



Systematics of north African *Agama* (Reptilia: Agamidae): a new species from the central Saharan mountains

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Abstract

We studied the taxonomic status of the north African *Agama* species *A. impalearis*, *A. castroviejoi*, and *A. boueti*. The study of recently collected specimens and museum material, as well as phylogenetic analyses of a short 16S ribosomal RNA gene fragment, revealed the presence of an undescribed species in Adrar des Ifoghas (Mali), Aïr Mountains (Niger), Ahaggar Mountains (Algeria) and Tassili n'Ajjer (Algeria, Lybia), previously mistaken either as *A. impalearis* or *A. agama*. The new species, *Agama tassiliensis* n. sp., clearly belongs to the *impalearis* – *boueti* – *spinosa* species group but differs from these species, among other characters, by its red, reddish-orange or orange vertebral stripe in males, long and angular head, long limbs and toes (with 4th toe usually slightly longer than 3rd toe), long but low nuchal crest made of 10 to 15 spines (rarely 8–9 spines) and large number of supralabials (10–16, usually around 12). Interspecific uncorrected *p*-distances based on the 16S rDNA gene fragment are high, ranging from 3.9% between *A. boueti* and *A. impalearis* to 7.9% between *A. spinosa* and *A. impalearis*. The new species is sympatric with *A. boueti* at least in the Aïr Mountains and exhibits average mtDNA divergences of 6.2%, 7.4%, and 7.6% with *A. spinosa*, *A. impalearis*, and *A. boueti*, respectively. *Agama boueti* is paraphyletic relative to *A. castroviejoi* in the mtDNA tree, and mtDNA genetic divergences between populations of both species are lower than 1.0%, suggesting that *A. castroviejoi* is better treated as a junior synonym of *A. boueti* pending more detailed analyses. Scattered mountain ranges in the Sahara seem to have promoted lineage divergence and ultimately speciation in this group. Further work should be done to study species taxonomy and evolution in those areas.

Key words: Ahaggar, Aïr, Algeria, Mauritania, Lybia, Niger, Mali, Sahara, Tassili n'Ajjer, taxonomy

Introduction

Although the most evocative images of the Sahara desert are vast expanses of dunes, the Saharan environment is largely occupied by scattered but large mountain ranges. In the western parts of the Sahara, the most important in extension and altitude are the Ahaggar (or Hoggar) Mountains in Algeria, the Tassili n'Ajjer in Algeria and Acacus Mountains (= Tadrart Acacus) in south-western Libya, the Aïr Mountains in northern Niger, the Adrar des Ifoghas in Mali and the Adrar Plateau (or Adrar Atar) and Tagant Plateau in Mauritania. These areas now constitute remarkable biogeographical crossroads for vertebrates, having acted as refugia for Sahelian (Dekeyser & Villiers 1956; Joger 1981; Kriska 2001; Lamarche 1988; Padial & de la Riva 2004; Padial 2006; Isenmann *et al.* 2010), Mediterranean (Dekeyser & Villiers 1956; Joger 1981) and even East African - Arabian species (Geniez & Gauthier 2008; Crochet *et al.* 2008). They also harbour several endemic species, a testimony to their role in the diversification of the Saharan vertebrate fauna (for reptiles see Wilms & Böhme 2001; Geniez & Arnold 2006). However, these mountain ranges have remained largely unexplored and have only recently received increased attention (for example Brito *et al.* 2011).

Several species of *Agama* have been reported for mountain areas in the Sahara. Padial (2005) described a new species closely related to *A. impalearis* Boettger, 1874: *A. castroviejoi* Padial, 2005 endemic to the Adrar Plateau of Mauritania, while relict populations of *A. boulengeri* Lataste, 1886, a Sahelian species, were reported from the Adrar and Tagant plateaus of Mauritania by Joger (1979) and Padial (2006). Depending on the authors, one or two *Agama* species inhabit the rest of the Saharan mountains. Joger (1981) and Schleich *et al.* (1996) mention only *A. impalearis* for the Ahaggar Mountains and Tassili n'Ajjer, and Joger (1979) lists only this species for the Air Mountains. Others, however, (Angel & Lhote 1938; Angel *et al.* 1954; Le Berre 1989) report both *A. impalearis* and *A. agama* (Linnaeus, 1758) in the Ahaggar Mountains and Tassili n'Ajjer. Kriska (2001) recognizes three species in the Air Mountains: *A. agama* in the central and southern Air, *A. impalearis* in the northern and central Air and two small areas in the south, with central areas thus having both species, and *A. boueti* Chabanaud, 1917 (a more ground dwelling species preferring flatter, often sandy, areas). Finally, Sindaco & Jeremčenko (2008) wrote: "The Central Saharan *Agama* (S. Algeria, Mali, Niger, SW. Libya and Tibesti between Libya and Chad) are usually ascribed to *A. impalearis*, but recently these populations are considered as belonging to the Afrotropical species *Agama agama* (IUCN 2007)". It should be noted that Anderson (1935) had some difficulties ascribing Agamas from the Ahaggar Mountains to species, and hesitated between *A. impalearis* and *A. spinosa* Gray, 1831.

This lack of agreement on the identification and taxonomic status of mountain populations of *Agama* in the Sahara seems to be the result of the recurrent endorsement of old literature records, the absence of recent collections and, consequently, of comprehensive molecular analyses, and the lack of a thorough morphological study of museum specimens. In this study we aim to clarify this confusing taxonomic scenario. For doing so, we studied qualitative, meristic and continuous quantitative morphological characters for old and recently collected museum specimens and photographed individuals of all North African *Agama* species: *A. impalearis*, *A. castroviejoi*, *A. boueti*, *A. boulengeri*, and *A. spinosa*. In addition, we used a short 16S ribosomal RNA gene fragment to infer relationships of those *Agama* species and calculate genetic divergences. We conclude that *Agama* populations from the Air Mountains, Ahaggar Mountains and Tassili n'Ajjer previously assigned either to *A. impalearis* or to *A. agama* represent an undescribed species that we name and describe herein.

Material and methods

Samples. We examined specimens housed in the following collections: the "Biogéographie et Ecologie des Vertébrés" herpetological collection of the UMR 5175 CEFE in Montpellier (BEV), the Muséum national d'Histoire naturelle in Paris (MNHN), and the Zoologisches Forschungsmuseum Alexander Koenig in Bonn (ZFMK). We also examined colour pictures of live specimens in the iconographic collections of P. Geniez in Montpellier (PGe xxx, see acknowledgements for the names of the photographers) and J. C. Brito in Porto (Brito code xxx). The list of examined specimens (voucher specimens or photographs) is available in Appendix I.

Morphological data. Twenty-four morphological variables have been measured: 14 quantitative morphometric variables [*SVL* = snout-vent length, *TL* = tail length, *FLL* = foreleg length, *HLL* = hindleg length, *FL1* to *FL5* = length of 1st to 5th fingers, *TL1* to *TL5* = length of 1st to 5th toes]; five quantitative pholidosis variables [*Dors* = number of longitudinal rows of dorsal scales counted around midbody, *Crest* = number of spines composing the nuchal crest, *Supral* = number of supralabials, *Infral* = number of infralabials, *CP* = number of pre-anal pores (only for males)], and five qualitative variables describing colour pattern [*HCol* = head colour, *BCol* = body colour, *VCol* = vertebral stripe colour, *TCol* = throat marbling colour, *BCol* = belly colour]. We do not report variation for all these variables in the results section: we only provide details for i) variables that have been used in the literature to identify species in this genus or ii) variables that were useful for species identification.

Molecular analyses. Collection numbers, localities and GenBank accession numbers for each sample used in this analysis are detailed in Table 1. Acronyms for DNA samples and associated vouchers, in addition to the ones listed above, are as follow: MNCN = Museo Nacional de Ciencias Naturales (Madrid); CET = private collection of J. Castroviejo at Centro de Estudios Tropicales in Sevilla; RIM = Mauritanian field numbers of J. M. Padial. Genomic DNA was extracted from ethanol-preserved tissues using standard phenol-chloroform extraction protocols. We amplified nearly 500 bp of the 16S mitochondrial gene with the primers 16Sar-5' (5'-CGCCTGTTTATCAAAAACAT-3') and 16Sbr-3' (5'-CCGGTCTGAACTCAGATCACGT-3') (Hillis *et al.* 1996). The polymerase chain reaction (PCR) amplification protocol was as follows: 95°C/15 s; 35 cycles of 95°C/30 s, 50°C/30 s, 72°C/1

min; and 72°C/10 min. PCR products were visualized in agarose gels, and unincorporated primers and dNTPs were removed from PCR products using ExoSap purification (ExoSap-it, GE Healthcare). Cycle sequencing reactions in both directions were completed using the corresponding PCR primers and BigDye Terminator 3.1 chemistry (Applied Biosciences), with a standard cycle sequencing profile (96°C/3 min; 35 cycles of 96°C/10 s, 50°C/15 s, 60°C/3 min; and 72°C/7 min). Reaction products were purified using ethanol precipitation and run in an ABI 3730xl analyzer. Gene fragments were aligned through a web server with Mafft (Katoh *et al.* 2005; Katoh & Toh 2008) under the Q-INS-i strategy, which takes into account secondary structure of RNA. The resulting alignment contained 512 characters, 362 characters were constant and 150 characters were variable including 119 characters that were parsimony-informative.

Maximum parsimony phylogenetic analyses were performed in PAUP* 4.0b10 (Swofford, 2002). The strict consensus tree was obtained using heuristic searches with tree bisection reconnection (TBR) and 100000 replicates using the ACCTRAN algorithm in PAUP. Gaps were considered a fifth character. Clade support was calculated by non-parametric bootstrapping using heuristic searches of 1000 replicate datasets with 10 random addition sequence replicates. Maximum likelihood analyses were performed in Garli 0.96 Beta (Zwickl 2006, available at http://www.nescent.org/informatics/download.php?software_id=4). We used default search parameters and implemented a GTR + I + G model of nucleotide evolution for the whole data matrix. We performed a total of 1000 runs (replicates) to reduce the probability of inferring a suboptimal likelihood solution. Node support was assessed by 500 bootstrap replicates and two search replicates per replicate. Sequences of *Agama agama*, *A. bouengeri* and *A. weidholzi* Wettstein, 1932 were used to root the trees following the phylogenetic hypothesis of Leaché *et al.* (2009). Bootstrap values (BSS) $\geq 80\%$ are usually considered to indicate strong support (Hillis & Bull 1993).

Results

Morphological examination of specimens. In total we examined 376 specimens (collection vouchers or photographs) of *Agama* from North West Africa (Morocco, Algeria, Libya, Mauritania, Mali, Niger), including numerous specimens from the Ahaggar Mountains, Tassili n'Ajjer and Air Mountains (see Appendix 1). We did not find any specimen of *Agama agama* or *A. impalearis* in these central Saharan massifs.

Most specimens from these areas belong to an undescribed taxon with colour characteristics similar to those of the *Agama agama* group (pale spots on the head and nuchal regions, blue body with yellow to red head and a red nuchal crest in breeding males), and with several meristics similar to the *Agama impalearis* group (shape and number of supralabial scales, conspicuous spines around the ear opening, short and high nuchal crest). The occurrence of characters associated with the *A. agama* species group and the *A. impalearis* species group in the central Saharan taxon probably explains why it has variously been assigned to one or the other of these species in the past. This new taxon will be described in detail below (see also ecological section).

In the Air Mountains, another species of *Agama* can be found alongside the central Saharan taxon. Comparisons of the specimens of this species with one of the types of *Agama boueti* as well as with characters given in Joger (1979) and Padial (2005) allowed us to identify these specimens as *Agama boueti*. In the Air Mountains and in the Adrar Plateau area, specimens of *A. boueti* have been found on flat grounds (plateaux, plains, valley bottoms, etc), while specimens of the new taxon have been observed on rocky slopes, outcrops etc. (pers. obs, Brito pers. com., Trape pers. com.). This ecological segregation agrees with the information given by Kriska (2001), where the new taxon is called *Agama impalearis*.

Our northernmost records of *Agama agama* (excluding the Sahelian areas of southern Mauritania where the species is widespread) come from 17°01'N 02°00'E in Mali (PGe 938, photo J.-F. Trape) and 50 km S of Tahoua in Niger (Brito code 399). The Malian record is only 180 km south of our closest locality for the new taxon, and further fieldwork will undoubtedly reduce the gap between the ranges of these two species. In addition, Kriska (2001) lists both *A. agama* and "*A. impalearis*" (in addition to *A. boueti*) for the Air Mountains, suggesting that the distributions of *A. agama* and of the new taxon could overlap there.

Genetic data. The amplified fragment starts at position 1879 and ends at position 2376 of the complete mitochondrial genome of *Pseudotrapelus sinaitus* (Heyden, 1827) deposited in GenBank under accession number NC_013603. Between 0 and 36 bp were missing depending on the specimens except for our two *Agama spinosa*, in which a fragment approximately 60 bp long was missing from the beginning of the sequence.

The maximum parsimony strict consensus of 42 equally parsimonious trees as well as the maximum likelihood best tree (GarliScore lnL=-1914.430641) rendered the same results. Both analyses support the monophyly of *A. castroviejoi*, *A. impalearis*, *A. spinosa* and a group made of Ahaggar, Tassili n'Ajjer and Air specimens (the central Saharan clade). *Agama boueti* is paraphyletic relative to *A. castroviejoi* (Fig. 1). The central Saharan clade and *A. spinosa* form a well-supported clade sister to another well-supported clade comprising *A. impalearis* and the *A. boueti*-*A. castroviejoi* lineage.

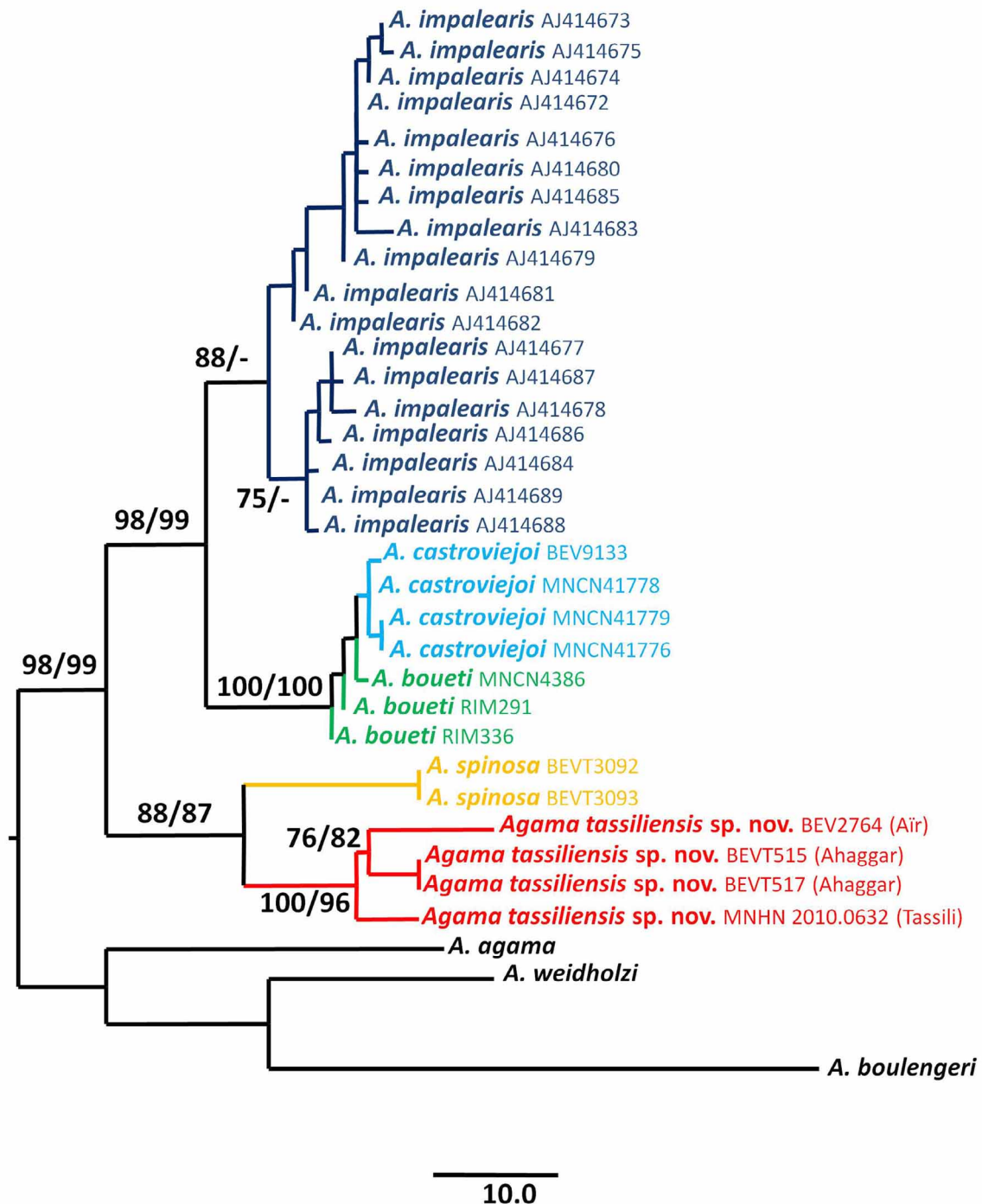


FIGURE 1. Maximum parsimony tree (one of 42 equally most parsimonious trees) with branch lengths measured as number of changes, and with identical topology to the maximum parsimony strict consensus tree and the best maximum likelihood tree (not shown), resulting from the phylogenetic analysis of a 512 base-pairs fragment of the mitochondrial 16S ribosomal RNA gene. Numbers on nodes are bootstrap support above 70% for maximum parsimony and maximum likelihood analyses respectively.

Table 1. Details for the tissue samples used for the genetic analyses. See text for abbreviation of collections.

Species	Locality	Voucher specimen or photograph	Tissue sample	Genbank
<i>Agama agama</i>	Mauritania: Hod El Gharbi: El Wad-Zouaina	CET (RIM 328)	MNCN-DNA20575	JN665050
<i>Agama boueti</i>	Mauritania: Tagant: Tidjikja, about 50 km E of Leckcheb	MNCN 43869	MNCN-DNA9849	JN665051
<i>Agama boueti</i>	Mauritania: Hodh el Gharbi: Ayoun el Atrous, nearby	CET (RIM 291)	MNCN-DNA20580	JN665052
<i>Agama boueti</i>	Mauritania: Hodh el Gharbi: Ayoun el Atrous, nearby	CET (RIM 336)	MNCN-DNA20579	JN665053
<i>Agama boulengeri</i>	Mauritania: Hodh el Gharbi: Ayoun el Atrous, nearby	CET (RIM 338)	MNCN-DNA20577	JN665054
<i>Agama boulengeri</i>	Mauritania: Hodh el Gharbi: Timbedgha - Ayoun el Atrous, between	CET (RIM 021)	MNCN-DNA20582	JN665055
<i>Agama boulengeri</i>	Mauritania: Tagant: Guelta Fanar	CET (RIM 344)	MNCN-DNA20584	JN665056
<i>Agama boulengeri</i>	Mauritania: Adrar: Oued Choum	CET (RIM 116)	MNCN-DNA20595	JN665057
<i>Agama boulengeri</i>	Mauritania: Adrar: Terjit	CET (RIM 066)	MNCN-DNA20598	JN665058
<i>Agama boulengeri</i>	Mauritania: Tagant: Zig well, between Lekcheb and Tichit	CET (RIM 174)	MNCN-DNA20597	JN665059
<i>Agama castroviejo</i>	Mauritania: Adrar: Aghmakoum, some km S of [21.1538°N/11.9103°W]	BEV.9133	BEV.T813	JN665060
<i>Agama castroviejo</i>	Mauritania: Adrar: Dahr Chinguetti, between Atar and Tidjikja [20.4424°N/12.8234°W]	MNCN 41778	MNCN-DNA20601	AY522928
<i>Agama castroviejo</i>	Mauritania: Adrar: Dahr Chinguetti, between Atar and Tidjikja [20.4424°N/12.8234°W]	MNCN 41779	MNCN-DNA20600	AY522929
<i>Agama castroviejo</i>	Mauritania: Adrar: Dahr Chinguetti, between Atar and Tidjikja [20.4424°N/12.8234°W]	MNCN 41776	MNCN-DNA20603	AY522926
<i>Agama impalearis</i>	Morocco: Bouarfa [32.54°N/1.97°W]	not traced	-	AJ414673
<i>Agama impalearis</i>	Morocco: Bouarfa [32.54°N/1.97°W]	not traced	-	AJ414675
<i>Agama impalearis</i>	Morocco: Bouarfa [32.54°N/1.97°W]	not traced	-	AJ414674
<i>Agama impalearis</i>	Morocco: Ouarzazate [30.75°N/6.63°W]	not traced	-	AJ414672

Continued on the next page...

Table 1. continued

Species	Locality	Voucher specimen or photograph	Tissue sample	Genbank
<i>Agama impalearis</i>	Morocco	not traced	-	AJ414676
<i>Agama impalearis</i>	Morocco: ain-el-Guettarra [33.93°N/3.38°W]	not traced	-	AJ414679
<i>Agama impalearis</i>	Morocco	not traced	-	AJ414680
<i>Agama impalearis</i>	Morocco	not traced	-	AJ414685
<i>Agama impalearis</i>	Morocco	not traced	-	AJ414683
<i>Agama impalearis</i>	Morocco: Assafid [30.62°N/9.37°W]	not traced	-	AJ414681
<i>Agama impalearis</i>	Morocco: Assafid [30.62°N/9.37°W]	not traced	-	AJ414682
<i>Agama impalearis</i>	Morocco	not traced	-	AJ414677
<i>Agama impalearis</i>	Morocco	not traced	-	AJ414687
<i>Agama impalearis</i>	Morocco: Sidi-Bou-Othmane [31.23°N/8.43°W]	not traced	-	AJ414684
<i>Agama impalearis</i>	Morocco	not traced	-	AJ414689
<i>Agama impalearis</i>	Morocco	not traced	-	AJ414688
<i>Agama impalearis</i>	Morocco	not traced	-	AJ414686
<i>Agama impalearis</i>	Morocco	not traced	-	AJ414678
<i>Agama tassiliensis n. sp.</i>	Algeria: Hoggar: Ahaggar mountains [23.1262°N/5.9890°E]	PGe.870	BEV.T515	JN665061
<i>Agama tassiliensis n. sp.</i>	Algeria: Hoggar: Ahaggar mountains [23.4788°N/5.7811°E]	PGe.910	BEV.T517	JN665062
<i>Agama tassiliensis n. sp.</i>	Algeria: Tassili: 13 km before Iherir coming from Djanet [25.3500°N/8.3911°E]	MNHN 2010.0632	BEV.T2973	JN665063
<i>Agama tassiliensis n. sp.</i>	Niger: Air: Zagado tributary, Kogo, base of Mt. Taghmerit [19.0015°N/9.3348°E]	BEV.2764	BEV.T803	JN665064
<i>Agama spinosa</i>	Egypt: Wadi el Gemal, 29 km upwaters from asphalted road [24.5640°N/34.9027°E]	PGe.1000	BEV.T3092	JN665065
<i>Agama spinosa</i>	Egypt: Wadi el Gemal, 26 km upwaters from asphalted road [24.5593°N/34.9286°E]	PGe.1001	BEV.T3093	JN665066
<i>Agama weidholzi</i>	Senegal: Tambacounda: Simenti [13.0330°N/13.2887°W]	no voucher	MNCN-DNA9785	JN665067

Interspecific uncorrected *p*-distances range from 3.9% between *A. boueti* and *A. impalearis* to 7.9% between *A. spinosa* and *A. impalearis* (Table 2) except for the clade *A. boueti* - *A. castroviejoii* where genetic distances between subclades are lower than 1.0% (mean=0.5, range=0.2–0.8). The central Saharan lineage shows average divergences of 6.2%, 7.4%, and 7.6% with *A. spinosa*, *A. impalearis*, and *A. boueti* - *A. castroviejoii*, respectively.

TABLE 2. Mean interspecific uncorrected *p*-distances for North West African *Agama* species based on mitochondrial 16S sequences (range is in parentheses).

	<i>A. boueti</i>	<i>A. impalearis</i>	<i>A. tassiliensis</i> n. sp.
<i>A. impalearis</i>	3.9 (3.0–4.9)	-	
<i>A. tassiliensis</i> n. sp.	7.6 (6.8–8.7)	7.4 (6.6–8.4)	-
<i>A. spinosa</i>	6.9 (6.5–7.3)	7.9 (7.7–8.4)	6.2 (5.8–6.6)

Intraspecific divergences largely vary across species. For *A. spinosa* the two haplotypes were identical, which is not surprising since the two samples were collected in the same locality. Divergences within the *Agama boueti* – *A. castroviejoii* clade are lower than 1% (see above). *Agama impalearis* shows divergences from 0.2–2.6% ($x=1.3$). Greater divergences are found within the central Saharan clade. Ahaggar and Aïr populations diverge by 2.6%, Tassili and Aïr populations by 3.0%, and Ahaggar and Tassili populations by 2.0%.

Given the results of phylogenetic analyses and interspecific distances we propose to consider provisionally *A. castroviejoii* as a junior synonym of *A. boueti*, pending results of detailed morphological and genetic studies, and refer to the clade *A. boueti* – *A. castroviejoii* as *A. boueti* subsequently. Samples across the distribution of *A. boueti*, including the type locality, will be required in order to assess the validity of this taxonomic hypothesis.

The central Saharan taxon occurs sympatrically with *A. boueti* in the Aïr Mountains (Joger 1979; Kriska 2001; J.C. Brito, L. Chirio and J.-F. Trape pers. com.), where they occupy different habitats (sandy flat areas for *A. boueti*, rocky outcrops and slopes for the central Saharan taxon), but they are not sister taxa. They are thus uncontroversial biological species. Since the genetic divergence between the central Saharan taxon and its closest relative *A. spinosa* is of the same magnitude (even if slightly lower) as between the central Saharan taxon and *A. boueti*, we describe this taxon as a new species below. We refrain from further dividing this taxon at this stage until the patterns of morphological and genetic variation among the three groups of populations (Ahaggar Mountains, Tassili n’Ajjer and Aïr Mountains) are better understood.

Agama tassiliensis sp. nov.

Holotype. MNHN 2010.0632, adult male collected on April 21th 2009 in the Tassili n’Ajjer (south-eastern Algeria), 5 km south-south-west from Iherir [WGS84 25.3500°N / 8.3911°E / 1428m a.s.l.] by P.-A. Crochet, P. Geniez and O. Peyre. See Figure 2.

Chresonyms. *Agama impalearis*: Joger 1979; 1981; Schleich *et al.* 1996; Kriska 2001. *Agama agama*: Angel and Lhote 1938; Angel *et al.* 1954; Le Berre 1989; Sindaco and Jeremčenko 2008.

Etymology. The name comes from the Berber word “tassili”, referring to sandstone plateaux of the Sahara. It also refers to the Tassili n’Ajjer, a Saharan massif where the holotype was collected.

Specimens examined. 68 specimens from the entire known distribution range of the species (cf. Distribution and Appendix I).

Diagnosis. A medium to large size *Agama* (reaching 13.4 cm of SVL and around 37 cm of total length) belonging to the *Agama impalearis* complex (medium proportions, dorsal scales regularly keeled, at least 3 spines on the anterior border of the ear opening, a nuchal crest in both sexes but no caudal crest, see also genetic data) and characterized by the following features (see also Tables 3, 4, 5, 6 and Fig. 2, 3, 4): head angular, 63 to 73 rows of dorsal scales at midbody, 4th toe slightly larger than 3rd (sometimes of same size), a relatively large number of supralabials (around 12, min. 10 max. 16), a large number of subdigital lamellae (15–20 under the 4th finger, average 17.37, and 18–24 under the 4th toe, average 20.47), a well-developed crest composed by (8) 10 to 15 spines and a frequently orange eye contour. Males in breeding condition can be brightly coloured: head and throat orange or red, body dark blue, legs and tail blue, crest and vertebral stripe generally reddish to red. Also, the new species is diagnosed by possessing 6 pure simple private nucleotide character states in the fragment of mitochondrial 16S gene

sequence when compared with the other members of the *impalearis* clade (all positions refer to the *Pseudotrapelus* complete mitochondrial sequence NC_013603, when they are dependent on ambiguous alignment this is indicated): A at positions 2127 (ambiguous alignment) and 2194; two Cs inserted immediately after position 1926; G at position 2218; and T, inserted after position 1926, 4bp after the two Cs.



FIGURE 2. *Agama tassiliensis* n. sp., holotype, MNHN 2010.0632, adult male from Algeria, Tassili n' Ajjer, 5.5km SSSW of Iherir [25.3500°N/8.3911°E], photo P. Geniez. A: dorsal view of the live specimen. B: ventral view of the live specimen.

Table 3. Mean (standard deviation), minimum-maximum (n=sample size) for selected characters in the *Agama imparealis* species group and *A. agama*.

	<i>Agama tassiliensis</i> n. sp.	<i>Agama imparealis</i>	<i>Agama spinosa</i>	<i>Agama boueti</i>	<i>A. boueti</i> , “ <i>castroviejei</i> ” phenotype	<i>Agama agama</i>
Adult SVL (males)	116.1 (11.23) 106-134 (n=9)	111.3 (11.37) 87-130 (n=36)	99.3 (8.14) 86-113 (n=13)	88.8 (10.38) 70-101 (n=9)	95.3 (8.38) 84-104 (n=4)	112.0 (12.69) 92-132 (n=9)
Adult SVL (females)	96.8 (11.18) 82-108 (n=4)	100.7 (7.20) 90-113 (n=17)	no voucher	85.1 (4.05) 81.6-90 (n=5)	84 (n=1)	101.6 (11.41) 91.2-115 (n=4)
Foreleg/SVL ratio (males)	0.44 (0.03) 0.40-0.48 (n=9)	0.43 (0.03) 0.39-0.52 (n=34)	0.44 (0.02) 0.41-0.47 (n=14)	0.46 (0.02) 0.45-0.48 (n=2)	0.45 (0.03) 0.41-0.47 (n=5)	0.46 (0.03) 0.43-0.50 (n=6)
Foreleg/SVL ratio (females)	0.45 (0.05) 0.39-0.52 (n=6)	0.44 (0.03) 0.39-0.48 (n=19)	no voucher	0.47 (0.02) 0.41-0.51 (n=5)	0.41 (n=1)	0.46 (0.04) 0.41-0.49 (n=6)
Hindleg/SVL ratio (males)	0.64 (0.03) 0.62-0.72 (n=9)	0.65 (0.04) 0.55-0.72 (n=35)	0.67 (0.03) 0.62-0.72 (n=14)	0.71 (0.02) 0.70-0.73 (n=2)	0.70 (0.04) 0.66-0.76 (n=5)	0.66 (0.04) 0.60-0.71 (n=6)
Hindleg/SVL ratio (females)	0.65 (0.09) 0.58-0.80 (n=6)	0.64 (0.04) 0.55-0.69 (n=18)	no voucher	0.73 (0.07) 0.60-0.77 (n=5)	0.67 (n=1)	0.67 (0.07) 0.56-0.75 (n=6)
Supralabials	12.10 (1.10) 10-16 (n=48)	12.18 (1.11) 10-17 (n=101)	10.57 (0.81) 9-12 (n=21)	11.02 (0.90) 9-13 (n=49)	11.93 (1.27) 10-14 (n=14)	9.12 (0.86) 7-11 (n=42)
Nb dorsal scales	68.00 (3.08) 63-73 (n=17)	69.22 (4.14) 57-83 (n=63)	64.83 (4.87) 59-77 (n=18)	58.37 (3.13) 53-65 (n=27)	60.71 (1.11) 60-63 (n=7)	68.19 (6.39) 57-78 (n=16)
Subd. lamellae 4th finger	17.37 (1.34) 15-20 (n=19)	13.76 (0.90) 12-16 (n=68)	14.86 (1.24) 13-18 (n=21)	12.45 (1.09) 10-14 (n=31)	14.38 (1.06) 13-16 (n=8)	19.68 (1.80) 16-22 (n=19)
Subd. lamellae 4th toe	20.47 (1.61) 18-24 (n=19)	15.84 (0.94) 14-18 (n=68)	17.10 (1.37) 16-20 (n=20)	18.06 (1.23) 16-21 (n=34)	21.22 (1.20) 19-23 (n=9)	22.38 (1.60) 19-25 (n=21)
Nb of crest spines (males)	11.88 (1.63) 8-15 (n=26)	9.58 (1.57) 6-13 (n=55)	11.07 (1.79) 8-16 (n=15)	7.25 (0.93) 6-9 (n=16)	7.11 (1.27) 5-9 (n=9)	14.68 (2.13) 10-19 (n=28)

Table 4. Frequency (in %) of vertebral stripe colour characters in each taxon (adult males only). I = indistinct, concolorous, GG = grey to greyish, WY = white to yellow, OR = orange to red. n = sample size.

	I	GG	YW	OR	n
<i>A. tassiliensis</i> n. sp.	3	0	18	79	33
<i>A. impalearis</i>	3	10	87	0	60
<i>A. spinosa</i>	8	15	77	0	13
<i>A. boueti</i> “castroviejoi” morphotype	11	22	67	0	9
<i>A. boueti</i>	17	72	11	0	18
<i>A. agama</i>	22	0	16	62	32

Table 5. Frequency (in %) of throat colouration characters in each taxon. W = white (no marbling); G = pale grey to brown grey marbling; D = dark grey, dark purple or black marbling; B = uniformly blue throat or blue marblings; O = uniformly orange to red throat or with orange to red marblings.

	Adult males						Adult females					
	W	G	D	B	O	n	W	G	D	B	O	n
<i>A. tassiliensis</i> n. sp.	0	17	26	0	56	23	0	25	75	0	0	16
<i>A. impalearis</i>	0	19	48	28	5	42	0	42	52	7	0	31
<i>A. spinosa</i>	10	10	0	0	80	10	25	50	0	0	25	4
<i>A. boueti</i> “castroviejoi” morphotype	0	57	43	0	0	7	0	50	50	0	0	4
<i>A. boueti</i>	40	47	13	0	0	15	57	37	3	3	0	35
<i>A. agama</i>	13	13	4	0	70	23	7	14	79	0	0	14

Table 6. Frequency (in %) of relative length of 3rd and 4th toes.

	3 rd > 4 th	3 rd = 4 th	3 rd < 4 th	n
<i>A. tassiliensis</i> n. sp.	0	17	83	6
<i>A. impalearis</i>	16	52	32	31
<i>A. spinosa</i>	0	21	79	14
<i>A. boueti</i> “castroviejoi” morphotype	0	75	25	8
<i>A. boueti</i>	70	19	11	27
<i>A. agama</i>	0	0	100	13

Comparison with similar species. Very similar to *Agama impalearis* (Fig. 5A) but the latter has a shorter, blunter head, 3rd and 4th toes often of equal length (see Table 6), a lower number of subdigital lamellae (12–16 under the 4th finger, 13.76 on average, 14–18 under the 4th toe, 15.84 on average, Table 3) and the vertebral stripe of males is whitish to yellowish, the throat frequently dark blue (never red) and the head yellow, brown, reddish-brown or blue.

Even more similar to the genetically closely related *A. spinosa* (Fig. 5B), but adult males of the latter exhibit a pure white crest and vertebral stripe, a much higher crest and the throat is more bloody red. In addition, most specimens (of all age and sex) of *A. spinosa* have a dark area just behind the gular fold (visible on preserved specimens) that is absent in *A. tassiliensis*.

Some specimens of *A. boueti* (Fig. 5C), especially the ‘castroviejoi’ morphotype (Fig. 5D) occurring in the western parts of the Sahara, can be very similar as well, but this species has a less slender head, a lower number of spines in the crest (5–9, 7 in average), less than 64 rows of dorsal scales (more than 62 in *A. tassiliensis*), and the head, throat or vertebral spine are never orange or red, but grey, greyish, whitish or yellowish. In addition, *A. boueti* (including the ‘castroviejoi’ morphotype) has a narrow (always 2 scales wide) and straight vertebral stripe, while *A. tassiliensis* has a more irregular, often poorly marked, and usually broader vertebral stripe.

Despite a similar general appearance, *A. agama* (Figs 6, 7) obviously differs from *A. tassiliensis* by a lower number of supra and infralabials, which are longer, a greater number of subdigital lamellae (16–22 beneath the 4th finger, average 19.68, 19–25 beneath the 4th toe, average 22.38), which are smooth while they are keeled (strongly so in *A. boueti*) in the members of the *A. impalearis* group, a different colouration for females and young specimens with turquoise blotches on the nape and frequently a diffuse orange zone on the flanks, and a different colouration

for nuptial males (wholly orange head and throat, black or blackish body, multicoloured tail with black, whitish, orange and black from base to tip, and lack of a coloured vertebral stripe).

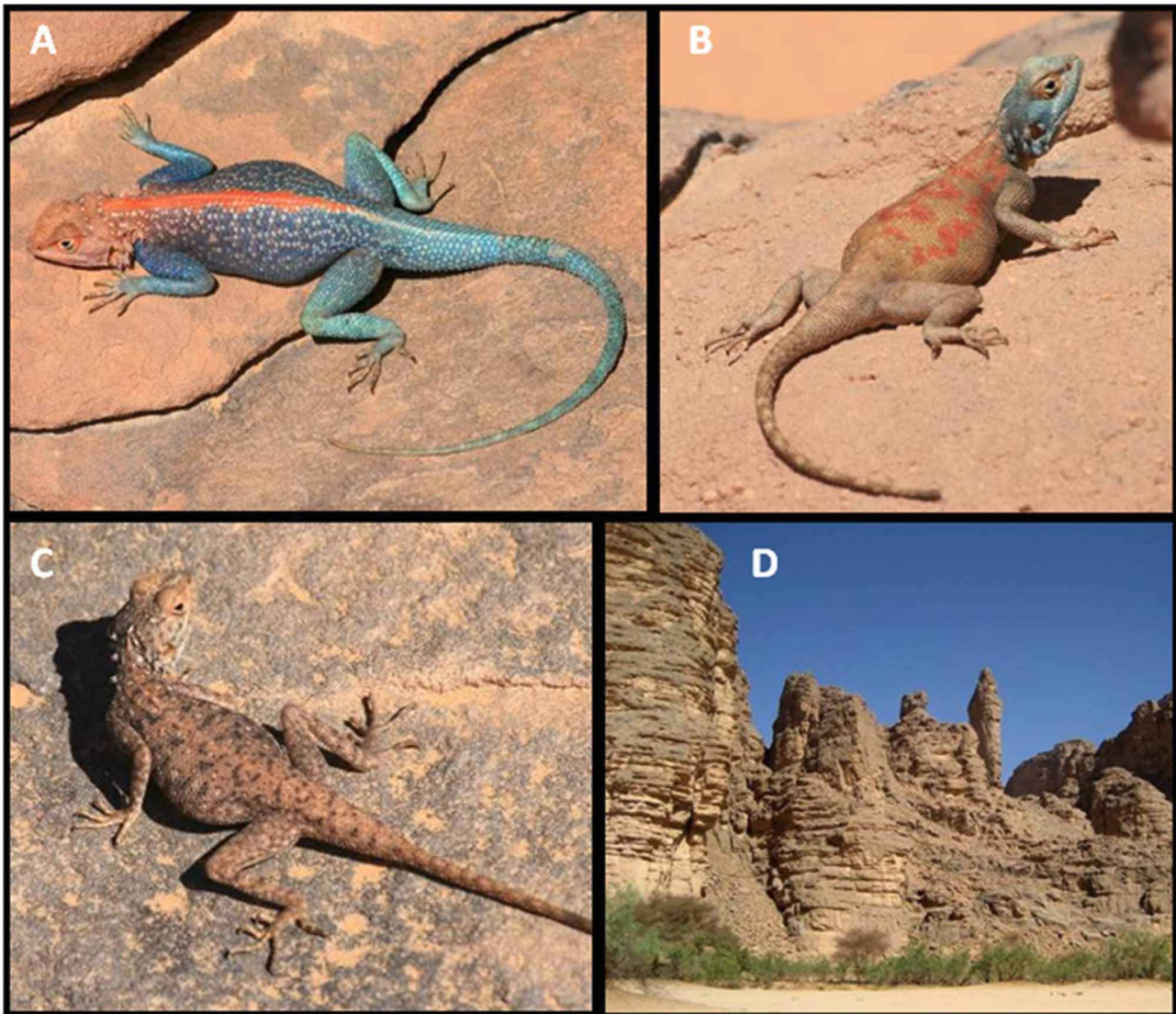


FIGURE 3. Variation in *Agama tassiliensis* n. sp. from Tassili n'Ajjer and Acacus Mountains. A: PGe.921, adult male in breeding colouration, Algeria, Tassili n'Ajjer, surroundings of Tamarit near Djanet, photo G. Vigo. Note the broad (3–4 scales wide), bright red vertebral stripe (can be orange to red in other specimens), a colour never encountered in the other members of the *A. implearis* group. In *A. agama* the crest area can be orange but this colour does not extend onto the back. B: PGe.991, gravid adult female, Algeria, Tassili n'Ajjer at 24.5847°N/9.3235°E, photo G. Vigo. Note that the colours are typical of gravid females of the *A. implearis* group, and very different from those of the *A. agama* group (cf. Fig. 6). C: PGe.999, juvenile, Libya, ca 100km N. of Ghat, Wadi Maghidet, photo G. Vigo. D: Habitat of *Agama tassiliensis* n. sp., Algeria, Tassili N'Ajjer, 5.5km downstream of Issendelene, photo P. Geniez.

Distribution. Only known from the central and southern Saharan mountains: the Acacus Mountains in south-western Libya, the Ahaggar Mountains (= Hoggar) and Tassili n'Ajjer in south and south-eastern Algeria, the Air Mountains in northern Niger and the Adrar des Iforas in north-eastern Mali (Fig. 8).

Ecology and conservation. The new species has only been seen on rocky substratum, especially prominent rocks, slopes, boulders, but also flatter areas such as rocky plateaux or river beds. It can occur on houses when they are adjacent to natural rocky habitats but nowhere truly colonizes human habitats, in contrast to *Agama agama* south of the Sahara. Like closely related species, it is a fully diurnal species that can bask in the sun even during the hottest hours of the day. It is usually common throughout its range, which lies in areas where human impact is still very limited. We are not aware of any direct threat, and the species does not seem to be specifically hunted, collected or destroyed by the local human populations in areas that we have visited. Its conservation status would thus probably qualify as “Least Concern” based on the current situation.

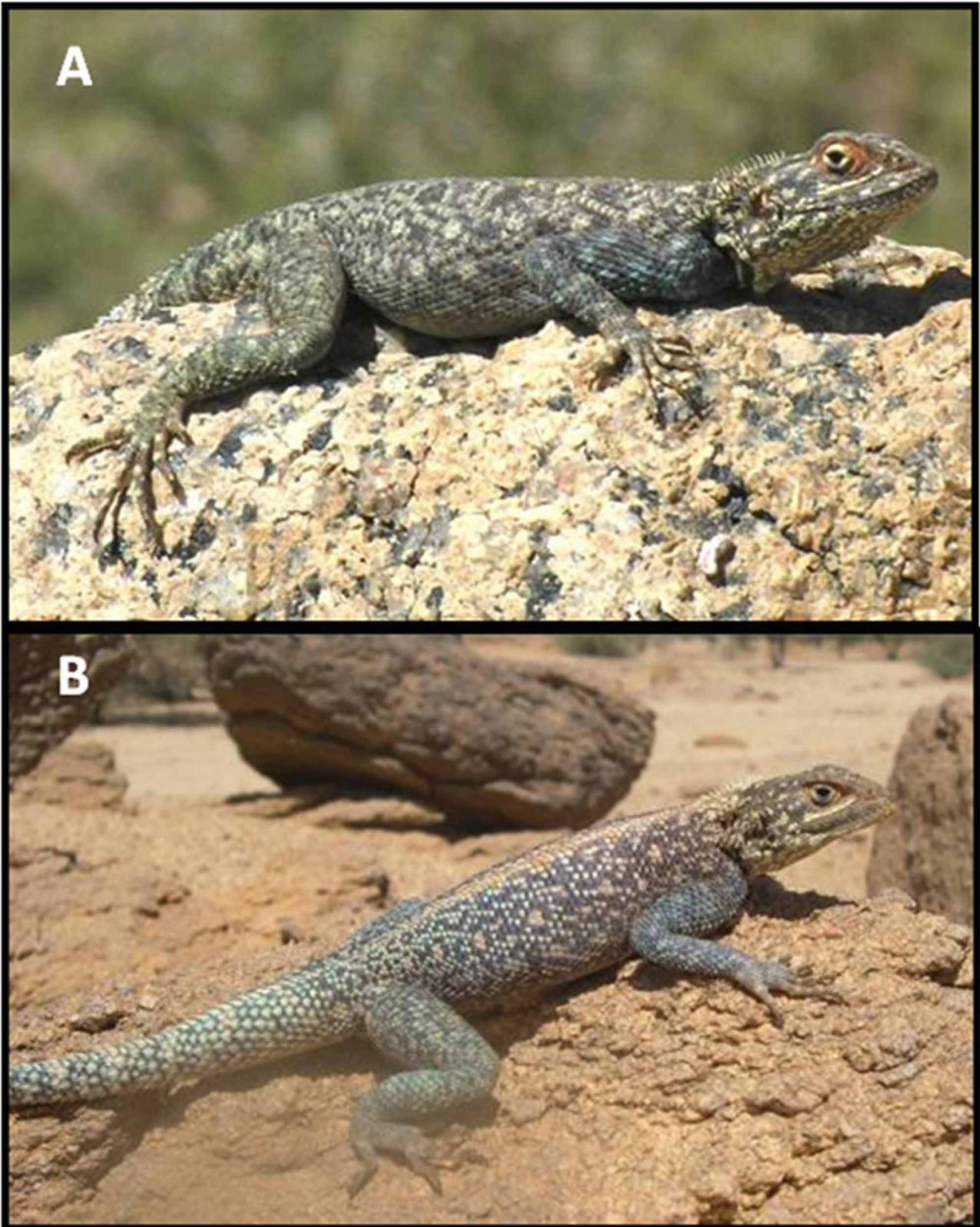


FIGURE 4. Variation in *Agama tassiliensis* n. sp. from Air Mountains, Niger. A: PGe.869, adult male from Idoukal'n Taghès, photo S. Sant. B: Brito code 362, adult male of from 20 km S. of Timia, photo J. C. Brito.

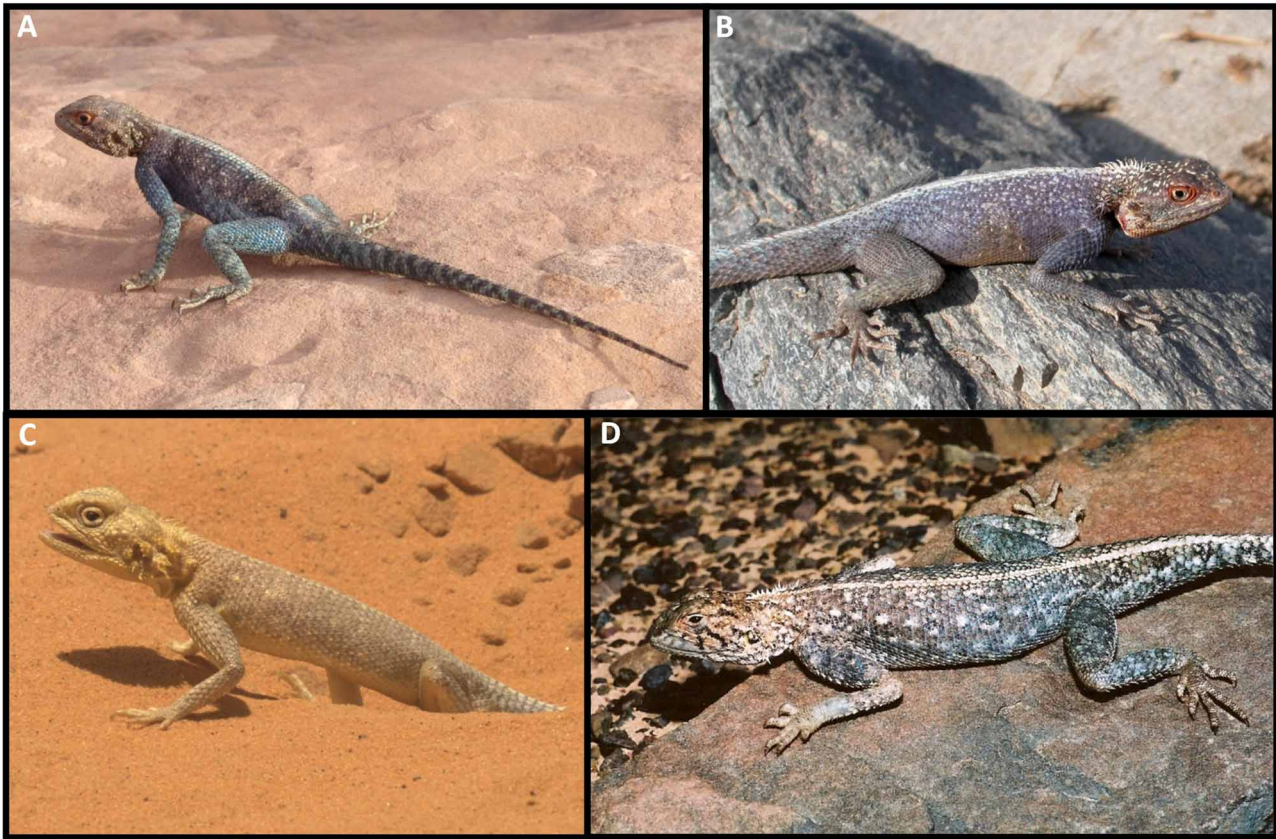


FIGURE 5. Adult males of the other members of the *Agama impalearis* group. A: *A. impalearis*, PGe.840, adult male, Algeria, Moudjebarah frescos near Ain Naga village, photo J. Viglione. Note the broad (3–4 scales wide), whitish vertebral stripe (orange to red in *A. tassiliensis* n. sp.) and the less pointed snout than in *A. tassiliensis*. B: *A. spinosa*, T3092, adult male. Egypt, Wadi el Gemal, photo P.-A. Crochet. Note the throat and the eye surround which are bloody red (not bright red, vermilion or orange as *A. tassiliensis* n. sp.), and the higher, pure white crest compared with *A. tassiliensis*. C: *A. boueti*, PGe.1002, adult male, Niger, Termit mountain, photo M. Ascani. Note the reduced number of crest spines (6 in this specimen), the relatively faded colouration and the uniformly pale throat. D: *A. boueti* of the “*castroviejo*” morphotype, PGe.847, adult male, Mauritania, track from Nouatil pass to Zerga, photo P. Geniez. Note the reduced number of crest spines (7 in this specimen) and the whitish vertebral stripe which is relatively narrow, not exceeding two scales in width.

Description of the holotype. Adult male in semi-nuptial colouration with the following features: SVL 166 mm, tail partly broken, pileus length 25.3 mm, pileus width 15.2 mm, foreleg length 51.1 mm, hind leg 81.3 mm, length of 1st to 5th fingers respectively 5.3, 8.7, 10.6, 10.2 and 8.2 mm, length of 1st to 5th toes respectively 6.8, 9.5, 13.7, 15.0 and 12.1 mm, 22 rows of pileus scales from the nose to the beginning of the crest and 18 between the eyes, 12 supralabials and 11 infralabials on each side, 67 rows of scales around midbody, 20 subdigital lamellae under the 4th finger and 23 under the 4th toe, a nuchal crest made of 13 vertical spines, 11 preanal pores, 8 spiny tufts on each side of the ear area and the neck, scales of the dorsum, forelegs, hindlegs and tail strongly and regularly keeled. Colouration (in the field, cf. Fig. 3): head reddish-brown with some yellowish small blotches, eye surround orange, dorsum dark purplish-grey, a broad dark orange vertebral stripe from the nape to the base of the tail extending from the orange crest, forelegs, hindlegs and tail greyish blue, fingers and toes yellowish, throat yellowish densely marbled purplish (orange on the gular fan), gular fold slightly darker, underparts whitish with a pale blue suffusion on the breast. GenBank accession number of the 16S gene fragment: JN665063.

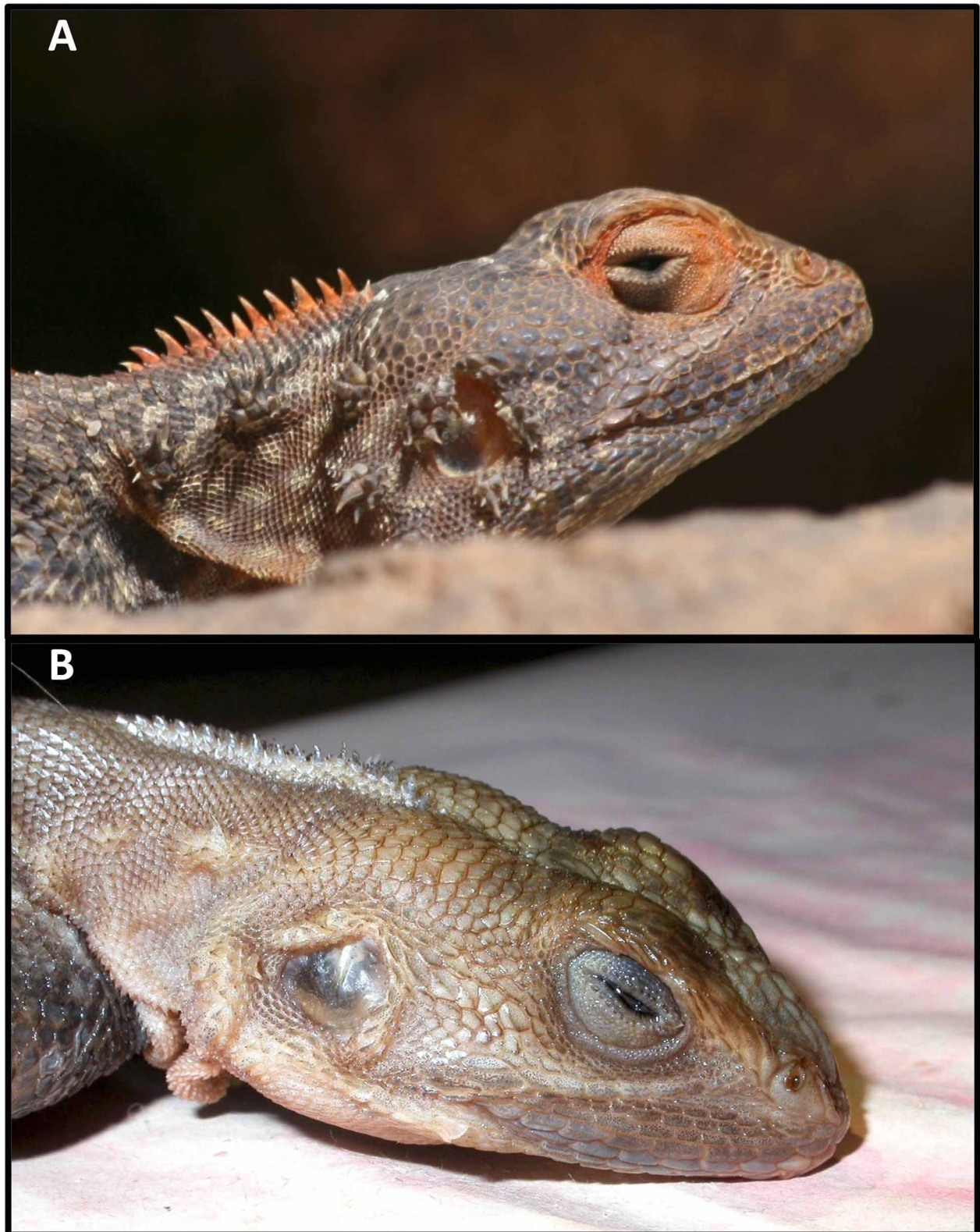


FIGURE 6. Comparisons of head characters in *Agama tassiliensis* n. sp. and *A. agama*. A: *A. tassiliensis* n. sp., PGe.998, non nuptial adult male from Algeria, Tassili n'Ajjer, 40 km NNW of Djanet, photo G. Vigo. Note the numerous, square-shaped labial scales (13 supralabials in this specimen), the numerous (12 in this specimen) and orange crest spines and the presence of spines around the ear opening. B: *A. agama*, MNHN 1990.4668, preserved adult male from Niger, Maradi, photo P.-A. Crochet. This species has fewer, more elongated labials (7 supralabials in this specimen), numerous crest spines (19 in this specimen) but a lower crest than *A. tassiliensis*. Note also the less developed spine tufts around the ear opening.

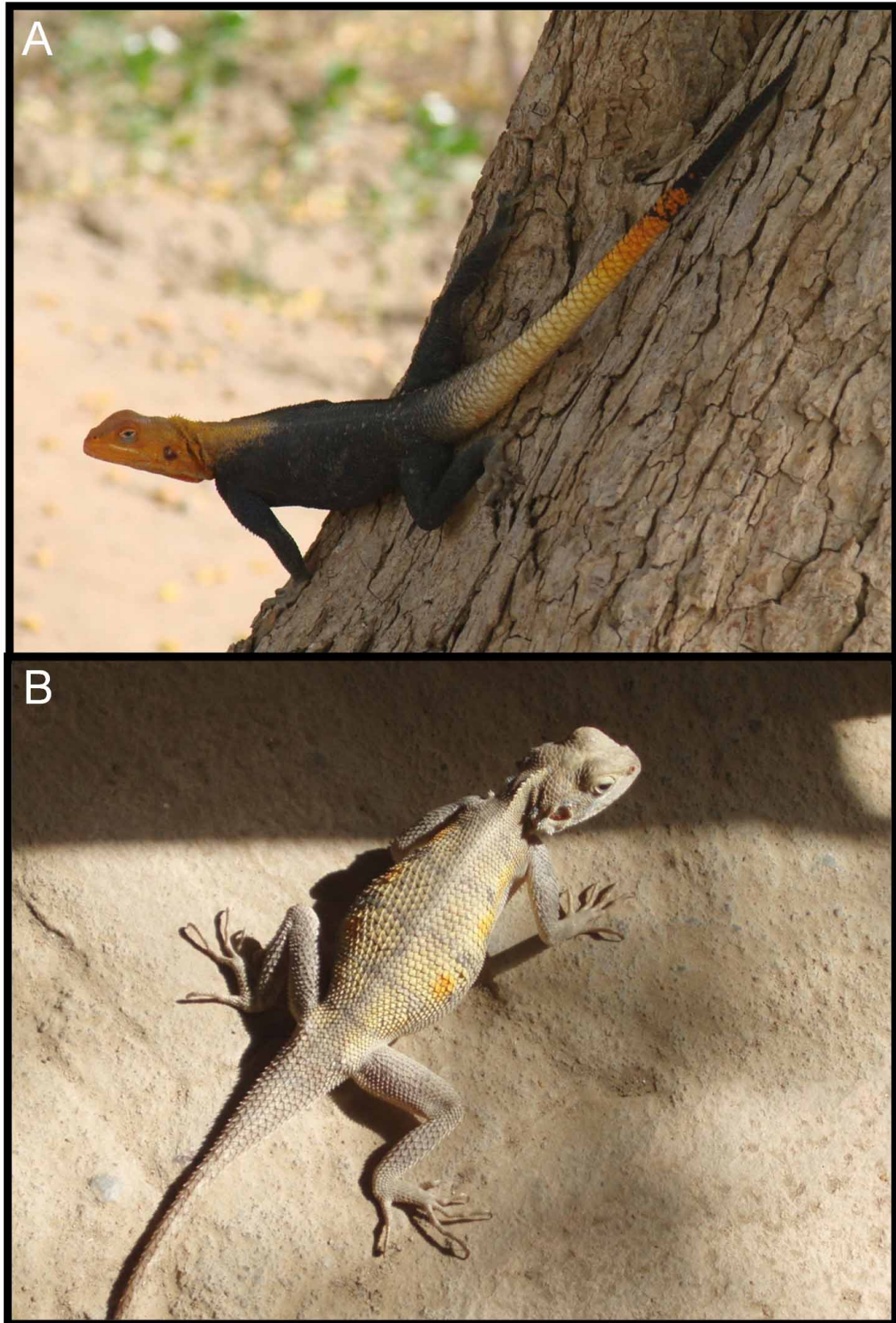


FIGURE 7. *Agama agama*. A: PGe.947, adult male in breeding colouration, Chad, N'Djamena, photo M. Braham-Chaouche. Note the orange colour of the head which does not extend onto the vertebral area, the uniformly black body and the yellow, orange and black tail, a colouration never found in members of the *Agama impalearis* group. B: PGe.1003, adult female, Mali, Djenné, photo A. Auricoste.

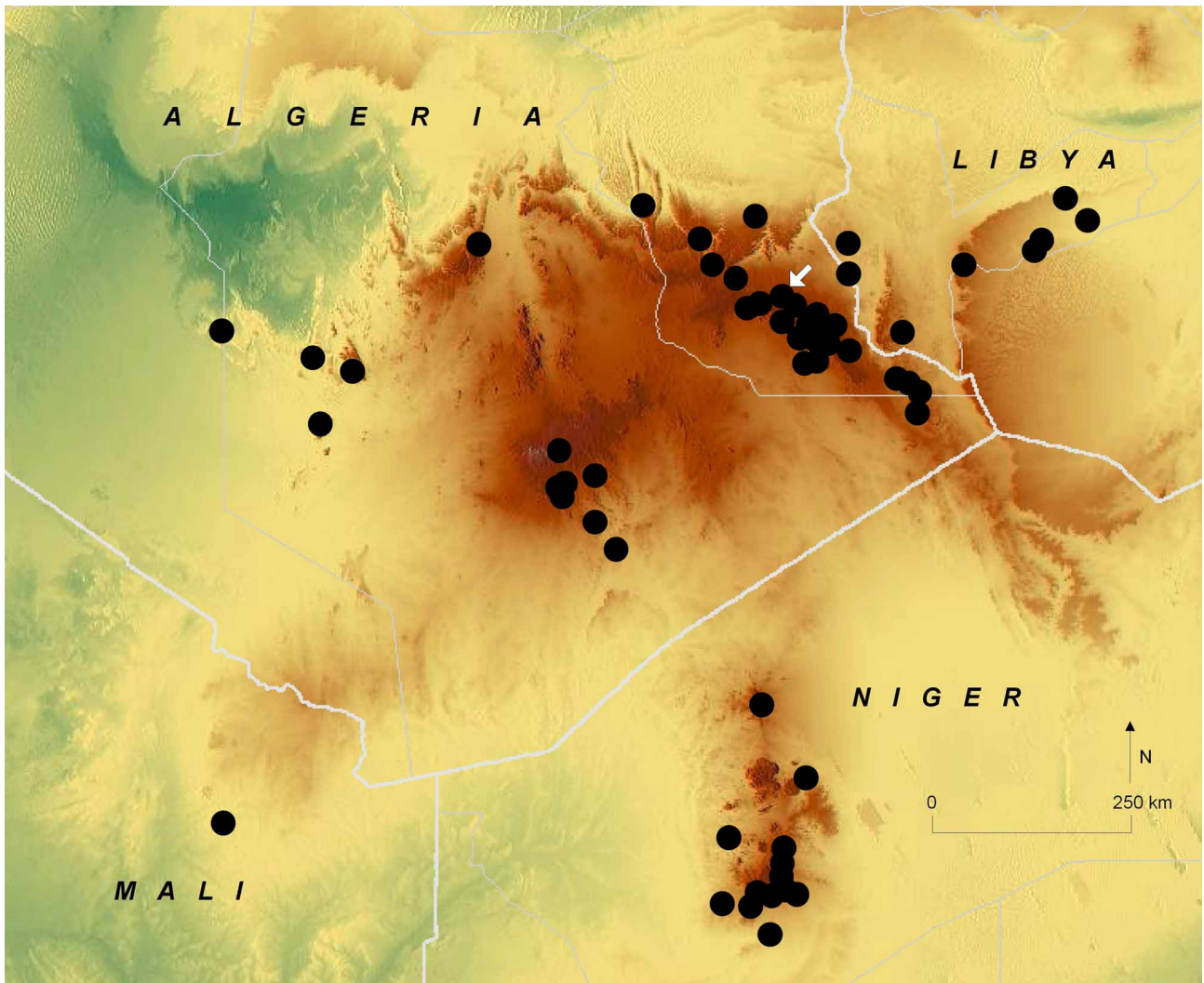


FIGURE 8. Distribution of *Agama tassiliensis* n. sp. based on the specimens or photographs that we have examined for this study. The arrow shows the type locality.

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Appendix. Specimens examined (as museum specimens or colour photographs) for the present study.

Locality, geographic coordinates in WGS84 decimal degrees, elevation, year and collector [museum or photographic number].

Note that many of the coordinates were extrapolated from the localities available with the specimens or photographs and thus do not correspond necessarily with the exact collection localities.

Agama tassiliensis n. sp.

Algeria: Approximately 260 km SSE of Reggane, 24.605°N/1.281°E, 390 m, 1962, H. Boutière [BEV.2760]; Adrar Taoudrat, 24.25°N/2.33°E, 720 m, 1965, Miss Cabi [MNHN 1965.200-201]; In Ziza (= Aguelmam I-n-Ziza, NW Ahaggar Mountains = Hoggar), 24.39°N/2.64°E, 485 m, Miss Cabi, 1965 [MNHN 1965.202]; Ahaggar Mountains, Mount Ilaman, 23.208°N/5.463°E, 2000 m [MNHN 1930.162]; Immidir, along the oued Tarit valley, 25.6654°N/ 4.5822°E, 1530 m, S. Sant, 2009 [PGe.912, 955]; 60-80 km SE of Tamanrasset, 22.36°N/6.01°E, 985 m, 2005, R. Le Fur [PGe.866]; Tamanrasset city, north-eastern exit, 22.800°N/5.541°E, 1390 m, 2007, O. Peyre [PGe.907]; Tamanrasset, slopes of the Djebel Adriane just north-east of the city, 22.807°N/5.540°E, 1402 m, 2007, G. Durand [PGe.908]; Ahaggar Mountains, oued Tahifet, east of Tamanrasset, 22.94°N/6.01°E, 1360 m, 2007, O. Peyre [PGe.909]; Ahaggar Mountains, at 21.8207°N/ 6.5226°E, 705 m, 2010, P. Lluch [PGe.922]; Ahaggar Mountains, at 25.9928°N/7.8407°E, 1310 m, 2007, G. Durand & O. Peyre [PGe.910]; Ahaggar Mountains, at 25.6063°N/8.0613°E, 1150 m, 2007, O. Peyre [PGe.910]; Tassili n'Ajjer, in the oued Tadjelahine valley, 26.25°N/6.63°E, 720 m, 2003, R. Le Fur [PGe.858]; Tassili n'Ajjer, 5 km SSW of Iherir, 25.3500°N/8.3911°E, 1428 m, 2009, P. Geniez, O. Peyre & P.-A. Crochet [holotype MNHN 2010.0632]; Tassili n'Ajjer, 5.5 km downstream of Issendelene, 24.9210°N/8.9600°E, 1150 m, 2009, P. Geniez, O. Peyre & P.-A. Crochet [PGe.911]; Tassili n'Ajjer, 1.2 km ENE of Télou Tedjert (36 km NW of Djanet), 24.7411°N/9.1867°E, 1185 m, 2009, P. Geniez, O. Peyre & P.-A. Crochet [BEV.10160]; Tassili n'Ajjer, oued Djerat, 26.16°N/8.61°, 850 m [MNHN 9003]; Tassili n'Ajjer, on the road near oued Tamanet, 24.8685°N/8.8263°E, 1150 m, 2010, O. Peyre [BEV.10928]; Tassili n'Ajjer, approximately 60 km N of Djanet, 25.01°N/9.17°E, 1700 m, 1988, P. Lluch [PGe.855]; Tassili n'Ajjer at 24.5847°N/9.3235°E, 1160 m, 2010, G. Vigo [PGe.991]; Tassili n'Ajjer, 40 km NNW of Djanet, 24.936°N/9.336°E, 1690 m, 2007, G. Vigo [PGe.997-998]; Tassili n'Ajjer, Jabbaren, 24.683°N/9.413°E, 1145 m, R. Le Fur [PGe.856-857], F. Moutou [PGe.859], M. Cheylan [PGe.865]; south of Adrar Adafar, 24.394°N/9.441°E, 990 m, 1962, H. Boutière [BEV.2761], south of Adrar Adafar, approximately at 24.4°N/9.5°E, 1050 m, 1962, H. Boutière [BEV.2762]; Tassili n'Ajjer, Djanet, 24.56°N/9.49°E, 1060 m [MNHN 1936.65]; Tassili n'Ajjer, 25 km N of Djanet, 24.8024°N/ 9.5355°E, 1630 m, 2010, G. Vigo [PGe.992]; Tassili n'Ajjer, plateau just 15 km E of Djanet, 24.52°N/9.61°E, 1500 m, 1993, P. Lluch [PGe.851-852]; Tassili n'Ajjer, reg of Tamarit near Djanet, 24.6034°N/9.6539°E, 1736 m, 2010, G. Vigo [PGe.921, 990]; Tassili n'Ajjer, oued Tin Itinen, 24.641°N/9.673°E, 1680 m, 2005, M. Cheylan [PGe.862-863, 906], Tassili n'Ajjer, Sefar, 24.670°N/9.736°E, 1545 m, 2005, M. Cheylan [PGe.864]; Tassili n'Ajjer, Tadrart at 24.0706°N/10.8028°E, 900 m, F. Begou-Pierrini [PGe.871], 2009, F. Dhermain [PGe.914]; Tassili n'Ajjer, Tadrart at 24.0482°N/10.8307°E, 880 m, 2009, F. Dhermain [PGe.915-916]; Tassili n'Ajjer, Tadrart at 24.0185°N/10.8894°E, 890 m, 2009, F. Dhermain [PGe.917]; Tassili n'Ajjer, canyon of In Djerane near Tin-Merzouga, 23.832°N/10.91°E, 1000 m, 2008, G. Vigo [PGe.993-996].

Libya: Erg Titersine, 40-80 km NNW of Ghat, 25.51°N/9.94°E, 647 m, 2004, P. Orsini [PGe.860]; Wadi Meseknan on the Messak Settafet plateau (between Ghat and Ubari), 25.5°N/11.5°E, 1035 m, 2006, R. Le Fur [PGe.867]; Wadi Matendus, 25.76°N/12.16°E, 675 m [ZFMK.63669]; Wadi Tekniwen on the Messak Settafet plateau, 26.1580°N/12.4858°E, 680 m, 2010, Y. Gauthier [PGe.920]; Wadi de Maghidet, 100 km N of Ghat, 25.8164°N/9.9704°E, 700 m, 2010, G. Vigo [PGe.999]; Acacus Mountains, Fozziaren Arch, 56 km SE of Ghat, 24.684°N/10.634°E, 860 m, 2002, A. Crochet [PGe.854].

Niger: Air Mountains, Kakimi, near Tafedek (50 km NNW of Agadez), 17.367°N/7.767°E, 510 m, 1990, A. Foucart [BEV.2763]; Air Mountains, exit of oued Temet, on the foothills of Mount Greboun, 20.212°N/8.664°E, 1055 m, 1990, A. Foucart [BEV.2765-2766]; Air Mountains, tributary of the Zagado river, at Kogo (foothills of Taghmert), 19.002°N/ 9.319°E, 765 m, 1990, A. Foucart [BEV.2764]; Tabelot area, 17.57°N/8.94°E, 840 m, 2005, B. Delprat [PGe.848-850]; Bagzane Mountains, Tadara, 17.3878°N/8.3782°E, 800 m, 2006, S. Sant [PGe.868]; near Idoukal'n Taghès, 17.7940°N/ 8.7205°E, 1740 m, 2006, S. Sant [PGe.869]; canyon of Ighalabélabène, 17.6857°N/8.8056°E, 1500 m, 2006, S. Sant [PGe.913]; Air Mountains, 5 km S of Timia (Agadez), 18.0984°N/8.7667°E, 1050 m, 2004, J.C. Brito [BEV.10433, Brito code 384]; Air Mountains, 10 km S of Timia (Agadez), 18.0125°N/8.7410°E, 1020 m, 2004, J.C. Brito [Brito code 367]; Air Mountains, 15 km S of Timia (Agadez), 17.9984°N/8.7540°E, 1110 m, 2004, J.C. Brito [Brito code 366]; Air Mountains, 20 km S of Timia (Agadez), 17.9856°N/8.7651°E, 1105 m, 2004, J.C. Brito [BEV.10432, Brito code 362]; Tourayet (Bilma-Agadez), 16.9517°N/8.6741°E, 540 m, 2004, J.C. Brito [BEV.10431, Brito code 343].

Mali: Adrar des Ifoghas, cercle de Kidal, 18.44°N/1.39°E, 575 m, 1987, Ehya Ag-Sidiyene [MNHN 1987.1863-1864].

Agama impalearis.

Algeria: Biskra, 34.85°N/5.73°E, 115 m, de Vauloger [MNHN 1974.338]; Moudjebarah frescos, Aïn Naga village, 34.691°N/ 6.086°E, 1 m, 2007, J. Viglione [PGe.840]; Djebel Elktef, Stitten, 33.77°N/1.23°E, 1400 m, 2007, J. Viglione [PGe.842]; Krekda, 31.87°N/0.76°E, 645 m, 2007, J. Viglione [PGe.841]; El Bayadh, 32.35°N/0.61°E, 810 m, 2007, J. Viglione [PGe.957]; Djelfa, 34.67°N/3.25°E, 1160 m, 2007, O. Peyre [PGe.958]; near Oran, 35.71°N/0.66°W, 110 m, 2004, O. Peyre [PGe.824]; 9 km N of Aïn Ourka, 32.02°N/0.08°W, 1100 m, 2006, O. Peyre [PGe.839]; 20 km W of Aïn Sefra,

32.69°N/0.78°W, 1170 m, 2005, O. Peyre [PGe.832]; 60 km W of Aïn Sefra, 32.76°N/1.22°W, 1370 m, 2004, O. Peyre [PGe.898]; Tlemcen area, 34.88°N/1.31°W, 800 m, 2008, B. Samraoui [PGe.959]; Algeria, without locality [MNHN 6927].

Morocco: Figuig palm grove, 32.10°N/1.23°W, 900 m, 2005, J. Cavailhes [PGe.831]; De Folia, near Figuig, 32.17°N/1.38°W, 950 m, 1982, J.-A. Rioux [BEV.2718-2719]; Djebel Grouz, 1 km S of Aïn Tanazara, 32.1943°N/1.9439°W, 1377 m, P. Geniez [PGe.825]; alfa steppe of Hassi El-Abiod (SE of Oujda), 34.8086°N/1.9152°W, 1170 m, 2004, P. Geniez [PGe.826]; Beni Snassen Mountains, 5 km N of Taforalta, 34.88°N/2.41°W, 485 m, 1988, P. Geniez [PGe.951]; approximately 50 km S of Gourrama, 32.01°N/3.95°W, 1150 m, 1962, J. Bons [BEV.2704, 2738]; palm grove at the oued Ziz bridge, north of Erfoud, 31.55°N/4.18°W, 824 m, 1962, J. Bons [BEV.2705]; Blarhima, near Aoufouss, 31.63°N/4.20°W, 890 m, 1972, J.-A. Rioux [BEV.2721-2722]; 6 km SW of Talrhemt, 32.56°N/4.49°W, 1800 m, 1962, J. Bons [BEV.2606]; Tizi-n-Talremt (N of Errachidia), 32.58°N/4.53°W, 1907 m, 1990, P. Geniez [PGe.810]; road from Fès to Taza, crossroad to the Moulay Idriss Premier dam, 34.12°N/4.62°W, 340 m, P. Escudie [PGe.948]; Ksar Set, approximately 5 km ENE of Tinejda, 31.54°N/5.01°W, 980 m, 1962, J. Bons [BEV.2740]; near Alnif, 31.12°N/5.17°W, 880 m, 2003, S. Doglio [PGe.949]; Rif Mountains, Beni Azi, bank of oued Laou, 35.26°N/5.27°W, 300 m, 1976, C.P. Guillaume [BEV.2729]; 15 km N of Azrou, 33.5427°N/5.3169°W, 1417 m, 2004, J.C. Brito [BEV.10430]; downstream exit of the Todgha gorges, 31.556°N/5.581°W, 1380 m, 1962, J. Bons [BEV.2734]; 14 km past El-Arba towards N'Kob, 30.82°N/5.65°W, 900 m, 1988, P. Geniez [PGe.804]; Tajalachte (Djebel Sagho), 31.06°N/5.88°W, 1555 m, 2005, A. Qninba [PGe.833]; Djebel Kebir near Tangier, 35.78°N/5.88°W, 150 m, 2003, D. Donaire [PGe.830]; Oulmès, 33.43°N/6.02°W, 1257 m, 1957, 1960, 1961, 1962 and 1963, J. Bons and R. Guillaume [BEV.2558, 2560, 2561, 2570, 2580, 2582, 2583, 2590, 2591, 2595, 2596, 2598, 2602-2604, 2611, 2616, 2662-2664, 2667, 2669, 2670, 2685, 2693, 2725]; Tarmilate, 33.40°N/6.07°W, 1000 m, 1962, J. Bons [BEV.2677-2678]; Tarmilate, wadi downstream of the dam, 33.334°N/6.036°W, 630 m, 1962, J. Bons [BEV.2687]; 6.9 km past the crossroad to the mines of Tazoult towards Zaouia Ahansal, 31.9511°N/6.0770°W, 1507 m, 2004, P. Geniez [PGe.827]; Oued El-Mahasser where crossed by the track from Aïn Sidi Abd-er-Rhamane to Zaouia Sidi Abd-en-Nebi (W of Mhamid), 29.91°N/6.15°W, 520 m, 2004, A. Cluchier [PGe.834]; foothills of the Djebel Bani, at 30.0947°N/6.2369°W, 832 m, 2003, A. Cluchier [PGe.822]; near Agdz, 30.71°N/6.45°W, 1000 m, 1998, R. Le Fur [PGe.815, 823]; 8 km past Agdz towards Ouarzazate, 30.71°N/6.59°W, 1600 m, 1988, P. Geniez [PGe.805]; 49 km past Agdz towards Tazenakht, 2 km past the crossroad to Tasla, 30.54°N/6.85°W, 1387 m, 1990, M. Geniez [PGe.809]; Aïn El-Hallouf canyon, approximately 12 km S of Rabat, 33.88°N/6.80°W, 150 m, 1989, P. Geniez [PGe.807]; south of Khouribga, 32.78°N/6.86°W, 655 m, 2004 [PGe.897]; north of Khouribga, 33.04°N/6.88°W, 640 m, 2004 [PGe.895]; Khattouat plateau, NW of Khouribga, 33.27°N/7.02°W, 580 m, 2004 [PGe.896]; Tizi-n-Bachkoum (Anti-Atlas), 30.70°N/7.28°W, 1700 m, 2002, M. TARRIER [PGe.819]; Taliouine, 30.53°N/7.92°W, 1040 m, 2002, M. TARRIER [PGe.820-821]; Akka Ighene, 29.99°N/7.53°W, 776 m, 1986, J.-A. Rioux [BEV.2754-2755]; Djebel Sirwa, 30.72°N/7.81°W, 1900 m, 2002, J. Delacre [PGe.817]; Ighil (ca 25 km S of Djebel Toubkal), 30.95°N/7.85°W, 1500 m, 1986, J.-A. Rioux [BEV.9285]; Aguer gour (Haut Atlas, E of Asni), 31.28°N/8.08°W, 950 m, 1985, P. Geniez [PGe.950]; 15 km before Asni from Ouirgane (Haut Atlas), 31.18°N/8.08°W, 870 m, 1971, A. Demaison [BEV.2715]; 8 km past Ijoukak towards Asni (Haut Atlas), 31.06°N/8.14°W, 1073 m, 1995, P.-A. Crochet [BEV.2759]; Oued Tata, 9 km past Souk-Tleta-Tagmoute towards Tata, 29.92°N/8.21°W, 1025 m, 1992, P. Geniez [PGe.811]; Amizmiz, 31.22°N/8.24°W, 1100 m, 1971, A. Demaison [BEV.2716-2717]; 15 km past Igherm towards Souk-Tleta-Tagmoute by the track 7160, 30.03°N/8.36°W, 1561 m, 1990, M. Geniez [PGe.953]; 10 km past Chichaoua towards Marrakech, 31.5742°N/8.6656°W, 350 m, 2007, P. Geniez [PGe.843-844]; near Aït-Baha along the road to Tafraoute (Anti-Atlas), 29.99°N/9.03°W, 1025 m, 2005, B. Baud [PGe.900]; Aït-Baha (Anti-Atlas), 30.08°N/9.15°W, 550 m, 2002, J. Delacre [PGe.818]; 1 km past Aït-Baha towards Tanalt (Anti-Atlas), 30.065°N/9.180°W, 525 m, 1996, P.-A. Crochet [BEV.2758]; 5 km N of Dar Lahoussine (Anti-Atlas, S of Aït-Baha), 29.94°N/9.29°W/650m, 1995, P. Geniez [PGe.813-814]; between El Jorf and Ademine forest house (Souss valley), 30.38°N/9.37°W, 105 m, 1990, M. Geniez [PGe.956]; 5 km past Targamait towards Guelmim, 28.8469°N/9.6148°W, 503 m, 2004, P. Geniez [PGe.828]; 11 km past Ounagha towards Essaouira, 31.5157°N/9.6540°W, 135 m, 2007, P. Geniez [PGe.838]; Paradis-Plage, south of N'Zala-de-Tiguert (N of Agadir), 30.53°N/9.69°W, 10 m, 1984, P. Geniez [PGe.803]; 14 km past Taïdalt towards Aouinet Torkoz, 28.66°N/9.71°W, 495 m, 1990, M. Geniez [PGe.952]; 33 km before Bou Izakarn from Tiznit, 29.4075°N/9.7180°E, 778 m, 2005, A. Cluchier [PGe.835-836]; surroundings of Tiznit, 29.72°N/9.72°W, 224 m, 2007, P. Evrard [PGe.954]; 15 km before Bou-Izakarn from Tiznit by the Tizi-n-Mighert, 29.40°N/9.74°W, 975 m, 1989, P. Geniez [PGe.808]; Rasoua village, 9 km S of Essaouira towards Agadir, 31.43°N/9.78°W, 75 m, 1988, P. Geniez [PGe.806]; Oued Siyad, 4 km E of Fask, 28.975°N/9.798°W, 340 m, 2007, R. León [PGe.899]; Cap Rhir, road from Agadir to Tamanar, 30.62°N/8.89°W, 40 m, 1971, A. Demaison [BEV.2714]; Souk El-Arba-des-Akhasass (Sidi Ifni area), 29.27°N/10.12°W, 286 m, 1972, J.-C. Bonaric [BEV.2739]; 18 km past Goulimine towards Tantan, 28.89°N/10.19°W, 250 m, 1992, M. Geniez [PGe.812]; Oued Draa at El-Aïoun du Drâa, 28.48°N/10.67°W, 220 m, 1974, G. Delye [BEV.2736]; 36 km before Abatteh from Tantan, 28.0954°N/11.3329°W, 65 m, 2002, P.-A. Crochet [PGe.816]; 12 km past El-Watia towards Laayoune, 28.4061°N/11.4037°W, 28 m, 2010, P.-A. Crochet [BEV.10854]; 18 km past Tantan-Plage (= El-Watia) towards Tarfaya, 28.3846°N/11.4257°W, 30 m, 2005, A. Cluchier [PGe.837]; desert south of the road, 9 km past Sidi Akhfennir towards Tarfaya, 28.0569°N/12.1339°W, 10 m, 2004, P. Geniez [PGe.829]; Morocco, without precise locality, J. Bons, J.-A. Rioux [BEV.2706, 2707, 2723, 2727, 2728, 2731, 2735].

Agama spinosa.

Egypt: Djebel Elba, 22.18°N/36.35°E [ZFMK.44174]; Wadi el Gemal, at 24.5640°N/34.9097°E, 200 m, 2009, P.-A. Crochet [BEV.T3092]; Wadi el Gemal, at 24.5593°N/34.9286°E, 180m, 2009, P.-A. Crochet [BEV.T3093].

Sudan: Arbeiat near Port-Sudan, 19.81°N/37.07°E, 110 m [ZFMK.40124-40127]; Erkowit (= Ar Kaweit), 18.767°N/31.117°E, 1110 m [ZFMK.32425-32433, 35375-35377, 38400].

Ethiopia: Alf Abed (locality not found) [ZFMK.19452-19453].

Agama boueti

Algeria: Ahaggar Mountains, In Abezou (= Irhzer oua-n-Abezzou), 24.083°N/5.050°E, 1050 m [MNHN 1936.64].

Mauritania: Tagant, Inikchâne, 18.3117°N/12.2341°W, 160 m, 2009, J.C. Brito [Brito code 2994]; Tagant, Oued Akneiker, 17.6672°N/12.1971°W, 250 m, 2009, J.C. Brito [Brito code 3158]; Tichit - Oualata, between Dahr Oualata and Guelb Aiche, 17.4074°N/7.2216°W, 250 m, 2003, J.C. Brito [Brito code 49]; Rosso - Nouakchott, 80 km S of Nouakchott, 17.3927°N/16.0621°W, 10 m, 2004, J.C. Brito [Brito code 489-490]; Tagant, extreme S of oued Lardedia, 17.3727°N/11.9158°W, 440 m, 2009, J.C. Brito [Brito code 3224]; Brakna, Chelkhet edh Dhîba, 17.1159°N/13.5752°W, 30 m, 2009, J.C. Brito [Brito code 3478]; Brakna, Oued Katchi, 17.0822°N/13.6357°W, 30 m, 2009, J.C. Brito [Brito code 3480]; Brakna, Poleti, 16.8361°N/13.2499°W, 90 m, 2009, J.C. Brito [Brito code 3474]; Brakna, oued Saouat, 16.7733°N/13.2103°W, 100 m, 2009, J.C. Brito [Brito code 3472]; Rosso - Kaedi, Lake Rkiz, SE of Mrea, 16.8912°N/15.2031°W, 10 m, 2007, J.C. Brito [Brito code 1292-1293, 1295-1296]; Rosso - Kaedi, E of Leroug, 16.7497°N/14.7339°W, 20 m, 2007, J.C. Brito [Brito code 1305]; Rosso - Kaedi, E of Bababé, 16.3008°N/13.8749°W, 40 m, 2007, J.C. Brito [Brito code 1313]; Between the Chott Boul and Dar Salam, 16.60°N/16.43°W, 4 m, 1994, C. Arvy and I. Ineich [MNHN 1996.2878-2880, 2883-2889, 2891-2892, 2895-2896, 2898, 2900-2901]; Mauritania without locality, 2007, "JFD" [PGe.901].

Niger: Agadez - Timia, 5 km S of Elkimi, 17.7108°N/8.2742°E, 700 m, 2004, J.C. Brito [Brito code 389]; Agadez - Timia, 50 km N of Agadez, 17.3025°N/8.1702°E, 660 m, 2004, J.C. Brito [Brito code 353a-b]; Aoudiras (= Aouderas), 17.634°N/8.409°E, 795 m, ca 1939, H. Lhote [MNHN 1932-129]; Termit Mountains, 16.07°N/11.27°E, 400 m, 2009, L. Chirio [PGe.904-905]; Gao (= Kao), 15.42°N/5.75°E, 470 m, de Gironcourt [MNHN 1910.6-8]; Ibohamane, on sandy ground, 14.80°N/5.93°E, 430 m, 1989, L. Chirio [MNHN 1990.4680]; near Malbaza, 160 km E of Maradi, 13.95°N/5.51°E, 310 m, 1986, L. Chirio [MNHN 1989.664]; track from Maradi to Dakoro, 13.95°N/6.98°E, 350 m [MNHN 1990.4685, 4687, 4688, 4690]; near Zinder, 13.79°N/8.98°E, 470 m, 1986, L. Chirio [MNHN 1989.665, 1990.4682]; Takieta, 13.68°N/8.53°E, 440 m [MNHN 1990.4684]; Kouré (SE of Niamey), 13.33°N/2.59°E, 255 m, 2010, L. Chirio [PGe.902-903]; Tahoua - Niamey, 20 km W of Birni N'Konin, 13.7872°N/4.9691°E, 290 m, 2004, J.C. Brito [Brito code 402]; Tahoua - Niamey, 15 km W of Birni N'Konin, 13.7859°N/5.0128°E, 270 m, 2004, J.C. Brito [Brito code 400].

Mali: Gao, 16.27°N/0.03°W, 250 m, before 1917, Dr. Bouet [MNHN 1917.45], syntype of *Agama boueti*.

Agama boueti, "castroviejoi" population

Mauritania: A few kilometers south of Aghmakoum at 21.1539°N/11.9103°W, 350 m, 2006, P.-A. Crochet [BEV.9132-9133]; Guelta of Eguemoun, 3 km W of Jreïf, 20.8710°N/12.4841°W, 322 m, 2006, P. Geniez [BEV.9174]; 28 km past Chinguetti towards Atar, 20.5619°N/12.5470°W, 608 m, 2005, P. Geniez [BEV.1111]; 44 km past Chinguetti towards Atar, 20.5459°N/12.6895°W, 703 m, 2005, P. Geniez [PGe.846]; track west of Zerga, 32 km ESE of Atar, 20.4385°N/12.7527°W, 649 m, 2007, P. Geniez [PGe.847]; Berbera, 19.9845°N/12.8221°W, 327 m, 2007, O. Peyre [BEV.10031-032]; 39 km past Akjoujt towards Atar, 19.9249°N/14.0653°W, 127 m, 2006, P.-A. Crochet [BEV.9118]; 10 km NW of Akjoujt, 19.8320°N/14.3678°W, 146 m, 2003, J.-F. Trape. Adrar, Aoueloul crater, 20.2426°N/12.6757°W, 570 m, 2008, J.C. Brito [Brito code 1919]; Adrar, 25 km SE of Aoueloul crater, 20.1455°N/12.5493°W, 450 m, 2008, J.C. Brito [Brito code 1922-1923]; Adrar, Oûdei Eker, 19.7643°N/13.0818°W, 170 m, 2008, J.C. Brito [Brito code 1841]; Dhar Chinguetti, on the road between Atar and Tidjikja, 20.4425°N/12.8235°W, 673 m, 2002, J.M. Padiàl [MNCN 41778-41779].

Agama agama

Chad: Fort Lamy (= N'Djamena) area, 12.14°N/15.04°E, 300 m, 1965, Stauch [MNHN 1966.303 BIS]; N'Djamena, 12.105°N/14.045°E, 295 m, 2009, M. Braham-Chaouche [PGe.946-947].

Niger: Tahoua - Niamey, 50km S of Tahoua, 14.5085°N/5.3770°E, 330 m, 2004, J.C. Brito [Brito code 399]; Simiri, 14.133°N/13.083°E, 280 m, 2004, J.-F. Trape [PGe.932-937]; track from Maradi to Dakoro, 13.95°N/6.98°E, 350 m, 1990, L. Chirio [MNHN 1990.4686-4687]; Maradi, walls of houses, 13.48°N/7.10°E, 352 m, 1990 and 1996, L. Chirio [MNHN 1990.4668-4674, 1996.2650-2651].

Mali: Southeastern Mali at 17.02°N/2.00°E, 350 m, 2004, J.-F. Trape [PGe.938]; Sévaré, near Mopti airport, 14.5201°N/4.09°W, 271 m, 2005, P. Beaubrun [BEV.8744]; F. Speyser [BEV.8869]; Mopti, 14.483°N/4.183°W, 270 m, 2005, A. Auricoste [PGe.943, 945]; Lanine Bougou, 14.067°N/6.033°W, 280 m, 2003, J.-F. Trape [PGe.926-931]; Bamako - Kayes, 210 km E of Kayes, 14.5115°N/9.7027°W, 240 m, 2004, J.C. Brito [Brito code 451]; Mosque of Djenné, 13.905°N/4.556°W, 275 m, 1980, J.-A. Mateo [PGe.960], 2005, P. Beaubrun [PGe.941]; Missira, 13.71°N/8.44°W, 330 m, 1986 [MNHN 1986.851-854]; Sandstone steep slopes at Baguineda, 30 km E of Bamako along the road to Ségou, 12.523°N/7.775°W, 350 m, 1994, J. Cuisin, B. Sicard & M. Tranier [MNHN 1994.6575, 6578].

Mauritania: Assaba, Tékent, 16.9043°N/12.8197°W, 10 m, 1990, J.C. Brito [Brito code 3464-3465]; Rosso - Kaedi, Lake Rkiz, SE of Mrea, 16.8912°N/15.2031°W, 10 m, 2007, J.C. Brito [Brito code 1297]; Rosso - Kaedi, Toldé Boussobé, river Senegal, 16.4152°N/14.0812°W, 20 m, 2007, J.C. Brito [Brito code 1308]; Hodh El Gharbi, 15 km W of Tîntâne,

16.3829°V/10.2871°W, 220 m, 2008, J.C. Brito [Brito code 2228]; Kaedi - Kankossa, SE of Lekseiba, 16.1728°N/13.0198°W, 30 m, 2007, J.C. Brito [Brito code 1320-1321]; Kankossa - Kiffa, N of Kankossa, 16.0768°N/11.5117°W, 70 m, 2007, J.C. Brito [Brito code 1362, 1364].

Senegal: Savannah with baobabs, some kilometers north of Mbour, along the road N1, 14.48°N/16.99°W, 10 m, 2002, M. Geniez [PGe.923].

France: Sète, in the harbour (département of Hérault, southern France), 43.401°N/3.710°E, 2 m, translocated individuals, probably from Ivory Coast, 2002, F. Catzefflis [PGe.925], 2002, P. Mayet [PGe.924], 2004, P. Mayet [PGe.961].

La Réunion island: introduced population, Le Port, 20.94°S/55.30°E, 30 m, 2008, J.-M. Probst [PGe.939-940, and 2 specimens without number].