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A multivariate analysis of the morphology of the colubrid snake *Malpolon monspessulanus* in Morocco and Western Sahara: biogeographic and systematic implications

Philippe Geniez, Alexandre Cluchier & Cornelius C. de Haan

Abstract. The largely circum-Mediterranean Montpellier Snake *Malpolon monspessulanus* appears to be highly differentiated in Morocco. Hill & Smith multivariate analyses performed on 68 specimens from south-western Europe and North Africa revealed the existence inside Morocco of three distinct parapatric populations with proper morphological features: (1) the nominal subspecies present in the major part of the country; (2) *Malpolon monspessulanus insignitus* in the North-East (high plateau), and (3) a new subspecies restricted to the coastal areas of south-western Morocco and Western Sahara. The main features of the new subspecies are 19 rows of dorsal scales at mid-body, with for adult males dorsally a general black pigmentation presenting a small whitish spot on every dorsal scale, while also throat and belly are whitish, longitudinally stained with dark grey, and for adult females dorsally a mostly more pronounced and contrasted expression of the specific, typical female colour pattern and markings, than seen in the females from elsewhere in Morocco. Adult male specimens morphologically intermediate between the new and the nominal subspecies, are recorded in the Souss valley. The Moroccan geographical distribution of the three subspecies is revised.

Key words. Squamata, Serpentes, Colubridae, Psammophiinae, *Malpolon monspessulanus*, systematics, new subspecies, geographical distribution, Morocco, Sahara.

Introduction

The Montpellier Snake *Malpolon monspessulanus* (Hermann, 1804) belongs to the Psammophines, a colubrid tribe or subfamily of mostly African snakes, consisting of 8 genera and about 44 species. These are characterized, in males, by their tiny hemipenes, quasi filiform and 3-4 subcaudals short (Bogert 1940) and, in both sexes, by their valvular nostril enabling "self-rubbing" (de Haan 2003, de Haan & Cluchier 2005). Moreover, lack of significant sexual dimorphism in tail length seems to be generalized in the whole tribe, anyway for sure in *Malpolon monspessulanus* (de Haan 1999).

This snake is the most widespread Mediterranean reptile, being present in all countries around the Mediterranean Sea, but absent in Italy between Istria and W-Liguria. Its distribution, originating from Africa (cf. Nagy et al. 2005) and depending of Mediterranean type climate (cf. Cheylan et al. 1981), extends to the East as far as easternmost Iran and Volgograd in the Caspian lowlands, and to the West up to and including the Atlantic coasts of Portugal, Morocco and Western Sahara, while altitudinal ranging is between sea level and at least 1200 m in the Caucasus, 1400 m in the Alps and 3000 m in the Atlas. (Bons & Geniez 1996, de Haan 1997, 1999).

Two subspecies are at present recognized: the nominal subspecies, *M. m. monspessulanus* (Hermann, 1804), distributed in W-Liguria (Italy), SE-France, Iberian Peninsula and the greater part of Morocco; *M. m. insignitus* (Geoffroy Saint Hilaire, 1827) from E-Morocco, through Algeria, Tunisia, Libya, N-Egypt, Palestine, Israel, Jordan, Syria, Turkey, into SE-Europe, including Cyprus and up to Istria (and perhaps sporadic in NE-Italy), and from Syria through Iraq up to E-Iran and northern wards up to

Volgograd in Ciscaucasian Europe. A third subspecies is currently in discussion, *M. m. fuscus* (Fleischmann, 1831) as a substitute for *M. m. insignitus* as far as most of its "Eurasian" distribution is concerned (cf. de Haan 1997). In addition, a new form was suspected to exist in SW-Morocco and in Western Sahara (Geniez & Geniez 1993, Bons & Geniez 1996, Geniez et al. 2004). These authors give a short description of this south-westernmost *M. monspessulanus* form and specify that it ranges from Tiznit in SW-Morocco, south through the coastal Western Sahara up to the Dakhla peninsula at the tropic of Cancer. They further point out morphological intergradations between this form and the nominal subspecies between Agadir and Tiznit. Interesting in this context is the fact that in the former Spanish Sahara, now called Western Sahara, Valverde (1992) noted the occurrence of a black *M. monspessulanus,* which he called *M. m. insignitus*. In the present paper we propose an analysis of the morphological variation of the Montpellier Snake in Morocco and Western Sahara.

Material and methods

Material examined

Considering the pronounced dimorphism encountered within *Malpolon monspessulanus*, including the high constancy of colour pattern observed in the different female forms, as well as the strong ontogenetic modifications of markings and colours in young males (de Haan 1999), the analyses were restricted to adult male specimens only.

The 68 examined specimens analysed in this study include 26 specimens collected from Moroccan localities. These localities extend from Western Sahara to Saïdia at the north-eastern border of Morocco with Algeria. The 42 specimens remaining were collected from the south of France (terra typica of *M. m. monspessulanus*), Spain, Portugal, Algeria, Tunisia and Egypt (terra typica of *M. m. insignitus*). The material examined is conserved in the Muséum National d'Histoire Naturelle in Paris, France (MNHN), the Estación Biologica de Doñana in Sevilla, Spain (EBD), the Zoologisches Forschungsmuseum Alexander Koenig in Bonn, Germany (ZFMK), the Institut Scientifique de Rabat, Morocco (ISR) and the Laboratoire de Biogéographie et Ecologie des Vertébrés of the Ecole Pratique des Hautes Etudes in Montpellier, France (BEV). These specimens, among about 90 others, are listed in the Appendix. In addition, many photos of live specimens with known origin were examined from the personal iconographical collection of one of the authors (PGe).

Characters studied – specimen identification

Sixteen characters were studied and taken into account for the analyses in this work (cf. Tab. 1 for total list and coding rules). They came from scalation, body proportions and colour pattern. Six quantitative characters concern body proportions and pholidosis, ten qualitative variables concern colour pattern. All characters were recorded by the same observer (AC), and with the same instrument so as to avoid any bias. Certain variables, such as the number of dorsal scale rows at mid-body which shows to be 19 among all specimens, were discarded. So were variables that could not be measured on every specimen, such as original length of incomplete tails and the corresponding number of subcaudals.

Each examined specimen was assigned a priori to a form: *monspessulanus*, *insignitus* or the new SW-Moroccan form. Specimens with intermediate features were not removed from the analysis. This *a priori* identification is not a character.

Statistical analyses

The aim of the analysis was to choose the most parsimonious process that would lead to a possible differentiation of the forms of

Variables	Description	Numerical codes
SVL	Snout-Vent length	x
LPil	Pileus length	x
WPil	Pileus width	x
RSL	Distance between the end of the last supralabial scale and the end of the rostral scale	x
ROc	Distance between the eye and the end of the rostral scale	x
VENT	Number of ventral scales	x
CH&N	General colour of the head and nape compared to the general colour of the dorsum at midbody	
	Color of the anterior part less dark than the color at midbody	1
	Color of the anterior part the same as the body	2
	Color of the anterior part darker than the color at midbody	3
SADL	Presence of the black saddle	
	No saddle	1
	Very light saddle	2
	Saddle present	3
	Saddle present extending on major part of the dorsum	4
CHD	Colour of the head	
CNK	Colour of the nape	
CBY	Colour of the body (dorsum behind the nape)	
	Light green or light grey	1
	Brownish or greyish, darker than (1)	2
	Light green or light grey, irregularly stained	3
	Brownish or greyish, darker than (1), irregularly stained	4
	Black	5
	Black with a white spot on each scale	6
	Sandish	7
	Russet-red	8
PGD	Pigmentation on the Dorsum	
	No spots	1
	Spots of <3 scales poorly contrasting	2
	Spots of >4 scales poorly contrasting	3
	Spots of <3 scales very contrasting	4
	Spots of >4 scales very contrasting	5
CFK	Colouration of the flanks	
	No black coloration	1
	Very light black coloration	2
	Neat black coloration	3
PGV	Pigmentation of the ventrals	
	Uniformly light coloured	1
	Marbled, stained	2
	Lined	3
	Uniformly dark coloured	4
SPS	Shape of the preocular light spot	
	Small horizontal rectangle	1
	Small square	2
	Vertical rectangle	3
	All the scale	4
SLS	Supralabial spots	
	No spots on supralabial scales	1
	Light spots very poorly borded with black	2
	Light spots borded with black	3

Tab. 1. List of morphological features used in this study and their coding rules.

Malpolon monspessulanus. Thus we undertook in the first place multivariate analyses, which do not depend on *a priori* specimen classification, and which are powerful tools that combine the information derived from several characters simultaneously, so as to objectively demonstrate the accuracy of our *a priori* identification. Neither discriminant-function analysis (DFA) nor between/within analysis were performed, their results depending on the *a priori* identification.

The main multivariate analysis method used in this study is the Hill & Smith analysis (Hill & Smith 1976), a technique which enables one to analyse simultaneously qualitative and quantitative variables. The quantitative and the qualitative characters are processed separately in the first place by respectively normalized principal component analysis (PCA) and multiple correspondence analysis (MCA) using the same row weights. The Hill & Smith technique then analyses both PCA and MCA statistical triplets and renders a single statistical triplet, allowing viewing of all the information analysed on the same axis. All multivariate analyses were implemented with the ADE-4 software package (Thioulouse et al. 1997).

(1) A first Hill & Smith analysis (H&S) was performed strictly on the Moroccan specimens. Its aim is to point out the different forms that occur in Morocco.

(2) A second H&S was run on all measured specimens. It aims at comparing the forms observed in Morocco with those present in south-western Europe (*monspessulanus*) and eastern North Africa (*insignitus*).

Means, standard deviations and ranges for quantitative variables can be found in Tab. 2, and the frequency of occurrence for each state of qualitative variables is given in Tab. 3.

The analysed specimens, the personal observations of the authors, the available published data including precise localities with precise description and/or photos of the observed specimens, as well as specimens preserved in accessible collections, were also used to elaborate a precise distribution map of the taxonomically distinguishable *Malpolon monspessulanus* forms of Morocco and Western Sahara.

Results

Existence of three forms of *Malpolon monspessulanus* in Morocco

The first analysis, run on Moroccan specimens exclusively (N=26), neatly separates 1) the specimen collected on the High Plateaux (HP), that we *a priori* assigned to *insignitus*, from the other forms on PC2 (Fig. 1), and 2) the three specimens collected on the coastal fringe of south-western Morocco and Western Sahara (SW) from the others on PC1/PC3 (Fig. 2). The HP specimen stands out according to the following characters: the general colour of both the head and the nape is rather light and resembles the light overall dorsum colour, the shape of the light preocular stain consists in a small square and the number of ventral scales is quite low (165). The SW specimens differentiate themselves from the other forms by a black saddle that extends on the major part of the dorsum and presents a single and contrasting white spot on each scale, by a more or less striped ventral pattern and by very contrasting light supralabial stains bordered with black. The eigenvalues, percent of explained variance, cumulated percent of explained variance, and contributions of the quantitative variables to the first three PCs can be found in Tab. 4. The contributions of the modalities of the qualitative variables to these same PCs are represented in Figures 3 and 4.

Two of the Moroccan forms of *Malpolon monspessulanus* fit the scatters of *monspessulanus* and *insignitus*. The third form does not fit any described subspecies. The second analysis, performed on all measured specimens, separates three forms on PC1 and PC2 (Fig. 5). The first form aggregates the SW-European and all the Moroccan specimens, except those of the High Plateaux and the coastal fringe of SW-Morocco and Western Sahara. This first form corresponds to the

Variable	SVL	LPil	WPil	RSL	ROc	Vent
monspessulanus (n=50)						
Mean	94,990	2,713	1,299	3,132	1,230	175,640
Standard deviation	19,842	0,414	0,197	0,495	0,229	4,637
Range	63.5-143	2.08-3.53	1-1.78	2.35-4.42	0.82-1.73	171-199
insignitus (n=11)						
Mean	90,773	2,517	1,171	2,901	1,142	169,545
Standard deviation	16,428	0,337	0,164	0,402	0,303	4,987
Range	65-119	2.01-3.02	0.905-1.39	2.38-3.53	0.8-1.88	162-177
saharatlanticus (n=3)						
Mean	116,500	3,210	1,550	3,883	1,437	174,333
Standard deviation	3,775	0,174	0,123	0,236	0,064	2,082
Range	113-120.5	3.01-3.33	1.41-1.64	3.66-4.13	1.39-1.51	172-176

Tab. 2. Means, standard deviations and ranges of the quantitative variables used in this study. (SVL= snout-vent length; LPil=pileus length; WPil=pileus width; RSL= distance between the end of the last supralabial scale and the end of the rostral scale; ROc= distance between the eye and the end of the rostral scale; VENT=number of ventral scales).

nominal subspecies: *Malpolon monspessulanus monspessulanus*. The second form aggregates the Moroccan High Plateaux specimen with those of eastern Maghreb and Egypt, and corresponds to *M. m. insignitus*. The features that differentiate *insignitus* from the two other forms are: the light colour of the head and nape which is the same as that of the dorsum at mid-body and everywhere else, lack of the black saddle, lack of dark colouration on the flanks, high occurrence frequency of a square or horizontal rectangle shaped light stain on the preocular, and, finally, a low number of ventral scales. The three specimens, however, collected along the coastal fringe of Western Sahara and SW-Morocco constitute a distinct population and do not fit any of the previously described forms and show to be representatives of a distinct population. They stand out thanks to the same features mentioned in the previous analysis. The multivariate analysis confirms the *a priori* identification. In Fig. 5, one can note the position of the intermediate specimens on the axis 1 and 2, depending on their origin. The specimen from Saïdia (BEV. 8412), those from Morocco without precise locality (BEV. 8426) and the one from Djurdjura (N-Algeria) (EBD. 19494) show an intermediate position between *monspessulanus* and *insignitus.* The specimen collected in the Souss valley (BEV. 8429) positions as an intermediate between *monspessulanus* and the third form. The eigenvalues, percent of explained variance, cumulated percent of explained variance, and contributions of the quantitative variables to the first two PCs can be found in Table 5. The contributions of the modalities of the qualitative variables to these same PCs are represented in Figure 6.

These two results confirm our field impressions: three distinct Moroccan forms of *Malpolon monspessulanus*, as long as adult males are concerned, are easily identifiable on colouration features. Two of these forms are already described and recognized as subspecies (cf. de Haan 1999): the one of the High Plateaux, which corresponds to *insignitus,* and the other one of the “rest of Morocco”, which corresponds to *monspessulanus*. However, specimens from SW-Morocco and Western Sahara correspond to a form that we propose to describe as a new subspecies as follows.

	CH&N		SADL		CHD		CNK		CBY		PGD		CFK		PGV		SPS		SLS	
monspessulanus	1	1.00	1	0	1	0.96	1	0	1	0	1	0.54	1	0	1	0.42	1	0	1	1.00
(n=50)	2	0	2	0.08	2	0.04	2	0	2	0.80	2	0.34	2	0.10	2	0.56	2	0.02	2	0
	3	0	3	0.92	3	0	3	0	3	0.02	3	0.08	3	0.90	3	0	3	0.98	3	0
			4	0	4	0	4	0.06	4	0.18	4	0.04			4	0.02	4	0		
					5	0	5	0.90	5	0	5									
					6	0	6	0.04	6	0										
					7	0	7	0	7	0										
					8	0	8	0	8	0										
insignitus	1	0.27	1	0.91	1	1.00	1	0.82	1	0.82	1	0.73	1	0.82	1	0.27	1	0.18	1	0.55
(n=11)	2	0.73	2	0.09	2	0	2	0.18	2	0.18	2	0.27	2	0	2	0.73	2	0.36	2	0.46
	3	0	3	0	3	0	3	0	3	0	3	0	3	0.18	3	0	3	0.36	3	0
			4	0	4	0	4	0	4	0	4	0			4	0	4	0.09		
					5	0	5	0	5	0	5	0								
					6	0	6	0	6	0										
					7	0	7	0	7	0										
					8	0	8	0	8	0										
saharatlanticus	1	1.00	1	0	1	1.00	1	0	1	0	1	0	1	0	1	0.33	1	0	1	0
(n=3)	2	0	2	0	2	0	2	0	2	0	2	0	2	0	2	0.33	2	0	2	0.33
	3	0	3	0	3	0	3	0	3	0	3	0	3	1.00	3	0.33	3	1.00	3	0.67
			4	1.00	4	0	4	0	4	0	4	1.00			4	0	4	0		
					5	0	5	0	5	0	5	0								
					6	0	6	1.00	6	1.00										
					7	0	7	0	7	0										
					8	0	8	0	8	0										

Tab. 3. Frequency of occurrence of each class of the qualitative variables.

Description of a new subspecies

***Malpolon monspessulanus saharatlanticus* ssp. n.**

Malpolon monspessulanus insignitus (non Geoffroy, 1824) – Valverde, 1992

Malpolon monspessulanus - Geniez & Geniez, 1993: 7.

Malpolon monspessulanus - Bons & Geniez, 1996: 242.

Malpolon monspessulanus monspessulanus - de Haan, 1999: 701.

Malpolon monspessulanus monspessulanus - Geniez et al., 2000: 156.

Malpolon monspessulanus ssp. - Geniez et al., 2004: 163.

Holotype: MNHN.2004.0076, adult male (roadkilled), collected by P. Geniez, 3 km south from Tah towards Laâyoune (Western Sahara) [27.653°N / 12.961°W], 6 May 1994 (Fig. 7).

Paratypes: BEV.286, adult male (roadkilled), collected by P. & M. Geniez, 36.5 km beyond Goulimine (= Guelmim) towards Tantan (south-western Morocco) [28.824°N / 10.387°W], 10 June 1989 (Fig. 8); ZFMK 49760, adult male (roadkilled), collected by W. Bischoff and U. Joger, 11 km east of Tantan-Plage towards Tantan (SW-Morocco), 28 May 1988; ZFMK 73034, adult male (killed by local people), collected by W. Böhme, near Igherm (Anti-Atlas, SW-Morocco).

Diagnosis: large colubrid snake (males 2.17 m and females 1.40 m maximum total length) showing general features of *Malpolon monspessulanus* (opisthoglyphous dentition, concave pileus, frontal plate clove-shaped — distally narrowing — almost always in contact with the large single preocular, two loreal scales, dorsal scales lengthwise grooved or smooth), dorsalia in 19 rows at mid-body, and for males, the major part of the dorsum black with one white spot on each scale, while the head and the nape are dark or light uniformly greenish or brownish like in *M. m. monspessulanus*; the distal part of the dark extension progressively vanishes near the cloaca; the tail is generally brown with more or less black patches; one light stain bordered with black on each supralabial scale (resembles the juvenile feature but not as contrasting as in females, cf. Tab. 6); the ground colour of the belly is generally white and presents a grey or blackish longitudinal marking, the rather contrasting pattern of the throat and anterior part of the belly suggests the typical juvenile and female ventral pattern (cf. Fig. 9); females present very contrasting patterns on head, throat and dorsum (Fig. 10); juveniles raise a similar pattern to those of *Malpolon monspessulanus monspessulanus*. For comparisons with the two other subspecies in Morocco see Table 6.

Description of the holotype (Fig. 7): An adult male measuring 120.5 cm of snout-vent length (total length about 160 cm) which presents the following features: 19 rows of dorsal scales at mid-body; head and nape uniformly greenish; upper part of the body black with one white spot on each scale of the dorsum and the flanks; tail ochrish presenting a black edge on each scale; the ground colour of the throat and the belly is whitish, longitudinally stained with dark grey, resembling the juvenile pattern; one large white stain outlined with black on each supralabial scale, resembling again the juvenile pattern.

Variation: Pronounced variations due to ontogenesis and sexual dimorphism exist and are mentioned in the diagnosis section above. In adult males of more than 140 cm overall length, the dark aspect (with one white spot on each black scale) is quite stable, but its extension on the body and its intensity get more pronounced following the age of the individual.

Etymology: The subspecific name refers to Atlantic Sahara (SW-Morocco and coastal Western Sahara) where all concerned specimens were found.

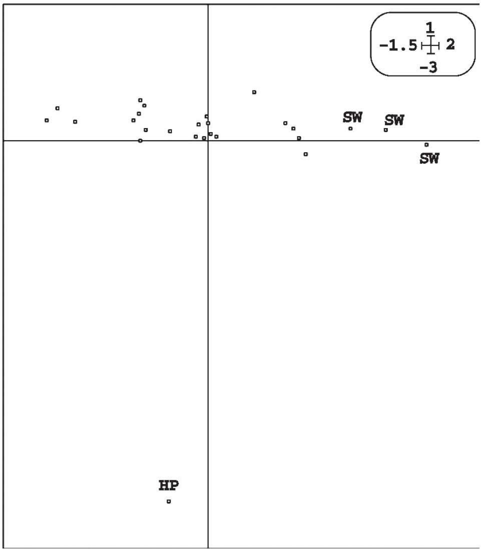

Fig. 1. Bivariate plot of PC1 and PC2 scores generated by a Hill & Smith analysis run on Moroccan specimens only. “SW” stands for the south-western specimens, “HP” for the High Plateaux specimen. All other dots represent the other Moroccan specimens.

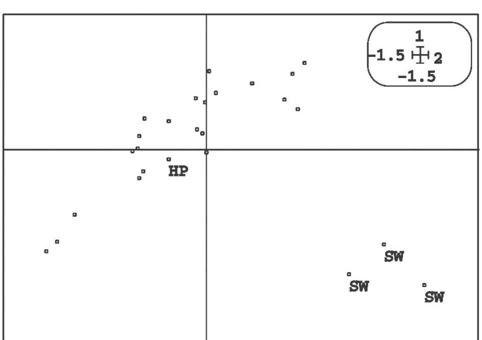

Fig. 2. Bivariate plot of PC1 and PC3 scores generated by a Hill & Smith analysis run on Moroccan specimens only. “SW” stands for the south-western specimens, “HP” for the High plateaux specimen. All other dots represent the other Moroccan specimens.

Iconography: Revista Española de Herpetologia 1991: 4; Schleich et al. 1996: 212, plate 45, 131; Geniez et al. 2004: 164, figs 189 and 190.

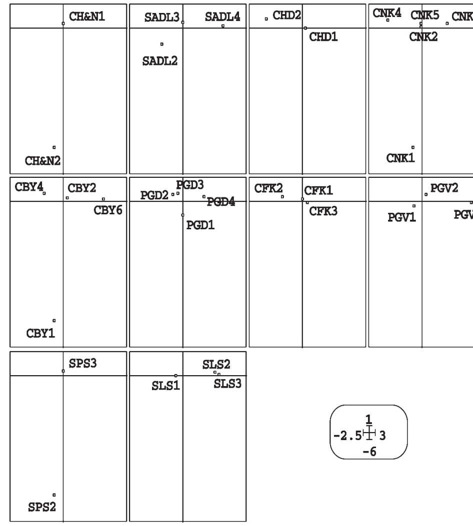

Fig. 3. Contribution of the modalities of the qualitative variables to the first and second axes of the first H & S analysis. See Tab. 4 for the contributions of the quantitative variables.

Distribution: along the north-western African Atlantic coast from Bou Izakarn (Morocco) to Dakhla (Western Sahara) with inland extensions up to Aoulouz and Tafraoute on the southern slopes of the western Atlases including the lower Drâa valley and upper Souss valley (cf. Map Fig. 11).

Habitat: semi-desert plains including beaches, sandy area with scarce vegetation, regs, cultivations around villages, certain rocky formations.

Subspecific distribution of *M. monspessulanus* in Morocco and Western Sahara

Our results establish the existence in north-western Africa of three distinct subspecies. Each of them shows distinct morphological features (Tab. 6). Their geographical distribution appears to be parapatric with morphological intergradations between them. Their respective distributions are (Fig. 11):

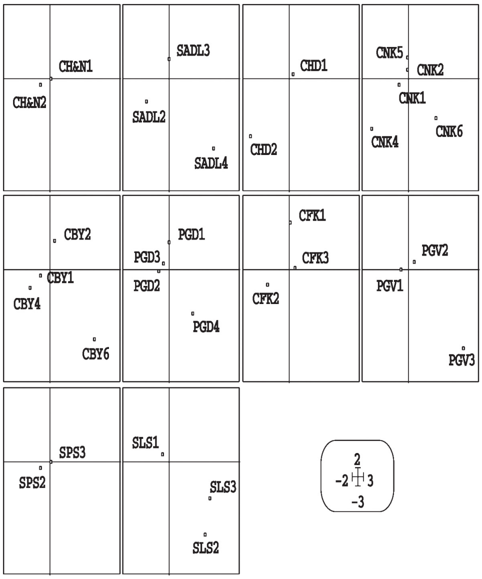

Fig. 4. Contribution of the modalities of the qualitative variables to the first and third axes of the first H & S analysis. See Tab. 4 for the contributions of the quantitative variables.

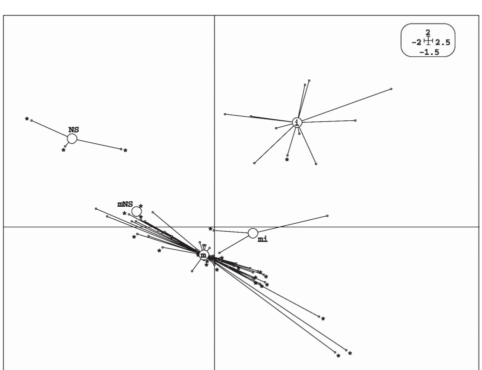

Fig. 5. Bivariate plot of PC1 and PC2 scores generated by a Hill & Smith analysis run on all specimens. In the barycentre circles "m" stands for *monspessulanus*, "i" for *insignitus*, "NS" for new subspecies, "mNS" for intermediate specimens between *monspessulanus* and the new subspecies and "mi" for intermediate specimens between *monspessulanus* and *insignitus*. The dots with a "*" refer to Moroccan specimens.

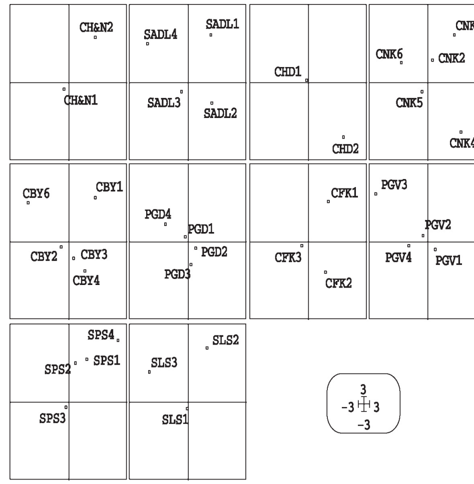

Fig. 6. Contribution of the modalities of the qualitative variables to the first and second axes of the second H & S analysis. See Tab. 5 for the contributions of the quantitative variables.

Malpolon monspessulanus monspessulanus: in the major part of Morocco. Absent on the High Plateaux east of the Moulouya wadi and in south-western Morocco south of Tiznit. Also absent in Western Sahara. Intergrading clines with *saharatlanticus* are observed in the western Souss valley and along the Atlantic coast between Agadir and Tiznit, and with *insignitus* at least at Saïdia (Mediterranean coast, north-eastern Morocco) and probably in north-western Algeria.

Malpolon monspessulanus insignitus (Fig. 12) occurs in Morocco only east of the Moulouya valley, especially on the High Plateaux, mostly on the dry steppes down south 27 km north of Tendrara but also more up north near Debdou in woody slopes (pers. obs.). An intermediate adult male specimen (in which the typical *monspessulanus* dark saddle and black flanks appear very light, the dorsum raises a sand colour and the belly is uniformly white) is known from Saïdia (BEV.8412). We suspect further occurrence of intermediate specimens between the Moulouya wadi and the eastern slopes of the Middle Atlas.

		PC1	PC2	PC3
N=26				
Eigenvalues		0.47	0.29	0.22
Percent of explained variance		28.1	17.2	20.0
Cumulated percent of explained variance		28.1	45.3	58.2
Contributions of the quantitative variables to the factors				
	SVL	0.88	-0.06	0.26
	LPil	0.93	-0.10	0.19
	WPil	0.91	-0.08	0.21
	RSL	0.94	-0.15	0.11
	ROc	0.89	-0.02	0.23
	VENT	0.01	0.63	0.12

Tab. 4. Eigenvalues and percent of explained variance of the first three axes of the first H & S analysis. Contributions of the quantitative variables to these axes are also given. For contribution of the qualitative variables, see Fig. 7 and 8.

Malpolon monspessulanus saharatlanticus is endemic in south-western Morocco and coastal Western Sahara, south to the Dakhla peninsula, which is the southernmost known location for the species. Intermediate specimens have been found in the lower Souss valley, between Aoulouz and Agadir and in the coastal area from Agadir to Tiznit. In these, the black saddle is much more extended than it is in *monspessulanus*, the dorsal light spots are less contrasting than those of *saharatlanticus*, the ground colour of the belly is white, strongly marbled with dark grey (BEV.8429).

Discussion and conclusion

The geographic pattern here described may raise the question: is the *saharatlanticus* subspecies only an ecotype adapted to extreme desert conditions? If so, the extension of the black colouration on practically all of the body of the Western Saharan Montpellier Snake could be a response to severe conditions in that area (Saharan bioclimatic stage, sensu BRIGNON & SAUVAGE 1962-63, enjoying warm winters and trade winds continually blowing). However, specimens raising features that can remind characters of *M. m. saharatlanticus*, i.e. dorsal black marks and scattered light spots, have been found in the Middle Atlas at 2000 m (2 km north of the Jbel Hebri, pers. obs., cf. BONS & GENIEZ 1996: picture p.243), area that presents drastically opposed climatic and habitat conditions (important rains, cold winters, abundant forests). On the contrary, typical *M. m. monspessulanus* specimens are found in continental pre-Saharan climate regions, i.e. in the Missour region and in the high Drâa valley between Ouarzazate and Zagora. These facts suggest more the establishment of an independent gene flow (subspecies) than a climatic adaptation (ecotype). However, several mentions of melanistic specimens of *Malpolon monspessulanus* outside of Morocco are given by the following authors: VALVERDE (1967) in the Coto Doñana natural park, and MEIJIDE (1981) in the province of Lugo in north-western Spain. Moreover, DE HAAN (cf. 1999: 698-704) documented several partially melanistic specimens preserved at the Bocage Museum in Lisbon, comparable with a 40% occurrence frequency of aberrant melanism (n=10) he observed in

		PC1	PC2
N=68			
Eigenvalues		0.43	0.31
Percent of explained variance		21.7	15.4
Cumulated percent of explained variance		21.7	37.1
Contributions of the quantitative variables to the factors			
	SVL	-0.81	0.33
	LPil	-0.86	0.25
	WPil	-0.88	0.18
	RSL	-0.88	0.27
	ROc	-0.75	0.29
	VENT	-0.27	-0.35

Tab. 5. Eigenvalues and percent of explained variance of the first and second axes of the second H & S analysis. Contributions of the quantitative variables to these axes are also given. For contribution of the qualitative variables, see Fig. 6.

the field in western Portugal. This 'aberrant' melanism concerns males with various extensions of the 'normal' black saddle, in which the whitish spots, typical for *saharatlanticus*, are lacking. Most extensions consist of irregular small and large black patches on the dorsum. Another saddle extension, never observed in *saharatlanticus*, goes plain dark forwards up to the snout (*M. monspessulanus* n° EN 226 at the Bocage Museum, Lisbon, photographed by CdH., Oct.1987, unpubl.). Perhaps the various black patterns of the west-Iberian Montpellier snakes are due to selection pressures, as for instance oceanic climate influences.

Throughout its vast distribution, the Montpellier snake finds in Morocco its highest rate of diversification with three subspecies. This distribution pattern can be explained by the occurrence of two major biogeographic barriers for species with Palearctic affinities. The first barrier is the Moulouya valley, in NE-Morocco, allowing a Saharan climate with cold winters (sensu Brignon & Sauvage 1962-63) to penetrate towards the north. Thus five taxa of reptiles, at a generic or a specific level, find here an eastern limit to their geographic range: *Psammodromus microdactylus* (Boettger, 1881), *Chalcides colosii* Hediger, 1935, *C. polylepis* Boulenger, 1890, *Macroprotodon brevis* (Günther, 1862) and the genus *Blanus*. And four taxa find in the same region a western limit to their distribution: *Psammodromus blanci* (Lataste, 1880), *Ophisops occidentalis* Boulenger, 1887, *Eryx jaculus* (Linnaeus, 1758) and *Macroprotodon abubakeri* Wade, 2001. The second major biogeographic barrier corresponds to the south-western part of the High Atlas, which, in the south-west, isolates a coastal fringe presenting an extremely soft climate with hardly contrasting seasons and hidden precipitations (arid and Saharan stages with warm winters, sensu Brignon & Sauvage 1962-63). This region shelters the last relictual savanna fauna elements: *Dasypeltis scabra* (Linnaeus, 1758), *Lamprophis fuliginosus* (Boie, 1827) and *Bitis arietans* (Merrem, 1820). Furthermore, five twin unities of reptile taxa find their biogeographical limits in this region: *Tarentola m. mauritanica* (Linnaeus, 1758) / *T. m. juliae* Joger, 1984, *Mesalina simoni* (Boettger, 1881) / *M. olivieri* (Audouin, 1829), *Acan-*

Fig. 7. Holotype of *Malpolon monspessulanus saharatlanticus* MNHN 2004.0076, adult male.

Fig. 8. Paratype of *Malpolon monspessulanus saharatlanticus* BEV.286, adult male.

thodactylus maculatus (GRAY, 1838) / *A. busacki* SALVADOR, 1982, *Chalcides ocellatus* (FORSSKÅL, 1775) / *C. polylepis* BOULENGER, 1890 and *C. m. mionecton* (BOETTGER, 1874) / *C. m. trifasciatus* (CHABANAUD, 1917). It is noteworthy that *Malpolon monspessulanus*, with three subspecies separated from each other by these two biogeographical barriers, seems to be a unique case among the Moroccan herpetofauna.

Fig. 9. Anterior ventral side of the holotype of *M. m. saharatlanticus* MNHN 2004.0076, adult male.

Fig. 10. Adult female of *Malpolon monspessulanus saharatlanticus* PGe.627.

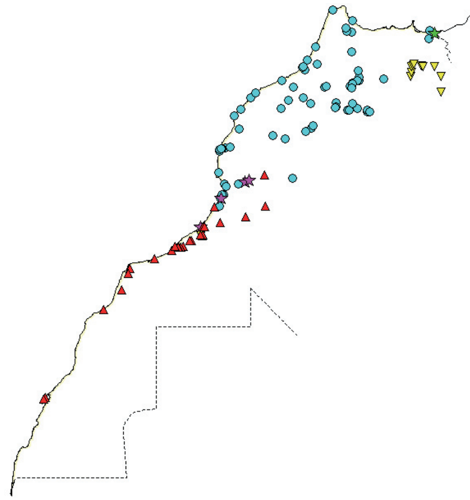

Fig. 11. Geographic distribution of *Malpolon monspessulanus* in Morocco and Western Sahara. Blue dots: *M. m. monspessulanus*, yellow inverted triangles: *M. m. insignitus*, red triangles: *M. m. saharatlanticus* subsp. nov., green star: intermediate specimen *monspessulanus* × *insignitus*, pink stars: intermediate specimens *monspessulanus* × *saharatlanticus*.

Fig. 12. *Malpolon monspessulanus insignitus* BEV.341, adult male, 13 km north from Debdou towards Taourirt, High Plateaux (NE-Morocco).

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males	**number of dorsal scale rows at midbody**	**dorsum**	**flanks**	**belly**	**supralabial scales**
Malpolon monspessulanus monspessulanus	19	uniformly greenish, ochre or brownish with a large dark 'saddle' two head lengths behind the head	blackish with a light stain on each scale, contrasting with the uniformly and more light dorsum	pale yellowish with for large males blackish suffusion or undefined large and confluent dark stains	uniformly greenish or pale greyish, no light stains, or very poorly contrasting
Malpolon monspessulanus insignitus	19 (rarely 17 in Algeria)	uniformly yellowish, beige or greyish, no dark saddle nor white spots	uniformly beige or greyish, no contrast with the dorsum	uniformly pale yellowish or whitish, no dark stains	uniformly yellowish or pale greyish, no light stains, or very poorly contrasting
Malpolon monspessulanus saharatlanticus	19	black 'saddle', starts generally one head length only behind the head, extends on the major part of the body, with bright white spots on each dorsal scale	black with one white spot on each scale, no contrasting with the dorsum	white, longitudinally stained of dark grey, reminding the juvenile pattern (cf. below), especially in the throat region	pale greenish or greyish with a light stain bordered of dark on each supralabial, reminds juvenile pattern (cf. below)
females	**number of dorsal scale rows at midbody**	**dorsum**	**flanks**	**belly**	**supralabial scales**
Malpolon monspessulanus monspessulanus	19	densely marbled with light and dark markings forming indistinct large stains; the black saddle appears in old females	densely marbled or spotted; the marks are not distinctly aligned	White, with an orange marking, very contrasting in the anterior part (as for juveniles, cf. below)	brown or russet-red with a strong light stain bordered of black on each supralabial
Malpolon monspessulanus insignitus	19 (rarely 17 in Algeria)	densely marbled with light and dark markings forming indistinct large stains; the black saddle is always absent	densely marbled and spotted; the marks are more or less contiguous, often forming a dark longitudinal stripe	White, with an orange marking, very contrasting in the anterior part (as for juveniles, cf. below)	brown or russet-red with a strong light stain bordered of black on each supralabial
Malpolon monspessulanus saharatlanticus	19	densely marbled with light and dark markings forming indistinct large stains and with sometimes one white spot on each scale; on old females, the black tint is more developed than in other forms	densely marbled with strong dark marks with sometimes one light spot on each scale; the marks can be aligned	White, with grey-blackish markings, more or less contrasting that can cover the orange colour habitually observed in the other subspecies	brown or russet-red with a strong light stain bordered of black on each supralabial

Tab. 6. Comparative table of morphological features of the three Moroccan subspecies of *Malpolon monspessulanus*

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Appendix

Detailed distribution data of *Malpolon monspessulanus* in Morocco with subspecific identification. Names between square brackets correspond to the observers when nor vouchers nor citations in museum catalogues are given. The localities are listed from the northernmost to the southernmost for each subspecies.

Malpolon monspessulanus monspessulanus: Tanger [BEV.8422]; 10 km from Chaouen towards Tetouan (western Rif mountain) [EBD.7495 and no number]; 3 km from the northern crossroad to Chaouen towards Tetouan (western Rif) [Ph. GENIEZ]; 1 km from the southern crossroad to Chaouen towards Tetouan (western Rif) [Ph. GENIEZ]; Tleta Oued-Laou beach (western Rif) [Ph. & M. GENIEZ]; Jbel Bou-Halla (western Rif) [EBD.19491]; Moulay-Bouchta, Jbel Amergou (southern slopes of the Rif mountains) [Ph.

Geniez]; Track above Tamjilt, south of Mousa-ou-Salah [Ph. Geniez]; 8 km N. Taforalt (Beni Snassen mountains) [Ph. Geniez]; 2.5 km E. Ras El-Ma (north-eastern Morocco) [M. Geniez]; Sidi Bou-Rhaba (N. Rabat) [ISR. 376019]; Mamora forest (near Rabat) [MNHN 1963.106]; Rabat [MNHN A.817, 1963.109, 111, ISR.381009]; Rabat Agdal [ISR.382002]; Casablanca [ZFMK 23038-23041]; Fort Gurgens, near Casablanca [MNHN 1912.192-193]; Chaouia, costal interland near Casablanca [MNHN 1921.553]; Bou-Regreg wadi dam [ISR. 378012]; El-Jadida [EBD.24670]; Dar Caïd Zerhouni, near El-Jadida [EBD.24671-24675]; Oualidia [EBD.24669]; Sidi Abed, Oualidia beach [EBD.23938, 23946]; Road 2301, near Sidi El-Hachemi [Ph. Geniez & P. Soto]; Road 1512, 24 km from Khourigba towards de El-Khattouat [Ph. Geniez]; 22 km from Sefrou towards Imouzzer du Kandar [Ph. Geniez]; 10 km S. Sefrou towards Fes [ZFMK 26240]; Oulmès (Central Plateau) [MNHN 1963.105, 108, 110, BEV.287, 349, 350, 8370, 8372]; Tarmilete (Central Plateau) [BEV.8371]; 4 km from the Dayet Ifrah towards Imouzzer du Kandar (Middle Atlas) [Ph. Geniez]; 5 km N. Dayet Ifrah (Middle Atlas) [PGe.616, Ph. Geniez, P.-A. Crochet, J.A. Mateo]; Ifrane (Middle Atlas) [EBD.24326]; 3 km from Ifrane towards Mischliffen (Middle Atlas) [Ph. Geniez]; 5 km SE Azrou (Middle Atlas) [EBD.18848]; 2 km N. Jbel Hébri, 2000 m (Middle Atlas) [PGe.624, Ph. Geniez & B. Delprat, S. Diochot]; Dayet Afourgha (Middle Atlas) [ZFMK 26241]; Slope going down to Itzer from the Aguelmam Azigza (Middle Atlas) [BEV.6562]; Sebt Gzoula [ISR. 380008]; 1 km from Afourer towards Bin El-Ouidane (northern slopes of the western High Atlas) [Ph. & M. Geniez & G. Trochard]; 14.3 km from the exit of Afourer towards Bin El-Ouidane by the road 508 (northern slopes of the western High Atlas) [MNHN 1981.30]; Ounagha, road P.10 [BEV.854]; Sidi Daoui, 2 km from Oued-Zem towards Romani [P. Escudié]; 13 km from Ben Ahmed towards Ras El-Aïn [Ph. Geniez & B. Delprat]; Road 1410, 11 km from Guissèr towards Mechra Ben-Abbou [Ph. Geniez & B. Delprat]; Khenifra [EBD.19618]; 23 km S. Khenifra [ZFMK 49807]; Road P.24, crossroad with the road P.33 towards El-Kebab (S. Khenifra) [Ph. Geniez & B. Delprat, S. Diochot]; Ouzoud falls (south-western High Atlas) [EBD.24327]; Road P.24, 3 km from Tamlelt towards Beni-Mellal [Ph. & M. Geniez & G. Trochard]; 18 km from the Tanout-ou-Filali towards Midelt [Ph. & M. Geniez & G. Trochard]; 22 km from the Tanout-ou-Filali towards Midelt [Ph. & M. Geniez & G. Trochard]; 10 km from Zeida towards Midelt [Ph. & M. Geniez & G. Trochard]; 3 km from the crossroad P.21 × S.329 towards Missour [Ph. & M. Geniez & G. Trochard]; 2 km from the Tizi-n-Talremt towards Essaouira [Ph. Geniez]; Road P.21, 17 km from Midelt towards Rich [E. Nancé]; 6 km from Sidi Bou Othmane towards Tamelelt [BEV.7777]; Road P.10, 6 km from Tleta Henchane towards Marrakech [Ph. & M. Geniez & G. Trochard]; Road P.10, 10 km from Essaouira towards Marrakech [Ph. & M. Geniez & G. Trochard]; Road P.10, 7 km from Essaouira towards Marrakech [Ph. & M. Geniez & G. Trochard]; Crossroad of Diabat, 8 km S. Essaouira [Ph. & M. Geniez]; Rasoua, 9 km S. Essaouira [PGe.611, Ph. & M. Geniez]; Road P.8, 8 km from the wadi Tamri bridge towards Essaouira [Ph. & M. Geniez & G. Trochard]; Agadir (lower Souss valley) [ZFMK 16082-16083]; Inezgane (lower Souss valley)[ZFMK 18875]; 9 km from Oulad Teïma towards Taroudant (Souss valley) [PGe.620, M. Geniez]; Sidi Rbat, wadi Massa mouth [PGe.623, Ph. Geniez, P. Soto & P. Escudié]; Sidi Boufdel (SW. Massa) [PGe.622, Ph. Geniez]; Between Azib Bouchaïba and Massa [Ph. Geniez]; Arbaa Aït Boutayeb (N. Tiznit) [BEV.314]; Tazenakht [PGe.614, M. Tarrier];

Intermediate specimens between *Malpolon m. monspessulanus* and *M. m. insignitus*: Saidia (north-eastern Morocco) [BEV.8412].

Malpolon m. insignitus (all on the High Plateaux): Track from Outat-Oulad El-Haj to Aïn-Benimathar, south of de Debdou [Bons 1960, pers. obs.]; 20 km W. Aïn Beni-Mathar [Bons 1960, pers. obs.]; South of the Debdou massif [MNHN 1961.323-324]; Road 5348, 63.5 km from Aïn Beni-Mathar towards Debdou [BEV.354]; 53 km from Aïn Beni-Mathar towards Debdou [P.-A. Crochet & S. Boissinot]; 6 km N. Debdou towards Taourirt [BEV.326]; 13 km N. Debdou towards Taourirt [BEV.341] (Fig. 12); 19 km N. Debdou towards Taourirt [BEV.346]; Road 5348 from Debdou towards Aïn Beni-Mathar, 1 km beyond the forest house of Aïn Serrak [BEV.334]; 30-35 km from Ain Beni-Mathar towards Tendrara [BEV.7759]. 27 km north of Tendrara towards Aïn Beni-Mathar [BEV.8504].

Intermediate specimens between *Malpolon m. monspessulanus* and *M. m. saharatlanticus*: Near Taroudant (Souss valley) [J.-M. Favrot]; Aït-Zoubia, ca 15 km E. Taroudant (Souss valley) [BEV.8429]; Between Sidi Boufdel and Issour (SW. Massa) [Ph. Geniez]; Between Plage Blanche and Foum Assaka [PGe.630, Ph. Geniez, P. Soto, P. Escudié].

Malpolon m. saharatlanticus: Aoulouz (eastern part of the Souss valley) [PGe.633, J. Garzoni]; Tafraoute (Anti-Atlas) [MNHN 1963.107]; Near Igherm (Anti-Atlas) [ZFMK 73034]. Road 7063, 17 km from Aglou towards Gourizim [M. Geniez]; Road P.30, 8 km from Bou-Izakarn towards Tiznit [Ph. Geniez, M. Geniez, G. Trochard]; Fort Bou-Jerif (near Guelmin) [PGe.631-632, Ph. Geniez, P. Soto & P. Escudié, M. Aymerich]; Road S.512, 36.5 km from Guelmim towards Tantan [paratype BEV.286] (Fig. 8); Road S.512, 31.5 km from Guelmim towards Tantan [Ph. Geniez, M. Geniez, G. Trochard]; 21 km from the wadi Draa bridge towards Gulemin by the "black track" [J. Garzoni]; 44.5 km from Tantan towards Guelmin [PGe.733, M. & E. Aymerich]; Chat Labiar [J.A. Valverde in Rev. Esp. Herpet., 6: 4 (1992)]; Some km N. Tantan [ISR no number]; 11 km E. Tantan-plage towards Tantan [paratype ZFMK 49760]; 12 km from Tantan-Plage towards Tantan [PGe.627, M. Geniez] (Fig. 10); 13 km from Tantan towards Tantan-Plage [Ph. Geniez, B. Delprat & S. Diochot]; 13 km from El-Quatia towards Tantan [PGe.731, M. & E. Aymerich]; 13 km from El-Quatia towards Tantan [PGe.732, M. & E. Aymerich]; 2 km from Tantan-Plage towards Tarfaya [M. Geniez]; 12 km from Tantan-Plage towards Tarfaya [M. Geniez]; 13 km from Tantan-Plage towards Tarfaya [Ph. Geniez & P. Soto]; North-eastern exit of Sidi Akhfennir [PGe.629, Ph. Geniez & P. Soto]; 14 km from Sidi Embarek de Tarfaya towards Tantan [M. Geniez]; 3 km from Tah towards Laayoune [holotype MNHN 2004.0076] (Fig. 7); 21 km from Dawra towards Tarfaya (Western Sahara) [M. Geniez]; Laayoune (Western Sahara) [EBD no number, 8 ind.]; 2 km from Lemsid towards Laâyoune (Western Sahara) [M. Geniez]; Botarja, near Villacisneros (Western Sahara) [EBD.2483]; Tafouarta, near Villacisneros (Western Sahara) [EBD no number].

Addendum

While the present paper was in the press, an interesting new phylogeny of Malpolon monspessulanus has been published (Carranza et al. 2006). This phylogeny seems to be in contradiction with our results on two important points:

1) Carranza et al. (2006) reveal, on the basis of phylogenetic analyses of mitochondrial DNA (combined sequences of 300 bp of the cytochrome *b* gene and 515 bp of 12S rRNA), that *insignitus* is very divergent from *monspessulanus*.

They estimate the time of divergence between these two clades at 3.5 to 6 million years. Based on this large divergence and the reciprocal monophyly of mitochondrial lineages as well as the main morphological differences cited from de Haan (1999), they conclude that *insignitus* is a species separate from *Malpolon monspessulanus* and consider *fuscus* as a subspecies of *Malpolon insignitus*.

This new combination, treating *insignitus* as specific rank, would not have surprised us that much, if it had been consistent with our morphological data from north-easternmost Morocco, which show intermediate specimens in a presumed contact zone between the coastal *monspessulanus* and the High Plateau-*insignitus*. So, if *monspessulanus* and *insignitus* are in fact distinct species and not subspecies, how to explain the morphologically intermediates we found in that zone?

2) Carranza et al. (2006) have found a *monspessulanus* haplotype north of Chrea (near Algiers) as well as another on the Algerian High Plateaus at 5 km N. of El Aouedj. These two specimens would constitute the first records for *M. m. monspessulanus* in Algeria.

However, no information is provided on their morphology, unless implicitely and a priori de Haan's (1999) subspecific/dimorphic criteria have been applied for these W-Algerian samples in particular. In that case the two specimens should be adult males, each having 19 dorsal scale rows at mid-body and a dark-pigmented dorsolateral region behind the nape (the "saddle complex"). If the Chrea specimen is actually such a 100 % *monspessulanus*, we wonder why Carranza et al. (2006) consider Algiers (near Chrea) as easternmost location for the *Malpolon monspessulanus* distribution, without showing what is to be found within the several 100 km between Algiers and Tunisia. Moreover, we regret they even do not present any *insignitus* sample west of Tunisia, i.e. neither in Algeria nor in Morocco.

Since the (about ten) adult male specimens we saw from the Moroccan/Algerian High Plateaus all have a typical *insignitus* morphology (unpublished data), the allocation of the El-Aouedj specimen to *monspessulanus* seems to be in contradiction with our findings.

We therefore look forward to further research and information, allowing a better understanding of how two of the former subspecies of *Malpolon monspessulanus* are distributed in Algeria. Such information would also help to determine if the El Aouedj specimen constitutes a range extension for *monspessulanus*, or an example of discordance between mitochondrial DNA and morphological characters.

We are pleased to note that Carranza et al. (2006) analysed their Essaouira sample (western Morocco, near the Atlantic coast) as rather divergent from all other Moroccan, the Iberian and the north-western Algerian ones. This may be a prefiguration of the supposable genetic divergence of *saharatlanticus* from *monspessulanus*.

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Author's addresses: Philippe Geniez, Alexandre Cluchier, Laboratoire de Biogéographie et Ecologie des Vertébrés, Ecole Pratique des Hautes Etudes, U.M.2, F-34095 Montpellier-cedex 5, France, E-Mail: geniez@univ-montp2.fr, cluchier@univ-montp2.fr; Cornelius C. de Haan, 8 route de St-Alban, Loiras, F-34700 Le Bosc, France, E-Mail: Haanpsam@aol.com.