






## Lifting the blue-headed veil – integrative taxonomy of the *Acanthocercus atricollis* species complex (Squamata: Agamidae)

Philipp Wagner <sup>a,b</sup>, Eli Greenbaum<sup>c</sup>, Aaron M. Bauer <sup>b</sup>, Chifundera Kusamba<sup>d</sup> and Adam D. Leaché <sup>e</sup>

<sup>a</sup>Department of Research & Conservation, Allwetterzoo, Münster, Germany; <sup>b</sup>Department of Biology, Villanova University, Villanova, PA, USA; <sup>c</sup>Department of Biological Sciences, University of Texas at El Paso, El Paso, TX, USA; <sup>d</sup>Laboratoire d’Herpétologie, Département de Biologie, Centre de Recherche en Sciences Naturelles, Lwiro, République Démocratique du Congo; <sup>e</sup>Department of Biology and Burke Museum of Natural History and Culture, University of Washington, Seattle, WA, USA

We present the first integrative review of the African agamid lizard *Acanthocercus atricollis*, a broadly distributed species found from Ethiopia through East Africa to Angola and South Africa. Since the original description of the species approximately 170 years ago six subspecies have been described, mainly on the basis of coloration characters. Our study presents new morphological and genetic data, which together suggest that *A. atricollis* is a complex of multiple species. External morphological characters and cranial osteology support some of the taxonomic differentiation implied by coloration. We also provide complementary 16S rRNA mitochondrial DNA (mtDNA) sequence data analysed in the context of species delimitation. Our integrated data support several systematic and taxonomic changes, including (1) *Acanthocercus branchi* is part of the *A. atricollis* complex, (2) the subspecies *A. gregorii*, *A. minutus*, *A. ugandaensis*, and *A. kiwuensis* merit species rank, (3) *A. atricollis loveridgei* is a synonym of *A. a. gregorii*, (4) *Agama cyanocephalus*, a former synonym of *A. atricollis*, is now recognized as full species distributed in Angola, Zambia and extreme northern Namibia. The distribution and diversity of the *A. atricollis* species complex supports the presence of a biogeographic arid corridor connecting eastern and southern Africa.

### ARTICLE HISTORY

Received 12 September 2017  
Accepted 28 January 2018  
Online 19 March 2018

### KEYWORDS

Squamata; Agamidae;  
*Acanthocercus atricollis*;  
*Acanthocercus cyanocephalus*; Africa

## Introduction

Cryptic species are defined as two or more taxa that are, or have been, recognized as a single nominal species, because they are at least superficially morphologically indistinguishable (Bickford et al. 2006). The revealing of cryptic species provides new opportunities to study mechanisms of speciation, biogeography, mate recognition and conservation management (Bickford et al. 2006). Integrative taxonomy can be described as a multisource approach for exploring biodiversity and resolving cryptic species complexes (Schlick-Steiner et al. 2010). The aim is to combine different sources of data

**CONTACT** Philipp Wagner  [wagner@allwetterzoo.de](mailto:wagner@allwetterzoo.de)

© 2018 Informa UK Limited, trading as Taylor & Francis Group

(e.g. morphology, genetics, bioacoustics and ecology) to increase the accuracy of species delimitation (Padiál et al. 2010). The approach has already been used to examine several agamid complexes (Wagner 2010; Wagner et al. 2011, 2013). In this paper we investigate a species complex using several types of morphological data (skull anatomy, pholidosis, morphometrics) and genetic data. Coloration and other descriptive characters are used to distinguish lineages and taxa. Our aim is to perform an integrative review of the species complex, which is important for informing studies of speciation and zoogeography across eastern and southern Africa.

*Acanthocercus* Fitzinger, 1843 are distributed along the south-western edge of the Arabian Peninsula, and on the opposite side of the Red Sea, across the Horn of Africa to East and southern Africa, with the most western populations reaching Angola and northern Namibia. The current species diversity is centred in the Horn of Africa and the adjacent Arabian Peninsula. The Arabian species *A. adramitanus* (Anderson, 1896) and *A. yemenensis* (Klausewitz, 1954) are genetically distinctive from the other taxa in the genus (Wagner 2010). The remaining species from the diversity centre (*A. annectans* [Blanford, 1870], *A. cyanogaster* [Rüppell, 1835], *A. guentherpetersi* Largen and Spawls, 2006 and *A. phillipsii* [Boulenger, 1895]) are all restricted to the Horn of Africa, while the only species outside this African range is *Acanthocercus atricollis* (Smith, 1849), a complex of several subspecies (Figure 1), and *A. branchi* Wagner, Greenbaum and Bauer, 2012b. *Acanthocercus atricollis* occurs from Ethiopia, through eastern Africa (Kenya, Uganda, Democratic Republic of the Congo [DRC], Rwanda, Burundi, Tanzania), to southern Africa (Zambia, Malawi, Mozambique, Zimbabwe, Botswana, South Africa, Swaziland, Namibia, Angola), whereas *A. branchi* was recently described from Zambia and Zimbabwe (Wagner et al. 2012b). Klausewitz (1957) established six subspecies of *A. atricollis* that are still recognized as valid (Wermuth 1967; Uetz et al 2017): *A. a. atricollis* (Smith, 1849) is mainly restricted to southern Africa with its northernmost limits in the DRC and Angola; *A. a. gregorii* (Günther, 1894) is known from coastal Kenya and Tanzania; *A. a. kiwuensis* (Klausewitz, 1957) occurs in the eastern DRC near Lake Kivu; *A. a. loveridgei* (Klausewitz, 1957) is recognized mainly from Tanzania; *A. a. minutus* (Klausewitz, 1957) is known only from Ethiopia and northern Kenya; and finally *A. a. ugandaensis* (Klausewitz, 1957) occurs in Uganda and western Kenya. The diagnostic characters presented by Klausewitz (1957) were minor and overlapping (e.g. few aspects of coloration of adult males, tail length, superficial pholidosis), and the geographic limits of the subspecies are unclear because many examined specimens lacked locality data. As a consequence, many authors have simply ignored these subspecies.

The ecology of the taxa within the *A. atricollis* complex is poorly known in many areas of their distributional range, but they are generally recognized as diurnal tree dwellers that inhabit dry forests, woodlands and forest/savannah mosaic up to 2500 m asl. *Acanthocercus a. atricollis* lives in structured colonies with one dominant adult male, and several females and juveniles (Reaney and Whiting 2003), whereas another taxon, *A. a. gregorii*, is a ground living lizard (Günther 1894). The taxa of the *A. atricollis* complex are classic ambush foragers spending most of the time waiting for potential prey on tree trunks or lateral branches. *Acanthocercus a. atricollis* is sexually dimorphic and dichromatic (Reaney and Whiting 2002) with adult males reaching larger body sizes than females, having a brilliant blue coloration on



**Figure 1.** Some subspecies within the *A. atricollis* complex: (a) *A. a. atricollis* from an unknown locality in South Africa by R. Günther. (b) *A. a. ugandaensis* from Buggala Island, Ssesse Islands, Uganda by D. Bygott. (c) *A. a. gregorii* from Kipini near Lamu, Kenya by S. Spawls. (d) *A. a. kiwuensis* from Gisenyi [type locality], Rwanda by K. Neil.

the body and throat and often a blue body with a yellowish vertebral stripe, whereas females remain inconspicuous olive-brown with black marbling. No sexual differences in diet or foraging behaviour have been recorded in the species (Reaney and Whiting 2002).

The East African arid corridor is a connection between the arid and semi-arid regions of south-western and north-eastern Africa through the eastern parts of the continent. Similarities in species composition between these parts of Africa have been noted by several authors (e.g. Poynton 1995; Wagner 2010). Disjunct distributions of isolated populations or sibling species in both African corners are examples of this 'hour-glass'-like distribution pattern (e.g. Kingdon 1990; Wagner 2010). The high number of examples of these disjunct distribution patterns across unrelated

taxa strongly suggests the existence of a historical biogeographic connection between both areas (Wagner 2010), which is supported by Kissling et al. (2016), who recognized these corridors as key predictors for present-day species richness. Research focused on the arid corridor distribution pattern is sparse and fine-scale analyses of possible refuge areas and potential West–East corridors within East Africa are needed.

In this paper, we conduct an integrative review of the *Acanthocercus atricollis* species complex using morphological and genetic data. We provide recommendations for a new taxonomy based on morphology, ecology, and genetic data, and provide updated morphological descriptions of valid taxa of the complex. Finally, we discuss the implications of these findings in light of the zoogeography of the region.

## Material and methods

### Material

In total 154 specimens were examined. Of these, 79 specimens were examined using a full dataset of 91 characters. The following material was included in the morphological analysis (numbers in brackets refer to the number of specimens examined for fine scale morphology): *Acanthocercus a. atricollis* = 21 (10); *A. a. gregorii* = 24 (14); *A. a. kiwuensis* = 19 (9); *A. a. loveridgei* = 18 (9); *A. a. minutus* = 15 (10); *A. a. ugandaensis* = 25 (9); *A. branchi* = 4 (2); '*A. cyanocephalus*' = 17 (8); *A. cyanogaster* = 11 (8)] (for details see Appendix 1). Females, juveniles, and damaged specimens were identified to the species and subspecies level and included for species descriptions, selected character analyses and distribution data, but only undamaged adult male specimens were used for detailed statistical comparisons. Additional material was used as geographic reference for distribution maps (for details see Appendix 2).

Name-bearing types of the following taxa were examined: *Acanthocercus branchi* Wagner, Greenbaum and Bauer, 2012b; *Agama atricollis* Smith, 1849; *Agama atricollis kiwuensis* Klausewitz, 1957; *Agama atricollis loveridgei* Klausewitz, 1957; *Agama atricollis minutus* Klausewitz, 1957; *Agama atricollis ugandaensis* Klausewitz, 1957; *Agama cyanogaster* Rüppell, 1835; *Agama gregorii* Günther, 1894. However, due to poor preservation, stuffed (*A. cyanogaster*) or damaged specimens, it was not possible to include all name-bearing types in the statistical analyses. All measurements were taken with a dial calliper to the nearest 0.01 mm, and, where necessary, under a stereomicroscope.

Material from the collections of the following institutes were used: The Natural History Museum (BMNH), London, UK; California Academy of Sciences (CAS), San Francisco, CA, USA; Museum of Comparative Zoology (MCZ), Harvard University, Cambridge, MA, USA; Naturhistorisches Museum (NHMW), Wien, Austria; Natural History Museum of Zimbabwe (NMZB), Bulawayo, Zimbabwe; Port Elizabeth Museum (PEM), Bayworld, South Africa; Philipp Wagner Private Collection (PW), Westbevern, Germany; Senckenberg Museum (SMF), Frankfurt, Germany; University of Texas at El Paso (UTEP), El Paso, TX, USA; Zoologisches Forschungsmuseum A. Koenig (ZFMK), Bonn,

Germany; Museum für Naturkunde (ZMB), Berlin, Germany; Zoologische Staatssammlung (ZSM), München, Germany.

### **Statistical morphological analysis**

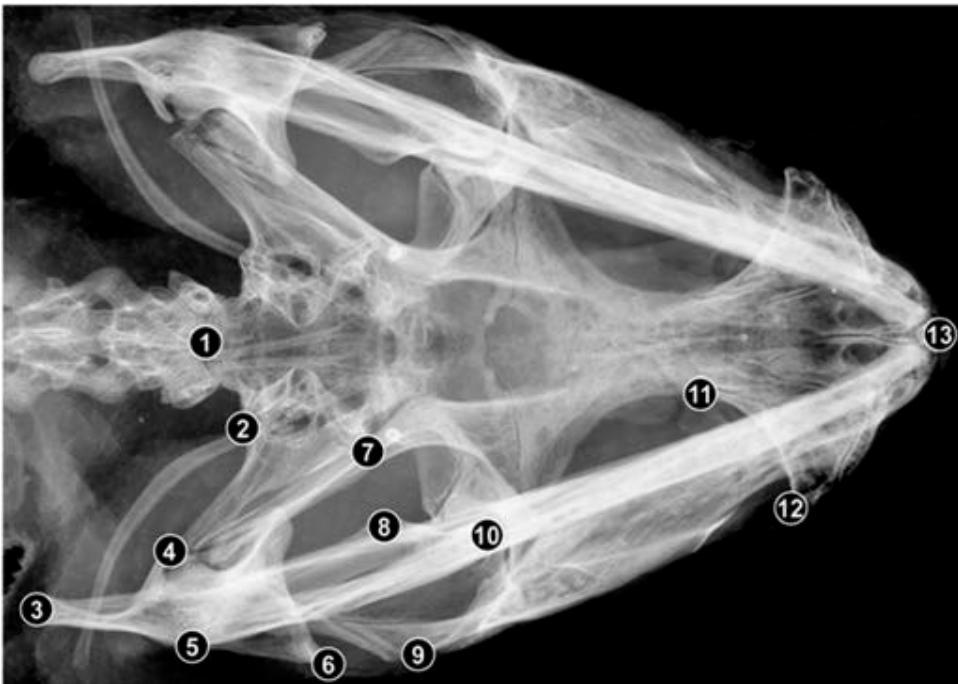
Principal component analysis (PCA) were performed with a correlation matrix to evaluate 19 mensural, 20 meristic, 12 qualitative, 17 ratio and nine selected morphological characters (see Table 1 for details) using the program PAST v.2.12 (Hammer et al. 2001). Characters that were identical or not evaluated in all specimens were excluded from analysis. For statistical analysis, mensural, meristic, and qualitative characters were size corrected and log-transformed to ensure normality (Burbrink 2001), and violations of non-independence in the PCA were avoided by taking measurements only from the left side of the body (Manly 1994). Preliminary analyses did show differences between sexes (data not shown), therefore only male specimens were statistically analysed.

### **Geometric morphometrics**

Undamaged specimens of the following taxa were examined for geometric morphometrics: *Acanthocercus adramitanus* ( $m = 10, f = 3$ ), *A. a. atricollis* ( $m = 10, f = 2$ ), *A. a. loveridgei* ( $m = 7, f = 2$ ), *A. a. ugandaensis* ( $m = 19, f = 13$ ) and *A. yemenensis* ( $m = 9, f = 6$ ). High resolution X-ray images of the skull were taken with a Faxitron LX60 Closed Cabinet (Tucson, USA). To ensure an equal orientation of all specimens, the mouth was aligned to a horizontal structure within the X-ray cabinet. Specimens were then X-rayed and homologous distances were measured and compared on both sides of the skull to make sure that the skull was not tilted. If any tilting was evident, the specimen was adjusted and the process repeated until a satisfactory image could be captured. Imagestacks were created using the program tpsUtil (Rohlf 2006a), and 13 homologous landmarks (Figure 2) were placed with the program tpsDig (Rohlf 2006b), following the criteria proposed by Zelditch et al. (2004). The landmarks were selected, to the extent possible, to cover the general shape of the skull. To increase the sample size, only one side of the skull was landmarked, as a high number of specimens had damage limited to one side only. Coordinate data were transformed to PAST-format, with the GMTP version 2.1 software (Taravati 2010). All further data transformations and analyses were performed in PAST (Hammer et al. 2001). A procrustes superimposition was calculated for the landmark configurations to remove effects of rotation, size and scale from the dataset, leaving only information about the shape for further analyses. Due to the limited sample size, only two taxa have been tested for sexual dimorphism: *A. a. ugandaensis* ( $m = 19, f = 13$ ) and *A. yemenensis* ( $m = 9, f = 6$ ). To remove potential noise caused by uninformative data, the individual residuals from the procrustes superimposition for all principle components (PCs) explaining  $\geq 0.05\%$  of the total variance within each species, were sorted by sex to perform a *t*-test for each PC. The null-hypothesis that both sexes have an equal mean shape was rejected at *p*-score of  $\leq 0.05\%$ . For all PCs, for which the null-hypothesis could be significantly rejected, visualizations of the described shape deformation and box-plots were computed. Due to the evident sexual dimorphism in the skull shape of the tested taxa, all further analyses were restricted to comparisons of males only. PCs explaining more than 5% of the total variance were compared pairwise in a scatter diagram to identify any disparities. Furthermore, a MANOVA was carried out with the specimens grouped by species. The level of constraint was set to 4 (Hammer

**Table 1.** Morphological characters (19 mensural, 27 meristic, 26 qualitative, 20 ratio and nine selected) used for the principal component analysis (PCA).

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)
TOT	Total length
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 at the angle of jaw
HH	Head height, maximum head height at angle of jaw
SEL	Snout–eye length, from snout tip to anterior margin of eye
EEL	Eye–ear length, from posterior margin of the eye to anterior margin of ear
ER	Eye length diameter, maximum horizontal eye diameter
EAR	Ear length, maximum horizontal ear diameter
SAL	Snout–arm length, from snout to anterior insertion 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
<b>Meristic characters</b>	
RPP	Number of rows of precloacal pores
PP	Total number of precloacal pores
SL	Number of supralabial scales
IL	Number of infralabial scales
NCR	Number of scales on the canthus between nasal scale and eye
SO	Number of scales on the canthus above the eye
CR	Number of scales on the canthus
NCS	Number of neck crest scales
T	Temporal scales between eye and ear
TCS	Number of tail crest scales
SaA	Anterior dorsal scale rows, counted transversely behind forelimbs
SaH	Posterior dorsal scale rows, counted transversely just at anterior insertion 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	Ventral scale numbers, counted longitudinally from shoulders to cloaca
CAS1-2	Caudal scales, counted around the tail at 10th and 15th scale row of the tail
Fi1-5	Subdigital lamellae of fingers 1–5
TOE1-5	Subdigital lamellae of toes 1–5
SRW1-3	Number of scale rings per whorl; anterior part dorsal (1), lateral (2), ventral (3)
SRW1_1-3	Number of scale rings per whorl; at midtail dorsal (1), lateral (2), ventral (3)
<b>Qualitative characters*</b>	
RPP	Row of cloacal pores continuous or not continuous
VFS	Vertebral scales large, same size or smaller than the scales on the flanks
DMS	Dorsal matrix scales absent, keeled, feebly keeled or smooth
FS	Flank scales keeled, feebly keeled or smooth
GS	Gular scales keeled, feebly keeled or smooth
UTS	Upper tail scales keeled, feebly keeled or smooth
LTS	Lower tail scales keeled, feebly keeled or smooth
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
AS	' <i>annectans</i> ' scale type present or absent
<b>Ratios</b>	
1–17	PP/RPP; TL/SVL; TL/TOT; TL/TH; TW/TH; HL/SVL; HL/HW; HW/HH; SEL/EEL; ER/EAR; SAL/AGD; AGD/TOT; HUL/RUL; FL/TFL; HUL+RUL/FL+TFL; SVL/FL+TFL; FL+TFL/TOL.



**Figure 2.** Overview of the 13 homologous landmarks used for the analysis.

2012). A Wilkins' lambda test was computed first, and if  $p$  was significant ( $\leq 0.05\%$ ) a pair wise Hotelling's T-squared statistic test was performed. The same was done with a principle components analysis combining taxa of both genera.

### **Molecular data**

A total of 42 specimens of *Acanthocercus atricollis* were included from the following countries: Botswana (1), DRC (12), Ethiopia (2), Kenya (4), Mozambique (3), Rwanda (3), South Africa (1), Tanzania (4), Uganda (4), and Zambia (8) (Table 2). Three other species were selected as outgroups, including *Acanthocercus annectens*, *A. cyanogaster*, and *Xenagama wilmsi* (Table 2). DNA was extracted with Qiagen DNeasy extraction kits (Qiagen). We PCR amplified a portion of the 16S rRNA (16S) mitochondrial DNA (mtDNA, Hilden, Germany) gene using primers and procedures from Leaché et al. (2009, 2017). DNA sequences were collected on an ABI 3730 or 3130xl automated sequencer with Big-Dye Terminator v. 3.1 (ABI, Waltham, USA). All sequences are deposited in GenBank (for accession numbers see Table 2). Complementary sequences were combined using Sequencher v4.8 (Gene Codes, Ann Arbor, USA). Multiple sequence alignments were generated using Muscle v3.6 (Edgar 2004).

### **Phylogenetic analysis**

We estimated the genealogical relationships for the samples using maximum likelihood (ML) and Bayesian inference (BI). ML analyses were conducted using RAXML v8

**Table 2.** Locality and voucher data for specimens included in the genetic analysis.

ID	Taxon	Voucher	Locality	Genbank accession number
BOT1	<i>A. a. atricollis</i>	ZFMK 41748	Botswana, Gabane	GU133322.1
DRC1	<i>A. a. kiwuensis</i>	UTEP 20389	DRC, Orientale, Bunia, 1248 m	MG837486
DRC2	<i>A. a. kiwuensis</i>	UTEP 20390	DRC, Orientale, Epulu (Ituri Forest), ca. 740 m	MG837487
DRC3	<i>A. a. kiwuensis</i>	UTEP 20388, UTEP 20363	DRC, North Kivu, Virguna National Park, Ndjuma lowland forest, 728 m	JX668131.1, MG837484
DRC4	<i>A. a. kiwuensis</i>	UTEP 20364	DRC, North Kivu, Kisanzi village near Mt. Teye, Ruwenzori Mts. 1702 m	MG837485
DRC5	<i>A. a. kiwuensis</i>	UTEP 20387	DRC, North Kivu, Kabasha escarpment in Virunga National park, 1202 m	MG837481
DRC6	<i>A. a. kiwuensis</i>	UTEP 20386	DRC, North Kivu, road just N of Goma, 1160 m	MG837480
DRC7	<i>A. a. kiwuensis</i>	UTEP 20391	DRC, South Kivu, ca. 100 m W of the shore of Lake Kivu in the village of Isale	MG837482
DRC8	<i>A. aff. atricollis</i>	EBG2167	DRC, South Kivu, road between Fizi and Lulimba, 1194 m	JX668132.1
DRC9	<i>A. branchi</i>	ELI322, ELI327	DRC, Katanga, Manono	MG837495 MG837496
DRC10	<i>A. aff. atricollis</i>	ELI005	DRC, Katanga, Mwaseini, Murungu elevation: 1667 meters above sea level	MG837491
ET1	<i>A. a. minuta</i>	MHNG 2679	Ethiopia, Lake Langano	MG837489
ET2	<i>A. a. loveridgei</i>	ZFMK 15866	Ethiopia, Kamba	MG837499
KE1	<i>A. a. loveridgei</i>	ZFMK 41655	Kenya, Masai Mara National Park	MG837497
KE2	<i>A. a. minuta</i>	PW_KE04.11_182	Kenya, Mt. Kulal	MG837490
KE3	<i>A. a. ugandaensis</i>	ZFMK 81963, ZFMK 81952	Kenya, Kakamega Forest, Buyangu Village	MG837507 MG837508
MOZ1	<i>A. a. atricollis</i>	ZFMK 41917	Mozambique, without further locality	MG837494
MOZ2	<i>A. a. atricollis</i>	ZFMK 41918	Mozambique, without further locality	MG837493
MOZ3	<i>A. a. atricollis</i>	MVZ 265804	Mozambique, Maputo	JX668133.1
RW1	<i>A. a. kiwuensis</i>	ZFMK 88200	Rwanda, Kibuye	MG837483
RW2	<i>A. a. loveridgei</i>	ZFMK 61662	Rwanda, Nasho	JX668134.1
RW3	<i>A. a. loveridgei</i>	ZFMK 61644	Rwanda, Mpanga	MG837498
SA1	<i>A. a. atricollis</i>	ZFMK 29397	South Africa, Durban	MG837492
TZ1	<i>A. a. loveridgei</i>	PEM 18898, PEM 18899	Tanzania, Serengeti, 6 km N of main Oldovai River, 8km N Maasai Village, and 32km N of Olobalol at bottom of N slopes of Ngorogoro foothills	MG837500 MG837501
TZ2	<i>A. a. ugandaensis</i>	JB41, JB42	Tanzania, Mount Meru	MG837504 MG837505
UG1	<i>A. a. kiwuensis</i>	CAS 201726, CAS 201727	Uganda, Rukungiri Dist., Byumba	GU128463.1, JX668130.1
UG2	<i>A. a. kiwuensis</i>	ZFMK 70546	Uganda, Kampala	MG837488
UG3	<i>A. a. ugandaensis</i>	PW_KE04.11_287	Uganda, Budongo	MG837506
ZA1	<i>A. cyanocephalus</i>	Z17, Z34	Zambia, Kalumbila	MG837509 MG837510
ZA2	<i>A. cyanocephalus</i>	ZFMK 88491, HF235_SN152, HF170_SN91, HF170_SN92	Zambia, Mwinilunga District, Ikelenge	MG837511 MG837512 MG837513 MG837514
ZA3	<i>A. branchi</i>	ZFMK 88682	Zambia, Chipata	MG837503
ZA4	<i>A. branchi</i>	ZFMK 88683	Zambia, Lusaka	MG837502
	<i>A. annectans</i>	CAS 227508	Somalia, 3 km N (by Bosasso Rd) of Karin, Lag	MG837516
	<i>A. cyanogaster</i>	MVZ 257928	Ethiopia, Mekelle University, Arid Campus	MG837517
	<i>Xenagama wilmsi</i>	AMCC 105545	Ethiopia, 16 km E Dodola on HWY	MG837515



(Stamatakis 2014). The RAxML analysis implemented the GTR+GAMMA model of nucleotide substitution. We used automatic bootstrapping for inferring confidence values on the branches of the gene tree using the extended majority rules method (Pattengale et al. 2009). BI was conducted with MrBayes v3.2.3 (Ronquist et al. 2012) with the GTR + I +  $\Gamma$  model. We ran two concurrent chains for 10 million generations each, logging every 1000 steps. The prior for branch lengths was unconstrained (exponential = 50), which sets a mean branch length prior = 0.02. We assessed convergence by comparing the two separate runs using the average standard deviation of split frequencies and the average potential scale reduction factor.

### **Species delimitation**

We conducted species delimitation tests using the general mixed Yule coalescent (GMYC; Pons et al. 2006) method. The GMYC estimates the number of species within a clade using a gene tree as the primary input. Using an ultrametric tree for a single locus, the GMYC identifies the point at which a Yule speciation process is replaced by a coalescent tree prior, which indicates the switch between the species and population level (Pons et al. 2006).

We conducted GMYC analyses using a Bayesian implementation called the bGMYC (Reid and Carstens 2012). The bGMYC differs from the traditional maximum likelihood implementation by taking phylogenetic uncertainty into account during the analysis. This is accomplished by sampling from a posterior distribution of gene trees. We estimated an ultrametric tree for the mtDNA data using BEAST v1.8.0 (Drummond et al. 2012). We assumed a Yule process speciation prior for the tree, and a strict clock for the rate of substitution (set to 1.0). The ploidy level was set to mitochondrial. We conducted two separate MCMC analyses for 10 million generations each, logging every 1000 steps. Convergence was assessed by inspecting burn-in plots for parameters using Tracer v1.6 (Rambaut and Drummond 2007), and by checking that the effective sample size of each parameter exceeded 200. Posterior probability values were obtained by summarizing the posterior distribution of trees (post burn-in) using TreeAnnotator (Bouckaert et al. 2014), which were mapped onto the maximum clade credibility (MCC) tree.

We ran the bGMYC analyses for 50,000 generations (sampling interval of 20) with a burn-in period of 1000. We set the minimum number of expected species at four (our analyses included three outgroup species and *Acanthocercus atricollis*), and we varied the maximum number of species from eight to 45 to quantify the sensitivity of the analysis to the species max prior. We summarized the bGMYC results using a sequence-by-sequence matrix that colours shared cells by the posterior probability that the corresponding sequences are conspecific (0 = separate species; 1 = conspecific). The results were mapped onto the MCC mtDNA gene tree.

## **Results**

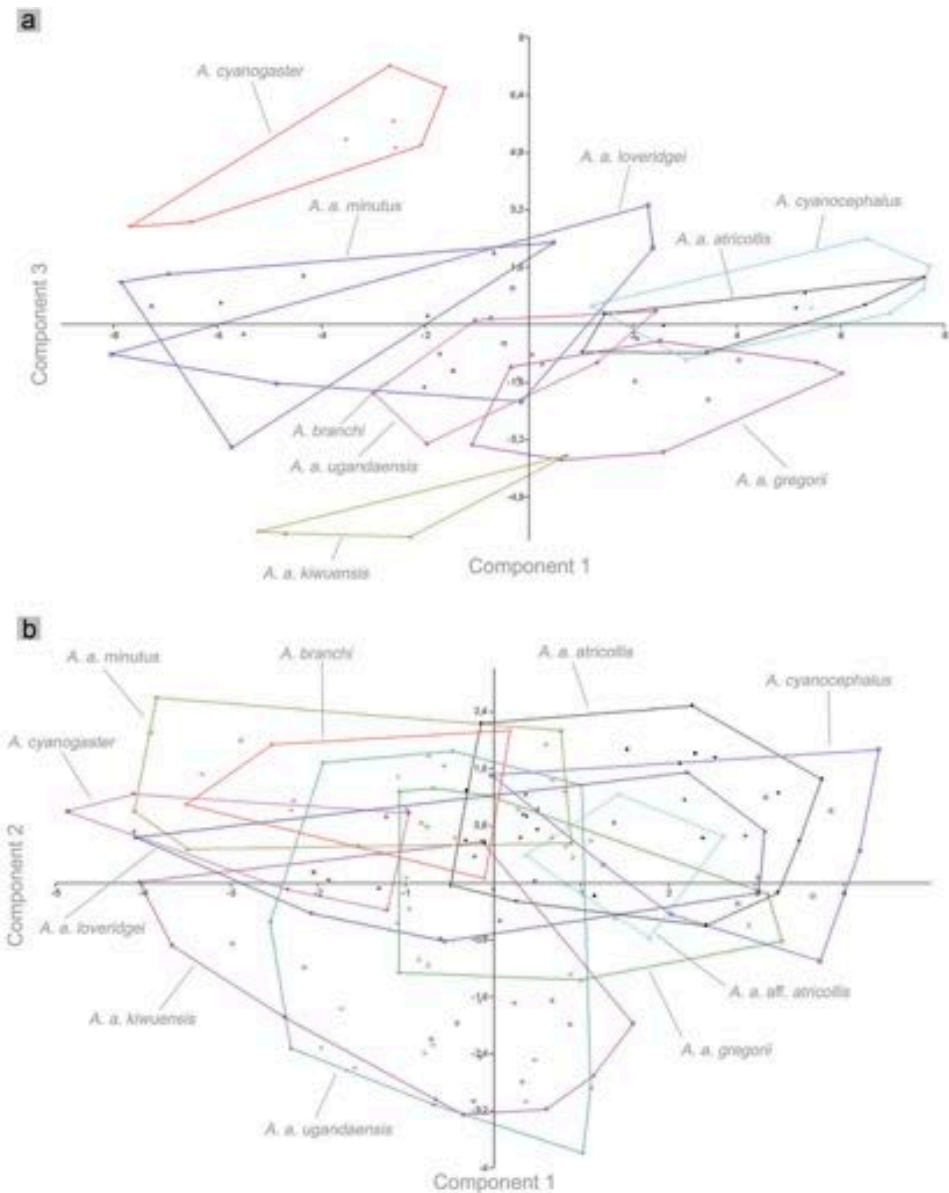
### **Morphology**

The longest (snout–vent length; SVL) taxa are *A. cyanocephalus*, *A. a. atricollis*, and *A. aff. atricollis*, whereas the smallest are *A. branchi*, *A. a. minuta* and *A. a. ugandaensis* (Supplemental Figure 1A). The longest tails can be found in *A. cyanocephalus*, *A. a. kiwuensis*

and *A. a. ugandaensis*; the shortest tails in *A. a. gregorii* and *A. a. branchi* (Supplemental Figure 1B). However, in relation to SVL, *A. a. kiwuensis* and *A. a. ugandaensis* have distinctly long tails (Supplemental Figure 1C). Compared with SVL, *A. a. minuta* has the broadest head, whereas *A. a. branchi* and *A. a. kiwuensis* have the most slender ones. Two subadult specimens (*A. aff. atricollis*) were placed on a dubious position by the molecular analyses (Figure 7). Therefore, those specimens were included by exception into the morphological analyses to prove a correct identification. The narrow head of *A. aff. atricollis* can be explained by the subadult age of the specimens, which do not exhibit the typical broad head of dominant adult males. According to our results, a correct identification of the specimens is not possible and we therefore place them as affinity to *A. atricollis*. The number of scale rows around midbody is overlapping in many taxa, with *A. a. atricollis* and *A. a. loveridgei* having the highest maximum numbers, and *A. a. kiwuensis* and *A. a. ugandaensis* having the lowest minimum numbers (Supplemental Figure 1E). The highest average counts are in *A. a. atricollis*, *A. a. gregorii*, *A. a. loveridgei* and *A. a. minuta*, whereas *A. a. kiwuensis* and *A. a. ugandaensis* have the lowest (Supplemental Figure 1E). The highest ranges are found in *A. a. atricollis*, *A. a. cyanocephalus*, *A. a. kiwuensis*, and *A. a. ugandaensis*. The highest average of longitudinal rows is found in *A. a. atricollis*, *A. a. branchi*, *A. a. loveridgei* and *A. aff. atricollis*, while the lowest is again in *A. a. kiwuensis* and *A. a. ugandaensis* (Supplemental Figure 1F). In general, all taxa have heterogeneous scalation, but are distinct in size, arrangement and density of the enlarged dorsal body scales. However, because in some taxa sexual dimorphism was recognized in these characters only adult males were used to distinguish and identify the taxa by these characters (see taxa accounts). The largest enlarged and undirected (not arranged in rows) scales can be found in *A. a. loveridgei* and *A. a. branchi*, the smallest in *A. a. minutus* and *A. a. atricollis* and the sole taxon with directed enlarged scales is *A. a. gregorii*. On the other hand taxa without scattered enlarged scales, like *A. a. ugandaensis*, have a uniform vertebral area consisting of enlarged scales only, but the similar *A. a. kiwuensis* has a vertebral area dominated by small matrix scales between the enlarged scales. Other details of the morphology are given in the respective species accounts (see below).

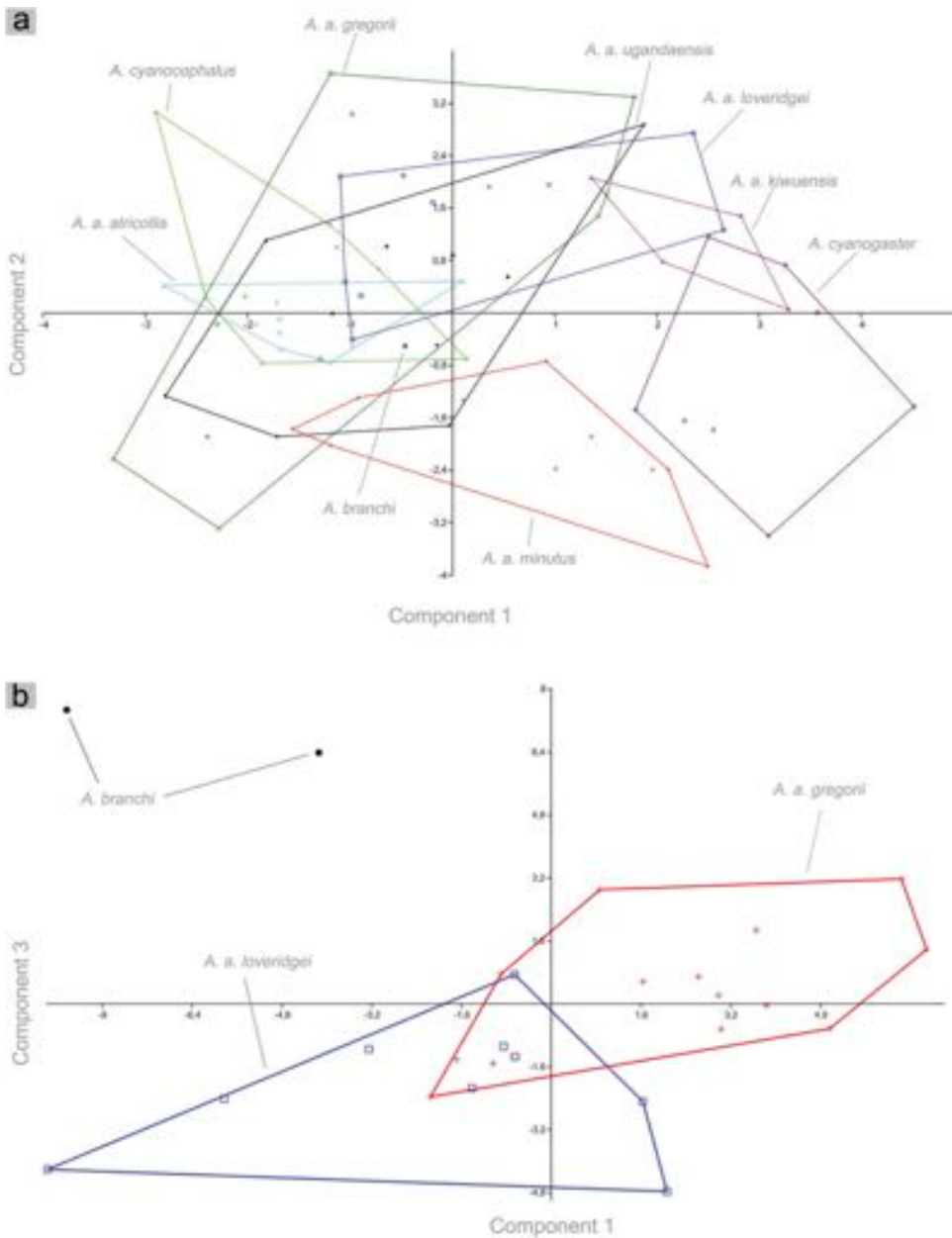
The PCA analyses were conducted on datasets including all *A. atricollis* group taxa as well as *A. cyanogaster*, the type species of the genus, as an outgroup. Generally, PCA analyses of mensural, meristic, quantitative and ratio values data do not show any specific partitioning and all different *A. atricollis* group taxa cluster together, often including *A. cyanogaster* as well.

In the first PCA of 60 characters (mensural, meristic, quantitative characters) for 70 specimens (Figure 3(a)), axes one and three explain 40.49% of the variance in the dataset (PC1: 28.89%; PC3 11.6%). This comparison yields a cluster of *A. cyanogaster* on one side and an overlapping cluster of all *A. atricollis* taxa on the other side. Within the latter cluster, *A. a. kiwuensis* is weakly differentiated from the remaining taxa, whereas *A. a. atricollis*, *A. a. loveridgei*, *A. a. gregorii*, *A. a. ugandaensis* and *A. a. cyanocephalus* cluster together and *A. a. minutus* is distinct from this cluster, only overlapping with *A. a. loveridgei*. The greatest intraspecific variation is exhibited by these last two taxa. Characters with the heaviest loading are SVL, HL, HH, SAL, RUL (PC1) and RPP, PP, CAS\_1, CAS\_2 (PC3), respectively. The first two axes explain 43.1% of the variance in the dataset (PC1: 28.89%; PC2: 14.21%), but do not show a separation of the taxa (see Table 1 for abbreviations).



**Figure 3.** (a) PCA of 60 characters (mensural, meristic, quantitative characters) for 70 specimens. (b) PCA of nine selected characters (SVL, TL, HL, HW, HH, SAM, D, V, PP) for 154 specimens. (Abbreviations are given in Table 1).

However, the pattern from the first PCA is not recognizable in the second PCA analysis (Figure 3(b)) in which all taxa form a single large cluster. Here, the PCA was done using nine selected characters (SVL, TL, HL, HW, HH, SAM, D, V, PP) for 154 specimens (Figure 3(b)). Plotting PC1 against PC2 shows an overlap of all taxa, including *A. cyanogaster*. The first two axes explain 71.86% of the variance in the dataset (PC1: 48.35%; PC2 23.51%).



**Figure 4.** (a) PCA of 16 ratio values of mensural data of 70 specimens. (b) PCA of 16 ratio values of mensural data of the cryptic taxa *A. branchi*, *A. a. gregorii* and *A. a. loveridgei*.

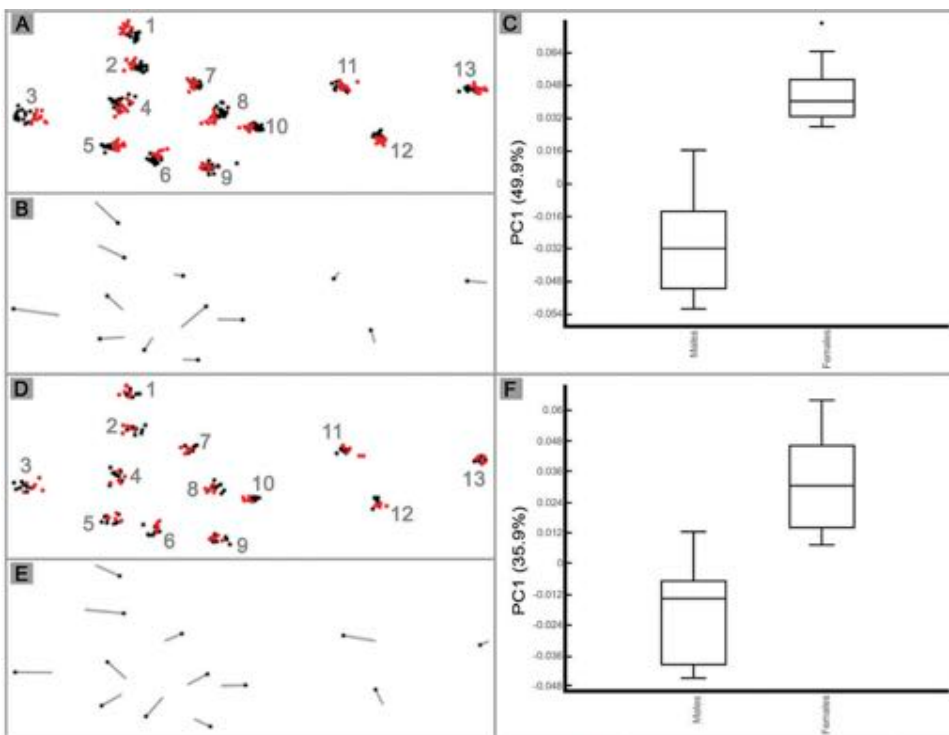
A third PCA analysis (Figure 4(a)) again shows *A. cyanogaster* and *A. a. minutus* somewhat distinct from a cluster containing all other taxa. For this analysis mensural data were used as 17 ratio values (see Table 1) for 70 specimens. The first two axes explain 40.79% of the variance in the dataset (PC1: 22.61%; PC2: 18.18%) and the comparison of PC1 against PC2 shows an overlap of all *A. atricollis* group taxa including the outgroup taxon, *A. cyanogaster*. Main loadings of ratio values are PC1: TL/TH, SEL/EEL

and PC2: TL/SVL, TL/TOTAL. Axes one and three explain 36.31% of the variance in the dataset (PC1: 22.61%; PC3: 13.7%) and show nearly the same clustering. However, in all analyses the taxa show high intraspecific variation.

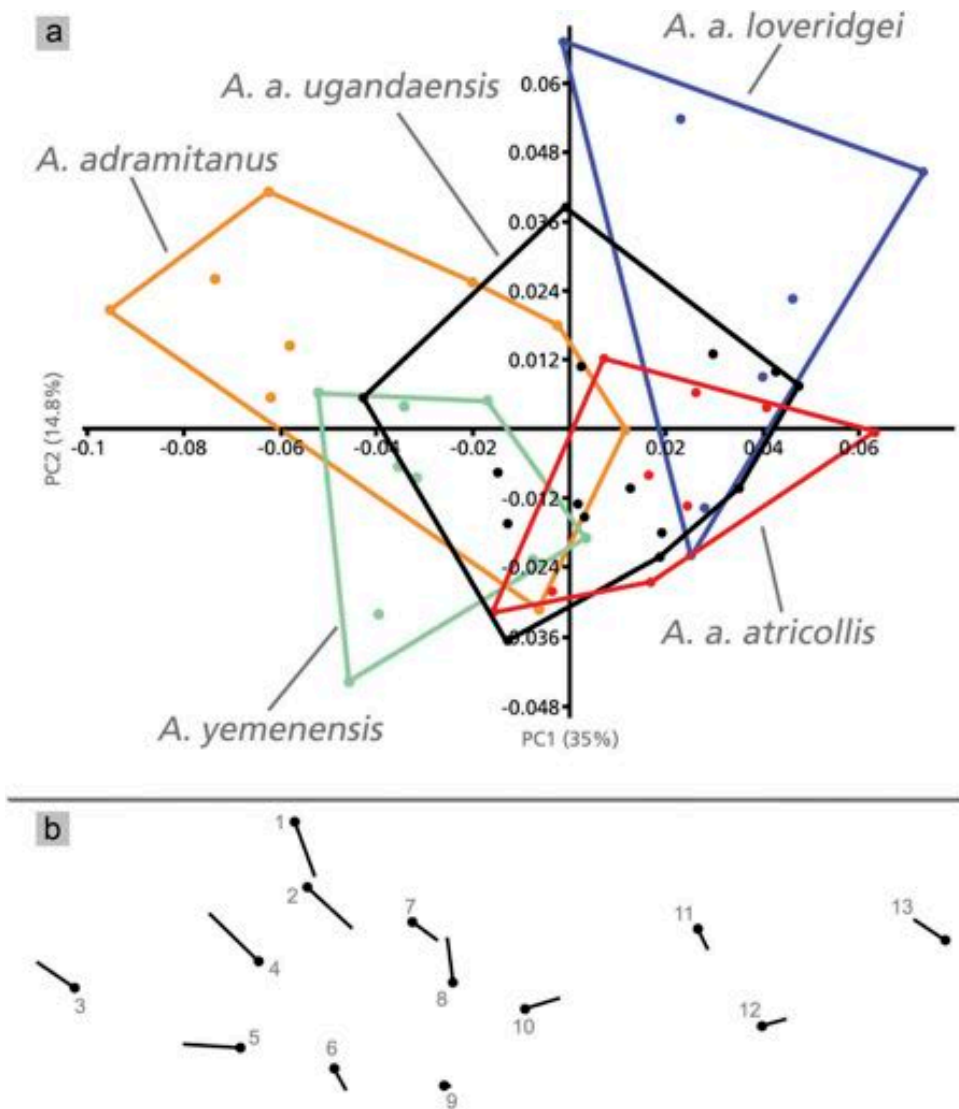
To analyse the status of the morphologically cryptic taxa *A. branchi*, *A. a. gregorii* and *A. a. loveridgei* a fourth PCA was conducted only using these taxa (Figure 4(b)). Here, the first and third axes explain 42.8% of the variance in the dataset (PC1: 28.82%; PC3: 13.98%) and the comparison shows that the morphospaces of *A. a. gregorii* and *A. a. loveridgei* overlap, whereas *A. branchi* is distinct, but the lack of more specimens of this taxon may cause a bias here. Main loadings of ratio values are PC1: SVL, HL and PC3: RPP, VFS, DMS, FS. Axes one and two explain 46.37% of the variance in the dataset (PC1: 28.82%; PC2: 17.55%, main loadings are Fi3, SRW1, SRW2) and show the same clustering.

### Geometric morphometrics

Evidence for sexual dimorphism in skull morphology was found in all taxa tested. A tendency for the grouping of the two sexes can be already recognized in the landmark plots (Figure 5(a), 5(d)), but it is more evident, among the tested taxa, in *A. a. ugandaensis* (Figure 5(a)), than in *A. yemenensis* (Figure 5(d)). Most individual landmarks congregate together, but some outliers can also be recognized, e.g. landmarks 9 and



**Figure 5.** Plots of landmarks following procrustes superimposition (red: females, black: males), visualizations of the deformation from the mean shape (vector length is proportional to contribution to total differentiation) and box-plots displaying the significant variation between sexes in PC1 (Supplemental Table 1): (a–c) *Acanthocercus ugandaensis*; (d–f) *Acanthocercus yemenensis*.



**Figure 6.** (a) Scatter plots of PC1 against PC2 with convex hulls. *Acanthocercus*: *adramitanus* (green), *A. a. atricollis* (red), *A. a. loveridgei* (blue), *A. a. ugandaensis* (black) and *A. yemenensis* (pink). (b) Visualizations of the deformation from the mean shape (vector length is proportional to contribution to total differentiation): *Acanthocercus* taxa, PC1 (35%).

11 of *A. a. ugandaensis* (Figure 6(a)); landmarks 3, 6 and 11 in *A. yemenensis* (Figure 5(d)). The total variance of sexual skull dimorphism is explained in *A. a. ugandaensis* by 26 PCs (the first five explain  $\geq 5\%$ ) and 82.3% total variance explained by the first five PCs versus 14 PCs in *A. yemenensis* (the first five explain  $\geq 5\%$ ) and 87.5% total variance explained by the first five PCs (Supplemental Table 1). In both taxa, it is only the first PC for which the null hypothesis can be rejected with significant support (Supplemental Table 2). The deformation from the mean skull shape, as explained by PC1, is visualized in Figure 5(b), 5(e) and shows the major variation in the relative length and width of the skull

(especially in posterior regions). This is supported by the vectors related to landmarks 1, 2 and 3, which are among the longest. If this is compared with the landmark plots (Figure 5(a), 5(d)) it is obvious that males generally have a more posterior placement of landmark 3, relative to landmark 1. Therefore, they possess a longer posterior jaw while females have a shorter and wider posterior jaw, which is supported by the more anterior placement of landmark 3 compared to the males and by the grouping of females above the males in landmark 1. Variation in length is greatest in the posterior parts of the jaw, but is also evident in the hinge region (landmarks 4, 5 and 6). Both taxa show an additional narrowing in females, but this is more pronounced in *A. yemenensis* (Figure 5(e)) than in *A. a. ugandaensis*. Some variation can be recognized in the width of the skull dorsum, supported by slight angles of the vectors from landmarks 1, 2 and 7, as well as in the anterior regions of the skull, supported by landmarks 11, 12 and 13. However, in *A. a. ugandaensis* it is mainly limited to a widening of the preorbital region (landmark 11 and 12; Figure 5(b)), whereas in *A. yemenensis* the greatest variation in the area is the shortening of the anterior skull, supported by the long anterior directed vector of landmark 11 (Figure 5(e)). The significant difference between the sexes can clearly be recognized in the box-plots (Figure 5(c), 5(f); Supplemental Table 2). There is no overlap in *A. a. ugandaensis* (Figure 5(c)), and just a slight overlap of the maximum values of males and the minimum of females in *A. yemenensis* (Figure 5(f)).

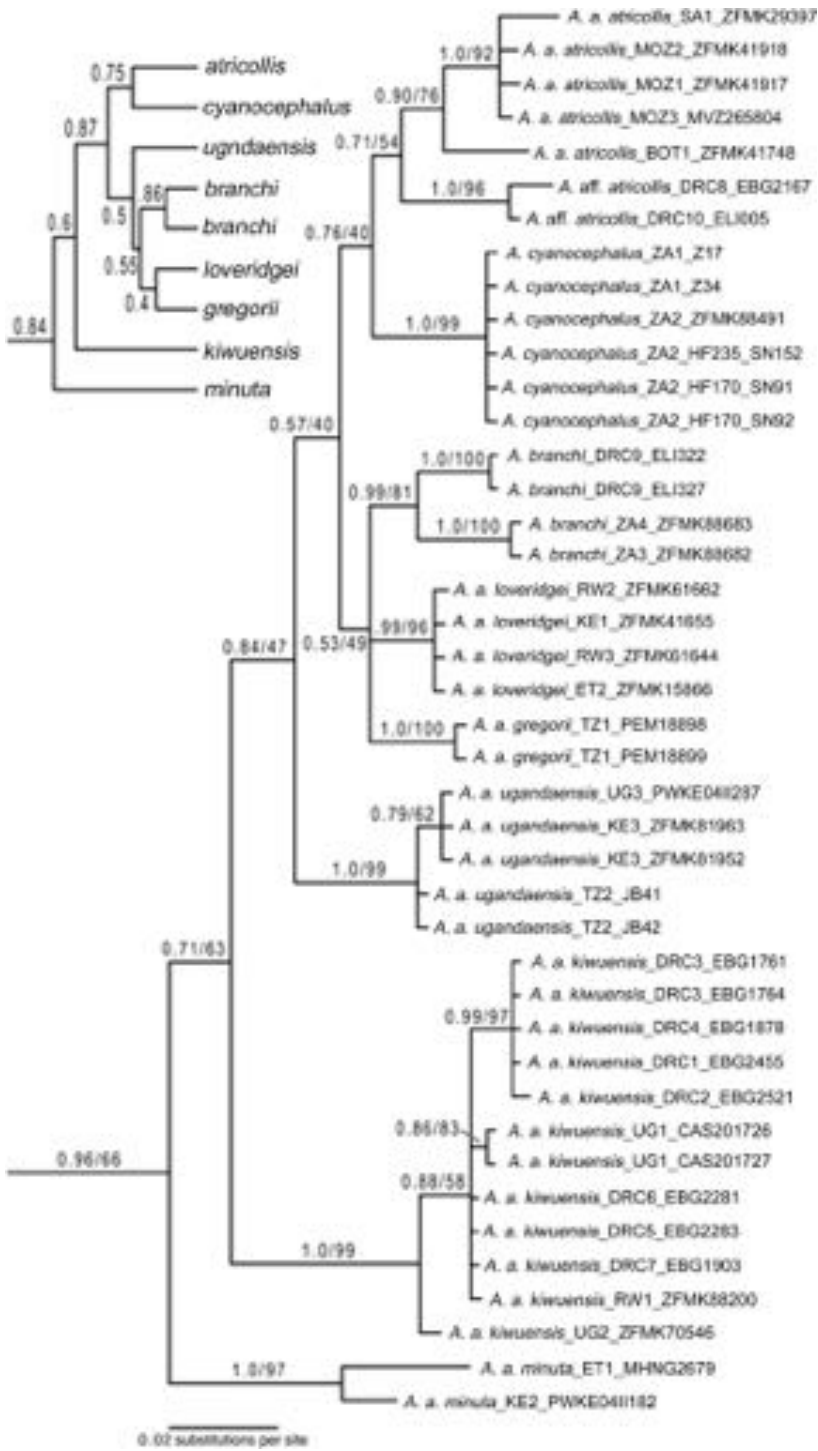
Interspecific comparison within *Acanthocercus* taxa results in no clear differences between or unique grouping of taxa. There is a slight tendency for *A. adramitanus* and *A. yemenensis* to group separately from all others, but there is always overlap with one or more of the other taxa (Figure 6(a)). A MANOVA resulted in a significant Wilks' lambda  $p$ -score ( $p = 4.098$ ). The pairwise comparison, with Hotelling's T-squared distribution, failed in all species pairs except for *A. a. ugandaensis* against *A. a. atricollis*, *A. adramitanus* and *A. yemenensis*, respectively. Only the comparison against *A. adramitanus* yielded a significant result of  $p = 0.0065$ . The greatest variation can be found with relative width and length of the skull, especially in the posterior regions, but also, to some extent, in the preorbital region (Figure 6(b))

### Gene tree analysis

The multiple sequence alignment included 599 aligned base pairs. ML and BI analyses supported similar topologies, and clades with high posterior probability values ( $\geq 0.95$ ) typically also had strong bootstrap support ( $\geq 70\%$ ) (Figure 7). The earliest divergence in the gene tree leads to *Acanthocercus a. minuta*, followed by *A. a. kiwuensis*, then *A. a. ugandaensis* (Figure 7). However, the topology among these clades is only weakly supported. The remaining samples are split into two clades with weak support, including (1) *A. a. gregorii*, *A. a. loveridgei* and *A. branchi* from the DRC and Zambia; and (2) *A. a. atricollis* and *A. cyanocephalus*. For the position of the outgroups see Supplemental Figure 2.

### Species delimitation

The bGMYC analyses of the 16S gene tree (the MCC tree from the \*BEAST analysis) are shown in Table 3. Our analyses included three outgroup species, and therefore we set



**Figure 7.** Mitochondrial DNA gene tree estimated for *Acanthocercus atricollis* using a portion of the 16S gene. The support for branches from BI and ML are shown on each branch, respectively. The \*BEAST species tree is shown in the top left with posterior probability values on branches.



**Table 3.** The number of species supported by bGMYC analyses of the 16S data.

Prior <sup>2</sup>	Number of species <sup>1</sup>	
	Posterior mean	95% HPD
Uniform [4, 8]	7	5 – 8
Uniform [4, 12]	8	5 – 12
Uniform [4, 16]	14	7 – 16
Uniform [4, 25]	17	10–23
Uniform [4, 45]	17	8 – 23

<sup>1</sup> Includes the three outgroup species.

<sup>2</sup> All values within the range have equal prior probability.

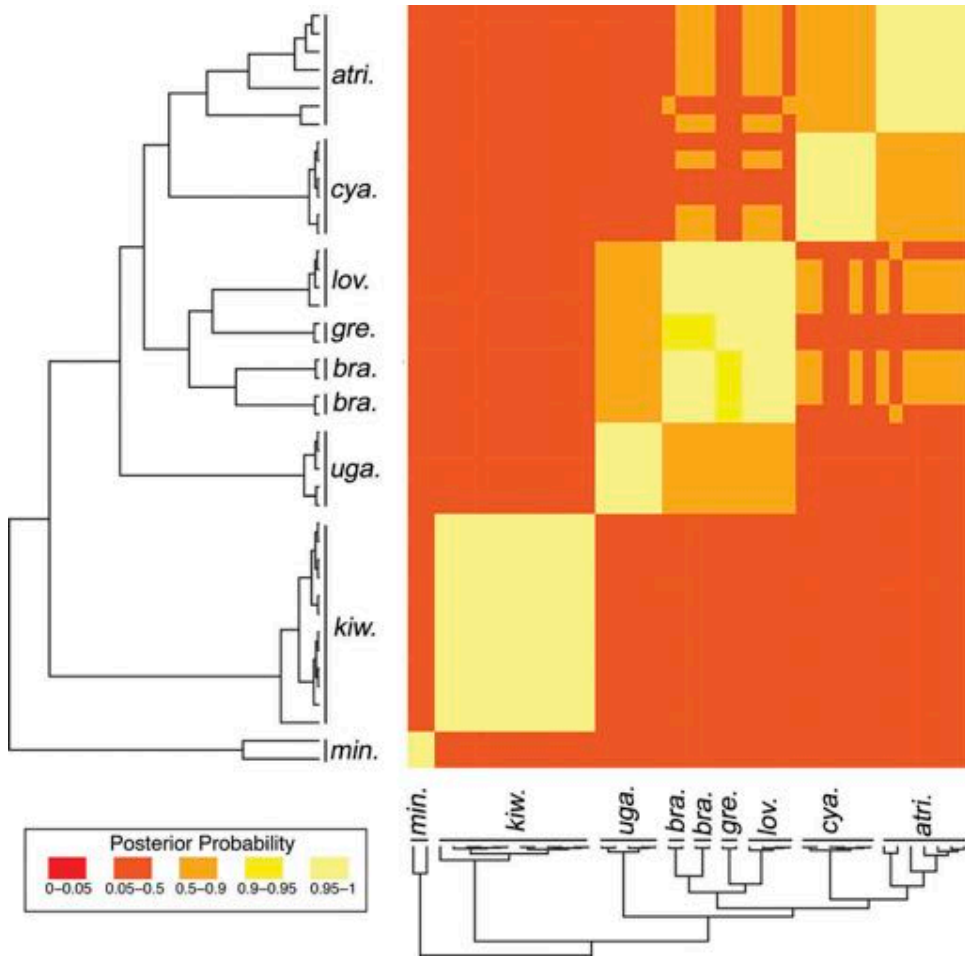
the expectation for the minimum number of species to four. However, we varied the expectation for the maximum number of species from eight to 45 (the maximum number of 16S sequences available). These analyses supported anywhere from three to 13 species within *A. atricollis*' (Table 3). We summarized the bGMYC results across 100 gene trees in the posterior distribution of trees from the \*BEAST analysis using a sequence-by-sequence matrix for the analysis that assumed a maximum of eight species. The bGMYC provides strong posterior probability > 0.90 that samples within the following clades are conspecific: *A. a. minuta*, *A. a. kiwuensis*, *A. a. ugandaensis*, *A. a. atricollis*, *A. a. loveridgei* + *A. a. gregorii*, *A. branchi* and *A. cyanocephalus* (Figure 8).

## Discussion

Lizards in the *Acanthocercus atricollis* complex are among the most conspicuous and frequently encountered lizards in Africa, yet the species complex remains understudied. Klausewitz (1957) produced the first review of the taxonomic status of the species and differentiated several subspecies chiefly using data on body proportions, scalation characters, and to a lesser extent, colour patterns. The species complex is of high interest for zoogeographical studies of the African eastern arid corridor in historic and recent times. Zoogeographical studies require a precise understanding of taxonomy and phylogenetic history, and the new data presented here provides a framework for more rigorous zoogeographical research in this part of sub-Saharan Africa.

The morphological analyses suggest that most taxa are overlapping in morphospace and only *Acanthocercus cyanogaster* (type species of the genus) and *A. a. kiwuensis* are somewhat distinct from the complex. Moreover, it seems obvious that using a more comprehensive dataset of characters seems to be a better method for distinguishing the different taxa, in comparison with selecting a subset of characters generally taken in morphological studies of lizards. However, without the integrative approach that includes genetic data, the morphological analyses alone would be insufficient for differentiating potential evolutionary lineages and resolving the taxonomy of the species complex. Alternatively, a self-standing genetic analysis would reveal lineages, but would require the addition of morphological data to diagnose those lineages.

The morphological characteristics of *Acanthocercus a. minutus* are largely overlapping with *A. a. loveridgei*, whereas *A. a. kiwuensis* is morphologically distinctive and only slightly overlaps with *A. a. gregorii*. The phylogenetic relationships among these species do not reflect these patterns of morphological variation, which would suggest a close relationship between *A. a. minutus* and *A. a. kiwuensis*, and perhaps a close relationship



**Figure 8.** The species delimitation model retrieved a maximum of eight species.

between *A. a. kiwuensis* and *A. a. gregorii*. Among the complex of three closely related taxa, *A. a. gregorii*, *A. a. loveridgei* and *A. branchi*, the first two are strongly overlapping in morphospace, whereas the last is quite distinct. The morphospaces of the African *A. a. atricollis*, *A. a. loveridgei* and *A. a. ugandaensis* and the Arabian *A. adramitanus* and *A. yemenensis* strongly overlap with each other, although the latter two are known to be genetically very distinct from the *A. atricollis* complex (Wagner 2010). Moreover, the morphometric analysis of *Acanthocercus* skulls, although hampered by the low number of specimens with undamaged heads, supports the view of cryptic and highly generalized agamid lizards with a highly conserved anatomy.

The genetic analysis of the 16S mtDNA revealed distinct lineages, although with weak support. This is especially true for the clade including the taxa *A. a. gregorii*, *A. a. loveridgei* and *A. branchi* (Figure 7). The species delimitation model retrieved a maximum of eight species with high support (Figure 8): *A. a. minuta*, *A. a. kiwuensis*, *A. a. ugandaensis*, *A. a. atricollis*, (*A. a. loveridgei* + *A. a. gregorii*), *A. branchi* and *A. cyanocephalus*. Although the analysis was only done with the 16S gene as a single

locus, it gives insight into the genetic structure of the complex. In addition, the species delimitation results are sensitive to the prior expectation for the maximum number of species expected. The gene tree supports the presence of several distinctive lineages in the same geographic region. This includes *A. a. atricollis* and *A. branchi* in the southern Albertine Rift, *A. a. loveridgei* and *A. a. minutus* in southern Ethiopia and *A. a. kiwuensis* and *A. a. loveridgei* in Rwanda and eastern DRC. This supports the view of a species complex composed of at least several sympatric lineages instead of a single highly variable species with clear geographic clustering of allopatric and/or parapatric populations.

Combining these results into an integrative taxonomic approach, several taxa are supported as specifically distinct: *A. a. atricollis*, *A. a. kiwuensis*, *A. a. minuta*, *A. a. ugandaensis* and *A. cyanocephalus*. The clade including *A. a. gregorii*, *A. a. loveridgei* and *A. branchi* is not as well supported at the species rank as are the other taxa, but it is clearly partitioned into two lineages, which is supported by the separation in morphospace of the lineages (*branchi* + *gregorii/loveridgei*) and several other morphological characters. Therefore, we recognize *A. a. gregorii* and *A. branchi* at the species level, whereas *A. a. loveridgei* is here regarded as a synonym of *A. a. gregorii* (see species account). Even though aspects of male coloration are important for the delimitation of agamid lizards (e.g. Boulenger and Power 1921; Wagner 2010) we did not use male coloration in the statistical analyses because precise information about adult male coloration was not available for all specimens and taxa. Furthermore, many characters, e.g. arrangement of scale pattern, found to be useful in distinguishing different taxa, are too subjective to include in statistical analyses. These characters are summarized in the taxon accounts (see below), where they are useful for the diagnosis of species.

The ecological variation within the complex is higher than previously acknowledged. *Acanthocercus atricollis*, recognized as a single species, was thought to be a tree dweller (e.g. Reaney and Whiting 2002), but data from literature and our own observations show that the other taxa are more variable. While *A. atricollis*, *A. ugandaensis*, *A. branchi*, and *A. cyanocephalus* are true tree dwellers (e.g. Reaney and Whiting 2002; pers. obs. P. Wagner), *A. gregorii* (including *A. loveridgei*) has been mentioned as ground living (Günther 1894; pers. obs. P. Wagner), *A. minutus* is a ground and rock dweller (Largen and Spawls 2010; pers. obs. P. Wagner) and *A. kiwuensis* uses both trees and rock substrates (E. Greenbaum pers. obs.).

Klausewitz (1957) suggested allopatric ranges for all taxa and restricted *A. atricollis* to southern Africa, *A. a. loveridgei* mainly to Tanzania, *A. kiwuensis* to Lake Kivu, *A. ugandaensis* to Uganda, *A. gregorii* to coastal East Africa and *A. minutus* to Ethiopia and Kenya. The results of our review reveal a more complex zoogeographic pattern (see distribution maps). Although *A. atricollis* is mainly restricted to southern Africa, two specimens are known from the southern Albertine Rift in the DRC. In this region *A. atricollis* overlaps with *A. cyanocephalus* and *A. branchi* as well as with *A. kiwuensis*, which is much more widespread than previously thought by Klausewitz (1957) and not restricted to Lake Kivu. *Acanthocercus ugandaensis*, previously thought to be restricted to Uganda, overlaps with *A. kiwuensis* in the northern Albertine Rift and with *A. gregorii* in Kenya and northern Tanzania. The latter taxon is the most widespread of the complex ranging from southern Tanzania and extremely northern Mozambique to central Ethiopia. However, *Acanthocercus* is most diverse in the Horn of Africa and two other species occur opposite

in the Arabian Peninsula. Kissling et al. (2016) have shown that in agamid lizards colonization from the Arabian Peninsula, dispersal limitations and arid corridors are the key predictors of present-day species richness. The *A. atricollis* complex shows the typical hour-glass pattern of the arid corridor and present day distribution (see taxon accounts) is obviously consistent with the findings of Kissling et al. (2016).

## Taxonomic revision

Class **REPTILIA** Laurenti, 1768  
 Family **AGAMIDAE** Gray, 1827  
 Genus ***Acanthocercus*** Fitzinger, 1843  
***Acanthocercus atricollis*** (Smith, 1849: 14)  
 (Figure 9)

1849 *Agama atricollis* Smith, Illustrations of the Zoology of South Africa. 3 (Reptiles, Appendix). Smith, Elder and Co., London: 14.

1851 *Stellio capensis* A. Duméril in Duméril & Duméril, Catalogue méthodique de la collection des reptiles du Muséum d'Histoire Naturelle. Paris: 106. Type locality: 'Cap de Bonne-Espérance' [=Cape of Good Hope], South Africa (fide Wermuth 1967).

1866 *Agama nigricollis* Barboza du Bocage (lapsus calami), Lista dos reptis das possessoes portuguezas d'Africa occidental que existem no Museu de Lisboa. Jornal de ciencias mathematicas, physicas, e naturaes, Lisboa 1: 43.

### Lectotype

BMNH 1946.8.28.1 (formerly 1865.5.4.5), from 'Port Natal' [=Durban], South Africa, designated by Klausewitz (1957).

### Taxonomic comments

Denzer et al. (1997) mentioned ZMB 16906 as the syntype of *A. a. atricollis*, and argued that (a) the specimen is topotypical material from the original type series and (b) no lectotype was designated before. First of all, Klausewitz (1957) designated the name-bearing lectotype (BMNH 1946.8.28.1), and therefore the ZMB specimen could only be a paralectotype, not a syntype. Second, the mentioned locality 'Rutenganio' [museum label] obviously refers to a mission station of the 'Herrnhuter Brüdergemeine' founded 1891 in Tanzania ('Deutsch-Ostafrika' at this time and therefore with a close relationship to the Berlin Museum). The station was situated in the Rungwe area in southern Tanzania, directly north of Lake Malawi (see no. 87 in Figure 14) and was often only referred to as 'Herrnhut, Nyasa'. Moreover, the presumed collector Adolf Ferdinand Stolz (1871–1917), a mission trader of the 'Herrnhuter Brüdergemeine' and famous collector of plants and animals (Harms 1918a, 1918b), was born decades after the description of *A. a. atricollis* by Smith (1849). Therefore, ZMB 16906 represents neither a former syntype nor a topotype of *A. atricollis*. However, this specimen still has type status as Klausewitz (1957, p. 163) included it in the paratype series of *A. loveridgei*.

Many authors (e.g. Loveridge 1957; Wermuth 1967) have recognized Bocage (1866) as the author of '*Stellio nigricollis*' but regarded the taxon as a synonym of *A. atricollis*. However,



**Figure 9.** Holotype (BMNH 1946.8.28.1) of *Acanthocercus atricollis*, from 'Port Natal' [=Durban], South Africa.

in his checklist of specimens collected in western Africa and present in the Lisbon collection, Bocage (1866) mentioned the name, but referred to an '*Agama nigricollis*' described by Smith with a type present in the British Museum. Furthermore, he mentioned that he previously thought that these specimens from Angola represented a new species which he meant to name '*St. angolensis*', but Albert Günther (curator at the British Museum at this

time), after an examination of these specimens, suggested them as conspecific with Smith's '*nigricollis*'. For that reason, Bocage declined to describe this form. Though it is mentioned in Bocage (1866), the type specimen of '*Agama nigricollis* Smith' is not present in the collection of the British Museum (C. McCarthy, pers. comm.) and the taxon is neither mentioned by Smith (1849) in the supposed publication of the description, nor by Boulenger (1885) in his catalogue of the specimens in the British Museum. Therefore, it is likely that (a) Bocage misread the letter he got from Günther, as Günther probably wrote *atricollis* rather than *nigricollis*; or (b) Günther intended to write *atricollis* and instead wrote *nigricollis* by mistake. This second theory might fit as *atricollis* is in fact described by Smith (1849) from southern Africa, with the types present in the British Museum, and also the first syllable of both species names, '*atri*' (Latin from *ater*) and '*nigri*' (Latin from *niger*), mean black. Bocage (1895) also recognized this mistake and stated *St. nigricollis* as 'lapsu', without mentioning reasons. On this basis, we also recognize '*St. nigricollis*' as a lapsus calami.

Denzer et al. (1997) mentioned '*Agama (Stellio) Antinorii*' as a name proposed by Peters & Doria in an unpublished type catalogue of the ZMB collection. However, the name was never published.

### Description

A large species with a total length up to 340 mm (SVL: 110–151 mm,  $x = 128.8$  mm,  $n = 12$ ), with the tail comparatively short, only one fourth to one third longer than the SVL. Head broad (particularly in males) and lacking the occipital scale. Nasal scale weakly convex, smooth, situated slightly below the canthus rostralis. Ear openings larger than eyes, tympanum conspicuously exposed. Nuchal crest or tufts of elongated scales absent. Body scales heterogeneous; dorsal matrix scales small, smooth and mucronate; irregularly intermixed with enlarged rhomboidal, mucronate and keeled scales. Vertebral scales larger than those on the flanks, very heterogeneous, larger scales strongly keeled, others smooth to weakly keeled. Body scales in 99–131 scale rows around midbody ( $x = 112.6$ ,  $n = 12$ ) and 52–74 ( $x = 50.5$ ,  $n = 12$ ) along the vertebrate. Gular scales smooth, slightly exposed. Ventral scales small and smooth, larger than the dorsal matrix scales in 76–94 ( $x = 83.2$ ,  $n = 12$ ) rows. Males with usually two continuous rows (2–3,  $x = 2.3$ ,  $n = 12$ ) with a total number of precloacal pores ranging between 10–12 (data from literature) or 15–34 (own data;  $x = 21.8$ ,  $n = 12$ ); absent in females. Scales on the upper surface of the basal part of the tail enlarged, thick and swollen, forming a distinct patch.

In males head, forelimbs and first half of the body blue; second half of the body and hind limbs reddish to yellow. Tail bicoloured, yellow in the proximal half, blue in the distal. Body coloration with a pale vertebral stripe and pale enlarged scales in the blue part, and yellow coloured enlarged scales in the reddish part. Throat of adult males pale to brilliant blue with a dark blue reticulated pattern. Females inconspicuous brownish with small black dots and fine lines. Males, females and even juveniles have a black spot at the shoulders. According to Klausewitz (1957) the body of adult males is dull blue to bluish, with yellow spiny scales, and a yellowish vertebral stripe, whereas Smith (1849) described the colour of the upper head and tail as greenish brown, or yellowish brown, the latter with narrow liver-brown rings. The latter author also mentioned a large black mark on the shoulders and described the upper and lateral parts of the body as intermediate between oil-green and yellowish brown and the throat greenish blue or straw yellow. Gough (1909) mentioned that males, when excited, have bright blue or

green heads and ventral surfaces, while females and juveniles do not appear to show the green or blue tints to the same extent.

### **Distribution**

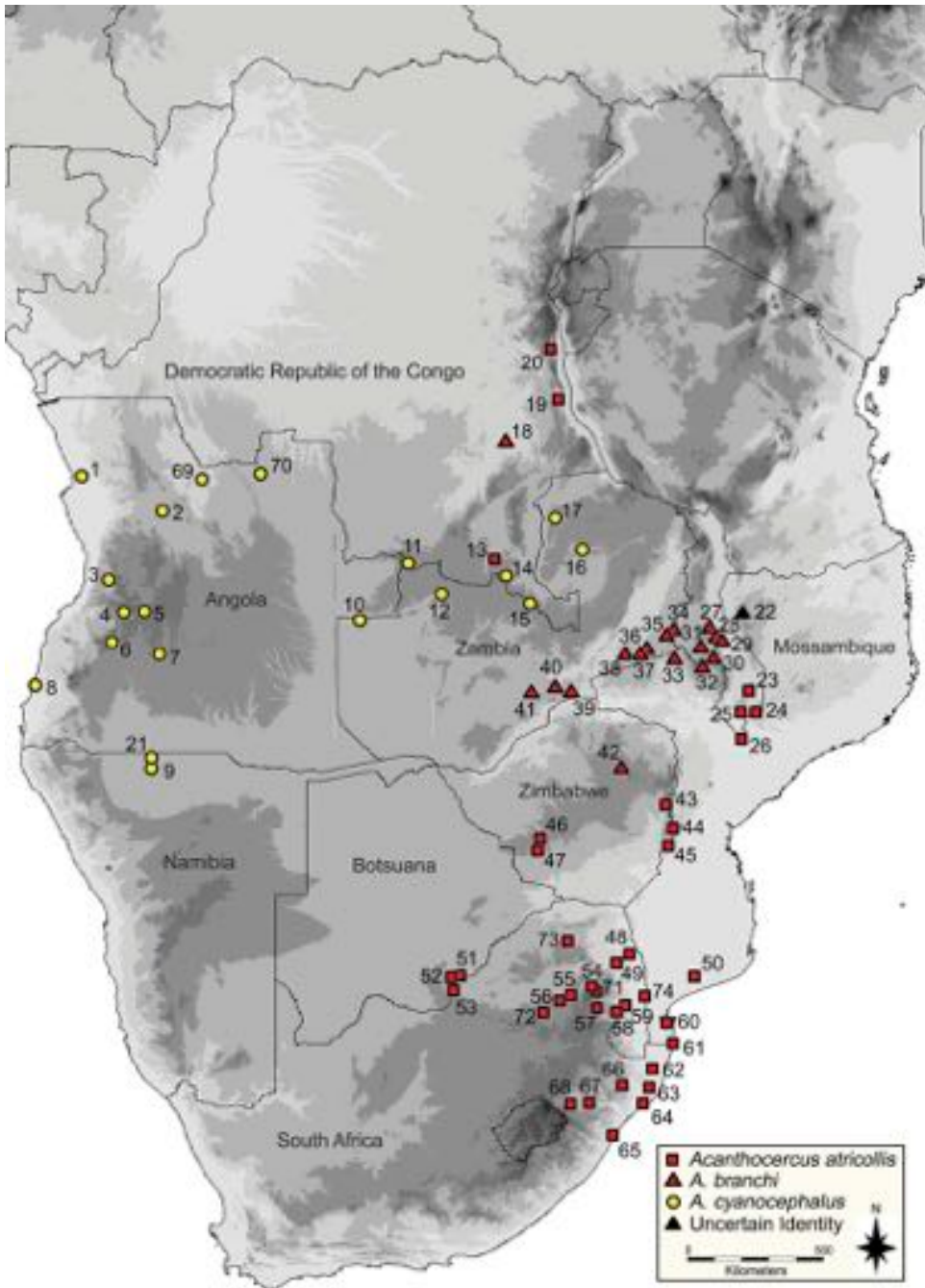
*Acanthocercus atricollis* is restricted to south-eastern Africa. There are confirmed records from South Africa, Swaziland, Botswana, Zimbabwe, Malawi and Mozambique (see [Figure 10](#)). Specimens previously recognized as *A. atricollis* from Namibia and Angola are now referred to *A. cyanocephalus* (see below). The detailed borders of the species' distribution remain unknown. Both [Klausewitz \(1957\)](#) and this study recognize *A. atricollis*-like specimens from south-eastern DRC, which is outside the main distributional range.

### **Habitat**

*Acanthocercus atricollis* is an arboreal lizard. [Gough \(1909\)](#) mentioned that he found the lizards invariably upon trees and that it seems that they take to the ground very unwillingly. According to [Reaney and Whiting \(2003\)](#) it lives in open savannah habitat and prefers thorn trees (46% *Vachellia karroo*), followed by sugarbush (*Protea caffra*) and unspecified dead trees. Their analysis shows that *A. atricollis* prefer trees with greater diameter, canopy cover, incidence of parasitic plants and presence of holes. However, according to the same authors, the last character could be an artefact as there was no significant evidence that the lizard uses holes as refuges or retreat sites. There are no differences in habitat use between the sexes or age classes ([Reaney and Whiting 2003](#)).

### **Ecology**

*A. atricollis* is ecologically the best known species of the complex. It lives in structured colonies of one dominant male and several females ([Reaney and Whiting 2002](#)), but often only few specimens are observed, giving the impression that only a single male with a single female live together, as mentioned e.g. by [Gough \(1909\)](#). Subordinate males are pushed completely out of the male's territory and have to establish their own outside the range of the dominant male (pers. comm. W.B. Branch). [Reaney and Whiting \(2002\)](#) found no differences in diet or foraging behaviour between the sexes. The diet mainly consists of ants and beetles, but grasshoppers also comprise a high proportion of their diet by volume ([Reaney and Whiting 2002](#)). Although generally known as diurnal, *A. atricollis* has also been mentioned as exhibiting some nocturnal activity by [Reaney and Whiting \(2003\)](#) and perches at greater heights at night than in the daytime. Both females and males were observed sleeping exposed on branches, but often under foliage ([Reaney and Whiting 2003](#)). In contrast, [Branch \(1998\)](#) mentioned hollow branches or holes as retreat sites. When chased the lizards slip over to the far side of the branch or to the other side of the trunk of the tree and when captured, they readily offer fight ([Gough 1909](#)). [Smart et al. \(2005\)](#) recorded higher densities of *A. atricollis* in degraded areas than in a nearby conserved area, but found that local residents had a negative perception of tree agamas. However, [Whiting et al. \(2009\)](#) identified *A. atricollis* as anthropophilic species. Even though they are killed by local residents (some indigenous people believe them to be poisonous, see [Gough 1909](#)), the population density in villages was higher than in adjacent disturbed communal rangelands or a nearby undisturbed protected area. The authors suggested three major contributing factors:



**Figure 10.** Distribution of *Acanthocercus atricollis*, *A. branchi* and *A. cyanocephalus*. The numbers refer to the specific localities.

1 = Dande; 2 = Malange; 3 = Mombolo; 4 = Cuma; 5 = Huambo; 6 = Caluquembe [=Kalukembé]; 7 = Capelongo [=Kuvango]; 8 = Namibe [=Mossamedes, Moçâmedes]; 9 = Ondangua; 10 = Chitau; 11 = Ikelenge; 12 = Kalumbila; 13 = Murungu; 14 = Lubumbashi; 15 = Mufulira; 16 = Lake Bangeulu; 17 = Kawambwa; 18 = Manono; 19 = Kalemie; 20 = Fizi; 21 = Oshikango; 22 = Serra Jeci Grasslands; 23 = Zomba Plateau; 24 = Mlanje Mountain; 25 = Cholo Mountain; 26 = Misala; 27 = Nchisi Mountain; 28 = Chitala River; 29 = Salima;



predators occur at a lower density, the primary prey is more abundant, and they may experience less competition for resources (Whiting et al. 2009).

***Acanthocercus branchi* Wagner, Greenbaum and Bauer, 2012b: 22, figs. 1–2a (Figure 11)**

2012 *Acanthocercus branchi* Wagner, Greenbaum & Bauer, A new species of the *Acanthocercus atricollis* complex (Squamata: Agamidae) from Zambia. *Salamandra* 48: 21–30.

**Holotype**

ZFMK 88682, from ‘dense Miombo woodland close to the ZAWA head office near Chipata’, Zambia.

**Description**

A small to medium sized species with a total length up to 313 mm (SVL: 83–131 mm,  $x = 113.2$  mm,  $n = 4$ ), tail short, about 1.4 times longer than SVL (SVL/TL: 0.65–0.75 mm,  $x = 0.71$  mm,  $n = 4$ ). Head distinctly broad in males, as in other species of the genus. Ear openings about the same size as the eyes, with the tympanum visible. Occipital scale lacking, but a parietal shield including a pineal window present. Nostril pear-shaped, slightly convex and below the canthus rostralis. Vertebral crest indistinct. Scales arranged in 103–130 ( $x = 115.5$ ,  $n = 4$ ) rows around midbody, and 67–81 ( $x = 71.2$ ,  $n = 4$ ) longitudinal rows along the vertebrae. Matrix scales small, usually smooth and scattered with pale, enlarged and keeled scales. Enlarged scales not organized into clusters, but indistinct transverse rows between the limbs present. Vertebral scales keeled, with a higher density of enlarged scales than on the flanks, sometimes giving an impression of a margin between the vertebral area and flanks. Gular scales flat, smooth, juxtaposed and becoming smaller towards the gular fold. Ventral scales small and smooth, in 79–95 ( $x = 87.8$ ,  $n = 4$ ) longitudinal rows. Males usually with two continuous rows of 21–25 ( $x = 22.8$ ,  $n = 4$ ) precloacal pores; it is assumed these are lacking in females, as is typical for most agamids.

**Distribution**

In Zambia the species is known from localities within the Luangwa (Chipata) and Zambezi (Lusaka) valleys (Figure 10). In Lusaka, it is known from three localities: Great

30 = Chongoni Forest Reserve; 31 = Lilongwe; 32 = 30 miles NNW of Furancungo; 33 = Chifumbazi; 34 = Chikowa; 35 = Chipata; 36 = Katete; 37 = 30 km W of Katete; 38 = Petauke; 39 = Chakwenga River; 40 = 80 km E of Lusaka; 41 = Lusaka; 42 = Ruwa near Harare; 43 = Fern Valley; 44 = Mt. Sei, Melsetter; 45 = Mt. Silinda; 46 = Bulawayo; 47 = Rhodes Grave, Matobo Hills; 48 = Krueger National Park; 49 = Hoedspruit Airforce base; 50 = 7 km N of Chibuto; 51 = Gaborone; 52 = Gabane; 53 = Otse; 54 = 12 km N of Lydenberg; 55 = Gerlachshoop [Mission Station]; 56 = Loskopdam; 57 = Waterval Onder; 58 = Barberton; 59 = Louwscreek; 60 = Delagoa Bay (Maputo); 61 = Ponta do Ouro; 62 = Mkuze Game Reserve; 63 = Somkele; 64 = Empangeni; 65 = Durban; 66 = Umfolozi; 67 = Tugela Estates [Farm]; 68 = Rustenberg [Farm]; 69 = Lunda; 70 = Malange; 71 = Lydenburg (=Mashishing); 72 = Wonderboom, near Pretoria; 73 = Woodbush; 74 = Komatipoort.



**Figure 11.** Holotype (ZFMK 88682) of *Acanthocercus branchi*, from Chipata, Zambia.

East Road and Makishi Road, both within the town, and the Pioneer Camp about 25 km outside Lusaka on the road to Malawi. In Malawi it is recognized from Lilongwe and the Chongoni Forest Reserve, south-east of Lilongwe. Moreover, new records show its presence in Zimbabwe (Ruwa, near Harare; P. Wagner pers. observation) and the Rift Valley in south-eastern DRC (Manono, Katanga Province) where the species could be sympatric with other members of the *A. atricollis* group.

### **Habitat and ecology**

This species is a tree dweller as is 'typical' for the *atricollis* complex. In Chipata it was collected in dense Miombo woodland with large trees and a structured canopy. In Lusaka it was captured on a solitary tree close to the Great East Road, near Manda Hill Shopping Mall. At both localities, small colonies were observed (Wagner et al. 2012b).

### ***Acanthocercus cyanocephalus* (Falk, 1925)**

(Figure 12)

1925 *Agama cyanocephala* Falk, Blätter für Aquarien und Terrarien-Kunde, Stuttgart 36: 83. Type locality as published: 'Angola'.

1866 *Stellio angolensis* Barboza du Bocage (nomen nudum), Jornal de ciencias mathematicas, physicas, e naturaes, Lisboa 1: 43. Type locality as published:

'Duque de Bragança' [=Huila Plateau, *fide* Loveridge 1957], Malanje Province, Angola.

### **Neotype**

ZFMK 88492, adult male, collected in a garden in Ikelenge (−11.241592, 24.273256), northern Mwinilunga District, North-Western Province, Zambia, by Philipp Wagner.

### **Taxonomic comments**

Falk (1925) described a rare agamid lizard, about 35 cm in total length (head length of 7 cm; body length of 15 cm), with a large, broad, triangular head, a brownish body and a blue head, which lived on trees in Angola. Additionally he mentioned that if this lizard is unknown, he would suggest the name '*Agama cyanocephala*'. Currently, only three large agamid lizards are known from Angola. *Agama mucosoensis* Hellmich, 1957 may be excluded based on the brief description in body and head coloration (see also Wagner et al. 2012a) and Falk (1925) was able to differentiate between *Agama planiceps schacki* Mertens, 1936 (mentioned as *Agama planiceps* Peters, 1862 by Falk) and the specimen described by him. Indeed, the few characters mentioned correspond well to a species of the *Acanthocercus atricollis* group, but the description is not adequate to identify the species itself and the type specimen was not deposited in a scientific collection. Based on the International Code of Zoological Nomenclature (ICZN 1999), this name has to be recognized. According to Article 12.1 every new name published before 1931 must satisfy the provisions of Article 11 and must be accompanied by a description of the taxon. The short description itself is in accordance to Article 11 and, moreover, Art. 11.5.1. explicitly mentions that a name proposed conditionally for a taxon before 1961 is not to be excluded on that account alone. Following Article 15.1 the conditional proposal is valid and the suggested name *Agama cyanocephala* Falk, 1925 is available.



**Figure 12.** Neotype (ZFMK 88492, designated herein) of *Agama cyanocephala*, from Ikelenge, Zambia.

This study has shown that populations from Angola, Zambia and the southern DRC are clearly distinct from all other taxa of the *atricollis* complex, and consequently Falk's name should be regarded as valid rather than as a synonym. The designation of a neotype herein is in accordance to Article 75 of the code. Kurt Falk (1925), who settled in Angola as a German anthropologist, obviously gave a conditional description as his entire article is a published summary of a letter he sent to Germany and together with his description of the specimen he mentioned that 'if it is a new species he would support the name (...) [translated from German]'. Accordingly, the male specimen he used for measurements and the brief description of the coloration was released or fed to his snakes, rather than preserved. To clarify the taxonomic status of the entire species group, we herein define a neotype for *Agama cyanocephala* Falk, 1925 and include a re-description of the taxon. A clear type locality is not given in the description. Kurt Falk studied different tribes in Angola and travelled extensively within the country. Therefore, the type locality can be restricted by original designation to Angola only. We chose a specimen from western Zambia (Ikkelenge), close to the border to Angola as a neotype, as it is identical with the few characters given by Falk (1925) and, in contrast to available material from Angola, it still retains colour pattern and is available for molecular analysis.

In his checklist of specimens from western Africa, present in the Lisbon collection, Bocage (1866) mentioned the name '*St. angolensis*'. He thought that these specimens from Angola represented a new species which he meant to name '*St. angolensis*', but Günther (curator at the British Museum at this time), after an examination of the specimens, suggested them as conspecific with Smith's '*nigricollis*' (= *Acanthocercus a. atricollis*, see comment there) and for that reason, Bocage (1866) mentioned that and abstained from providing a description. Therefore, we recognize '*Stellio angolensis*' as a nomen nudum.

### Diagnosis

*Acanthocercus cyanocephalus* is characterized by its large size and the relatively short tail. There are relatively few enlarged, keeled, spinose scales on a matrix of small smooth scales, vertebral region with only very slightly enlarged scales, only half of the size or smaller than the enlarged keeled, spinose scales.

It is a large member of the genus with a total length up to 350 mm (SVL: 113–147 mm,  $x = 136.8$  mm,  $n = 8$ ), tail short, about 1.3 times longer than the SVL. Head distinctly broad in males like in other species of the genus. Ear openings about the same size or slightly smaller than the eyes, with the tympanum visible. Occipital scale lacking. Nostril slightly below the canthus rostralis. No vertebral crest. Scales arranged in 100–119 ( $x = 109.8$ ,  $n = 8$ ) rows around midbody and 58–78 ( $x = 71.4$ ,  $n = 8$ ) longitudinal rows along the vertebrate. Matrix scales small, usually smooth and scattered with enlarged keeled scales. Enlarged scales usually not organized in rows or clusters. Vertebral scales keeled, with a higher density of enlarged scales as on the flanks. Gular scales flat, smooth, juxtaposed and becoming smaller towards the gular fold. Ventral scales small and smooth, in 74–94 ( $x = 83$ ,  $n = 8$ ) longitudinal rows. Males with usually two continuous rows of 24–26 precloacal pores, which are lacking in females.

### **Differential diagnosis**

*Acanthocercus cyanocephalus* is clearly distinct from all other species in the coloration of adult males: head and throat uniform blue, body black with numbers of whitish coloured scales forming a spotted pattern, first half of tail brownish, second half banded black and blue.

From some of the other species this taxon differs as follows: from (a) *A. a. ugandaensis* it differs in possessing a vertebral region without rows of enlarged, keeled scales or small scales which are framed by a row of enlarged scales, by its larger size (113–148 mm vs. 96–125 mm in adult males) and a shorter tail; from (b) *A. a. kiwuensis* it differs by its larger size, the shorter tail and it does not possess transverse rows of enlarged scales; from (c) *A. a. minutus* it differs by its larger size and a strikingly different coloration.

*Acanthocercus cyanocephalus* is similar in size and some aspects of pholidosis to *A. atricollis* and *A. gregorii*. However, it is clearly distinct from (a) *A. gregorii* by its slightly smaller size, a shorter tail, having smooth versus keeled gular scales, in not possessing longitudinal rows of enlarged pale dorsal scales, in possessing many fewer enlarged body scales and the enlarged scales are smaller, the vertebral region of *A. gregorii* is covered with enlarged, keeled scales only, whereas in the vertebral region of *A. cyanocephalus* small scales are scattered among enlarged ones, and the pelvic and femoral regions of *A. gregorii* are dominated by enlarged scales whereas in *A. cyanocephalus* there is a mixture of one half each of both scale types; and finally from (b) *A. atricollis* in possessing a significantly lower number of enlarged body scales, especially on the lateral parts of the body and in *A. atricollis* the vertebral region has a broad band of enlarged scales whereas in *A. cyanocephalus* there is a mixture of small and enlarged scales.

### **Description of the neotype**

Adult male; habitus stout, with a large triangular head distinct from the body; tail short. **Measurements.** SVL 143.2 mm, tail length (TL) 187.0 mm, head length (HL) 42.3 mm, head with (HW) 39.8 mm, head height (HH) 21.8 mm, left forelimb 58.5 mm, left hind limb 84.8 mm. **Pholidosis.** Large teardrop-shaped nasal scale slightly below the canthus rostralis, directed laterally, pierced by the round nostril in its posterior part. Scales of anterior, lateral and central part of the head large, from the level of the ear scales are abruptly smaller, only about one fourth the size of the large head scales; head scales unequal in size, not directed, usually smooth, sporadically heavy keeled, free anterior margins of head scales only sporadically with sensory pits. 15 supralabial scales, 15 infralabial scales on both sides; supraocular scales smooth, 9 on each side; no parietal shield and pineal organ visible. Ear opening large, about the same size as the eye, margin bordered by a semicircle of ten spinose mucronate scales, tympanum superficial. No nuchal crest. Gular scales flat, smooth, juxtaposed and becoming smaller towards the gular fold. Dorsal body scales a mixture of small, usually smooth but sometimes keeled scales, some giving the impression of granular scales; and scattered enlarged keeled and sometimes mucronate or spinose scales, enlarged scales not organized in rows or clusters. Seventy-five dorsal scales in the vertebral region from midpoint of pectoral region to midpoint of pelvic region, consisting of a mixture of small and enlarged scales, not distinct from the rest of the body but all scales in the vertebral region are keeled. Ventral body scales smooth, slightly imbricate at their posterior margins, in 83 scales from midpoint of pectoral region to preloacal pores. Around midbody there are 125

rows of scales. Preloacal scales in two rows, 13 pores in the anterior, 11 in the posterior row. Scales on the dorsum of the forelimb unequal in size and strongly keeled, smooth on the underside, on the upper arm scales somewhat larger than the largest dorsal body scales, becoming smaller ventrally and distally. Scales on the dorsum of the hind limb keeled to smooth becoming completely smooth ventrally, on the upper thighs unequal in size and a mixture of small and scattered enlarged scales, enlarged scales as large as the enlarged dorsal body scales. In both, manus and pes, 4th digit is the longest, digital length decreasing 3-2-5-1, subdigital lamellae keeled and mucronate, 21 under left 4th digit. Tail arranged in whorls of four scale rings at the basal part of the tail, whorls becoming indistinct towards the tail tip, tail scales keeled and mucronate. First third of the tail extremely swollen, heavily built and laterally compressed, scales extremely large and thick, feebly to heavily keeled, much larger than the head or enlarged body scales. In the second third the tail is much thinner and slightly depressed. *Coloration* (after two years of preservation in ethanol): Head and neck blue. Ground colour of body and limbs black, sometimes with a bluish tint but dominated by a pattern of short whitish stripes and dots. Tail greyish at the base, followed by blue and brownish bands. Throat uniform bright blue, belly white mottled with black dots, underside of the tail dirty white.

### *Coloration in life*

*Males.* Head, neck and parts of the shoulders brilliant blue. Body and limbs black, with a pattern of white stripes and dots. Tail at the base yellowish, followed by blue and brownish bands. Throat uniform bright blue, framed by yellowish dots on a blue background. *Females.* Female coloration is unknown but presumably similar to the other subspecies. *Juveniles.* Only known from juvenile males, which are uniform brownish with a pattern of pale brown and black stripes and dots and a banded tail. The black bar on the shoulders, typical for *A. atricollis*, is more distinct in juveniles than in adult males. The throat is white with a reticulated pattern of blue stripes. Belly and underside of the tail creamy white, belly marbled with a greyish pattern.

### *Variation*

All examined specimens are similar in aspects of scalation and body proportions. One adult male (ZFMK 88491) shows three dark transverse bands between the limbs. The typical broad heads of adult males are absent in juvenile and subadult males.

### *Habitat*

Specimens were collected on trees in Miombo woodland, gardens and plantations. One specimen was hiding in a termite mound, directly beside a large tree. In northern Namibia (Ovamboland) specimens were abundant and conspicuous on trees and particularly on isolated trees surrounding water bodies (pers. obs. A. Bauer.) In Manono (DRC) the individuals were collected on man-made walls from small rocks and on buildings in the town in human disturbed areas, but not on trees.

### *Diet*

A stomach content analysis of vouchers (PEM 6360–6373) from the type locality and Sanolumba Village (southern DRC) found several types of arthropods: spiders, caterpillars, ants, termites, Diptera, Hymenoptera, Orthoptera and Coleoptera.

### Distribution

*Acanthocercus cyanocephalus* is currently known from far northern Namibia, Angola, north-western Zambia, southern and south-eastern DRC (Figure 10). Especially around the type locality it is known from several localities not noted on Figure 10, because they are too close to each other to show on a continental scale: Hillwood Farm (NMZB 10521, 10574; ZFMK 88491); Hillwood Farm: Nature Reserve (ZFMK 88493); Ikelenge (NMZB 1606; ZFMK 88495–97); Isombo Stream (NMZB 10659); Sakeji School (NMZB 10485, 10613; ZFMK 88494); Zambezi Bridge, NW of Ikelenge (NMZB 7081) and from Sanolumba Village opposite the border within southern DRC (PEM 6367–68, 6371).

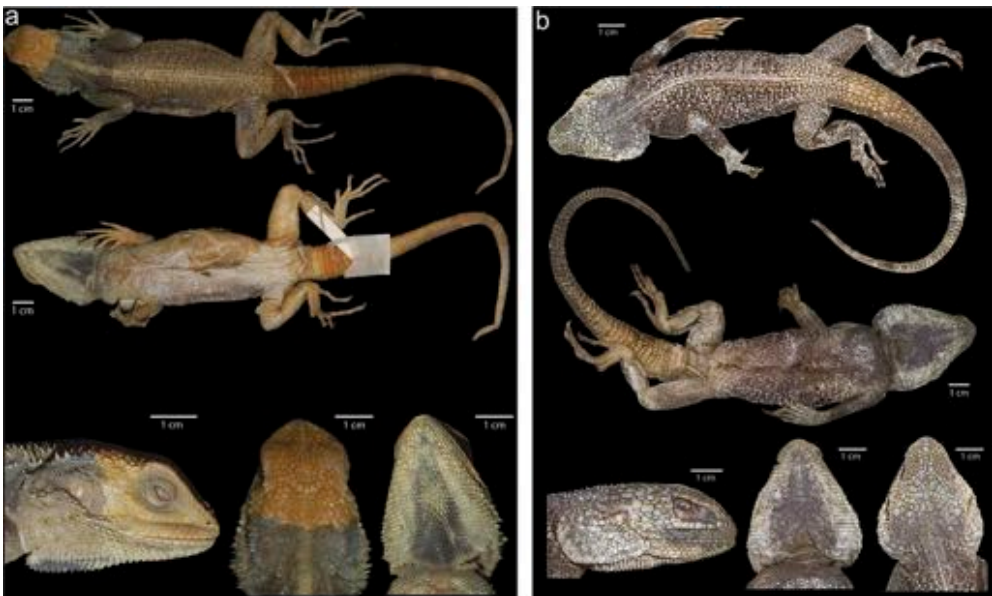
### Mythology

The Lunda people of north-western Zambia consider the blue-headed agama as poisonous and do not hunt or eat them (pers. observ. P. Wagner). They are relatively frightened to touch these lizards and the lizards are usually killed by children only.

### *Acanthocercus gregorii* (Günther, 1894: 86) (Figure 13(a))

1894 *Agama gregorii* Günther, Report on the collection of reptiles and fishes made by Dr J. W. Gregory during his expedition to Mount Kenia [sic]. Proceedings of the Zoological Society, London 1894: 84–91.

1957 *Agama atricollis loveridgei* Klausewitz, Eidonomische Untersuchungen über die



**Figure 13.** (a) Lectotype (BMNH 1946.8.28.67) of *Acanthocercus gregorii*, from Mkonumbi, Kenya. (b) Holotype (SMF 10138) of *Acanthocercus atricollis loveridgei*, from 'Kakoma, O-Afrika' [=Tanzania], East Africa.



Rassenkreise *Agama cyanogaster* und *Agama atricollis*. 2. Die Unterarten von *Agama atricollis*. Senckenbergiana biologica 38: 157–174: 163. Holotype: SMF 10138, from 'Kakoma, O-Afrika' [=Tanzania], East Africa (Figure 13(b)).

### Lectotype

BMNH 1946.8.28.67, from 'Mkonumbi, a grassy coast district with salt-swamps', Coast Province, Kenya, East Africa.

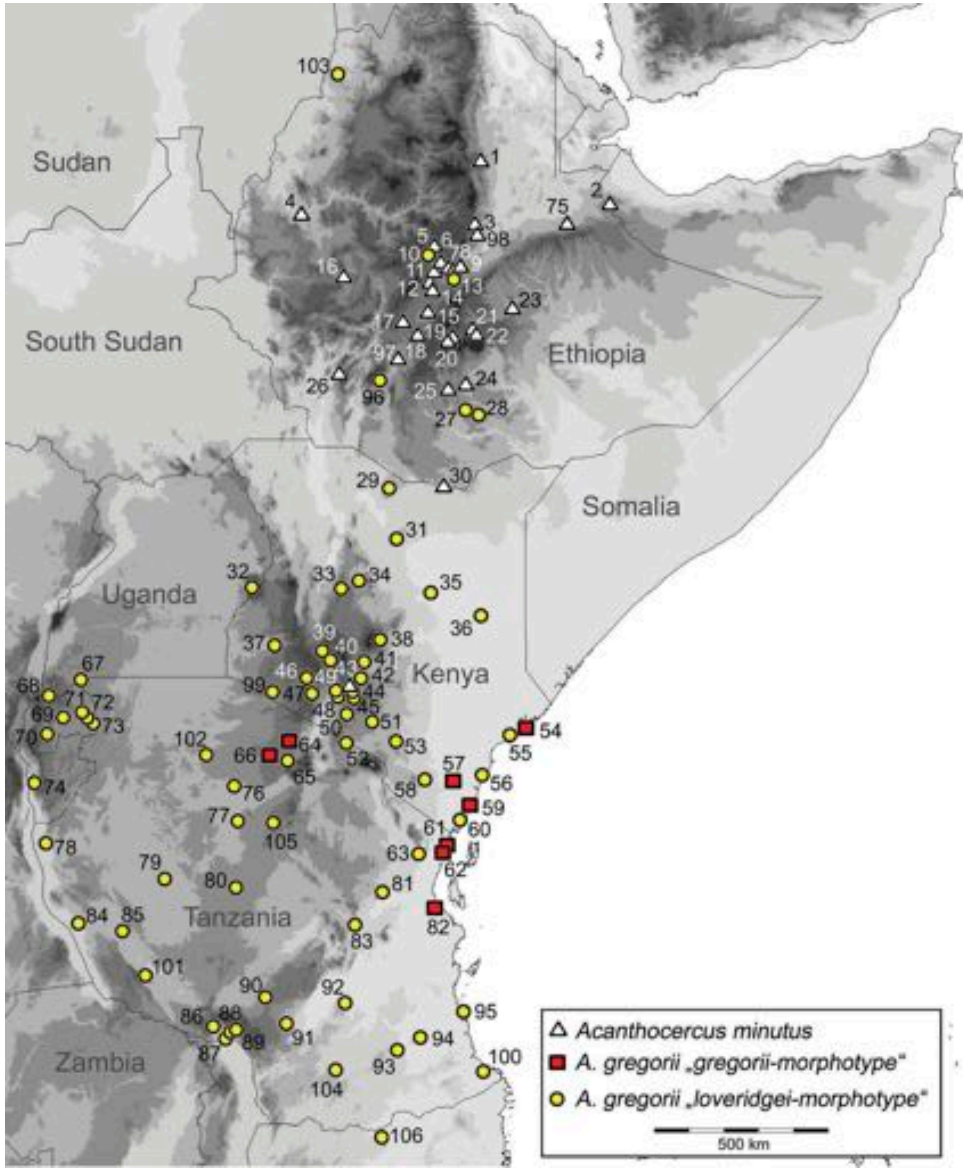
### Description

The largest species (total length of adult males up to 360 mm [adult males SVL: 91–138 mm,  $x = 119.2$  mm,  $n = 23$ ], adult females to 300 mm) of the genus, but similar in body size to *A. atricollis*; tail a third to a half longer than the SVL, but there is a series of specimens from one locality in the Serengeti that have extremely short tails, shorter than the SVL. Head distinctly broad in males, lacking the occipital scale. Ear opening as large as the eye, tympanum conspicuous. Nasal scale not convex, smooth and slightly below the canthus rostralis. Nuchal crest absent. Distinct from *A. atricollis* in possessing many enlarged, white coloured dorsal scales, forming a dotted pattern (= *A. loveridgei* morphotype) or forming a dotted pattern with up to five transverse scale rows (= *A. gregorii* morphotype). Body scalation heterogeneous, dorsal matrix scales small, smaller than ventral scales, irregularly intermixed by enlarged scales, sometimes forming distinct transverse scale rows. Enlarged scales keeled, most concentrated at the vertebrae. Vertebral zone covered by enlarged scales intermixed with smaller matrix scales, not separated by distinct rows of enlarged scales from the lateral parts of the body. Body scales are arranged in 88–126 ( $x = 103.8$ ,  $n = 23$ ) rows around midbody and 52–85 ( $x = 66.5$ ,  $n = 23$ ) longitudinal rows along the vertebrae. Ventral scales smooth, smaller than the enlarged dorsal scales, but larger than the matrix scales, in 77–92 ( $x = 83.3$ ,  $n = 23$ ) longitudinal rows. Gular scales small, smooth to feebly keeled, but erect and about the same size as the ventral scales. Males with one to three continuous rows ( $x = 2.0$ ,  $n = 22$ ) with a total number of 7–37 ( $x = 19.0$ ,  $n = 22$ ) precloacal pores, lacking in females. Dorsal scales of the basal part of the tail larger than those on the other parts of the tail, often forming a distinct patch of thick and swollen scales.

The coloration in life is poorly known. Günther (1894), in the first description, mentioned the throat and upper parts of the body bluish, but head, enlarged scales and basal portion of the tail yellow, while Sternfeld (1912) described the throat, chest and sometimes belly as reticulated blue and the dorsally enlarged body scales yellow. According to Klausewitz (1957) the throat of adult males is uniform greenish blue, head bluish green, body uniform blue and the tail bi-coloured yellowish at the base and brownish at the tip.

### Distribution

*Acanthocercus gregorii* has the widest distribution within the *A. atricollis*-complex (Figure 14). It is known from Ethiopia, Kenya, Tanzania, Rwanda, Burundi and extreme northern Mozambique. Klausewitz (1957) mentioned specimens from Uganda (as *A. loveridgei*) but it was not possible to confirm this and the presence of *A. gregorii* in Uganda is dubious. He (Klausewitz 1957) also recognized '*A. loveridgei*' from Lake Bengweulu and the southern margins of the Luangwa Valley in Zambia. The previous



**Figure 14.** Distribution of *Acanthocercus gregorii* and *A. minutus*. The numbers refer to the specific localities.

1 = Gojam; 2 = Batia; 3 = Lit Marafia; 4 = Didessa [Oromia]; 5 = Addis; 6 = Adda; 7 = Modjo; 8 = Adama [Nazareth]; 9 = Welenchiti; 10 = Akaki; 11 = Mount Zaguala; 12 = Maki River; 13 = Wonji; 14 = Harra, Lake Zuai; 15 = Lake Langan; 16 = Didessa; 17 = without locality; 18 = Lake Awasa; 19 = between Dodola and Adaba; 20 = Dodola; 21 = Mount Gaysay; 22 = Dinshu; 23 = Sheikh Husein; 24 = Sidam Bale bridge; 25 = Kebre Mengist; 26 = Felenguai; 27 = just N of Neghelli; 28 = Neghelli; 29 = Huri Hills; 30 = Moyala; 31 = Marsabit; 32 = Elgonyi; 33 = Maralal; 34 = Ntumot Lagga; 35 = Gorba Tula; 36 = Guaso Nyiro; 37 = Kericho Valley; 38 = Kirui; 39 = Lake Elmenteita; 40 = Naivasha; 41 = Fort Hall; 42 = Thika; 43 = Nairobi; 44 = Nairobi National Park; 45 = Attui; 46 = Narok; 47 = South N'guassa Mjiro River; 48 = Ngong Hills; 49 = SW of Ngong Hills; 50 = Kajiado; 51 = Sultan Hamud; 52 = Namanga; 53 = Makneni; 54 = Lamu island; 55 = Mkonumbi; 56 = Gede; 57 = Malindi district; 58 = Mount Sagalla; 59 = Mombasa; 60 = Mnambe Village; 61 = Tanga; 62 = Maweni; 63 = Korogwe;

record is now referred to *A. cyanocephalus* and the latter to *A. branchi*. Therefore, '*A. loveridgei*' (= *A. gregorii*) does not occur in Zambia. Specimens of the *A. gregorii* morphotype are known from coastal East Africa between Lamu Island, Kenya in the north and Tanga, Tanzania in the south, as well as from two localities in the Serengeti National Park (see [Figure 15](#)). All other records refer to the *A. loveridgei* morphotype. *Acanthocercus gregorii* is sympatric with *A. minutus* in Ethiopia, with *A. kiwuensis* in Rwanda and Burundi, and with *A. ugandaensis* in Kenya and northern Tanzania. However, the detailed limits of its distribution are still incompletely known.

### **Habitat and ecology**

Detailed information is sparse and inconsistent. Günther (1894) mentioned *A. gregorii* as ground living and described the habitat as 'a grassy coast-district with salt-swamps'. In the Serengeti specimens were observed in rocky areas and on the ground hiding, even in skulls of large mammals, but also on acacia trees (PW, own observation). According to these observations, *A. gregorii* seems not to be a strictly tree-dwelling species, in contrast to e.g. *A. atricollis*. Sternfeld (1912) mentioned gravid females in December from Uvira Kasongo.

### ***Acanthocercus kiwuensis* (Klausewitz, 1957: 167)** ([Figure 15](#))

1957 *Agama atricollis kiwuensis* Klausewitz, Eidonomische Untersuchungen über die Rassenkreise *Agama cyanogaster* und *Agama atricollis*. 2. Die Unterarten von *Agama atricollis*. Senckenbergiana biologica 38: 157–174.

### **Holotype**

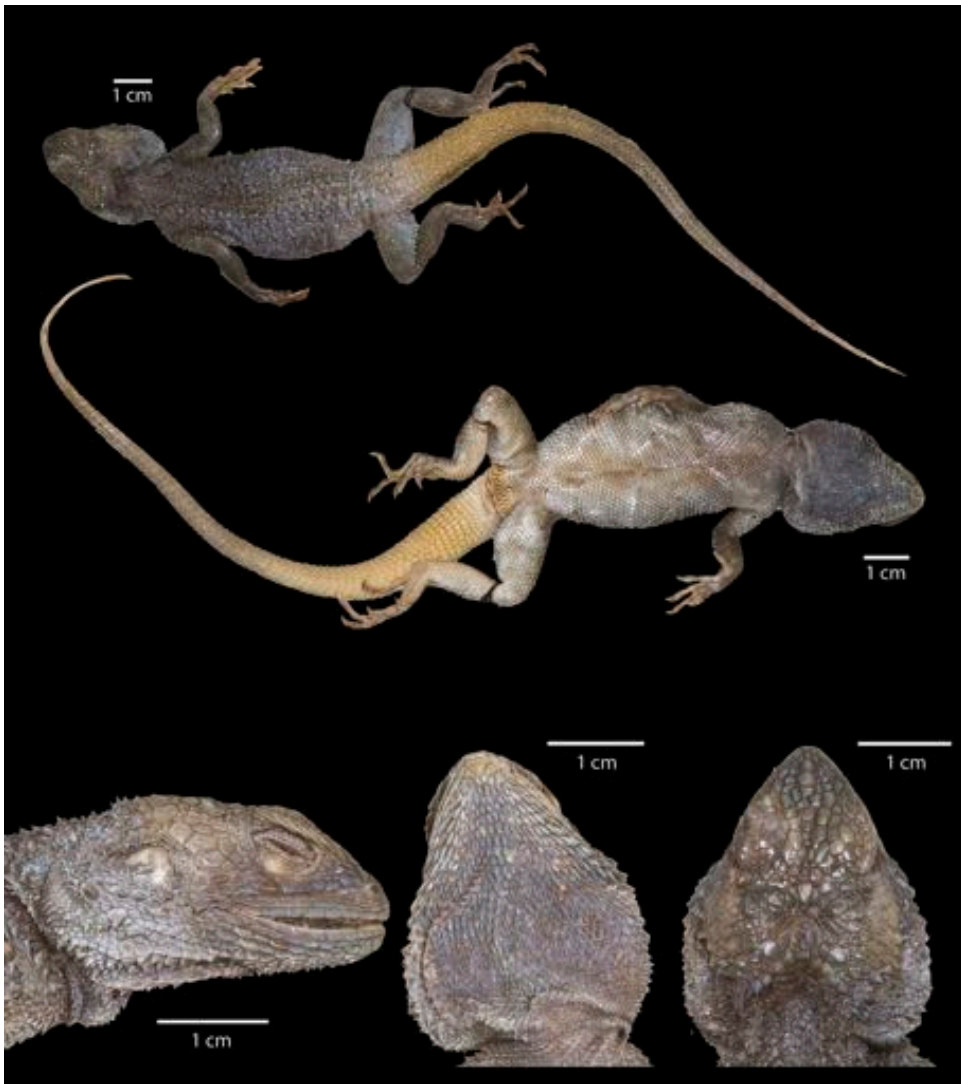
ZMB 23906, from 'Kissenji [=Gisenyi] north-east shore of Lake Kivu', Rwanda, East Africa.

### **Description**

A small species of the genus (SVL 87.3–130.3,  $x = 116.1$ ,  $n = 15$ ) with a total length usually about 300 mm, tail more than half again longer than the SVL in adult males. Head narrow (particularly in males), occipital scale lacking. Nasal scale not convex, smooth, below the canthus rostralis, often not visible from above. Ear openings as large as eyes, with the tympanum conspicuous. No nuchal crest. Dorsal scalation heterogeneous, matrix scales keeled and mucronate, irregularly intermixed with enlarged keeled and mucronate scales of two sizes, but not as distinct as in *A. gregorii*. Vertebral scales enlarged, becoming continuously smaller to the flanks, not as distinct as

---

64 = northern slopes Ngorongoro; 65 = Olduvai Gorge, Arusha; 66 = Serengeti, Naabi Gate; 67 = Kakitumba; 68 = Ntaruka; 69 = Kibale; 70 = Mpanga; 71 = Ntaruka?; 72 = Lake Nasho; 73 = Mpanga?; 74 = Bujumbura; 75 = Digg's Farm nr. Amoressa; 76 = Sanga; 77 = only coordinates; 78 = Tabora Udjidji; 79 = Kakoma; 80 = Ukimbu; 81 = Nguru Mountains; 82 = Bagamoyo; 83 = Kilosa; 84 = Karema; 85 = Kakokwe; 86 = Tukuyu; 87 = Rutenganio; 88 = Mwaya; 89 = Matema; 90 = Utengule; 91 = Ilolo; 92 = Uhehe; 93 = Liwale; 94 = Manengue; 95 = Kilwa; 96 = Arba Minch; 97 = Lake Shala; 98 = Mahal Uonz; 99 = Masai Mara NP; 100 = Lyanza; 101 = Kikambo; 102 = Sanga; 103 = Metemna; 104 = NE Songea District; 105 = Singida; 106 = Niassa Game Reserve.



**Figure 15.** Holotype (ZMB 23906) of *Acanthocercus kiwuensis*, from Kissenji, Rwanda.

in other species. Body scales in 73–96 rows [up to 116 mentioned by (Sternfeld 1912) around midbody ( $x = 83.6$ ,  $n = 29$ ) and 55–77 ( $x = 62.7$ ,  $n = 15$ ) longitudinal rows along the vertebrae. Ventral scales smooth and small, as large as the medium-sized dorsal scales, in 57–74 ( $x = 63.9$ ,  $n = 15$ ) longitudinal rows. Gular scales small, keeled, and exposed, slightly smaller than the ventral scales. Males with two to three continuous rows ( $x = 2.2$ ,  $n = 18$ ) and a total number of 16–28 precloacal pores ( $x = 20.2$ ,  $n = 18$ ), absent in females. Dorsal scales of the tail base not as distinctly swollen as in e.g. *A. gregorii* or *A. atricollis*, but distinct from other scales of the tail.

According to Klausewitz (1957) this species has a very characteristic coloration: adult males with a yellowish green to greenish blue head, throat whitish to blue, body deep blue with some pale blue dots, base and first third of the tail yellow, followed by

yellowish green second third and a brownish tip. Sternfeld (1912) mentioned male specimens from 'Kissenje' [=Gisenyi] having the entire body blue and the tail uniform olive-yellow. However, the non-nuptial coloration shows a pattern of yellow spots and stripes on the body as well.

### **Distribution**

Since its description (Klausewitz 1957), *A. kiwuensis* had been considered restricted to the mountainous areas around Lake Kivu (Rwanda and DRC). Herein, it is recognized as a wide-ranging species from Lake Kivu in the south to central Uganda and north-eastern DRC in the north (Figure 16).

### **Habitat and ecology**

*Acanthocercus kiwuensis* has been found on trees in savannah woodland, but also on man-made structures (e.g. houses, old walls) near cities and towns (EG, pers. obs.).

## ***Acanthocercus minutus* (Klausewitz, 1957: 170)** (Figure 17)

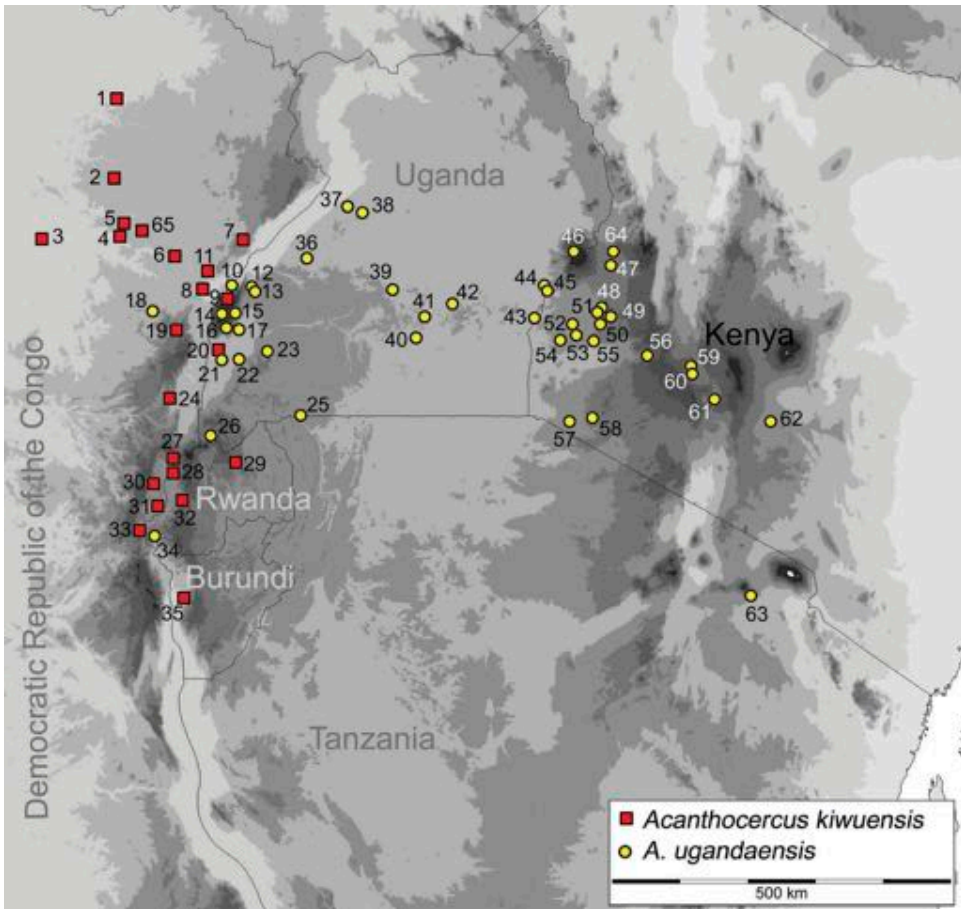
1957 *Agama atricollis minuta* Klausewitz, Eidonomische Untersuchungen über die Rassenkreise *Agama cyanogaster* und *Agama atricollis*. 2. Die Unterarten von *Agama atricollis*. Senckenbergiana biologica 38: 157–174.

### **Holotype**

ZMB 29089, from 'Dscheffedenza [=Ciaffedenza], Shoa', Ethiopia (for comment see distribution).

### **Description**

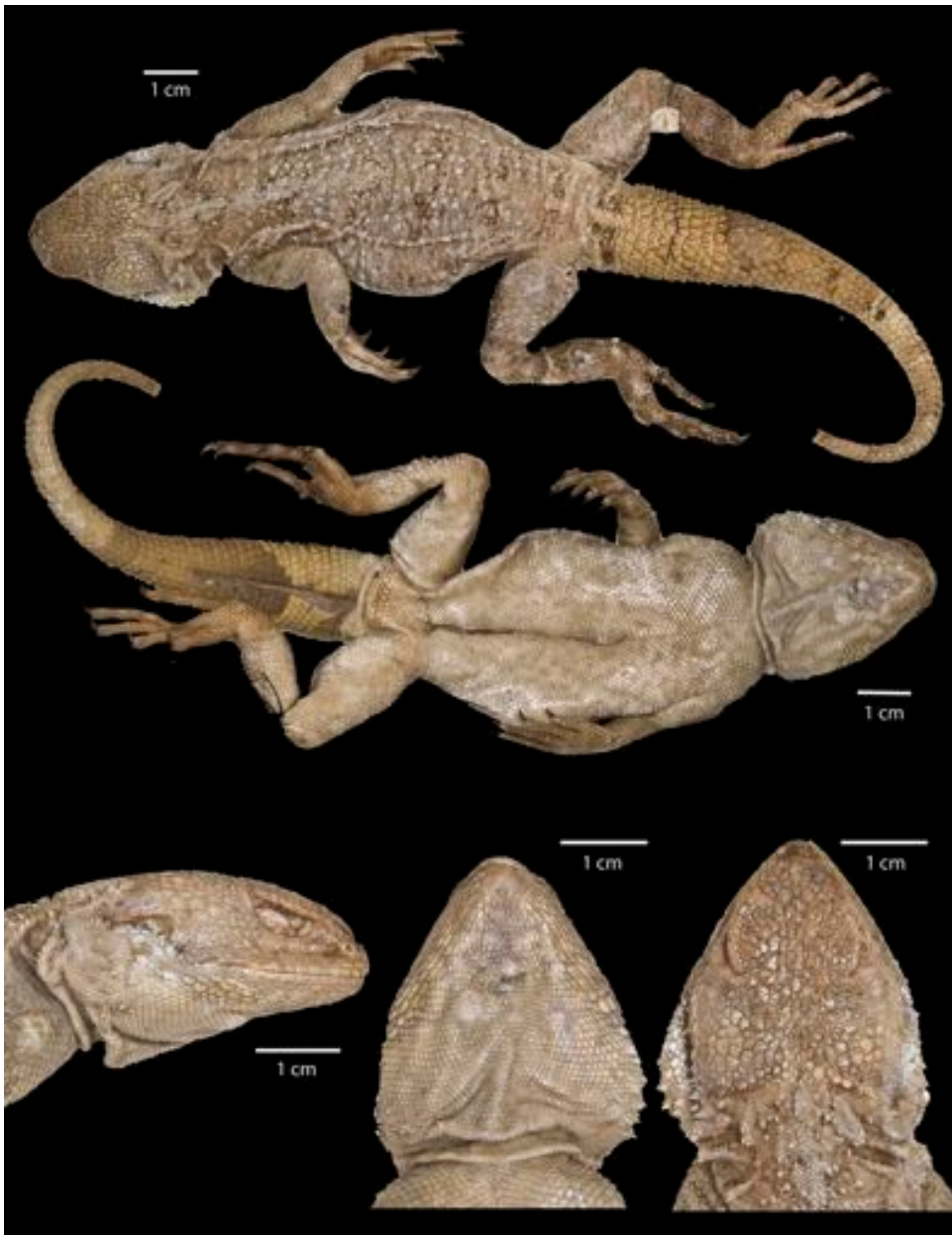
A small species of the genus with a total length below 290 mm (SVL: 93–117 mm,  $x = 108.2$  mm,  $n = 3$ ), tail only one fourth longer than SVL, shorter than in *A. ugandaensis* or *A. kiwuensis*. Both Loveridge (1920) and Klausewitz (1957) noted the small size of this species. The head seems to be only moderately broad because of the small size, but in relation to SVL length it is broader than in other species of the genus. Ear openings as large as eyes, with the tympanum visible. Occipital scale lacking. Nostril slightly below the canthus rostralis. No vertebral crest. Scales arranged in 104–114 ( $x = 109.7$ ,  $n = 3$ ) rows around midbody and 72–85 ( $x = 79.7$ ,  $n = 3$ ) longitudinal rows along the vertebrae. Matrix scales small, rhomboidal and keeled, scattered with enlarged scales. These larger scales are not as large and distinct as in *A. gregorii*. Vertebral scales keeled, enlarged scales intermixed with matrix scales but distinct to the lateral scalation, not arranged in distinct vertebral bands or framed by scales which are larger than the scales of the centre of the band. Gular scales small, smooth and flat. Ventral scales small and smooth, in 71–75 ( $x = 73.7$ ,  $n = 3$ ) longitudinal rows. Males usually with two (sometimes three) continuous rows of 14–17 precloacal pores, which are lacking in females.



**Figure 16.** Distribution of *Acanthocercus kiwuensis* and *A. ugandaensis*. The numbers refer to the specific localities.

1 = without locality [03.21°N, 28.52°E]; 2 = Okapi Faunal Reserve, Kayumaga stream; 3 = Avakubi, Ituri Forest; 4 = Epulu; 5 = Okapi Faunal Reserve; 6 = without locality [1.12°N, 29.25°E]; 7 = Bunia; 8 = Ndjuma Forest; 9 = Kisanzi [village near Mt. Teye]; 10 = Hakitengya; 11 = Byumba; 12 = Fort Portal; 13 = Semliki Forest; 14 = Nyakalengijo; 15 = Kyehundwe; 16 = Jambo Village; 17 = Kasese; 18 = Mount Ruwenzori; 19 = Butembo; 20 = Lake Edward; 21 = Kazinga channel; 22 = Kichwamba; 23 = Ibanda; 24 = Kabasha Escarpment; 25 = Kasese; 26 = Nyakabande; 27 = near Goma; 28 = Gisenyi [Rutshuru]; 29 = Buyumba; 30 = Isale; 31 = Upper Mulinga River, Idjwi Island; 32 = Kibuye; 33 = Bukavu; 34 = Cyamudongo; 35 = Bujumbura; 36 = Kikonda; 37 = Budongo Forest; 38 = Masinde; 39 = Kabulamuliro; 40 = Entebbe; 41 = Kampala; 42 = Mabira Forest; 43 = Jinja; 44 = Ntotoro; 45 = Osukuru; 46 = Elgonyi; 47 = Kitale; 48 = Kisere; 49 = Kamwega; 50 = Kakamega Forest; 51 = Buyangu Village; 52 = Kaimosi; 53 = Siaya; 54 = Ngiya; 55 = Kisumu; 56 = Lumbwa; 57 = Migori; 58 = Loita Plains; 59 = Nakuru; 60 = Nakuru National Park; 61 = Lake Naivasha; 62 = Thika; 63 = Mount Meru; 64 = Kitosh; 65 = without locality [1.52°N, 28.59°E].

There is no information about life coloration available. According to Klauswitz (1957) this species, like *A. ugandaensis*, is uniform brownish with a reticulated blue pattern on the throat. However, this description seems to be based on preserved specimens.



**Figure 17.** Holotype (ZMB 29089) of *Acanthocercus minutus*, from Dscheffedenza, Ethiopia.

### ***Distribution***

*A. minutus* is mainly restricted to Ethiopia with few records from Kenya (e.g. adult female from Nairobi mentioned by Klausewitz 1957, Figure 14). The published type locality is Dscheffedenza in 'Shoa', which seems to be the German name for 'Ciaffedenza', a town east of Addis Ababa.

### **Habitat and ecology**

Little information about habitat or ecology is available. Within a species account on *A. atricollis*, Largen and Spawls (2010) mentioned Ethiopian populations of small, frequently less colourful and ground-living specimens which probably refer to *A. minutus*. These populations are distributed within an altitudinal range of 1500–3000 m asl and inhabit dry savannah and woodland habitats. Largen and Spawls (2006, 2010) mentioned that they do not show affinity for trees and that the specimens were most frequently encountered in open environments in holes or beneath rocks. However, they only mentioned that there was uncertainty about which name to apply to these populations, but did not give citations or mention particular taxon names.

### ***Acanthocercus ugandaensis* (Klausewitz, 1957: 169)** (Figure 18)

1957 *Agama atricollis ugandaensis* Klausewitz, Eidonomische Untersuchungen über die Rassenkreise *Agama cyanogaster* und *Agama atricollis*. 2. Die Unterarten von *Agama atricollis*. Senckenbergiana biologica 38: 157–174.

### **Holotype**

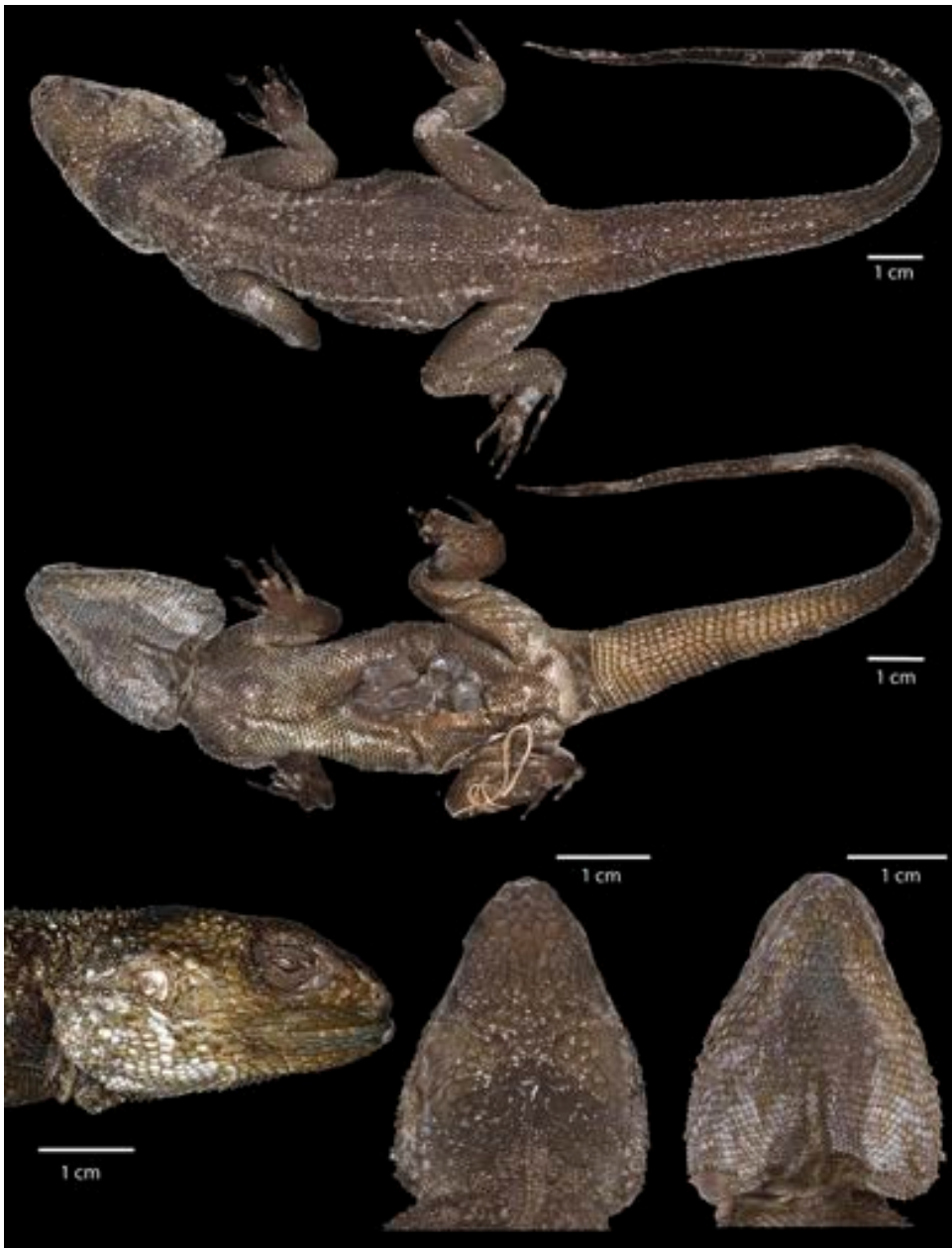
ZMB 11904, from 'Uganda', East Africa.

### **Description**

A medium sized species with a total length up to 350 mm in adult males (SVL: 90–124,  $x = 106$  mm,  $n = 16$ ), tail long, about 1.6 times longer than the SVL (*vide* Klausewitz 1957), longer than in *A. gregorii* and *A. kiwuensis*. Head broad (particularly in males) lacking the occipital scale. Ear openings slightly larger than eyes, with the tympanum visible. Nostril slightly below the canthus rostralis. No or very weakly developed nuchal crest. Scales arranged in 75–110 ( $x = 88.4$ ,  $n = 16$ ) rows around midbody and 54–69 ( $x = 60.2$ ,  $n = 16$ ) longitudinal rows along the vertebrate. Dorsal body scalation consists of small, smooth to feebly keeled, rhomboidal matrix scales, scattered with enlarged keeled scales. Vertebral scales strongly keeled, enlarged, usually larger than other enlarged body scales, forming a distinct vertebral band framed by scales which are larger than the scales of the centre of the band. Ventral scales small and smooth (sometimes very feebly keeled on the margins of the belly), in 56–80 ( $x = 65.7$ ,  $n = 16$ ) longitudinal rows. Gular scales small and keeled. Males usually with two (sometimes three) continuous rows of 12–17 precloacal pores, which are poorly developed in females.

According to Klausewitz (1957) the coloration is brownish, without any pale or yellowish pattern, but this seems to be a description of preserved specimens. In nuptial males, the head, forelimbs and distal half of the tail are brilliant blue. Hind limbs and first half of the tail yellowish-greenish. On the upper surface of neck and body, the matrix scales are dark brown to black, with the enlarged scales yellow and blue on the flanks and blue along the vertebrate. Sometimes also some yellow spots on the head and the forelimbs. Females light brown, with a dark green to brown dorsolateral stripe on each side and a pale vertebral stripe.





**Figure 18.** Holotype (ZMB 11904) of *Acanthocercus ugandaensis*, from 'Uganda'.

### ***Distribution***

*Acanthocercus ugandaensis* was described from unspecified localities in Uganda, and since, the description has not been recorded elsewhere. Herein, we recognize it from Rwanda (Cyamudongo), Kenya (Kakamega, Nairobi) and Tanzania (Mount Meru) as well (Figure 15).

## Habitat and ecology

*Acanthocercus ugandaensis* is a tree dweller and occurs in secondary dry forest, but also in plantations, large hedges along streets and on solitary trees in gardens (pers. observ. E. Greenbaum). There is no information about the social structure of the species, but solitary specimens only were trapped by the senior author around Kakamega forest, Kenya.

## Acknowledgements

We appreciate the loan of type specimens, specimens and the presentation of images by Jens Vindum (California Academy of Sciences), Colin McCarthy (The Natural History Museum, London), William Branch (Bayworld, Port Elizabeth Museum) Mark-Oliver Rödel (Museum für Naturkunde, Berlin) and Gunther Köhler (Senckenberg Museum, Frankfurt). Colin McCarthy and Wolfgang Böhme (Zoologisches Forschungsmuseum Koenig, Bonn) are especially thanked for fruitful discussions on nomenclatural issues about *A. atricollis*-synonyms. We are grateful to Tomáš Mazuch and Vlada Trailin for their help with Ethiopian localities. We thank the Ambrose Monell Cryo Collection of the American Museum of Natural History (AMNH) in New York, William Branch (PEM), Wolfgang Böhme (ZFMK) and Jens Vindum (CAS) for providing tissue loans. We are grateful to the authorities of the Zambian Wildlife Authority and the Ministry of Environment and Tourism of Namibia for the respective permits allowing collecting and exporting important specimens. PW is grateful to two Zambian scientists he is co-operating with in the ZamBio Project: Dr Victor Siamudala and Dr Humphrey Simukoko; and especially to Robert Chiwala for his friendship and help during his stay. Finally, PW is very thankful to Esther Townsend and Helen Finney for their continuing help (also with healing from snake bites) and to the Fischer family for their hospitality during the field trip. EG and CK thank our field companions Mwenebatu M. Aristote, Wandege Mastaki Moninga, Angalikiana Mulamba Marcel, Mululema Zigabe and Maurice Luhumyo. Baluku Bajope and Muhimanyi Manunu of CRSN provided project support and permits, and we thank the Institut Congolais pour la Conservation de la Nature for permits to work in protected areas. Technician Ana Betancourt of the UTEP DNA Analysis Core Facility sequenced samples for this study.

## Disclosure statement

No potential conflict of interest was reported by the authors.

## Funding

This work was supported by the National Science Foundation [DEB 1019943, DEB-0844523]; Lemole Endowed Chair in Integrative Biology Fund at Villanova University. The field excursion by PW was funded by the Deutsche Gesellschaft für Herpetologie & Terrarienkunde (DGHT) and the Alexander-Koenig-Stiftung of the Zoologisches Forschungsmuseum A. Koenig. Fieldwork by EG in DRC was funded by the Percy Sladen Memorial Fund, an IUCN/SSC Amphibian Specialist Group Seed Grant, research funds from the Department of Biology at Villanova University, a National Geographic Research and Exploration Grant [number 8556-08], and University of Texas at El Paso (UTEP). Sample sequencing was funded by National Institutes of Health [grant #5G12RR008124].

## ORCID

Philipp Wagner  <http://orcid.org/0000-0002-0460-2688>  
Aaron M. Bauer  <http://orcid.org/0000-0001-6839-8025>  
Adam D. Leaché  <http://orcid.org/0000-0001-8929-6300>

## References

- Anderson J. 1896. A contribution to the Herpetology of Arabia, with a preliminary list of the reptiles and batrachians of Egypt. London: R. H. Porter; p. 124.
- Bickford D, Lohmann DJ, Sodhi NS, Ng PKL, Meier R, Winker K, Ingram KK, Das I. 2006. Cryptic species as a window on diversity and conservation. *Trends Ecol Evol.* 22:148–155.
- Blanford WT. 1870. Observations of the geology and zoology of Abyssinia, made 1867–68. London: McMillan; xii + p. 487.
- Bocage BDJV. 1866. Lista dos reptis das possessoes portuguezas d’Africa occidental que existem no Museu de Lisboa. *J Sci Math Phys Nat Lisboa.* 1:37–56.
- Bocage BDJV. 1895. Herpétologie d’Angola et du Congo. Lisbonne: Ministère de la Marine et des Colonies. + XIX plates. p. xx + 203.
- Bouckaert R, Heled J, Kühnert D, Vaughan T, Wu CH, Xie D, Suchard MA, Rambaut A, Drummond AJ. 2014. BEAST 2: a software platform for bayesian evolutionary analysis. *PLoS Comput Biol.* 10: e1003537.
- Boulenger GA. 1885. Catalogue of the Lizards in the British Museum (Nat. Hist.) I. Geckonidae, Eublepharidae, Uroplatidae, Pygopodidae, Agamidae. London: British Museum (Natural History). + XXXII plates. p. 450.
- Boulenger GA. 1895. XXIV.— On the reptiles and batrachians obtained by Mr. E. Lort-Phillips in Somaliland. *Ann Mag nat Hist.* 16:165–169. doi:10.1080/00222939508680248
- Boulenger GA, Power JH. 1921. A revision of the South African agamas allied to *Agama hispida* and *A. atra*. *Transact Roy Soc S Africa.* 9:229–287.
- Branch B. 1998. A field guide to snakes and other reptiles of Southern Africa. 3rd ed. Cape Town (South Africa): Struik Publishers.
- Burbrink FT. 2001. Systematics of the eastern rat-snake complex (*Elaphe obsoleta*). *Herp Monogr.* 15:1–53.
- Denzer W, Günther R, Manthey U. 1997. Kommentierter Typenkatalog der Agamen (Reptilia: Squamata: Agamidae) des Museums für Naturkunde der Humboldt-Universität zu Berlin (ehemals Zoologisches Museum Berlin) [Commented Type Catalogue of the Agamidae of the Museum of Natural History of the Humboldt University in Berlin (former Zoological Museum Berlin)]. *Zoosyst Evol.* 73:309–332.
- Drummond AJ, Suchard MA, Xie D, Rambaut A. 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Mol Biol Evol.* 29:1969–1973.
- Edgar RC. 2004. Muscle: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Res.* 32:1792–1797.
- Falk K. 1925. Herpetologische Berichte aus Angola (Portugiesisch West-Afrika) [Herpetological reports from Angola (Portuguese West-Africa)]. *Blätter Für Aquarien Und Terrarienkunde.* 36:81–83.
- Fitzinger L. 1843. Systema Reptilium, fasciculus primus, Amblyglossae. Wien: Braumüller et Seidel; p. 106.
- Gough LH. 1909. The South African species of *Agama*. *Transact Transvaal Mus.* 1:183–194, XXIV plates.
- Gray JE. 1827. XI. A synopsis of the genera of saurian reptiles, in which some new genera are indicated, and the others reviewed by actual examination. *Philosophical Magazine.* 2 (2): 54–58. doi:10.1080/14786442708675620
- Günther A. 1894. Report on the collection of reptiles and fishes made by Dr. J. W. Gregory during his expedition to Mount Kenia [sic]. *Proc Zool Soc London.* 1894:84–91.
- Hammer Ø. 2012. PAST: paleontological Statistics, version 2.15 Reference manual. Oslo: Natural History Museum, University of Oslo.
- Hammer Ø, Harper DAT, Ryan PD. 2001. PAST: paleontological Statistics software package for education and data analysis. *Palae Elec.* 4(1):1–9.
- Harms H. 1918a. Nachruf auf Adolf Stolz [Obituary of Adolf Stolz]. *Notizblatt Des Königlich Botanischen Gartens Und Museums Zu Berlin.* 7(66):281–285.

- Harms H. 1918b. Nachschrift zu vorstehendem Nachrufe auf A. Stolz [Apostil to the aforementioned obituary of A. Stolz]. Notizblatt des Königl. Botanischen Gartens Und Museums Zu Berlin. 7(66):285–288.
- International Commission on Zoological Nomenclature (ICZN). 1999. International code of zoological nomenclature. 4th ed. London: The International Trust for Zoological Nomenclature.
- Kingdon J. 1990. Island Africa: the evolution of Africa's Rare animals and plants. London: Collins.
- Kissling WD, Blach-Overgaard A, Zwaan RE, Wagner P. 2016. Historical colonization and dispersal limitation supplement climate and topography in shaping species richness of African lizards (Squamata: Agamidae). *Sci Rep.* 6:34014.
- Klausewitz W. 1954. Eidonomische Untersuchungen über die Rassenkreise *Agama cyanogaster* und *Agama atricollis*. 1. Der Rassenkreis der *Agama cyanogaster*. *Senckenb Biol.* 35:137–146.
- Klausewitz W. 1957. Eidonomische Untersuchungen über die Rassenkreise *Agama cyanogaster* und *Agama atricollis*. Die Unterarten von *Agama atricollis* [Eidonomic studies about the species complex of *Agama cyanogaster* and *Agama atricollis*. The subspecies of *Agama atricollis*]. *Senckenb Biol.* 38:157–174.
- Largen MJ, Spawls S. 2006. Lizards of Ethiopia (Reptilia Sauria): an annotated checklist, bibliography, gazetteer and identification. *Trop Zool.* 19:21–109.
- Largen MJ, Spawls S. 2010. Amphibians and reptiles of ethiopia and eritrea. Frankfurt: Edition Chimaira; p. 694.
- Laurenti JN. 1768. Specimen medicum, exhibens synopsis reptilium emendatam cum experimentis circa venena et antidota reptilium austriacorum. Vienna: J.T.N. de Trattnern; p. 214.
- Leaché AD, Chong RA, Papenfuss TJ, Wagner P, Böhme W, Schmitz A, Rödel MO, Lebreton M, Ineich I, Chirio L, et al. 2009. Phylogeny of the genus *Agama* based on mitochondrial DNA sequence data. *Bonn Zool Beitr.* 56:273–278.
- Leaché AD, Grummer JA, Miller M, Krishnan S, Fujita MK, Böhme W, Schmitz A, Lebreton M, Ineich I, Chirio L, et al. 2017. Bayesian inference of species diffusion in the West African *Agama agama* species group (Reptilia, Agamidae). *Syst Biodiv.* 15:192–203.
- Loveridge A. 1920. Notes on East African lizards collected 1915–1919, with the description of a new genus and species of skink and new subspecies of gecko. *Proc Zool Soc London.* 1920:131–167.
- Loveridge A. 1957. Checklist of the reptiles and amphibians of East Afrika (Uganda, Kenya, Tanganyika, Zanzibar). *Bull Mus Comp Zool Harvard.* 117:153–363.
- Manly BFJ. 1994. Multivariate statistical methods: a primer. 2nd ed. London: Chapman & Hall; p. 119.
- Padial JM, Miralles A, De la Riva I, Vences M. 2010. The integrative future of taxonomy. *Front Zool.* 7:16.
- Pattengale ND, Alipour M, Bininda-Emonds OR, Moret BM, Stamatakis A. 2009. Research in computational molecular biology. How many bootstrap replicates are necessary? Berlin (Heidelberg): Springer; p. 184–200.
- Peters WCH. 1862. Übersicht einiger von dem, durch seine afrikanische Sprachforschungen, rühmlichst bekannten, Hrn. Missionär C.H. Hahn bei Neu-Barmen, im Hererolande, and der Westküste von Afrika, im 21° südl. Br. gesammelten Amphibien, nebst Beschreibungen der neuen Art. *Monatsber Akad Wiss Berlin.* 1862: 15–26.
- Pons J, Barraclough TG, Gomez-Zurita J, Cardoso A, Duran DP, Hazell S, Kamoun S, Sumlin WD, Vogler AP. 2006. Sequence-based species delimitation for the DNA taxonomy of undescribed insects. *Syst Biol.* 55:595–609.
- Poynton JC. 1995. The “arid corridor” distribution in Africa: a search for instances among amphibians. *Madoqua.* 19:45–48.
- Rambaut A, Drummond AJ. 2007. TRACER. Oxford: University of Oxford.
- Reaney LT, Whiting MJ. 2002. Life on a limb: ecology of the tree agama (*Acanthocercus a. atricollis*) in southern Africa. *J Zool London.* 257:439–448.
- Reaney LT, Whiting MJ. 2003. Picking a tree: habitat use by the tree agama, *Acanthocercus atricollis atricollis*, in South Africa. *Afr Zool.* 38:273–278.

- Reid NM, Carstens BC. 2012. Phylogenetic estimation error can decrease the accuracy species delimitation: A Bayesian implementation of the General Mixed Yule Coalescent model. *BMC Evol Biol.* 12:196.
- Rohlf FJ. 2006a. TPSutil: utilities, version 1.38. Stony Brook (NY): State University at Stony Brook.
- Rohlf FJ. 2006b. TPSdig, version 2.10. Stony Brook (NY): State University at Stony Brook.
- Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Syst Biol.* 61:539–542.
- Rüppell E. 1835. Neue Wirbelthiere zu der Fauna von Abyssinien gehörig, entdeckt und beschrieben: amphibien. Frankfurt am Main (Germany): S. Schmerber.
- Schlick-Steiner BC, Steiner FM, Seifert B, Stauffer C, Christian E, Crozier RH. 2010. Integrative taxonomy: a multisource approach to exploring biodiversity. *Annu Rev Entomol.* 55:421–438.
- Smart RM, Whiting MJ, Twine W. 2005. Lizards and landscapes: integrating field surveys and interviews to assess the impact of human disturbance on lizard assemblages and selected reptiles in a savanna in South Africa. *Biol Con.* 122:23–31.
- Smith A. 1849. Illustrations of the Zoology of South Africa. vol. 3 (Reptiles). Appendix. London: Smith, Elder, and Co; p. 28.
- Stamatakis A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics.* 30:1312–1313.
- Sternfeld R. 1912. Wissenschaftliche Ergebnisse der Deutschen Zentral-Afrika Expedition 1907–1908, unter Führung A. Friedrichs, Herzogs zu Mecklenburg. Klinkhard und Biermann, Leipzig. IV. Zoologie II. Lfg. Reptilia; p. 197–279 [the volume was published in parts from 1911 to 1913 but this part was published in 1912].
- Taravati S. 2010. GMTP, version 2.1. Iran: Biology Department-Ferdowsi University of Mashhad.
- Uetz P, Freed P, Hošek J, editors. 2017. The reptile database [Internet]. [accessed 2017 Feb 22]. <http://www.reptile-database.org>.
- Wagner P. 2010. Diversity and distribution of African lizards [dissertation]. Bonn (Germany): University of Bonn.
- Wagner P, Bauer AM, Wilms TM, Barts M, Böhme W. 2012a. Miscellanea acrodontia: notes on nomenclature, taxonomy and distribution. *Russ J Herp.* 19:177–189.
- Wagner P, Greenbaum E, Bauer AM. 2012b. A new species of the *Acanthocercus atricollis* (Squamata: Agamidae) complex from Zambia. *Salamandra.* 48:21–30.
- Wagner P, Mazuch T, Bauer AM. 2013. An extraordinary tail – integrative review of the agamid genus *Xenagama*. *J Zool Systematics Evol Res.* 51:144–164.
- Wagner P, Melville J, Wilms TM, Schmitz A. 2011. Opening a box of cryptic taxa? A review of the morphology and current taxonomy of the lizard genus *Trapelus* (Squamata: Agamidae) in northern Africa and description of a new species. *Zool J Linn Soc.* 163:884–912.
- Wermuth H. 1967. Liste der rezenten Amphibien und Reptilien: agamidae [Checklist of the recent amphibians and reptiles: agamidae]. *Das Tierreich.* 86:XIV + 1–127.
- Whiting MJ, Chetty K, Twine W, Carazo P. 2009. Impact of human disturbance and beliefs on the tree agama *Acanthocercus atricollis atricollis* in a South African communal settlement. *Oryx.* 43:586–590.
- Zelditch ML, Swiderski DL, Sheets D, Fink WL. 2004. Geometric morphometrics for biologists: a primer. San Diego (CA): Elsevier.

## Appendix 1. Material examined for fine scale morphology.

***Acanthocercus atricollis*. BOTSWANA.** Gabane (ZFMK 41647); Gaborone (ZFMK 41747–748, 42967–701); Otse (ZFMK 44647). **MOZAMBIQUE.** Without detailed locality (ZFMK 41917–918). **SOUTH AFRICA.** Cape Province [in error] (ZFMK 7423–424); Durban (ZFMK 18394); ‘Port Natal’ [=Durban], (BMNH 1946.8.28.1); Natal (ZFMK 29397); Transvaal, Gaanskuil, Rustenberg [=NW Province] (ZFMK 2691–692).

***Acanthocercus aff. atricollis*. DRC.** Katanga, Murungu Highlands, Mwaseini (ELI005); South Kivu, road between Fizi and Lilimba, 1194 m (EBG2167).

***Acanthocercus branchi*. MALAWI.** Chongoni Forest Reserve (ZMB 76267); Lilongwe (ZMB 76264). **ZAMBIA.** Chakwenga river (NMZB-UM 4463); Chikowa (NMZB-UM 27144-45); Chipata (ZFMK 88682); Kalikali Dam (NMZB-UM 27143); Katete (NMZB-UM 32631-32); 30 km W of Katete (NMZB-UM 4634-35); Lusaka (ZFMK 88683-684); 80 km ENE of Lusaka (NMZB-UM 4622-23); Petauke Old Boma (NMZB-UM 27151); Sayiri court (NMZB-UM 27146-50).

***Acanthocercus cyanocephalus*. ANGOLA.** Kalukembé (= Caluquembe) (MHNG 1545.24-26). **DRC.** Sanolumba Village (PEM R-6367-68, 6371). **ZAMBIA.** NW Province, Mwinilunga District, Ikelenge (NMZB 1606, ZFMK 88492, 88495-97); Ikelenge, Hillwood Farm (NMZB 10521, 10574, ZFMK 88491); Ikelenge, Hillwood Farm, Nature Reserve (ZFMK 88493); Ikelenge, Isomo Stream (NMZB 10659); Ikelenge, Sakeji School (NMZB 10485, 10613, PEM R-6360-66, 6369-70, 6372-73, ZFMK 88494); NW of Ikelenge, Zambezi Bridge (NMZB 7081); NW Province, Kalumbila Village (PEM R-6372).

***Acanthocercus gregorii*. KENYA.** Mkonumbi (BMNH 1946.8.28.67). **TANZANIA.** Serengeti, 6 km N of main Oldovai River, 8 km N Maasai Village, and 32 km N of Olobalol at bottom of N slopes of Ngorogoro foothills, 02°55'24.5"S, 35°10'41.2"E, 1595 m (PEM 18899); Serengeti, Naabi Gate (ZFMK 21073-086).

***Acanthocercus kiwuensis*. DRC.** North Kivu, road just N of Goma, 1160 m (UTEP 20386, formerly EBG2281); North Kivu, Kisanzi Village near Mt. Teye, Ruwenzori Mts., 1702 m (UTEP 20364); North Kivu, Virunga NP, Kabasha Escarpment, 1202 m (UTEP 20387 formerly EBG2283); North Kivu, Virunga NP, Ndjuma lowland forest, 728 m (UTEP 20388 formerly EBG1761); Orientale, Bunia, 1248 m (UTEP 20389 formerly EBG2455); Orientale, Epulu (Ituri Forest), 740 m (UTEP 20390 formerly EBG2521); South Kivu, 100 m W of the shore of Lake Kivu in the village Isale (UTEP 20391 formerly EBG1903). **RWANDA.** Kibuye at Lake Kivu (ZFMK 88200); 'Kissenji' [=Gisenyi] (ZMB 23906). **UGANDA.** Kampala (ZFMK 68489, 70546-549); Rukungiri Dist., Byumba (CAS 201726-727).

***Acanthocercus loveridgei*. ETHIOPIA.** Kaffa Province, Arba Minch (ZFMK 15865-866); Kaffa Province, Kambe (ZFMK 15867); Kaffa Province, Wonji (ZFMK 15868); Shoa Province, Akaki, Lake Haraironi (ZFMK 2685). **KENYA.** Masai Mara NP (ZFMK 41655); Narok (ZFMK 19161). **RWANDA.** Kibungo, Nasho (ZFMK 61662); Kibungo, Mpanga (ZFMK 61664); Kibungo, Ntaruka (ZFMK 61661); Kigali (ZFMK 61665). **TANZANIA.** Kakoma (SMF 10138); Tabora Ujdjidi (ZFMK 20854).

***Acanthocercus minuta*. ETHIOPIA.** Dscheffedenza, Shoa (ZMB 29089); Gojam, Blue Nile Canyon (ZFMK 56655); Oromia, Didessa, a Woreda (ZFMK 56656); Shoa Province, Akaki, Modjo (ZFMK 2683-84, -2686-88); Shoa, Descheffedenza (ZMB 29089); Shoa Province, Lake Langano (ZFMK 55356-357, 55553, 56654); Shoa Province, Nazareth, road to Wonji (ZFMK 16229-230).

***Acanthocercus ugandaensis*. KENYA.** Kakamega Forest (ZFMK 81952-963). **RWANDA.** Cyamudongo (ZFMK 55710-717). **UGANDA.** Budongo Forest (ZFMK 88792); Kilembe, Jambo Village (ZFMK 65181); Mount Ruwenzori (ZFMK 63335); Ruwenzori, Fort Portal (ZFMK 63355-359); Ruwenzori, Kasese (ZFMK 63143-145, 63275-281); Ruwenzori, Nyakalengijo (ZFMK 63236); Ruwenzori, Semliki Forest (ZFMK 64489, 63294-295); Uganda (ZMB 11904).

***Acanthocercus sp. n.* | DRC.** Katanga (MHNG 778.23); Katanga, Manono (ELI322, 327).

## Appendix 2. Additional material (not examined in detail, used as geographic reference)

***Acanthocercus atricollis*. Malawi.** MCZ R-50544: Chutala River, nr Salima; MCZ R-50552: Likabula River, Mlanje Mt.; MCZ R-50547: Nchisi Mt., nr Bowa House; MCZ R-50549: Zomba Plateau, nr Bowa House. **Mozambique.** R-PEM 15570: 7 km N of Chibuto; R-PEM 16124: Lechengwe village, Niassa Game Reserve; ZMB 27579: Missala. **SOUTH AFRICA.** R-PEM 5099: Empangeni; R-PEM 8692: Hoedspruit Airforce base; MCZ R-184444: Limpopo, R-PEM 437, PEM 439: Louwscreek; ~12 km N of Lydenberg Rd on Wildebeeskraal Rd; R-PEM 8698: Mkuze Game Reserve camp site; MCZ

R-41861: Natal, Tugela Estates, Weenen; ZMB 7882: Port Natal; MCZ R-41860: Transvaal: Barberton; ZMB 6544: Transvaal, Gerlachshoop; ZMB 2551: Transvaal, Ha-Schokama; SMF 43929: Transvaal, Loskopdam; ZMB 27227: Transvaal, Mpoma; MCZ R-41859: Transvaal, Waterval Onder; MCZ R-18282: Zululand, Somkele; SMF 46928: Zululand, Umfolozi River, Camp Masimba. **Zimbabwe.** MCZ R-12624: Bulowayo; MCZ R-21550: Rhodes Grave, Matopo Hills; MCZ R-29187: Mt. Sei, Melsetter; MCZ R-44461: Mt. Silinda.

***Acanthocercus cyanocephalus.* ANGOLA.** AMNH 48162-72: Capelongo; AMNH 48173-8, AMNH 48191-2: Chitau; MCZ R-34965: Cuma; AMNH 48179: Dande; AMNH 48180-1, AMNH 48183-7: Huambo; MCZ R-74124, MCZ R-169585: Lunda; ZMB 10027: Malange; AMNH 48188-90: Mombolo. **DRC.** SMF 40863: Élisabethville [=Lubumbashi]. **NAMIBIA.** MCZ R-190193-94: Oshikango. USNM 154114: Ovamboland, Ondangua; MCZ R-190193-94: near Oshikango, 200 m S of St. Mary's Mission; NMB R07427: Ovamboland, Ompundja; ZSM 13/1960: nördl. Ovamboland; AMNH 97756: Ovamboland Reg[ion], Ondangua; TM 17105-06, 17111-12, 17116, 17122: Eenhana, Oshikango; TM 38574-76: Ovamboland, Odimbo; TM 38604: Opuwo, Oshakati; TM 38583-85: Ovamboland, Odangwa; TM 45111: Opwuo, Ondangwa, 24 KM SE – Oshivelo; TM 38597: Ovamboland, Onguediva. **ZAMBIA.** AMNH 130261-62: Ndola, Mufulira.

***Acanthocercus 'loveridgei'.* BURUNDI.** ZMB 22578: Usumbura [=Bujumbura]. **Ethiopia.** MCZ R-34963: Metemna, Denboa; MCZ R-119625: just N of Neghelli. **TANZANIA.** AMNH 50788-89: Blanketti River; MCZ R-54769: Central Province, Singida; SMF 10138: Kakoma; ZSM 99/1908: Korogwe; MCZ R-54554: Lyanza; MCZ R-54556: Manengue; MCZ R-30747: Matema, nr Myaya; MCZ R-54557, MCZ R-169637: Milepa; MCZ R-54555: Mucembe; MCZ R-18589: Mwanza, Sanga; MCZ R-30748: Mwaya, Lake Nyasa; ZMB 24993: Nguru Mountains; MCZ R-50190: NE Songea District; MCZ R-54551: Rukwa, Kakokwe; MCZ R-54552, MCZ R-169653: Rukwa, Kapombo; MCZ R-54549: Rukwa, Kikambo; MCZ R-30752: Rungwe, Ilolo; MCZ R-30749: Rungwe, Tukuyu; ZMB 16906: Rutenganio; MCZ R-52416: Southern Province, Kilwa; MCZ R-50188, MCZ R-52417: Southern Province, Liwale; ZMB 15771: Uhehe; ZMB 15772: Ukimbu; ZMB 15447: Utengule, Iringa. MCZ R-54768: Western Province, Karema, Mpanda; **ZAMBIA.** SMF 22879: Usombo, Lake Bangweulu.

***Acanthocercus gregorii.* KENYA.** MCZ R-7987, MCZ R-29641: Guass Nyiro; MCZ R-41096-100, ZMB 15116: Lamu island. **TANZANIA.** ZMB 13152: Bagamoyo; SMF 10139: Maweni near Tanga; ZMB 11897: Tanga.

***Acanthocercus kiwuensis.* DRC.** AMNH 10485-87, AMNH 10490-91: Avakubi, Ituri Forest; MCZ R-19762: Lake Edward; MCZ R-24764: Rutshuru; MCZ R-169578, MCZ R-47356: Upper Mulinga River, Idjwi Id. **RWANDA.** MCZ R-169615, MCZ R-47355, MCZ R-24761, ZMB 22577: Kissenji [=Gisenyi], Lake Kivu.

***Acanthocercus minuta.* ETHIOPIA.** ZMB 19740: Adis Abeba; MCZ R-118108: Amoressa, Digg's Farm; AMNH 37898-99: Bishoftu [= Debre Zeyit]; ZMB 24528: Floden Ngara; AMNH 13519, AMNH 20151-52: Harrar; MCZ R-8064: Hassan; MCZ R-34967: Lake Shala; ZMB 10306: Lit Marafia; ZSM 44/21: Modjo; ZMB 19739: Omo area; ZMB 10305: Shoa, Mahal Unz. **KENYA.** MCZ R-29643: Mt. Sagalla; MCZ R-18587-88, SMF 41203: Nairobi.

***Acanthocercus ugandaensis.* KENYA.** MCZ R-41067: Bukori, Kitosh; MCZ R-68773: Kisumu, 60 km E; MCZ R-68972: Lumbwa; MCZ R-131085: Ngiya. **UGANDA.** MCZ R-30757: Jinja; AMNH 48039-40: Kichwamba; MCZ R-47353: Kigezi Distr., Nyakabande.