

Chorological analysis and morphological variations of Saurians of the genus *Uromastix* (Reptilia, Agamidae) in western Sahara. Description of two new taxa.

JOSÉ ANTONIO MATEO^{1,3}, PHILIPPE GENIEZ², LUIS FELIPE LÓPEZ-JURADO³ & JACQUES BONNS²

¹ Estación Biológica de Doñana-CSIC, Apartado 1056, E-4108 Sevilla, Spain.

² Laboratoire de Biogéographie et Ecologie des Vertébrés-EPHE, Université Montpellier 2, Place Eugène Bataillon, F-34095 Montpellier, France.

³ Departamento de Biología, Universidad de Las Palmas de Gran Canaria, 35017 Las Palmas de Gran Canaria, Spain. E-mail: luisfelipe.lopez@biologia.ulpgc.es

Abstract: The description of a new species of the genus *Uromastix* is proposed on the basis of two specimens from the Adrar Souttoug in Western Sahara. This taxon differs greatly from *U. acanthinura* on account its larger size, the much larger number of scales, the arrangement of tubercles on its upper thighs, the different habitus and colouring. These morphological features mean it closely resembles *U. aegyptia*. The existence of a relictual *U. aegyptia*-group throughout the Sahara is suggested. In addition, the morphological variations in Spiny-tailed agamas (or Mastigures) of the *Uromastix acanthinura* group in the west of the Sahara are briefly analysed. This produces evidence for the existence of a species proper to Western Sahara and surrounding areas, *Uromastix flavifasciata*, represented by two subspecies: *U. f. flavifasciata* in the north and *U. f. obscura* subsp. nov. in the south. The latter new form is characterised by uniformly black colouring, even in active individuals. This work also demonstrates that *Uromastix acanthinura wernerii* does not penetrate Western Sahara and that its distribution is parapatric with that of *U. flavifasciata*. Lastly, the presence of *U. maliensis* is suspected in the Adrar Atar (Mauritania) and the Adrar Souttoug (Western Sahara).

Key words: Agamidae, *Uromastix*, chorology, systematics, Sahara.

Resumen: Análisis corológico y variaciones morfológicas en los saurios del género *Uromastix* (Reptilia, Agamidae) de la región occidental del Sahara. Descripción de dos nuevos taxones.- Se describe una nueva especie del género *Uromastix* sobre la base de dos especímenes procedentes del Adrar Sutuf (Sahara Occidental). Los individuos del nuevo taxón difieren fuertemente de *Uromastix acanthinura* por el gran tamaño que llegan a alcanzar los adultos, su siempre mayor número de escamas, la disposición diferente de los tubérculos en los muslos, y por su diseño y coloración. Sus características generales se asemejan a las de *Uromastix aegyptia*, un hecho que sugiere la posible existencia de lagartos del complejo *U. aegyptia* en poblaciones relicticas a lo largo del desierto del Sahara. Se han analizado también las variaciones morfológicas de los lagartos de cola espinosa del grupo *Uromastix acanthinura* en la región occidental del Sahara, cuyos resultados ponen de manifiesto la existencia de una especie propia al Sahara Occidental y sus alrededores, *Uromastix flavifasciata*, representada por dos subspecies: *U. f. flavifasciata* en el norte y *U. f. obscura* subsp. nov en el sur. Esta última forma se caracteriza por su coloración negra homogénea incluso en animales activos. Este trabajo también demuestra que *Uromastix acanthinura wernerii* no penetra en el Sahara Occidental y que su distribución es parapátrica con *U. flavifasciata*. Finalmente, nuestras observaciones también dan como posible la existencia de *Uromastix maliensis* en el Adrar Atar (Mauritania) y en el Adrar Sutuf (Sahara Occidental).

Palabras Clave: Agamidae, *Uromastix*, corología, sistemática, Sahara.

INTRODUCTION

The genus *Uromastix*, of the family Agamidae and the subfamily Uromastycinae, comprises ten species (WILMS, 1995; JOGER & LAMBERT, 1996). It has a typically Saharo-Sindian range covering the whole of the Sahara, Somalia, Ethiopia, the Arabian peninsula, Palestine, Syria, Iraq, Iran, southern Afghanistan, Pakistan and north-west India (WILMS, 1995). In Africa, lizards of the genus *Uromastix* are not evenly distributed throughout the Sahara and there are whole areas where this animal is unknown. If the range of the genus *Uromastix* in the western half of the Sahara is compared with a map of ergs (Saha-

ran wind- dunes) the two can be seen to complement each other quite closely (Figure 1). As SCHLEICH *et al.* (1996) point out, it is clear that Spiny-tailed agamas (or Mastigures) avoid the ergs which may well constitute barriers for these animals (GRENOT & VERNET, 1972). As is evidenced by the distribution maps of the genus published by WILMS (1995), the emplacement of these ergs probably gave rise to the isolation of *Uromastix* in the west of the Sahara from those in central Sahara. The range of Spiny-tailed agamas in the west Sahara corresponds to an area oriented north-east / south-west starting in south-east Morocco and extending south-westwards over the entire foothills of the Moroccan Anti-

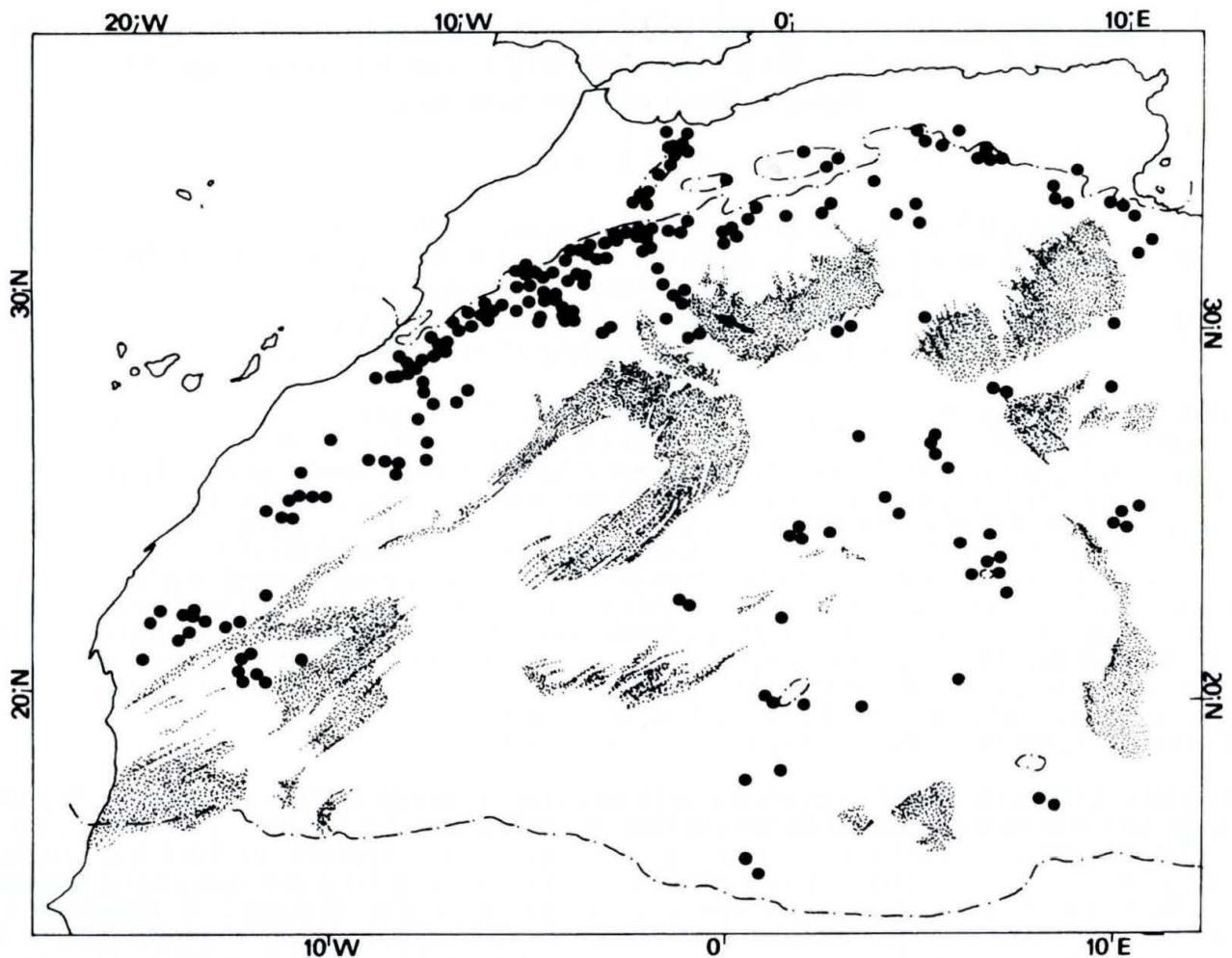


Figure 1.- Distribution map of ergs (in grey) and of *Uromastyx* (full circles), all taxons confused. The dashed line is the isoline for 200 mm of anual rainfall.

Figure 1.- Disposición de los ergs (punteado) y de los lagartos del género *Uromastyx* (puntos negros). La línea punteada corresponde a la isoyeta de 200 mm anuales.

Atlas, and covering Western Sahara, north-east Mauritania and the Adrar Atar region also in Mauritania. It is limited to the north-west by the Moroccan Atlas axis, to the west by Saharan zones under strong oceanic influences (Saharan bioclimatic zone with warm winters), to the south and east by a succession of ergs which probably constitute an impassable barrier: the Trarza and Ouarane sands (cf. ANGEL & LOTHE, 1938), the Majâbat al-Koubrâ (cf. MONOD, 1958), the Iguidi, Chech and Er-Raoui ergs and, lastly, the Great Western erg (Figure 1).

Historical background to the systematics of Spiny tailed agamas (or Mastigures) in the west of the Sahara

In the north of this western region, i.e. Morocco, PASTEUR & BONIS (1962) do not recog-

nise any particular forms and ascribe the forms *nigriventris* Rothschild & Hartert, 1912, *nigerrimus* Hartert, 1913, *weneri* L. Müller, 1922, and *pluriscutata* Féjerváry, 1927, to manifestations of the species' considerable morphological and chromatic variation. They do not comment on the chromatic differences, observed by VALVERDE (1957), between animals from south Morocco and those from the Western Sahara. In VALVERDE's opinion, Spiny-tailed agamas from the former Spanish colony are sufficiently distinct to deserve a separate subspecific status. Five years later, MERTENS (1962) suggested the existence of three subspecies in the western area: *Uromastyx acanthinura acanthinura* Bell, 1825, for north-west Africa, *U. a. weneri* for north-west Algeria and eastern Morocco (wadi Mouloya valley) and *U. a. flavifasciata* Mertens,

1962. This last form was described on the basis of a specimen which this author reported to have come from 50 km. north-east of Dakar (Senegal). MERTENS (1962) also mentioned the existence of this taxon in Western Sahara (after the illustrations published by VALVERDE, 1957), and recalled the occurrence of *U. acanthinura* in the Adrar of Mauritania but he stated that it had not yet been established whether or not these Mauritanian populations belonged to the subspecies *flavifasciata*. The terra typica of *U. a. flavifasciata* was rightly questioned by BÖHME (1978) who suggested locating it at Atar, in the Adrar of Mauritania, but without giving reasons for this, possibly the result of a report by GRENOT (1974, p.162). Probably following the two latter authors, WILMS & BÖHME (1993) and SCHLEICH *et al.* (1996) recognised the existence of *Uromastix a. flavifasciata* in the Adrar Atar. Within the species *Uromastix acanthinura*, WILMS & BÖHME (1993) recognised four subspecies: *Uromastix a. acanthinura* in north-west Sahara; *U. a. geyri* in south central Sahara; *U. a. dispar* in southern east Sahara; and *U. a. flavifasciata* only in the Atar region of Mauritania. Curiously, WILMS (1995) considered *Uromastix acanthinura flavifasciata* synonymous with the nominal form and because of lack of information he did not pronounce on the status of *U. a. weneri*. At the same time, he omitted from his *U. acanthinura* distribution map the whole of Western Sahara, a region where Spiny-tailed agamas are well represented (cf. VALVERDE, 1957, and own data). SCHLEICH *et al.* (1996) accepted the validity of the subspecies *flavifasciata*, but they too restricted it solely to the Atar region, and were "unsure" of the validity of the subspecies *weneri*. Lastly, BONIS & GENIEZ (1996) ignored *U. a. weneri* and assigned all the Spiny-tailed agamas from north Morocco (as far south as Bas Drâa region) to the nominal subspecies, recognised the existence of *U. a. flavifasciata* which, in their opinion occupies the northern half of Western Sahara and did not pronounce on the status of Spiny-tailed agamas from the southern half of Western Sahara. They observed that animals from the latter region have a uniformly blackish colouring and could therefore be related to the subspecies *nigerrima*.

The conclusion that can be drawn from this bibliographic analysis is that slight contradictions exist between authors as to the taxo-

nomy of Spiny-tailed agamas from the west of the Sahara and, in particular, that in the Western Sahara this is almost completely unknown. The examination of a large sample of Spiny-tailed agamas from the west of the Sahara has enabled us to demonstrate the importance of this region for understanding the phylogeography of this genus, the existence of a new species of the genus *Uromastix* as well as large morphological and chromatic variations within the *Uromastix acanthinura* group.

MATERIAL AND METHODS

We examined 154 Spiny tailed agamas from the following scientific collections: Estación Biológica de Doñana-Sevilla, (E.B.D.), (n=75), Muséum National d'Histoire Naturelle de Paris (M.N.H.N.), (n= 40), Laboratoire de Biogéographie et Ecologie des Vertébrés de l'E.P.H.E., Montpellier (E.P.H.E), (n= 37), Departamento de Biología University of Las Palmas (U.L.P.G.C), (n= 2). Of these 154 animals, 124 come from the area of the present publication, namely 60 from Morocco and north-west Algeria, 58 from Western Sahara, 5 from Mauritania and one from the Hamada of Tindouf in Algeria. The other 30 individuals were from regions and taxons which are outside the framework of this study; they were used for purposes of comparison. They are *Uromastix a. acanthinura* (2 specimens from central and east Algeria), *U. a. geyri* (8 individuals from south Algeria and north Niger), *U. a. dispar* (1 from Tchad), *U. maliensis* (1 from south Algeria), *U. ocellata ocellata* (2 from Egypt), *U. ocellata ornata* (2 from Egypt and Arabia), *U. aegyptia aegyptia* (4 from Egypt), *U. macfadyeni* (1 from Djibouti), *U. princeps* (3 from Somalia), *U. benti* (1 from Arabia), *U. loricata* (1 example of unknown provenance), *U. hardwickii* (4 specimens from Pakistan). As well as 69 animals of diverse origins and which are not held in museum collections.

The 177 specimens from scientific collections were photographed, measured and their scales counted. We have used the following abbreviations: SVL: snout-vent length; TAIL: tail length; %TAIL: proportion of tail length to snout-vent length; DORS: number of longitudinal scale rows counted at mid-body; VENL: number of ventral scale rows counted from the gular fold to the inguinal fold; CAUD: number of scaly verticillae on the up-



Figure 2.- a: *Uromastix acanthinura weneri*, yellow form, from 24 km after Saka towards Guercif (NE Morocco) (photo Ph. Geniez); b: *U. a. weneri*, orange form, from 25 km after Taïdalt towards Aouinet-Torkoz (SW Morocco) (photo M. Geniez); c: *U. flavifasciata flavifasciata* from Rabounet-Tindouf (Algeria) (photo D. Donaire); d: *Uromastix cf. maliensis*, from djebel Koudiat Laghnam (Adrar Souttouff, Western Sahara)(photo E. Mahé).

Figura 2.- a: *Uromastix acanthinura weneri*, forma amarilla, procedente de una localidad situada a 24 km de Saka en dirección a Guercif (NO de Marruecos) (Fotografía P. Geniez); b: *U. a. weneri*, forma naranja, de un punto situado a 25 km de Taidalt en dirección a Aouinet Torkoz (Suroeste de Marruecos); c: *U. flavifasciata flavifasciata*, procedente de Rabounet-Tinduf (Argelia) (Fotografía D. Donaire); d: *Uromastix af. maliensis*, procedente de yebel Kudiat Lajnam-Adrar Sutuf (Sahara Occidental) (Fotografía E. Mahé).

per tail; SUBC: number of transversal SCALE rows on underside of tail; POAN: presence or non-presence of pre-anal pores; PRAN: presence or non-presence of femoral pores; NPOR: total number of pre-anal and femoral pores; SSTV: presence or non-presence of small scales inserted between the tail verticillae; FLAT: tail distinctly flattened or with a nearly circular section; FEPO: presence or non-presence of scaly tubercles or enlarged scales on the flanks; TUBB: presence or non-presence of scaly tubercles on the back.

RESULTS AND DISCUSSION

The examination of our sample of Spiny-tailed agamas from the west of the Sahara (western area, cf. Figure 1) revealed a clear

division into two sets: on one hand, a very large majority of animals can be ascribed to variations of the group *Uromastix acanthinura* (sensus JOGER, 1986); on the other, two very different specimens which are related, at least from a morphological point of view, to species considered much more oriental, in particular *Uromastix aegyptius*.

1.- Spiny-tailed agamas of the group *Uromastix acanthinura* in the west of the Sahara

The north-east of the western area (the west of the Algerian high plateaus and the wadi Moulouya valley in Morocco) is occupied by the form *Uromastix acanthinura weneri* (MERTENS, 1962; SCHLEICH *et al.*, 1996), characterised by the bright yellow colour of the

Table 1: Meristic and folioidotic characters of Spiny-tailed agamas. SVL: snout-vent length; TAIL: tail length; DORS: number of scale rows at midbody; VENL: number of transversal rows of ventral scales; CAUD: number of scaly verticillae on upper tail; SUBC: number of transversal rows of sub-caudal scales; NPOR: total number of pre-anal and femoral pores. The holotype of *Uromastix acanthinurus flavifasciatus* (SMF 58032) has been included in *U. Flavifasciata flavifasciata*; their meristic and biometric characteristics are the following: SVL: 265 mm; TAIL: 165 mm; %: percent of TAIL LENGTH/SVL LENGTH; DORS: 200; VENL: 108; CAUD: 21; NPOR: 30.

Tabla 1: Caracteres merísticos y folioidóticos de los lagartos de cola espinosa. SVL: longitud cabeza-cuerpo; TAIL: longitud de la cola; DORS: escamas alrededor del cuerpo; VENL: número de filas transversales de escamas ventrales; CAUD: número de verticilos en la cola; SUBC: número de filas transversales de escamas subcaudales; NPOR: número de poros preanales y femorales. El Holotipo de *Uromastix acanthinurus flavifasciatus* (SMF 58032) ha sido incluido en *U. Flavifasciata flavifasciata*; sus características merísticas y biométricas son las siguientes: SVL: 265 mm; TAIL: 165 mm; %: porcentaje de Longitud cola/Longitud cabeza-cuerpo; DORS: 200; VENL: 108; CAUD: 21; NPOR: 30.

Species		SVL	TAIL	%	DORS	VENL	CAUD	SUBC	NPOR
<i>U. occidentalis</i>	\bar{x}	308	228	74.0	299.0	121.5	23.0	49.0	0
	\pm	-	-		1.0	0.3	0.0	0.0	-
	n	1	1		2	2	2	2	2
<i>U. aegyptia aegyptia</i>	\bar{x}	270	195	72.2	271.5	133.5	23.0	56.0	31.5
	\pm	-	-		12.8	5.2	0.0	1.4	1.8
	n	1	1		4	4	4	4	4
<i>U. acanthinura. acanthinura</i>	\bar{x}	182.5	113.8	62.4	174.7	81.0	21.0	39.8	28.0
	\pm	13.7	7.7		3.5	3.2	0.4	1.9	2.2
	n	2	2		4	4	4	4	4
<i>U. a. geyri</i>	\bar{x}	181.3	157.8	86.8	171.0	80.1	23.3	47.7	33.1
	\pm	8.5	13.3		8.9	2.6	0.5	1.8	3.6
	n	6	6		8	8	8	8	7
<i>U. a. wernerii</i>	\bar{x}	186.7	116.4	62.3	168.4	79.7	20.0	40.1	26.1
	\pm	12.7	7.8		6.7	2.2	0.4	1.3	1.7
	n	60	60		55	57	58	58	55
<i>U. a. dispar</i>	\bar{x}	181	122	67.4	180	89	22	37	34
	\pm	-	-		-	-	-	-	-
	n	1	1		1	1	1	1	1
<i>U. flavifasciata flavifasciata</i>	\bar{x}	226.6	142.8	63.2	181.7	96.7	19.3	47.9	32.0
	\pm	16.0	9.3		3.1	2.1	0.5	1.3	1.3
	n	28	28		34	36	33	31	28
<i>U. f. obscura</i>	\bar{x}	231.6	144.6	62.4	183.3	97.7	19.4	47.2	28.7
	\pm	15.1	9.1		2.2	3.4	0.4	1.4	1.5
	n	6	6		19	23	19	17	14
<i>U. sp (Mauritania)</i>	\bar{x}	166.0	118.5	71.4	188.2	94.0	21.3	46.7	28.0
	\pm	10.6	7.8		4.2	4.9	0.6	1.5	2.2
	n	5	5		4	4	4	3	4
<i>U. maliensis</i>	\bar{x}	187.4	114.6	61.2	182	88	20.0	40	25.0
	\pm	17.2	10.1		-	-	0.7	-	1.6
	n	9	9		1	1	10	1	10
<i>U. ocellata ocellata</i>	\bar{x}	134.0	130.0	97.0	244.0	107	28.5	46.5	30.0
	\pm	3.0	5.0		1.0	3.5	0.4	1.3	-
	n	2	2		2	2	2	2	1
<i>U. o. ornata</i>	\bar{x}	168.0	131.5	78.3	171.0	81.0	22.5	29.0	24.0
	\pm	11.5	8.3		11.0	0.0	0.2	1.5	3.0
	n	2	2		2	2	2	2	2
<i>U. macfadyeni</i>	\bar{x}	100.0	91	91.0	176	96	26	48	28
	\pm	-	-		-	-	-	-	-
	n	1	1		1	13	1	1	1
<i>U. princeps</i>	\bar{x}	125	60	48.0	151.3	93.3	13.0	25.5	6
	\pm	-	-		3.3	5.2	0.5	1.7	0.8
	n	1	1		3	3	2	2	3
<i>U. benti</i>	\bar{x}	162	151	93.2	150	70	27	33	0
	\pm	-	-		-	-	-	-	-
	n	1	1		1	1	1	1	1
<i>U. loricata</i>	\bar{x}	240	170	70.8	206	93	26	55	21
	\pm	-	-		-	-	-	-	-
	n	1	1		1	1	1	1	1
<i>U. hardwickii</i>	\bar{x}	152.0	119.5	78.6	212.5	121.7	35.5	99.3	29.5
	\pm	9.0	9.3		6.1	2.8	0.9	1.8	1.9
	n	4	4		4	4	4	3	4

adults (Figure 2a).

In south Morocco, from Tafilalet to the foothills of djebel Ouarkiz, polychromatic populations are found, with orange to red animals predominating in some cases, and yellowish green ones in others, together with a not so negligible number of individuals that are both orange and green (Figure 2b; cf. also HOOGLMOED, 1972; 1974; WILMS, 1995; BONS & GENIEZ, 1996) and which, according to SCHLEICH *et al.* (1996) and WILMS (pers. com.), are also related to *U. a. wernerii*. The entirely yellow form is relatively rare and is found sporadically within orange and green populations. These polychromatic populations penetrate the south-east along the wadi Guir-Saoura corridor, the only passage southwards between The Chech erg and the Great Western Sandsea, extending as far as the Ougarta mountains (cf. GRENOT, 1974). Because of the colour patterns observed there, this region, located in Algeria, could be the southernmost meeting point between subspecies *U. a. acanthinura* and *U. a. wernerii*.

South of the Ouarkiz range, that is to say, in the north of Western Sahara, one strain appears characterised by large-sized individuals (up to 290 mm snout-vent length compared to 230 mm for the largest *Uromastix a. wernerii* of our sample), a significantly higher number of transversal rows of ventral scales ($\alpha < 1\%$, Mann-Whitney U test: $Z = 8,18$ for 57 *U. a. wernerii* and 51 specimens from Western Sahara) (cf. Table I) which means a proportionally longer body, a higher average number of rows of sub-caudal scales (cf. Table I), and, above all, by its black colouring enhanced by 5 to 7 sharply contrasting greenish to bright yellow transversal stripes on its back. An analysis of the main components (MCA) (Figure 5) based on seven biometric and meristic characteristics taken over 85 adult individuals allows us to clearly separate the strain of the western Moroccan Sahara from the rest thanks, above all, to said characteristics. This MCA reveals, moreover, that the variables used do not allow us to separate the males from the females with any degree of clarity, neither in *Uromastix acanthinura wernerii* nor in the Western Sahara strain. Juveniles also have light-coloured transversal stripes on their backs (Figure 2c; cf. also VALVERDE, 1957; MERTENS, 1962; GRENOT, 1974; SCHOUTEN & THEVENOT, 1978). This easily recognisable and scarcely variable

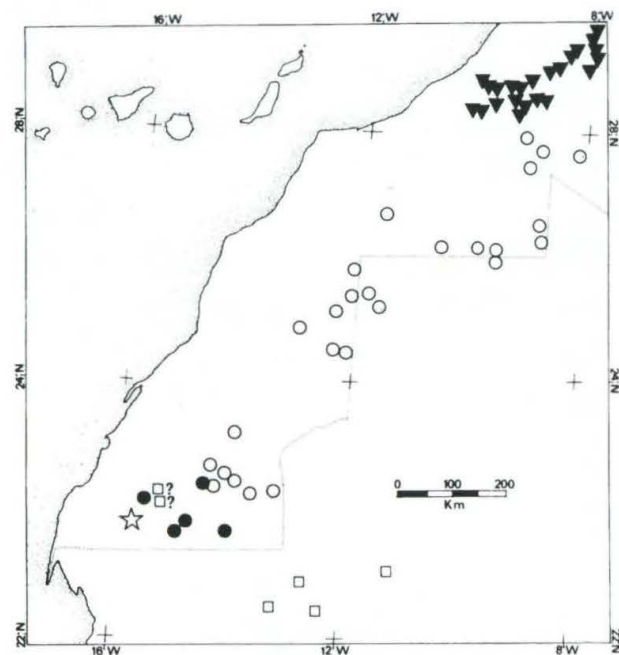


Figure 3.- Distribution of saurians of the genus *Uromastix* in the west of the Sahara. Triangles: *Uromastix acanthinura wernerii*; hollow circles: *U. flavifasciata flavifasciata*; full circles: *U. f. obscura*; squares: *U. cf. maliensis*; star: *U. occidentalis*.

Figura 3.- Distribución de los saurios del género *Uromastix* en la región occidental del Sahara. Triángulos: *U. acanthinura wernerii*; puntos blancos: *U. flavifasciata flavifasciata*; puntos negros: *U. f. obscura*; cuadrados: *U. cf. maliensis*; estrella: *U. occidentalis*

strain fits the diagnosis of *Uromastix acanthinura flavifasciata* given by MERTENS (1962) (cf. Table I). This taxon is distributed throughout all Western Sahara, south to around Awserd and Agüenit; it is also found in the region of Tindouf (far west of Algeria), in the Zemmour of Mauritania (GRENOT, 1974; obs pers.), and according BÖHME (1978) and Th. WILMS (Com. pers.), in the Mauritanian region of Atar. Its northern limits are near the southern foothills of djebel Ouarkiz.; In the lower wadi Draâ valley, located immediately north of the Ouarkiz range, only *U. a. wernerii* is found represented by orange, green and mixed green and orange forms. We do not know of any morphologically intermediate specimens between *Uromastix a. wernerii* and *U. a. flavifasciata*. Djebel Ouarkiz constitutes a sizeable barrier to exchanges between populations from south Morocco and from Western Sahara. Besides the case of these Spiny-tailed agamas, this barrier is a decisive feature in the separation of *Acanthodactylus dumerili* (in the north) from *A.*



Figure 4.- a: *Uromastix occidentalis* (Holotype) from Aagtel Agmumuit - Western Sahara (Photo. José A. Mateo). b: *Uromastix occidentalis* (Paratype) from Aagtel Agmumuit - Western Sahara (Photo. José A. Mateo). c: *Uromastix flavifasciata obscura* (Holotype) from Zoug - Western Sahara (Photo. José A. Mateo).

Figura 4.- a: *Uromastix occidentalis* (Holotipo) procedente de Aagtel Agmumuit (Fotografía José A. Mateo). b: *Uromastix occidentalis* (Paratipo) procedente de Aagtel Agmumuit (Fotografía José A. Mateo). c: *Uromastix flavifasciata obscura* (Holotipo) procedente de Zug -Sahara Occidental (Fotografía José A. Mateo).

aureus (in the south), as well as between *Sphenops boulengeri* (in the north) and *S. sphenopsiformis* (in the south) (BONS & GENIEZ, 1996). In the Ougarta mountains (Algeria) GRENOT (1974) observed a striped specimen reminiscent of the form *flavifasciata*

(cf. plate II, photo «d» in GRENOT, 1974) but differing on account of its orange background colour and less contrasted transversal stripes.

In the most southerly quarter of Western Sahara, starting in the Awserd region and, still further south, in the Tiris (Figure 3), there occurs another form of Spiny-tailed agama which replaces the form *flavifasciata* from which it differs due to its overall black colouring even in active animals, the absence of light-coloured transversal stripes (R. SORIGUER, pers. com.; M. GENIEZ, pers. com.; pers. obs.) (Figure 4b). It greatly resembles *flavifasciata*, however, due to its large size (max. SLV: 275 mm), a large number of ventral scales (up to 116 transversal rows counted from the gular fold to the inguinal fold), which also means a longer body than *U. acanthinura*, and a larger number of rows of subcaudal scales (cf. Figure 5 and Table 1). In the Awserd region, the contact area between the *flavifasciata* strain and the black strain, mixed populations occur containing striped and entirely black specimens are present (Figure 6). The existence of the striped *flavifasciata* strain in the Mauritanian region of Atar (BÖHME, 1978; TH. WILMS com. pers.) would seem to indicate that this strain is constantly present from the Zemmour to the Atar region and the black strain is restricted to the Southern region of the Western Sahara.

The southern limit of the genus *Uromastix* in the west of the Sahara is in the Adrar Atar, Mauritania, (Figure 3). The four specimens we examined differ from the form *flavifasciata* due to the absence of striped colour pattern (Figure 7b). They differ from the *flavifasciata* and from the black strains on account of their smaller size (cf. Table I), a proportionally less elongated body, a larger number of scale rows between the eye and the supralabials, and smaller, blunter head scales. They are similar in their overall high number of scales (DORS, VENL, SUBC, cf. Table I). Their colour pattern is only slightly contrasted, with diffused blackish and yellowish hues; the underside and, in some individuals, the upperside of the fingers are pale yellow, thus contrasting with the blackish forelimbs. Their biometric characters and their colour pattern would appear to relate them to *Uromastix maliensis* (Figure 7a), known from Mali and southern Algeria, i.e. around one thousand kilometers distant from the Adrar Atar. On one of these animals, however, darker barely visible transversal

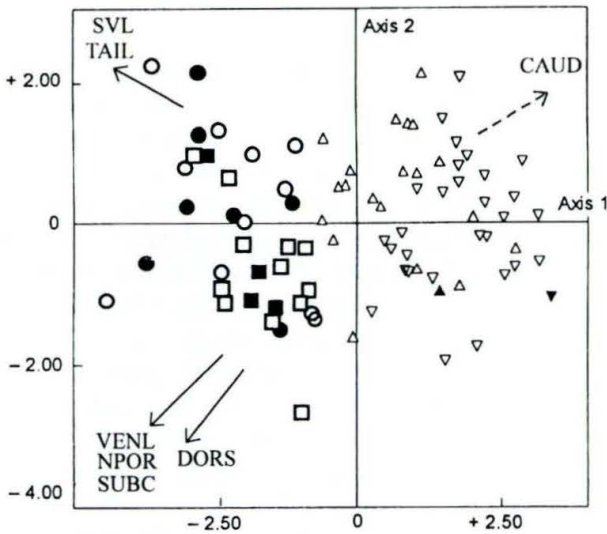


Figure 5.- Principal component analysis for morphological differences between *Uromastix acanthinura* and *U. flavifasciata*. Empty circles and squares: *U. f. flavifasciata* males and females respectively; black circles and squares: *U. f. obscura* males and females; empty upturned triangles and triangles: *U. acanthinura weneri* males and females; black upturned triangles and triangles: *U. a. acanthinura*. SVL: snout-vent length; TAIL: tail length; DORS: number of longitudinal scale rows counted at midbody; VENL: number of ventral scale rows counted from the gular fold to the inguinal fold; CAUD: number of scale verticillae on the upper tail; SUBC: number of transversal scale rows on underside of tail; NPOR: total number of pre-anal and femoral pores.

Figura 5.- Representación sobre los ejes 1 y 2 de un análisis de componentes principales (PCA) entre *Uromastix acanthinura* y *U. flavifasciata*. Círculos y cuadrados vacíos: *U. f. flavifasciata* machos y hembras, respectivamente; círculos y cuadrados negros: *U. f. obscura* machos y hembras; triángulos y triángulos invertidos vacíos: *U. a. weneri* machos y hembras; triángulos y triángulos invertidos negros: *U. a. acanthinura*, machos y hembras; SVL: longitud cabeza-cuerpo; TAIL: longitud de la cola; DORS: número de escamas dorsales en la región media corporal; VENL: número de series transversales de escamas ventrales; CAUD: número de verticilos en la zona superior de la cola; SUBC: número de series transversales de escamas subcaudales; NPOR: número de poros preanales y femorales.

stripes can be perceived on the back, which is inconsistent with the diagnosis given by JOGER & LAMBERT (1996). The discovery, some 20,000 years ago (see WILLIAMS, 1984), of the large ergs in the south of the Sahara could explain an allopatric type of distribution for *U. maliensis*. But the small number of specimens examined from the Atar region does not allow us to pronounce with certainty on their systematic status. Further research is ne-

cessary to look for possible morphologically intermediate specimens between the *flavifasciata* strain and the animals from the Adrar Atar. Nevertheless, the confirmation of the presence of *flavifasciata* in this region (cf. BÖHME, 1978) would support the idea that the two species may concur in Mauritania. Lastly, we indicate that an examination of photographic documents (E. MAHÉ, pers. com.) (Figure 2d) suggests the occurrence in the Adrar Souttoug (south of Western Sahara, cf. map I) of Spiny-tailed agamas similar to those from the Adrar Atar.

We have seen that the *flavifasciata* strain, as described by MERTENS (1962), does not present any morphological intergradation with *Uromastix acanthinura weneri* on the northern fringes of its range. On the other hand, in the south of the striped strain's range mixed population occur (striped and black strains). Even further south, i.e. south of Aswerd, in the Adrar Souttoug, at Zoug and Tichla, only black individuals are found. Finally, in the Adrar Atar, Mauritania, there exist animals whose morphology recalls that of *U. maliensis*. The latter are separated from the black strain of southern Western Sahara by the Aze-fâl ergs. These biogeographical reasons lead us to consider the striped and the black Spiny-tailed agamas to be a distinct species, itself divided into two parapatric subspecies. We suggest the following new combinations:

Uromastix flavifasciata Mertens, 1962
comb. nat. nov.

comprising two *subspecies*:

Uromastix flavifasciata flavifasciata
Mertens, 1962

and

Uromastix flavifasciata obscura subsp. nov.

Holotype- DB.ULPGC-7 (Fig. 4c), an adult male from Gor el Carrashit (Western Sahara) (21°23'N/14°27'W), collected by M. Hasi, June 10th 1995 and deposited in the collection of the Department of Biology of the University of Las Palmas de Gran Canaria (Las Palmas, Spain).

Paratypes: DB.ULPGC- 10, an adult male from Zoug (21°34'/14°10'W)(SVL: 232 mm;



Figure 6.- Mixed population of *Uromastix flavifasciata* from 10 km after Auserd in the direction of Tichla (Western Sahara). The striped specimens belong to the nominal form and the black ones to the form *obscura* (photo R. Soriguer).

Figura 6.- Población mezclada de *U. flavifasciata* procedente de un punto situado a 10 km de Auserd en dirección a Tichla (Sahara Occidental). Los individuos rayados presentan las características de la subespecie nominal, mientras que los lagartos negros presentan las de *U. f. obscura* (fotografía R. Soriguer).

TAIL: 148 mm - 63.8%; DORS: 180; VENL: 112; CAUD: 21; SUBC: 48; NPOR: 30), and DB.ULPGC-11, an adult female from Gor el Garrashit (SVL: 212 mm; TAIL: 130 mm - 61.3%; DORS: 181; VENTL: 99; CAUD: 21;

SUBC: 45; NPOR: 27). Collected by M. Hasi in June 1995, and deposited in the collection of the Department of Biology (University of Las Palmas de Gran Canaria).

Diagnosis- Agamid of the genus *Uromastix* presenting the following characters: relatively large size; proportionally long body; large number of transversal ventral scale rows (up to 116); average-sized flattened tail (54 to 71 % of snout-vent length), a fairly low number of tail verticillae (18 to 21) and a fairly large number of sub-caudal scale rows (42 to 52);

presence of pre-anal and femoral pores (24 to 34 overall); presence on upper thighs of adjacent spiny enlarged scales; absence of small scales interposed between the caudal verticillae, of a pre-anal plate, and of tubercles on the flanks and back; uniformly black overall colouring; the underside is uniformly dark grey.

Etymology- The name *obscura* is proposed because of the particularly dark colouring of all the animals examined, whether alive or dead, active or at rest.

Description of holotype- Adult male measuring 194 mm SVL; 185 scales round body; 97 ventral scales between gular fold and inguinal fold; 5 rows of subocular scales; short tail (62.37% of SVL), flattened, not tapering

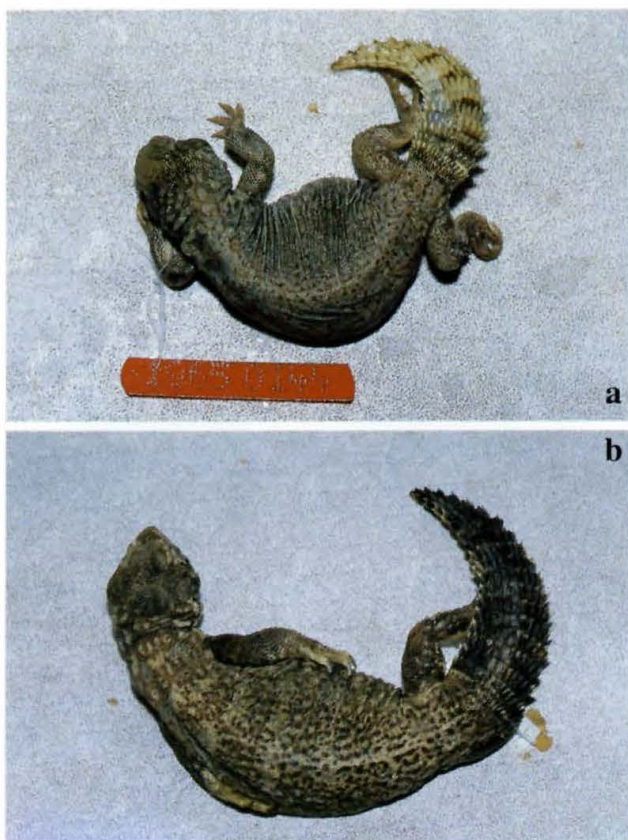


Figure 7.- a: *Uromastyx* cf. *maliensis*, from Adrar Atar (Mauretania)(photo Ph. Geniez in MNHN-Paris); b: Paratype of *Uromastyx maliensis*, from Taoudrart (West side of Hoggar Mountains - Algeria) (photo Ph. Geniez in MNHN-Paris).

Figura 7.- a: *Uromastyx* cf. *maliensis*, individuo del Adrar Atar (Mauritania) (Fotografía P. Geniez en MNHN-Paris); b: Paratipo de *Uromastyx maliensis* procedente de Taoudrart (contrafuertes occidentales del macizo del Hoggar) (Fotografía P. Geniez en MNHN-Paris).

to a point at the end, and possessing 21 verticillae of scales; 46 transversal rows of subcaudal scales; no small scales between verticillae; 28 femoral and preanal pores (14 + 14). Absence of tubercles on the flanks and on the back. The fore-edge of the ear possesses four spiny scales; the back, the tail and the ventral side are uniformly black.

2- The giant Spiny-tailed agama of Adrar Souttouf.- The second group of Spiny-tailed agamas from Western Sahara is represented by a large sized species, which to our knowledge has not been described. We propose the following description:

Uromastyx occidentalis sp. nov.

Holotype- DB.ULPGC-5 (Fig. 4a), an adult

male from Aagtel Agmumuit, between Yeloua and Mades (Adrar Souttouf, Western Sahara) [21°52'N, 15°31'W] (Fig. 3), collected by M. Hasi June 25th 1995 and deposited in the collection of the Department of Biology- University of Las Palmas de Gran Canaria. Las Palmas de Gran Canaria (Spain).

Paratype- E.B.D.29495 (Fig. 4b), a juvenile from the same location as the holotype, also collected by M. Hasi on June 25th 1995 and conserved in the collection of the Estación Biológica de Doñana (Seville, Spain).

Diagnosis- Agamid of the genus *Uromastyx* presenting the following characters: large size; head proportionally very small; large number of transversal rows of ventral scales (121-122) and round the body (297-301); flattened and relatively long tail (*circa* 75% of snout-vent length in adults) possessing a fairly large number of scaly verticillae (23); several transversal rows of subcaudal scales per verticilla; 7 rows of sub-ocular scales; 6 large blunt scales on the fore-edge of the ear orifice; presence on upper thighs of tiny scales and spiny tubercles well separated from each other; absence of small scales inserted between the tail verticillae, of tubercles on flanks, of pre-anal plate and of pre-anal and femoral pores; overall colouring of adults dark reddish brown; the young are yellowish brown with scattered darker spots and faint vermiculation.

Etymology- The name *occidentalis* is proposed because of the region where the animals occur (Western Sahara) and more especially because of the geographic location of its range which is the most westerly of the genus *Uromastyx*.

Description of holotype- Adult male (well developed testicles and epididymus on the examined specimen), measuring 308 mm SVL and 228 mm tail length. Head proportionally very small (67 mm, i.e. 22 % of snout-vent length). 297 scales round body, 122 ventral scales between gular fold and inguinal fold, 7 rows of sub-ocular scales; fairly long tail (74 % of snout-vent length) horizontally flattened, not tapering to a point at the end, possessing 23 verticillae of relatively blunt scales; 56 transversal rows of sub-caudal scales; no small scales inserted between the verticillae.

Absence of pre-anal and femoral pores, as of tubercles on the flanks and on the back. The upper side of thighs have regularly arranged, well separated spiny tubercles inserted between very tiny scales. The fore-edge of the ear possesses 6 large scales with a relatively rounded profile. Acrodont teeth on the back of the maxilla and dentary; fore region of jaws without teeth, forming a bony beak. The animal is uniformly dark reddish brown, including on the ventral face. Only the rear of the back, the thighs and the base of the tail are a slightly lighter colour.

Description of paratype-juvenile measuring 70 mm snout-vent length and 43.5 mm tail length. 301 scales round body, 121 ventral scales between gular fold and inguinal fold, 7 rows of sub-ocular scales; relatively short tail (62.1 % of body length), ventrally flattened, not tapering to a point at its end, possessing 23 verticillae of relatively blunt scales; 53 transversal rows of subcaudal scales; no small scales inserted between the verticillae. Absence of pre-anal and femoral pores, as well as of tubercles on flanks and back. Upper thighs have regularly arranged, well separated spiny tubercles inserted between very tiny scales. The fore-edge of the ear possesses 6 large scales with a relatively rounded profile. Teeth present on the entire maxilla and dentary. The animal is yellowish brown with scattered darker spots on the back and indistinct irregularly patterned vermiculation.

3) Comparison of *Uromastix occidentalis* sp. nov. with other morphologically similar members of the genus or with specimens whose habitat is the same region.

The differences between *Uromastix occidentalis* sp. nov. and other *Uromastix* genus members, whose names are hereinafter listed, are the following:

-from *Uromastix maliensis* Joger & Lambert, 1996 (south Algeria, Mali), *U. a. acanthinura* Bell, 1825 (Algerian, Tunisian and Lybian Sahara), *U. a. weneri* L. Müller, 1922 (west Algeria and Morocco), *U. a. dispar* Heyden, 1827 (south-eastern fourth of the Sahara) and *U. flavifasciata* (Western Sahara, Hamada de Tindouf in Algeria, and the Mauritanian Zemmour), by more numerous body scales (DORS and VENTL), a longer tail with a larger number of scaly verticillae, the presence on the upper thighs of more regularly

arranged separated spiny tubercles, its larger overall size and the absence of pre-anal and femoral pores.

-from *Uromastix acanthinura geyri* L. Müller, 1922 (south Algeria, Mali), by more numerous body scales, a slightly shorter tail, the absence of tubercles on the flanks, more developed scales on the fore edge of the ear orifice, the presence on the upper thighs of more regularly arranged and separated spiny tubercles, its much larger overall size and the absence of pre-anal and femoral pores.

-from *Uromastix aegyptia aegyptia* (Forskål, 1775) (north Egypt east of the Nile, Sinai, Palestine) by slightly fewer body scales, the absence of tubercles on the flanks, the absence of pre-anal and femoral pores (on occasions, the females of this subspecies do not have these pores or possess them in very small numbers; TH. WILMS, com. pers., and own data) and different colouring.

-from *Uromastix aegyptia microlepis* (Blanford 1874) (Arabian peninsula, Irak, extreme south-west Iran) by the absence of pre-anal and femoral pores (as in the previous case, some females of this sub-species also lack preanal or femoral pores or when such are present, they are reduced in size; TH. WILMS, com. pers.) and different colouring.

Consequently, *Uromastix occidentalis* n. sp. does not resemble any previously described taxon. However, as the following comparative analysis demonstrates, it seems to be related, at least morphologically, to *U. aegyptia*, in particular to the subspecies *microlepis*, the areas of distribution of these are separated, however, by over 5000 km of desert.

CONCLUSION

We have seen that Spiny-tailed agamas from the west of the Sahara can be divided into two distinct groups. The first group comprises Spiny-tailed agamas of the group *Uromastix acanthinura* (sensus JOGER, 1986) and is represented in this region by four taxons:

-*Uromastix acanthinura weneri*, in Morocco

-*U. flavifasciata flavifasciata*, in the northern three-quarters of Western Sahara, the Hamada de Tindouf in Algeria, and Zemmour and Atar regions in Mauritania.

-*Uromastix flavifasciata obscura* in the southern fourth of Western Sahara

-*Uromastix* sp. in the Adrar Atar of Mau-

ritania and probably in the Adrar Souttoug in Western Sahara; this taxon may be conspecific with *U. maliensis*.

In its complexity this distribution pattern is comparable with that observed in the Central Saharan zone, i.e. between the High Plateaus of Algeria and Mali, through central Sahara, the Hoggar and Tassili-n-Ajjer mountains. But, unlike in the western area, there is a gradual morphological transition from north to south between *U. a. acanthinura* and *U. a. geyri* giving the latter taxon a subspecific status (WILMS & BÖHME, 1993). *U. a. geyri* is itself sympatric with *U. maliensis* and could be considered the ultimate stage of a character displacement resulting from contact with *U. maliensis*.

The second group is represented by the new species, *Uromastix occidentalis*, a Spiny-tailed agama which is morphologically similar to *Uromastix* of the group *aegyptia* (cf. JOGER, 1986). If a phylogenic relationship could be demonstrated between *U. occidentalis* and *U. aegyptia*, it would then be particularly important to pursue research in the central Sahara in order to try and discover new populations of *Uromastix* of the same group. Although *U. aegyptia* is not known west of the Nile (around 5,000 km between the range of *U. aegyptia* and that of *U. occidentalis*), it should not be forgotten that several authors have reported this species in north central Sahara. TRISTRAM (1860, apend. VI, p. 406) appears to have been the first person to mention *Uromastix spinipes* (= *U. aegyptia*) west of the Nile in the Sahara. He refers to its presence in « the desert of south Algeria » and we know that on this occasion TRISTRAM did not venture further south than the latitude of Touggourt. This mention was quoted again by STRAUCH (1862). LALLEMANT (1886) included *U. spinipes* in his catalogue of the Reptiles of Algeria; according to this author, it « inhabits the southern desert. A fairly rare species ». Furthermore, OLIVIER (1894) says he found it in Algeria « in hills, north of Biskra, in the neighbourhood of the wadi »; the description he gives coincides perfectly with the diagnosis of *U. aegyptia*. This mention is quoted again by DOUMERGUE (1901) while BOULENGER (1891) considered its existence in «Barbary» as unlikely. What should we think of the comments of TRISTRAM (1860), and more especially of OLIVIER (1894) concerning regions where *U. a. geyri*, the only taxon these

authors could have confused with *U. aegyptia*, is unknown? *Uromastix aegyptia* was reported from the south of Cyrenaica (Lybia) by LE BERRE (1989) while GAUTHIER (1967) observed a very large specimen of *Uromastix* of a « Prussian blue » colour in rocky ground near Béni Abbès in the west of Algeria. The confirmation of the existence of *U. aegyptia* in central Sahara, supported by a demonstration that *U. occidentalis* and *U. aegyptia* are two phylogenetically close species, would suggest the existence of a *U. aegyptia* group comprising *U. a. aegyptia*, *U. a. microlepis* and *U. occidentalis*. This group could then have a relictual existence throughout the Sahara where the dominant species is *U. acanthinura*. This type of pattern, with oriental species persisting here and there in the Sahara is known for other species, for example, *Chalcides ocellatus* (Sauria, Scincidae), the *Trapelus savignyi* group (Sauria, Agamidae), the *Tropicolotes steudneri/nattereri* group (Sauria, Gekkonidae), *Leptotyphlops macrorhynchus* (Serpentes, Leptotyphlopidae), the *Telescopus dhara* group (Serpentes, Colubridae) and *Coluber rhodorachis* (Serpentes, Colubridae). Similar distribution patterns can be observed in Sahelian related species such as lizards of the genus *Philochortus* (Sauria, Lacertidae), *Scincopus fasciatus* (Sauria, Scincidae) *Tarentola ehippiata* and *T. annularis* (Sauria, Gekkonidae), or Mediterranean ones such as *Macroprotodon cucullatus* (Serpentes, Colubridae).

Acknowledgements

The authors would like to thank Michel Geniez, Pierre-André Crochet, Stéphane Boissinot, Ramón C. Soriguer and M. Hasi for the data they collected during field trips in Morocco and Western Sahara and which has been incorporated into the present work. They are also grateful to Elizabeth Allberry Guilloson for translating the French manuscript into English.

REFERENCES

- ANGEL, F. & LHOTE, H. (1938): Reptiles et amphibiens du Sahara Central et du Soudan recueillis par M.H. Lhote chargé de Mission du Muséum National d'Histoire Naturelle. *Bull. Com. Et. Hist. Sci. Afr. Occ. Fr.*, 21: 345-384.

- BÖHME, W. (1978): Zur Herpetofaunistik des Senegal. *Bonn. zool. Beitr.*, 29: 360-417.
- BONS, J. & GENIEZ, P. (1996): *Amphibiens et reptiles du Maroc (Sahara Occidental compris)*. Atlas Biogéographique. Asociación Herpetológica Española., Barcelona, 320 pp.
- BOULENGER, G.A. (1891): Catalogue of the reptiles and batrachians of Barbary (Morocco, Algeria and Tunisia) based chiefly upon the notes and collections made in 1880-1884 by M. Fernand Lataste. *Trans. Zool. Soc. London*, 13: 93-164.
- DOUMERGUE, F. (1901): *Essai sur la faune herpétologique de l'Oranie*. Fouque éd., Oran, 404 pp.
- GAUTHIER, R. (1967): Ecologie et éthologie des reptiles du Sahara nord-occidental (région de Béni Abbès). *Bull. Mus. Royal Afr. Centr., Tervuren (Sci. Zool)*, 155: 1-83.
- GRENOT, C. (1974): Polymorphisme chromatique du lézard agamide *Uromastix acanthinurus* Bell dans les populations du Sahara nord-occidental. *Bull. Soc. Zoo. Fr.*, 99: 153-164.
- GRENOT, C. & VERNET, R. (1972): Les reptiles dans l'écosystème au Sahara occidental. *C. R. Soc. Biogéogr. France*. 433: 96-112.
- HOOGMOED, M.S. (1972): Doornstaart-agemen. *Het Aquarium*, 43: 2-7.
- HOOGMOED, M.S. (1974): Echsen aus Nordafrik. Herpetologische Impressionen aus Südmarokko. *Aquariem Mag.*, 8: 304-310.
- JOGER, U. (1986): Phylogenetic analysis of *Uromastix* lizards, based on albumin immunological distances. *Stud. Herp.*, Roček Z. (de.), Prague: 187-191.
- JOGER, U. & LAMBERT, M.R.K. (1996): Analysis of the herpetofauna of the Republic of Mali, I. Annotated inventory, with description of a new *Uromastix* (Sauria: Agamidae). *Journ. Af. Zool.*, 110: 21-51.
- LALLEMANT, C. (1886): *Herpétologie de l'Algérie ou catalogue synoptique et analytique des reptiles et amphibiens de la Colonie*. F. Savy, Paris, 41 p.
- LE BERRE, M. (1989): *Faune du Sahara. I. Poissons-amphibiens-reptiles*. Lechevalier, R. Chabaud, Paris, 332 pp.
- MERTENS, R. (1962): Bemerkungen über *Uromastix acanthinurus* als Rassenkreiss (Reptila, Sauria). *Senck. Biol.*, 43: 425-432.
- MONOD, T. (1958): Majâbat al Koubrâ. Contribution a l'étude de l'"empty quarter" ouest-saharien. *Mém. I.F.A.N.*, 52: 1-407.
- OLIVIER, E. (1894): Herpétologie algérienne ou Catalogue raisonné des reptiles et des batraciens observés jusqu'à ce jour en Algérie. *Mem. Soc. Zool. Fr.*, 7: 1-36.
- PASTEUR, G. & BONS, J. (1962): Catalogue des reptiles actuels du Maroc. Révision des formes d'Afrique, d'Europe et d'Asie. *Trav. Inst. Sci. Chér. Maroc, ser. Zool.*, 21: 1-132.
- SCHLEICH, H.H., KÄSTLE, W. & KA-BISCH, K. (1996): *Amphibians and Reptiles of North Africa*. Koeltz Scientific Books, Koenigstein, 630 pp.
- SCHOUTEN, J.R. & THEVENOT, M. (1978): Terrestrial fauna. *Tarfaya Oil Project Environmental Study*, Liverpool University; Schell de. 72-78.
- STRAUCH, A. (1862): Essai d'une herpétologie de l'Algérie. *Mém. Acad. Impériale Sci. St. Pétersbourg*, VII° sér., 4: 1-86.
- TRISTRAM, H.B. (1860): *The Great Sahara wandering south of the Atlas Mountains*. John Murray Pub., London. 435 p.
- VALVERDE, J.A. (1957): *Aves del Sahara Español. Estudio Ecológico del Desierto*. Inst. Est. Africanos, Madrid. 487 p.
- WILLIAMS, M. (1984): Geology. In J.L. Cloudley-Thompson (Ed.), *Sahara Desert*, pp: 31-39. Pergamon Press, Oxford.
- WILMS, T. (1995): *Dornschwanzagamen. Lebensweise, Pflege und Zucht*. Herpeton-Verlag, Offenbach, 130 pp.
- WILMS, T. & BÖHME, W. (1993): Über die intraspezifische Systematik von *Uromastix acanthinurus* Bell 1825 (Sauria; Uromastycinae). *Zusammenfassungen D.G.H.T. Jahrestagung 1993. Idar-Oberstein*: 8-9.

Recibido: 07/04/98

Aceptado: 03/11/98