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Taxonomy and evolution of the North African ocellated lizard, *Lacerta pater* (Lataste, 1880) (Sauria: Lacertidae)

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Abstract. Morphological variations (biometry, pholidosis, pattern and colour) were studied in the North African lizard *Lacerta pater*. Whereas biometric characters do not vary geographically there are some pholidotic and colour pattern differences between eastern (Tunisian and Algerian) and western (Moroccan) populations. The data confirm the validity of the subspecies *Lacerta pater tangitana* (Boulenger, 1887).

Key words. Lacertidae, taxonomy, NW Africa, *Lacerta pater*.

Introduction

The systematics of *Lacerta pater* have been little studied in comparison with those of the closely related species *Lacerta lepida* Daudin, 1802.

The ocellated lizards of north Africa were described by Lataste (1880) as a subspecies of *Lacerta ocellata*. However, Boulenger (1887) reported morphological differences between two populations of this lizard, and described a new subspecies found near Tangier: *Lacerta ocellata tangitana*. Separation between *Lacerta ocellata pater* and *Lacerta ocellata tangitana* was based on the number of femoral pores and dorsal scales.

Some 30 years later Boulenger (1920) retracted his earlier proposal that *Lacerta ocellata tangitana* was a subspecies and synonymized the taxon on the basis of occurrence of animals around Oran with the characteristics of *Lacerta ocellata tangitana*, together with other animals which had the characteristics of the nominal subspecies.

From that time, to the present, almost all the published works on this subject appear to have avoided describing any difference between the populations, although there are some exceptions (e. g. Angel 1946).

Recently, Bischoff (1982) brought the matter to light again when he showed that *Lacerta lepida* and *L. pater* were two different species because it was difficult to find crosses and back-crosses and he questioned whether the *tangitana* subspecies could be considered a valid subspecies.

This paper considers the most notable differences between these populations in an attempt to resolve this taxonomic problem, and also to provide new information on the evolution of the species.

Material and Methods

A total of 209 adult specimens of *Lacerta pater* were used in this study. The specimens belong to the collections of the British Museum, London (53); the Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (26); the Musée National d'Histoire Naturelle, Paris (15); the Naturhistorisches Museum, Vienna (2); the Institut de Recherche, Rabat (16), and the Estación Biológica de Doñana, Seville (97). The area enclosed by the places of capture constitutes an acceptable coverage of the species distribution.

The specimens were grouped on the following medium-sized natural regions: the Rif and surrounding area, the Middle Atlas mountains, the Great Atlas mountains, Tell and the Western Algerian plateau (W. Algeria), Aures and Kabilia (E. Algeria), and Kroumiria and Dorsal Tunisian mountains (Tunisian distribution).

Measurements were made of the following biometric and pholidotic characters of each specimen: snout-vent length (Svl), head length (Hl), head width (Hw), snout length from preocular scale to front region of rostral plate (Sntl), distance between nostrils (Nosd), mentonian groove length (Menl), length of posterior extremity (Legl), width of occipital scale (Occ), width of the frontal scale (Fron), number of dorsal scales in a transversal row (Dor), number of ventral scales in transverse and longitudinal rows (Vent & Venl), number of femoral pores (Fem), number of collar scales (Col), number of gular scales from the mentonian groove to collar (Gul), number of supraciliary granules (Scg), and number of scales around preanal plate (Sap).

The differences of colour and patterns were evaluated on the basis of the presence or absence in each individual of the following characteristics: dorsal ocelli, ocelli on tail, open ocelli, sharp band, blue spots, blue spots only on front, encircled blue spots, background screen, green colour in the tail, pattern on neck, pattern on head, pattern on hindlegs and pattern on forelegs.

The data clusters were constructed using a matrix of euclidean distances and the groupings of the different Operative Taxonomical Units (OTU's) were obtained by the sum of squares method. All these operations and the discriminant analysis were carried out using the P2M and P7M programs, respectively, of BMDP packet (Dixon, 1983).

Results

Biometry and Pholidosis

After applying two discriminant function analyses (for males and females) to pholidotic and biometric data, only two variables gave significant F values in each analysis. These were femoral pores (Fem) (for males $F_{(5,103)} = 19.15$; for females $F_{(2,92)} = 13.78$) and the number of dorsal scales (Dor) (for males $F_{(10,206)} = 9.42$; for females $F_{(4,184)} = 7.32$).

Table 1: Hemimatrices of F interpopulational values resulting from the two discriminant analyses applied to biometric and pholidotic data.

Males		Rif 1	Mid. Atl. 2	Gr. Atl. 3	W. Alg. 4	E. Alg. 5	Tunisia 6
1	Rif	—			**	**	**
2	Middle Atlas	2.27	—		**	**	**
3	Great Atlas	0.24	1.47	—	**	**	**
4	W. Algeria	20.96	13.59	23.80	—		*
5	E. Algeria	26.14	18.84	28.18	1.78	—	
6	Tunisia	43.23	37.28	53.99	4.79	0.15	—
Females		1	2	3	4	5	6
1	Rif	—			**	**	**
2	Middle Atlas	1.32	—		**	**	**
3	Great Atlas	0.67	0.99	—	**	**	**
4	W. Algeria	6.12	11.17	20.78	—		
5	E. Algeria	12.37	12.52	12.27	0.27	—	
6	Tunisia	23.42	27.17	15.14	1.54	0.22	—

* sign. $p \leq 0.05$; ** sign. $p \leq 0.01$

The F values for each population are given in Table 1 and they show that the Moroccan populations (Rif, Middle Atlas and Great Atlas) show no significant differences among themselves. This is also apparent with the Algerian and Tunisian populations, except in males from Western Algeria and Tunesia ($p \leqq 0.05$). On the contrary, each of the Moroccan populations differs significantly from all of the rest ($p \leqq 0.01$).

Mean values for every variable used in this analysis can be seen in Table 2.

Pattern and Coloration

Unlike *Lacerta lepida* (Mateo 1988), the coloration of one population of the African ocellated lizards displays as much variation as is seen in the remaining species

Table 2: Population average values of the biometric and pholidotic variables used in this paper. (Abbreviations can be read in the paragraph Material and Methods).

	Rif	Midd. Atl.	Great Atl.	W. Alger.	E. Alger.	Tunisia
Males						
Dor	83.000	79.620	79.960	79.860	77.110	65.320
Venl	7.500	8.000	7.520	7.670	8.000	7.870
Vent	30.170	29.930	28.910	30.500	30.660	29.800
Fem	18.830	18.330	18.540	17.830	15.200	14.880
Col	12.370	12.390	12.070	12.670	12.680	12.750
Gul	26.870	27.330	27.370	28.330	25.700	24.210
Scg	6.120	6.810	7.130	5.670	5.600	5.580
Svl	141.310	138.150	139.980	141.420	140.220	144.360
Hl/Svl	0.263	0.261	0.261	0.276	0.261	0.269
Hw/Hl	0.486	0.493	0.482	0.486	0.494	0.516
Nosd/Hl	0.145	0.148	0.144	0.141	0.154	0.143
Sntl/Hl	0.355	0.359	0.359	0.346	0.368	0.365
Menl/Hl	0.369	0.381	0.371	0.380	0.383	0.385
Legl/Svl	0.497	0.505	0.495	0.496	0.493	0.486
Occ/Fron	0.927	0.967	0.991	0.850	0.870	0.929
No.	12	18	17	21	15	24
Females						
Dor	83.640	80.100	78.640	76.120	73.690	75.140
Venl	6.640	7.940	7.580	8.000	7.800	8.000
Vent	31.090	31.110	30.170	31.820	31.290	31.070
Fem	18.900	17.110	17.080	15.310	14.050	14.860
Col	12.780	12.140	11.870	12.110	12.320	12.280
Gul	25.890	26.110	26.620	25.540	25.000	25.780
Scg	5.890	6.610	7.120	6.560	5.470	5.560
Svl	137.690	133.160	138.690	138.560	133.680	144.410
Hl/Svl	0.236	0.231	0.244	0.235	0.221	0.235
Hw/Hl	0.441	0.489	0.473	0.489	0.488	0.480
Nosd/Hl	0.147	0.151	0.140	0.149	0.159	0.143
Sntl/Hl	0.377	0.376	0.353	0.370	0.389	0.371
Menl/Hl	0.395	0.386	0.374	0.392	0.381	0.399
Legl/Svl	0.458	0.475	0.453	0.474	0.451	0.460
Occ/Fron	0.792	0.812	0.867	0.735	0.766	0.808
No.	10	20	15	14	13	28

distribution. The only exceptions are the unique presence of an intense-yellow on the throat of the males of the eastern populations and the absence of green colour in the tails of the western lizards. It should be pointed out that even if the colouring of the tail is easily seen in all the specimens, dead or live, the yellow throat coloration is only seen in live specimens.

In contrast to the small variation in coloration, the designs of these animals display considerable modifications throughout their area of distribution. The clusters in Figure 1 were obtained from the presence-absence data for patterns and coloration (Table 3). These schematic trees always tend to group the populations of the eastern region on one hand, and the Moroccan populations on the other and this separation is the same for both males and females, however, the females display wider differences.

Table 3: Regional presence proportions of each character used in this paper.

	Rif	M. Atl.	G. Atl.	W. Alg.	E. Alg.	Tunis.
Males						
Presence of Ocelli	0.60	0.36	0.38	0.33	0.36	0.47
Ocelli on Tail	0.20	0.43	0.00	0.00	0.29	0.20
Open Ocelli	0.00	0.00	0.00	0.00	0.07	0.00
Sharp Bands	0.00	0.07	0.00	0.00	0.14	0.00
Blue Spots	1.00	0.86	1.00	1.00	1.00	1.00
Blue Spots only on Front	0.00	0.00	0.00	0.00	0.00	0.00
Encircled Blue Spots	1.00	0.64	0.77	0.67	0.78	0.27
Background Screen	0.60	0.93	0.92	1.00	0.86	0.87
Green Colour on Tail	0.20	0.21	0.08	0.67	1.00	1.00
Pattern on Neck	0.60	0.29	0.38	0.67	0.36	0.47
Pattern on Pileum	0.00	0.00	0.00	0.00	0.07	0.07
Pattern on Hindlegs	0.40	0.36	0.54	0.67	0.57	0.80
Pattern on Forelegs	0.00	0.07	0.08	0.00	0.36	0.40
No.	10	14	13	6	14	15

	Rif	M. Atl.	G. Atl.	Alg.	Tunis.
Females					
Presence of Ocelli	0.88	0.87	0.83	0.79	0.84
Ocelli on Tail	0.88	0.47	0.58	0.79	0.63
Open Ocelli	0.00	0.00	0.00	0.42	0.47
Sharp Bands	0.38	0.07	0.00	0.42	0.42
Blue Spots	1.00	0.93	1.00	0.95	1.00
Blue Spots only on Front	0.13	0.27	0.00	0.16	0.11
Encircled Blue Spots	0.88	0.87	0.83	0.58	0.79
Background Screen	0.88	0.93	1.00	0.05	0.21
Green Colour on Tail	0.13	0.13	0.00	1.00	1.00
Pattern on Neck	0.88	0.73	0.83	0.47	0.47
Pattern on Pileum	0.00	0.00	0.00	0.05	0.05
Pattern on Hindlegs	0.80	0.67	0.42	0.63	0.47
Pattern on Forelegs	0.25	0.27	0.00	0.21	0.21
No.	7	15	12	19	19

G. Atl.: Great Atlas; M. Atl.: Middle Atlas; Rif: Rif; W. Alg.: West Algeria; E. Alg.: East Algeria; Alg.: Algeria; Tunis.: Tunisia.

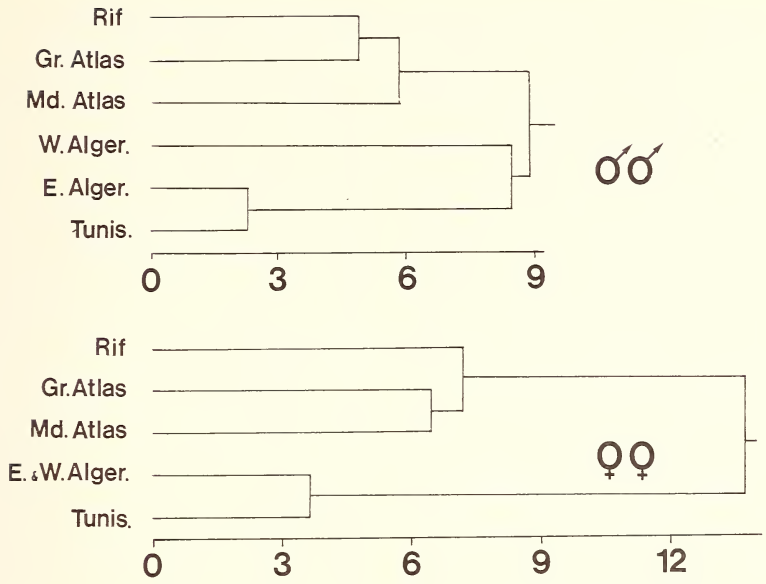

Fig. 1: Cluster of populations based on pattern and coloration of the specimens. In the case of the Algerian females, western and eastern specimens were included in a unique group.

Applying the Chi-squared test to the patterns of males and females of the two extremes of the distribution (Table 4) revealed that for the western animals there were significant differences between sexes in only two of the thirteen characters employed in this paper (Presence of dorsal ocelli, of ocelli on the tail), while for the eastern animals, six of these characters (Presence of dorsal ocelli, of ocelli on the tail, of open ocelli, of well-defined dorsal ocelli, of the background reticular pattern, and of pattern on the forelegs) had significant values ($p \leqq 0.05$) (Figure 2).

Discussion

It is noteworthy that the biometric characters and the coloration characters presented the least variation. In contrast, the pholidotic characters and the patterns allowed individual specimens from one or other extreme of the species distribution to be identified.

These results are both contrasted and complemented by those obtained in a study using an electrophoretic method (Mateo et al., in prep.) in which the same geographically extreme populations display genetic distances between themselves as large as those existing between them and *Lacerta lepida*, a species in which the morphological variations are almost always associated with appreciable bioclimatic variations (Mateo 1988). Consequently, it can be said that it is precisely those characters supposedly subjected to the strongest selection pressures that present the least variations.

The absence of geographical variations in those characters subjected to the strongest selection pressures (for example, animal size, the length of its limbs, the size

Table 4: Chi-squared values between sexes for each pattern and colour character in the populations of the eastern (Tunisia, W. Algeria and E. Algeria) and western (Rif, Middle Atlas and Great Atlas) distribution areas.

	Chi-squared values	
	East	West
Presence of Ocelli	4.12*	4.55*
Ocelli on Tail	10.04*	6.33*
Open Ocelli	11.74*	0.00
Sharp Bands	8.56*	3.58
Blue Spots	0.02	0.06
Blue Spots on Front	0.50	3.20
Encircled Blue Spots	0.07	0.00
Background Screen	24.92*	0.08
Green Colour on Tail	0.00	0.00
Pattern on Neck	0.00	2.67
Pattern on Pileum	0.16	0.00
Pattern on Hindlegs	1.20	1.32
Pattern in Forelegs	5.71*	3.52

* sign. $p \leqq 0.05$

of its snout, or its coloration) is understandable when one considers that the species distribution extends along a narrow east-west coastal fringe that lies between the Sahara Desert and the Mediterranean Sea and that the most important present-day phytoclimatic variations occur in a steep north-south gradient, the steepness of which must have oscillated enormously during the whole of the Quaternary period. On the other hand, those characters that are modified with time in a more random way by being exposed to less intense selection pressures, display important systematic differences.

In the narrow coastal distribution area described above, there are two population nuclei that may be said to be extremes, both located in areas where the range of bioclimatic conditions is optimum for the species: one in the Moroccan Atlas Mountains, and another in Kroumiria and Kabilia regions, in the east. The extensive area which lies between the two has a much more irregular climate; in the case of the valley of the river Moulouya, the desert reaches the sea, and the sparse populations there are almost always limited to vegetation bordering the few rivers of the region. Consequently, and in accordance with morphological data, there is no cline between western and eastern lizards, but a disjunction with tendency to a secondary contact zone.

Throughout the Pleistocene period, pluvial and interpluvial intervals would have separated and rejoined the two extreme areas (Faure 1986, Livingstone 1975) to provoke an intermittent speciation process that is still incomplete today.

This is an appropriate point to mention the subspecific taxonomical differences within the *Lacerta pater* species. As explained above, these differences are extreme between the most geographically separated populations within species distribution and consequently, they may be considered as two different subspecies. Their individual characteristics are as follows:

Fig. 2: Photographs illustrating the main differences in the observed dorsal pattern in females. Right: Middle Atlas female with background reticular pattern and indistinct closed ocelli. Left: Tunisian female, without reticular pattern and with clearly defined, open ocelli.

Lacerta pater pater (Lataste, 1880)

Syntypes studied: BM 1946.9.2.21 (♂, Setif, Algeria), BM 1946.9.2.22 (♀, Setif, Algeria), BM 1946.9.2.23 (♂, Setif, Algeria), BM 1946.9.2.24 (♀, Batna, Algeria), and BM 1946.9.2.25 (♂, Batna, Algeria). Collected by F. Lataste and deposited in the British Museum (Natural History) collections, London.

Diagnosis: Lizards with less femoral pores (X♂ = 15.99; X♀ = 14.78) than the ones of the other subspecies (Appendix 1). Males show patterns similar to those in males and females of the *tangitana* subspecies, but the females included in this subspecies are well differenciated since most of them present patterns on a plain colour base and have very nitid ocelli, generally open at their end and longitudinally aligned (Figure 2). Both sexes almost always have hind legs and tail base the same colour as the back; while in adult males the gular region is a bright yellow, sometimes with blue reflections. The animal size and the proportions of legs, snout and head, are very similar to the other subspecies (Appendix 2).

Distribution: Tellian Atlas, Aures area, Tunisian Mountains and isolated populations of the Saharian Atlas.

Etymology: The nominal "pater" refers, according to Lataste (in Bedriaga 1886), to the intermediate morphology between *Lacerta ocellata* and *Lacerta viridis* and to their supposed common ancestry.

Lacerta pater tangitana (Boulenger, 1887)

Syntypes studied: BM 1884.6.30.3 (♂), BM 1884.6.30.4 (♂), BM 1884.6.30.5 (♀), BM 1946.9.2.11 (♀), BM 1946.9.2.12 (♀), all from the neighbourhood of Tangiers, and collected by H. Vaucher and deposited in the British Museum (Natural History), London.

Diagnosis: The individuals from species distribution western end generally present more femoral pores than the nominal ones (X♂ = 18.53; X♀ = 17.53) and mild gradual variations in characters such as dorsal (Appendix 1). Unlike Algerian and Tunisian lizards, they do not present a sexual dimorphism in pattern as noticeable as in *Lacerta pater pater*, ocelli being as a rule not very marked and the base of not a plain pattern. Ocelli are always closed at their ends though they are aligned longitudinally to the body axis (Figure 2).

Both males and females usually have hind legs and tail base dark brown, even when the back may be bright green. Males nevertheless will almost never present bright colours in the gular region as in the nominal subspecies.

Distribution: Rif, Middle Atlas, Great Atlas, Moroccan Central Plateau and isolated populations on the Atlantic coast, valleys of the Ziz and Draa rivers. The river Moulouya is considered to be the limit between the subspecies.

Etymology: Although "tangitana" refers to Tangiers, it is neither a latinization of the name of the people of Tangiers (tangerina or tangeriana), nor is it Latin (tingitana), however, it will continue to be employed as the nominal for the subspecies.

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Zusammenfassung

Die Arbeit befaßt sich mit der Variation der morphologischen Merkmalscharakteristik — Biometrie, Pholidose, Zeichnungsmuster und Färbung — der nordafrikanischen Art *Lacerta lepida*. Es ergaben sich keine geographischen Variationen im gesamten Verbreitungsgebiet für die biometrischen Meßwerte. Bei einigen Pholidose- und Färbungsmerkmalen jedoch und hauptsächlich, was das Zeichnungsmuster angeht, konnten bedeutende Unterschiede zwischen östlichen (tunesischen und algerischen) und westlichen (marokkanischen) Populationen festgestellt werden. Die Ergebnisse dieser Untersuchung bestätigen die Existenz der Unterart *Lacerta lepida tangitana* (Boulenger, 1887).

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Appendix 1: Mean values, standard deviations and range of the pholidotic characters in each subspecies.

	Males		Females		Males		Females	
	pater	*tangit.*	*pater*	*tangit.*	*pater*	*tangit.*	*pater*	*tangit.*
	Sap				Dor			
mean	6.48	6.21	6.43	6.32	72.35	79.84	75.05	80.40
st. dev.	0.74	0.70	0.83	0.93	4.29	6.07	3.82	6.58
maximum	8	7	8	8	90	99	85	98
minimum	4	5	4	4	67	68	65	70
	Venl				Vent			
mean	7.83	7.70	7.94	7.53	30.26	29.57	31.31	30.79
st. dev.	0.30	0.78	0.30	0.97	1.21	1.34	1.12	1.45
maximum	8	8	8	9	34	34	34	33
minimum	6	6	6	6	28	27	29	28
	Fem				Col			
mean	15.99	18.53	14.78	17.53	12.70	12.25	12.25	12.19
st. dev.	1.54	1.55	1.42	1.45	1.09	1.13	1.47	1.15
maximum	19	23	18	21	16	15	16	15
minimum	12	16	12	15	11	10	9	10
	Gul				Scg			
mean	26.02	27.23	25.53	26.23	5.61	6.75	5.79	6.62
st. dev.	2.34	2.18	2.34	2.71	1.50	1.84	1.32	2.03
maximum	31	31	33	34	9	10	9	11
minimum	20	23	23	22	2	2	3	1
No.					60	47	55	45

Appendix 2: Mean values, standard deviations and range of the biometric characters in each subspecies.

	Males		Females		Males		Females	
	pater	*tangit.*	*pater*	*tangit.*	*pater*	*tangit.*	*pater*	*tangit.*
	Svl				Hl/Svl			
mean	142.30	139.62	140.38	136.33	0.269	0.262	0.232	0.236
st. dev.	16.34	17.08	15.36	12.66	0.024	0.018	0.016	0.022
maximum	179.00	166.00	170.00	163.30	0.330	0.285	0.253	0.300
minimum	109.10	96.30	112.10	114.00	0.205	0.193	0.175	0.195
	Hw/Hl				Nosd/Hl			
mean	0.504	0.486	0.484	0.473	0.146	0.145	0.148	0.146
st. dev.	0.048	0.029	0.031	0.047	0.019	0.013	0.016	0.017
maximum	0.749	0.549	0.618	0.578	0.189	0.173	0.195	0.180
minimum	0.387	0.411	0.441	0.340	0.104	0.119	0.128	0.101
	Sntl/Hl				Menl/Hl			
mean	0.359	0.358	0.375	0.369	0.382	0.375	0.390	0.386
st. dev.	0.045	0.019	0.030	0.034	0.024	0.024	0.023	0.034
maximum	0.495	0.435	0.463	0.443	0.430	0.428	0.433	0.484
minimum	0.280	0.328	0.347	0.292	0.331	0.330	0.330	0.316
	Legl/Svl				Occ/Fron			
mean	0.490	0.499	0.460	0.464	0.887	0.965	0.779	0.826
st. dev.	0.034	0.032	0.031	0.030	0.112	0.156	0.121	0.173
maximum	0.554	0.572	0.503	0.531	1.125	1.413	1.075	1.186
minimum	0.423	0.434	0.386	0.425	0.649	0.701	0.527	0.569
No.					60	47	55	45