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Studies on African *Agama* VI. Taxonomic status of the West African *Agama* (Sauria: Agamidae) with prominent tail crests: *Agama boulengeri* Lataste 1886, *Agama insularis* Chabanaud, 1918 and *Agama cristata* Mocquard, 1905

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Abstract. This publication reviews the taxonomy of three West African *Agama* species, *A. boulengeri*, *A. cristata*, and *A. insularis*, each characterized by a prominent tail crest in adult males. Following the results from morphological and genetic analyses, *Agama insularis* is recognized as a synonym of the revalidated *Agama cristata*, whereas this species is clearly distinct from *Agama boulengeri*. We present a detailed distribution map for these *Agama* species, as well as for *A. weidholzi*. Following the results of recent publications, *Agama atra knobeli* is herein regarded as a full species.

Key words. Africa, Guinea, Los Islands, Île de Roumé; Sauria, Agamidae, *Agama cristata*, *A. insularis*, *A. boulengeri*, *A. knobeli*, *Agama weidholzi*.

Introduction

Despite an increasing amount of work on the taxonomy and phylogeny of African lizards in the genus *Agama* (Böhme et al. 2005, Padial 2005, Wagner 2007, Wagner et al. 2008a, Wagner et al. 2008b, Wagner et al. 2009a, Wagner et al. 2009b) several species are only poorly known, and the validity of some taxa remains questionable (e.g. *A. bocourti* Rochebrune, 1884; *A. bottegi* Boulenger, 1897; *A. cornii* Scortecci, 1928; *A. insularis* Chabanaud, 1918 and *A. agama boensis* Monard, 1940 [regarded as a synonym of *A. weidholzi* by Grandison 1969]). Many species are only diagnosable based on adult male coloration (Loveridge 1933, Thys van den Audenaerde 1963, McLachlan 1981, Böhme et al. 2005, Wagner 2007, Wagner et al. 2008a, Wagner et al. 2008b), and the lack of appropriate comparative material coupled with inadequate descriptions of the adult coloration in life prevents formal taxonomic evaluations.

Three species in West Africa are characterized by possessing a prominent tail crest in adult males: *Agama boulengeri*, *A. insularis* and *A. cristata*. The taxonomic status of these taxa is the focus of this study.

Agama insularis, was described by Chabanaud (1918) on the basis of a juvenile and a subadult female collected by Dr. G. Bouet in 1914 on Île Roumé, which is part of the Îles de Los archipelago located in the Atlantic Ocean just several kilometres (ca. 8 km) offshore from Conakry, Guinea. In his description of *A. insularis,* Chabanaud (1918) only compared his new species with *Agama kirkii*

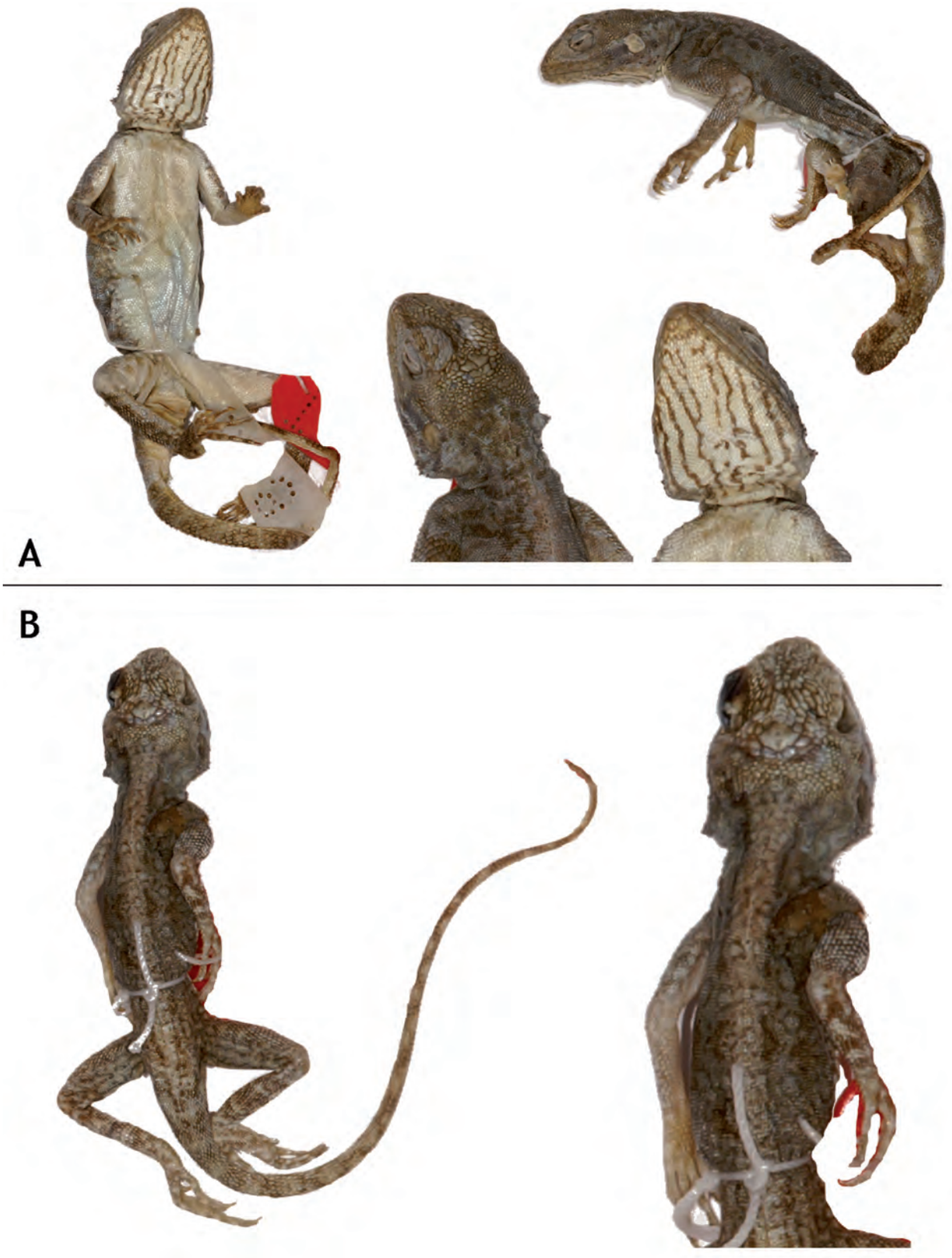

Fig. 1. The two syntypes of *Agama insularis* Chabanaud, 1918 (MNHN 1918.041-042).

Boulenger, 1884 from southern Africa and stated both as closely related. The only morphological differences noted were related to (1) head shapes (more elongate in *A. insularis*) and (2) body scalation (*A. insularis* has smaller scales, 120–130 scale rows around midbody versus about 90 in *A. kirkii,* and *A. insularis* had dorsal scales that are smaller compared to ventral scales.

Based on a larger series of specimens collected from the type locality, which included adult specimens, PARKER (1939) reassessed the validity of *A. insularis* (material of the IRSNB, Appendix 1). In this publication PARKER (1939) also compared *A. insularis* with *A. boulengeri* Lataste, 1886, a morphologically similar species distributed in Mauritania and Mali. He distinguished *A. insularis* from *A. boulengeri* by its more strongly carinate scales, especially on the occiput and lower surfaces of the tail; larger nasal, separated from the rostral by a single elongate scale; larger number of labial scales, 8–9 versus 11 and the colouration of adult males. Nevertheless, PARKER (1939) only described the adult colouration from preserved specimens. Adult males are brownish black above with light specking, especially on the vertebral region; lower surfaces of the head, chest and abdomen are blackish-grey; middle of the gular region is jet black. JOGER (1979) described the adult male colouration of living *A. boulengeri* as follows: (1) ground colour pale gray-brown with transverse rows of white spots; (2) throat dirty white with longitudinal stripes, parts of the head gray-blue; (3) tail gray-blue and (4) a characteristic half-moon shaped black bar on the anterior margin of the shoulder. LAMBERT & MULLIÉ (1998) refer, beside the tail crest of the males, to the nuptial colouration of females as the most striking difference between the sexes of *A. boulengeri*. They describe the males as drab with uniform purple-grey coloured scales dorsally, whereas the females have a brilliant yellow mid-dorsal band with three approximately bat-shaped transverse bands on a bright orange background.

LAURENT (1947) reported a series of *Agama insularis* from Iles Roumé and a neighboring island, Île Kassa, and mentioned that the characters given by PARKER (1939) were in agreement with his specimens. However, LAURENT (1947) described additional sources of morphological variation, including 10 to 13 precloacal pores, 8 to 10 supralabial and 7 to 10 infralabial scales. Because of differences in the number of scale rows around midbody (Île Roumé: 115 to 125; Île Kassa: 143 to 147) he suggested that the Île Kassa population deserved subspecific status.

The taxonomic status of *Agama insularis* has been changed since these early studies. GUIBÉ (1954) listed *A. insularis* as valid in the type catalogue of the collection of the Muséum national d'histoire naturelle in Paris, although WERMUTH (1967) regarded this species as questionable, since it was only known at this time from its type locality. JOGER (1979) reasserted the validity of *A. insularis*; however, MOODY (1980) placed *A. insularis* in synonymy of *A. boulengeri*, but without giving a reason. Nevertheless, BÖHME (1985) followed JOGER (1979) and stated that *A. insularis* and *A. boulengeri* are both valid species and probably closely related. Finally, BRYGOO (1988) and ULBER & BARTS (1997) treated *A. insularis* as a valid species, although without offering additional comments regarding this decision.

Interestingly, another species of *Agama* from West Africa possessing a prominent tail crest has remained mostly overlooked since its description. *Agama cristata* was described by MOCQUARD (1905) from a single specimen collected from Bomanesco (Sankaran) in Guinea by M. A. Chevalier, and later donated to the Muséum national d'histoire naturelle in Paris by M. Maurice de Rothschild. MOCQUARD (1905) did not compare his new species with any other species and characterized it mainly by the large crest proceeding from the neck to the tail. Later, *A. cristata* was apparently regarded as a synonym of *A. sankaranica* Chabanaud, 1918 by GUIBÉ (1954) and WERMUTH (1967), presumably because both taxa share the same type locality (*A. sankaranica*: Moussaia, Sankaran, Guinea; *A. cristata*: Bomanesco, Sankaran, Guinea). Later, BRYGOO (1988) confirmed the validity of *A. cristata* in his type catalogue presumably because of the tail crest, but again he was not followed by ULMER & BARTS (1997).

Despite the presence of a prominent tail crest in adult males shared between *Agama cristata, A. boulengeri* and the island endemic species, *Agama insularis,* a comparison of these species remains to be conducted. In contrast to the previous three species, *A. sankaranica* and *Agama weidholzi* Wettstein, 1932 are small and solitary-living species. The latter was included in the comparison, because it is endemic to this region and so far only known from Senegal (e.g. WETTSTEIN 1932), Gambia (BÖHME 2005), Mali (e.g. GRANDISON 1969) and Guinea-Bissau (MONARD 1940). Additionally, MONARD (1940) included specimens of *A. weidholzi* and *A. sankaranica* in the type series of *A. boensis*. (GRANDISON 1969, BÖHME 2005) and for that reason a close relation to *A. sankaranica* could be possible.

Our aim is therefore to compare the species of *Agama* with prominent tail crests in adult males (*Agama cristata, A. boulengeri* and the island endemic species, *Agama insularis*) to clarify their taxonomic status, distribution, and phylogenetic relationships. We also include other species of West African *Agama* in our study that lack prominent tail crests in adult males, but that are hypothesized to be close relatives because they occur in the same areas.

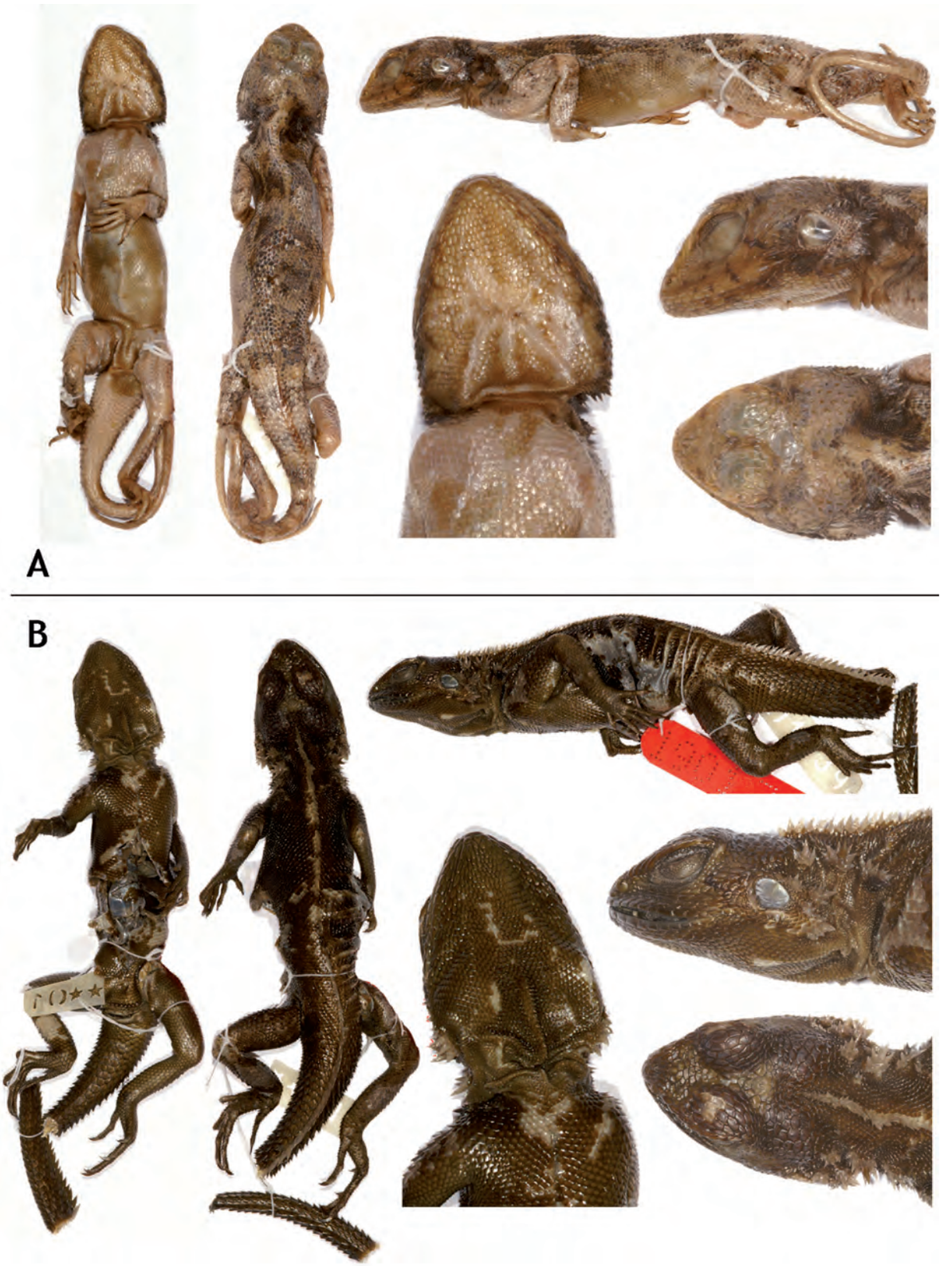

Fig. 2. The holotypes of a) *Agama sankaranica* (MNHN 1901.0395) and b) *Agama cristata* (MNHN 1901.0394).

Material & Methods

The voucher specimens examined in this study are accessioned in the following natural history collections: Collection of Jean François Trape, deposited in Institut de Recherche pour le Développement (IRD) Dakar, Senegal (TR); Institut royal des Sciences naturelles de Belgique (IRSNB); Museum national d'histoire naturelle de Paris, France (MNHN; Museum für Naturkunde, Berlin, Germany (ZMB) and Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany. The type specimens of *Agama cristata* and *A. insularis* were included, however, the type specimens of *A. insularis* are juveniles and therefore topotypical material was also used for this taxon.

Since several studies have now shown that DNA barcoding, especially when using the mitochondrial 16S rRNA gene, is a reliable tool in reptile or amphibian taxonomy (e.g. Vences et al. 2005; Bwong et al. 2009) molecular data were collected to calculate a simple neighbour-joining phylogeny (fig. 4) and to analyse the sequence variation between species. A portion of the mitochondrial 16S rRNA gene of *Agama insularis* (ZFMK 88247; GenBank accession number: GU133326) from the type locality, as well as *Agama cristata* (TR555; GenBank accession number: GU133325) from Guinea, *Agama boulengeri* (MNHN; Gen-Bank accession number: GU133324) from Mauritania, *Agama weidholzi* (ZFMK 75001; GenBank accession number: GU133328) from Gambia, *Agama sankaranica* (ZFMK 84992; GenBank accession number: GU133327) from an unknown locality and *Agama agama* (ZFMK 15222 [neotype]; GenBank accession number: GU133323) were sequenced. *Acanthocercus atricollis* (ZFMK 41748; GenBank accession number: GU133322) was used as outgroup.

DNA was extracted using QuiAmp tissue extraction kits (Quiagen) or a modified Chelex-Protocol (Walsh et al. 1991, Schmitz 2003). The primers 16sar-L (light chain; 5' – CGC CTG TTT ATC AAA AAC AT – 3') and 16sbr-H (heavy chain; 5' – CCG GTC TGA ACT CAG ATC ACG T – 3') of Palumbi et al. (1991) were used to amplify a portion of the mitochondrial 16S ribosomal RNA gene. PCR cycling procedure was as described in Schmitz et al. (2005). PCR products were purified using Quiaquick purification kits (Quiagen). Sequences were obtained using an automatic sequencer (ABI 377). Sequences were aligned using ClustalX (Thompson et al. 1997; default parameters) and manually checked using the original chromatograph data in the program BioEdit (Hall 1999). A preliminary phylogenetic tree was calculated in the program Paup* 4.0b10 (Swofford 2002) using the Neighbor-joining algorithm (NJ) and 20000 pseudo-replicates to estimate node support. This program was also used to compute the uncorrected pairwise distances for all sequences.

The following measurements and scale counts were used to compare the different species in statistical analysis (for selected characters see table 1): Snout-vent length (SVL): measured from mental scale to cloaca; tail length (TL): measured from cloaca to tip of tail; Tail crest length (TcL): length of the tail crest from midpoint of pelvic region to tip of crest; head length (HL): measured from jugale to rostral scale; head height (HH): measured at the jugal-postorbital region; head width (HW): measured across the jugal-postorbital region just anterior to the external auditory meatus; Midbody scales (MS): scale rows around midbody; tail crest scales (TcS): number of tail crest scales, counted from midpoint of pelvic region to tip of crest; dorsal scales (DS): number of midline longitudinal dorsal scales, counted from midpoint of pectoral region to midpoint of pelvic region; cloacal pores (CP).

Excel 2000 and SPSS (10.0) software packages were used to run statistical analyses. Hierarchical Cluster analysis and Principal Component Analysis (PCA) were used to evaluate the morphological data and to explore the phenetic relationships between the taxa examined.

Results & Disussion

Morphology. Significant differences were found when the effect of body sizes was removed from analyses (see fig. 3), but there is still a high level of overlap among species in all PC's. Best results were found in PC 1 and 2 (PC 1= 41.379% of variance; PC 2= 25.825% of variance; PC 3= 24.098% of variance; PC 4= 8.699% of variance) and are visualized in fig. 3. *Agama insularis* has a significantly larger relative head height, head width and head length than *A. boulengeri*, but lower average of mid-body scale rows and significantly smaller relative head length than *A. cristata*. *Agama cristata* differs significantly in a higher average of mid-body scale rows and larger relative head length from both *A. insularis* and *A. boulengeri*. *Agama boulengeri* differs significantly in smaller relative head height, head width and head length from both *A. insularis* and *A. cristata*. Males have significantly lower tail-crest-scales and tail-crest-length than either *A. insularis* or *A. cristata*. Differences in pholidosis between *A. boulengeri* and *A. cristata* are low and mostly overlapping (see table 1), which is unsurprising within the genus *Agama*. But in average, *A. cristata* has a higher count of scale rows around midbody than *A. boulengeri*. Also the differences in colouration between *A. boulengeri* and *A. cristata* are low. Small differences in colouration were found between *Agama boulengeri* on one hand and *A. cristata* on the other hand. Especially the colouration of the throat in adult

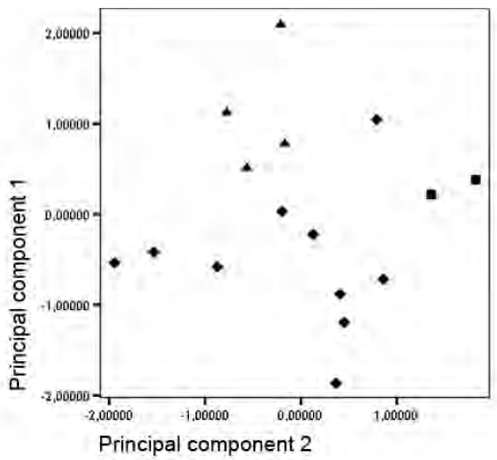

Fig. 3. Projection of the first and second principal component from a PCA run on 16 individuals assigned to ◆ = *Agama boulengeri*, ▲ = *Agama insularis* ■ = *Agama cristata*.

males is distinct. In *A. boulengeri* the throat is dirty white with longitudinal stripes, whereas in *A. cristata* the basal parts of the throat are dark bluish-black.

Genetics. As obvious from fig. 4, *Agama boulengeri* is very distinct from the two other known species with tail crests (*A. insularis*; *A. cristata*), and it is found in a basal position to all other *Agama* species included in this study (NJ: 70). In contrast, the two other species, *A. insularis* and *A. cristata* form a maximally supported clade (NJ: 100) that is the sister clade of *A. weidholzi* (NJ: 84) with this subclade significantly separated from its sister clade containing *A. agama* and *A. sankaranica* as sister taxa, though this latter subclade receives hardly any support (NJ: 56). This low support comes as no surprise as other studies show clearly that *A. agama* and *A. sankaranica* are not very closely related (Leaché et al. 2009).

Table 2 summarizes the uncorrected p-distances for 496 bp of the 16S rRNA gene. *Agama boulengeri* shows the highest genetic differences to all other species with values ranging from 12.1%–15.9% thus showing that it is not closely related to any of the other included *Agama* species, and is far removed from the two other taxa with tail crests (*A. insularis*: 15.5% *A. cristata*: 14.1%). Thus the genetic data clearly confirm the specific distinctness of *A. cristata*/*A. insularis* from *A. boulengeri*.

Although genetic interspecific differences range at moderately high values ranging from 8.0%–11.9%, the genetic distance between *A. insularis* and *A. cristata* is low at only ca. 0.7% (corresponding to only differing basepairs). The low level of sequence divergence observed between *A. cristata* and *A. insularis* is consistent with the hypothesis that these taxa represent a single species.

Agama boulengeri is distinct in pholidosis, colouration and genetics from *A. insularis* and *A. cristata*. But no significant differences in morphology and genetics were found between *A. cristata* and *A. insularis.* It is important to note that this result is based on an examination of type specimens, topotypical material, and freshly collected material (see appendix). Therefore we consider *Agama insularis* Chabanaud, 1918 as a junior synonym of the revalidated *Agama cristata* Mocquard, 1905.

Agama cristata Mocquard, 1905

1905 *Agama cristata* Mocquard, Bull. Mus. Hist. Nat. 11: 288.
1918 *Agama insularis* Chabanaud, Bull. Mus. Hist. Nat., 3: 2, 3. Terra typica: "île Rooma (groupe des îles de Las)" (= Roumé Island, Los Islands), Guinea; Syntypes. MHNP 1918.41, 1918.42
1939 *Agama insularis* – Parker, Mém. Mus. Roy. Hist. Nat. Belg., Sér. 2, 15: 89.
1947 *Agama insularis* – Laurent, Bull. Mus. Roy. Hist. Nat. Belg., 23 (16): 5.
1954 *Agama insularis* – Guibé, Catalogue des Types de Lézards du Muséum national d'Histoire naturelle: 26.
1954 *Agama cristata* – Guibé, Catalogue des Types de Lézards du Muséum national d'Histoire naturelle: 26.
1967 *Agama cristata* – Wermuth, Das Tierreich, 86: 11.
1967 *Agama insularis* – Wermuth, Das Tierreich, 86: 16.
1979 *Agama insularis* – Joger, Salamandra 15: 36.
1982 *Agama insularis* – Welch, Herpetology of Africa: 48.
1985 *Agama insularis* – Böhme, Proc. Intl. Symp. Afr. Vertebr., Bonn, 1985: 471.
1988 *Agama insularis* – Brygoo, Bull. Mus. Nat. Hist. Naturelle 10, supplement 3, 1–-56.
1997 *Agama insularis* – Ulber & Barts, Herprint International, Bredell, South Africa, 418 pp.
2008 *Agama maria* nom. nov. Barabanov, Russ. J. Herp. 15: 206.
2009 *Agama cristata* – Wagner & Böhme, Russ. J. Herp. 16: 161–162.

Holotype. MNHN 1901.0394.

Terra typica. Bomanesco, Sankaran, Guinea.

Comment on Nomenclature. Barabanov (2008) recently proposed a nomen novum for *Agama cristata* Mocquard, 1905 because he recognized this taxon as a primary junior homonym of *Agama cristata* Merrem, 1820, recently known as the iguanid lizard *Corytophanes cristatus*. However, Wagner & Böhme (2009) did not accept this suggestion because in accordance to article 23.9.5 of the ICZN (1999) the author failed to refer the case to the Com-

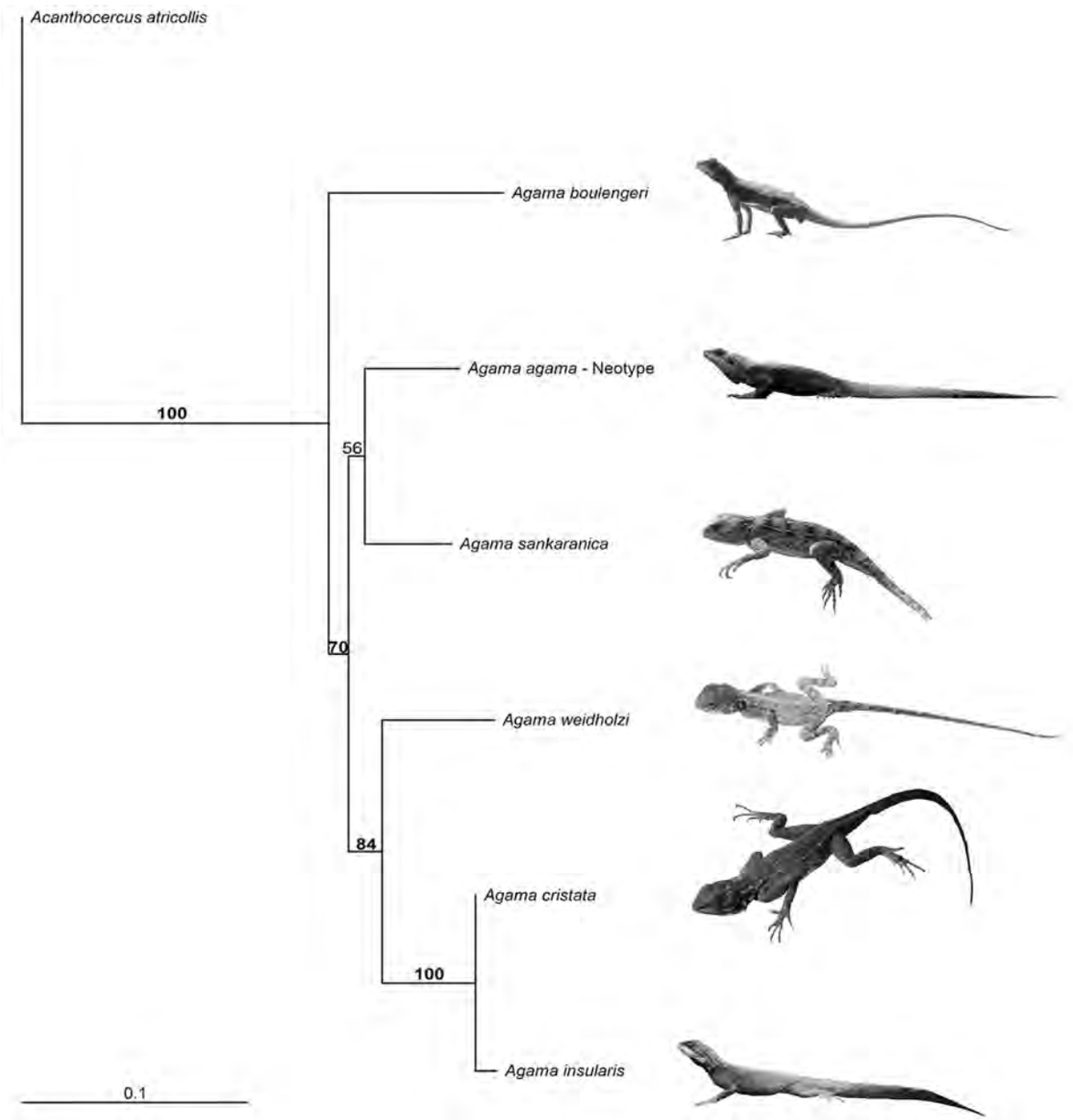

Fig. 4. Neighbor-joining tree based on 496 bp of the mitochondrial 16S rRNA gene. Values above the nodes represent bootstrap (20000 pseudo-replicates) values in percent for the neighbor-joining analysis. Significantly supported values are in bold. Values below 50% are not shown.

mission of Zoological Nomenclature which would be necessary because both taxa are not congeneric since 1827, where BOIE (in SCHLEGEL 1827) connects Merrem's *cristata* as type species with his newly described genus *Corythophanes*.

Diagnosis. A large species of *Agama* (total length of adult male up to 340 mm), which is characterized by its bluish-black colouration on the throat and the large nuchal and tail crests of adult males.

The species differs from nearly all other *Agama* species in having a large tail crest, usually reaching the last third of the tail. Only three other species, *A. boulengeri*, *A. kirkii* and *A. knobeli*, have such a prominent tail crest.

Agama cristata differs in detail from:

(1) *A. boulengeri* in (a) higher numbers of scales rows around midbody (97 to 123 in *A. boulengeri* and 111 to 147 [latter value fide LAURENT 1947] in *A. cristata*); in

Table 1. Comparison of measurements and pholidosis.

	Agama boulengeri average (min–max), n	*Agama cristata* average (min–max), n	*Agama weidholzi**	*Agama gracilimembris**
SVL	**88.4** (62.5–129.8), 22	**92.0** (69.0–123.0), 16	54–65	44–57
TL	**185.0** (119.2–236.2), 12	**149.3** (98.8–215.0), 12	–	–
HH	**11.0** (8.1–16.3), 22	**12.3** (8.6–17.6), 16	–	–
HW	**16.1** (12.0–24.0), 22	**17.5** (11.1–23.8), 16	–	–
HL	**23.8** (17.0–33.6), 22	**25.3** (20.1–33.3), 16	–	–
SAM	**112.9** (97–123), 22	**121.4** (111–136), 13	68–82	70–85
TCS	**71.3** (62–78), 10	**77.5** (75–80), 6	–	–
PP	**11.3** (8–14), 12	**11.4** (10–13), 7	–	–

SVL= snout-vent length; **TL**= tail length; **HH**= head height; **HW**= head width; **HL**= head length; **SAM**= scale rows around midbody; **TCS**= tail crest scales; **PP**= precloacal pores. All measurements in mm;.*= after GRANDISON 1969

Table 2. Uncorrected p-distances for 496 bp of the mitochondrial 16SrRNA sequences used in this study.

	Taxa	**1**	**2**	**3**	**4**	**5**	**6**	**7**
1	*Acanthocercus atricollis* ZFMK 41748	–						
2	*Agama boulengeri* MNHN	0.2135	–					
3	*Agama agama* ZFMK 15222	0.2029	0.1348	–				
4	*Agama cristata* TR555	0.1937	0.1405	0.1040	–			
5	*Agama insularis* ZFMK 88247	0.2022	0.1553	0.1123	0.0072	–		
6	*Agama sankaranica* ZFMK 84992	0.1929	0.1209	0.0803	0.1036	0.1192	–	
7	*Agama weidholzi* ZFMK 75001	0.2117	0.1590	0.1069	0.0892	0.1002	0.1068	–

(b) having smaller relative head height, head width and head length; and (c) males of *A. boulengeri* have a lower number of tail-crest-scales and a lower length of the tail-crest. (d) male coloration (larger ocelli, lower parts of the throat and gular fold deep bluish-black).

(2) *A. kirkii* in (a) having smaller body scales; (b) dorsal scales are smaller than ventral scales; and (c) in having no narrow blue and white banded tail (d) a geographic distribution confined to northern parts of southern Africa (Malawi, Zambia, Zimbabwe, Mozambique, Botswana).

(3) *A. knobeli* is herein recognized as a valid species, because we recognized striking dissimilarities in morphology between *A. knobeli* and the former nominate form *A. atra*: *Agama atra* is lacking the prominent large tail crest and has more spinose scales as *A. knobeli*, but further research on the relationships of these two species is in need. However, *A. knobeli* differs from *A. cristata* in (a) having larger body scales, (b) dorsal scales in same size as ventral scales and (c) in having a pale vertebral stripe in nuptial coloured adult males, and (d) a geographic distribution restricted to Namibia.

Colouration in alcohol. The holotype of *A. cristata* is uniform brown. Syntypes of *A. insularis* are grey to brown in different shades, but typical ocelli of *Agama* females and juveniles are visible. One subadult female specimen (TR 2353) from the island Île de Roumé (Los islands) is uniform brown with scattered orange stripes and bars on the body and shows dark stripes on a white throat. Even juveniles from the same locality show dark framed ocelli on the body and white dots on the head. In both juveniles (MNHN 2008.0023, TR 2352) a lateral orange stripe is obvious.

Fig. 5. Images of the following *Agama* species (in life):
A= '*Agama insularis*' from island Roumé (photo by Dr. Guy Kremer). **B=** *Agama cristata*, male, from Kindia, Pastoria, Guinea (photo by Ivan Ineich). **C=** *Agama cristata*, male, from Chutes de Kinkon, Guinea (photo by Ivan Ineich). **D=** *Agama cristata*, female, from Chutes de Kinkon, Guinea (photo by Ivan Ineich). **E=** *Agama boulengeri*, male, from Mauritania (photo by Hemmo Nickel). **F=** *Agama boulengeri*, female, from Mauritania (photo by Hemmo Nickel). **G=** *Agama boulengeri*, male, from Chûtes de Félou, Mali (photo by Ulrich Joger). **H=** *Agama weidholzi*, male, from Mali (photo by Ulrich Joger). **I=** *Agama cristata*, male, from Kindia, Pastoria, Guinea (tail crest in detail) (photo by Ivan Ineich).

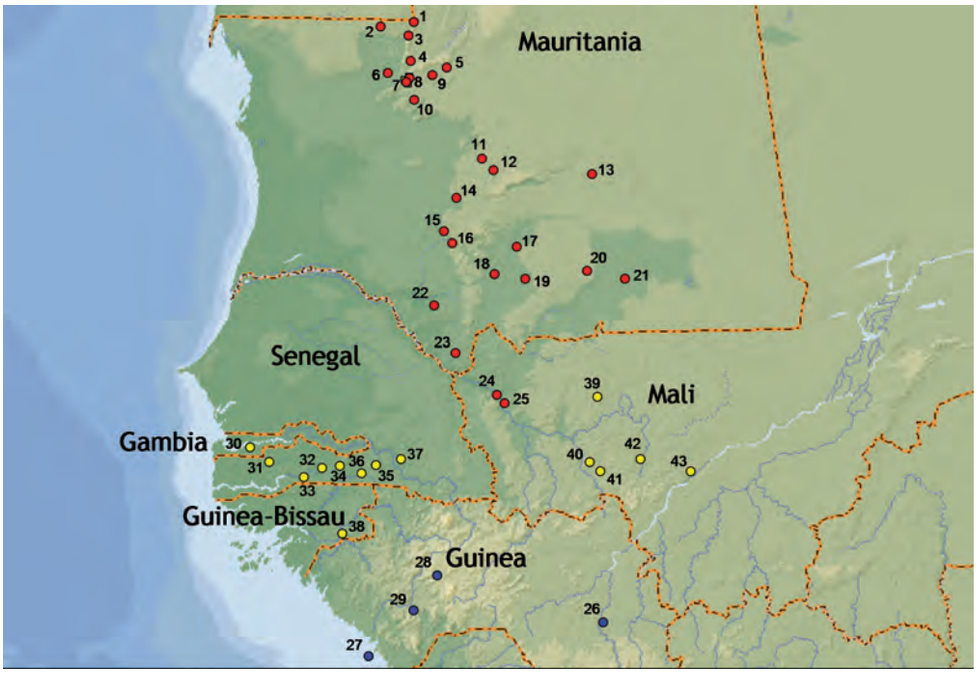

Fig. 6. Distribution map of *Agama boulengeri*, *A. cristata* and *A. weidholzi.*
*Agama boulengeri***:** Mauritania: **1=** Choûm; **2=** Ben Amira; **3=** Aggui; **4=** Guelta Molomhar; **5=** Chinguetti; **6=** Guelta Hamdoun; **7=** Kanoal; **8=** Terjît; **9=** Zerga Mountains; **10=** Tintâne; **11=** Iriji; **12=** Tidjikja; **13=** Tîchît; **14=** Guelta Fanar; **14=** Guelta Matmata; **15=** Achram; **16=** Aïn El Ghaire; **17=** Bou Bleïîne; **18=** Kîfa; **19=** Bougari; **19a=** Guelta Oumm Lebare; **19b=** Guelta Metraucha; **19c=** Oumm El Khez; **20=** Ayoûn El Atroûs; **21=** between Timbedgha and Ayoûn El Atroûs; **22=** Mbout; **23=** Sélibabi (for details see Padial 2006). Mali: **24=** Medine (type locality of *A. boulengeri*); **25=** Chûtes du Félou (Joger 1981).
Agama cristata: Guinea: **26=** Moussaia, Sankaran (type locality of *A. cristata*); **27=** Île Rooma, Îles de Los (type locality of *A. insularis*); **28=** Chutes de Kinkon near Pita; **29=** Kindia. *Agama weidholzi:* The Gambia: **30=** Bwiam. Senegal: **31=** Boughari, Casamance; **32=** between Tiara and Mantiankani; **33=** 13 km Southwest of Kolda; **34=** Tabadienke, 30 km South of Diallakoto; **35=** 20 km S of Médina Gounas; **36=** 12 km West of Kounkané; **37=** 5 km East of Darsalam (Niokolo-Koba National Park). Guinea-Bissau: **38=** Madina do Boé, Pitche. Mali: **39=** 9 km North of Fatao (14°24'N, 9°29'W); **40=** 20 km West of Kita (13°03'N, 9°42'W); **41=** 5 km East of Kita (13°03'N, 9°25'W); **42=** between Négala and Kassaro (12°55'N, 8°40'W); **43=** Négala (12°52'N, 8°27'W)

Colouration in life (see fig. 5)**.** *Males*. Body brownish, scattered with dark framed white to creamy ocelli, usually bigger ocelli form distinct rows. Lips creamy to bluish-creamy. Head and neck brownish with a pale stripe underneath the eye. Lower parts of the throat and gular fold deep bluish-black with strips running to the chin. Posterior part of the neck, body, parts of the hindlimb and tail sometimes speckled with white and dark scales. Sometimes a pale vertebral band between the limbs is obvious. Tail at the base pale speckled black, downwards brownish. Belly and underside of the limbs creamish to dark grey.

Females. Body brownish, scattered with dark framed white to creamy ocelli, when pregnant with dark orange to red coloured bands on the lateral body sides between the limbs. Sometimes lateral parts of the body white followed by a darker band and pale brownish on vertebral parts. Head and neck brownish with pale to yellow dots on the upper head and a pale stripe underneath the eye. Lips creamy to white.

Fig. 7. Mite pocket-like structure (indicated by an arrow) at a specimen of *Agama cristata* from Kindia, Pastoria in Guinea.

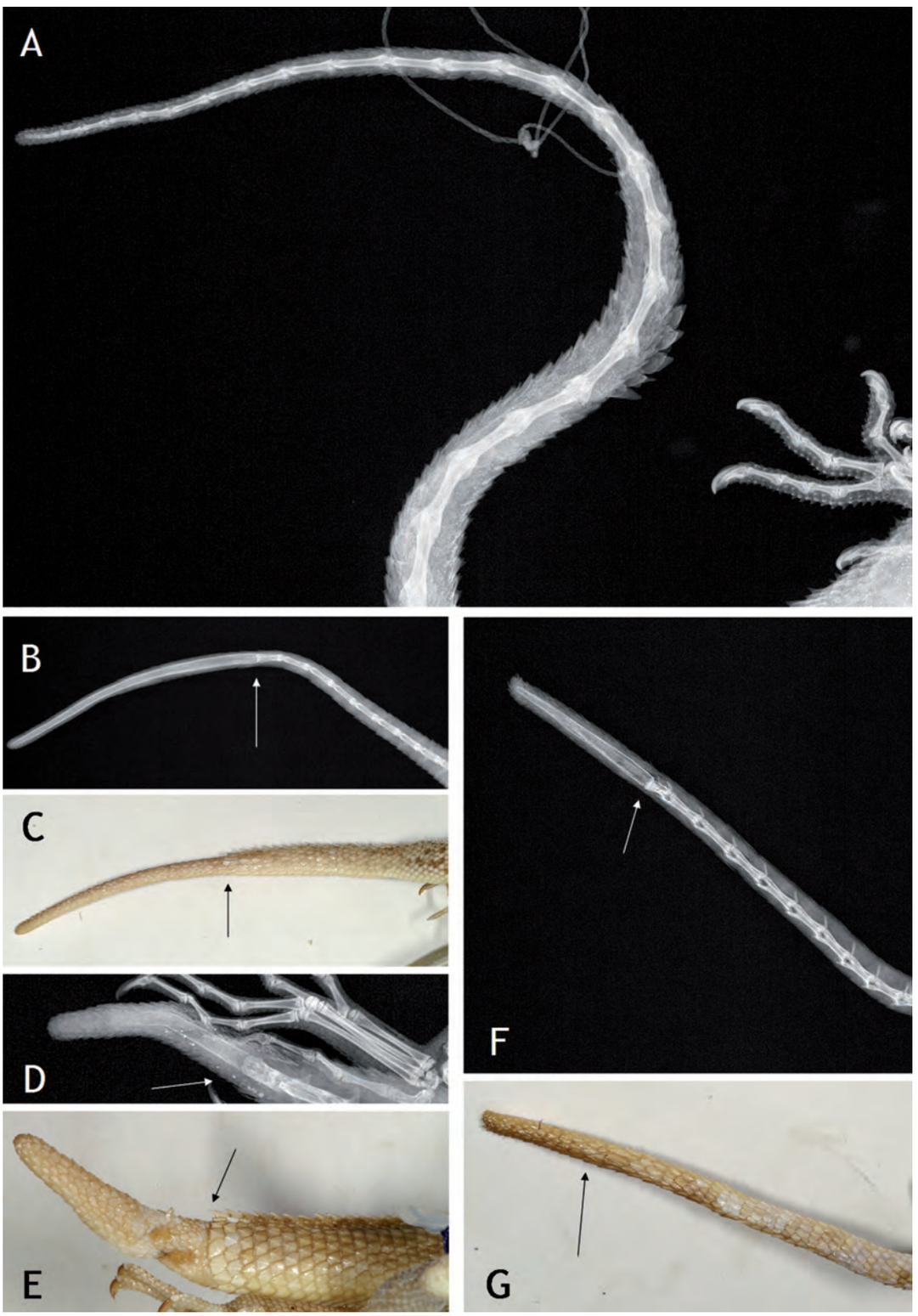

Fig. 8. Comparison of tail regenerates with x ray images (point of fracture indicated by arrows): **A)** original tail of *Agama boulengeri* (ZMB 22922). **B, C)** long tail regenerate of *A. boulengeri* (ZMB 55884). **D, E)** short tail regenerate of *A. boulengeri* (ZMB 55885). **F, G)** short tail regenerate of *A. boulengeri* (ZMB 55887)

Fig. 9. A remarkable bifurcated tail in a specimen of *Agama lionotus lionotus* (Kenya: Kitui District, NMK L/1252).

Juveniles. Juveniles are only known from preserved vouchers.

Distribution. *A. cristata* is so far only known from Guinea. Beside the type localities of the two taxa, the species is also recorded from the hydroelectrical power station at Kinkon water falls (11°2'54.9"N 12°27'1.8"W; about 820 m a.s.l.) and the Pastoria station (former Institute Pasteur) (10°5'36.5"N 12°50'21"W; about 388 m a.s.l.).

Agama boulengeri is endemic to the oriental region from Senegal, western Mali and Mauritania (Geniez et al. 2004), which is a similar distribution pattern as in *Tarentola parvicarinata* Joger, 1980 (Sauria: Phyllodactylidae) (Joger 1980). Joger (1979) regarded the species as endemic for the Variscian Fold Mountains between the Adrar Mountains in Mauritania and northern Senegal (see fig. 6). The limits of the geographic distribution of *Agama cristata* are less clear, and it is therefore more difficult to discuss their speciation and biogeography. However, the Senegal River, which separates *A. boulengeri* from *A. cristata* may have functioned to keep these lineages separated.

Relationships. Morphologically, *A. cristata* is very similar to *A. boulengeri*. But preliminary phylogenetic results indicate a sister taxa relation between *A. cristata* and *A. weidholzi*, with *A. boulengeri* placed as the sister taxon to all species analyzed (fig. 4). These results do not correlate with morphology, because *A. weidholzi* is a small, ground dwelling species without any tail crest, and is similar in morphology to the west and central African species *A. gracilimembris*. Grandison (1969) compared series of the two species and stated both as closely related. Gartshore (1985) also mentioned similarities in the colouration of gravid females between *A. gracilimembris*, *A. doriae* and *A. sankaranica*. There are also similarities between *A. weidholzi*, *A. gracilimembris* and *A. sankaranica* in behavioural aspects. All these are solitary species that lack social interactions outside of the breeding season (Gartshore 1985), and males occupy home ranges but do not defend territories.

Unfortunately, *A. gracilimembris* could not be included in the phylogenetic analysis because of a lack of fresh DNA samples of this rare species.

Biology. *Agama cristata,* like *A. boulengeri*, is a rupicolous species living on rocks in syntopy with *Trachylepis quinquetaeniata* (Sauria: Scincidae). Also *Trachylepis affinis* was recorded in the area nearby. In males, a mite pocket behind the tympanum is sometimes obvious (see fig. 7). These mite pocket-like structures are rare in agamid lizards. Arnold (1986) described nuchal pockets from iguanian lizards whereas Bertrand & Modry (2004) reported the first pocket-like structures in an *Agama* lizard (*Agama caudospinosa*). In this case, the newly described mite *Pterygosoma livingstonei* was found heavily concentrated in a skin-fold in front of the forelimb. Here, we report a similar pocket-like structure in front of the forelimb of an *Agama cristata* specimen (fig. 7, indicated by an arrow), which is similar to the pocket shown in Bertrand & Modry (2004). However, these species are not closely related, and we predict that these structures are more common in *Agama* lizards than they are currently believed to be.

Remarks on caudal anatomy. Some specimens of *Agama cristata* and *A. boulengeri* (e.g. a subadult female; TR 2353) show remarkable tail regeneration (fig. 8). Complete caudal regeneration in Agamid lizards is relatively rare, and regenerated tails are normally short and possess a knob-like end (e.g. *Agama lionotus*, see fig. 9). This is probably because Agamidae, like Chamaeleonidae and Platynota, lack a cartilaginous stratum or plane (Ananjeva 1985, Ananjeva & Danov 1991). As an example, the total length of a specimen of *A. cristata* (TR 2352) is 89.5 mm; with a tail length (TL) in total of 68.8 mm and a regenerate length (RL) of 36.2 mm (RL/TL= 0.53). Therefore, the regenerate measures a bit more than half of the length of the tail. The total length of the regenerate is longer than the documented bifurcated tail of *Laudakia caucasia* (Ananjeva & Danov 1991) with a length of 23.1 mm.

This phenomenon is also visible in *A. boulengeri*. Three specimens of the ZMB collection show a relatively long, slender and not knobbly regenerated tail. ZMB 55885 has a TL of 45.8 mm with a RL of 19.7 mm (RL/TL= 0.43). ZMB 55887 has a TL of 75.2 mm with a RL of 16.8 mm (RL/TL= 0.22), whereas ZMB 55884 has a TL of 109.6 mm with a RL of 46.4 mm (RL/TL= 0.42) (see fig. 8).

Also a specimen of the species *Agama lionotus lionotus* Boulenger, 1896 from East Africa (Kenya: Kitui District, NMK L/1252) shows a remarkable bifurcated tail, but here, in difference to the bifurcated tail reported by Ananjeva & Danov (1991) from *Laudakia caucasia*, only one tail tip is a regenerate (see fig. 9).

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REFERENCES

ANANJEVA, N. B. (1985): Autotomy and regeneration in agamid lizards. Questions of Herpetology, Soviet All.-Union Herp. Conf. Nauka: 8–9.

ANANJEVA, N. B. & R. A. DANOV (1991): A rare case of bifurcated caudal regeneration in the Caucasian agama, *Stellio caucasius*. Amphibia-Reptilia **12**: 346–356.

ARNOLD, E. N. (1986): Mite pockets of lizards: a possible means of reducing damage by ectoparasites. Biol. J. Linn. Soc. **29**: 1–21.

BARABANOV, A. (2008): A case of homonymy in the genus *Agama* (Reptilia: Sauria: Agamidae). Russian Journal of Herpetology **15**: 206.

BERTRAND, M. & D. MODRY (2004): The role of mite pocket-like structures on *Agama caudospinosa* (Agamidae) infested by *Pterygosoma livingstonei* sp. n. (Acari: Prostigmata: Pterygosomatidae). Folia Parasitologica **51**: 61–66.

BÖHME, W. (1985): Zoogeographical patterns of the lizard fauna of the African sub-Saharan savvana belt, with preliminary description of a new chameleon. Proc. Intl. Symp. Afr. Vertebr., Bonn: 471–478.

BÖHME, W. (2005): Presence of *Agama weidholzi* Wettstein, 1932 in The Gambia, West Africa. Salamandra **41**: 155–157.

BÖHME, W., WAGNER, P., MALONZA, P., LÖTTERS, S & J. KÖHLER (2005): A new species of the *Agama agama* group (Squamata: Agamidae) from Western Kenya, East Africa, with comments on *Agama lionotus* Boulenger 1896. Russian Journal of Herpetology **12**: 143–150.

BRYGOO, É. R. (1988): Les types d'Agamidés (Reptiles, Sauriens) du Muséum national d'Histoire naturelle. Catalogue critique. Bull. Mus. nation. Hist. nat. Paris **10** 4e sér.: 1–56.

BWONG, B.A., CHIRA, R., SCHICK, S., VEITH, M. & S. LÖTTERS (2009): Diversity of Ridged Frogs (Ptychadenidae: *Ptychadena*) in the easternmost remnant of the Guinea-Congolean rain forest : an analysis using morphology, bioacoustics and molecular genetics. Salamandra **45** (3): 129–146.

CHABANAUD, P. (1918) : Etude d'une collection de reptiles de l'Afrique occidentale francais. Bull. Mus. nation. Mist. nat. Paris **24**: 160–166.

GARTSHORE, M. E. (1985): *Agama gracilimembris* Chabanaud, 1918 (Reptilia: Sauria: Agamidae) in Nigeria. Herpetological Journal **1**: 23–25.

GENIEZ, P. MATEO, J. A., GENIEZ, M. & PETHER, J. (2004): The Amphibians and Reptiles of the Western Sahara. Frankfurt Contributions to Natural History, Edition Chimaira, Volume **19**, 229 pp.

GRANDISON, A. G. C. (1969): *Agama weidholzi* of West Africa and Its Relationsship to *A. gracilimembris*. Bull. Inst. Fond. Afr. Noire (Ser. A) **31**: 666–675.

GUIBÉ, J. (1954): Catalogue des Types de Lézards du Muséum national d'Histoire naturelle. Bayeux, Colas, pp. 26.

HALL, T. A. (1999): BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symposium Series **41**: 95–98.

ICZN (International Commission of Zoological Nomenclature) (1999), *International Code of Zoological Nomenclature. 4th Edition Adopted by the International Union of Biological Sciencees*, International Trust of Zoological Nomenclature, London.

JOGER, U. (1979): Zur Ökologie und Verbreitung wenig bekannter Agamen Westafrikas (Reptilia: Sauria: Agamidae). Salamandra **15**: 31–52.

JOGER, U. (1980): Eine neue Art der Gattung *Tarentola* aus Westafrika. Amphibia-Reptilia **1**: 137–147.

LAMBERT, M. R. K. & W. C. MULLIÉ (1998): Sexual dichromatism of *Agama boulengeri* observed in southern Mauritania. British Herpetological Society Bulletin **65**: 42–44.

LAURENT, R. (1947): Notes sur quelques reptiles appartenant a la collection du Musée royal d'Histoire naturelle de Belgique. Bull du Musée royal d'Histoire naturelle de Belgique **23**: 1–12.

LEACHÉ, A. D., CHONG, R. A., PAPENFUSS, T. J., WAGNER, P., BÖHME, W., SCHMITZ, A., RÖDEL, M.-O., LEBRETON, M., INEICH, I., CHIRIO, L., BAUER, A., ENIANG, E. A. & S. BAHA EL DIN (2009): Phylogeny of the genus *Agama* based on mitochondrial DNA sequence data. Bonner Zoologische Beiträge **56**: 273–278.

LOVERIDGE, A. (1933): Reports on the scientific results of an expedition to the Southwestern highlands of Tanganyika territory, VII, Herpetology. Bulletin of the Museum of Comparative Zoology at Harvard College **74**: 195–416.

MCLACHLAN, G. R. (1981): Taxonomy of *Agama hispida* (Sauria: Agamidae) in southern Africa. Cimbebasia ser. a **5** (6): 219–227.

MOCQUARD, M. F. (1905): Note préliminaire sur une collection de reptiles et de batraciens offerte au Muséum par M. Maurice de Rothschild. Bulletin du Museum nationale d'Histoire naturelle Paris **11**: 285–290.

MONARD, A. (1940): Résultats de la mission scientifique du Dr. MONARD en Guinée Portugaise (1937–1938). VIII Reptiles. Arq. Mus. Bocage, Lisboa **11**: 147–180.

MOODY, S. M. (1980): Phylogenetic and Historical Biogeographical Relationships of the Genera in the Family Agamidae (Reptilia: Lacertilia). Unpublished Ph.D. Thesis, Univ. of Michigan, 373 pp.

PADIAL, J. M. (2005): A new species of *Agama* (Sauria: Agamidae) from Mauritania. Herpetological Journal **15** (1): 27–35.

PALUMBI, S. R., MARTIN, A., ROMANO, S., MCMILLAN, W. O., STICE, L. & G. GRABOWSKI (1991): The simple fool's guide to PCR. Department of Zoology and Kewalo Marine Laboratory, Hawaii, 47 pp.

PARKER, H. W. (1939): Résultats scientifiques des croisières du Navire-École Belge 'Mercator'. V. Reptilia et Amphibia. Mém. Mus. Roy. Hist. Nat. Belg., Sér. 2, **15**: 85–90.

SCHLEGEL, H. (1827): Notice sur l'Erpétologie de l'île de Java par M. Boie. Bull. Sci. Nat. Géol. **9**: 233–240.

SCHMITZ, A. (2003): Taxonomic and phylogenetic studies on scincid lizards (Reptilia: Scincidae). Unpubl. PhD thesis, University of Bonn, 262 pp.

SCHMITZ, A., INEICH, I. & L. CHIRIO (2005): Molecular review of the genus *Panaspis* sensu lato in Cameroon, with special reference to the status of the proposed subgenera. Zootaxa, **863**: 1–28.

SWOFFORD, D. L. (2002): PAUP*: Phylogenetic analysis using Parsimony (*and other methods), version 4.0b10. Sunderland, MA: Sinauer Associates.

THOMPSON, J. D., GIBSON, T. J., PLEWNIAK, F., JEANMOUGIN, F. & D. G. HIGGINS (1997): The ClustalX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic Acids Research **24**: 4876–4882.

THYS VAN DEN AUDENAERDE, D. F. E. (1963): Les Agamidae du Congo: les espèces et leur distribution géographique. Revue de Zoologie et de Botanique Africaines **68**: 203–250.

ULBER, T. M. & M. BARTS (1997): Catalogue of valid species and synonyms Volume 4 (Agamidae/Uromastycidae). Herprint International, Bredell, South Africa, 418 pp.

VENCES, M., M. THOMAS, M., VAN DER MEIJDEN, A., CHIARI, A. & D. R. VIEITES (2005): Comparative performance of the 16S rRNA gene in DNA barcoding of amphibians. Frontiers in Zoology, **2**: 5.

WAGNER, P. (2007): Studies in African *Agama* I: On the taxonomic status of *Agama lionotus usambarae* Barbour & Loveridge, 1928 (Squamata, Agamidae). Herpetozoa **20**: 69–73.

WAGNER, P. & W. BÖHME (2009): On the status in nomenclature of *Agama cristata* Mocquard, 1905. A reply to Andrei Barabanov. Russian Journal of Herpetology **16** (2): 161–162.

WAGNER, P., BURMANN, A. & W. BÖHME (2008a): Studies on African *Agama* II. Resurrection of *Agama agama kaimosae* Loveridge, 1935 (Squamata: Agamidae) from synonymy and its elevation to species rank. Russian Journal of Herpetology **15**: 1–7.

WAGNER, P., KRAUSE, P., BURMANN, A. & W. BÖHME (2008b): Studies on African *Agama* III. Resurrection of *Agama agama turuensis* LOVERIDGE, 1932 (Squamata: Agamidae) from synonymy and its elevation to species rank. Salamandra **44**: 35–42.

WAGNER, P., WILMS, T., BAUER, A. & W. BÖHME (2009a): Studies on African *Agama* V. On the origin of *Lacerta agama* Linnaeus, 1758 (Squamata: Agamidae). Bonner Zoologische Beiträge **56** (4): 215–223.

WAGNER, P., BAREJ, M. F. & A. SCHMITZ (2009b): Studies on African *Agama* VII. A new species of the *Agama agama*-group (Linnaeus, 1758) (Sauria: Agamidae) from Cameroon & Gabon, with comments on *Agama mehelyi* Tornier, 1902. Bonner Zoologische Beiträge **56** (4): 285–297.

WALSH, P. S., METZGER, D.A. & R. HIGUCHI (1991): Chelex 100 as a medium for simple extraction of DNA for PCR–based typing from forensic material. BioTechniques **10**: 506–513.

WETTSTEIN, O (1932): Eine neue Eidechse aus Senegambien. Zool. Anz., Leipzig **99**(11/12): 303–305.

WERMUTH, H. (1967): Liste der rezenten Amphibien und Reptilien: Agamidae. Das Tierreich **86**, i–xiv, 1–127.

Appendix. Material examined

Agama boulengeri: MALI. Kayes: Chûtes de Félou (ZFMK 20058, 22176 – 180, 25481 – 485). MAURITANIA. Adrar: Terjit (ZFMK 76917); 20km N Atar (ZFMK 79729); Ayoun-el Atrons (ZFMK 83825 – 827); Guelta Metraucha (ZFMK 76862 – 864, 76868); Galoula (=Passe de Galoula) (ZMB 32583, ZMB 55882 – 888, ZMB 32584).

Agama cristata: GUINEA. Chûtes Kinkon (MNHN 2006.0553, MNHN 2006.0554); Kindia, Institut Pasteur (MNHN 2006.0555, MNHN 2006.0556).

'Agama insularis': GUINEA. Îles des Los, Île Roumé (MNHN 2008.0023, TR 2352 – 53; IRSNB 1392 a–c, 1728, 1733, 1729 a–e; MNHN 2008.0023, ZFMK 88247).

Agama weidholzi: GAMBIA. Bwiam (ZFMK 75001). MALI. 8km E Kassaro (ZFMK 20060); 5km E Kita (ZFMK 20061); 20km W Kita (ZFMK 20062); 9km N Fatao (ZFMK 20063 – 65); between Negala and Kassaro (ZFMK 20059). SENEGAL. 5km SO Darsalam (ZFMK 20066 – 068); 20km S Medina Gounas (ZFMK 20069); 13km SE Kolda (ZFMK 20066 – 078); 12km W Kounkané (ZFMK 20070 – 071); between Tiara and Mantiankani (ZFMK 20072).