



## Bioclimatic discriminant capacity of terrestrial mammal faunas

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### ABSTRACT

A new method of environmental inference is presented. This method uses the climatic restriction index (CRI) for each mammal species, based on its geographical range within different climatic regimes, and a set of calculated summary indexes known as the bioclimatic spectrum. Analysis of 50 faunas throughout the world shows that terrestrial mammal communities are effective tools for accurate climatic inference at large spatial scale. The results also indicate that the use of entire mammalian fauna is the best inference system, followed by those based on separate groups such as Insectivora,

Rodentia, micromammals and macromammals. Removing Chiroptera from the analysis does not change the results significantly. Bioclimatic analysis appears to be a good method for environmental interpretation. This new method ensures a high qualitative precision. It provides an empirical model for mammal community characterization that must be taken into account for palaeoclimatic reconstructions of continental environments.

**Key words** bioclimatic spectrum, bioclimatology, biome, discriminant analysis, macroecology, mammalia, mammalian communities, methodology, palaeoclimatology.

### RESUMEN

Se presenta un nuevo método de inferencia ambiental. Este método utiliza el índice de restricción climática (CRI) para cada especie de mamífero, basado en su distribución geográfica, y en una serie de índices porcentuales conocida como espectro bioclimático. El análisis de cincuenta faunas de todo el mundo muestra que las comunidades de mamíferos terrestres son una herramienta eficiente para la inferencia climática de gran resolución a una escala espacial amplia. Los resultados indican que el uso de la fauna completa es el mejor sistema de inferencia, seguido por aquellos que utilizan grupos separados

tales como Insectivora, Rodentia, micromamíferos y macromamíferos. La eliminación de Chiroptera del análisis no cambia los resultados significativamente. El análisis bioclimático parece ser un buen método para la interpretación ambiental. Este nuevo método asegura una gran precisión cualitativa. Provee un modelo empírico para la caracterización de comunidades de mamíferos que debe ser tenido en cuenta en las reconstrucciones palaeoclimáticas de ambientes continentales.

**Palabras clave** análisis discriminante, bioclimatología, bioma, comunidades de mamíferos, espectro bioclimático, macroecología, mammalia, metodología, paleoclimatología.

### INTRODUCTION

Palaeoclimatical studies contribute significantly to an understanding of the biogeographical history of many animal groups and of how climatic

tendencies from the past may still be acting currently. It is generally assumed that past macroclimatic factors may be recognized by the study of fossil mammal assemblages (van de Weerd & Daams, 1978; Andrews *et al.*, 1979;

Artemiou, 1984; Bonis *et al.*, 1992; Andrews, 1995). This assumption is based on the fact that climate imposes a habitat series which in turn imposes a community structure (Walter, 1970; Blondel, 1979; Currie, 1991; Kerr & Packer, 1997; Shepherd, 1998). In addition, many studies have focused on indirect climate effects on mammal communities, such as types of vegetation, to explain mammal community organization and differentiation (Valverde, 1967; Fleming, 1973; van de Weerd & Daams, 1978; Legendre, 1986; Kay & Madden, 1997). Therefore, mammal fossil assemblages, especially those of rodents, have been considered as a suitable climatic indicator for qualitative (van de Weerd & Daams, 1978; Daams & van der Meulen, 1984; Sesé, 1991; van der Meulen & Daams, 1992) and quantitative (Montuire, 1996; Montuire *et al.*, 1997) climatic reconstructions.

Palaeoclimatic studies based on whole or nearly whole mammal faunas are relatively recent. Some of these (Andrews *et al.*, 1979; Legendre, 1986) are based on Fleming's (1973) or Valverde's (1967) classical studies, which were conceived as an adequate system for mammal community description, but not for environmental inference. Palaeoclimatic studies focused on the inference of past climatic conditions are based on a wide variety of methods, including: the study of habitat preference of living related species (van de Weerd & Daams, 1978; Van Couvering, 1980; Evans *et al.*, 1981; Ruiz Bustos, 1994, 1995), functional morphology (Kappelman, 1991; Plummer & Bishop, 1994; Kappelman *et al.*, 1997), taxonomic categories of the fauna (Bonis *et al.*, 1992) and, recently, the quantitative application of Andrews *et al.*'s (1979) method (Kay & Madden, 1997; Reed, 1998).

In general, the results from these palaeo-environmental studies are relatively vague (cool-warm, wet-dry, temperate-sub-tropical-tropical, forest-open land, etc.) (Mosbrugger & Schilling, 1992) and therefore a new method that allows the inference of more accurate climatic typologies is needed. According to Mosbrugger & Schilling (1992), multivariate statistical analysis should be applied to allow a refinement of the climatic inference methods. However, the application of multivariate techniques is not sufficient in itself to ensure greater refinement, as palaeoclimatic reconstruction methods also require a reference to present communities in an extensive geographical framework (see Rodríguez, 1997).

The aims of this paper are to present a new multivariate method for palaeoclimatic inference and to test its accuracy with extant faunas. The intent of the present study is to determine if this new method allows the recognition of different biomes using multivariate analysis. For this purpose, a specific climatic typology is used that will hopefully achieve greater qualitative accuracy than previous palaeoenvironmental reconstruction methods. Furthermore, fossil assemblages do not always represent fully the past mammal communities, depending on palaeo-ecological and/or taphonomical processes. Therefore, the accuracy of the method will be tested, applying it to single orders or groups of orders (macromammals, micromammals, etc.).

## MATERIALS AND METHODS

The bioclimatic characterization of the therio-faunas is based on the climatic typology of Walter (1970), summarized in Table 1, and mapped in Allué (1990). This typology has been selected because it has a simple nomenclature and coincides with traditional biomes (Odum, 1971; Lacoste & Salanon, 1973; Lieth, 1975; Strahler & Strahler, 1987).

Fifty localities from all over the world (with the exception of Australia) and from all climates form the database of this study (Appendix 1). Five localities containing both faunistic 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 so that the localities from a single climate zone were as widely scattered as possible all over the world. The surface of each sample area is roughly 10 000 km<sup>2</sup>. This size is adequate to take into consideration spatial variation in climate (O'Brien, 1993) and all possible regional habitats. In order to avoid high climate variations imposed by differences in topography (mainly mountain ranges), the selected localities are mostly below 1000 m above sea level. Only two localities exceed that altitude, since it is necessary to find determinate climate conditions in certain geographical areas.

The faunal list of each locality has been obtained from the references in Appendix 1. In addition to the references on faunal lists given in

**Table 1** Climatic typology used in this paper (modified from Walter, 1970; Walter considers II/III as a zonoecotone between tropical forests and deserts but I apply it as a zonobioma because it is traditionally used in palaeoecology because of its unique faunistic community) and its relationships with world vegetation types

Climate		Zonobiome (mainly vegetation type)	
I	Equatorial	I	Evergreen tropical rain forest
II	Tropical with summer rains	II	Tropical deciduous forest
II/III	Transition tropical semi-arid	II/III	Savanna
III	Sub-tropical arid	III	Sub-tropical desert
IV	Winter rain and summer drought	IV	Sclerophyllous woody plants
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

Appendix 1, data from Haltenorth *et al.* (1979), Burton & Pearson (1987), Lekagul & McNeely (1988), Heptner *et al.* (1989) and Heptner & Sludskii (1992) were used for information about species geographical ranges. These lists also contain species that became extinct during the last two centuries. Species introduced by man are omitted. Taxonomy has been standardized according to Wilson & Reeder (1993).

The analytical methodology in this work shows some similarity to the Taxonomic Habitat Index method conceived by Evans *et al.* (1981) and developed by Andrews (1990) and Fernández-Jalvo *et al.* (1998). In the sections below, I will consider their methods to clarify the features of the new methodology proposed here.

First, a species by climate matrix is made for every locality (Appendix 2). The value of one species in a climate zone is 0 when the species does not live in that climate zone. When the species inhabits that climate zone the value is determined by the climatic restriction index (CRI). This index corresponds to the formula:

$$CRI_i = 1/n$$

in which  $n$  is the number of climate zones inhabited by the species and  $i$  is climate zone  $i$ , in which the species occurs. The more climatically restricted species have consequently higher CRI values and they offer a better climatic indication because of more specific environmental requirements. Consequently, the sum of the different CRI of a species equals 1. CRI is

analogous to the THI weightings of Andrews (1990). The main difference is that one species' THI scores are dependent on the proportions of each habitat occupied by the species, while CRI is fixed for all the climate zones occupied by the species. In this manner, to assess the index values of one species is simplified because is not necessary to know the habitat preference of the species, only its climate zone occurrence.

The number of climate zones inhabited by a species is determined by the relative size of its geographical range. If 15% or more of the geographical range of a species is situated within a climate zone, the species is considered to occupy that climate zone. It is also considered to occupy a specific climate zone when the species inhabits 50% or more of one climatic dominion. A climatic dominion is a continuous terrestrial area within one climate zone only. For instance, part of the winter rain and summer drought climate zone is present around the Mediterranean Sea and it consists of several climatic dominions. One is formed by the larger part of the Iberian Peninsula–South France, consisting of a continuous terrestrial area, and another climatic dominion is, for instance, north-western Africa. The criteria used for this climatic assignation were adopted after a preliminary chorological survey of the species considered.

In this paper, the term bioclimatic component (BC) is used, which is the representation in a specific locality of each of the 10 existing climates,

analogous to habitat types of Evans *et al.* (1981) and Andrews (1990). The CRI of each separate species is calculated and situated in correspondent BCs that the species inhabits. Each BC locality value is calculated according to the formula:

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

in which *i* is climate zone *i* and *S* is the number of species in the locality. All BC values of one locality constitute its bioclimatic spectrum (Appendix 2). One could consider the value of each BC as the relative frequency of the species from the locality that occupy the corresponding climate zone.  $BC_i$  is analogous to the cumulative index of Andrews (1990) or the percentage THI of Fernández-Jalvo *et al.* (1998).

Concluding, bioclimatic analysis of a locality is an ordination method using weighted averages (Gauch, 1982) on a climatic presence/absence matrix, in which weights for species are defined by CRI and the ordination scores for each bioclimatic component are calculated as proportions to obtain the BC values in that locality.

In order to verify if localities within the same climate zone have more similar bioclimatic spectra than those of other climate zones, a discriminant analysis was performed. In the analysis, the variables used are the different  $BC_i$  that form the bioclimatic spectrum. Therefore, each locality is an operational faunistic unit characterized by 10 variables. The minimal tolerance level used was 0.0001.

Subsequently, each mammal order was studied independently to determine if all provide similar results or if some orders are better climatic predictors than others. Furthermore, the analysis was also applied to: macromammals as a group (Xenarthra, Scandentia, Dermoptera, Primates, Carnivora, Proboscidea, Perissodactyla, Hyracoidea, Tubulidentata, Artiodactyla, Pholidota); micromammals as a group (Didelphimorphia, Paucituberculata, Microbiotheria, Insectivora, Chiroptera, Rodentia, Lagomorpha, Macroscelidea); and the entire fauna without Chiroptera, and micromammals without Chiroptera, since bats are usually separated in ecological analysis (Wilson III, 1974; McCoy & Connor, 1980; Shvarts *et al.*, 1995) and they are excluded in palaeoecological analysis because they are rarely found as fossils (Andrews *et al.*, 1979).

## RESULTS AND DISCUSSION

### Bioclimatic spectra

Table 2 shows bioclimatic spectra of each locality obtained from the analysis of the whole fauna. In this table it is observed that the highest BC generally corresponds to the climate zone in which the locality is situated. Furthermore, other relatively high bioclimatic components from a locality correspond to other climate zones that may be closely related to the one in which the locality is situated.

### Discriminant analysis

#### *Whole fauna*

Nine functions have been calculated using the 50 localities and nine of the 10 bioclimatic components. Each function is highly correlated with one or two of the studied bioclimatic components, allowing the separation of localities belonging to the corresponding climate zones. This analysis generated correct classification for 98% of the studied localities (Table 3). Appendix 3 shows the results for each locality.

Among the 50 studied localities, only one (Voi in Kenya, number 39 in Appendix 3) has been wrongly grouped in the whole fauna discriminant analysis. It is a savanna community, but calculated discriminant functions group it as a tropical deciduous forest community. This may be explained by a number of factors. First of all, it is located in a small climatic dominion and it belongs to a biome in which the fauna is related strongly to the ones from the adjacent tropical deciduous forest biome. Furthermore, this locality has a relatively short dry period (7.44 months) divided into two different dry epochs per year (Griffiths, 1972) and it is situated near the savanna–tropical deciduous forest ecotone. Finally, there is a great variety of habitats in that region, from dry forest and closed woodland to open grassland (P. Andrews, personal communication).

#### *Mammal orders*

The use of discriminant analysis hindered inclusion of six mammal orders in our analysis of single orders because they contain one species only (Paucituberculata, Microbiotheria, Dermoptera, Tubulidentata), because they inhabit

**Table 2** Whole mammal faunal bioclimatic spectra of the localities. Each column represents a bioclimatic component (see Table 1), and  $BC_i$  values ( $BC_i = \Sigma CRI_i / 100/S$ ) are shown for each locality. For more explanation see the text and Appendix 2

Locality	I	II	II/III	III	IV	V	VI	VII	VIII	IX
Barrow	0.000	1.209	1.209	1.890	3.794	2.162	10.540	7.366	31.969	39.860
Port Harrison	0.000	0.794	0.794	1.814	4.671	3.243	15.385	13.005	22.528	37.766
Malye-Karmaerly	0.000	1.587	1.587	3.628	3.628	3.628	3.628	3.628	25.057	53.628
Mys Chelyuskin	0.000	1.235	1.235	1.235	1.235	1.235	4.938	1.235	32.716	54.938
Mys Schmidta	0.000	0.694	0.694	0.694	1.944	0.694	7.674	3.507	42.049	42.049
Fairbanks	0.000	0.705	2.584	2.055	4.416	3.463	22.101	9.601	45.712	9.363
Fort Smith	0.605	1.209	4.293	3.840	5.523	4.849	22.808	12.887	37.944	6.041
Kajaani	0.726	1.043	0.635	1.043	8.166	2.737	25.546	9.594	41.737	8.773
Serov	0.518	0.745	0.454	0.745	7.873	2.465	26.241	10.764	43.928	6.267
Erbogachen	0.876	1.259	0.766	0.766	4.822	2.121	12.293	7.121	55.397	14.579
Rapid City	1.139	3.505	8.216	8.641	9.934	6.575	19.718	31.769	8.907	1.596
Puerto Santa Cruz	2.105	4.142	14.050	7.661	9.883	11.272	15.849	34.420	0.617	0.000
Fort Schevchenko	1.675	2.215	1.506	5.052	16.491	2.342	8.619	58.973	2.160	0.966
Urumchi	0.926	1.296	1.296	2.963	9.574	1.963	8.741	65.963	5.407	1.870
Paotou	0.236	0.777	1.202	2.925	7.322	2.038	8.386	72.570	3.578	0.966
Prince Rupert	0.309	1.080	4.837	3.911	6.411	4.698	28.726	15.763	29.559	4.707
Cleveland	1.858	4.685	5.093	4.665	5.982	11.677	33.470	14.304	16.121	2.146
Evangelistas	1.458	4.887	11.554	8.284	11.169	12.900	30.876	17.964	0.908	0.000
Vlissingen	0.968	1.587	1.239	1.587	20.066	3.643	41.814	10.368	15.710	3.018
Tsingtao	5.474	6.821	3.862	1.539	8.314	16.193	37.658	14.952	4.418	0.770
New Orleans	5.451	9.355	6.650	5.194	5.021	37.883	17.542	8.641	3.938	0.325
Puerto Montt	1.723	5.245	7.291	4.942	17.367	42.518	13.308	6.533	1.073	0.000
Corrientes	17.391	32.869	18.115	1.612	1.694	25.219	1.284	1.612	0.205	0.000
Foochow	16.255	22.343	5.595	1.038	3.873	33.804	12.685	2.340	1.916	0.152
Kagoshima	5.659	6.770	2.663	1.687	4.627	36.085	34.085	3.020	4.270	1.130
Fresno	2.016	5.462	11.794	12.429	29.435	4.620	13.306	13.632	6.423	0.882
Santiago de Chile	2.298	4.690	12.432	12.217	37.701	13.131	10.251	6.518	0.762	0.000
Sanlucar de Barrameda	2.310	4.430	3.372	4.113	39.896	6.303	24.266	9.690	4.610	1.009
Aleppo	2.026	5.589	6.517	8.739	41.271	5.354	15.299	11.684	2.763	0.757
Esfahan	0.577	3.276	4.601	10.608	44.282	3.979	11.668	16.912	3.065	1.032
Phoenix	2.772	9.240	21.504	27.371	10.326	4.266	7.427	13.490	3.452	0.152
Arica	5.177	5.177	15.025	40.783	18.056	8.207	2.146	4.419	1.010	0.000
Assuan	2.676	13.027	16.360	37.127	17.451	5.831	3.146	2.584	1.400	0.397
Mascate	2.450	11.919	13.368	34.279	22.685	5.293	2.830	4.486	1.587	1.104
Lüderitz Bay	5.537	13.146	21.003	37.146	14.527	8.027	0.408	0.204	0.000	0.000
Las Piedras	30.769	32.491	28.788	1.170	0.768	4.541	0.521	0.775	0.175	0.000
Catamarca	7.615	18.742	44.514	5.594	3.773	11.581	2.088	5.655	0.437	0.000
Zinder	6.485	27.304	37.145	12.637	7.510	8.510	0.272	0.136	0.000	0.000
Voi	8.378	36.424	29.066	10.615	6.434	8.832	0.167	0.084	0.000	0.000
Jaipur	14.233	29.296	33.831	10.802	5.130	3.904	1.723	1.082	0.000	0.000
Roque Saenz Peña	15.817	33.237	24.583	2.660	1.891	18.686	1.250	1.635	0.240	0.000
Ziguinchor	16.192	39.272	21.434	8.928	5.980	7.839	0.236	0.118	0.000	0.000
Moundou	11.124	39.671	24.726	8.432	6.379	9.313	0.236	0.118	0.000	0.000
Mtwara	11.150	46.505	19.326	7.148	5.198	10.394	0.187	0.093	0.000	0.000
Patna	17.398	38.922	28.207	6.551	3.660	3.303	1.469	0.490	0.000	0.000
Tumaco	44.932	28.115	19.003	1.137	0.746	4.926	0.363	0.609	0.170	0.000
Paramaribo	46.245	29.179	18.401	0.686	0.361	4.488	0.227	0.347	0.067	0.000
Kribi	69.971	17.420	5.558	2.360	1.799	2.819	0.073	0.000	0.000	0.000
Yangambi	65.496	19.607	5.950	2.774	2.274	3.820	0.079	0.000	0.000	0.000
Medan	69.883	20.111	5.002	0.612	0.522	2.588	0.990	0.196	0.098	0.000

**Table 3** Summary of locality classification on the basis of whole mammal faunal bioclimatic spectra (total sum of well-classified localities = 98%)

Present climate	Predicted climate zone										Well-classified localities %
	I	II	II/III	III	IV	V	VI	VII	VIII	IX	
I	5 100%	0 0%	0 0%	0 0%	0 0%	0 0%	0 0%	0 0%	0 0%	0 0%	100%
II	0 0%	5 100%	0 0%	0 0%	0 0%	0 0%	0 0%	0 0%	0 0%	0 0%	100%
II/III	0 0%	1 20%	4 80%	0 0%	0 0%	0 0%	0 0%	0 0%	0 0%	0 0%	80%
III	0 0%	0 0%	0 0%	5 100%	0 0%	0 0%	0 0%	0 0%	0 0%	0 0%	100%
IV	0 0%	0 0%	0 0%	0 0%	5 100%	0 0%	0 0%	0 0%	0 0%	0 0%	100%
V	0 0%	0 0%	0 0%	0 0%	0 0%	5 100%	0 0%	0 0%	0 0%	0 0%	100%
VI	0 0%	0 0%	0 0%	0 0%	0 0%	0 0%	5 100%	0 0%	0 0%	0 0%	100%
VII	0 0%	0 0%	0 0%	0 0%	0 0%	0 0%	0 0%	5 100%	0 0%	0 0%	100%
VIII	0 0%	0 0%	0 0%	0 0%	0 0%	0 0%	0 0%	0 0%	5 100%	0 0%	100%
IX	0 0%	0 0%	0 0%	0 0%	0 0%	0 0%	0 0%	0 0%	0 0%	5 100%	100%

one climate zone only (Paucituberculata, Microbiotheria, Scandentia, Dermoptera), or because they were found in only one locality in each inhabited climate zone (Macroscelidea).

Insectivora and Rodentia are the orders that give the best discriminant results. For the Insectivora, 97.3% of the 37 localities in which this order is present were well classified, and for the Rodentia, these numbers are 94% of 50 localities (Fig. 1). Currie (1991) demonstrated a close relationship of the Rodentia and Insectivora with climate. This is probably due to the limited geographical ranges and relative stenotopy of many of their species (Brown *et al.*, 1996). Therefore, it is understandable that the Rodentia have been used widely to infer palaeoenvironmental conditions (van de Weerd & Daams, 1978; Daams & van der Meulen, 1984; Sesé, 1991; van der Meulen & Daams, 1992; Vianey-Liaud, 1991; Denys, 1992; Avery, 1993; Montuire, 1996; Motuzco & Ivanov, 1996; Montuire *et al.*, 1997). On the other hand, the use of Insectivora as climatic indicators is much less extensive (de Jong, 1988; Reumer, 1995), because this group is scarce in

fossil assemblages and the taxonomic studies in this group are, for this reason, less numerous. Better knowledge of this group will improve the accuracy of the palaeoclimatic reconstructions based on it.

Carnivora form the third best group, with 86% of 50 localities well classified. The remaining orders contain about 80% of well-classified localities (Fig. 1). Perissodactyla and Hyracoidea have a smaller discriminant capacity (around 70% of well-classified localities) and Proboscidea provides the least predictability (< 40%).

The reasons that the major part of the mammal orders have a smaller discriminant capacity than Insectivora or Rodentia may be because they contain few species (Proboscidea, Hyracoidea, Pholidota); because their species have wide geographical ranges and occupy numerous climatic zones (Carnivora, Artiodactyla, Lagomorpha); or because there are few localities (Didelphimorphia, Xenarthra, Primates, Proboscidea, Perissodactyla, Hyracoidea, Pholidota). The discriminant analysis of three groups that are present in few localities (Didelphimorphia,

Xenarthra, Primates) shows few wrongly classified localities. A more exhaustive study may confirm their validity as environmental indicators. As an example, the Primates from our localities inhabit tropical and sub-tropical climates only, but among them they show a significant discriminant capacity (only climates II and II/III are little differentiated, Fig. 1).

The Chiroptera form a special case. They are traditionally good climatic markers and they are correlated strongly with climatic parameters (McCoy & Connor, 1980), but in the bioclimatic analysis they show a lesser discriminant capacity than other small mammals, probably because bat species have generally larger geographical ranges than other similar-sized mammals (Rapoport, 1982). Furthermore, Rabenold (1993) recorded that animals that make long-distance migrations show different biogeographic patterns from non-migratory ones. Many bat species have migratory behaviour (McNab, 1982; Hill & Smith, 1984) and they can avoid climate restrictions and resource scarcity (Patterson *et al.*, 1996). This can be understood as an opportunist species character (Margalef, 1977) resulting in little climatic specialization. Fleming (1973) and Willig & Selcer (1989) have expressed the view that bat species are highly eurytopic and usually occur in several biomes. This pattern is clear in the altitudinal gradient of south-eastern Peru, where Patterson *et al.* (1996, 1998) have observed that bat faunas found at successively higher elevations are mainly impoverished and attenuated lowland faunas, while mouse faunas show a neat differentiation into various communities concurrent with vegetation types along the elevational gradient. This altitudinal gradient represents a habitat series analogous to that of biomes in a latitudinal gradient (Walter & Breckle, 1986). Therefore, this altitudinal pattern of bat species zonation may be similar to the latitudinal biome gradient pattern, making the use of Chiroptera more difficult than other micromammals for climate discrimination.

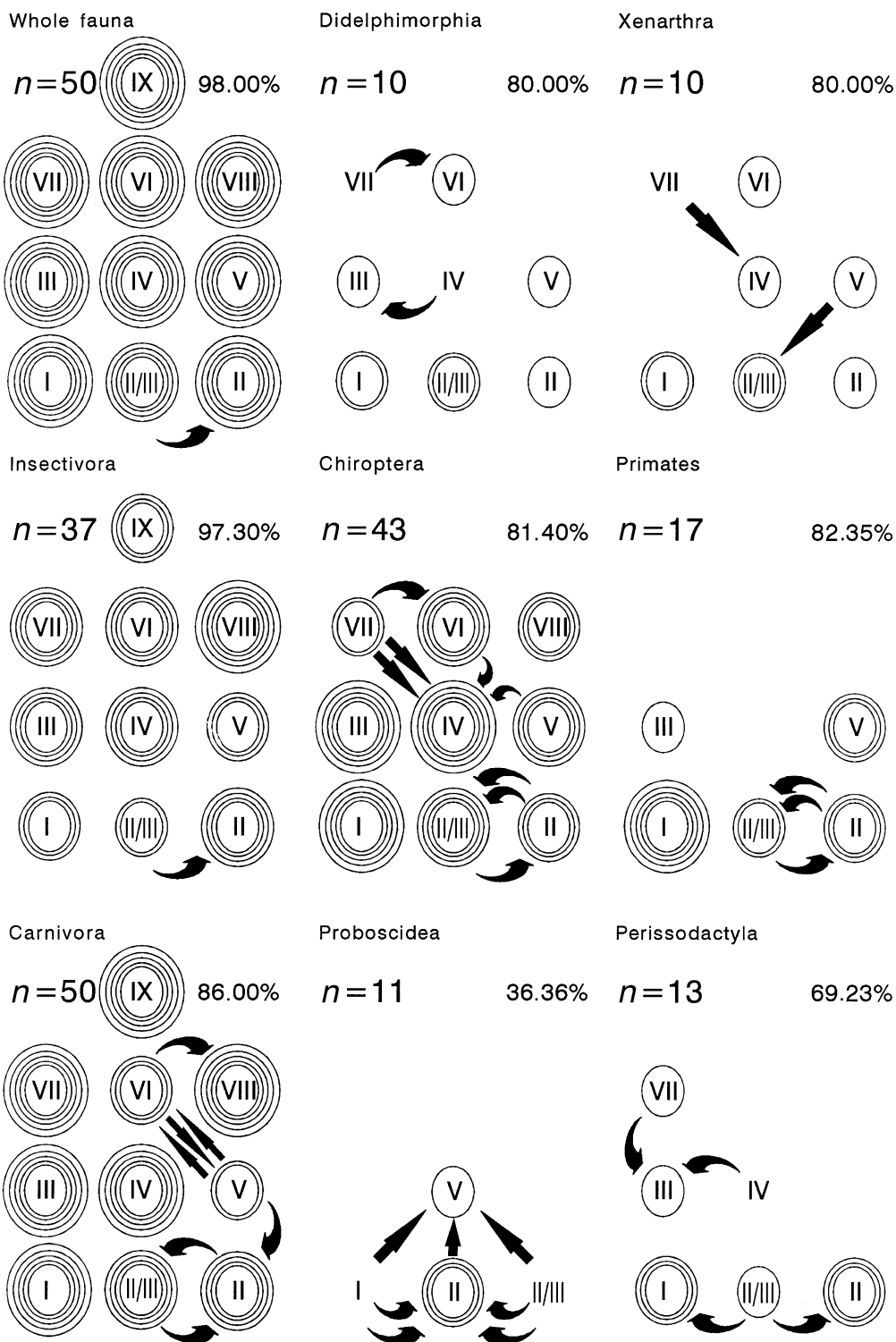
On the other hand, some orders with low climatic discriminant capacity at the biome level may be used to differentiate environments at another level. For example, Perissodactyla clearly separate temperate from tropical localities (Fig. 1).

#### *Micromammals vs. macromammals*

Better predictions are obtained by grouping the orders. Macromammal discriminant analysis generated 90% of well-classified localities. This proportion is 96% in micromammal analysis (Fig. 1). Geographic ranges of micromammals are usually small (Brown *et al.*, 1996), as mentioned above, and the majority of their species occur in few biomes, whereas larger mammals occur in many biomes (Brown & Nicoletto, 1991). This observation corroborates results of the present study. Micromammals have a greater discriminant capacity than macromammals probably because they are more climatically specialized. There are several reasons that may account for the greater climatic specialization in small mammals than in larger mammals, and which may thus affect the pattern observed in this work. (1) There are fewer macromammal species than micromammal species (Hutchinson & MacArthur, 1959; Van Valen, 1973; Dial & Marzluff, 1988; Brown & Nicoletto, 1991; Maurer *et al.*, 1992). Consequently, the number of possible competitive interactions among similar-sized small mammal species within feeding guilds is greater than among large mammals (Brown & Nicoletto, 1991). Therefore, to avoid this competition, small species need to be more stenotopic (Brown & Nicoletto, 1991). (2) Energetic and physiological constraints create a high degree of specialization in small species (Brown & Nicoletto, 1991). (3) Generation interval is correlated positively with body size (Eisenberg, 1990), which could allow micromammals to reach greater degrees of specialization than macromammals.

#### *Faunas without bats*

Whole fauna analysis, excluding the Chiroptera, results in 96% well-classified localities. Analysis of micromammals without bats generate the same proportion of well-classified localities (Fig. 1). Discriminant analyses without Chiroptera (both whole fauna and micromammals) generated results similar to those containing bats. In these analyses, the locality of Prince Rupert (Canada) was classified incorrectly since it belongs to climate zone VI and not to climate zone VIII. The main causes of this error may be the small size of the climatic dominion and the proximity of the Canadian taiga climatic dominion. The



**Fig. 1** Discriminant analysis results. Each ring represents a well-classified locality. The arrow stands for a locality from a climate zone (see Table 1) classified as belonging to another ( $n$  = localities used in analysis; % = proportion of well-classified localities).



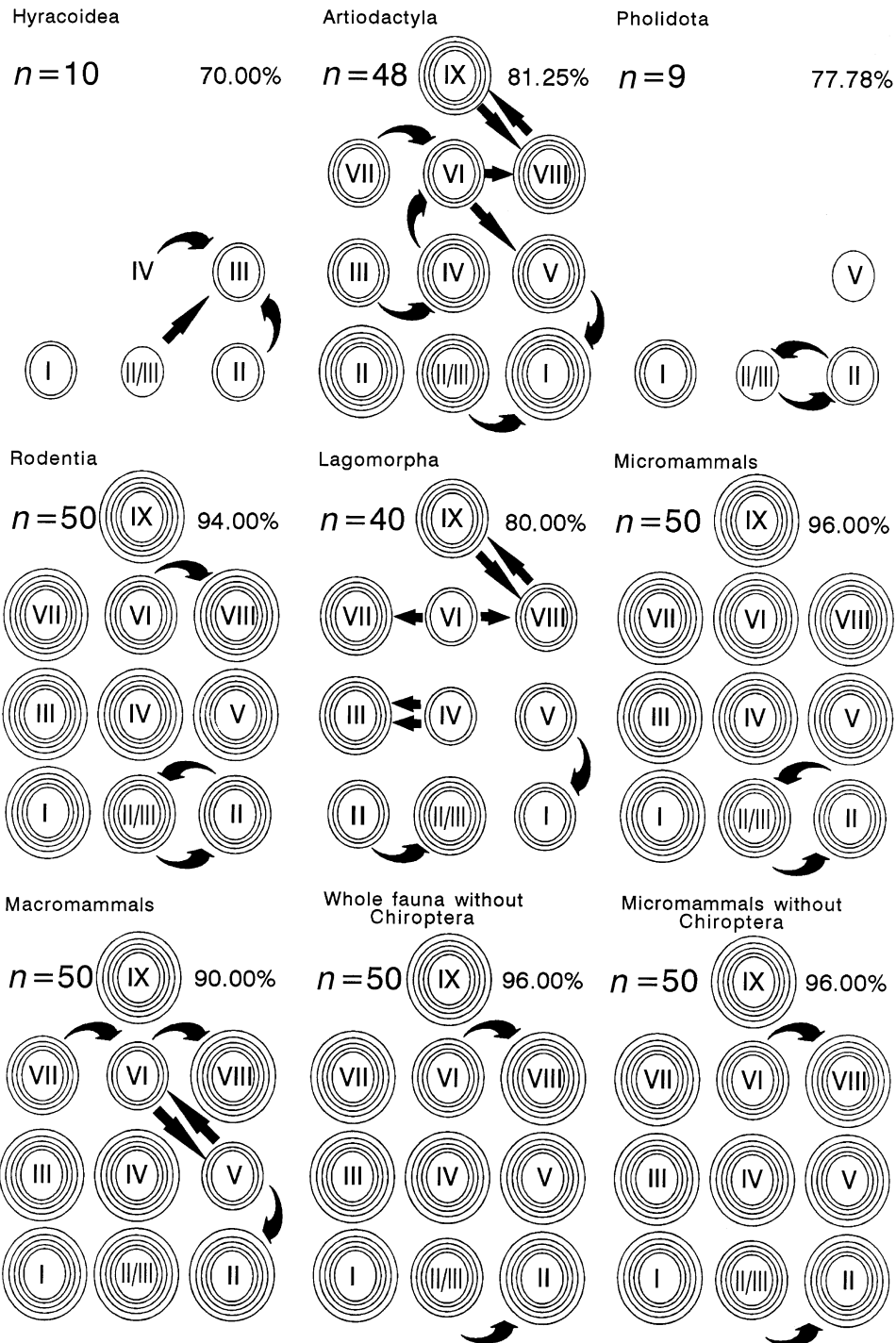


Fig. 1 continued.

Voi community from Kenya was also classified wrongly in these analyses; most probably for the reasons given above.

## CONCLUSIONS

Results of this work suggest that a new bioclimatic method, employing a multivariate (discriminant functions) analysis of climatic and mammalian distributional data, can be applied as an efficient tool in palaeoclimatical studies of continental environments. This new method, based on studies of extant mammal faunas, appears to be very accurate. The qualitative results obtained for each mammal association are based on a specific climatic typology. Therefore, one of the appealing attributes of the new method is that it allows the use of different mammal groups (micromammals, macromammals, rodents, etc.) to obtain comparable results. The present results indicate that the bioclimatic method for palaeoenvironmental inference will allow us to improve our knowledge of climatic events that happened in past times (Neogene–Quaternary).

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**Appendix I** Characteristics of studied localities (Cl., climate zone)

N	Cl.	Locality	Country	Latitude	Longitude	Altitude	References
1	IX	Barrow	USA	71°18' N	156°47' W	7 m	Hall, 1981
2	IX	Port Harrison	Canada	58°27' N	78°08' W	6 m	Hall, 1981
3	IX	Malye-Karmaerly	Russia	72°23' N	52°44' E	16 m	Corbet, 1978
4	IX	Mys Chelyuskin	Russia	77°43' N	104°17' E	6 m	Corbet, 1978
5	IX	Mys Schmidta	Russia	68°55' N	179°17' E	6 m	Corbet, 1978
6	VIII	Fairbanks	USA	64°49' N	147°52' W	133 m	Hall, 1981
7	VIII	Fort Smith	Canada	60°01' N	11°58' W	62 m	Hall, 1981
8	VIII	Kajaani	Finland	64°17' N	27°41' E	134 m	Corbet, 1978
9	VIII	Serov	Russia	59°36' N	60°32' E	132 m	Corbet, 1978
10	VIII	Erbogachen	Russia	61°16' N	108°01' E	287 m	Corbet, 1978
11	VII	Rapid City	USA	44°02' N	103°03' W	965 m	Hall, 1981
12	VII	Puerto Santa Cruz	Argentina	50°01' S	68°32' W	12 m	Redford & Eisenberg, 1992
13	VII	Fort Schevchenko	Kazakhstan	44°33' N	50°17' E	23 m	Corbet, 1978
14	VII	Urumchi	China	43°47' N	87°37' E	912 m	Corbet, 1978
15	VII	Paotou	China	40°34' N	109°50' E	1044 m	Corbet, 1978
16	VI	Prince Rupert	Canada	54°17' N	136°23' W	16 m	Hall, 1981
17	VI	Cleveland	USA	41°24' N	81°51' W	237 m	Hall, 1981
18	VI	Evangelistas	Chile	52°24' S	75°06' W	55 m	Redford & Eisenberg, 1992
19	VI	Vlissingen	Holland	51°27' N	3°36' E	12 m	Corbet, 1978
20	VI	Tsingtao	China	36°04' N	120°19' E	77 m	Corbet, 1978
21	V	New Orleans	USA	29°57' N	90°04' W	3 m	Hall, 1981
22	V	Puerto Montt	Chile	41°28' S	72°57' W	13 m	Redford & Eisenberg, 1992
23	V	Corrientes	Argentina	27°28' S	58°49' W	60 m	Redford & Eisenberg, 1992
24	V	Foochow	China	26°05' N	119°18' E	88 m	Corbet & Hill, 1992
25	V	Kagoshima	Japan	31°34' N	130°33' E	4 m	Corbet, 1978
26	IV	Fresno	USA	36°46' N	119°42' W	100 m	Hall, 1981
27	IV	Santiago de Chile	Chile	33°27' S	70°42' W	520 m	Redford & Eisenberg, 1992
28	IV	Sanlucar de Barrameda	Spain	36°47' N	6°21' W	30 m	Corbet, 1978
29	IV	Aleppo	Syria	36°11' N	37°13' E	395 m	Corbet, 1978
30	IV	Esfahan	Iran	32°37' N	51°40' E	1598 m	Corbet, 1978
31	III	Phoenix	USA	33°26' N	112°01' W	340 m	Hall, 1981
32	III	Arica	Chile	18°28' S	70°22' W	29 m	Redford & Eisenberg, 1992
33	III	Assuan	Egypt	23°58' N	33°40' E	194 m	Corbet, 1978
34	III	Mascate	Oman	23°37' N	58°35' E	4 m	Corbet, 1978

**Appendix I** *continued.*

N	Cl.	Locality	Country	Latitude	Longitude	Altitude	References
35	III	Lüderitz Bay	Namibia	26°38' S	15°06' E	23 m	Kingdon, 1971–82; Nowak, 1991; Dorst & Dandelot, 1973
36	II/III	Las Piedras	Venezuela	11°42' N	70°12' W	15 m	Eisenberg, 1989
37	II/III	Catamarca	Argentina	28°26' S	65°46' W	547 m	Redford & Eisenberg, 1992
38	II/III	Zinder	Niger	13°48' N	8°59' E	510 m	Kingdon, 1971–82; Nowak, 1991; Dorst & Dandelot, 1973
39	II/III	Voi	Kenya	3°24' S	38°34' E	560 m	Kingdon, 1971–82
40	II/III	Jaipur	India	26°49' N	75°48' E	390 m	Corbet & Hill, 1992
41	II	Roque Saenz Peña	Argentina	26°49' S	60°27' W	92 m	Redford & Eisenberg, 1992
42	II	Ziguinchor	Senegal	12°35' N	16°16' W	10 m	Kingdon, 1971–82; Nowak, 1991; Dorst & Dandelot, 1973
43	II	Moundou	Chad	8°37' N	16°04' E	420 m	Kingdon, 1971–82; Nowak, 1991; Dorst & Dandelot, 1973
44	II	Mtwara	Tanzania	10°16' S	40°16' E	113 m	Kingdon, 1971–82
45	II	Patna	India	25°37' N	85°10' E	53 m	Corbet & Hill, 1992
46	I	Tumaco	Colombia	1°49' N	78°47' W	4 m	Eisenberg, 1989
47	I	Paramaribo	Surinam	5°51' N	55°10' W	3 m	Eisenberg, 1989
48	I	Kribi	Cameroon	2°57' N	9°54' E	624 m	Kingdon, 1971–82; Nowak, 1991; Dorst & Dandelot, 1973
49	I	Yangambi	Zaire	0°49' N	24°29' E	487 m	Kingdon, 1971–82; Nowak, 1991; Dorst & Dandelot, 1973
50	I	Medan	Indonesia	3°40' N	98°35' E	14 m	Corbet & Hill, 1992

**Appendix 2** Bioclimatic characterization of one of the localities studied in this paper, Fort Smith (North-west Territories, Canada). For explanation see the text (0.000, species do not inhabit the climate zone; rest of the values represent  $CRI = 1/n$ ; BC, bioclimatic component value; S, locality species number; i, climate i)

Species	CRI									
	I	II	II/III	III	IV	V	VI	VII	VIII	IX
<i>Sorex arcticus</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.000	0.000
<i>Sorex cinereus</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.250	0.250	0.250	0.250
<i>Sorex hoyi</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.500	0.000	0.500	0.000
<i>Sorex monticolus</i>	0.000	0.000	0.333	0.000	0.000	0.000	0.333	0.000	0.333	0.000
<i>Sorex palustris</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.500	0.000	0.500	0.000
<i>Myotis lucifugus</i>	0.000	0.000	0.143	0.143	0.143	0.143	0.143	0.143	0.143	0.000
<i>Alopex lagopus</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.500	0.500
<i>Canis latrans</i>	0.000	0.143	0.143	0.143	0.143	0.000	0.143	0.143	0.143	0.000
<i>Canis lupus</i>	0.000	0.111	0.111	0.111	0.111	0.111	0.111	0.111	0.111	0.111
<i>Vulpes vulpes</i>	0.000	0.000	0.000	0.143	0.143	0.143	0.143	0.143	0.143	0.143
<i>Lynx canadensis</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.250	0.250	0.250	0.250
<i>Puma concolor</i>	0.111	0.111	0.111	0.111	0.111	0.111	0.111	0.111	0.111	0.000
<i>Lontra canadensis</i>	0.000	0.000	0.000	0.000	0.200	0.200	0.200	0.200	0.200	0.000
<i>Mephitis mephitis</i>	0.000	0.000	0.143	0.143	0.143	0.143	0.143	0.143	0.143	0.000
<i>Gulo gulo</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.333	0.000	0.333	0.333
<i>Martes americana</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.500	0.000	0.500	0.000
<i>Martes pennanti</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.500	0.000	0.500	0.000
<i>Mustela erminea</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.250	0.250	0.250	0.250
<i>Mustela nivalis</i>	0.000	0.000	0.000	0.000	0.200	0.000	0.200	0.200	0.200	0.200
<i>Mustela vison</i>	0.000	0.000	0.000	0.000	0.200	0.200	0.200	0.200	0.200	0.000
<i>Ursus americanus</i>	0.000	0.000	0.143	0.143	0.143	0.143	0.143	0.143	0.143	0.000
<i>Ursus arctos</i>	0.000	0.000	0.000	0.000	0.250	0.000	0.250	0.250	0.250	0.000
<i>Alces alces</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.000	0.000
<i>Odocoileus hemionus</i>	0.000	0.000	0.167	0.167	0.167	0.000	0.167	0.167	0.167	0.000
<i>Odocoileus virginianus</i>	0.143	0.143	0.143	0.143	0.000	0.143	0.143	0.143	0.000	0.000
<i>Rangifer tarandus</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.500	0.500
<i>Bison bison</i>	0.000	0.000	0.000	0.000	0.000	0.250	0.250	0.250	0.250	0.000
<i>Marmota monax</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.500	0.000	0.500	0.000
<i>Tamias minimus</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.500	0.500	0.000
<i>Tamiasciurus hudsonicus</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.500	0.000	0.500	0.000
<i>Glaucomys sabrinus</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.500	0.000	0.500	0.000
<i>Castor canadensis</i>	0.000	0.000	0.000	0.000	0.200	0.200	0.200	0.200	0.200	0.000
<i>Zapus hudsonius</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.333	0.333	0.333	0.000
<i>Clethrionomys gapperi</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.333	0.333	0.333	0.000
<i>Microtus pennsylvanicus</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.333	0.333	0.333	0.000
<i>Microtus xanthognathus</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.000	0.000
<i>Ondatra zibethicus</i>	0.000	0.000	0.000	0.000	0.000	0.250	0.250	0.250	0.250	0.000
<i>Phenacomys ungava</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.000	0.000
<i>Synaptomys borealis</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.000	0.000
<i>Peromyscus maniculatus</i>	0.000	0.000	0.167	0.167	0.167	0.000	0.167	0.167	0.167	0.000
<i>Erethizon dorsatum</i>	0.000	0.000	0.200	0.200	0.000	0.000	0.200	0.200	0.200	0.000
<i>Lepus americanus</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.500	0.000	0.500	0.000
<b>Sum of CRI <math>\Sigma CRI_i</math></b>	0.254	0.508	1.803	1.613	2.320	2.037	9.579	5.413	15.937	2.537
<b>Bioclimatic spectrum</b>										
<b><math>BC_i = (\Sigma CRI_i) 100/S</math></b>	<b>0.605</b>	<b>1.209</b>	<b>4.293</b>	<b>3.840</b>	<b>5.523</b>	<b>4.849</b>	<b>22.808</b>	<b>12.887</b>	<b>37.944</b>	<b>6.041</b>
<b>Bioclimatic components</b>										

**Appendix 3** Whole mammal faunas discriminant analysis results for all 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)

N	Climate zone	Locality	Country	Highest probability climate zone	$P_1$	2nd highest probability climate zone	$P_2$
1	IX	Barrow	USA	IX	1.0000	=	
2	IX	Port Harrison	Canada	IX	1.0000	=	
3	IX	Malye-Karmaerly	Russia	IX	1.0000	=	
4	IX	Mys Chelyuskin	Russia	IX	1.0000	=	
5	IX	Mys Schmidta	Russia	IX	1.0000	=	
6	VIII	Fairbanks	USA	VIII	1.0000	VI	0.0000
7	VIII	Fort Smith	Canada	VIII	1.0000	VI	0.0000
8	VIII	Kajaani	Finland	VIII	1.0000	VI	0.0000
9	VIII	Serov	Russia	VIII	1.0000	VI	0.0000
10	VIII	Erbogachen	Russia	VIII	1.0000	=	
11	VII	Rapid City	USA	VII	0.9404	VI	0.0596
12	VII	Puerto Santa Cruz	Argentina	VII	0.9999	VI	0.0001
13	VII	Fort Schevchenko	Kazakhstan	VII	1.0000	VI	0.0000
14	VII	Urumchi	China	VII	1.0000	VI	0.0000
15	VII	Paotou	China	VII	1.0000	=	
16	VI	Prince Rupert	Canada	VI	0.6717	VIII	0.3283
17	VI	Cleveland	USA	VI	1.0000	VIII	0.0000
18	VI	Evangelistas	Chile	VI	1.0000	VII	0.0000
19	VI	Vlissingen	Holland	VI	1.0000	VIII	0.0000
20	VI	Tsingtao	China	VI	1.0000	VII	0.0000
21	V	New Orleans	USA	V	1.0000	=	
22	V	Puerto Montt	Chile	V	1.0000	=	
23	V	Corrientes	Argentina	V	0.9953	II	0.0047
24	V	Foochow	China	V	1.0000	II	0.0000
25	V	Kagoshima	Japan	V	1.0000	VI	0.0000
26	IV	Fresno	USA	IV	1.0000	VI	0.0000
27	IV	Santiago de Chile	Chile	IV	1.0000	=	
28	IV	Sanlucar de Barrameda	Spain	IV	1.0000	=	
29	IV	Aleppo	Syria	IV	1.0000	=	
30	IV	Esfahan	Iran	IV	1.0000	=	
31	III	Phoenix	USA	III	1.0000	VII	0.0000
32	III	Arica	Chile	III	1.0000	=	
33	III	Assuan	Egypt	III	1.0000	=	
34	III	Mascate	Oman	III	1.0000	=	
35	III	Lüderitz Bay	Namibia	III	1.0000	=	
36	II/III	Las Piedras	Venezuela	II/III	0.9981	II	0.0019
37	II/III	Catamarca	Argentina	II/III	1.0000	II	0.0000
38	II/III	Zinder	Niger	II/III	1.0000	II	0.0000
39	II/III	Voi	Kenya	II	0.9298	II/III	0.0702
40	II/III	Jaipur	India	II/III	1.0000	II	0.0000
41	II	Roque Saenz Peña	Argentina	II	1.0000	II/III	0.0000
42	II	Ziguinchor	Senegal	II	0.9999	II/III	0.0001
43	II	Moundou	Chad	II	0.9999	II/III	0.0001
44	II	Mtwara	Tanzania	II	1.0000	II/III	0.0000
45	II	Patna	India	II	0.5906	II/III	0.4094
46	I	Tumaco	Colombia	I	1.0000	II/III	0.0000
47	I	Paramaribo	Surinam	I	1.0000	II/III	0.0000
48	I	Kribi	Cameroon	I	1.0000	=	
49	I	Yangambi	Zaire	I	1.0000	=	
50	I	Medan	Indonesia	I	1.0000	=	