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# The distribution patterns of reptiles in the Riff region, northern Morocco

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## Summary

A biogeographical classification of reptiles in the Riff region (northern Morocco, Africa) was carried out to look for shared distribution patterns, here termed chorotypes. Baroni-Urbani & Buser's similarity index was applied to the presence/absence data of reptiles in 10 × 10 km UTM (Universal Transverse Mercator) squares, and then UPGMA (Unweighted Pair-Group Method using arithmetic average) was used to classify the species. A probabilistic method was employed to assess the statistical significance of the groups obtained. An ordination method, the Canonical Correspondence Analysis, was also used to study the distribution of the reptiles within a continuous framework.

A gradual longitudinal replacement of reptile species was found throughout the Riff, with no sharp discontinuities for the distributions of most of the species. This may be due to the biogeographical northward movement of the Saharan boundaries, which have not yet reached biogeographical equilibrium. Thus, Saharan reptiles enter the Riff region from the east, through the lower basin of the River Moulouya.

Seven reptile chorotypes were identified in the Riff, and these comprise Mediterranean species and others endemic to the Maghreb (the region that spans most of North-western Africa, excluding the Sahara). These chorotypes have a western distribution, and are segregated from one another according to altitude. Historical and ecological processes can account for the distributions shared by these species, which have inhabited the Riff for longer than eastern reptiles.

*Key words:* biogeography, distribution, Morocco, reptiles, Sahara

## Résumé

Une classification biogéographique des reptiles a été réalisée dans la région du Riff, au nord du Maroc, pour étudier les schémas de distribution partagés, appelés ici chorotypes. On a appliqué l'index de Baroni-Urbani & Buser aux données sur la présence ou l'absence de reptiles dans des quadrilatères de 10 km/10 UTM (Universal Transverse Mercator), puis l'UPGMA (Unweighted Pair-Group Method using arithmetic Average) pour classifier chaque espèce. Une méthode de probabilité a été utilisée pour évaluer la signification statistique des groupes obtenus. Une méthode de classification, la Canonical Correspondence Analysis, fut aussi employée pour étudier la distribution des reptiles dans

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un cadre continu. On a découvert un remplacement longitudinal graduel des espèces de reptiles le long du Riff, sans discontinuité abrupte dans la distribution de la plupart des espèces. Ceci peut être dû au mouvement biogéographique vers le nord des limites sahariennes, qui n'ont pas encore atteint un équilibre biogéographique. Donc, les reptiles sahariens pénètrent dans le Riff par l'est, par le bas du bassin de la rivière Moulouya. On a identifié dans le Riff un total de sept chorotypes, et ceux-ci comprennent des espèces méditerranéennes et d'autres qui sont endémiques au Maghreb (la région qui couvre la plus grande partie du nord-ouest africain, à l'exclusion du Sahara). Ces chorotypes ont une distribution occidentale et sont séparés l'un de l'autre en fonction de l'altitude. Des processus historiques et écologiques peuvent avoir influencé les distributions partagées par ces espèces qui ont occupé le Riff depuis plus longtemps que les reptiles orientaux.

## Introduction

The Maghreb, the region that collectively spans most of North-western Africa, excluding the Sahara, has the highest percentage of endemic reptiles in the Mediterranean Basin (Busack, 1986; Saint-Girons, 1986). Within the Maghreb, the Riff (a compact mountain range in Northern Morocco), probably has the highest diversity of reptilian species (Fahd, 1993; Schleich, Kästle & Kabisch, 1996), although they are possibly the least known members of the Moroccan herpetofauna (Fahd & Pleguezuelos, 1992).

The biogeographical characteristics of the Riff mountains are of great interest due to the unusual geographical and climatic features of the region, and the variability of its landscape (Bons, 1973; Busack, 1986; Bennas, Sainz & Alba, 1992). The Riff has a close biogeographical relationship with the Iberian Peninsula, because the Betic-Riff massif acted as a continental bridge between Europe and Africa until 5 million years ago (Steininger, Rabeder & Rogl, 1985), allowing reptile fauna to cross from one continent to the other (Busack, 1986). At that time, the marine transgression that separated the Betic-Riff massif from the Atlas mountains (Maldonado, 1986) favoured the evolution of endemic reptiles.

The climate is also unusual in the Riff. Although the Riff mountains are not very high they represent the wettest zones, not only in Morocco, but also in the whole of North Africa. To the east, however, the influence of the Sahara extends to the Mediterranean border through a geographical depression. This implies an eastward longitudinal replacement of wet environments for arid ones, which strongly affects the faunal composition of the Riff.

Along this environmental gradient, some species may share distribution patterns and thereby constitute discontinuous biogeographical entities, named 'chorotypes' by Baroni-Urbani (1978). Alternatively, it is possible that the species are distributed independently and are therefore using the space as a continuum (see, for instance, McCoy, Bell & Walters, 1986; Austin & Smith, 1989). If the former is true, then classification methods are appropriate to study their biogeographical relations, but if the latter is true, then ordination methods are more suitable. Several recent techniques (McCoy *et al.*, 1986; Real, Vargas & Guerrero, 1992) help to distinguish between the two possibilities.

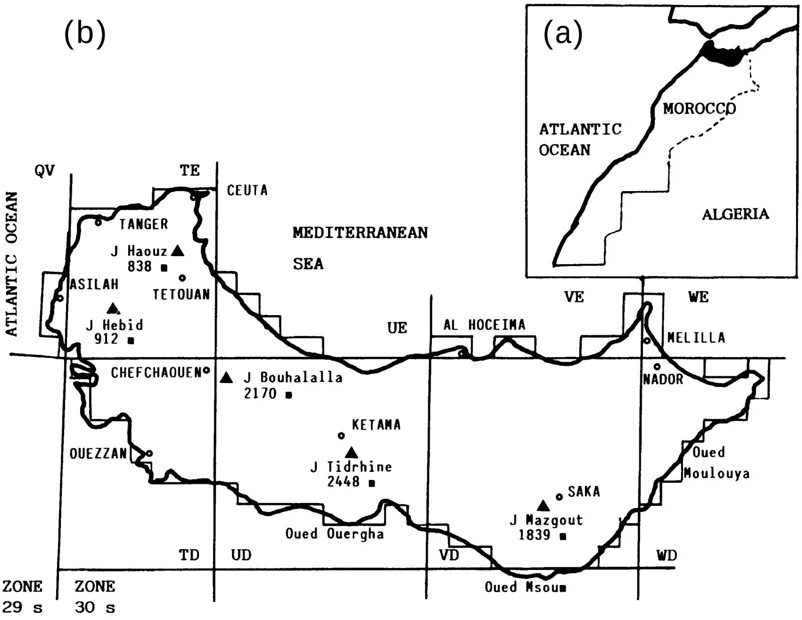

**Fig. 1.** Study area: (a) Location with respect to Morocco; (b) Riff region with the 100 × 100 km UTM grid, and the main geographical names.

The aim of this paper is to determine whether the reptilian fauna constitutes well established and discontinuous biogeographical entities along the Riff, which are here termed chorotypes, or whether there is a gradual replacement of reptile species from west to east. The possible causes of their biogeographical patterns are discussed, taking into account the geological history of the region, its climate, and the current characteristics of its landscape.

## Materials and methods

### *Study area*

The study area, located in Northern Morocco, occupies a geographical strip close to the Mediterranean Sea, 90 km wide from north to south and 340 km long from east to west, with an approximate area of 30,000 km$^2$ (Fig. 1). It roughly coincides geologically with the Riff Massif. The left side of the lower basin of the river Moulouya, also called the Eastern Riff, has also been included as several cases of allopatry between reptile species have been reported there (Caputo, 1993).

The climate of the Riff is influenced by the sea, both by the Atlantic Ocean and the Mediterranean Sea. The Atlantic side of the Riff is affected by heavy precipitation, with an average annual rainfall higher than 1000 mm. On the Mediterranean side, the precipitation is usually less than 500 mm annually, decreasing to less than 200 mm at some points in the Moulouya basin. The temperature range in the northern zone, influenced by the Mediterranean Sea, is lower than in the southern zone, which has a more continental climate (Maurer, 1968).

### *Sampling method*

We used 10 × 10 km UTM (Universal Transverse Mercator) squares as the geographical sampling unit. Nine expeditions were made to the study area from 1989 to 1993, totalling 54 sampling days (four observers per day). The unit of sampling effort was established as one observer in one biotope for 30 min. We also established a sampling effort of 4 h per square. Field data were obtained from 136 squares, as we did not sample those squares where the landscape had been strongly altered by humans.

In addition, published data were included (see revision in Fahd, 1993), and data from the following institutions' collections: Estación Biológica de Doñana, Seville; Museo Nacional de Ciencias Naturales, Madrid; Institute Scientifique, Rabat; Departamento de Biología Animal, Granada; Museum National d'Histoire Naturelle, Paris; Département de Biologie, Tétouan. Species not observed during the sampling carried out in the 1989–93 period were excluded from the analysis, as were those with a very restricted distribution in the study area (*Chalcides polylepis* Boulenger 1890; *C. mionecton* [Boettger 1874]; *C. mauritanicus* [Dumeril & Bibron 1839]; *Psammodromus microdactylus* [Boettger 1881]; *Acanthodactylus lineomaculatus* Duméril & Bibron 1839; *Eryx jaculus* [Linné 1758]). We also excluded squares from which we did not obtain data. The distribution maps of the species can be found in Fahd (1993) and Fahd & Pleguezuelos (1996).

After the field data were gathered, two new species belonging to the superspecies *Chalcides chalcides* Laurenti 1768 were described, *C. pseudostriatus* Caputo 1993 and *C. minutus* Caputo 1993 whose theoretical distribution ranges included our study area, (Caputo, 1993). As all the specimens we found are morphologically similar to the new species *C. pseudostriatus*, we provisionally consider that this is the only species of the complex *C. chalcides* that inhabits the study area (but see Mateo, Geniez & Bons, 1995). We also prefer the name *C. paralellus* instead of *C. ghiarai* Caputo & Mellado 1992 (Mateo *et al.*, 1995).

### *Statistical methods*

To classify the species according to their distribution, we applied the similarity index of Baroni-Urbani & Buser (1976) to each pair of species *a* and *b*:

$$B = \frac{\sqrt{C.D} + C}{\sqrt{C.D} + A + B + C},$$

where $A$ is the number of squares where only species $a$ is present, $B$ is the number of squares where only species $b$ is present, $C$ is the number of squares where both species are present, and $D$ is the number of squares from which both species are absent.

A dendrogram of the biogeographical relationship between the species was obtained applying the UPGMA (Unweighted Pair-Group Method using arithmetic Average) algorithm (Sneath & Sokal, 1973) to the matrix of values of Baroni-Urbani & Buser's similarity index. The statistical significance of each similarity value was calculated according to the statistical table in Baroni-Urbani & Buser (1976). In this way a matrix of significant similarities was obtained by substituting the similarity values with a '+', '0', or '−' when the similarities were, respectively, higher, similar, or lower than would be expected at random. The statistical significance of each group shown in the dendrogram was assessed by using the method of McCoy *et al.* (1986) as modified by Real *et al.* (1992a). For each comparison, we took a submatrix of significant similarities which we divided into three zones: zone A and zone B, corresponding to each group compared; and zone A × B corresponding to the intersection of both groups. When similarities higher than expected at random (+) tended to be located in zones A and B, but not in A × B, we considered that the groups belonged to two biogeographically segregated chorotypes. If, on the other hand, the similarities lower than expected ( − ) tended to be located in A × B, but not in A or in B, then we considered the two groups of species to be strongly segregated.

The parameters DW(A × A) and DW(B × B) measure the internal homogeneity of each group, whereas DS measures strong segregation between groups (see McCoy *et al.*, 1986). The statistical significance of the segregations between groups was assessed by independence analysis (*G*-test) of the distribution of the signs '+', ' − ', and '0' in each submatrix, yielding the parameters GW for weak segregation and GS for strong segregation. A group of species was considered to be a weakly segregated chorotype when $DW>0$ and GW was statistically significant, and a strongly segregated one when $DS>0$ and GS was statistically significant.

In addition, using CANOCO software (ter Braak, 1988a, 1988b) a Canonical Correspondence Analysis was performed (ter Braak, 1986) of the species according to their presence or absence at each sampling site, to place the species in a continuous sequence. We used the geographical longitude, latitude and elevation of each site as environmental variables, so that the axes of the Canonical Correspondence Analysis were lineal combinations of these variables.

## Results

Thirty-five species of reptiles were found in the Riff (see Appendix 1). The dendrogram in Fig. 2 shows the similarity between the species according to their geographical distributions. Table 1 shows the matrix of significant similarities between the distributions of the 35 reptile species. This table was divided into the different submatrices analysed to assess the statistical significance of the groups obtained in the dendrogram of Fig. 2. Table 2 shows the results obtained after the application of the method of McCoy *et al.* (1986) to each of the submatrices.

Only 13 species of reptiles can be considered as belonging to any of the seven chorotypes significantly segregated from the other species. The most numerous chorotype is composed of five species; two chorotypes of two species each; and four chorotypes of only one species. The other 22 species do not significantly aggregate with or segregate from these chorotypes, but are more or less related to the chorotypes in a gradual way, with no sharp discontinuities.

Chorotype I: *B. tingitanus*, *E. orbicularis*, *Ch. colosii*, *T. graeca* and *M. cucullatus*. Most of these species are typically Mediterranean reptiles. They have a western distribution in the Riff and inhabit sites at relatively high elevations, with the exception of *T. graeca*, which is found at low and medium elevations.

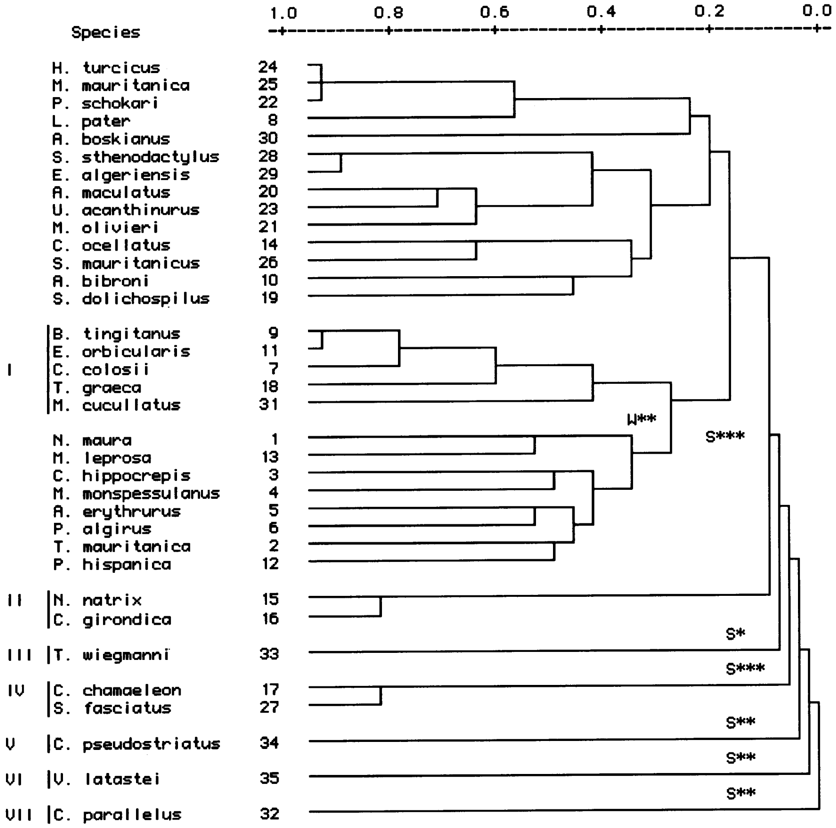

**Fig. 2.** Chorotypes detected in the study area according to the distribution of reptile species. S, Strong segregation; W, Weak segregation. *$P<0{\cdot}05$; **$P<0{\cdot}01$; ***$P<0{\cdot}005$.

Chorotype II: *N. natrix* and *C. girondica*. They are distributed at high elevations, that is, not under 1100 m for *N. natrix*, with *C. girondica* being more abundant between 1600 and 2000 m (Fahd, 1993). These are two typical Palearctic species that probably colonized Africa during the Messinian Period or a period prior to the formation of the Strait of Gibraltar. In the study area the distribution of these species is restricted to the continental islands formed by the mountain range of the Riff.

Chorotype III: *T. wiegmanni*. This species is endemic to the Maghreb, being discontinuously distributed over the study area.

Chorotype IV: *C. chamaeleon* and *S. fasciatus*. These species are Maghrebian reptiles characterized by the low altitude of their sampling sites, which are less than 600 m (Fahd, 1993).

Chorotype V: *C. pseudostriatus*. This is an Moroccan endemic species distributed in the study area in western localities of low elevation.

Chorotype VI: *V. latastei*. This is a Iberian-Riff species with a discontinuous distribution in the Riff, present mainly in western localities of high elevation.

Chorotype VII: *C. parallelus*. This reptile is also endemic to the Maghreb with a distribution limited to the eastern edge of the study area.

**Table 1.** Matrix of significant similarities between the distributions of the 35 reptile species observed in the Riff. Species numbers as in Fig. 2

| Species | 25 | 22 | 8 | 30 | 28 | 29 | 20 | 23 | 21 | 14 | 26 | 10 | 19 | 9 | 11 | 7 | 18 | 31 | 1 | 13 | 3 | 4 | 5 | 6 | 2 | 12 | 15 | 16 | 33 | 17 | 27 | 34 | 35 | 32 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 24 | + | + | 0 | + | − | − | 0 | + | − | 0 | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| 25 |  | + | 0 | − | − | − | − | − | − | 0 | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| 22 |  |  | 0 | − | − | − | 0 | − | + | + | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| 8 |  |  |  | − | − | − | − | − | − | − | − | − | − | 0 | 0 | 0 | − | 0 | − | − | 0 | − | 0 | − | − | − | − | − | − | 0 | 0 | − | − | − |
| 30 |  |  |  |  | − | − | 0 | + | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| 28 |  |  |  |  |  | + | + | 0 | + | 0 | + | 0 | − | − | − | − | 0 | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| 29 |  |  |  |  |  |  | 0 | − | − | − | − | − | − | − | − | − | + | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| 20 |  |  |  |  |  |  |  | + | + | + | 0 | 0 | 0 | − | − | 0 | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| 23 |  |  |  |  |  |  |  |  | + | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| 21 |  |  |  |  |  |  |  |  |  | + | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| 14 |  |  |  |  |  |  |  |  |  |  | + | 0 | 0 | − | − | 0 | − | − | − | − | 0 | − | − | − | − | − | − | − | 0 | − | − | − | − | − |
| 26 |  |  |  |  |  |  |  |  |  |  |  | − | − | − | − | − | 0 | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| 10 |  |  |  |  |  |  |  |  |  |  |  |  | − | − | − | − | 0 | − | − | − | − | − | 0 | − | 0 | − | − | − | − | − | − | − | − | − |
| 19 |  |  |  |  |  |  |  |  |  |  |  |  |  | − | − | − | − | − | 0 | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| 9 |  |  |  |  |  |  |  |  |  |  |  |  |  |  | + | + | + | + | 0 | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| 11 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | + | + | − | 0 | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| 7 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 0 | + | 0 | − | − | − | 0 | 0 | 0 | − | + | − | − | − | − | − | − | − |
| 18 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | − | 0 | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| 31 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| 1 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 0 | − | − | − | − | − | − | 0 | − | − | − | − | − | − | − |
| 13 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| 3 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 0 | 0 | − | − | 0 | − | − | − | − | − | − | − | − |
| 4 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | − | 0 | − | − | − | − | − | − | − | − | − | − |
| 5 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 0 | − | − | − | − | − | − | − | − | − | − |
| 6 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 0 | 0 | − | − | − | − | − | − | − | − |
| 2 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 0 | − | − | − | − | − | − | − | − |
| 12 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | − | − | − | − | − | − | − | − |
| 15 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | + | − | − | − | − | − | − |
| 16 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | − | − | − | − | − | − |
| 33 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | − | − | − | − | − |
| 17 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | + | − | − | − |
| 27 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | − | − | − |
| 34 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | − | − |
| 35 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | − |

+: Similarity significantly higher than random expectation; −: Similarity significantly lower than random expectation; 0: Similarity without significant difference with the random expectation.

**Table 2.** Statistical significance of the groups obtained in Fig. 2, according to the method of McCoy *et al.* (1986)

| Groups obtained by UPGMA | | | Aggregation | | Segregation | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | Weak | | Strong | | |
| Group A | Group B | Coefficient | DW(AxA) | DW(BxB) | GW | P | DS | GS | P |
| 9–7 | 18 | 0·562 | 0·209 | −0·498 | 0·002 | NS | −0·498 | 0 | NS |
| 24–22 | 8 | 0·538 | 0·7071 | 0 | 2·911 | NS | 0 | 0 | NS |
| 28–29 | 20–21 | 0·409 | 0·4157 | 0·4157 | 0·2918 | NS | 0 | 0·1961 | NS |
| 9–18 | 31 | 0·377 | 0·2561 | −0·3841 | 0·1145 | NS | 0 | 1·045 | NS |
| 14–26 | 10–19 | 0·315 | 0·7071 | −0·7071 | 0·1297 | NS | −0·2911 | 0·7134 | NS |
| 28–21 | 14–19 | 0·265 | 0·1799 | −0·4027 | 2·4148 | NS | −0·253 | 1·9609 | NS |
| 9–31 | 1–12 | 0·248 | 0·3837 | −0·5362 | 7·1295 | ** | −0·0896 | 6·0483 | * |
| 24–8 | 30 | 0·213 | 0·204 | −0·212 | 0·0021 | NS | 0·3352 | 3·1367 | NS |
| 24–30 | 28–19 | 0·155 | −0·0102 | −0·2291 | 5·6279 | * | −0·1469 | 12·1154 | *** |
| 24–19 | 9–12 | 0·141 | −0·3335 | −0·4818 | 32·8102 | *** | −0·4194 | 35·0324 | *** |
| 24–12 | 15–16 | 0·0648 | −0·5653 | 0·6892 | 1·8837 | NS | 0·0576 | 11·1514 | *** |
| 24–16 | 33 | 0·055 | −0·5623 | 0 | 1·3983 | NS | 0·0547 | 4·421 | * |
| 24–33 | 17–27 | 0·0457 | −0·5716 | 0·7071 | 4·2431 | * | 0·0509 | 9·6221 | *** |
| 24–27 | 34 | 0·0277 | −0·5846 | 0 | 1·2692 | NS | 0·0663 | 7·6389 | ** |
| 24–34 | 35 | 0·0257 | −0·5925 | 0 | 1·1895 | NS | 0·0618 | 7·2843 | ** |
| 24–35 | 32 | 0·0084 | −0·5996 | 0 | 1·1159 | NS | 0·0578 | 6·9569 | ** |

*$P<0·05$; **$P<0·01$; ***$P<0·005$; NS: Non significant.

The species *N. maura*, *M. leprosa*, *C. hippocrepis*, *M. monspessulanus*, *A. erythrurus*, *P. algirus*, *T. mauritanica* and *P. hispanica* do not aggregate significantly, but are more closely related to Chorotype I than to the other species (Fig. 2). On the other hand, the species *H. turcicus*, *M. mauritanica*, *P. schokari*, *L. pater*, *A. boskianus*, *S. sthenodactylus*, *E. algeriensis*, *A. maculatus*, *U. acanthinurus*, *M. olivieri*, *Ch. ocellatus*, *S. mauritanicus*, *A. bibroni* and *S. dolichospilus*, although not significantly aggregated, are more related to one another than to the rest of species (see Fig. 2).

The results of the CCA can be seen in Fig. 3. The species appearing in the upper left quadrant have an eastern distribution in the Riff. The species in the upper right quadrant have a high elevation distribution, and those that occur towards the right of this quadrant have a more westerly distribution. The rest of the species recorded have a low elevation distribution, and those shown towards the lower right side of the graph occupy a more westerly distribution.

## Discussion

### *The statistical significance applied to the classification method*

The method of McCoy *et al.* (1986) as modified by Real *et al.* (1992a) allowed us to distinguish between the significant chorotypes and the groups of species that are merely artefacts of the cluster analysis.

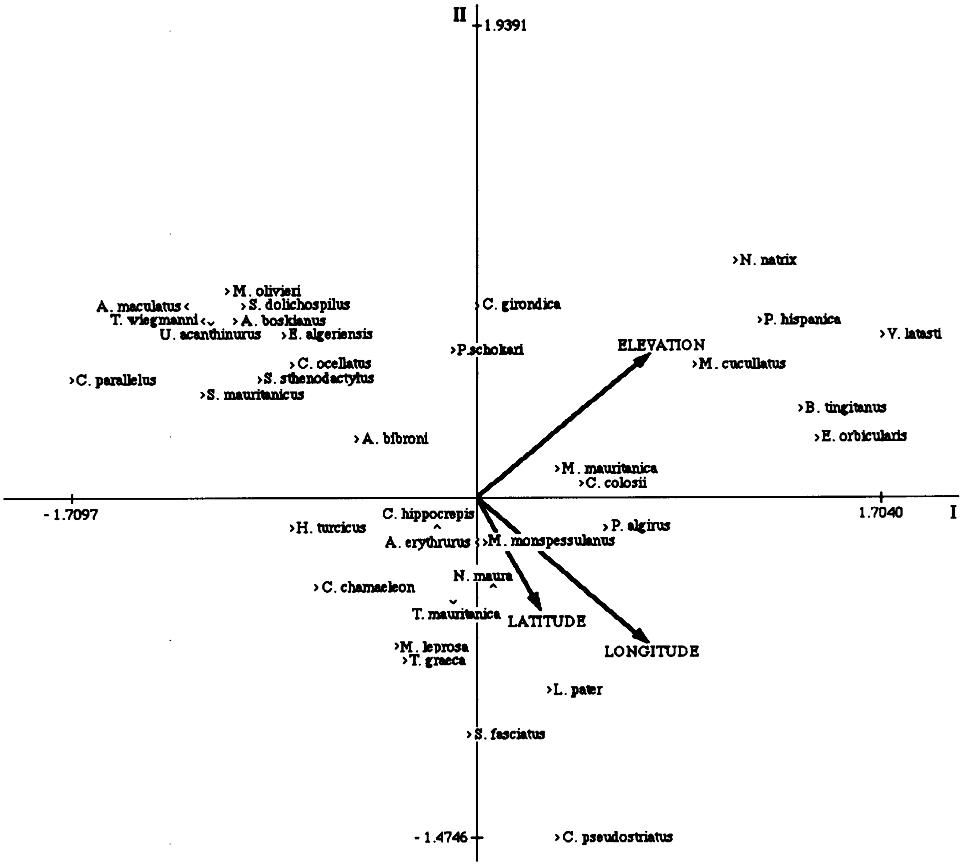

**Fig. 3.** Results of the Canonical Correspondence Analysis (CCA): species scores and biplot scores of geographical variables according to the presence of reptile species at each sampling point. Horizontal: axis 1; vertical: axis 2. ∧: score of the species whose name appears above; <: score of the species whose name appears on the left; >: score of the species whose name appears on the right; ∨: score of the species whose name appears below.

Whittaker (1975), Birks (1976), McCoy *et al.* (1986) and Belbin & McDonald (1993), among others, pointed out that some distortion is caused by the arbitrary assumption of a hierarchical structure in the data when using cluster analysis. This distortion can lead to the acceptance of artificial groups of species that do not correspond with what is actually found in nature (Vargas, 1993). Thus, the mere visual analysis of the groups of species appearing in a dendrogram does not indicate whether the groups are artificial or reflect natural phenomena.

In most studies, the groups are formed by dividing the dendrogram at an arbitrary level of similarity (see, for instance, Baroni-Urbani, 1978; Baroni-Urbani & Collingwood, 1976, 1977; Dzwonko & Kornas, 1978). However, the method of McCoy *et al.* (1986), as modified by Real *et al.* (1992a), has been used by Real, Guerrero & Ramírez (1992) for detecting biotic boundaries between biogeographic regions. In the present study, we have used this method in an analogous way for the detection of significant chorotypes. The main advantages of this method are that the necessary calculation is simple, and the significant groups are obtained on a probabilistic basis. Thus, the species are not considered as chorotypes when the relationships between their distributions is compatible with that expected at random.

### *The chorotypes of reptiles in the Riff*

Seven chorotypes were obtained, which included only thirteen species. These species can be considered to belong to discontinuous biogeographical entities, on the basis of their presence in the 10 × 10 km squares. These thirteen species have a mainly Mediterranean distribution or are Maghrebian endemics with peculiar distributions (with the exception of *E. orbicularis* and *N. natrix*, which have a wider distribution).

The chorotypes have a mainly western distribution in the Riff, and segregate from one another according to altitude. These western species have inhabited the Riff for longer than the eastern reptiles, and so historical and ecological processes can account for their shared distributions.

### *The gradual replacement of species*

Twenty-two species do not significantly aggregate or segregate from one other, or from the seven chorotypes. This may be due to the lack of biogeographical equilibrium of the Saharan species penetrating through the River Moulouya, as most of these 22 species are found in the eastern extreme of the Riff region (Fahd, 1993). In any case, the longitudinal replacement of species along the Riff has to be considered gradual in the main, with no sharp discontinuities for the majority of species. The biogeographical relationship between these 22 species and also their relationship with the previous seven chorotypes can only be analysed in a continuous framework.

The CCA enabled us to consider all the species as a whole, in a surface related to the geographical longitude and the elevation of the sampling site. Figure 3 shows a gradual eastward replacement of the European and Ibero-Berber fauna by Saharan fauna throughout the Riff region.

The species of the upper left quadrant of Fig. 3 inhabit arid environments with annual precipitation lower than 300 mm, mainly consisting of large plains with bare soil or covered only by stunted grassland and scrub. Most of these species are typically Saharan (*S. sthenodactylus*, *U. acanthinurus*, *A. boskianus*, *S. dolichospilus*) and their presence in northern latitudes close to the Mediterranean Sea was unknown until very recently (Géniez *et al.*, 1991; Fahd & Pleguezuelos, 1992; Mellado & Mateo, 1992). *E. algeriensis* shows a wide distribution in North Africa, from the Atlantic coast to Egypt and the Middle East (Levinton *et al.*, 1992), but in the Riff only the subspecies *E. a. meridionalis* Doumergue 1901 is found, which is typical of the most arid zones of eastern Morocco (Bons, 1967). Only a few kilometres south of the study area, but still within the Moulouya River basin, the Saharan species *Mesalina guttulata* (Lichtenstein 1823), *Eryx jaculus* and *Cerastes cerastes* (Linné 1758) are also present (Laurent, 1935; Bons, 1960; Mellado & Mateo, 1992).

Le Houerou (1992) reconstructed the progress of the limits of the Sahara desert from 18,000 years BC up to the present, studying the vegetation and the fossil dunes. He concluded that the northern limit of the desert has moved northwards, nearing the Mediterranean Sea. The lower basin of the River Moulouya has received annual precipitation of less than 200 mm during the last 16 years, close to the climatic limit of the Sahara Desert (Donadieu, 1977). Our results confirm a biogeographical northward movement of the Saharan limit, and show that this movement has probably not yet reached a biogeographical equilibrium. We consider that the Saharan reptiles must have colonized the eastern Riff from the Tafilalt, through the Rekkan plain and the Moulouya Valley (the 'Western Arid Steppe Zone' of Le Houerou, 1990), some of them doing this very recently (Fahd, 1993). Nowadays, these species are distributed between the eastern foothills of the Riff and the River Moulouya, an area consequently very rich in species (Fahd & Pleguezuelos, 1992).

Most of the species displayed in the other quadrants of Fig. 3 are typically Mediterranean, and occupy areas with annual precipitation exceeding 500 mm, with woodlands (*Quercus rotundifolia*, *Q. suber*, *Q. pyrenaica*, *Abies pinsapo*) or related types of ecological successions of vegetation. Many species are present on both sides of the Strait of Gibraltar (*E. orbicularis*, *T. graeca*, *P. hispanica*, *M. cucullatus*, *M. monspessulanus*, *C. hippocrepis*, etc.), or are represented in the Iberian Peninsula by a vicariant species (*B. tingitanus*–*B. cinereus*, *C. pseudostriatus*-*C. striatus*, *L. pater*–*L. lepida*). Some of these species might have originally inhabited the Betic-Riff Massif, but the opening of the Straits of Gibraltar, some 5 million years ago (Steininger *et al.* 1985), probably gave rise to allopatric speciation processes that eventually gave rise to the vicariant species. These species have the closest distribution to the Strait of Gibraltar. *Emys orbicularis*, with a wide Palearctic distribution, is only limited, in the study area, to the wettest environments of the western foothills of the Riff.

The species of the lower half of Fig. 3 (*H. turcicus*, *A. erythrurus*, *C. chamaeleon*) are mainly distributed on the northern slopes of the Riff mountains, in low elevation areas close to the coast, where the temperatures are mild (Maurer, 1968).

Thus, the distribution of two-thirds of the species may be explained either by the prior existence of a continental union between Europe and Africa or by the current penetration of aridity in the Mediterranean area through the Moulouya Valley (Fahd & Pleguezuelos, 1992, 1996; Fahd, 1993). The other species either have a wide distribution in North Africa, or are Maghrebian endemics. As a result, the Riff region has a high reptilian species richness (Fahd & Pleguezuelos, 1992) and a high rate of replacement of species in a limited geographical range, and so it is a suitable territory for further biogeographical analyses. In the future, we intend to study the environmental factors that affect the distribution of each species in this region, and to explain in environmental terms the longitudinal replacement of species.

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## Appendix 1

Reptile fauna found in the Riff region during the sampling period (1989–93).

CHELONIA
  Testudinidae
    *Testudo graeca graeca* (Linné 1758)
  Emydidae
    *Mauremys leprosa* (Schweigger 1812)
    *Emys orbicularis* (Linné 1758)

AMPHISBAENIA
  Amphisbaenidae
    *Blanus tingitanus* Busack, 1988
  Trogonophidae
    *Trogonophis wiegmanni wiegmanni* Kaup, 1830
    *Trogonophis wiegmanni elegans* (Gervais 1835)

SAURIA
  Gekkonidae
    *Hemidactylus turcicus turcicus* (Linné 1758)
    *Saurodactylus mauritanicus mauritanicus* (Duméril & Bibron 1836)
    *Saurodactylus fasciatus* Werner, 1931
    *Stenodactylus sthenodactylus mauritanicus* Guichenot, 1850
    *Tarentola mauritanica mauritanica* (Linné 1758)
  Agamidae
    *Agama bibroni* Duméril, 1851
    *Uromastix acanthinurus acanthinurus* Bell, 1825

Chamaeleonidae
  *Chamaeleo chamaeleon chamaeleon* (Linné 1758)
Scincidae
  *Chalcides pseudostriatus* Caputo, 1993
  *Chalcides colosii* Lanza, 1957
  *Chalcides ocellatus subtypicus* Werner, 1931
  *Chalcides parallelus* (Doumergue 1901)
  *Eumeces algeriensis algeriensis* Peters, 1864
Lacertidae
  *Acanthodactylus boskianus* (Daudin 1802)
  *Acanthodactylus erythrurus belli* Gray, 1845
  *Acanthodactylus maculatus* (Gray 1838)
  *Lacerta pater tangitana* (Boulenger 1887)
  *Mesalina olivieri olivieri* (Audouin 1829)
  *Podarcis hispanica vaucheri* (Boulenger 1905)
  *Psammodromus algirus algirus* (Linné 1758)

SERPENTES
Colubridae
  *Coluber hippocrepis hippocrepis* Linné, 1758
  *Coronella girondica* (Daudin 1803)
  *Macroprotodon cucullatus brevis* (Günther 1862)
  *Malpolon monspessulanus monspessulanus* (Hermann 1804)
  *Natrix maura* (Linné 1758)
  *Natrix natrix astreptophora* (Seoane 1884)
  *Psammophis schokari* (Forsskal 1775)
  *Spalerosophis dolichospilus* (Werner 1923)
Viperidae
  *Vipera latastei gaditana* Saint-Girons, 1977
  *Macrovipera mauritanica* (Gray 1849)