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Complex patterns of morphological and mtDNA variation in *Lacerta perspicillata* (Reptilia; Lacertidae)

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Lacerta perspicillata is a north-west African lacertid lizard that shows considerable intraspecific variation, with three subspecies described on the basis of colour pattern and body size. Recent observations of a population containing two morphological forms and more than one deep genetic lineage, as well as an apparent lack of concordance between forms and genetic lineages, suggest that the complexity is greater than previously thought. To analyse and quantify this variation, we studied the variability within this species at two levels: (1) external morphology (multivariate analysis of scalation, body dimensions, and colour pattern) and (2) mtDNA (sequencing and single-strand confirmation polymorphism analysis). Fifty-two individuals were studied at Taza, northern Morocco. Two morphological groupings (ostensibly representing two previously described subspecies) and two deep mtDNA lineages were detected at this site, with complete correspondence between the two. This, together with an apparent lack of hybrids, would normally support respective full species recognition. However, analysis of 98 individuals from other populations demonstrated that the situation is highly complex with the same genetic lineages having reversed morphotypes in other areas, making such a designation difficult. Across the other studied populations, we found no support for any of the currently recognized subspecies. The lack of congruence between mtDNA lineages and morphometric patterns (in some cases) and the morphological similarity among lizards from different lineages suggest ecophenotypic convergence or multiple introgressive hybridization. The study highlights the tremendous complexity that may exist within a taxon and the inadequacy of older alpha-taxonomy based designations in describing it.

ADDITIONAL KEYWORDS: Balearic Islands – genetic variation – lizard – morphology – North Africa.

INTRODUCTION

Lacerta perspicillata Duméril & Bibron, 1839 is a small lacertid endemic to north-west Africa. Its present-day distribution includes Morocco (Middle and High Atlas, Oulmés Plateau, Rabat, Salé), Algeria (Tellian Atlas, Oran, Algiers, Habibas Islands), and a non-African introduced population on the island of Menorca (Balearic Islands, Spain; Bons & Geniez, 1996; Mateo, 1997). The exact origin of the latter population remains uncertain, but a recent introduction from the Algerian coastal populations has been suggested (Richter, 1986; Mateo, 1997). The phylogenetic relationships and taxonomy of *L. perspicillata* have been debated in the literature, with the species having been assigned to several different genera (Bons & Geniez, 1996).

Intraspecific variation is considerable and complex. Bons (1968) recognized three different North African subspecies based on their size, coloration, colour pattern and distribution.

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1. *Lacerta perspicillata perspicillata* is a small-sized form from the high plateaus of Algeria and Morocco and southern parts of the eastern High Atlas. It is characterized by a largely uniform bronze dorsum with an almost indistinct spotted pattern. The Menorcan populations have been assigned to this subspecies (Richter, 1986).
2. *Lacerta perspicillata chabanaudi* is a large spotted form with light dots on a dark background, distributed across the High and Middle Atlas, Central Plateau, Fez, and Rabat.
3. *Lacerta perspicillata pellegrini* is of small body size with two light dorsolateral stripes on a spotted dorsum and is found in the High and Middle Atlas (Bons & Geniez, 1996).

If racial categories are to be of use, they clearly need to predict variation in a range of characteristics (Thorpe, 1976). This does not appear to be the case for the aforementioned subspecies, with several authors questioning their validity (Bons & Geniez, 1996; Mayol, 1997).

A recent preliminary study on intraspecific variability based on mtDNA sequence variation (12S rRNA) showed that the current subspecies designations do not necessarily correspond to genetically identified lineages and indicated that *L. perspicillata* may be a species complex (Harris *et al*., 2003). Although morphology was not quantified, two different forms (corresponding to *L. p. chabanaudi* and *L. p. pellegrini*) were found to exist syntopically at Taza, northern Morocco (Bons & Geniez, 1996; Harris *et al*., 2003). Two ostensibly morphologically differentiated specimens from this site were found to have highly divergent mtDNA, which tentatively pointed towards both mtDNA and morphological separation.

Here, we extend the previous study by quantifying morphological variation and describing mtDNA lineages within this species group, the latter based on a more rapidly evolving mtDNA gene. A detailed analysis of morphology and mtDNA at the Taza site was aimed at assessing potential speciation within this group. Individuals from five further sample localities (representing all three subspecies) were also used to help describe mtDNA diversity across morphological forms and provide a framework against which variability and speciation could be assessed.

MATERIAL AND METHODS

Morphological data and tissue samples for DNA analyses were collected in April 2003 and April 2004 from the following localities: Oukaimeden, Gaada of Debdou, Balcon d'Ito, Caves of Chiker and Taza in Morocco; and Menorca, in the Balearic Islands (Fig. 1). The two morphological forms at Taza (Harris *et al*., 2003) were sampled separately. Additional data were obtained from three other Moroccan localities: Jbel Bour, Mischliffen and Tizi-n-test (Fig. 1) to increase the sampling area, although these were not included in the morphological analyses due to small sample sizes.

Individuals were sexed, measured and tail tips collected for DNA analyses. Ventral, lateral, and dorsal pictures were taken of all individuals before release at the capture site.

MORPHOLOGICAL ANALYSES

Adult individuals (males, $N = 83$; females, $N = 88$) were sexed on the basis of head and body robustness and development of femoral pores (Richter, 1986; Perera, 2005). Juveniles could not be sexed and so were excluded from morphological analyses. Males and females were sexually dimorphic and were analysed separately. Seven body measurements, three scalation characters, and seven colour pattern characters (see Appendix) were recorded by the first author in all cases. Snout–vent length (SVL) was measured to the nearest 0.5 mm using a ruler, and the remaining body measurements with a Vernier calliper to the nearest 0.1 mm. Bilateral measurements (FLL and HLL) were taken from the right side of the animal. Data could not be obtained in 14 cases (1.3% of the data) and hence they were substituted by group means (adjusted for body size, if necessary). Scalation and coloration characters (see Appendix) were recorded at least twice from photographs.

All body measurements were log-transformed to meet normality assumptions, and adjusted to a standard SVL using the pooled within-group regression coefficients, after testing for homogeneity of slopes. New values were used in posterior multivariate analyses.

Generalized variation in the colour pattern was analysed with a correspondence analysis (CA) and a multiple correspondence analysis (MCA), which allowed simultaneous visualization of the relationships between the coloration characters and the individuals analysed (McGarigal, Cushman & Stafford, 2000). Morphometric and scalation characters were analysed using principal component analyses (PCA) and canonical discriminant function analysis (CDFA). The presence of two divergent maternal lineages at Taza had already been established (Harris *et al*., 2003), thus PCAs were performed on correlation matrices (McGarigal *et al*., 2000) across all individuals from this site. This allowed objective assessment of morphological differentiation without a priori assignment to putative groups. CDFA was used to maximize variation between a priori defined groups (populations) and to classify individuals based on the canonical discriminant functions (CDF).

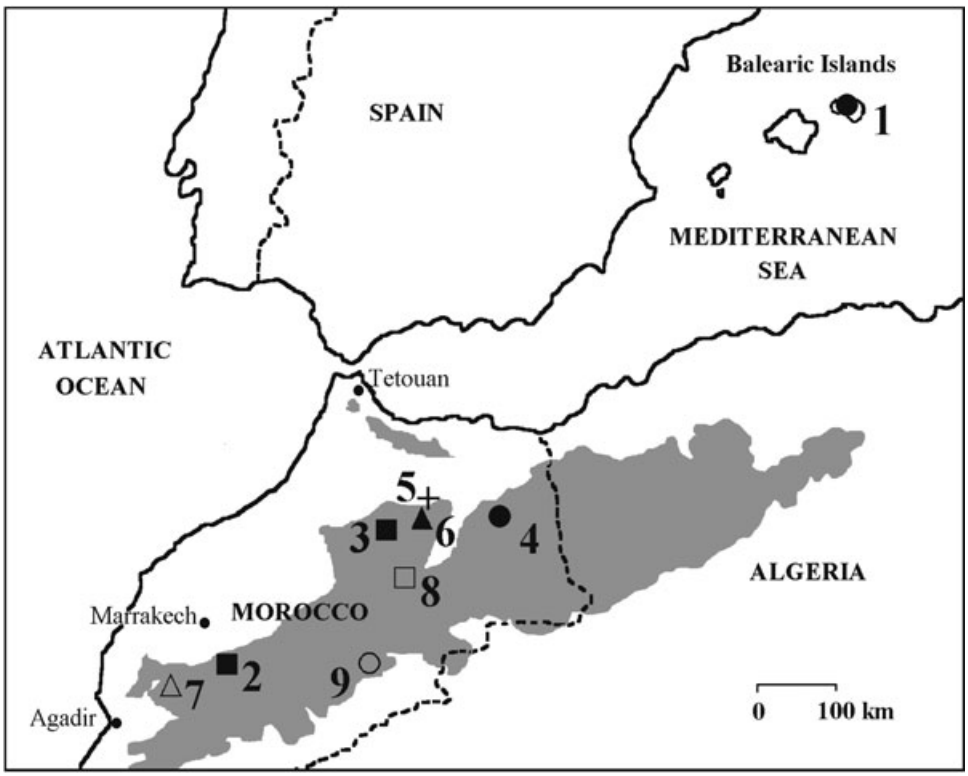

Figure 1. Localities under study. Symbols show current subspecies designation: □, *Lacerta perspicillata chabanaudi*; △, *Lacerta perspicillata perspicillata*; △, *Lacerta perspicillata pellegrini*; +, sympatry of *L. p. chabanaudi* and *L. p. pellegrini*. Solid symbols indicate localities with morphometric and genetic data, whereas open symbols indicate only genetic data. Localities: (1) Menorca, (2) Oukaimeden, (3) Balcon d'Ito, (4) Debdou, (5) Taza, (6) Caves of Chiker, (7) Tizi-n-test, (8) Mischliffen, and (9) Jbel Bour.

LABORATORY METHODS

Primers published by Arévalo, Davis & Sites (1994) were used to initially sequence 12 individuals for a region of the ND4 gene and adjacent tRNAs (light and heavy strands) using an automated sequencer (ABI310). This marker was chosen because it evolves more rapidly than the 12S rRNA (which had indicated the existence of two deeply divergent lineages but could not reveal diversity within lineages) (Harris *et al*., 2003). Sequences were aligned with two outgroup sequences using Clustal W (Thompson *et al.*, 1994): *Podarcis hispanica* and *Podarcis muralis*. From these sequences, the most variable region was identified by eye. Two new primers were designed (5′-GAT TAATCCGCATTTCAC-3′ and 5′-AGGGCTGAAGAT GTTAGGC-3′) to amplify this 253-bp region. 150 samples (Table 1) were amplified using these primers, and variation was identified using the single-strand confirmation polymorphism (SSCP) approach. PCR product (1 μL) was mixed with 5 μL of denaturing loading buffer, and samples were denatured for 4 min at 94 °C. A further sample (5 μL) was run on a 12% polyacrylamide gel (49 : 1) with 1 × TBE buffer on a vertical electrophoresis system at a constant 250 V and temperature (12 °C) for 18 h. The results were visualized by silver-staining. Preliminary results were compared against the initial samples of known sequences, and

Table 1. Distribution of the 13 haplotypes determined from 150 individuals from nine localities (including two morphological forms from Taza) determined using single-strand confirmation polymorphism

Origin	*N*	Haplotypes
Balcon d'Ito	29	27A, 2L
Taza *pellegrini*	27	27C
Taza *chabanaudi*	25	25B
Caves of Chiker	29	27C, 2I
Debdou	5	3E, 2K
Oukaimeden	5	5F
Mischliffen	5	1G, 4H
Menorca	23	21D, 2J
Jbel Bour	1	1A
Tizi-n-test	1	1N
Total	150	13 haplotypes

all new conformers were sequenced to identify the haplotypes. Analyses were concentrated where two syntopic forms are found (Harris *et al*., 2003).

Phylogenetic analyses

Mitochondrial DNA sequences were imported into PAUP* 4.0b10 (Swofford, 2003) for phylogenetic analyses based on maximum likelihood (ML) and maximum parsimony (MP). MrBayes was used for Bayesian inference (Huelsenbeck & Ronquist, 2001). For the former, we used the approach outlined by Huelsenbeck & Crandall (1997) to test 56 alternative models of evolution, employing PAUP* 4.0b10 and Modeltest (Posada & Crandall, 1998). The best model was subsequently used to estimate a tree using ML (Felsenstein, 1981) with random sequence addition (100 replicate heuristic search). The MP analysis was also performed with random sequence addition (100 replicate heuristic search), and support for nodes was estimated using the nonparametric bootstrap technique (Felsenstein, 1985) with 1000 replicates. Bayesian analyses were conducted with random starting trees, run 0.5×10^6 generations, and sampled every 100 generations using a general-time-reversible model of evolution (Rodriguez *et al*., 1990) with a gamma model of among site rate variation. In both searches, 'burn-in' data sampled from generations preceding stationarity of the Markov chain were discarded. All data collected at stationarity were used to obtain a 50% majority-rule consensus tree with posterior probabilities for internal nodes. Two independent replicates were conducted and inspected for consistency to check for local optima (Huelsenbeck & Bollback, 2001).

RESULTS

Morphological and genetic differentiation in sympatry

The first objective was to examine whether the two sympatric forms living in Taza were morphologically and genetically distinct. Not all colour pattern characters varied between individuals. For males, only ventral dark spots in the longitudinal rows (VRP), dorsal design (DD) and degree of contact among spots (DCS) were analysed using CA. Only two characters varied between females (i.e. DD and DCS) and so multivariate techniques were not applied. In males, the first CA axis (71% of total variation) distinguished two clearly non-overlapping colour pattern groupings (Fig. 2), with similar differentiation being observed for female dorsal pattern (Table 2). Thus, the two colour pattern morphs could be objectively assigned to the *L. p. pellegrini* and *L. p. chabanaudi* subspecies, and so will be referred to as Taza *pellegrini* and Taza *chabanaudi* from this point onwards. Without exception, the former had a striped dorsal pattern formed by spots and lines whereas the latter showed a dorsal spotted pattern with no stripes. All *pellegrini* males were homogeneously grouped in the CA, whereas vari-

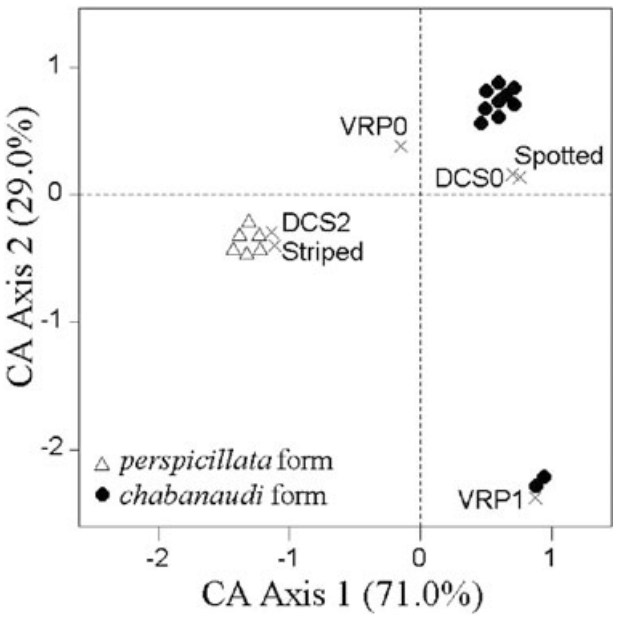

Figure 2. Correspondence analysis (CA): plot of male colour pattern characters (CA, % variance) and individuals from Taza on the first two axes. Colour pattern acronyms are followed by states, as given in the Appendix (e.g. 'DCS2' indicates character DCS, with state two, 'spots in contact').

Table 2. Female colour pattern variation at the Taza site (frequencies)

	Dorsal design		Contact among spots		
	Spotted	Striped	DCS0	DCS1	DCS2
Lacerta perspicillata pellegrini	0	13	0	0	13
Lacerta perspicillata chabanaudi	13	0	2	11	0

For an explanation of the codes, see both the text and Appendix.

ation within *chabanaudi* individuals was reflected along the second CA axis (Fig. 2). The *chabanaudi* morph generally lacked ventral dark pigmentation, although two males had dark pigmentation reduced to the first external scale row. A dorsal pattern with spots not in contact was found in males (Fig. 2), although some degree of contact in females was also found (Table 2).

PCAs on body dimensions and scalation characters also suggested two subspecies-concordant morphological groupings at Taza, although, unlike colour pattern, there was some limited overlap (Fig. 3). For males, HW had a low contribution to the retained principal components (communalities $c < 0.6$), thus we did not include it in the analyses presented here. Characters that contributed most to the male PC1 (30.6% of total variation) were limb length (FLL and HLL), pileus dimensions (PL and PW) and ventralia (Table 3). For PC2 (22.1%), the three most important characters were gularia, HLL, and SVL, whereas HH had the biggest influence on PC3 (14.2%). These character loadings were similar to some extent in females, with limb length (FLL, HLL), pileus dimensions (PL, PW), and HW variables contributing most to PC1 (41.3%); gularia, ventralia, and SVL to PC2 (15.0%); and gularia and HH to PC3 (12.2%).

The SSCP analysis showed that all 25 Taza individuals with the *chabanaudi* colour morph were fixed for a single haplotype (B; Table 1), whereas all lizards ($N = 27$) with a striped morph (*pellegrini*) corresponded to a different haplotype (C). Thus, in all individuals from Taza, there was perfect concordance between the morphological- and the mtDNA-based separation of the two forms.

MORPHOLOGICAL AND GENETIC DIFFERENTIATION AMONG LOCALITIES

Our second aim was to assess whether there was general concordance between external morphology and genetic lineage. For the colour pattern analyses, the first two axes of the MCA explained 60.8% and 59.3% of the variance in males and females, respectively, with similar patterns observed in both sexes (Fig. 4). The presence of dark pigmentation in the ventral areas (gular, chest, ventral, and cloacal areas) contributed most to the first axis (39.6% and 38.2% of total male and female variation, respectively). Second axes variances (21.2% in males and 21.1% in females) were explained mainly by dorsal coloration characters in both sexes: the presence of linked spots, the presence of dorsolateral lines and reduced dorsal pigmentation. Individuals assigned to *L. p. pellegrini* formed a homogeneous group but *L. p. chabanaudi* and *L. p. perspicillata* individuals did not, as reflected by within-group variation along the first and second axes, respectively.

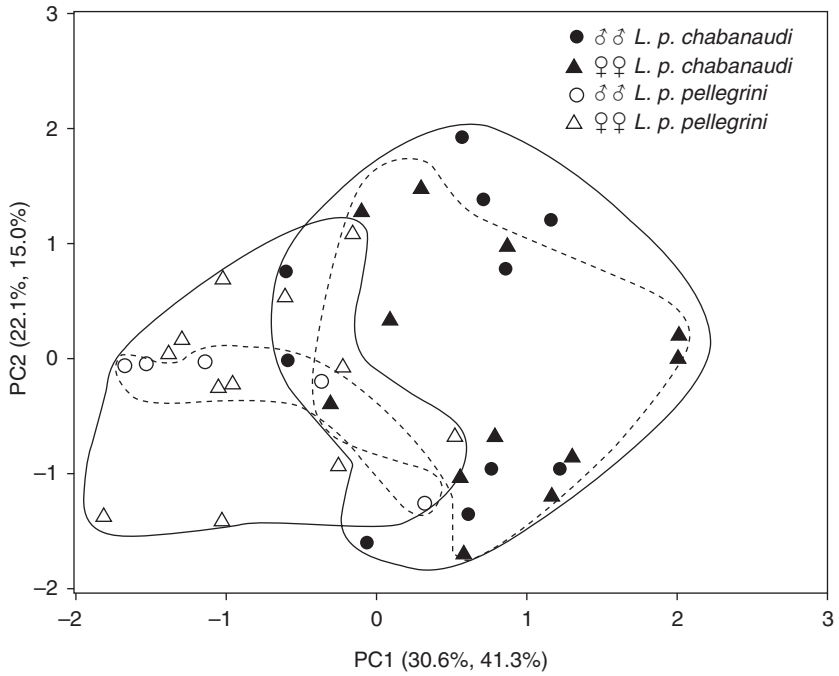

Figure 3. Plot of the first two principal components (PC1 and PC2 with percentage variation for males and females, respectively) from the analyses of body dimension and scalation variation in Taza. For brevity, the results of the separate male and female principal component analyses were included on the same plot.

Table 3. Summary results of the principal component analyses (PCA) (Taza individuals only) and the canonical discriminant function analysis (CDFA) (all sites)

	Taza (PCA)						All localities (CDFA)					
	Males			Females			Males			Females		
	PC1	PC2	PC3	PC1	PC2	PC3	CDF1	CDF2	CDF3	CDF1	CDF2	CDF3
PW	–0.840	0.053	0.329	0.790	0.041	–0.230	–0.358	0.230	0.333	0.060	0.133	0.590
PL	–0.500	–0.070	–0.440	0.901	0.000	0.004	–0.169	0.200	0.141	0.325	0.534	0.278
HH	–0.350	0.482	0.680	0.460	0.014	–0.560	–0.730	–0.138	0.058	–0.415	0.258	0.457
HW	–	–	–	0.937	0.048	0.023	–0.083	–0.383	0.394	0.208	0.662	0.060
FLL	0.699	0.452	–0.150	0.728	0.355	0.355	0.161	0.013	–0.030	0.403	0.450	0.342
HLL	0.529	0.598	0.013	0.828	0.222	0.265	–0.030	–0.213	0.549	0.248	0.560	0.380
SVL	0.047	0.778	0.208	–0.250	0.594	0.454	0.192	–0.345	0.017	0.036	0.089	–0.570
Gularia	0.310	–0.670	0.498	0.274	–0.550	0.548	0.524	0.349	–0.216	0.551	–0.272	–0.156
Collaria	0.242	–0.260	0.430	0.316	0.244	–0.390	0.087	–0.207	0.096	0.200	0.101	–0.010
Ventralia	0.870	–0.260	0.138	–0.390	0.779	–0.050	0.271	0.543	0.360	0.166	–0.402	0.104
Eigenvalue	2.756	1.988	1.281	4.130	1.503	1.219	6.701	1.106	0.738	4.960	2.354	0.799
%variance	30.600	22.100	14.200	41.300	15.000	12.200	71.100	11.700	7.800	57.000	27.000	9.200

Factor loadings of body measurements and scalation characters for the first three principal components (PC1, PC2 and PC3) are shown for individuals from Taza. Also shown are discriminant loadings for male and female morphometric and scalation characters, eigenvalues and percentage variance of the first two canonical variables. All body measurements were log-transformed and adjusted by the snout–vent length (SVL) (see text for details). For character abbreviations, see Appendix.

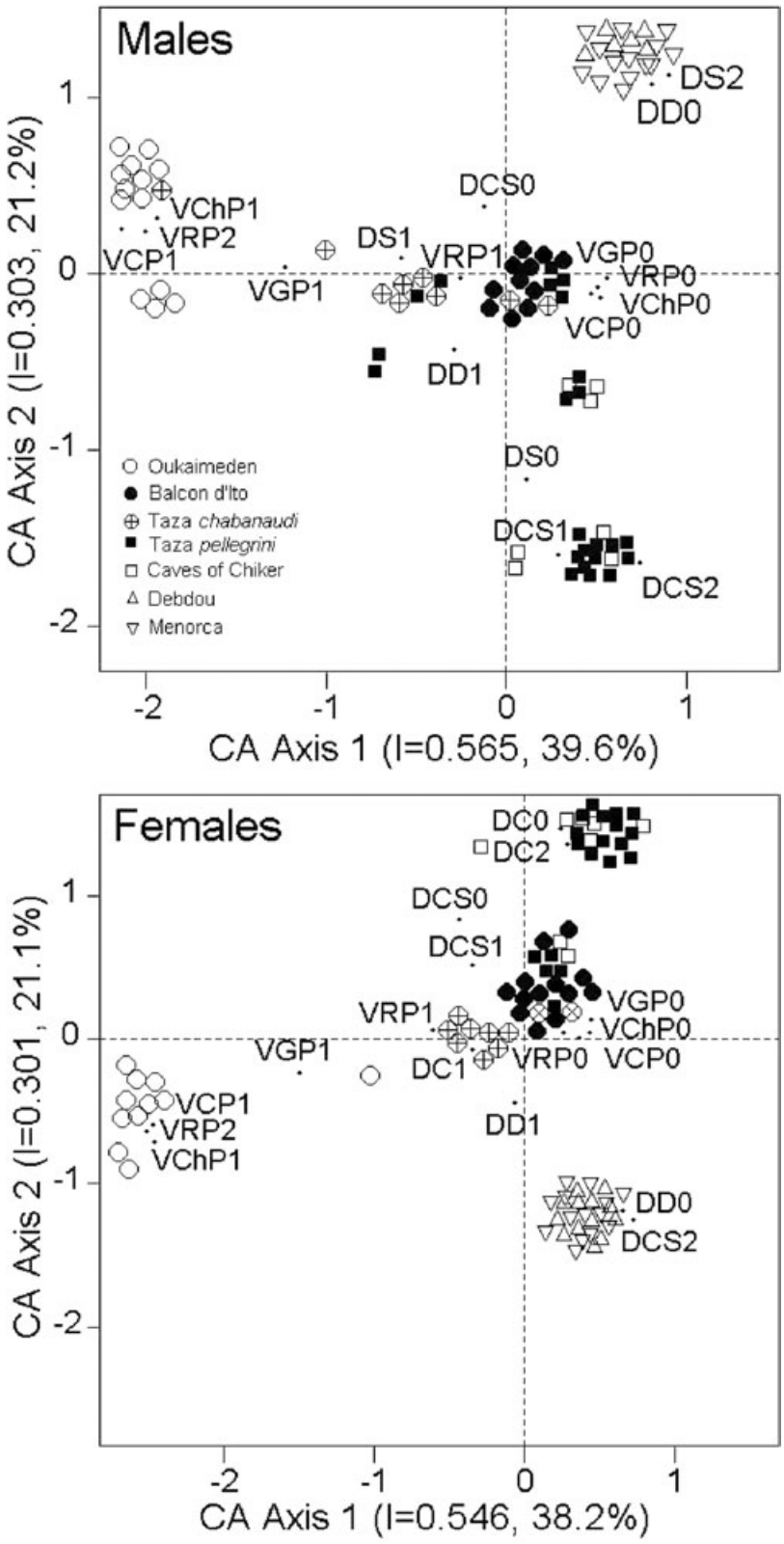

Figure 4. Plots of all individuals and their coloration characters against the first two multiple correspondence analysis axes (inertia, % variance) for males and females. Open and solid symbols represent the two different genetic lineages. Colour pattern characters and states are described in the Appendix.

For body dimensions and scalation characters (Fig. 5), the variables that contributed most to CDF1 (representing 71.1% of male and 57.0% of female variation) were HH and gularia in males and gularia in females (Table 3). Ventralia in males and PL, HW, and HLL in females contributed most to CDF2 (representing 11.7% in males and 27.0% in females). HLL in males and SVL and PW in females contributed most to CDF3 (7.8% and 9.2%, respectively; Table 3). A total of 85.5% of males and 85.3% of females were correctly assigned to their populations. The best-discriminated populations were Menorca (100% of individuals were correctly classified), Debdou (100%) and Taza *chabanaudi* (100%) for males, and Menorca (100%), Balcon d'Ito (90%) and Taza *chabanaudi* (92.3%) for females (Table 4).

The most appropriate model of sequence evolution for the data set was the HKY model, with sites assigned to discrete rate categories based on the γ distribution (*ts*/*tv* ratio = 5.064, γ shape parameter = 0.222). Using this model, the heuristic search found a single tree of –lnL = 3046 (Fig. 6). This was identical to the estimate of topology derived from both MP (one tree of 431 steps, 184 informative characters) and Bayesian inference (Fig. 6). This estimate of relationships is similar to that derived from 12S rRNA sequences (Harris *et al*., 2003) inasmuch as it identifies two main clades (i.e. one clade containing *L. p. perspicillata* from Menorca and Taza *chabanaudi* which is reciprocally monophyletic with a second clade containing all three subspecies of *L. perspicillata*). However, the faster evolving marker used here allowed additional well-supported lineages to be identified within each of these two main clades (e.g. the reciprocal monophyly of Menorca and Taza individuals in the first clade). Of the 150 samples analysed using SSCP, 13 different electromorphs were determined, corresponding to the distinct haplotypes (Table 1). Nevertheless, the phylogeny bears no correspondence with either subspecies, nor does it provide coherent geographical patterns (Fig. 6).

DISCUSSION

The mtDNA analysis confirms the prima facie suggestion that there are two distinct syntopic lineages of *L. perspicillata* at Taza (Harris *et al*., 2003), and that these lineages correspond to two distinct external morphologies: (1) a *L. p. chabanaudi* form (i.e. a spotted dorsal pattern, larger, longer limbs and a greater number of gular scales) and (2) a *L. p. pellegrini* form (i.e. a striped dorsal pattern, smaller size, shorter limbs and lower number of gular scales). This fact, together with the degree of genetic divergence between them, the strict syntopy in which they are found, and the lack of gene flow, would normally be considered evidence of specific differentiation. The main criterion for the Biological species concept (Mayr, 1942) (the dominant nonphylogenetic species concept) appears to be met in that there is no evidence of interbreeding between the two forms. The complete separation into two divergent lineages would also make them good phylogenetic species (Nixon & Wheeler, 1990). However, what would appear to be a

Table 4. Classification of individuals by locality based on the canonical discriminant function analysis

	Oukaimeden	Debdou	Menorca	Balcon d'Ito	Taza *chabanaudi*	Taza *pellegrini*	Caves of Chiker
Males							
Oukaimeden	10 (76.9%)	1 (7.7%)		1 (7.7%)			1 (7.7%)
Debdou		7 (100%)					
Menorca			21 (100%)				
Balcon d'Ito	2 (18.2%)			7 (63.6%)	1 (9.1%)	1 (9.1%)	
Taza *chabanaudi*					11 (100%)		
Taza *pellegrini*						3 (50%)	3 (50%)
Caves of Chiker						2 (14.3%)	12 (85.7%)
Females							
Oukaimeden	8 (72.7%)					1 (9.1%)	2 (18.2%)
Debdou	1 (12.5%)	6 (75%)				1 (12.5%)	
Menorca			19 (100%)				
Balcon d'Ito				9 (90%)			1 (10%)
Taza *chabanaudi*				1 (7.7%)	12 (92.3%)		
Taza *pellegrini*		1 (7.7%)				11 (84.6%)	1 (7.7%)
Caves of Chiker		1 (7.1%)				3 (21.4%)	10 (71.4%)

The percentage values indicate assignment success in a posterior jacknife analysis.

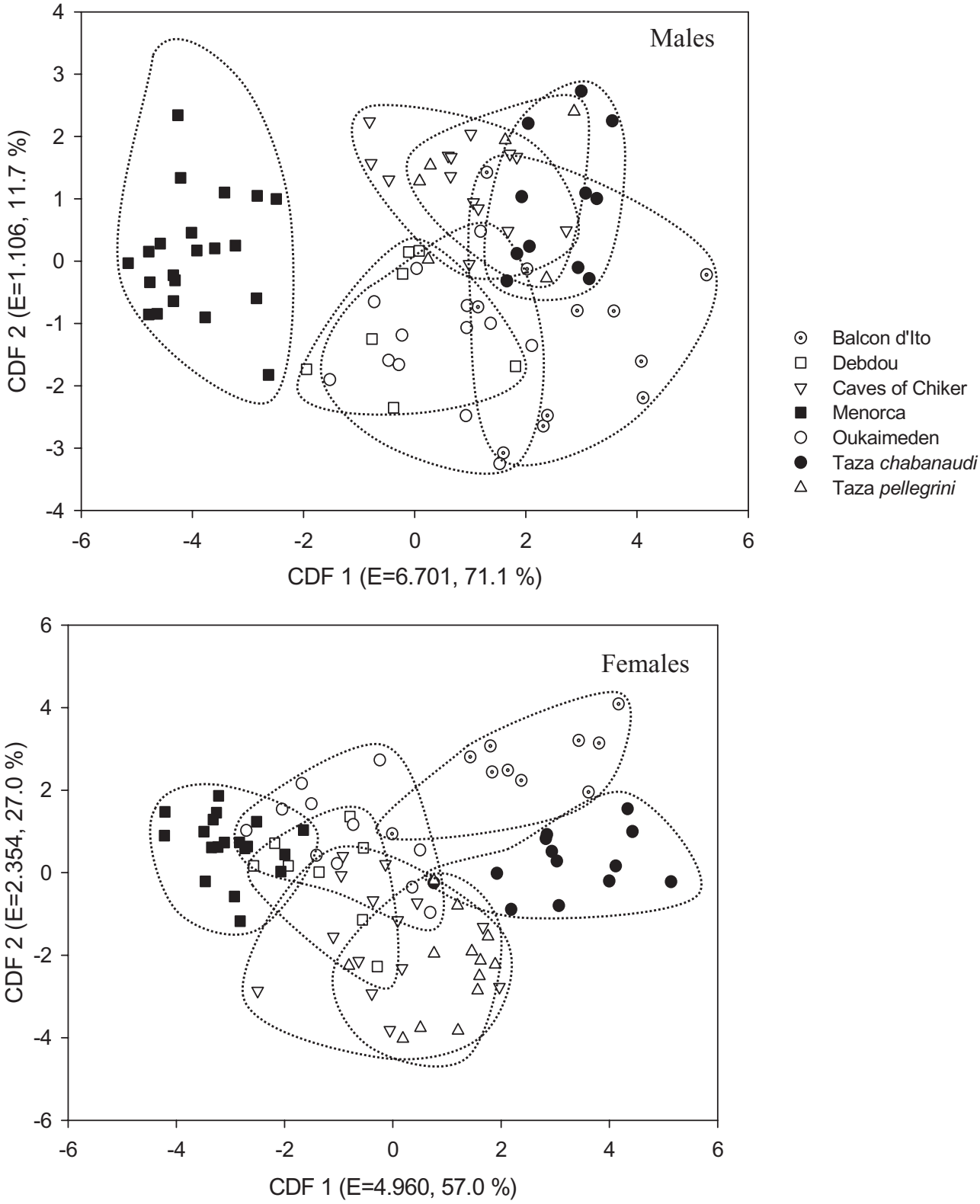

Figure 5. Plots of individual canonical discriminant function scores (CDF 1 and CDF 2) for males and females. Graphs are based on morphometric and scalation characters. Simples represent subspecific designations: circles, *Lacerta perspicillata chabanaudi*); squares (*Lacerta perspicillata perspicillata*); triangles (*Lacerta perspicillata pellegrini*). Open symbols represent individuals from genetic lineage 1 and solid symbols represents individuals belonging to genetic lineage 2.

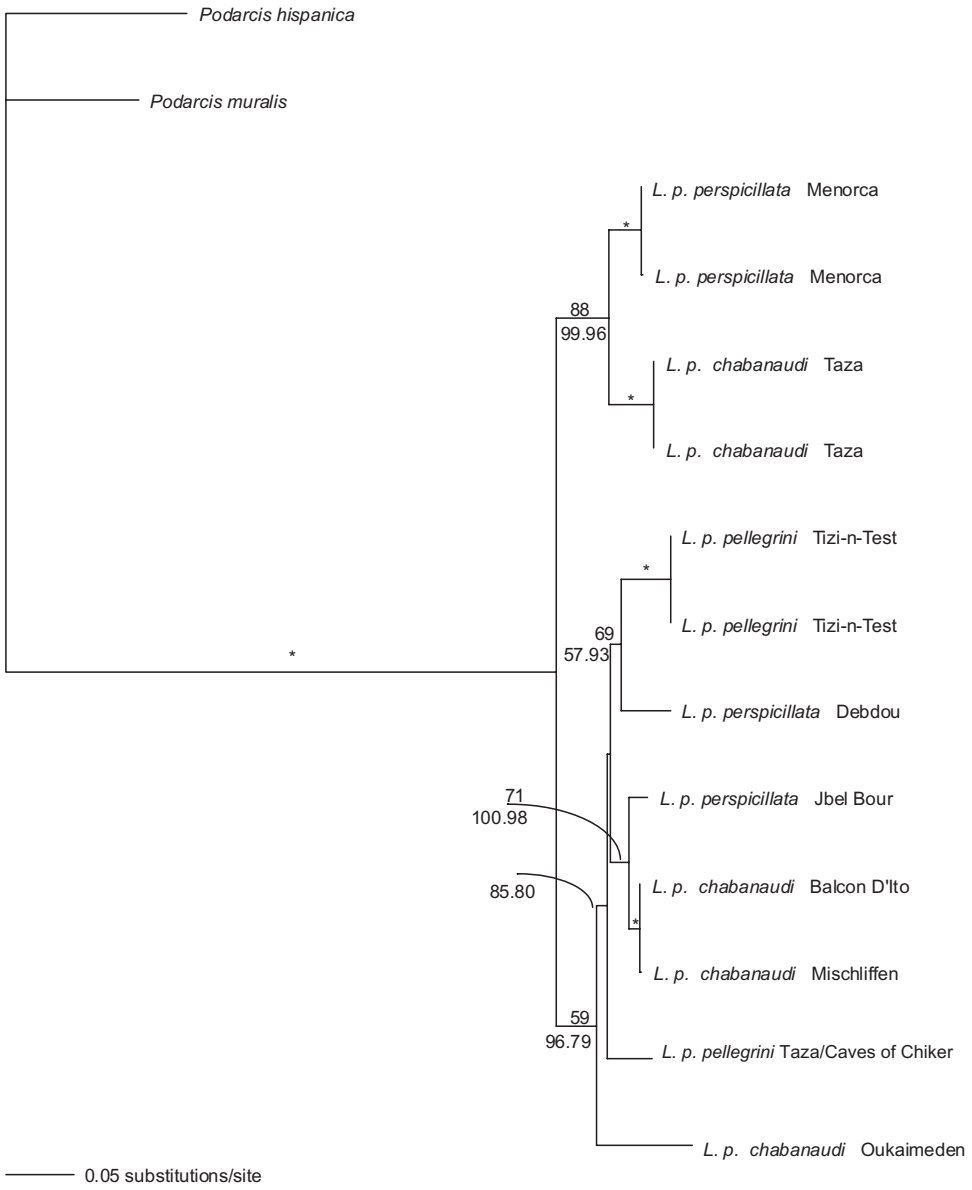

Figure 6. Estimate of relationships derived using maximum likelihood (ML), maximum parsimony (MP), and Bayesian analyses results. Numbers above nodes are MP bootstrap support values, numbers below nodes are ML, and Bayesian support/credibility values. *All methods have 100% support.

indisputable case of speciation at Taza is complicated by the information available from other sites, where the same genetic lineages have reversed morphotypes. This shows how the wider geographical sampling was vital to the analysis of this species complex, even if the finding of an additional level of complexity has hindered immediate taxonomic conclusions from being reached.

All populations could be assigned to one of the three current subspecies on the basis of the external morphology, particularly colour pattern. However, in most cases, heterogeneity among populations with similar external morphology is evident. In *L. p. perspicillata*, the two populations included in this study (i.e. Debdou and Menorca) had similar uniform or low-contrast spotted dorsal patterns but different generalized body dimensions and scalation values. We could not rule out the possibility that this differentiation is due to the insular nature of the Menorcan population: habitat structure and quality might influence, at least partially, some morphological traits in lizards (Losos, 1990; Vitt, Zani & Avila-Pires, 1997; Herrel, De Grauw & Lemos-Espinal, 2001; Glor *et al*., 2003). However, mtDNA analysis revealed that both popu-

lations belong to two different lineages. *L. p. chabanaudi* follows a similar pattern to the *perspicillata* form. All populations had a very contrasted spotted dorsal body, with pale spots on a very dark or black bottom, but differences in other morphological characters were evident in some cases. Thus, Oukaimeden was well differentiated by the presence of dark pigmentation along the ventral body whereas, in Balcon d'Ito and most Taza *chabanaudi*, ventral pigmentation was mainly reduced or non-existent. Generalized morphology of individuals from Oukaimeden was relatively different from the ones from Balcon d'Ito and Taza *chabanaudi*. Again, mtDNA analyses showed that this subspecies does not form a monophyletic group. Finally, *L. p. pellegrini* forms a homogeneous group, with individuals from the two analysed populations highly similar in body dimensions, scalation characters, and coloration pattern. This fact is congruent with the genetic results, where both *pellegrini* populations share a common haplotype. The two populations are only 15 km from each other, close to the Middle Atlas, so this result is not unexpected. Interestingly, Bons & Geniez (1996) noted differences between *L. p. pellegrini* populations from Middle Atlas and the ones from the High Atlas, and the sample of *L. p. pellegrini* from this latter region is not a sister taxon to the individuals from the Middle Atlas. More phylogenetic and morphological analyses, including population based sampling from both areas, are needed to better understand the variation within this form.

The present analysis provides no support for any of the currently recognized subspecies. By contrast, the lack of congruence between mtDNA lineages and morphometric patterns in some cases and the high morphological similarity among lizards from different lineages may suggest ecophenotypic convergence or multiple introgressive hybridization. However, this remains speculative because sampling across the full range of this complex is incomplete (Algerian populations are absent) and we may not have yet described the full range of morphological and mtDNA diversity in this complex.

In summary, the results obtained for *L. perspicillata* are of relevance to the historical biogeography of this understudied region. In particular, we have demonstrated that this is another cryptic species complex, as seen in *Agama* (Brown, Suárez & Pestano, 2002) and *Podarcis* (Harris *et al*., 2002), suggesting that complex intraspecific biodiversity is common in north-west African lizards. In addition, our analysis of the intraspecific variation within *L. perspicillata* shows that, despite the genetic separation and morphological distinctiveness observed in the two syntopic forms from Taza, we are unable to recommend respective species status for the two forms. This highlights how obtaining more data on different character systems can actually make it more difficult to group low-level taxa together under a particular species concept.

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APPENDIX

MORPHOLOGICAL AND SCALATION CHARACTERS MEASURED

Morphometric characters (mm)

- SVL (snout-vent length)
  - PL (pileus length)
  - PW (pileus width)
  - HH (head height)
  - HW (total head width)
  - FLL (fore-limb length)
  - HLL (hind-limb length)
- Scalation characters
  - Gularia (number of gular scales)
  - Ventralia (number of ventral scales)
  - Collaria (number of collar scales)
- Colour pattern characters
  - Ventral
    - VGP: Dark spots in the gular area (0 = absence, 1 = presence)
    - VChP: Dark spots in the chest area (0 = absence, 1 = presence)
    - VRP: Dark spots in the longitudinal rows (0 = absence, 1 = reduced to the first two external rows, 2 = not reduced to the two external rows)
    - VCP: Dark spots in the cloacal scales (0 = absence, 1 = presence)
  - Dorsal
    - DD: Design (0 = striped, 1 = spotted)
    - DCS: Contact among spots (0 = not in contact, 1 = in contact but irregularly, 2 = in contact forming stripes)
    - DC: Contrast (0 = high contrast in all the dorsal area, 1 = high contrast reduced to the vertebral area, 2 = low contrast)