CONTRIBUTION TO THE SYSTEMATICS OF THE LIZARD ACANTHODACTYLUS ERYTHRURUS (SAURIA, LACERTIDAE) IN MOROCCO

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We have analysed several scalation characters and the geographic distribution of lizards of the Acanthodactylus erythrurus group to verify the validity of these criteria. These data are collated with biogeography to demonstrate the existence of two distinct species within what are known as common fringe-toed lizards: Acanthodactylus erythrurus, consisting of three subspecies, and Acanthodactylus lineomaculatus, monotypic and endemic to Morocco. Hypotheses concerning the population history of these animals are proposed.

INTRODUCTION

At the beginning of the last century common fringe-toed lizards were described from Europe (Lacerta erythrura Schinz 1833, and Acanthodactylus vulgaris Duménil & Bibron 1839) and from North Africa (Acanthodactylus lineomaculatus Duménil & Bibron 1839). Since then, they have been the subject of many investigations. Boulenger’s revision in 1878 was the first attempt to introduce some order to the genus Acanthodactylus, often considered as one of the most difficult in the Palearctic. The increase in the number of specimens collected, and the use of often contradictory terminology by different authors, led Salvador (1982) and Arnold (1983) to make a revision of the numerous species that this genus comprises and to clarify the phylogensis. Other authors have confined their research to a single group, e.g. Squalli-Houssaini (1991) on the fringe-toed lizards of the erythrurus group.

Since we had access to abundant material from North Africa and precise data on these animals’ ecology and distribution in Morocco, our intention was to readdress the problem, restricting our analysis to certain scalation characters that, in our opinion, are discriminative. These characters were then collated with the ecological and biogeographical characteristics of the populations being studied. We restricted our study to the different forms of the common fringe-toed lizard in Morocco because it is the country where the widest diversity of forms and habits is found.

The common fringe-toed lizard, Acanthodactylus erythrurus (Schinz 1833), is the only representative of the genus occurring in Europe, where it is confined to the southern two thirds of the Iberian Peninsula, extending its range as far north as Gerona (Barbadillo Escriva, 1987), Zaragoza, Burgos (old record) and Leon (old record) (Salvador in Böhme, 1981). It is also the only fringe-toed lizard to occupy the whole of Morocco, north and west of the Atlas. This distribution stretches eastwards along a large part of the Algerian coast. However, it does not appear to be known from Tunisia.

Morphologically, it is characterised by the presence of three complete rows of scales round the fingers and small dorsal scales, either keeled or unkeeled, on the back, with the underside of the tail bright red in juveniles and subadults. The combination of these three characters distinguishes Acanthodactylus erythrurus within the genus. Three subspecies have been recognised in Morocco (Pasteur & Bons, 1960; Bons & Girot, 1962):

— ssp. belli Gray 1845, in the Rif, on the coast and plateaux east of the Altasles, the southern slopes of the High Atlas and the far west of the Anti-Atlas (this subspecies is the only representative of Acanthodactylus erythrurus in Algeria; Salvador, 1982).


— ssp. lineomaculatus Duménil & Bibron 1839, on the Atlantic coast from Tangiers to Essaouira (endemic to Morocco).

The nominate subspecies is confined to the Iberian peninsula.

The two recent revisers of the genus, Salvador (1982) and Arnold (1983), do not retain the subspecies atlanticus. They consider it as intermediate between A. erythrurus belli and A. erythrurus lineomaculatus. Whereas Squalli Houssaini (1991), without adopting a definite position, considers that the Moroccan subspecies have little taxonomic value and are only a reflection of their distribution, and that the Iberian fringe-toed lizards are sufficiently differentiated from their Moroccan counterparts to merit a distinct specific status.

MATERIALS AND METHODS

We examined 496 Moroccan individuals from 22 localities, or groups of localities, throughout the country. For comparative purposes, we added 11 individuals
from Andalusia (Spain) (Fig. 1). The samples varied in size depending on the localities, ranging from 1 to 69 specimens (average: 22.55). The examined samples are as follows:

<table>
<thead>
<tr>
<th>Location</th>
<th>Number of Individuals</th>
</tr>
</thead>
<tbody>
<tr>
<td>MOROCCO</td>
<td></td>
</tr>
<tr>
<td>Larache</td>
<td>(47 individuals)</td>
</tr>
<tr>
<td>Mehdia, Kenitra</td>
<td>(36 individuals)</td>
</tr>
<tr>
<td>Mamora Forest</td>
<td>(41 individuals)</td>
</tr>
<tr>
<td>Rabat-Agdal</td>
<td>(55 individuals)</td>
</tr>
<tr>
<td>Temara, Sables d’or</td>
<td>(14 individuals)</td>
</tr>
<tr>
<td>Zafr Forest</td>
<td>(47 individuals)</td>
</tr>
<tr>
<td>Casablanca</td>
<td>(47 individuals)</td>
</tr>
<tr>
<td>Doukkala</td>
<td>(4 individuals)</td>
</tr>
<tr>
<td>Essaouira</td>
<td>(6 individuals)</td>
</tr>
<tr>
<td>Region of Lakes</td>
<td>(5 individuals)</td>
</tr>
<tr>
<td>Ifrane</td>
<td>(34 individuals)</td>
</tr>
<tr>
<td>Azrou</td>
<td>(17 individuals)</td>
</tr>
<tr>
<td>Tioumliline, Agdal Plateau</td>
<td>(9 individuals)</td>
</tr>
<tr>
<td>Tarmilale, Oulmes</td>
<td>(69 individuals)</td>
</tr>
<tr>
<td>Haouz, Marrakech</td>
<td>(3 individuals)</td>
</tr>
<tr>
<td>Rif</td>
<td>(18 individuals)</td>
</tr>
<tr>
<td>Eastern Morocco</td>
<td>(13 individuals)</td>
</tr>
<tr>
<td>Eastern High Atlas</td>
<td>(13 individuals)</td>
</tr>
<tr>
<td>Jbel Saghro</td>
<td>(4 individuals)</td>
</tr>
<tr>
<td>40 km W. of Tazenakht</td>
<td>(11 individuals)</td>
</tr>
<tr>
<td>Jbel Siroua</td>
<td>(2 individuals)</td>
</tr>
<tr>
<td>Oued Noun</td>
<td>(1 individual)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Location</th>
<th>Number of Individuals</th>
</tr>
</thead>
<tbody>
<tr>
<td>SPAIN</td>
<td></td>
</tr>
<tr>
<td>Benidorm</td>
<td>(1 individual)</td>
</tr>
<tr>
<td>Almeria</td>
<td>(2 individuals)</td>
</tr>
<tr>
<td>Huescar</td>
<td>(2 individuals)</td>
</tr>
<tr>
<td>Torre de la Higuera</td>
<td>(3 individuals)</td>
</tr>
<tr>
<td>unknown locality</td>
<td>(3 individuals)</td>
</tr>
</tbody>
</table>

Five scale characters were monitored: (1) dorsal scales strongly keeled or not; (2) position of the subocular in relation to the edge of the upper lip; (3) number of scales and granules arising from the fragmentation of the first supraocular, right and left; (4) number of interfrontal granules; and (5) internasal divided or not.

We then compared the percentage of individuals within each population that presented different configurations of each character.

The specimens examined come from the collection of the Laboratoire de Biogéographie et Ecologie des Vertébrés de l’E.P.H.E., Montpellier, France. The results of these examinations were collated with numerous observations made in the field in Morocco and the Iberian Peninsula.
RESULTS

The results of the pholidotic analyses are ordered according to scale characters.

DORSAL SCALATION (FIG. 2)

An examination of the dorsal scales reveals a partition of our samples into two groups: (1) lizards from the Atlantic coastal area, between Tangiers and Essouira, possess strongly and sharply keeled dorsal scales, starting on the back and sides of the neck; (2) lizards from all other localities (Morocco and Spain) possess smooth scales on the anterior part of the back. In some populations they become tectiform or weakly keeled at the rear of the back.

We did not observe any individuals presenting intermediate characters between these two types of scalation, nor any mixed populations. Consequently, strongly keeled dorsal scales make it possible to distinguish with certainty Atlantic coast animals from all the other common fringe-toed lizards examined from Morocco and Spain. A later examination of a sample (c. 30 individuals) from the Aures in Algeria, put at our disposal by Laurent Chirio, also confirmed our findings for Algeria.

POSITION OF THE SUBOCULAR (FIG. 3)

Four positions of this scale in relation to the upper lip were observed. This is the most commonly used character for the recognition and distinction of the North African subspecies (Bons & Girot, 1962).

Position 1: The subocular is wedged between the 4th and 5th upper labials, but does not touch the lip (labials 4 and 5 are still in contact). This is characteristic of the form lineomaculatus.

Position 2: The subocular is separated from the lip by a small trapezoidal scale that appears to result from the fragmentation of the 4th supralabial.

Position 3: The subocular is separated from the lip by a small "independent" rectangular scale. This position is characteristic of the form atlanticus.

Position 4: The subocular is in wide or narrow contact with the upper lip. This subocular/edge of lip contact is characteristic of the form beli.

The analysis of our samples shows that only animals from the Rif, the southern slopes of the High Atlas and the east of Morocco are 100% consistent with position 4.

Position 3 is characteristic of animals from the Middle Atlas and the Haouz plain, in percentages varying from 87 to 100%. The other situations are infrequent in these regions: 0 to 8.7% of position 1, 0 to 20% of position 4.

The coastal animals are distributed along a band running north-east/south-west. In localities north of Rabat they mostly (75 to 95%) possess a small trapezoidal upper labial (position 2) that is usually absent (57.1 to 95%) in specimens from south of Rabat (position 1).

Consequently the traditional criterion of the position of the subocular used to distinguish subspecies of Acanthodactylus erythrurus should be used with care. Position 4 certainly enables animals from the Rif, eastern Morocco, the southern slopes of the High Atlas and the far west of the Anti-Atlas, (i.e. belonging to the subspecies beli), to be identified unequivocally. However, positions 1 and 3, that were traditionally used to identify respectively the lineomaculatus and atlanticus forms, are not absolute and cannot be used for the determination of all individuals.

Position 3 (small rectangular supralabial) is peculiar to the form atlanticus, but a small percentage of individuals from the Middle Atlas present situations 1 and 4.
Position 1, characteristic of *lineomaculatus*, can be used to identify a large proportion of animals from the Atlantic coastal area south of Rabat, but becomes infrequent north of Rabat. It is replaced by position 2 (fragmented supralabial), a configuration that may sometimes be confused with position 3.

SUPRAOCULAR SHIELDS (FIG. 4)

The genus *Acanthodactylus* is characterized by the presence of four large supraocular shields that have a tendency to fragmentation. In common fringe-toed lizards, only shields 2 and 3 remain entire, while the 4th, and to a lesser extent the 1st, are fragmented into granules or small scales.

The Atlantic samples are the most affected by this fragmentation, since between 85.7% and 100% of specimens, depending on localities, have the 1st supraocular fragmented into over five scales and granules on at least one side. (From 50 to 100% of individuals possess over five scales in the place of the 1st supraocular on both sides).

In samples from the Rif, the Atlases, western Morocco and Iberia, the 1st supraocular is nearly always fragmented into fewer than six scales on both sides (from 76.9 to 100% of individuals, depending on localities).

The division of the 1st supraocular into more than five fragments is an identifying feature for individuals from the Atlantic coast. However, this situation is also found, though in very low percentages, in Andalusia, the Rif, the Middle Atlas and the East.

EXISTENCE OF INTERPREFONTAL GRANULES (FIG. 5)

In some fringe-toed lizards, one or several granules are intercalated between the prefrontal scales. These granules exist in 75 to 95.8% of individuals from the Atlantic coast, except those from the extreme north (Mehdiya, 47.2%; Larache, 25%).

On the other hand, the absence of interprefrontal granules is the most common situation in animals from the rest of Morocco and Andalusia (80 to 100% of individuals, depending on localities, with values always higher than in the Atlantic localities). Some animals from the Rif, the Middle Atlas, the East and Spain have one granule (5.9 to 20% of individuals depending on localities), while it is absent in all specimens examined from the High Atlas, Haouz and the far west of the Anti-Atlas.

The presence of one or two interprefrontal granules, characteristic of the form *lineomaculatus*, is therefore predominant in animals from the coast south of Rabat and infrequent in the north. It is rare or exceptional in animals from other areas.

DIVISION OF THE INTERNASAL (FIG. 6)

The division of the internasal is a recognition character of the subspecies *lineomaculatus*.

With the exception of those from the extreme north (Larache and Mehdiya), the majority of individuals from the Atlantic coast have a divided internasal (66.7 to 85.7%, depending on localities), whereas the other populations show few cases of internasal division (Middle Atlas, 2.9 to 5.9%, depending on localities), or none (Anti-Atlas, High Atlas, Haouz, Rif, East and Spain).

All the fringe-toed lizards from the Atlantic coast between Tangiers and Essaouira, i.e. those that always present strongly keeled scales, when compared to the other forms, also have a much more pointed snout, a more slender head, a sharper angle between the pileus and the cheeks, more angular lateral edges to the frontal, which is markedly concave, and variably keeled temporal scales. Squalli-Houssaini (1991) adds other distinctive characters such as the number of rows of supraciliary granules (two for *lineomaculatus*, one for the other taxa of the group), and the frequent pres-
Acanthodactylus erythrurus that it is not recognised by Salvador (1982) and Arnold (1983). The absence of intermediate animals may mean that the supposed contacts do not exist, the two subspecies being allopatric in the southern part of their range.

We have no knowledge of contacts between atlanticus and belli along the ridge of the High Atlas, even though the two subspecies are separated by only a few kilometres. The very high altitude of the High Atlas mountains may mean that the supposed contacts do not exist, the two subspecies being allopatric in the southern part of their range. We know several areas where populations of lineomaculatus and belli or atlanticus live in immediate proximity. No morphologically intermediate animals have been observed. This apparent absence of intermediates between the two forms, together with diagnostic morphological differences (dorsal scalation, head shape) and other important differences (position of subocular, divided internasal, shape of frontal) indicate that we are dealing with two distinct species: Acanthodactylus lineomaculatus on the one hand, and Acanthodactylus erythrurus, represented in Maghreb by the subspecies belli and atlanticus, on the other.

Within the range of Acanthodactylus lineomaculatus, disparity in several characters is observed between animals from south of Rabat and those from the north: divided internasal, number of interprefrontal granules, fragmented 4th supralabial. However these variations are of a clinal nature, with the transition consisting of a progressive inversion of frequency, so the town of Rabat is only a reference mark. Consequently, it is impossible to establish the existence of two subspecies for A. lineomaculatus. Besides, other characters are invariant throughout the whole of this species range (keeled dorsal scales, slim pointed snout, concave frontal, strongly fragmented 1st supraocular), providing supplementary evidence for A. lineomaculatus specific status.

Of course, there are no contacts between the nominal subspecies, confined to the Iberian peninsula, and the other forms that are peculiar to the Maghreb. However, from a strictly morphological point of view, the European animals are very similar to A. erythrurus.
belli and atlanticus, to such an extent that the Spanish
animals, whose subocular is in contact with the lip, are
practically indistinguishable, apart from slight
colouration variations, from A. erythrurus bell. They
have a rounded snout, low headscale fragmentation
and smooth dorsal scales. So A. erythrurus bell and A.
erythrurus atlanticus should be considered as
conspecific with A. erythrurus erythrurus, in spite of the
electrophoretic differences observed by Squalli
Houssaini (1991) between animals from the Iberian
peninsula and those from Morocco.

In fact, this author has found a \(D_{Nat}\) genetic distance
of 0.327 between his Spanish samples (Alicante) and
those from Morocco. This distance is higher than that
observed between his oceanic coast population and
both Rifain and Middle Atlas samples \(D_{Nat} = 0.081\).
In Busack's (1986) study of Acanthodactylus erythrurus,
the genetic distance between different samples
from Tingitane Peninsula (north of Morocco)
was no different from that between Tingitane and An­
dalusia \(D_{Nat} = 0.10\) and 0.09 respectively. The genetic
similarity between Spanish and Moroccan populations
found by Busack (1986) is in partial contradiction of
those of Squalli-Houssaini (1991) but agrees with our
morphological results: we observe a closer phenotypic
similarity between Acanthodactylus erythrurus erythrurus
(Spain), A. e. bell (northern, eastern and
southern Morocco) and A. e. atlanticus (central Mo­
rocco) than between these and A. lineomaculatus.

Moreover, the weaker electrophoretic polymor­
phism in Spanish populations (six diagnostic alleles
for 10 individuals, \(D_{Nat} = 0.01\)) compared to one of the
Moroccan populations (12 diagnostic alleles for 9 indi­
viduals, \(D_{Nat} = 0.10\)) (Busack, 1986), suggest the
Iberian peninsula was colonized from North Africa by
a small number of individuals. This led to a 'founder
effect' characterized by the large genetic homogeneity
of Spanish populations. This homogeneity approaches
the phenotypic uniformity observed in Andalusia.

**SYSTEMATIC REVIEW OF THE FRINGE-TOED LIZARDS
OF THE GROUP ERTHRURUS**

Common fringe-toed lizards are distributed in the
Iberian peninsula and the Maghreb, except Tunisia.
They are represented by two geographically parapatric
species, one of which is monotypical and the other
comprising three subspecies. They are all character­
ized by three entire rows of scales round the fingers,
small dorsal scales, and the bright red underside of the
tail in juveniles and subadults.

*Acanthodactylus erythrurus erythrurus* (Schinz, 1833)

**Diagnosis:** Smooth dorsal scales (or weakly keeled on
rear of back), rounded snout, barely concave frontal,
entire internasal, usually no interprefrontal granules
(exceptionally one), 1st supraocular generally frag­
mented into fewer than six scales on both sides
(sometimes into six scales on both sides), subocular
usually in contact with lip (sometimes it is separated
from the lip by the 4th and 5th labials that are joined in
this case).

**Distribution:** The southern two-thirds of the Iberian
Peninsula, extending northwards along the Mediterra­
nean coast as far as the environs of Gerona.

*Acanthodactylus erythrurus bell* Gray, 1845

**Diagnosis:** Smooth dorsal scales (or weakly keeled on
rear of back), rounded snout, barely concave frontal,
etire internasal, usually no interprefrontal granules
(exceptionally one), 1st supraocular generally frag­
mented into fewer than six scales on both sides
(exceptionally six on one or both sides), subocular in
contact with lip.

**Distribution** (Fig. 7): Rif mountains and foothills, east­
er Morocco, southern slopes of the High Atlas and far
west of the Anti-Atlas (Foum Assaka, Ifni), as well as
Mediterranean Algeria.

*Acanthodactylus erythrurus atlanticus* Bouleneger,
1918

**Diagnosis:** Smooth dorsal scales (or weakly keeled on
rear of back), rounded snout, barely concave frontal,
eternal nearly always whole (exceptionally di­
vided), no interprefrontal granules (sometimes one,
exceptionally two), 1st supraocular generally frag­
mented into fewer than six scales on both sides
(exceptionally six on one or both sides), subocular gen­
erally separated from the lip by a small rectangular
or oval scale (exceptionally this small scale is absent
and the subocular may or may not be in contact with the
lip).

**Distribution** (Fig. 7): Morocco only; Middle Atlas in­
cluding the Central Plateau, northern slopes of the
High Atlas, plains to the north and west of the Atla­
ses, with the exception of an Atlantic coastal fringe.

*Acanthodactylus lineomaculatus* Duméril & Bibron,
1839

**Diagnosis:** Strongly keeled dorsal scales, slim pointed
snout, concave frontal (with sharply angled lateral
edges), internasal usually divided, except north of
Rabat, usually one or two granules, except north of
Rabat where they are generally absent, 1st supraocular
usually fragmented into more than six scales or gran­
ules, subocular usually separated from the lip by the
4th and 5th supralabials, the 4th being usually frag­
mented at the rear by a small trapezoidal scale in
localities north of Rabat.

**Distribution** (Fig. 7): Moroccan endemic along the At­
lantic coast from Tangiers to Essaouira.

*Acanthodactylus (erythrurus) lineomaculatus* has been
frequently reported from Agadir and the plain of the
Oued Souss. However, all fringe-toed lizards of this
area that we examined in collections or in the field, be­
long to the *pardalis* group, especially *Acanthodactylus
busacki* Salvador, 1982. Raxworthy et al. (1984) also
mentions the problem in identifying Cap Rhir's ani­
mals (northern Agadir) and suggests that only
**Acanthodactylus pardalis** s.l. was present in this area. So we must accept that *A. lineomaculatus* reaches its geographical limit 15 km south of Essaouira and that further south it is replaced by another species, *A. busacki*. This taxon is found in the plain of Oued Souss and the Atlantic coast from Tamri, in the North, to Boujdour, in the South.

**CONCLUSION**

On the basis of several scalation characters, we have been able to demonstrate that there is a larger disparity between animals from the Atlantic coast of Morocco and those from the rest of the country, than exists between the latter and the fringe-toed lizards from the Iberian Peninsula. This disparity is largely confirmed by the morphological analysis of Squalli Houssaini (1991) but is contrary to her genetic findings. This author used electrophoresis, to show that the Iberian animals she studied differ from those from Morocco in two diagnostic loci (*FUM* and *ME.1*) and by a fixed allele (*LDH-2(90]*) that is not shared by their Moroccan counterparts. On the other hand, the three Moroccan forms are barely distinguishable from each other on the basis of electrophoresis with the exception of *lineomaculatus*, which presents a more developed enzymatic polymorphism with a higher number of rare alleles.

We have also observed that animals from the Mediterranean coast of Morocco, and those from both the Mediterranean and Atlantic coast of Iberia, did not display any of the morphological characters of *Acanthodactylus lineomaculatus*. This suggests that these lizards have been isolated on the Atlantic coast for a long time and enables us to reject the hypothesis of a single ecotypical adaptation to sandy habitats, where thermal variations are mitigated by the proximity of the Atlantic. This also suggests that Spain was colonised by a small group of individuals from Morocco. This idea is reinforced by Busack (1986) who obtained an insignificant genetic distance (*D_{Nei} = 0.01*) between his different Iberian samples and found for Spanish samples only six diagnostic alleles for 10 individuals, as opposed to 12 diagnostic alleles for nine individuals in northern Morocco. This type of biogeographical scenario is found in other species, for example *Podarcis hispanica, Lacerta lepida* and...
Macroprotodon cucullatus (cf. Busack, 1986; Table 3).

The presence of Acanthodactylus erythrurus atlanticus in the plains to the north-west of the Atlases suggests the recent colonisation of this low altitude habitat by a form that could have been differentiated by long isolation in high mountains and selective pressures associated with these extreme conditions. It is conceivable that this colonisation is still taking place and that this form could come into contact with A. lineomaculatus. Would this develop into competition between the two forms, or even lead to the elimination of the coastal form with its more demanding ecological requirements? Alternatively, will the present situation stabilise, with the sandy substrate and the presence of a well-adapted species to this environment proving an insuperable barrier for A. erythrurus atlanticus?

Another hypothesis can be put forward to explain the presence of the form atlanticus in the plains. This subspecies could have been much more widespread during the pluvial periods and the last glaciations than at present. The general warming and aridification that have led to the present climate could have reduced the range of atlanticus to small isolated populations, in which case this form would be retreating in the plains to the north-west of the High Atlas.

Patterns of interspecific diversity within other species groups which are comparable to Acanthodactylus erythrurus are known from Morocco. In the Acanthodactylus genus, two species groups are known (Salvador, 1982; Bons & Geniez, in press). The pardalis group contains one species, Acanthodactylus maculatus, which has a wide extension in arid steppes in the East of the Atlas (and in Algeria), where there are cold or cool winters (sensus Brignon & Sauvage, 1962). The same species group also includes an endemic Moroccan species, Acanthodactylus busacki, which is restricted to the oceanic coast from Tamri to Boujdour and the plain of Oued Souss, an area with hot winters.

Within the scutellatus group, Acanthodactylus dumerili is linked to the Sahara's sand dunes with temperate winters. On the other hand, Acanthodactylus aureus, also in the scutellus group, occurs from the Sahara's Atlantic littoral sands (from Agadir to Senegal), where winters are hot.

These patterns are also observable in other reptile genera (in particular Saurodactylus, Chalcides and Sphenops; cf. Table 1), as well as some mammals (Aulagnier & Thévenot, 1986), members of the Gerbillidae belonging to the genus Gerbillus and Gerbillus pyramidum group. They are represented in Morocco by a Saharan and sand-loving species, Gerbillus pyramidum, located in all the Sahara, and four endemic species in sand from both the Moroccan oceanic coast and western Sahara (from the north to the south, Gerbillus hesperinus, G. hoogstralli, G. occiduus and G. riggenbachii) where there are hot winters.

Caputo et al. (1993) used Sue's works (1984, 1989) to explain the history of the specific distinction between Sphenops sepoids and S. sphenopsiformis. These authors state that "these two species may have diverged as a result of allopatry during the drastic climatic fluctuations of the Plio-Pleistocene. During the most mesic climatic periods, the pluvial phases in the

### Table 1. Bioclimatic characteristics of ranges of several vicariant species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Atlantic sides of Morocco &amp; W. Sahara</th>
<th>Eastern and southern sides of Morocco</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>endemic?</td>
<td>hot</td>
</tr>
<tr>
<td>A. erythrurus</td>
<td>N</td>
<td></td>
</tr>
<tr>
<td>A. lineomaculatus</td>
<td>Y</td>
<td>**</td>
</tr>
<tr>
<td>A. maculatus</td>
<td>N</td>
<td></td>
</tr>
<tr>
<td>A. busacki</td>
<td>Y</td>
<td></td>
</tr>
<tr>
<td>A. dumerili</td>
<td>N</td>
<td></td>
</tr>
<tr>
<td>A. aureus</td>
<td>N</td>
<td>**</td>
</tr>
<tr>
<td>Sph. boulenageri</td>
<td>N</td>
<td></td>
</tr>
<tr>
<td>Sph. sphenopsis</td>
<td>N</td>
<td>**</td>
</tr>
<tr>
<td>Saur. mauritianicus</td>
<td>N</td>
<td></td>
</tr>
<tr>
<td>Saur. brosseti</td>
<td>Y</td>
<td>**</td>
</tr>
<tr>
<td>Ch. ocellatus</td>
<td>N</td>
<td></td>
</tr>
<tr>
<td>Ch. polylepis</td>
<td>Y</td>
<td>**</td>
</tr>
<tr>
<td>Ch. minutus</td>
<td>?</td>
<td></td>
</tr>
<tr>
<td>Ch. pseudostriatus</td>
<td>Y</td>
<td></td>
</tr>
</tbody>
</table>
Saharan region (corresponding to high-latitude glaciations) would have caused the contraction of the once more-or-less continuous desert into separate arid refuges'. The explanation given by these authors may also apply to taxa listed in Table 1.

These examples illustrate the biological originality of the north-west African Atlantic littoral region. This originality is reinforced by the existence of a cortege of species endemic to this area. Pelobates varaldii (Amphibia, Anura, Pelobatidae), Geckonia chazalliae (Reptilia, Sauria, Gekkonidae), Chalcides mionecton (Reptilia, Sauria, Scincidae) and Crocidura tarfayensis (Mammalia, Insectivora, Soricidae) are some examples of this cortege. These last species do not present oriental or non coastal vicariance.

In the Miocene, the climate of palaearctic Morocco was arid, with vegetation consisting of mainly sclerophyll forests (Axelrod, 1978). This period coincided with the start of orogenic movement leading to the formation of the Atlas mountains. We believe that these two events played a major role in the differentiation of endemic species. This differentiation was accelerated by alternate pluvial and dry periods which isolated populations in either mountains or plains. Moreover, Morocco is the only north-west African country which has both Mediterranean and Atlantic coasts. The arid depression of Oued Moulouya and the Sahara Desert provide further barriers to the east and south respectively. Populations tend to be separated by these geographical partitions. In addition, Morocco itself can be divided into nine distinct geographical units: the Rif; the Oued Souss valley; the Middle Atlas; the Mediterranean coastal fringe between Melilla and Oran; the High Atlas; the Hauts Plateaux; the Anti-Atlas; the Sahara; and the Atlantic plains.

This geographical partitioning has induced an exceptional diversification of the Moroccan herpetofauna (105 species of amphibians and reptiles, of which 22 are endemics (Bons & Geniez, in prep.). The fringe-toed lizards of the erythrurus group follow the same pattern, with one endemic species on the oceanic coast (Acanthodactylus lineomaculatus) and another one living in the rest of palaearctic Morocco (A. erythrurus). The latter is split into two subspecies: one, an endemic (subsp. atlanticus) in the mountains and the hills of the Atlantic side, the other one found everywhere else in the Moroccan mountains. With nine species, including two endemics in Morocco (Salvador, 1982), the Acanthodactylus genus is less diversified than the Chalcides genus which has no less than 11 species, eight of which are endemic to Morocco (Mateo et al., in prep.).

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REFERENCES


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