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Similarity relationship between Mammal faunas and biochronology from Latest Miocene to Pleistocene in the Western Mediterranean area

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Key words: Biochronology, Large mammal faunas, neogene-quaternary, Western Europe

ABSTRACT

The multivariate analysis is a successful tool in biochronological studies, and it is here applied to the biochronology of the Western Mediterranean area from latest Miocene to Pleistocene. Multiple local mammal faunal assemblages were analyzed using clustering and non-linear ordination techniques to discover their interrelationships and to which degree they can be put together to form a sequence of non-overlapping "zones of homogeneity". Each set is assumed to be a mammal assemblage living together in space and time. The discontinuities between them reflect successive changes in mammal communities, which are apparently related to episodes of biotic and abiotic environmental variations. Three informal hierarchical ranks of faunal organization are recognized after the analysis: "Superages", "Ages" and "Units", which are in contrast to previous biochronological schemes. The beginning of "Superage I" can be correlated with the end of the Mediterranean salinity crisis, at the Mio-Pliocene boundary. The "Superage II" is correlated with the "Glacial Pleistocene", around 1.0 Ma, and is characterized by the presence of a modern fauna. European Land Mammal Ages are correlated with «Ages» and seem to be an adequate biochronologic framework of reference for the Plio-Pleistocene. Major discrepancies occur between «Units» and previous biochronological units.

RÉSUMÉ

Les méthodes multivariées constituent des outils valables dans les études biochronologiques et elles ont ici été utilisées dans la biochronologie de la Méditerranée occidentale dès la fin du Miocène au Pléistocène. On analyse les associations de grands mammifères livrés par multiples sites fossilifères au moyen des méthodes agglomératives et d'ordination, de sorte qu'on puisse mettre en relief leurs relations de similitude et jusqu'à quel point elles peuvent être regroupées en constituant une séquence de «zones d'homogénéité» sans recouvrement. On assume que chacun de ces groupements représente un assemblage de mammifères vivant ensemble dans l'espace et le temps. Le discontinuités entre eux traduisent les changements successifs dans les communautés de mammifères, qui apparemment sont reliés aux épisodes de variation biotique et abiotique de l'environnement. Trois niveaux hiérarchiques peuvent être reconnus: «Superâges», «Âges» et «Unités», ils ont été comparés avec les schèmes biochronologiques précédents. Le début du «Superâge I» semble être relié avec la fin de la «Crise de salinité de la Méditerranée» à la limite Mio-Pliocène. Celui du «Superâge II», caractérisée par la présence d'une faune moderne, est relié au «Pléistocène Glacial» environ 1.0 Ma. Les «Âges Mammaliens» d'Europe occidentale se correspondent avec les «Âges» reconnus d'après notre analyse et semblent être un cadre de référence approprié pour le Plio-Pléistocène. Les différences les plus remarquables sont entre nos «Unités» et les divers unités biochronologiques des escales précédentes.

Introduction

It has been difficult to apply the geologic time scale to continental sediments given that these are usually less extensive, that superposition is more difficult to demonstrate and that interdigitation of non marine and marine rocks is rare. To reach a hypothesis of temporal position for such cases it may be necessary to study the evolution stages (Lindsay & Tedford 1990). A chronologic system based mainly on the stage of evolution of selected, well-defined lineages of mammals (traditionally rodents) rather than by superposition has been advanced by vertebrate paleontologists.

First appearance datum (FAD), often an immigrant, and last appearance datum (LAD) of individual taxa are generally used to define boundaries. As Pickford (1990) points out, there are some drawbacks in using changes in the distribution patterns of organisms in biochronology. In some cases, intra- or intercontinental dispersal events can be shown to be heterochronous, particularly if impeded by barriers, and fluctuations in distribution patterns of organisms make it difficult to distinguish whether an immigration or an extinction event has occurred. This kind of problem also makes it difficult to recognize whether two local faunal assemblages are contemporary or superposed in time.

Because direct observation of temporal relationships is rarely available in fossiliferous continental deposits, especially

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in fissure and cave deposits, the use of temporal range of taxa, often estimated from the supposed biochronological position of localities, in the definition of biochrons might be criticized as circular.

We propose a multivariate approach based on similarity that intends to solve in part these problems. Biochronological units, characterized by a particular faunal assemblage, are assumed to represent lapses of time during which faunas have certain taxonomic homogeneity, the discontinuity between them denoting faunal restructuration associated with major changes in environmental conditions. The local faunal assemblage (LFA) furnished by a locality represents a partial record or sample of these homogeneous faunas obtained through the span of the deposition. Multiple LFAs have been analyzed using multivariate techniques to discover their interrelationships and to which degree they can be put together to form a sequence of non-overlapping "zones of homogeneity" trying to minimize the taphonomic and sampling bias.

These "zones of homogeneity" are characterized by a particular set of taxa regardless of their ranges. The use of time intervals based on the overlapping temporal ranges of numerous taxa allows both greater repeatability of age estimate (similar to statistical concepts of precision) and better likelihood of close approximation between this age and the true temporal interval for these taxa (similar to statistical accuracy) (Flynn et al. 1984).

The method does not include circular and *a priori* reasoning in verifying that faunal assemblages (major clusters in a dendrogram) are present before the selection of various taxa for their recognition is determined. Furthermore, the use of independent geochronologic techniques is possible to test hypotheses of temporal position and for correlation of faunas.

The contributions resulting from its application to the biochronology of the Northwestern Mediterranean region from Late Miocene to Middle Pleistocene corroborate the reliability of this approach.

In recent years, several multivariate approaches have been developed trying to abandon the similarity and association concepts. These methods based on temporal correlation of local series can not be applied to the continental records because most of the mammal localities are stratigraphically isolated. The parsimony-based method of disjunct distribution ordination (DDO) of Alroy (1992) is more appropriate. This method tries to order FADs and LADs based solely on conjunct data (i.e., records that pairs of taxa have overlapping distributions across set of taxonomic list). Nevertheless, the obtaining ordination may be the result of ecological or biogeographic factors, not necessarily of temporal gradients alone (Alroy 1994).

Biochronological framework

The Neogene-Quaternary formations of the Northwestern Mediterranean region contain thick sedimentary sequences especially well exposed and with abundant fossils, making it possible to document faunal changes with increased temporal resolution. Despite the impressive number of taxonomic, phylogenetic and biochronologic studies of the Northwestern Mediterranean continental Neogene deposits and their fossil mammal faunas, the chronologic time scale and its calibration are still imprecise. In this regard, considerable efforts to establish an adequate biochronological framework have been made (Ambrosetti et al. 1972; Mein 1975, 1990; Azzaroli 1977, 1982, 1983; Guérin 1982; Aguilar & Michaux 1987; Agustí et al. 1987; De Bruijn et al. 1992), but none of them encompasses the complete time interval analyzed here; besides, there are discrepancies among them, making it difficult to establish accurate equivalences.

The most largely used biochronologic time scale for Neogene Southwest European continental deposits is that established on the basis of the successive mammal communities, essentially rodents, by Mein (1975), lately revised by Mein (1990) and De Bruijn et al. (1992). This scale ends at the beginning of the Middle Pleistocene and is replaced, up to the Holocene, by a less accurate one proposed by Guérin (1982) approximately derived from MN "zones" but of dubious value due to overlapping (Azzaroli 1977). Many studies have been addressed to these MN "zones" and detailed relevant references and correlations can be found in Steininger et al. (1990). The MN "zones" were developed from the biozones of Thaler (1966) based on mammal assemblages from well-known European sites, a type locality was designated for each zone and each zone is bounded by specific guide fossils (*niveaux-repères*, following Hartenberger 1969). Most of the reference faunas designated by Thaler had previously been correlated with marine stages, so the sequential ordering of these zones had already been placed in a chronologic framework (Lindsay & Tedford 1990). Regardless of the lack of geologic context, the MN scale has been used with a biostratigraphic meaning. Mein's scale is not a true biozonation, but a hypothesis of bioevent succession. Both projects are valid and not necessarily contradictory, however they must not be mixed, as it occurs in the MN "zones" (Agustí & Moyà 1991). Some criticisms have been made: MN "zones" may be diachronous; the selected taxa were heterogeneous; the boundaries were not well defined (Daams & Freudenthal 1981; Jaegger 1990; Agustí & Moyà 1991).

An alternative scale was established for Southwest France by Aguilar (1982) and Aguilar & Michaux (1987) for the Miocene-Pliocene. The former proposed that the mammal faunas should be referred directly to marine stages assuming hypothetical marine-continental correlation. The latter used the amount of evolutionary change within rodent lineages to attribute a longer or shorter duration to some of their biozones.

A second approach was proposed by Agustí et al. (1987) for the Pleistocene, following the methodology developed by De Bruijn & van Meurs (1967), Van der Weerd (1976) and Daams & Freudenthal (1981). These authors worked in isolated basins of Spain with sections where the relative position of the different sites is well known from a stratigraphic point of

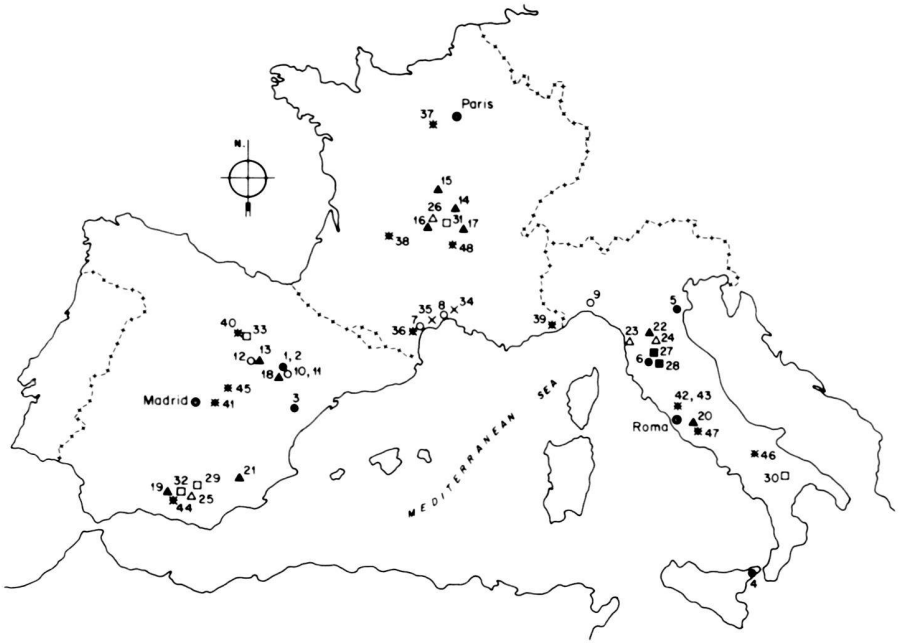


Fig. 1. Geographical distribution of the selected localities from Spain, Italy and France. Symbols correspond to each main cluster recognized as "Unit" in Figure 3 (A-B-C-D-E-F-G-H). Locality numbers as in Table 2.

view. This situation allowed the definition of true biozones and continental-stages, according to the rules of the International Stratigraphic Code. Moreover, these were greatly based on micromammals that have demonstrated a high temporal resolution, but only in a basin or relatively small area, making it difficult to correlate them to a regional or continental scale.

A third approach was developed by Ambrosetti et al. (1972), Azzaroli (1977, 1982, 1983, 1991), Torre et al. (1992) and Sala et al. (1992) for the Italian Plio-Pleistocene, following the methodology proposed for the definition of the North American LMAs. In some cases, the boundaries of these mammal units were designated by erosional phases calibrated by K/Ar ages and magnetostratigraphic data (Ambrosetti et al. 1972; Arias et al. 1979, 1980).

In a similar way, the European literature is also full of terms such as Turolian, Ruscinian, Villafranchian, Galerian, . . . defining supposed LMAs or proposed as continental-stages of dubious value since none of them has been referred to any formal stratotype. A biostratigraphic definition was provided later for the Turolian by Van der Weerd (1976). Mein et al. (1989–90) proposed the Alfambrian stage corresponding to the Ruscinian LMA, even though its use is not yet generalized.

The mammal chronology for Europe would become indecipherable if each country or each research group were to employ its own chronological structure.

Our aim is to quantify the similarities among the local mammal assemblages, which allow us to establish the successive faunal changes during this time, and to contrast these patterns with the previously established biochronological schemes. The calibration is based on K/Ar ages (Berggren et al. 1985, 1995), several correlations with the marine time scale by the use of interstratified marine levels (Montenat et al. 1975; Aguilar & Michaux 1984; Clauzon & Cravatte 1985; Clauzon et al. 1990) and magnetostratigraphic data (Lindsay 1985; Hilgen & Langereis 1988; Biquand et al. 1990; Opdyke et al. 1990).

Material and methods

LFAs from selected localities of Spain, France and Italy (Fig. 1) are summarized in Table 1. They have been chosen because of their unusually complete faunal record. Sites including more than one faunal level are separated as different LFAs. On the other hand, we excluded from this study localities which include several fossiliferous sites or levels whose relative stratigraphic positions are not well established, such as Senèze, France (Thouveny & Bonifay 1984; Bonadonna & Alberdi 1987).

The initial localities-by-taxa data matrix is compiled in Table 2 based on our critical review of the up-to-date record for each locality. Only terrestrial large mammals were considered since most of the analyzed LFAs do not include significant small mammal faunas, due to taphonomic and monographic reasons. The presence of a taxon in a locality was coded 1 in Table 2. The use of the specific taxonomic level is due to: 1) the species is the basic biologic unit, and there is more consensus on the species concept than on the genus concept; 2) for a quantitative approach, genera introduce a greater bias than species, since some groups such as carnivores include many monospecific genera, while others such as equid genera group many species. A common problem in this study was the confidence level of taxonomic identifications. In quantitative biochronology, working with the same species concept is essential. We standardized the taxonomy, including forms identified as confer (cf.) within the nominated taxon, and considered the affinis (aff.) species as different taxa.

Tab. 1. Summary of the selected localities, countries and the most important references about each.

Localities	Countries	References
1- El Arquillo, Teruel	Spain	Azanza and Menéndez 1989-90; Cerdeño 1992; Alcalá 1994.
2- Las Casiones, Teruel	Spain	Alcalá 1994.
3- Venta del Moro, Valencia	Spain	Morales 1984; Alberdi and Bonadonna 1988; Azanza and Menéndez 1989-90; Alcalá 1994.
4- Gravitelli, Messina	Italy	Seguenza 1902; Kotsakis 1984; Alberdi and Bonadonna 1988.
5- Brisighella, Faenza	Italy	De Giuli 1989; Rook 1992; Masini and Rook 1993.
6 - Baccinello V3, Grosseto	Italy	Hürzeler and Engesser 1976; De Giuli et al. 1983; Kotsakis 1984; Alberdi and Bonadonna 1988.
7- Montpellier, Languedoc	France	Guérin and Mein 1971; Michaux 1975.
8- Perpignan, Roussillon	France	De Bruijn et al. 1992.
9- Triversa,Villafranca d'Asti	Italy	Masini et al. 1994.
10- La Calera, Teruel	Spain	Azanza et al. 1989; Alcalá 1994.
11- La Gloria 4, Teruel	Spain	Azanza et al. 1989; Alcalá 1994.
12- Layna, Soria	Spain	Pérez and Soria 1989-90; Alcalá 1994.
13- Villarroya, Logroño	Spain	Villalta 1952; Azanza et al. 1989; Aguirre 1989; Alcalá 1994.
14- Les Etouaires, Puy-de-Dôme	France	Schaub 1949; Heintz et al. 1974; de Lumley 1976.
15- Pardines, Perrier, Puy-de-Dôme	France	Heintz et al. 1974; de Lumley 1976.
16- Chilhac, Haute-Loire	France	Heintz et al. 1974; de Lumley 1976; Boeuf 1983, 1992; Geraads 1990.
17- Saint-Vallier, Montrebut, Drôme	France	Viret 1954; Heintz et al. 1974; de Lumley 1976; de Bruijn et al. 1992.
18- La Puebla de Valverde, Teruel	Spain	Heintz 1970, 1978; Azanza et al. 1989; Alcalá 1994.
19- San Giacomo, Anagni	Italy	Bidditu et al. 1979; Bonadonna and Alberdi 1987; Masini et al. 1994.
20- Montopoli, Pisa	Italy	De Giuli and Heintz 1974a,1974b; Azzaroli et al. 1982; De Giuli et al. 1983; Azzaroli 1992; Masini et al. 1994.
21- Huélago, Granada	Spain	Alberdi et al. 1989; Azanza and Menédez 1989-90.
22- El Rincón, Albacete	Spain	Alberdi et al. 1982.
23- Olivola, Val di Magra	Italy	Azzaroli 1982, 1992; Bonadonna and Alberdi 1987; Azzaroli and Mazza 1993; Masini et al.1994
24- Casa Frata, Arezzo	Italy	Borselli et al. 1980; De Giuli and Masini 1983, 1987; Azzaroli 1992.
25- Venta Micena, Granada	Spain	Moyà and Menéndez 1986; Moyà-Solà et al. 1987; Lister 1990a; Martínez 1992.
26- Blassac-La-Gironde, Haute-Loire	France	Heintz et al. 1974; de Lumley 1976; Prat 1980; Geraads 1990; Boeuf et al. 1992.
27- Selvella, Val di Chiana, Umbria	Italy	De Giuli 1987; Azzaroli et al. 1982; Azzaroli 1992; Azzaroli and Mazza 1993.
28- Pietrafitta, Perugia	Italy	Azzaroli and Mazza 1993; Mazza et al. 1993; Masini et al. 1994.
29- Huéscar-1, Granada	Spain	Mazo et al. 1985; Aguirre 1989; Alberdi et al. 1989.
30- Venosa, Basilicata	Italy	Caloi and Palombo 1979a, 1979b; Alberdi et al. 1988.
31- Solilhac, Haute-Loire	France	De Lumley 1976; Prat 1980; Crégut 1981; Bonifay 1986; Geraads 1990; Lister 1990a.
32- Cúllar de Baza-1, Granada	Spain	Ruiz Bustos 1976; Moyà and Menéndez 1986; Aguirre 1989; Alberdi et al. 1989.
33- Atapuerca TD4, Burgos	Spain	Aguirre 1989; Azanza and Sánchez 1990; Cerdeño 1990; Cervera 1992.
34- L'Escale, Bouches-du-Rhône	France	Bonifay 1971; de Lumley 1976.
35- Lunel-Viel, Hérault	France	Bonifay 1971; de Lumley 1976; Crégut 1981.
36- La Caune de l'Arago, US, Tautavel	France	De Lumley 1976; Crégut 1980, 1981; Lister 1990a, 1990b.
37- Abîmes de la Fage, Corrèze	France	Bouchud 1972; de Lumley 1976; Crégut 1981.
38- Combe Grenal, Domme, Dordogne	France	de Lumley 1976; Crégut 1981.
39- Lazaret, Nize, Alpes-Maritimes	France	De Lumley 1976; Crégut 1981.
40- Atapuerca TD10-11, Burgos	Spain	Aguirre 1989; Azanza and Sánchez 1990; Cerdeño 1990; Cervera 1992.
41- Pinilla del Valle, Madrid	Spain	Alférez 1985; Alférez et al. 1982, 1985a, 1985b; Alférez and Iñigo 1990; Aguirre 1989; Cerdeño 1990.
42- Torre in Pietra, Roma	Italy	Caloi and Palombo 1978; Masini et al. 1994.
43- Malagrotta, Roma	Italy	Caloi and Palombo 1979c; Masini et al. 1994.
44- La Solana del Zamborino, Granada	Spain	Martín Penela 1988; Aguirre 1989; Cerdeño 1990.
45- Cueva del Congosto, Guadalajara	Spain	Alberdi et al. 1977; Aguirre 1989; Cerdeño 1990.
46- Isernia La Pineta, Molise	Italy	Sala 1983; Masini et al. 1994.
47- Fontana Ranuccio, Anagni	Italy	Bidditu et al. 1979; Masini et al. 1994.
48- Châtillon-Saint-Jean, Drôme	France	Mourer-Chauvire 1972; de Lumley 1976; Crégut 1981.

Tab. 2. Data matrix

TAXA	1 El Arquillo	2 Las Casiones	3 Venta del Moro	4 Gravitelli	5 Brisighella	6 Baccinello V3	7 Montpellier	8 Perpignan	9 Triversa	10 La Calera	11 La Gloria 4	12 Layna	13 Villarroya	14 Etouaires	15 Pardines	16 Chilhac	17 Saint Vallier	18 La Puebla de Valverde	19 San Giacomo	20 Montopoli	21 Huélago	22 El Rincón	23 Olivola	24 Casa Frata	25 Venta Micena	26 Biassac-la-Gironde	27 Selvella	28 Pietrafita	29 Huéscar	30 Venosa	31 Solilhac	32 Cúllar 1	33 Atapuerca TD4	34 L'Escale	35 Lunel-Viel	36 La Caune de l'Arago US	37 Abîmes de la Fage	38 Combe grenal	39 Lazaret	40 Atapuerca TD10	41 Pinilla del Valle	42 Torre in Pietra	43 Malagrotta	44 La Solana del Zamborino	45 El Congosto	46 Isernia La Pineta	47 Fontana Ranuccio	48 Châtillon-Saint-Jean
PRIMATES																																																
1 *Macaca florentina*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
2 *Macaca sylvana*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1	_	_	_	_
3 *Mesopithecus monspessulanus*	_	_	_	_	_	_	1	1	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
4 *Dolichopithecus ruscinensis*	_	_	_	_	_	_	_	1	_	_	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
5 *Paradolichopithecus sp. 1*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
6 *Paradolichopithecus sp. 2*	_	_	_	_	_	_	_	_	_	_	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
7 *"Pithecus maritimus"*	_	_	_	_	_	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
CARNIVORA																																																
8 *Nyctereutes donnezani*	_	_	_	_	_	_	_	1	_	_	1	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
9 *Nyctereutes magamastoides*	_	_	_	_	_	_	_	_	_	_	_	_	1	1	1	1	1	1	_	1	_	1	_	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
10 *Vulpes alopecoides*	_	_	_	_	_	_	_	_	_	_	_	_	1	1	_	_	1	1	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
11 *Vulpes praeglacialis*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1	_	_	_	_	_	_	_	_	1	_	1	_	_	_	_	_	_	_	_	_	_	_	_
12 *Vulpes vulpes*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1	1	_	_	_	_	_	1	1	_	_	_	_	_	_
13 *Vulpes (Xenocyon) falconeri*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1	_	_	_	_	_	1	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
14 *Canis michauxi*	_	_	_	_	_	_	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
15 *Canis adoxus*	_	_	_	_	_	_	_	1	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
16 *Canis etruscus*	_	_	_	_	_	_	_	_	_	_	_	_	_	1	_	_	_	_	1	_	_	_	1	1	1	1	1	_	1	_	1	1	1	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_
17 *Canis lupus*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1	1	1	_	1	_	1	1	_	_	_	_	1
18 *Canis monticinensis*	_	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
19 *Cuon alpinus*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1	1	_	_	_	_	_	1	_
20 *Cuon stehlini*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_
21 *Cuon priscus*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1	1	_	_	_	_	_	_	_	_	_	_	_	_
22 *Baranogale antiqua*	_	_	_	_	_	_	_	_	_	_	_	_	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
23 *Baranogale helbingi*	_	_	_	_	_	_	_	_	1	_	_	_	_	_	_	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
24 *Enhydrictis ardea*	_	_	_	_	_	_	_	_	1	_	_	_	1	1	_	_	1	_	_	_	_	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
25 *Aonyx bravardi*	_	_	_	_	_	_	_	_	_	_	_	_	_	1	_	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
26 *Lutra affinis*	_	_	_	_	_	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
27 *Lutra gennevauxi*	_	_	_	_	_	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
28 *Mustela nivalis*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1	_	_	_	_	_	_	_
29 *Mustela palerminea*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1	1	_	_	_	_	_	_	_	_	_	_	_	_	_
30 *Plesiogulo crassa*	_	_	_	_	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
31 *Plesiogulo monspessulanus*	_	_	1	_	_	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
32 *Gulo gulo schlosseri*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_
33 *Meles spelaeus*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_
34 *Meles thorali*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
35 *Meles meles*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1	_	_	_	_
36 *Sivaonix lluecai*	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
37 *Mellivora bienfeldi*	_	_	_	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
38 *Pannonictes nestii*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
39 *Megaviverra apenninica*	_	_	_	_	_	_	_	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
40 *Viverra pepraxi*	_	_	_	_	_	_	1	1	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
41 *Agriotherium insigne*	_	_	_	_	_	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
42 *Agriotherium roblesi*	_	1	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
43 *Ursus minimus*	_	_	_	_	_	_	_	_	1	_	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
44 *Ursus ruscinensis (= arvernensis, minutus)*	_	_	_	_	_	_	1	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
45 *Ursus etruscus*	_	_	_	_	_	_	_	_	_	_	_	_	1	1	1	1	1	1	_	_	_	_	1	1	1	1	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
46 *Ursus spelaeus*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1	_	_	_	1
47 *Ursus denningeri*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1	_	_	1	1	1	1	_	_	_	_	_	_	_	1	1	_
48 *Ursus praearctos*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
49 *Ursus arctos*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1	_	_	_	_	_	_	_	1
50 *Hyaena prisca*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1	1	_	_	_	_	_	_	_	_	_	_	_	_	_
51 *Pachycrocuta pyrenaica*	_	_	_	_	_	_	_	1	_	1	1	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
52 *Pachycrocuta perrieri*	_	_	_	_	_	_	_	_	_	_	_	_	1	1	1	1	1	1	_	1	_	_	_	_	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
53 *Pachycrocuta brevirostris*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1	1	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
54 *Crocuta spelaea*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_
55 *Crocuta crocuta*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1	1	_	_	_	_	_	_	1	1	_	_	1	_	_	_	_
56 *Chasmaportetes lunensis*	_	_	_	_	_	_	_	_	1	_	_	1	1	1	1	_	1	1	1	_	_	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
57 *Thalassictis hyaenoides*	_	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
58 *Thalassictis hipparionum*	1	1	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
59 *Thalassictis gr. chaerethis-macrostoma*	_	_	_	1	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
60 *Adcrocuta eximia*	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
61 *Plioviverrops faventinus*	_	_	_	_	1	_	_	_	_	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
62 *Metailurus parvulus*	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
63 *Metailurus major*	_	_	_	_	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
64 *Parailurus hungaricus*	_	_	_	_	_	_	_	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
65 *Dinofelis diastemata*	_	_	_	_	_	_	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
66 *"Felis" christoli (gr. attica-christoli)*	_	_	1	_	1	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
67 *Felis maniculata*	_	_	_	_	_	_	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
68 *Felis issiodorensis*	_	_	_	_	_	_	_	1	1	1	1	1	1	1	1	_	1	1	_	_	_	1	1	1	_	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
69 *Felis lunensis*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
70 *Felis monspessulana*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1	_	_	_	_	_	_	_	_	_	_	_	_	_
71 *Felis sylvestris*	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1	_	_	_	1	1	_	_	1	1	_	_	_

TAXA	1 El Arquillo	2 Las Casiones	3 Venta del Moro	4 Gravitelli	5 Brisighella	6 Baccinello V3	7 Montpellier	8 Perpignan	9 Triversa	10 La Calera	11 La Gloria 4	12 Layna	13 Villarroya	14 Etouaires	15 Pardines	16 Chilhac	17 Saint Vallier	18 La Puebla de Valverde	19 San Giacomo	20 Montopoli	21 Huélago	22 El Rincón	23 Olivola	24 Casa Frata	25 Venta Micena	26 Blassac-la-Gironde	27 Selvella	28 Pietrafitta	29 Huéscar	30 Venosa	31 Solihac	32 Cúllar 1	33 Atapuerca TD4	34 L'Escale	35 Lunel-Viel	36 La Caune de l'Arago US	37 Abimes de la Fage	38 Combe grenal	39 Lazaret	40 Atapuerca TD10	41 Pinilla del Valle	42 Torre in Pietra	43 Malagrotta	44 La Solana del Zamborino	45 El Congosto	46 Isernia La Pineta	47 Fontana Ranuccio	48 Châtillon-Saint-Jean
72 Felis (Lynx) spelaea																																		1	1	1			1									
73 Felis (Lynx) pardina																																			1									1				
74 Viretailurus schaubi													1				1	1				1																										
75 Panthera gr. toscana-gombaszoegensis																							1					1	1				1	1	1													
76 Panthera (Leo) fossilis																																								1								
77 Panthera (Leo) spelaea																																			1	1	1		1					1				
78 Panthera lunellensis																																			1													
79 Panthera pardus																																				1			1									
80 Acinonyx pardinensis									1			1	1	1			1	1		1			1	1																								
81 Homotherium sainzelli														1	1		1																																
82 Homotherium crenatidens									1				1				1	1					1	1																								
83 Megantereon cultridens																							1																									
84 Megantereon megantereon													1	1	1	1	1	1								1																						
85 Machairodus sp.						1	1																																									
86 Amphimachairodus giganteus	1	1	1			1																																										
87 Paramachairodus orientalis		1																																														
88 Paramachairodus maximiliani			1																																													
PROBOSCIDEA																																																
89 Tetralophodon longirostris	1	1																																														
90 Zygolophodon turicensis	1	1		1																																												
91 Zygolophodon borsoni								1	1					1																																		
92 Anancus arvernensis			1				1	1	1				1	1	1	1	1		1	1																												
93 Mammuthus trogontherii																																1												1				
94 Mammuthus meridionalis																1	1	1	1	1	1		1	1	1	1	1	1																				
95 Elephas (Paleoxodon) antiquus																													1		1			1								1	1	1		1	1	
PERISSODACTYLA																																																
96 Tapirus arvernensis (= minor)							1	1	1					1																																		
97 Hipparion sp.			1			1																																										
98 Hipparion primigenium	1	1	1																																													
99 Hipparion concudense	1																																															
100 Hipparion gromovae	1	1	1																																													
101 Hipparion periafricanum	1	1																																														
102 Hipparion fissurae										1	1	1																																				
103 Hipparion rocinantis													1																																			
104 Hipparion crassum						1	1	1																																								
105 Equus stenonis stenonis																							1			1																						
106 Equus stenonis livenzovensis																				1	1	1																										
107 Equus stenonis granatensis																									1																							
108 Equus stenonis vireti																	1	1	1																													
109 Equus stenonis guthi																1																																
110 Equus altidens																													1	1	1	1																
111 Equus stehlini																								1																								
112 Equus sussenbornensis																													1	1	1	1	1															
113 Equus steinheimensis																																																1
114 Equus hydruntinus																																		1			1											
115 Equus bressanus															1											1																						
116 Equus caballus caballus																																				1	1				1							
117 Equus caballus pivetaui																																								1								
118 Equus caballus mosbachensis																																		1	1							1	1		1		1	
119 Equus caballus germanicus																																						1		1								
120 Equus caballus torralbae																																												1				
121 Lartetotherium schleiermacheri	1	1	1																																													
122 Stephanorhinus megarhinus					1	1	1	1																																								
123 Stephanorhinus miquelcrusafonti								1		1		1																																				
124 Stephanorhinus jeanvireti									1					1							1																											
125 Stephanorhinus hundsheimensis																												1																			1	
126 Stephanorhinus etruscus													1	1	1	1	1	1	1		1	1	1	1	1	1			1	1	1	1	1															
127 Stephanorhinus mercki																															1			1		1												
128 Stephanorhinus hemitoechus																																			1	1		1		1	1	1	1	1	1			
129 Coelodonta antiquitatis																																					1	1										1
130 Chalicotherium sp.						1																																										
HYRACOIDEA																																																
131 Pliohyrax graecus		1					1																																									
ARTIODACTYLA																																																
132 Microstonyx major				1																																												
133 Korynochoerus provincialis			1				1	1																																								
134 Sus arvernensis (= minor)								1	1					1																																		
135 Sus strozzii																			1				1																									
136 Sus scrofa																																1					1	1			1	1	1	1	1	1	1	

TAXA	1 El Arquillo	2 Las Casiones	3 Venta del Moro	4 Gravitelli	5 Brisighella	6 Baccinello V3	7 Montpellier	8 Perpignan	9 Triversa	10 La Calera	11 La Gloria 4	12 Layna	13 Villarroya	14 Etouaires	15 Pardines	16 Chilhac	17 Saint Vallier	18 La Puebla de Valverde	19 San Giacomo	20 Montopoli	21 Huélago	22 El Rincón	23 Olivola	24 Casa Frata	25 Venta Micena	26 Blassac-la-Gironde	27 Selvella	28 Pietrafita	29 Huéscar	30 Venosa	31 Solihac	32 Cúllar 1	33 Atapuerca TD4	34 L'Escale	35 Lunel-Viel	36 La Caune de l'Arago US	37 Abîmes de la Fage	38 Combe grenal	39 Lazaret	40 Atapuerca TD10	41 Pinilla del Valle	42 Torre in Pietra	43 Malagrotta	44 La Solana del Zamborino	45 El Congosto	46 Isernia La Pineta	47 Fontana Ranuccio	48 Châtillon-Saint-Jean
137 *Hexaprotodon crusafonti*	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
138 *Hippopotamus antiquus (= major)*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
139 *Hippopotamus tiberinus*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
140 *Paracamelus aguirrei*	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
141 *"Capreolus" australis*	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
142 *Pliocervus matheroni*	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
143 *Pliocervus turolensis*	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
144 *"Cervus" cusanus*	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
145 *Capreolus sussenbornensis*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
146 *Capreolus capreolus*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	1	-	1	1	1	1	-	-
147 *Croizetoceros pyrenaicus*	-	-	1	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
148 *Croizetoceros ramosus*	-	-	-	-	-	-	-	-	-	1	1	-	1	1	1	1	1	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
149 *Pseudodama pardinensis*	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
150 *Pseudodama rhenanus (= philisi)*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
151 *Pseudodama perolensis*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
152 *Pseudodama lyra*	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
153 *Pseudodama nestii*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
154 *Pseudodama farnetensis*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
155 *"Cervus" perrieri*	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
156 *Arvernoceros ardei*	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
157 *Dama sp.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-	1	1	1	1	1	1	1	1	1	-	1	-	-
158 *"Cervus" aff. elaphoides / nov.sp.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
159 *Cervus sp.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
160 *Cervus elaphus*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	1	1	1	1	1	1	1	1	1	1	1	1
161 *Eucladoceros tegulensis (= senezensis)*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	1	1	-	1	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
162 *Cervalces carnutorum*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
163 *Eucladoceros falconeri*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
164 *Eucladoceros dicranios*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
165 *Praemegaceros boldrinii*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
166 *Praemegaceros verticornis*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
167 *Praemegaceros solhilacus*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
168 *Dolichodoryceros savini*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
169 *Megaloceros giganteus*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1
170 *Rangifer tarandus*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	-	-	-	-	-	-	-	-	-	1
171 *Birgerbohlinia sp.*	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
172 *Tragoportax gaudryi*	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
173 *Tragoportax ventiensis*	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
174 *Tragoreas oryxoides*	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
175 *Gazella deperdita*	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
176 *Gazella nov. sp.*	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
177 *Gazella borbonica*	-	-	-	-	-	-	-	1	-	-	-	1	1	1	1	-	1	1	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
178 *Hispanodorcas nov. sp.*	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
179 *Gazellospira torticornis*	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	1	1	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
180 *Protoryx sp. 1*	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
181 *Protoryx sp. 2*	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
182 *Parabos soriae*	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
183 *Parabos cordieri*	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
184 *Alephis lyryx*	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
185 *Leptobos elatus*	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
186 *Leptobos etruscus*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
187 *Leptobos stenometopon*	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
188 *Leptobos vallisarni*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
189 *Leptobos gr. merlai-furtivos*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
190 *Bos primigenium*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	-	1	-	-	1	1	1	1	-	-	-	-
191 *Bison priscus*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	1	-	-	-	1
192 *Bison schoetensacki*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	1	-	1
193 *Bubalus sp.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
194 *Ovis ammon cf. antiqua*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
195 *Praeovibos priscus*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
196 *Hesperidoceras merlae*	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
197 *Soergelia minor*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
198 *Gallogoral meneghinii*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
199 *Procamptoceras brivatense*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
200 *Hemitragus bonali*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	1	-	-
201 *Samotragus occidentalis*	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
202 *Capra alba*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
203 *Capra pyrenaica*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
204 *Capra ibex*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	-	-	-	-	-	-	-	-	-
205 *Rupicapra rupicapra*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	1	-	-	-	-	-	1	-	-	-
206 *Saiga tatarica*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
207 *Pliotragus ardeus*	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
TUBULIDENTATA																																																
208 *Orycteropus depereti*	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

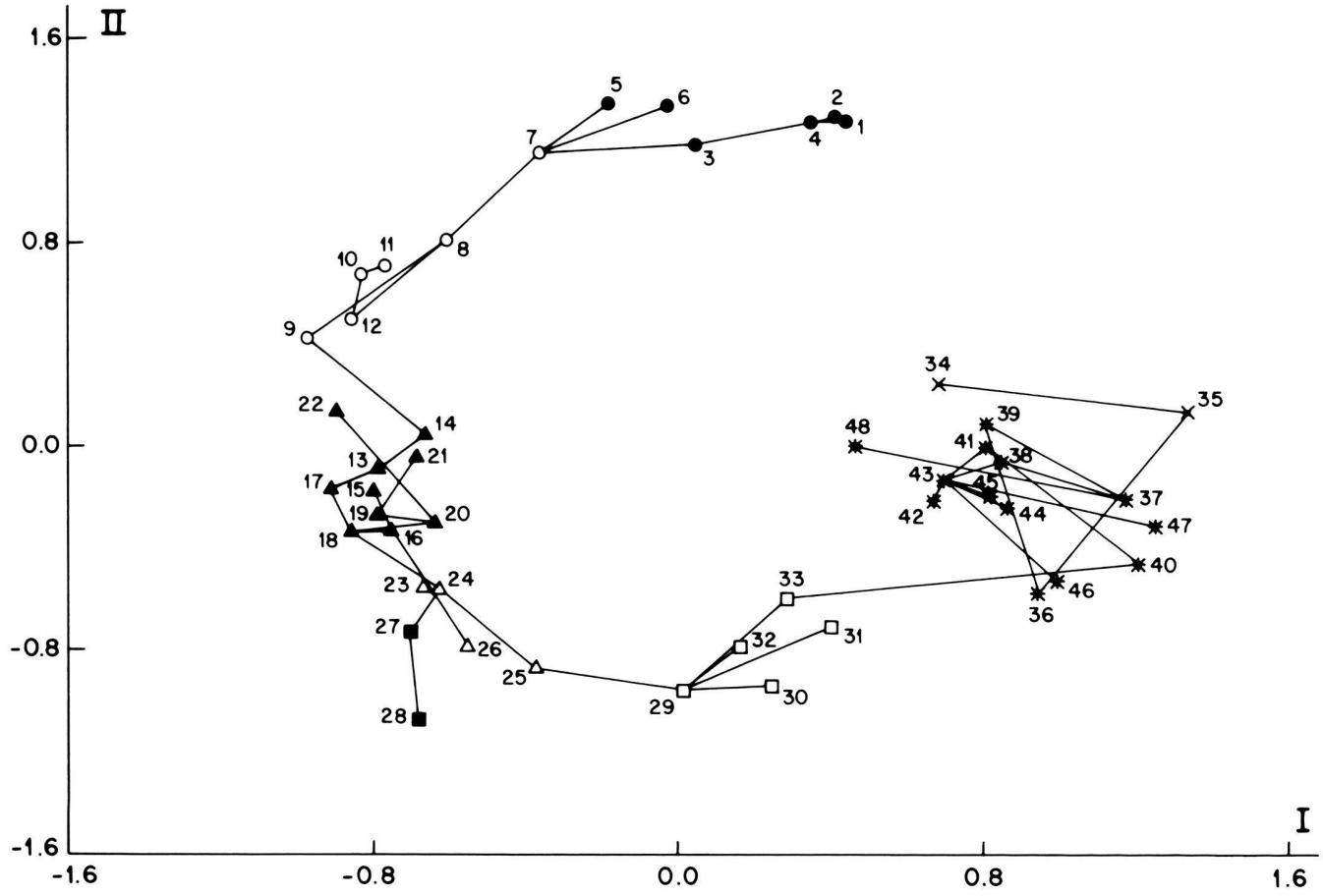


Fig. 2. Two dimensional solution for nonmetric multidimensional scaling of the 48 local faunal assemblages based on principal coordinate analysis. A minimum spanning tree connects closer local faunal assemblages. Symbols and locality numbers as in Figure 3 and Table 2.

The NTSYS-PC program, version 1.7 (Rohlf 1992) was used in the analysis. The initial matrix has been edited and effectively manipulated by the multivariate method and computing programs to be used. To avoid the introduction of noise and to reduce the matrix size, outliers and incomparable data have been deleted prior to quantitative analysis. From the statistical point of view, rare taxa should be removed from a quantitative analysis (Maples & Archer 1988). No further data transformations have been made in the data-editing step.

The presence of a taxon in a sample is the basic data unit, and therefore binary coefficients can be used in most biostratigraphic work (Hazel 1970). Absence of a taxon in a locality may derive from ecological and/or biogeographical bias, differential preservations, and/or poor sampling, rather than from temporal factors. So, the common absence conveys no precise information and can not be interpreted as an indication of similarity. Several conventional binary similarity coefficients available in the literature do not consider mutual absences. Among them, the Jaccard coefficient satisfies also the following conditions (Shi 1993) that are preferable in our analysis:

- it has only positive values ranging from 0 (totally different) to 1 (identical)
- it is metric and symmetrical
- it is little affected by differences in sample sizes
- it has a near-linear relationship with the increase of the number of shared taxa

The Jaccard coefficient is one of the most widely used. As Simpson (1960) pointed out, it is the most obvious and intuitively most acceptable of the measures. It is simply the proportion of objects present in two units being compared. Relative to other coefficients, the Jaccard coefficient tends to emphasize differences (Hazel 1970).

An integrated multivariate approach combining cluster analysis and non-linear ordinations is used to analyze the large, heterogeneous, binary data set, because both procedures make no assumptions about the data structure. An ordination is used first to derive an ordination space of LFAs. Ordination assumes data continuities and therefore it is useful for displaying interrelationships of data points, testing the null hypothesis

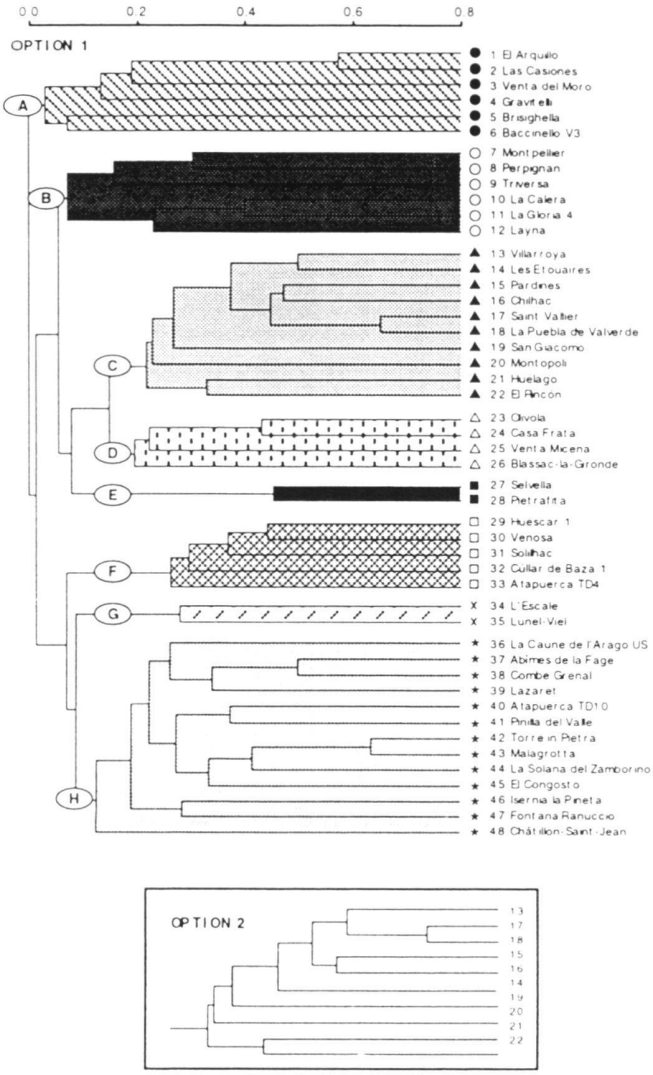


Fig. 3. Q-mode dendrogram for 48 local faunal assemblages based on unweighted data of 117 species. Outliers and no comparable data are removed. CCC = 0.91693 and 0.91736 for options 1 and 2 respectively.

that LFAs are randomly distributed through time. Cluster analysis assumes data discontinuities as being useful to undertake partitioning of the ordination space and for classification.

The ordination technique was non-metric multidimensional scaling (NMDS), using principal coordinate analysis (PCO) as the initial configuration (Kruskal 1964). PCO does not use strictly the Euclidean distances, which are rarely met by binary data (Gower 1966). This method was used to transform a symmetric similarity matrix to a scalar product form, so that its eigenvalues and eigenvectors could be computed. NMDS has no underlying assumptions about normality or linearity of the data because it uses only the rank order information rather than the metric information (Shi 1993). The assumption of linearity is replaced by the weaker and less problematic assumption of monotonicity (Gauch 1982). Comparative studies have found that NMDS normally provides better low-dimensional displays or coordinates in terms of distances in the display than do linear ordination techniques (Hughes 1973). We used the statistic Stress1 as a measure of how well a configuration matches the similarity matrix (Kruskal 1964).

We superposed a minimum spanning tree (Rohlf 1970) over the two dimensional ordination plot resulting from the NMDS analysis. This method is useful to detect local distortions, such as pairs of points which look close together in a plot, but are actually far apart if other dimensions are taken into account. The minimum spanning tree was obtained from the same similarity matrix used in the NMDS.

The clustering technique was the unweighted pair-group method using arithmetic averages (UPGMA). In the UPGMA, the level at which a member will join an existing cluster is based on average similarities of all the existing members calculated from the original matrix of coefficients. Thus, each member of a cluster has equal weight at all levels of clustering. The cophenetic correlation coefficient (CCC) was computed as a measurement of distortion (Farris 1969). Among the agglomerative hierarchical clustering techniques, UPGMA yield a greater CCC indicating less amount of distortion in the dendrogram relative to the original similarity matrix (Hazel 1970; Shi 1993).

Q-mode analysis relates LFAs to each other on the basis of the present species. In individual sections where fossils are abundant, the dendrogram reproduces the stratigraphic position of the samples in the section and indicates their relative faunal similarities (Hazel 1970). R-mode analysis relates species to each other on the basis of the LFAs where they are found. Ideally, dendrograms resulting from clustering of R-mode similarities will reveal which species are responsible for the clusters of localities obtained in Q-mode. However, care must be taken because eventually all species are forced into cluster (Hazel 1970).

Results

The two dimensional ordination from NMDS analysis is shown in Figure 2. The measurement of goodness of fit shows an interval between fair and good levels, according to Kruskal's (1964) evaluation of Stress1 coefficient. A minimum spanning tree is superimposed on the plot as an informative mean of gauging distance relationships among localities. As expected, the LFAs appear distributed in several groups which have been interpreted according to the pattern obtained by cluster analysis (Fig. 3). There is a clear arrangement of these groups according to time. Some discrepancies appear to occur between both results, for instance, the transitional positions of Montpellier and Triversa. However, the examination of the distance within the minimum spanning tree supports the relation shown by the dendrogram.

Figure 3 shows the Q-mode dendrogram resulting from the clustering of similarities among LFAs based on the occurrences of species. There is a high goodness of fit between the cophenetic value matrix and the original matrix being clustered (CCC = 0.917). There are three main clusters that reflect two main ruptures. The first main cluster (cluster A) gathers the latest Miocene localities that have been included in this analysis.

The second main cluster (cluster B+C+D+E) joins the Pliocene localities to the Early Pleistocene ones. A clear break between Ruscinian (cluster B) and Villafranchian (cluster C+D+E) localities is detected. The only exception is Triversa that appears included in cluster B. The Villafranchian localities are divided into three minor clusters. Most of them are grouped in cluster C. Within this cluster, the most likely grouping is the subgroup: Pardines+Chilhac and Saint-Vallier+La Puebla de Valverde. This subgroup is closer to Villarroya and Les Etouaires than to the other sites gathered within cluster C (San Giacomo, Montopoli, Huélago and El Rincón). Two equal options have been supplied by the Q-mode analysis. Villarroya and Les Etouaires could form a single cluster joined to this subgroup or Villarroya could be closer to Saint-Vallier+La Puebla de Valverde which presents the highest similarity.

The third main cluster includes all Middle Pleistocene localities which group, in turn, into three minor clusters: the cluster F gathers the earliest Middle Pleistocene localities; L'Escale and Lunel-Viel form a single cluster (G); and the rest of the localities are grouped into the cluster H. All correspond to the Galerian LMA.

Figure 4 shows the R-mode dendrogram resulting from the clustering of similarities among species based on the localities where they are found. There is a goodness of fit between the cophenetic value matrix and the original matrix being clustered (CCC = 0.833). The hierarchical arrangement of species indicates that three major groupings are related at a very low level and each one contains several subordinate groups. These groups are here considered as associations (A). Association 1 (A1) corresponds to the Turolian and Ruscinian faunas, Association 2 (A2) corresponds to Villafranchian faunas and Association 3 (A3) to Galerian faunas. Within these associations several groupings of minor order are retained. Some of them reveal which species are responsible for the cluster of localities obtained in Q-mode. Thus, A1.3 and A1.4 correspond to cluster A; A1.2 corresponds to cluster B; A2.1.3, A2.1.5 and A2.1.6 correspond to cluster C; A3.3.1 corresponds to cluster F and A3.2.2 and A3.2.4 correspond to cluster H. In other cases, they grouped long-term taxa. For instance, A1.1 contains species present in cluster A, B and C; A2.1.2 species present in cluster B, C, D and E and A3.1 species present in cluster D, F, G and H. The integration of long-term taxa is generally produced with the taxa typical of the cluster in which the long-term taxa have more weight (Fig. 4). Their first or last occurrences have less importance. It is worth mentioning that Q-mode and R-mode dendrograms have some discrepancies concerning Ruscinian LFAs and species. The Ruscinian LFAs in Q-mode dendrogram are joined to Villafranchian localities, while in R-mode dendrograms most Ruscinian species are joined to Turolian ones and only some long-term taxa present in Triversa are attached to Villafranchian ones.

Analysis of the data set

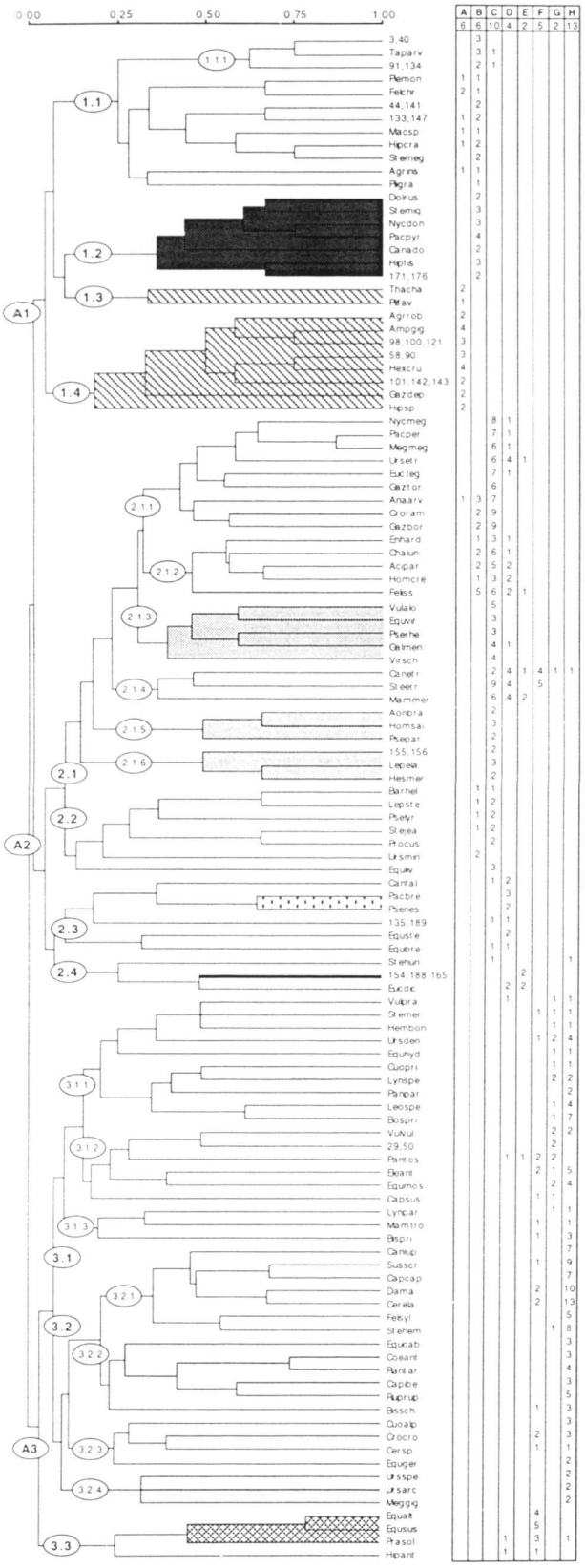
Cluster A

Localities. El Arquillo, Las Casiones, Venta del Moro, Gravitelli, Brisighella and Baccinello V3.
Available datations. Venta del Moro was placed in the magnetostratigraphic chrons 3An.1n or 3An.2n (Opdyke et al. 1990) recently calibrated as 5.89–6.18 and 6.27–6.57 Ma respectively (Cande & Kent 1995).
Biochronological equivalences. Mein's "zone" MN13 and latest Turolian (Ventian).
Faunal associations. A1.3 *(Thalassictis* gr. *chaerethis-macrostoma + Plioviverrops faventinus)* and A1.4 *(Agriotherium roblesi + Amphimachairodus giganteus + Hipparion primigenium + Hipparion gromovae + Lartetotherium schleiermacheri + Thalassictis hipparionum + Zygolophodon turicensis + Hexaprotodon crusafonti + Tetralophodon longirostris + Hipparion periafricanum + Pliocervus matheroni + Pliocervus turolensis + Gazella deperdita + Hipparion* sp.).
Discussion. Cluster A includes some localities previously referred to the Ventian representing the transition between the Turolian s.s. levels and the early Ruscinian (Aguirre et al. 1976). According to Alberdi & Bonadonna (1988) only Baccinello V3 and Venta del Moro would correspond to the Ventian age. The ordination multivariate analysis shows a short distance among the most certain Turolian localities such as El Arquillo, Las Casiones and Gravitelli. Nevertheless, combining the results from both analyses, they do not allow the separation of these three localities from the rest of cluster A. On the other hand, the age of Baccinello V3 has been variously interpreted between MN13 and MN14 and some authors pointed out the possibility of a somewhat older age than Brishigella (De Giuli 1989; Engesser 1989).

The separation between clusters A and B+C+D+E can be related to the Pliocene transgression, placed at the Mio-Pliocene boundary dated around 5.4 Ma (Steininger et al. 1985).

Cluster B

Localities. Montpellier, Perpignan, Triversa, La Calera, La Gloria and Layna.
Available datations. Based on an unpublished paleomagnetic section from the Pichegu quarry (France), Lindsay et al. (1980) pointed out that the Ruscinian could be correlated with the Gilbert magnetic chron, a correlation also proposed by Clauzon et al. (1990). Triversa was placed in the magnetostratigraphic chron 2An.2n (Lindsay et al. 1980) recently calibrated as 3.11–3.22 Ma (Cande & Kent 1995).



Biochronological equivalences. It corresponds to Ruscinian, Mein's "zones" MN14 and MN15, and Perpignan level (Torre et al. 1992). Triversa is the oldest locality of the MN16 (de Bruijn et al. 1992) and was chosen by the Italian authors as the reference level for the lowest Villafranchian unit.

Faunal associations. A1.2 *(Dolichopithecus ruscinensis + Stephanorhinus miguelcrusafonti + Nyctereutes donnezani + Pachycrocuta pyrenaica + Canis adoxus + Hipparion fissurae + Birgerbohlinia* sp.).

Appearance of long-term taxa. A1.1.1 (Zygollophodon borsoni + Sus arvernensis + Tapirus arvernensis + Mesopithecus monspessulanus + Viverra pepraxi) and A2.1.2 *(Enhydrictis ardea + Chasmaportetes lunensis + Acynonix pardinensis + Homotherium crenatidens + Felis issiodorensis).* Also *Baranogale helbingi + Leptobos stenometopon + Pseudodama lyra + Stephanorhinus jeanvireti* integrated into A2.2.1 and *Croizetocerus ramosus + Gazella borbonica* integrated in A2.1.1.

Discussion. The Ruscinian faunas are usually separated into two biochrons, MN14 (Montpellier and La Calera) and MN15 (Perpignan and Layna) (de Bruijn et al. 1992). This separation has not been confirmed by the analysis.

The transition between Ruscinian and Villafranchian LMAs corresponds to an intercontinental faunal dispersal event, related to a global climatic change. Two outstanding arrivals to Eurasia are those of the elephants from Africa and of *Equus* from North America. This has been called the *Leptobos-Equus*-elephant event (Steininger et al. 1985), and could be correlated with the "Great American Biotic Interchange", dated around 3.0 Ma (Webb 1985). Azzaroli et al. (1988) divided this event into two migration waves: first, the arrival of *Leptobos* at the beginning of the Villafranchian, and later the arrival of elephant-*Equus* in the last part of the Early Villafranchian. Azzaroli et al. (1988) placed the Triversa fauna between both events. The transitional situation of Triversa is confirmed by our analyses. This locality (locality 9) appears in the Q-mode dendrogram included in cluster B, but in the ordination analysis it occupies a more intermediate position, between clusters B and C, slightly closer to Les Etouaires (locality 14). This is also marked by the R-mode dendrogram. A1.2 and A1.1.1 are integrated in the main A1 joined to the Turolian fauna, thus representing a certain disagreement with the Q-mode analysis.

Cluster C

Localities. Villarroya, Les Etouaires, Pardines, Chilhac, Saint-Vallier, La Puebla de Valverde, Huélago, San Giacomo, El Rincón and Montopoli.

Fig. 4. R-mode dendrogram for 117 species. Outliers and no comparable data are removed. Opposite the end points of the dendrogram, values for occurrence of species in the main cluster recognized as "Unit" in Figure 3 are given. CCC = 0.83296. Abbreviations for species are composed by the three first letters of genus and of species, and species number as in Table 2.

Available datations. Les Etouaires was considered older than 3.0 Ma following fission track data obtained from a reworked deposit where several volcanic events are represented (Chambaudet & Couthures 1981). Ly et al. (1982) proposed a younger age around 2.6–2.4 Ma for this locality. Afterwards, all these data were discussed, concluding that they cannot be used accurately (Bonadonna & Alberdi 1987; Azzaroli et al. 1988). Les Etouaires has been correlated with Triversa by magnetostratigraphy (Bonadonna & Alberdi 1987). El Rincón1 has been indirectly dated as 2.5–2.6 Ma by Leone (1985). Boeuf (1983) reported several K/Ar ages for a basalt flow overlying the faunal level of Chilhac, between 1.6 and 2.3 Ma. Based on paleomagnetic and radiometric data, Bonadonna & Alberdi (1987) later assigned this fossiliferous level to the beginning of the Olduvai subzone, around 1.95 Ma.
Biochronological equivalences. Mein's "zones" MN16 and MN17, partially with MN17 of Agustí et al. (1987), and with the Italian faunal units Triversa (in part), Montopoli and Saint-Vallier (Torre et al. 1992). Early, Middle and the beginning of Late Villafranchian.
Faunal associations. A2.1.5 *(Aonyx bravardi + Homotherium sainzelli + Pseudodama pardinensis)*, A2.1.6 *(Cervus perrieri + Arvernoceros ardei + Leptobos elatus + Hesperidoceras merlai)*, A2.1.3 *(Vulpes alopecoides + Equus stenonis vireti + Pseudodama rhenanus + Viretailurus shaubi)*.
Appearance of long-term taxa. A2.1.4 *(Canis etruscus + Stephanorhinus etruscus + Mammuthus meridionalis)*. *Gallogoral meneghini* is included in A2.1.3. *Nyctereutes megamastoides + Pachycrocuta perrieri + Megantereon megantereon + Ursus etruscus + Eucladoceros tegulensis + Gazellospira torticornis* are integrated in A2.1.1, and *Canis falconeri + Sus strozzi + Leptobos merlai + Equus bressanus* are included in A2.3.
Discussion. In previous biochronological scales the localities, included in cluster C appear in two or three "zones" (Fig. 4) corresponding to MN16a, MN16b, and MN17. This distribution does not appear clearly in our analysis. As we point out above, two options have resulted for the relationships of Villarroya and Les Etouaires, but both appear closer to MN17 localities (Pardines, Chilhac, Saint-Vallier, La Puebla de Valverde) than to MN16b localities (San Giacomo, Montopoli, Huélago, El Rincón). Villarroya and Les Etouaires are included in MN16a along with Triversa. These two localities share almost 40 per cent of species (mainly carnivorous taxa) with MN17 localities and less than 25 per cent with Triversa. MN16a represents a time span previous to the *Equus*-elephant dispersal event (Azzaroli et al. 1988). It is worth mentioning that this idea is based on the presence of *Hipparion* instead of *Equus* in Villarroya, the absence of equids in Triversa and Les Etouaires and the absence of elephants in these three localities. The common absences (negative evidences) are intentionally excluded in our analysis.

Cluster D

Localities. Olivola, Casa Frata, Venta Micena and Blassac-La-Gironde.
Available datations. Olivola is situated at the top of a fluviatile complex with evidence of an intensive erosion, the so-called Aullan erosional phase, and the beginning of this erosional phase has been placed at the end of the Olduvai palaeomagnetic episode (Azzaroli et al. 1988). In addition, at Blassac-La-Gironde, there is an overlaying lava flow dated around 1.9 Ma. This deposit shows a positive polarity referred to the Olduvai palaeomagnetic episode (Boeuf et al. 1992).
Biochronological equivalences. MN18 and most of MN19 (Guérin 1982), upper part of MN17 and MmQ1 of Agustí et al. (1987) and the Italian faunal units Senèze, Olivola and Tasso (Torre et al. 1992): Late late Villafranchian.
Faunal associations. Pachycrocuta brevirostris + Pseudodama nestii and *Equus stehlini + Leptobos etruscus* are included in A2.3 along with other taxa already present in cluster C.
Appearance of long-term taxa. Stephanorhinus hundsheimensis, Eucladoceros dicranius, Vulpes praeglaciaris, Panthera toscana, Hippopotamus antiquus, and *Praemegaceros solhilacus* are included in diverse associations.
Discussion. The beginning of the cluster D corresponds to the Olivola faunal unit. This faunal transition was called the "Wolf" event (Azzaroli et al. 1988), and was characterized by the massive expansion of *Canis etruscus* in Europe. However, this species was previously recorded at San Giacomo and possibly at Les Etouaires, both within cluster C. Casa Frata locality was placed in the Tasso faunal unit characterized by the appearance of *Canis (Xenocyon) falconeri* (Torre et al. 1992). In our analysis, Olivola and Casa Frata show the highest similarity within cluster D, and a break between them is not supported, in agreement with Agustí et al. (1987).

Cluster E

Localities. Selvella and Pietrafita.
Biochronological equivalences. From the upper part of MN19 to the lower part of MN20 (Guérin 1982), MmQ2 of Agustí et al. (1987) and the Farneta faunal unit (Torre et al. 1992). This is the latest Villafranchian.
Faunal associations: Pseudodama farnetensis + Leptobos vallisarni + Praemegaceros boldrinii integrated in A2.4.

Cluster F

Localities. Huéscar, Venosa, Solilhac, Cullar de Baza 1 and Atapuerca TD4.
Available datations. Solilhac was placed in the Jaramillo palaeomagnetic episode, dated around 0.99–1.07 Ma (Thouveny & Bonifay 1984). At Atapuerca-TD4, the palaeomagnetic inversion detected between levels TD2 and TD4 was correlated with the Matuyama-Brunhes boundary, around 0.78 Ma (Carracedo et al. 1987). Recently, Parés & Pérez González (1995) situated the TD4 level as older than the Matuyama-Brunhes boundary.
Biochronological equivalences. Upper part of MN20, MN21 and lower part of MN22 (Guérin 1982) and MmQ3 of Agustí et al. (1987). Early Galerian.

Faunal associations. Equus altidens + Equus sussenbornensis integrated in A3.3 along with *Praemegaceros solhilacus* and *Hippopotamus antiquus,* already present in cluster D.
Appearance of long-term taxa. Crocuta crocuta, Ursus deningeri, Elephas antiquus, Mammuthus trogontherii, Stephanorhinus mercki, Sus scrofa, Capreolus capreolus, Dama sp., *Cervus elaphus, Bison priscus, Bison schoetensacki.*
Discussion. The beginning of cluster F corresponds to the main interruption observed among the faunal assemblages here analyzed. This faunal turnover supposes the appearance of many modern mammal lineages, such as the first caballine-*Equus sussenbornensis*-, and the present association of deer *Dama + Cervus elaphus + Capreolus. Mammuthus trogontherii, Elephas antiquus* and *Ursus deningeri* are also recorded for the first time as typical Middle-Late Pleistocene mammals, and *Dolichodoryceros savini* is the first representative of the *Megaloceros* group within the Megacerini.

Cluster G

Localities. L'Escale and Lunel-Viel.
Available datations. L'Escale is considered younger than the Matuyama-Brunhes boundary from palaeomagnetic data (Thouveny & Bonifay 1984).
Biochronological equivalences. Upper part of MN22 (Guérin 1982), lowermost part of MQ4 of Agustí et al. (1987). Middle Galerian.
Appearance of long-term taxa. Vulpes vulpes, Cuon priscus, Mustela palerminia, Hyaena prisca, Felis (Lynx) spelaeus, Felis (Lynx) pardina, Panthera (Leo) spelaea, Equus hydruntinus, Equus caballus mosbachensis, Stephanorhinus hemitoechus, Hemitragus bonali and *Bos primigenius,* most of them integrated in A3.1.1.

Cluster H

Localities. La Caune de l'Arago US, Abîmes de la Fage, Combe Grenal, Lazaret, Atapuerca TD10, Pinilla del Valle, Torre in Pietra, Malagrotta, La Solana del Zamborino, El Congosto, Isernia La Pineta, Fontana Ranuccio and Châtillon-Saint-Jean.
Available datations. Fontana Ranuccio was dated by K-Ar around 0.5 Ma (Biddittu et al. 1979), Isernia around 0.7 Ma (Coltorti et al. 1982) and Pinilla del Valle ca. 0.2 Ma (Alférez 1985), by electron spin resonance (ESR).
Biochronological equivalences. MN23 and MN24 of Guérin (1982), most of the lower part of MQ4 of Agustí et al. (1987). Late Galerian.
Faunal associations. A3.2.2 *(Equus caballus caballus + Coelodonta antiquitatis + Rangifer tarandus + Capra ibex + Rupicapra rupicapra)* and A3.2.4 *(Ursus spelaeus + Ursus arctos + Megaloceros giganteus).*
Appearance of long-term taxa. Canis lupus, Felis sylvestris, Panthera pardus, Cuon alpinus, Capreolus capreolus and *Equus caballus germanicus.*

Temporal resolution

As expected, groupings of LFAs based on the common presence of species have been revealed by multivariate techniques. Comparing our results with previous bio- and geochronological data, a clear arrangement of these groups according to time is evidenced (Fig. 5).

The characteristic features of each group, and in several cases the similarity between faunas of adjacent ones, lead to the recognition of three informal hierarchical ranks of organization (Fig. 5). These are, from higher to lower levels within the hierarchy: "Superages", "Ages" and "Units", which do not exactly correspond to previous biochronological schemes.

Apart from cluster A that could be grouped with an older Turolian association, the dendrogram (Fig. 3) and Figure 5 show the existence of two large distinct aggregates of LFAs (clusters B+C+D+E and clusters F+G+H). We informally named them "Superage I" and "Superage II". In the sense that both aggregates have scarce common taxa between them suggesting that each one form part of "an ecologically adjusted group of animals with specific geographic limits and chronologic range" (Tedford 1970, p. 602), the level of "Superage" could be equivalent to the Chronofauna concept (*sensu* Tedford 1970; Emry et al. 1987). The rise and fall of both "Superages" seem to be governed by concurrent environmental change and community reorganization associated with the major pulses in the late Neogene glacial trend.

The beginning of "Superage I" can be correlated with the end of the Mediterranean salinity crisis (Hsü et al. 1977). Oxygen isotopic evidence indicates high but variable $\delta^{18}O$ values around the Mio-Pliocene boundary that resembles glacial/interglacial cycles but only one-third the amplitude of the Late Pleistocene signal (Hodell et al. 1986). These authors interpreted this variability as a reflection of instability in the Antarctic ice sheet. Paleomagnetic correlation points to an isotopic event coinciding with the isolation and desiccation of the Mediterranean basin around 5.0 Ma ago. The termination of the salinity crisis and restoration of open-marine conditions coincided with a glacial retreat and marine transgression marked by a rapid decrease in $\delta^{18}O$.

On the other hand, the beginning of the "Superage II" could be calibrated, based on Solilhac locality, with the Jaramillo magnetic event around 1.0 Ma (Thouveny & Bonifay 1984) or slightly older. It can also be correlated with another great climatic event, the so-called "Glacial Pleistocene". For the interval 1.30–0.91 Ma, it is fairly well documented that the character of the isotope record changes from low amplitude, 40–50 ka quasiperiodic cycles (orbital obliquity), to lower frequency (100 ka cycles, orbital eccentricity) and higher amplitude nature of the signal (Williams et al. 1988).

As important dispersal events are time synchronous and relative sea level drop favours the correlation, the European and North American biochronologic scales are coincident (Opdyke 1990). Thus European LMAs and North American LMAs are coincident for every boundary from the base of the

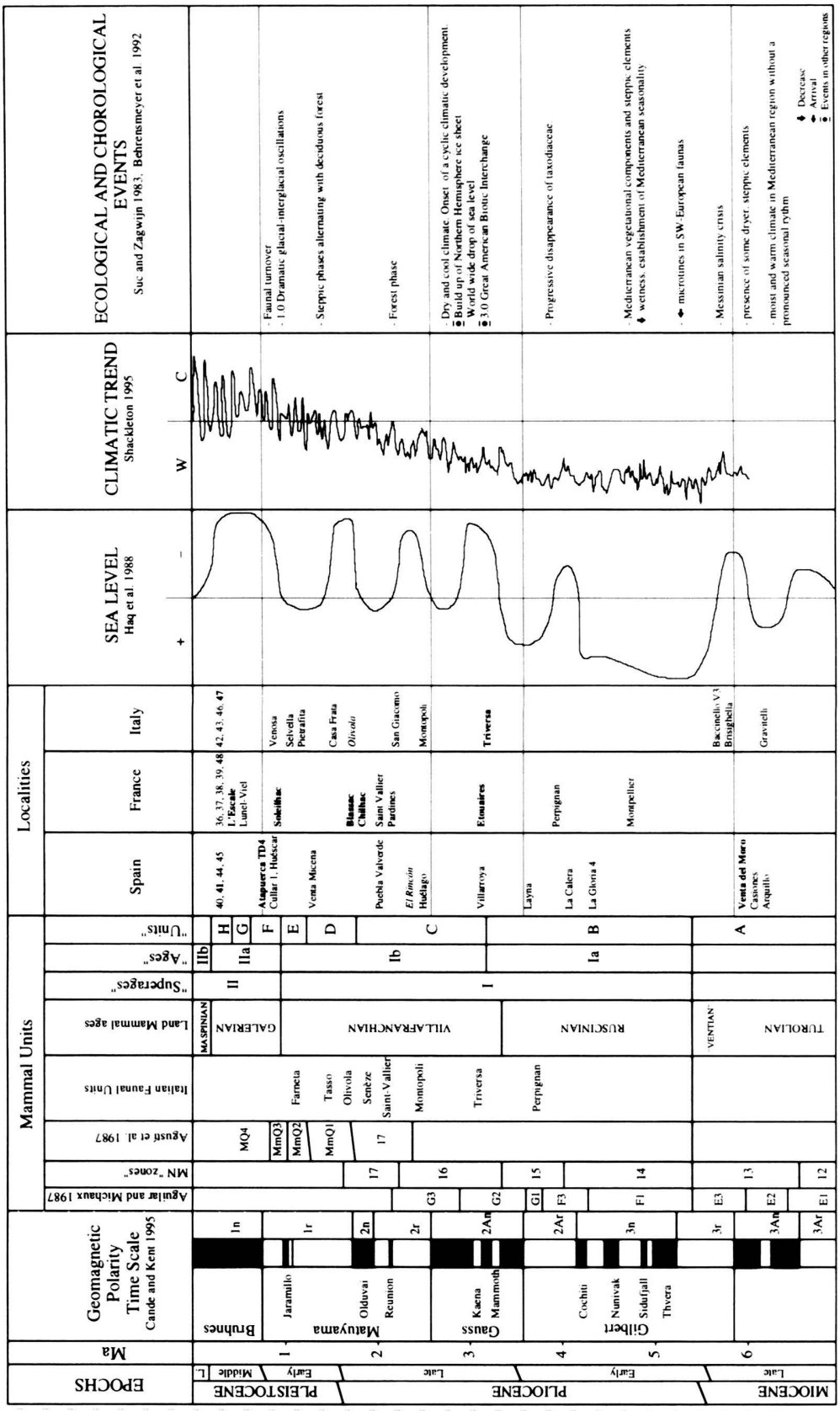


Fig. 5 Chronostratigraphic situation of the selected localities from Spain, Italy and France in the Mediterranean area, during the last 6 Ma. The localities with radiometric or magnetostratigraphic datations are shown: bold for direct and italic for indirect correlation. The equivalence between biochronological units are based mainly on the included localities. There is a large variation among the authors about FADs.

Miocene to the Pliocene, except in the Plio-Pleistocene epochs where it is distorted (Opdyke 1990). Our results seem to be in agreement with this idea. "Superages" I and II appear to be correlated with the Blancan and Irvingtonian North American LMAs respectively.

The "Ages" or second hierarchical level recognized in the Q-mode dendrogram (Fig. 2 and 5) basically correspond to the European LMAs proposed by different authors (e.g. Ambrosetti et al. 1972; Aguirre et al. 1976; Fahlbusch 1976; Alberdi & Aguirre 1977; see Fig. 5). At this level of analysis, independent biochronologic techniques, such as a classical approach based on qualitative analysis and an approach based on multivariate analysis, can be productively used to test hypotheses of faunal correlation.

Each "Age" includes one or more "Units" corresponding to clusters of Figure 3. There is only little correspondence with any of the previous biochronological scales (MN "zones", Mammal Units, biozones) as is indicated in Figure 5. This lack of agreement is likely to be due to: 1) the absence of micromammals in the analysis, 2) the clustering was only based on mutual presences and 3) our analysis was computed at specific taxonomical level.

Minor pulses in the Late Neogene glacial trend are also detected and they are suspected as base of the lower hierarchical levels. There is evidence of a moderate climatic deterioration during the Villafranchian, between 3.2 and 3.1 Ma, interpreted as reflecting the first accumulation of a Northern Hemisphere ice sheet (Thunell 1979; Shackleton et al. 1984). At this moment, the *Equus*-elephant event occurred, corresponding to be boundary of our Ages Ia/Ib (Fig. 5).

Thus, clustering reflects changes in the mammal communities apparently related to episodes of biotic and abiotic environmental variation, either of different magnitude or of different cumulative effects. The clusters could represent spans of time during which the faunas have a certain taxonomic homogeneity. The discontinuity between them may denote a faunal restructuration associated with major changes in environmental conditions, clearly correlated with worldwide phenomena.

Conclusions

The definition of biochronological units implies two steps. First, the recognition of a succession of non-overlapping, ecologically adjusted assemblages of animals living together in space and time. Second, the boundary definitions following the first appearance datums (FADs) in the lower boundary.

The multivariate approach provides a successful tool in the first step of recognition of biochrons and helps in the selection of FADs. It supposes an important contribution to continental biochronology.

The application of this methodology to the biochronology from latest Miocene to Middle Pleistocene in the Western Mediterranean area proves that European LMAs constitute an adequate biochronologic framework of reference for this time interval, especially when large mammals are considered.

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