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Morphological variability of the Lataste's viper (*Vipera latastei*) and the Atlas dwarf viper (*Vipera monticola*): patterns of biogeographical distribution and taxonomy

José C. Brito[1], Xavier Santos[2,3], Juan M. Pleguezuelos[2], Soumia Fahd[4],
Gustavo A. Llorente[3], Xavier Parellada[5]

Abstract. The Lataste's viper *Vipera latastei* is a medium-sized viper distributed throughout almost the entire Iberian Peninsula and north-west of Africa. Former morphological studies noted the existence of two subspecies, *V. l. gaditana* and *V. l. latastei,* as well as a full species, *V. monticola,* in the High Atlas, corresponding to the prior overall range described for *V. latastei*. However, some results remained unclear in these former studies, e.g. the specific status of the Medium Atlas populations, the intra-subspecific differences in *V. l. gaditana* and, the true status of some isolated populations of the northern range. For this reason, 45 morphological characters were analysed in 672 preserved specimens covering the entire range. Categorical Principal Components Analysis (CATPCA) and Discriminant Function Analysis (DFA) were used to assess geographic variability, treating specimens individually or assigning them *a priori* to groups, respectively. Geographic groups were established according to the origin of specimens in isolated areas of mountain chains. As the percentage of correct assignment was low in DFA, initial groups were combined to maximize the percentage. The results from the multivariate analysis suggest morphological differentiation between populations. Some variables accounted for geographic variability: e.g. rows of dorsal scales at mid-body are taxonomically stable and clearly separate the African populations; and number of ventral scales showed a clinal variation from 126 to 143 ventrals in extreme populations. The three African groups manifested clear morphological differences, and especially specimens from the High Atlas (*V. monticola*) and Alger. On the contrary, a large number of initial Iberian groups were merged because of the low scores in the correct classification. The final groups showed a vast central area with low morphological differentiation as well as isolated populations in the NW, NE and SW Iberian Peninsula. This conclusion matches well with allopatric speciation processes during the Quaternary ice ages, which contributed to the contraction/expansion of range, isolation events, and peripheral population refugia. Morphological differentiation in external characters of *V. latastei* exhibited similar results with respect to *V. aspis* and *V. ammodytes*, the vipers occupying other southern European peninsulas. Molecular markers will contribute to elucidate the relationships between *V. latastei* populations and the history of colonisation across the Strait of Gibraltar.

Introduction

The family Viperidae includes modern and venomous snakes widely distributed around the world except in Oceania (McDiarmid et al., 1999). There is a general consensus on the African origin of the family which afterwards colonized Eurasia and America (Rage, 1987; Greene, 1992; Lenk et al., 2001). The family includes four subfamilies (McDiarmid et al., 1999) with unclear definition in their phylogenetic relationships (Ash and Marx, 1988; Marx et al., 1988; Herrmann and Joger, 1997; Herrmann et al., 1999; Lenk et al., 2001). One of these subfamilies, the Viperinae, is found in Africa and Eurasia, and includes the true viper species grouped in 13 genera. The genus *Vipera* is the best represented in Europe, with 10 species (Gasc et al., 1997). The oldest European *Vipera* fossils, from the Miocene and Pliocene, were found in several localities both in Eastern and Western Europe (Bailón et al., 2002; see a review in Szyndlar and Rage, 2002).

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1 - Centro de Investigação em Biodiversidade e Recursos Genéticos da Universidade do Porto (CIBIO/UP), Instituto de Ciências Agrárias de Vairão, R. Padre Armando Quintas, 4485-661 Vairão, Portugal
Corresponding author; e-mail: jcbrito@mail.icav.up.pt
2 - Departamento de Biología Animal y Ecología, Facultad de Ciencias, Universidad de Granada, 18071 Granada, Spain
3 - Departament de Biologia Animal (Vertebrats), Universitat de Barcelona, Av. Diagonal 645, 08028 Barcelona, Spain
4 - Département de Biologie, Faculté des Sciences, Université Abdelmalek Essaadi, Tétouan, Morocco
5 - Servei Protecció Fauna, Dep Medi Ambient, Generalitat Catalunya, 08071 Barcelona, Spain

These palaeontological data suggest that, until the upper Pliocene, a group of "small" true vipers (g. *Vipera*) inhabited northern and western Europe, whereas southern and eastern Europe was occupied by large true vipers, ancestors of the present genus *Macrovipera* (Saint Girons, 1980; Barbadillo et al., 1997; Nilson and Andrén, 1997; Ivanov et al., 2000; Crespo, 2001; Szyndlar and Rage, 2002). During the Quaternary, climatic shifts in Europe reduced the distribution range of the "large" true vipers, and probably favoured the geographic expansion of the small true vipers (Crespo, 2001; Szyndlar and Rage, 2002).

Saint Girons (1980) proposed that the current distribution of the viper species in Europe evolved from the old distribution of three ancestors which occupied three well-defined climatic regions: i) a steppe-form, precursor of the *ursinii* group, ii) a viper of wet and cold forests, precursor of the *berus-seoanei* group, and iii) a viper of hot and dry forests, precursor of the *ammodytes-aspis-latastei* group. Climatic shifts during the Pleistocene (i.e. glaciations) prompted specialization processes for isolated populations in the Mediterranean Peninsulas (*V. latastei* in Iberian one, *V. aspis* in Italian one, and *V. ammodytes* in the Balkans). Later phylogenetic studies based on ecological traits (Nilson and Andrén, 1997) and blood albumins (Herrmann et al., 1992, 1999; Herrmann and Joger, 1997), also differentiated a group of small vipers, including the endemic vipers of the three major southern European Peninsulas. Recent studies based on mitochondrial DNA sequences have supported these conclusions (Lenk et al., 2001).

Saint Girons (1980) suggested that the three endemic vipers in southern Europe appeared in the first cold period (Upper Pliocene or Lower Pleistocene). Successive glaciations during the Pleistocene modified the latitudinal range of the European vipers, favoured the isolation of small populations, and consequently gave rise to geographic differentiation (subspecies). Geographic variation in several morphological traits in the three species supports recent allopatric speciation processes: a) there is morphological variation in *V. aspis* throughout its entire distribution range (Zuffi and Bonnet, 1999) and Zuffi (2002) proposed specific rank for some of the subspecies; b) studies based on morphological traits confirm geographic variation in qualitative and meristic characters for *V. ammodytes* in the Balkans (Tomović and Džukić, 2003); c) *Vipera latastei* shows the most complex scenario, as the contact between the Iberian Peninsula and Morocco had contributed to the expansion of this viper through north-western Africa to the High Atlas Mountains, Morocco (Saint Girons, 1980). Subsequent allopatric processes, similar to those that occurred in the other vipers, had favoured the strong differentiation of the populations of the High Atlas. These populations were initially described as a subspecies (Saint Girons, 1953a, b), but later, raised to a full species: *V. monticola* (Beerli et al., 1986). In the rest of the area occupied by *V. latastei*, Saint Girons (1977, 1978) described two subspecies based on some morphological traits: *V. l. latastei* in a great part of the Iberian Peninsula, and *V. l. gaditana* in south-western Iberian Peninsula and north-eastern Africa. This author also detected wide variability within the *gaditana* subspecies but the small sample he used precluded a better discrimination. The existence of a geographic barrier, the Strait of Gibraltar, separating the European from the African populations of these subspecies, suggests that strong differentiation patterns may occur, as in the case of other reptile species (Bons, 1973; Busack, 1986; Busack and Maxson, 1987; Harris et al., 2002, 2004a). For these reasons, a complex scenario for *V. latastei* is expected following the results found for *V. aspis* and *V. ammodytes*. The goal of this study is the analysis of the morphological variation in the *Vipera latastei-monticola* populations throughout their entire geographic range, including samples of vipers from a larger number of localities both in African and European populations. It is expected to identify morphological differentiation patterns, draw hypothesis for evolutionary scenarios of these vipers and revise current systematics.

Materials and methods

Study area and samples

The study area includes the Iberian Peninsula and northwestern Africa (fig. 1). Preserved specimens were examined from the collections of the following institutions (acronym and sample size included): Muséum Nationale d'Histoire Naturelle, Paris (MNHN, 15 specimens); Laboratoire de Biogéographie et Écologie des Vertébrés, Université de Montpellier II (LBEV, 2 specimens); Museu Bocage, Lisbon (MBL, 6 specimens), Museu de História Natural, Porto University (MHN, 3 specimens), Departamento de Biología Animal y Ecología, Granada University (DBAG, 54 specimens), Departament de Biologia Animal, Barcelona University (DBAUB, 17 specimens), Museo Nacional de Ciencias Naturales, Madrid (MNCN, 250 specimens), Museu de Ciències Naturals of Barcelona (MCNB, 16 specimens), Estación Biológica de Doñana, Seville (EBD, 133 specimens), Instituto Pirenaico de Ecología, Jaca (IPE, 14 specimens), Monestir de Montserrat (MMO, 15 specimens), Department de Biologie of the Abdelmalek Essaâdi University, Tetuan (DBAEU, 3 specimens), and the private collection of J.C. Brito (JCB, 125 specimens). Additional data from 19 specimens was recorded from the literature (Dolfus and Beaurieux, 1928; Wettstein, 1933; Beerli et al., 1986; Pillet, 1994).

A total of 672 specimens were examined, although 106 specimens with unrecognizable sex (mainly newborns and juveniles) were excluded; thus, 564 specimens (334 males and 230 females) were used in the analysis.

Despite *Vipera latastei* is distributed throughout a substantial part of the Iberian Peninsula, the present distribution of the species and, consequently, the origin of the majority of preserved specimens coincides with discrete and isolated areas of mountain chains (Godinho et al., 1999; Pleguezuelos and Santos, 2002). For this reason, geographic groups to test morphological variability were established according to the distribution of these mountains (fig. 1). Specimens from closely related mountains were pooled when the sample size was insufficient for performing the statistical analysis. A similar pattern occurred in Africa. Four specimens from the following localities were not used in the analysis, but were tested for group assignment: Columbretes islands (Valencia, Spain), Gata cape (Almería, Spain), Rhibat al Khayr (Taza, Morocco) and Azrou (Ifrane, Morocco). Overall, 19 geographic groups for males and 18 for females (no specimens were available for the SW Iberian group) were assembled. Sample sizes for geographic groups and sexes are listed in Appendices 1, 2 and 3.

Characters

For each specimen a total of 45 characters were recorded: seven morphometric, 18 meristic and 20 qualitative.

Morphometric traits included: snout-vent length (SVL); tail length (TLENG); head length, measured from the tip of the snout to the posterior tip of the quadrate (HLENG); head width, measured across the widest part of the head (HWIDT); head height, measured at the highest point of the head (HHEIG); mouth length, measured from tip of the snout to the posterior border of the last supralabial scale (MLENG). Body characters were measured with a measuring tape to 1 cm precision and head characters using a calliper to 0.1 mm precision. Furthermore, the relative length of the tail to total length (TBODY) and the dorsal head area (HAREA), as the area of a triangle with the head length and width as the sides of this triangle, were calculated.

Meristic traits when bilateral were considered on the left (L) and the right (R) sides and were: number of ventral scales, excluding preventrals and anal, following the method used by Saint Girons (1978) (NVENT); subcaudal scales (SUBCA); scale rows at mid-body (DMBOD); apical scales (APICA); cantal scales (CANTL, CANTR); supralabial scales (SUPRL, SUPRR); infralabial scales (INFRL, INFRR); periocular scales (PERIL, PERIR); scale rows between the periocular and the supralabial scales (RPSL, RPSR); loreal scales (LOREL, LORER); intercantal plus intersupraocular scales (INTER); dorsal marks between the head and the vent (DMARK).

Qualitative traits when bilateral were considered on the left (L) and the right (R) sides and were: cantal scales enter the eye (CANEL and CANER with states 0 – no, 1 – yes); nasorostral scale entire or fragmented (NASOL and NASOR, with states: 0 – entire, 1 – fragmented); fragmentation of the parietal scales (FPARI, with states: 0 – partial, 1 – total); fragmentation of the frontal scale (FFRON, with states 0 – partial, 1 – total); most common dorsal body pattern (BPATT, with states: 0 – opposed marks, 1 – zigzag, 2 – both); most common shape of the dorsal marks (SMARK, with states: 0 – angled, 1 – rounded, 2 – spots); general broadness of the dorsal marks (BROAD, with states: 0 – wide, 1 – medium, 2 – narrow); contrast between the background dorsal colour and the dorsal marks (CONTR, with states: 0 – strong, 1 – medium, 2 – weak); dark margin around the dorsal marks present (BMARG, with states: 0 – yes, 1 – no); bright margin around some of the dorsal marks present (WMARG, with states: 0 – yes, 1 – no); most common shape in the union of the dorsal marks (SUNIO, with states: 0 – wide, 1 – narrow, 2 – discontinuous spots); contrast between lateral marks and lateral background colour (CLATE, with states: 0 – lateral marks absent, 1 – weak, 2 – strong); shape of the dorsal head marks (HMARK, with states: 0 – head marks absent, 1 – two points, 2 – V-shaped; 3 – horse-shoe); contrast between the background colour and the lateral stripe of the head (SCONT, with states: 0 – stripe absent, 1 – dark stripe, 2 – black stripe); contact between the lateral stripe with the eye (SCONN, with states: 0 – stripe absent, 1 – contacts, 2 – does not contact); coloration of the supralabial scales

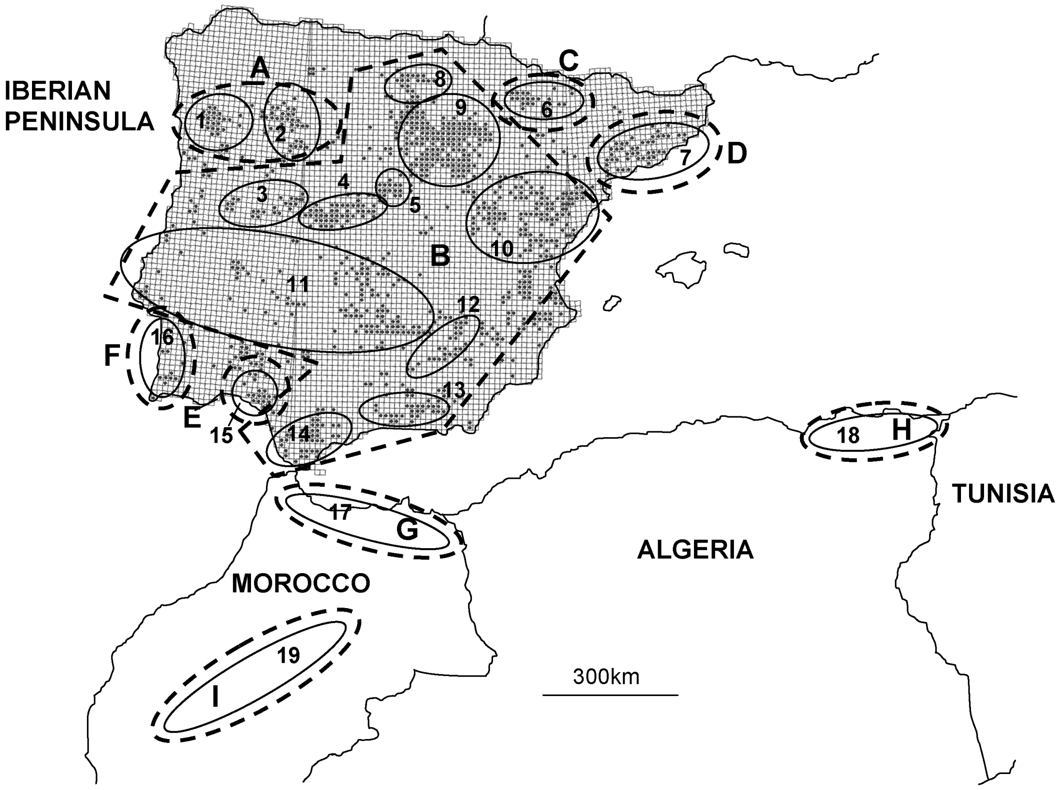

Figure 1. Distribution range of *Vipera latastei* in the Iberian Peninsula by UTM10 × 10 km squares. Solid lines and numbers: location of the 19 geographic groups considered for analysis. 1 – NW Portugal (including Gerês, Alvão and Montemuro Mountains), 2 – León Mountains (including La Culebra and Montesinho Mountains), 3 – Estrela-Gata Mountains, 4 – Gredos Mountain, 5 – Guadarrama Mountain, 6 – Pre-Pyrenees (including Guara and S. Juan de la Peña Mountains), 7 – coastal Catalonia, 8 – western Iberian System, 9 – central Iberian System, 10 – eastern Iberian System, 11 – Montes de Toledo and Sierra Morena (including a vast plain region from the Atlantic coast to La Mancha region), 12 – Cazorla and Alcaraz Mountains, 13 – Sierra Nevada Mountains, 14 – Serranía de Ronda Mountains, 15 – Doñana, 16 – SW Iberian Peninsula, 17 – Rif Mountains, 18 – Algeria, and 19 – High Atlas Mountains. Discontinuous lines and capital letters: location of the final 9 groups (called populations in the text) following the discriminant function analysis method (see Material and methods section). A – NW Iberian Peninsula (groups 1 and 2 merged), B – central Iberian Peninsula (groups 3 to 5 and 8 to 14 combined), C – Pre-Pyrenees, D – coastal Catalonia, E – Doñana, F – SW Iberian Peninsula, G – Rif Mountains, H – Alger, I – High Atlas Mountains.

(SCOLO, with states: 0 – whitish, 1 – whitish spotted, 2 – other); dark spot below the eye present (LMARK, with states: 0 – no, 1 – yes); and colour of the ventral side of the tail differentiated (TDIFF, with states: 0 – no, 1 – yes).

Statistical analysis

A total of 21 variables (14 meristic and 7 metric) were tested for sexual dimorphism in *V. latastei*. Meristic characters were compared with adult and juvenile specimens pooled as there are no ontogenic shifts, whereas metric characters were compared only among adult vipers (SVL > 245 mm in males and 260 mm in females, unpubl. data). All variables were tested for normality, for each sex separately, before comparisons. For both sexes, only the number of ventral scales and number of subcaudals scales were not normally distributed (males: NVENT: K-S = 0.096, df = 38, $P = 0.2$, SUBCA: K-S = 0.107, df = 38, $P = 0.2$; females: NVENT: K-S = 0.125, df = 12, $P = 0.2$, SUBCA: K-S = 0.148, df = 12, $P = 0.2$). Meristic variables (tail length and head measures) were compared by ANCOVA tests using SVL as covariable after testing for parallelism of the distributions and homogeneity of variances. To compare SVL between sexes, the entire sample of adult vipers was used due to the small differences in size at sexual maturity. Furthermore, the upper decile of the sample was used to test sexual differences in the maximum size attained. Comparisons were made for the total sample, the whole Iberian sample, and some Iberian groups with sample enough: Doñana, Central Iberian Peninsula, and NW Portugal-León Mountains.

Multivariate statistics were used on 34 meristic and qualitative traits. Specimens were eliminated from the analysis when they had more than 25% of the traits with missing values, leaving a total of 429 specimens (251 males and 178 females) for the analysis. Because of sexual dimorphism in some traits, analyses were performed separately for males and females.

Categorical Principal Components Analysis (CATPCA) and Discriminant Function Analysis (DFA) were used to determine geographic variability, treating specimens individually or assigning them *a priori* to groups, respectively. CATPCA is a procedure for data reduction to find structural relationships among specimens without *a priori* subdivision of the specimens into discrete groups (Nilson and Andrén, 2001). Although having a less discriminatory power than methods that define *a priori* groups such as DFA, CATPCA is useful to perform analysis without prejudgment of the distinctiveness of the groups (Malhotra and Thorpe, 2004). With the CATPCA procedure, new orthogonal axes were constructed that were linear combinations of the original variables (not standardized). The loading scores on the first two extracted principal components were used as a measure of the association between individual and trait variability. The total variance accounting for each eigenvalue was used to evaluate the level of explanation of the analysis.

DFA was performed to clarify the relative importance of such traits as discriminators between *a priori* groups and the relative positions of the centroids of those groups (Tomovíc and Džukic, 2003). With the DFA procedure, significant traits for group assignment were accessed with stepwise methods. A classification procedure based on a matrix of Mahalanobis distances was used to evaluate group membership, without prior analysis of variance. As the discriminant functions computed by the DFA are the linear combinations of the original variables that maximized differences between given groups, DFA depends on which individuals were assigned to each group before the computation, and it was less parsimonious than CATPCA (Crochet et al., 2003).

For this reason, several groups combining different populations were tested using an interactively procedure. Initially, a DFA analysis was performed with the 19 initial groups (18 for females, as explained above). The results of the percentage of correct classification of specimens in each group were used to determine which groups should be merged. For instance, if the specimens of a certain group were consistently classified as belonging to another group, then these groups were combined. The procedure was repeated using the new combinations of groups until the percentage of correct assignments of group membership was maximized.

Hierarchical Cluster Analysis (HCA) based on the matrix of Mahalanobis distances determined with DFA was used to evaluate group relationships (relatedness). HCA procedure categorized homogeneous groups based on distances, using an algorithm that started with each case in a separate cluster and combined clusters until only one was left. The hierarchical clustering process was represented as a tree, or dendrogram, where a join of the tree illustrated each step in the clustering process. The minimum variance clustering method or Ward's method was used with the squared Euclidean distances, because it emphasised the greatest inter-group distances (Werner et al., 1999).

Statistical analyses were performed with the statistical packages Statistica 6.0 for Windows and SPSS 12.0 for Windows.

Results

Sexual dimorphism

There were small differences in the characters tested for sexual dimorphism with the exception of those related to the tail (tail length and number of subcaudals). Male and female *V. latastei* were similar in body length (SVL females 406.8 mm, males 404.4 mm, $t = 0.3$, $df = 431$, $P = 0.7$, $n_1 = 184$, $n_2 = 249$). Male and female *V. monticola* also showed no sexual differences in body length (SVL females 263.9 mm, males 266.6 mm, $t = 0.1$, $df = 21$, $P = 0.9$, $n_1 = 10$, $n_2 = 13$). Geographic groups with sufficient samples exhibited similar results. However, analyses using the upper decile of the sample from the Central Iberia group indicated than males were larger than females (SVL females 516.9 mm, max: 545 mm, males 548.7 mm, max: 596 mm, $t = 3.5$, $df = 24$, $P = 0.001$, $n_1 = 11$, $n_2 = 15$) suggesting that in some populations males attained larger sizes than females.

The tail was larger in males than in females in both *V. latastei* (ANCOVA test $F_{1,406} = 237.3$, $P < 0.001$) and *V. monticola* (ANCOVA test $F_{1,16} = 7.0$, $P = 0.02$). Sexual differences in tail length were also significant in all the Iberian groups.

No sexual differences were found in head length and height or in mouth length. On the contrary, the head width differed significantly between male and female *V. latastei* (ANCOVA $F_{1,282} = 3.98$, $P = 0.047$), females having wider heads than males. Comparisons in single groups were significant in only the NW Iberian Peninsula (ANCOVA $F_{1,55} = 7.09$, $P = 0.01$), the head of females being wider than that of males. Moreover, in the NW Iberian Peninsula, females also had larger head areas than males (ANCOVA $F_{1,19} = 6.16$, $P = 0.02$), a characteristic not observed in other groups.

Males had more subcaudals than did females (females 34.6, males 41.4; Mann-Whitney U test $Z = 15.04$, $P < 0.000001$). Differences were also significant in all the Iberian groups but not in the Rif or in Alger, perhaps due to the small sample sizes. Specimens from the High Atlas showed no differences in the number of subcaudals although males had more scales than females (Appendix 2). Some Iberian groups also significantly differed between males and females in such characters as PERIOR (Doñana), PERIOL (coastal Catalonia), LOREL (NW Iberian Peninsula), INFRR and LORER (Pre-Pyrenees), although there were no patterns of sexual differences in these variables among groups.

Sexual differences were also observed in APICA and INTER in *V. latastei* (APICA: females 5.1, males 4.7, $Z = 3.48$, $P = 0.0005$; INTER: females 36.1, males 34.8, $Z = 2.27$, $P = 0.02$). By groups, differences were significant only in the final group of the Central Iberian Peninsula.

Multivariate analysis

Four meristic traits were excluded due to a lack of geographic variance: cantal scales on the left and right side of the head (CANTL and CANTR) and scale rows between the periocular and the supralabial scales on the left and right side of the head (RPSL and RPSR).

The variance accounted by the two most explicative dimensions on the CATPCA for males and females were 7.66% and 9.24%, respectively, indicating a low explanatory power. The loadings on the first and second principal components for males and females (table 1) show intersexual differences in meristic and qualitative traits explaining variation. The number of dorsal marks, infralabial scales, intercantal and intersupraocular scales, and loreal scales, explained the variation in both males and females. Other traits contributing to variability were the number of ventral scales, the presence of a dark margin around the dorsal marks, the contrast of the lateral stripe with the rest of the head, the contact between the lateral stripe with the head, and the coloration of the supralabial scales for males. For females these traits were the number of scale rows at mid-body and the number of periocular scales (table 1).

Table 1. Loading scores on the first two principal components extracted according to the Categorical Principal Components Analysis using meristic and qualitative traits of individual male and female *Vipera latastei-monticola* complex. * – Significant loadings.

Variable	Males		Females	
	PC1	PC2	PC1	PC2
APICA	0.272	−0.212	0.115	0.447
BMARG	0.548*	0.030	0.321	−0.341
BPATT	−0.120	0.205	0.252	−0.349
CANTL	−0.262	−0.164	0.340	−0.182
CANTR	−0.231	−0.187	0.311	−0.187
CONTR	−0.419	−0.097	−0.492	0.391
DMBOD	0.367	0.123	0.178	0.532*
DMARK	−0.337	0.502*	−0.548*	0.137
FFRON	0.314	−0.389	0.248	−0.207
FPARI	0.317	−0.197	0.190	−0.147
HMARK	0.148	0.116	−0.478	−0.128
INFRL	0.430	0.410	−0.043	0.636*
INFRR	0.528*	0.293	0.142	0.792*
INTER	0.519*	−0.360	0.717*	0.311
LMARK	0.310	−0.095	0.530*	−0.303
LIPMA	0.129	0.492	−0.404	−0.040
LOREL	0.637*	−0.306	0.827*	0.196
LORER	0.606*	−0.384	0.773*	0.352
MCONN	0.168	0.171	−0.263	0.321
MPATT	0.303	−0.027	0.361	−0.352
MRANG	0.184	−0.367	−0.124	0.418
NASOL	−0.054	−0.354	0.562*	−0.037
NASOR	−0.070	−0.272	0.494	−0.019
PERIL	0.339	−0.216	0.302	0.632*
PERIR	0.378	−0.226	0.387	0.388
SCONN	0.447	0.646*	−0.317	0.219
SCONT	0.453	0.638*	0.200	−0.275
SUBCA	0.115	0.227	0.085	0.329
SCOLO	0.205	0.502*	−0.457	0.048
SUPRL	0.405	−0.067	0.372	0.305
SUPRR	0.425	−0.104	0.106	−0.228
TDIFF	−0.062	−0.075	−0.026	0.263
VENTR	−0.018	0.607*	0.028	−0.167
WMARG	0.415	0.041	0.438	−0.337

The correct classification of specimens of the initial groups on the DFA for males and females was relatively low (table 2), suggesting that a large number of groups should be combined. Nevertheless, specimens were accurately classified in the following groups: Pre-Pyrenees, Alger and High Atlas for both sexes; in the SW

Table 2. Percentage of correct classification of individual male and female *Vipera latastei-monticola* complex belonging to the initial and final groups, according to meristic and qualitative traits, by the first two canonical variates using Mahalanobis distances.

Initial groups	Males	Females	Final groups	Males	Females
1. NW Portugal	86.1	81.0	A. NW Iberian Pen.	78.6	73.9
2. León Mts.	83.3	50.0	B. Central Iberian Pen.	92.8	94.3
3. Estrela-Gata Mts.	46.1	88.9	C. Pre-Pyrenees	100.0	66.7
4. Gredos Mts.	66.7	83.3	D. Coastal Catalonia	60.0	75.0
5. Guadarrama Mt.	76.5	68.8	E. Doñana	78.9	93.8
6. Pre-Pyrenees	100.0	100.0	F. SW Iberian Pen.	100.0	–
7. Coastal Catalonia	73.3	75.0	G. Rif Mts.	66.7	66.7
8. Western Iberian System	60.0	77.8	H. Alger	100.0	100.0
9. Central Iberian System	78.9	81.0	I. High Atlas Mts.	100.0	100.0
10. Eastern Iberian System	33.3	63.6			
11. Toledo & Morena Mts.	75.0	100.0			
12. Cazorla & Alcaraz Mts.	70.0	57.1			
13. Nevada Mt.	81.5	80.0			
14. Ronda Mt.	80.0	60.0			
15. Doñana	84.2	93.8			
16. SW Iberian Pen.	100.0	–			
17. Rif Mts.	66.7	100.0			
18. Alger	100.0	100.0			
19. High Atlas Mts.	100.0	100.0			
Total	75.3	79.7		87.6	90.4

Iberian Peninsula for males; and in the Central Iberian Peninsula and Rif for females. The final groups (populations) designated by the interactive procedure had correct classification rates above 87 and 90% for males and females, respectively (table 2). These groups were: NW Iberian Peninsula (including NW Portugal and León Mountains); Central Iberian Peninsula (including the mountains of Estrela-Gata, Gredos, Guadarrama, Cazorla and Alcaraz, Sierra Nevada, and the Serranía de Ronda, as well as the entire Iberian System); Pre-Pyrenees; Coastal Catalonia; Doñana; SW Iberian Peninsula; Rif; High Atlas and Alger. The DFA analysis showed that the number of scale rows at mid-body, the number of ventral, subcaudal and apical scales, and the fragmentation of the nasorostral scale, significantly contributed to the discrimination among the final groups of males (table 3). For females, the number of scale rows at mid-body and the number of ventral and loreal scales, most explained geographic variation (table 3).

Among the final groups, the mean number of ventral scales varied significantly between 124 in Alger and 143 in the NW Iberian Peninsula (Kruskal-Wallis test $H_{8,384} = 113.7$, $P < 0.0001$), and a clinal variation pattern was clearly discernible (fig. 2). The number of subcaudal scales varied significantly between 35 in Alger and 46 in the Pre-Pyrenees for males ($H_{8,225} = 36.6$, $P < 0.00001$), while differences for females were also pronounced ($H_{7,163} = 23.6$, $P = 0.001$). The number of apical scales varied significantly between 4 in the Pre-Pyrenees and 7 in the Rif ($H_{8,418} = 28.0$, $P = 0.0005$). The number of loreal scales on the left side of the head ranged between 6.5 in the High Atlas and 11 in the SW Iberian Peninsula ($H_{8,385} = 55.4$, $P < 0.00001$). The number of scale rows at mid-body also varied significantly between 19 in the High Atlas and 23 in Alger ($H_{8,419} = 107.3$, $P < 0.0001$). The percentage of specimens with the nasorostral scale fragmented ranged from 0% for the NW and SW Iberian Peninsula, Pre-Pyrenees, and High Atlas; around 30% for Coastal Catalonia and the Rif; and about 80% for Alger (fig. 2).

Descriptive statistics on morphometric variation of adult males and females among the ini-

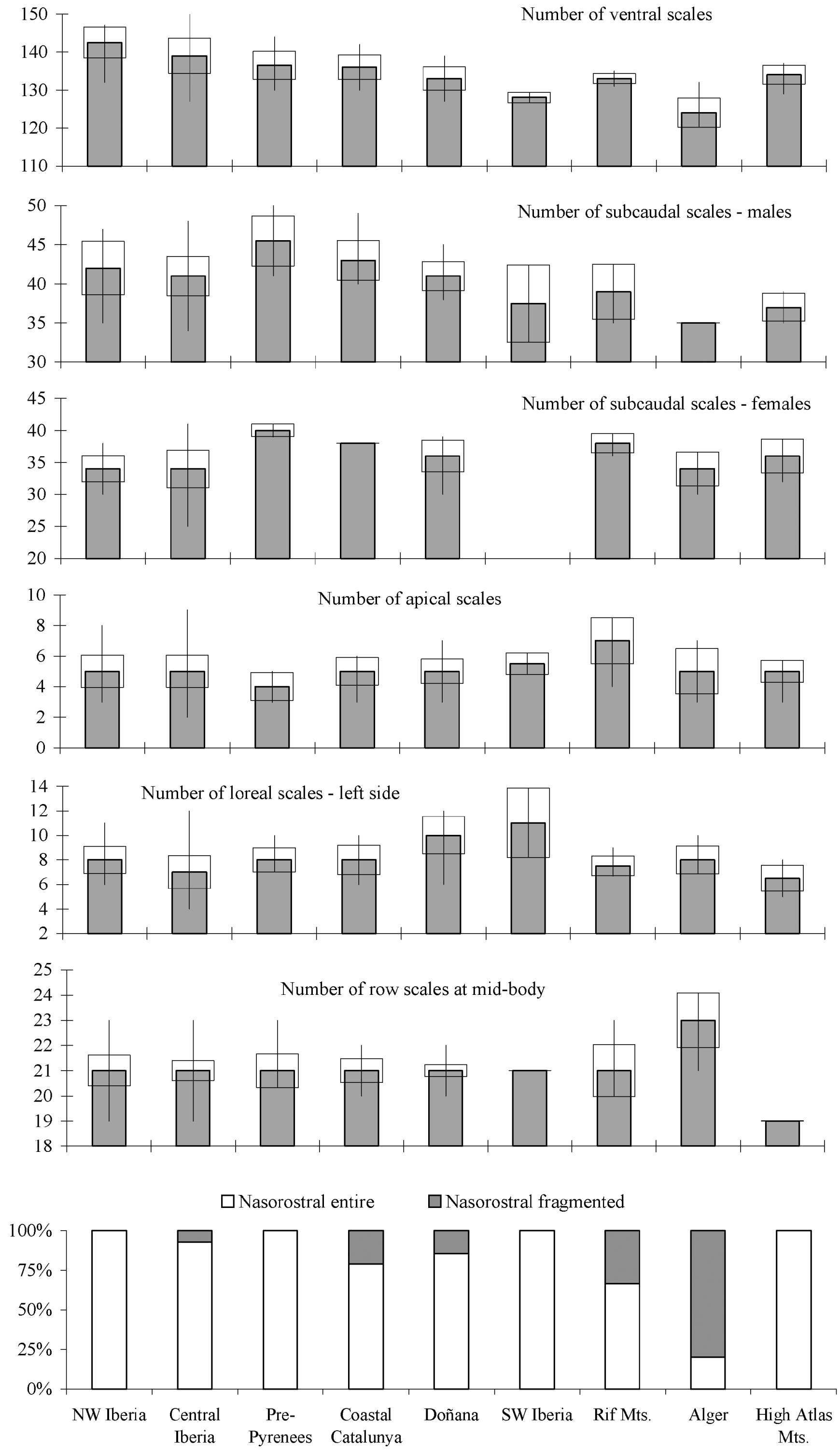

Figure 2. Mean, range and standard deviation of five meristic traits and percentage of character states in one qualitative trait that explain *Vipera latastei-monticola* morphological variation in the nine final groups selected by the Discriminant Function Analysis. Number of subcaudals is given for each sex due to significant sexual dimorphism in this trait.

Table 3. Meristic and qualitative traits related with geographic variability in male and female *Vipera latastei-monticola* complex. Traits were selected using a stepwise procedure with a Discriminant Function Analysis.

Sex	Variables	Significance of F	Wilks' Lambda
Males	DMBOD	0.000	0.077
	NASOL	0.001	0.048
	SUBCA	0.002	0.041
	VENTR	0.014	0.035
	APICA	0.030	0.032
Females	DMBOD	0.001	0.047
	VENTR	0.012	0.019
	LOREL	0.017	0.016

tial groups is presented in Appendix 1. Descriptive statistics on the meristic traits and frequencies of states in qualitative traits that discriminate among the initial and final groups are presented in Appendices 2 and 3.

The scatter plots of the relative position of individual specimens and group centroids in the projection of the first two discriminant axes showed that for males the variability of samples from the Coastal Catalonia, Rif, High Atlas, and Alger, did not overlap with the rest of the samples, whereas for females, discrimination was higher in the groups Doñana, High Atlas, and Alger (fig. 3). The remaining Iberian groups were less significantly discriminated in both sexes. The specimens from Columbretes islands, Gata cape, and Azrou (Medium Atlas, Morocco) were classified as belonging to the Nevada group, while the specimen from Rhibat al Khayr (Morocco) was classified as belonging to the Rif group.

Hierarchical Cluster Analysis for the initial groups showed unclear patterns of group association and of difficult interpretation, as expected from the results of the percentage of correct classification of group assignment (fig. 4). However, the African groups clearly differ from the Iberian groups, but in females the Rif group clustered with the Iberian groups. Also in females the groups Coastal Catalonia and Pre-Pyrenees clustered together. For the final groups, HCA showed a strong association between the geographic Coastal Catalonia with Pre-Pyrenees groups, and between the NW and central Iberian groups (fig. 4). The Rif group clustered consistently with the Iberian groups, whereas in males the SW Iberian group clustered with the High Atlas group. The African groups High Atlas and Alger were the most differentiated groups in both sexes despite their small sample size.

Discussion

Sexual dimorphism

There were few sexual morphological differences between male and female *V. latastei-monticola* complex. For example, male and female *V. latastei* do not differ in body size. However, males were larger than females when only the upper deciles of SVL were compared. In Gerês (northern Portugal), males grow faster, attain sexual maturity sooner, and the asymptotic body size is larger, than in females. However, mortality increased after sexual maturity in both sexes and was higher in males than in females. Probably, the sexual difference in mortality annulled an age-specific sexual size dimorphism in favour of males, and produced a minor sexual size dimorphism in mean adult body size in this group (Brito and Rebelo, 2003).

Sexual differences are important in the number of subcaudal scales and tail length, both traits being larger in males than in females. The number of subcaudal was reported from the literature as varying geographically and presenting sexual dimorphism (Saint Girons, 1977, 1978). According to our study, populations from the SW Iberian Peninsula, the High Atlas, and Alger had a mean of 37 subcaudals in both sexes; populations from the Rif and Doñana had 40 and 37 subcaudals, respectively; populations from central and NW Iberian had 42 and 34; and other populations had 43 and 37 subcaudals, respectively. For males, both larger tails and higher number of subcaudals are related to the presence of the hemipenis in the tail, as in many snake species (Shine, 1993). In the SW

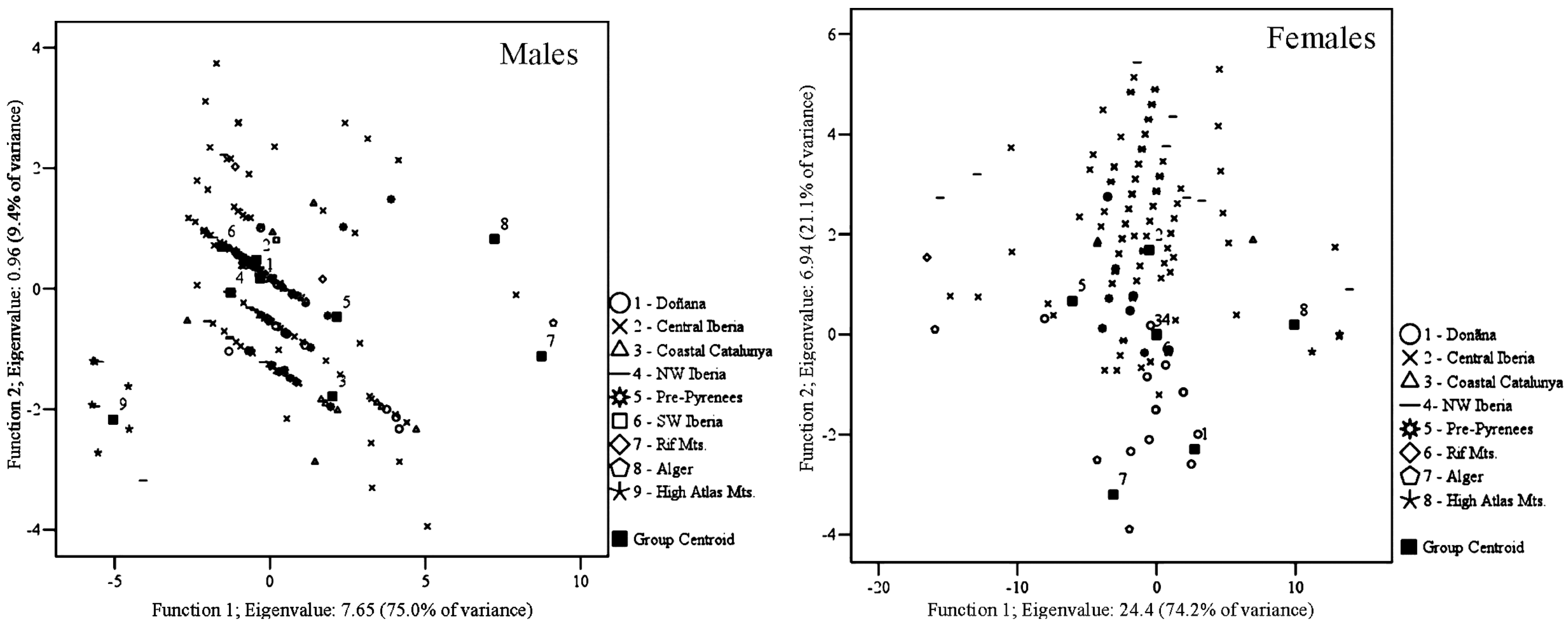

Figure 3. Relative position of individual male and female *Vipera latastei-monticola* specimens belonging to nine geographic groups in the projection of the first two canonical variates according to the Discriminant Function Analysis using meristic and qualitative traits.

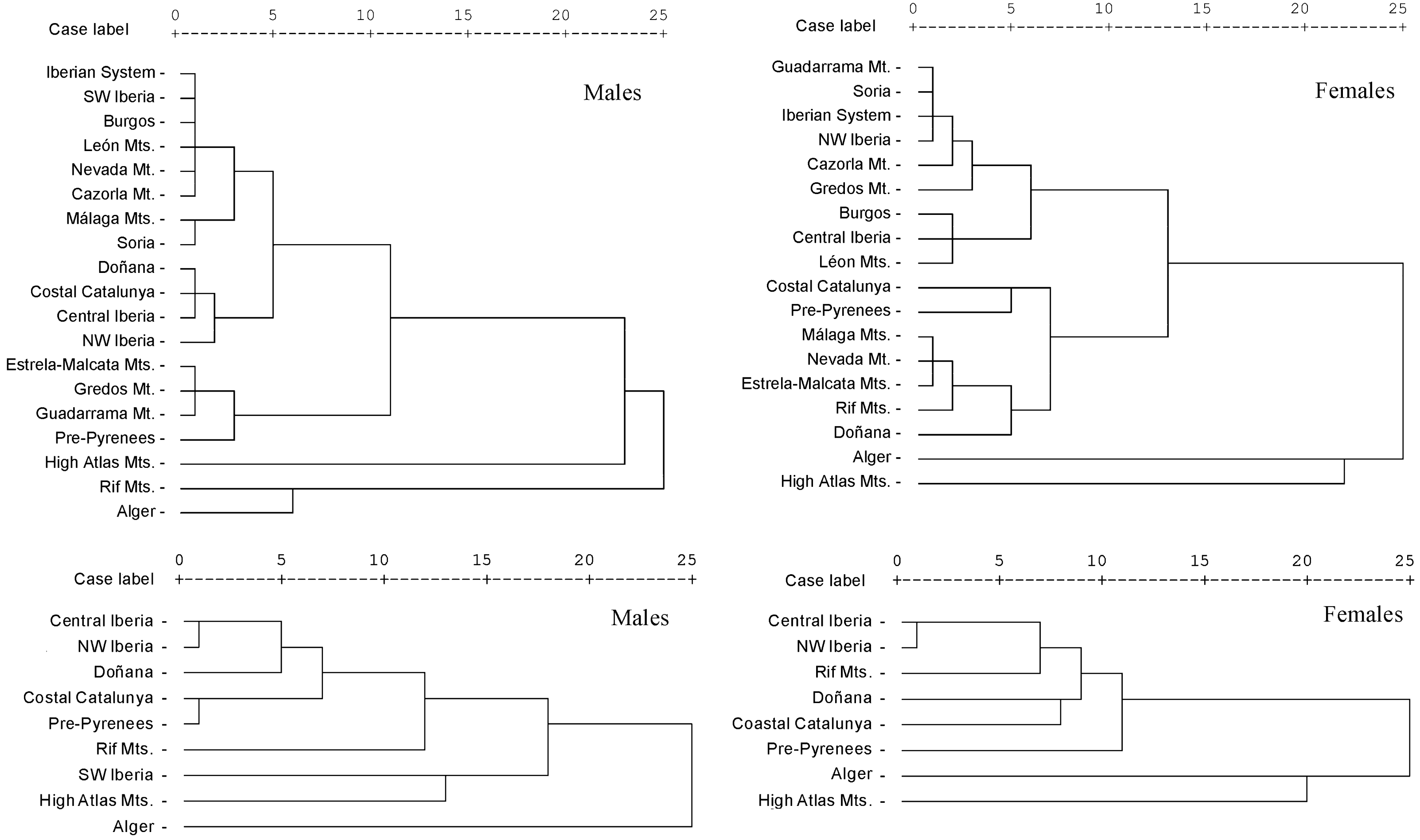

Figure 4. Male and female *Vipera latastei-monticola* complex initial (above, 19 regions) and final (below, 9 regions) group relationships based on Mahalanobis distances and meristic as well as qualitative traits. Trees were estimated by Hierarchical Cluster Analysis using Wards method of clustering.

Iberian Peninsula, Rif, High Atlas, and Alger, males and females of these areas showed reduced sexual dimorphism in these characters, although this result may be due to the small sample sizes for these populations. For females, the relative length of the tail and subsequently the number of subcaudals could be related to reproductive effort. Amongst the factors affecting sexual size dimorphism (review by Shine, 1994), fecundity-selection pressure can favour a larger female body size by reducing the number of subcaudals, in order to accommodate a larger number of embryos. This trend should be stronger in viviparous species (Madsen and Shine, 1992), as is the case for the vipers here considered. This would apply perfectly to *V. latastei*, where the proportion of variation explained by the regression of clutch size on body size ($r^2 = 0.7$, $n = 19$, unpubl. data) is rather high (see comparative data for 61 snake species in Seigel & Ford, 1987).

Geographical analysis and taxonomic implications

The analysis of meristic and qualitative characters from *Vipera latastei* and *Vipera monticola* revealed a complex pattern of biogeographical distribution of morphological variability. Principal Components Analysis and Discriminant Function Analysis showed that the variables accounting for much of the geographical variability were the number of ventral, subcaudal, apical, and loreal scales, the rows of dorsal scales at mid-body, and the level of fragmentation of the nasorostral scale.

These results confirmed previously reported data (Saint Girons, 1977, 1978; Beerli et al., 1986) concerning the taxonomic relevance of the number of ventral scales. Our analysis also showed a clinal variation pattern in an approximately SE-NW axis within the total distribution area of the species: populations from the SW Iberian Peninsula and Alger with a mean of 126 ventrals; from Doñana, the High Atlas, and Rif with 133 ventrals; from the Central Iberian Peninsula, Pre-Pyrenees and coastal Catalonia with 137 ventrals; and from the NW Iberian Peninsula with a mean of 143 ventral scales. As larger individuals often have more ventral scales than smaller ones in many snake species (Klauber, 1945; Lindell et al., 1993), this clinal pattern in the number of ventral scales (more in the north) agrees with the Bergmann' rule. Although Bergmann' rule was applied primarily to endotherms, it also applies to certain ectotherms (e.g. Ray, 1960; Atkinson, 1994), including some snake species (Ashton, 2001; Ashton and Feldman, 2003; Santos and Pleguezuelos, 2003). The evolutionary forces that acted to increase the number of ventral scales in the northern populations remain unclear, but some authors have suggested that the seasonality of climatic variables could be a good predictor of intraspecific variation in size-related traits of ectotherms (Boyce, 1979).

The number of apical scales and loreal scales were previously reported as having geographic variation (Saint Girons, 1977). Nevertheless, concerning the number of apical scales, the present study shows that populations from the Pre-Pyrenees had a mean number of 4 apicals, while populations from the Rif had 7 apicals and from the remaining areas a mean of 5 apical scales. In the Pre-Pyrenees, there is a contact area with *V. aspis*, and morphological convergence between the two species has been reported (Duguy et al., 1979): specimens from *V. latastei* in this region have a short nose covered by only two or three scales. A similar trend was observed in the north part of Burgos province (western Iberian System) where *V. latastei* and *V. aspis* have another contact area (Pleguezuelos and Santos, 2002; Gosá, 2002). There are no reports of confirmed hybridization between these two species, but genetic studies could provide insights on a probable gene flow between these two vipers. The number of loreal scales apparently also has taxonomic relevance, as populations from the SW Iberian Peninsula and Doñana have a mean of 11 loreal scales, whereas the remaining populations had a mean of 8 loreal scales.

The number of row scales at mid-body was previously regarded as taxonomically stable, and used to separate the three populations: a) High Atlas, exclusively with 19 rows, b) Alger, mostly with 23 rows, and c) the remaining areas, mostly with 21 rows (Saint Girons, 1977; Beerli et al., 1986). This is the most stable character separating the populations of the High Atlas from the other areas, and has contributed significantly to determine the specific status of these populations (Beerli et al., 1986). Our study confirms previous results: all the specimens analysed from the High Atlas had 19 rows of scales, the majority from Alger had 23 rows (60%), and most specimens from the remaining areas had 21 rows (95%).

It is known that in interspecies comparisons among snakes, larger species had more dorsal rows than do smaller species (Klauber, 1956; Arnold, 1993), because more scales are necessary to envelop a larger body (Fabien et al., 2004). This simple morphological hypothesis fits well for the number of dorsal rows in the small-sized High Atlas *V. monticola* populations (all individuals with 19 rows), but does not fit for the also small-sized *V. latastei* from Argel (most individuals with 23 rows). Shine (2002) also proposed the existence of morphological adaptation (i.e. number of dorsal rows) to different dietary habits in snakes: a high number of dorsal rows would facilitate the ingestion of larger, bulk prey, giving the skin of the snake more ability to stretch (Gans, 1974; Fabien et al., 2004). However, lack of data on geographic variation of diet composition from the African populations precludes testing this hypothesis.

The results from the multivariate analysis suggest that: 1) there is a strong morphological differentiation for the population of the High Atlas. Clearly, the populations occurring in the High Atlas share particular characters, such as exclusively 19 rows of scales at mid-body, a low number of subcaudals, and a small body size. 2) There is a complex variation pattern among the populations of southern Iberian Peninsula and northern Africa. For instance, one specimen from Chefchaouen (the Rif) was systematically classified as belonging to the Central-Iberian group, males from the SW Iberian Peninsula clustered with the African clad, while males and females from the Rif clustered with the Iberian Peninsula clad. Although some characters exhibit geographical stability, such as a low number of ventral scales and high frequency of specimens with the nasorostral scale fragmented in Alger, or a large number of apical scales in the Rif, there is a large overlap between the ranges of character variation among these populations. 3) There is a certain degree of differentiation among the groups the NW Iberian Peninsula, Pre-Pyrenees and coastal Catalonia, with respect to central-Iberian group (fig. 1). The specimens from these populations present particular characters, such as large number of ventral scales in the NW Iberian population or low number of apical scales in Pre-Pyrenees, but there is again a marked overlap among these populations with the rest of the Iberian populations.

The current taxonomic status of *V. latastei-monticola* populations in the Atlas Mountains is unclear. Saint Girons (1953a, b) attributed a subspecies status to the populations from the High Atlas, whereas Beerli et al. (1986) recognized them as a species, *V. monticola*. Nevertheless, in the Medium Atlas, there are specimens with 21 rows of scales at mid-body, as in Ribat-al-Khayr plateau (ancient Ahermoumou) and Azibs Aghous (High Atlas; Roux, 1939), suggesting that the status of *V. monticola* should be re-evaluated (Bons and Geniez, 1996). The present analysis classified the specimen from Ribat-al-Khayr (available in the MNHN collection) as belonging to the Rif group. Therefore, *V. monticola* probably occupies all of the High Atlas as well as the Medium Atlas, with the exception of the north-eastern plateau, east of Fez. The specific status for the populations in the High Atlas should be maintained pending further analysis of specimens from the Medium Atlas.

The taxonomic status of the remaining populations is also unclear. According to Saint Girons (1977, 1978), the populations from the south-western Iberian Peninsula and northern Africa belong to the subspecies *V. latastei gaditana*, whereas the remaining populations belong to the nominal subspecies: *V. latastei latastei*. However, Saint Girons (1977) noted that, despite that all specimens from Algeria belonged to the *gaditana* subspecies, the variability of the Algerian sample, mostly from the Tell Mountains, was larger than the variability between the populations from the Rif Mountains and south-western Iberian Peninsula. The small sample of analysed specimens precluded the author of assigning further subspecies, despite the recognition that other taxa could be present in the study area. The analyses of the present study also suggest that the Algerian populations belong to an undescribed taxa. Nevertheless, the small sample size and the complex pattern of morphological variation across the Strait of Gibraltar do not confirm or invalidate of the morphological trends. The opening of the Gibraltar Strait (c. 5.3 m. y.; Maldonado, 1986) acted as a vicariate agent of diversification between the amphibians and reptiles of the Iberian Peninsula and northern Africa (Busack, 1986). This crucial event separated the faunas inhabiting the southern Iberian Peninsula from those in northern Africa, turning them into allopatric taxa. Complex patterns of genetic variation have been described in other taxa, such as salamanders, geckos, and lizards (Busack, 1988; Harris et al., 2002, 2004a, b; Batista et al., 2004), and this is probably also the case for the *V. latastei* populations.

Our results for the geographic differentiation of the populations of the Iberian Peninsula agree with the distribution limits of the subspecies proposed by Saint Girons (1977). However, our analyses also indicate a certain degree of differentiation in the north-western and north-eastern populations. The climatic shifts since the Last Glacial Maximum probably contributed to isolation events, population refugia, and contraction/expansion processes, as observed in other taxa (e.g. Alexandrino et al., 2000). The genetic changes in the fragmented refugial populations were not probably substantial enough to produce full speciation (the most recent ice age ended about 10,000 years ago) but could accelerate the process of allopatric speciation, contributing to present intraspecific differentiation (Ridley, 2004). In conclusion, the Iberian *Vipera latastei* groups show a morphologically homogeneous central area with differentiation in isolated populations at the range limits. This scenario matches well with a classical model of speciation proposed by Mayr (1963) in the sense that most new species arise from peripheral isolated populations. These allopatric speciation processes could also have been favoured by a very fragmented distribution area, thereby contributing to the present-day morphological variation (Godinho et al., 1999; Pleguezuelos and Santos, 2002).

The question arises as to whether the model described above is similar to the models found in *V. aspis* and *V. ammodytes*. Some morphological traits (ventral scales, dorsal rows, dorsal pattern) similarly function as appropriate external characters to divide the populations into the three species (Zuffi, 2002; Tomović and Džukić, 2003; this study). As snakes are morphologically simple, there are limited number of ways in which populations can differ (Shine, 2000). This could result in similar patterns of intraspecific differentiation in the three viper species, also increased by the fact that they have been exposed to similar recent geological events (i.e. glaciations) in similar biogeographical areas (i.e. three major Mediterranean Peninsulas).

The use of molecular markers could help in determining the relationships between *V. latastei* populations, in evaluating the role of the opening of the Strait of Gibraltar as a barrier to gene flow and as a diversification agent, as well as in understanding the colonisation history of *V. latastei* across the entire geographic distribution range. Such study would certainly help in the revision of the systematic and taxonomical status of *V. latastei-monticola* populations in northern Africa that morphologically exhibit a puzzling scenario.

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Appendix 1. Descriptive statistics of morphometric variation of adult male (M) and female (F) of *Vipera latastei-monticola* complex in 19 groups (see Materials and methods section for abbreviations).

Character	SVL		TLENG		TBODY		HLENG	
Group/Sex	M	F	M	F	M	F	M	F
NW Portugal; n	53	42	53	42	53	42	13	9
Mean ± SD	396.6 ± 77.0	411.1 ± 80.2	64.2 ± 15.4	55.0 ± 12.7	13.9 ± 1.6	11.8 ± 1.1	20.2 ± 2.0	21.9 ± 3.3
Min-Max	250-580	270-560	35-100	30-80	9-16	9-14	18-25	17-28
León Mts.; n	3	3	3	3	2	3	2	2
Mean ± SD	383.1 ± 36.7	403.0 ± 59.8	60.0 ± 10.0	49.0 ± 1.7	13.1 ± 0.6	11.0 ± 1.2	20.8 ± 0.4	21.7 ± 2.5
Min-Max	345-418	334-440	50-70	47-50	13-14	10-12	21	20-24
Estrela-Gata Mts.; n	13	13	10	12	10	11	9	10
Mean ± SD	404.7 ± 43.8	401.1 ± 54.7	64.8 ± 12.8	56.8 ± 8.0	14.0 ± 2.2	12.5 ± 1.0	23.4 ± 3.4	22.3 ± 2.4
Min-Max	350-495	294-487	35-83	45-70	8-15	11-14	19-29	19-25
Gredos Mts.; n	11	6	9	6	7	6	9	6
Mean ± SD	380.7 ± 84.0	420.7 ± 23.1	66.2 ± 13.4	63.0 ± 5.5	14.7 ± 1.1	13.0 ± 0.5	22.4 ± 3.6	23.1 ± 2.1
Min-Max	270-504	395-455	43-82	58-73	13-16	12-14	16-27	19-26
Guadarrama Mt.; n	16	11	15	9	15	9	11	10
Mean ± SD	405.2 ± 90.3	407.7 ± 74.7	65.1 ± 15.1	61.7 ± 9.4	13.9 ± 1.0	12.9 ± 0.7	22.6 ± 3.6	22.9 ± 3.1
Min-Max	254-523	263-501	36-88	48-80	12-15	12-14	17-27	16-26
Pre-Pyrenees; n	8	4	7	4	6	4	7	4
Mean ± SD	420.7 ± 76.2	438.5 ± 18.4	78.3 ± 15.7	67.5 ± 7.1	15.9 ± 0.7	13.3 ± 0.8	23.7 ± 3.4	25.3 ± 2.0
Min-Max	259-499	414-455	50-96	57-73	15-17	12-14	17-27	23-28
Coastal Catalonia; n	11	5	11	5	9	2	7	4
Mean ± SD	409.6 ± 118.6	539.1 ± 69.5	74.6 ± 20.7	71.6 ± 7.0	15.7 ± 1.7	11.1 ± 0.3	23.5 ± 5.2	27.9 ± 1.8
Min-Max	270-567	457-640	44-103	64-79	14-19	11	17-30	26-30
W Iberian System; n	12	9	11	9	10	9	5	7
Mean ± SD	450.7 ± 62.0	432.4 ± 61.8	74.3 ± 7.5	64.3 ± 6.3	14.4 ± 1.1	13.1 ± 1.3	24.7 ± 1.6	23.9 ± 2.6
Min-Max	315-533	338-520	56-84	51-71	13-16	11-15	22-26	20-28
C Iberian System; n	16	21	15	18	14	16	11	15
Mean ± SD	425.2 ± 61.6	406.7 ± 63.6	70.8 ± 9.5	56.9 ± 9.1	14.3 ± 0.9	12.3 ± 0.9	24.0 ± 1.9	22.2 ± 2.4
Min-Max	309-572	294-533	52-87	43-74	12-16	11-14	20-27	18-28
E Iberian System; n	15	11	15	10	15	9	13	8
Mean ± SD	397.5 ± 88.7	381.4 ± 57.9	67.2 ± 14.5	56.5 ± 6.0	14.5 ± 1.4	12.7 ± 1.0	22.1 ± 2.5	21.9 ± 3.0
Min-Max	268-596	276-466	49-101	49-65	11-17	12-15	18-25	17-26
Toledo-Morena; n	16	4	16	4	15	3	12	3
Mean ± SD	381.7 ± 85.2	382.9 ± 63.9	67.3 ± 13.1	53.8 ± 12.5	15.1 ± 1.3	12.2 ± 1.1	23.5 ± 4.3	24.3 ± 4.9
Min-Max	256-592	316-462	40-86	43-70	13-17	11-13	18-31	20-30
Cazorla-Alcaraz; n	8	7	8	7	8	7	5	6
Mean ± SD	404.4 ± 64.4	408.3 ± 55.1	66.1 ± 8.3	57.3 ± 9.6	14.1 ± 0.6	12.3 ± 0.7	25.3 ± 4.1	24.7 ± 3.7
Min-Max	302-525	330-499	53-83	44-73	14-15	11-13	21-32	20-30
Nevada Mt.; n	30	20	26	18	23	18	21	13
Mean ± SD	427.7 ± 75.6	408.8 ± 62.3	71.0 ± 13.6	56.8 ± 8.9	14.5 ± 1.1	12.3 ± 1.1	25.1 ± 4.9	25.0 ± 3.2
Min-Max	255-549	275-545	41-103	38-69	13-17	10-14	15-32	18-29
Ronda Mt.; n	14	8	13	7	12	7	13	7
Mean ± SD	452.2 ± 73.6	424.5 ± 98.8	77.9 ± 9.9	61.0 ± 16.0	14.6 ± 0.8	12.5 ± 1.4	27.0 ± 3.7	26.8 ± 3.6
Min-Max	333-571	275-543	64-97	34-79	14-16	11-15	21-33	20-31
Doñana; n	15	14	15	14	15	14	12	12
Mean ± SD	386.9 ± 80.5	364.4 ± 64.3	68.9 ± 15.0	57.1 ± 10.4	15.1 ± 1.0	13.6 ± 1.0	24.0 ± 3.6	22.7 ± 2.6
Min-Max	265-504	275-455	50-96	44-75	13-17	12-16	18-29	19-27
SW Iberian Pen.; n	3	1	3	0	3	1	1	
Mean ± SD	315.0 ± 60.6	500.0	55.0 ± 15.0		14.7 ± 1.2	4.8	16.7	
Min-Max	260-380	500	40-70		13-16	5	17	
Rif Mts.; n	3	2	3	2	3	2	3	2
Mean ± SD	236.3 ± 11.8	344.5 ± 2.1	40.0 ± 5.0	53.5 ± 7.8	14.4 ± 1.1	13.4 ± 1.8	14.9 ± 0.8	21.7 ± 1.1
Min-Max	229-250	343-346	35-45	48-59	13-15	12-15	14-16	21-23
Alger; n	2	3	1	3	1	3	2	3
Mean ± SD	295.0 ± 14.1	274.7 ± 42.3	45.0	38.0 ± 4.0	13.6	12.2 ± 1.3	17.3 ± 0.7	17.2 ± 0.7
Min-Max	285-305	238-321	45	34-42	14	11-14	17-18	17-18
High Atlas Mts.; n	13	10	10	10	10	10	5	3
Mean ± SD	266.6 ± 61.5	263.9 ± 34.7	40.0 ± 5.7	38.0 ± 3.7	14.1 ± 1.0	12.7 ± 1.0	13.3 ± 1.3	15.9 ± 0.8
Min-Max	205-450	211-307	32-51	33-45	12-16	12-15	12-15	15-17

Character	HWIDT		HHEIG		MLENG	
Group/Sex	M	F	M	F	M	F
NW Portugal; n	31	24	27	24	13	10
Mean ± SD	13.8 ± 2.4	15.0 ± 2.7	8.6 ± 2.0	8.9 ± 2.0	18.7 ± 1.6	18.8 ± 2.3
Min-Max	10-19	10-21	5-16	6-12	16-22	15-22
León Mts.; n	1	1	1	1	2	2
Mean ± SD	13.8	18.3	8.2	9.6	18.7 ± 0.1	19.3 ± 2.6
Min-Max	14	18	8	10	19	17-21
Estrela-Gata Mts.; n	8	11	6	9	9	10
Mean ± SD	15.9 ± 1.6	15.3 ± 1.9	9.6 ± 1.8	9.2 ± 1.3	20.2 ± 2.7	19.4 ± 2.0
Min-Max	14-18	12-18	8-13	7-11	18-25	16-22
Gredos Mt.; n	9	5	7	4	9	6
Mean ± SD	15.3 ± 3.5	15.8 ± 2.6	9.5 ± 1.3	9.5 ± 0.7	18.7 ± 3.8	19.6 ± 2.2
Min-Max	9-19	13	7-11	9-10	13-25	15-22
Guadarrama Mt.; n	11	8	7	8	11	11
Mean ± SD	14.8 ± 2.1	15.3 ± 2.2	7.9 ± 1.4	9.1 ± 1.1	19.1 ± 3.2	19.5 ± 2.8
Min-Max	11-18	12-19	6-10	8-10	14-23	13-23
Pre-Pyrenees; n	7	4	7	4	7	4
Mean ± SD	15.4 ± 4.3	17.9 ± 2.4	9.6 ± 1.8	9.7 ± 0.7	19.8 ± 2.5	22.2 ± 1.0
Min-Max	8-20	16-21	6-11	9-11	15-23	21-23
Coastal Catalonia; n	6	3	6	3	7	4
Mean ± SD	16.0 ± 3.7	17.6 ± 2.6	10.9 ± 2.7	10.9 ± 1.7	19.9 ± 4.7	22.6 ± 1.2
Min-Max	11-21	15-20	7-14	10-13	13-25	21-24
W. Iberian System; n	4	7	3	7	5	7
Mean ± SD	15.1 ± 0.7	15.8 ± 3.3	8.7 ± 1.3	9.6 ± 1.2	21.1 ± 1.7	19.9 ± 2.5
Min-Max	14-16	10-20	7-10	8-11	19-23	16-23
C Iberian System; n	11	15	11	10	12	17
Mean ± SD	15.2 ± 1.8	14.2 ± 1.7	9.9 ± 1.1	9.1 ± 0.7	20.4 ± 2.0	19.0 ± 2.0
Min-Max	12-18	10-18	8-12	8-10	16-23	15-23
E Iberian System; n	12	8	11	7	13	8
Mean ± SD	14.0 ± 2.2	14.7 ± 2.9	8.8 ± 1.5	9.3 ± 2.0	18.3 ± 2.1	18.2 ± 2.8
Min-Max	10-18	12-20	6-11	6-12	14-22	15-22
Toledo–Morena; n	10	3	9	3	12	3
Mean ± SD	15.8 ± 3.7	17.2 ± 4.2	10.7 ± 3.8	10.7 ± 3.0	19.6 ± 3.1	21.2 ± 5.1
Min-Max	11-22	14-22	7-20	8-14	15-24	17-27
Cazorla-Alcaraz; n	5	6	6	6	5	6
Mean ± SD	16.5 ± 2.7	18.4 ± 5.1	10.5 ± 1.8	10.0 ± 2.0	20.7 ± 2.8	20.2 ± 4.7
Min-Max	15-21	12-27	8-13	8-13	18-25	12-26
Nevada Mt.; n	17	13	17	11	21	15
Mean ± SD	17.0 ± 3.3	18.0 ± 2.8	10.4 ± 1.8	10.8 ± 1.5	21.1 ± 3.8	21.0 ± 2.8
Min-Max	11-23	13-23	7-14	8-13	13-27	16-24
Ronda Mt.; n	11	6	11	5	12	7
Mean ± SD	18.4 ± 1.8	18.5 ± 2.3	10.4 ± 2.2	11.7 ± 2.1	23.3 ± 2.8	22.5 ± 2.5
Min-Max	15-21	16-22	7-13	8-14	19-28	18-25
Doñana; n	11	7	9	6	13	10
Mean ± SD	16.8 ± 3.4	15.8 ± 2.6	8.9 ± 1.2	9.4 ± 1.1	19.6 ± 2.9	19.0 ± 2.4
Min-Max	12-22	14-22	7-11	8-11	15-24	16-22
SW Iberian Pen.; n	2	0	2	0	2	0
Mean ± SD	12.5 ± 23		8.2 ± 0.5		16.2 ± 1.9	
Min-Max	11-14		8-9		15-18	
Rif Mts.; n	3	2	3	2	2	2
Mean ± SD	10.2 ± 1.6	15.1 ± 1.7	5.8 ± 0.7	9.1 ± 1.0	12.1 ± 0.4	18.3 ± 0.4
Min-Max	9-12	14-16	5-7	8-10	12-12	18-19
Alger; n	2	3	2	3	2	3
Mean ± SD	9.4 ± 1.3	10.9 ± 1.6	6.3 ± 0.5	7.5 ± 0.5	15.3 ± 0.7	14.8 ± 1.4
Min-Max	9-10	9-12	6-7	7-8	15-16	14-17
High Atlas Mts.; n	5	3	5	3	5	3
Mean ± SD	8.0 ± 0.9	9.5 ± 1.6	5.7 ± 0.5	6.3 ± 0.3	12.3 ± 1.4	13.6 ± 0.5
Min-Max	7-9	9-11	5-6	6-7	11-15	13-14

Appendix 2. Descriptive statistics of seven meristic traits explaining morphological variation of the male (M) and female (F) *Vipera latastei-monticola* complex in 19 groups, according to the Discriminant Function Analysis (see Materials and methods section for abbreviations).

Character	VENTR		SUBCA		DMBOD		APICA		PERIL		LOREL	
Group/Sex	M	F	M	F	M	F	M	F	M	F	M	F
NW Portugal; n	34	20	32	19	35	21	36	21	31	20	31	19
Median ± SD	142 ± 3.9	145 ± 3.7	43 ± 3.4	35 ± 2.0	21 ± 0.6	21 ± 0.8	5 ± 1.0	5 ± 1.1	9 ± 0.8	10 ± 0.6	8 ± 1.1	8 ± 1.0
Min-Max	132-146	135-147	35-47	30-38	19-21	19-23	3-7	3-8	8-11	9-11	6-10	6-10
León Mts.; n	6	2	5	2	6	2	6	2	6	2	6	2
Median ± SD	141 ± 3.7	138 ± 7.8	37 ± 2.2	32 ± 0.7	21 ± 0.0	21 ± 0.0	5 ± 0.8	5 ± 0.7	10 ± 0.9	10 ± 1.4	8 ± 1.4	8 ± 0.7
Min-Max	136-145	132-143	37-42	31-32	21	21	3-5	4-5	9-11	9-11	7-11	7-8
Estrela-Gata Mts.; n	10	14	10	17	12	17	13	18	12	18	12	18
Median ± SD	135 ± 4.5	138 ± 3.6	40.5 ± 2.2	33 ± 3.5	21 ± 0.6	21 ± 0.3	4 ± 1.0	5 ± 1.0	10 ± 0.5	10 ± 0.7	7 ± 2.1	7 ± 0.9
Min-Max	127-139	130-143	38-45	25-39	21-23	21-22	3-5	3-7	9-10	9-11	4-11	6-9
Gredos Mt.; n	14	6	14	6	15	6	14	6	15	6	15	6
Median ± SD	140 ± 4.7	141 ± 1.9	40 ± 1.5	36 ± 1.6	21 ± 0.5	21 ± 0.8	5 ± 0.9	5 ± 0.0	10 ± 1.0	9 ± 0.5	7 ± 1.1	8 ± 0.5
Min-Max	131-148	139-144	39-43	33-37	21-23	19-21	3-7	5	8-12	9-10	5-9	7-8
Guadarrama Mt.; n	17	15	15	13	17	16	16	16	17	16	17	14
Median ± SD	141 ± 4.2	143 ± 3.1	42 ± 2.3	36 ± 2.6	21 ± 0.7	21 ± 0.5	5 ± 1.3	5 ± 1.2	10 ± 0.6	10 ± 0.6	7 ± 0.6	7 ± 1.4
Min-Max	136-153	139-150	38-47	31-40	20-23	21-23	3-9	2-8	9-11	8-11	6-8	6-11
Pre-Pyrenees; n	9	3	8	3	8	3	9	3	9	3	8	3
Median ± SD	137 ± 4.1	135 ± 2.0	46 ± 3.2	40 ± 1.0	21 ± 0.7	21 ± 0.6	4 ± 0.9	5 ± 0.6	10 ± 0.7	10 ± 0.6	8 ± 0.7	7 ± 1.7
Min-Max	130-144	133-137	41-50	39-41	21-23	21-22	3-5	4-5	9-11	9-10	7-9	7-10
Coastal Catalonia; n	15	2	15	4	14	4	15	4	14	4	15	4
Median ± SD	136 ± 3.3	138 ± 3.5	43 ± 2.5	38 ± 0.0	21 ± 0.5	21 ± 0.5	5 ± 1.0	5 ± 0.0	10 ± 0.8	9 ± 1.4	8 ± 1.1	7 ± 1.9
Min-Max	130-142	135-140	40-49	38-38	20-22	20-21	3-6	5	8-11	6-9	6-10	6-10
W Iberian System; n	9	7	10	9	10	9	9	9	7	7	6	7
Median ± SD	143 ± 3.6	140 ± 3.4	40 ± 2.4	33 ± 1.7	21 ± 0.0	21 ± 0.3	4 ± 1.2	5 ± 1.0	9 ± 0.9	9 ± 0.7	6 ± 0.5	7 ± 1.3
Min-Max	138-148	133-142	38-45	30-35	21	20-21	2-5	3-6	8-10	8-10	6-7	5-9
C Iberian System; n	16	16	17	19	19	21	19	20	19	20	16	20
Median ± SD	139 ± 3.9	141 ± 3.3	40 ± 2.3	34 ± 2.3	21 ± 0.2	21 ± 0.2	5 ± 1.1	5 ± 0.7	9 ± 0.7	9 ± 0.7	6 ± 0.7	7 ± 1.1
Min-Max	133-145	136-147	36-44	30-39	21-22	21-22	3-7	3-7	8-11	8-11	5-8	5-10
E Iberian System; n	15	10	14	10	15	11	15	11	15	11	14	11
Median ± SD	138 ± 5.5	140 ± 3.0	41 ± 3.1	34 ± 3.0	21 ± 0.0	21 ± 0.6	5 ± 1.3	5 ± 0.7	9 ± 0.8	10 ± 1.0	8 ± 1.7	7 ± 1.0
Min-Max	131-150	133-142	38-48	28-38	21	19-21	3-8	3-6	8-10	7-11	5-11	5-8
Toledo-Morena; n	12	4	11	4	12	4	12	4	10	4	8	2
Median ± SD	134 ± 4.3	135 ± 4.0	40 ± 2.9	34 ± 4.5	21 ± 0.3	21 ± 0.0	5 ± 1.0	6 ± 1.5	10 ± 0.7	10 ± 0.9	9 ± 1.5	8 ± 0.7
Min-Max	127-143	131-140	34-44	26-36	20-21	21	3-7	5-8	10-12	9-11	6-11	7-8

Character	VENTR		SUBCA		DMBOD		APICA		PERIL		LOREL	
Group/Sex	M	F	M	F	M	F	M	F	M	F	M	F
Cazorla-Alcaraz; n	10	6	9	6	10	7	10	7	8	7	9	6
Median ± SD	136 ± 3.8	138 ± 6.2	40 ± 3.3	37 ± 2.7	21 ± 0.0	21 ± 0.7	5 ± 1.2	5 ± 1.2	9 ± 0.7	9 ± 0.8	7 ± 1.0	7 ± 1.2
Min-Max	128-140	130-146	37-48	32-39	21	20-22	3-8	3-7	8-10	8-10	5-8	5-8
Nevada Mt.; n	23	16	23	19	27	19	27	19	23	19	25	19
Median ± SD	139 ± 4.3	137 ± 4.1	43 ± 2.0	35 ± 2.9	21 ± 0.0	21 ± 0.2	5 ± 0.6	5 ± 0.8	10 ± 0.9	10 ± 0.7	8 ± 1.1	8 ± 1.4
Min-Max	127-146	132-145	38-46	28-41	21	21-22	3-6	5-8	8-11	9-11	6-10	6-12
Ronda Mt.; n	13	9	14	8	15	10	15	9	15	10	15	9
Median ± SD	136 ± 3.4	137 ± 1.7	42 ± 2.6	35 ± 3.1	21 ± 0.3	21 ± 0.4	5 ± 1.2	5 ± 1.3	10 ± 0.7	10 ± 0.8	9 ± 1.6	8 ± 2.0
Min-Max	130-141	134-139	37-46	32-40	21-22	21-22	4-8	4-8	9-11	8-11	6-11	5-12
Doñana; n	16	15	19	15	18	16	17	16	16	14	15	14
Median ± SD	133 ± 3.5	134 ± 2.7	41 ± 1.9	36 ± 2.5	21 ± 0.2	21 ± 0.3	5 ± 0.7	5 ± 0.8	10 ± 0.9	10 ± 1.1	9 ± 1.4	10 ± 1.6
Min-Max	127-139	127-138	38-45	30-39	20-21	21-22	3-6	3-7	8-11	7-11	7-11	6-12
SW Iberian Pen.; n	2	0	2	0	2	0	2	0	2	0	2	0
Median ± SD	128 ± 1.4		38 ± 5.0		21 ± 0.0		5.5 ± 0.7		8.5 ± 0.7		11 ± 2.8	
Min-Max	127-129		34-41		21		5-6		8-9		9-13	
Rif Mts.; n	3	3	3	3	3	3	3	3	3	3	3	3
Median ± SD	133 ± 0.6	133 ± 2.0	39 ± 3.5	38 ± 1.5	21 ± 1.2	21 ± 1.2	7 ± 1.7	7 ± 1.5	10 ± 0.6	10 ± 3.2	7 ± 0.6	8 ± 1.0
Min-Max	132-133	131-135	35-42	36-39	21-23	21-23	4-7	5-8	10-11	5-11	7-8	7-9
Alger; n	2	3	1	3	2	3	2	3	2	3	2	3
Median ± SD	123.5 ± 0.7	124 ± 4.9	35	34 ± 2.6	23 ± 0.0	21 ± 1.2	5.5 ± 0.7	5 ± 2.0	10.5 ± 0.7	10 ± 0.6	7.5 ± 0.7	9 ± 1.0
Min-Max	123-124	123-132	35	30-35	23	21-23	5-6	3-7	10-11	9-10	7-8	8-10
High Atlas Mts.; n	6	3	5	3	6	3	6	3	6	3	5	3
Median ± SD	135 ± 2.8	132 ± 1.7	37 ± 1.8	36 ± 2.6	19 ± 0.0	19 ± 0.0	5 ± 0.8	5 ± 0.6	9 ± 0.8	9 ± 1.5	6 ± 1.1	7 ± 1.0
Min-Max	129-137	132-135	35-39	32-37	19	19	3-5	4-5	8-10	7-10	5-8	6-8

Appendix 3. Frequencies (N – %) of three qualitative character states explaining the morphological variation of the male (M) and female (F) *Vipera latastei-monticola* complex in 19 groups, according to the Discriminant Function Analysis (see Materials and methods section for abbreviations and variable state descriptions).

Character		NASOL		CONTR			WMARG	
Group	Sex	0	1	0	1	2	0	1
NW Portugal	M	36-100	0-0	17-52	16-48	0-0	2-6	29-94
	F	21-100	0-0	3-17	11-61	4-22	5-29	12-71
León Mts.	M	6-100	0-0	1-17	5-83	0-0	2-40	3-60
	F	2-100	0-0	0-0	1-100	0-0	1-100	0-0
Estrela-Gata Mts.	M	9-69	4-31	2-29	3-43	2-29	1-17	5-83
	F	13-72	5-28	0-0	2-50	2-50	3-60	2-40
Gredos Mt.	M	13-87	2-13	4-36	7-64	0-0	4-40	6-60
	F	6-100	0-0	2-33	4-67	0-0	1-25	3-75
Guadarrama Mt.	M	16-94	1-6	3-30	6-60	1-10	6-60	4-40
	F	15-94	1-6	0-0	5-63	3-38	9-90	1-10
Pre-Pyrenees	M	9-100	0-0	1-13	4-50	3-38	8-100	0-0
	F	3-100	0-0	0-0	0-0	2-100	2-100	0-0
Coastal Catalonia	M	11-73	4-27	1-9	5-45	5-45	7-88	1-13
	F	4-100	0-0	0-0	0-0	1-100	1-100	0-0
W Iberian System	M	9-90	1-10	3-33	5-56	1-11	3-38	5-63
	F	9-100	0-0	1-11	4-44	4-44	8-89	1-11
C Iberian System	M	18-95	1-5	4-36	5-45	2-18	1-10	9-90
	F	21-95	1-5	0-0	5-83	1-17	4-67	2-33
E Iberian System	M	13-87	2-13	8-67	3-25	1-8	5-45	6-55
	F	11-100	0-0	1-33	1-33	1-33	3-75	1-25
Toledo-Morena Mts.	M	11-92	1-8	1-13	7-88	0-0	1-13	7-88
	F	4-100	0-0	0-0	0-0	1-100	1-100	0-0
Cazorla-Alcaraz Mts.	M	10-100	0-0	1-11	2-22	6-67	4-57	3-43
	F	7-100	0-0	1-50	1-50	0-0	3-75	1-25
Nevada Mt.	M	27-100	0-0	5-26	8-42	6-32	7-32	15-68
	F	19-100	0-0	0-0	2-29	5-71	6-86	1-14
Ronda Mt.	M	15-100	0-0	3-30	4-40	3-30	1-8	12-92
	F	9-90	1-10	0-0	2-33	4-67	6-100	0-0
Doñana	M	16-84	3-16	15-83	2-11	1-6	1-7	13-93
	F	13-87	2-13	9-64	4-29	1-7	1-7	13-93
SW Iberian Pen.	M	2-100	0-0	1-50	0-0	1-50	0-0	2-100
	F	–	–	–	–	–	–	–
Rif Mts.	M	1-33	2-67	1-50	0-0	1-50	2-100	0-0
	F	3-100	0-0	0-0	0-0	1-100	1-100	0-0
Alger	M	0-0	2-100	1-50	1-50	0-0	0-0	2-100
	F	1-33	2-67	2-100	0-0	0-0	1-33	2-67
High Atlas Mts.	M	6-100	0-0	0-0	4-67	2-33	6-100	0-0
	F	3-100	0-0	1-33	1-33	1-33	2-100	0-0