



The bioclimatic model: a method of palaeoclimatic qualitative inference based on mammal associations

MANUEL HERNÁNDEZ FERNÁNDEZ*†‡ and PABLO PELÁEZ-CAMPOMANES‡

*Department of Geology and Geophysics, Kline Geology Laboratory, Yale University, PO Box 208109, New Haven, Connecticut 06520–8109, U.S.A. E-mail: manuel.hernandez@yale.edu; †Departamento y UEI de Paleontología, Facultad de Ciencias Geológicas (Universidad Complutense de Madrid) e Instituto de Geología Económica (Consejo Superior de Investigaciones Científicas), Ciudad Universitaria, 28040, Madrid, Spain. E-mail: hdezfdz@geo.ucm.es; ‡Departamento de Paleobiología, Museo Nacional de Ciencias Naturales (Consejo Superior de Investigaciones Científicas), José Gutiérrez Abascal 2, 28006, Madrid, Spain. E-mail: mcnp177@mncn.csic.es

ABSTRACT

Aim The bioclimatic model is a new method for palaeoclimatic reconstruction built on the assumption of a significant correlation between climate and mammal community composition. The goal of this approach is to infer past climatic conditions using mammal fossil associations as source data.

Location The study used mammal faunas from all over the world to develop the bioclimatic model. As an example of the potential of the model, we have applied it to Quaternary faunas from Eurasia.

Methods The proposed model was constructed by applying multivariate discriminant analysis to modern mammal faunas and climates from throughout the world. The model was validated with a different set of modern faunas than those used in the discriminant analysis, including some from transitional zones between different climates (ecotones). To test the reliability of the method in the Pleistocene, the results have been compared to those obtained with data from other disciplines, such as palaeobotany.

Results The results obtained in the validation of the model show that more than 90% of the localities have been classified correctly. Comparisons of results in the late Pleistocene–Holocene of Barová between a palaeobotanical study and the bioclimatic analysis show the latter to be highly accurate. The results for early Pleistocene faunas show somewhat drier and more open climatic conditions for Europe than the present day, with larger areas of steppe environments.

Main Conclusions The bioclimatic model could be used to infer climatic conditions from mammal faunas. The results presented in this work provide a preliminary example of the potential that bioclimatic analysis has as a tool for palaeoclimatic inference. Finally, this method offers the opportunity to standardize data coming from vertebrate palaeontology for use in the construction and evaluation of climatic models.

Key words Bioclimatology, discriminant analysis, Europe, Mammalia, mammalian communities, palaeoclimatology, palaeoecological method, Pleistocene, Rodentia.

INTRODUCTION

During the last 30 years numerous studies have been carried out in order to reconstruct past climates and to build models to help us understand how, when, and why the global climate changes happened. These studies have focused on aspects

such as marine and atmospheric circulation, tectonics and palaeovegetation (CLIMAP, 1976; COHMAP, 1988; PRISM, 1995; Prentice & Webb III, 1998; Kohfeld & Harrison, 2000), and little attention has been paid to the important source of data available from disciplines like vertebrate palaeontology, particularly from mammal palaeontology.

There are abundant works on palaeoecological and palaeoclimatic reconstruction based on mammals (van de Weerd & Daams, 1978; Andrews *et al.*, 1979; Legendre, 1986; de Bonis *et al.*, 1992; van der Meulen & Daams, 1992; van Dam, 1998; Hernández Fernández *et al.*, 2003). The approaches of

Correspondence: Department of Geology and Geophysics, Kline Geology Laboratory, Yale University, PO Box 208109, New Haven, Connecticut 06520–8109, U.S.A. E-mail: manuel.hernandez@yale.edu

Climate		Zonobiome (mainly vegetation type)	
I	Equatorial	I	Evergreen tropical rain forest
II	Tropical with summer rains	II	Tropical deciduous woodland
II/III	Transition tropical semiarid	II/III	Savanna
III	Subtropical arid	III	Subtropical desert
IV	Winter rain and summer drought	IV	Sclerophyllous woodland-shrubland
V	Warm-temperate	V	Temperate evergreen forest
VI	Typical temperate	VI	Nemoral broadleaf-deciduous forest
VII	Arid-temperate	VII	Steppe to cold desert
VIII	Cold-temperate (boreal)	VIII	Boreal coniferous forest (Taiga)
IX	Arctic	IX	Tundra

Table 1 Climatic typology used in this paper (modified from Walter, 1970) and its relationships with world vegetation types. Walter (1970) considers II/III as a zonoecotone between tropical forests and deserts but we apply it as a zonobiome because it is traditionally used in palaeoecology due to its unique faunal community

those authors, nevertheless, offered interpretations at a quite restricted scale. They are important to the understanding of ecological or climatic evolution through time at a local scale but are difficult to extrapolate to a wider scale and thus to compare with data from other areas. Therefore, it is important to develop new methods that can be used to make climatic reconstruction and environmental interpretations at a much broader geographical scale. Hernández Fernández (2001a) developed just such a methodology, bioclimatic analysis, to make palaeoclimatic interpretations based on mammal associations. He showed the high correlation attainable between mammal associations and specific climatic and vegetation typologies (Walter, 1970; see Table 1), and thus the power of the analysis of mammal associations as a proxy for climatic reconstruction. In the same paper he also analysed the climatic discrimination among several sets of mammal groups, such as entire mammal faunas, rodent faunas, macromammal faunas and whole faunas without bats. The reason for doing these analyses is because in the fossil record it is quite common to have fossil associations composed only of large mammals or small mammals due to taphonomic or sampling biases.

The aim of the present paper is to present models for each of the mammal groups indicated above and validate them with modern faunas not used to build the model. Additionally, the model will be applied to several fossil mammal faunas, comparing the interpretations obtained using mammal assemblages with interpretations based on data from different sources, such as palynological studies.

MATERIALS AND METHODS

Hernández Fernández (2001a) described the analytical methodology in detail. In the following paragraphs we will present only a summary of the approach.

Faunal data for 50 localities from all over the world (with the exception of Australia) and from all climates (following

the climatic typology of Walter, 1970; Table 1) form the database of this study (Appendix 1 in Hernández Fernández, 2001a). Five localities containing both faunal and climatic information were selected from each climate zone in order to have comparable data for all biomes. Each locality was selected in such a way that it represents the average climatic conditions within its climate zone and that the localities from a single climate zone were as widely scattered as possible all over the world. The faunal list of each locality has been obtained from the literature (see References in Hernández Fernández, 2001a).

For every locality a species by climate matrix is made. The value assigned to each of the species in each climate is 0 when the species does not live in that climate zone or $1/n$ (called the Climatic Restriction Index, CRI; Hernández Fernández, 2001a) when it does live in it, being n the number of climates in which the species is present. See Hernández Fernández (2001a) for a more detailed description on the determination of the climate zones inhabited by a species. The Bioclimatic Component (BC) is the representation in a specific locality of each of the 10 existing climates. Each of the 10 BC values for every locality is calculated according to the formula:

$$BC_i = (\sum CRI_i)100/S$$

where i is climate zone i and S is the number of species in the locality. The 10 BC values of a locality constitute its bioclimatic spectrum. The latter are the data used in the multivariate analysis. The bioclimatic spectra (calculated for the whole faunas, rodent faunas, macromammal faunas and whole faunas without bats) of the 50 recent faunas, distributed all over the world (Hernández Fernández, 2001a), are available as supplementary material (Appendix 1) in the journal's web site and in the web page of one of the authors (M.H.F.) at the National Museum of Natural Sciences of Madrid web site (<http://www.mncn.csic.es/>).

Table 2 New modern localities studied in this work. N, locality numbers are consecutive to those in Hernández Fernández (2001a)

N	Climate zone	Locality	Country	Latitude	Longitude	Altitude	References
51	VIII/IX	Ust Kamchatsk	Russia	56°14'-N	162°28'-E	6 m	Corbet (1978)
52	VI/VIII	Saskatoon	Canada	52°08'-N	106°38'-W	157 m	Hall (1981)
53	VI/VIII	Riga	Latvia	56°58'-N	24°04'-E	3 m	Corbet (1978)
54	VI/VII	Budapest	Hungary	47°31'-N	19°02'-E	120 m	Corbet (1978)
55	VI	Dairen	China	38°54'-N	121°38'-E	96 m	Corbet (1978)
56	IV/VI	Portland	USA	45°32'-N	122°40'-W	9 m	Hall (1981)
57	V	Charleston	USA	32°54'-N	80°02'-W	100 m	Hall (1981)
58	IV/VI	Niza	France	43°40'-N	7°12'-E	5 m	Corbet (1978)
59	II/V	Kweilin	China	25°15'-N	110°10'-E	167 m	Corbet (1978); Corbet & Hill (1992)
60	III	Smara	Sahara W	26°44'-N	11°26'-W	140 m	Corbet (1978)
61	II	Puerto Ayacucho	Venezuela	5°41'-N	67°38'-W	99 m	Eisenberg (1989)
62	I/II	Tabou	Ivory Coast	4°55'-N	7°22'-E	4 m	Kingdon (1971–82); Dorst & Dandelot (1973); Nowak (1991)
63	I	Kuala Lumpur	Malaysia	3°07'-N	101°42'-E	34 m	Corbet & Hill (1992)

The proposed models have been built using discriminant analysis. In this analysis, we used the different BC_i that form the bioclimatic spectrum as variables. Therefore, each locality is an operational faunistic unit characterized by 10 variables. Then, based on the obtained bioclimatic spectra, we calculate a series of discriminant functions (Appendix 2, and at <http://www.mncn.csic.es/>) and calculate to which climate zone a locality has the highest probability of association. All calculations were done using SPSS version 11.01.

The validation of the model was done using 13 new recent faunas (Table 2), distinct from the 50 used to calculate the discriminant functions. Some of these localities, distributed throughout the world, are located in the proximity of ecotones between two or more climate zones. Since the main application of the model will be the inference of past climatic conditions and its evolution through time, we have decided to include these ecotone faunas to check the power of the model and its reliability for faunas with transitional climatic characterization. Bioclimatic spectra of whole faunas, rodent faunas, macromammal faunas and whole faunas without bats of the 13 new localities are shown in Appendix 3 and at <http://www.mncn.csic.es/>.

As set out above, the purpose of this model is to allow a climatic classification of fossil faunas and thus, to provide a tool to relate past faunal variation through time and space. As an example of the results that could be obtained and its reliability, when compared with other sources of data and interpretations, rodent faunas from two late Pleistocene–Holocene superposed levels from the Barová Cave (Czech Republic), where faunal and palynological data are available (Svoboda *et al.*, 2000), have been studied. The lower selected level is

layer 12. The upper selected level, composed of layers 10b, 10c and 9, has a minimum sample size of rodent fossils adequate to obtain accurate palaeoclimatic inferences (Daams *et al.*, 1999). These three layers show a qualitatively homogeneous faunal composition and the results would not be affected by their combination.

In addition, 12 early Pleistocene fossil mammal assemblages from Eurasia (of an approximate age of 1.8 ma; Table 3, Fig. 1) were analysed by the method developed in this study. Since most of these assemblages have reported exclusively small mammals, we will use the model developed for rodent faunas. There are no data available on how much time is represented by each faunal assemblage. The length of the concentration period varies from hours in some catastrophic fossil sites (Behrensmeyer & Schindel, 1983) to a century in macromammals fossil sites with eschatological origin (Behrensmeyer, 1982). According to Behrensmeyer (1982), time resolution for attritional assemblages could be 10^2 – 10^3 years, and possibly more, in small mammal fossil sites, because of condensation and reelaboration (or reworking) processes (*sensu* Fernández-López, 2000). Nevertheless, Agustí & Martín Suárez (1986) and Álvarez Sierra *et al.* (1990) consider that micromammal fossils are unlikely to be reelaborated (or reworked) because of their fragility. Furthermore, any shift in the biome due to climatic variation has to be reflected in sedimentary changes. Since the sampling methodology considers as a fossil fauna only the specimens coming from a single stratum, we consider that the climatic conditions were probably similar, despite the time involved in the formation of some of our fossil localities. Therefore, application of the bioclimatic analysis would not suffer from the

Table 3 Literature sources of the Eurasian early Pleistocene sites used in this work. N, numbers in Fig. 1. Cl., current climate zone (see Table 1). S, number of rodent species. E, sedimentary environment (K, karstic; A, alluvial)

N	Fossil site	Country	Cl.	S	E	References
1	Quibas	Spain	IV	5	K	Montoya <i>et al.</i> (1999)
2	Bagur 2	Spain	IV	9	K	López Martínez <i>et al.</i> (1976); Martín Suárez & Mein (1991); Laplana (1999)
3	Mas Rambault 1	France	IV	8	K	Chaline & Michaux (1966); Chaline (1972); Chaline & Michaux (1974); Martín Suárez & Mein (1991); Aguilar <i>et al.</i> (1993)
4	Les Valerots	France	VI	16	K	Chaline (1972); Chaline & Michaux (1974); Bartolomei <i>et al.</i> (1975); Nadachowski (1991); Nadachowski & Garapich (1998)
5	Neuleiningen 5	Germany	VI	6	K	Maul (1996)
6	Monte Peglia A	Italy	IV/VI	8	K	van der Meulen (1973); Nadachowski & Garapich (1998)
7	Chlum 6	Czech Republic	VI	19	K	Bartolomei <i>et al.</i> (1975); von Koenigswald & Heinrich (1999)
8	Villany 5	Hungary	VI	16	K	Kretzoi (1956); van der Meulen (1974); Jánossy (1986); Montuire (1995)
9	Kamyk	Poland	VI	20	K	Kowalski (1975); Nadachowski (1990a); Nadachowski (1990b); Daoud (1993); Garapich & Nadachowski (1996); Nadachowski (1998)
10	Betfia 9a	Rumania	VI	14	K	Terzea (1995); Terzea (1996); Hír & Venczel (1998)
11	Tiligul	Ukraine	VII	21	A	Rekovets & Nadachowski (1995)
12	Dodogol 1	Russia	VII	5	A	Alexeeva (1998)

time-averaged sample present in some small mammal fossil assemblages.

Application of the bioclimatic analysis to ancient mammal faunas deals with a very common problem in palaeoecology: the occurrence of nonanalogous faunas, or so-called disharmonic faunas (Lundelius *et al.*, 1987). Mammal species must migrate if they are to survive climate change. Palaeoecologists have demolished the notion that ecological communities can be considered as ancient, coevolved entities, since climate change evokes differential responses in the constituent taxa. Thus, the taxonomic composition of biomes during one climatic phase can be very different from that during another phase (FAUNMAP, 1996). Climatic oscillations on the Milankovitch time scale enables repeated mixing of faunas during some phases, and disjunctions during others. These data require a dynamic perspective on mammal biogeography and raise the problem of the incidence of nonanalogous faunas. Bioclimatic analysis assigns climate zones (biomes) to

the localities on the basis of the taxonomic composition of communities or fossil associations, but the bioclimatic spectrum is an emergent property of the locality based on functional bioclimatic characteristics of its constituent taxa. Thus, two mammal assemblages need not have any taxa in common in order to be assigned to the same climate zone, making the bioclimatic analysis fairly independent from modern analogues in terms of mammal communities.

Potential limitations in this methodology include the possible existence of unknown biomes in the past or that modern biomes have different characteristics than in the past. This problem is stronger when the age of taxa or localities increases, although we think that Plio-Pleistocene biomes have been substantially similar to modern ones (CLIMAP, 1976; PRISM, 1995). Nevertheless, we are developing a complementary model for quantitative inference that will be useful in addressing this problem (M. Hernández Fernández & P. Peláez-Campomanes, in prep.).

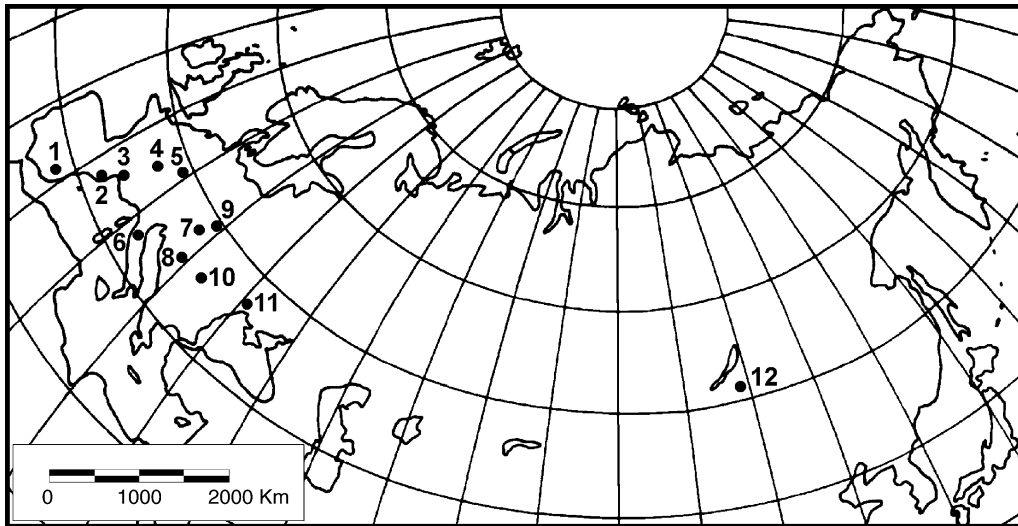


Fig. 1 Location of the 12 early Pleistocene fossil sites used in this work. Numbers as in Table 3.

RESULTS AND DISCUSSION

The bioclimatic model

The discriminant functions used for the model are shown in Appendix 2. The percentages of localities classified correctly are 98% for whole faunas, 94% for rodent faunas, 90% for macromammal faunas and 96% for whole faunas without bats (Hernández Fernández, 2001a).

The bioclimatic spectra of the 13 localities used for validation (Appendix 3) show, in general, more even distribution of the different bioclimatic components (BC, *sensu* Hernández Fernández, 2001a) than the 50 localities used to build the model. Our interpretation of this observation is that the differences of distribution of the bioclimatic spectra are due to the relative position of the localities in the climatic zone. The 50 localities used in the model come from areas in the middle of climatic dominions, thus *a priori* with a higher proportion of taxa characteristic of the corresponding climatic zone, while several of the validation localities come from ecotone areas between two climate zones and thus include a higher degree of mixed taxa.

The result obtained in the validation of the model shows that more than 90% of the 13 localities have been classified correctly. The differences between the groups of mammals show that, as for the 50 original localities used to construct the model (Hernández Fernández, 2001a), the reliability of the rodent faunas, whole faunas and whole faunas without bats is very high, with the macromammal fauna the least accurate (Table 4). Despite the small differences in the classifications obtained for each of the four groups of mammal faunas, it is important to note the high degree of accuracy

expressed by all. This is important since, as was discussed above, the associations of fossil mammals are frequently composed exclusively of only one of these groups due to sampling or taphonomic bias. This method could therefore be used to infer climatic conditions from micromammals, macromammals, or entire faunas.

It is possible to obtain additional information and interpretations by carefully studying the characteristics of the localities where the model fails. Puerto Ayacucho belongs to the tropical with summer rains climate zone (II) but it has been classified as transitional tropical semiarid climate zone (II/III) by the bioclimatic analysis of the whole fauna, macromammals and the whole fauna without bats. This is probably due to the fact that the landscape physiognomy of Los Llanos (Venezuela) corresponds to a savanna due to edaphic conditions (Walter, 1970). The rodent fauna, on the other hand, classifies this locality correctly. The higher discriminant capacity of the latter group could be due to a stronger relationship with vegetation physiognomy in the macromammals while rodents do not have this stronger dependence and thus reflect a closer relationship with climatic conditions. This observation is supported by the results of Hernández Fernández (2001a). In that work, Voi (Kenya) was assigned to a macroclimate of tropical forest by the rodent fauna, while the macromammals classified it as savanna. The climate of that locality is not typical of savanna, which perhaps explains the incorrect assignment from the rodent fauna. Another possible cause of the different identified climate by the two mammal groups could be that the landscape perception scale is different in rodents and in macromammals. The former can find a greater variety of appropriate microhabitats while the

Table 4 Discriminant analysis results for 13 new localities (P_1 , probability of the highest probability climate zone; P_2 , probability of the second highest probability climate zone; =, the second highest probability climate zone is the same as the highest probability climate zone)

Climate zone	Locality	Whole faunas				Rodent faunas			
		highest probability climate zone	P_1	2nd highest probability climate zone	P_2	highest probability climate zone	P_1	2nd highest probability climate zone	P_2
VIII/IX	Ust Kamchatsk	VIII	1.000	=		IX	0.996	VIII	0.004
VI/VIII	Saskatoon	VI	0.792	VIII	0.208	VIII	0.985	VI	0.015
VI/VIII	Riga	VI	1.000	VIII	< 0.001	VI	0.999	VIII	0.001
VI/VII	Budapest	VI	1.000	VII	< 0.001	VI	1.000	VIII	< 0.001
VI	Dairen	VI	1.000	VIII	< 0.001	VI	1.000	VIII	< 0.001
IV/VI	Portland	VI	1.000	VII	< 0.001	VI	1.000	VIII	< 0.001
V	Charleston	V	1.000	=		V	1.000	=	
IV/VI	Niza	IV	0.956	VI	0.044	VI	0.999	IV	< 0.001
II/V	Kweilin	V	1.000	II	< 0.001	V	1.000	II	< 0.001
III	Smara	III	1.000	=		III	1.000	=	
II	Puerto Ayacucho	II/III	0.974	II	0.026	II	0.997	II/III	0.003
I/II	Tabou	I	1.000	=		I	1.000	=	
I	Kuala Lumpur	I	1.000	=		I	1.000	=	

Climate zone	Locality	Macromammal faunas				Whole faunas without bats			
		highest probability climate zone	P_1	2nd highest probability climate zone	P_2	highest probability climate zone	P_1	2nd highest probability climate zone	P_2
VIII/IX	Ust Kamchatsk	VIII	1.000	VI	< 0.001	VIII	1.000	VI	< 0.001
VI/VIII	Saskatoon	VI	0.890	VIII	0.110	VIII	0.745	VI	0.255
VI/VIII	Riga	VI	0.963	VIII	0.037	VI	0.999	VIII	< 0.001
VI/VII	Budapest	VI	0.998	IV	0.002	VI	1.000	VIII	< 0.001
VI	Dairen	VI	0.955	V	0.045	VI	1.000	VIII	< 0.001
IV/VI	Portland	VI	0.999	VIII	0.001	VI	1.000	VIII	< 0.001
V	Charleston	VI	0.561	V	0.424	V	1.000	=	
IV/VI	Niza	VI	0.988	IV	0.012	VI	0.795	IV	0.205
II/V	Kweilin	V	1.000	VI	< 0.001	V	1.000	=	
III	Smara	III	0.999	=	< 0.001	III	1.000	=	
II	Puerto Ayacucho	II/III	0.980	II	0.020	II/III	0.945	II	0.055
I/II	Tabou	I	1.000	=		I	1.000	=	
I	Kuala Lumpur	I	1.000	=		I	1.000	=	

macromammals have a more restricted range of habitats because of their larger body size. Perhaps for this reason the rodents are more greatly influenced by climate than large mammals, while the macromammals may be more influenced by landscape scale characteristics, that is to say, by the major habitats in an area.

A similar explanation can be determined for the classification of Charleston in the temperate climate zone (VI) using macromammals, although it actually belongs in the warm temperate climate zone (V). This incorrect classification could be due to the similarity of, and the gradual change between, the large mammal faunas from climate zones V and VI of

eastern North America. There is a relatively low number of large mammal species exclusive to the temperate evergreen forest of the south-eastern North America climatic dominion. Most of its large mammal species also inhabit the nemoral broadleaf-deciduous forest of the eastern North America climatic dominion. This similarity is more pronounced in localities near the ecotone V/VI. Therefore, relatively low values of BC V are attained in localities close to the north edge of the south-eastern North America climatic dominion.

Hence, the results shown in Table 4 indicate that it is possible to detect situations where the fauna comes from an ecotone, the boundary area between two climate zones. Another

Table 5 Bioclimatic spectra of the Eurasian rodent fossil sites used in this work. Numbers for fossil sites as in Fig. 1

Fossil site	I	II	II/III	III	IV	V	VI	VII	VIII	IX
<i>Late Pleistocene-Holocene</i>										
Barová 9–10c–10b	0.000	0.000	0.000	0.000	9.259	0.000	53.704	9.259	24.074	3.704
Barová 12	0.000	1.389	1.389	1.389	6.944	0.000	21.759	7.870	36.574	22.685
<i>Early Pleistocene</i>										
1 Quibas	2.857	22.857	2.857	2.857	29.524	2.857	6.667	19.524	10.000	0.000
2 Bagur 2	0.000	11.111	0.000	2.222	25.370	0.000	14.259	30.926	16.111	0.000
3 Mas Rambault 1	0.000	12.500	0.000	2.500	34.792	0.000	22.292	16.042	11.875	0.000
4 Les Valerots	0.000	0.000	0.000	6.667	15.000	6.250	25.417	26.458	13.958	6.250
5 Neuleiningen 5	0.000	0.000	0.000	14.444	14.444	0.000	8.889	25.556	22.778	13.889
6 Monte Peglia A	0.000	0.000	0.000	10.833	23.333	12.500	15.000	23.333	15.000	0.000
7 Chlum 6	0.000	0.000	0.000	5.614	12.807	0.000	34.737	20.702	21.579	4.561
8 Villany 5	0.893	0.893	0.000	13.750	25.060	0.893	14.643	29.226	12.560	2.083
9 Kamyk	0.000	0.625	0.625	12.625	18.458	0.000	19.292	13.458	3.125	0.000
10 Betfia 9a	1.020	1.020	0.000	7.619	8.639	1.020	22.925	40.782	14.592	2.381
11 Tiligul	1.276	1.276	0.595	13.294	22.863	2.228	13.339	35.561	9.569	0.000
12 Dodogol 1	0.000	0.000	0.000	10.667	10.667	0.000	10.667	47.333	20.667	0.000

example is that of Saskatoon, located in the ecotone between climate zones VI (temperate climate zone) and VIII (boreal climate zone). It can be observed that the highest probable climate is different depending on the group used to classify it. Using the whole fauna and the macromammals the most probable climate is VI, while using rodents and whole fauna without bats, climate VIII is identified. Furthermore, the highest probability climate (P_1 in Table 4) is usually lower than 0.90, while in situations where the locality is located in the more central parts of the dominion, the probability of the most probable climate is always close to 1.00. For those cases where the ecotone is not detected, the reason could be due to: (1) young boundaries (the boundaries were established recently) (2) the relative geographical extent of both climate zones, one of them being much larger than the other and thus the main source of taxa, or (3) one of the climates showing a higher proportion of characteristic taxa for that climate. The latter case indicates that there are climate zones in which faunas have more cosmopolitan taxa with a low proportion of typical taxa for that climate zone, while in others the proportions of these characteristic taxa may be quite high (Appendix 1) (M. Hernández Fernández & E.S. Vrba, in prep.).

Bioclimatic classification of fossil associations

Barová Cave (late Pleistocene–Holocene)

The bioclimatic spectra of both fossil rodent associations are shown in Table 5. The results obtained from the model show a change from a boreal climate in Barová 12 (the highest probability climate zone is VIII, $P_1 = 1.000$; the second highest

probability climate zone is VI, $P_2 < 0.001$) to a temperate climate in Barová 9–10c–10b (the highest probability climate zone is VI, $P_1 = 1.000$; the second highest probability climate zone is VIII, $P_2 < 0.001$). These results agree with the palynological analysis presented by Svobodová (1992), showing a change from a landscape dominated by tree genera representative of boreal coniferous forests (*Pinus*, *Picea*, *Juniperus* and *Salix*) in the lower level (layer 12) to a nemoral broadleaf-deciduous forest dominated by *Corylus* and *Betula* in the upper level (layers 9–10c–10b).

Eurasian early Pleistocene

The bioclimatic characterization of the extinct species from the early Pleistocene Eurasian sites has been carried out by studying the dental morphology of the species and comparing it with the morphology of modern taxa, assigning the extinct species to the morphologically closest living species or group of species (Hernández Fernández, 2001b; Hernández Fernández & Peláez-Campomanes, 2003). For those extinct taxa included in a phylogenetic clade in which the extant representatives all have a similar climatic distribution, we assume they had the same distribution as the extant species.

Problems derived from actualism force us to be cautious. Correlation between dental morphology and climatic ranges could be different for fossil taxa, and climatic ranges of extinct taxa could be unlike those of extant taxa. Thus we have adopted a conservative approach to the study of climatic ranges of fossil taxa. Extinct genera have been analysed as a whole for comparison with extant genera (Hernández Fernández & Peláez-Campomanes, 2003). Relatively little uncertainty is introduced when all of the species in a taxon present

Table 6 Qualitative bioclimatic analysis results for rodent faunas from the Eurasian basal early Pleistocene (P_1 , probability of the highest probability climate zone; P_2 , probability of the second highest probability climate zone)

Fossil site	Qualitative bioclimatic analysis			
	Highest probability climate zone	P_1	2nd highest probability climate zone	P_2
1 Quibas	IV	1.000	VI	< 0.001
2 Bagur 2	VII	0.561	VI	0.432
3 Mas Rambault 1	IV	1.000	VI	< 0.001
4 Les Valerots	VI	0.999	VII	< 0.001
5 Neuleiningen 5	VIII	0.486	VII	0.339
6 Monte Peglia A	VI	0.902	VII	0.097
7 Chlum 6	VI	0.999	VIII	0.001
8 Villany 5	VII	0.840	IV	0.120
9 Kamyk	VII	0.538	VI	0.462
10 Belfia 9a	VII	0.570	VI	0.430
11 Tiligul	VII	0.999	VI	0.001
12 Dodogol 1	VII	1.000	VI	< 0.001

similar bioclimatic characterization, and indeed this is often the case. However, it is sometimes necessary to assign taxa to numerous different BC. Such taxa have reduced discriminatory power, but they still can provide useful information for a global analysis to help distinguish, for example, between forests and open lands.

It can be admitted that some climatic range assignments may be over- or under-estimated. However, the intention is not to define species as key climatic indicators, thus they must not be used directly as evidence for the climate of localities that contain those taxa. This bioclimatic characterization is an important methodological step for the bioclimatic analysis. Nevertheless, the latter is robust against a limited number of errors in the assignments. The influence of small errors associated with the incorrect assignment of species is weak because the whole fauna (or the rodent fauna) is used for the climatic inference for a locality.

The obtained bioclimatic spectra of the studied fossil rodent associations are shown in the Table 5. The results of the qualitative bioclimatic analysis shown in Table 6 indicate that there is a set of localities where the model assigns them a climate with a high probability, above 90%, such as Quibas, Mas Rambault 1, Les Valerots, Monte Peglia A, Chlum 6, Tiligul and Dodogol 1, while for others the probabilities for the two more probable climates are similar, such as in Bagur 2, Neuleiningen 5, Kamyk and Belfia 9. This difference among localities could be due, as pointed out in the validation of the model, to the position of each locality within the climatic zones. Localities where the probability is high would be situated

far away from the climate zone boundaries, while those with low probabilities could be situated close to the boundary between climatic zones.

Initially examining localities classified with a high probability, we can infer that during the early Pleistocene the Mediterranean climate (IV) was established along the Mediterranean coast at least at its western part. East Europe and Central Asia at that time showed a typical steppe climate (VII) as indicated by the results obtained for Tiligul (Ukraine) and Dodogol 1 (Russia). Finally, a third group of localities indicate the presence of a broadleaf-deciduous forest biome (VI). The localities of climate zone VI are Les Valerots (France), Monte Peglia A (Italy) and Chlum 6 (Czech Republic). So far, the results obtained are similar to what we observe in present day climatic distribution (Allué Andrade, 1990). The differences arise when we study the localities classified with low probabilities. All those localities but Neuleiningen 5 (Germany) have steppe (VII) as the most probable climate, although the probability of the broadleaf-deciduous forest biome (VI) is only slightly lower. This could be interpreted as indicative of more open and drier conditions in central Europe than nowadays, with the steppe penetrating more deeply into central Europe from the East. With the few localities studied here it is not possible to establish if the steppe zonobiome formed a continuous band reaching Spain (Bagur 2), or if there were just small patches scattered through a more extended zonobiome VI. The presence nearby of areas of climatic zone VI could be the reason for the high probability of this climate as the second probable climatic zone. Neuleiningen 5 has a very specific climatic classification. The most probable climate zone is boreal (VIII), with climatic zone VII as the next most probable. One interpretation could be that the boreal climate zone, at that time, occupied a small patch related to mountain ranges, as can be observed in the present day. However, the high proportion of BC VII on the bioclimatic spectrum of this locality could indicate that the steppe zonobiome was also present in western Germany during the Early Pleistocene, indicating boundary conditions between steppe and taiga (VII/VIII).

CONCLUSIONS

The results presented in this work provide a preliminary example of the potential that bioclimatic analysis has as a tool for palaeoclimatic inference. The application of the model to fossil mammal associations from large areas and with similar ages offers the possibility to construct palaeoclimatic maps when combined with palaeogeographical reconstructions. It also offers the potential to study climatic evolution at different scales in time and space. Finally, the method offers the opportunity to standardize data coming from vertebrate palaeontology for use in the construction and evaluation of palaeoclimatic models.

ACKNOWLEDGMENTS

We thank Drs M.A. Álvarez Sierra, N. López Martínez and J.L. Tellería (Complutense University, Madrid) and B. Luna (Castilla-La Mancha University, Toledo) for comments and valuable suggestions. Comments and questions by Dr R. Graham (Denver Museum of Nature and Science) greatly helped to improve the final document. We also thank Dr R.A. Martin (Murray State University) for his critical comments of this work and help with the English.

This study was supported by the Spanish CICYT (PB98-0691-C03-01; PB98-0691-C03-02) and MCYT (BTE2002-00410). One of the authors (M.H.F.) has been funded by postdoctoral grants from the Fulbright Visiting Scholar Program, with the financial sponsorship of the Spanish Ministry of Education, Culture and Sports, and from the Education Council of the Comunidad Autónoma de Madrid (CAM), financed by the CAM and by the European Social Fund. P.P.-C. has a CSIC contract from the I3P program supported by the European Social Fund.

SUPPLEMENTARY MATERIAL

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/GEB/GEB057/GEB057sm.htm>

Appendix 1.1 Whole mammal faunal bioclimatic spectra of the localities.

Appendix 1.2 Rodentia faunal bioclimatic spectra of the localities.

Appendix 1.3 Large mammal faunal bioclimatic spectra of the localities.

Appendix 1.4 Whole mammal without Chiroptera faunal bioclimatic spectra of the localities.

Appendix 2.1 Coefficients for discriminant functions calculated from whole mammal faunal bioclimatic components and centroids, for each discriminant function, for every locality's biome group.

Appendix 2.2 Coefficients for discriminant functions calculated from rodent faunal bioclimatic components and centroids, for each discriminant function, for every locality's biome group.

Appendix 2.3 Coefficients for discriminant functions calculated from large mammal faunal bioclimatic components and centroids, for each discriminant function, for every locality's biome group.

Appendix 2.4 Coefficients for discriminant functions calculated from whole mammal without Chiroptera faunal bioclimatic components and centroids, for each discriminant function, for every locality's biome group.

Appendix 3.1 Whole mammal faunal bioclimatic spectra of the 13 new localities used for the validation of the bioclimatic model.

Appendix 3.2 Rodentia faunal bioclimatic spectra of the 13 new localities used for the validation of the bioclimatic model.

Appendix 3.3 Large mammal faunal bioclimatic spectra of the 13 new localities used for the validation of the bioclimatic model.

Appendix 3.4 Whole mammal without Chiroptera faunal bioclimatic spectra of the 13 new localities used for the validation of the bioclimatic model.

REFERENCES

- Aguilar, J.-P., Bachelet, B., Bonnet, A., Lesage, J.-L. & Michaux, J. (1993) Le gisement karstique du Grand Serre (Commune de Montclus, Gard). Données nouvelles sur les faunes de rongeurs du Pliocène terminal dans le Sud de la France. *Geobios*, **26**, 633–640.
- Agustí, J. & Martín Suárez, E. (1986) Un proyecto de análisis ecoestratigráfico en el Plio-Pleistoceno de la depresión de Guadix-Baza. *Memorias I Jornadas de Paleontología* (Coord. by E. Villas), pp. 21–32. Diputación General de Aragón, Departamento de Cultura y Educación, Zaragoza.
- Alexeeva, N. (1998) Paleoeecology of Transbaikalian *Allophaiomys* faunas. *Paludicola*, **2**, 16–19.
- Allué Andrade, J.L. (1990) Atlas fitoclimático de España. *Monografías del Instituto Nacional de Investigaciones Agrarias*, **69**, 1–223.
- Álvarez Sierra, M.A., Díaz Molina, M., Lacombe, J.L. & López Martínez, N. (1990) Taphonomic and sedimentary factors in the fossil record of mammals. *European neogene mammal chronology* (ed. by E.H. Lindsay, V. Fahlbusch and P. Mein), pp. 461–474. Plenum Press, New York.
- Andrews, P., Lord, J.M. & Evans, E.M.N. (1979) Patterns of ecological diversity in fossil and modern mammalian faunas. *Biological Journal of the Linnean Society*, **11**, 177–205.
- Bartolomei, G., Chaline, J., Fejfar, O., Jánossy, D., Jeannet, M. & von Koenigswald, W. & Kowalski, K. (1975) *Pliomys lenki* (Heller 1930) (Rodentia, Mammalia) en Europe. *Acta Zoologica Cracoviensia*, **20**, 394–465.
- Behrensmeyer, A.K. (1982) Time resolution in fluvial vertebrate assemblages. *Paleobiology*, **8**, 211–227.
- Behrensmeyer, A.K. & Schindel, D. (1983) Resolving time in Paleobiology. *Paleobiology*, **9**, 1–8.
- de Bonis, L., Bouvrain, G. & Geraads, D. & Koufos, G. (1992) Multivariate study of late Cenozoic mammalian faunal compositions and paleoecology. *Paleontologia i Evolució*, **24–25**, 93–101.
- Chaline, J. (1972) *Les Rongeurs du Pléistocène Moyen et Supérieur de France (Systématique, Biostratigraphie, Paléoclimatologie)*. *Cahiers de Paléontologie*. CNRS, Paris.
- Chaline, J. & Michaux, J. (1966) Résultats préliminaires d'une recherche systématique de micromammifères dans le Pliocène et le Quaternaire de France. *Comptes Rendus de l'Académie des Sciences de Paris, Series D*, **262**, 1066–1069.
- Chaline, J. & Michaux, J. (1974) Les Rongeurs du Pléistocène inférieur de France. *Mémoires du Bureau de Recherches Géologiques et Minières*, **78**, 89–96.

- CLIMAP Project Members (1976) The surface of the Ice-Age Earth. *Science*, **191**, 1131–1137.
- COHMAP Members (1988) Climatic changes of the last 18 000 years: observations and model simulations. *Science*, **241**, 1043–1052.
- Corbet, G.B. (1978) *The mammals of the Palaearctic region: a taxonomic review*. Cornell University Press, London.
- Corbet, G.B. & Hill, J.E. (1992) *The mammals of the Indomalayan region: a systematic review*. Oxford University Press, Oxford.
- Daams, R., van der Meulen, A.J., Peláez-Campomanes, P. & Álvarez Sierra, M.A. (1999) Trends in rodent assemblages from the Aragonian (Early-Middle Miocene) of the Calatayud-Daroca Basin, Aragon, Spain. *Hominoid evolution and climatic change in Europe*, Vol. 1. *The evolution of neogene terrestrial ecosystems in Europe* (ed. by J. Agustí, L. Rook and P. Andrews), pp. 127–139. Cambridge University Press, Cambridge.
- van Dam, A. (1998) The small mammals from the Upper Miocene of the Teruel-Alfambra region (Spain): Paleobiology and paleoclimatic reconstructions. *Geologica Ultraiectina*, **156**, 1–203.
- Daoud, A. (1993) Evolution of Gliridae (Rodentia, Mammalia) in the Pliocene and Quaternary of Poland. *Acta Zoologica Cracoviensia*, **36**, 199–231.
- Dorst, J. & Dandelot, P. (1973) *A field guide to the larger mammals of Africa*. Collins, London.
- Eisenberg, J.F. (1989) *Mammals of the Neotropics*, Vol. 1: *the northern Neotropics: Panama, Colombia, Venezuela, Guyana, Suriname, French Guiana*. The University of Chicago Press, Chicago.
- FAUNMAP Working Group (1996) Spatial response of mammals to Late Quaternary environmental fluctuations. *Science*, **272**, 1601–1606.
- Fernández-López, S.R. (2000) *Temas de Tafonomía*. Departamento de Paleontología, Universidad Complutense de Madrid, Madrid.
- Garapich, A. & Nadachowski, A. (1996) A contribution to the origin of *Allophaiomys* (Arvicolidae, Rodentia) in Central Europe: the relationship between *Mimomys* and *Allophaiomys* from Kamyk (Poland). *Acta Zoologica Cracoviensia*, **39**, 179–184.
- Hall, E.R. (1981) *The mammals of North America*, Vols I–II. John Wiley & Sons, New York.
- Hernández Fernández, M. (2001a) Bioclimatic discriminant capacity of terrestrial mammal faunas. *Global Ecology and Biogeography*, **10**, 189–204.
- Hernández Fernández, M. (2001b) *Análisis paleoecológico y paleoclimático de las sucesiones de mamíferos del Plio-Pleistoceno ibérico*. PhD Thesis. Universidad Complutense de Madrid, Madrid.
- Hernández Fernández, M. & Peláez-Campomanes, P. (2003) Ecomorphological characterization of Murinae and hypsodont ‘Cricetidae’ (Rodentia) from the Iberian Plio-Pleistocene. *Coloquios de Paleontología, Volumen Extraordinario*, **1**, 237–251.
- Hernández Fernández, M., Salesa, M.J., Sánchez, I.M. & Morales, J. (2003) Paleoeología del género *Anchitherium* von Meyer, 1834 (Equidae, Perissodactyla, Mammalia) en España: evidencias a partir de las faunas de macromamíferos. *Coloquios de Paleontología, Volumen Extraordinario*, **1**, 253–280.
- Hír, J. & Venczel, M. (1998) The *Allophaiomys* populations of Betfia IX (Romania, Bihor County). *Paludicola*, **2**, 37–49.
- Jánossy, D. (1986) *Pleistocene vertebrate faunas of Hungary*. Akadémiai Kiadó, Budapest.
- Kingdon, J. (1971) *East African mammals. An atlas of evolution in Africa*, Vol. I. Academic Press, London.
- Kingdon, J. (1974a) *East African mammals. An atlas of evolution in Africa*, Vol. II. Part A (Insectivores and bats). Academic Press, London.
- Kingdon, J. (1974b) *East African mammals. An atlas of evolution in Africa*, Vol. II. Part B (Hares and rodents). Academic Press, London.
- Kingdon, J. (1977) *East African mammals. An atlas of evolution in Africa*, Vol. III. Part a (Carnivores). Academic Press, London.
- Kingdon, J. (1979) *East African mammals. An atlas of evolution in Africa*, Vol. III. Part B (Large mammals). Academic Press, London.
- Kingdon, J. (1982a) *East African mammals. An atlas of evolution in Africa*, Vol. III. Part C (Bovids). Academic Press, London.
- Kingdon, J. (1982b) *East African mammals. An atlas of evolution in Africa*, Vol. III. Part D (Bovids). Academic Press, London.
- von Koenigswald, W. & Heinrich, W.-D. (1999) Mittelpleistozäne Säugetierfaunen aus Mitteleuropa-der Versuch einer biostratigraphischen Zuordnung. *Kaupia*, **9**, 53–112.
- Kohfeld, K.A. & Harrison, S.P. (2000) How well can we simulate past climates? Evaluating the models using global palaeoenvironmental datasets. *Quaternary Science Reviews*, **19**, 321–346.
- Kowalski, K. (1975) Earliest appearance of lemmings in the Quaternary of Poland. *Trabajos sobre Neógeno/Cuaternario*, **4**, 99–104.
- Kretzoi, M. (1956) Die altpleistozänen Wirbeltier Faunen des Villányer Gebirges. *Geologica Hungarica, Serie Palaeontologie*, **27**, 1–264.
- Laplana, C. (1999) Presencia de *Microtus (Allophaiomys) chalinei* Alcalde, Agustí y Villalta 1981 (Arvicolidae, Rodentia) en el yacimiento de Bagur-2 (Pleistoceno inferior, Girona, España). *Treballs del Museu de Geologia de Barcelona*, **8**, 25–32.
- Legendre, S. (1986) Analysis of mammalian communities from the Late Eocene and Oligocene of Southern France. *Palaeovertebrata*, **16**, 191–212.
- López Martínez, N., Michaux, J. & Villalta, J.F. (1976) Rongeurs et Lagomorphes de Bagur-2 (Province de Gérone, Espagne), nouveau remplissage de fissure du début du Pléistocène Moyen. *Acta Geológica Hispánica*, **11**, 46–54.
- Lundelius, E.L., Jr Downs, T., Lindsay, E.H., Semken, H.A., Zakrzewski, R.J., Churcher, C.S., Harington, C.R., Schultz, G.E. & Webb, S.D. (1987) The North American Quaternary sequence. *Cenozoic Mammals of North America: Geochronology and Biostratigraphy* (ed. by M.O. Woodburne), pp. 211–235. University of California Press, Berkeley.
- Martín Suárez, E. & Mein, P. (1991) Revision of the genus *Castillomys* (Muridae, Rodentia). *Scripta Geologica*, **96**, 47–81.
- Maul, L. (1996) Biochronological implications of the arvicolids (Mammalia: Rodentia) from the Pliocene and Pleistocene faunas of Neuleiningen (Rheinland-Pfalz, southwest Germany). *Acta Zoologica Cracoviensia*, **39**, 349–356.
- van der Meulen (1973) Middle Pleistocene smaller mammals from the monte Peglia, (Orvieto, Italy) with special reference to the phylogeny of *Microtus* (Arvicolidae, Rodentia). *Quaternaria*, **17**, 1–144.
- van der Meulen (1974) On *Microtus (Allophaiomys) deucalion* (Kretzoi, 1969), (Arvicolidae, Rodentia), from the Upper Villányian (Lower Pleistocene) of Villány-5, S. Hungary. *Proceedings of the Koninklijke Nederlandse Akademie Van Wetenschappen, Series B*, **77**, 259–266.

- van der Meulen, A.J. & Daams, R. (1992) Evolution of Early-Middle Miocene rodent faunas in relation to long-term palaeoenvironmental changes. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **93**, 227–253.
- Montoya, P., Alberdi, M.T., Blázquez, A.M., Barbadillo, L.J., Fumanal, M.P., van der Made, J., Marín, J.M., Molina, A., Morales, J., Mure-laga, X., Peñalver, E., Robles, F., Ruiz Bustos, A., Sánchez, A., Sanchiz, B., Soria, D. & Szyndlar, Z. (1999) La fauna del Pleistoceno Inferior de la Sierra de Quibas (Abanilla, Murcia). *Estudios Geológicos*, **55**, 127–161.
- Montuire, S. (1995) Évolution climatique et diversité chez les mammifères en Europe centrale depuis del Pliocène. *Geobios, Memoire Special*, **18**, 313–327.
- Nadachowski, A. (1990a) Review of fossil Rodentia of Poland (Mammalia). *Senckenbergiana Biologica*, **70**, 229–250.
- Nadachowski, A. (1990b) Lower Pleistocene rodents of Poland: faunal succession and biostratigraphy. *Quartärpaläontologie*, **8**, 215–223.
- Nadachowski, A. (1991) Systematics, geographic variation, and evolution of snow voles (*Chionomys*) based on dental characters. *Acta Theriologica*, **36**, 1–45.
- Nadachowski, A. (1998) Faunal succession of small mammal assemblages at the Pliocene–Pleistocene boundary in Poland. *Mededelingen Nederlands Instituut Voor Toegepaste Geowetenschappen TNO*, **60**, 281–286.
- Nadachowski, A. & Garapich, A. (1998) *Allophaiomys* evolutionary stage in extant *Microtus*. *Paludicola*, **2**, 91–94.
- Nowak, R.M. (1991) *Walker's mammals of the world*, Vols I–II, 5th edn. Johns. Hopkins University Press, Baltimore.
- Prentice, I.C. & Webb, T., III (1998) BIOME 6000: reconstructing global mid-Holocene vegetation patterns from palaeoecological records. *Journal of Biogeography*, **25**, 997–1005.
- PRISM Project Members (1995) Middle Pliocene paleoenvironments of the Northern Hemisphere. *Paleoclimate and Evolution, with Emphasis on Human Origins* (ed. by E.S. Vrba, G.H. Denton, T.C. Partridge and L.H. Burckle), pp. 197–212. Yale University Press, New Haven.
- Rekovets, L. & Nadachowski, A. (1995) Pleistocene voles (Arvicolidae) of the Ukraine. *Paleontologia i Evolució*, **28–29**, 145–245.
- Svoboda, J., Horáček, I., Ložek, V., Svobodová, H. & Šilar, J. (2000) The Pekárna Cave. Magdalenian stratigraphy, environment, and the termination of the loess formation in Moravian Karst. *Sborník Geologických Véd (Antropozoikum)*, **24**, 61–79.
- Svobodová, H. (1992) Palaeobotanical evidence on the Late Glacial in the Moravian Karst. *Palaeovegetational development in Europe and the regions relevant to its palaeofloristic evolution* (ed. by J. Eder-Kovar), pp. 81–85. Naturhistorisches Museum, Wien.
- Terzea, E. (1995) Mammalian events in the Quaternary of Romania and correlations with the climatic chronology of Western Europe. *Acta Zoologica Cracoviensia*, **38**, 109–120.
- Terzea, E. (1996) Biochronology of the Pleistocene deposits at Betsia (Bihor, Romania). *Acta Zoologica Cracoviensia*, **39**, 531–540.
- Walter, H. (1970) *Vegetationszonen und Klima*. Eugen Ulmer, Stuttgart.
- van de Weerd, A. & Daams, R. (1978) Quantitative composition of rodent faunas in the Spanish Neogene and paleoecological implications (I–II). *Proceedings of the Koninklijke Nederlandse Akademie Van Wetenschappen, Serie B*, **81**, 448–473.

BIOSKETCHES

Manuel Hernández Fernández has a broad interest in the area of evolutionary biology, encompassing a wide variety of problems related to the biological and climatic evolution of the Neogene-Quaternary Earth. He is particularly interested in the interface between macroecology and palaeoclimatology and the focus of his current research is in the use of mammal faunas for high precision palaeoenvironmental inference.

Pablo Peláez-Campomanes is interested in the structure of Cenozoic mammal communities integrating evolutionary and community ecology theories in studies with a multispecies perspective. His studies also provide extensive data sets for subsequent analyses of the evolution of mammalian lineages.