

Biogeography of the White-Bellied Carpet Viper *Echis leucogaster* Roman, 1972 in Morocco, a study combining mitochondrial DNA data and ecological niche modeling

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Key words: biogeographic patterns; saharan discontinuity; subtropical snakes.

Paraules clau: discontinuitat sahariana; patrons biogeogràfics; serps subtropicals.

Abstract: In northwest Africa some species from Sahelian origin appear with relict populations and apparently isolated by the extreme aridity of the Sahara desert. However very tolerant to aridity species could maintain continuous populations as might be the case for *Echis leucogaster* as indicated by results from genetic analysis and bioclimatic models.

Resum: Al nord-oest d'Àfrica apareixen un grup d'espècies d'origen saheliana en poblacions relictas i aparentment aïllades pel desert del Sàhara. No obstant això espècies molt tolerants a l'aridesa podrien mantenir poblacions contínues, com podria ser el cas de *Echis leucogaster* segons indiquen els resultats de l'anàlisi genètica i els models bioclimàtics.

The carpet or saw-scaled vipers of the genus *Echis* Merrem, 1820 are nocturnal, small (less than 90 cm), fairly stout snakes with a pear-shaped head covered with small scales, prominent eyes with vertical pupils set near the front of the head, and a thin neck. These snakes are found across the semiarid regions of the old world, from Sri Lanka through India, Pakistan, Afghanistan north to Uzbekistan, parts of Iran and the Middle East and in west, northern and east Africa (Gasperetti, 1988; Spawls and Branch, 1995; Wüster, 1997; Arnold *et al.* 2009). All species have a distinctive threat display, forming c-shaped coils with the body, rubbing their lateral scales with serrated keels to make a hissing sound (stridulation) and striking vigorously. They have a very potent venom and, in many areas, are a common cause of fatal snake bite in people

(Gasperetti, 1988; Spawls and Branch, 1995; Gutierrez *et al.* 2006). It has been shown that venom chemistry sometimes varies greatly between different species or populations of *Echis*, which makes it even more relevant to have a good knowledge of the systematics of the genus.

Unfortunately, the saw-scaled or carpet vipers are one of the most taxonomically problematic groups of venomous snakes and, up to date, it is still not certain exactly how many species and subspecies exist within the group (Wüster *et al.*, 1997). For a long time (until the 1980's) only two species of *Echis* were recognized: the Burton's carpet viper, *E. coloratus* Günther, 1878, from Arabia, Jordan, Israel and eastern Egypt; and *E. carinatus* (Schneider, 1801), believed to occur over most of the range of the genus, from west Africa to India and Sri Lanka (described on the basis of specimens collected in Madras, India).

The taxonomy of Burton's carpet viper has been unproblematic and the only taxonomic changes include the description of a new species endemic to northern Oman, *E. omanensis* Babocsay, 2004, and a subspecies from Israel and Jordan named *E. coloratus terraesanctae* Babocsay, 2003. Molecular analyses (Arnold *et al.* 2009) have supported the specific status of *E. omanensis*, while *E. c. terraesanctae* remains recognized on the basis of morphology only.

On the other hand, the systematics of *E. carinatus* in its broad sense has been confused and unstable in recent decades, especially as a result of the revision by Cherlin (1990), who described several species and subspecies, although his analyses have not been widely accepted by subsequent herpetologists. Morpho-logical taxonomy of the *Echis carinatus* complex is problematic due to the existence of climatic clines affecting the number of ventral scales (Cherlin, 1981). Recent molecular analyses by Arnold *et al.* (2009) have shown that *E. carinatus sensu stricto* is confined to the eastern Arabian Peninsula and Asia, with *E. multisquamatus* Cherlin, 1990, being genetically very similar to *E. c. sochureki* Stemmler, 1969, something that had been already shown by Auffenberg and Rehman, (1991) using external morphology. Other subspecies as for instance *E. c. astolae* Mertens, 1970, from Astolae Island in Pakistan and *E. c. sinhaleyus* Deriyalaga, 1951 from Sri Lanka have not been tested using molecular data. The study by Arnold *et al.* (2009) also showed that two further species could be recognized from the Arabian Peninsula: the name *E. khosatzkii* Cherlin, 1990 being available

for the morphologically distinct populations from Dhofar, southern Oman and the Hadhramaut, eastern Yemen, and a still undescribed species from Yemen, for which the name *E. borkini* Cherlin, 1990 may be available. These results suggest that *E. pyramidum* may not be present in the Arabian Peninsula.

The situation in Africa is much more complex and still far from being solved (see for instance Cherlin 1990, Largen and Rasmusen 1993, Spawls and Branch 1995, Wüster *et al.* 1997, Mazuch 2005; Arnold *et al.* 2009). Therefore, as suggested by Spawls and Branch (1995), it seems safest to regard the African carpet vipers of the “*E. carinatus*” group as belonging to three species. These are: the west African carpet viper, *E. ocellatus* Stemmler, 1970, found in the savannah of west Africa, from southern Mauritania and Senegal east to Nigeria, southwestern Chad and northern Cameroon; the northeast African carpet viper, *E. pyramidum* (E. & I. Geoffroy St. Hilaire, 1827), found in oases, semi-desert, dry savannah and rocky areas including lava fields across northeast Africa, with apparently isolated populations in northern Egypt, Lybia and Algeria; and the white-bellied carpet viper, *E. leucogaster* Roman, 1972, found in arid savannah, Sahel, semi-desert and well vegetated wadis across the whole western Sahelian region from the southern half of Mauritania, Senegal and northern Guinea in the west, through central Mali, into western Niger and into the the Hoggar in Algeria, with presumably isolated populations in northern Mauritania, western Sahara and southern Morocco (see Figure 1). This latter species has a similar cephalic scalation than *E. carinatus*, 27 - 33 rows of dorsal scales at midbody and 165 - 180 ventrals (Hughes, 1977).

According to Spawls and Branch (1995) and Wüster *et al.* (1997), it is not clear if the northwestern populations of *E. leucogaster* from Morocco are really isolated from the Sahelian populations or are the result of lack of collecting in the always-difficult intermediate areas. If these had been truly isolated for a long time, the large geographical area between the northwestern and southern populations might have acted as a barrier preventing contact and promoting genetic divergence. Apart from the obvious biogeographical and evolutionary interest that this may have, this would also be very relevant from a toxicological point of view. It has been shown that antivenoms raised against venom from a population of *Echis* in one area may be ineffective in treating bites elsewhere, for

venom chemistry sometimes varies greatly between them (Warrell and Arnett, 1976; Gillisen *et al.* 1994).

Although the number of reported localities for *E. leucogaster* from the northern populations is still very low in the northwestern area (northern Mauritania, Western Sahara and Morocco), it has increased from two specimens from the same locality in Morocco (Auinet-Torkoz) reported by Bons and Geniez (1996), to a total of nine reported by Aymerich *et al.* (2004). Of these, two specimens were from two different localities in northern Mauritania and the remaining seven specimens were all from Morocco (see Fig. 1). Most of the Moroccan specimens have been found near Auinet Torkoz, and the northern-most specimen found so far comes from Amazer, 50 Km south of Ouarzazate; 350 Km northeast in a straight-line from Auinet Torkoz (Fig. 1).

During a recent fieldtrip carried out by the authors in May 2009, a specimen of *Echis leucogaster* was found at 20:45h dead on the road, close to the Oued Tensif, less than 5 Km up road (northeast) from Tassawant and 10 Km southwest of Agz, Morocco (geographical coordinates in decimal degrees: 30.64212 / -6.58195). For its state of preservation, we could deduce that the animal had been lying there for several days (see Fig. 9A and C in appendix of pag. 127). The area where the specimen was found was a relatively barren, semidesertic and stony plateau at 1059 m of altitude (see Fig. 9B in appendix of pag.127). Bioclimatic data from the nearest meteorological station (Ouarzazate) indicate that the region is within the upper thermomediterranean low arid bioclimate belt, with oceanic-high semicontinental conditions (Rivas-Martinez, 2009). The climate of the locality is characterized by an annual mean temperature of 19.9°C, with annual precipitation of 119 mm and minimum temperature of coldest month of 1.4°C (Worldclim dataset, Hijmans *et al.*, 2005). The specimen shares the typical pattern of coloration and body size of the species but as a result of its poor conservation state it was not possible to carry out any scale counts (see Fig. 9A in appendix of pag. 127). Other species found 5 Km further down the road from the new locality of *E. leucogaster* (at Tassawant) include several adults and larvae of *Bufo brongersmai*, *Epidalea boulengeri* and *Bufo mauritanicus*, near irrigation canals in cultivated land, and *Agama impalearis* and *Tropicolotes tripolitanus* in the stony semidesert.

This specimen constitutes the northern-most record of *Echis leucogaster* ever reported, being 40 Km further north than Amazer (Aymerich *et al.* 2004; see Fig. 1). Although the specimen was in a poor state of conservation, some details, as for instance the two big inoculating fangs, were very evident (see Fig. 9C in appendix of pag. 127), as well as its stomach content, which included the remains of a *Scorpion maurus* (see Fig. 9D in appendix of pag. 127).

This specimen of *E. leucogaster*, not only was very relevant from a biogeographical point of view but also constituted a unique opportunity to try to test the degree of genetic isolation of the northwestern populations of *E. leucogaster* from the Sahelian populations using information from its DNA. In order to do so, a small tissue sample including dry skin, muscle and bone was taken in the field, with special care to avoid the stomach area, and it was kept in absolute ethanol. The specimen was preserved dry at 4°C as a voucher for further morphological and genetic Studies. Once in the laboratory of the Institute of Evolutionary Biology (CSIC-UPF) in Barcelona, the tissue sample was processed using methods described elsewhere (Carranza *et al.* 2004; 2006) and with special care to avoid contamination. The extracted DNA was used to amplify and sequence the cytochrome *b* and 16S rDNA mitochondrial fragments, using exactly the same primers and conditions as described by Arnold *et al.* (2009). The mitochondrial DNA sequences of the new population of *E. leucogaster* from Morocco were aligned with other *Echis* samples from GenBank (Table 1) using ClustalX with default parameters (Thompson *et al.* 1997). The resulting alignment included 1117 base pairs (bp) (731 bp of cytochrome *b* and 386 bp of 16S rDNA) of which 343 were variable positions. JModeltest v.0.1.1 (Posada, 2008) was used to select the most appropriate model of sequence evolution using the Akaike Information Criterion (AIC). The model selected was the GTR+G, for the data set containing the cytochrome *b* sequences and the GTR+I+G for the 16S rDNA dataset. The computer program RAxML v.7.0.3 (Stamatakis, 2006) was used for the ML analyses using the “Hard & slow” option, with a heuristic search of 100 trees. The reliability of the ML trees was assessed by bootstrap analysis (Felsenstein, 1985) involving 1000 bootstrap replications. Bayesian analyses were performed using MrBayes v.3.1.2 (Huelsenbeck and Ronquist, 2001), with independent models and model parameters applied to each mitochondrial gene partition. All analyses started with randomly generated trees and ran for

2×10^6 generations. After checking that stationary had been reached, the first 4000 trees were discarded, and a majority rule consensus tree with branch lengths was generated from the remaining 16,000 trees.

In order to interpret the results of the phylogenetic analyses in the light of both the known and the potential distribution ranges of *Echis leucogaster*, an ecological niche modeling projection was performed. Twenty-five presence localities were digitally georeferenced based on information from Gasperetti (1988), Aymerich *et al.* (2004) and the new specimen found, using the software Ozyexplorer. Nineteen localities outside the described area for the species were considered as absences. Nineteen climate variables (Worldclim dataset, Hijmans *et al.*, 2005) were extracted using DIVA GIS (Hijmans *et al.*, 2004) with a very low resolution ($0,166^\circ$), in order to minimize the effect of possible errors in the accuracy of the georeferenced localities. As the correlation matrix showed that the environmental variables were highly correlated, a principal components regression (PCR) was applied to the variables in order to reduce the dimensions and to identify to the most explanatory variables. All statistical analysis were performed using Statistica 6.0.

The results of the phylogenetic analyses are shown in Fig. 3 and clearly indicate that the *E. leucogaster* from Agz, Morocco is very closely related to the two *E. leucogaster* samples from Ayoun el'Atrous (Mauritania). Despite being separated by more than 1600 Km, these samples present an uncorrected genetic divergence (*p*-distance) of only 1% in the 731 bp of cytochrome *b* analyzed for this study and are identical in the 386 bp of the 16S rDNA. Since the specimen from Agz is the northernmost sample of *E. leucogaster* known to date, we can confidently conclude that the genetic divergence between the northwestern and Sahelian populations of *E. leucogaster* is very low, indicating that these populations are either connected or, if in isolation, the separation occurred very recently.

The results of the PCR suggest that the presence of *Echis leucogaster* in the region might be positively correlated with the increase of temperature and inversely correlated with precipitation (Table 2). This is expected as the species has a mainly Sahelian and perisaharan distribution (see Gasperetti, 1988). The most significant variables identified by PCR were successively included in the model excluding variables with highly correlated coefficients. Finally, the selected variables (Table 2) were used in a niche modeling simulation performed with Maxent, a general-

purpose algorithm which makes accurate predictions using data sets that only contain information on the known presence (Philips et al., 2006) and even from small sample sizes (Pearson et al., 2007). In order to determine the accuracy of the model several agreement statistics for the three different thresholds were computed: lowest presence threshold (minimum predicted area with omission error equal to 0, Pearson et al., 2007); OC, optimal cut-off with minimum misclassification rate; and 50, the highest of the 50% predicted values (Table 3). The area under the curve for the model was 0.98, suggesting that climatic variables correctly explained the distribution of *Echis leucogaster* in the region. The projection map is shown in Fig. 4 and indicates that, under the present climatic conditions, *E. leucogaster* is likely to have a continuous distribution along the western boundary of the Sahara desert. This is in agreement with the results of the phylogenetic analyses, which suggest that there is almost no genetic divergence between the populations of *E. leucogaster* analyzed (see Fig. 3). However, the high inaccuracy of the available data jeopardizes the results of the modeling. Future discovery of new localities of this rare species will allow us to either ratify or refute this hypothesis.

This apparent continuous distribution in *Echis leucogaster* predicted by the niche modeling analysis and supported by the genetic data might also apply to other subtropical species with supposedly isolated populations in northwest Africa as for instance *Crocodylus suchus*, *Dasypeltis scabra*, *Bitis arietans*, *Lamprophis fuliginosus* (Bons and Geniez, 1996; Duplessy et al., 1989). Most probably, these species had a continuous range during the Pleistocene, when much of this northwestern area that is now covered by the Sahara Desert was much more vegetated and would have provided suitable habitat for them. What is not so clear is if, like in the case of *E. leucogaster*, the actual climatic conditions still allow some contact. The lack of data in the intermediate areas between the Sahel and northwest Africa might be the result of poor sampling caused by the difficult political situation in the region. The present work demonstrates that in cases like this niche modeling can be a very useful tool. However, the degree of geographical isolation, genetic divergence and taxonomic status of these apparently relict populations will only be elucidated when molecular and niche modeling data are available for them, as it is available now for *E. leucogaster*.

Acknowledgements

This work was carried out under a permit from the Moroccan Government (Department of Water and Forestry resources) to David Donaire.

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Table 1.- Details of material and sequences used in the present study. The question mark indicates that the *cytb* and 16S rRNA sequences of the specimen of *E. ocellatus* by Lenk *et al.* 2001 are probably the result of a misidentification of an *E. leucogaster* specimen by an *E. ocellatus* (see Fig. 3).

Taxa	Locality	Accession Numbers Cyt b / 16SrRNA	References
<i>Cerastes cerastes</i>	Erfoud (Morocco)	AJ275703 / AJ275755	Lenk <i>et al</i> 2001
<i>Cerastes vipera</i>	Djebil (Tunisia)	AJ275705 / AJ275757	Lenk <i>et al</i> 2001
<i>Echis coloratus</i>	Wadi Rishrash (Egypt)	AJ275708 / AJ275760	Lenk <i>et al</i> 2001
<i>Echis omanensis</i> -1	Jebel Akhdar (north Oman)	EU642590 / EU642581	E3026.8
<i>Echis omanensis</i> -2	North of Tanuf (north Oman)	EU642587 / EU642578	E3026.9
<i>Echis omanensis</i> -3	Wadi Beni Habib (north Oman)	EU642588 / EU642579	E3026.10
<i>Echis omanensis</i> -4	Wadi Beni Khalid (north Oman)	EU642589 / EU642580	E23116.1
<i>Echis carinatus</i> subsp.	(Pakistan)	AJ275706 / AJ275758	Lenk <i>et al</i> 2001
<i>Echis multisquamatus</i>	(Turkmenistan)	AJ275702 / AJ275763	Lenk <i>et al</i> 2001
<i>Echis carinatus sochureki</i>	Manah (north Oman)	EU642591 / EU642582	E3026.2
<i>Echis ocellatus</i> -1	West Africa	AF292568 /	W _{ster} , unpublished
<i>Echis ocellatus</i> -2	West Africa	AF191579 /	Malhotra & Thorpe 2000
<i>Echis ocellatus</i> -3	10Km N. of Tapoua (Niger)	EU642592 / EU642593	SPM0050
<i>Echis sp.</i>	(Yemen)	AJ275707 / AJ275759	Lenk <i>et al</i> 2001
<i>Echis khozatskii</i>	NW. of Ayun pools (Dhofar, Oman)	EU642584 / EU642575	E3026.15
<i>Echis pyramidum</i>	(Egypt)	AJ275709 / AJ275761	Lenk <i>et al</i> 2001
<i>Echis ocellatus?</i>	(Mali)	AJ275710 / AJ275762	Lenk <i>et al</i> 2001
<i>Echis leucogaster</i> -1	Ayo ^o n el'Atrous (Mauritania)	EU642585 / EU642576	E3026.3
<i>Echis leucogaster</i> -2	Ayo ^o n el'Atrous (Mauritania)	EU642586 / EU642577	E3026.4
<i>Echis leucogaster</i> -3	Agz (Morocco)	GU078718 / GU078719	ME2

Variables	SL
<u>annual precipitation</u>	-0.348835355
precipitation of wettest quarter	-0.32551582
precipitation of wettest month	-0.322842296
isothermality	-0.230488934
precipitation seasonality	-0.226351542
precipitation of warmest quarter	-0.222125223
precipitation of coldest quarter	-0.147846466
minimum temperature of coldest month	-0.132308049
precipitation of driest month	-0.130139678
mean temperature of coldest quarter	-0.119962559
precipitation of driest quarter	-0.115355614
mean temperature of driest quarter	0.0297552291
annual mean temperature	0.0385694298
mean temperature of wettest quarter	0.0791138993
mean diurnal range	0.176126922
mean temperature of warmest quarter	0.223325155
<u>maximum temperature of warmest month</u>	0.236764966
temperature annual range	0.259127201
<u>temperature seasonality</u>	0.286243262

Table 2. Environmental variables selected to be included in the model (underlined) using a principal components regression method. SL= Sum of loadings.

Kappa	0.8099	0.9545	0.8409
Comission	0.2105	0	0
Omission	0	0.08	0.28

Table 3. Accuracy assessment of the thresholds displayed in Fig. 4.

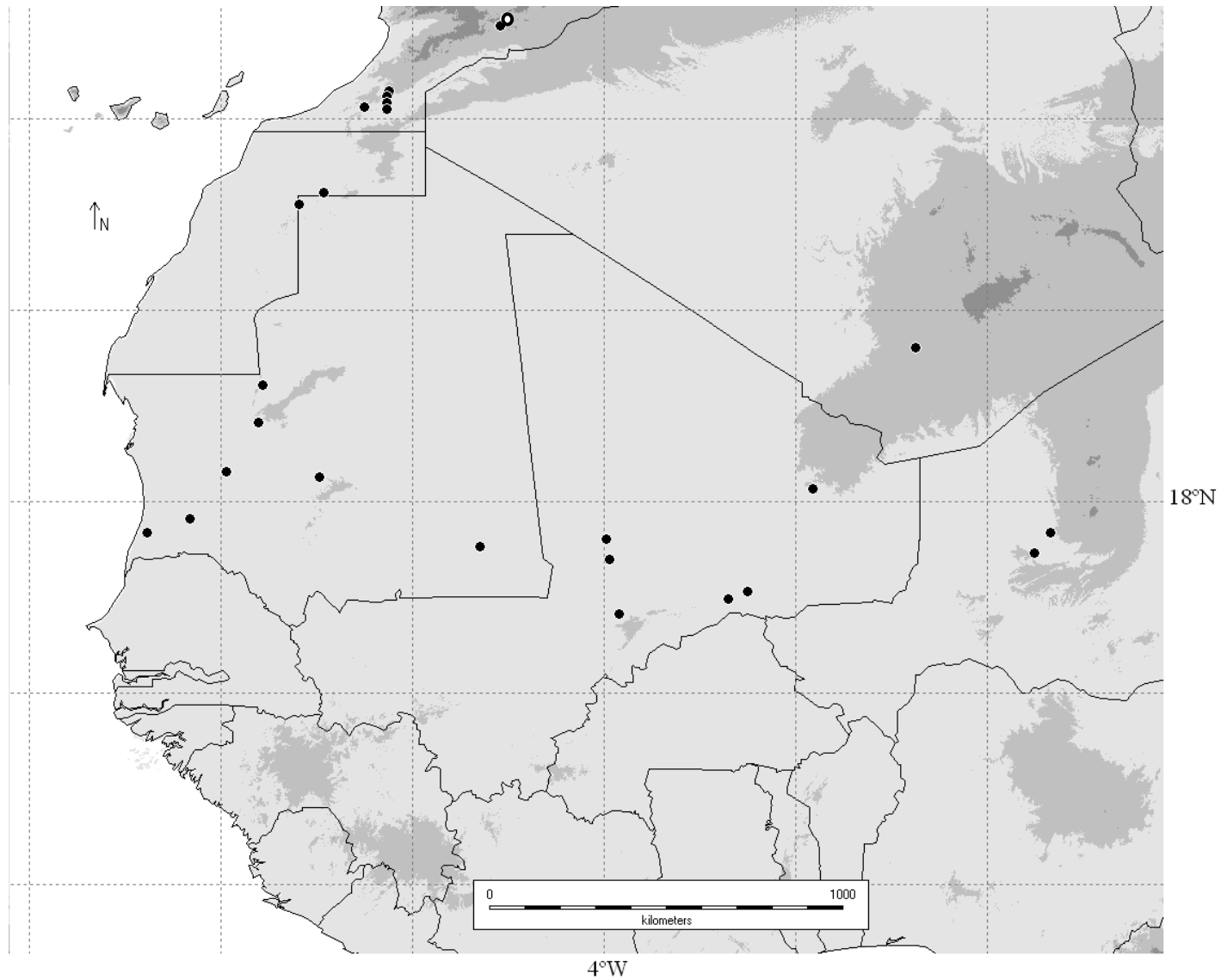


Figure 1.- Distribution of *Echis leucogaster* in Northwestern Africa (according to Gasperetti, 1988; Aymerich et al., 2004). All known populations are marked with black dots. The new locality described in this paper is marked with a white circle.

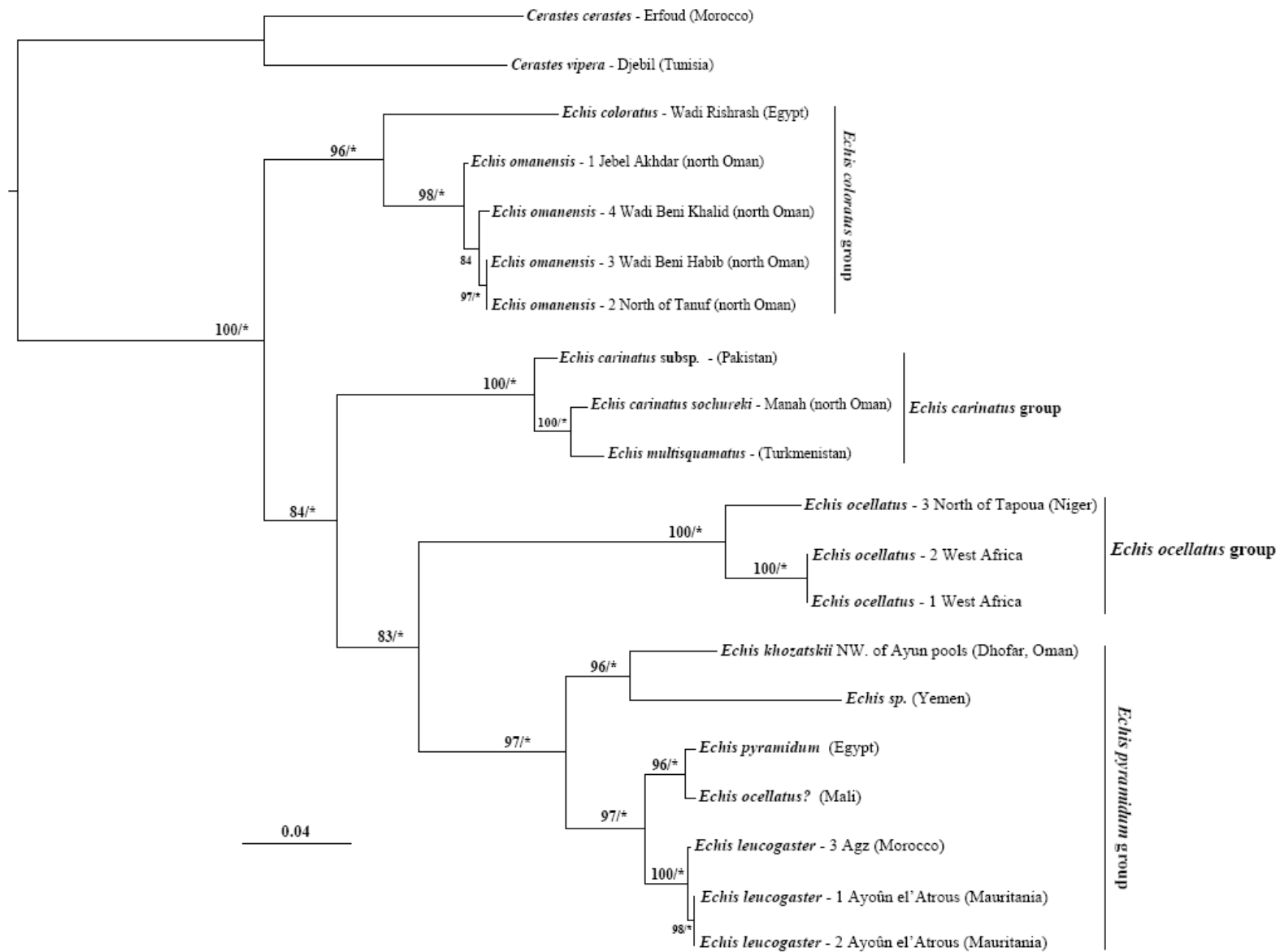


Figure 3. Maximum-likelihood tree including cytochrome b and 16S rRNA sequences from all the specimens from Arnold *et al.* (2009) plus the new specimen from near Agz, Morocco. Bootstrap support values are shown above the branches to the left of the forward slash and posterior probability values above 0.95 are also indicated above branches by an asterisk to the right of the forward slash.

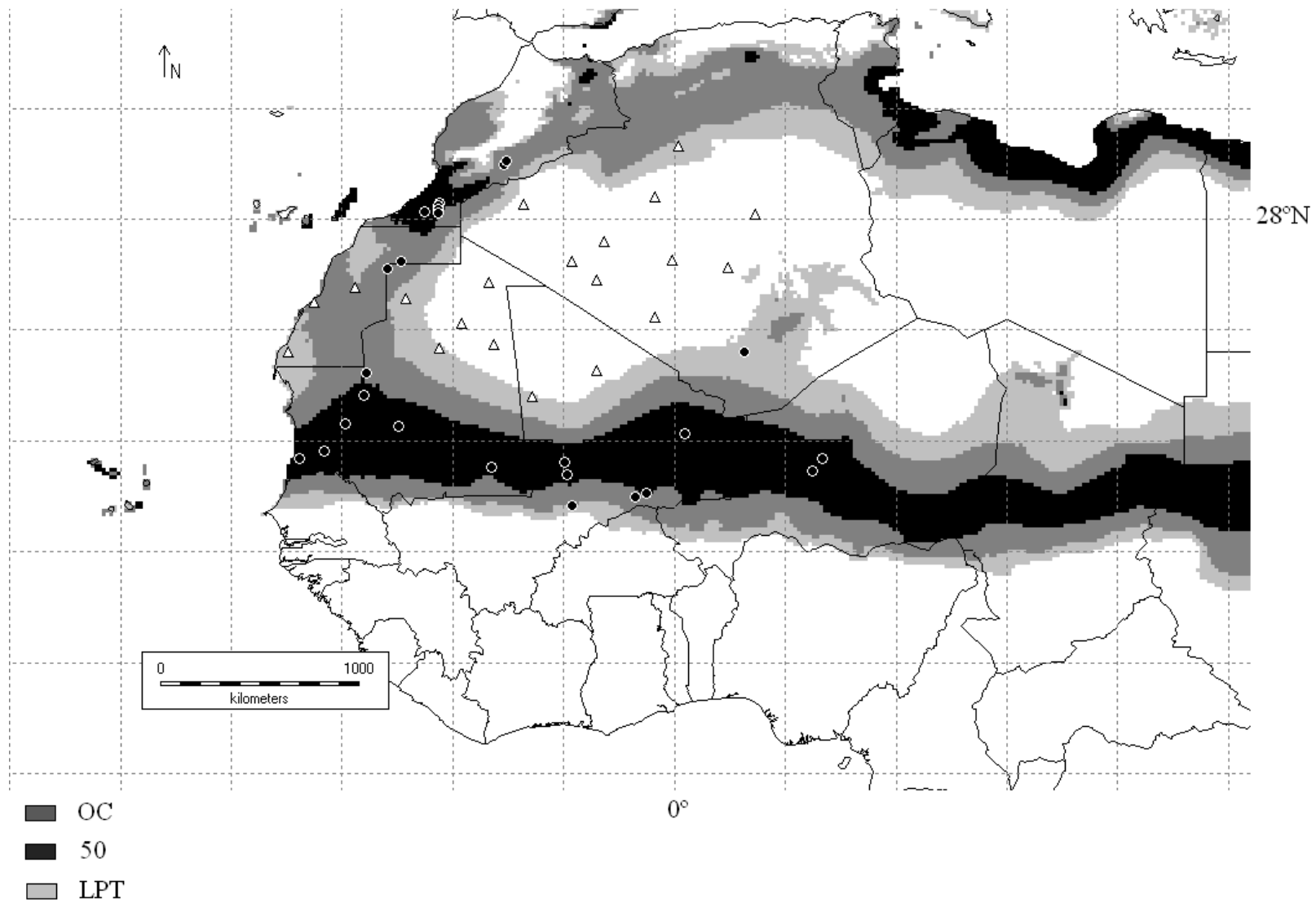


Figure 4.- Projected distribution of *Echis leucogaster* in northwest Africa. Circles: presence localities. Triangles: absence localities. 50: 50% of the highest probability localities; OC: optimal cut-off; LPT: lowest presence threshold.

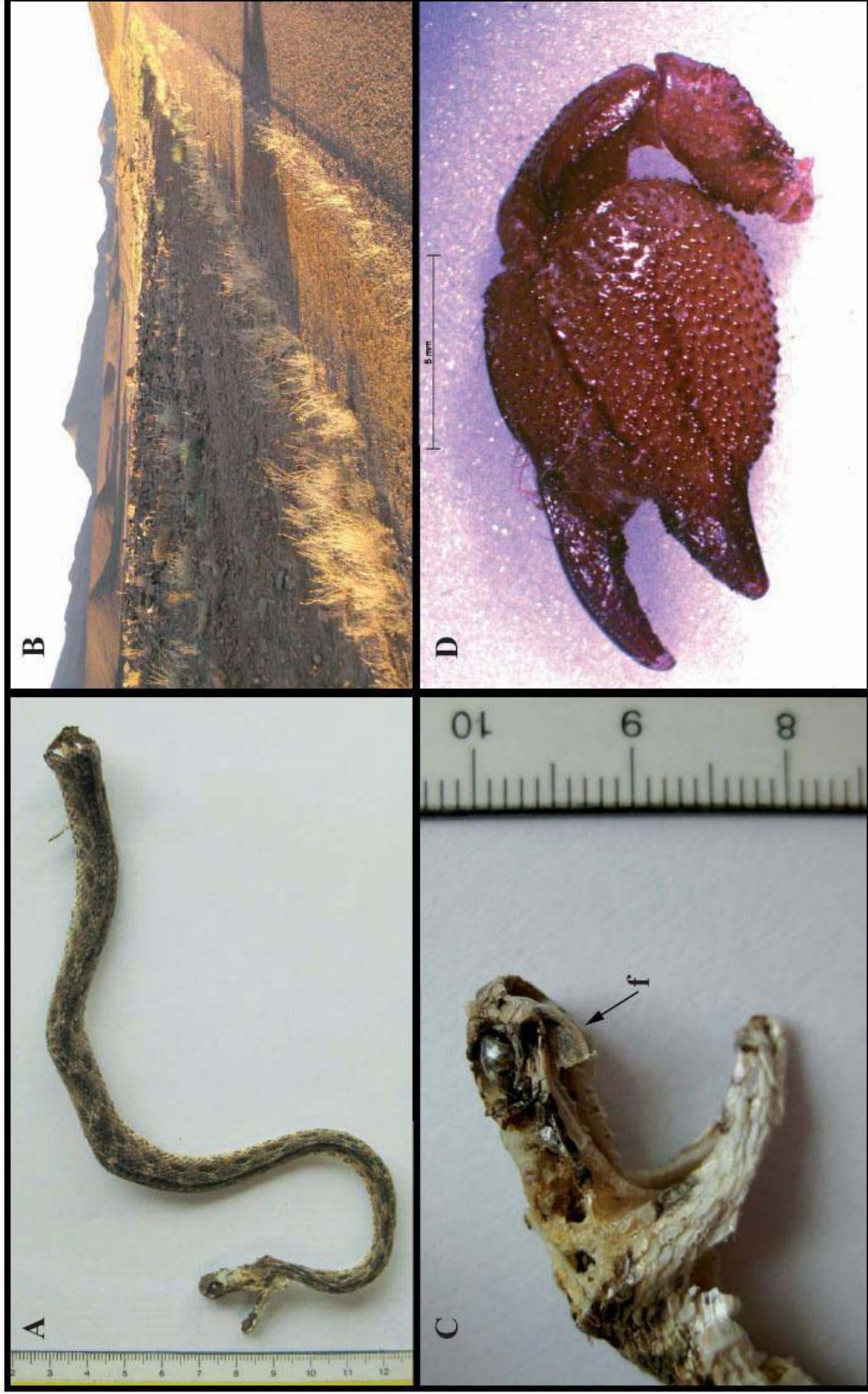


Figure 9.- Pictures showing A) *E. leucogaster* found on the road 10 Km southwest of Agz; B) habitat where the specimen was found; C) detail of the head showing the fangs (f); D) *Scorpion maurus* chelicerae found in the stomach of *E. leucogaster*, which confirms that scorpions are part of the diet of these snakes. (referenced in the pág. 58 and 59). Photographs: Salvador Carranza