An update about the genus *Uromastyx* in Morocco: distribution limits and phenotypic variability

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Fecha de aceptación: 20 de febrero de 2025.
Key words: contact areas, hybridization, spiny-tailed, intermediate, Sahara.

Resumen: La información publicada sobre el género *Uromastyx* en Marruecos es claramente incompleta. En el presente artículo se actualiza la información sobre las tres especies descritas en Marruecos. *U. occidentalis* sigue sin ser encontrado en la naturaleza, lo que aumenta la incertidumbre sobre esta especie. *U. nigriventris* no está aislado como se podía suponer y existen varias zonas potenciales de contacto con *U. dispar*.

The genus *Uromastyx* Merrem, 1820, belongs to the family Agamidae and the subfamily Uromastycinae. It comprises 15 species distributed across Africa and the Middle East and is the sister genus of Saara, which includes three species native to the Irano-Turanian region (Sindaco & Jeremcenko, 2008; Wilms *et al.*, 2009; Uetz *et al.*, 2024). In Morocco (including Western Sahara), three species of *Uromastyx* are currently recognized: *Uromastyx nigriventris* Rothschild & Hartert, 1912, *U. dispar* Heyden, 1827 and *U. occidentalis* Mateo, Geniez, Lopez-Jurado & Bons, 1999 (Martínez del Mármol *et al.*, 2019; Bouazza *et al.*, 2021).

Despite ongoing interest in the evolutionary biology and ecology of *Uromastyx*, some gaps remain in our understanding of the genus in Morocco. For instance, the phylogenetic relationships among the recognized species remain partially unresolved (Harris *et al.*, 2007; Wilms *et al.*, 2009; Tamar *et al.*, 2018). Furthermore, while some morphological traits have been described, the variability of color patterns and coloration among populations, especially in transitional zones, has been understudied. This variability may conceal significant adaptive traits and evolutionary processes.

This study aims to provide an updated overview of *Uromastyx* species in Morocco. We first provide comments on the status of *U. occidentalis*, including the origin of its type specimens and we provide an overview of the *U. acanthinura* group to contextualize these species within a broader taxonomic framework. Subsequently, we explore the distribution limits and present new morphological data from specimens collected in the potential contact zone between *Uromastyx dispar* and *U. nigriventris* in southern Morocco, spanning the region from Merzouga to Smara.

Uromastyx occidentalis was described based on two specimens deposited by M. Hasi, a truck driver of the "Polisario" (Mateo Miras, personal communication.), in the collection

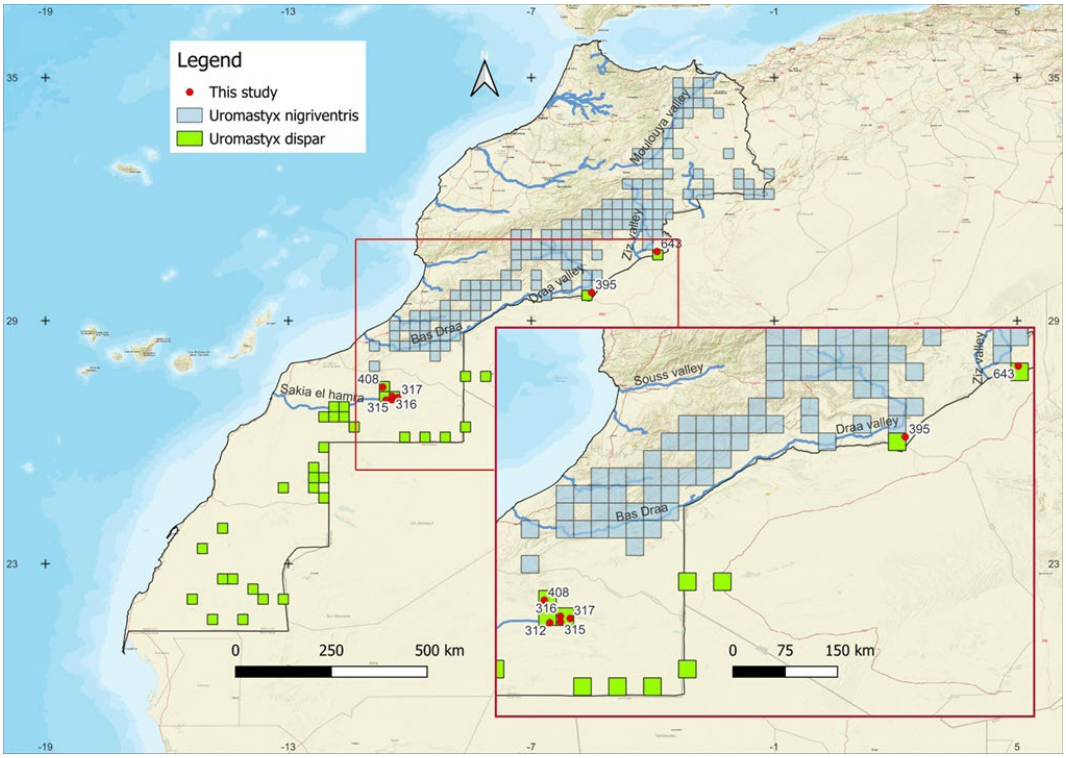

Figure 1: Updated distribution map (25x25 UTM grid) of *Uromastyx nigriventris* (blue) and *U. dispar* (green) in Morocco, based on color variation (Bons & Geniez, 1996; Martínez del Mármol et al., 2019; this study). Red circles indicate specimens in the potential contact zone. Numbers show the code in the registry of the first author of the present note (see Figure 2).

Figura 1: Mapa de distribución actualizado (cuadrícula UTM 25x25) de *Uromastyx nigriventris* (azul) y *U. dispar* (verde) en Marruecos, basado en la variación de color (Bons & Geniez, 1996; Martínez del Mármol et al., 2019; este estudio). Los círculos rojos indican especímenes en la posible zona de contacto. Los números muestran el código en el registro del primer autor de la presente nota (ver Figura 2).

of the Department of Biology of the University of Las Palmas de Gran Canaria. The paratype was donated to the Doñana Biological Station (Seville, Spain), the two specimens were apparently found in Adrar Souttouf between Aagtel Agmumuit and Mades (M. Hasi in Mateo *et al.*, 1998). However, over the past 20 years, several expeditions have been conducted in this specific area, finding several other agamid species of smaller size (*Agama boueti*, *Uromastyx dispar*), but *U. occidentalis* was never observed (Mediani & Chevalier, 2016; F. Martínez Freiría, personal communication; J.A. Mateo Miras, personal communication; A. Qninba, personal communication). This species is notable for its size, which adults can grow up over 50 cm of total length (Mateo *et al.*, 1998). A phylogenetic analysis including *U. occidentalis* is needed to better understand the origin of these specimens and their relationship to other species within the genus, particularly the morphologically similar *U. aegyptia* (Forskal, 1775). Notably, our research has revealed that the paratype at the Doñana Biological Station appears to be lost, while the holotype is now housed at the Nature Museum of Tenerife (López Jurado, personal communication).

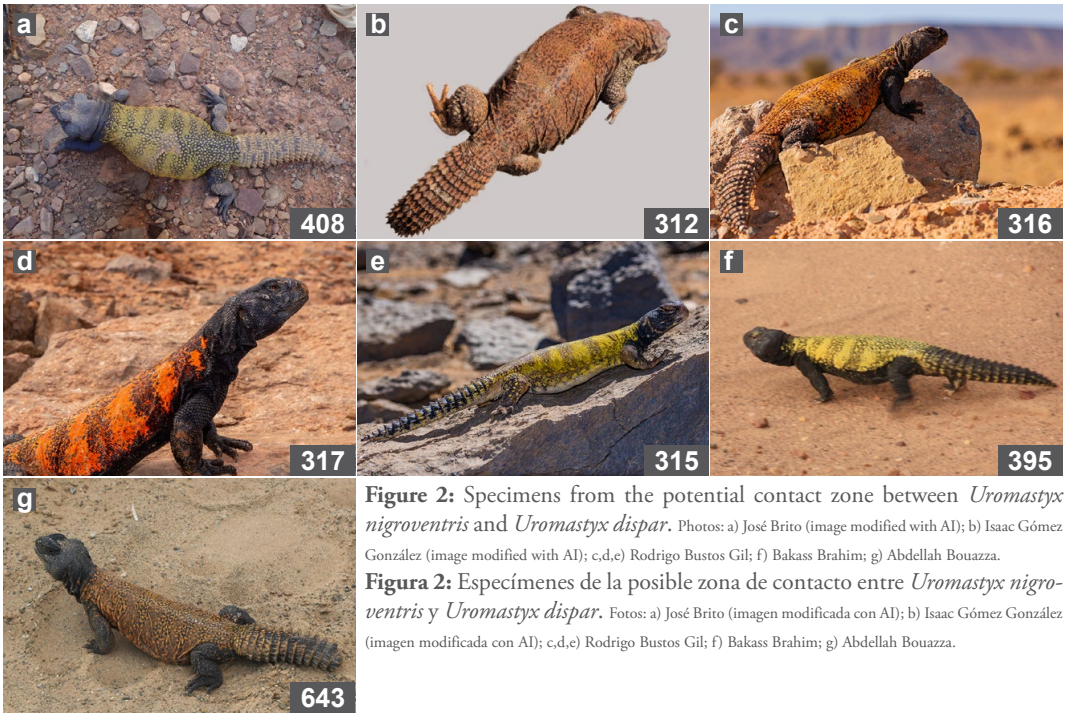

Figure 2: Specimens from the potential contact zone between *Uromastyx nigroventris* and *Uromastyx dispar*. Photos: a) José Brito (image modified with AI); b) Isaac Gómez González (image modified with AI); c,d,e) Rodrigo Bustos Gil; f) Bakass Brahim; g) Abdellah Bouazza.

Figura 2: Especímenes de la posible zona de contacto entre *Uromastyx nigroventris* y *Uromastyx dispar*. Fotos: a) José Brito (imagen modificada con AI); b) Isaac Gómez González (imagen modificada con AI); c,d,e) Rodrigo Bustos Gil; f) Bakass Brahim; g) Abdellah Bouazza.

Uromastyx nigriventris (including its synonyms *U. acanthinurus werneri* Müller, 1922 and *U. acanthinurus* var. *pluriscutata* Fejérváry, 1927; fide Wilms *et al.*, 2009) was historically described as a subspecies of *Uromastyx acanthinura* (Mateo *et al.*, 1999; Wilms & Böhme, 2001). Molecular analysis showed that *U. nigriventris* is a sister taxon of *U. acanthinura* and *U. dispar* (Wilms *et al.*, 2009). Older adult individuals of *U. nigriventris* are characterized by a black venter, which inspired the scientific name "nigri-ventris" and a uniform orange-yellow-greenish coloration on the head and dorsum. Inmature specimens are uniform brown (rarely whitish). Commonly referred to as the Moroccan Dob or Moroccan Spiny-Tailed Lizard (despite its holotype being collected in Algeria), this species has a wide distribution across Morocco (Martínez del Mármol *et al.*, 2019). Its range extends from the Guelmim-Labyar-Tilemsoune areas in the west to Figuig in the east and approaches the Mediterranean Sea in the north by the arid Moulouya valley (Figure 1). The southern limit of *U. nigriventris* was tentatively identified in earlier literature as the Bas Draa-Djebel Ouarkziz region (Wilms *et al.*, 2009). However, subsequent expeditions recorded the species further south (Kane *et al.*, 2019), prompting debate regarding its true southern boundary. Recently, one of the authors (A.B.) recorded its presence approximately 30 km north of Zag (lat. 28.279, long. -9.333). Additionally, an observation on *iNaturalist* showing a picture of a typical adult *U. nigriventris*, placed the species 20 km southwest of MSied (October 16, 2009, X. Rufray, personal communication), which represents the southernmost confirmed record to date.

Uromastyx dispar, commonly known as the banded Dob, is a typical Saharan species with a wide distribution in the Sahara Desert, from Morocco, to Algeria, Mauritania, Sudan, Chad or Mali. In Morocco it has an irregular known distribution, probably because of the danger to

visit areas far of roads and trails due to the areas with mines (Mine Action Review, 2024). The subspecies present in Morocco is only *U. d. flavifasciata* Mertens, 1962 (Martínez del Mármol *et al.*, 2019), considering that *Uromastyx flavifasciata obscura* Mateo *et al.*, 1999 is genetically identical to *U. d. flavifasciata*. Both of them with a low genetic distance to the nominate subspecies *U. dispar dispar* (Wilms *et al.*, 2009). Mateo *et al.* (1998) also reported some specimens of *Uromastyx d. cf. maliensis* north of the Adrar Souttouf, but considering that the distribution of *U. dispar maliensis* Joger & Lambert, 1996 is in Mali and Algeria, this must be a confusion with subadult or juvenile specimens of *U. dispar flavifasciata* that did not show the typical black body coloration with "5–7 wide, clearly defined yellow, white or red dorsal crossbands". Females are sand colored with small black dots and ocelli at their backs (Wilms *et al.*, 1999). In Mauritania, 130 kms northeast of Nouakchott, one of the authors (G.M.M) could observe an adult *Uromastyx* with uniform yellowish color with transverse bands of similar color and several ocelli, that would be according to the denominated ocellata morphotype described in the Atar region in Mauritania (Trape *et al.*, 2012). The habitat at this locality, seems to be more suitable for *U. nigriventris*, and specimens have been found mostly in stony areas like *U. nigriventris* but they can also survive in steppes without stones, using deep holes in the ground (hard substrate, not sand), as refuge.

Like *U. nigriventris*, *U. dispar* is rare or absent in the coastal areas, where the weather during the biggest part of the year is colder than inland. The limits between both species in Morocco remains unclear, partly due to historical difficulties in traveling between Smara and Zag. The northernmost records of *U. dispar* are located a few kilometers north of Smara, in the Echdeira area (Figure 1). Several individuals observed within contact zone displayed a distinctive bright orange coloration on their dorsal surfaces, tail, head, and forelimbs, with faintly visible transverse bars on their dorsum (number 312 in Figure 2). Two specimens with *U. dispar* phenotype were found in Tidri-Mhamid el Ghizlane (number 395 in Figure 2) and Taouz (number 643 in Figure 2) suggesting that probably there are many contact zones between *U. nigriventris* and *U. dispar* in the Moroccan territories. This unusual coloration warrants further investigation, as it may reflect hybridization or an adaptation to local environmental conditions. Conversely, other specimens from Echdeira area displayed color patterns typical of *U. dispar*, which partially overlap with those of *U. nigriventris*, raising questions about the morphological boundaries between these closely related species.

Future expeditions in the area between MSied and Echdeira are recommended to better understand the southern distribution limit of *U. nigriventris*. Additionally, molecular analyses (mitochondrial and nuclear) of specimens from Echdeira, Tidri, and Taouz are crucial to determine whether these areas represent a natural hybridization zone between *U. dispar* and *U. nigriventris*, or if they reveal a new phenotypic variation within *U. dispar flavifasciata* in Morocco, comparable to the *ocellata* morphotype (Trape *et al.*, 2012). It would be also convenient to determine if these areas are ecologically intermediate (Tamar, *et al.*, 2018; Kechnebbou *et al.*, 2020).

Ackowledgments: To P. Wagner and T. Wilms for his revision of the article. To E. Fernández, J.A. Mateo Miras and L.F. López Jurado for the information. To B. Brahim and J. Brito for the permission to use their photos in the article.

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