Cryptic variation in the Moroccan high altitude lizard *Atlantolacerta andreanskyi* (Squamata: Lacertidae)

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**Abstract.**—*Atlantolacerta andreanskyi* is a mountain specialist lacertid lizard, restricted to areas above 2400 m of the High Atlas Mountains of Morocco, with apparently no geographic connection between different populations. In a recent molecular study, populations from *A. andreanskyi* collected across its distribution area were analysed, showing unprecedented levels of genetic differentiation for mitochondrial markers, which were also partially differentiated for nuclear markers. Here we aim to investigate, for the first time, the phenotypic variability of this species, using univariate and multivariate analyses on linear measurements, pholidotic and coloration characters in six populations of *A. andreanskyi* previously analysed genetically and covering most of its distribution range. The results show that despite the high genetic divergence previously detected, morphological variation among populations was low. Thus, although some genetic lineages could be partially discriminated morphologically at a multivariate level, single diagnostic traits could not be identified, and thus, they can be considered as cryptic lineages. Although the extreme genetic diversity observed supports the existence of six independent entities, more prospecting and analysis of additional populations will be needed to confirm the evolutionary independence of the lineages before their formal description.

**Key words.** —Cryptic species; high altitude; lacertid; Morocco; morphology

**INTRODUCTION**

Delimiting species, despite being a controversial issue, is of major importance since species are the basic unit in areas such as ecology, biogeography and evolution, with strong implications in taxonomy, and consequently conservation actions (Myers *et al.* 2000; Sites & Marshall 2003). Determining if a population constitutes an independent evolving lineage poses more difficulties in recently separated species, which are less likely to achieve criteria such as morphological distinctiveness, reproductive isolation, ecological divergence and monophyly (de Queiroz 2007). Moreover, speciation is not always accompanied with phenotypic changes, potentially leading to an underestimation of the actual levels of biodiversity. Cryptic species are an example that can be difficult to classify, particularly because morphology has been traditionally the main tool for identifying and classifying new species. Although in the past two decades the study of cryptic species has increased (Padial & de la Riva 2009; Detwiler *et al.* 2010; Florio *et al.*
mainly due to the advances in molecular and analytical methods, cryptic diversity remains a challenge for taxonomists. Additionally, delimitation of allopatric forms is a further challenge, as it is difficult to measure objectively some of the criteria that, usually, determine reproductive isolation.

Cryptic species are found across all biogeographical regions and major metazoan groups (Pfenninger & Schwenk 2007). In North Africa, new cryptic diversity has recently been described in several taxa such as plants (Abdelaziz et al. 2011), spiders (Duncan et al. 2010), mammals (Ben Faleh et al. 2012) and reptiles (Perera & Harris 2010; Rato et al. 2012). The diverse geographical and geological features and the variety of climates exert different selective pressures that have promoted speciation processes in the region, and some areas, such as the Atlas Mountains, are especially interesting. This mountain system formed at the Africa–Eurasia plate boundaries, uplifted during the Cenozoic (Gómez et al. 2000) and has been identified as refugia during the Pleistocene climatic fluctuations (Medail & Diadema 2009), harbouring a diversity that is still underexplored. Moreover, there are an increasing number of examples (Brown et al. 2002; Fritz et al. 2006; Recuero et al. 2007; Rato et al. 2010) demonstrating a role of the Atlas system in species diversification. The most recent study of the Moroccan day gecko (genus *Quedenfeldtia*), endemic to the Atlas region, reveals high levels of genetic diversity and confirms once more the interest of this region as source of cryptic speciation (Barata et al. 2012b).

*Atlantolacerta andreanskyi* (Werner 1929) is a small lacertid lizard endemic to the western and central High Atlas Mountains of Morocco. It is the lacertid found at higher altitudes, being restricted to areas between 2 400 m and 3 800 m a.s.l. (Bons & Geniez 1996; Schleich et al. 1996). It is often found near watercourses and in the base of cushion-like thorny plants (Bons & Geniez 1996) that offer a buffered microclimate with humidity, food, and protection against predators and wind (Schleich et al. 1996). In a recent study, individuals from eight different geographic populations, covering the distribution range of *A. andreanskyi*, were compared using a multilocus approach, which included two mitochondrial and five nuclear markers (Barata et al. 2012a). Results revealed an extreme genetic diversity among seven of the eight populations analysed in mtDNA, showing divergence levels ranging from 1.6% to 6.6% in 12S rRNA and 5.5% to 16.5% in ND4. The nuclear markers (ACM4, MC1R, C-MOS, PDC and RAG1) were concordant with the mtDNA pattern, although monophyly was not retrieved in some populations. In view of these results, the authors suggested the possibility that *A. andreanskyi* might be a complex of species. Unfortunately, due to the restricted, and in many cases inaccessible distribution range, there is a profound lack of knowledge regarding this species, and the few existing studies (Werner 1929, 1931, 1935; Saint Girons 1953; Pasteur & Bons 1960; Klemmer 1969; Stemmler 1972; Busack 1987; Volobouev et al. 1990) are mostly based on individuals from two geographically close populations from the High Atlas (Oukaimeden and Toubkal). The only available studies on morphology and sexual dimorphism are also based on these populations (Busack 1987; Rykena & Bischoff 1992; Schleich et al. 1996), although Destre et al. (1989) and Joger & Bischoff (1989) mention the population from Jebel Ayache and the possibility that this population is distinct from the others at a subspecific or specific level, but without any detailed explanation other than its geographical isolation.

In consequence, there is an urgent need to collect data concerning the morphological variation across the distribution range of the species, in order to evaluate its real “cryptic nature”. In this study we investigate the morphological variation within *A. andreanskyi* in
six different populations, in order to assess if the genetic lineages detected in Barata et al. (2012a) represent cryptic lineages. To achieve this, analyses of body measurements, pholidosis and coloration characters were performed.

**MATERIALS AND METHODS**

**Sampling and Data Collection**

The study area comprises the western and central parts of the High Atlas Mountains of Morocco, across the distribution range of *A. andreanskyi* (Bons & Geniez 1996). Sampling took place between 2008 and 2011. A total of 139 specimens from 6 of the 8 populations genetically characterized in Barata et al. (2012a), covering most of the species distribution range, were sampled (Figure 1): Jebel Sirwa (13 males (M) and 9 females (F)), Oukaimeden (14M, 17F), Tizin Tichka (12M, 12F), Jebel Azourki (10M, 21F), Outabati (6M, 5F) and Jebel Ayache (8M, 12F). Populations sampled ranged from 2 390 to 3 000 m altitude (Figure 1). Despite considerable effort to sample in the other two populations included in the genetic study (Toubkal and Jebel Awlime), only two and three specimens could be found, respectively, and thus, they were not included in the morphological analysis. Specimens were caught by hand, identified and sexed on the basis of external features (Schleich et al. 1996).

![Figure 1. Distribution map and altitude of the populations of *Atlantolacerta andreanskyi* included in the study and phylogenetic relationships of the mitochondrial lineages retrieved in the study by Barata et al. (2012a). White small dots represent the known distribution of the species as available in Bons & Geniez (1996). See Barata et al. (2012a) for more information regarding the genes included and support values of the clades. Jebel Awlime and Toubkal localities were not included in the study but are highlighted on the map since they were included in the genetic study by Barata et al. (2012a).](image)
In total, seven linear measurements, nine pholidotic characters, and seven coloration characters were recorded. Snout vent length (SVL) was measured from the tip of the snout to the cloacal opening; trunk length (TRL) was measured from the posterior edge of the forelimb insertion to the anterior edge of the hindlimb insertion; head length (HL) was measured from the tip of the snout to the collar, head width (HW) at its widest part, usually at the level of the temporal region, and head height (HH) from occiput to jaws. The total lengths of frontlimbs (FLL) and hindlimbs (HLL) were measured from the longest toe to the base of the limb. Also, detailed pictures of dorsal, lateral and ventral body were taken in the field, and nine pholidotic variables recorded \textit{a posteriori} from them: number of ventral scales (VSN) including all the large scales counted in a midline from the collar to the anterior insertion of hindlimbs; number of gular scales (GSN) in a midline from the collar to the chin shields scales; number of collar scales (CSN), number of femoral pores (FPN) counted in males only; number of supratemporal scales (STSN); number of supralabial scales (SLSN); number of supraciliary scales (SCSN); number of supraciliary granules (SCGN), and number of enlarged side to side lamellae under the fourth toe (Lam). Regarding colour pattern, the following variables were also recorded from pictures: presence of black pigmentation (spots) in the lateral head (HPL, 1 = absent, 2 = scarce, 3 = abundant), dorsal head (HPD, 1 = absent, 2 = scarce, 3 = abundant), ventral head (HPV, 1 = absent, 2 = scarce, 3 = abundant), ventral body (VBP, 1 = absent, 2 = scarce, 3 = abundant) and cloacal region (CD, 0 = absent, 1 = one single dot in the anal plate, 2 = two dots in the anal plate; 3 = three dots in the anal plate); presence of a central dorsal line (CBL, 1 = absent, 2 = discontinuous, 3 = continuous) and presence of light dorsolateral lines (Wline, 1 = absent, 2 = present).

Since morphological measurement techniques can vary between observers (Roitberg et al. 2011), all linear measurements were recorded in the field by the same author (MB) to the nearest 0.01 mm, using a digital calliper. Pholidotic and colour variables were also retrieved from digital pictures by the same author (MB) at least twice and the mean value was recorded. In 4.83% of the cases (141 of the 2,919 cases), data could not be collected due to missing limbs or toes, or poor picture quality, and thus they were replaced by the group mean (both sex and population).

Only adult individuals were included in this study. Individuals were released in the same place where they were caught after recording the coordinates of the location with a GPS. Tissue samples from the localities in this study were already characterized genetically in Barata et al. (2012a) (Figure 1).

\textbf{Statistical Analysis}

Body measurements and pholidotic variables were log-transformed and checked for homoscedasticity (Levene's test, lawstat R package) and normality (Shapiro–Wilks test, R Development Core Team 2011) assumptions. Since linear measurements were highly correlated to body size (SVL, Pearson correlation in all cases $p < 0.01$, R Development Core Team 2011), we used an isometric correction (Somers 1986) to estimate body-size-corrected variables that were then used to investigate the existence of possible differentiation shape patterns. For this, all linear measurements (log transformed) were projected on an isometric vector, in order to obtain a multivariate representation of the isometric size of each individual (mSIZE). Each variable was then regressed on this isometric vector and the residuals obtained were used as size-corrected variables. Thus,
the multivariate representation of isometric size (mSIZE) was used as a size estimator, whereas the remaining isometric-size corrected variables (residuals) were used as a representation of shape (Kaliontzopoulou et al. 2010). All this procedure was manually implemented in the R package (R Development Core Team 2011).

Given the different sample sizes among populations, we used a nonparametric (permutational) analysis of the variance (MANOVAs) based on euclidean distance matrices to investigate the effects of the factors POPULATION, SEX and its interaction (POPULATION*SEX) on size (mSIZE), shape (isometric-size corrected variables) and pholidotic characteristics of the lizards. This approach partitions the sum of squares of distance matrices among groups to generate F statistics, whose significance is determined by comparing the observed effects against random permutations of the data. These analyses were done using the function adonis implemented in the R package Vegan (Oksanen et al. 2011). Additionally, sexual dimorphism within each population was investigated at univariate level using the same nonparametric permutational approach but including sex as a single factor.

To investigate the generalized morphological relationships among the different A. andreanskyi populations at a multivariate level Canonical Discriminant Function Analyses (CDA) were performed on measurements (isoSIZE and shape variables) and pholidosis separately. Due to the sexual dimorphism existent, CDA analyses were performed separately in males and females. We used the leave-one-out option, which is based on the Jackknife resampling method, to cross-validate the classification results. Since this procedure generates individual classifications using discriminate functions based on all observations except the given case, it provides a more accurate estimate of the classification values. This analysis was performed using the function lda implemented in the R package MASS (Venables & Ripley, 2002).

Finally, variation in colour pattern between populations was investigated at a multivariate level using a Multiple Correspondence Analysis (MCA) using the dudi.acm function implemented in the R package ade4 (Dray & Dufour 2007).

All analysis and graphics were performed in an R environment (R Development Core Team 2011). In all cases, significance level was considered at $p < 0.05$.

## Results

Detailed descriptive statistics for all the linear measurements and pholidotic variables are presented in the online supplementary material (Table S1).

### Inter-lineage Variation

**Linear measurements.**—The permutational multivariate analysis of variance (MANOVA) showed general differences between POPULATION, SEX and its interaction in both size (mSIZE) and shape (Table 1). Regarding differences among populations, individuals from Jebel Azourki and Jebel Ayache had higher mSIZE values than the other populations, and this pattern was congruent in males and females (Figure 2). Populations also differed in all shape related variables (isometric-size corrected variables) (Table 1). Regarding differences between sexes, males had higher mSIZE values than females (Figure 2; Table 1). Males of A. andreanskyi had wider, higher and longer heads (HH, HL, HW), and longer front limbs (FLL) than females, but females had longer trunks (TRL, AFRICAN JOURNAL OF HERPETOLOGY 64(1) 2015 5
Table 1. Summary of the permutational analysis of variance (MANOVA) results regarding the effect of population (Pop), Sex and its interaction on multivariate size (mSIZE), shape (iso-corrected linear measurements) and pholidosis (log transformed variables). Significant values ($p < 0.05$) are in bold.

|       | TOTAL |       |       |       |       |       |       |
|-------|-------|-------|-------|-------|-------|-------|-------|
|       | Pop   | Sex   | Pop*Sex | Males | Females |
|       | F     | p     | F      | p     | F      | p     | F      | p     |
| mSIZE | 34.328 | 0.001 | 32.348 | 0.001 | 5.167   | 0.001 | 16.658 | 0.001 |
| shape | 9.840  | 0.001 | 38.567 | 0.001 | 1.945   | 0.005 | 5.438  | 0.001 |
| scales| 8.177  | 0.001 | 2.117  | 0.098 | 1.584   | 0.078 | 4.030  | 0.001 |
| TrL   | 10.862 | 0.001 | 303.110 0.001 | 5.620  | 0.001 | 6.229  | 0.001 | 5.222  | 0.001 |
| HL    | 2.865  | 0.016 | 23.891 | 0.001 | 1.306   | 0.271 | 0.974  | 0.470 |
| HW    | 11.731 | 0.001 | 50.561 | 0.001 | 1.654   | 0.145 | 8.534  | 0.001 |
| HH    | 9.149  | 0.001 | 20.685 | 0.001 | 1.887   | 0.105 | 4.121  | 0.003 |
| FLL   | 2.847  | 0.012 | 8.813  | 0.002 | 1.160   | 0.323 | 2.315  | 0.064 |
| HLL   | 11.880 | 0.001 | 3.110  | 0.088 | 0.788   | 0.572 | 6.767  | 0.001 |
| VSN   | 12.551 | 0.001 | 139.375 | 0.001 | 0.934   | 0.463 | 6.990  | 0.002 |
| FPN   | –     | –     | –      | –     | –      | –     | –      | –     |
| Lam   | 10.080 | 0.001 | 1.049  | 0.31  | 1.240   | 0.296 | 11.280 | 0.001 |
| STSN  | 5.838  | 0.001 | 0.791  | 0.375 | 2.162   | 0.054 | 3.204  | 0.019 |
| GSN   | 5.736  | 0.001 | 3.708  | 0.059 | 1.047   | 0.417 | 4.726  | 0.004 |
| CSN   | 10.521 | 0.001 | 2.911  | 0.082 | 1.488   | 0.2   | 2.669  | 0.033 |
| SCGN  | 9.913  | 0.001 | 0.532  | 0.481 | 1.073   | 0.38  | 4.292  | 0.003 |
| SCSN  | 2.161  | 0.06  | 0.217  | 0.613 | 3.767   | 0.004 | 1.812  | 0.107 |
| SLSN  | 6.547  | 0.001 | 1.543  | 0.239 | 1.550   | 0.163 | 6.040  | 0.001 |

Figure 2. Variation in multivariate size (mSIZE) in males (solid lines) and females (dashed lines) of the *A. andreanskyi* populations included in this study. For each population, mean values ± standard deviation is shown. JAy: Jebel Ayache, Jsir: Jebel Sirwa, Tizin: Tizin Tichka, Ouk: Oukaimeden, Jaz: Jebel Azourki, Out: Outabati. Symbols for each population correspond to the ones described in Figure 1.
Males and females had similar hindlimb length (HLL, Table 1, Figure S1). The degree of sexual dimorphism (POPULATION*SEX interaction) was similar among populations, with the exception of trunk length (TRL) (Table 1). Considering only males, we did find differences among populations in multivariate size (mSIZE) and shape (Table 1), as well as in most of the iso-corrected measurements with the exception of head length (HL) and front limb length (FLL) (Table 1). Regarding females, general differences in size and shape were also observed, and all linear measurements were significantly different among populations with the exception of the forelimbs (Table 1).

At a multivariate level, the Canonical Discriminant Function Analyses (CDFAs) showed a partial discrimination of the lineages, with different patterns in males and females (Table 2). In males, the first discriminant function (CDF1), which explains 63.3% of the total variation was mostly represented by mSIZE, TRL and HW (Table 2). The second function (CDF2) explains 19.48% of the total variation and has hindlimb

| Body measurements | Males     | Females   |
|------------------|-----------|-----------|
|                  | CDF1      | CDF2      | CDF3 | CDF1 | CDF2 | CDF3 |
| mSIZE            | -0.77     | -0.52     | 0.20 | 0.91 | -0.20 | -0.14 |
| TRL              | 0.47      | -0.62     | 0.06 | 0.18 | -0.73 | -0.14 |
| HL               | 0.02      | 0.33      | 0.24 | -0.27 | -0.26 | -0.26 |
| HW               | -0.46     | 0.13      | -0.85 | -0.12 | 0.62 | 0.15 |
| HH               | 0.32      | -0.32     | -0.27 | -0.18 | 0.78 | -0.10 |
| FLL              | -0.09     | -0.23     | 0.29 | 0.08 | -0.14 | -0.48 |
| HLL              | -0.34     | 0.70      | 0.40 | 0.24 | -0.17 | 0.80 |

| Eigenvalues     | 5.70      | 3.16      | 2.50 | 6.75 | 3.32 | 2.42 |
| % explained      | 63.33     | 19.48     | 12.19 | 68.56 | 16.59 | 8.83 |
| % cumulative     | 63.33     | 82.81     | 95.00 | 68.56 | 85.15 | 93.98 |

| Scales | Males | Females |
|--------|-------|---------|
|        | CDF1  | CDF2    | CDF3 | CDF1  | CDF2 | CDF3 |
| VSN    | -0.45 | -0.28   | 0.91 | 0.25  | 0.49 | 0.21 |
| FPN    | 0.49  | 0.57    | 0.17 | —     | —    | —    |
| Lam    | 0.58  | -0.49   | -0.13 | 0.28  | -0.02 | 0.07 |
| STSN   | 0.27  | -0.32   | -0.14 | 0.17  | -0.50 | 0.13 |
| GSN    | 0.42  | 0.34    | -0.01 | 0.20  | -0.01 | -0.41 |
| CSN    | 0.17  | -0.20   | 0.31 | 0.50  | 0.18  | -0.45 |
| SCGN   | -0.42 | 0.29    | -0.14 | -0.29 | 0.50  | -0.43 |
| SCSN   | 0.22  | 0.12    | -0.08 | -0.09 | 0.31  | 0.41 |
| SLSN   | 0.49  | -0.01   | 0.49 | 0.20  | 0.22  | 0.21 |
| Eigenvalues | 3.13  | 0.78    | 0.56 | 1.90  | 0.95  | 0.51 |
| % explained     | 62.00 | 15.40   | 11.20 | 53.40 | 26.60 | 14.3 |
| % cumulative    | 62.00 | 77.40   | 88.50 | 53.40 | 79.90 | 94.2 |

Table 2. Summary of the Canonical Discriminant Function Analyses (CDFA) performed on the linear measurements (including the multivariate size [mSIZE] and shape [remaining iso-corrected linear measurements]) and pholidosis. For each analysis the factor structure, eigenvalues, and partial and cumulative variation (as a percentage) of the first three canonical discriminant functions (CDFs) is given. Analyses were made separately for males and females. More contributing variables (> ± 0.40) are in bold. Femoral pores (NFP) are absent in females and thus this variable was not included in the CDFA analysis.
length (HLL) and again mSIZE and trunk length (TRL) as the most contributing variables (Table 2). Regarding the third discriminant function (CDF3), it explains 12.19% of the variation, and has head width (HW) and hindlimb length (HLL) as the most contributing variables (Table 2). In females, variation across CDF1 represented 68.56% of the total variation observed and was mostly represented by the variable mSIZE (Table 2). CDF2 (16.59% variation) was mostly explained by the variables trunk length (TRL), head height (HH), and head width (HW) (Table 2). Finally, CDF3, which represents 8.83% of the variation, was mostly explained by the length of the limbs (FLL and HLL) (Table 2).

The moderate discrimination power of the canonical functions was reflected in the correct classification percentages (Table 3). In males, the higher classification rates were 76.9% of individuals correctly classified for Jebel Sirwah and 75% for Jebel Ayache (75%), while Tizin Tichka (33.3%) and Jebel Azourki (20%) were the worst classified (Table 3). Regarding females, classification percentages were higher than in males. The better classified populations were Jebel Azourki (90.4%) and Outabati (80%), while Jebel Ayachi (33.3%) was the worst classified (Table 3).

**Pholidosis.**——MANOVA analysis of scales revealed generalized differences among populations, but not between sexes or the interaction POPULATION*SEX (Table 1). Populations differed in all the scalation variables analysed with the exception of SCSN (Table 1). Sexual differentiation in pholidosis was restricted to the number of ventral scales (VSN, Table 1) with a higher number in females than in males (Figure S2 in the online supplementary material). Interaction POPULATION*SEX revealed a different pattern of sexual dimorphism among populations only in the number of supraciliary scales (SCSN) (Table 1). Considering only males, we did find differences among populations in all the pholidotic variables analysed with the exception of number of supraciliary scales (SCSN) (Table 1). In females, differences among populations were observed in all the pholidotic variables analysed (Table 1).

However, in both sexes, the level of discrimination of the CDFA among populations was low and not congruent with the pattern retrieved from the body measurements analysis. In males, the first canonical function explains 62% of the total variation, with the main contribution of ventral (VSN), femoral (FPN), gular (GSN), supraciliar (SCGN) and supralabial (SLSN) scales and lamellae (Lam; Table 2). Regarding CDF2 (15.4% of the variation), the main contributing variables were the number of femoral pores (FPN) and the number of lamellae (Lam; Table 2). CDF3 (11.2% of the variation) was mostly explained by the number of ventral scales (VSN) and the number of supralabial scales (SLSN; Table 2). Regarding females, CDF1 explains 53.4% of the total variation and is mainly represented by the number of collar scales (CSN), while CDF2 explains 26.6% of the variation being the number of ventral (VSN) and supratemporal (STSN) scales and the number of supraciliary granules (SCGN) the most contributing variables (Table 2). CDF3 represents 14.3% of the variation and is mostly represented by the number of gular (GSN), collar (CSN) and ciliar (SCGN and SCSN) scales (Table 2).

As expected, the degree of discrimination was low in both sexes (Table 3). The discriminant functions did not provide good results as seen in the correct identification percentages (Table 3). In males, Oukaimeden was the best discriminated population (85.7%), while Jebel Azourki and Outabati had the lowest discrimination percentages (20% and 33.3% respectively, Table 3). In females, Oukaimeden also had the highest classification rate (82%, Table 3), while the worst classified population was Outabati (none of the individuals was correctly classified, Table 3). This might be the result of the
Table 3. Classification matrices based on the discriminant functions obtained from the analyses of the linear measurements (mSIZE and remaining isocorrected variables) and pholidotic variables (scales). For each pair of populations the percentage and frequency (in parentheses) are shown.

| Linear measurements | Population | Sex   | J. Sirwa | Oukaimeden | Tizin Tichka | J. Azourki | Outabati | J. Ayache |
|---------------------|------------|-------|----------|------------|--------------|------------|----------|-----------|
| J. Sirwa            | Males      | 76.9 (10) | –         | 7.7 (1)    | 7.7 (1)      | –          | 7.7 (1)  |
|                     | Females    | 44.4 (4)  | 22.2 (2)  | 11.1 (1)   | 11.1 (1)     | –          | 11.1 (1) |
| Oukaimeden          | Males      | –       | 64.3 (9)  | 28.6 (4)   | –            | 7.1 (1)    | –         |
|                     | Females    | 5.9 (1)  | 76.5 (13)| 11.8 (2)   | –            | –          | 5.9 (1)   |
| Tizin Tichka        | Males      | 8.3 (1)  | 41.7 (5)  | 33.3 (4)   | 16.7 (2)     | –          | –         |
|                     | Females    | –       | 33.3 (4)  | 50 (6)     | –            | –          | 16.7 (2)  |
| J. Azourki          | Males      | 30 (3)   | –         | 10 (1)     | 20 (2)       | 10 (1)     | 30 (3)   |
|                     | Females    | 4.8 (1)  | –         | –          | 90.4 (19)    | –          | 4.8 (1)  |
| Outabati            | Males      | –       | 16.7 (1)  | 16.7 (1)   | –            | 66.7 (4)   | –         |
|                     | Females    | –       | 20 (1)    | –          | –            | 80 (4)     | –         |
| J. Ayache           | Males      | 12.5 (1) | –         | –          | 12.5 (1)     | –          | 75 (6)   |
|                     | Females    | 8.3 (1)  | 8.3 (1)   | 16.7 (2)   | 33.3 (4)     | –          | 33.3 (4) |

| Scales | Population | Sex   | J. Sirwa | Oukaimeden | Tizin Tichka | J. Azourki | Outabati | J. Ayache |
|--------|------------|-------|----------|------------|--------------|------------|----------|-----------|
| J. Sirwa | Males      | 61.5 (8) | 7.7 (1)  | 7.7 (1)   | 7.7 (1)      | 15.4 (2)   | –        |
|         | Females    | 44.4 (4)| –        | 85.7 (12) | 7.1 (1)      | –          | 22.2 (2) | 33.0 (3)  |
| Oukaimeden | Males      | –      | 11.8 (2) | 82.4 (14)| 5.9 (1)      | –          | –        | –         |
|          | Females    | 11.8 (2)| 82.4 (14)| 5.9 (1)   | –            | –          | –        | –         |
| Tizin Tichka | Males      | 25.0 (3)| 16.7 (2) | 41.7 (33)| 8.3 (1)      | 8.3 (1)    | –        | –         |
|           | Females    | 18.3 (2)| 16.7 (2) | 5.9 (1)   | –            | –          | –        | –         |
| J. Azourki | Males      | 40.0 (4)| –        | 20.0 (2)  | 20.0 (2)     | 10.0 (1)   | 10.0 (1) | –         |
|            | Females    | 4.8 (1) | 4.8 (1)  | 19.0 (4)  | 61.9 (13)    | –          | 9.5 (2)  | –         |
| Outabati   | Males      | 16.7 (1)| –        | 16.7 (1)  | 16.7 (1)     | 33.3 (2)   | 16.7 (1) | –         |
|           | Females    | 16.7 (1)| –        | 20.0 (1)  | 80.0 (4)     | –          | –        | –         |
| J. Ayache | Males      | –      | –        | –         | –            | 38.0 (3)   | 62.5 (5) | –         |
|           | Females    | 8.3 (1)| 8.3 (1)  | –         | 25.0 (3)     | –          | 58.3 (7) | –         |
small sample size available for this population (only five females). Notably also the population with the largest number of analysed individuals (Oukaimeden) also had the highest percentage classified correctly.

**Colour pattern.**—Colour pattern variation showed a similar pattern in males and females (Figure 3), with three main groups: (1) Jebel Ayache and Outabati; (2) Tizin Tichka and Jebel Azourki; and (3) Jebel Sirwa and Oukaimeden. However, this pattern differs with the one observed in the pholidotic and body measurements analysis. In males, the first group, which includes the most oriental populations (Outabati and Jebel Ayache had, in general, a trend towards the absence of light dorsolateral lines (Wlline.1) and central dorsal line (CBL.1)). The second group, formed by the central populations of Tizin Tichka and Jebel Azourki, tend to have black spots in the ventral head (HPV.3) and two black dots in the anal plate (CD.2). The third group, formed by the occidental populations of Oukaimeden and Jebel Sirwa, showed a general trend towards a lack of black pigmentation in the ventral (VBP.1), head (HPL.1, HPV.1, HPD.1) and presence of continuous bright dorsolateral lines (Wllines.2). In females, the oriental group (Outabati and Jebel Ayache), tend to lack a central dorsal line (CBL.1) and light dorsolateral lines (Wlline.1), and to have slightly or unspotted heads (HPD.1, HPV.1, Figure 3). The central group (Tizin Tichka and Jebel Azourki) had, in general, a quite intense spotted pattern in ventral (HPV.3, VBP.3, CD3), lateral (HPL.3) and dorsal areas (HPD.3, HPD.2, CBL.3, CBL.2), continuous or discontinuous bright dorsolateral lines (Wlline.2), and more intense pigmentation in the anal plate (CD.2, CD.3, Figure 3). Finally, the occidental group (Oukaimeden and Jebel Sirwa), showed a trend towards an absence of pigmentation in the cloacal plate (CD.0), laterals of the head (HPL.1), and ventral body (HPV.1 and VBP.1).
Intra-lineage Sexual Dimorphism

Males had higher multivariate size (mSIZE) than females, but only in three of the populations analysed were results significant (Table 1, Table 4, Figure S1). Regarding shape, females had comparatively larger trunks than males in all the populations analysed (Table 4, Figure S1). Sexual dimorphism in shape was more accentuated in Jebel Sirwa, Jebel Azourki and Tizin Tichka (Table 4). In these populations, males had significantly more robust heads than females (Figure S1). Moreover, Jebel Sirwa was the only population where males had significantly longer forelimbs than females (Table 4, Figure S2). On the other hand, Oukaimeden and Jebel Ayache had the lower degree of sexual dimorphism (Table 4). In these populations, males and females only differed in the trunk length, which was longer in females (Table 4, Figure S2). Finally, Outabati population had females with longer trunk and males with higher heads (Table 4, Figure S2).

Regarding pholidosis, only two variables were able to discriminate consistently males and females across all the populations: number of femoral pores (FPN) and the number of ventral scales (VSN) (Table 4). Males had developed femoral pores, and females, generally absent or incomplete lines. Regarding VSN, females had a higher number of ventral scales than males in all populations (Table 4, Figure S2). For the other variables, we found punctual differences in some of the populations analysed (Table 4, Figure S2), but with no consistent pattern. Thus, males had higher number of lamellae and supraciliar scales (SCSN) in Jebel Sirwa, more supratemporal scales (STSN) in Jebel Azourki and a larger number of supraciliar granules (GSN) in Jebel Ayache in comparison with their respective females (Table 4, Figure S2).

Finally, males and females also exhibited differences in colour pattern (Figure 3). Females had, in general, more uniform pattern than males. Males tend to have more pigmentation in the dorsum, and lines tend to be more discontinuous than in females. Moreover, while lateral dark bands tend to be reticulated in males, in females they tend to be uniform in coloration. Regarding the ventral region, males are generally more spotted than females. Moreover, when orange pigmentation is present, in males it tends to cover entirely the ventral body, while in females, it is usually reduced to the cloaca, femoral region and ventral tail (Figure 3).

DISCUSSION

Despite the high genetic divergence found between the six analysed populations of *A. andreanskyi* (Barata *et al.* 2012a), no diagnostic morphological characters supporting the genetic divergence were identified. The analysis of linear measurements and pholidotic characters detected some morphological variability among genetic lineages, although these had limited diagnostic value due to the overlap among populations. We do not discard the possibility that this finding might be the result of some limitations, such as the study of a single population per lineage, and the small sample size of some of the localities analysed. The most contributing variable for the discrimination of the populations was mSIZE. Interestingly, the population with the largest body size was Jebel Ayache, which has the highest altitude among all the populations analysed. On the other hand, the smallest body size population was Outabati, which is found at the lowest altitude among the populations analysed. This pattern interestingly does not support the results from previous studies suggesting that lizards follow a reverse Bergmann’s rule.
Table 4. Summary of the permutational multivariate analysis of variance (MANOVA) results regarding the effect of the factor SEX on size (mSIZE, multivariate size), shape (iso-corrected linear measurements) and pholidosis (log transformed variables). Results are given for each population separately. Significant values \((p' < 0.05)\) are in bold.

|          | Jebel Ayache |                         | Jebel Azourki |                         | Jebel Sirwa |                         | Oukaimeden |                         | Outabati |                         | Tizin Tichka |                         |
|----------|--------------|--------------------------|--------------|--------------------------|--------------|--------------------------|------------|--------------------------|----------|--------------------------|--------------|--------------------------|
|          | F            | p                        | F            | p                        | F            | p                        | F          | p                        | F        | p                        | F            | p                        |
| mSIZE    | 42.769       | **0.001**                | 0.414        | 0.560                    | 1.507        | 0.225                    | 5.174      | **0.027**                | 11.402   | **0.003**                | 2.022        | 0.140                    |
| Shape    | 5.023        | **0.002**                | 10.956       | **0.001**                | 8.273        | **0.001**                | 4.316      | **0.001**                | 6.778    | **0.005**                | 9.039        | **0.001**                |
| Scales   | 1.323        | 0.241                    | 1.853        | 0.130                    | 3.963        | **0.003**                | 0.801      | 0.463                    | 0.753    | 0.497                    | 2.449        | 0.079                    |
| TrL      | 11.571       | **0.006**                | 107.866      | **0.001**                | 93.423       | **0.001**                | 26.823     | **0.001**                | 44.734   | **0.002**                | 99.665       | **0.001**                |
| HL       | 4.144        | 0.059                    | 10.529       | **0.003**                | 7.999        | **0.018**                | 0.028      | 0.863                    | 1.771    | 0.229                    | 10.995       | **0.004**                |
| HW       | 2.635        | 0.123                    | 29.762       | **0.001**                | 17.412       | **0.002**                | 3.759      | 0.072                    | 2.243    | 0.177                    | 16.420       | **0.001**                |
| HH       | 0.093        | 0.783                    | 10.123       | **0.004**                | 0.003        | 0.957                    | 3.144      | 0.083                    | 7.375    | **0.038**                | 9.744        | **0.005**                |
| FLL      | 2.186        | 0.165                    | 0.522        | 0.487                    | 11.606       | **0.004**                | 1.897      | 0.194                    | 4.145    | 0.080                    | 0.171        | 0.693                    |
| HLL      | 0.072        | 0.783                    | 2.114        | 0.163                    | 0.748        | 0.402                    | 0.001      | 0.991                    | 8.514    | 0.018                    | 1.401        | 0.261                    |
| VSN      | 13.870       | **0.003**                | 16.771       | **0.001**                | 40.803       | **0.001**                | 74.907     | **0.001**                | 14.097   | **0.007**                | 27.282       | **0.001**                |
| FPN      | –            | –                        | –            | –                        | –            | –                        | –          | –                        | –        | –                        | –            | –                        |
| Lam      | 0.787        | 0.372                    | 1.199        | 0.281                    | 21.906       | **0.001**                | 0.247      | 0.618                    | 0.117    | 0.742                    | 0.139        | 0.709                    |
| STSN     | 1.880        | 0.211                    | 4.886        | **0.044**                | 3.099        | 0.083                    | 1.073      | 0.300                    | 2.506    | 0.252                    | 0.051        | 0.881                    |
| GSN      | 4.899        | **0.027**                | 1.538        | 0.217                    | 0.242        | 0.656                    | 0.010      | 0.926                    | 2.049    | 0.174                    | 0.877        | 0.356                    |
| CSN      | 0.178        | 0.727                    | 0.808        | 0.403                    | 0.650        | 0.433                    | 0.444      | 0.522                    | 2.238    | 0.266                    | 3.358        | 0.092                    |
| SCGN     | 0.873        | 0.393                    | 0.002        | 0.980                    | 0.775        | 0.508                    | 0.319      | 0.611                    | 0.162    | 0.711                    | 4.195        | 0.061                    |
| SCSN     | 0.059        | 1.000                    | 2.905        | 0.109                    | 8.056        | **0.012**                | 0.784      | 0.477                    | 1.322    | 0.370                    | 0.528        | 0.571                    |
| SL SN    | 2.253        | 0.166                    | 0.042        | 0.868                    | 3.668        | 0.053                    | 2.517      | 0.192                    | 0.907    | 0.461                    | 0.006        | 1.000                    |
(Ashton & Feldman 2003). However, this pattern was only evident in males, and despite the altitudinal gradient of the populations analysed, we did not observe a gradient in body size with altitude in the other localities. Different social, environmental or ecological selective pressures (Case 1976; Wikelski 2005; Collar et al. 2011) might also be playing a role in shaping body size at a local level. For example, in Jebel Sirwa, several studies on the lizards of the genera Acanthodactylus and Podarcis have found a distinctive pattern of Jebel Sirwa regarding other nearby populations and rather a link with populations from Eastern Maghreb, and this may be a general biogeographic pattern (Harris et al. 2002; Pinho et al. 2007; Fonseca et al. 2009; Lima et al. 2009).

Regarding sexual dimorphism, A. andreanskyi males are, in general, larger than females, although this pattern was significant only in some of the populations analysed. Again, the limited sampling in some of the populations might be one of the reasons for the lack of consistency in body size sexual dimorphism. We did find a consistent female-biased dimorphism across all populations in trunk length, and related to that, a higher number of ventral scales than males. This pattern, commonly observed in lacertids (see a review in Cox et al. 2003), supports the fecundity advantage hypothesis (Darwin 1874). According to this hypothesis, larger female body sizes would be favoured in species with a short reproductive season, to maximize clutch success on each reproductive episode. This seems to be the case of A. andreanskyi living in high mountain areas, where the harsh environmental conditions impose a long hibernation period of six to eight months (Schleich et al. 1996).

Moreover, males presented enlarged femoral pores, less developed or absent in females. Femoral pores are known to be important in intraspecific communication, playing an important role in sex recognition, mating selection and territory marking (Gómez et al. 1993; Kaliontzopoulou et al. 2005; Martín et al. 2007). Absence of femoral pores in females of some populations of A. andreanskyi was already described (Barata et al. 2011). Regarding the other characters, males present, in general and for the same size, more robust heads and larger forelimbs. This pattern is congruent with other studies on lacertids, and represents an advantage in intersexual encounters, feeding and escaping from predators (Herrel et al. 1996, 1999, 2001a, 2001b). The degree of sexual dimorphism may reflect the competition and selective pressures acting on a population (Kaliontzopoulou et al. 2007). However despite the greater human pressure observed in Oukaimeden (this locality has a ski station), A. andreanskyi is present in high densities (Busack 1987; and M.B. personal observation). On the other hand, since sexual dimorphism in this population is low, we might expect segregation in diet or niche resources in order to reduce intraspecific competition. Interestingly, the only quantitative study on diet composition in this species showed no differences in the diet of males and females in Oukaimeden (Carretero et al. 2006). Regarding habitat use, the populations analysed presented variation in habitat characteristics including altitude (600 m variation), presence of water, different refuge availability and different spectrum of sympatric species. For example, in Oukaimeden, Atlantolacerta was found under small rocks while in other localities they chose the protection of spiky bushes (Alyssum spinosum, Bupleurum spinosum, Cytisus balansae; Rykena & Bischoff 1992). The Jebel Ayache and Jebel Azourki populations were found in dry places, while in Oukaimeden individuals were found near a water source. Furthermore, Oukaimeden and Jebel Azourki had a larger number of sympatric reptile species, including Podarcis vaucheri, Tarentola mauritanica, Timon tangitanus, Natrix maura, Quedenfeldtia trachyblepharus, Scelarcis perspicillata and Vipera monticola, while in other populations this number was apparently lower.
Unfortunately, as far as we know, there is no information regarding intraspecific microhabitat segregation. More studies need to be done to unveil what mechanisms are behind intraspecific segregation for resources in *A. andreanskyi*.

Although our analyses did show a partial discrimination at the multivariate level, this study failed to find diagnosable characters that allow a simple morphological identification of the lineages. Similar results were found in another cryptic species complex, *Podarcis hispanica* (Kaliontzopoulou et al. 2012). Unfortunately, our results must be considered preliminary due to the fact that only one population per genetic lineage was analysed. Analysis of more populations of the same lineage will allow more definitive conclusions regarding its cryptic nature to be developed.

As described in Barata et al. (2012a), *A. andreanskyi* has high levels of genetic diversity. Our study also highlights another facet of ‘cryptic’ taxa, in which lineages do have morphological differences, but for them to be identified based on these requires analysis of many individuals and characters, a situation similar to that observed in the *Podarcis hispanica* complex (Kaliontzopoulou et al. 2012). Thus, while they might not be strictly ‘cryptic’, from a practical point of view such forms essentially are until some simple diagnostic characters are identified. The conclusions of this study are still preliminary for a formal description, since we only were able to sample a single population for each lineage, and in some of the cases, with a small number of individuals per population. Increased sampling of more populations per lineage and screening of areas with possible intermediate populations are still needed to assess the extent and diversity of the lineages and a more statistically robust assessment of the morphological variation within and between lineages.

A future taxonomic revision will have enormous implications for the conservation status of *Atlantolacerta* as the present species, already with a small distribution, possibly represents at least six different evolving lineages with very restricted areas (Barata et al. 2012a). There is now only one known population for each lineage. Furthermore, the mountain habitat is difficult to sample and the possibility of other cryptic forms occurring is high. Additionally, this work has implications for the study of other mountain species in the region, since cryptic diversity might have been overlooked due to a lack of morphological variation. The processes that promoted this kind of speciation most probably have implications for other species living in similar habitats, and thus further attention to other high altitude Atlas Mountain endemics is warranted.

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**Supplementary Material**

Online Supplementary Material is available for this article which can be accessed via the online version of this journal available at www.tandf.co.uk/journals/THER.

**REFERENCES**

ABDELAZIZ, M., J. LORITE, A.J. MUÑOZ-PAJARES, M.B. HERRADOR, F. PERFECTTI & J.M. GÓMEZ. 2011. Using complementary techniques to distinguish cryptic species: a new *Erysimum* (Brassicaceae) species from North Africa. Am. J. Bot. 98: 1049–1060.

ASHTON, K.G. & C.R. FELDMAN. 2003. Bergmann’s rule in non-avian reptiles: turtles follow it, lizards and snakes reverse it. Evolution 57: 1151–1163.

BARATA, M., D.J. HARRIS & A. PERERA. 2011. *Atlantolacerta andreanskyi* (Atlas Dwarf Lizard). Abnormal scelation. Herpetol. Rev. 42: 599.

BARATA, M., S. CARRANZA & D.J. HARRIS. 2012a. Extreme genetic diversity in *Atlantolacerta andreanskyi* (Werner, 1929): A mountain cryptic species complex. BMC Evol. Biol. 12: 167.

BARATA, M., A. PERERA, F. MARTÍNEZ-FREIRIA & D.J. HARRIS. 2012b. Cryptic diversity within the Moroccan endemic day geckos *Quedenfeldtia* (Squamata: Gekkonidae): a multidisciplinary approach using genetic, morphological and ecological data. Biol. J. Linn. Soc. 106: 828–850.

BEN FALEH, A., L. GRANJON, C. TATARD, Z. BORATYNSKI, J.F. COSSON & K. SAID. 2012. Phylogeography of two cryptic species of African desert jerboas (Dipodidae: *Jaculus*). Biol. J. Linn. Soc. 107: 27–38.

BICKFORD, D., D.J. LOHMAN, N.S. SODHI, P.K.L. NG, R. MEIER, K. WINKER, K.K. INGRAM & I. DAS. 2007. Cryptic species as a window on diversity and conservation. Trends Ecol. Evol. 22: 148–155.

BONS, J. & P. GENIEZ. 1996. Amphibiens et reptiles du Maroc (Sahara Occidental compris), Atlas Biogéographique. Asociación Herpetologica Española, Barcelona, Spain.

BROWN, R.P., N.M. SUAREZ & J. PESTANO. 2002. The Atlas mountains as a biogeographical divide in North-West Africa: evidence from mtDNA evolution in the Agamid lizard *Agama impalearis*. Mol. Phylogenet. Evol. 24: 324–332.

BUSACK, S.D. 1987. Notes on the biology of *Lacerta andreanszkyi* (Reptilia: Lacertidae). Amphibia-Reptilia 8: 231–236.

CARRETERO, M.A., A. PERERA, D.J. HARRIS, V. BATISTA & C. PINHO. 2006. Spring diet and trophic partitioning in an alpine lizard community from Morocco. Afr. Zool. 41: 113–122.

CASE, T.J. 1976. Body size differences between populations of the chuckwalla, *Sauromalus obesus*. Ecology 57: 313–323.

COLLAR, D.D., J.A. SCHULTE III & J.B. LOSOS. 2011. Evolution of extreme body size disparity in monitor lizards (*Varanus*). Evolution 65: 2664–2680.

COX, R.M., S.L. SKELLY & H.B. JOHN-ALDER. 2003. A comparative test of adaptive hypotheses for sexual size dimorphism in lizards. Evolution 57: 1653–1669.

DARWIN, C. 1874. The Descent of Man, and Selection in Relation to Sex. 2nd edition. Appleton, New York.

DE QUEIROZ, K. 2007. Species concepts and species delimitation. Systematic Biol. 56: 879–886.

DESTRE, R., P. ROUX, P. GENIEZ, M. THEVENOT & J. BONS. 1989. Nouvelles observations sur l’herpétofaune marocaine. Bull. Soc. Herp. Fr. 51: 19–26.

DETWILER, J.T., D.H. BOS & D.J. MINCHIELLA. 2010. Revealing the secret lives of cryptic species: Examining the phylogenetic relationships of echinostome parasites in North America. Mol. Phylogenet. Evol. 55: 611–620.

DRAY, S. & A.B. DUFOUR. 2007. The ade4 package: implementing the duality diagram for ecologists. J. Stat. Soft. 22: 1–20.

DUNCAN, R.P., M.R. RYNERSON, C. RIBERA & G.J. BINFORD. 2010. Diversity of *Loxosceles* spiders in Northwestern Africa and molecular support for cryptic species in the *Loxosceles rufescens* lineage. Mol. Phylogenet. Evol. 55: 234–248.
FLORIO, A.M., C.M. INGRAM, H.A. RAKOTONDRAVONY, E.E. LOUIS & C.J. RAXWORTHY. 2012. Detecting cryptic speciation in the widespread and morphologically conservative carpet chameleon (*Furcifer lateralis*) of Madagascar. J. Evolution. Biol. 25: 1399–1414.

FONSECA, M.M., J.C. BRITO, O.S. PAULO, M.A. CARRETERO & D.J. HARRIS. 2009. Systematic and phylogeographical assessment of the *Acanthodactylus erythrurus* group (Reptilia: Lacertidae) based on phylogenetic analyses of mitochondrial and nuclear DNA. Mol. Phylogenet. Evol. 51: 131–142.

FRITZ, U., M. BARATA, S.D. BUSACK, G. FRITZSCH & R. CASTILHO. 2006. Impact of mountain chains, sea straits and peripheral populations on genetic and taxonomic structure of a freshwater turtle, *Mauremys leprosa* (Reptilia, Testudines, Geoemydidae). Zool. Scr. 35: 97–108.

GÓMEZ, A., E. FONT & E. DESFILIS. 1993. Chemoreception in the Lacertidae: exploration and conspecific discrimination in the Spanish wall lizard, *Podarcis hispanica*. Pp. 213–230. In E.D. Valakos, W. Böhme, V. Pérez-Mellado & P. Maragou (Eds.), Lacertids of the Mediterranean Region: A Biological Approach. Hellenic Zoological Society, Athens.

GÓMEZ, F., W. BEAUCHAMP & M. BARAZANGI. 2000. Role of the Atlas Mountains (northwest Africa) within the African-Eurasian plate-boundary zone. Geology 28: 775–778.

HARRIS, D.J., S. CARRANZA, E.N. ARNOLD, C. PINHO & N. FERRAND. 2002. Complex biogeographical distribution of genetic variation within *Podarcis* wall lizards across the Strait of Gibraltar. J. Biogeogr. 29: 1257–1262.

HERREL, A., R. VAN DAMME & F. DE VREE. 1996. Sexual dimorphism of head size in *Podarcis hispanica atrata*: Testing the dietary divergence hypothesis by bite force analysis. Neth. J. Zool. 46: 253–262.

HERREL, A., L. SPITHOVEN, R. VAN DAMME & F. DE VREE. 1999. Sexual dimorphism of head size in *Gallotia galloti*: testing the niche divergence hypothesis by functional analyses. Funct. Ecol. 13: 289–297.

HERREL, A., E. DE GRAUW & J.A. LEMOS-ESPINIAL. 2001a. Head shape and bite performance in Xenosaurid lizards. J. Exp. Zool. 290: 101–107.

HERREL, A., R. VAN DAMME, B. VANHOODYONCK & F. DE VREE. 2001b. The implications of bite performance for diet in two species of lacertid lizards. Can. J. Zool. 79: 662–670.

JAGER, U. & W. BISCHOFF. 1989. Erste Ergebnisse einer herpetologischen Forschungsreise nach Nordwest-Afrika. Tier und Museum (Bonn) 1: 99–106.

KALIONTZOPOULOU, A., M.A. CARRETERO & G.A. LLORENTE. 2005. Differences in the pholidotic patterns of *Podarcis bocagei* and *P. carbonelli* and their implications for species determination. Rev. Esp. Herp. 19: 71–86.

KALIONTZOPOULOU, A., M.A. CARRETERO & G.A. LLORENTE. 2007. Multivariate and geometric morphometrics in the analysis of sexual dimorphism variation in *Podarcis* lizards. J. Morphol. 268: 152–165.

KALIONTZOPOULOU, A., M.A. CARRETERO & G.A. LLORENTE. 2010. Intraspecific ecomorphological variation: linear and geometric morphometrics reveal habitat-related patterns within *Podarcis bocagei* wall lizards. J. Evol. Biol. 23: 1234–1244.

KALIONTZOPOULOU, A., M.A. CARRETERO & G.A. LLORENTE. 2012. Morphology of the *Podarcis* wall lizards (Squamata: Lacertidae) from the Iberian Peninsula and North Africa: patterns of variation in a putative cryptic species complex. Zool. J. Linn. Soc. Lond. 164: 173–193.

KLEMMER, K. 1969. Beobachtungen an den Hochgebirgsreptilien *Quedenfeldtia trachyblepharus* (Gekkonidae) und *Lacerta andreanskyi* (Lacertidae) des Hohen Atlas, Marokko. Zool. Anz. 3: 325–327.

LIMA, A., C. PINHO, S. LARBES, M.A. CARRETERO, J.C. BRITO & D.J. HARRIS. 2009. Relationships of *Podarcis* wall lizards from Algeria based on mtDNA data. Amphibia-Reptilia 30: 483–492.

MARTIN, J., P.L. MOREIRA & P. LÓPEZ. 2007. Status-signalling chemical badges in male Iberian rock lizards. Funct. Ecol. 21: 568–576.

MEDAIL, F. & K. DIADEMA. 2009. Glacial refugia influence plant diversity patterns in the Mediterranean Basin. J. Biogeogr. 36: 1333–1345.

MYERS, N., R.A. MITTERMEIER, C.G. MITTERMEIER, G.A.B. DA FONSECA & J. KENT. 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853–858.

OKSANEN J., F.G. BLANCHET, R. KINDT, P. LEGENDRE, P.R. MINCHIN, R.B. O’HARA, G.L. SIMPSON, P. SOLYMOS, M.H.H. STEVENS & H. WAGNER. 2011. Vegan: Community Ecology Package. R package version 2.0-3.
PADIAL, J.M. & I. DE LA RIVA. 2009. Integrative taxonomy reveals cryptic Amazonian species of *Pristimantis* (Anura: Strabomantidae). Zool. J. Linn. Soc. Lond. 155: 97–122.

PASTEUR, G. & J. BONS. 1960. Catalogue des reptiles actuels du Maroc. Travaux de l’Institut Scientifique Chérifien, Rabat.

PERERA, A. & D.J. HARRIS. 2010. Genetic variability within the Oudri’s fan-footed gecko *Ptyodactylus oudrii* in North Africa assessed using mitochondrial and nuclear DNA sequences. Mol. Phylogenet. Evol. 54: 634–639.

PFENNINGER, M. & K. SCHWENK. 2007. Cryptic animal species are homogeneously distributed among taxa and biogeographical regions. BMC Evol. Biol. 7: 121.

PINHO, C., D.J. HARRIS & N. FERRAND. 2007. Comparing patterns of nuclear and mitochondrial divergence in a cryptic species complex: the case of Iberian and North African wall lizards (*Podarcis*, Lacertidae). Biol. J. Linn. Soc. 91: 121–133.

R DEVELOPMENT CORE TEAM. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.R-project.org/.

RATO, C., S. CARRANZA, A. PERERA, M.A. CARRETERO & D.J. HARRIS. 2010. Conflicting patterns of nucleotide diversity between mtDNA and nDNA in the Moorish gecko, *Tarentola mauritanica*. Mol. Phylogenet. Evol. 56: 962–971.

RATO, C., S. CARRANZA & D.J. HARRIS. 2012. Evolutionary history of the genus *Tarentola* (Gekkota: Phyllodactylidae) from the Mediterranean Basin, estimated using multilocus sequence data. BMC Evol. Biol. 12: 14.

RECUERO, E., A. IRAOLA, X. RUBIO, A. MACHORDOM & M. GARCIA-PARIS. 2007. Mitochondrial differentiation and biogeography of *Hyla meridionalis* (Anura: Hylidae): an unusual phylogeographical pattern. J. Biogeogr. 34: 1207–1219.

ROITBERG, E.S., V.F. ORLOVA, V.N. KURANOVA, N.A. BILAKHOVA, O.I. ZINENKO, K. LJUBISAVLJEVIC, R. R. SHAMGUNOVA, M.A. CARRETERO, A. CLASEN, M. FORT & W. BÖHME. 2011. Inter-observer and intra-observer differences in measuring body length: a test in the common lizard, *Zootoca vivipara*. Amphibia-Reptilia 32: 477–484.

RYKENA, S. & W. BISCHOFF. 1992. On reproductive biology of the High Atlas Mountain lizard *Lacerta andreanskyi* Werner, 1929. Pp. 399–402. In Proceedings of the 6th Ordinary General Meeting of the Societas Europaea Herpetologica, Budapest.

SAINT GIRONS, H. 1953. Une vipère naine: *Vipera latastei montana*. B. Soc. Zool. Fr. 78: 24–28.

SITES, J.W. & J.C. MARSHALL. 2003. Delimiting species: a Renaissance issue in systematic biology. Trends Ecol. Evol. 18: 462–470.

SOMERS, K.M. 1986. Multivariate allometry and removal of size with principal components analysis. Syst. Zool. 35: 359–368.

STEMLER, O. 1972. Herpetologische Beobachtungen in Marokko XII. Im Hochtal des Oued Rhirhaia. Aquaterra 9: 8–12.

VENABLES, W.N. & B.D. RIPLEY. 2002. Modern Applied Statistics with S. Fourth edition. Springer, New York.

VOLOBOUEV, V., G. PASTEUR, J. BONS, C.P. GUILLAUME & B. DUTRILLAUX. 1990. Sex chromosome evolution in reptiles: divergence between two lizards long regarded as sister species *Lacerta vivipara* and *Lacerta andreanskyi*. Genetica 83: 85–91.

WERNER, F. 1929. Wissenschaftliche Ergebnisse einer zoologischen Forschungsreise nach Westalgerien und Marokko. Sitz. Akad. Wiss. Wien 138: 1–34.

WERNER, F. 1931. Ergebnisse einer zoologischen Forschungsreise nach Marokko. I. Einleitung und Reisebericht. Sitz. Akad. Wiss. Wien 140: 235–259.

WERNER, F. 1935. Auf Fang seltener Lacerten in drei Erdteilen. Bl. Aquar. Terrarienkunde 46: 33–37 [reprint in Die Eidechse 3 (5): 25–29].

WIECZKSI, M. 2005. Evolution of body size in Galapagos marine iguanas. P. Roy. Soc. Lond. B. Bio. 272: 1985–1993.

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