

A MOLECULAR STUDY OF THE GENUS *Agama* (SQUAMATA: AGAMIDAE) IN WEST AFRICA, WITH DESCRIPTION OF TWO NEW SPECIES AND A REVIEW OF THE TAXONOMY, GEOGRAPHIC DISTRIBUTION, AND ECOLOGY OF CURRENTLY RECOGNIZED SPECIES

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Submitted March 25, 2011.

We conducted field studies in 15 West African countries and collected one thousand specimens of lizards of the genus *Agama*. Based on these collections, literature, molecular analysis of selected specimens, and examination of Linnean type-specimens of *A. agama*, we review the phylogeny, taxonomy, geographic distribution and ecology of the West African species of the genus *Agama*. Seventeen different species are recognized in the genus *Agama* in West Africa, northern Cameroon and Chad: *A. africana*, *A. agama*, *A. boensis*, *A. boueti*, *A. boulengeri*, *A. castroviejoi*, *A. cristata*, *A. doriae benueensis*, *A. gracilimembris*, *A. insularis*, *A. lebretoni*, *A. paragama*, *A. sankaranica*, *A. weidholzi*, and three new species. We design a lectotype for *A. agama* (Linnaeus, 1758) and attribute to *A. wagneri*, sp. nov., the populations from northern and central Cameroon of the *A. agama* complex. *Agama parafricana*, sp. nov., is described from wet savanna areas of Togo and Benin. *Agama sylvanus* from southern Ghana is a junior synonym of *A. africana*. *Agama* cf. *impalearis* from northern Niger and Mali corresponds to an undescribed species. *Agama boensis* is resurrected from the synonymy of *A. sankaranica*. According to biogeographic areas, four species are Sahelian, seven species are Sudanian, four species are Guinean, and two species are ubiquitous.

Keywords: Reptilia; phylogeny; taxonomy; geographic distribution; Linnaeus; Linnean type-specimens; *Agama agama*; *Agama parafricana* sp. nov.; *Agama wagneri* sp. nov.; *Agama impalearis* complex; *Agama boensis*.

INTRODUCTION

Lizards of the genus *Agama* Daudin are among the most common reptiles in West Africa. They are abundant everywhere in towns and villages. In rural areas, they are common from some of the most arid areas of the Sahelo-Saharan region to the Guinean rainforest. However, despite several comprehensive earlier works (Grandison, 1968, 1969; Joger, 1979) and a rapidly increasing amount of recent work (Padial, 2005, Leaché et al., 2009; Wagner et al., 2009a, 2009b, 2009c; Trape, 2011), the composition, distribution and ecology of *Agama* remains poorly known since several taxa still pose some difficult species delimitation problems and the status of other taxa appears uncertain.

The mitochondrial genome, with its fast substitution rate and their maternal inheritance mode constitute one of the most suitable markers for phylogenetic studies (Anderson et al., 1981; Boore et al., 1999). Moreover, mitochondrial loci are generally considered as a more sensitive indicator of population structure than are nuclear loci, although it is not always indisputable (Zink and Barrowclough, 2008). For lizards as for other reptiles and organisms, molecular methods have proven a very effective tool to resolve species limits and often contributed to the recognition of new species (Adalsteinsson et al., 2009; Pook et al., 2009; Trape et al., 2009, Wagner et al., 2009c).

From 2003 to 2010, we conducted comprehensive field surveys on the lizard fauna of 200 study sites in 15 West African countries as part of a research program on tick-borne borreliosis, a poorly known tropical infectious disease (Trape et al., 1996). About 1000 specimens of agamas were collected and determined to species either by using classical morphological identification criteria or by molecular methods. Based on these data, literature,

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and examination of Linnean type-specimens of *A. agama*, we review here the phylogeny, taxonomy, geographic distribution and ecology of the West African species of the genus *Agama*.

MATERIAL AND METHODS

1. Field surveys

Field surveys were conducted in Mauritania, Morocco (including Western Sahara), Mali, Niger, Senegal, Guinea Bissau, Guinea, Liberia, Burkina Faso, Ghana, Togo, Benin, Nigeria, Cameroon, and Chad. Since the primary objective of the field surveys was to map the geographic distribution of the soft tick *Ornithodoros sonrai* by investigating rodent burrows along meridians and parallels on a square degree scale, most study sites were selected along North-South and West-East transects. To help to resolve some systematic issues regarding *Agama*, additional field sampling was conducted in or nearby the type localities of the following species: *Agama africana* Hallowell, 1844 (type locality: "Liberia"), *Agama bocourti* Rochebrune, 1884 (type locality: "Gambie, Casamance, Mélécorée"), *Agama boensis* Monard, 1940 (type locality: "Madina Boé," Guinea Bissau), *Agama boueti* Chabanaud, 1917 (type locality: "Gao," Mali), *Agama castroviejoi* Padial, 2005 (type locality: "Dahr Chinguetti," Mauritania), *Agama cristata* Mocquard, 1905 (type locality: "Sankaran, Soudan français," southern Mali or northeastern Guinea), *Agama insularis* Chabanaud, 1918 (type locality: "île Rooma, groupe des îles de Las," Guinea), *Agama lebretoni* Wagner, Barej and Schmitz, 2009 (type locality: "north-east of Mamfe, Mukwecha, Amebisu," Cameroon), *Agama paragama* Grandison, 1968 (type locality: "Zaria City," Nigeria), *Agama picticauda* Peters, 1877 (type locality: "Afa Foah, Accra und Cameruns"), *Agama sankaranica* Chabanaud, 1918 (type locality: "Moussaïa, pays Sankaran," Guinea), and *Agama savattieri* Rochebrune, 1884 (type locality: "Gambie, Casamance, Mélécorée, Albréda, Bathurst"). In the case of *Agama agama* (Linnaeus, 1758), the type locality "America" was erroneous (Lönnberg, 1896; Andersson, 1900), and thus our initial approach was to consider that either the coast of Senegambia or the coast of Ghana, where most of the oldest European settlements in Africa were established during the 16th and 17th centuries, could reasonably be proposed as a corrected type locality for this species (Harris 1964). However, the recent designation of a neotype of *A. agama* from northern Cameroon by Wagner et al. (2009a) despite the fact that presumed syntypes of *A. agama* still exist in the Linnean collections kept in the Museum of Evolution of the Uppsala University (ZMUU) and the

Swedish Museum of Natural History in Stockholm (NRM), prompted us to conduct further investigations on Linnean type-specimens in Uppsala and Stockholm museums and *Agama* specimens from northern Cameroon.

Most *Agama* specimens collected were preserved in ethanol, others in formaldehyde. They were entered in the collection of the Institut de Recherche pour le Développement in Dakar, Senegal (IRD), except for a few specimens that were deposited in the Muséum national d'Histoire naturelle de Paris (MNHN) or the Institut Royal des Sciences Naturelles de Bruxelles (IRSNB). Based on the literature and the original description of types, all specimens were initially determined by using classical morphological identification criteria. In addition, selected specimens were studied by molecular methods, notably those belonging to the *Agama agama* complex and related species.

2. Molecular study

DNA from 100 mg of homogenized muscular tissue conserved in ethanol was extracted using the BioRobot MDx Workstation (Qiagen, Courtaboeuf, France) with customized extraction protocol and stored at 4°C until use in PCR amplifications. For most samples we amplified a portion of the 16S mt rDNA gene with the universal vertebrate primers 16SA-2290, CGCCTGTTTACCAAAAACAT and 16SB-2860, CCGGTCTGAACTCAGATCACGT (Kochern et al., 1989). In some cases, when the repeated amplification of samples produced no positive bands, we used the primers Aga-dif-F AGGTACCGCCTGCCAGTGA and Aga-dif-R ATCGTTGAACAAACGAACC designed on conserved regions of amplified 16S rDNA from others *Agama* (Table 1). All primers were manufactured by Eurogentec, Seraing, Belgium. DNA extracted from uninfected hard ticks from colonies at the Unité des Rickettsies, Marseille, France, and sterile water were used as negative controls. Polymerase chain reactions were performed in automated DNA control cyclers (GeneAmp 2400 and 9700; Applied Biosystems, Foster City, CA, USA). PCR products were visualized by electrophoresis on a 1.5% agarose gel, stained with ethidium bromide and examined using an ultraviolet transilluminator. The PCR products were purified using a QIAquick Spin PCR Purification Kit (Qiagen) according to the manufacturer's instructions. Sequencing of amplicons was performed using the BigDye Terminator Cycle Sequencing Kit (Perkin Elmer Applied Biosystems) with ABI automated sequencer (Applied Biosystems). Sequences obtained from studied lizards as well as from most available 16S rDNA sequences of West African species of *Agama* from GenBank (Table 2) were aligned with CLUSTAL W

TABLE 1. List of the Specimens Used for Molecular Studies in this Article

No	Species according to present article	Voucher	Country	Locality	GenBank number	Sequence length
1	<i>Agama africana</i>	TR3106	Ghana	Akutuaso forest, topotype of <i>A. sylvanus</i>	JF520638	497
2	<i>Agama africana</i>	TR3089	Ghana	Krokosua forest	JF520639	497
3	<i>Agama africana</i>	TR2769	Guinea	Balassou	JF520640	497
4	<i>Agama africana</i>	TR2780 [#]	Guinea	Balassou	JF520641	497
5	<i>Agama africana</i>	TR2811	Guinea	Konsankoro	JF520642	497
6	<i>Agama africana</i>	7326X	Guinea	Dakakoura	JF520643	497
7	<i>Agama africana</i>	7312X [#]	Guinea	Daramagnaki	JF520644	497
8	<i>Agama africana</i>	7313X [#]	Guinea	Daramagnaki	JF520645	497
9	<i>Agama africana</i>	7318X	Guinea	Diandian	JF520646	497
10	<i>Agama africana</i>	TR2138	Guinea	Nzérékoré	JF520647	497
11	<i>Agama africana</i>	TR2544 [#]	Guinea	Yatia	JF520648	497
12	<i>Agama africana</i>	TR2545	Guinea	Yatia	JF520649	497
13	<i>Agama africana</i>	TR2546 [#]	Guinea	Yatia	JF520650	497
14	<i>Agama africana</i>	TR2591 [#]	Liberia	Bopolu	JF520651	498
15	<i>Agama africana</i>	TR2592	Liberia	Bopolu	JF520652	498
16	<i>Agama africana</i>	TR2659	Liberia	Kpaytuo	JF520653	498
17	<i>Agama africana</i>	TR2663	Liberia	Mile 48	JF520654	497
18	<i>Agama africana</i>	TR2730	Liberia	West of Sapo	JF520655	498
19	<i>Agama agama</i>	TR3306	Benin	Guiguisso	JF520656	499
20	<i>Agama agama</i>	TR3209	Benin	Gorouberi	JF520657	499
21	<i>Agama agama</i>	TR3238*	Benin	Kargui	JF520658	426
22	<i>Agama agama</i>	TR3199*	Benin	Kokoro	JF520659	426
23	<i>Agama agama</i>	7005X	Benin	Pendjari	JF520660	499
24	<i>Agama agama</i>	TR30	Chad	Mataya	JN385281	500
25	<i>Agama agama</i>	TR09	Chad	Willicouré	JN791278	500
26	<i>Agama agama</i>	TR10	Chad	Willicouré	JN791276	500
27	<i>Agama agama</i>	TR11	Chad	Willicouré	JN791277	500
28	<i>Agama agama</i>	TR3019	Ghana	Abusuapeade	JF520661	499
29	<i>Agama agama</i>	TR3112*	Ghana	Anomabu	JF520662	426
30	<i>Agama agama</i>	TR3109	Ghana	Elmina	JF520663	499
31	<i>Agama agama</i>	TR2956	Ghana	Mankuma	JF520664	499
32	<i>Agama agama</i>	TR2374	Guinea	Kalan-Kalan	JF520665	499
33	<i>Agama agama</i>	TR2375 [#]	Guinea	Kalan-Kalan	JF520666	499
34	<i>Agama agama</i>	TR2381 [#]	Guinea	Kalan-Kalan	JF520667	499
35	<i>Agama agama</i>	TR2384 [#]	Guinea	Kalan-Kalan	JF520668	499
36	<i>Agama agama</i>	TR2394 [#]	Guinea	Kalan-Kalan	JF520669	499
37	<i>Agama agama</i>	TR2535	Guinea	Pont Gambie	JF520670	499
38	<i>Agama agama</i>	TR2537 [#]	Guinea	Pont Gambie	JF520671	499
39	<i>Agama agama</i>	TR2538 [#]	Guinea	Pont Gambie	JF520672	499
40	<i>Agama agama</i>	TR8623X	Guinea	Mont Going	JN791274	499
41	<i>Agama agama</i>	TR8540X	Guinea	Mont Going	JN791276	499
42	<i>Agama agama</i>	TR3558	Guinea Bissau	Bubaque	JF520673	499
43	<i>Agama agama</i>	TR3559 [#]	Guinea Bissau	Bubaque	JF520674	499
44	<i>Agama agama</i>	TR3820	Guinea Bissau	Madina-Boé	JF520675	491
45	<i>Agama agama</i>	TR3891 [#]	Guinea Bissau	Médina-Thialé	JF520676	499
46	<i>Agama agama</i>	TR3939 [#]	Guinea Bissau	N'Thiané	JF520677	499
47	<i>Agama agama</i>	TR2644	Liberia	Monrovia	JF520678	499
48	<i>Agama agama</i>	TR2645 [#]	Liberia	Monrovia	JF520679	499
49	<i>Agama agama</i>	TR1893	Mali	Kourougé	JF520680	500
50	<i>Agama agama</i>	TR3466	Mali	Npiébougou	JF520681	499
51	<i>Agama agama</i>	TR3470* [#]	Mali	Npiébougou	JF520682	426
52	<i>Agama agama</i>	6487X*	Niger	Park du W	JF520683	426

TABLE 1 (continued)

No	Species according to present article	Voucher	Country	Locality	GenBank number	Sequence length
53	<i>Agama agama</i>	TR2851	Niger	Tékhé	JF520684	499
54	<i>Agama agama</i>	TR3618	Nigeria	Idanré	JF520685	499
55	<i>Agama agama</i>	TR3575	Nigeria	Riyom	JF520686	499
56	<i>Agama agama</i>	TR3590 [#]	Nigeria	Riyom	JF520687	499
57	<i>Agama agama</i>	TR3504 [#]	Nigeria	Zaria	JF520688	499
58	<i>Agama agama</i>	TR3505	Nigeria	Zaria	JF520689	499
59	<i>Agama agama</i>	TR2886	Senegal	Dakar	JF520690	499
60	<i>Agama agama</i>	TR3807	Senegal	Djibonker	JF520691	499
61	<i>Agama agama</i>	TR3862 [#]	Senegal	Mlomp	JF520692	499
62	<i>Agama agama</i>	TR1730	Togo	Agoté	JF520693	499
63	<i>Agama agama</i>	TR2303	Togo	Konkoré	JF520694	499
64	<i>Agama agama</i>	TR2304	Togo	Pont Kéran	JF520695	499
65	<i>Agama boensis</i>	7324X	Guinea	Dakacoura	JF520696	500
66	<i>Agama boensis</i>	7320X	Guinea	Diandian	JF520697	500
67	<i>Agama boensis</i>	7496X [#]	Guinea	Kogon-Lenguéré	JF520698	500
68	<i>Agama boensis</i>	7577X [#]	Guinea	Missidé-Balouta	JF520699	500
69	<i>Agama boensis</i>	7604X [#]	Guinea	Kogon-Lenguéré	JF520700	500
70	<i>Agama boensis</i>	7355X [#]	Guinea	Yama	JF520701	500
71	<i>Agama boensis</i>	TR3871	Guinea Bissau	Madina-Boé	JF520702	500
72	<i>Agama boensis</i>	TR3873 [#]	Guinea Bissau	Madina-Boé	JF520703	500
73	<i>Agama boensis</i>	TR3952	Senegal	Kédougou	JF520704	500
74	<i>Agama boueti</i>	6020X	Niger	Agadez	JF520705	500
75	<i>Agama boueti</i>	TR3508*	Niger	Ayrou	JF520706	427
76	<i>Agama boueti</i>	6132X [#]	Niger	Ayrou	JF520707	500
77	<i>Agama boueti</i>	6088X	Niger	Gougaram	JF520708	500
78	<i>Agama boueti</i>	6089X [#]	Niger	Gougaram	JF520709	500
79	<i>Agama boueti</i>	6309X	Niger	Kao	JF520710	500
80	<i>Agama boueti</i>	7297X	Niger	Kouré	JF520711	500
81	<i>Agama boueti</i>	6069X	Niger	Mataene	JF520712	500
82	<i>Agama boueti</i>	6092X	Niger	Tasha Ibrahim	JF520713	500
83	<i>Agama boueti</i>	6015X [#]	Niger	Tchin-Tabaraden	JF520714	500
84	<i>Agama boueti</i>	6075X	Niger	Tchin-Telloust	JF520715	500
85	<i>Agama castroviejoii</i>	TR107	Mauritania	Akjoujt	JF520716	498
86	<i>Agama cristata</i>	TR3449	Mali	Zambouroula	JF520717	500
87	<i>Agama cristata</i>	TR3450	Mali	Zambouroula	JF520718	500
88	<i>Agama doriae benueensis</i>	TR3577	Nigeria	Riyom	JF520719	500
89	<i>Agama doriae benueensis</i>	TR3593	Nigeria	Riyom	JF520720	500
90	<i>Agama gracilimembris</i>	TR3301*	Benin	Guiguissou	JF520721	426
91	<i>Agama impalearis</i>	TR1838	Morocco	Tata	JF520722	499
92	<i>Agama insularis</i>	TR2435	Guinea	Pastoria	JF520723	501
93	<i>Agama lebretoni</i>	TR3771	Cameroon	Ebinsi	JF520724	499
94	<i>Agama lebretoni</i>	TR 3765	Cameroon	Ejagam lake	JF520725	499
95	<i>Agama lebretoni</i>	TR3784	Cameroon	Mamfè	JF520726	499
96	<i>Agama lebretoni</i>	TR 3670	Cameroon	Widikum	JF520727	500
97	<i>Agama parafricana</i>	TR3200	Benin	Bassila	JF520728	497
98	<i>Agama parafricana</i>	TR3248*	Benin	Guiguissou	JF520729	424
99	<i>Agama parafricana</i>	TR3249*	Benin	Guiguissou	JF520730	424
100	<i>Agama parafricana</i>	TR3311	Benin	Guiguissou	JF520731	497
101	<i>Agama parafricana</i>	TR3964	Benin	Koto	JN791273	497
102	<i>Agama parafricana</i>	TR2957*	Ghana	Nsonsomea	JF520732	424
103	<i>Agama parafricana</i>	TR2968*	Ghana	Nsonsomea	JF520733	424
104	<i>Agama parafricana</i>	TR3130	Togo	Forêt d'Asrama	JF520734	497

TABLE 1 (continued)

No	Species according to present article	Voucher	Country	Locality	GenBank number	Sequence length
105	<i>Agama paragama</i>	6919X	Niger	Kouré	JF520735	497
106	<i>Agama paragama</i>	TR2849	Niger	Tékhé	JF520736	497
107	<i>Agama paragama</i>	TR2850a	Niger	Tékhé	JF520737	497
108	<i>Agama paragama</i>	TR3502	Nigeria	Zaria	JF520738	497
109	<i>Agama sankaranica</i>	7068X	Benin	Boribansifa	JF520739	499
110	<i>Agama sankaranica</i>	7072Xa	Benin	Boribansifa	JF520740	498
111	<i>Agama sankaranica</i>	TR2377	Guinea	Kalan-Kalan	JF520741	499
112	<i>Agama sankaranica</i>	TR3467	Mali	Npiébougou	JF520742	501
113	<i>Agama sankaranica</i>	TR3468	Mali	Npiébougou	JF520743	500
114	<i>Agama sankaranica</i>	6109X	Niger	Alambaré	JF520744	501
115	<i>Agama sankaranica</i>	7228X	Niger	Gaya	JF520745	501
116	<i>Agama sankaranica</i>	TR2202	Togo	Fazao	JF520746	499
117	<i>Agama</i> sp.	6026X	Niger	East of Gougaram	JF520747	502
118	<i>Agama</i> sp.	6090X	Niger	Gougaram	JF520748	502
119	<i>Agama</i> sp.	6080X	Niger	Haut-Zagado	JF520749	502
120	<i>Agama</i> sp.	6070X	Niger	Mataene	JF520750	502
121	<i>Agama wagneri</i>	TR 3674	Cameroon	Mangeng	JF520751	497
122	<i>Agama wagneri</i>	TR3750	Cameroon	Mokolo	JF520752	498
123	<i>Agama wagneri</i>	TR3751	Cameroon	Mokolo	JF520753	498
124	<i>Agama wagneri</i>	TR3753	Cameroon	Ngaoundéré	JF520754	498
125	<i>Agama wagneri</i>	TR3754	Cameroon	Yaoundé	JF520755	497
126	<i>Agama wagneri</i>	TR3755	Cameroon	Yaoundé	JF520756	497
127	<i>Agama weidholzi</i>	TR2399	Guinea	Kalan-Kalan	JF520757	499

GenBank accession number is that of mitochondrial 16S rDNA sequence. Indicated length corresponds to a sequence deposited in GenBank and used for the phylogenetic studies.

* Sequences obtained by amplification with Aga-dif primers.

Sequences that were not used for the construction of phylogenetic trees presented in Figs. 1 and 2.

program and then corrected manually to preserve conserved motifs. The evolutionary history was inferred using Bayesian phylogenetic analysis (Ronquist and Huelsenbeck 2003) by TOPALi 2.5 software (Biomathematics and Statistics Scotland) with integrated MrBayes application (<http://mrbayes.csit.fsu.edu>) with HKY substitution model for the whole alignments. Minimum evolution and maximum parsimony phylogenetic trees, within group average calculation and between group average calculation (Maximum Composite Likelihood method), were performed by MEGA 4.0.2 software (Kumar et al., 2008). The sequence of *Trapelus mutabilis* (voucher ZFMK 64395) was used as outgroup. All sequenced amplicons were registered in GenBank (Table 1).

RESULTS AND DISCUSSION

1. Phylogenetic analyses

A total of 171 specimens were included in the phylogenetic analyses, including 127 specimens from our field collections and 44 specimens from GenBank. At least

one specimen of each species of *Agama* previously known from West Africa was included. Special attention was carried to the *Agama agama* complex and related species (86 specimens of our collection tested, including topotype specimens of *A. paragama*, *A. sylvanus*, *A. lebretoni*, *A. africana*, *A. savattieri*, *A. picticauda*, *A. agama* sensu Wagner et al. 2009a and *A. agama* sensu Mediannikov et al., this paper).

A phylogenetic tree (Bayesian interference) including all West African species and the most distinct *Agama agama* sensu lato vouchers is presented in Fig. 1. All species morphologically attributable to the *A. agama* complex belong to the same clade. The sahelo-saharian species are distributed in two clades, one including only *A. boulengeri*, the other including *A. boueti*, *A. castroviejoi*, *A. impalearis* (from southern Morocco) and a yet undescribed species from Air mountains (Niger) previously confused with *A. impalearis*. The remaining species belong to three clades, one including only *A. cristata*, second including *A. insularis*, *A. gracilimembris*, and *A. weidholzi*, the third including *A. doriae*, *A. sankaranica*, and all species of the *A. agama* complex. Two

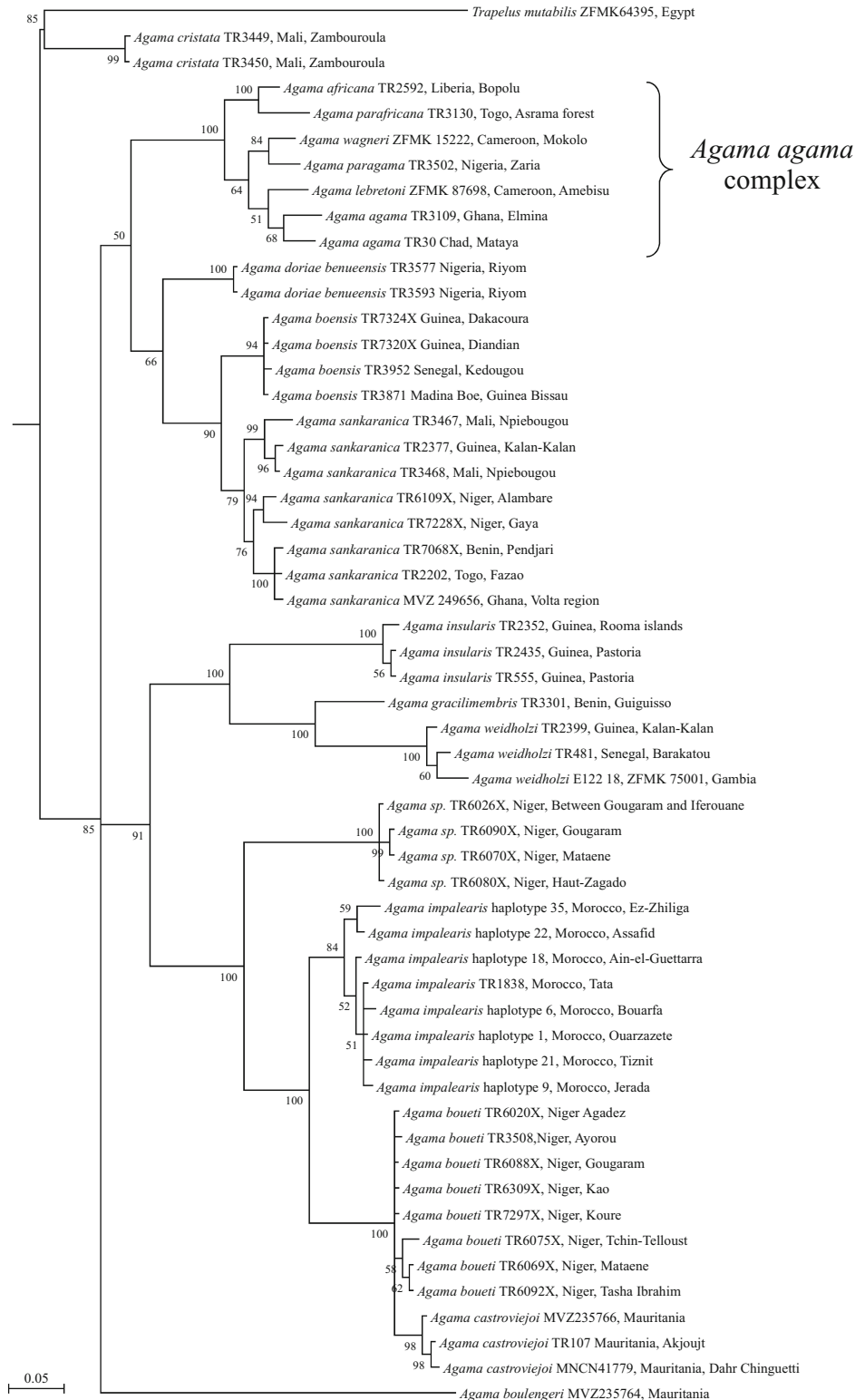


Fig. 1. Evolutionary relationships of the West-African *Agama* species. The evolutionary history was inferred using Bayesian phylogenetic analysis with HKY substitution model for the whole alignments based on 16S rDNA sequences. The confidence probability (multiplied by 100) that the interior branch length is greater than 0, as estimated using the bootstrap test (100 replicates is shown next to the branches). The tree is drawn to scale, with branch lengths in the same units as those of the evolutionary distances used to infer the phylogenetic tree.

TABLE 2. List of Mitochondrial 16s rDNA Sequences Obtained from GenBank and Used for Phylogenetic Tree Construction with Notes on the Origin of the Voucher

No.	GenBank number	Species according GenBank	Species according present article	Voucher or another specimen designation	Country of voucher origin	Locality	Length of sequence	Reference
1	GU128443	<i>A. agama</i>	<i>A. agama</i>	MVZ 238891	Niger	Niamey	474	Leache et al., 2009
2	GU128439	<i>A. agama</i>	<i>A. agama</i>	MVZ 249617	Ghana	Volta region	474	Leache et al., 2009
3	GU128436	<i>A. agama</i>	<i>A. agama</i>	ZFMK 73185	Gabon	Tchimbelle	474	Leache et al., 2009
4	GU133310	<i>A. agama</i>	<i>A. agama</i>	E122 13 MHNG 2689 53	Benin		499	Wagner et al., 2009b
5	GU128433	<i>A. agama</i>	<i>A. agama</i>	MCZ 184561	Cameroon	Yaoundé	474	Leache et al., 2009
6	FJ159558	<i>A. agama</i>	<i>A. agama</i>	983	Mali	Bandiagara cliff	443	Vasconcelos et al., 2009
7	FJ159562	<i>A. agama</i>	<i>A. agama</i>	RV	Cape Verde	Santo Antao Island	442	Vasconcelos et al., 2009
8	GU128437	<i>A. agama</i>	<i>A. agama</i>	LSUMZ H20336	Ghana	Tessano	474	Leache et al., 2009
9	FJ159561	<i>A. agama</i>	<i>A. agama</i>	399	Niger	50 km S of Tahoua	443	Vasconcelos et al., 2009
10	GU128441	<i>A. agama</i>	<i>A. agama</i>	AMNH 109799	Mali	unknown	476	Leache et al., 2009
11	FJ159559	<i>A. agama</i>	<i>A. agama</i>	1364	Mauritania	N of Kankossa	444	Vasconcelos et al., 2009
12	FJ159560	<i>A. agama</i>	<i>A. agama</i>	425	Burkina-Faso	15 km W Fada-Ngourma	444	Vasconcelos et al., 2009
13	GU128438	<i>A. agama</i>	<i>A. agama</i>	LSUMZ H20085	Ghana	Buipe	474	Leache et al., 2009
14	GU128445	<i>A. agama</i>	<i>A. agama</i>	2906 1	Chad	Bol	474	Leache et al., 2009
15	GU128442	<i>A. agama</i>	<i>A. agama</i>	ZFMK 76838	Mauritania	Selibabi	475	Leache et al., 2009
16	GU133311	<i>A. agama</i>	<i>A. agama</i>	BM ZFMK 73845	Senegal	Dakar	499	Wagner et al 2009c
17	GU128440	<i>A. agama</i>	<i>A. africana</i>	ULM 200	Guinea	Diaragbela	473	Leache et al., 2009
18	GU128434	<i>A. agama</i>	<i>A. wagneri</i>	MCZ184562	Cameroon	Yaoundé	472	Leache et al., 2009
19	GU133323	<i>A. agama</i>	<i>A. wagneri</i>	AL ZFMK 15222	Cameroon	Mokolo	474	Wagner et al., 2009b
20	GU128435	<i>A. agama</i>	<i>A. lebretoni</i>	CAS 207958	Equ. Guinea	Bioko island	475	Leache et al., 2009
21	GU128444	<i>A. agama</i>	<i>A. lebretoni</i>	MVZ 253099	Nigeria	Cross river National parc	474	Leache et al., 2009
22	GU128432	<i>A. agama</i>	<i>A. lebretoni</i>	X3853	Cameroon	Mende, Mont Takamanda	474	Leache et al., 2009
23	GU128449	<i>A. Boulengeri</i>	<i>A. Boulengeri</i>	MVZ235764	Mauritania	Nouakchott district	473	Leache et al., 2009
24	AY522929	<i>A. castroviejoi</i>	<i>A. castroviejoi</i>	MNCN41779	Mauritania	Dahr Chinguetti	498	Padiati, 2005
25	GU133325	<i>A. cristata</i>	<i>A. insularis</i>	AL GN TR555	Guinea	Pastoria	475	Wagner et al., 2009b
26	GU133314	<i>A. finchi</i>	<i>A. agama finchi</i>	ZFMK 83652	Kenya	Malaba	499	Wagner et al., 2009c
27	GU128452	<i>A. finchi</i>	<i>A. agama finchi</i>	ZFMK 83653	Kenya		475	Leache et al., 2009
28	AJ1414673	<i>A. impalearis</i>	<i>A. impalearis</i>	Haplotype 6	Morocco	Bouarfá	467	Brown et al., 2002
29	AJ1414676	<i>A. impalearis</i>	<i>A. impalearis</i>	Haplotype 9	Morocco	Jerada	467	Brown et al., 2002
30	AJ1414679	<i>A. impalearis</i>	<i>A. impalearis</i>	Haplotype 18	Morocco	Ain-el-Guetiara	467	Brown et al., 2002
31	AJ1414672	<i>A. impalearis</i>	<i>A. impalearis</i>	Haplotype 1	Morocco	Ouarzazete	467	Brown et al., 2002
32	AJ1414680	<i>A. impalearis</i>	<i>A. impalearis</i>	Haplotype 21	Morocco	Tizi-Mighert (Tiznit)	467	Brown et al., 2002
33	AJ1414681	<i>A. impalearis</i>	<i>A. impalearis</i>	Haplotype 22	Morocco	Assafid	467	Brown et al., 2002
34	AJ1414689	<i>A. impalearis</i>	<i>A. impalearis</i>	Haplotype 35	Morocco	Ez-Zhliga	467	Brown et al., 2002
35	GU128454	<i>A. impalearis</i>	<i>A. castroviejoi</i>	MVZ235766	Mauritania	Nouakchott district	474	Leache et al., 2009
36	GU133326	<i>A. insularis</i>	<i>A. insularis</i>	AL 2008 023 ZFMK (TR2352)	Guinea	Ile Rooma	412	Wagner et al., 2009b
37	GU133318	<i>A. lebretoni</i>	<i>A. lebretoni</i>	E90 20 ZFMK 75376	Cameroon	Nguengue	499	Wagner et al., 2009c
38	GU133317	<i>A. lebretoni</i>	<i>A. lebretoni</i>	AL ZFMK 73241	Cameroon	Fougamou	499	Wagner et al., 2009c
39	GU133316	<i>A. lebretoni</i>	<i>A. lebretoni</i>	ZFMK 87698	Cameroon	Amebisu	499	Wagner et al., 2009c
40	GU13332	<i>A. paragama</i>	<i>A. paragama</i>	AL ZFMK 15244	Cameroon	Waza	497	Wagner et al., 2009c
41	GU128460	<i>A. sankaranica</i>	<i>A. sankaranica</i>	MVZ 249656	Ghana	Volta region	475	Leache et al., 2009
42	GU128462	<i>A. weidholzi</i>	<i>A. weidholzi</i>	TR481	Senegal	Barakatou	474	Leache et al., 2009
43	GU133328	<i>A. weidholzi</i>	<i>A. weidholzi</i>	E1 22 18 ZFMK 75001	Gambia		473	Wagner et al., 2009b
44	GU128465	<i>Trapelus mutabilis</i>	<i>Trapelus mutabilis</i>	ZFMK 64395	Egypt		473	Leache et al., 2009

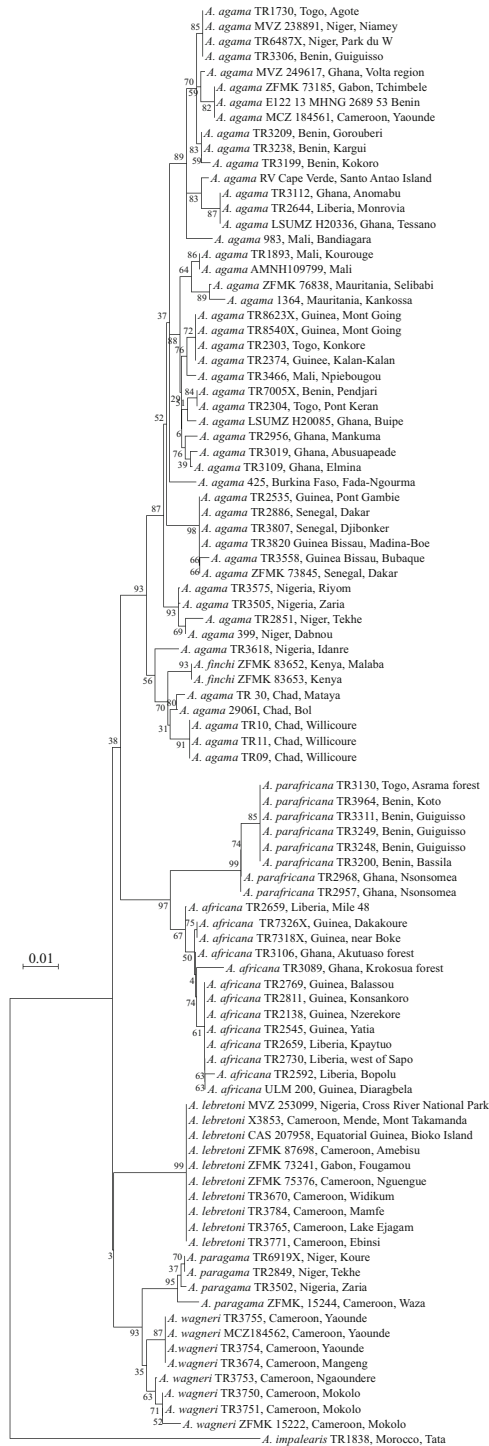


Fig. 2. Evolutionary relationships of the West-African species of the *Agama agama* complex. The evolutionary history was inferred using Minimum Evolution analysis with maximum composite likelihood substitution model. The confidence probability (multiplied by 100) that the interior branch length is greater than 0, as estimated using the bootstrap test (100 replicates is shown next to the branches). The tree is drawn to scale, with branch lengths in the same units as those of the evolutionary distances used to infer the phylogenetic tree.

well-supported lineages exist within geographically distinct specimens classically attributed to *A. sankaranica*, one including all specimens from the westernmost part of West Africa (Senegal, Guinea Bissau, and western Guinea), the other one including all specimens from the central and eastern parts of West Africa. The calculated genetic distance between these two lineages (0.038) appears higher than between some well recognized species of the *A. agama* complex, suggesting that *A. boensis* Monard, 1940, described from Guinea Bissau, should be resurrected from the synonymy of *A. sankaranica*.

A phylogenetic tree of the *A. agama* complex and related species including a large number of specimens from most areas of West Africa is shown in Fig. 2. At least six phylogeographic groups correspond to distinct species. *A. lebretoni* from southwestern Cameroon, southeastern Nigeria and Bioko Island is the most homogeneous species. Another well supported phylogeographic group, which represents a new species described in this paper, comprises specimens from wet savanna areas of Benin, Togo and Ghana that are both morphologically and genetically distinct from sympatric *A. agama* specimens. Topotypes of *A. sylvanus* from Akutuaso forest (Ghana) and of *A. africana* from forest areas of Liberia belong to the same phylogeographic group which also includes most specimens from forest and wet savanna areas of Guinea. The topotype of *A. paragama* from Zaria (Nigeria) belongs to a well supported phylogeographic group which is also distributed in Niger. Vouchers from northern and central Cameroon constitute a distinct species related to *A. paragama* which is described in this paper. The largest clade, which comprises most of the specimens classically attributed to *A. agama*, is distributed in all Sahelian and Sudanian areas investigated, in the Dahomey gap where it reaches the coastal areas of Ghana, Togo and Benin, in large cities along the Atlantic coast such as Accra, Monrovia, and Dakar, and in villages of forest areas of Ghana and inselbergs of forest areas of Nigeria but not in villages of forest areas of Guinea or Liberia where only *A. africana* was found. Within this

TABLE 3. Genetic Distances within Each Group of the *Agama agama* Complex

Species	Maximum composite likelihood
<i>Agama agama</i>	0.014
<i>Agama africana</i>	0.004
<i>Agama lebretoni</i>	0.000
<i>Agama paragama</i>	0.005
<i>Agama parafricana</i>	0.002
<i>Agama wagneri</i>	0.008
<i>Agama agama</i> cf. <i>finchi</i>	0.008



Fig. 3. *Agama africana* Hallowell, 1844.

clade, there is clear evidence for several distinct geographic lineages requiring further morphological and genetical investigations with additional specimens and/or molecular markers to determine if some of them may represent distinct species or subspecies. We calculated distances within (Table 3) and between (Table 4) the different species or more distinct geographic lineages of the *A. agama* complex, including *A. finchi* from Kenya and related specimens from Chad and southern Nigeria. We found that distances within each species or lineage does not exceed 0.014 (maximum composite likelihood), and that distances between species is between 0.021 and 0.057.

2. Species account

Based on these data, literature, and examination of Linnean type-specimens of *A. agama*, at least 17 different species can be recognized in the genus *Agama* in West Africa, northern Cameroon and Chad. For each species, our own records are given with an asterisk, and a square-degree distribution map and some ecological notes are provided. References are given with each species when they are used in the systematic account, the distribution map and/or the ecological notes.

2.1. *Agama africana* Hallowell, 1844 (Figs. 3 and 4)

1844 *Tropidolepis africanus* Hallowell, *Proc. Acad. Nat. Sci. Philadelphia*, **1844**, 171. Type locality: Liberia.

1884 *Agama savattieri* (pro parte) — Rochebrune, *Faune Sénégalie*, Rept., **89**, 11; Figs. 1, 2.

TABLE 4. Genetic Distances Between Groups of the *Agama agama* Complex

	Maximum composite likelihood					
	1	2	3	4	5	6
[1] <i>Agama agama</i>						
[2] <i>Agama africana</i>	0.042					
[3] <i>Agama lebretoni</i>	0.045	0.038				
[4] <i>Agama paragama</i>	0.045	0.041	0.038			
[5] <i>Agama parafricana</i>	0.051	0.030	0.058	0.050		
[6] <i>Agama wagneri</i>	0.038	0.036	0.037	0.021	0.047	
[7] <i>Agama agama</i> cf. <i>finchi</i>	0.026	0.038	0.035	0.039	0.057	0.032

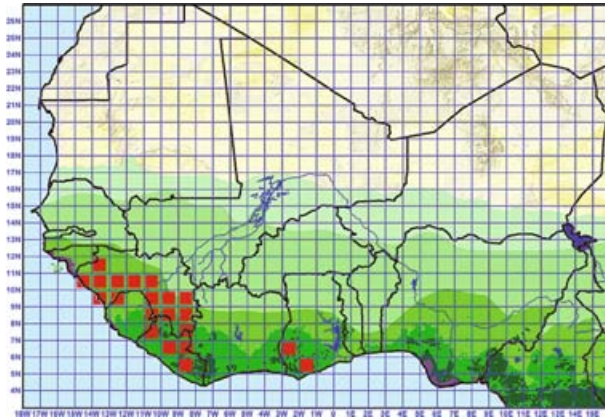


Fig. 4. Geographic distribution of *Agama africana* Hallowell, 1844.

1941 *Agama agama africana* — Loveridge, *Proc. U.S. Natl. Mus.*, **91**, 116.

1981 *Agama sylvanus* — Macdonald, *J. Zool. Lond.*, **193**, 191.

Geographic distribution (confirmed by molecular studies only). **Ghana:** Akutuaso forest* (05°16' N 01°28' W, type locality of *A. sylvanus* Macdonald 1981), Krokosua forest* (06°29' N 02°45' W). **Guinea:** Balassou* (08°23' N 09°18' W), Boké* (10°57' N 14°16' W), Dakakoura* (10°52' N 13°38' W), Daramagnaki* (10°52' N 13°47' W), Diandian* (11°00' N 13°46' W), Diaragbéla (10°35' N 09°58' W), Diéké forest* (07°30' N 08°53' W), Kalékouré* (09°57' N 12°48' W), Kilissi* (09°57' N 12°49' W), Kindia* (10°03' N 12°51' W), 25 km SW of Kindia* (09°55' N 13°02' W), Konsankoro* (09°02' N 08°59' W), vicinity of Nianfou-rando* (09°31' N 10°24' W), Oueye* (08°02' N 08°56' W), Kouroumaya* (09°56' N 12°49' W), Pastoria* (10°06' N 12°50' W), Yatia* (10°01' N 10°58' W), vicinity of Yatia* (10°02' N 11°01' W). **Liberia:** Bopolu* (07°03' N 10°29' W), Kpaytuo* (06°48' N 08°48' W), Miles 48* (05°35' N 08°32' W), track west of Sapo* (05°42' N 08°58' W).

Systematics. Both our molecular and field data indicate that *A. africana* must be resurrected from the synonymy of *A. agama* and that *A. sylvanus* is a junior synonym of *A. africana*. Coloration of adult males and the number of vertebral scales (33 – 40 in *A. africana*, 42 – 58 in *A. agama*, counts according to Grandison, 1968) are the best criteria to distinguish these two species where they are parapatric, e.g., in Kérouané and Konsankoro areas in Guinea where *A. africana* is distributed along the Milo river valley and *A. agama* in the surrounding hills and mountains.

Ecological notes. *A. africana* is widely distributed in the most humid areas of West Africa. It inhabits clearings

and tracks in the rain forest, plantations, and villages adjacent to rain forest, mosaics forest — savanna, forest galleries, and adjacent villages in Guinean savanna areas. It is a semi-arboreal species, living in groups consisting of a single adult male, one or more females, and a number of young animals.

References. Macdonald (1981).

2.2. *Agama agama* (Linnaeus, 1758) (Figs. 5 and 6)

1758 *Lacerta agama* Linnaeus, *Syst. Nat. Ed. 10*, **1**, 207.— Type locality: “America” (in error; coast of West Africa, probably Senegal or Ghana, this study).

1802 *Agama colonorum* Daudin (nomen substitutum pro *Lacerta agama* Linnaeus, 1758), *Hist. nat. gén. part. rept.*, **3**, 358.

1877 *Agama picticauda* (pro parte) — Peters, *M. Berk. K. preuß. Akad. Wiss. Berlin*, 612.

1884 *Agama savattieri* (pro parte) — Rochebrune, *Faune Sénégal, Rept.*, **89**, 11, Figs. 1, 2.

Geographic distribution (confirmed by molecular studies only). **Benin:** Batia* (10°53' N 01°28' E), Gorouberi* (12°07' N 03°08' E), Guiguissou* (09°03' N 01°40' E), Kargui Hill* (11°55' N 03°12' E), Kokoro* (08°17' N 02°38' W). **Burkina Faso:** 15 km W of Fada-Ngourma (12°06' N 00°14' E). **Cameroon:** Yaoundé (03°51' N 11°30' E). **Cape Verde Islands:** Lagedos, Santo Antão (17°01' N 25°05' W). **Chad:** Bol (13°27' N 14°42' E), Mataya* (11°59' N 17°59' E), Willicouré-Sounoute* (14°09' N 21°50' E). **Gabon:** Tchimbéle Dam (00°37' N 10°24' E). **Ghana:** Abusuaapeade* (06°52' N 02°52' W), Anomabu* (05°10' N 01°08' W), Buipe (08°47' N 01°28' W), Elmina* (05°08' N 01°18' W), Monkuma* (09°09' N 02°29' W), Tesano (05°36' N 00°14' W). **Guinea:** Balagbeni* (09°12' N 08°53' W), Kalan-Kalan* (10°06' N 08°53' W), Mont Going, Simandou PK0* (09°09' N 08°56' W), Pont Gambie* (11°59' N 11°49' W). **Guinea Bissau:** Bubaque* (11°18' N 15°50' W), Madina Boé* (11°44' N 14°12' W), Madina Tiané* (11°58' N 14°14' W), N'Tchalé* (11°59' N 14°48' W). **Liberia:** Monrovia* (06°17', 10°46' W). **Mali:** Bandiagara cliff (14°36' N 03°12' W), vicinity of Kourougé* (14°09' N 09°08' W), Npiébougou and vicinity* (10°58' N 08°00' W; 10°58' N 07°58' W; 11°01' N 08°01' N; 11°00' N 07°59' W), Laminibougou* (14°04' N 06°02' W). **Mauritania:** N of Kankossa (16°04' N 11°30' W), Selibabi (15°09' N 12°11' W). **Niger:** 50 km S of Tahoua (14°09' N 05°21' E), Niamey (13°30' N 02°06' E), Tékhé* (14°01' N 06°01' N), vicinity of Tékhé* (14°01' N 05°58' E; 13°58' N 05°59' E; 13°59' N 06°01' N). **Nigeria:** Idanré* (07°06' N 05°06' E), Riyom* (09°37' N



Fig. 5. *Agama agama* (Linnaeus, 1758).

08°44' E), Zaria* (11°09' N 07°47' E). **Senegal:** Dakar* (14°43' N 17°26' W), Djibonker* (12°32' N 16°21' W), Mlomp* (12°33' N 16°34' W). **Togo:** Agoté* (07°15' N 00°47' E), Konkoré* (10°45' N 00°12' E), Pont Keran* (10°09' N 00°49' E).

Systematics. Wagner et al. (2009a) designated a neotype for *A. agama*, arguing that Linnaeus (1758) referred to a plate of Seba (1734) and that no syntype corresponding to the Agamid lizards illustrated by Seba was available. In fact, Linnaeus (1758) also explicitly referred to descriptions of specimens in the collection of the Prince, later King Adolf Fredrik. One part of the collection was donated to the Academy in Uppsala and described by Linnaeus (1749). A larger collection remained in the King's possession and was described by Linnaeus (1754, 1764). Linnaeus (1749: 288 – 289) gave a detailed description of *Lacerta cauda tereti longa, pedibus pentadactylis, dorso antice denticulato, collo patiteque pone aculeato* based on the material in the Uppsala collection, even addressing sex differences, suggesting that more than one specimen was at hand. This description is referred to in the diagnosis of *Lacerta agama* in Linnaeus (1758) and the specimens referred to are syntypes. Catalogues and several publications on the Linnean type specimens indicate that ZMUU 32, a specimen kept in the Zoological Museum of the Uppsala University, has always been registered as formerly belonging to the Adolphi Friderici collection and was the basis for the description of the lizard on pp. 288 – 289 (Lönnerberg, 1896;

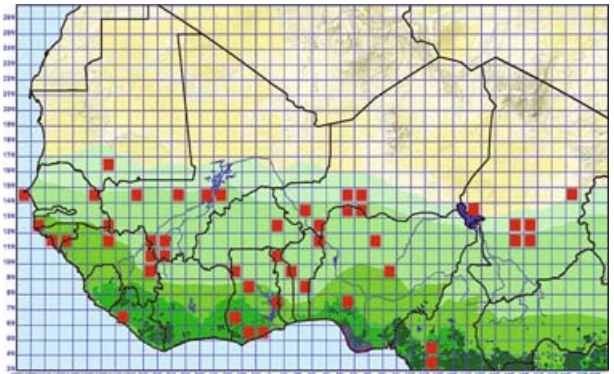


Fig. 4. Geographic distribution of *Agama agama* (Linnaeus, 1758).

Olofsson circa 1915; Holm, 1957; Wallin, 1997). It is consequently a syntype of *A. agama*. We examined this specimen which is a male of *A. agama* (Fig. 7). Importantly, both its vertebral (47) and mid-dorsal counts (71) match with *A. agama* specimens from Senegal or the coast of Ghana and exclude *A. africana*. Linnaeus (1754: 44) briefly diagnosed *Agama amphibia*, referring to the earlier description in Linnaeus (1749) and mention in Linnaeus (1748). The majority of the specimens catalogued in Linnaeus (1754) are presently in the Swedish Museum of Natural History. Andersson (1900: 11) identified three specimens in this collection as representing Linnaeus's (1754) *Lacerta amphibia*, and which thus are syntypes of *A. agama*. Only one of these, however, pres-

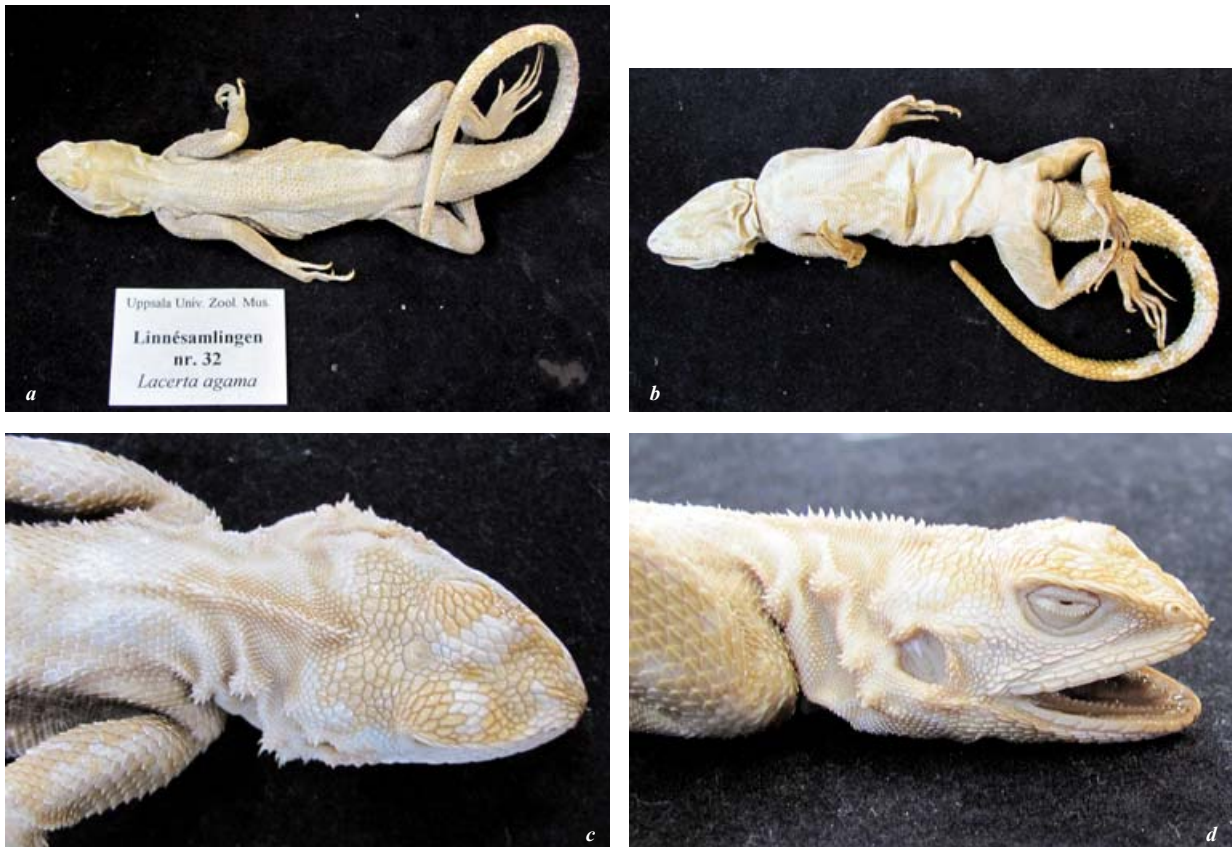


Fig. 7. Views of ZMUU 32, the lectotype of *Lacerta agama* Linnaeus, 1758.

ently catalogued as NRM 108, is definitely referable to *Agama agama*, and its vertebral (45) and mid-dorsal counts (72) are close to those of ZMUU 32. Linnaeus (1749, 1754, 1758) persistently referred specimens described and figured by Seba (1734) as *Salamandra americana* and *Salamandra amphibia* to *A. agama* and those Seba specimens are consequently also syntypes of *A. agama*. Although it remains possible that one or more of the Seba specimens were acquired by King Adolf Fredrik for his collection, we have not been able to fully correlate any of the three specimens in the Adolf Fredrik collection with Seba's figures and descriptions. Since at least four syntypes of *A. agama* still exist (ZMUU 32, NRM 107, 108, 112), the designation of a neotype by Wagner et al. (2009a) is hereby invalidated (International Commission on Zoological Nomenclature, 1999: Article 75.8). Because the type series, including Seba's material, is a composite, we select here ZMUU 32 as lectotype of *Lacerta agama* Linnaeus, 1758. This specimen has a consistent record of attachment to the description in Linnaeus (1749: 288 – 289), and is fully compatible with the current concept of *Agama agama*. Its meristic data sug-

gest that it comes from an area in western Africa that was included in the route of ships traveling between Europe and Africa or South America in the 18th Century. The specimen, catalogued in the Museum of Evolution, Uppsala University with the catalogue number ZMUU 32, conforms to the detailed description by Linnaeus (1749), and is figured here in dorsal and ventral aspect (Fig. 7). The neotype proposed by Wagner et al. (2009a), ZFMK 15222, and similar specimens from northern and central Cameroon in our collection belong to a new species (see below).

Ecological notes. The most widespread *Agama* species in West Africa. All savanna areas, where it is also very abundant in villages and towns. Introduced populations in towns, villages and other human-impacted areas of previously rain forest areas of West and Central Africa, but excluded from many parts of human-impacted areas of the Guinean forest block by *A. africana* and from the Nigerian/southwestern Cameroonese part of the Congolese forest block by *A. lebretoni*. Semi-arboreal, but also rock dweller and appreciates concrete man-made



Fig. 8. *Agama boensis* Mocquard, 1886.

structures. Groups consisting of a single adult male, several females, and a number of young animals.

References. Holm (1957), Harris (1964), Wallin (1997), Leaché et al. (2009), Vasconcelos et al. (2009), Wagner et al. (2009a).

2.3. *Agama boensis* Mocquard, 1886 (Figs. 8 and 9)

1940 *Agama boensis* Monard, *Arq. Mus. Bocage*, **11**, 155. Type locality: Madina Boé, Guinea Bissau.

Geographic distribution. **Guinea:** Dakacoura* (10°52' N 13°38' W), Diandian* (11°00' N 13°46' W), Kogon-Lenguéré* (11°06' N 13°48' W), vicinity of Linsan* (10°08' N 12°32' W), Missidé-Balouta* (10°55' N 13°39' W), Yama* (11°07' N 13°39' W). **Guinea Bissau:** Madina Boé* (11°44' N 14°12' W). **Mali:** Bangaya* (13°14' N 10°43' W). **Senegal:** Bandafassi* (12°32' N 12°18' W), 30 km SE Dar Salam (13°09' N 12°55' W), Kédougou* (12°32' N 12°10' W), 34 km NW of Mako (13°00' N 12°36' W), 10 km NW of Nafadji (12°41' N 11°40' W), Satatougou-Bafé (12°38' N 11°25' W).

Systematics. Monard (1940) mentioned two *Agama* species in Madina Boé (Guinea Bissau): *A. colonorum*

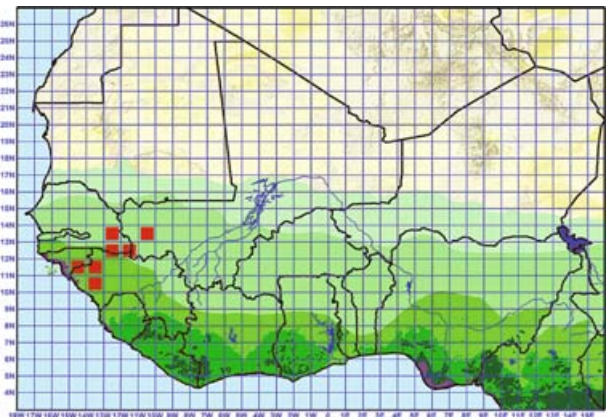


Fig. 9. Geographic distribution of *Agama boensis* Mocquard, 1886.

Daudin, 1802 (= *A. agama*), and *A. boensis* sp. nov., a new species that was represented by four specimens in his collection. Grandison (1968) examined the four syntypes of *A. boensis* and concluded that three of the syntypes belonged to *A. sankaranica* and the fourth syntype was conspecific with *A. weidholzi*. During our field survey in Madina Boé, we collected specimens of *A. agama*



Fig. 10. *Agama boueti* Chabanaud, 1917.

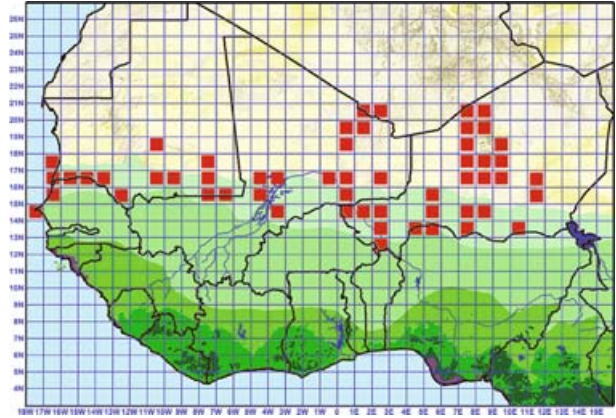


Fig. 11. Geographic distribution of *Agama boueti* Chabanaud, 1917.

(confirmed by molecular studies), *A. weidholzi*, and a third species similar to the description and photograph of *A. boensis* published by Monard (1940). Both molecular data (see Fig. 1) and differences in scale counts (midbody scale count 70 – 83, vertebral scales 39 – 50 for *A. boensis*; midbody scale count 60 – 75, vertebral scales 31 – 39 for our specimens of *A. sankaranica* from eastern and central Guinea, southeastern Mali, Togo, Benin, and Niger) (L. Chirio and J.-F. Trape, unpublished data) suggest that *A. boensis* is a valid species, distributed in the westernmost part of West Africa, that must be resurrected from the synonymy of *A. sankaranica*.

Ecological notes. The distribution of *A. boensis* corresponds to the western part of Fouta Djallon mountains in Guinea and the lateritic hills and tables of eastern Guinea Bissau, southeastern Senegal and western Mali. Specimens are solitary and live on the ground. They are often seen perching on stones or termite mounds.

References. Monard (1940), Grandison (1968), Joger and Lambert (2002).

2.4. *Agama boueti* Chabanaud, 1917

(Figs. 10 and 11)

1917 *Agama boueti* Chabanaud, *Bull. Mus. Hist. nat., Paris*, **23**, 85.— Type locality: Gao, Niger.

Geographic distribution. **Mali:** Adrar des Iforhas (20°00' N 2°00' E, approx.), 93 km S of Aguelhok (18°38' N 00°11' E), Ansongo (15°40' N 00°30' E), Bandiagara (14°21' N 03°37' W), Dabaye* (15°07' N 07°57' W), Dabi* (15°55' N 04°08' W), Douentza (15°00' N 02°57' W), Gao (16°15' N 00°03' W), vicinity of Gaoudel* (16°00' N 04°06' W), Goundam (16°25' N 03°40' W), vicinity of Haoussa Foulane* (16°03' N 00°08' E), NW of Ménaka* (16°05' N 02°10' E), Tessalit (20°12' N 01°00' E), 64 km S of Tessalit (19°38' N

00°57' E), NW of Tiderméné* (17°02' N 02°08' E), SW of Abibara* (19°01' N 01°50' E). **Mauritania:** Ayoûn El Atrouïs (16°39' N 09°37' W), Boghé* (16°35' N 14°15' W), Bougari (16°32' N 10°47' W), Chott Boul (16°36' N 16°26' W), Lakarich* (15°59' N 06°30' W), W of Lekhcheb* (18°27' N 10°50' W), Leqceiba* (16°13' N 13°08' W), Mahmûdé lake (16°29' N 07°42' W), Metraucha (16°33' N 10°45' W), 80 km S of Nouakchott (17°23' N 16°04' W), N of Rosso (16°30' N 15°48' W). **Niger:** 10 km NW of Abalak (15°37' N 06°25' E), Ayorou* (14°44' N 00°55' E), 42 km N of Agadez (17°20' N 07°58' E), vicinity of Agadez* (16°56' N 07°57' E), 15 km W of Birni N'Konin (13°47' N 05°01' E), 20 km W of Birni N'Konin (13°47' N 04°58' E), vicinity of Elmeki (17°43' N 08°16' E), N of Farié* (14°03' N 01°32' E), Gidyo* (13°59' N 10°02' E), Iférouane* (19°03' N 08°25' E), 25 km SE of Iférouane* (18°54' N 08°33' E), vicinity of Kolifo* (13°59' N 04°00' E), Kouré* (13°19' N 02°35' E), Maradi* (13°30' N 07°06' E), Mazadaoua* (14°00' N 08°00' E), vicinity of Mazadaoua (14°02' N 07°58' E), vicinity of Simiri* (14°02' N 02°05' E), 15 km NW of Tahoua (14°54' N 05°23' E), Zagado* (18°37' N 09°05' E). **Senegal:** Dakar* (14°44' N 17°26' W), Keur Massar (14°47' N 17°19' W), Malika (14°48' N 17°21' W), Mboro-sur-Mer (15°11' N 16°54' W).

Ecological notes. Inhabits sandy places with vegetation in the Sahel: fixed dunes on the southern edge of the Sahara desert, sandy bed of oued in Aïr mountains (Niger) and Adrar des Ifhoras (Mali), coastal dunes in Senegal and southern Mauritania. Lives on the ground. Eat



Fig. 12. *Agama boulengeri* Lataste, 1886.

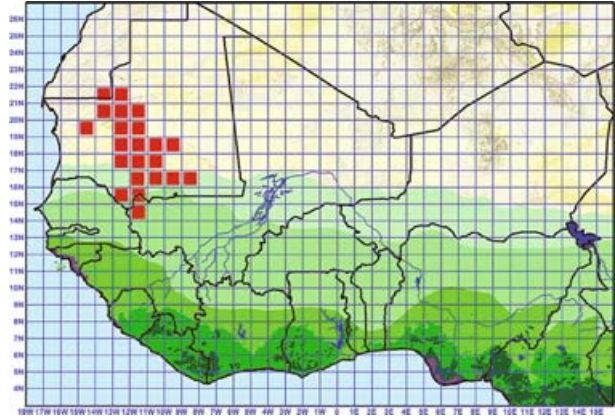


Fig. 13. Geographic distribution of *Agama boulengeri* Lataste, 1886.

mainly insects but also succulent plants. Solitary and territorial.

References. Brito et al. (2008), Böhme (1978), Joger (1979, 1981), Joger and Lambert (1996), Karns and Cissé (1975), Kriska (2001), Padiál (2006).

2.5. *Agama boulengeri* Lataste, 1886

(Figs. 12 and 13)

1917 *Agama boulengeri* Lataste, *Le Naturaliste, Paris*, **8**, 212. Type locality: vallon des singes à Médine, Haut Sénégal, Mali.

Geographic distribution. **Mali:** Médine (14°22' N 11°21' W), chutes du Félou (14°21' N 11°20' W), chutes de Gouina* (14°01' N 11°06' W). **Mauritania:** Achram (17°21' N 12°23' W), 5 km SE of Aggui* (21°08' N 13°05' W), guelta Agmeïmine* (19°45' N 12°50' W), Agueni* (20°31' N 13°08' W), Aïn El Ghaire (17°11' N 12°14' W), Ayoûn El Atroûs (16°39' N 09°37' W), guelta Azougui* (20°38' N 13°08' W), Ben Amira (21°13' N 13°40' W), Bou Bleï'ine (17°07' N 10°59' W), Bougari (16°32' N 10°47' W), Chinguetti (20°27' N 12°22' W), oued Choûm (21°17' N 13°06' W), Dar el Oula* (16°35' N 09°48' W), Drayya Imougayene* (19°46' N 12°14' W), guelta El Berbera* (19°59' N 12°49' W), guelta Fanar (18°00' N 12°10' W), Hamdoun* (20°20' N 13°09' W), Iriji Adrar (20°31' N 13°03' W), Iriji Tagant* (18°45' N 11°40' W), guelta Ilij* (20°38' N 13°38' W), Kaonal (20°18' N 13°11' W), vicinity of Louths (17°14' N 12°06' W), between Lekhcheb (18°30' N 10°30' W) and Tîchît (18°26' N 09°26' W), guelta Matmata* (17°53' N 12°07' W), M'bout (16°01' N 12°34' W), guelta Metraucha (16°33' N 10°45' W), guelta Molomhar* (20°34' N 13°07' W), Moudjeria* (17°53' N 12°19' W), Nbeïka* (17°58' N 12°14' W),

20 km NE of Nbeïka* (18°08' N 12°02' W), Nkedeï* (19°37' N 12°48' W), Oujeft* (20°00' N 13°03' W), Oumm El Khez (17°03' N 10°57' W), guelta Oumm Lebare (16°29' N 10°49' W), Rachid* (18°47' N 11°41' W), Sélibabi (15°09' N 12°10' W), Soufa* (15°56' N 12°02' W), Swiyia (20°16' N 13°07' W), guelta Tachot* (13°24' N 13°06' W), guelta Taoujafet* (18°52' N 11°49' W), Ted (20°44' N 13°01' W), Terjît* (20°15' N 13°05' W), vicinity of Timbedgha (16°26' N 09°14' W), Tidjkdja (18°33' N 11°25' W), Tintâne (16°23' N 10°10' W), guelta Toungad (20°03' N 13°07' W), Zerga (20°19' N 12°40' W).

Ecological notes. A rupicolous species, living in socially organized groups on hot, dry rock surfaces of the Adrar, Tagant, Affolé, and Assaba mountains of Mauritania, and the gorges of the Senegal river in southwestern Mali. In the most arid part of its range (Aïr mountains in Mauritania), populations of this species are particularly abundant on rocks surrounding permanent or semi-permanent gueltas but rare elsewhere.

References. Joger (1979), Padiál (2006), Wagner et al. (2009b), Trape (2009).

2.6. *Agama castroviejoï* Padiál, 2005

(Figs. 14 and 15)

2005 *Agama castroviejoï* Padiál, *Herpetol. J.*, **15**, 27. Type locality: Dahr Chinguetti, Mauritania.

Geographic distribution. **Mauritania:** near Akjoujt* (19°48' N 14°25' W; 19°50' N 14°22' W), 19 km N of Atar* (20°41' N 13°00' W), 30 km E of Atar (20°34' N 12°52' W), Dahr Chinguetti (20°26' N 12°49' W), Ebnu Pass (20°33' N 12°36' W), 3 km SW of Hamdoun* (20°18' N 13°10' W), 19 km before the Nouatil Pass (20°32' N 12°17' W).



Fig. 14. Female of *Agama castroviejoi* Padial, 2005.

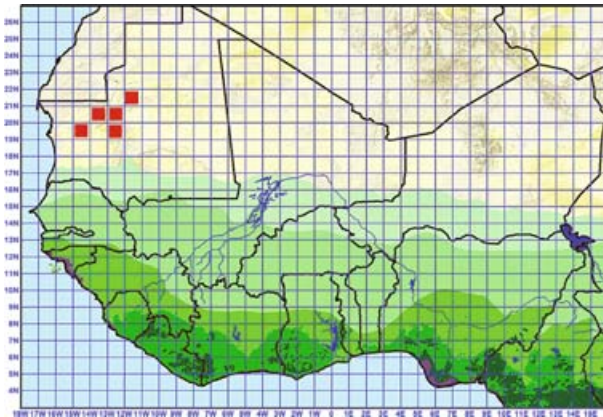


Fig. 15. Geographic distribution of *Agama castroviejoi* Padial, 2005.

Ecological notes. Inhabits hot dry rocky areas of central Mauritania. Individuals are solitary, often perching on stones around the middle of the day. Although genetically and morphologically close to *A. boueti*, ecologically very distinct and unique color pattern of gravid females (see Fig. 14) evocating the related *A. impalearis* from southern Morocco rocky areas.

Reference. Padial (2005).

2.7. *Agama cristata* Mocquard, 1905

(Figs. 16 and 17)

1905 *Agama cristata* Mocquard, *Bull. Mus. Hist. nat., Paris*, **11**, 288. Type locality: Sankaran, Soudan Français.

2009 *Agama cristata* (pro parte) — Wagner et al., *Bonn. zool. Beitr.*, **56**, 239.

Geographic distribution. **Mali:** Bomanesco (not located); Zambouroula* and vicinity (11°34' N 07°33' W; 11°36' N 07°34' W); Npiébougou* and vicinity (11°58' N 08°00' W; 12°03' N 08°02' W; 12°02' N 07°59' W).



Fig. 16. *Agama cristata* Mocquard, 1905.

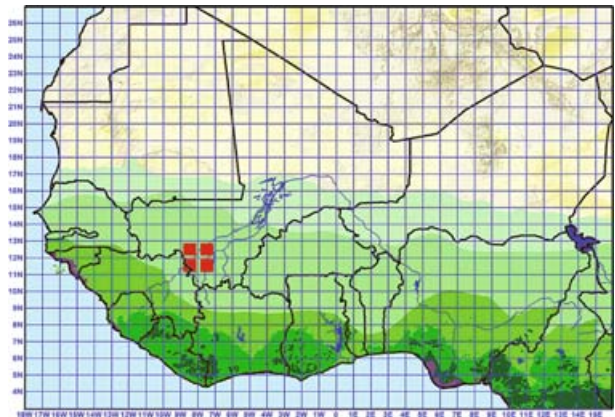


Fig. 17. Geographic distribution of *Agama cristata* Mocquard, 1905.

Ecological notes. A semi-arboreal species that inhabits flat wooded savanna areas of southern Mali and probably adjacent similar savanna areas of Guinea and Ivory Coast. Individuals seem solitary, but almost no ecological data are available.

Reference. Trape (2011).

2.8. *Agama doriae benueensis* Monard, 1951

(Figs. 18 and 19)

1885 *Agama doriae* Boulenger, *Ann. Mus. Civ. Stor. Nat. Giacomo Doria*, **2**, 127. Type locality: Keren, Eritrea.

1951 *Agama benueensis* Monard, *Mém. Inst. Fr. Afr. noire*, **1**, 131. Terra typica: Bénoué, Cameroon.

1968 *Agama benueensis* Grandison, *Bull. Br. Mus. Nat. Hist. (Zool.)*, **17**, 78.

1984 *Agama doriae benueensis* Moody and Böhme, *Bonn. zool. Beitr.*, **35**, 107.

Geographic distribution. **Cameroon:** see Grandison (1968) and Chirio and Lebreton (2007). **Central African Republic:** see Chirio and Ineich (2006). **Ghana:** Accra (?) (05°33' N 00°11' W). **Nigeria:** between Benisheik and Auno (11°50' N 12°43' W, approx.), Igbetti



Fig. 18. *Agama doriae benueensis* Monard, 1951.



Fig. 20. *Agama gracilimembris* Chabanaud, 1918.

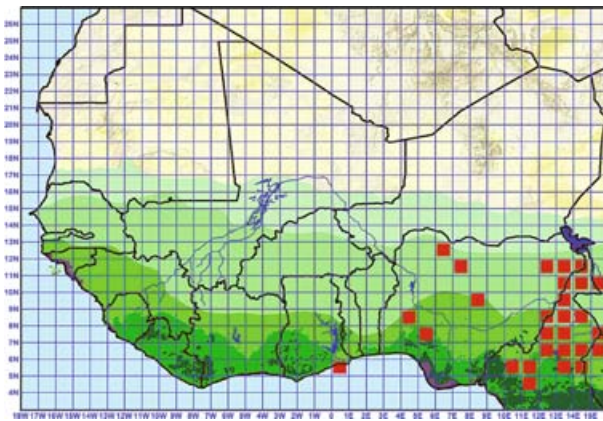


Fig. 19. Geographic distribution of *Agama doriae benueensis* Monard, 1951.

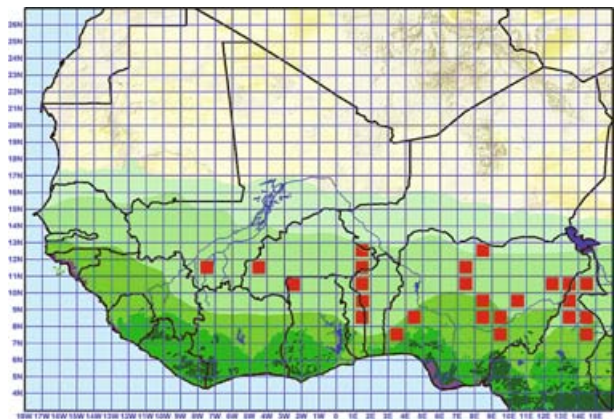


Fig. 21. Geographic distribution of *Agama gracilimembris* Chabanaud, 1918.

(08°44' N 04°08' E), Idanre* (07°06' N 05°06' E), Jos (09°56' N 08°53' E), Kwatarakwashi rock (12°23' N 06°49' E, approx.), Maiduguri (11°50' N 13°09' E), Riyom* (09°37' N 08°44' E), Zaria (11°04' N 07°43' E).

Ecological notes. A large sized *Agama* strictly confined to large rocky outcrops such as the vast gneiss inselbergs where it is common in Nigeria both in the savanna and in the forest. Conduct its feeding and sexual activities on the actual surface of the rock. Socially organized communities, with males very conspicuous in defense of territories and control of access to females.

References. Grandison (1968), Moody and Böhme (1984), Chirio and Lebreton (2007).

2.9. *Agama gracilimembris* Chabanaud, 1918
(Figs. 20 and 21)

1918 *Agama gracilimembris* Chabanaud, *Bull. Mus. Hist. nat., Paris*, **24**, 106. Type locality: Dahomey.

Geographic distribution. **Benin:** Guiguissou* (09°03' N 01°40' E); Igbéré* (08°59' N 01°57' E); Pendjari* (11°26' N 01°23' E); Tanougou* (10°48' N 01°26' E). **Burkina Faso:** 10 km SW of Bobo Dioulasso* (11°07' N 04°48' W), vicinity of Mangou* (12°03' N 01°53' E). **Cameroon:** see Chirio and Lebreton (2007); **Central African Republic:** see Chirio and Ineich (2006). **Ghana:** Wa (10°03' N 02°29' W), **Guinea:** vicinity of Kinkon* (11°05' N 12°27' W). **Mali:** vicinity of Zambouroula* (11°36' N 07°34' W). **Nigeria:** see Grandison (1968) and Gartshore (1985).

Ecological notes. A small sized *Agama* living on the ground and occurring in a wide variety of habitats in Sudan and Guinea savannas. Generally considered as the rarest of the West African *agamas*. A solitary species, males do not apparently defend territories or attempt to secure sole access to females. Often seen sunning on small termite mounds or other vantage points.



Fig. 22. *Agama insularis* Chabanaud, 1918.



Fig. 24. *Agama lebretoni* Wagner, Barej et Schmitz, 2009.

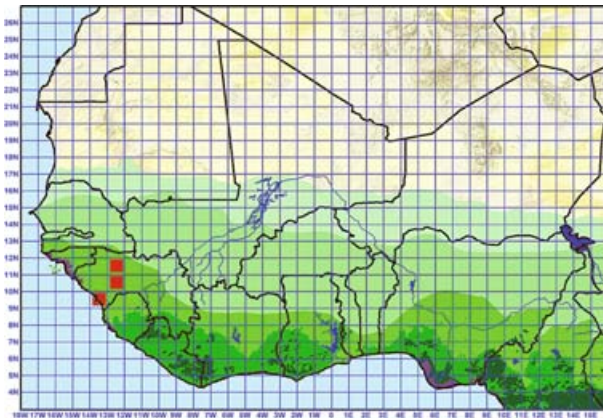


Fig. 23. Geographic distribution of *Agama insularis* Chabanaud, 1918.

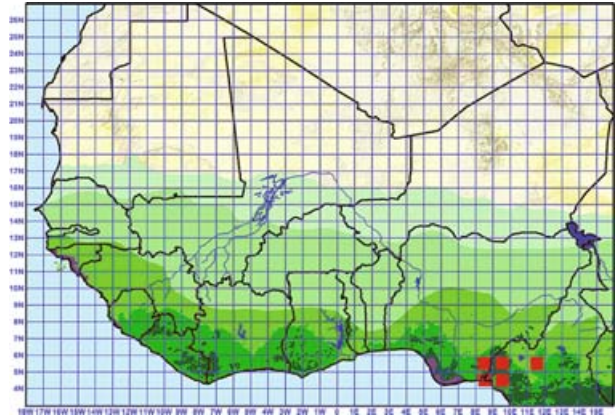


Fig. 25. Geographic distribution of *Agama lebretoni* Wagner, Barej et Schmitz, 2009.

References. Grandison (1968), Gartshore (1985).

2.10. *Agama insularis* Chabanaud, 1918

(Figs. 22 and 23)

1918 *Agama insularis* Chabanaud, *Bull. Mus. Hist. nat., Paris*, **24**, 161. Type locality: île Rooma (groupe des îles de Las), Guinée Française.

Geographic distribution. **Guinea:** île Kassa (09°28' N 13°45' W), île Rooma* (09°27' N 13°47' W), chutes de Kinkon* (11°02' N 12°27' W); Pastoria* (10°05' N 12°50' W).

Ecological notes. A large sized rupicolous species living in socially organized groups on the wet rock surfaces of the southern part of the Fouta Djallon mountains (Guinea) and the adjacent rocky islands of the Los Archipelago.

References. Parker 1939, Laurent 1947, Wagner et al., 2009b, Trape, 2011.

2.11. *Agama lebretoni* Wagner, Barej et Schmitz, 2009

(Figs. 24 and 25)

2006 *Agama* sp. Chirio and Lebreton, *Atlas des reptiles du Cameroun*, p. 166.

2009 *Agama lebretoni* Wagner, Barej et Schmitz, *Bonn. zool. Beitr.*, **56**, 291. Type locality: north-east of Mamfe, Mukwecha, Amebisu, Cameroon.

Geographic distribution (type series and/or confirmed by molecular studies only). **Cameroon:** Douala (04°02' N 09°41' E), Ebinsi* (05°41' N 09°09' E), Lake Ejagam* (05°45' N 08°59' E), Magba (05°58' N 11°13' E), Mundemba (04°58' N 08°53' E), Mukwecha (05°53' N 09°33' E), Mamfé* (05°44' N 09°18' E), Nguengue (04°54' N 09°56' E), Rumpi Hills (04°50' N 09°10' E, approx.), Taboh* (05°43' N 09°07' E), Widikum* (05°50' N 09°42' E). **Equatorial Guinea:** Bioko Island, Malabo (03°45' N 08°46' E). **Gabon:** Fougamou



a



b



c



d

Fig. 26. *Agama parafricana* sp. nov. J.-F. Trape, O. Mediannikov et S. Trape.

(01°12'S, 10°35' E). **Nigeria:** Cross River National Park (05°44' N 08°44' E, approx.).

Ecological notes. A semi-arboreal species living in socially organized groups in towns, villages, plantations and forest areas of southeastern Nigeria, southwestern Cameroon and Gabon where it is very common.

References. Chirio and Lebreton (2007), Leaché et al. (2009), Wagner et al. (2009c).

2.12. *Agama parafricana* sp. nov. J.-F. Trape, O. Mediannikov et S. Trape (Figs. 26 – 28)

Holotype. MNHN 2010.0630 (GenBank: JF520734), previously IRD TR.3130, an adult male collected on 1 March 2010 in Asrama forest* (07°00' N 01°23' E), Togo, by J.-F. Trape (Fig. 26).

Paratypes. MNHN 2010.0631 (GenBank: JF520728), previously IRD TR.3200, a gravid female collected on 4 March 2010 at Bassila* (09°01' N

01°39' E), Benin, by J.-F. Trape (Fig. 28a, b); IRSNB 2662 (GenBank: JF520729), previously IRD TR.3248, an adult female collected on 7 March 2010 at Guiguisso* (09°03' N 01°40' E), Benin, by a villager (Fig. 28c);

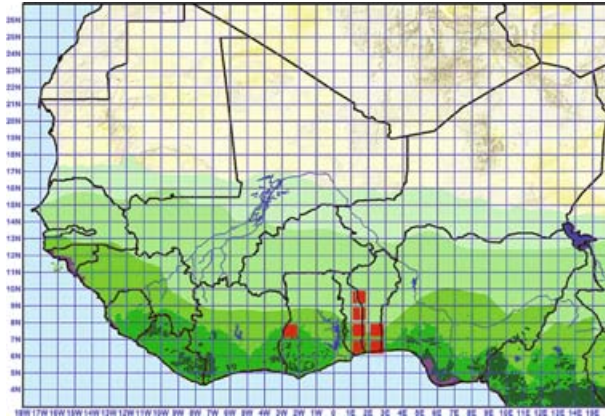


Fig. 27. Geographic distribution of *Agama parafriicana* sp. nov. J.-F. Trape, O. Mediannikov et S. Trape.

IRSNB 2663 (GenBank: JF520730), previously; IRD TR.3249, a gravid female collected on 7 March 2010 at Guiguisso* by a villager (Fig. 28d); IRD TR.3311 (GenBank: JF520731), a male collected on 7 March 2010 at Guiguisso* by a villager; IRD TR.3316, a female collected on 7 March 2010 at Guiguisso* by a villager.

Other specimens. IRD TR.2957 (GenBank: JF520732), an adult male collected on 20 February 2010 at Nsosomea* (07°51' N 02°47' W), Ghana, by J.-F. Trape; IRD TR.2968 (GenBank: JF520733), an adult male collected on 20 February 2010 at Nsosomea* (07°51' N 02°47' W), Ghana, by J.-F. Trape; IRD TR.3964, an adult female collected on 4 April 2011 in Lama forest* (06°58' N 02°10' E) by J.-F. Trape.

Diagnosis. The genetic results and the following characters: a species resembling *A. agama*, *A. paragama*, and *A. africana* but characterized by a much smaller snout-vent length of adult males (82 – 101 mm instead of 115 – 140 mm), a low vertebral count (29 – 34 instead of 40 – 56 in sympatric specimens of *A. agama*), and strongly carinated and mucronate dorsal scales (feebly



a



b



c



d

Fig. 28. Female paratypes of *Agama parafriicana*.

carinated and mucronate scales in sympatric specimens of *A. agama*).

Etymology. The name of the new species refers to its close relationship to *A. africana*.

Description of holotype. The holotype is an adult male of the following dimensions: total length 279 mm, snout-vent length 101 mm, tail length 178 mm, ratio total length: tail length 1.57, head length 30 mm, head width 20 mm, head height 13 mm. Nostril on the canthal ridge, situated on the posterior half of the nasal. Anterior part of the nasal keeled. Ten supralabial scales on each side. Supraorbital and other scales between the eyes smooth. Head scales between posterior end of the eyes and neck keeled. Head scales of the temporal region keeled. Gular scales flat and smooth. Occipital scale large, its diameter about three quarter of tympanum diameter. Pineal organ visible, pierced in the middle of the occipital. Ear hole large, but slightly smaller than the eye, its edge with a few spiny scales. Five tufts of scale posterior to ear hole. Nuchal crest low, consisting of twelve lanceolate scales. No dorsal crest and no caudal crest. Dorsal body scales strongly keeled and mucronate, those near the vertebral line almost twice as large than those on the flanks. Ventral scales small and smooth. Midbody scale count 72. Vertebral scale count 35 (measured along the vertebral line from forelimbs, on a level with the axillae, to hind limbs, on a level with the groin). One row of 12 preanal pores. Tail scales strongly keeled and mucronate. Fourth toe and fourth finger the longest. Subdigital lamellae 18 on both side under the fourth toe, 21 on both side under the fourth finger.

Color in life and just killed similar, with the head dull whitish, the upper surfaces of the body and forelimbs

blue, the vertebral region, part of the flanks and the lower limbs whitish, the tail successively whitish on the major part of its length then banded in black and grayish, the throat and the underside of the belly and the tail whitish (Fig. 26).

Variation. The main characteristics of the five paratypes (one male and four females) and the two males from Ghana are given in Table 5. The snout-vent length ranges from 76 to 87 mm for the males and from 73 to 85 mm for the females (79 and 85 mm for the two breeding females). The midbody scale count ranges from 56 to 63 for the males and from 54 to 60 for the females. The vertebral count ranges from 32 to 34 for the males and from 29 to 31 for the females. Coloration in males and females is variable, but all present a more or less banded pattern of the last part of the tail. One male from Ghana (IRD TR.2957) had the head and throat orange in life. The other males in life had a brownish or grayish head and the throat whitish. Their dorsum and upper surface of limbs was bluish and the anterior part of the vertebral region whitish. The females were brown with an orange or red-brown pattern on the flanks and three or four irregular transversal bars of the same color on the dorsum (Fig. 28).

Comparison with other species. Molecular studies indicate that *A. parafricana* is closely related to the other species of the *A. agama* complex. In Guiguissou (Benin), where we collected most specimens of the type series, we also obtained 15 specimens of *A. agama*. It has been possible to immediately separate on the field these two species on the basis of the vertebral count and the aspect of the dorsal scales. In this area, the vertebral count of *A. agama* ranged from 40 to 56 (mean: 46.8, $n = 15$), in-

TABLE 5. Main Characteristics of *A. parafricana* Specimens from Togo, Benin, and Ghana

Characteristics	Collection numbers							
	MNHN 2010.0630	MNHN 2010.0631	IRSNB 2662	IRSNB 2663	IRD TR 3311	IRD TR 3316	IRD TR 2957	IRD TR 2968
Country	Togo	Benin	Benin	Benin	Benin	Benin	Ghana	Ghana
Locality	Asrama	Bassila	Guiguissou	Guiguissou	Guiguissou	Guiguissou	Nsomsoméa	Nsomsoméa
GenBank	yes	yes	yes	yes	yes	no	yes	yes
Sex	♂	♀	♀	♀	♂	♀	♂	♂
Snout-vent length, mm	101	79	85	73	76	75	82	87
Tail length, mm	178	76+	137	44+	47+	29+	139	147
Midbody scale count	72	57	60	54	60	60	63	56
Vertebral count	34	31	31	29	34	30	32	33
Preanal pores	12	0	0	0	12	0	13	12
Supralabials	10	9	10	11	11	9	9	10
Longest finger	4 th	4 th = 3 rd	4 th	4 th	4 th	4 th	4 th	4 th
Longest toe	4 th	4 th	4 th	4 th = 3 rd	4 th	4 th	4 th	4 th
Lamellae 4 th finger	18/18	16/17	16/17	16/16	17/17	17/17	17/17	18/19
Lamellae 4 th toe	21/21	19/19	20/20	18/19	21/22	19/19	19/20	20/21



Fig. 29. *Agama paragama* Grandison, 1968.

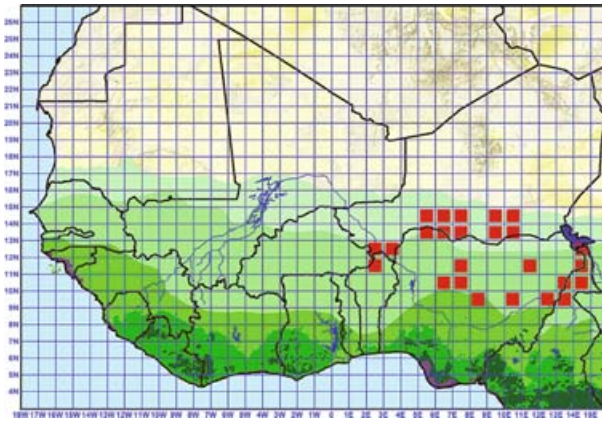


Fig. 30. Geographic distribution of *Agama paragama* Grandison, 1968.

stead of 29 – 35 in *A. parafricana*. Both the nuptial coloration and size of adult males of the new species differ from those of the other species of the *A. agama* complex in West Africa. In particular, the snout-vent length of dominant males of *A. agama*, *A. africana*, *A. paragama*, *A. lebretoni*, and *A. wagneri* is usually comprised between 115 and 140 mm instead of 82 – 101 mm in *A. parafricana*. All other West African *Agama* also present both marked genetic (see Fig. 1) and morphological

differences with the new species. *A. insularis*, *A. boulengeri* and *A. doriae benueensis* have a much higher mid-dorsal count (111 – 147, 97 – 123, and 74 – 98, respectively); *A. gracilimembris* is a much smaller species (maximum SVL: 56 mm) with heterogeneous scales and lacking rosettes of erected scales on the side of the head; *A. weidholzi* is a smaller species (maximum SVL: 65 mm), has a very different coloration and only a few isolated erected scales on the side of the head; *A. sankaranica* and *A. boensis* have a very different coloration and are two of the rare species with the nostril under the canthal ridge; *A. cristata* has two black spots on each side of the neck and often presents a marked nuchal, dorsal and caudal crest. *A. boueti* and *A. castroviejoi* are two sahelian species with a very different coloration and the third finger longer than the fourth (fourth finger the longest in *A. parafricana*).

2.13. *Agama paragama* Grandison, 1968

(Figs. 29 and 30)

1968 *Agama paragama* Grandison, *Bull. Br. Mus. Nat. Hist. (Zool.)*, 17, 75. Type locality: Zaria City, Nigeria.

Geographic distribution (type series and/or confirmed by molecular studies only). **Cameroon:** see Grandison (1968). **Niger:** Kouré* (13°19' N 02°35' E), Rifilamiram* and vicinity (14°00' N 10°02' E), Tekhé* and vicinity (14°01' N 06°01' E). **Nigeria:** Birnin Gwari



Fig. 31. *Agama sankaranica* Chabanaud, 1918.

(11°02' N 06°47' E), Jos (09°56' N 08°53' E), Naraguta (09°58' N 08°54' E), Potiskum (11°42' N 11°04' E), Yo (09°15' N 12°25' E), Zaria* (11°09' N 07°47' E), Zonkwa (09°46' N 08°16' E).

Ecological notes. A semi-arboreal species living in socially organized groups. In southern Niger and northern Nigeria, a densely populated area where fields have replaced most of the original Sahelo-Sudanian savanna, very common in acacia trees but absent from the villages where it is replaced by *A. agama*.

Reference. Grandison (1968).

2.14. *Agama sankaranica* Chabanaud, 1918

(Figs. 31 and 32)

1918 *Agama sankaranica* Chabanaud, *Bull. Mus. Hist. nat., Paris*, **24**, 105. Type locality: Moussaïa, pays Sankaran (Guinea).

Geographic distribution: **Benin:** Barabon (11°43' N 02°42' E), Guiguissou* (09°03' N 01°40' E), Oké-Owo* (07°57' N 02°17' E), Pendjari* (11°24' N 01°35' E). **Burkina Faso:** near Ouagadougou (12°21' N 01°32' W), chutes de Koudou (11°40' N 02°18' E). **Ghana:** Accra (05°33' N 00°11' W), Donkorkrom (07°03' N 00°06' W), Legon (05°38' N 00°13' W), Madina (05°38' N 00°12' W), Tafo (06°12' N 00°22' W), Tamalé (09°24' N 00°51' W), Wa (10°03' N 02°29' W). **Guinea:** Beyla (08°41' N 08°38' W), Diaka* (11°33' N 12°27' W), Kalan-Kalan* (10°06' N 08°53' W), Kankan (10°23' N 09°18' W), Kérouané* (09°16' N 09°00' W), Moussaïa (10°07' N 09°22' W). **Ivory Coast:** Comoé National Park (08°30' N 03°30' W, approx.). **Mali:** Doussoudiana* (11°09' N 07°48' W), Niakoni* (11°11' N 07°48' W), Npiébougou* (11°59' N 08°00' W), between Sefeto and Diougounté* (14°08' N 09°57' W), Ségou

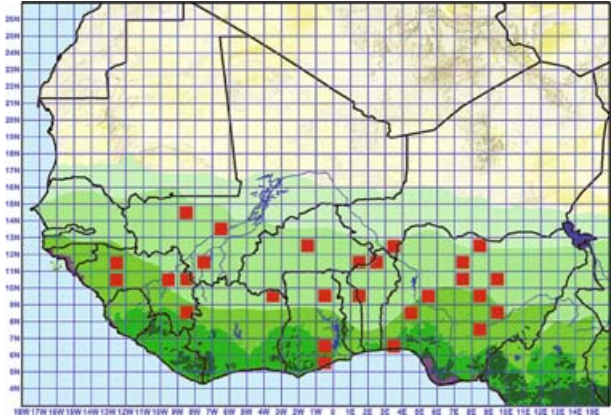


Fig. 32. Geographic distribution of *Agama sankaranica* Chabanaud, 1918.

(13°27' N 06°16' W). **Niger:** SE of Boukagorou* (12°38' N 03°12' E). **Nigeria:** Bauchi (10°18' N 09°50' E), Lagos (06°25' N 03°22' E), Kano (12°00' N 08°31' E), Makurdi (07°44' N 08°32' E), Rimi SE of Kaduna (10°31' N 07°27' E), Shendam (08°53' N 9°28' E), Zaria (11°09' N 07°47' E), Zonkwa (09°47' N 08°17' E). **Togo:** Alédjo* (09°15' N 01°12' E), Fazao* (08°42' N 00°48' E). **Additional possible localities of *A. sankaranica* in Mali** (specimens from western Mali previously attributed to *A. sankaranica* by Joger and Lambert 1996, but not compared to *A. boensis*): 14 km S of Fatao (14°12' N 09°29' W), 17 km E of Kita (13°04' N 09°19' W), Kita (13°03' N 09°29' W), SW of Monsombougou (14°57' N 10°00' W), Nioro du Sahel (15°14' N 09°35' W), 10 km W of Sandaré (14°42' N 10°24' W).

Ecological notes. Among specimens previously attributed to *A. sankaranica* in West Africa, molecular data indicate that specimens collected in Guinea Bissau, Senegal and western Guinea belong to *A. boensis* (see above). *A. sankaranica* is distributed in central and eastern Guinea, Mali, Ivory Coast, Burkina Faso, Togo, Benin, Niger, and Nigeria. Specimens are solitary and live on the ground in the Sudan and Guinea savanna.

References. Böhme et al. (1996), Chirio (2009), Grandison (1956, 1968), Hughes in litt. (2010), Joger (1981), Joger and Lambert (1996, 2002), Rödel et al. (1997).

2.15. *Agama wagneri* sp. nov. J.-F. Trape, O. Mediannikov et S. Trape (Figs. 33 and 34)

2009 *Agama agama* Wagner et al., *Bonn. zool. Beitr.*, **56**, 221.

Holotype. ZFMK 15222 (GenBank: GUI133323), an adult male collected on 14 February 1974 at Mokolo



Fig. 33. *Agama wagneri* sp. nov. J.-F. Trape, O. Mediannikov et S. Trape.

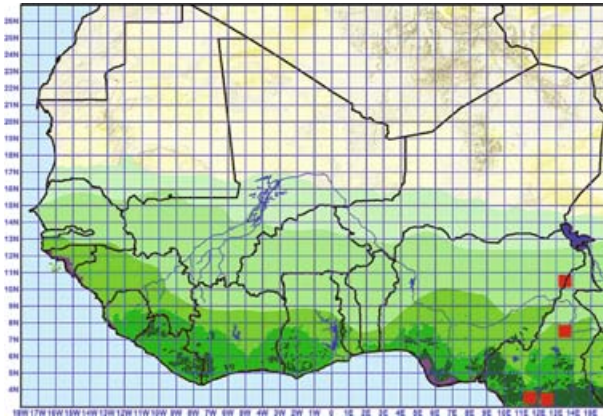


Fig. 34. Geographic distribution of *Agama wagneri* sp. nov. J.-F. Trape, O. Mediannikov et S. Trape.

(10°44' N 13°47' E), Cameroon, by W. Böhme and W. Hartwig.

Other specimens. MCZ.184562 (GenBank: GUI128434), Yaoundé, Cameroon; IRD TR.3674 (GenBank: JF520751), vicinity of Mengang*, Cameroon (03°54' N 12°07' E), collected on 6 December 2010 by

J.-F. Trape; IRD TR.3750 (GenBank: JF520752) and IRD TR.3751 (GenBank: JF520753) two adult males collected on 20 December 2010 at Mokolo* (10°44' N 13°47' E), Cameroon, by M. Talla Kouete; IRD TR.3753 (GenBank: JF520754), collected on 21 December 2010 at Ngaoundéré* (07°19' N 13°35' E), Cameroon, by M. Talla Kouete; IRD TR.3754 (GenBank: JF520755) and IRD TR.3755 (GenBank: JF520756), collected on 23 December 2010 at Yaoundé* (03°52' N 11°30' E), Cameroon, by M. Talla Kouete.

Diagnosis. A large species of the *Agama agama* complex related to *A. paragama* that can be safely distinguished from other species of this complex only by its genetics. *A. wagneri* differs from sympatric *A. paragama* by the coloration of males, by a much higher vertebral count (42 – 54 instead of 26 – 34) and by the aspect of the dorsal scales that are less carinated and mucronate in *A. wagneri* than in *A. paragama*.

Etymology. This species is dedicated to Philipp Wagner in recognition to his contribution to the study of the genus *Agama*.

Description of holotype. A detailed description of the holotype has been previously published by P. Wagner



Fig. 35. *Agama weidholzi* Wettstein, 1923.

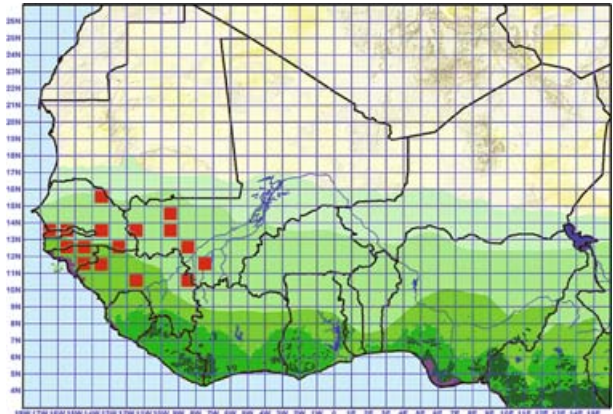


Fig. 36. Geographic distribution of *Agama weidholzi* Wettstein, 1923.

(*Bonn. zool. Beitr.*, 2009, **56**, 220 – 222) as neotype of *A. agama*.

Systematics. As mentioned above (see *A. agama*), the designation by Wagner et al. (2009a) of ZFMK 15222 as neotype of *A. agama* (Linnaeus, 1758) was invalid since syntypes of *A. agama* are still extant and correspond to what is currently known as *A. agama*. Molecular data show that ZFMK 15222 and our additional specimens from northern and central Cameroon represent a new species that is more related to *A. paragama* than to *A. agama*, *A. africana*, *A. lebretoni*, and *A. parafricana*. The new species is also distributed in Yaoundé and along some roads near Yaoundé. It seems excluded from town, villages, plantations and roads of forest areas of southwestern Cameroon by *A. lebretoni*. Interestingly, the presence of some specimens of *A. agama* genetically almost identical to those of Benin, Ghana and Togo has also been documented in Yaoundé (Leaché et al., 2009) where they are probably in competition with *A. wagneri*.

2.16. *Agama weidholzi* Wettstein, 1923

(Figs. 35 and 36)

1923 *Agama weidholzi* Wettstein, *Zool. Anz., Leipzig*, **99**, 304.

Type locality: Tabadienka, 30 km südlich von Diakkoto, Senegambien.

Geographic distribution. **Gambia:** near Kiang West National Park (13°18' N 15°55' W, approx.). **Guinea:** Kalan-Kalan* (10°06' N 08°53' W), Yatia* (10°01' N 10°58' W), vicinity of Sandénia* (10°10' N 11°12' W). **Guinea Bissau:** Madina Boé* (11°44' N 14°12' W). **Mali:** Bamako (12°38' N 07°59' W), SW of Bamako* (12°30' N 08°08' W), Doussoudiana* (11°09' N 07°48' W), 9 km N of Fatao (14°24' N 09°29' W), Kassama* (13°03' N 11°07' W), 5 km E of Kita (13°03' N 09°25' W), 20 km W of Kita (13°03' N 09°42' W), vicinity of Laminina* (11°14' N 07°46' W), Niakoni* (11°11' N 07°48' W), Négala (12°52' N



Fig. 37. *Agama* sp.

08°27' W), between Négala and Kassara (12°55' N 08°40' W). **Senegal:** Barakatou* (13°02' N 13°43' W), Boughari (12°59' N 15°50' W), 5 km SE of Darsalam (13°14' N 13°09' W), vicinity of Kédougou* (12°27' N 12°02' W), 13 km SW of Kolda (12°49' N 14°58' W, approx.), 12 km W of Kounkané (12°54' N 14°10' W, approx.), Médina Djikoye* (13°37' N 16°18' W), 20 km S of Médina Gonas (12°59' N 13°41' W), Mont Rolland (14°55' N 16°58' W), Namâri (15°04' N 13°38' E), Tabadian (13°11' N 13°28' W), NE of Tiara (12°56' N 14°32' W, approx.).

Ecological notes. A small species (maximum snout-vent length: 65 mm) living on the ground in the Sudan and Guinea savanna of the most occidental part of West Africa. Individuals are solitary.

Reference. Böhme (1978), Cissé and Karns (1978), Emms et al. (2007), Grandison (1969), Joger, (1981, 1982), Joger and Lambert (1996, 2002).

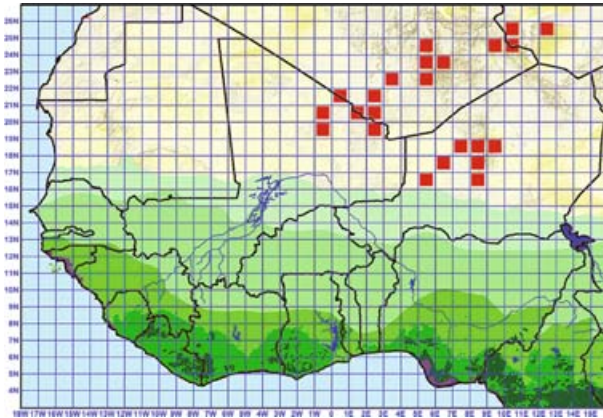


Fig. 38. Geographic distribution of *Agama sp.*

2.17. *Agama sp.* (Figs. 37 and 38)

2008 *Agama cf. impalearis* Brito et al., *Herpetol. Bull.*, **105**, 19–27.

Geographic distribution. **Algeria:** Tassili, Hoggar, and Tanezrouft (see Sindaco and Jeremcenko, 2008, under *A. impalearis*). **Libya:** Tassili (see Sindaco and Jeremcenko, 2008, under *A. impalearis*). **Mali:** Adrar Ouzzeïne* (19°01' N 01°50' E), between Tisserlitine and Timétrine (20°36' N 00°11' W), Tessalit and vicinity (10°12' N 01°00' E), Ti-N-Zaouâtene (19°50' N 02°58' E, approx.). **Niger:** Abardokh (17°31' N 08°39' E), 50 km N of Agadez (17°18' N 08°10' E), Gougaram* (18°27' N 07°48' E), East of Gougaram* (18°28' N 07°51' E), near guelta Iloukloukané* (19°05' N 08°53' E), In Abezou (17°15' N 05°20' E, approx.), 8 km E of Tchintoulous* (18°34' N 08°51' E), Tchintoulous* (18°34' N 08°47' E), 5 km S of Timia (18°06' N 08°45' E), 20 km S of Timia (17°58' N 08°45' E), Zagado* (18°37' N 09°06' E).

Remarks. This new species will be described by Geniez et al. (in press). Specimens were previously confounded with *A. impalearis* or *A. agama*. Individuals are solitary and lives on rocks in the mountains of central Sahara (Aïr, Adrar des Ifoghas, Hoggar, Tassili, Tanezrouft).

References. Brito et al. (2008), Joger and Lambert (1996), Papenfuss (1969), Sindaco and Jeremcenko (2008), Trape et al. (in press).

Acknowledgments. We are grateful to Y. Mané, G. Diatta, M. Talla Kouete, and L. Chirio for assistance in the field and for collecting some of the specimens used in the study. We thank S. Kullander and E. Sjölin for invaluable help in Stockholm and Uppsala when one of us (JFT) examined the *Lacerta agama* Linnean types of the Museum Adolphi Friderici collection.

We thank P.-A. Crochet and P. Geniez for very useful discussions about *Lacerta agama* and the Sahelo-Saharan *Agama* species. J. Brito provided useful data on specimens deposited in his collection. G. Chauvancy contributed to the distribution maps and G. Subramanian to the molecular study. S. Kullander and an anonymous reviewer provided very useful comments and suggestions for improving a preliminary draft of this paper.

REFERENCES

- Anderson S., Bankier A. T., Barrell B. G., de Bruijn M. H., Coulson A. R., Drouin J., Eperon I. C., Nierlich D. P., Roe B. A., Sanger F., Schreier P. H., Smith A. J., Staden R., and Young I. G. (1981), "Sequence and organization of the human mitochondrial genome," *Nature*, **290**, 457–465.
- Andersson L. G. (1900), "Catalogue of Linnean type-specimens of Linnaeus's reptilian in the Royal Museum in Stockholm," *Bihang Till K. Svenska Vet.-Akad. Handlingar*, **26**, 1–29.
- Boore J. L. (1999), "Animal mitochondrial genomes," *Nucl. Acids Res.*, **27**, 1767–1780.
- Adalsteinsson S. A., Branch W. R., Trape S., Vitt L. J., and Hedges S. B. (2009), "Molecular phylogeny, classification, and biogeography of snakes of the Family Leptotyphlopidae (Reptilia: Squamata)," *Zootaxa*, **2244**, 1–50.
- Böhme W. (1978), "Zur Herpetofaunistik des Senegal," *Bonn. zool. Beitr.*, **29**, 360–417.
- Böhme W., Menig H., and Rödel M. O. (1996), "New records of amphibians and reptiles from Burkina Faso and Mali," *Br. Herpetol. Soc. Bull.*, **56**, 7–26.
- Brito J. C., Rebelo H., Crochet P.-A., and Geniez P. (2008), "Data on the distribution of reptiles and amphibians from North and West Africa, with emphasis on *Acanthodactylus* lizards and the Sahara desert," *Herpetol. Bull.*, **105**, 19–27.
- Brown R. P., Suarez N. M., and Pestanob J. (2002), "The Atlas mountains as a biogeographical divide in North-West Africa, evidence from mtDNA evolution in the Agamid lizard *Agama impalearis*," *Mol. Phylog. Evol.*, **24**, 324–332.
- Chabanaud P. (1918), "Etude complémentaire de deux *Agama* de l'Afrique Occidentale et description de quatre espèces nouvelles de reptiles de la même région," *Bull. Mus. natl. d'Hist. Nat.*, **24**, 104–112.
- Chirio L. (2009), "Inventaire des reptiles de la région de la réserve de Biosphère Transfrontalière du W (Niger/Bénin/Burkina-Faso, Afrique de l'Ouest)," *Bull. Soc. Herpétol. Fr.*, **132**, 13–41.
- Chirio L. and Lebreton M. (2007), *Atlas biogéographique des Reptiles du Cameroun*, IRD/MNHN, Paris.
- Cissé M. and Karns D. R. (1978), "Les sauriens du Sénégal," *Bull. l'Inst. Fond. d'Afr. Noire. Sér. A*, **40**, 144–211.
- Emms C., Jambang M., Bahl O., Mankali B., Paziaud L., and Barnett L. (1987), "The reptile fauna of The Gambia," *Herpetol. Bull.*, **99**, 3–18.
- Gray R. (1975), *The Cambridge History of Africa. Vol. 4*, Cambridge Univ. Press, pp. 1600–1790.

- Gartshore M. E.** (1985), “*Agama gracilimembris* Chabanaud, 1918 (Reptilia: Sauria: Agamidae) in Nigeria,” *Br. J. Herpetol.*, **1**, 23 – 25.
- Grandison A. G. C.** (1956), “On a collection of lizards from West Africa,” *Bull. l’Inst. Fr. d’Afr. Noire. Série A*, **18**, 224 – 245.
- Grandison A. G. C.** (1969), “Nigerian lizards of the genus *Agama* (Sauria: Agamidae),” *Bull. Br. Mus. Nat. Hist. (Zool.)*, **17**, 67 – 90.
- Grandison A. G. C.** (1969), “*Agama weidholzi* (Sauria: Agamidae) of West Africa and its relationship to *Agama gracilimembris*,” *Bull. l’Inst. Fond. d’Afr. Noire. Sér. A*, **31**, 666 – 675.
- Harris V. A.** (1964), *The Life of the Rainbow Lizard*, Hutchinson, London.
- Holm Å.** (1957), “Specimina Linnaeana. I Uppsala bevarade zoologiska samlingar från Linnés tid,” *Uppsala Univ. Årsskrift*, **6**, 5 – 68.
- International Commission on Zoological Nomenclature** (1999), *International Code of Zoological Nomenclature. Fourth Edition*, International Trust for Zoological Nomenclature, London.
- Joger U.** (1979), “Zur Ökologie und Verbreitung wenig bekannter Agamen Westafrikas (Reptilia: Sauria: Agamidae),” *Salamandra*, **15**, 31 – 52.
- Joger U.** (1981), “Zur Herpetofaunistik Westafrikas,” *Bonn. zool. Beitr.*, **32**, 297 – 340.
- Joger U.** (1982), “Quatre lézards nouveaux pour la faune du parc national du Niokolo-Koba,” in: *Recherches Scientifiques dans les parcs nationaux du Sénégal, Mémoires de l’Institut Fondamental d’Afrique Noire*, No. 92, 177 – 183.
- Joger U. and Lambert M. R. K.** (1996), “Analysis of the herpetofauna of the Republic of Mali. I. Annotated inventory, with description of a new *Uromastix* (Sauria: Agamidae),” *J. Afr. Zool.*, **110**, 21 – 51.
- Joger U. and Lambert M. R. K.** (2002), “Inventory of amphibians and reptiles in SE Senegal including the Niokolo-Koba National Park, with observations on factors influencing diversity,” *Tropical Zool.*, **15**, 165 – 185.
- Karns D. R. and Cissé M.** (1975), “Découverte d’*Agama boueti* Chabanaud (Reptilia: Sauria: Agamidae) au Sénégal avec notes systématiques et écologiques,” *Bull. l’Inst. Fond. d’Afr. Noire. Sér. A*, **37**, 939 – 940.
- Kochern T., Thomas W., Meyer A., Edwards S., Paabo S., Villablanca F., and Wilson A.** (1989), “Dynamics of mitochondrial DNA evolution in animals, amplification and sequencing with conserved primers,” *Proc. U.S. Natl. Acad. Sci.*, **86**, 6196 – 6200.
- Kumar S., Dudley J., Nei M., and Tamura K.** (2008), “MEGA: A biologist-centric software for evolutionary analysis of DNA and protein sequences,” *Briefings Bioinformatics*, **9**, 299 – 306.
- Kriska M. A.** (2001), “Contribution à l’inventaire chorologique des biogéocénoses de l’Aïr et du Tamesna nigérien,” *Montpellier, Ecole Pratique des Hautes Etudes, Mémoire*, No. 24.
- Laurent R. F.** (1947), “Notes sur quelques reptiles appartenant à la collection du Musée Royal d’Histoire Naturelle de Belgique,” *Bull. Mus. roy. d’Hist. nat. Belg.*, **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., and Baha El Din S.** (2009), “Phylogeny of the genus *Agama* based on mitochondrial DNA sequence data,” *Bonn. zool. Beitr.*, **56**, 273 – 278.
- Linnaeus C.** (1748), *Systema naturae sistens regna tria naturae, in classes et ordines, genera et species redacta tabulisque aeneis illustrata. Secundum sextam Stockholmiensem emendatam and auctam editionem*, Lipsiae.
- Linnaeus C.** (1749), “Museum Adolpho-Fridericianum,” *Amoenitates academicæ seu dissertationes variae physicae, medicae botanicae antehac seorsim editae nunc collectae et auctae cum tabulis aeneis*, **1**, 277 – 326.
- Linnaeus C.** (1754), *Adolphi Friderici Regis Svecorum, Gothorum, Vandalorumque & c. in quo Animalia Rariora Imprimis et Exotica, Quadrupedia, Aves, Amphibia, Pisces, Insecta, Vermes Describuntur et Determinatur, Latine et Suetice cum Iconibus*, Typ. Regia, Holmiae, Stockholm.
- Linnaeus C.** (1758), *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima. Tomus 1*, Laurenti Salvi, Holmiae, Stockholm.
- Linnaeus C.** (1764), *Museum S:æ R:æ M:tis Adolphi Friderici regis Svecorum, Gothorum, Vanalorumque & c. & c. & c. In quo Animalia rariora Imprimis and Exotica, Aves, Amphibia, Pisces Describuntur. Tomi Secundi Prodomus*, Laurentius Salvius, Holmiae.
- Lönnberg E.** (1896), “Linnean type-specimens of birds, reptiles, batrachians and fishes in the Zoological Museum of the R. University in Upsala,” *Bihang Till K. Svenska Vet.-Akad. Handlingar*, **22**, 1 – 45.
- Loveridge A.** (1936), “African reptiles and amphibians in Field Museum of Natural History,” *Field Mus. Nat. Hist. Chicago. Zool. Ser.*, **22**, 1 – 111.
- Macdonald M. A.** (1981), “A new species of agamid lizard from Ghana,” *J. Zool.*, **193**, 191 – 199.
- Mertens R.** (1938), “Herpetologische Ergebnisse einer Reise nach Kamerun,” *Abh. senckenberg. naturforsch. Ges.*, **442**, 1 – 52.
- Moody S. M. and Böhme W.** (1984), “Merkmalsvariation und taxonomische stellung von *Agama doriae* Boulenger, 1885 und *Agama benueensis* Monard, 1951 (Reptilia: Agamidae) aus dem Sudangürtel Afrikas,” *Bonn. zool. Beitr.*, **35**, 107 – 128.
- Monard A.** (1940), “Résultats de la mission scientifique du Dr Monard en Guinée Portugaise, 1937 – 1938. VIII. Reptiles,” *Arq. Mus. Bocage*, **11**, 147 – 182.
- Olofsson O.** (circa 1915), *Linneana*, Uppsala University, unpublished document.
- Padial J. M.** (2005), “A new species of *Agama* (Sauria: Agamidae) from Mauritania,” *Herpetol. J.*, **15**, 27 – 35.
- Padial J. M.** (2006), “Commented distributional list of the reptiles of Mauritania (West Africa),” *Graellsia*, **62**, 159 – 178.

- Papenfuss T. J.** (1969), "Preliminary analysis of the reptiles of arid central West Africa," *Wasman J. Biol.*, **27**, 249 – 325.
- Parker H. W.** (1939), "Résultats scientifiques des croisières du navire-école belge «Mercator». V. Reptilia et Amphibia," *Mém. Mus. roy. d'Hist. nat. Belg.* 2^{ème} sér., **15**(II), 85 – 90.
- Pook C. E., Joger U., Stumpel N., and Wuster W.** (2009), "When continents collide: Phylogeny, historical biogeography and systematics of the medically important viper genus *Echis* (Squamata: Serpentes: Viperidae)," *Mol. Phylog. Evol.*, **53**, 792 – 807.
- Rödel M.-O., Grabow J. K., Hallerman J., and Böckler C.** (1997), "Die Echsen des Comoé-Nationalparks, Elfenbeinküste," *Salamandra*, **33**, 225 – 240.
- Ronquist F. and Huelsenbeck J. P.** (2003), "MrBayes 3: Bayesian phylogenetic inference under mixed models," *Bioinformatics*, **19**, 1572 – 1574.
- Sindaco R. and Jeremcenko V. K.** (2008), *Reptiles of the Western Palearctic*, Edizioni Belvedere, Latina.
- Seba A.** (1734), *Locupletissimi Rerum Naturalium Thesauri Accurata Descriptio, et Iconibus Artificiosissimis Expressio, per Universam Physices Historiam. Opus, cui, in hoc Rerum Genere, Nullum per Exstitit, Ex Toto Terrarum Orbe Collegit, Digessit, Descripsit, et Depingendum Curavit Albertus Seba, Etzela Oostfrisius, Academiae Caesareae Leopoldino Carolinae Naturae Curiosorum Collega Xenocrates dictus; Societatis Regiae Anglicanae, et Instituti Bononiensis, sodalis. Tomus I*, Janssonio-Waesbergios and J. Wetstenium and Gul. Smith, Amsterdam.
- Trape J.-F.** (2011), "*Agama cristata* Mocquard, 1905 and *Agama insularis* Chabanaud, 1918 (Squamata: Agamidae), two valid West African species," *J. Herpetol.*, **45**, 352 – 354.
- Trape J.-F., Godeluck B., Diatta G., Rogier C., Legros F., Albergel J., Pépin Y., and Duplantier J.-M.** (1996), "The spread of tick-borne borreliosis in West Africa and its relation to sub-saharan drought," *Am. J. Trop. Med. Hyg.*, **54**, 289 – 293.
- Trape J.-F., Chirio L., Broadley D. G., and Wüster W.** (2009), "Phylogeography and systematic revision of the Egyptian cobra (Serpentes: Elapidae: *Naja haje*) species complex, with the description of a new species from West Africa," *Zootaxa*, **2236**, 1 – 25.
- Trape J.-F., Trape S., and Chirio L.** (in press), *Lézards, crocodiles et tortues d'Afrique occidentale et du Sahara*, IRD Editions, Marseille.
- Trape S.** (2009), "Impact of climate change on the relict tropical fish fauna of central Sahara, threat for the survival of Adrar mountains fishes, Mauritania," *Plos one* **4**, **2**, e4400, 1 – 10.
- Vasconcelos R., Rocha S., Brito J. C., Carranza S., and Harris D. J.** (2009), "First report of introduced African Rainbow Lizard *Agama agama* (Linnaeus, 1758) in the Cape Verde Islands," *Herpetozoa*, **21**, 183 – 186.
- Wagner P., Wilms T. M., Bauer A., and Böhme W.** (2009a), "Studies on African *Agama*. V. On the origin of *Lacerta agama* Linnaeus, 1758 (Squamata: Agamidae)," *Bonn. zool. Beitr.*, **56**, 215 – 223.
- Wagner P., Ineich I., Leaché A. D., Wilms T. M., Trape S., Böhme W., and Schmitz A.** (2009b), "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," *Bonn. zool. Beitr.*, **56**, 239 – 253.
- Wagner P., Barej M. F., and Schmitz A.** (2009c), "Studies on African *Agama* VII. A new species of the *Agama agama*-group (Linnaeus, 1758) (Sauria: Agamidae) from Cameroon and Gabon, with comments on *Agama mehelyi* Tornier, 1902," *Bonn. zool. Beitr.*, **56**, 285 – 297.
- Wallin L.** (1997), *Catalogue of Type Specimens. 4. Linnaean specimens*, Uppsala University Zoological Museum.
- Wermuth H.** (1967), "Liste der rezenten Amphibien und Reptilien: Agamidae," *Das Tierreich*, **86**, 1 – 127.
- Zink R. M. and Barrowclough G. F.** (2008), "Mitochondrial DNA under siege in avian phylogeography," *Mol. Ecol.*, **17**, 2107 – 2121.