_i is the total number of individuals of the ith species. The result is that the Shannon–Wiener indices (Figs. 8A and 9A) and the Simpson indices (Figs. 8B and 9B) provide the same information.

The Shannon–Wiener index is higher when different species are represented equally (when there is no clear dominance of one species over others, i.e. when the specific variability is high).

The Simpson index is designated with the character L and corresponds to the following mathe-

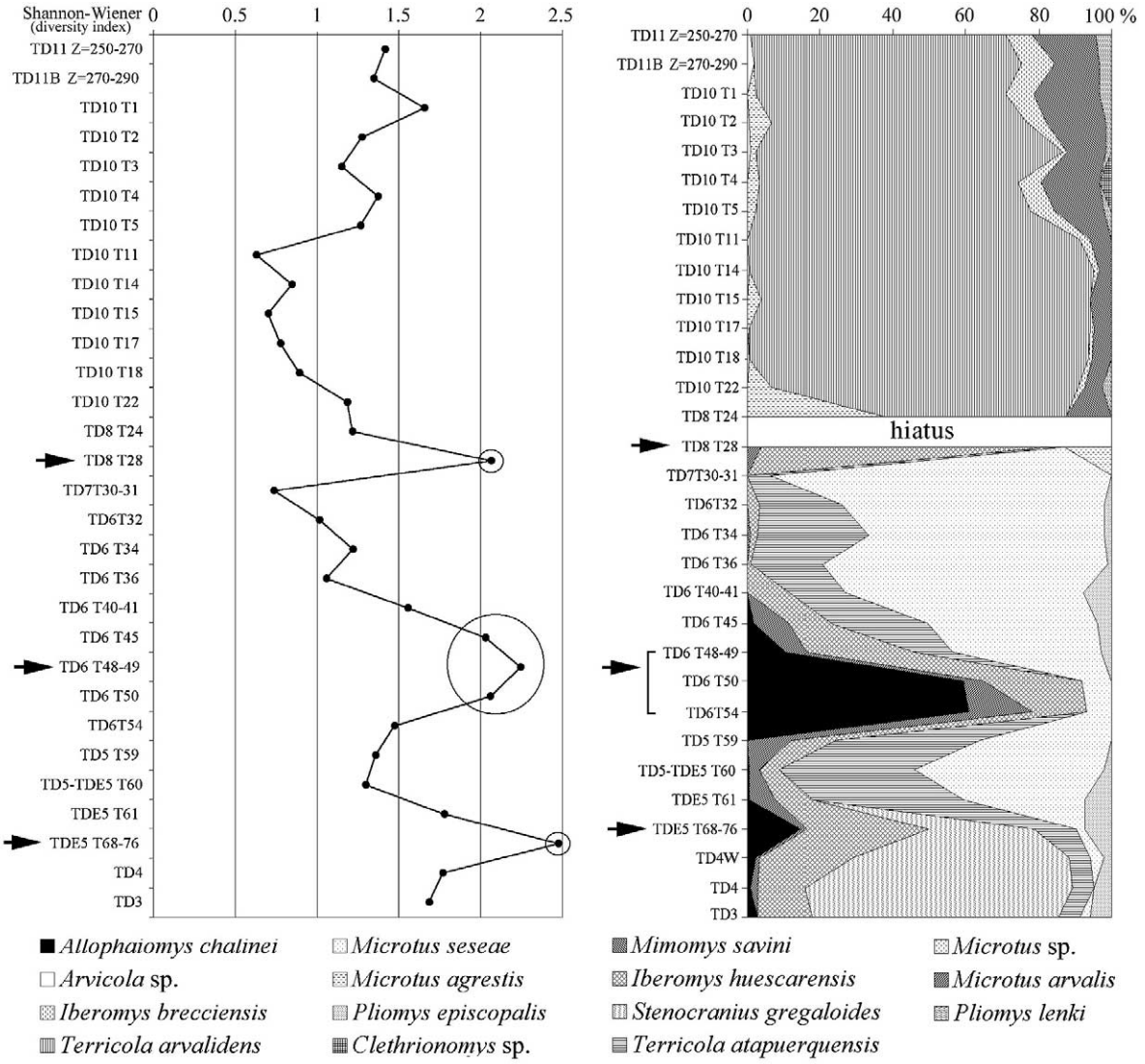

Fig. 10. (A) Shannon–Wiener index along the whole sequence of Gran Dolina. (B) Variation in the arvicoline associations along the whole sequence of Gran Dolina showing that the more important community changes are coincident with the peaks of maximal diversity obtained by the Shannon–Wiener index.

matical formula:

$$L = \sum_{i=1}^{s} (n_i\ (n_i - 1))/N\ (N-1))$$

where n_i is the minimum number of individuals of the ith species, N the total number of individuals, and S the number of species.

The index increases when one species is dominant (when the specific diversity of the community decreases). There is a negative correlation between diversity and the manifestation of dominance (Margalef, 1986).

Generally, an increase in the diversity index has been taken as indicator of an increase in the organisation of the ecosystem and favourable ecological conditions (López-Martínez and Truyols, 1994). In the present work, there is clear evidence

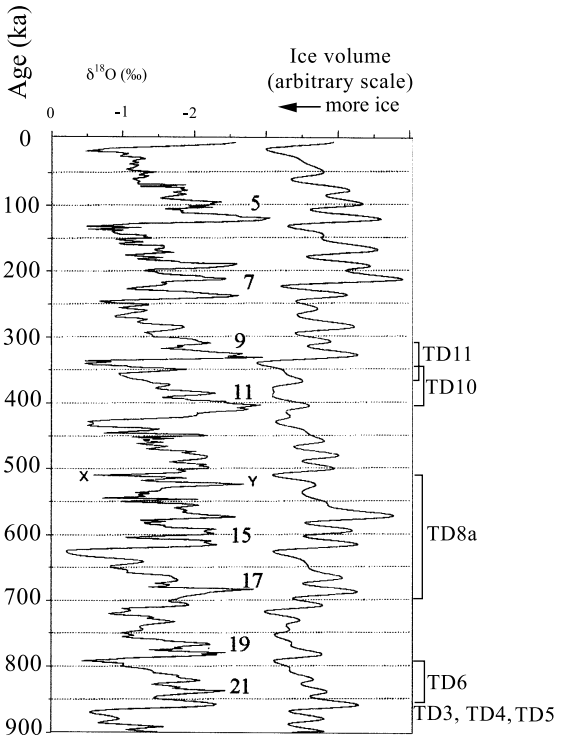

Fig. 11. Correlation of the different levels of Gran Dolina with oxygen isotope stages of Bassinot et al. (1994).

for an increased diversity at the points of climatic shift (when communities overlap) (see Fig. 10).

The maximum diversity at Gran Dolina coincides with a maximum Shannon–Wiener index and a minimum Simpson index (Figs. 8A,B and 9A,B).

A detailed interpretation of the curves of specific diversity is given below.

3.5.1. TD3, TD4

The Shannon–Wiener indices are relatively low and the Simpson indices are quite high, implying a low specific diversity. That reflects a community of species adapted to the prevailing climatic conditions (a cold climate in this case).

3.5.2. TD5

Lower TD5: The Shannon–Wiener index reaches a maximum value while the Simpson index has its minimal value. The high specific diversity is related to a mixed fauna, which indicates the transition from a cold to warm climate. The species adapted to the cold climate have not yet disappeared but have decreased significantly. The species adapted to the new conditions start to invade the niches left by the former species. Therefore, this increase in the diversity reflects the coexistence of the two groups of species and does not prove better conditions.

Upper TD5: The Shannon–Wiener indices decrease progressively whereas the Simpson indices increase gradually. The lower specific diversity reflects the disappearance of the species that were not adapted to the new climatic conditions. It also shows the dominance of a few species (*Terricola arvalidens* and *Microtus seseae*).

3.5.3. TD6

Lower TD6: This sub-unit includes archaeological sublevels 54–45. The Shannon–Wiener and Simpson indices show a progressive increase in the specific diversity. This is due to a climate change reflected by a mixed fauna. This fauna includes species that are experiencing more favourable conditions and others that have increasingly unfavourable conditions.

Upper TD6: In this sub-unit (archaeological sublevels 45–32) a progressive decrease in specific diversity indicates that new species are occupying ecological niches left by the species disappeared therein.

3.5.4. TD7

In this level there is a low specific diversity probably because the fossil samples are quite poor. No inference is made from the diversity indices.

3.5.5. TD8

Lower TD8 (TD8a): The Shannon–Wiener and Simpson indices show in TD8 T28 the last of the three peaks in diversity (the last important climatic change at Gran Dolina). This again reflects a mixed association characterised by the overlap of species that have not yet disappeared completely and the arrival of new ones that begin to occupy niches left by the former.

Upper TD8 (TD8b): In this sub-unit, the Shannon–Wiener and Simpson indices show a low spe-

cific diversity that might be due to the scarcity of the material found.

3.5.6. TD10, TD11

The specific diversity is quite low throughout these levels. Contrary to what is observed in the Lower Pleistocene part, the curves do not suggest important changes or important climatic oscillations during the time of deposition. That reflects a micromammal association adapted to its environment. In archaeological sublevels 4 and 2, there is a slight increase in diversity, which is probably the result of a slight decrease in the dominance of *Terricola atapuerquensis*. The general aspect of the ecosystem is rather uniform.

In conclusion, the changes experienced by the community structure of Gran Dolina due to climatic oscillations, as deduced from the Shannon–Wiener and Simpson indices, display the following pattern:

(1) The succession starts with an association of species A fully adapted to their environment. The diversity is low.

(2) A climatic change occurs, causing the regression of the association of species A and the arrival of the association of species B, which are adapted to the new climate. The diversity is very high, reflecting the mixed nature of the fauna that includes elements of A and B (A+B).

(3) The association of species A disappears and the association of species B, which is adapted, occupies the ecological niches left by A. The diversity decreases once again.

(4) A climatic change occurs, and the cycle starts again.

4. Correlation with the oxygen isotope stages

The chronology of the Gran Dolina site was established based on U-series/ESR methods (Falguères et al., 1999). Fig. 11 shows the correlations of the levels of Gran Dolina with the curve of oxygen isotope stages (OIS) provided by Bassinot et al. (1994).

The average age is 372 ± 33 ka for TD10 and 337 ± 29 ka for TD11 (Falguères et al., 1999). Due to the normal uncertainty of these values, they cannot be assigned to OIS 9, 10 or 11. However, OIS 10 can be excluded based on the climate inferences obtained in the present work since it is related with a glacial period. Therefore, TD10 and TD11 can be correlated with either OIS 9 (lowest dating) or 11 (highest dating).

The micromammal record reveals a quite important gap at the level TD8. Hence, this unit is subdivided into two quite different parts. The upper section (TD8b) presents an association of micromammals characteristic of an interglacial climate. It has not been dated but should be between 372 ± 33 ka (presumed age of TD10) and 602 ± 92 ka (presumed age of TD8a). Therefore, a correlation with OIS 13 or 15 may be inferred for TD8b.

The lower part of the level TD8 is dated as 602 ± 92 ka (Falguères et al., 1999). It is characterised, as mentioned above, by a cold climate. Therefore, it can be correlated with OIS 16 (lowest dating) or OIS 18 (highest dating). Due to the stratigraphical proximity of the Matuyama/Brunhes geomagnetic reversal (780 ka), the lack of attested stratigraphical discontinuities, and the faunal continuity, the lower TD8 is more probably to correlate with OIS 18.

The Matuyama/Brunhes boundary is located in the upper part of TD7 (Parés and Pérez-González, 1999), suggesting that it is to correlate with OIS 19. However, it cannot be excluded that it also correlates with OIS 18 and/or 20. Unfortunately, its fossil content is very scarce and does not permit more precise climatic inferences.

The dates for TD6 in Falguères et al. (1999) are 770 ± 116 ka, 762 ± 114 ka, and 676 ± 101 ka. TD6 is below the Matuyama/Brunhes geomagnetic reversal and, therefore, it should be older than 780 ka. As the highest dating of TD6 is 886 ka (Falguères et al., 1999), its age should be between 780 ka and 886 ka. Since it is related to an interglacial climate, it can finally be correlated with OIS 21.

Although TD3, TD4, and lower TD5 have not been dated, their age must be between 780 ka and 980 ka because they are between the Matuyama/Brunhes boundary and the Jaramillo event (which is located in TD1 (Parés and Pérez-González, 1999)). A single transition from a cold to a warm climate occurs between these lower units

of the succession and TD6 (interglacial). In addition, in view of the continuity of the faunas, there is no evidence of a sedimentary break. Therefore, it can be assumed that there are two consecutive OIS within TD3–TD6. Hence, the lower levels of Gran Dolina may be correlated with OIS 22 (Fig. 11).

5. Results

5.1. TD3, TD4, TD4W

These levels are characterised by arid steppe species (*Allocricetus bursae*) and cold climate species (*Stenocranius gregaloides*) associated with murines (*Apodemus* gr. *sylvaticus-flavicollis*), glirids (*Eliomys quercinus*), and insectivores (*Erinaceus europaeus*). The environment would be continental with a dry and rather cold climate and dominant steppe, although forest patches may persist in sheltered areas. The Iberian Peninsula was probably in a cold phase.

Due to the scarcity of pollen, these results cannot be contrasted with the palynological analysis in García Antón (1995) but they coincide with those of Hoyos and Aguirre (1995), who attribute dry and cold conditions to these levels.

Lower TD5: A slight warming and increased dryness are revealed by a decrease in the percentage of *Stenocranius gregaloides* and the expansion of *Allocricetus bursae*, respectively. The landscape would be similar to that inferred for the previous unit: a steppe-like environment with a clear continental influence (as revealed by typical species of open and dry areas) and forest patches in sheltered areas.

These results are consistent with those of Hoyos and Aguirre (1995), who interpret the deposits as an alternation of colder and drier climatic conditions than present day, with important winter frosts followed by pulsations of moister and less harsh weather. Similarly, this level is dry for García Antón (1995), even more than the previous one.

Upper TD5: The substitution of *Stenocranius gregaloides* by *Terricola arvalidens* and *Microtus seseae*, together with the increase of *Mimomys savini* and *Pliomys episcopalis*, indicates interglacial conditions. The upper TD5 is composed of three archaeological sublevels, i.e. T61, T60, and T59. Due to reasons mentioned above (cf. 3.2. Relative abundance of soricines and cricetines as indicators of humidity–dryness), they have been grouped in Fig. 5. However, interestingly enough, although their faunal content is similar, their ratio of cricetines/soricines is quite different. In fact, upper TD5 could be divided into two parts, the lower one (T61) being rather moister. The increase in dryness at the top of this unit is in agreement with the results of García Antón and Sainz-Ollero (1991). However, these authors report that the increased aridity is accompanied by a decrease in temperature, which is not revealed by our data. Hoyos and Aguirre (1995) associate the upper part of upper TD5 with a warmer and drier climate than the lower one, and they notice a shift towards colder and moister conditions in the top of the upper TD5. However, this trend has not been observed in the present work.

The landscape would be characterised by humid valleys (inhabited by humid meadow species), forests (as revealed by warm forest species) and drier and higher zones (in which the steppe species would develop).

Lower TD6: This part of the level reflects an increase in the dryness. *Terricola arvalidens* and *Microtus seseae* decrease whereas *Allophaiomys chalinei*, *Mimomys savini* and *Iberomys huescarensis* increase. Despite the replacement of some species, as a result of climatic changes, both fossil associations correspond to interglacial faunas. The environment would be mostly open with scarce forests.

For García Antón (1995), this lower section corresponds to a cold and dry climate, which disagrees with the results presented in this paper. This may be explained by imprecise pollen sampling.

Upper TD6: A slight temperature drop and increased dryness can be inferred. The environment was probably more open than it was in the lower sub-unit. *Microtus seseae* and *Terricola arvalidens* would have occupied the humid meadow. *Allocricetus bursae* would have developed in the most arid areas and the forest patches would have still

been inhabited by typical species of forest environments. The association recorded may still correspond to an interglacial environment. The appearance of *Sus scrofa* (wild boar) at TD6 (Van der Made, 1998) confirms the clemency of the weather. This animal lives in large forests and cannot feed if the soil is frozen or covered by a thick layer of snow. According to Delpech et al. (1983, p. 167), this is one of the best indicators of the warmer periods of the Pleistocene.

5.2. TD7

Few micromammals have been found at this level so no inferences are made about the environment or climate. Nevertheless, the presence of *Ovibos* cf. *suessenbornensis* (Van der Made, 1998) may suggest a rather cold climate, prelude to the glacial period of the lower TD8. In fact, this species is morphologically close to the modern *Ovibos mostachus*, which inhabits the tundra of northern Canada and Iceland.

5.3. TD8

Lower TD8 (TD8a): The record of *Microtus* aff. *ratticepoides*, an indicator of a cold climate, is remarkable. The appearance of *Hippopotamus amphibius* is merely related to the nearby river Arlanzón. The coexistence of steppe-like species, cold climate species and forest inhabitants argues for an environment of low temperatures, somewhat moist, with open areas and forest. The Iberian Peninsula was probably experiencing a glacial period. Hoyos and Aguirre (1995) also infer a cold and humid climate for the lower TD8.

Upper TD8 (TD8b): The record of micromammals is poor and only representatives of the subfamily Arvicolinae are found. The association is characteristic of an interglacial period. This result fits with those of García Antón (1998) and Hoyos and Aguirre (1995), who infer that the climate was then not very harsh.

5.4. TD10, TD11

All samples show a similar faunal association that would correspond to an interglacial period with slight fluctuations in relative moisture. These fluctuations are also described by Hoyos and Aguirre (1995), although these authors infer colder conditions for the lower part of TD10, which have not been evidenced in this work.

The proportion of insectivores remains constant throughout the unit. The percentage of cricetines is high whereas the murines are nearly insignificant. The arvicolines persist as the best represented subfamily, *Terricola atapuerquensis* being the most abundant species.

The environment would be constituted by moist valleys, inhabited by humid meadow species (*Terricola atapuerquensis*), and forests of pines and *Quercus*, inhabited by warm forest species such as *Eliomys quercinus*, *Erinaceus europaeus*, and *Apodemus* gr. *sylvaticus-flavicollis*. *Allocricetus bursae* would be present in the open and most arid zones.

6. Conclusions

The study of micromammal associations from the Early to Middle Pleistocene at Gran Dolina evidences several climatic oscillations. The lower part of the succession (TD3, TD4, TD4W to lower TD5) reveals a continental, dry climate. The micromammals of the upper part of TD5 and TD6 reflect a complex interglacial period with fluctuations in the degree of relative humidity. TD7 and the lower part of TD8 correspond to cold and relatively moist conditions. The upper part of the succession (TD8b, TD10, TD11) yields a homogeneous fossil record, suggesting interglacial conditions with slight fluctuations in relative moisture.

The different levels of Gran Dolina have also been correlated with OIS. Levels TD5, TD4 and TD3 are correlated with OIS 22, TD6 with OIS 21, TD8a with OIS 16 or 18, TD8b with OIS 13 or 15 and TD10 and TD11 with OIS 9 or 11.

The climatic cycles of the Pleistocene affected the Iberian Peninsula and northern Europe in different ways, but the exceptional micromammal fossil record at Gran Dolina demonstrates warm–cold alternations quite far south. As a result of the climatic oscillations, there were several

migrations and local extinctions of different species. During climatic shifts, an overlapping of communities, and thus an increase in the specific diversity, is observed.

The glacial periods correspond to environments with more steppe-like species such as cricetines (e.g. *Allocricetus bursae*) and some cold climate arvicolines (e.g. *Stenocranius gregaloides* and *Microtus* aff. *ratticepoides*). Interglacial periods were not only reflected by increased moisture: they were affected by fluctuations in humidity/dryness.

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