



urn:lsid:zoobank.org:pub:63D950B1-10B3-4EC1-B4E6-8558F5618DF6

## Another Angolan Namib endemic species: a new *Nucras* Gray, 1838 (Squamata: Lacertidae) from south-western Angola

<sup>1,2</sup>William R. Branch, <sup>1,3,\*</sup>Werner Conradie, <sup>4,5,6</sup>Pedro Vaz Pinto, and <sup>7,8</sup>Krystal A. Tolley

<sup>1</sup>Port Elizabeth Museum, P.O. Box 13147, Humewood, Port Elizabeth 6013, SOUTH AFRICA <sup>2</sup>Department of Zoology, Nelson Mandela University, Port Elizabeth 6031, SOUTH AFRICA <sup>3</sup>School of Natural Resource Management, George Campus, Nelson Mandela University, George 6530, SOUTH AFRICA <sup>4</sup>Fundação Kissama, Rua 60 Casa 560, Lar do Patriota, Luanda, ANGOLA <sup>5</sup>CIBIO/InBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Universidade do Porto, Campus de Vairão, Vairão, PORTUGAL <sup>6</sup>TwinLab CIBIO/ISCED, Instituto Superior de Ciências da Educação da Huila, Rua Sarmento Rodrigues s/n, Lubango, ANGOLA <sup>7</sup>South African National Biodiversity Institute, Kirstenbosch Research Centre, Private Bag X7, Claremont 7735, Cape Town, SOUTH AFRICA <sup>8</sup>Centre for Ecological Genomics and Wildlife Conservation, Department of Zoology, University of Johannesburg, Auckland Park, 2000, Johannesburg, SOUTH AFRICA

**Abstract.**—A new endemic Sandveld Lizard, genus *Nucras*, is described from south-western Angola. Morphologically it resembles members of the *Nucras tessellata* group, but it is genetically separated and is sister to the larger *tessellata* + *lalandii* group. Although the genus is generally very conservative morphologically, the new species differs from other congeners in a combination of scalation, overall dorsal color pattern, and geographic separation. The new species is known from fewer than 12 specimens collected over a period spanning 120 years from arid south-western Angola. This brings the total number of species in the genus to 12 and adds another species to the growing list of endemic species of the Namib region of Angola. This new finding further reinforces the idea that this Kaokoveld Desert region is a key biodiversity area worthy of conservation and long-term protection.

**Keywords.** Sandveld Lizard, taxonomy, Africa, endemism, Kaokoveld, biodiversity hotspot

**Citation:** Branch WR, Conradie W, Vaz Pinto P, Tolley KA. 2019. Another Angolan Namib endemic species: a new *Nucras* Gray, 1838 (Squamata: Lacertidae) from south-western Angola. *Amphibian & Reptile Conservation* 13(2) [Special Section]: 82–95 (e199).

**Copyright:** © 2019 Branch et al. This is an open access article distributed under the terms of the Creative Commons Attribution License [Attribution 4.0 International (CC BY 4.0): <https://creativecommons.org/licenses/by/4.0/>], which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited. The official and authorized publication credit sources, which will be duly enforced, are as follows: official journal title *Amphibian & Reptile Conservation*; official journal website: [amphibian-reptile-conservation.org](http://amphibian-reptile-conservation.org).

**Received:** 8 May 2019; **Accepted:** 8 August 2019; **Published:** 8 November 2019

### Introduction

The recorded reptile diversity in Angola (278 species, Marques et al. 2018; Branch et al. 2019) is significantly lower than that of South Africa (407 species, Tolley et al. 2019), a nearby country of comparable size and habitat diversity. This incongruity has been attributed to the lack of recent faunal surveys and/or taxonomic revision of groups in the country (Marques et al. 2018; Branch et al. 2019). That this gap simply represents under-sampling of the Angolan herpetofauna is evidenced by the recent discovery of numerous new species, including lacertids of genus *Pedioplanis* (Conradie et al. 2012), girdled lizards of genus *Cordylus* (Stanley et al. 2016; Marques et al. 2019b), and a new skink of genus *Trachylepis* (Marques et al. 2019a), as well as several candidate new species of lacertids (Branch and Tolley 2017), and geckos (Branch et al. 2017).

At present, the family Lacertidae is represented in Angola by 13 species in six genera; *Heliobolus* (one species), *Holaspis* (one), *Ichnotropis* (three), *Meroles* (three), *Nucras* (two), and *Pedioplanis* (three; see Marques et al. 2018; Branch et al. 2019). The lacertid generic diversity is comparable to that of other herpetologically rich areas in sub-Saharan Africa, e.g., eight genera in Tanzania, Kenya, and South Africa, and five in Namibia (Branch 1998; Spawls et al. 2018). However, the lacertid species diversity in Angola (13 species) is notably lower: Kenya (15), Tanzania (16), Namibia (25), and South Africa (28) [Branch 1998; Spawls et al. 2018; Branch et al. 2019; Bauer et al. 2019].

The taxonomy of the lacertid genus *Nucras* Gray, 1838 is complicated by the relatively secretive habits and conservative morphology of known species, and this has confounded early attempts to resolve species

**Correspondence.** \* [werner@bayworld.co.za](mailto:werner@bayworld.co.za)

boundaries and geographical distributions within the genus. Currently, *Nucras* comprises eleven species that are mainly restricted to southern Africa, with a northern outlier (*Nucras boulengeri* Neumann, 1900) occurring in East Africa, although there is a single, isolated record from Isoka, northern Zambia (Haagner et al. 2000; Spawls et al. 2018).

Taxonomy of the Western (or Striped) Sandveld Lizard, *Nucras tessellata*, has proven to be particularly problematic, as have the species boundaries within the *N. tessellata* species complex. Broadley (1972) recognized four subspecies (*Nucras taeniolata taeniolata*, *Nucras taeniolata ornata*, *Nucras tessellata tessellata*, and *Nucras tessellata livida*), as well as a number of taxonomically unresolved non-specific forms, i.e., *Nucras tessellata tessellata* var. “T,” *Nucras taeniolata ornata* var. *holubi*, and *Nucras tessellata tessellata* var. *elegans*. Broadley (1972) examined the morphology of over 800 specimens and concluded that the dorsal color pattern and the number of subdigital lamellae under the 4<sup>th</sup> toe are reliable taxonomic characters to differentiate species within the *N. tessellata* complex. In recent years, several subspecies and varieties were elevated to full species, e.g., *Nucras taeniolata*, *N. holubi*, *N. ornata* (Jacobsen 1989), and *N. livida* (Branch and Bauer 1995). A number of historically problematic Angolan specimens were considered to form part of the *Nucras tessellata* (Smith, 1838) complex, best representing *Nucras tessellata tessellata* var. “T.” However, Broadley (1972) deferred making a decision on their taxonomic status pending the collection of additional material. The only other Angolan member of the genus, *Nucras scalaris* Laurent, 1964, was described on the basis of material from northern Angola and is not currently regarded to be included in the *N. tessellata* complex.

Bocage (1895) was the first to record *N. tessellata* from Angola, but noted only that (translated from the original French): “Mr. Anchieta met this species at two different locations, Maconjo and Caconda, from where he sent us a few individuals. All of these individuals belong to the variety *taeniolata*, separated from the typical form not only by its coloration, with a back striped longitudinally in white and blackish-brown, but is also slimmer.” He provided no further details of the specimens, leaving out information on scalation and size. Fortunately, the late Donald G. Broadley visited the Museu Bocage Lisboa, Portugal (currently Museu Nacional de História Natural e da Ciência) in 1968, before the disastrous fire of 1978 destroyed its collections. Broadley was only able to locate the three specimens from Maconjo listed by Bocage (1895). Boulenger (1910) first assigned specimens from Moçâmedes (=Namibe) district to *Nucras tessellata* var. *taeniolata*. In subsequent years, he referred the same material as part of *Nucras intertexta* var. *holubi* under a different color variation A and called this the most ‘primitive form’ (Boulenger 1917, 1921). Monard (1937)

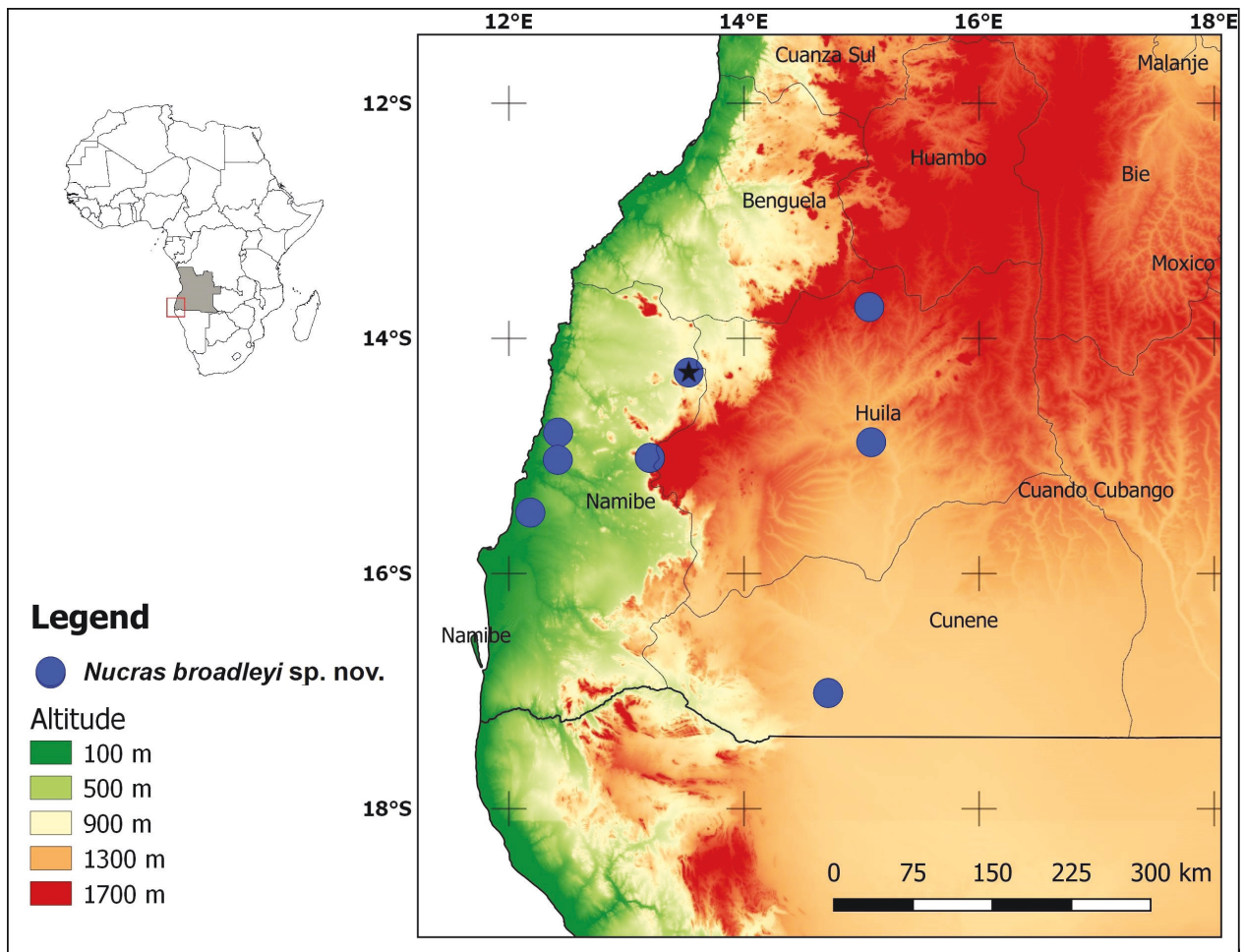
recorded three additional juvenile specimens from Kapelongo (= Capelongo) and reported that they exhibit typical coloration of *taeniolata*, and thus assigned his material to the *N. tessellata* complex. The most detailed description to follow was a specimen collected from “km 34 de la route de Moçâmedes à Sa da Bandeira” (= 34 km from Namibe on Lubango road) and documented by Laurent (1964). All the above specimen data are pooled in the summary tables of scalation in the revision of the *N. tessellata* complex (Broadley 1972), and he concluded that the Angolan material represents an undescribed species.

During recent surveys in south-western Angola, several individuals of *Nucras* were collected. This new material is compared with historical material of the species known from Angola and supplemented with phylogenetic analyses to investigate their taxonomic status, and to advance our understanding of the *N. tessellata* complex.

## Materials and Methods

**Sampling and material examined.** During a recent expedition to south-western Angola, two *Nucras* individuals were collected from Namibe Province (Fig. 1). Each specimen was collected as a voucher, fixed in 10% formalin and thereafter transferred to 70% ethanol for long-term storage at the Port Elizabeth Museum (PEM). Prior to fixation, a tissue sample was collected and preserved in 99% ethanol. Material from the following museums was examined (Table 1) by Donald Broadley: Museu Bocage Lisboa, Portugal (MBL), Museu Regional do Dundo, Dundo, Angola (MD), and the British Museum (now Natural History Museum, London) [NHML]. WRB examined material in the Transvaal Museum (now Ditsong National Museum of Natural History Northern Flagship Institute, Pretoria) [TM], and re-examined and photographed the NHML specimens. Photographs of Monard’s (1937) material from the Musée d’Histoire Naturelle, La-Chaux-de-Fond, Switzerland (MHNC, formerly LCFM) were made available by Luis Ceriaco. The Angolan material was further compared to other material housed in the PEM.

**Morphological data.** To quantify morphology for the species diagnoses, the following measurements were recorded from each individual: snout-vent length (SVL): tip of snout to anterior edge of cloaca; tail length (Tail): tip of tail to posterior edge of cloaca; total length (TL): combined SVL and tail length; head length (HL): from anterior edge of occipital/parietal scale to tip of snout; head width (HW): width of head (just behind eye); snout length (SL): from anterior corner of eye to tip of snout; eye length (EL): horizontal diameter of eye; ear-eye length: from posterior corner of eye to anterior edge of ear opening.



**Fig.1.** Map showing distribution of *Nucras broadleyi* sp. nov. in Angola.

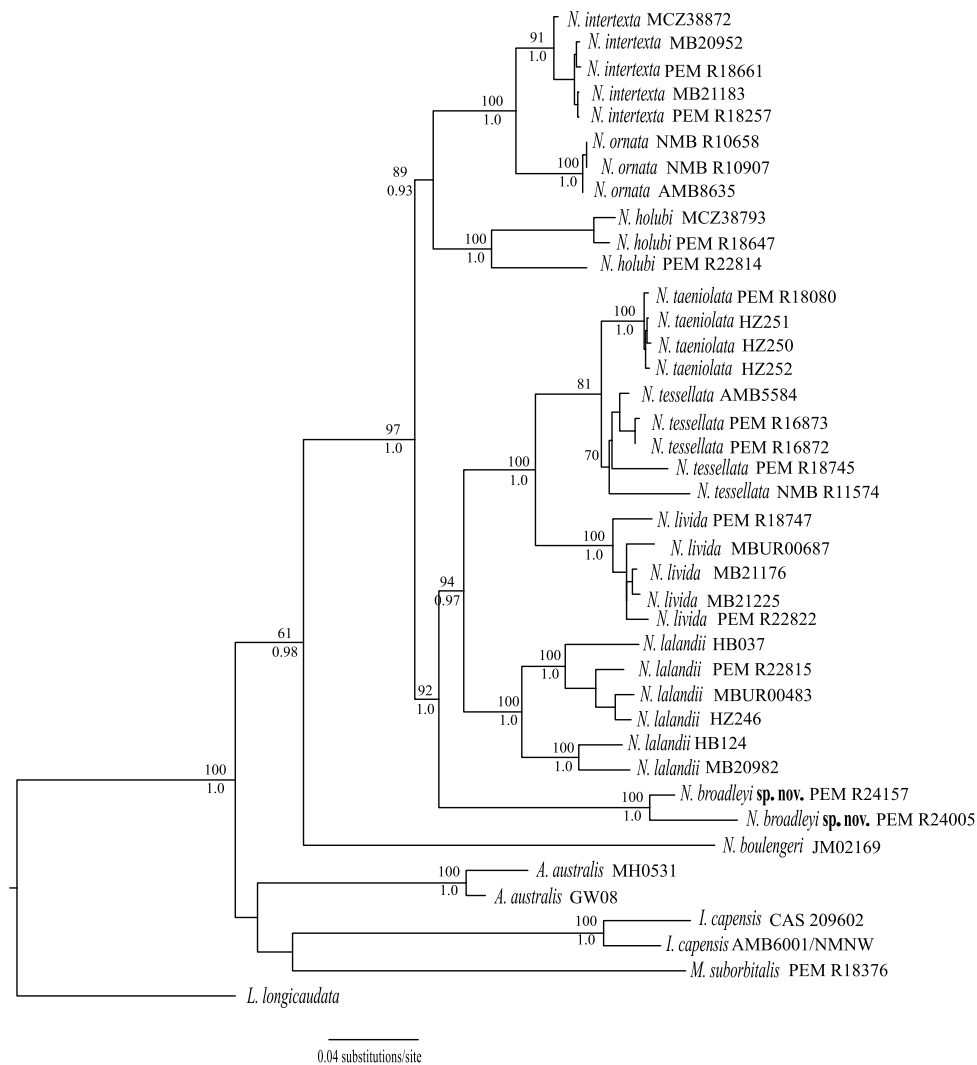
The following scalation details were recorded: upperlabials (UL): in front of subocular and after subocular; lowerlabials (LL), transverse rows of ventrals, longitudinal ventral scale rows, supraciliars (SC), granules between supraciliars (SC) and subocular, number of subdigital lamellae below 4<sup>th</sup> toe, and number of femoral pores. All counts were performed on both left and right sides. The presence of interparietal and whether it was in contact with occipital were also recorded.

**Phylogenetic analyses.** To place the two *Nucras* individuals recently collected from Angola in a phylogenetic context, one nuclear (RAG-1) and two mitochondrial (ND4, 16S) genes were sequenced (Table 2). DNA was extracted using salt extraction (Aljanabi and Martinez 1997), with PCR amplification, and cycle sequencing following standard procedures. A 25  $\mu$ l PCR reaction included 3  $\mu$ l of 1 mM dNTPs, 3  $\mu$ l of 25 mM MgCl<sub>2</sub>, 0.2  $\mu$ l of 10 pmol forward and reverse primers, 3  $\mu$ l of buffer solution (20 mM Tris-HCl ~pH 8.0, 100 mM NaCl, 0.1 mM EDTA, 1 mM DTT), 0.1  $\mu$ l (0.5U) Taq polymerase, and 1–2  $\mu$ l of 25 ng/ $\mu$ l genomic DNA. Thermal cycling was run with initial denaturation for 4 min at 94 °C followed by: 35 cycles with denaturation for 30 s at 94 °C, annealing for 40 s at 55–57 °C, extension

for 40 s at 72 °C, and final extension for 4 min at 72 °C. Primers used for amplification were ND4: ND4 (Forstner et al. 1995) and Leu1 (Arévalo et al. 1994), 16S: L2510 and H3080 (Palumbi 1996); and RAG-1: RAG1-F0 and RAG1-R1 (Mayer and Pavlicev 2007). PCR products were run on a 1% agarose gel and visualized under a UV light to verify amplification. Amplicons were sequenced directly using the forward primers at Macrogen (Amsterdam, Netherlands). Sequences were edited and aligned using Geneious software v4.7 (Kearse et al. 2012). New sequences have been deposited in GenBank (Table 2). In addition, gene sequences for multiple individuals of all *Nucras* species (except *N. scalaris*) and sequences representing outgroup taxa were downloaded from GenBank (Table 2).

A Bayesian analysis of 2,052 characters from the two mitochondrial genes and one nuclear gene (ND4: 678 bp, 16S: 482 bp, RAG-1: 892 bp) was used to investigate optimal tree space using MrBayes v3.2.2 (Huelsenbeck and Ronquist 2001) at the CIPRES Science Gateway (Miller et al. 2010). To determine which evolutionary model best fit the data, jModeltest was initially run (Posada 2008). The AIC test specified the GTR+G model for both mitochondrial markers and HYK+G for RAG-1. Therefore, three unlinked data partitions were created, specifying six





**Fig. 2.** Maximum likelihood topology for *Nucras* with bootstrap values (top) and Bayesian posterior probabilities (bottom) at each node. Bootstrap values <60%, posterior probabilities <0.90, and node support within each species is not shown.

(mitochondrial genes) and two (RAG-1) rate categories, including the gamma distribution, with uniform priors for all parameters. For 16S, 38 bases were excluded due to poor alignment. To ensure the robustness of results, the MCMC was run twice in parallel for 20 million generations (four chains in each run), with trees sampled every 1,000 generations. A 10% burn-in was examined (2 million generations, 2,000 trees) in Tracer v1.6 (<http://beast.bio.ed.ac.uk>) to check that the effective sample size (ESS) of all parameters met a threshold of 200 after burn-in. A 50% majority rule tree was constructed and nodes with  $\geq 0.95$  posterior probability were considered supported.

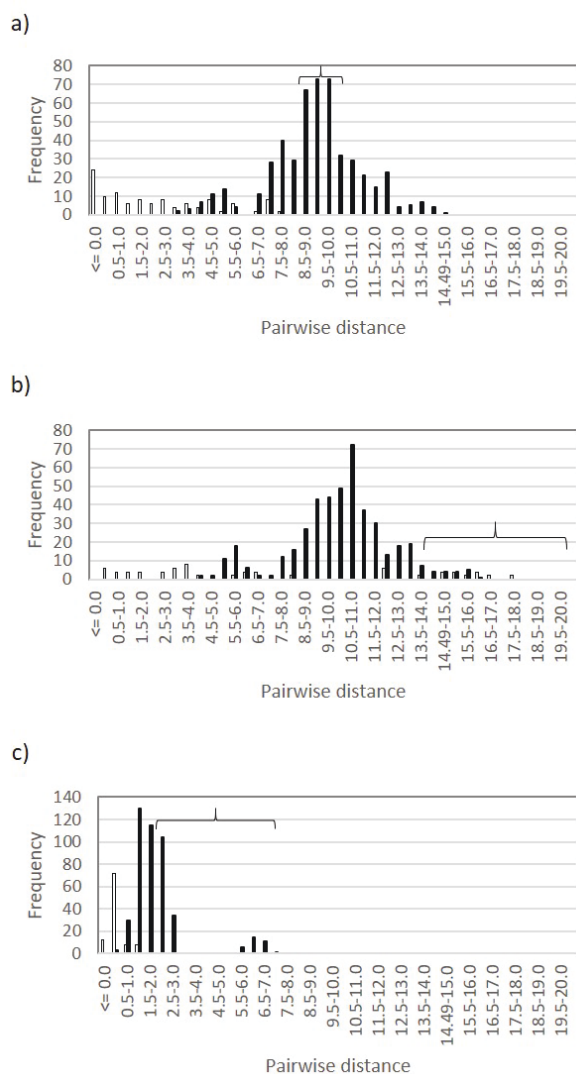
In addition to the Bayesian analysis, a maximum likelihood (ML) search was run using RAxML HPC 7.2.8 (Stamatakis 2006) on the CIPRES Science Gateway ([http://www.phylo.org/sub\\_sections/portal/](http://www.phylo.org/sub_sections/portal/)) for the combined dataset. The datasets were partitioned as in the Bayesian analysis, with a GTR+I+G model for all markers and 1,000 bootstrap replicates (Stamatakis et al. 2008). This analysis was run three times to ensure that independent ML searches produced the same topologies. Nodes with a bootstrap value

of  $\geq 70\%$  were considered as supported in this analysis.

Pairwise sequence divergence values (uncorrected net *p*-distances) were estimated between species for both markers using MEGA v7 (Kumar et al. 2016). In addition, a barcoding approach was used to compare inter- and intra-specific sequence divergences, using SpeciesIdentifier v1.8 (Meier et al. 2006). Pairwise comparisons were generated for all *Nucras* individuals in the phylogeny for each gene, and frequency distributions of inter- and intra-specific comparisons were made. The ND4 gene was truncated 433 bp, as some GenBank sequences had only partial sequences for that gene.

## Results

**Phylogenetic analyses.** The phylogenetic analyses show that the two individuals from Angola are in the same clade, and it is sister to a clade containing *N. livida*, *N. taeniolata*, and *N. tessellata* (Fig. 2). The new Angolan clade is well-supported by both Bayesian and likelihood analyses. Uncorrected net *p*-distances for each of the genes are



**Fig. 3.** Frequency distribution of pairwise sequence divergences for *Nucras* species for a) 16S, b) ND4, and c) RAG-1. Inter-specific differences shown as black bars, and intra-specific differences as white bars. The ranges of values relating *Nucras broadleyi* sp. nov. with other members of the *N. tessellata* clade are indicated by brackets.

similar to those found for other species of *Nucras* (Table 3), and the frequency distribution of pairwise differences shows that these Angolan individuals fall in the range of inter-specific divergence values (Fig. 3).

**Systematics.** Based on the minor morphological differences and the distinct dorsal coloration differences observed among material examined, combined with the abovementioned genetic evidence, the Angolan material is described below as a new species. No historical names are available for this clade, thus leaving no outstanding taxonomic issues (Broadley 1972; Uetz et al. 2017).

***Nucras broadleyi* sp. nov.**  
Angolan Sandveld Lizard

urn:lsid:zoobank.org:act:C82E3A75-96FF-4D2A-9B52-3ABF4B58BC2B

(Figures 4–6)

**Chernonymy.** *Nucras tessellata* var. *taeniolata* (Bocage 1895: 30), *Nucras tessellata* var. *taeniolata* (Boulenger 1910: 474), *Nucras tessellata* var. *holubi* (Boulenger 1917: 210), *Nucras intertexta* var. *holubi* (Boulenger 1920: 20), *Nucras tessellata* (Monard 1937: 73; Laurent 1964: 56), *Nucras ornata* (Broadley 1965: 23), *Nucras tessellata* (Broadley 1972: 30; Ceriaco et al. 2016: 56; Burger 2014: 171), *Nucras* aff. *tessellata* (Marques et al. 2018: 221; Branch et al. 2019: 317).

**Type material.** The type series is comprised of the three most recently collected specimens, which are housed in PEM and TM.

**Holotype.** A subadult male (PEM R24005, AG 018), 10 km west of Lola, edge of Bentiaba River valley, Namibe Province, Angola (-14.29028, 13.53056, WGS 84, 802 m asl). Collected by W.R. Branch, P. Vaz Pinto, and J.S. de Almeida on 2 November 2015.

**Paratypes (2).** a) A subadult female (PEM R24157, AG 166), 8.8 km southwest of Farm Mucungo, Namibe Province, Angola (-14.80167, 12.41917, WGS 84, 385 m asl). Collected by W.R. Branch, P. Vaz Pinto, and J.S. de Almeida on 8 November 2015. b) An unsexed adult (TM 40392), “34 km S of Moçâmedes to Porto Alexandre, Angola, 1512Ca” (= 34 km S Namibe to Tômbwa), Namibe Province, Angola (approx. -15.48220, 12.18289). Collected by W.D. Haacke on 30 March 1971.

**Additional referred material:** The following additional material was used to expand the description of variation within the species: a) an adult male (MD 1967, Laurent 1964), “km 34 de la route de Moçâmedes à Sa da Bandeira” (=34 km from Namibe on Lubango road, -15.03333, 12.41667), collected 24 October 1949, b) MBL 646, 647a, 647b (Bocage 1895: 30) from Maconjo (approx. -15.01667, 13.20000), c) BM 1970.6.29.10–11 (Boulenger 1910: 474) from Ponang Kuma (= Donguena, approx. -17.01667, 14.71667), and d) MHNC 91.0524 (Monard 1937) from Capelongo (approx. -14.88333, 15.083333), collected April 1933.

**Etymology.** The specific epithet is a patronym in honor of Donald G. Broadley for his numerous contributions to the herpetofauna of Africa. Don (as most of us knew him) was the first to recognize the Angolan population as a separate species (Broadley 1972). The name is constructed in the masculine genitive.

**Diagnosis.** Assigned to *Nucras* due to a well-defined collar (absent in *Ichnotropis*), toes not serrated or fringed (versus serrated or fringed in *Meroles*), subdigital lamellae smooth (versus keeled in *Pedioplanis* and *Heliobolus*), subocular

**Table 1.** Meristic and scalation data for Angolan *Nucras broadleyi* sp. nov. PEM – Port Elizabeth Museum, BM – Natural History Museum, London (formerly British Museum), MD – Museu Dundo Regional do Dundo, Angola, TM – Ditsong Museum of Natural History, South Africa (formerly Transvaal Museum), MBL – Museu Bocage Lisboa, Portugal (material destroyed), MHNC – Musée d' Histoire Naturelle de La Chaux-de-Fonds, Chaux-de-Fonds, Switzerland.

Museum number	PEM R24005	PEM R24157	TM 40397	MD 1967	MBL 646	MBL 647a	MBL 647b	BM 1907.6.29.10	BM 1907.6.29.11	MHNC 91.0524-5
Status	Holotype	Paratype	Paratype	Additional specimen	Additional specimen	Additional specimen	Additional specimen	Additional specimen	Additional specimen	Additional specimens
Sex	Male	Female	Male	Male						Juveniles
SVL	36	44	58	40 (39)	57	63	52	74	60	
Tail	t	t	110	90 (91)	120+	133	135	144+	114	
Total	-	-	168	130	177+	193	187	218	174	
Head length (HL)	10.5	9.7	12.4	9.5	12.1	13.8	12.8			
Head width (HW)	5.88	6.4	6.2							
HW/HL ratio	0.56	0.7	0.5							
Snout length	3.8	4.1	4.9							
Eye length	2.11	2.1	2.4							
Ear-eye length	3.74	3.5	4.2							
UL *	4 (2)	4 (2)	4 (2)					4 (2)	4 (2)	
LL **	6 (3)	6 (3)	6 (3)					6 (3)	6 (3)	
MSR	42	48	46	48 (50)	38	44	46	48	48	42-43
Ventrals (transverse)	8	8	8	8	8	8	8	8	8	
Ventrals (longitudinal)	28	29	27	29	33	30	29	33	29	27-29
Granules SC-SO	1/0	3/4	2/3	3	1	2	6/3	3/2	3/3	0-2
Supraciliaries	6/6	7/8	6/6	6	5	6	7	7/6	6	
Interparietal Y/N	Y	Y	Y	Y				Y	Y	
IP contact with occipital	contact	contact	contact	contact	separate	broad contact	broad contact	contact	contact	
Subdigital lamellae below 4 <sup>th</sup> toe	23/25	27/27	23/25	28/29 (27)	27/26	28/27	28/28	28/28	26/26	25
Femoral pores	13/13	15/15	14/16	13/13	14/13	12/12	15/14	14/14	13/13	

\* anterior subocular (posterior subocular), \*\* total (largest number, t = truncated)

bordering lip, the nostril is pierced between two nasals, nasal well separated from upper labial, and dorsal scales small, smooth, and juxtaposed.

The new species can be diagnosed from other *Nucras* species based on a combination of the following characters: series of transversely enlarged plates present under forearm (versus absent or only feebly enlarged in *Nucras lalandii*), a small series (0–6) of small granules present between

supraciliaries and supraoculars (versus mostly absent in *N. boulengeri* and *N. lalandii*), 23–29 lamellae under 4<sup>th</sup> toe (versus less than 22 in *N. lalandii*), dorsum with a series of longitudinal pale stripes (versus dark cross bands present in *N. lalandii* and *N. scalaris* or a series of pale vertebral spots, sometimes forming irregular transverse bands in *N. intertexta* or lack of any dorsal patterns in *N. aurantiaca*), four pale stripes on nape with outer stripes forming a

**Table 2.** Samples used in genetic analysis. Museum abbreviations: CAS – California Academy of Science, PEM – Port Elizabeth Museum, NMB – National Museum Bloemfontein.

Genus	Species	Field accession ID	Museum accession number	16S	ND4	RAG1	Locality
<i>Nucras</i>	<i>broadleyi</i> sp. nov.	AG18	PEM R24005	MN265869y	—	MN265872y	Angola, Namibe Province
<i>Nucras</i>	<i>broadleyi</i> sp. nov.	AG166	PEM R24157	MN265870y	MN265871y	MN265873y	Angola, Namibe Province
<i>Nucras</i>	<i>boulengeri</i>	JM02169		HG005184	HG005212	HG005233	Kenya
<i>Nucras</i>	<i>holubi</i>	MBUR00260	PEM R22814	HG005188	HG005216	HG005237	South Africa, Limpopo Province
<i>Nucras</i>	<i>holubi</i>	MCZ38793	CAS 234138	HG005186	HG005214	HG005235	South Africa, Limpopo Province
<i>Nucras</i>	<i>holubi</i>	RSP420	PEM R18647	HG005187	HG005215	HG005236	South Africa, Limpopo Province
<i>Nucras</i>	<i>intertexta</i>	MB20952		HG005193	HG005221	HG005242	South Africa, Northern Cape Province
<i>Nucras</i>	<i>intertexta</i>	MB21183		HG005194	HG005222	—	South Africa, Northern Cape Province
<i>Nucras</i>	<i>intertexta</i>	MCZ38872	CAS 234212	HG005192	HG005220	HG005241	South Africa, Limpopo Province
<i>Nucras</i>	<i>intertexta</i>	RSP030	PEM R18257	HG005191	HG005219	HG005240	South Africa, Northern Cape Province
<i>Nucras</i>	<i>intertexta</i>	RSP277	PEM R18661	HG005190	HG005218	HG005239	South Africa, Northern Cape Province
<i>Nucras</i>	<i>lalandii</i>	HB037		HF951554	HF951533	HF951538	South Africa, KwaZulu-Natal Province
<i>Nucras</i>	<i>lalandii</i>	HB124		HF951553	HF951532	HF951537	South Africa, Eastern Cape Province
<i>Nucras</i>	<i>lalandii</i>	HZ246		HF951555	HF951534	HF951539	South Africa, Eastern Cape Province
<i>Nucras</i>	<i>lalandii</i>	MB20982		HG005197	HG005225	HG005245	South Africa, Western Cape Province
<i>Nucras</i>	<i>lalandii</i>	MBUR00414	PEM R22815	HG005195	HG005223	HG005243	South Africa, Eastern Cape Province
<i>Nucras</i>	<i>lalandii</i>	MBUR00483		HG005196	HG005224	HG005244	South Africa, Eastern Cape Province
<i>Nucras</i>	<i>livida</i>	KTH08-071	PEM R18747	HG005200	HG005227	HG005247	South Africa, Western Cape Province
<i>Nucras</i>	<i>livida</i>	MB21176		HG005201	HG005228	HG005248	South Africa, Northern Cape Province
<i>Nucras</i>	<i>livida</i>	MB21225		HG005202	HG005229	HG005249	South Africa, Northern Cape Province
<i>Nucras</i>	<i>livida</i>	MBUR00670	PEM R22822	HG005198	—	HG005246	South Africa, Eastern Cape Province
<i>Nucras</i>	<i>livida</i>	MBUR00687		HG005199	HG005226	—	South Africa, Western Cape Province
<i>Nucras</i>	<i>ornata</i>	AMB8635	PEM R17591	HG005206	—	HG005252	South Africa, Limpopo Province
<i>Nucras</i>	<i>ornata</i>	MBUR01226	NMB R10907	HG005203	—	HG005250	South Africa, KwaZulu-Natal Province
<i>Nucras</i>	<i>ornata</i>	MBUR01230	NMB R10658	HG005204	—	HG005251	South Africa, KwaZulu-Natal Province
<i>Nucras</i>	<i>taeniolata</i>	HZ250		HG005207	—	HG005253	South Africa, Eastern Cape Province
<i>Nucras</i>	<i>taeniolata</i>	HZ251		HG005208	HG005230	HG005254	South Africa, Eastern Cape Province
<i>Nucras</i>	<i>taeniolata</i>	HZ252		HG005209	—	HG005255	South Africa, Eastern Cape Province
<i>Nucras</i>	<i>taeniolata</i>	PEM R18080	PEM R18080	HG005210	HG005231	HG005256	South Africa, Eastern Cape Province

**Table 2 (continued).** Samples used in genetic analysis. Museum abbreviations: CAS – California Academy of Science, PEM – Port Elizabeth Museum, NMB – National Museum Bloemfontein.

Genus	Species	Field accession ID	Museum accession number	16S	ND4	RAG1	Locality
<i>Niocras</i>	<i>tessellata</i>	AMB5584	CAS 206725	HG005211	HG005232	HG005257	South Africa, Northern Cape Province
<i>Niocras</i>	<i>tessellata</i>	KTH08-069	PEM R18745	HF951559	—	HF951543	South Africa, Western Cape Province
<i>Niocras</i>	<i>tessellata</i>	MB20650	PEM R16873	HF951556	HF951535	HF951540	South Africa, Northern Cape Province
<i>Niocras</i>	<i>tessellata</i>	MB21061	NMB R11574	HF951558	—	HF951542	South Africa, Northern Cape Province
<i>Niocras</i>	<i>tessellata</i>	MB20687	PEM R16872	HF951557	HF951536	HF951541	South Africa, Northern Cape Province
Outgroup							
<i>Latastia</i>	<i>longicaudata</i>			AF080358	—	EF632229	GenBank
<i>Australolacerta</i>	<i>australis</i>	MH0531	NA	DQ871152	FR751398	DQ871208	South Africa, Western Cape Province
<i>Australolacerta</i>	<i>australis</i>	GW08	NA	HF547772	HF547725	HF547691	South Africa, Western Cape Province
<i>Ichnotropis</i>	<i>capensis</i>	AMB6001	NMNW	DQ871148	HF547732	DQ871206	Namibia, Kamanjab
<i>Ichnotropis</i>	<i>capensis</i>	AMB6067	CAS 209602	DQ871149	HF547733	DQ871207	South Africa, KwaZulu-Natal Province
<i>Merolius</i>	<i>suborbitalis</i>	SVN049	PEM R18376	HF547800	HF547759	HF547718	South Africa, Western Cape Province

continuous light stripe with the outer edges of the parietals (similar to Broadley's (1972) *N. tessellata tessellata* var. "T," differs from *N. livida* and *N. tessellata* where the outer stripes often do not form a continuous light stripe with the outer edges of the parietals; differs from *N. caesicaudata* and *N. ornata* where there are only three longitudinal stripes present on nape and sometimes the vertebral ones are absent), well defined occipital scale separating parietals (versus reduced or absent in northern Namibia *N. holubi*, which is referred to as *N. intertexta damarana* Parker; as well as absent in *N. caesicaudata*), parietal foramen absent (often present in all other species except *N. taeniolata*), and postnasals separated (usually fused in *N. taeniolata*).

In the phylogenetic analysis, the uncorrected *p*-distances show that this clade differs by >8% for 16S, >14% for ND4, and >1% for RAG1 sequence divergence from other members of the *N. tessellata* clade.

**Description of Holotype (Fig. 4).** Body relatively slender (SVL approx. 4.5 times the head length, tail truncated), with hindlimbs larger than forelimbs (femur of hind limb equal to length of tibia); head narrow and elongated (56% longer than wide) with narrow pointed but blunt snout, that is slightly longer than distance from back of eye to rear of ear opening. Rostrum protruding and visible from below. Nasals paired and in contact (0.2 mm suture length), not swollen, nostril directed backwards separating postnasals. Frontonasal single, wider than long (1.1 × 1.8 mm). Prefrontals paired and in broad median contact with one another (0.6 mm suture length), wider than long (1.1 × 1.2 mm). Frontal entire, longer than wide (2.7 × 1.9 mm). Two large rounded supraoculars, both in contact with the frontal, with anterior supraocular preceded by a single large scale in contact with prefrontal, frontonasal, and posterior loreal, with posterior supraocular bordered by a single large scale in contact with parietal and frontoparietal. Paired frontoparietal in broad contact (1.3 mm suture length), nearly as wide as long (1.7 × 1.5 mm). Parietals twice as long as wide (3.1 × 1.8 mm), fully separate by a large, pentagonal interparietal (2.5 × 1.2 mm) that is twice as long as wide, slightly shorter than frontoparietals and nearly equal to length of frontonasal and prefrontal combined. Small subtriangular occipital (0.5 × 0.7 mm). Two loreals, second much larger than first. Six supraciliaries on each side, 1<sup>st</sup> is the longest. A single minute granule scale between supraocular and supraciliaries on right side, none on left side. Four supralabials anterior to subocular and three supralabials posterior to subocular, on both sides. Subocular slightly elevated medial and bordering the lip, its lower border being shorter than the upper. Three temporal scales, first longer than others, smooth. Tympanic shield as wide as long, border of ear opening. No ear lobes. Lower eyelid with transparent brille formed by five larger scales, surrounded by numerous smaller scales. Lower eyelid separated from subocular and enlarged temporal scales by a series of 10 smaller scales. Small scale above 3<sup>rd</sup> supralabial separating the posterior loreal and subocular.



## A new *Nucras* species from Angola

**Table 3.** Pairwise uncorrected net *p*-distances for species of *Nucras*: a) 16S, b) ND4, c) RAG-1. Comparisons not made due to missing data indicated by *na*.

a)	1	2	3	4	5	6	7	8	9
1 <i>broadleyi</i> <b>sp. nov</b>	0.048								
2 <i>lalandii</i>	0.083	0.047							
3 <i>livida</i>	0.097	0.058	0.019						
4 <i>taeniolata</i>	0.098	0.056	0.084	0.000					
5 <i>tessellata</i>	0.075	0.043	0.026	0.073	0.027				
6 <i>boulengeri</i>	0.105	0.101	0.117	0.116	0.103	<i>na</i>			
7 <i>holubi</i>	0.074	0.044	0.066	0.063	0.053	0.079	0.048		
8 <i>intertexta</i>	0.084	0.068	0.090	0.085	0.078	0.105	0.043	0.008	
9 <i>ornata</i>	0.083	0.067	0.091	0.082	0.076	0.108	0.050	0.043	0.000

b)	1	2	3	4	5	6	7	8	9
1 <i>broadleyi</i> <b>sp. nov</b>	<i>na</i>								
2 <i>lalandii</i>	0.139	0.124							
3 <i>livida</i>	0.194	0.115	0.045						
4 <i>taeniolata</i>	0.208	0.147	0.121	0.003					
5 <i>tessellata</i>	0.198	0.138	0.112	0.006	0.018				
6 <i>boulengeri</i>	0.219	0.188	0.233	0.277	0.267	<i>na</i>			
7 <i>holubi</i>	0.153	0.092	0.137	0.156	0.146	0.199	0.115		
8 <i>intertexta</i>	0.208	0.141	0.175	0.196	0.193	0.239	0.118	0.017	

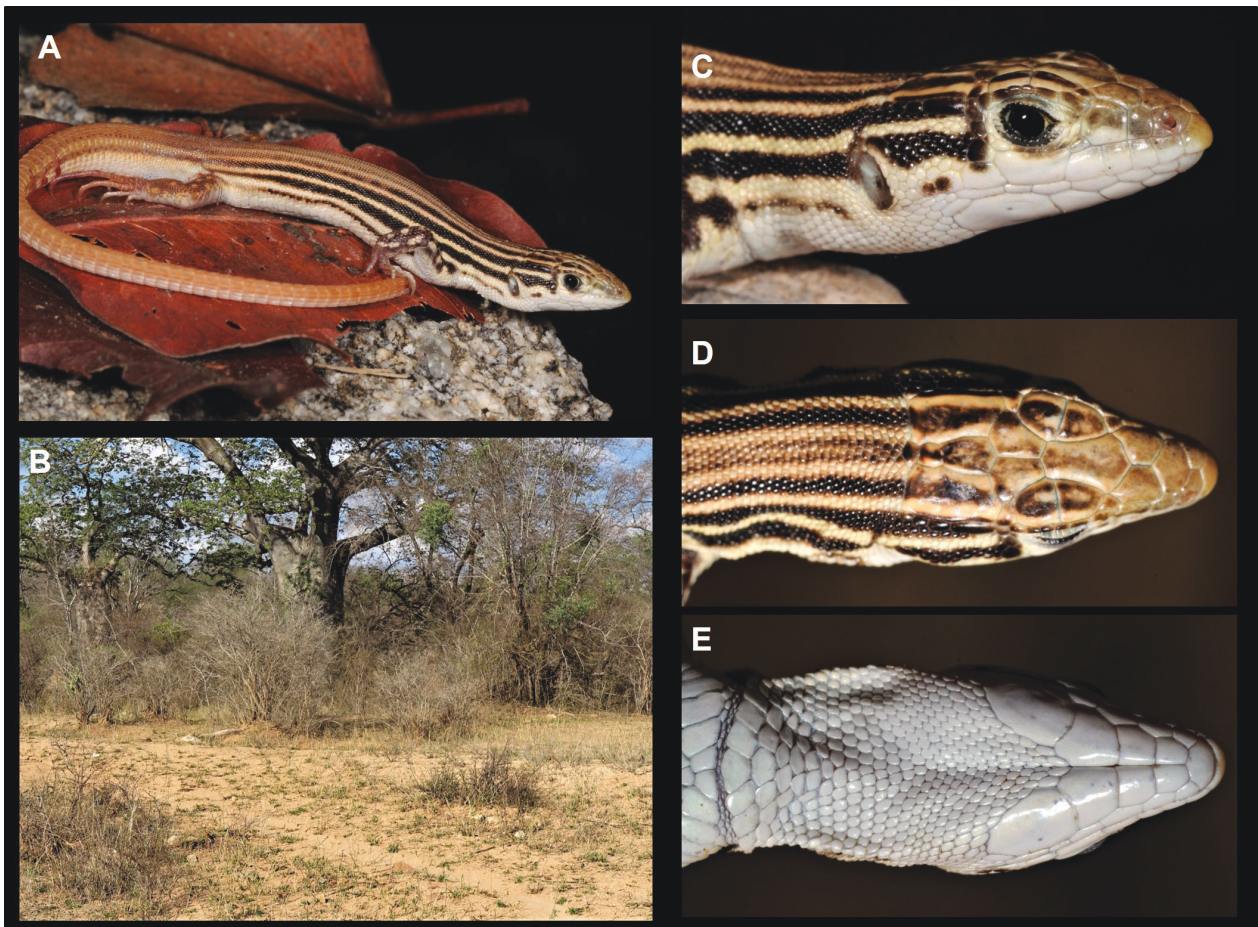
  

c)	1	2	3	4	5	6	7	8	9
1 <i>broadleyi</i> <b>sp. nov</b>	0.001								
2 <i>lalandii</i>	0.012	0.002							
3 <i>livida</i>	0.014	0.009	0.004						
4 <i>taeniolata</i>	0.013	0.007	0.009	0.004					
5 <i>tessellata</i>	0.012	0.006	0.008	0.007	0.008				
6 <i>boulengeri</i>	0.066	0.059	0.064	0.064	0.058	<i>na</i>			
7 <i>holubi</i>	0.020	0.015	0.017	0.016	0.016	0.068	0.004		
8 <i>intertexta</i>	0.017	0.012	0.013	0.012	0.013	0.064	0.015	0.001	
9 <i>ornata</i>	0.021	0.016	0.016	0.016	0.017	0.064	0.019	0.004	0.001

Enlarged scale bordering 1<sup>st</sup> post subocular, supralabial, and the subocular. Six infralabials on both sides, with 3<sup>rd</sup> being longest; four enlarged pairs of chin shields, last largest and first three in broad contact. Twenty-four gular scales in a straight line between symphysis of chin shields and median collar plate, equal in size except last 4–5 larger. Collar free, comprising seven enlarged plates (median subtriangular) and extending slightly onto side of neck as a crease, bordered by 2–3 smaller scales. Dorsal scales small, juxtaposed, granular, smooth, larger on sides toward ventrals. Midbody scales 42. Ventral plates eight longitudinal and 28 transverse rows (from collar to groin), plates of the innermost rows longer than broad, with outer row notably smaller than other rows, transverse row of ventrals across chest just behind collar longer than broad; preanal scales irregular, median ones larger. Scales on upper surface of forearm large, smooth or slightly keeled. Scales on lower surface of forearm with eight enlarged plates, at least twice the width of scales on upper forearm.

Scales on upper surface of tibia rhombic, subimbricate, smooth, and much larger than dorsal scales. Tibia below with a series of large plates. Subdigital lamellae under fourth toe 23R/25L. Femoral pores 13R/15L. Dorsal scales on tail oblique, strongly keeled diagonally, and truncate behind, ventral scales on tail obtusely keeled.

*Coloration.* Dorsum with eight pale cream to white dorsolateral longitudinal stripes, separated by dark brown to black stripes. These stripes are more boldly patterned anteriorly, fading posteriorly. No light vertebral stripe. The two pale paravertebral stripes are separated by a very narrow strip of darker scales that starts on the interparietal through the occipital scale and fades posteriorly onto body and tail. The dorsolateral stripe extending along outer borders of parietals continues onto the tail. It is followed by the upper lateral stripe extending from posterior of the eye onto the head through the mid-temporal with a brief break above the ear opening, and continues onto the tail. The lower lateral stripe starts at the subocular, through the



**Fig. 4.** *Nuocras broadleyi* sp. nov. A – holotype, adult male, PEM R24005 (AG 18) in life; B – general habitat photo of type locality, 10 km west of Lola, edge of Bentiaba River valley, Namibe Province, Angola; C – lateral close-up of head of holotype; D – dorsal close-up of head of holotype; E – ventral close-up of head of holotype (Photos: Bill Branch).

ear opening, broken briefly above the arm, after which it continues all the way onto the tail. Ventrums white and lower limbs oblique white. Fore limbs upper surface black with scattered pale blotches. Hind limbs light brown with pale blotches. Upper surface of tail red-brown, similar to hind limbs. Scales bordering the orbit are black edged.

**Variation (Figs. 5–6).** Meristic and escalation data are summarized in Table 1. The largest specimen examined is (BM 1907.6.29.10) 74 +144 mm (tail regenerated). Regarding coloration, there seem to be three main variations among material examined: 1) 8–9 longitudinal stripes as in holotype (in PEM R24005, MBL 647a, 647b, MHNC 91.0524–5), 2) 4–5 pale longitudinal stripes broken up posteriorly with flanks spotted (in BM 1970.6.29.10–11, TM 40392, MD 1967), and 3) broken paravertebral stripes, continuous dorsolateral line and barred flanks (in PEM R24157), similar to *N. intertexta*.

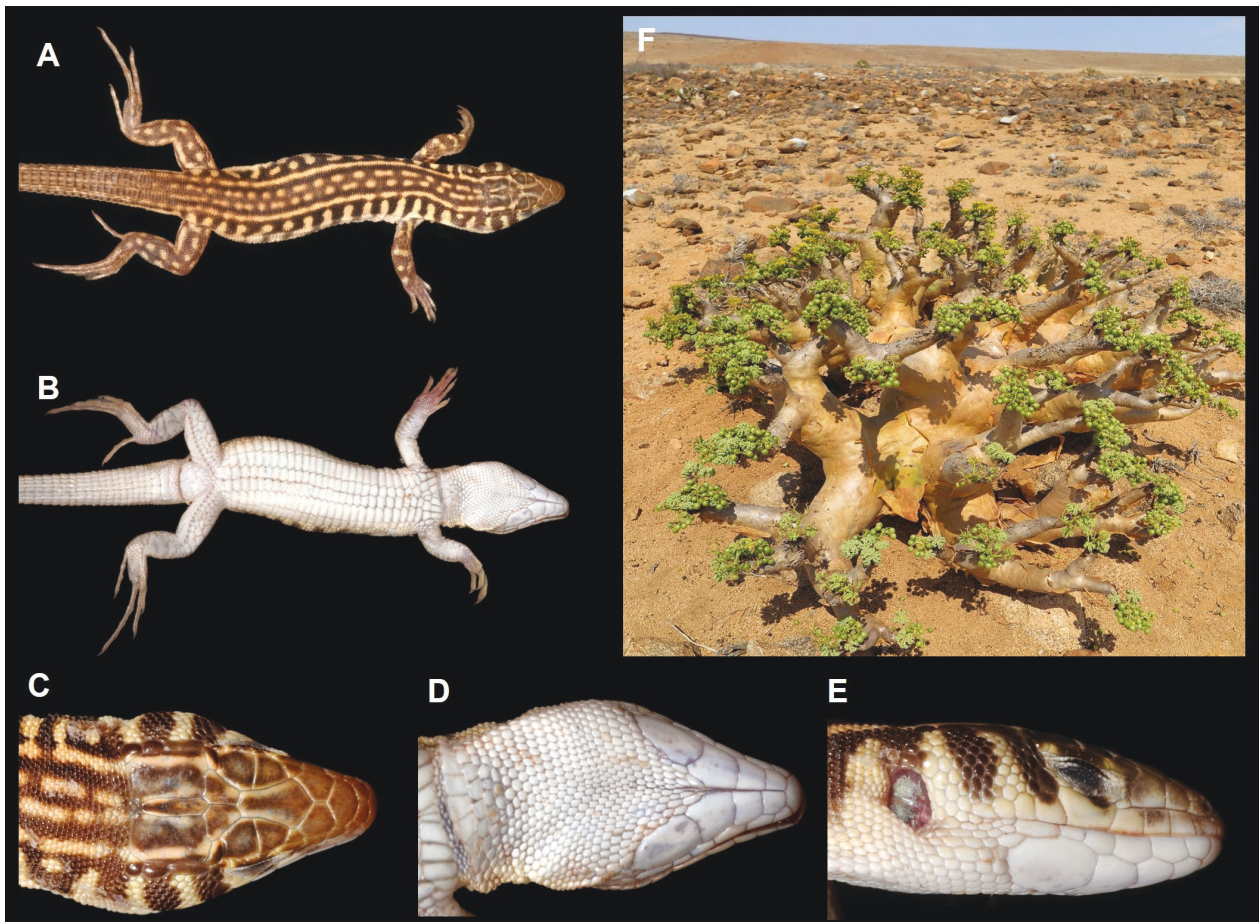
**Distribution.** Found only in semi-arid south-western Angola, throughout much of Namibe Province and extending onto the escarpment of southern Huíla and Cunene Provinces (Fig. 1). Known localities include: Maconjo (Bocage 1895: 30), Ponang Kuma (=Donguena)

(Boulenger 1910: 472), 34 km from Namibe on Lubango road (Laurent 1964: 56), 34 km south of Tombwa (TM 40397), 8.8 km southwest of Farm Mucungo (this study), 10 km west of Lola (this study), and Capelongo (Monard 1937: 73). The locality of Caconda (Bocage 1895) extends the species distribution further north into Huíla Province, but the specimens could not be critically evaluated by Broadley (1972) and are now presumably lost.

**Habitat.** The species appears to be associated with mopane woodlands, dry savannas, and semi-desert shrublands (Barbosa 1970). The new material was found in sandy plains with scattered low granite outcrops, with varying degrees of short grass cover and scattered bushes. Vegetation included *Colophospermum mopane*, *Ficus* sp., *Senegalia* (=Acacia) *mellifera*, *Commiphora* sp., *Boscia foetida*, and *Salvadora persica*. The confirmed historical records were also obtained within the dry woodland zone, even though the possible occurrence of the species in Caconda would place the species above 1,500 m asl and well into the mesic conditions of *Brachystegia* habitats (Barbosa 1970).

**Conservation.** Population estimates for the species





**Fig. 5.** *Nucras broadleyi* sp. nov. A – paratype, adult female, PEM R24157 (AG 166) dorsal view; B – ventral view; C – dorsal close-up of head of paratype; D – ventral close-up of head of paratype; E – lateral close-up of head of paratype; F – general habitat photo of type locality, 8.8 km southwest of Farm Mucongo, Namibe Province, Angola (Photos: Bill Branch).

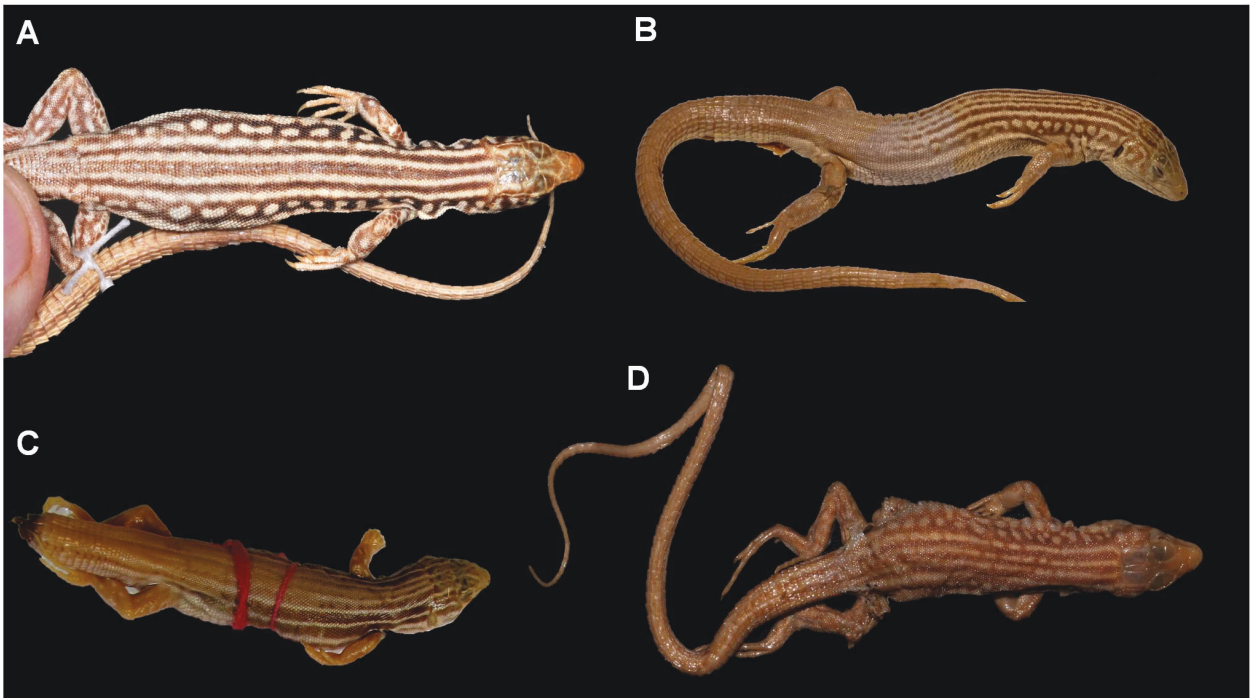
are unknown, and only few scattered specimens (~12) are known, of which four specimens were destroyed in the Museu Bocage Lisboa fire and one of the Monard specimens is unaccounted for. However, Sandveld Lizards are secretive and less conspicuous than many other lacertids, so additional surveys are required to determine the full range of the species and to identify potential habitat threats in order to accurately assess its conservation status.

## Discussion

Broadley (1972) was the first to suggest the Angolan population of *Nucras tessellata* to be different from other described species, but took no taxonomic action. Here, we present evidence to support his assumptions and formally describe the Angolan population as a new species. Thus, Angola now has two endemic species of *Nucras* and the genus now comprises 12 recognized species. As our phylogeny is built on the work of Edwards et al. (2013) we retrieved the same general topology, except for the inclusion of the new species. Although different samples and genetic markers were used, Bauer et al. (2019) retrieved the same species relationships except for the inclusion of their newly described species, *N. aurantiaca*. Thus, we can conclude that the current species relationships are

well resolved. Due to the secretive nature of members of this genus, disjunct distribution, and previously recognized varieties (see Broadley 1972), it is possible that there are other undiscovered species, particularly in areas that remain poorly surveyed.

The species appears restricted to the arid biomes of southwestern Angola at relatively low to moderate altitudes, while the records from Caconda remain problematic and may have been misidentified or incorrectly labelled. In recent years, the number of endemic species described from the arid south-western Angola has increased, e.g., *Kolekanus plumicaudus* (Haacke 2008), *Pedioplanis huntleyi* and *P. haackei* (Conradie et al. 2012), *Cordylus namakuivus* (Stanley et al. 2016), *Cordylus phonolithos* (Marques et al. 2019b), *Poyntonophrynus pachnodes* (Ceriaco et al. 2018), and now *Nucras broadleyi* sp. nov. This region also harbors numerous other endemic species, such as *Afrogecko ansorgii*, *Pachydactylus angolensis*, *Poyntonophrynus grandisonae*, *Pedioplanis benguellensis*, *Rhoptropus taeniostictus*, *Typhlacontias rudebecki*, and *T. punctatissimus bogerti* (Ceriaco et al. 2016, 2018; Marques et al. 2018; Branch et al. 2019). The growing body of information suggests there could be a unique and diverse endemic Angolan-Namib reptile fauna (Ceriaco et al. 2016; Marques et al. 2018; Branch



**Fig. 6.** Variation of *Nucras broadleyi* nov. sp. dorsal color pattern. A – TM 40392 from “34 km S of Moçâmedes to Porto Alexandre;” B – BM 1970.6.29.10 from Ponang Kuma (=Donquena); C – MHNC 91.0524 from Capelongo; D – MD 1967 from “km 34 de la route de Moçâmedes à Sa da Bandeira” (Photos: A,B – Bill Branch, C, D – Luis Ceriaco).

et al. 2019), with additional discoveries yet to be made.

**Acknowledgements.**—We thank José Luis Alexandre and Fernanda Lages for organizing the export permits for the vouchers, done within the framework of a SASSCAL Project sponsored by the Federal Ministry of Education and Research (BMBF) - ISCED permit issued 12 November 2015. We thank Lemmy Mashinini (Ditsong Museum, Pretoria, South Africa) and Patrick Campbell (Natural History Museum, London, United Kingdom) for allowing WRB to inspect material in their care. Shiela Broadley kindly provided access to the late Don Broadley’s data, noting that Don was one of the last researchers that managed to study the Bocage material before a fire destroyed the collection. Aaron Bauer and Luis Ceriaco are thanked for providing additional data and comparative photographs of Angolan material, and their excellent reviews which improved the quality of this paper. João Simões de Almeida is thanked for his field assistance. This work was supported in part by the National Research Foundation of South Africa and the South African National Biodiversity Institute.

## Literature Cited

- Aljanabi SM, Martinez I. 1997. Universal and rapid salt-extraction of high quality genomic DNA for PCR based techniques. *Nucleic Acids Research* 25: 4,692–4,693.
- Arévalo E, Davis SK, Sites JJW. 1994. Mitochondrial DNA sequence divergence and phylogenetic relationships among eight chromosome races of the *Sceloporus grammicus* complex (Phrynosomatidae) in central Mexico. *Systematic Biology* 43: 387–418.
- Barbosa LAG. 1970. *Carta Fitogeográfica de Angola*. Instituto de Investigação Científica de Angola, Luanda, Angola. 323 p.
- Bauer AM, Childers JL, Broeckenhoven C, Mouton PLN. 2019. A new *Nucras* Gray, 1838 (Squamata: Lacertidae) from the Strandveld of the Western Cape, South Africa. *Zootaxa* 4560(1): 149–163.
- Bocage JVB. 1895. *Herpétologie d'Angola et du Congo*. Ministério da Marinha e das Colónias, Lisbonne, Portugal. 203 p., 20 pls.
- Boulenger GA. 1910. A revised list of South African reptiles and batrachians, with synoptic tables, special reference of specimens in the South African Museum, and descriptions of new species. *Annals of the South African Museum* 5: 455–538.
- Boulenger GA. 1917. A revision of the lizards of the genus *Nucras*, Gray. *Annals of the South African Museum* 13: 195–216.
- Boulenger GA. 1920. *Monograph of the Lacertidae*. Volume 1. Trustees of the British Museum (Natural History), London, United Kingdom. x + 352 p.
- Branch WR, Bauer AM. 1995. The herpetofauna of the Little Karoo, Western Cape, South Africa, with notes on life history and taxonomy. *Herpetological Natural History* 3: 47–89.
- Branch WR, Tolley KA. 2017. Oral presentation (Abstract). New lacertids from Angola. *African Herp News* 66: 11.
- Branch WR. 1998. *Field Guide to the Snakes and other Reptiles of Southern Africa*. Struik, Cape Town, South Africa. 368 p.



- Branch WR. 2016. Preface, Amphibian & Reptile Conservation special Angola-Africa issue. *Amphibian & Reptile Conservation* 10(2): i–iii (e128).
- Branch WR, Haacke W, Vaz Pinto P, Conradie W, Baptista N, Verburt L. 2017. Loveridge’s Angolan geckos, *Afroedura karroica bogerti* and *Pachydactylus scutatus angolensis* (Sauria, Gekkonidae): new distribution records, comments on type localities, and taxonomic status. *Zoosystematics and Evolution* 93: 157–166.
- Branch WR, Baptista N, Vaz Pinto P, Conradie W. 2019. The reptiles of Angola – History, updated checklists, endemism, hot spots, and future directions for research. Pp. 283–326 In: *Biodiversity of Angola. Science and Conservation: A Modern Synthesis*. Editors, Huntley BJ, Ferrand N, Russo V, Lages F. Springer Open, Cham, Switzerland. 552 p.
- Broadley DG. 1965. Some problems presented by sand lizards of the *Nucras tessellata* group. *Journal of the Herpetological Association of Africa* 1: 18–23.
- Broadley DG. 1972. A review of the *Nucras tessellata* group (Sauria: Lacertidae). *Arnoldia* 20: 1–35.
- Burger M. 2014. *Nucras tessellata* (A. Smith, 1838). Pp. 171–172 In: *Atlas and Red List of the Reptiles of South Africa, Lesotho, and Swaziland*. Editors, Bates MF, Branch WR, Bauer AM, Burger M, Marais J, Alexander GJ, de Villiers MS. Suricata 1. South African National Biodiversity Institute, Pretoria, South Africa. 485 p.
- Ceríaco LMP, Marques MP, Bandeira S, Agarwal I, Stanley EL, Bauer AM, Heinicke MP, Blackburn DC. 2018. A new earless species of *Poyntonophrynus* (Anura, Bufonidae) from the Serra da Neve Inselberg, Namibe Province, Angola. *ZooKeys* 780: 109–136.
- Ceríaco LMP, de Sá SC, Bandeira S, Valério H, Stanley EL, Kuhn AL, Marques M, Vindum JV, Blackburn DC, Bauer AM. 2016. Herpetological survey of Iona National Park and Namibe Regional Natural Park, with a synoptic list of the amphibians and reptiles of Namibe Province, Southwestern Angola. *Proceedings of the California Academy of Sciences* 63(2): 15–61.
- Conradie W, Branch WR, Measey GJ, Tolley KA. 2012. Revised phylogeny of Sand lizards (*Pedioplanis*) and the description of two new species from south-western Angola. *African Journal of Herpetology* 60: 91–112.
- FitzSimons VFM. 1943. The lizards of South Africa. *Memoirs of the Transvaal Museum* 1: 1–528.
- Forstner MRJ, Davis SK, Arevalo E. 1995. Support for the hypothesis of Anguimorph ancestry for the suborder Serpentes from phylogenetic analysis of mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution* 4: 93–102.
- Haacke WD. 2008. A new leaf-toed gecko (Reptilia: Gekkonidae) from south-western Angola. *African Journal Herpetology* 57(2): 85–92.
- Haagner GV, Branch WR, Haagner AJF. 2000. Notes on a collection of reptiles from Zambia and adjacent areas of the Democratic Republic of the Congo. *Annals of Amphib. Reptile Conserv.*
- the Eastern Cape Museum* 1: 1–25.
- Huelsenbeck JP, Ronquist F. 2001. MrBayes: Bayesian inference of phylogenetic trees. *Bioinformatics* 17: 754–755.
- Jacobsen NHG. 1989. *A Herpetological Survey of the Transvaal*. Ph.D. Dissertation, University of Natal, Department of Biological Sciences, Durban, South Africa. 1,621 p.
- Kearse M, Moir R, Wilson A, Stones-Havas S, Cheung M, Sturrock S, Buxton S, Cooper A, Markowitz S, Duran C, et al. 2012. Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* 28(12): 1,647–1,649.
- Kumar S, Stecher G, Tamura K. 2016. MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution* 33: 1,870–1,874.
- Laurent RF. 1964. Reptiles et amphibiens de l’Angola (troisième contribution). *Publicações Culturais Companhia de Diamantes de Angola* 67: 1–165.
- Marques MP, Ceríaco LMP, Bandeira S, Pauwels OSG, Bauer AM. 2019a. Description of a new long-tailed skink (Scincidae: *Trachylepis*) from Angola and the Democratic Republic of the Congo. *Zootaxa* 4568(1): 51–68.
- Marques MP, Ceríaco LMP, Stanley EL, Bandeira S, Agarwal I, Bauer AM. 2019b. A new species of Girdled Lizard (Squamata: Cordylidae) from the Serra da Neve Inselberg, Namibe Province, southwestern Angola. *Zootaxa* 4668(4): 503–524.
- Marques MP, Ceríaco LMP, Blackburn DC, Bauer AM. 2018. Diversity and distribution of the amphibians and terrestrial reptiles of Angola: atlas of historical and bibliographic records (1840–2017). *Proceedings of the California Academy of Sciences Series 4*, 65(Supplement II): 1–501.
- Mayer W, Pavlicev M. 2007. The phylogeny of the family Lacertidae (Reptilia) based on nuclear DNA sequences: convergent adaptations to arid habitats within the subfamily Eremiainae. *Molecular Phylogenetics and Evolution* 44: 1,155–1,163.
- Meier R, Kwong S, Vaidya G, Ng PKL. 2006. DNA barcoding and taxonomy in Diptera: a tale of high intraspecific variability and low identification success. *Systematic Biology* 55: 715–728.
- Miller MA, Pfeiffer W, Schwartz T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. Pp. 1–8 In: *Proceedings of the Gateway Computing Environments Workshop (GCE), 14 November 2010, New Orleans, Louisiana, USA*. Institute of Electrical and Electronics Engineers (IEEE), Piscataway, New Jersey, USA. 115 p.
- Monard A. 1937. Contribution à l’herpétologie d’Angola. *Arquivos do Museu Bocage* 8: 19–154.
- Neumann O. 1900. Description of a new lizard of the genus *Nucras* from Usoga, British East Africa. *Annals and Magazine of Natural History, including*

*Zoology, Botany, and Geology* 7(5): 56.

Posada D. 2008. jModelTest: phylogenetic model averaging. *Molecular Biology and Evolution* 25: 1,253–1,256.

Smith A. 1838. Contributions to the natural history of Southern Africa. Article VIII. *Magazine of Natural History* 2(14): 92–94.

Spawls S, Howell K, Drewes R, Ashe J. 2018. *A Field Guide to the Reptiles of East Africa*. 2<sup>nd</sup> Edition. Bloomsbury Natural History, London, United Kingdom. 624 p.

Stamatakis A, Hoover P, Rougemont J. 2008. A rapid bootstrap algorithm for the RAxML web servers. *Systematic Biology* 57: 758–771.

Stamatakis A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22: 2,688–2,690.

Stanley EL, Ceriaco, LMP, Bandeira S, Valerio H, Bates MF, Branch WR. 2016. A review of *Cordylus machadoi* (Squamata: Cordylidae) in southwestern Angola, with the description of a new species from the Pro-Namib desert. *Zootaxa* 4061(3): 201–226.

Tolley K, Weeber J, Maritz B, Verburgt L, Bates M, Conradie W, Hofmeyr R, Turner A, Da Silva J, Alexander G. 2019. No safe haven: protection levels show imperiled South African reptiles not sufficiently safe-guarded despite low average extinction risk. *Biological Conservation* 233: 61–72.



**Bill Branch** (William R. Branch) was born in London, United Kingdom. Bill was employed as Curator of Herpetology at the Port Elizabeth Museum for over 30 years (1979–2011), and upon his retirement he was appointed Curator Emeritus Herpetology until his death in October 2018. Bill’s herpetological studies concentrated mainly on the systematics, phylogenetic relationships, and conservation of African reptiles, but he has been involved in numerous other studies on the reproduction and diet of African snakes. He has published over 300 scientific articles, as well as numerous popular articles and books. The latter include: *South African Red Data Book of Reptiles and Amphibians* (1988), *Dangerous Snakes of Africa* (1995, with Steve Spawls), *Field Guide to the Reptiles of Southern Africa* (1998), *Tortoises, Terrapins,*

*and Turtles of Africa* (2008), and *Atlas and Red Data Book of the Reptiles of South Africa, Lesotho, and Swaziland* (multi-authored, 2014), as well as smaller photographic guides. In 2004, Bill was the 4<sup>th</sup> recipient of the “Exceptional Contribution to Herpetology” award of the Herpetological Association of Africa. Bill has undertaken field work in over 16 African countries, and described nearly 50 species, including geckos, lacertids, chameleons, cordylids, tortoises, adders, and frogs.



**Werner Conradie** holds a Masters in Environmental Science (M. Env. Sc.) and has 12 years of experience with the southern African herpetofauna, with his main research interests focusing on the taxonomy, conservation, and ecology of amphibians and reptiles. Werner has published numerous principal and collaborative scientific papers, and has served on a number of conservation and scientific panels, including the Southern African Reptile and Amphibian Relisting Committees. He has undertaken research expeditions to many African countries including Angola, Botswana, Lesotho, Malawi, Mozambique, Namibia, South Africa, Zambia, and Zimbabwe. Werner is currently the Curator of Herpetology at the Port Elizabeth Museum (Bayworld), South Africa.



**Pedro Vaz Pinto** is Angolan and was born in Luanda, Angola, in 1967. Pedro graduated in Forest Engineering at the Technical University of Lisbon, and obtained a doctoral degree in Biology from the University of Porto, Portugal. Over the past 20 years, he has worked in biodiversity conservation in Angola addressing rare or endangered species, and protected area management. Pedro is a director for the local NGO Kissama Foundation, and a researcher for CIBIO-InBio. His studies on Angolan vertebrates have focused mostly on genetics, biogeography, and conservation in antelopes, birds, reptiles, and amphibians. Pedro travels the country extensively and has received three international environmental awards for his biodiversity conservation work in Angola.



**Krystal Tolley** is a Principal Researcher at the South African Biodiversity Institute in South Africa. Krystal studies patterns of biodiversity and adaptation of African reptiles by combining phylogenetics, phylogeography, performance-based data, species distribution models, and morphology.