

Application of Unitary Associations to biochronological scales based on mammals: the case of Miocene rodents from some localities in western Europe

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Abstract. The method of biochronological analysis known as "Unitary Associations" was developed in the late 1970s in order to establish concurrent range zones taking virtual associations into account (e. g., synchronous species that never coexisted for ecological reasons). We have here used three successions of Miocene localities as synthetic sections. They are characteristic of the three biochronological scales currently used in western Europe. Only those rodent species common to at least two of the three successions have been considered. Besides pointing to some problems of chronology, the use of this method in continental environments in which the succession order of the localities is often inferred on the basis of evolutionary stages makes apparent some taxonomic discrepancies between authors.

Key words: biochronology, Unitary Associations, virtual associations, mammals, rodents, Miocene, western Europe.

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I. INTRODUCTION

Like almost all the stratotypes of the Universal Geological Time Scale, those of the Miocene have been defined on marine series. Numerous strata deposited in continental environments (lakes, rivers, alluvial aprons, etc.) contain fossil mammals. In order to provide ages for these sediments, paleomammalogists have long used the terminology of the stages in the Universal Geological Time Scale. To do this they have had to establish marine/continental correlations using three methods: lateral facies changes, marine intercalations in continental beds (or vice versa) and continental faunas in marine sediments (animals swept along by coastal streams and deposited in marine environments) (GINSBURG 1975). Such correlations are always geographically limited and it is also necessary to establish purely continental mammalian biochronologies.

Since the working unit for paleomammalogists is the locality, THALER suggested referring to mammalian "zones" by the names of type localities. In 1965 he proposed the first mammal biochronology for the European Tertiary, based on the succession of mammalian faunas in western

Europe. Zones and sub-zones were based on the evolutionary stages of the representatives of certain lineages.

This zonation was replaced by that developed by MEIN expounded at the VIth Congress of the Regional Committee on Mediterranean Neogene Stratigraphy (RCMNS), in 1975. Later, MEIN introduced some corrections to this zonation and described its philosophy more precisely (MEIN 1979, 1981).

Each mammal, or MN, unit was initially defined by characteristic species (one species is theoretically sufficient to define a zone), mammalian associations determined at the generic level and first occurrences, most frequently due to migrations.

A revised version of the MN zonation was recently proposed (MEIN 1989). It is based, for the Miocene, on the 14 following reference levels: Paulhiac, Montaigu, Laugnac, Wintershof-West, La Romieu, Pontlevoy-Thenay, Sansan, Steinheim, Anwil, Can Llobateres, Masia del Barbo, Crevillente 2, Los Mansuetos and El Arquillo 1. Several participants at the Reims Congress in 1990 expressed their doubts regarding the stratigraphic succession of Steinheim and Anwil. The two corresponding mammal units were grouped into a single one, the reference locality for which is the fauna from La Grive M (DE BRUIJN et al. 1992).

In 1982, AGUILAR proposed a new biozonation for the Miocene of western Europe, based on the evolutionary stages of rodents (cricetids, eomyids and murids). Species associations, immigrations and extinctions were also taken into account. This scale supposedly gives greater weight to biogeographical differentiation. On the other hand, correlations with the marine stratigraphic scales were proposed using radiometric dates or localities (reference levels) more or less directly correlated with marine beds. Subsequently, the calibration of the successions of localities allowed this author to estimate the resolution obtained with the rodents to 750 000 years in the lower Neogene and 250 000 years in the upper Neogene (AGUILAR & MICHAUX 1987).

A third zonation, mainly subdividing the Aragonian, has been proposed. The Aragonian was formerly defined as the time interval separating the first occurrences of the tridactyl equids *Anchitherium* and *Hipparion* in western Europe (FAHLBUSCH 1976). This zonation, established in the Calatayud-Teruel Basin (Spain), has known several versions; the last one, due to DAAMS & FREUDENTHAL (1988), has been improved by VAN DER MEULEN & DAAMS (1992). Mainly based on the rodents, it is built on the following criteria: presence of one or several taxa, absence of one or several taxa, evolutionary stages, abundance.

Thus, three mammalian time scales for the Miocene of western Europe are currently in use, although DAAMS & FREUDENTHAL (1988) admit to the possibility that their biozonation is of only local value.

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II. UNITARY ASSOCIATIONS

The principles on which the Unitary Associations method is based will not be reviewed here. For further details, the reader is referred to previous papers on the subject (GUEx 1977, 1980, 1991). Originally, this method was developed to analyse sparse, incomplete and conflicting stratigraphic data. The aim of the method is to construct sequences of inter-species coexistence intervals of minimal duration. Such sequences can be used as a biochronological framework for stratigraphic correlations. Therefore, the biochronological scale is defined as a succession of mutually exclusive biological events (co-occurring taxa).

The Unitary Associations method makes use of graph theory. A graph is a set of vertices joined by edges (undirected graph), arcs (directed graph) or both (semidirected graph). An arc is an edge with an arrow indicating a direction for an ordered pair of vertices (Fig. 1).

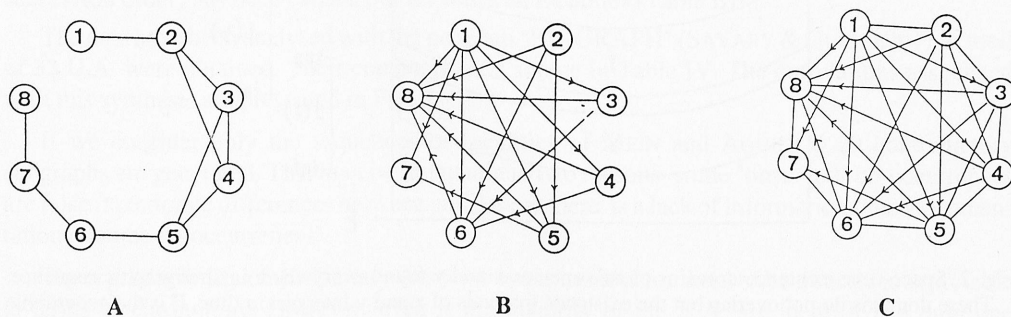


Fig. 1. A – undirected graph representing the coexistence of eight species. B – directed graph representing the superpositions of the same eight species. C – biostratigraphic graph representing the coexistences and superpositions of the same eight species; this semidirected graph results from the combination of A and B. After GUEX 1991.

The following analogies can be made:

- each vertex is the stratigraphic range of a species;
- two compatible species (i. e., two species having coexisted during at least a part of their stratigraphic ranges) are joined by an edge;
- two incompatible species (i. e., two species that never coexisted but the stratigraphic relationships of which are known) are joined by an arc;
- two species the coexistence or the stratigraphic relationships of which can not be demonstrated are not joined.

A Unitary Association (U.A.) is represented by a maximal set of vertices joined together by edges ("maximal cliques"), i. e., a maximal set of species compatible with each other.

The Unitary Associations method identifies mutually exclusive species associations. It can also identify virtual co-occurrences: two synchronous species may never be found together for taphonomic reasons (differential fossilization) or ecological reasons (species that were never sympatric). Absences are not significant; the virtual co-occurrences are simply deduced from the effective occurrences or co-occurrences.

An important premise of the Unitary Associations method is the diachronic nature of the "datums". In the theoretical example of Fig. 2, the last appearance datum of species X precedes the first appearance datum of species Y, whatever place is considered; nevertheless, the respective coexistence intervals of X and Y overlap in time.

In the case of continental localities with fossil mammals, one problem is the lack of superpositional time control. The working unit for the paleomammalogist is the locality, considered as a "snapshot" in the geological time scale. The problem of correlation treated in the present paper does not concern normal stratigraphic data (with local faunal sequences) but data of archaeological type: the fossil localities are not known in stratigraphic superposition and the "sequences" are inferred from the evolutionary stages of the mammals.

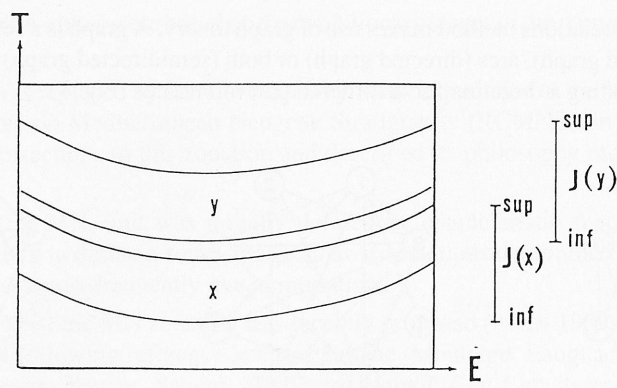


Fig. 2. Space-time existence domains of two species x and y found everywhere in stratigraphic sequence. These domains do not overlap but the existence intervals of x and y intersect in time. E is the geographic space, T is the time, J(x) and J(y) are the respective chronological ranges of x and y. After GUEX 1991.

III. APPLICATION OF UNITARY ASSOCIATIONS TO MIOCENE MAMMALIAN BIOCHRONOLOGY

We have used the Unitary Associations method to test three successions of Miocene localities characteristic of the three mammalian biochronologies currently used in western Europe. The three successions have been considered as three synthetic sections, where each locality represents a "fossil level" (Table I). The succession order is not actually observed but inferred on the basis of

Table I

List of the localities composing the three studied "sections"

"SECTION" MEIN		"SECTION" AGUILAR		"SECTION" DAAMS	
El Arquillo 1	13	Castelnou 3	25	Pedregueras 2A	14
Los Mansuetos	12	Lissieu	24	Nombrevilla	13
Crevillente 2	11	Stade de Cucuron	23	Toril	12
Masia del Barbo	10	Pertuis	22	Manchones 1	11
Can Llobateres	9	Montredon	21	Las Planas 5B	10
La Grive M	8	Castelnou 1B	20	Valalto 2C	9
Sansan	7	La Grenatière	19	Las Planas 4A	8
Pontlevoy-Thenay	6	Lo Fournas 3	18	Valdemoros 3E	7
La Romieu	5	Lo Fournas 2	17	Valdemoros 3B	6
Wintershof-West	4	Lo Fournas 10	16	Olmo Redondo 9	5
Laugnac	3	Luc-sur-Orbieu	15	Vargas 1A	4
Montaigu	2	Baixas	14	Villafeliche 2A	3
Paulhiac	1	Ste Catherine 8	13	Moratilla	2
		Port-la-Nouvelle	12	Navarrete	1
		Ste Catherine 7	11		
		Beaulieu	10		
		Serre de Vergès	9		
		Estrepouy	8		
		Bouzigues	7		
		Lespignan	6		
		Caunelles	5		
		La Paillade	4		
		Plaissan	3		
		Coderet	2		
		Cap Janet 1-2	1		

evolutionary stages (according to the opinion of each author). Only those rodent species common to at least two of the three successions have been taken into account (a total of 67 species: 9 sciurids, 1 castorid, 25 glirids, 7 eomyids, 1 zapodid, 16 cricetids and 8 murids). The apparent stratigraphic ranges of the species are indicated in Table II. A separate analysis (i. e., without inferring any succession order) has been carried out for fourteen localities (Table III).

The data have been analysed with the program "BIOGRAPH" (SAVARY & GUÉX 1991). A total of 33 U.A. were obtained. Their composition is shown in Table IV. The correlations associated with this synthesis are presented in Fig. 3.

If we consider only the sequences of localities of MEIN and AGUILAR, 29 contradictory subgraphs are generated. This may be imputable to two reasons: some "observed" co-occurrences are false (taxonomic differences between authors) or there is a lack of information (non-documentation of some co-occurrences).

The reproducibility of the Unitary Associations is too low for them to be directly interpretable in terms of chronology. However, even if the majority of the U.A. are identified in only one sequence of localities, some are shared by two successions. They confirm the subcontemporaneity of some localities (e. g., Laugnac and Bouzigues), while pointing to problems with the relative ages of other localities. We here give some examples of correlations that are more or less consistent with the recently published opinions of different authors.

A correlation between Sansan and Manchones has recently been proposed (AGUILAR et al. 1994). The main argument is the co-occurrence of *Megacricetodon gersii* and *Megacricetodon crusafonti* in the French locality of Castelnou 6. The association of these two species would allow a correlation of Castelnou 6 with both Sansan in France and Manchones in Spain. The problem is that without any superpositional data there is no way of knowing the exact stratigraphic ranges of the species. The fact that *Megacricetodon gersii* is known at Sansan, *Megacricetodon crusafonti* at Manchones and both at Castelnou 6 does not mean that these three localities automatically are contemporaneous. We can alternatively suppose that Manchones is younger than Sansan, and that *Megacricetodon gersii* and *Megacricetodon crusafonti* co-occur in the time span between these two localities. That is exactly the result suggested by the Unitary Associations: Castelnou 6 may be chronologically intermediate between Sansan and Manchones, the latter being closer to La Grive M. However, it has been pointed out (MEIN personal communication) that the faunal assemblages from Castelnou are unique. Does this indicate that the fissure fillings from Castelnou are reworked and that their faunal content is chronologically heterogeneous? Sedimentological and taphonomic data could answer this question. In 1982, AGUILAR placed Manchones in an intermediate position between Sansan and La Grive M (also in HEISSIG 1990); Sansan was situated in zone C3 (Langhian) while La Grive M was in zone C4 (Serravalian), together with Manchones. The result given by the U.A. is consistent with this opinion.

The French locality of Montredon, with its two supposedly isochronous fossiliferous levels, was formerly correlated with the Spanish locality of Masia del Barbo, with an age estimated between 9 and 10 million years (AGUILAR 1982). If we assume the chronological significance of the succession of U.A. 26, 27 and 28, Montredon would be intermediate between Can Llobateres and Masia del Barbo. According to AGUILAR & MICHAUX (1987), Montredon and Can Llobateres are about 11 and 11.5 million years old, respectively. This is consistent with the result given by the U.A., but the U.A. identified in Montredon is not the same as that identified in Masia del Barbo.

This analysis has been realized using the reference localities of MEIN's zonation as given by DE BRUIJN et al. (1992), i. e., without considering Steinheim and Anwil (former type localities of MN7 and MN8) as "levels" in MEIN's sequence. According to DE BRUIJN et al. (1992), the faunas from Steinheim (Germany) and Anwil (Switzerland) show only minor differences in their stage-of-evolution. Thus, these authors suggested replacing them by the French fauna of La Grive M,

Table II
 Apparent existence intervals of the 67 studied species. Each species is given with its level of first occurrence (F.O.) and last occurrence (L.O.); for each section, the numbers correspond to those given in Table I

"SECTION" MEIN	F.O.	L.O.	"SECTION" AGUILAR	F.O.	L.O.	"SECTION" DAAMS	F.O.	L.O.
<i>Apodemus gudrunae</i>	13	13	<i>Apodemus gudrunae</i>	25	25	<i>Apodemus gudrunae</i>	-	-
<i>Blackia miocaenica</i>	8	8	<i>Blackia miocaenica</i>	5	5	<i>Blackia miocaenica</i>	-	-
<i>Bransatoglis cadeoti</i>	5	5	<i>Bransatoglis cadeoti</i>	-	-	<i>Bransatoglis cadeoti</i>	-	-
<i>Bransatoglis concavidens</i>	1	1	<i>Bransatoglis concavidens</i>	2	2	<i>Bransatoglis concavidens</i>	-	-
<i>Bransatoglis fugax</i>	1	1	<i>Bransatoglis fugax</i>	2	6	<i>Bransatoglis fugax</i>	-	-
<i>Chalicomys jaegeri</i>	9	10	<i>Chalicomys jaegeri</i>	-	-	<i>Chalicomys jaegeri</i>	-	-
<i>Cricetodon sansaniensis</i>	7	7	<i>Cricetodon sansaniensis</i>	15	15	<i>Cricetodon sansaniensis</i>	-	-
<i>Cricetodon occidentalis</i>	11	11	<i>Cricetodon occidentalis</i>	22	22	<i>Cricetodon occidentalis</i>	-	-
<i>Democricetodon affinis</i>	8	8	<i>Democricetodon affinis</i>	20	20	<i>Democricetodon affinis</i>	-	-
<i>Democricetodon brevis</i>	8	8	<i>Democricetodon brevis</i>	12	17	<i>Democricetodon brevis</i>	-	-
<i>Democricetodon gaillardi</i>	7	7	<i>Democricetodon gaillardi</i>	-	-	<i>Democricetodon gaillardi</i>	10	10
<i>Eliomys truci</i>	11	12	<i>Eliomys truci</i>	25	25	<i>Eliomys truci</i>	14	14
<i>Eomuscardinus sansaniensis</i>	7	7	<i>Eomuscardinus sansaniensis</i>	21	24	<i>Eomuscardinus sansaniensis</i>	-	-
<i>Eomyops catalaunicus</i>	8	9	<i>Eomyops catalaunicus</i>	21	24	<i>Eomyops catalaunicus</i>	11	11
<i>Eucrietodon aquitanicus</i>	3	3	<i>Eucrietodon aquitanicus</i>	7	7	<i>Eucrietodon aquitanicus</i>	-	-
<i>Eucrietodon gerandianus</i>	2	2	<i>Eucrietodon gerandianus</i>	6	6	<i>Eucrietodon gerandianus</i>	-	-
<i>Eucrietodon hesperius</i>	1	1	<i>Eucrietodon hesperius</i>	3	4	<i>Eucrietodon hesperius</i>	-	-
<i>Fahlbuschia larteti</i>	8	8	<i>Fahlbuschia larteti</i>	19	19	<i>Fahlbuschia larteti</i>	-	-
<i>Glirudinus glirulus</i>	1	1	<i>Glirudinus glirulus</i>	2	3	<i>Glirudinus glirulus</i>	-	-
<i>Glirudinus gracilis</i>	4	4	<i>Glirudinus gracilis</i>	9	10	<i>Glirudinus gracilis</i>	-	-
<i>Glirudinus modestus</i>	4	5	<i>Glirudinus modestus</i>	5	12	<i>Glirudinus modestus</i>	2	4
<i>Glirudinus undosus</i>	9	9	<i>Glirudinus undosus</i>	-	-	<i>Glirudinus undosus</i>	-	-
<i>Heteroxerus grivensis</i>	8	9	<i>Heteroxerus grivensis</i>	15	20	<i>Heteroxerus grivensis</i>	5	12
<i>Heteroxerus lavocati</i>	1	1	<i>Heteroxerus lavocati</i>	2	5	<i>Heteroxerus lavocati</i>	-	-
<i>Heteroxerus paulhiacensis</i>	1	2	<i>Heteroxerus paulhiacensis</i>	1	5	<i>Heteroxerus paulhiacensis</i>	-	-
<i>Heteroxerus rubricati</i>	5	5	<i>Heteroxerus rubricati</i>	9	14	<i>Heteroxerus rubricati</i>	1	10
<i>Huerzelerimys vireti</i>	11	11	<i>Huerzelerimys vireti</i>	22	22	<i>Huerzelerimys vireti</i>	-	-
<i>Keramidomys pertesunatoi</i>	8	9	<i>Keramidomys pertesunatoi</i>	-	-	<i>Keramidomys pertesunatoi</i>	-	-
<i>Ligerimys antiquus</i>	4	5	<i>Ligerimys antiquus</i>	8	10	<i>Ligerimys antiquus</i>	1	2
<i>Ligerimys florancei</i>	5	5	<i>Ligerimys florancei</i>	11	13	<i>Ligerimys florancei</i>	3	3
<i>Ligerimys lophidens</i>	4	4	<i>Ligerimys lophidens</i>	9	9	<i>Ligerimys lophidens</i>	-	-
<i>Megacricetodon collongensis</i>	6	6	<i>Megacricetodon collongensis</i>	12	14	<i>Megacricetodon collongensis</i>	6	8
<i>Megacricetodon crusafonti</i>	-	-	<i>Megacricetodon crusafonti</i>	-	-	<i>Megacricetodon crusafonti</i>	11	11
<i>Megacricetodon gersii</i>	7	7	<i>Megacricetodon gersii</i>	15	15	<i>Megacricetodon gersii</i>	-	-

Table II cont.

"SECTION" MEIN	F.O.	L.O.	"SECTION" AGUILAR	F.O.	L.O.	"SECTION" DAAMS	F.O.	L.O.
<i>Megacricetodon gregarius</i>	8	8	<i>Megacricetodon gregarius</i>	19	20	<i>Megacricetodon gregarius</i>	-	-
<i>Megacricetodon minor</i>	7	8	<i>Megacricetodon minor</i>	15	19	<i>Megacricetodon minor</i>	10	13
<i>Melissiodon dominans</i>	4	4	<i>Melissiodon dominans</i>	9	14	<i>Melissiodon dominans</i>	-	-
<i>Microdyromys koenigswaldi</i>	5	5	<i>Microdyromys koenigswaldi</i>	6	18	<i>Microdyromys koenigswaldi</i>	-	-
<i>Microdyromys miocaenicus</i>	7	7	<i>Microdyromys miocaenicus</i>	20	20	<i>Microdyromys miocaenicus</i>	-	-
<i>Microdyromys aegercii</i>	7	7	<i>Microdyromys aegercii</i>	14	18	<i>Microdyromys aegercii</i>	-	-
<i>Miodyromys biradiculus</i>	4	5	<i>Miodyromys biradiculus</i>	10	16	<i>Miodyromys biradiculus</i>	-	-
<i>Miodyromys hamadryas</i>	-	-	<i>Miodyromys hamadryas</i>	10	10	<i>Miodyromys hamadryas</i>	-	-
<i>Muscardinus hispanicus</i>	-	-	<i>Muscardinus hispanicus</i>	21	21	<i>Muscardinus hispanicus</i>	13	14
<i>Muscardinus thaleri</i>	-	-	<i>Muscardinus thaleri</i>	-	-	<i>Muscardinus thaleri</i>	7	12
<i>Myoglis meini</i>	7	9	<i>Myoglis meini</i>	-	-	<i>Myoglis meini</i>	11	12
<i>Occitanomys adroveri</i>	12	13	<i>Occitanomys adroveri</i>	23	25	<i>Occitanomys adroveri</i>	-	-
<i>Occitanomys sondaari</i>	11	11	<i>Occitanomys sondaari</i>	22	22	<i>Occitanomys sondaari</i>	-	-
<i>Palaeosciurus feignouxii</i>	2	2	<i>Palaeosciurus feignouxii</i>	4	5	<i>Palaeosciurus feignouxii</i>	1	1
<i>Palaeosciurus fissurae</i>	4	4	<i>Palaeosciurus fissurae</i>	-	-	<i>Palaeosciurus fissurae</i>	-	-
<i>Paraglitulus werenfelsi</i>	9	9	<i>Paraglitulus werenfelsi</i>	-	-	<i>Paraglitulus werenfelsi</i>	9	9
<i>Parapodemus barbarae</i>	12	12	<i>Parapodemus barbarae</i>	23	23	<i>Parapodemus barbarae</i>	-	-
<i>Parapodemus lugdunensis</i>	11	11	<i>Parapodemus lugdunensis</i>	-	-	<i>Parapodemus lugdunensis</i>	-	-
<i>Peridyromys brailtoni</i>	3	3	<i>Peridyromys brailtoni</i>	7	9	<i>Peridyromys brailtoni</i>	-	-
<i>Peridyromys gregarius</i>	4	5	<i>Peridyromys gregarius</i>	8	8	<i>Peridyromys gregarius</i>	-	-
<i>Peridyromys murinus</i>	1	4	<i>Peridyromys murinus</i>	1	13	<i>Peridyromys murinus</i>	1	5
<i>Peridyromys occitanus</i>	3	5	<i>Peridyromys occitanus</i>	8	8	<i>Peridyromys occitanus</i>	-	-
<i>Plesioimithus myarion</i>	2	2	<i>Plesioimithus myarion</i>	4	4	<i>Plesioimithus myarion</i>	-	-
<i>Progonomys cathalai</i>	9	10	<i>Progonomys cathalai</i>	21	21	<i>Progonomys cathalai</i>	-	-
<i>Pseudodyromys ibericus</i>	4	5	<i>Pseudodyromys ibericus</i>	5	13	<i>Pseudodyromys ibericus</i>	1	6
<i>Pseudothieridomys parvulus</i>	1	3	<i>Pseudothieridomys parvulus</i>	4	10	<i>Pseudothieridomys parvulus</i>	-	-
<i>Rhodanomys schlosseri</i>	2	2	<i>Rhodanomys schlosseri</i>	4	4	<i>Rhodanomys schlosseri</i>	-	-
<i>Rhodanomys transiens</i>	1	1	<i>Rhodanomys transiens</i>	1	3	<i>Rhodanomys transiens</i>	-	-
<i>Ruscinomys schaubi</i>	12	13	<i>Ruscinomys schaubi</i>	23	23	<i>Ruscinomys schaubi</i>	-	-
<i>Spermophilinus besana</i>	5	6	<i>Spermophilinus besana</i>	-	-	<i>Spermophilinus besana</i>	3	5
<i>Spermophilinus bredai</i>	7	9	<i>Spermophilinus bredai</i>	9	21	<i>Spermophilinus bredai</i>	8	12
<i>Stephanomys ramblensis</i>	13	13	<i>Stephanomys ramblensis</i>	24	24	<i>Stephanomys ramblensis</i>	-	-
<i>Tempestia hartenbergeri</i>	10	10	<i>Tempestia hartenbergeri</i>	-	-	<i>Tempestia hartenbergeri</i>	-	-

U.A.	MEIN	AGUILAR	DAAMS & FREUDENTHAL
33	El Arquillo 1	<i>La Tour</i>	Castelnou 3
32		<i>Ratavoux</i>	Lissieu
31	Los Mansuetos		Stade de Cucuron
30	Crevillente 2	<i>Mollon</i>	Pertuis
29			Pedregueras 2A
28	Masia del Barbo		
27		Montredon	Nombrevilla
26	Can Llobateres	<i>Soblay</i>	
25	La Grive M		
24		Castelnou 1B La Grenatière	Toril Manchones
23	<i>Anwil</i>		
22	<i>Cases de Penes</i>	Lo Fournas 3	
21	<i>Steinheim</i>		
20		Castelnou 6	
19	Sansan	Lo Fournas 2	
18		Lo Fournas 10 Luc-sur-Orbieu	Las Planas 5B Valalto 2C
17		<i>Veyran</i>	
16		<i>Ste Catherine</i> 1	
15			Las Planas 4A Valdemoros 3E
14		Baixas	Valdemoros 3B
13			Olmo Redondo 9
12	Pontlevoy-Thenay	Lo Fournas 1	Ste Catherine 8 Port-la-Nouvelle
11	La Romieu		Ste Catherine 7
10			Beaulieu
9	Wintershof-West		
8		<i>Ste Catherine</i> 2	Serre de Vergès Estrepouy
7	Laugnac		Bouzigues
6			
5			Navarrete
4		Lespignan	
3	Montaigu	Caunelles	
2		La Paillade	
1	Paulhiac	Venelles	Plaissan Coderet Cap Janet 1-2

Fig. 3. Position of the studied localities in the succession of the 33 identified Unitary Associations.

Table IV ctd

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
<i>Democricetodon brevis</i>												x	x	x	x	x	x	x	x	x	x	x	x	x	x								
<i>Heteroxerus grivensis</i>												x	x	x	x	x	x	x	x	x	x	x	x	x	x								
<i>Myodromys aegercii</i>													x	x	x	x	x	x	x	x	x	x	x	x	x								
<i>Muscardinus thaleri</i>														x	x	x	x	x	x	x	x	x	x	x	x								
<i>Megacricetodon gersii</i>															x	x	x	x	x	x	x	x	x	x	x								
<i>Megacricetodon minor</i>																x	x	x	x	x	x	x	x	x	x								
<i>Microdromys miocaenicus</i>																	x	x	x	x	x	x	x	x	x								
<i>Cricetodon sansaniensis</i>																		x	x	x	x	x	x	x	x								
<i>Democricetodon gaillardi</i>																		x	x	x	x	x	x	x	x								
<i>Paraglitulus wernfelsi</i>																			x	x	x	x	x	x	x								
<i>Eomuscardinus sansaniensis</i>																			x	x	x	x	x	x	x								
<i>Myoglis meini</i>																				x	x	x	x	x	x								
<i>Megacricetodon crusafonii</i>																				x	x	x	x	x	x								
<i>Megacricetodon gregarius</i>																					x	x	x	x	x								
<i>Democricetodon affinis</i>																					x	x	x	x	x								
<i>Glirudinus undosus</i>																						x	x	x	x								
<i>Eomyops catalaunicus</i>																						x	x	x	x								
<i>Fahlbuschia larteti</i>																							x	x	x								
<i>Keramidomys perlesunatoi</i>																								x	x								
<i>Chalicomys jaegeri</i>																								x	x								
<i>Progonomys cathalai</i>																								x	x								
<i>Muscardinus hispanicus</i>																								x	x								
<i>Tempestia hartenbergeri</i>																								x	x								
<i>Eliomys truci</i>																								x	x								
<i>Cricetodon occidentalis</i>																									x	x							
<i>Occitanomys sondaari</i>																									x	x							
<i>Parapodemus lugdunensis</i>																									x	x							
<i>Huerzelerimys vireti</i>																									x	x							
<i>Parapodemus barbae</i>																									x	x							
<i>Occitanomys adroveri</i>																										x	x						
<i>Ruscinomys schaubi</i>																										x	x						
<i>Stephanomys ramblensis</i>																										x	x						
<i>Apodemus gudrunae</i>																											x	x					

chosen as the reference locality of a new unit MN7+8. However, using the Unitary Associations method, separate analysis of Steinheim and Anwil situates them between Sansan and La Grive M. Moreover, they are arranged in a way (Steinheim before Anwil) that would confirm the previous zonation of MEIN, with Steinheim and Anwil being the respective type localities of two distinct units MN7 and MN8. In the former zonation of MEIN, La Grive M was placed in MN7, together with Steinheim. The intermediate location of the succession Steinheim-Anwil, between Sansan and La Grive M, could indicate a slightly greater age for Anwil than previously thought.

From other paleontological criteria including not only rodents but also ungulates, especially artiodactyls, some authors agree with the separation of MN7 and MN8 and with the question of the diachroneity of Sansan and Manchones (AGUSTÍ & MOYÁ-SOLÁ 1991). A biochronological method based on parsimony analysis has recently been proposed (MARTINEZ 1995) and leads to similar results.

IV. CONCLUSIONS

If we assume the chronological significance of these results, the precision of the Miocene mammalian biochronologies seems more apparent than real. However, we must keep in mind that: 1) the result provided by the U.A. is correct only if we assume that the succession order given by each author is correct; 2) this succession is inferred and not really observed. Theoretically, nothing precludes an extension of the Unitary Associations method to problems of correlation in mammalian biochronology; sequences of localities established on a regional scale can be then treated as synthetic sections. When stratigraphic superposition is not clearly demonstrated, a succession order must be inferred on the basis of evolutionary stages. In that case, the main obstacles are represented by differences between different authors regarding taxonomy, by possible errors in estimating the evolutionary stages and by circular reasoning due to the fact that the evolutionary lineages used in biochronology are not always defined independently of the pre-established biochronological framework. Pointing out these contradictions is not without interest insofar as it can lead to some revisions of species or lineages.

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