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To cite this article: Thore Koppetsch & Wolfgang Böhme (2022): On the identity of west Saharan geckos of the *Tarentola ehippiata* complex (Squamata: Phyllodactylidae), with comments on an extreme case of syntopy with their close relative *T. annularis*, African Journal of Herpetology, DOI: [10.1080/21564574.2022.2055652](https://doi.org/10.1080/21564574.2022.2055652)

To link to this article: <https://doi.org/10.1080/21564574.2022.2055652>



Published online: 07 Apr 2022.



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On the identity of west Saharan geckos of the *Tarentola ehippiata* complex (Squamata: Phyllodactylidae), with comments on an extreme case of syntopy with their close relative *T. annularis*

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ABSTRACT

Tarentola geckos have a widespread geographic distribution and occur both in the Palearctic and Afrotropical realms, as well as the Neotropical region. Particularly, across North Africa phenotypically similar and cryptic species can be found, like the west Saharan members of the *T. ehippiata* complex. However, the taxonomic relationships and phylogeographic patterns of these geckos are not fully understood. Here we show that some specimens of *Tarentola* geckos from Mauritania and southern Morocco previously identified as *T. hoggarensis* can actually be assigned to *T. panousei*, a taxon treated as a synonym until now. Because the corresponding type specimen has apparently been lost, we designate a neotype for *T. panousei* referring to a suitable specimen from the type locality. Based on a morphological examination of the neotype and comparative material we provide a detailed redescription of *T. panousei* and evaluation of its diagnostic characters. Moreover, we report on a syntopic occurrence of *T. annularis* and *T. panousei* on an isolated acacia tree in the Western Sahara and the (micro) habitat use of both species.

ARTICLE HISTORY

Received 16 June 2021
Accepted 16 March 2022

ASSOCIATE EDITOR

S Edwards

KEYWORDS

biogeography; ecology; Mauritania; Morocco; systematics; *Tarentola panousei*

Introduction

Among squamates, the gekkotan genus *Tarentola* is biogeographically peculiar, because it is distributed over the borderline between the western Palearctic and the Afrotropical realms and even occurs in the Neotropical region (Joger 1984; Sprackland and Swinney 1998), a pattern that is known for some other geckos (Laurent 1979), but also for a single representative of the predominantly Afro-Arabian *Trachylepis* skinks only (apart from the doubtful status of *T. maculata* and its possibly erroneous type locality in Demerara, Guyana), the island endemic *T. atlantica* (Mausfeld et al. 2002; Carranza and Arnold 2003; Lyra and Vences 2018). Similarly, the three trans-Atlantic *Tarentola* geckos in the Caribbean (Cuba, Bahamas, Jamaica) are doubtlessly old endemics that diverged approximately 23 million years ago from an earlier stage of the Atlantic Ocean and have

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African Journal of Herpetology is co-published by NISC Pty (Ltd) and Informa Limited (trading as Taylor & Francis Group)

nothing to do with anthropogenic translocation (Carranza et al. 2000; Gamble et al. 2011; Vasconcelos et al. 2012). In contrast to *T. atlantica* they are considered to represent a subgenus of their own. A more complex pattern can be found off the West African coast: The Palearctic Canary Islands were colonised twice via long transmarine dispersal, once the eastern islands by the *T. mauritanica* group, then independently the central and western islands by the subgenus *Makariogecko*. In contrast, a single species of *Makariogecko* gave rise to the whole radiation of the Afrotropical Cape Verdian Islands approximately seven million years ago (Carranza et al. 2000), which, however, in contrast to scincids (*Chalcides* (Carranza et al. 2008) and *Chioninia*, respectively (Carranza et al. 2001; Miralles et al. 2011)), do not represent different subfamilies, but even the same subgenus. However, for *Tarentola* remarkable biogeographical patterns are not only to be found on islands, but also across their continental distribution range. Although the Mediterranean *T. mauritanica* group is widespread from northern Italy and southern France southwards to the Morocco-dominated Western Sahara, it is replaced in the south by the *T. annularis/ephippiata* group, which extends from the Western Sahara down to West and Central Africa (Joger 1984; Trape et al. 2012; Carranza et al. 2002; Rato et al. 2012).

Studying this transition between the Mediterranean, western Palearctic, and the Afrotropical biogeographical zones was also the inducement for a three-month mission to the western margin of the Sahara desert conducted by the Zoologisches Forschungsmuseum Alexander Koenig (ZFMK) in Bonn in the winter of 1999/2000. As an exemplary case study, the acquisition of reptile communities along a north-south gradient should shed some light on faunal and landscape history (Böhme et al. 2001), considering the fact that the transition has always been a dynamic oscillating process in geological history.

During this expedition, one night was spent close to a single acacia tree (*Vachellia tortilis* (formerly known as *Acacia raddiana*)) (Figure 1) south of the Mauritanian harbour city of Nouadhibou in a monotonous sandy and nearly treeless desert landscape. The isolated acacia at this site (20°57' N, 16°31' W) was the only tree in a radius of at least 3 km, and when we inspected it after nightfall with torchlights, it turned out to be populated by two *Tarentola* species in relatively high densities: by *T. annularis* on the one hand (Figure 2A) and by a member of the *T. ephippiata* complex on the other (Figure 2B). Syntopic occurrence of both species on acacia trunks has only been briefly mentioned once, by Sow et al. (2015) from the Banc d'Arguin National Park, which extends not far south from Nouadhibou, along the Mauritanian coast. These authors referred to the second species as *T. ephippiata hoggarensis*, pending additional clarification of its taxonomic status. This paper aims to resolve the taxonomic position of this member of the *T. ephippiata* complex, and to discuss the syntopy between it and *T. annularis* at this specific site.

Taxonomic assignment of these west Saharan members of the *T. ephippiata* complex is problematic. According to the distribution maps in Joger (1984), Bons and Geniez (1996), Trape et al. (2012), Colacicco (2015) and Martínez de Mármol et al. (2019), they should belong to the taxon *hoggarensis* Werner, 1937. However, the type locality of *T. hoggarensis*, the south Algerian Hoggar Mountains, is situated approximately 2000km eastwards in the interior of the Sahara. Werner (1937) had described it originally as a subspecies of *Tarentola delalandii*, a species endemic to the Canary Islands, whereas Pasteur (1960) treated it as a species, even a polytypic one, because he regarded the taxon



Figure 1. The isolated *Vachellia tortilis* acacia tree SE of Nouadhibou on which the two closely syntopic *Tarentola* species were found. Photograph by W Böhme

panousei, which he had described the year before (Pasteur 1959) as a subspecies of *T. hoggarensis*.

Joger (1984), in his great taxonomic revision of the genus *Tarentola*, again placed *hoggarensis* as a subspecies of *T. ehippiata* and considered *panousei* as its synonym and some subsequent authors (Bons and Geniez 1996; Colacicco 2015) followed this view. In contrast, Trape et al. (2012) again treated *hoggarensis* as a full species, followed by Martínez de Mármol et al. (2019), but the name *panousei* was no longer mentioned. However, because Joger (1984) had already given hints about some morphological, geographically correlated interpopulational differences within the huge distribution range of *hoggarensis*, the possible validity of *Tarentola (hoggarensis) panousei* again merits some attention. Joger and Bischoff (1989) listed specimens of this complex, which they had collected south of the Lesser Atlas (Icht), not far from the type locality of Pasteur's *panousei*, simply as *T. ehippiata*.

Tarentola ehippiata O'Shaughnessy, 1875 (*sensu stricto*) had been described from 'West Africa', restricted by Joger (1984) to Nigeria. He subsumed the morphological differences between this form and *hoggarensis* and saw evidence for intergrades between both populations from Niger and the Lake Chad area on the one hand; but on the other hand also infrasubspecific differentiation in various populations living in so-called 'favorable regions' ('Gunstregionen') within the Sahara.

The taxon *senegambiae* Joger, 1984, likewise raised to specific rank by Trape et al. (2012), occurs only west of 13° longitude between the 11° and 17° north latitude, therefore extending beyond the Senegal River to a noteworthy degree. It is distinguished from *hoggarensis*, apart from its more southwestern distribution by its markedly bigger size, a higher midbody scale count (99–125 vs 68–98), and a higher interorbital scale count (14–18 vs 10–14) (Joger 1984; Trape et al. 2012).



Figure 2. A: *Tarentola annularis* inhabiting the acacia tree of [Figure 1](#). B: Second, syntopic *Tarentola* species on the same tree assigned here to *T. panousei*. Photographs by W Böhme

Materials and methods

Morphological analysis

To evaluate the possible distinctness and validity of Pasteur's taxon *panousei*, we performed a morphological analysis of 24 *T. hoggarensis* (*sensu lato*) specimens from the collection of the Zoologisches Forschungsmuseum A. Koenig (ZFMK), Bonn (see Appendix I: Material examined). The characters were partially selected and modified, based on

previous taxonomic studies of *Tarentola* by Pasteur (1960), Joger (1984) and Vasconcelos et al. (2012).

Scale counts were made using a stereomicroscope, and morphological measurements were taken with a Vernier calliper to the nearest 0.1 mm. For all specimens we examined the sex and the following 25 characters and six ratios were determined: snout-vent length (SVL); tail length (TaL, measured only in specimens with complete original tails); total length (TL, as the sum of SVL and TaL); trunk length (TrL, from the posterior end of forelimb insertion to anterior end of hind limb insertion); tail width (TW, at the widest point of tail); head width (HW, widest part of head, usually at the temple); head height (HH, from the base of the maxilla to the top of head); nostril-eye distance (NED, posterior margin of nostril to anterior edge of eye); snout-eye distance (SED, tip of snout anterior margin of eye); ear-eye distance (EED, anterior margin of ear to posterior margin of eye); number of supralabial scales (SLS, counted from rostral to posterior end of mouth cleft); number of non-divided lamellae under first hind toe (Lam1); number of undivided lamellae under fourth hind toe (Lam4); number of transverse dorsal tubercles (Trow, counted paramedially); gular scales (GS, from mental to gular fold); number of interorbital scales (IOS); shape of dorsal tubercles (DTshape): dorsal tubercles arranged in longitudinal rows, clearly distinct (D) or indistinct (ID) from neighbouring dorsal scales; supranasal scales (SNcontact) in contact (C) or separated (S); shape of internasal (IN shape) similar in size as supranasals (L) or smaller (S); shape of ear opening (Eoserr) anteriorly serrated (Serr) or smooth (Sm); contact between nostril and rostral (NRcontact) pointy (O) or broad (B); shape of lamellae at the base of 4th toe (Lbshape) replaced by scale row (R) or uniform (U); supraocular integument (SOIshape) soft (S) or ossified (O); shape of postocular stripe (POstripe) reaching axilla (A) or elbow (E). The colour pattern of each individual was carefully recorded.

Principal component analysis of the morphological data

A principal component analysis (PCA) of the above listed characters was conducted using the Ade4 package (Dray and Dufour 2007) in R (R Development Core Team 2012). Tal, TL, and ratios were excluded from the PCA, because of the presence of incomplete tails in many specimens. One specimen (ZMFK 84913) was excluded, because of its poor state of preservation that allowed no clear identification of some categorical characters. To control for the effect of body size, continuous variables were regressed on SVL and sex, and the residuals were used in the subsequent PCA. The analysis was performed by using mixed variables. All variables were included in a single PCA, in order to evaluate the meaningfulness of the categorical characters based on Pasteur's original description and compare them with both the quantitative traits used in his original description and additional traits used in the present study. Based on both quantitative and categorical variables, the first two principal components (PCs) are visualised in Figure 3. We applied ANOVAs to PCA results and SVL separately in order to investigate whether the specimens from south-east of Nouadhibou in Mauritania and southern Morocco differ significantly from those of southern Mauritania and Algeria.

Results and discussion

Resurrection of Tarentola panousei based on morphological and statistical analyses

There are diagnostic differences between the three Operational Taxonomic Units (OTUs) classified as *T. hoggarensis* on the one hand and on the other hand, the series from Nouadhibou, plus two specimens from South Morocco used in this analysis (Table 1). Some of them are weaker, but some are strong enough to define Pasteur's (1959) nomen *panousei* as a distinct taxon at the species level.

According to our PCA analysis based on the morphological examination of *Tarentola* specimens from various localities in north-western Africa the first three components explained 30.6%, 13%, 10.6% of the total variation, respectively. The first component was clearly discriminative between the specimens from southern Mauritania and Algeria assigned to *T. hoggarensis* on the one hand, and the other operational taxonomic unit (OUT) (Figure 3). The highest loading for the first component refers to the continuous variable GS, and the highest loadings for the same component referring to categorical variables are DTshape, EOser, POstripe and NRcontact. Based on the first component, the populations from Nouadhibou and South Morocco show a lower number of gular scales than the other OTUs. They also differ by the presence of smooth dorsal tubercles, a serrated ear opening, a postorbital stripe reaching only to the axilla and often a pointy contact of nostril and rostral scales, whereas none or only single of the other OTUs show the presence of these characters. The first axis did not separate different sexes in any of the OTUs. Based on the ANOVA, the two OTUs from Algeria and southern Mauritania were

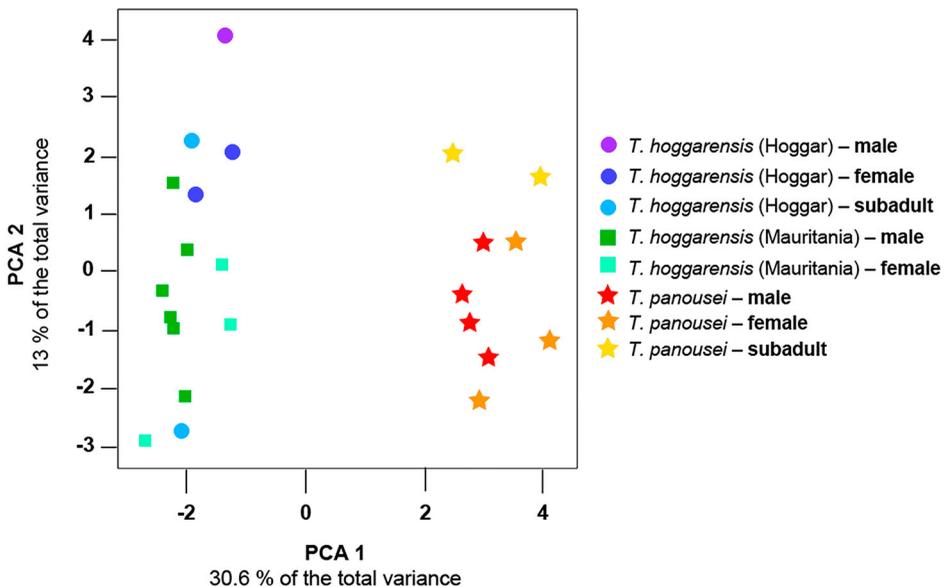


Figure 3. Principal component analysis (PCA) of morphological differences between *Tarentola hoggarensis* from the type locality (Hoggar, Algeria) (male/female/subadult), *T. hoggarensis* from Mauritania (male/female), and *T. panousei* from Nouadhibou and South Morocco (male/female/subadult). Principal component axes refer to the first two principal components

Table 1. Mensural and meristic comparisons between *Tarentola panousei* and *T. hoggarensis* from Mauritania and Hoggar, Algeria. Linear measurements (in mm) and scale counts are given as mean values (Mean) ± standard deviation (SD) and sample size (n), minimum (Min) and maximum (Max) are shown. See Materials and methods for explanation of the single character abbreviations

Species	<i>Tarentola hoggarensis</i> (Mauritania)				<i>Tarentola hoggarensis</i> (Hoggar)				<i>Tarentola panousei</i>			
	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max
	n = 9				n = 5				n = 10			
Country	Mauretania				Hoggar, Algeria				Mauretania			
Sex	Males + Females				Males + Females				Males + Females			
SVL	62.7	6.5	50.7	72.6	49.8	10.3	34.9	58.5	73.1	13.1	47.1	85.4
TaL	59.9	2.8	56.8	64.1	49.3	10.3	39.0	59.2	45.6	1.7	43.6	46.7
TL	122.7	5.2	114.4	126.9	98.0	21.7	73.9	117.3	105.0	17.6	93.8	125.2
TrL	27.7	4.1	21.8	36.0	23.2	3.8	18.2	27.1	33.1	6.0	19.8	37.8
TW	7.0	1.3	5.2	9.3	6.4	1.8	4.6	9.2	10.6	2.2	6.6	12.7
HW	14.2	1.6	11.4	16.3	10.9	1.7	9.0	12.7	15.6	3.3	8.6	18.8
HH	9.4	1.2	7.8	11.5	6.8	1.3	5.3	8.4	10.9	2.5	5.6	13.3
NED	5.6	0.7	4.8	7.1	4.4	0.9	3.5	5.6	6.4	1.3	4.2	7.7
SED	8.1	0.6	7.2	9.3	6.0	0.7	5.1	6.7	8.4	1.5	5.6	9.8
EED	6.7	0.8	5.3	7.6	5.1	1.1	3.7	6.3	7.9	1.8	4.7	9.6
SLS	9	1	8	10	8	1	7	9	8	0	8	9
ILS	8	1	7	9	7	1	6	8	7	0	6	7
Lam1	13	1	12	14	15	1	14	17	14	1	12	15
Lam4	16	1	15	17	16	1	15	18	16	1	14	17
Trow	15	1	15	17	16	1	15	17	15	2	12	17
GS	34	3	29	37	35	2	33	37	29	1	27	31
IOS	14	1	12	15	12	1	11	13	12	1	11	15
DTshape			D				D		ID			
SNcontact			C-S				C				S	
INshape			L-S				S				L	
EOserr			Sm				Sm				Serr	
NRcontact			B				B				P-(B)	
LBshape			U-R				U				U-R	
SOshape			S-O				S-O				S-O	
POstripe			E				E				A	
TaL/SVL	0.96	0.09	0.83	1.03	1.02	0.07	0.97	1.12	0.81	0.20	0.59	0.99
TrL/SVL	0.44	0.03	0.41	0.50	0.47	0.03	0.44	0.52	0.45	0.02	0.42	0.48
HW/SVL	0.23	0.01	0.22	0.24	0.22	0.03	0.21	0.27	0.21	0.01	0.18	0.23
HH/SVL	0.15	0.01	0.12	0.16	0.14	0.02	0.11	0.17	0.15	0.01	0.12	0.16
TW/SVL	0.11	0.02	0.09	0.15	0.13	0.02	0.11	0.16	0.14	0.01	0.13	0.16
SED/SVL	0.13	0.01	0.12	0.14	0.12	0.02	0.11	0.15	0.11	0.01	0.10	0.12

significantly different from the population from southern Morocco and Nouadhibou ($F = 567.4$, p -value $< 2.2e^{-16}$). Likewise, the SVL differed between the two taxa ($F = 45.2$, p -value $< 1.5e^{-6}$).

According to our morphological investigation of both *T. hoggarensis* from southern Mauritania and the type material from Algeria (Hoggar) and individuals of *Tarentola* from locations in southern Morocco and Nouadhibou in western Mauritania, and the significant statistical distinctness of the two groups, we consider the latter OTU as distinct at the species level and assign it to the previously described *T. panousei*.

Neotype designation and redefinition of *Tarentola panousei*

Facing the complicated situation within the *T. ephippiata* complex in general, and within the taxon *hoggarensis* in particular, a clear definition of *T. panousei* based on type material is warranted. However, Pasteur's type specimen, which was published with an informal (private) catalogue no. (BGP 2.54), was stated by its author to be finally deposited in the Muséum d'Histoire Naturelle (MNHN) in Paris, is definitely not there (I Ineich and N Vidal, pers. comm.). The (unlikely) possibility of recovering it in the Natural History Museum (NHMUK in London), because Grandison (1961) had access to the specimen for her revision of West African *Tarentola*, where the specimen was included and figured, was investigated by P Campbell (pers. comm.) and can also be ruled out, because we were additionally told by I Ineich, that Georges Pasteur had informed the former curator in Paris, ER Brygoo, in July 1989, that he had given the specimen to the Institut Scientifique Chérifien in Rabat instead. However, our inquiry at this institution (Prof. M Fekhaoui) was also unsuccessful, and we were assured that the specimen was not in Morocco (S Fahd, pers. comm.). In view of the complex taxonomic situation within the *T. ephippiata* complex in general and in the taxon *hoggarensis* in particular, designation of a neotype for *T. panousei* is warranted. A suitable specimen from within the type locality (Bassin du Draa moyen) was available. Its redefinition, preceded by a short synonymy/chresonymy list, is given below:

***Tarentola panousei* Pasteur, 1959**

Tarentola panousei Pasteur, 1959 ('Hamada du Dra, Bassin du Draa moyen', South Morocco)

Tarentola panousei – Bons, 1959 (see above)

Tarentola ephippiata – Bons, 1959 (Aouinet-Torkoz, South Morocco; citing Pasteur 1959, the same specimen identified later by Bons and Geniez (1996) is listed next to *P. panousei*)

Tarentola hoggarensis panousei – Pasteur, 1960 (see above)

Tarentola hoggarensis panousei – Pasteur and Bons, 1960 (see above)

Tarentola ephippiata – Grandison 1961 (see above)

Tarentola ephippiata – Salvador and Peris, 1976 (Rio de Oro, West Sahara)

Tarentola ephippiata hoggarensis – Joger, 1984 (SW Morocco, West Sahara)

Tarentola ephippiata – Mahé 1985 (Nouadhibou, Mauritania)

Tarentola ephippiata – Joger and Bischoff, 1989 (Icht, Morocco)

Tarentola ephippiata hoggarensis – Bons and Geniez, 1996 (SW of Aouinet-Torkoz, South Morocco)

Tarentola cf. *ephippiata* ('*T. ephippiata*-Gruppe') – Böhme et al. 2001 (south of Nouadhibou, NW Mauritania)

Tarentola hoggarensis – Herrmann and Herrmann 2003 (20 km south of Aounet-Torkoz, South Morocco)

Tarentola ephippiata hoggarensis – Colacicco, 2015 (in part, South Morocco, West Sahara, Mauritania)

Tarentola ephippiata hoggarensis – Sow et al. 2015 (Parc National du Banc d'Arguin, Mauritania)

Tarentola hoggarensis – Martínez del Marmol et al. 2019 (in part, South Morocco, Western Sahara)

Diagnosis: A relatively large (up to 85.4 mm SVL) member of the *Tarentola ephippiata* complex with a lumpy habitus, which is distinguished from its former conspecific *T. hoggarensis* (Figure 5A) by its greater snout-vent length (max. 85 mm vs. 73 mm), a lower number of gular scales (27–31 vs. 29–37), and often a higher tail width/snout-vent length ratio (0.13–0.16 vs. 0.09–0.16). Ear openings small, sometimes concealed, with a serrated (vs. smooth) anterior margin. Dorsal tubercles irregularly arranged (vs. in longitudinal rows) and only indistinctly differentiated from the surrounding scalation. Colour pattern more or less uniformly greyish beige with, in adults, only four indistinct pale dorsal blotches and a postocular dark stripe reaching the axillary region.

T. panousei can be distinguished from *T. ephippiata* by the presence of indistinct and flat dorsal tubercles (vs. slightly keeled), and from *T. senegambiae* by a lower number of interorbital scales (11–15 vs. 14–18) and a shorter snout-vent length (maximum 85 mm vs. 129 mm).

Less marked is a different arrangement of the rostral/nasal contact (less broad and more pointy in some *T. panousei*), the shape of the basal lamellae at the fourth toe (in some *T. panousei* replaced by scale row and not uniform), and the degree of ossification of the supraocular lamina (no clear differences). For additional differences in scalation see Table 2.

Neotype: ZFMK 73503, subadult female from 20 km south of Aouinet-Torkoz, Oued Torkoz, at its mouth into the Oued Dra (28°29.00' N, 09°51.17' W), SW Morocco, collected by Hans-Werner Herrmann, on 4 October 2000 on an *Vachellia tortilis* acacia trunk (Herrmann and Herrmann 2003).

The half-grown female (Figure 4, Table 2) has a total length of (52.3 + 43.6) 95.9 mm and is consequently smaller than the lost holotype, the snout-vent length of which was 67 mm (Pasteur 1960). Broad head (HW 10.7 mm; HH 7.3 mm) with blunt snout (SED/SVL 0.11) (Figures 4C to 4E) (Figures 4C to 4E). Eight supralabial scales, seven infralabial scales. Supranasal scales separated, internasal scale, large with a similar size like the supranasalia. Point contact between nostril and rostral. Supraocular integument smooth, ear opening serrated. Under the first hind toe, thirteen undivided lamellae, and under the fourth hind toe fourteen. Seventeen longitudinal rows of dorsal tubercles, although irregularly arranged and partially indistinct from the surrounding dorsal scalation. Fifteen interorbital scales, thirty scales from mental scale to the gular fold.

In a preservative, brownish ground colouration dorsally, yellowish ventrally. Four white dorsal patches from snout to vent. Postocular stripe reaching axilla.

Table 2. Mensural and meristic measurements of the specimens assigned to *Tarentola panousei* (linear measurements in mm). Absence (–) of characters are indicated in specimens with regenerated or incomplete tails. See Materials and methods for explanation of the single character abbreviations

Collection number	ZFMK 73503 (NEOTYPUS)	ZFMK 79522 SO	ZFMK 79523 SO	ZFMK 79524 SO	ZFMK 79525 SO	ZFMK 79526 SO	ZFMK 79527 SO	ZFMK 79528 SO	ZFMK 79529 SO	ZFMK 84913 no precise locality
Location	Aouinet Torkoz	Nouadhibou	Morocco							
Country	Morocco	Mauritania	Morocco							
Sex	Female (subadult)	Female	Female	Female	Male	Male	Male	Male	Juvenile	Male
SVL	52.3	82.7	82.1	75.0	85.4	82.3	78.7	72.2	47.1	73.1
TaL	43.6	–	–	–	–	–	46.5	–	46.7	–
TL	95.9	–	–	–	–	–	125.2	–	93.8	–
TrL	24.9	36.6	37.3	34.4	37.8	36.5	36.3	34.4	19.8	33.3
TW	6.6	10.7	12.3	11.7	12.3	12.7	11.9	11.5	6.9	9.6
HW	10.7	17.0	17.8	15.3	18.8	18.1	17.0	15.8	8.6	16.7
HH	7.3	13.0	13.0	10.8	13.3	12.1	11.4	11.2	5.6	11.3
NED	4.2	6.9	7.7	6.4	7.7	7.5	7.1	6.6	4.3	5.1
SED	6.0	8.4	9.7	8.3	9.8	9.2	9.5	8.2	5.6	8.9
EED	4.9	9.1	9.4	8.1	9.6	9.3	7.6	8.5	4.7	7.8
SLS	8	9	8	8	8	8	8	8	8	8
ILS	7	7	7	7	7	7	7	6	6	7
Lam1	13	12	13	14	15	14	15	15	14	13
Lam4	14	16	16	16	16	16	16	16	17	17
Trow	17	13	13	15	12	15	15	16	16	15
GS	30	29	29	31	31	27	29	29	28	30
IOS	15	11	13	12	12	12	11	12	12	13
DTshape	ID	ID	ID	ID	ID	ID	ID	ID	ID	ID
SNcontact	S	S	S	S	S	S	S	S	S	?
INshape	L	L	L	L	L	L	L	L	L	?
EOserr	Serr	Serr	Serr	Serr	Serr	Serr	Serr	Serr	Serr	Serr
NRcontact	P	(P)	P	P	P	(B)	P	(B)	P	?
LBshape	U	R–U	U	R	R	R	U	U	R	U
SOshape	S	O	O	O	O	O	O	O	S	O
POstripe	A	A	A	A	A	A	A	A	A	A
TaL/SVL	0.83	–	–	–	–	–	0.59	–	0.99	–
TrL/SVL	0.48	0.44	0.45	0.46	0.44	0.44	0.46	0.48	0.42	0.46
HW/SVL	0.20	0.21	0.22	0.20	0.22	0.22	0.22	0.22	0.18	0.23
HH/SVL	0.14	0.16	0.16	0.14	0.16	0.15	0.14	0.16	0.12	0.15
TW/SVL	0.13	0.13	0.15	0.16	0.14	0.15	0.15	0.16	0.15	0.13
SED/SVL	0.11	0.10	0.12	0.11	0.11	0.11	0.12	0.11	0.12	0.12

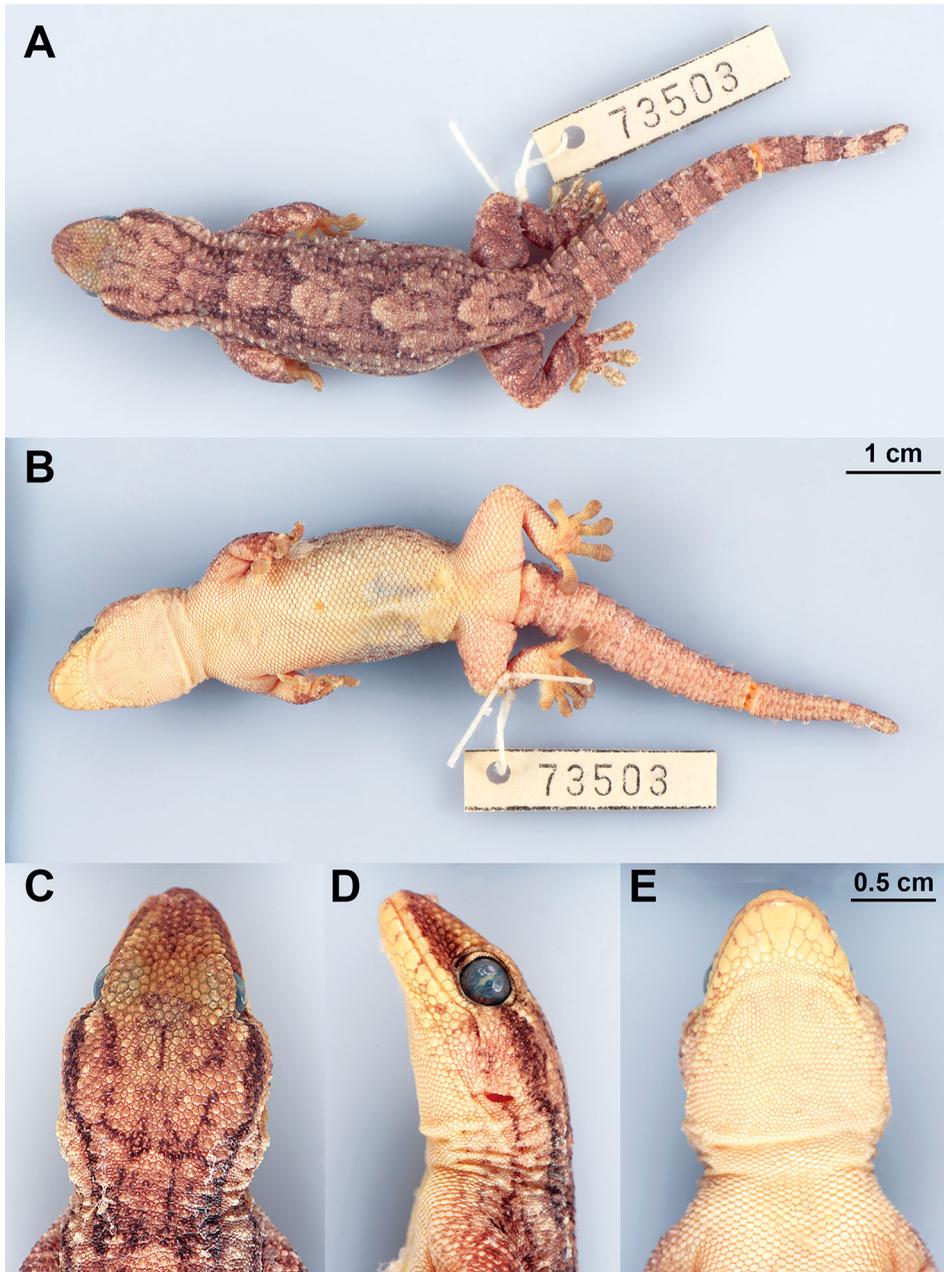


Figure 4. Neotype for *Tarentola panousei* Pasteur, 1959, (ZFMK 73503) from near Aouinet Torkoz, S Morocco, designated here, (A) in dorsal and (B) ventral view. Head in (C) dorsal, (D) lateral and (E) ventral view. Photographs by T Koppetsch

Variation: A second specimen from southern Morocco (ZFMK 84913) is bigger than the neotype but also not full grown (Table 2). The series collected from the acacia tree south of Nouadhibou contained eight specimens (Figure 5B) with SVL values from

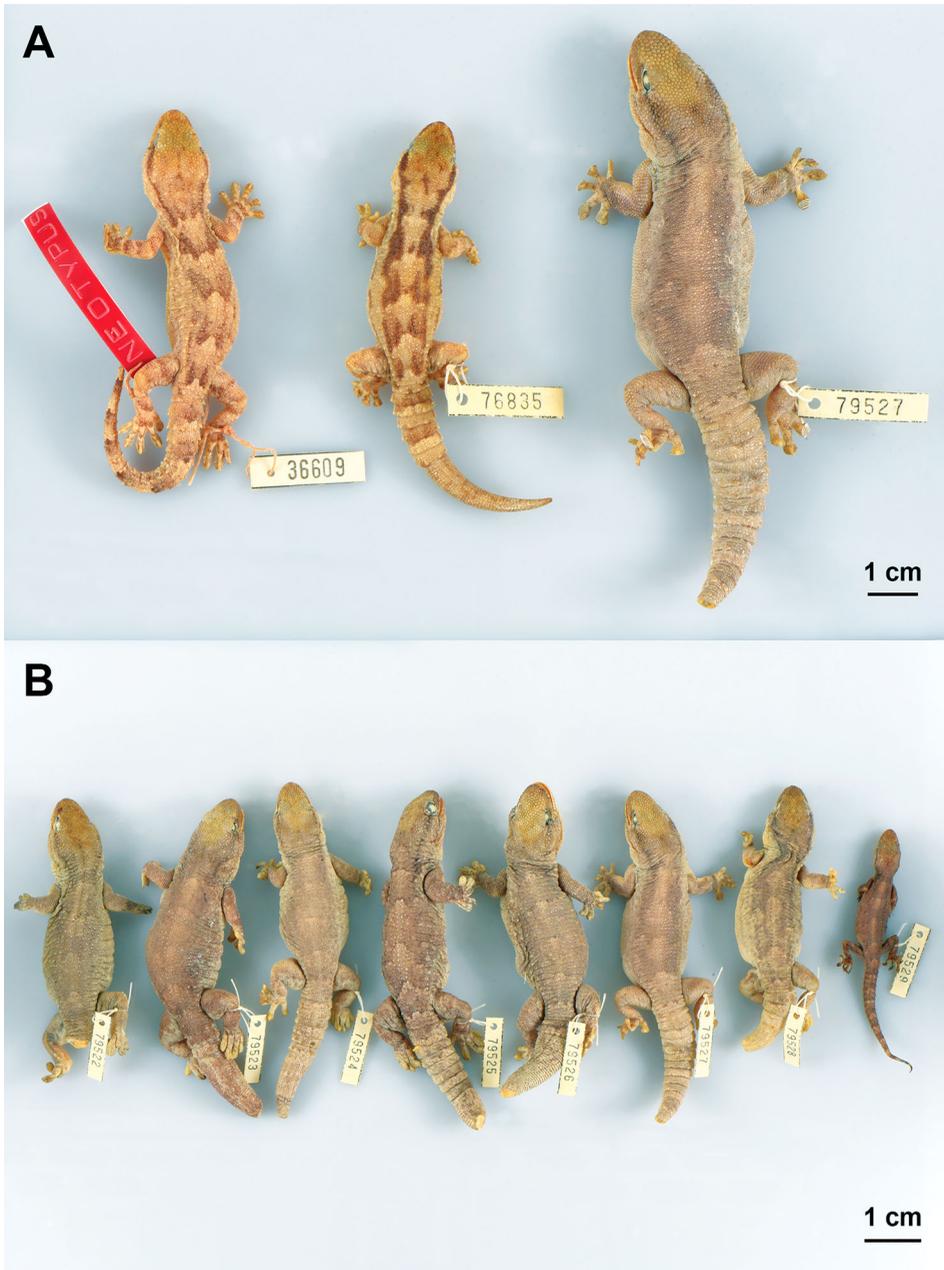


Figure 5. A: Comparison of *Tarentola hoggarensis* from the type locality, Hoggar, Algeria (ZFMK 36609; neotype) and from Tamourt Bougari, Mauritania (ZFMK 76835), and *T. panousei* from Nouadhibou, Mauritania (ZFMK 79527). B: Series of *T. panousei* (ZFMK 79522–79529) from the acacia tree SE of Nouadhibou. Photographs by T Koppetsch

47.1 to 85.4 mm (Table 2), consequently not reaching the size class of its syntopic congener *T. annularis* (up to 140 mm SVL), but with a markedly stout, robust habitus (Figure 6).

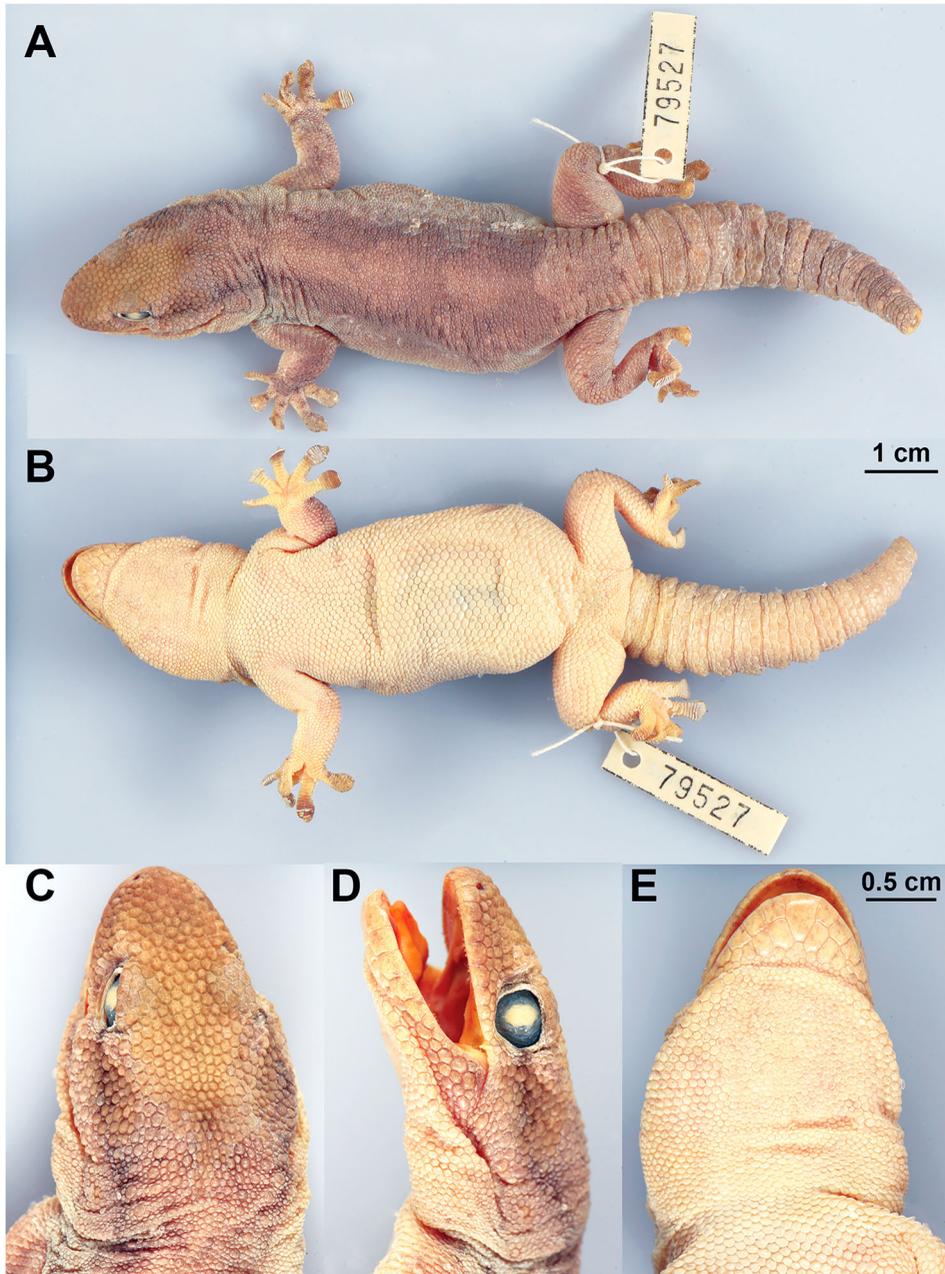


Figure 6. Specimen of *Tarentola panousei* (ZFMK 79527) from the isolated *Vachellia tortilis* acacia tree SE of Nouadhibou, (A) in dorsal and (B) ventral view. Head in (C) dorsal, (D) lateral and (E) ventral view.. Photographs by T Koppetsch

Systematics

Based on our morphological analysis, *Tarentola panousei* is phenotypically most similar to *T. hoggarensis* (Figure 5A), with which it was confused by previous authors, who

considered both names to be synonymous (see the synonymy-chresonymy list above). However, adult *T. panousei* show a higher maximal snout-vent length (up to 85.4 mm) with a lumpy appearance, compared with *T. hoggarensis* (Figure 5A) and a more or less uniform greyish beige with only four indistinct, pale dorsal patches from snout to vent.

Although some of Pasteur's (1960) qualitative diagnostic characters can be considered as strong and justified traits for the definitive identification of *T. panousei* based on our comparative examination of, for example, shape of ear opening (Eoserr) (in *T. panousei*: ear opening serrated), shape of postocular stripe (POstripe) (in *T. panousei*: postocular stripe up to the axilla) and shape of dorsal tubercles (DTshape) (in *T. panousei*: dorsal tubercles not in rows and indistinct from surrounding dorsal scales), others do not allow a clear separation from individuals of *T. hoggarensis*, for example, contact between nostril and rostral (Nrcontact), shape of lamellae at the base of 4th toe (Lbshape) and shape of the supraocular integument (SOIshape).

In addition to the characters based on Pasteur's diagnosis (Pasteur 1959, 1960), we showed that *T. panousei* have a slightly lower range of gular scale counts, compared with *T. hoggarensis* (27–31 vs 29–37) (Table 1).

Overall, we conclude that Pasteur's (1959) recognition of a new species was correct, and that a revalidation of *T. panousei* as a species is fully justified. If one considers the differences between newly described or revalidated species within the *T. mauritanica*/*T. deserti* complex (Joger 1984; Joger and Bshaenia 2010), the differences between *T. hoggarensis* and *T. panousei* are at least equivalent. Nonetheless, a future genetic corroboration of our conclusion would be highly desirable. Moreover, it must still be demonstrated that the subpopulations of *T. panousei* in southwest Morocco and those from south of Nouadhibou, separated by an air-distance of ca. 1 000 km (Figure 7, map), are identical, despite their strong resemblance regarding mensural and meristic characteristics shown. It must also be determined whether the geographically intermediate populations, in particular the coastal ones, will have to be assigned to *T. panousei* as well.

Habitat selection

Our nocturnal survey of the single, isolated acacia tree mentioned in the introduction (Figure 1), which harboured two closely coexisting species of *Tarentola*, yielded 23 specimens, of which seven *T. annularis* (four adults, three juveniles: ZFMK 79476–482) and eight *T. panousei* (seven adults and one juvenile: ZFMK 79522–529) were collected, the remaining specimens being released. The old acacia tree (Figure 1) offered two types of shelter or hiding places, larger clefts in the wood and small knotholes (Figure 8), of which the former (Figure 9A) were occupied by *T. annularis*; whereas the latter (Figure 9B) were used even by adult *T. panousei* specimens, which filled these holes completely with their bodies. Nearly all geckos were found and observed exclusively on the tree trunk. Only one big *T. annularis* male of 22 cm total length descended from the trunk and caught a migratory locust of c. 8–9 cm length, which was attracted by the headlight of our truck, at <1 m distance from the trunk, the distal parts of its toes were bent upwards in the fine desert sand in order to keep the adhesive lamellae clean. Three *T. annularis* juveniles (Figure 10) were also seen on the sandy ground, but escaped immediately to the nearby tree trunk. No *T. panousei* was observed outside of its arboreal microhabitat.

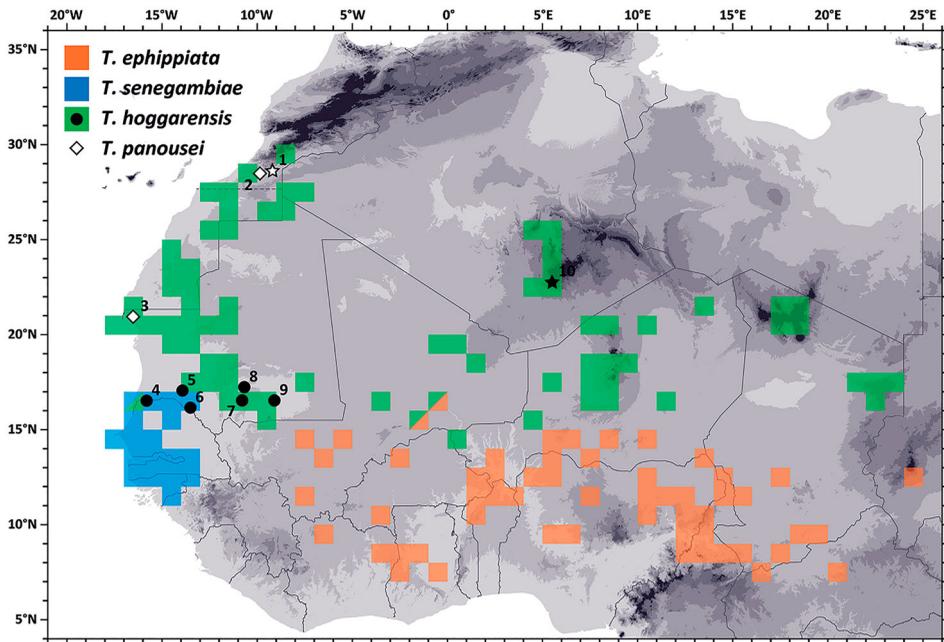


Figure 7. Distribution map of the *Tarentola ehippiata* species complex in NW and W Africa, inspired by the grid maps in Trape et al. (2012). The numbered localities refer to the localities where specimens were studied. *T. panousei*: 1 – Bassin du Dra moyen, Morocco (white star: type locality); 2 – S of Aouinet Torkoz, Morocco; 3 – SE of Nouadhibou, Mauritania; *T. hoggarensis*: 4 – Parc National Diawling; 5 – Lac Aleg, Mauritania; 6 – Kaedi, Mauritania; 7 – Tamourt Bougari, Mauritania; 8 – Tamchekket, Mauritania; 9 – Chlim, Mauritania; 10 – N of Tamanrasset, Algeria (black star: type locality). Map by M Flecks

Close syntopy on one single isolated tree trunk

This extreme syntopic situation of two similarly large gecko species suggested that *T. annularis* was superior in competition, because it occupied the more spacious shelter types. The smaller *T. panousei* specimens, in contrast, had to be content with the much smaller knotholes where adult specimens were hardly fitting in (Figures 8 and 9), as already indicated by Böhme et al. (2001). This was surprising, because *T. annularis* is otherwise a rupicolous species, whereas *T. hoggarensis* and its close relative *T. panousei* seem to be specialised tree dwellers. Even if *T. annularis* was, in contrast to *T. panousei*, also observed on the sandy ground, but very close to the acacia trunk, it is extremely unlikely for both species to have had genetic exchange with conspecifics in neighbouring trees, because these were virtually absent for a radius of at least several kilometres, a distance impossible to cross for either species. Given the extreme isolation of their habitat, we hypothesise that both micropopulations might have faced a long period of inbreeding, but without breakage of the isolating mechanism between these two congeners. This is important to note, because Grandison (1961) had reported on specimens intermediate between *T. annularis* and '*T. ehippiata*' (currently *T. senegambiae*) from Senegal, Gambia and Guinea Bissau and speculated on 'a breakdown in whatever mechanism isolates' both species from each other. However, these two species are also more similar to each other

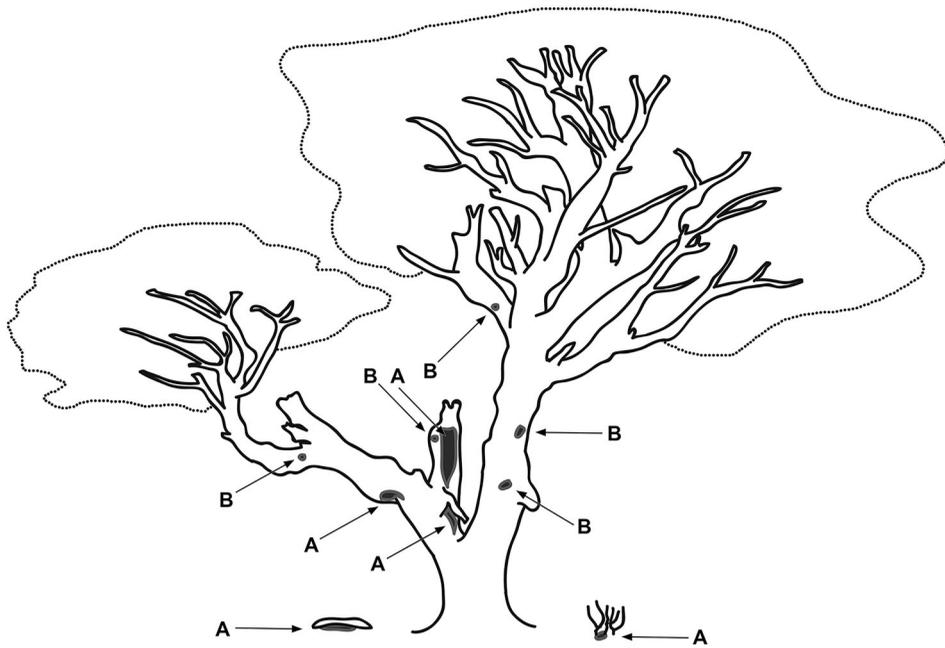


Figure 8. Sketch of the *Vachellia tortilis* acacia tree investigated (see Figure 1) to show the different shelter places of both syntopic *Tarentola* species. Labelled with 'A' for *T. annularis*, and 'B' for *T. panousei*. Drawing by T Koppetsch

with respect to their body size. In contrast, the two strictly syntopic subpopulations of *T. panousei* and *T. annularis*, in the isolated acacia tree described here, were well separated from each other morphologically, including in respect to size, despite the presumably long duration of their isolation from any other conspecific of either species.

Senegambian representatives of the *T. ehippiata* complex were separated as a subspecies *T. e. senegambiae* by Joger (1984) and raised to specific rank by Trape et al. (2012). According to the grid map by these authors, its Sahelian distribution range is separated from that of the Saharan *T. hoggarensis*, whereas *T. annularis*, sympatric with *T. hoggarensis* farther northwards, is missing from the *T. senegambiae* range, except for two rocky sites near Dakar (Yoff and Cap Manuel) and the rocky offshore islands Gorée, Ngor and Ile Madeleine (Cissé 1974; Böhme 1978; Cissé and Karns 1979; Joger 1982). According to Böhme et al. (2001), these marginal points were relictual occurrences where the likewise large, robust *T. senegambiae* was unable to follow. *Tarentola senegambiae* is also a primary, but obviously less specialised tree-dweller, sometimes even referred to as 'fig-tree gecko' (Cissé 1974; Cissé and Karns 1979), because it was found, in contrast to the obviously strictly tree-dwelling *T. hoggarensis* and *T. panousei*, next to trees, as well as on buildings in human settlements, for example, by WB (still as '*T. ehippiata*') behind shutters of an ORSTOM Institute building at Richard-Toll (Böhme 1978).

The only reference reporting '*T. ehippiata*' from coastal Mauritania on house walls is by Ineich (1996). He found these geckos close to and in Nouakchott, on the walls of a veterinary station and of a military post, here in sympatry with *Hemidactylus brookii* (currently *H. angulatus*). All other discoveries of this species, made farther northwards, were



Figure 9. A: Details of the *Vachellia tortilis* acacia trunk with larger clefts as hides of *T. annularis*. B: Small knotholes as hides for *T. panousei*. The one Ouguiya coin serving as a scale is 21 mm in diameter. Photographs by W Böhme

on trees (acacia). To the south, in the Diawling National Park in the Senegal River delta, close to the Senegalese border, the geckos were found on Baobab (*Adansonia digitata*) trees, with *T. annularis* already largely missing in this area.

However, the exact taxonomic identity of these geckos, in the light of Joger's (1984) revision and the present paper, should be reinvestigated, because now three taxa of the *T. ephippiata* species complex, viz. *T. panousei*, *T. hoggarensis* and, in the south,



Figure 10. Juvenile *T. panousei* from the acacia tree investigated. Photograph by W Böhme

perhaps also *T. senegambiae*, might be involved. The grid maps in Trape et al. (2012) suggest sympatry between the latter and *T. hoggarensis* in the Senegal River delta area.

The assumption of the competitive superiority of *T. senegambiae* over equal-sized *T. annularis*, as implied by Böhme (1978) can certainly not be applied to the situation of the syntopic presence of the otherwise strictly rupicolous *T. annularis* with *T. panousei*, because in this case it seemed that the latter, because of its smaller size, was the inferior competitor, pushed back to the less favourable shelter and hiding places. *T. annularis*, otherwise known from Egypt and the Sudan to North Cameroon and Mauritania predominantly as a rock-dweller, has been observed on trees so far only by Sow et al. (2015) and in the present study. However, although Sow et al. (2015) found their '*T. e. hoggarensis*' only in bare areas in holes of acacia trees, they only occasionally found *T. annularis*, which they observed three times more often, in syntopy with the former. At our site near Nouadhibou, *T. annularis* proved to be superior in competition in a habitat structure absolutely atypical for it, whereas it was the primary microhabitat for its smaller congener.

The obviously less narrow ecological specialisation of *T. annularis*, compared with the taxa of the *T. ephippiata* complex, might also explain why it is taxonomically uniform from Egypt and the Sudan to the Atlantic Ocean, whereas the more stenoecious *T. ephippiata* complex is partitioned to several taxa within the same geographic area. The distribution pattern of the here revalidated *T. panousei* appears to be biogeographically peculiar, with only patchy and locally isolated subpopulations known so far. However, an overlooked more broad occurrence in this region cannot be ruled out, because other records assigned to *T. ephippiata sensu stricto* might actually represent *T. panousei*. These broad gaps in

known distribution ranges are also known for other African geckos, for example, *Hemidactylus pseudomuriceus* (Koppetsch and Böhme 2017). Nevertheless, it can only be speculated whether the localities where *T. panousei* had been recorded might rather be the result of a relictual patchy distribution. The underlying determinants, for example, different dispersal abilities, and possible scenarios, for example, transformation relictual refugia in the past to the present fragmented distribution of the *T. ephippiata* complex as a whole, which had caused or shaped those distinct biogeographic patterns, might be identified by future more comprehensive phylogeographic analyses.

Acknowledgements

We thank Ivan Ineich and Nicolas Vidal (Muséum National d'Histoire Naturelle, Paris), Soumia Fahd (Université de Tétouan), and Patrick Campbell (Natural History Museum London), for confirming that the *T. panousei* type specimen had been lost. Ivan Ineich helped additionally with literature advice. Fabrizia Ronco (Zoological Institute, Basel) and Becky Cramer (Natural History Museum, Oslo) supported our statistical analysis. As always, Ursula Bott (Museum Koenig, Bonn), assisted again in finalizing the manuscript, and Morris Flecks (Museum Koenig, Bonn) provided the distribution map. We are grateful to Salvador Carranza (Institute of Evolutionary Biology, Barcelona), Aaron Bauer (Villanova University) and an anonymous reviewer, for their helpful comments on our manuscript.

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Appendix I: Material examined

Tarentola panousei:

MOROCCO: Aouinet-Torkoz, Oued Torkoz, at its mouth into the Oued Dra (28°29.00' N, 09°51.17' W) (ZFMK 73503 [neotype]); no precise locality, southern Morocco (ZFMK 84913)
MAURITANIA: Nouadhibou (20°57' N, 16°31' W) (ZFMK 79522–79529)

Tarentola hoggarensis:

ALGERIA: 40 km N Tamanrasset, Hoggar (ZFMK 36609 [neotype], ZFMK 38953–38956)
MAURITANIA: Chlim (ZFMK 76790); Kaedi (ZFMK 76824); Lac Aleg (ZFMK 76901); Parc National Diawling (ZFMK 76842); Tamchekket (ZFMK 76843); Tamourt Bougari (ZFMK 76833–76836)