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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* Duméril & Bibron 1839) and from North Africa (*Acanthodactylus lineomaculatus* Duméril & 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 phylogenesis. 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 occuring 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 Atlases. 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 Atlases, 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. *atlanticus* Boulenger 1918, in the Middle Atlas, the northern slopes of the High Atlas and the plains situated north of the High Atlas (endemic to Morocco).

— ssp. *lineomaculatus* Duméril & 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

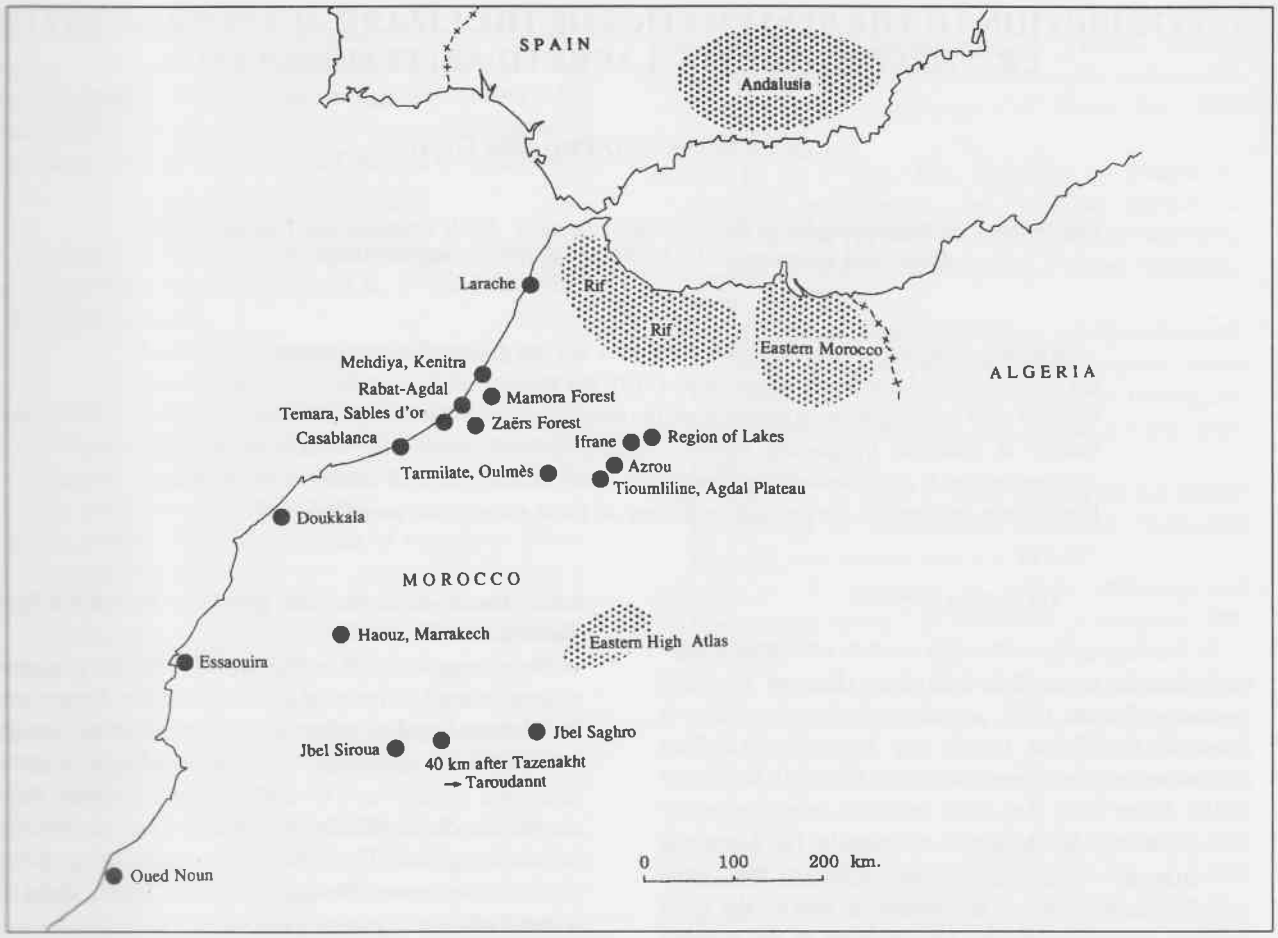


FIG. 1. Location of populations studied.

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 :

MOROCCO	
Larache	(47 individuals)
Mehdiya, Kenitra	(36 individuals)
Mamora Forest	(41 individuals)
Rabat-Agdal	(55 individuals)
Temara, Sables d'or	(14 individuals)
Zaërs Forest	(47 individuals)
Casablanca	(47 individuals)
Doukkala	(4 individuals)
Essaouira	(6 individuals)
Region of Lakes	(5 individuals)
Ifrane	(34 individuals)
Azrou	(17 individuals)
Tioumliline, Agdal Plateau	(9 individuals)
Tarmilate, Oulmès	(69 individuals)
Haouz, Marrakech	(3 individuals)
Rif	(18 individuals)
Eastern Morocco	(13 individuals)
Eastern High Atlas	(13 individuals)
Jbel Saghro	(4 individuals)
40 km W. of Tazenakht	(11 individuals)
Jbel Siroua	(2 individuals)
Oued Noun	(1 individual)
SPAIN	
Benidorm	(1 individual)
Almeria	(2 individuals)
Huescar	(2 individuals)
Torre de la Higuera	(3 individuals)
unknown locality	(3 individuals)

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 interprefrontal 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.

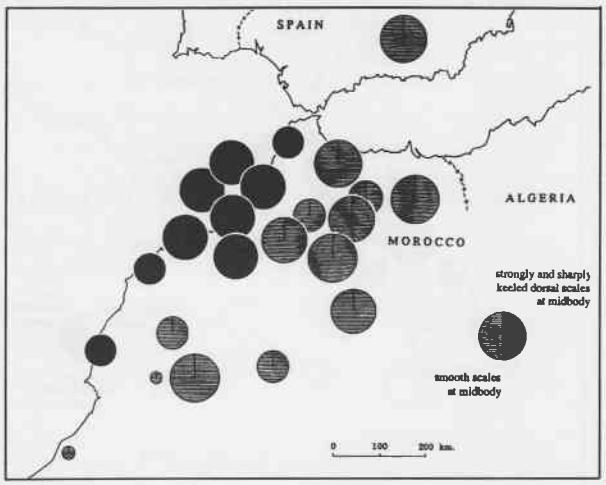


FIG. 2. Texture of dorsal scales, expressed in percentages of individuals per site.

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 Essaouira, 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 Aurès in Algeria, put at our disposal by Laurent Chirio, also confirmed our findings for Algeria.

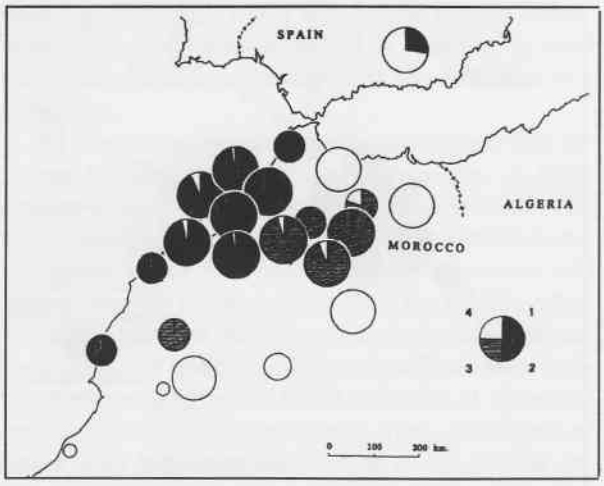
POSITION OF THE SUBOCULAR (FIG. 3)

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*.



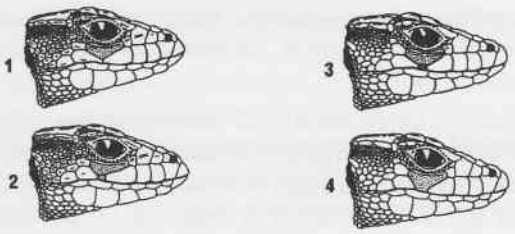


FIG. 3. Position of subocular scale, expressed in percentages of individuals per site.

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 *belli*.

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 *belli*), 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.

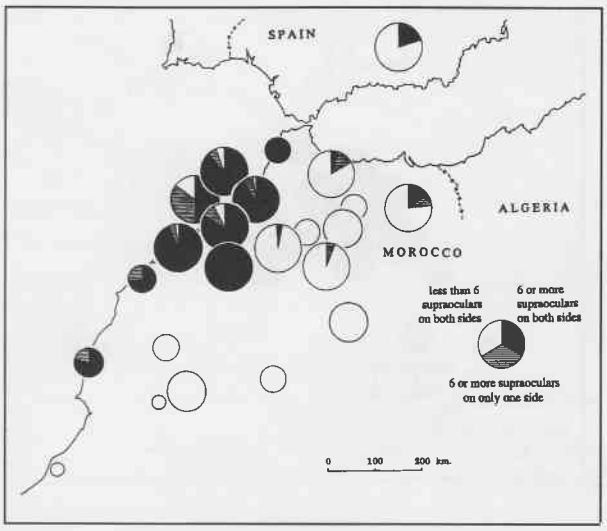


FIG. 4. Number of fragments of the 1st supraocular scale, expressed in percentages of individuals per site.

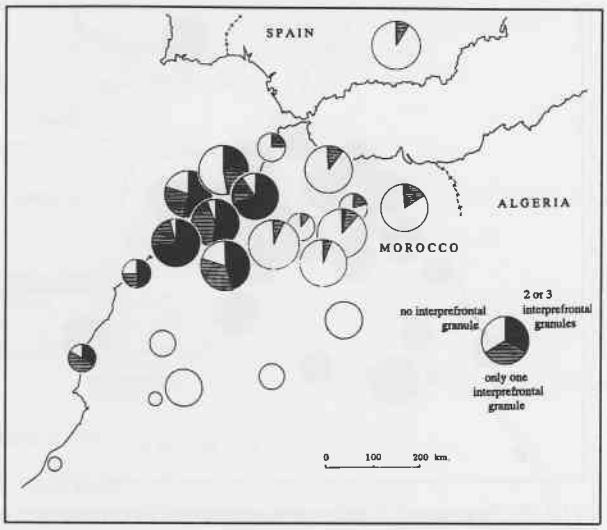


FIG. 5. Presence or absence of interprefrontal granules, expressed in percentages of individuals per site.

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 taxons of the group), and the frequent pres-

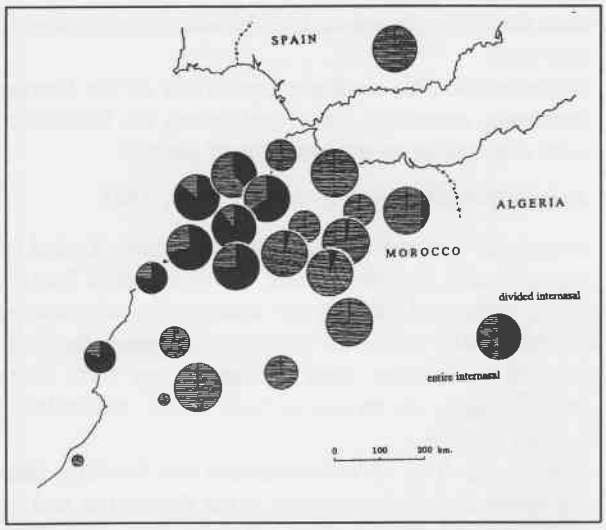


FIG. 6. Division of internasal scale, expressed in percentages of individuals per site.

ence (41%) of occipital granules in the former and their rarity in the others. These characters were not monitored during our analyses but they have been largely confirmed by our studies in the field.

DISCUSSION

It is therefore established that the head scalation criteria used to identify the subspecies of *Acanthodactylus erythrurus* should not be taken into account if used in isolation or on a single specimen. On the other hand, if applied together, they are very interesting and easy to use. They also make it possible to show up three geographic regions, which are occupied by three morphologically different types. These correspond to the three traditionally accepted subspecies of Morocco: ssp. *lineomaculatus*, ssp. *belli* and ssp. *atlanticus* (Pasteur & Bons, 1960; Bons & Girot, 1962). In spite of the total confirmation of these characters and percentages by Squalli-Houssaini (1991), this author could not adopt the same conclusions as ours because of the low number of populations studied.

Concerning the form *atlanticus*, it should be noted that it is not recognised by Salvador (1982) and Arnold (1983). They consider it an intermediate between *A. erythrurus belli* and *A. erythrurus lineomaculatus.* Yet the homogeny of its scalation characters, distributed over a well defined geographical area (the Middle Atlas, northern slopes of the High Atlas and Haouz), make it quite different from the other subspecies. Furthermore this form, usually considered as mountainous (Pasteur & Bons, 1960; Bons & Girot, 1962), is found in plains at Haouz of Marrakech. The hypothesis that the form *atlanticus* could be a mountain ecotype of *Acanthodactylus erythrurus* can therefore not be retained. Lastly, the absence of intermediate animals between the subspecies *lineomaculatus* and *belli,* as well as the absence of intermediate morphological characters between these two forms, is contrary to the claims of Salvador (1982) and Arnold (1983). *Acanthodactylus erythrurus atlanticus* is therefore a valid subspecies perfectly consistent with the definition of a subspecies.

We then investigated the nature of contacts and relations between these different subspecies. A large number of specimens, observed in many localities (cf. Fig. 2), enabled us to make the following clarifications.

Contact zones between the forms *atlanticus* and *belli* exist in the northern foothills of the Middle Atlas. The transition from one subspecies to the other occurs via a mosaic of small populations in which all the individuals possess either the labial character of *atlanticus* (position 3) or of *belli* (position 4). Thus, 5 km north of Dayet Ifrah (region of lakes, north of the Middle Atlas), all individuals of *Acanthodactylus erythrurus* possess the headscale pattern of *belli,* while the surrounding populations belong to the subspecies *atlanticus*.

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 invariable 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 belli*. They have a rounded snout, low headscale fragmentation and smooth dorsal scales. So *A. erythrurus belli* 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_{Nei} 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_{Nei} = 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 Andalusia (D_{Nei} = 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. belli* (northern, eastern and southern Morocco) and *A. e. atlanticus* (central Morocco) than between these and *A. lineomaculatus*.

Moreover, the weaker electrophoretic polymorphism in Spanish populations (six diagnostic alleles for 10 individuals, D_{Nei} = 0.01) compared to one of the Moroccan populations (12 diagnostic alleles for 9 individuals, D_{Nei} = 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 *ERYTHRURUS*

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 characterized 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 fragmented 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 Mediterranean coast as far as the environs of Gerona.

Acanthodactylus erythrurus belli Gray, 1845

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 fragmented 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, eastern 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 Boulenger, 1918

Diagnosis: Smooth dorsal scales (or weakly keeled on rear of back), rounded snout, barely concave frontal, internasal nearly always whole (exceptionally divided), no interprefrontal granules (sometimes one, exceptionally two), 1st supraocular generally fragmented into fewer than six scales on both sides (exceptionally six on one or both sides), subocular generally 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 including the Central Plateau, northern slopes of the High Atlas, plains to the north and west of the Atlases, 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 granules, subocular usually separated from the lip by the 4th and 5th supralabials, the 4th being usually fragmented at the rear by a small trapezoidal scale in localities north of Rabat.

Distribution (Fig. 7): Moroccan endemic along the Atlantic 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, belong to the *pardalis* group, especially *Acanthodactylus busacki* Salvador, 1982. Raxworthy *et al.* (1984) also mentions the problem in identifying Cap Rhir's animals (northen Agadir) and suggests that only

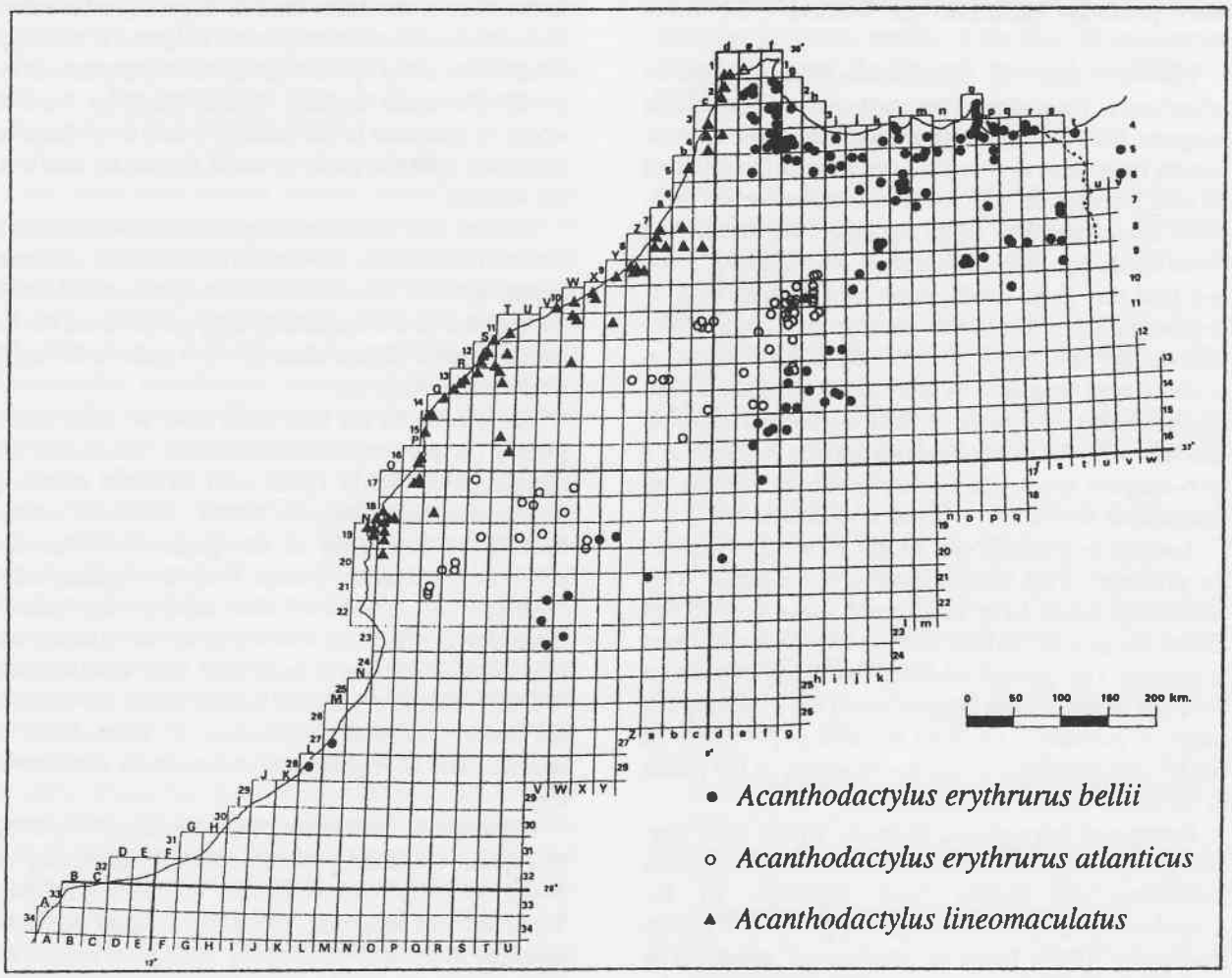


FIG. 7. Distribution of common fringe-toed lizards in Morocco (from Bons & Geniez,in press).

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 differentiatied 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 Saraha'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. riggenbachi*) where there are hot winters.

Caputo *et al.* (1993) used Suc's works (1984, 1989) to explain the history of the specific distinction between *Sphenops sepsoides* 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. end., endemic to Morocco; temp., substage with temperate winter; ** , species well represented in substage; * , marginal species in substage.

		Atlantic sides of Morocco & W. Sahara				Eastern and southern sides of Morocco			
Species	endemic?	hot	temp.	cool	cold	hot	temp.	cool	cold
A. erythrurus	N					*	**	**	**
A. lineomaculatus	Y	**	**						
A. maculatus	N						*	**	**
A. busacki	Y	**	*						
A. dumerili	N						**	**	
A. aureus	N	**							
Sph. boulengeri	N						**		
Sph. sphenopsif.	N	**							
Saur. mauritanicus	N						**	**	
Saur. brosseti	Y	**	**	*					
Ch. ocellatus	N					**	**	**	
Ch. polylepis	Y	**	**	**	*				
Ch. minutus	?						**	**	**
Ch. pseudostriatus	Y	*	**	**	*				

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 chazaliae* (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 palearctic 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 palearctic 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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