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A new species of the *Acanthocercus atricollis* complex (Squamata: Agamidae)

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Abstract. We describe a new species of the agamid genus *Acanthocercus* from Namibia and Angola, based on morphological and molecular evidence. The phylogenetic analysis of a fragment of the mitochondrial 16S rRNA gene suggests that the new species is closely related to the other taxa from southern Africa and is distinct from species from eastern and northeastern Africa. The new species is characterized by its high scale counts (mean scale rows around midbody 136, mean dorsal scale rows 103, mean ventral scale rows 101) and displaying males showing a blue coloration of the head, forelimbs, flanks of the anterior part of the body and distal half of the tail; a very distinct pale vertebral stripe between the blue flanks and enlarged yellowish dorsal scales on the posterior part of the body. In Namibia the species is restricted to a small area of grassland with mopane and Maklani palms in northern Ovamboland, but its distribution in Angola spans a diversity of habitats. We also recognize a potential new species from northern Angola and discuss the preliminary distribution of *Acanthocercus* in Angola.

Key words. *Acanthocercus* sp. n., Africa, Namibia, Angola.

Resumo. Descrevemos neste artigo uma nova espécie de Agamídeo do género *Acanthocercus* da Namíbia e de Angola, com base em evidências morfológicas e moleculares. A análise filogenética de um fragmento do gene mitocondrial 16S rRNA sugere que a nova espécie é relacionada com outros taxa do sul de África e distinta das espécies do leste e nordeste de África. A nova espécie é caracterizada pelo seu maior número de escamas (média de escamas à volta do corpo de 136, média de escamas em fiada dorsal 103, média de escamas em fiada ventral 101) e pelos machos em coloração exibitiva apresentarem um cor azulada na cabeça, braços, flancos da parte anterior do corpo e parte segunda metade distal da causa; uma linha vertebral pálida bem marcada entre os flancos azuis e as escamas dorsais amareladas presentes no parte posterior do corpo. Na Namíbia a espécie encontra-se restrita a uma pequena área de pradaria com Mutiate e palmeiras Malklani no norte da Ovambolândia, mas a sua distribuição em Angola engloba uma maior diversidade de habitats. Reconhecemos também a existência de uma potencial nova espécie no norte de Angola e discutimos uma potencial e preliminar distribuição do género *Acanthocercus* em Angola.

Palavras-chave. *Acanthocercus* sp. n., África, Namíbia, Angola.

Introduction

The agamid genus *Acanthocercus* Fitzinger, 1843 is distributed from the southwestern corner of the Arabian Peninsula, across the Horn of Africa and south to southern Africa. The area outside Arabia and the Horn of Africa is occupied only by the *Acanthocercus atricollis* (Smith, 1849) species complex, occurring from Ethiopia to the eastern and northern parts of South Africa. Klausewitz (1957) first reviewed the species complex and recognized six subspecies, which have since been elevated to species rank or recognized as synonyms by Wagner et al. (2018): *A. atricollis* from Botswana, Malawi, Mozambique, South Africa, Eswatini and Zimbabwe; *A. gregorii* (Günther, 1894)

from Burundi, Ethiopia, Kenya, Mozambique, Rwanda and Tanzania (including the synonym *A. loveridgei* [Klausewitz, 1957]); *A. kiwuensis* (Klausewitz, 1957) from DRC and Uganda; *A. minutus* (Klausewitz, 1957) from Ethiopia and Kenya; and *A. ugandaensis* (Klausewitz, 1957) from Kenya, Rwanda, Uganda, and Tanzania. Moreover, Wagner et al. (2012) described an additional species, *A. branchi*, from Zambia, and Wagner et al. (2018) revalidated the name *A. cyanocephalus* for individuals occurring in NW Zambia, Angola and northern Namibia. The phylogenetic relationships of the *A. atricollis* complex were examined by Wagner et al. (2018), who showed that the constituent taxa are very similar in morphology but genetically distinct and represent a cryptic group of closely related species. The availability of more extensive material of the complex from southern Angola, and the examination of specimens from northern Namibia (Ovamboland), both initially referred to *A. cyanocephalus* by Wagner et al. (2018), prompted a reassessment of these far-southwestern populations of *Acanthocercus*. Using an integrative approach incorporating morphological features as well as genetic data we demonstrate that *A. cyanocephalus* occupies only portions of Angola, and that southern Angola and adjacent northern Namibia support a previously undescribed member of the genus.

Material & methods

Material

In total 172 specimens [*A. atricollis* (21); *A.* cf. *atricollis* (4); *A. branchi* (6); *A. cyanocephalus* (13); *A. cyanogaster* (8); *A. gregorii* (52); *A. kiwuensis* (19); *A. minutus* (20); *A. ugandaensis* (25); *Acanthocercus* sp. n. (4)] were examined for morphological analysis (for details see appendix 1). Females, juveniles, and damaged specimens were excluded from the statistical data analysis but were used to compare the different species. Name-bearing types of the following taxa were examined: *Acanthocercus branchi* Wagner, Greenbaum & Bauer, 2012; *Agama cyanocephalus* Falk, 1925; *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, dry taxidermied (*A. cyanogaster*) or damaged specimens, it was not possible to include all name-bearing types in the statistical analysis.

Material from the collections of the following institutes were used: The Natural History Museum (BMNH), London, England; California Academy of Sciences (CAS), San Francisco, California, USA; Museu de História Natural e da Ciência da Universidade do Porto (MHNC-UP); Museum of Comparative Zoology (MCZ), Harvard University, Cambridge, Massachusetts, USA; Naturhistorisches Museum (NHMW), Wien, Austria; Natural History Museum of Zimbabwe (NMZB), Bulawayo; Port Elizabeth Museum (PEM) (Bayworld), South Africa; Senckenberg Museum (SMF), Frankfurt, Germany; University of Texas at El Paso (UTEP), Texas, USA; Zoologisches Forschungsmuseum A. Koenig (ZFMK), Bonn, Germany; Museum für Naturkunde (ZMB), Berlin, Germany; Zoologische Staatssammlung (ZSM), München, Germany.

Morphology

Measurements were taken with a digital caliper under a dissecting microscope to the nearest 0.1 mm. Forty-five measurements and scale counts and 27 other qualitative characters were scored and are shown in Table 1. Mensural and meristic characters have been used for PCA, while qualitative characters helped to distinguish the potential new species from other taxa. Specimens were grouped as operational taxonomic units (OTUs) on a species level. Juveniles were defined as specimens with a snout–vent length (SVL) less than 50% of the SVL of the largest specimen of the same OTU and excluded from the statistical analyses. Due to sexual dimorphism, only males were analyzed. The number of available female specimens was too small to conduct a separate analysis. *Acanthocercus cyanogaster* is not closely related to the *A. atricollis* group, but was included in the dataset as comparison for morphological similarities within the *A. atricollis* group.

Two different data sets have been analyzed: A large one with 172 specimens but only 14 characters and a small one with only 91 specimens but a higher number of 45 characters (see Table 1). All metric data were log-transformed to ensure normal distribution. Regression residuals were calculated on the morphometric variables using SVL as a covariable to account for allometry, i.e. to avoid size dependent intercorrelation effects, prior to conducting a principal component analysis (PCA) to assess the overall morphological variation between the putative taxa. PCAs were computed using the program PAST v.2.12 (Hammer et al. 2001).

Genetics

New DNA sequence data were obtained from eleven *Acanthocercus* individuals collected from Angola, northern Namibia, and South Africa (for GenBank accessions see Supplementary Table 1). Additional *Acanthocercus* sequences were downloaded from GenBank to have a nearly complete representation of the genus and to serve as outgroup taxa. Some sequences downloaded from GenBank PopSet 1579201217 were observed to have ~120 basepairs pertaining to the ND4 mitochondrial region appended to the 16s sequence. These regions were trimmed for the genetic analyses. Genomic DNA was extracted using a salt DNA extraction protocol (Aljanabi & Martinez 1997). Gene amplification of the mitochondrial 16s ribosomal RNA locus (16s) was performed using Polymerase Chain Reactions (PCR). Primer sequences follow Palumbi et al. (1991), and PCR reactions were carried out with 34 cycles at an anneal-

Table 1. Morphological characters (19 mensural, 26 meristic, 27 qualitative) used for the principal component analysis (PCA). Bold are those characters used in the large dataset, all mensural and meristic characters have been used in the small dataset, qualitative characters have been used for the description only.

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
Meristic characters	
RPP	Number of rows of precloacal pores
PP	Total number of precloacal pores
SL	Number of supralabial scales
IL	Number of infralabial scales
SO	Number of scales on the canthus above the eye
T	Temporal scales between eye and ear
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
SRW:1-3	Number of scale rings per whorl; anterior part dorsal (1), lateral (2), ventral (3)
Qualitative characters	
VFS	Vertebral scales large, same size or smaller than scales on flanks
DS	Dorsal scales homogeneous or heterogeneous
EDS	Enlarged dorsal scales smooth, keeled, no enlarged scales
DMS	Dorsal matrix scales absent, smooth, feebly keeled, keeled
FS	Flank scales smooth, feebly keeled, keeled
VS	Ventral scales smooth, feebly keeled, keeled
GS	Gular scales smooth, feebly keeled, keeled
UTS	Upper tail scales smooth, feebly keeled, keeled
LTS	Lower tail scales smooth, feebly keeled, keeled
OTS	Outer tail scales thorn like, not thorn like, strongly thorn like
PO	Pineal window visible, not visible
NS1	Nasal scale on or below the canthus rostralis
NS2	Nasal scale smooth or keeled
NS3	Nasal scale round or pear-shaped
NS4	Nasal scale flat or convex
ST	Scale tufts around the ear present, not present
Sli	Lifestyle pairs, colony, solitary
SDL	Subdigital lamellae keeled, not keeled
SBT	Scales between last tail spine
CV	No. of caudal vertebrae
FV	No. of vertebrae of the tail filament
CR	Caudal ribs absent or present
AS	annectans-type scale present, not present
LT	Longest toe 4th, equal, 3rd
TC	Male throat colored with a network, not with a network
AUS	Upper arms keeled, strongly keeled, normal
ECO	Living on tree, ground, rock

ing temperature of 50°C. PCR product was confirmed using gel electrophoresis and a negative control. A magnetic-bead solution (Rohland & Reich 2012) was used to clean successful PCR products before sequencing with Big-Dye v3.1 chemistry. An additional magnetic bead clean-up was performed prior to analyzing cycle sequencing product on an ABI 3730xl sequencer. Forward and reverse raw sequences were imported into Geneious v11.0.2 and contigs were created from extensive overlapping regions. Muscle 3.8.425 (Edgar 2004) implemented in Geneious was used to align sequences. Phylogenetic trees were estimated using maximum likelihood (ML) and Bayesian inference (BI) methods. ML tree inference was performed using RAxML v8.2.12 (Stamatakis 2014) with a GTRGAMMA substitution model and 1000 rapid bootstrap iterations. BI tree inference was performed using MrBayes v3.2.6 (Ronquist et al. 2012) with a GTR+I+G substitution model, sampling from the posterior distribution every 2000 generations for

20 million generations. Tracer v1.7.1 was used to check ESS values for convergence, while FigTree v1.4.4 was used to visualize all trees and manually root the ingroup clade using the (*A. annectans*, *A. cyanogaster*, *A. adramitanus*, and *A. yemensis*) sister clade. Uncorrected pairwise distances between and within groups were estimated in MEGA 7.0.26 (Kumar et al. 2016) using the same sequence alignment as described above, except for sites with missing data or gaps, which were ignored. Groupings were specified at the species level using GenBank identifications and phylogenetic clustering.

Nomenclatural act

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, as it is registered at Zoobank under the LSID (Life Science Identifier): urn:lsid:zoobank.org:pub:F8A2CC7C-593F-49B7-9C28-81EDBA149962. Therefore, the new name contained herein is available under the Code. The electronic edition of this work was published in a journal with a Zoobank registration and an ISSN, it has been archived, and it is available from the following digital repositorys: www.salamandra-journal.com.

Results

Morphology

Both PCA analyses of the mensural characters show the morphospace of the OTU of the putative new species overlapping with that of several other species of the complex. In the large dataset (Fig. 1) it overlaps with nearly all other OTU's, excluding only *A.* cf. *atricollis* (see Fig. 1, = *A.* sp. DRC), whereas it overlaps only with *A. cyanogaster*, *A. ugandaensis*, *A. minutus* and *A. gregorii* in the small dataset (see Fig. 2). Both PCA analyses of the meristic characters show the morphospace of the OTU of the potential new species clearly distinct from all other OTU's.

Genetics

The 16S tree (see Fig. 3) of the sequenced specimens plus sequences obtained from GenBank show the clade with specimens of the putative new species in only a moderate supported clade including *A. atricollis* group lineages from southern Africa and two specimens from the Democratic Republic of Congo (DRC). The relationships within this clade are weak, resulting in a polytomy, but the branch length of the putative new species is distinct from and comparable to lengths of other valid taxa. Both of the DRC specimens are subadults and a correct morphological identification is not possible. This clade comprises part of a polytomy with "*Acanthocercus cyanocephalus*" from Malanje in northern Angola and the lineage of specimens including *A. cyanocephalus* from the type locality in Zambia. The former clade likely represents yet another new species, but requires further investigation (Marques et al., own data). All of these clades are part of a more expansive lineage, including *A. atricollis* sensu stricto from southern Africa. Support values are too low to establish a robust pattern of the genetic diversity in this subgroup, but collectively these taxa are highly distinct from other species of the *A. atricollis* complex from East and NE Africa.

Uncorrected pairwise distances for the 16S sequences (see Supplementary Table 2) show the putative new species to be between 3.66 and 6.17% divergent from other members of the southern African *A. atricollis* complex, and 10.19–13.86% divergent from *Acanthocercus* species from the Horn of Africa and the Arabian Peninsula.

Acanthocercus margaritae **sp. n.**

(Figs. 4, 5, 6)

LSID: urn:lsid:zoobank.org:act:8C642E13-B26D-44A0-A924-40B94C84A642.

Stelio atricollis: Bocage (1895: 22)
Agama (*Stellio*) *atricollis* Monard (1931: 92)
Agama atricollis Monard (1937: 58)
Agama colonorum Angel (1923: 159)
Agama cyanogaster Loveridge (1957: 195)
Acanthocercus atricollis Branch (1998: 218)
Acanthocercus cyanocephalus [part] Wagner et al. (2018: 27), Branch et al. (2019: 313)
Acanthocercus sp. Marques et al. (2018: 27), Butler et al. (2019: 235), Baptista et al. (2019: 107)

Holotype. MCZ R190193 (Fig. 4), adult male from "near Oshikango, 200 m S of St. Mary's Mission," Kunene Region, Namibia [-17.471145 N, 15.935669 E], collected on November 26th 2011 by A.M. Bauer, M. Heinicke, W.R. Branch and J. Marais.

Paratypes. MCZ R190194, male with the same data as the holotype; CAS 263908 (field number AMB 10159), male from Bicuar National Park, camp headquarters [-15.10161 N, 14.83986 E], Huila Province, Angola, collected on July 26th 2017 by L.M.P. Ceríaco, M. Marques, S. Bandeira, T. Julio, B. Butler, and M. Heinicke; CAS 263911 (field number AMB 9358), male from Lubango, Kimbo do Soba [-14.93419 N, 13.46925 E], Huila Province, Angola, collected on July 21st 2017 by M. Marques, L.M.P. Ceríaco, S. Bandeira, M. Heinicke, T. Julio, and B. Butler; MHNC-UP/REP 422 (field number AMB 10987), male from Matunto, Bicuar National Park [-15.36345 N, 15.28316 E], Huila Province, Angola, collected on March 10th 2018 by L.M.P. Ceríaco, M. Marques, H. Valério, S. Elizalde and D. Elizalde.

Diagnosis. The new species is included in the genus *Acanthocercus* because of the combination of a heterogeneous body scalation and a tail that is segmented in distinct whorls. Within this genus, the heterogeneous body

scalation refers it to the *cyanogaster*/*atricollis* group and the high density of enlarged scales in combination with a black patch on the shoulders places it into the *A. atricollis* complex. *Acanthocercus margaritae* sp. n. is a medium sized lizard (mean SVL 112 mm [96–129 mm], mean total length 258 mm [217–299 mm]) of its genus and overall is very similar in morphology to *A. atricollis* and *A. cyanocephalus*. However, it is distinct from all other species of the complex in its meristic characters. The new species is characterized by its high numbers of scale counts (mean scale rows around midbody 136, mean dorsal scale rows 103, mean ventral scale rows 101). Displaying males are characterized by a blue coloration of the head, forelimbs, flanks of the upper part of the body and second half of the tail; a pale vertebral band, very distinct between the blue flanks and enlarged yellowish dorsal scales on the lower part of the body.

Differential comparison. *Acanthocercus margaritae* sp. n. can be distinguished from other taxa of the *A. atricollis* complex by the following characters (see also Table 2):

(a) *Acanthocercus atricollis* is larger in SVL (mean 129 mm vs. 112 mm) and in total length (mean 302 mm vs. 258 mm). The mean counts of scale rows around midbody (112 vs. 136), dorsal scales (67 vs. 103), and ventral scales (87 vs. 101) are all lower than in the new species. The ranges of these characters are also higher in *A. margaritae* sp. n. than in *A. atricollis* (see Table 2). The mean number of precloacal pores is higher in *A. atricollis* than in the new species (22 vs. 14).

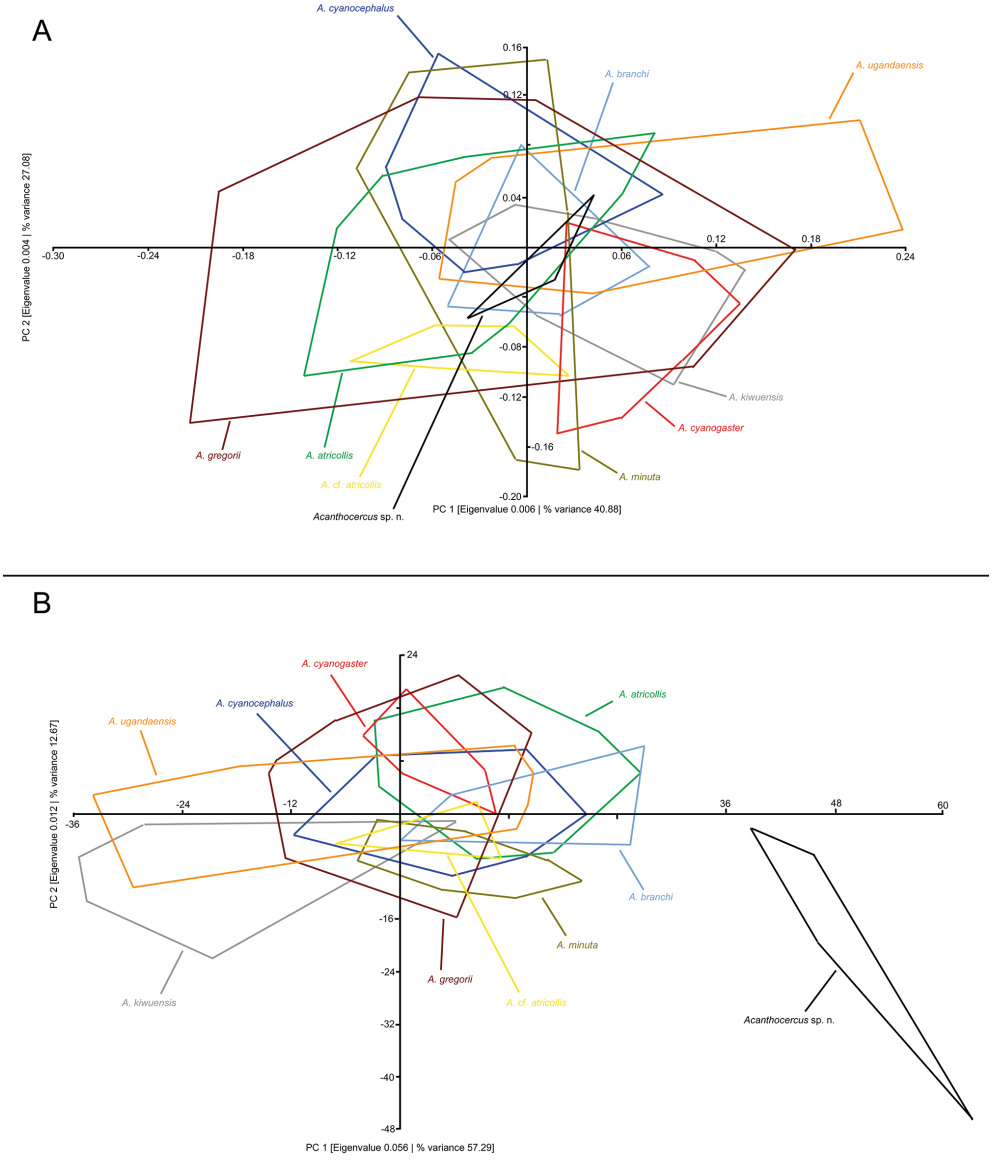

Figure 1. PCA plot of the "large" dataset using 168 specimens and 14 characters. A) showing the comparison of mensural character;, B) showing the meristic characters. For characters see Table 1.

Table 2. Characters and values to distinguish *Acanthocercus margaritae* sp. n. from its closest relatives. Values are given in the format: min–max (mean) n.

	SVL (mm)	TOTAL (mm)	SaM	D	V	PP
A. atricollis	107-151 (129) 21	248-347 (302) 21	103-125 (112) 21	52-83 (67) 21	76-102 (87) 21	(22) 21
A. branchi	83-131 (109) 6	194-313 (262) 6	103-130 (117) 6	67-81 (73) 6	79-95 (88) 6	17-23 (20) 6
A. cyanocephalus	113-149 (138) 13	276-372 (334) 13	96-119 (108) 13	58-78 (68) 13	69-94 (80) 13	15-33 (22) 13
A. cyanogaster	80-118 (101) 8	176-303 (255) 8	104-115 (109) 8	59-75 (65) 8	69-82 (76) 8	26-54 (38) 8
A. gregorii	74-138 (119) 52	189-360 (291) 52	88-119 (104) 52	52-85 (64) 52	70-96 (81) 52	7-37 (22) 52
A. kiwuensis	78-130 (111) 19	200-334 (290) 19	76-108 (87) 19	55-77 (63) 19	57-88 (67) 19	8-12 (10) 19
A. minutus	85-120 (101) 20	189-288 (234) 20	100-120 (108) 20	69-88 (79) 20	71-88 (78) 20	9-34 (26) 20
A. ugandaensis	91-126 (103) 25	221-351 (275) 25	75-117 (94) 25	54-74 (63) 25	59-95 (73) 25	18-35 (24) 25
A. margaritae sp. n.	96-129 (112) 4	217-299 (258) 4	131-143 (136) 4	81-133 (103) 4	94-107 (101) 4	9-19 (14) 4

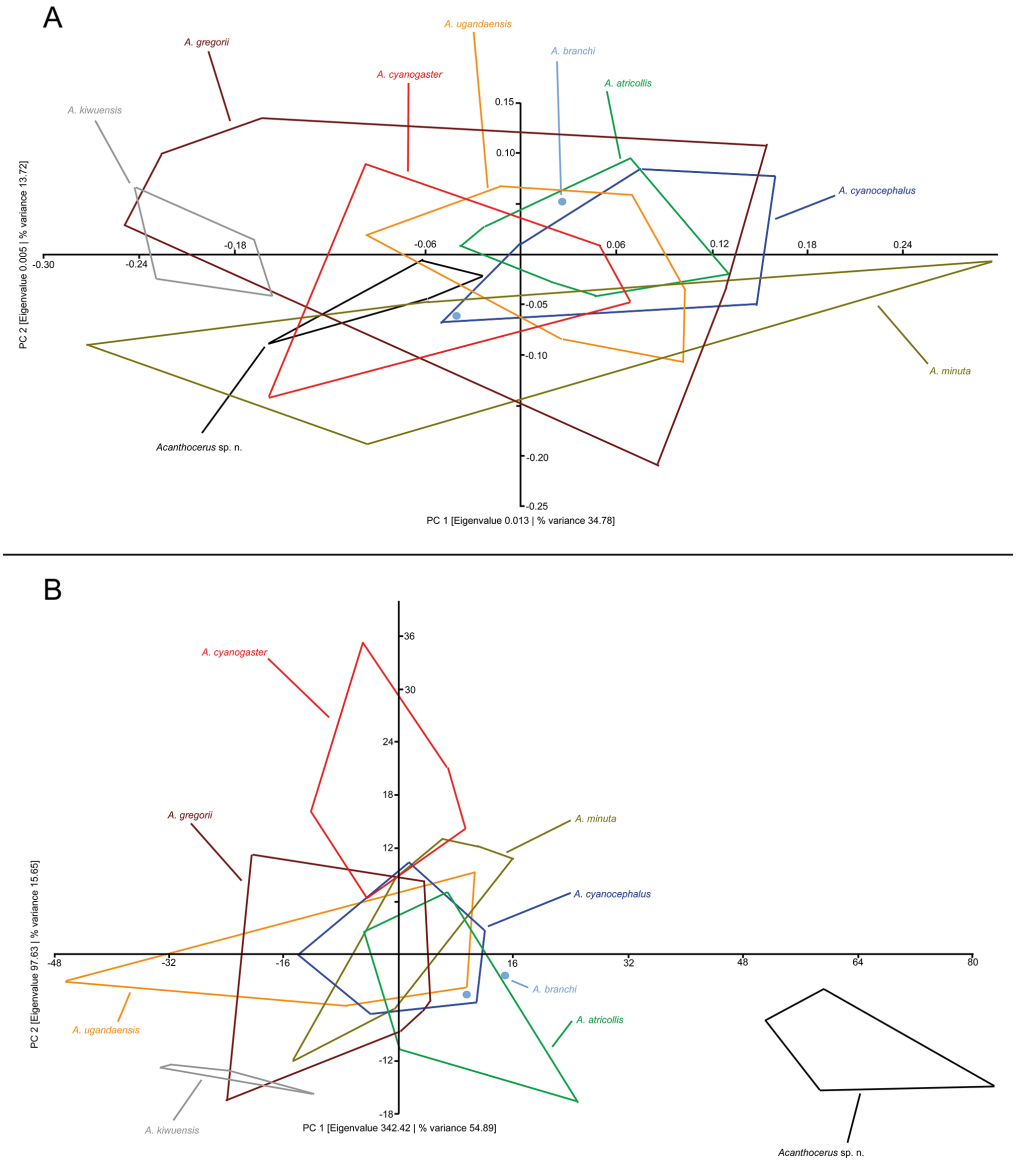

Figure 2. PCA plot of the "small" dataset using 91 specimens and 45 characters. A) showing the comparison of mensural character;, B) showing the meristic characters. For characters see Table 1.

(b) *Acanthocercus branchi* has lower mean counts of scale rows around midbody (117 vs. 136), dorsal scales (73 vs. 103), and ventral scales (88 vs. 101) than the new species. The ranges of these characters are higher in *A. margaritae* sp. n. than in *A. branchi* (see Table 2). The mean number of precloacal pores is higher in *A. branchi* than in the new species (20 vs. 14).

(c) *Acanthocercus cyanocephalus* is larger in size than *A. margaritae* sp. n. (SVL mean 138 vs. 112| mean total length 334 vs. 258) and has lower mean counts of scale rows around midbody (108 vs. 136), dorsal scale (68 vs. 103), and ventral scales (80 vs. 101). The ranges of these characters are also distinctly higher in *A. margaritae* sp. n. than in *A. cyanocephalus* (see Table 2). The mean number of precloacal pores is higher in *A. cyanocephalus* than in the new species (22 vs. 14).

(d) *Acanthocercus cyanogaster* has lower mean counts of scale rows around midbody (109 vs. 136), dorsal scales (65 vs. 103), and ventral scales (76 vs. 101) than the new species. The ranges of these characters are higher in *A. margaritae* sp. n. than in *A. cyanogaster* (see Table 2). The mean number of precloacal pores is higher in *A. cyanogaster* than in the new species (38 vs. 14).

(e) *Acanthocercus gregorii* has lower mean counts of scale rows around midbody (104 vs. 136), dorsal scales (64 vs. 103), and ventral scales (81 vs. 101) than the new species. The ranges of these characters are higher in *A. margaritae* sp. n. than in *A. gregorii* (see Table 2). The mean number of precloacal pores is higher in *A. gregorii* than in the new species (22 vs. 14).

(f) *Acanthocercus kiwuensis* has lower mean counts of scale rows around midbody (87 vs. 136), dorsal scales (63 vs. 103), and ventral scales (67 vs. 101) than the new species. The ranges of these characters are higher in *A. margaritae* sp. n. than in *A. kiwuensis* (see Table 2). The mean number of precloacal pores is lower in *A. kiwuensis* than in the new species (10 vs. 14).

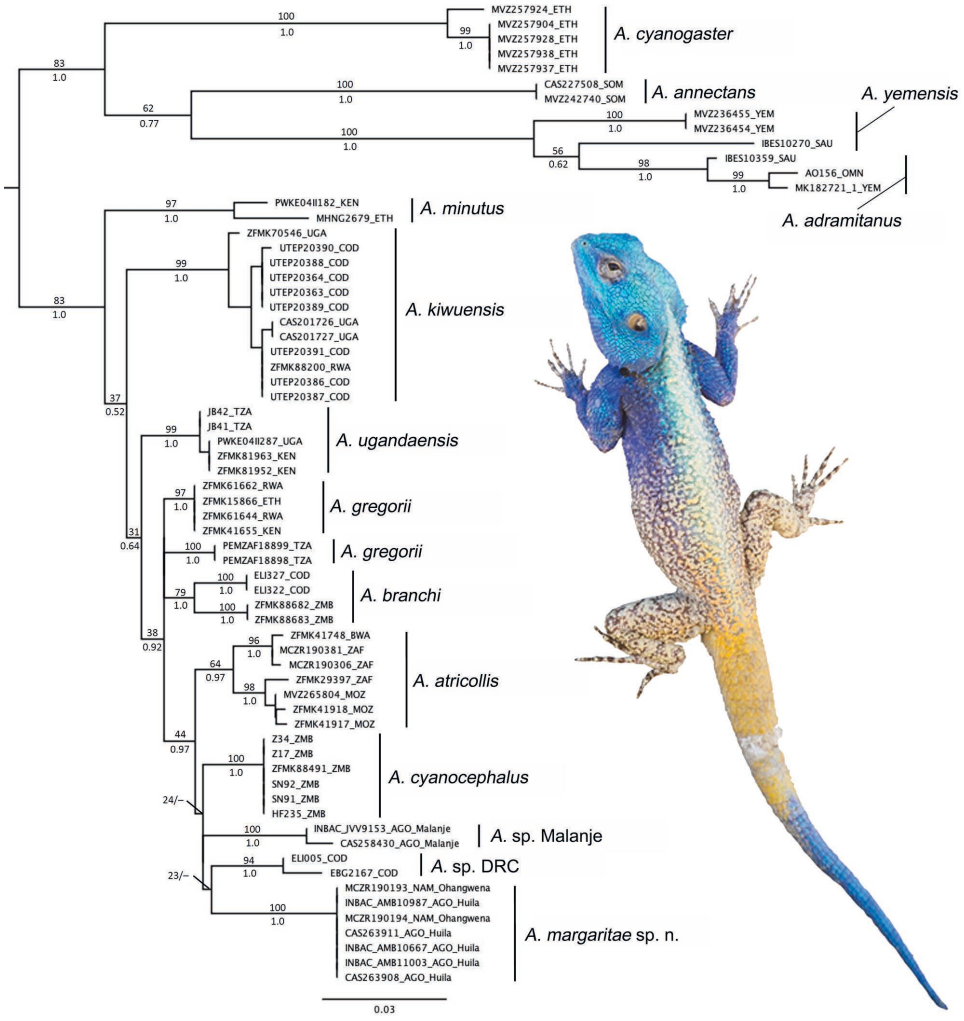

Figure 3. Maximum Likelihood (ML) phylogeny (best tree) based on a sequence of ~500 bp of 16S ribosomal RNA inferred by using the GTRGAMMA model of nucleotide substitution in RAxML. Support values (bootstrap/posterior probabilities) are shown at each node.

(g) *Acanthocercus minutus* is smaller in SVL (mean 101 mm vs. 112 mm) and in total length (mean 234 mm vs. 258 mm). It has lower mean counts of scale rows around midbody (108 vs. 136), dorsal scales (79 vs. 103), and ventral scales (78 vs. 101) than the new species. The ranges of these characters are higher in *A. margaritae* sp. n. than in *A. minutus* (see Table 2). The mean number of precloacal pores is higher in *A. minutus* than in the new species (26 vs. 14).

(h) *Acanthocercus ugandaensis* is smaller in SVL (mean 103 mm vs. 112 mm) but longer in total length (mean 275 mm vs. 258 mm). It has lower mean counts of scale rows around midbody (94 vs. 136), dorsal scales (63 vs. 103), and ventral scales (73 vs. 101) than the new species. The ranges of these characters are higher in *A. margaritae* sp. n. than in *A. ugandaensis* (see Table 2). The mean number of precloacal pores is higher in *A. ugandaensis* than in the new species (24 vs. 14).

Description of the holotype. Adult male. Measurements: snout–vent length (SVL) 144.4 mm, tail length (TL) 176.6 mm, head length (HL) 37.4 mm, head width (HW) 34.9 mm, head height (HH) 17.7 mm, left forelimb 39 mm, left hind limb 51 mm. Habitus stout, with a large triangular head that is distinct from the body; tail relatively short. Nasal scale flat to faintly convex, smooth, oval and situated slightly below canthus rostralis, pierced by a round nostril in the posterior part of scale, directed laterally. Scales on anterior, lateral and central parts of head large, but abruptly smaller from behind ear opening, only about one fourth of the size of large head scales; head scales unequal in size, not oriented in the same direction, usually smooth, sporadically heavily keeled or with a rough surface, with free anterior margins and only sporadically with sensory pits. Fourteen supralabial scales and twelve sublabial scales on both sides; supraocular scales smooth, eleven scales along canthus rostralis from nasal to behind eye; six scales from nasal to anterior margin of eye; parietal shield an elongate hexagon; pineal organ small, visible in posterior part of parietal shield. Ear opening large, about same size as eye, margin lacking a semicircle of spinose mucronate scales; tympanum superficial. No nuchal crest present. Gular scales flat, smooth, juxtaposed and becoming smaller towards gular fold. Dorsal body scales a mix of small and smooth matrix scales, sometimes giving the impression of granular scales, and scattered, pale white-edged, enlarged scales. Large scales keeled, sometimes mucronate or spinose, not arranged in clusters, but rather in four, very indistinct, transverse rows between limbs. Ninety dorsal scales along vertebral column from midpoint of pectoral region to midpoint of pelvic region. Vertebral region covered by a mix of small and large scales, forming a pattern distinct from rest of lateral parts of body. Large vertebral scales keeled, rarely some feebly keeled, smaller scales. Ventral body scales smooth, slightly imbricate at their posterior margins, in 94 scale rows from midpoint of pectoral region to precloacal pores. One hundred thirty-seven scale rows around the body behind the forelimbs; 143 around midbody and 129 around the body in front of the hind limbs. Precloacal scales in two rows (the second one weakly developed), eleven pores in anterior row, six in posterior. Scales on upper side of forelimb unequal in size and strongly keeled, smooth on underside; upper arm scales somewhat larger than largest dorsal body scales, becoming smaller towards underside and manus. Fourth finger longest, digital length decreasing 3–2–5–1, subdigital lamellae keeled and mucronate, 20 under left 4th finger. Scales on upper side of hind limb keeled to smooth, becoming completely smooth on underside; scales on upper thighs unequal in size, and a mix of small and scattered enlarged scales that are as large as the enlarged dorsal body scales. Fourth toe longest, digital length decreasing 3–2–5–1, subdigital lamellae keeled and mucronate, 22 under left 4th toe. Tail with indistinct whorls of four scale rings (one ring consists of distinctly smaller scales) in its basal portion, whorls becoming slightly more distinct towards tip and comprise three scale rings only, caudal scales keeled and mucronate. First third of tail slightly swollen, scales larger than in other parts of the body, strongly robust and keeled. Distal portion of the tail much thinner and slightly compressed.

Figure 4. Holotype (MCZ R190193) of *Acanthocercus margaritae* sp. n. from "near Oshikango, 200 m S of St. Mary's Mission," Namibia [-17.471145 N, 15.935669 E].

After formalin fixation and ten years of preservation in ethanol (see Fig. 4), head dark brown with some white scales. Throat bluish at base, whitish at the centre and upper parts. Black patch on shoulders. Ground color of dorsum grayish, enlarged scales on upper and lateral parts of body and limbs plain white to dirty white. Ventral side of body, limbs and tail dirty grayish. Enlarged scales on upper side of tail base distinctly whitish. Scales becoming more brownish-dirty white striped towards tail tip.

Variation. Some variation of the type series is shown in Table 2. Snout–vent length 96–129 mm (mean 112 mm). Tail length 121–177 mm (mean 148 mm), with the ratio TL/SVL 1.23–1.44 (mean 1.32); head length 29–39 mm (mean 34 mm); supralabial scales on the left side 12–14 (mean 13); infralabial scales on the left side 12–12; supraocular scales on the left side 5–6 (mean 6); temporal scales on the left side 5–9 (mean 7); scale rows around fore body 132–153 (mean 141); scale rows around hind body 112–136 (mean 125); subdigital lamellae under Fi1 11–12 (mean 11), Fi2 14–15 (mean 15), Fi3 19–20 (mean 20), Fi4 20–23 (mean 21), Fi5 15–17 (mean 16); subdigital lamellae under TOE1 10–23 (mean 15), TOE2 14–16 (mean 15), TOE3 20–23 (mean 21.5), TOE4 22–24 (mean 23), TOE5 19–20 (mean 20); rows of precloacal rows one or two (mean 1.5).

Coloration. Coloration in freshly dead male animals (see Fig. 5) brownish, with a gray and black patterning and a ringed tail. Lateral and ventral parts of the head and parts of the forelimbs blue and partly gray or brown. Ventral parts of the body, limbs and tail dirty whitish with a brown patterning. In displaying males (see Fig. 6) head, fore limbs, upper parts of the flanks blue and second half of the tail brilliant blue; a pale vertebral band from the neck to the tail is present, distinct anteriorly between the blue flanks becoming more indistinct posteriorly; enlarged dorsal scales of the lower part of the body yellowish, matrix scales bluish and becoming black on the hind limbs; first half of the tail greenish. Coloration of females in life unknown.

Coloration of displaying males (Fig. 7) is overall more similar to *A. atricollis* than to *A. cyanocephalus*. However, in *A. margaritae* sp. n. the blue coloration on the flanks is not intermixed with yellowish colored scales. The new species is clearly distinct from *A. cyanocephalus* and *A. branchi*, in that both of the latter species have a dark brown to black body coloration with intermixed yellowish to white scales and lack blue coloration on the flanks.

Relationships. *Acanthocercus margaritae* sp. n. is closely related to specimens of an unknown species from the Democratic Republic of the Congo (DRC), specimens hitherto identified as "*Acanthocercus cyanocephalus*" [= *A.* sp. Malanje, see Fig 3] from Cangandala National Park, Malanje Province in northern Angola (e.g., Ceríaco et al. 2018), *A. cyanocephalus* and *A. atricollis*. Interspecific relationships within this clade are all poorly supported, precluding meaningful resolution of relationships. This clade as a whole, however, is supported by a high (0.97) posterior probability and is, in turn, closely related to *A. branchi* and *A. gregorii*, while the morphologically very similar species

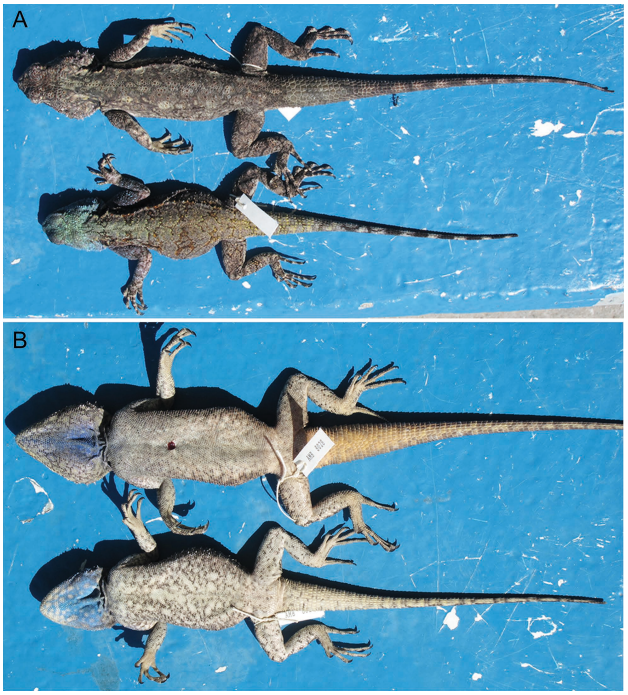

Figure 5. Freshly dead holotype (MCZ R190193) and paratype (MCZ R190194) from "near Oshikango, 200 m S of St. Mary's Mission," Kunene Region, Namibia [-17.471145 N, 15.935669 E].

Figure 6. Living paratypes. (A) CAS 263908 from Bicuar National Park, camp headquarters [-15.10161 N, 14.83986 E], Huila Province, Angola; (B) MHNC-UP_REP 422 from Matunto, Bicuar National Park [-15.36345 N, 15.28316 E], Huila Province, Angola.

A. ugandaensis and *A. kiwuensis* are genetically more distantly related and *A. minutus* is basal to the entire species group (see Fig. 3).

Distribution. The new species is so far known from the two localities of the type series and several additional localities from Namibia and Angola (see Fig. 8). However, we suggest that it is also present in the intervening area. The distribution in Namibia includes the following specimens and localities: 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.[iches] 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;" SMF 65987: "Onguediva;" SMF 66928–9: "Oshikango."

All specimen-vouchered Namibian localities are concentrated in the northern Oshana Region and the adjacent

Figure 7. Images of displaying males of *Acanthocercus margaritae* sp. n. (A) from Onesi, Omusati Region, Namibia (-17.478164 N, 14.650651 E). Photo by Jukka Jantunen and available from iNaturalist under the observation code 1963735. (B) from near Ondjiva, Cunene Province, Angola [-17.674433 N, 15.799167]. Photo by Pedro Martins [7 December 2018] and available from iNaturalist under the observation code 19293652.

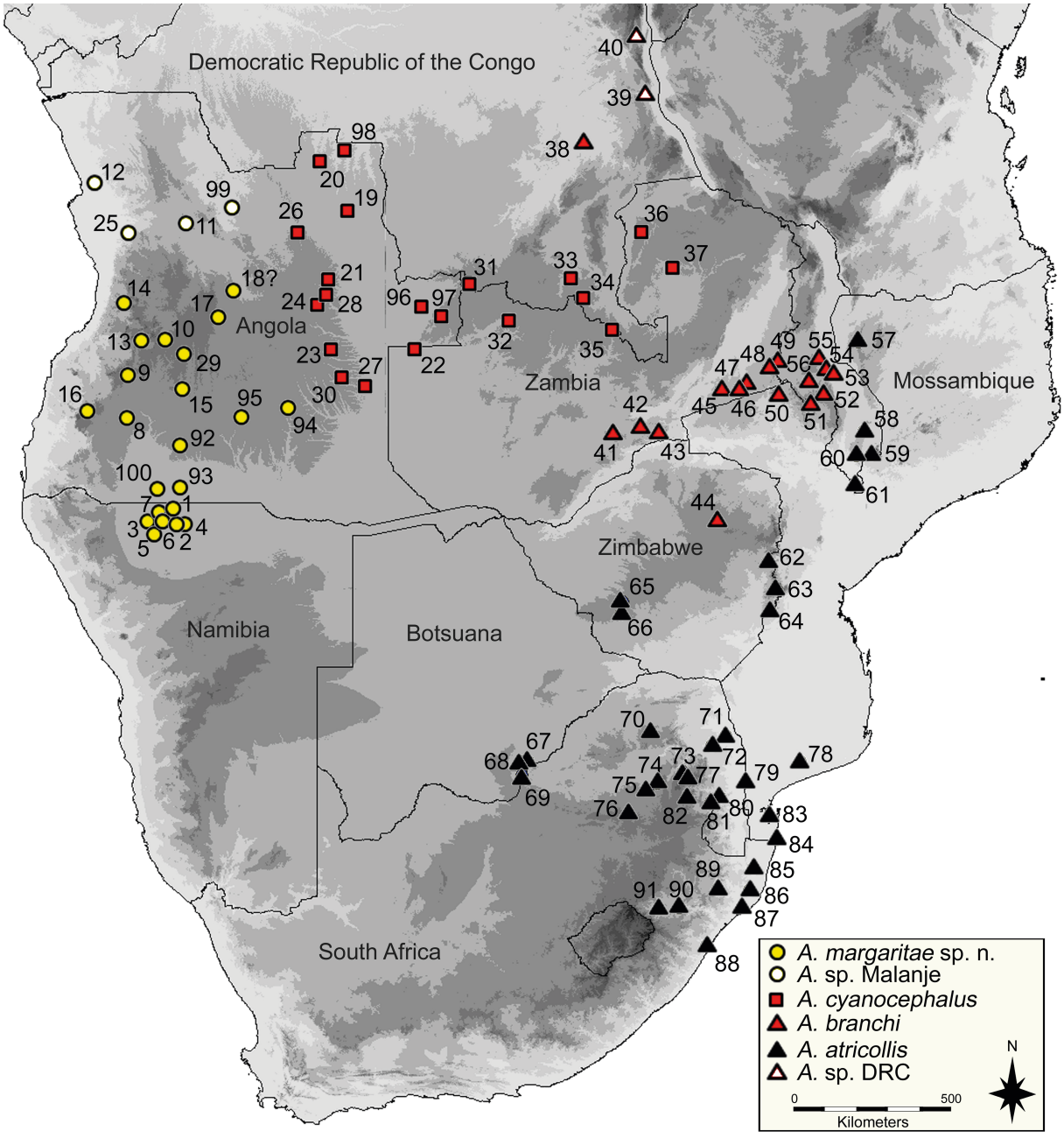

Figure 8. Distribution of *Acanthocercus* taxa in southern and southern central Africa. 1= Oshikango; 2= Odangwa; 3= Oshakati; 4= Mafa; 5= Ompundja; 6= Onguediva; 7= Odimbo; 8= Bicuar National Park, Matunto; 9= Kalukembé; 10= Huambo; 11= Cangandala; 12= Dande; 13= Cuma; 14= Mombolo; 15= Capelongo; 16= Lubango; 17= Kuito; 18= Pavalange, Kimbango; 19= De Beers Lucapa; 20= Lake Carumbo, Base camp; 21= Luma Cassai; 22= Chitau (Zambia); 23= Cassamba; 24= Fazenda Santa Cruz; 25= Calombe; 26= Cacolo; 27= Vila Gago Coutinho; 28= Luso; 29= Cachingues; 30= Serra Luchazes; 31= Ikelenge; 32= Kalumbila; 33= Murungu; 34= Lubumbashi; 35= Mufulira; 36= Kawambwa; 37= Lake Bangeulu; 38= Manono; 39= Kalemie; 40= Lulimba; 41= Lusaka; 42= 80 km E of Lusaka; 43= Chakwenga River; 44= Ruwa near Harare; 45= Petauke; 46= Katete; 47= 30 km W of Katete; 48= Chipata; 49= Chikowa; 50= Chifumbazi; 51= 30 miles NNW of Furancungo; 52= Chongoni Forest Reserve; 53= Salima; 54= Chitala River; 55= Nchisi Mountain; 56= Lilongwe; 57= Serra Jeci Grasslands; 58= Zomba Plateau; 59= Mlanje Mountain; 60= Cholo Mountain; 61= Misala; 62= Fern Valley; 63= Mt.Sei, Melsetter; 64= Mt.Silinda; 65= Bulawayo; 66= Rhodes Grave, Matobo Hills; 67= Gaborone; 68= Gabane; 69= Otse; 70= Woodbush; 71= Krueger National Park; 72= Hoedspruit Airforce base; 73= 12 km N of Lydenberg; 74= Gerlachshoop [Mission Station]; 75= Loskopdam; 76= Wonderboom, near Pretoria; 77= Lydenburg (=Mashishing); 78= 7 km North of Chibuto; 79= Komatipoort ; 80= Louwscreek; 81= Barberton; 82= Waterval Onder; 83= Delagoa Bay (Maputo); 84= Ponta do Ouro; 85= Mkuze Game Reserve; 86= Somkele; 87= Empangeni; 88= Durban; 89= Umfolozi; 90= Tugela Estates [Farm]; 91= Rustenberg [Farm]; 92= Mupa; 93= Mupanda; 94= Région du Kwito, affluent du Kubango; 95= Kakindo; 96= Cazombo; 97= Calunda; 98= Dundo; 99= Cassange; 100= Ondjiva.

western Ohangwena Region and northwestern Oshikoto Region. This area lies to the north of Etosha National Park in the area formerly constituting the "Bantustan" of Ovamboland. Although this entity ceased to exist as a separately administered "ethnic zone" with the independence of Namibia in 1989, the heavily populated northern areas of these three regions, plus that of the Omusati Region further to the west, are collectively still commonly referred to as Ovamboland. This area seems to be the southernmost distribution of *Acanthocercus margaritae* sp. n., which enters northern Namibia from southern Angola. Auerbach (1987) plotted a locality for "*A. atricollis*", 30 km NW of Sepupa in far northwestern Botswana based on a NMZB specimen. This lies at the western periphery of the Okavango Panhandle, about 45 km south of the western Caprivi Strip (Kavango Region). This locality is more than 600 km distant from the nearest *A. margaritae* sp. n. locality and on biogeographic grounds is more likely to be assignable to *A. cyanocephalus*. It is 400 km or more away from the more-or-less contiguous populations of tree agamas in eastern Botswana. Griffin (2003) mentions the species' occurrence in Etosha National Park, but this is unsupported by voucher specimens or by photo-vouchered records on relevant online sites. The northern boundary of Etosha lies at 18.5° S, about 64 km south of the nearest *Acanthocercus* record near 18.0° S. Griffin (2003) also mentioned a record from Rundu and the possible occurrence in the Caprivi parks (now Zambezi Region). However, there is no evidence for *Acanthocercus* in Namibia east of about 16.20°E. The westernmost record is supported by a photo voucher (iNaturalist.org/observations/19637354) from -17.478164, 14.650651, showing a male in full color (see Fig. 7).

In Angola, *Acanthocercus* spp. are widely distributed, occurring in all provinces except those in the far northwest and in Namibe in the far southwest (Marques et al. 2018). A locality given by Wagner et al. (2018) for Namibe is doubtful as it is not linked with a specimen and most likely refers to *Agama schacki* or may be a historical record representing the point of shipment or a generalization for southwestern Angola a whole. Based on Wagner et al. (2018) and the preliminary results of this study, Marques et al. (2018) allocated Angolan tree agamas to either *A. cyanocephalus*, occurring north of about 14°S or *Acanthocercus* sp. (= *A. margaritae* sp. n.) with localities in Huila, Cunene and northern Cuando Cubango provinces. This decision was followed by Butler et al. (2019) and Baptista et al. (2019). From our genetic data (see Fig. 3) northern Angolan specimens are closely related to both *A. margaritae* sp. n. and *A. cyanocephalus*, but a detailed reexamination in light of the current information is required. From a purely biogeographic perspective it seems likely that the Malanje species has a broad distribution in the northwest of the country, in miombo dominated areas, whereas *A. cyanocephalus* is present in Moxico and the Lundas, where the habitats include both Angolan and Central Zambezian miombo and southern Congolian forest-savanna mosaic on aeolian soils. Angolan localities possibly attributable to *A. margaritae* sp. n. include Vila da Ponte, Capelongo and Huila in the Province of Huila (Bocage 1895, Monard 1937, Marques et al. 2018), Mupa and Mupanda in Cunene Province (Monard 1937, and Fig. 8), and Kwito and Kakindo in Cuando Cubango (Angel 1923, Monard 1937). The proximity of our genotyped Huila localities to the two more western historical Huila records and of the Kunene records to the Namibian records certainly argues strongly for these records, at a minimum, being *A. margaritae* sp. n. The three more eastern *Acanthocercus* sp. (those of Kwito and Kakindo in Cuando Cubango; Angel 1923; Monard 1937) are tentatively identified as also belonging to this species, but all these specimens require reexamination.

In addition to the Namibian localities, it seems likely that most of the Angolan localities plotted as *A. cyanocephalus* by Wagner et al. (2018) are either referable to *A. margaritae* sp. n. or to the as-yet-unnamed taxon represented in our genetic data set from Malanje Province. However, numerous localities from northeastern Angola plotted by Marques et al. (2018) are probably true *A. cyanocephalus*. The area occupied by *A. margaritae* sp.

Figure 9. Habitat of *Acanthocercus margaritae* sp. n. in area of Maklani palms (*Hyphaene petersiana*) near the Calueque-Oshakati canal system south of Oshikango, Namibia.

n. spans a significant rainfall gradient (~400 – >1000 mm/yr) and elevation range (1100–2000 m). All of the Namibian and Cunene Province populations correspond roughly to the Western Zambezian Grasslands ecoregion (Olson et al. 2001), although more northern candidate populations lie in the much more extensive Angolan Miombo Woodlands ecoregion (see Marques et al. 2018:18).

Ecology. *Acanthocercus margaritae* sp. n. is a tree dweller as is typical for most of the taxa of the species complex (Reaney & Whiting 2002, Wagner et al. 2018). In Namibia it occupies areas on the interior plain of northern Ovamboland at elevations around 1100 m corresponding roughly to the Cuvelai River drainage. The area receives about 400 mm of rain per year, falling mostly in late summer (January through April). Vegetation is characterized by grasslands mixed with open mopane (*Colophospermum mopane*) woodlands with stands of Maklani palms (*Hyphaene petersiana*) (Fig 9). However, the area is the most densely populated region in Namibia with significant small-scale agriculture, many villages, and some larger urban centers. *Acanthocercus* is often seen on both native trees and ornamental trees and shrubs in gardens, as well as on the walls of buildings, although it seems to avoid areas of high human activity. In Angola the species occurs in considerably different habitats (see e.g., Fig. 10), from miombo forest areas to open mopane woodlands (Grandvaux-Barbosa 1970) and anthropogenically transformed landscapes such as farms or even within major urban areas such as Lubango.

Etymology. The species epithet "*margaritae*" is formed as a genitive Latin noun to honor the Greek scientist Dr. Margarita Metallinou (1985 –2015) whose promising career was tragically cut short on the 2nd of July 2015 by a wildlife encounter in Zambia. This new species is a special tribute to her memory from all the authors of this publication to recognize her enthusiasm, passion and dedication to herpetology.

Figure 10. Habitat of *Acanthocercus margaritae* sp. n. at the Matunto Post, Bicuar National Park, Huila, where paratype MHN-CUP_REP 422 was collected.

Discussion

The population of *Acanthocercus* in Namibia was historically recognized as *Acanthocercus atricollis* (see e.g., Klausewitz 1957), but Wagner et al. (2018) tentatively placed them in the revalidated species *Acanthocercus cyanocephalus*. However, the correct identity was still questionable as specimens from Namibia were not included in the analysis by Wagner et al. (2018) and were only used for geographic information. The aim of this study was to clarify the status of the Namibian and southern Angolan population of *A. cyanocephalus* and both the morphological and genetical analysis have clearly shown that the population is distinct to this taxon and is described here as *Acanthocercus margaritae* sp. n.

The geographic range of the species is not entirely resolved. Obviously, the populations in northern Namibia are the southwesternmost records, as the genus *Acanthocercus* is not known elsewhere in the country. *Acanthocercus margaritae* sp. n. enters Namibia from southern Angola and while we have a good knowledge about the distribution in Namibia, the new species is so far only known with certainty from Bié, Cunene and Huila provinces in Angola.

However, the correct status of specimens from northwestern Angola (Malanje) and the DRC remains unknown. While material of adult specimens from Malanje is available, the specimens from DRC are subadults and the identity will not be clarified until adult specimens are available. Further research includes the clarification of the correct distribution areas of the species in Angola. Even though the male coloration of *A. margaritae* sp. n. is similar to *A. atricollis* from South Africa, it is clearly distinct from that of *A. cyanocephalus*, the other *Acanthocercus* species occurring in Angola. Moreover, scale counts of *A. margaritae* are quite distinctive to all other species of the *Acanthocercus atricollis* complex. Therefore, even citizen scientist contributions like iNaturalist can contribute meaningfully to a good understanding of the distribution of *Acanthocercus* in Angola, if males with display coloration are figured.

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Appendix 1

Material examined, excluding the type series.

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 [=NWProvince] (ZFMK 2691–692).

Acanthocercus aff. *atricollis*.––DRC. Haut-Katanga, Marungu Highlands, Mwaseini (ELI005); South Kivu,road ca. 4 km NE of Lulimba, 1194 m (EBG2167).

Acanthocercus branchi.––DRC. Tanganyika, Manono (ELI322, 323). MALAWI. Chongoni Forest Reserve (ZMB 76267); Lilongwe (ZMB 76264). ZAMBIA. Chakwenga river (NMZB-UM 4463); Chikowa (NMZB-UM 27144–45); Chipata (ZFMK88682); 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.––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. Mkonumbi (BMNH 1946.8.28.67); 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. Serengeti, 6 km Nof 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 (ZFMK21073–086). Kakoma (SMF 10138); Tabora Udjidji (ZFMK 20854).

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); Ituri, Bunia,1248 m (UTEP 20389 formerly EBG2455); Ituri, Epulu (Ituri Forest), 740 m (UTEP 20390 formerly EBG2521); South Kivu, 100 m W of the shore of Lake Kivu at Isale (UTEP 20391 formerly EBG1903). RWANDA. Kibuye at Lake Kivu (ZFMK 88200); 'Kissenji'[=Gisenyi] (ZMB23906). UGANDA. Kampala (ZFMK 68489, 70546–549); Rukungiri Dist., Byumba (CAS 201726–727).

Acanthocercus minutus.––ETHIOPIA. Dscheffedenza, Shoa (ZMB 29089); Gojam, Blue Nile Canyon (ZFMK 56655); Oromia, Didessa, Woreda (ZFMK 56656); Shoa Province, Akaki, Modjo (ZFMK2683–84, -2686–88); Shoa, Descheffedenza (ZMB 29089); Shoa Province, Lake Langano (ZFMK55356–357,55553, 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, JamboVillage (ZFMK 65181); Mount Ruwenzori (ZFMK 63335); Ruwenzori, Fort Portal (ZFMK63355–359); Ruwenzori, Kasese (ZFMK 63143–145, 63275–281); Ruwenzori, Nyakalengijo (ZFMK63236); Ruwenzori, Semliki Forest (ZFMK 64489, 63294–295); Uganda (ZMB 11904).

Acanthocercus spec. n.–– DRC. Katanga (MHNG 778.23).

Supplementary data

The following data are available online:

Supplementary document 1. GenBank accession numbers of the sampled used in this study, including vouchers and localities.

Supplementary document 2. Uncorrected pairwise distances for within (bold diagonal) and between (under diagonal) *Acanthocercus* species with the 16S ribosomal RNA locus.