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A new cryptic species of the *Agama lionotus* complex from south of the Ngong Hills in Kenya

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Abstract. East Africa, especially if including the Horn of Africa, is a centre of diversity for African Agamid lizards and harbours the endemic lineage of the *Agama lionotus* complex, which currently comprises nine species. Species of the complex are mainly characterized by their throat pattern in adult males, which can be used for species identification. Among them, *Agama lionotus* and *Agama dodomae* show a very distinct colouration of a blue body and a white/blue annulated tail – a colour pattern that is otherwise only known from the southern African *Agama kirkii*. Within the complex, *Agama lionotus* is the most widely distributed taxon, ranging from Ethiopia to northern Tanzania and being replaced by *Agama dodomae* farther south in Tanzania. Other taxa of the complex are more restricted in their distribution. In this study, specimens from a larger area south of the Ngong Hills are examined and compared with other members of the complex, because they show an overall similarity to *Agama lionotus*, but are distinctly smaller. Examining the morphological (62 characters) and genetical (16S, ND4, CMOS) data indicates that these specimens represent a new species. Furthermore, phylogenetic analyses support the new taxon as not closely related to *Agama lionotus* itself, but as a member of the complex. The new species is especially characterized by its small size. Adult males have a vertebral stripe, a blue body colouration and an annulated white/blue tail. Further typical characters are the low number of scale rows around midbody, the pear-shaped and keeled nasal scale, the minute nuchal crest, and the feebly keeled vertebral scales, followed by dorsal and lateral keeled scales. The results of this study improve our understanding of the diversity of agamid lizards in East Africa and support the value of adult male throat coloration for the identification of species within the *Agama lionotus* complex.

Key words. Agamidae, *Agama*, *Agama dodomae*, new species, East Africa, Tanzania.

Introduction

"I had a farm in Africa, at the foot of the Ngong Hills." With this sentence starts one of the most famous books about Kenya: 'Out of Africa' by Karen Blixen (1937 [under the nom-de-plume Isak Dinesen]). The Ngong Hills Karen Blixen wrote about are the peaks of a ridge along the Great Rift Valley situated to the southwest of Nairobi and reaching 2,483 m a.s.l. at their highest peak, Point Lamwia. They are actually the remains of a massive volcano that formed the hills by depositing basalt lava between 5 and 6.5 million years ago. Even though the Ngong Hills themselves are a well-known place even to tourists, their biodiversity and especially that of the larger area south of the hills is still poorly known and specific studies on the amphibians and reptiles of the area are lacking. The area was therefore visited by a student of the German BIOTA programme in 2004 and a few specimens of a medium-sized *Agama* were collected that were provisionally identified as *Agama lionotus* Boulenger, 1896. A second locality, Elangata Wuas, is situated south of the Ngong Range in the Kajiado District. Within this area, the Elangata Wuas Ecosystem Management Program (EWEMP) was initiated in 1992 as a project to identify community-driven sustainable dryland natural resource options. During a field study of the local amphibians and reptiles in 1992, several *Agama* specimens were collected and this time identified as *Agama agama* (Linnaeus, 1758).

Within the Agaminae, the Africa-endemic genus *Agama* Daudin, 1802 contains the highest species diversity in Africa. These lizards occupy nearly all arid environments and are only absent from rainforests and hot sand deserts. *Agama* contains several geographic lineages (Leaché et al. 2014) and comprises a total of ~45 valid species and several species candidates (Wagner 2010a). One lineage, the *Agama lionotus* complex, is endemic to East Africa including the Horn of Africa and currently comprises nine species: *A. caudospinosa* Meek, 1910, *A. dodomae* Loveridge, 1923, *A. doriae* Boulenger, 1885, *A. kaimosae* Loveridge, 1935, *A. lionotus* Boulenger, 1896, *A. mwanzae* Loveridge, 1923, *A. persimilis* Parker, 1942, *A. rueppelli* Vaillant, 1882, and *A. turuensis* Loveridge, 1932. Our knowledge about this lineage is reasonably good and its members have been intensively studied in the last years (e.g., Wagner et al. 2008a, b, Wagner 2010b). Moreover, Wagner (2010a) has shown that the adult male colour pattern, especially the throat pattern, is a good character for identifying East African *Agama* species. In this study, morphological and molecular data are used to reassess the identification of the specimens collected in the Ngong and Elangata Wuas areas in comparison with other East African *Agama* species.

Material and methods

In addition to an adult female of the proposed new species, only adult male specimens were examined for the morphological analysis (Appendix 1). Females, juveniles, and damaged specimens were identified to species level and included for distribution data.

The following taxa of the *Agama lionotus* complex were part of the morphological analysis: *Agama dodomae, A. kaimosae, A. l. lionotus, A. l. elgonis, A. mwanzae, A. turuensis, A. ufipae*, and *A. usambarae*. *Agama caudospinosa*, *A. doriae*, and *A. rueppelli*, which are also members of this complex, were not included in the statistical analysis, because they are morphologically very distinct from the examined taxa and genetic analysis supports them as basal within the complex (Wagner 2010a, Leaché et al. 2014). For each specimen, 68 character states were examined (Tab. 1). Character states that could not be collected from every specimen and those equal throughout all specimens were excluded from analysis (see Tab. 1). Measurements were taken with a dial calliper to the nearest 0.01 mm, and/or, where necessary, under a stereomicroscope. All bilateral characters were recorded from the left side to avoid violations of non-independent data in the Principal Component Analysis (PCA) (Manly 1994, Burbrink 2001). Morphological differences are interpreted in this study as a measure of genetic differentiation. Discrete mensural and meristic differences between groups of phenotypically uniform individuals are considered to be the result of a lack of gene flow. Therefore, morphological analyses are useful for resolving the taxonomic position of taxa when genetic data is not available.

Specimens from the following institutions were examined: California Academy of Sciences (CAS), San Francisco, CA, U.S.A.; Museum d'histoire naturelle (MHNG), Genève, Switzerland; Museum of Comparative Zoology (MCZ), Harvard, MA, U.S.A; National Museums of Kenya (NMK), Nairobi, Kenya; Zoologisches Forschungsmuseum A. Koenig (ZFMK), Bonn, Germany. Other used abbreviations are: CA – Cameroon; ET – Ethiopia; KE – Kenya; RW – Rwanda; S – Somalia; TZ – Tanzania; $\bar{x}$ – average.

The name-bearing types of *Agama elgonis*, *A. kaimosae*, *A. rueppelli*, *A. turuensis*, *A. ufipae*, and *A. usambarae* were examined. Moreover, data and descriptions presented by Spawls et al. (2002), Wagner (2007), Wagner et al. (2008a, b), and the relevant original descriptions were considered. Distributional data are based on specimens with precise locality data and identified to species level. Additional data was obtained from GBIF and Herpnet.

A total of 41 adult male specimens of *Agama* were included in present morphological analyses, including *A. dodomae* (4), *A. kaimosae* (2), *A. l. lionotus* (12), *A. l. elgonis* (3), *A. mwanzae* (9), *A. turuensis* (7), *A. ufipae* (1, holotype), *A. usambarae* (1, holotype), and three specimens of the proposed new *Agama* (one of which is an adult female) from Elangata Wuas. Principal component analyses (PCA, correlation matrix) were used to evaluate 62 morphological characters (Tab. 1) using the software PAST v.2.12 (Hammer et al. 2001). For morphological analysis, mensural, meristic, and ratio characters were size-corrected, $\log_{10}$-transformed and analysed both separately and together. Taxa with only one available specimen were analysed using the morphopoint rather than the morphospace. Qualitative data was used for species delimitation.

All nine species of the *Agama lionotus* complex were included in these phylogenetic analyses, but further details, including more specimens and the position of the complex within the genus, can be obtained from Leaché et al. (2014). All sequences (Tab. 2) of the 16S, ND4 and CMOS genes were imported from Genbank (Benson et al. 2013) and originally published by Leaché et al. (2014). Details like, e.g., number of samples and total number of basepairs can be obtained from this publication. Taxa of the *Agama agama* complex (*A. agama*, *A. picticauda;* only shown as *Agama agama* complex) were used as outgroup. Contiguous DNA sequences were aligned and edited using Sequencer v4.8, and multiple sequence alignments were generated using Muscle v3.6 (Edgar 2004). Phylogenetic relationships were estimated using maximum likelihood (ML) and Bayesian inference (BI). Maximum likelihood analyses were conducted using RAxML-VI-HPC v7.0.4 (Stamatakis 2006). The RAxML analyses used the GTRGAMMA model of nucleotide substitution. Support values were estimated from 1,000 non-parametric bootstrap replicates. The nucleotide substitution model for Bayesian phylogenetics was selected using JModelTest v0.1 (GTR+I+Γ; Posada 2008). Bayesian phylogenetic analysis was conducted using parallel MrBayes v3.1.2 (Ronquist & Huelsenbeck 2003). The analysis was run for 1 million generations using four heated Markov chains.

Results

The phylogeny (Fig. 1) places *Agama doriae* from the Horn of Africa with full support as basal to all other taxa of the *Agama lionotus* complex. Within this latter clade, *A. rueppelli* is fully supported as a sister species to the remaining clade. This lineage is the core group of this publication and *Agama lionotus* is well supported (bootstrap = 89%; posterior probability = 1.0; Fig. 1) as basal to a reasonably well supported clade, including the putative new species (bootstrap = 68%; posterior probability = 0.98) and *A. turuensis*, *A. kaimosae*, *A. mwanzae*, and *A. dodomae*. *Agama ufipae* (herein recognized as a subspecies of

Table 1. Mensural, meristic, and qualitative characters taken from each examined specimen. For ratio characters see Table 3. Characters marked with an asterisk were not used in the statistical analysis.

	Mensural Characters
SVL	Snout–vent length, from tip of snout to cloaca
TL	Length of tail, from tip of tail to cloaca (only specimens with entire tails were used)
TW	Tail width, maximum tail width at the tail base
TH	Tail height, maximum tail height at the tail base
HL	Head length, from tip of snout to angle of jaw
HW	Head width, maximum head width across angles of jaw
HH	Head height, maximum head height at angle of jaw
*CRL	Nuchal crest length, from before the first to behind the last crest scale
SEL	Snout–eye distance, from snout tip to anterior margin of eye
EEL	Eye–ear distance, from posterior margin of eye to anterior margin of ear
ER	Eye length diameter, maximum horizontal eye diameter
EAR	Ear length, maximum horizontal ear diameter
SAL	Snout–arm distance, from snout tip to anterior insertion point of forelimb
AGD	Axilla–groin distance
HUL	Humerus length
RUL	Radius–ulna length
FL	Femur length
TFL	Tibia–fibula length
TOL	Length of 4th toe, excluding the claw
	Meristic Characters
RPP	Number of rows of precloacal pores
PP	Total number of precloacal pores
SL	Number of supralabial scales
IL	Number of infralabial scales
CR	Number of scales on the canthus rostralis
NCR	Number of scales on the canthus between nasal scale and eye
SupraO	Number of supraocular scales
NCS	Number of nuchal crest scales
T	Temporal scales between eye and ear
TCS	Number of caudal crest scales
SaA	Anterior dorsal scale rows, counted transversely behind forelimbs
SaH	Posterior dorsal scale rows, counted transversely just anterior to insertion point of hind limbs
SaM	Dorsal scale rows at midbody, counted transversely at midpoint between fore and hind limbs
D	Dorsal scale numbers, counted longitudinally from shoulders to posterior margin of hind limbs
V	Number of ventral scale, counted longitudinally from shoulders to cloaca
CAS1–2	Number of caudal scales, counted around the tail at 10th and 15th scale rows of the tail
Fi1-5	Number of subdigital lamellae of fingers 1–5
TOE1–5	Number of subdigital lamellae of toes 1–5
*ET	Number of scale tufts around the ear
*NT	Number of scale tufts on the neck
	Qualitative characters*
DS	Dorsal body scales homogenous (scales of similar size and shape) or heterogeneous (small scales intermixed with larger scales)
DFS	Dorsal scales larger or smaller than, or same size as the flank scales
VDS	Vertebral scales keeled, feebly keeled or smooth
DMS	Dorsal scales keeled, feebly keeled or smooth
FS	Flank scales keeled, feebly keeled or smooth
VS	Ventral scales keeled, feebly keeled or smooth
GS	Gular scales keeled, feebly keeled or smooth
UTS	Upper caudal scales keeled, feebly keeled or smooth
LTS	Lower caudal scales keeled, feebly keeled or smooth
PO	Position of the parietal eye visible or not visible
NS1	Nasal scale on or below the canthus rostralis
NS2	Nasal scale smooth or keeled
NS3	Nasal scale round or pear-shaped
NS4	Nasal scale flat or convex
SDL	Subdigital lamellae keeled or smooth
LT	Longest toe 3rd, 4th or both equal
PPR	Row of precloacal pores continuous or discontinuous
TSU	Tympanum superficial or not
HS	Head scales smooth, rugose or keeled
ETS	Tufts of scales around the ear strongly, moderately or feebly developed, or lacking

Table 2. Voucher numbers and citation data for specimens used in the study. All sequences are deposited in GenBank and were adopted from Leaché et al. (2014). CA – Cameroon; ET – Ethiopia; KE – Kenya; SO – Somalia; TZ – Tanzania.

Species ID this paper	Species ID Leaché et al. (2014)	Voucher	Locality	Genbank voucher numbers 16S	ND4	CMOS	New Taxonomy
A. agama complex	*A. agama*	MCZ 184560	CA, Yaounde	JX668144	JX857595	JX838903	
A. caudospinosa	*A. caudospinosa*	ZFMK 83662	KE, Naru Moru	GU128450	GU128487	JX838926	
A. dodomae	*A. dodomae*	ZFMK 84983	TZ	JX668167	JX857552	JX838927	
A. doriae	*A. doriae*	MVZ 257967	ET, Aynalem	JX668168	JX857614	JX838928	
A. kaimosae	*A. kaimosae*	ZFMK 82075	KE, Masai Mara	JX668183	JX857630	–	
A. lionotus	*A. lionotus*	ZFMK 83646	KE, Tsavo East	GU128456	GU128493	JX838956	
A. mwanzae	*A. mwanzae*	ZFMK 82076	KE, Masai Mara	GU128457	–	JX838961	
A. rueppelli	*A. rueppelli*	MVZ 241336	SO, Borama	JX668208	JX857599	JX838972	
A. turuensis	*A. turuensis*	ZFMK 74930	TZ, Jorodom	JX668214	–	–	
Agama sp. n.	*A. lionotus*	CAS 199008	KE, Kajiado Dist.	JX668193	JX857597	JX838955	*A. hulbertorum* sp.n.

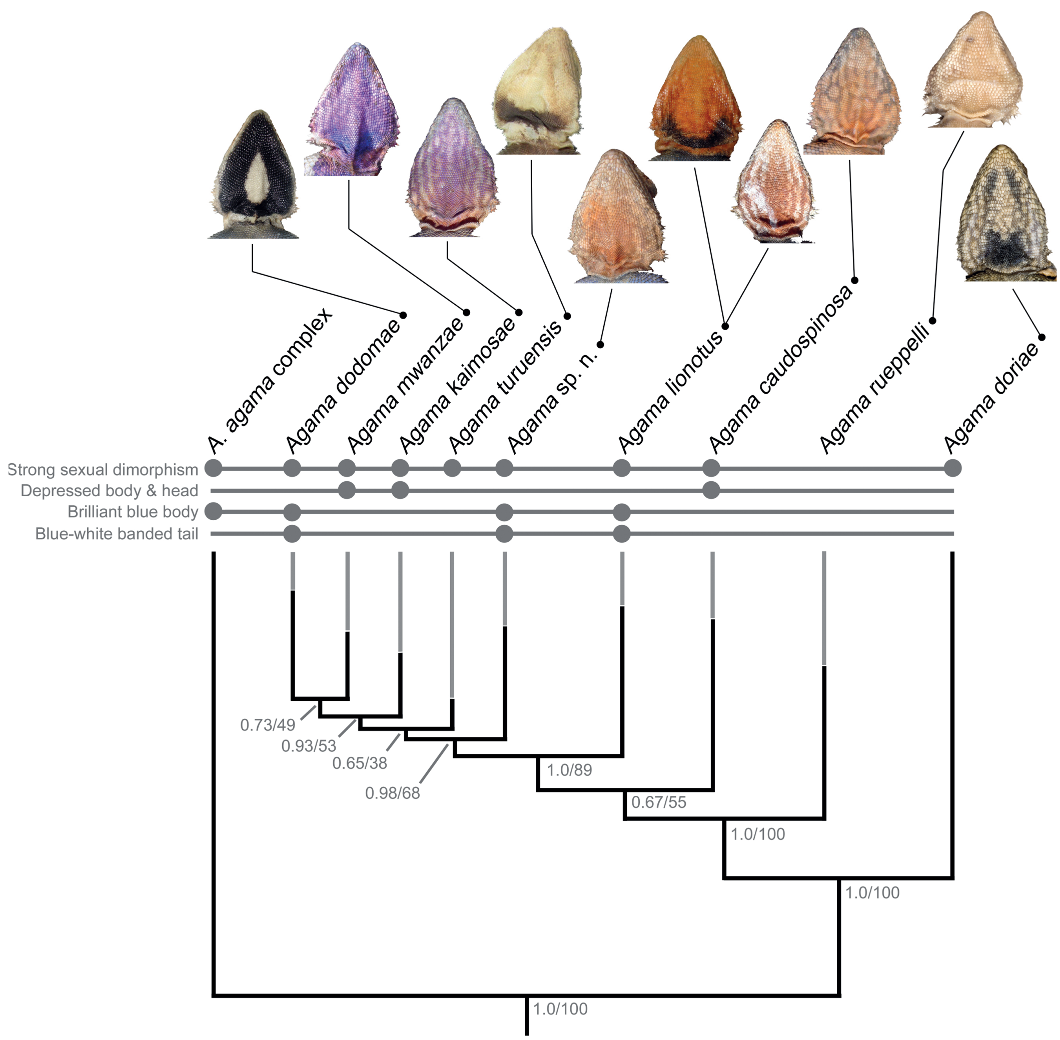

Figure 1. Concatenated data phylogeny (mtDNA + four nuclear genes) for the *Agama lionotus* complex based on a Bayesian phylogenetic analysis using MrBayes. Posterior probability values ≥ 0.50 and RAxML bootstrap values < 50% are shown on branches. With regard to the throat colouration of *A. lionotus*, the left illustration refers to *A. l. elgonis*, the right one to *A. l. lionotus*.

A. dodomae, see Discussion) and *Agama usambarae* (recognized as a synonym of *A. lionotus fide* Wagner 2007) are not shown, as no tissue samples were available. Within this clade, most of the nodes are supported by bootstrap values higher than 70% and a PP of 0.7.

The PCA analyses were conducted on datasets containing *A. dodomae, A. kaimosae, A. l. lionotus, A. l. elgonis, A. mwanzae, A. turuensis*, and three specimens of the putative new species (including the name-bearing type specimens of *A. elgonis*, *A. kaimosae, A. turuensis, A. ufipae,* and *A. usambarae*), and included 62 characters (18 mensural, 17 mensural ratios, 27 meristic) for 42 specimens. In a general PCA of mensural, meristic, and ratio data (Fig. 2), the first two axes explain 39.15% of the variance in the dataset (PC1: 27.6%; PC2 11.55%). The third and fourth axes explain 25.47% of the variance in the dataset (PC3: 8.6%; PC4: 7.65%) and show a similar pattern. Generally, main contributors are scattered about the entire dataset (see Tab. 3 for detailed analyses), but the highest loadings to PC1 and PC2 were mainly mensural characters (e.g., PC1: SVL, HL, EEL, SAL, ADG, TFL; PC2: HW/HH, TW/TH). Generally, this PCA shows a phenotypic partitioning of the putative new species and *Agama mwanzae* from Rwanda (= *A. mwanzae*_RW), being most distinctive from other East African agamas. Most of the remaining species show an overlap, which is strongest between *Agama mwanzae* from Masai Mara/Serengeti and *A. turuensis* from the same region, but *Agama dodomae* is slightly distinct in its morphospace.

Agama l. lionotus has the highest variance in its morphospace, followed by *A. turuensis* and *A. mwanzae* from Rwanda, while *A. dodomae* and *A. l. elgonis* have the smallest morphospaces. A first detailed PCA was conducted using only mensural characters, where the first and second axes explain 79.96% of the variance (PC1: 74.69%; PC2: 5.26%; Jolliffe cut-off: 0.7). Plotting PC1 against PC2 (Fig. 3A; for PCA loadings see Tab. 3) shows an extreme overlap of *A. l. lionotus*, *A. l. elgonis*, *A. kaimosae* and *A. turuensis*. *Agama mwanzae* overlaps slightly with this group, whereas *A. dodomae* and *A. mwanzae* from Rwanda are slightly distinct. The putative new species is strongly distinct in its morphospace from the other examined taxa and separated from *A. mwanzae* Rwanda, *A. usambarae* and *A. dodomae* on the first axis and all other taxa on the second axis. Comparing PC1 with PC3 and PC4 generally shows the same pattern of morphospace, but the taxa are more distinct. These comparisons explain 78.83% and 78.66% of the variance, respectively. *Agama l. lionotus* shows the largest variance in its morphospace, followed by *A. mwanzae* from Rwanda, while *A. l. elgonis* and *A. mwanzae* have the smallest morphospaces. Only ratio characters were used in a second detailed PCA, and the

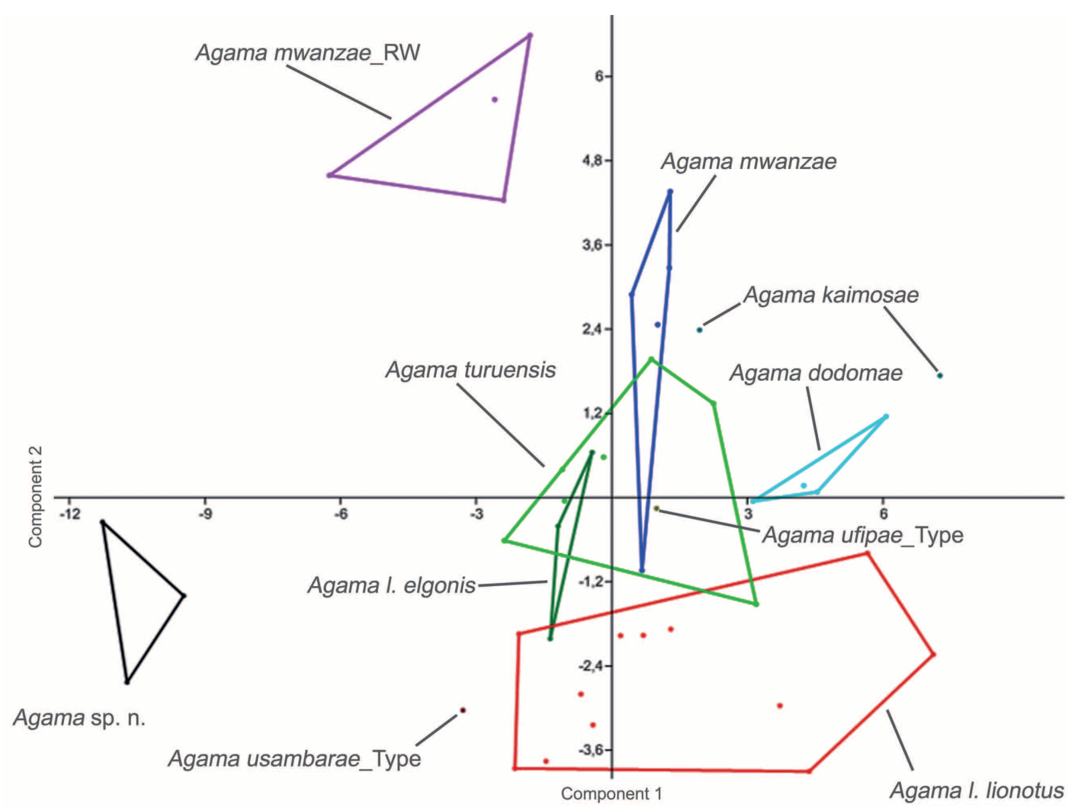

Figure 2. Plot of specimen scores of principal component analyses of size-corrected and $\log_{10}$-transformed data of the *A. lionotus* group. Mensural, meristic and ratio characters were analysed together. Populations of *A. mwanzae* from Rwanda (*A. mwanzae*_RW) versus those from Kenya/Tanzania (*A. mwanzae*) were analysed separately, because of their disjunctive geographic separation.

Table 3. Principal component analysis (correlation matrix) elements of the unit eigenvectors for size-corrected and $\log_{10}$-transformed data of PC1 and PC2 for specimens of the *A. lionotus* complex (see Fig. 2). Partitioned mensural, ratio and meristic values. See Table 1 for explanation of variables.

Mensural Characters	PC 1	PC 2	Ratio Characters	PC 1	PC 2	Meristic Characters	PC 1	PC 2
SVL	0.2317	0.05826	TL/SVL	-0.107	0.05422	RPP	0.04868	0.08717
TL	0.1742	0.09907	TL/TOTAL	-0.1058	0.04794	PP	0.08971	0.09873
TW	0.1935	0.1315	TL/TH	-0.0989	0.2097	SL	-0.0008939	-0.08907
TH	0.2032	-0.0971	TW/TH	-0.004294	0.2846	IL	0.06623	-0.1026
HL	0.2222	0.1124	HL/SVL	-0.0732	0.1752	NCR	-0.03761	0.05042
HW	0.1928	0.1231	HL/HW	0.06027	-0.01339	SupraO	0.01193	0.1326
HH	0.211	-0.06522	HW/HH	-0.03013	0.2533	CR	-0.01613	0.1364
SEL	0.2083	0.1003	SEL/EEL	-0.04986	0.05773	T	-0.04593	-0.1983
EEL	0.2162	0.05915	ER/EAR	-0.06336	-0.1455	NCS	0.02478	-0.2802
ER	0.1382	0.03667	SAL/ADG	-0.01185	0.06543	TCS	0.05079	-0.2331
EAR	0.1556	0.1606	ADG/TOTAL	0.07132	-0.0896	SaA	0.1173	-0.02299
SAL	0.2238	0.06687	HUL/RUL	-0.04223	0.03283	SaM	0.1047	0.007923
ADG	0.2171	0.02842	FL/TFL	-0.0372	0.1635	SaH	0.05698	-0.0003537
HUL	0.2054	0.1047	HUL+RUL/FL+TFL	0.006409	-0.07859	D	0.07591	0.0417
RUL	0.2076	0.06727	SVL/FL+TFL	0.07463	-0.1106	V	0.1279	-0.06491
FL	0.1886	0.1503	FL+TFL/TOL	0.01376	0.166	CAS_1	0.1069	-0.2526
TFL	0.218	0.07504	PP/RPP	0.05567	0.02483	CAS_2	0.1153	-0.2204
TOL	0.1865	0.005297				FI_1	0.1425	-0.05953
						FI_2	0.08444	-0.02833
						FI_3	0.08719	-0.1248
						FI_4	0.0982	-0.1422
						FI_5	0.132	-0.05124
						TOE_1	0.05666	-0.07259
						TOE_2	0.05328	-0.1624
						TOE_3	0.1225	-0.1166
						TOE_4	0.1051	-0.1669
						TOE_5	0.1235	-0.1427
	Eigenvalue	% Variance						
PC 1	17.1133	27.602						
PC 2	7.16146	11.551						

first and second axes explain 43.1% of the variance (PC1: 27.02%; PC2: 16.09%; Jolliffe cut-off: 0.7; for PCA loadings see Tab. 3). Plotting PC1 against PC2 (Fig. 3B) shows an extreme overlap of all taxa other than *A. mwanzae* from Rwanda. *Agama mwanzae* and *A. turuensis* have the strongest variance in their morphospaces, followed by *A. l. lionotus* and *A. mwanzae* from Rwanda, while *A. dodomae*, *A. l. elgonis*, and the putative new species have the smallest. Comparing PC1 with PC3 (13.36%) and PC4 (8.41) produces the same result. The putative new species is separated from *A. mwanzae* Rwanda and *A. l. lionotus* on the first axis and all other taxa on the second axis.

The third detailed PCA (Fig. 3C) compared meristic characters. The first and second axes explain 38.81% of the variance (PC1: 24.15%; PC2: 14.66%; Jolliffe cut-off: 0.7). Plotting these axes shows overlaps of most taxa with the new species and *Agama mwanzae* from Rwanda being slightly distinct in its morphospace. *Agama mwanzae* shows the highest variance in its morphospace, followed by *A. l. lionotus* and *A. turuensis*, while *A. mwanzae* from Rwanda and *A. l. elgonis* have the smallest variance. Comparing PC1 with PC3 (10.39%) and PC4 (7.37) produces the same result, but the taxa do not overlap as strongly as in PC1 against PC2. The putative new species is separated from all species other than *A. mwanzae* Rwanda and *A. turuensis* on the first axis and except of *A. mwanzae* and *A. dodomae* on the second axis.

Comparing the morphology and genetic data shows one main result: The provisional identification of the specimens from Elangata Wuas as *Agama agama* was wrong and they instead represent a new species, which is herein described as:

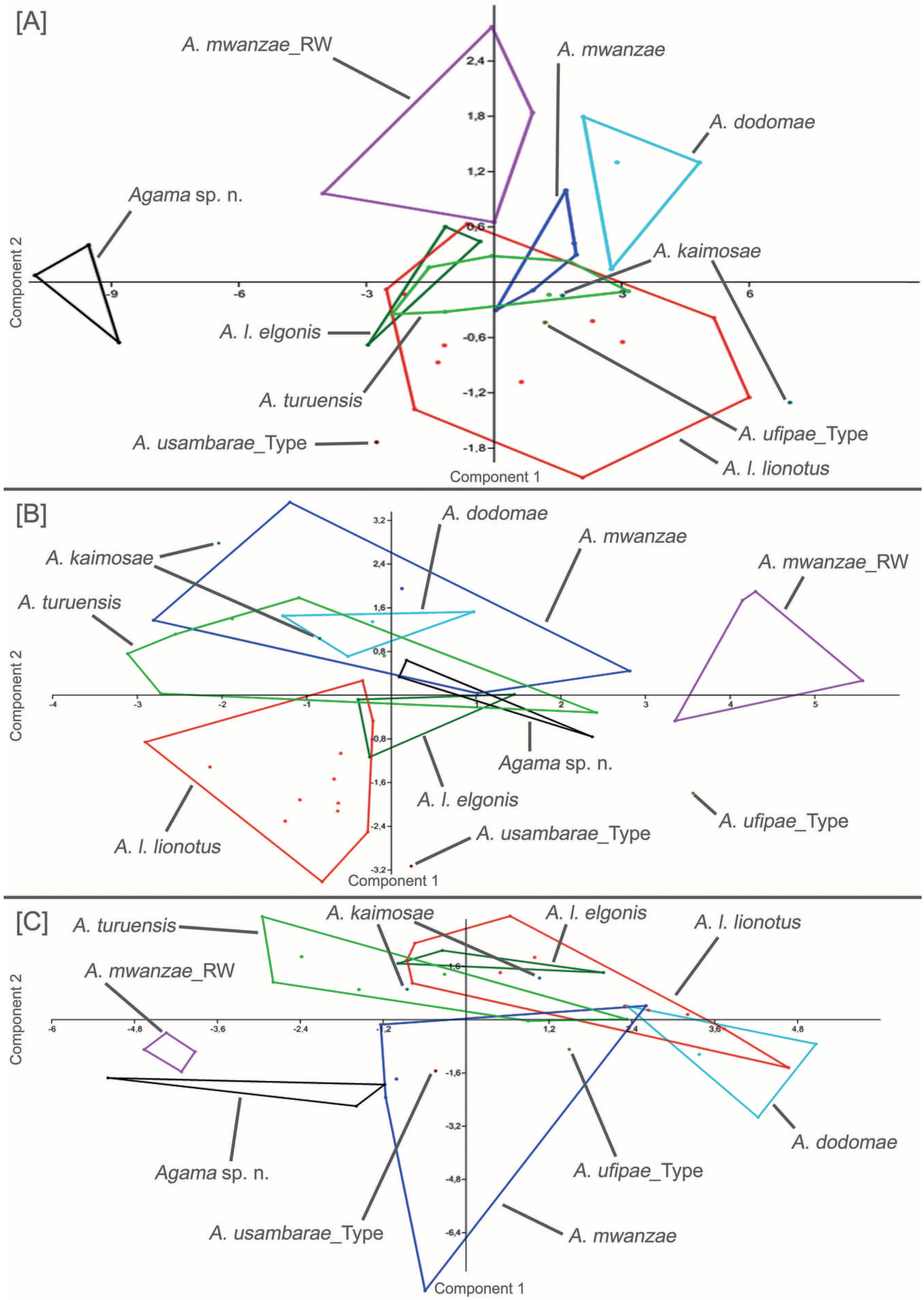

Figure 3. Plot of specimen scores of principal component analyses (PCA) of size-corrected and $\log_{10}$-transformed data of the *A. lionotus* group: A) first two axes of PCA of mensural data; B) first two axes of PCA of ratios; C) first two axes of PCA of meristic data. Populations of *A. mwanzae* from Rwanda (*A. mwanzae*_RW) versus those from Kenya/Tanzania (*A. mwanzae*) were analysed separately, because of their disjunctive geographic separation.

Table 4. Selected morphological characters of examined species. See Table 1 for explanation of variables.

	Agama hulbertorum	*Agama l. lionotus*	*Agama l. elgonis*	*Agama dodomae*	*Agama turuensis*	*Agama kaimosae*	*Agama mwanzae*	*Agama mwanzae_RW*
SVL [mm]	77.2–84.9 [80.5]	106.3–138.6 [120.0]	99.5–117.4 [107.9]	126.0–136.7 [130.4]	99.0–134.8 [114.6]	122.8–143.9 [133,4]	115.3–127.8 [120.6]	95.3–118.5 [109.4]
SaM	58–67 [63.3]	67–91 [74.5]	84–88 [83.9]	74–78 [75.5]	71–85 [76.3]	79–95 [85.3]	59–78 [71.4]	68–75 [72.5]
D	50–69 [58.7]	56–71 [65.3]	66–70 [68]	66–75 [70.8]	66–70 [68]	59–68 [63.5]	60–73 [65.6]	63–78 [69.3]
V	76–82 [78.7]	83–97 [90.3]	92–93 [92.3]	95–102 [98.5]	91–99 [96.1]	92–97 [94.5]	74–93 [82.5]	80–85 [82.5]

Agama hulbertorum sp. n.
(Fig. 4, Tab. 4)

Holotype: CAS 198880, adult male from Elangata Wuas, 26 km bearing 266 (true North) from Kajiado, (1°52'18.7" S, 36°33'46.6" E), ca 1,300 m, collected by M. Cheptumo, P. Matolo & J.V. Vindum on 3.VI.1995 [this holotype and name were registered at Zoobank under LISD FA8C667B-C1C4-44B2-8083-F245230C3566].

Paratypes: CAS 198908–914, all from Elangata Wuas, 20.8 km bearing 248 (true North) from Kajiado (1°55'38.6" S, 36°37'22.0" E), collected by M. Cheptumo, P. Matolo & J.V. Vindum on 30.V.1995. CAS 198995–199008, all from Elangata Wuas, Base Camp Sinya Omelok, 20.4 km bearing 247 (true North) from Kajiado (1°55'45.9" S, 36°37'41.1" E), collected by M. Cheptumo, P. Matolo & J.V. Vindum on 28.V.1995.

Additional specimens: NMK L/2732/4 adult male, NMK L/2732/3 adult female, NMK L/2732/1 juvenile, ZFMK 83643 juvenile, all from southern slopes of the Ngong Hills (1°27'4.997" S, 36°37'54.242" E) and collected by Alexander Burmann on 7.IV.2004.

Diagnosis: A small *Agama* of the *A. lionotus* complex. It can be identified by the following combination of characters: nasal scale pear-shaped, keeled and tubular; nasal scale in contact with the first canthus scale; nuchal crest minute, consisting of few, indistinctly raised scales; ear opening surrounded by five tufts of spiny scales, with two additional tufts on the neck; vertebral scales feebly keeled, dorsal and lateral scales keeled, ventral and gular scales smooth; dorsal and lateral caudal scales keeled, ventral caudal scales smooth; and males with one discontinuous row of precloacal pores. Males in nuptial colouration exhibit a red throat, without any pattern, a vertebral stripe, and a narrowly annulated blue and white colour pattern on the tail.

Description: Maximum length 228 mm (CAS 198995), with an SVL between 77 and 85 mm. Head round to moderately convex, body scarcely depressed, hind limbs strong. Head scales moderately large, smooth, with a medium-sized occipital scale as large as the largest head scale and half the diameter of the tympanum, pierced by a visible pineal foramen in its centre. Gular fold present, gular pouch missing. Tail about one and a half times longer than SVL (143 mm at 85 mm SVL in CAS 198995). Nasal scale pear-shaped, keeled and strongly convex, pierced by a laterally positioned and slightly posterodorsally directed nostril in its posterior part, situated on the canthus rostralis. A minute nuchal is present in males, consisting of 11–12 small erect scales that are as large as other body scales. Five tufts of spinose scales around the ear and an additional two on the sides of the neck, longest spines about half of the diameter of the ear opening. Body scales of medium size, imbricate and homogeneous; vertebral scales feebly keeled, dorsal and lateral scales keeled, ventral and gular scales smooth, both smaller than the dorsals, and gular scales smaller than ventral scales. Body scales in 58–67 ($\bar{x}$ = 63.3) rows around midbody, 50–69 ($\bar{x}$ = 58.7) vertebral scales and 76–82 ($\bar{x}$ = 78.7) scales down the length of the belly. Fourth and third fingers equal in length, fourth toe longest. Tail slightly compressed, covered dorsally and laterally with strongly keeled scales that are larger than the body scales, ventrocaudal scales smooth and smaller, becoming keeled towards the tail tip. One discontinuous row of ten or eleven precloacal pores in adult males.

Differential diagnosis: In general, adult males of *A. hulbertorum* sp. n. are distinct from most other species of the genus (excluding *A. dodomae*, *A. lionotus*, and *A. kirkii*) by their colouration of a bright blue body with a vertebral stripe and a blue/white annulated tail.

Within the *Agama lionotus* complex s. str. (Tab. 4), *Agama hulbertorum* sp. n. is distinct from *A. l. lionotus* by its smaller adult size ($\bar{x}$ = 80.5 mm versus 120.0 mm), a lower number of ventral scales (76–82 versus 83–97), a lower number of scale rows around midbody (58–67 versus 67–91), a keeled versus a smooth nasal scale, and by having a distinct vertebral stripe extending to the hind limbs.

Agama hulbertorum sp. n. is distinct from *A. l. elgonis* by its smaller size (SVL $\bar{x}$ = 80.5 mm versus 108.0 mm), having a lower number of scale rows around midbody (58–67 versus 84–88), a lower number of ventral scales (76–82 versus 92–93), the lack of a U-shaped dark bar at the base of

Figure 4. Male holotype (CAS 198880) of *Agama hulbertorum* sp. n. From top to bottom: dorsal, ventral, and lateral views of the entire specimen. Bottom from left to right: dorsal, ventral, and profile views of the head.

the throat of adult males, as is typical for *A. l. elgonis,* and by having a distinct vertebral stripe extending to the hind limbs.

Agama hulbertorum sp. n. is distinct from *A. dodomae* by its smaller size (SVL $\bar{x}$ = 80.5 mm versus 130.0 mm), having a lower number of scale rows around midbody (58–67 versus 74–78), a lower number of ventral scales (76–82 versus 95–102), the lack of a rhombic dark bar at the base of the throat of adult males, as is typical for *A. dodomae,* and by having a distinct vertebral stripe extending to the hind limbs.

Agama hulbertorum sp. n. is distinct from *A. turuensis* by its smaller size (SVL $\bar{x}$ = 80.5 mm versus 117.0 mm), having a lower number of scale rows around midbody (58–67 versus 71–85), a lower number of ventral scales (76–82 versus 91–99), a blue/white annulated tail, the lack of large dark bar at the base of the throat of adult males, as is typical for *A. turuensis,* and by having a distinct vertebral stripe extending to the hind limbs.

Agama hulbertorum sp. n. is distinct from *A. kaimosae* by its smaller size (SVL $\bar{x}$ = 80.5 mm versus 133.0 mm), having a lower number of scale rows around midbody (58–67 versus 79–95), a lower number of ventral scales (76–82 versus 92–97), a blue/white annulated tail, and by having a distinct vertebral stripe extending to the hind limbs.

Agama hulbertorum sp. n. is distinct from *A. mwanzae* by its smaller size (SVL $\bar{x}$ = 80.5 mm versus 115.0 mm), having a lower number of scale rows around midbody (58–67 versus 86–95), an entirely blue body colouration and a blue/white annulated tail, and by having a distinct vertebral stripe extending to the hind limbs.

The new species is distinct from both *Agama rueppelli* and *A. persimilis* by the brilliant colouration of adult males, showing a blue body and a blue/white annulated tail.

Only one species outside the *A. lionotus* complex is similar in colouration. From *Agama kirkii*, the new species is distinct by its smaller size (SVL $\bar{x}$ = 80.5 mm versus 115.0 mm), having a lower number of scale rows around midbody (58–67 versus 99–114), the lack of a large dark spot at the base of the throat of adult males, and by having a distinct vertebral stripe extending to the hind limbs.

Description of the holotype (CAS 198880, Fig. 4): Adult male with a complete tail. Measurements: SVL 79.3 mm; TL 141.1 mm; HL 22.5 mm; HW 19.0 mm; HH 10.6 mm; crest length 9.5 mm; length of humerus 19.0, of radius/ulna 13.5 mm; of femur 22.8 mm, of tibia/fibula 21.3 mm.

Description: Head and body depressed. Nostril tubular and a third of the size of the nasal scale, directed more or less laterally and slightly posterodorsally, located in the posterior part of a convex, keeled, pear-shaped nasal scale that is situated on the canthus rostralis. Nasal scale partly visible from above, not separated by smaller scales from the first canthal scale. Nostril visible from above. The first three canthal scales not in contact with the eye. Scales on the head smooth, interorbital scales as large as or smaller than the supraorbital scales; imbrications of temporal scales not uniformly directed, some ventrally and others posteriorly orientated. Occipital medium-sized, as large as the largest head scale and half the diameter of the tympanum, pierced by a visible pineal foramen in its centre. Eleven upper and 9 lower labial scales on the left side. Ear opening smaller than the eye, surrounded at its borders by five tufts of spinose scales, two additional tufts on the dorsolateral parts of the neck. Spinose scales of the tufts long, consisting of scales of the same size and one elongated scale in the centre. Gular fold present, but gular pouch absent. Minute nuchal crest of 9.5 mm in length present, composed of twelve tiny and somewhat erect scales. Dorsal scales homogeneous, in 67 scale rows around the body just behind the forelimbs, in 58 scale rows around midbody, and in 64 scale rows around the body in front of the hind limbs. There are 50 vertebral scales and 76 medioventral scales between the anterior border of the shoulders and cloaca. One row of ten precloacal pores. Dorsal and lateral body scales keeled, with the keel extending along the entire scale, slightly mucronate and erect. Scales directly along the vertebral column feebly keeled. Gular and ventral scales smooth. Fifteen keeled lamellae under the left fourth finger, 19 keeled lamellae under the left fourth toe. Relative length of digits of left manus 1<2=5<3<4; relative length of digits of left pes 1<2<5=3<4. Tail depressed at its base behind cloaca. Large hemipeneal pockets absent. Dorsal and lateral tail scales moderately keeled, slightly mucronate, and somewhat larger than the body scales. Ventral tail scales smooth at its base, becoming moderately keeled towards the tail tip. Tail scales not arranged in distinct whorls of scale rings, but indistinct whorls of three scale rings present.

Colouration (after fixation and 19 years of preservation; Fig. 4): Upper parts of the head and body somewhat rufous brown to dark dirty grey. Forelimbs still with some bluish colouration. Head and neck with few indistinct pale ocelli. Throat dirty whitish without any pattern. Dirty whitish vertebral stripe present. Tail dirty brown with some indistinct bands. Underside of the body and tail dirty whitish.

Variation in colouration: Similar in all preserved specimens, with the vertebral stripe being only present in males. Live specimens from the Ngong Hills are described by Burmann (2006): adult males in nuptial colouration with orange to red head and neck; body, including the limbs, blue with a whitish vertebral stripe. Throat uniform red, without any pattern. Tail blue with an indistinct thin white banding. Underside of the body and limbs blue, underside of the tail white. Males in non-nuptial colouration (Fig. 5) reddish-brown above with a pale vertebral stripe, legs blue, tail dirty white to bluish with indistinctly coloured rings; throat red with no pattern, belly and underside of legs blue, tail dirty white. Females and juveniles similar to other *Agama* species. Females brown with a pattern of dark-framed pale to orange ocelli on the head. Body with a similar pattern and additionally with indistinct dark brown bands. Tail banded light and dark brown. Underside of the head, body and tail whitish. Juveniles similar, but ocelli and bands more distinct. Gravid females display a broad orange stripe on the flanks.

Relationships: Despite the fact that adult males of *Agama hulbertorum* sp. n. are similar in colour pattern to *A. l. lionotus*, the species is the sister taxon to a lineage including *A. turuensis*, *A. kaimosae*, *A. mwanzae*, and *A. dodomae* (Fig. 1), while *A. lionotus* is the sister species to this entire lineage.

Etymology: This species is named in honour of Andrea and Felix Hulbert, in recognition of their contributions to the captive breeding of African reptiles and, of course, our glorious friendship.

Distribution and habitat: The type series was collected in the area of Elangata Wuas at the southern tip of the Kenyan Rift Valley close to the border with Tanzania (Fig. 6). The general topology is characterized by plains with occasional volcanic hills and valleys. The vegetation of this semi-arid region is dominated by *Acacia-Commiphora-Balanites* woodland with an annual precipitation of 600 mm. An unpublished comparison of the 16S gene between specimens from Elangata Wuas and those from the southern slopes of the Ngong Hills (see Wagner 2010a) shows that both belong to the same taxon. Here, several specimens were collected at the southern slopes of the Ngong Hills at an elevation of 1,730 m. Therefore, the species could occupy at least the area between these two localities. Furthermore, the new species was sighted by Stephen Spawls (pers. comm. 2. VIII 2014) west of the Ngong Hills (south of the Mt. Suswa Conservancy; 1°18'37.213" S, 36°20'57.527" E) in rocky habitats with sparse vegetation (Fig. 7) and in the area of Olorgesaile (1°34'40.012" S, 36°26'59.791" E).

Figure 5. Live male of *Agama hulbertorum* sp. n. in non-nuptial colouration from Olorgesaile (1°34'40.012" S, 36°26'59.79" E), Kenya. Dorsal view above, ventral view below. Photo courtesy of Stephen Spawls.

Ecology: A rupicolous lizard with individuals inhabiting rocky outcrops or solitary larger stones and rocks in an arid landscape with *Acacia* shrub vegetation. It is diurnal and lives in harem groups of one dominant male and several females and juveniles (A. Burmann, pers. com. 2006). Specimens at the Ngong Hills were active around noon at temperatures of about 27°C and a humidity of 60% (Burmann 2006).

Discussion

Both morphological and genetic analyses support the taxonomic distinctiveness of the specimens from the area south of the Ngong Hills. Generally, *Agama* species are very similar in morphology and show high variations of characters within species, resulting in large overlaps of characters between species (Wagner 2010b). The PCA analyses show a large overlap within the *Agama lionotus* complex, but specimens of *Agama hulbertorum* sp. n. are nevertheless distinct from this group. Genetic analyses place *A. hulbertorum* sp. n. apart from *Agama lionotus* and basal to a group including *A. turuensis*, *A. kaimosae*, *A. mwanzae*, and *A. dodomae*. Consequently, these specimens are considered as a distinct, although cryptic, new species.

Moreover, the genetic results emphasise the value of the adult male throat colouration for the identification of species within the *Agama lionotus* complex, which was in the past suggested for this complex by Wagner (2010a). The throat colouration (Fig. 1) varies between uniform light (*A. hulbertorum* sp. n., *A. rueppelli*), a pattern of dark and pale red stripes (*A. caudospinosa*, *A. kaimosae, A. l. lionotus, A. mwanzae*), uniform with basal dark bars (*A. doriae*, *A. l. elgonis*, *A. turuensis*), a dark rhombic pattern (*A. d. dodomae*), and the uniformly dark throat of *A. d. ufipae*. The latter taxon was recognized as a subspecies of *A. lionotus* (Böhme et al. 2005), but as its gular pattern is more similar to *A. dodomae* and as it is bordering the distribution range of this taxon, while *A. lionotus* is mainly a Kenyan endemic species and only reaches the extreme North of Tanzania (Fig. 6), it should be consequently recognized as a subspecies of this taxon (see also Wagner 2010a). *Agama usambarae* was suggested to be a synonym of *A. l. lionotus* (Wagner 2007). Morphological PCA analyses show the previous taxon most often in close morphospatial proximity to the latter, and Wagner (2007) did not find any differences between *A. l. lionotus* and the holotype of *A. usambarae*, supporting the latter's status as a synonym.

In spite of the fact that several new agamid lizards were recently described from the Horn of Africa (Wagner & Bauer 2011, Wagner et al. 2013a, Wagner et al. 2013b), the discovery of a new *Agama* lizard from Kenya is surprising. Apart from South Africa, Kenya is regarded as one of the best herpetologically studied countries in Africa. Moreover, the area is geographically close to Nairobi and reasonably well known. The reason why this species was not discovered earlier is obviously due to its cryptic similarity to *Agama lionotus*, however, its vertebral stripe and smaller adult size identify *Agama hulbertorum* sp. n. as clearly distinct. *Agama lionotus* has a wide distribution (Fig. 6) on the eastern side of the Rift Valley within Kenya and is found reasonably close to the type locality of *A. hulbertorum* sp. n. However, *Agama l. lionotus* appears to be a more lowland-adapted species, while the new species and especially *A. l. elgonis* appear to range in mid-altitude situations. Both taxa, *A. l. lionotus* and *A. l. elgonis,* seem to overlap in their distribution at Arusha, but they are most probably microspatially separated. The Kenya-Tanzania border areas seem to coincide with the species border between *A. lionotus* and *A. dodomae*, but no geological structure has so far been identified that would explain this pattern.

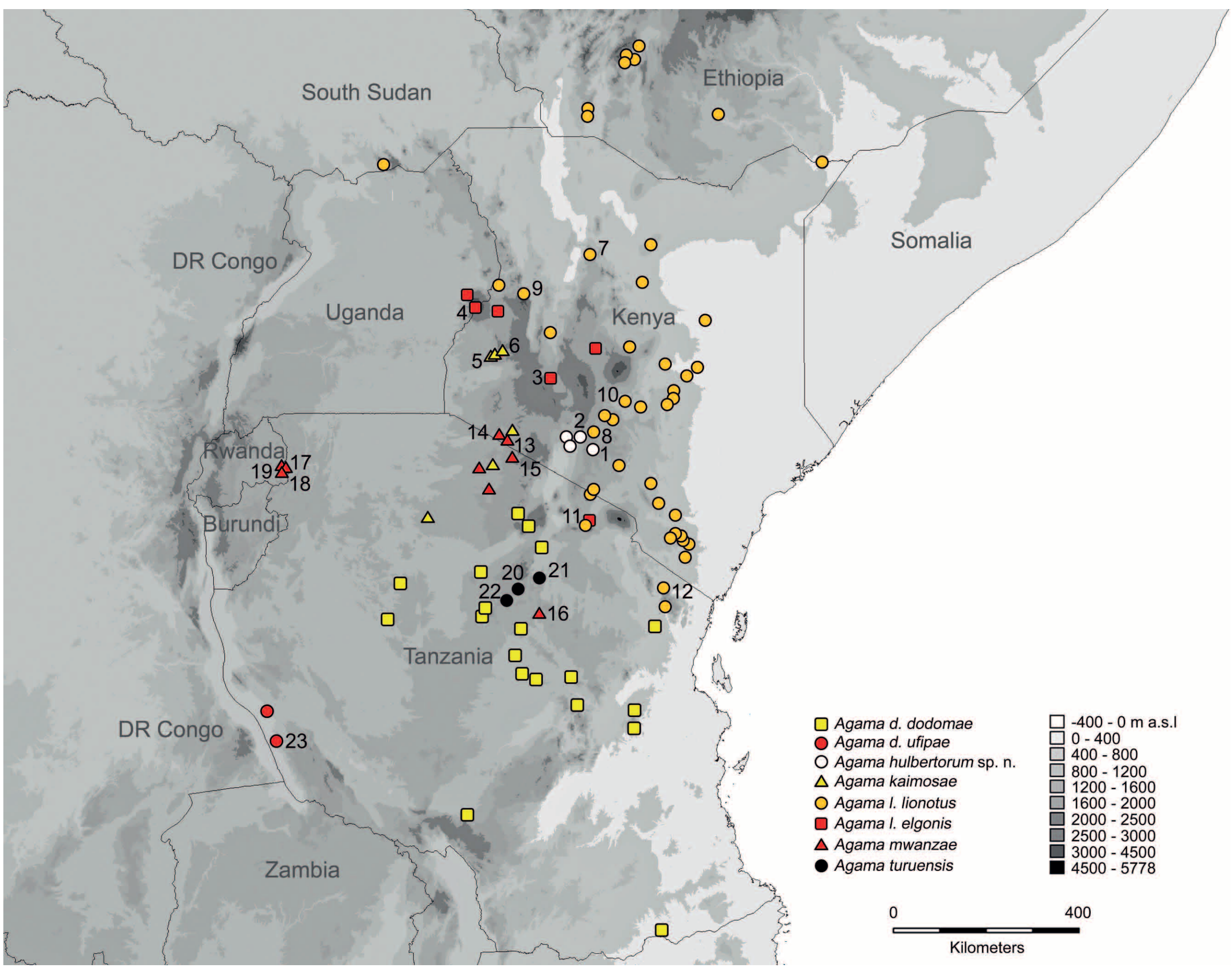

Figure 6. Distribution of the *Agama lionotus* complex, excluding *A. caudospinosa, A. doriae, A. lucyae, A. rueppelli* and *A. persimilis*. Localities extracted from GBIF, museum collections and own unpublished data. Numbers refer to localities of specimens examined herein:1=area north of Kajiado (type locality of *A. hulbertorum* sp. n.); 2 – southern slopes of the Ngong Hills; 3 – Nakuru NP; 4 – Mt. Elgon; 5 – Kaimosi; 6 – Ngoromosi; 7 – South Horr; 8 – Nairobi; 9 – Sebit, Cherangani Hills; 10 – Kindaruma; 11 – Arusha; 12 – Usambara Mountains; 13 – Keekorok, Masai Mara; 14 – Mara Serena Lodge, Masai Mara; 15 – Klein's Camp, Serengeti; 16 – Hambi; 17 – Ntaruka; 18 – Rugarama; 19 – Lake Mpanga; 20 – Mount Hanang; 21 – Mount Kwaraha; 22 – Unyanganyi, Singada; 23 – Kipili; 24 – Soni, Usambara Mountains.

Figure 7. Habitat of *Agama hulbertorum* sp. n. west of the Ngong Hills (1°18'37.213" S, 36°20'57.527" E), Kenya. Photo courtesy of Stephen Spawls.

Because of the disjunctive geographic separation of the populations of *Agama mwanzae* from Rwanda versus those from Tanzania/Kenya, their morphological data were analysed separately. The results show these populations to be distinct from each other, but the analysis only included specimens from central Tanzania and Rwanda and lacked specimens from the area south of Lake Victoria. Their distinctiveness could therefore be an artefact resulting from missing data. However, the status of the specimens from Rwanda should be clarified.

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Appendix 1
Material examined

Agama caudospinosa: Kenya: Lake Elementaita: NMK L/2722/1–2; Kiamatongu: NMK L/2730/2–3, ZFMK 83667; Naro Moru: NMK L/2726/3–6, ZFMK 83661–663; Meru: Nkunga NMK L/2728/2–3, 6, ZFMK 83664–666; Nairobi (locality questionable): ZFMK 8701, 9025. ***Agama dodomae dodomae***: Tanzania: ZMB 12980, ZFMK 83706, 84983–85. ***Agama dodomae ufipae***: Tanzania: MCZ 30741: Kipili, Ufipa (holotype). ***Agama kaimosae***: Kenya: Kaimosi: MCZ 40136 (holotype); Ngoromosi: NMK L/2715/1, 3–4, ZFMK 83658–660; Tanzania: Kishapu District: Mwamalasa: MHNG 877.65, MHNG 2684.001–006. ***Agama lionotus elgonis***: Kenya: Mount Elgon: MCZ 32797 (syntype); Nakuru: CAS 147880; NMK L/2721/1, 3, ZFMK 83637; Lake Nakuru NP: ZFMK 82064–065. ***Agama lionotus lionotus***: Kenya: Cherangani Hills: Sebit: NMK L/2718/1, 3–4, 7–8, ZFMK 83634–636; Cherangani Hills: Sigor: ZFMK 82062–063; CAS 154486: btw Kapenguria and Marich Pass; Lake Baringo: NMK L/2720; Ngong Hills: NMK L/2732/1, 3–4, ZFMK 83643; Namanga: NMK L/2733/2–4, ZFMK83644; Nairobi NP: Masai Gate: NMK L/2724/3–5, ZFMK 83639–640; South Horr: ZFMK 70772–775; Of Ngomeni Dam: CAS 161269, 161272; Ol Doinyo Sapuk NP: NMK L/2734/2, ZFMK 83645; Sultan Hamud: NMK L/2742/1, ZFMK 83651; Isiolo: NMK L/2727/1, 3–4, ZFMK 83641; Kindaruma: NMK L/2729/1, 3, ZFMK 83642; Kibwezi: NMK L/2740; Taita Hills: NMK L/2736; Tsavo East NP: NMK L/2735/1, 4–5, 7, ZFMK 83646–648; Tsavo West NP: NMK L/2739/1–4; Sagala Hills: NMK L/2737/1, ZFMK 83649; Rukinga Ranch: NMKL/2738/1, 3–4, ZFMK 83650. Tanzania: ZFMK 7485; Tanga: ZFMK 44713; Arusha: ZFMK 66617–618; Mbunyani: ZFMK 77336. ***Agama mwanzae***: Kenya: Masai Mara: NMK L/2723/1–3, ZFMK 83657, 82075–077. Rwanda: Mpanga: ZFMK 51195; Kibungu: Rugurama: ZFMK 55797–800; Kibungu: Nasko: ZFMK 61664; Kibungu: Ntaruka: ZFMK 61663. Tanzania: Dodoma, Kondoa, Hambi: CAS 162643. ***Agama turuensis***: Tanzania: Mt. Hanang: ZFMK 74930–943, 82192–194, 82324–328, 82357–360, 82278–279; MCZ 30686: Unyanganyi, Turu (Singida) (holotype). ***Agama usambarae***: Tanzania: MCZ 24129: Soni, near Lushoto, (Usambara Mts.) (holotype).