



A reevaluation of records of Sandveld lizards, *Nucras* Gray, 1838 (Squamata: Lacertidae), from northern Namibia

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Abstract.—Data relating to the Sandveld lizards (*Nucras*) occurring in Namibia, southwest Africa are reviewed. In particular, we investigated records of *N. holubi*, a chiefly southeastern African species, and attempted to identify recently collected material that could not be assigned to any species currently recognized in Namibia. A phylogenetic analysis of *Nucras* based on three mitochondrial markers revealed a deep divergence between Namibian *Nucras holubi* and two presumably conspecific clades from Limpopo Province, South Africa. In addition, the coloration pattern and scalation of the Namibian material differ from those of the eastern forms, supporting its recognition as a separate species. The name *Nucras damarana* Parker, 1936, long relegated to the synonymy of *N. holubi*, is here resurrected for this apparently endemic northern Namibian species. *Nucras damarana* is restricted to the Kunene, Omusati, Oshikati, Kavango, and Otjozondjupa regions of north-central Namibia. A distinctive specimen of *Nucras* from near Ruacana in the Kunene Region was identified as allied to *Nucras broadleyi*, a species recently described from southwestern Angola, on the basis of genetic data, although it differs substantially in color pattern. With the addition of *N. aff. broadleyi* and the resurrected *N. damarana* to its fauna, as well as the removal of *N. holubi* from the nation's species list, four species of *Nucras* are confirmed to be present in Namibia. Although the conservation status of *N. damarana*, *N. tessellata*, and *N. intertexta* is Least Concern, the uncertain taxonomic status of *N. aff. broadleyi* precludes a meaningful threat assessment.

Keywords. Distribution, endemism, *Nucras damarana*, *Nucras broadleyi*, *Nucras holubi*, phylogeny, taxonomy

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Introduction

Three species of Sandveld lizards, *Nucras* (Lacertidae), are currently regarded as occurring in Namibia: *N. intertexta* (Smith, 1838), *N. tessellata* (Smith, 1838), and *N. holubi* (Steindachner, 1882) (Branch 1998; Griffin 2003; Herrmann and Branch 2013). Paradoxically, the first species recorded from what is now Namibia was a species that does not occur in the country. Boulenger (1887) reported *N. delalandii* (= *N. lalandii*), from “Damaraland,” an area corresponding to most of interior central and northern Namibia. This record was repeated by Werner (1910), Boulenger (1910), and Sternfeld (1911a), with the last author adding a second record from Gobabis. However, both Hewitt (1910) and Boulenger (1917) questioned the locality, the latter noting that the

specimen had been obtained by purchase in 1865 without an indication of the collector. Indeed, this specimen is part of a collection of specimens obtained from W. Stevens, all from Damaraland (BMNH 65.6.18.1–13, 65.8.28.1–31). In fact, it is likely that none of this material originated in the area then referred to as Damaraland. In addition to *N. lalandii*, the collection included specimens of *Afrogecko porphyreus* (BMNH 65.6.18.11), which is endemic to the southern and southwestern portions of the Cape provinces; *Philothamnus natalensis* (BMNH 65.6.18.1) and *P. hoplogaster* (BMNH 65.6.18.2), which are both limited to eastern southern Africa; and the types of *Chamaeleon damaranum* = *Bradypodion damaranum* (BMNH 65.6.18.4–5), which is endemic to the south coast of the Western and Eastern Cape provinces. Boulenger (1920) presented data for a specimen of *N. delalandii* from “Great Namaqualand,” but by the

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time of the subsequent genus revision, this species was recognized as being restricted to the eastern portions of the subcontinent (FitzSimons 1943).

Fischer (1888) first recorded *N. tessellata* from between Aus and Bethanie, with further records given by several authors: Boettger (1893, 1894: Bethanien, Rehoboth, and environs), Werner (1910: Okahandja and Kubub, 1915: Usakos), Sternfeld (1911a,b: Deutsch Südwest-Afrika), and Methuen and Hewitt (1914: Kraikluft and between Nakeis and Groendoorn). However, subsequent authors (e.g., Broadley 1972; FitzSimons 1943; Mertens 1955) interpreted some of these (Okahandja and Usakos) records as representing other species. FitzSimons (1943) considered *N. tessellata* to be widespread, although his knowledge of it was based on the published German colonial records noted above. Mertens (1955) likewise reported older localities but noted that he knew the species with certainty only from Rehoboth. Broadley (1972) accepted the same southern Namibian localities as Mertens (1955), i.e., as far north as the area around Rehoboth, but added a record 20 km N of Rosh Pinah. The current concept of the species limits its Namibian distribution to the far south and southeast of the country, thereby excluding most of the historical records (Branch 1998), although Rehoboth area records were accepted by Visser (1984) and Griffin (2003).

Hoesch and Niethammer (1940) first reported *Nucras intertexta* from Namibia from the area of the Waterberg. FitzSimons (1943) further recorded it from Sandfontein near Gobabis, whereas Mertens (1955) added Okahandja and Boettger's (1893) record of *N. tessellata* from Bethanie to the *N. intertexta* records. Broadley (1972) added many records from northwestern Namibia and considered *N. intertexta* to be widespread across the northern half of Namibia (plus Bethanie), most of Botswana, northern South Africa, southern Zimbabwe, and southern Mozambique. The Bethanie record has since been considered to be an error by Branch (1998), but the northern Namibian records form a diagonal from the Omaheke Region northwest to the Angolan border in the Kunene Region (Branch 1998; Visser 1984).

Nucras intertexta holubi was first recorded from Namibia by FitzSimons (1943) based on Werner's (1910, 1915) earlier records of *N. tessellata* from Okahandja and Usakos, respectively, and new records from Outjo, Kaoko Otavi, and Otjitondua. Mertens (1955) listed the same records but called into question both the identity of the specimens and the validity of the taxon. Broadley (1972) included this form in his concept of *N. taeniolata ornata*, with records from Kombat, Opuwo, Ombombo, Oshakati, Kaoko Otavi, Otjitondua, Otjivakandu, Outjo, and Sissekab, all in northern Namibia in the current Kunene, Oshana, and Otjozondjupa regions, in addition to a single southern record from Stamprietfontein (2418AD, Hardap Region). Jacobsen

(1989) subsequently elevated *N. ornata* to full species and treated *N. t. holubi* as subspecifically distinct within *taeniolata*, and Bates (1996) later demonstrated the specific validity of *N. holubi*, although neither of them explicitly reevaluated the Namibian "*holubi*." Branch (1998) mapped the distribution in Namibia and apparently treated the northern and western records as referable to *N. intertexta*, but without comment. Visser (1984) and Griffin (2003), however, recognized as valid records from as far northwest as Opuwo.

A fourth taxon, *N. intertexta damarana*, was described by Parker (1936) from Sissekab in north central Namibia. It was considered a valid subspecific form with a small area of endemism by both FitzSimons (1943) and Mertens (1955, 1971). However, Broadley (1972) included it, along with *N. i. holubi*, in the synonymy of *N. taeniolata ornata*. This nominal taxon has not been accepted as valid since, nor has its status been reevaluated, although Branch et al. (2019a) suggested that the name *damarana* was applicable to northern Namibian *N. holubi*, without commenting on its validity.

As currently construed, both *Nucras tessellata* and *N. intertexta* have broad distributions, the Namibian portions of which are contiguous with the rest of their respective ranges (Branch 1998; Visser 1984). However, *Nucras holubi* is currently recognized as having a disjunct distribution in southern Africa. The main area of occurrence extends from about 31°S in the northern Eastern Cape Province of South Africa, to the north and east to include the central and northeastern provinces of South Africa, Eswatini (formerly Swaziland), eastern Botswana, Zimbabwe, southern Malawi, and almost certainly parts of Mozambique; while the second area is in north central Namibia (Bourquin 2004; Branch 1998; Burger 2014; De Waal 1978; Griffin 2003; Jacobsen 1989). The large gap between these two areas (> 900 km) has long suggested to herpetologists that the status of the Namibian population required further investigation

Here morphological and molecular data from northern Namibian specimens of *Nucras* were used to reevaluate the status of *N. holubi* and *N. damarana* in the country. The possibility that a recently described Angolan species might also occur in Namibian territory was also investigated. The *Nucras* in southwestern Angola had variously been referred to either *N. tessellata* (Bocage 1895), *N. t. taeniolata* (Boulenger 1910), or *N. intertexta holubi* (Boulenger 1917, 1920), and was considered to represent a new species by Broadley (1972; see review therein). Branch et al. (2019a) stabilized the situation in Angola by describing the species known from Namibe, Huila, and Cunene provinces in southwestern Angola as *Nucras broadleyi*, the southernmost record of which is from Donguena, Cunene Province (-17.01667, 14.71667), only 42 km north of the Namibian border.

Materials and Methods

Specimens. Standard institutional codes used in this paper are: CAS (California Academy of Sciences, San Francisco, California, USA), MCZ (Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA), NHMUK (The Natural History Museum, London, United Kingdom), NMB (National Museum, Bloemfontein, South Africa), NMNW (National Museum of Namibia, Windhoek, Namibia), NMW (Naturhistorisches Museum Wien, Vienna, Austria), PEM (Port Elizabeth Museum, Port Elizabeth, South Africa), SAM (Iziko, South African Museum, Cape Town, South Africa), DNMNH (Ditsong National Museum of Natural History, Pretoria, South Africa), and ZFMK (Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany). Additional tissue samples were derived from the collections of Vincent Egan (LMH), Marius Burger (MB/MBUR), Michael Cunningham (MH), and Raymond B. Huey (RBH).

Morphology. The following mensural features were recorded to the nearest 0.1 mm using digital calipers: SVL (snout-vent length), TrW (trunk width), TailL (tail length), TailW (maximum tail width), AGL (axilla-groin length), HumL (humerus length), ForeL (forearm length), FemL (femur length), CrusL (shank length from knee to heel), PesL (pes length from heel to tip of 4th toe), HeadL (head length), HeadW (head width), HeadD (Head depth), CSn (collar-snout length), OrbD (eye diameter = width of eye), NEye (nostril to eye distance), EyeE (eye to ear distance), EarD (maximum height of ear opening), and EarW (maximum width of ear opening). Details of pholidosis including head scalation, as well as femoral pore disposition, were also recorded. Except in the case of MCZ R-190201 (see below), scalation and pore data were collected unilaterally, for head scalation from the right side of the body and femoral pores from the left side of the specimen only. Morphological data are presented in Table 1. Additional data for *N. holubi* were derived from Broadley (1972) and Jacobsen (1989). Comparisons were made with all other described species of *Nucras* based on material listed in Bauer et al. (2019) and from literature sources (e.g., Branch et al. 2019a; Broadley 1972).

Molecular data. New sequence data were generated for specimens of *Nucras* sp. ($n = 1$) and *N. holubi* from South Africa ($n = 4$) and Namibia ($n = 1$), and were combined with sequence data generated for a previous phylogenetic study on South African *Nucras* (Bauer et al. 2019) from 48 individuals of seven *Nucras* species (*N. boulengeri*, *N. holubi*, *N. intertexta*, *N. ornata*, *N. lalandii*, *N. tessellata*, and *N. livida*). Further data from Branch et al. (2019a) were downloaded from GenBank for additional sequences of *N. intertexta* ($n = 3$), *N. holubi* ($n = 1$), *N. taeniolata* ($n = 2$), *N. tessellata* ($n =$

1), *N. livida* ($n = 1$), *N. lalandii* ($n = 2$), and *N. broadleyi* ($n = 2$), and for five outgroup taxa belonging to the southern African radiation of Eremiadinae (Engledler et al. 2013): *Australolacerta australis*, *Meroles knoxii*, *M. suborbitalis*, *Pedioplanis laticeps*, *P. namaquensis*, and *Heliobolus lugubris*. All of the sequences combined resulted in a final dataset of 73 individuals (see Table 2). Genomic DNA was extracted using the Qiagen DNAeasy Kit from whole tissues consisting of tail tips, liver, or skeletal muscle and stored in 95% ethanol. PCR amplification was performed on an Eppendorf Mastercycler gradient thermocycler using the primer pairs METF1 (5'-AAGCTTTTCGGGCCCATACC-3') (Macey et al. 1997) and CO1R1 (5'-AGRGTG CCAATGTCTTTGTGRTT-3') (Arèvalo et al. 1994) for ND2, ND4F (5' CACCTATGACTAC CAAAAGCTCATGTAGAAGC-3') and Leu (5'-CATTACTTTTACTTTGGATTTGCACCA-3') (Arèvalo et al. 1994) for ND4, and 16Sa-1 (5'-CGCCTGTTTATCAAAAACAT-3') and 16S-H (5'-CCGGTCTGAACTCAGATCACGT-3') (Palumbi et al. 1991) for 16S. PCR products were visualized using 1.5% agarose gels before being purified with the AMPure magnetic bead solution kit (Agencourt Bioscience, Beverly, Massachusetts, USA). Cycle sequencing was performed using the BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, California, USA) and then samples were purified using the CleanSeq magnetic bead kit (Agencourt Bioscience, Beverly, Massachusetts, USA). Sequences were analyzed on an ABI 3730xl DNA analyzer and subsequently assessed in Geneious Prime v2020.0.5, where an initial sequence alignment was constructed using the MUSCLE v3.8.31 alignment tool and then manually adjusted by eye.

Phylogenetic analysis. Phylogenetic tree reconstruction used 1,686 base pairs (bp) derived from three mitochondrial markers (16S, ND2, and ND4). Variable and parsimony informative sites were summarized using the tool AMAS (Alignment Manipulation and Summary) (Borowiec 2016). Maximum likelihood (ML) and Bayesian inference (BI) analyses were performed on the CIPRES Science Gateway v3.3 (Miller et al. 2010). Analyses were performed on each individual gene and on the concatenated set of mitochondrial genes. Each dataset was partitioned using PartitionFinder v2.1.1 (Lanfear et al. 2017), employing the partitioning schemes supported by the Bayesian Information Criterion (BIC) score for each analysis. The analysis resulted in three partitions for the concatenated mtDNA analysis: (1) the first codon position of ND2 and the third codon of ND4; (2) the second codon position of ND2, the first codon position of ND4, and the entire 16S gene; and (3) the third codon position of ND2 and the second codon position of ND4. All ML partitions were run under the GTR+ Γ model of evolution using RAXML v8.1.24 (Stamatakis 2014) for

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Table 1. Measurements and scale counts from Namibian specimens of *Nucras damarana* and *N. aff. broadleyi*. Scale counts are provided for the right side of the body only and femoral pore counts from the left, except for MCZ R190201, which serves as the basis for the redescription of *Nucras damarana* provided in this paper.

	<i>N. damarana</i>	<i>N. damarana</i>	<i>N. damarana</i>	<i>N. damarana</i>	<i>N. damarana</i>	<i>N. aff. broadleyi</i>
	MCZ R190201	CAS 180421	CAS 193676	CAS 193807	CAS 193668	CAS 214642
SVL	57.6	41.6	31.8	42.6	38.8	58.2
TrW	9.4	6.5	3.8	6.7	5.5	9.7
TailL	107.0	101.0	67.5	89.0	95.0	120
TailW	5.0	3.3	2.2	3.3	3.4	4.7
AGL	32.0	20.8	14.7	24.7	20.0	31.5
HumL	5.0	4.7	3.2	4.6	4.4	5.8
ForeaL	5.5	4.8	3.7	3.9	3.8	5.5
FemL	7.7	6.9	5.5	5.5	5.3	7.5
CrusL	8.5	7.4	5.5	6.2	6.5	8.2
PesL	12.2	12.4	9.8	11.3	11.0	12.2
HeadL	11.6	11.4	8.4	10.6	9.9	13.1
HeadW	7.6	6.7	4.3	5.3	5.5	7.2
HeadD	5.5	4.6	3.1	4.3	4.2	5.5
CSn	17.8	15.2	11.6	13.4	14.5	19.1
OrbD	2.0	2.0	1.2	1.9	1.9	2.0
Neye	3.8	3.1	2.3	3.1	2.6	3.7
Eyee	4.5	3.9	2.4	3.6	3.8	5.0
EarH	2.2	1.9	1.3	1.7	1.7	2.1
EarW	1.3	0.8	0.5	1.1	0.9	1.3
Chin Shields	4/4	4	4	4	4	4
Femoral pores (per thigh)	12/12	13	13	13	13	13
Supralabials	8/8	7	7	7	7	6
Infralabials	8/8	6	7	6	6	6
Supraoculars	4/4	4	4	4	4	4
Supraciliaries	7/8	7	7	7	7	7
Supraciliary granules	5/5	6	4	6	6	6
Supratemporals	2/3	2	3	2	3	4
Dorsal scale rows at midbody	36	40	37	37	36	38
Ventral scale rows	8	8	8	8	8	8
Ventral scales in longitudinal series	33	28	28	28	29	34
Subdigital lamellae	9/9-14/13-18/18-26/25-?/14	7-13-18-25-12	8-13-18-24-14	9-13-18-24-14	10-13-17-24-14	10-13-18-23-13

Table 2. Samples used in molecular phylogenetic analysis with associated GenBank accession numbers. Specimen collection standard abbreviations are detailed in **Materials and Methods**.

Taxon name	Specimen	Field/tissue #	Country	Province/Region	Specific locality	Latitude	Longitude	GenBank accession number		
								ND2	16S rRNA	ND4
<i>Nucras aurantiacus</i>	NMB R11626	USHNS01	South Africa	Western Cape	Lamberts Bay	32°05'04.36"S	18°21'26.9"E	MH023414	MH023413	—
<i>Nucras aurantiacus</i>	NMB R11627	USHNS02	South Africa	Western Cape	Lamberts Bay	32°05'04.36"S	18°21'26.9"E	MH023415	—	—
<i>Nucras boulengeri</i>	PEM R16773	KC 20	Tanzania	Mara	Klein's Camp	01°49'16.2"S	35°14'30.5"E	MG846513	MG846603	—
<i>Nucras</i> aff. <i>broadleyi</i>	CAS 214642	AMB 6405	Namibia	Kunene	59 km W of Kamanjab	19°39'14"S	14°21'03"E	MT137656	MT139873	MT137653
<i>Nucras broadleyi</i>	PEM R24005	AG 018	Angola	Namibe	10 km W Lola	14°17'25"S	13°31'50"E	—	MN265869	—
<i>Nucras broadleyi</i>	PEM R24157	AG 166	Angola	Namibe	8.8 km SW Farm Mucungo	14°48'06"S	12°25'09"E	—	MN265870	MN265871
<i>Nucras damarana</i>	MCZ R190201	AMB 8037	Namibia	Omusati	60 km SE of Ruacana Crossroads	17°29'8.1"S	14°51'57.9"E	MT137660	MT139875	MT137655
<i>Nucras holubi</i>	—	MB 21672	South Africa	Limpopo	Farm Kalkfontein	24°54'47"S	30°04'17"E	MT137657	—	—
<i>Nucras holubi</i>	CAS 234138	MCZ F38793	South Africa	Limpopo	Farm Pylkop	22°45'52"S	29°44'28"E	MG846533	MG846601	MG846580
<i>Nucras holubi</i>	MCZ R184459	AMB 8313	South Africa	Limpopo	Farm Celine	22°41'29"S	29°31'42"E	MG846532	MG846582	MG846563
<i>Nucras holubi</i>	NMB R11613	MBUR 01001	South Africa	Limpopo	Greater Kuduland Safaris	22°38'28"S	30°18'50"E	MG846534	MG846596	MG846577
<i>Nucras holubi</i>	NMB R11615	MBUR 01027	South Africa	Limpopo	Greater Kuduland Safaris	22°38'28"S	30°18'50"E	MG846515	MG846597	MG846578
<i>Nucras holubi</i>	PEM R17430	—	South Africa	KwaZulu-Natal	Mkhuze Game Reserve	27°37'17"S	32°10'40"E	MT137661	—	—
<i>Nucras holubi</i>	PEM R18647	RSP420	South Africa	Limpopo	Venetia Limpopo Reserve	22°19'08"S	29°20'53"E	—	HG005187	HG005215
<i>Nucras holubi</i>	PEM R22813	MBUR 00232	South Africa	Limpopo	Bochum	23°16'52"S	29°08'10"E	MT137658	—	—
<i>Nucras holubi</i>	PEM R22814	MBUR 00260	South Africa	Limpopo	Bochum	23°16'52"S	29°08'10"E	MT137659	MT139874	MT137654
<i>Nucras intertexta</i>	—	LMH 000095	South Africa	Limpopo	Bergplaats Game Lodge	24°00'1.9"S	29°58'56.6"E	MG846550	MG846583	MG846564
<i>Nucras intertexta</i>	—	MB 20952	South Africa	Northern Cape	Farm Blackridge	28°49'02"S	22°32'42"E	MG846542	MG846587	MG846568
<i>Nucras intertexta</i>	—	MBUR 21183	South Africa	Northern Cape	Farm Lemoenfontein	30°51'10"S	23°37'36"E	—	HG005194	HG005222

Sandveld lizards (*Nucras*) of Namibia**Table 2 continued.** Samples used in molecular phylogenetic analysis with associated GenBank accession numbers. Specimen collection standard abbreviations are detailed in **Materials and Methods**.

Taxon name	Specimen	Field/tissue #	Country	Province/Region	Specific locality	Latitude	Longitude	GenBank accession number		
								ND2	16S rRNA	ND4
<i>Nucras intertexta</i>	CAS 234193	MCZ F38851	South Africa	Limpopo	Lajuma Wilderness Camp	23°02'21"S	29°26'59"E	MG846541	MG846602	MG846581
<i>Nucras intertexta</i>	CAS 234212	MCZ F38872	South Africa	Limpopo	Lajuma	23°02'10"S	29°25'41"E	MG846540	—	—
<i>Nucras intertexta</i>	PEM R18257	RSP030	South Africa	Northern Cape	Rooipoort	28°36'45"S	24°08'41"E	—	HG005191	HG005219
<i>Nucras intertexta</i>	PEM R18661	RSP 277	South Africa	Northern Cape	Tswalu	27°17'52"S	22°27'14"E	—	HG005190	HG005218
<i>Nucras intertexta</i>	PEM R20958	MB 21288	South Africa	Northern Cape	Farm Mansfield	27°41'28"S	23°25'00"E	MG846525	—	—
<i>Nucras intertexta</i>	PEM R21065	MB 21406	South Africa	North West	About 1 km SE of Majankeng	27°07'04"S	23°57'31"E	MG846543	—	—
<i>Nucras lalandii</i>	—	MB 20982	South Africa	Western Cape	11 km ESE Herbertsdale	34°02'49"S	21°53'07"E	—	HG005197	HG005225
<i>Nucras lalandii</i>	—	MBUR 00483	South Africa	Eastern Cape	Farm Bamboesberg	31°36'52"S	26°18'50"E	—	HG005196	HG005224
<i>Nucras lalandii</i>	NMB R10904	MBUR 00484	South Africa	Eastern Cape	Bamboesberg, Farm Bamboeshoek	31°36'52"S	26°18'50"E	MG846549	MG846591	MG846572
<i>Nucras lalandii</i>	PEM R21025	MBUR 00414	South Africa	Eastern Cape	1 km S of Siphpheto village	30°33'03"S	28°50'22"E	MG846548	MG846590	MG846571
<i>Nucras lalandii</i>	PEM R21026	MBUR 00415	South Africa	Eastern Cape	1 km S of Siphpheto village	30°33'03"S	28°50'22"E	MG846544	—	—
<i>Nucras lalandii</i>	PEM R22815	MBUR 00411	South Africa	Eastern Cape	1 km W of Siphpheto village	30°32'08"S	28°49'38"E	MG846547	MG846589	MG846570
<i>Nucras lalandii</i>	PEM R22816	MBUR 00412	South Africa	Eastern Cape	1 km W of Siphpheto village	30°32'08"S	28°49'38"E	MG846546	—	—
<i>Nucras lalandii</i>	PEM R22817	MBUR 00432	South Africa	Eastern Cape	Near Fever village	30°32'07"S	28°49'37"E	MG846545	—	—
<i>Nucras lalandii</i>	PEM R22818	MBUR 00485	South Africa	Eastern Cape	Bamboesberg, Farm Bamboeshoek	31°36'52"S	26°18'50"E	MG846516	MG846592	MG846573
<i>Nucras lalandii</i>	PEM R22819	MBUR 00550	South Africa	Eastern Cape	1.5 km E of Toisekraal	31°49'45"S	26°45'36"E	MG846560	MG846593	MG846574

Table 2 continued. Samples used in molecular phylogenetic analysis with associated GenBank accession numbers. Specimen collection standard abbreviations are detailed in **Materials and Methods**.

Taxon name	Specimen	Field/tissue #	Country	Province/Region	Specific locality	Latitude	Longitude	GenBank accession number			
								ND2	16S rRNA	ND4	ND4
<i>Nucras lalandii</i>	PEM R9707	—	South Africa	Eastern Cape	Mientu River nr. Holy Cross Mission	31°09'19"S	29°44'44"E	MG846517	—	—	—
<i>Nucras livida</i>	PEM R18747	KTH 08-071	South Africa	Western Cape	Little Karoo	33°32'50"S	21°12'55"E	—	HG005200	HG005227	—
<i>Nucras livida</i>	PEM R19087	MB 21209	South Africa	Northern Cape	Farm Kareehook	30°10'37"S	23°28'54"E	MG846535	MG846588	MG846569	—
<i>Nucras livida</i>	PEM R19094	MB 21216	South Africa	Northern Cape	~44 km SW of Strydenburg	30°08'27"S	23°15'31"E	MG846536	—	—	—
<i>Nucras livida</i>	PEM R19103	MB 21225	South Africa	Northern Cape	Farm Goodhope	30°07'28"S	23°18'48"E	MG846519	—	—	—
<i>Nucras livida</i>	PEM R19108	MB 21230	South Africa	Northern Cape	Farm Kareehook	30°10'37"S	23°28'54"E	MG846537	—	—	—
<i>Nucras livida</i>	PEM R19116	MB 21238	South Africa	Northern Cape	Farm Goodhope	30°07'28"S	23°18'48"E	MG846538	—	—	—
<i>Nucras livida</i>	PEM R22820	MBUR 00632	South Africa	Eastern Cape	Farm Suurhoek	32°51'37"S	24°27'25"E	MG846520	MG846594	MG846575	—
<i>Nucras livida</i>	PEM R22821	MBUR 00646	South Africa	Eastern Cape	Farm Matjiesfontein	32°50'50"S	24°25'12"E	MG846521	—	—	—
<i>Nucras livida</i>	PEM R22822	MBUR 00670	South Africa	Eastern Cape	Farm Matjiesfontein	32°50'06"S	24°26'28"E	MG846539	—	—	—
<i>Nucras livida</i>	PEM R22823	MBUR 00687	South Africa	Western Cape	Farm Tierberg	33°09'12"S	22°15'56"E	MG846518	MG846595	MG846576	—
<i>Nucras ornata</i>	NMB R10657	MBUR 01169	South Africa	KwaZulu-Natal	Manyiseni region	26°54'55"S	32°03'04"E	MG846529	—	—	—
<i>Nucras ornata</i>	NMB R10658	MBUR 01230	South Africa	KwaZulu-Natal	Manyiseni region	26°54'55"S	32°03'04"E	MG846527	—	—	—
<i>Nucras ornata</i>	NMB R10659	MBUR 01251	South Africa	KwaZulu-Natal	Usutu Gorge	26°51'58"S	32°09'17"E	MG846551	—	—	—
<i>Nucras ornata</i>	NMB R10660	MBUR 01262	South Africa	KwaZulu-Natal	1.5 km SE of Ekuhleleni	26°51'38"S	32°03'08"E	MG846552	—	—	—
<i>Nucras ornata</i>	PEM R17591	AMB 8635	South Africa	Mpumalanga	N of Swaziland border	25°05'27"S	31°59'23"E	MG846526	—	—	—
<i>Nucras ornata</i>	PEM R5906	—	South Africa	KwaZulu-Natal	Manjiseni region	27°04'45"S	32°02'25"E	MG846531	—	—	—
<i>Nucras taeniolata</i>	—	HZ251	South Africa	Eastern Cape	—	—	—	—	HG005208	HG005230	—
<i>Nucras taeniolata</i>	PEM R18080	—	South Africa	Eastern Cape	Nyati Camp	32°59'03"S	26°50'01"E	—	HG005210	HG005231	—

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Table 2 continued. Samples used in molecular phylogenetic analysis with associated GenBank accession numbers. Specimen collection standard abbreviations are detailed in **Materials and Methods**.

Taxon name	Specimen	Field/tissue #	Country	Province/Region	Specific locality	Latitude	Longitude	GenBank accession number			
								ND2	16S rRNA	ND4	ND4
<i>Nucras tessellata</i>	—	MB 20724	South Africa	Northern Cape	Farm Donkiedam	30°55'27"S	19°02'51"E	MG846557	MG846586	MG846567	—
<i>Nucras tessellata</i>	—	RBH 3468	South Africa	Northern Cape	Kgalagadi Transfrontier Park	26°24'12.1"S	20°41'1.46"E	MG846524	MG846604	—	—
<i>Nucras tessellata</i>	CAS 201917	AMB 5070	South Africa	Northern Cape	Richtersveld National Park	28°6'40"S	17° 1' 10" E	MG846522	—	MG846561	—
<i>Nucras tessellata</i>	CAS 206723	AMB 5582	South Africa	Northern Cape	Groenriviermond	30°51'29"S	17° 34' 43" E	MG846553	—	MG846562	—
<i>Nucras tessellata</i>	CAS 206725	AMB 5584	South Africa	Northern Cape	Groenriviermond	30°51'29"S	17° 34' 43" E	MG846555	—	—	—
<i>Nucras tessellata</i>	NMB R10781	MBUR 21061	South Africa	Northern Cape	Farm Good Hope	29°52'04"S	22°33'22"E	MG846559	—	—	—
<i>Nucras tessellata</i>	NMB R11497	MBUR 1393	South Africa	Northern Cape	Farm Leeuberggrivier	30°27'48"S	19°26'52"E	MG846523	MG846598	—	—
<i>Nucras tessellata</i>	NMB R11514	MBUR 1394	South Africa	Northern Cape	Farm Narosies	30°33'03"S	19°34'53"E	MG846558	MG846599	MG846579	—
<i>Nucras tessellata</i>	PEM R16872	MB 20687	South Africa	Northern Cape	Farm Kamas	30°35'28"S	18 49 20 E	—	HF951557	HF951536	—
<i>Nucras tessellata</i>	PEM R16873	MB 20650	South Africa	Northern Cape	Farm Loerkop	30°39'23"S	19°20'33"E	MG846554	MG846584	MG846565	—
<i>Australolacerta australis</i>	—	MH 0531	South Africa	Western Cape	Buffelshoek Corner	33°28'19"S	19°23'41"E	DQ871094	DQ871152	—	—
<i>Heliobolus lugubris</i>	CAS 234139	MCZ F37894	South Africa	Limpopo	Farm Pylkop	22°45'52"S	29°44'28"E	DQ871084	DQ871142	—	—
<i>Heliobolus lugubris</i>	R184277	MCZ F37870	Namibia	Kunene	Kamanjab Rest Camp	19°37'47"S	14°48'56"E	DQ871083	DQ871141	—	—
<i>Meroles knoxii</i>	CAS 206782	AMB 5629	South Africa	Northern Cape	Port Nolloth	29°15'11.4"S	16°52'40.8"E	DQ871088	DQ871146	—	—
<i>Meroles suborbitalis</i>	PEM R16978	MB 20696	South Africa	Northern Cape	Farm Kamans	30°35'17"S	18°50'49"E	MG846556	MG846585	MG846566	—
<i>Pedioplanis laticeps</i>	PEM R17212	JSM 018	South Africa	Northern Cape	Bezantsgat Farm	32°29'34"S	19°35'34"E	DQ871067	DQ871125	—	—
<i>Pedioplanis namaquensis</i>	CAS 200033	AMB 4558	South Africa	Northern Cape	vic. Kodas Ruins	28°14'58"S	16°56'41"E	DQ871043	DQ871101	—	—

1,000 rapid nonparametric bootstrap replicates (BS), with values greater than 70% considered to be indicative of support. The BI PartitionFinder analysis resulted in the same partitioning scheme recovered for the ML analysis (Partitions 1–3 listed above) and were run using the GTR+I+ Γ (Partitions 1 and 2) and HKY+ Γ (Partition 3) models of evolution. MrBayes v3.2.7 (Ronquist et al. 2012) was used to perform the BI analysis, and it was run for 50,000,000 generations sampling every 10,000 generations. Convergence of the Markov chains was assessed by eye using Tracer v1.6 (Rambaut et al. 2014) and the initial 25% of trees were discarded as burn-in. Posterior probabilities (PP) greater than 0.95 were considered to be indicative of support.

Results

Molecular phylogenetics. Final alignments for the three mitochondrial markers were as follows: ND2, 403 bp (226 variable, 193 parsimony informative); ND4, 732 bp (329 variable, 278 parsimony informative); and 16S, 551 bp (157 variable, 123 parsimony informative). There were no conflicts in the tree topologies between the BI and ML analyses and both analyses retrieved generally high nodal support, with some notable exceptions, throughout their respective trees (Fig. 1). *Nucras boulengeri* and *N. broadleyi* (including our *Nucras* sp. from northern Namibia) form a clade sister to all other *Nucras* species (BS = 89%, PP = 0.92). Among the remaining named taxa there are two major clades (although this split received weak nodal support; BS = 46%, PP = 0.58): one which includes *N. holubi* (BS = 100%; PP = 1.0), and sister taxa *N. intertexta* and *N. ornata* (BS = 100%, PP = 0.99), and another which is comprised of all remaining *Nucras* species. The latter includes *N. aurantiacus*, which is sister (BS = 99%, PP = 1.0) to a clade containing *N. livida* which is itself sister (BS = 99%, PP = 1.0) to a clade (BS = 95%, PP = 0.99) containing *N. tessellata* and *N. taeniolata*, with *N. taeniolata* appearing nested within the broader *N. tessellata* clade (BS = 90%, PP = 0.92). Pairwise uncorrected ND4 distances between *N. taeniolata* and sister *N. tessellata* samples (CAS 201917, 206723) were 0.45–6.08% (mean 3.26%).

Within *N. holubi* there appear to be three highly divergent clades. The first is comprised of individuals from the Limpopo and KwaZulu-Natal provinces of South Africa (BS = 100%, PP = 1.0), which is sister (BS = 100%, PP = 1.0) to a second clade comprised of an individual from Namibia, which is sister (BS = 80%, PP = 0.89) to another set of specimens collected from Limpopo, South Africa—thus rendering the South African *N. holubi* paraphyletic with respect to the single specimen collected in northern Namibia (MCZR190201). Pairwise uncorrected ND2 distances from the Namibian *N. holubi* were 12.30–12.84% (mean 12.50%) to their sister South African *N. holubi*, and 14.25–14.56% (mean 14.40%) to the remaining (outgroup) South African *N.*

holubi. For 16S, there was a 19.14% mean difference between the Namibian specimen and its sister clade of *N. holubi*, a 12.83% difference from the other South African *N. holubi*, and a 19.66% mean divergence between the two South African *N. holubi* clades. Comparable values for ND4 were 13.1%, 17.84%, and 15.58%. The mean intraclade divergences for the sister clade to the Namibian sample was 2.01% for ND2 (range 0.26–3.42%). Divergences were 2.85% for ND4 and 1.09% for 16S for the only two samples available for these markers. Pairwise uncorrected distances between the Angolan *N. broadleyi* and its Namibian sister were 15.03–15.69% and 8.24% for 16S and ND4, respectively, and there was a 7.83% 16S difference between the two Angolan samples (noting that no ND2 data were available for the Angolan samples and ND4 was available only for PEM R24157).

Morphology

Nucras damarana. The Namibian specimen genotyped as a member of the *N. holubi* clade (MCZ R190201) was compared to specimens of *N. holubi* from Limpopo Province, South Africa, from which the original syntype series was derived (Limpopo Valley, Transvaal; Steindachner 1882). It was also compared to the type material of *N. intertexta damarana* (Fig. 2). Parker (1936) distinguished *N. i. damarana* from its congeners by its small size (maximum 54 mm SVL) and the shortening of the interparietal such that the parietals form a suture behind it. Broadley (1972) recorded 24 specimens of *Nucras taeniolata ornata* from Southwest Africa [=Namibia], all of which may be assumed to be the same taxon described by Parker (1936). He further demonstrated that one of Parker's distinguishing features for *N. i. damarana*, the contact of the parietals separating the interparietal from the occipital, was not constant among the Namibian material and that it also occurred in other congeners.

However, Broadley (1972) did find that his Namibian “*ornata*” were smaller than all other members of the *N. tessellata* group, except for *N. taeniolata ornata* (today *N. holubi*) from Gaborone, Botswana, with no individuals larger than 57 mm SVL. He also demonstrated that the Namibian specimens had the lowest mean number of transverse scale rows at midbody (39), with almost no overlap between this group and his other populations of *N. ornata* (= *N. ornata* + *N. holubi*). This group also exhibited one of the lowest total numbers of femoral pores (lowest minimum number of 21, and second only in mean to the Kimberley District specimens [of *N. holubi*] of < 26).

MCZ R190201 (Figs. 3, 4A) is only slightly larger than the largest specimen recorded by Broadley (1972: 57.6 vs. 57 mm SVL), and has only 36 midbody scale rows and a total of only 24 femoral pores. Four additional specimens of Namibian “*N. holubi*” examined here

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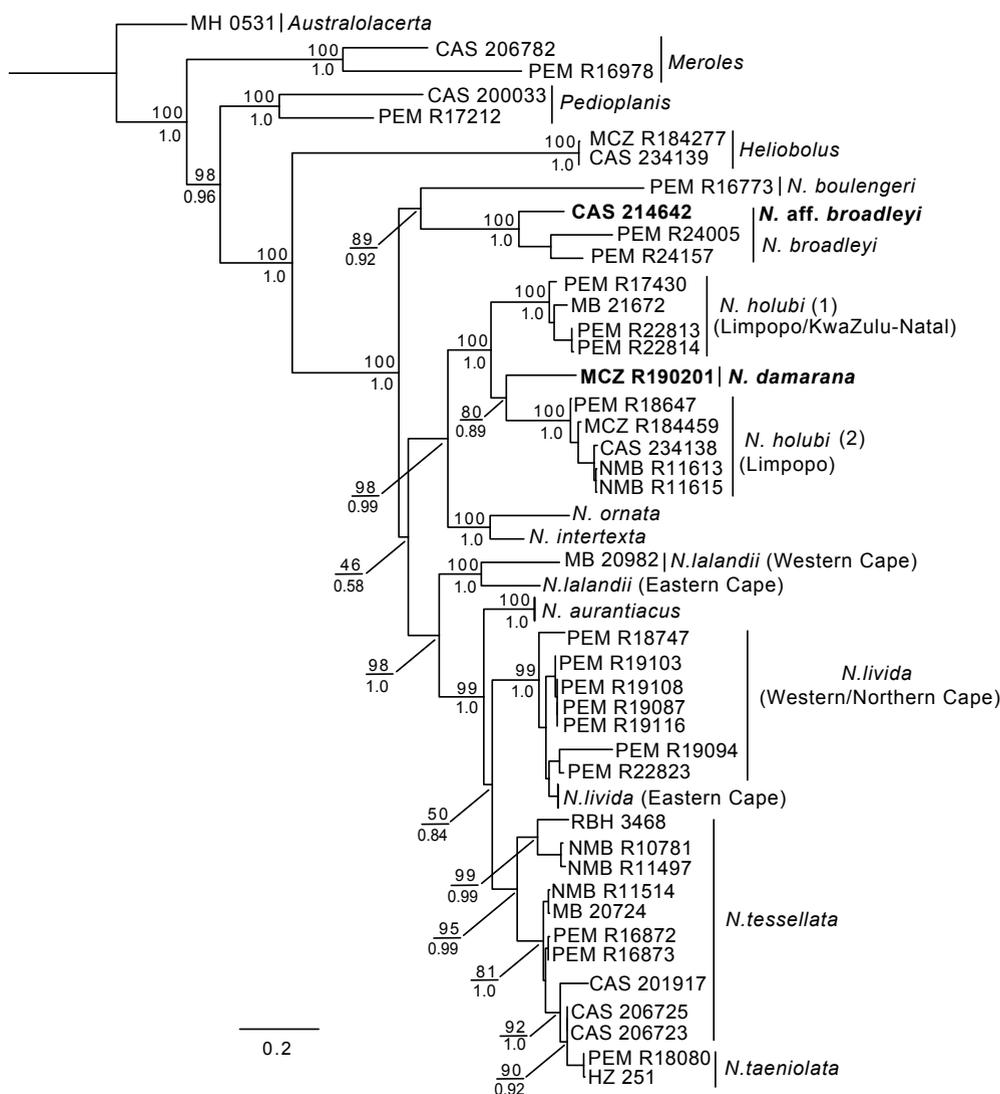


Fig. 1. Concatenated mitochondrial RaxML phylogram of the genus *Nucras* and outgroups used in this study. Bootstrap support (above) and posterior probabilities (below) are shown for the species level and more inclusive nodes. Select nodes containing individuals with identical or minor sequence divergence (less than 2%) from shared localities and from non-focal taxa have been collapsed in order to condense overall tree size; but a full list of the specimens used in this study can be found in Table 1.

(CAS 180421, 193807, 193668, 193676) are likewise consistent, with maximum counts of 40 midbody scale rows and 26 femoral pores. Further, Parker's (1936) statement that the occipital scale was reduced in his new taxon is also borne out by our specimens, two of which have a small occipital scale and three of which have no distinct occipital scale (Fig. 3C). These features separate the disjunct Namibian "*N. holubi*" from the southeastern African *N. holubi sensu stricto* and, along with the large genetic divergence and geographic disjunction between them, support the resurrection of *Nucras damarana* Parker, 1936 as a distinct taxon that is apparently endemic to northern Namibia.

Parker's (1936) description of *Nucras intertexta damarana* was written at a time of great confusion over species boundaries within *Nucras*. Indeed, despite its obvious similarity to *N. holubi* and *N. ornata*, his

comparisons were chiefly with *N. intertexta*. This confusion still existed through the revisionary work of Broadley (1972), who synonymized several taxa now considered distinct from one another. Parker's (1936) diagnosis was brief and is now inadequate to unambiguously distinguish the taxon among all of its congeners. As a consequence, we provide a new diagnosis for the taxon and a detailed description of MCZ R190201.

Nucras damarana Parker, 1936

Nucras tessellata [part]: Werner (1910: 329).

Nucras intertexta damarana Parker, 1936: 135.

Syntypes: NHMUK 1946.8.6.17–24 [originally 1936.8.1.534–541]. Sessekab [=Sissekab], N.W. of Otavi, 1,300 m. Coll. Karl Jordan, 10–12 November 1933.



Fig. 2. Syntype series of *Nucras intertexta damarana* Parker, 1936 (NHMUK 1946. 1946.8.6.17–24) from Sissekab (-19.328645, 17.196238), Otjozondjupa Region, Namibia. The image has been modified to provide a uniform background and some extraneous string has been deleted. Photo by A.M. Bauer.

Nucras intertexta holubi [part]: FitzSimons (1943: 320).
Nucras taeniolata ornata [part]: Broadley (1972: 13).
Nucras taeniolata holubi [part]: Jacobsen (1989: 453).
Nucras holubi: Bates (1996: 35) [by implication]; Branch (1998: 169) [explicit for Namibian populations].

Referred material

Kunene Region: Otjivakundu (-17.120881, 13.258644) DNMNH 38806–07; 25 km N of Etengua (-17.292402, 12.945191) DNMNH 49033; 15 km N of Opuwo (-17.944228, 13.857124) DNMNH 48964–65; Opuwo (-18.061608, 13.83867) NMW 35352, DNMNH 24479, DNMNH 32352 [given as DNMNH 32351 by Broadley (1972)], DNMNH 33021, DNMNH 38911–14, DNMNH 71317; 57.9 km SW of Opuwo on Opuwo-Orupembe Rd. (-18.25533, 13.50200) CAS 193807; Okamangudona (-18.264261, 13.513046) DNMNH 71284; Hoarusib River, 92 km S of Opuwo (-18.269277, 13.216553) DNMNH 51219; Kaoko Otavi (-18.299656, 13.654006) SAM ZR-017494; Otjitundua (-18.65000, 14.23333) SAM ZR-017535; 35 km W of

Kamanjab on Kamanjab-Torrabaai Rd. (-19.57617, 14.59877) CAS 193668; Torrabaai Rd., 48.6 km W of Farm Franken entrance (-19.63633, 14.38267) CAS 180421; 59.3 km W of Kamanjab on Kamanjab-Torrabaai Rd. (-19.65167, 14.35558) CAS 193676; Outjo (-20.116667, 16.15000) SAM ZR-017507; Farm Kaokokroou [487] (-20.35948, 14.905159) NMW 31109. **Omusati Region:** 60 km SE of Ruacana crossroads (-17.48558, 14.86608) MCZ R190201; Ombombo (-17.940000, 14.310000) SAM ZR-017519. **Oshana Region:** Emono, 2 km SW of Onayena (-17.775004, 15.678522) NMB R07448; Oshakati (-17.785131, 15.698611) DNMNH 38613, DNMNH 45761. **Oshikoto Region:** Namutoni (-18.807768, 16.940231) ZFMK 18579–80; Chudop Waterhole (-18.856125, 16.923499) NMNW 5482; DNMNH 57024–25; Halali, Etosha National Park (-19.033333, 16.466667) DNMNH 56393. **Otjozondjupa Region:** Sissekab (-19.328645, 17.196238) NHMUK 1946.8.6.17–24; Kombat (-19.713265, 17.710345) DNMNH 30464. **Note:** Broadley (1972) listed DNMNH 22225 from Stamprietfontein in the Hardap

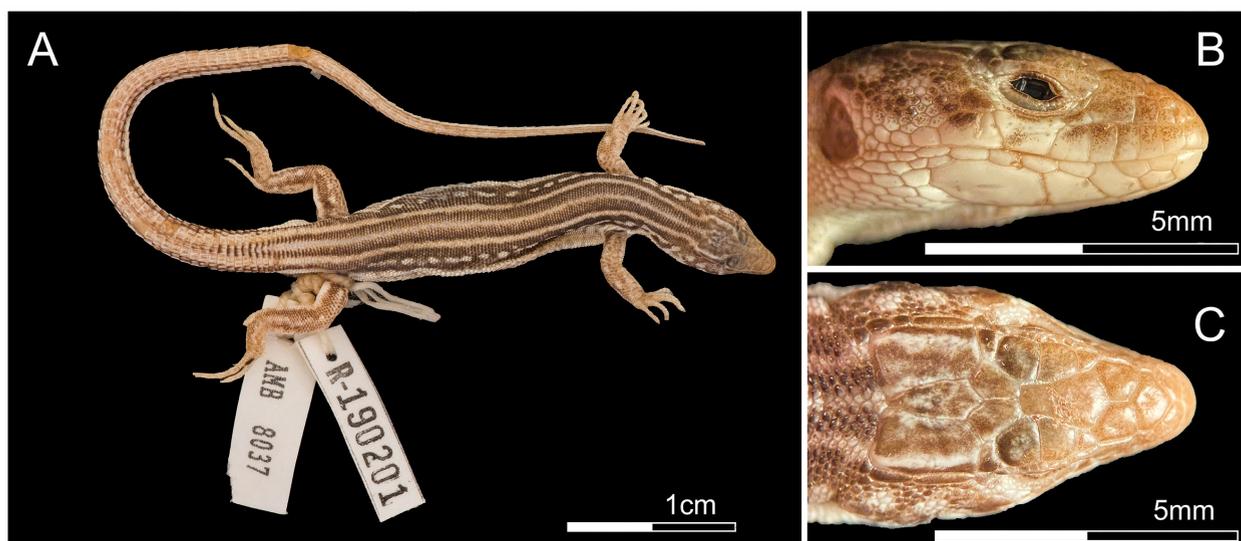


Fig. 3. *Nucras damarana* (MCZ R-190201). (A) Whole body dorsum, (B) lateral view of head, and (C) dorsal view of head. Note the single row of spots and dashes on each flank, and the absence of a discrete occipital scale. Photos by M. Murdoch.

Region (-24.33333, 18.40000), however, this specimen is listed in the DNMNH database as being from Opuwo, Kunene Region. Given the large geographic disjunction between Stamprietfontein and all other localities and the fact that there is another anomalous specimen record from Stamprietfontein in the Ditsong collection (*Causus rhombeatus*; DNMNH 22222), we consider the record as dubious and have omitted it.

Diagnosis. A small *Nucras* (maximum 57.6 mm SVL) with eight longitudinal series of enlarged ventral plates, a series of small granules between the supraoculars and supraciliaries, occipital scale reduced or absent, and enlarged plates on the underside of the forearm. Adult dorsal color pattern characterized by three distinct pale longitudinal stripes extending from the nape to the tail base, an additional pale stripe at ventrolateral margin of flanks, flank markings comprise spots or horizontal dashes typically in a single line, and tail not brightly colored (Figs. 3A, 4A).

The new species may be distinguished from *N. lalandii* by the presence of enlarged plates under the forearms and from *N. lalandii* and *N. boulengeri* by the presence of a series of small granules between the supraoculars and supraciliaries. In its color pattern (see above), it is distinct from *N. aurantiaca* (no dorsal markings), *N. scalaris* (dark crossbands), *N. lalandii* (dark blotches or ocelli or both, forming transverse bands, but never stripes), *N. intertexta* (pale dorsal spots and/or irregular thin crossbands or reticulations), *N. livida* (six stripes on nape), *N. tesellata* (two or four stripes on nape, stripes generally not extending to sacrum; tail and hindbody reddish), *N. broadleyi* (usually four stripes on nape, see section on this taxon below), *N. taeniolata* (8–11 stripes on nape), *N. caesicaudata* (5–7 pale dorsal stripes; tail pale blue), and *Nucras ornata*

(vertebral line often lacking; markings on flanks oriented vertically; tail reddish). *Nucras damarana* is most similar to *N. holubi*, with which it has long been confused. Both taxa share three prominent pale stripes and other basic pattern elements. However, the former species is much smaller, reaching only 57.6 mm SVL, whereas true *N. holubi* may reach 73 mm SVL (Jacobsen 1989), and has a lower number of midbody dorsal scale rows (34–42 (36–40 in our sample of five)) versus 41–65 in *N. holubi* in the former Transvaal (Jacobsen 1989) and 44–58 in Botswana (Broadley 1972). In addition, the vertebral stripe in *N. damarana* does not typically have crisply demarcated edges (Figs. 3A, 4A; vs. cleanly demarcated by a dark brown border in *N. holubi*, Fig. 4B) and flank markings in *N. damarana* generally form a single line of irregularly shaped pale spots, sometimes anteriorly the spots are connected (vs. frequently forming two or rarely more lines of irregularly shaped pale spots in *N. holubi*).

Description of MCZ R190201 (field number AMB 8037). Measurements are given in Table 1. Body moderately slender and elongate (AGL/SVL 0.56), trunk longer than hind limbs (AGL/[FemL + CrusL + PesL] 1.11), tail longer than SVL (TailL/SVL 1.86), moderately slender and tapering. Limbs short, pes longer than shank or femur (PesL/FemL 1.62; PesL/CrusL 1.47). Head moderately large (HeadL/SVL 0.20), distinct from neck, slightly elongate (HeadW/HeadL 0.66), not depressed (HeadD/HeadL 0.47). Snout blunt, short (NEye/HeadL 0.33), almost twice eye diameter (NEye/OrbD 1.9). Eye relatively large (OrbD/HeadL 0.17); lower eyelid scaly, with four large translucent/semi-opaque scales surrounded by a rim of small granules. Eye to ear distance more than 1.5 times diameter of eye (EyeE/OrbD 2.25).

Ear opening vertical, much taller than wide (EarH/EarW 1.62), without projecting lobules, bordered

posteriorly by a series of tiny granules and anteriorly by a series of slightly larger, elongate scales and anterior to this a vertical row of enlarged juxtaposed scales; tympanic shield narrow, three times the size of cheek scales. Rostral approximately as wide as deep, strongly gabled, separating supranasals for most of their length; loreal region flat to very slightly concave. Supralabials 8R/8L; increasing in size posteriorly to the sixth right, fifth left, which is largest; in subocular position and possessing a strong longitudinal furrow running the length of the scale in continuation with the contact border between the anteriormost supralabial and loreal. Infralabials 8R/8L, all much longer than wide.

Nostrils semicircular, surrounded by enlarged supranasal, and two postnasals, each approximately one-fourth the size of supranasal. Two loreal scales; anterior loreal trapezoidal, bordered anteriorly by two postnasals, dorsally by frontal and prefrontal, ventrally by second supralabial (fully) and supralabials one and three (point contact only); posterior loreal five-sided, posterior face much taller than anterior, twice as long as anterior loreal, bordered dorsally by prefrontal, posteriorly by first (point contact only) supraocular, first supraciliary, three preocular scales, and ventrally by supralabials three and four. Supranasals in narrow contact with one another posteromedially; frontonasal roughly hexagonal, wider than long, with lateral apices projecting posteriorly, gabled anteriorly; prefrontals in broad contact with one another. Frontal scale approximately two times wider anteriorly than posteriorly, lateral terminus of frontal-frontoparietal suture lies posterior to border between

second and third supraoculars. Four supraocular scales on both sides, second and third much larger than first and fourth, 7R/8L supraciliary scales, smallest at midorbit, where there is a row of five supraciliary granules separating supraorbitals from main row of supraciliaries on each side. Parietals five-sided, much longer than wide, with slight forward projection wedged between frontoparietal and fourth supraciliary. Interparietal scale narrow and elongate, tapering to a point posteriorly, separating posteriormost portion of frontoparietals from one another and completely separating left and right parietals; parietal window small but distinct; no clear occipital scale present (Fig. 3C). 2R/3L supratemporal scales, anterior narrow and elongate, posterior less than half the size of anterior, but much larger than scales of cheek region.

Mental roughly semicircular, broader than deep, roughly same width as rostral, bordered posteriorly by a pair of small chin shields in midline contact with one another and bordering first and second infralabials. Second set of chin shields larger and also in contact with each other medially, extending dorsolaterally to the margin of the jaw, resulting in a loss of contact between second and third infralabials (condition not seen in other specimens; Fig. 3B). Third pair larger still and also in contact with each other medially, bordering third and fourth infralabials. Fourth pair of chin shield pairs 1.5 times as large as third and widely separated from one another medially, bordering infralabials 4–7. Indistinct gular fold present, scales anterior to this roughly hexagonal and becoming longitudinally elongate and



Fig. 4. (A) Life photo of *Nucras damarana* (MCZ R-190201) from 60 km SE of Ruacana crossroads (-17.48558, 14.86608), Omusati Region, Namibia. (B) Life photo of *Nucras holubi* from Alldays, Limpopo Province, Republic of South Africa. Note differences in dorsal and lateral patterning. Photos copyright by Johan Marais.

angled medially at approximately the level of the angle of the jaws; scales between gular fold and collar enlarged and rectangular. Twenty-seven scales between chin and collar; collar border comprising a series of eight enlarged scales, the largest in median position and rhomboidal in shape, decreasing in size dorsolaterally and anteriorly.

Dorsal pholidosis homogeneous, 36 longitudinal rows of small granules at midbody, becoming slightly larger and more flattened on flanks. Eight longitudinal rows of transversely widened ventral plates plus, lateralmost considerably smaller than the rest. Thirty-three transverse rows of ventral plates between axilla and groin.

Femoral pores extending to knee, 12 on each thigh, with left and right series separated by a diastema of two scales of roughly equal size. Scales in row immediately posterior to femoral pore row oval, approximately half the size of pore-bearing scales. Scales of rows anterior to pores much larger, one (distal) to three (middle and proximal) rows between pore-bearing scales and enlarged preaxial plates. Large, roughly semicircular patch of preloacal plates anterior to cloaca, constituent scales extremely large, largest bordering posterior margin medially, bordered laterally by one plate on each side, each one-sixth size of median plate, and anteriorly by two scales, each half the size of median plate, a semi-circular series of much smaller scales bordering the preloacal plates laterally and anteriorly.

Preaxial surface of forelimb covered with a series of transversely enlarged scales; postaxial surface covered by smaller, flattened juxtaposed scales. Scales on palms small, flattened, juxtaposed to subimbricate. Manual digits 4>3>5>2>1, all clawed. Preaxial aspect of thigh with large transverse plates, continuing on to shank and dorsum of pes, postaxial aspect with small, smooth, subimbricate scales, granular on shank. Scales on the sole small, smooth, granular to slightly elongate. Digits of pes 4>3>5>2>1, all clawed, bearing a series of smooth narrow subdigital lamellae, lamellar formulae: (L) 9-14-18-26-[5th toe missing], (R) 9-13-18-25-14.

Tail original, 107 mm in length, 22 elongate rectangular scales per whorl at level of knee of adpressed hindlimb. One row of dorsal scales for each ventral row. Basal portion of tail with most scales smooth and only scattered keeled scales, rapidly transitioning to keeled dorsal scales, and most of the tail with all scales keeled.

Color in alcohol (Fig. 3). Dorsum medium brown with three cream-colored longitudinal stripes, vertebral stripe narrower than lateral stripes and with less well-defined edges. Lateral stripes carry forward to the lateral edges of the parietal scales and fade out on the posterior frontal, adjacent to the posterior supraocular scales. Median stripe continuous with an irregular whitish marking centered on the interparietal scale. Flanks dark brown, bordered above by dorsolateral cream stripe and below by a thicker cream-colored stripe that is confluent with the white of the lateral surface of the neck and extends to the hindlimb insertion.

This stripe is bordered ventrally by a brown line that begins inconspicuously behind the axilla and widens posteriorly to include the lowest 2–3 rows of dorsal scales and the edges of the lateralmost ventral plates, terminating at the hindlimb insertion. Dark area of the flanks encompassing a discontinuous longitudinal series of white dashes and spots extending from the temporal region to the posterior edge of the hindlimb insertion.

Anterior portion of head densely speckled with brown pigment, fading on the ventral portion of the rostral and supralabials; infralabials without dark pigmentation; rims of eyelids with a narrow dark brown margin. Posterior supraoculars dark brown, this coloration continuing posteriorly along the dorsolateral margins of the head and confluent with the dark surfaces of the flanks. Forelimbs a mottled pale brown with darker posterior portions to most scales and a series of diffuse whitish spots. Hindlimbs with an irregular dark brown line running from the limb insertion onto the postaxial surface of the foot; another such line on the preaxial surface of the limb, passing over the front of the knee and terminating at the flexure of the ankle. The area between these lines occupied by a series of partly joined white spots with diffuse margins. The central cream stripe of the dorsum fades out on pygal portion of tail, but the lateral stripes widen and fuse posterior to this, yielding a more-or-less uniform pale brown dorsum of the tail. The darker coloration of the flanks continues as a diffuse stripe on the lateral surfaces of the proximal half of the tail before fading entirely. All ventral surfaces immaculate cream.

Color in life (Fig. 4A). Pattern as above. Dorsal ground color dark brown. Middorsal stripe an orange-brown, dorsolateral stripes off-white, ventrolateral stripes cream, spots on flanks a pale yellowish-cream, with diffuse orange-brown markings between some spots. Venter immaculate white.

Distribution. *Nucras damarana* has a broad distribution across northwestern Namibia, including the Kunene Region (exclusive of the Namib and pro-Namib in the west), as well as the Omusati, Oshana, and Oshikoto Regions and in the northwest of the Otjozondjupa Region (Fig. 5). Although unsupported by vouchers, it is likely to be present in the Ohangwena Region and into the southern Angolan Cunene Province.

Natural history. Parker (1936) recorded *Nucras damarana* only from Sessekab, which he described as “open forest.” The species occurs in several of the major landscape divisions of Namibia, including the Kalahari Sandveld, Kunene Hills, Cuvelai System, Central-western Plains, and Kamanjab Plateau, and spans a broad annual precipitation gradient from 150 mm in the west to approximately 500 mm in the east (Goudie and Viles 2015). Its distribution falls entirely within the Tree and Shrub Savanna biome, with the majority of localities within areas characterized

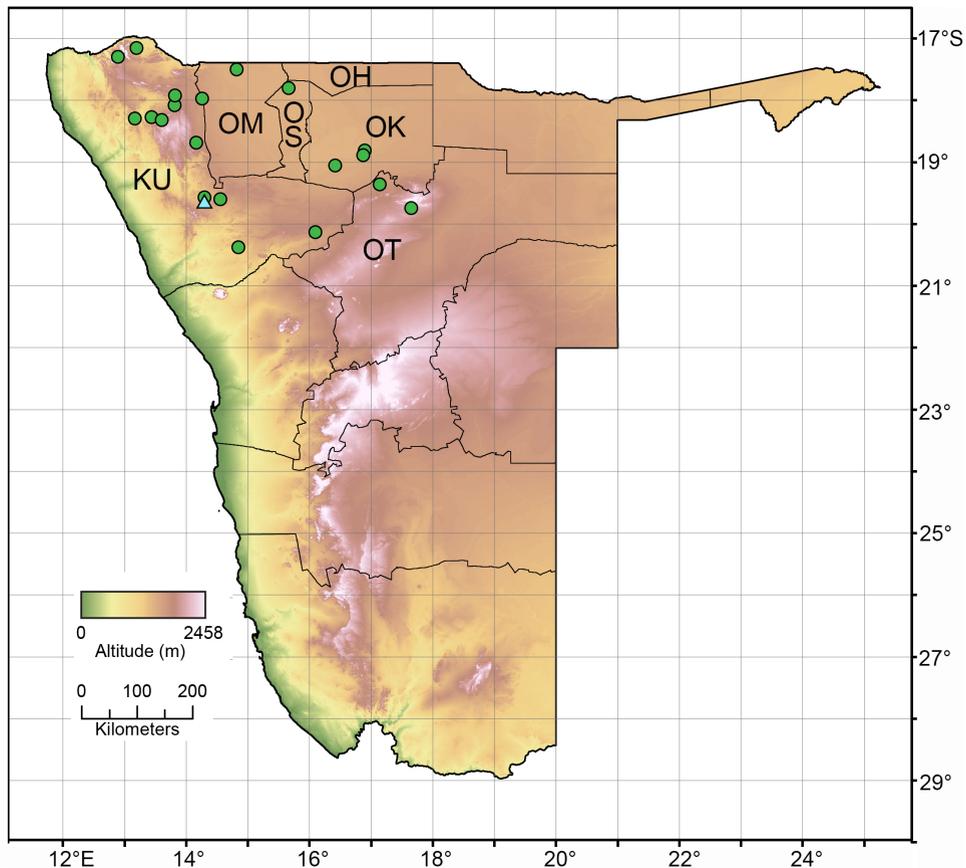


Fig. 5. Map of Namibia showing the distribution of *Nucras damarana* (green circles) and *N. cf. broadleyi* (blue triangle). Black borders indicate regional boundaries. Regions mentioned in the text are: KU – Kunene, OH – Ohangwena, OM – Omasati, OS – Oshana, OK – Oshikoto, and OT – Otjozondjupa. *Map courtesy of Edward L. Stanley.*

as woodland, but extending into areas of sparse shrubland (Atlas of Namibia 2002). *Nucras damarana* is an uncommonly encountered terrestrial species, usually found in relatively mesic microhabitats in areas with at least some vegetation as ground cover. Although the diet has not been studied in this species, most congeners have a broad diet of arthropods including various insects, spiders, and centipedes (van der Meer et al. 2010), and this is likely the case for *N. damarana*.

Conservation. Although this species, like many *Nucras*, is not commonly encountered, it has a large extent of occurrence (> 80,000 km²) and its entire range falls within an area of relatively low human density. In Ovamboland, localized agricultural activity may be a threat to this terrestrial lizard, but it likely experiences minimal disruption in other portions of its range, particularly in the Kunene Region. It is protected in Etosha National Park as well as several communal conservancies and is of Least Concern.

Nucras aff. broadleyi. CAS 214642, from 48 km west of Kamanjab on the road to Torra Bay (-19.65389,

14.35083), in the Kunene Region, Namibia (Fig. 5), was strongly supported as the sister to the two Angolan samples sequenced and identified as *Nucras broadleyi* by Branch et al. (2019a). There was a 15.03–15.69% divergence in the 16S sequence between the Angolan and Namibian specimens, compared to a 7.83% divergence between the two Angolan samples. While these divergences are relatively high, they are likely artificially inflated because of ambiguities in base calls and alignment in part of the sequences obtained. When compared with the diagnostic features proposed for *N. broadleyi*, our specimen is consistent with respect to scale characters, most notably the presence of granules between the supraoculars and supraciliaries, the well-defined occipital scale separating the parietals posteriorly, and the absence of a distinct parietal window in the interparietal scale (Fig. 6C). It is also consistent in size (58.2 mm SVL vs. a maximum of 63 mm) and falls within the range of all standard but non-diagnostic features of scalation presented by Branch et al. (2019a) for *N. broadleyi*. However, the specimen differs significantly in color pattern. Branch et al. (2019a) describe the diagnostic dorsal pattern as having a series of longitudinal pale stripes, including four pale stripes

on the nape with the lateralmost of these forming a light stripe that is continuous with the outer edges of the parietals. In contrast, the Namibian specimen has a pattern entirely lacking solid longitudinal stripes and instead exhibits pale spots or dashes anteriorly and a series of irregular transverse bars posteriorly (Figs. 6–7). This most closely resembles the pattern seen in adult specimens of *N. intertexta*, which was, indeed, the field identification given to the specimen by the senior author. However, Namibian *N. intertexta* are much larger (up to 91 mm SVL) and have a larger number of dorsal midbody scale rows (40–56 vs. 38–48 in Angolan *N. broadleyi* and 38 in CAS 214642) and usually have the parietals in contact posteriorly (comparative data from Broadley 1972 and Branch et al. 2019a). The mismatch in color is noteworthy, however, both *N. intertexta* and *N. broadleyi* show significant variation in their patterns (Branch et al. 2019a: Fig. 6; Broadley 1972: Pl. III), with elements of the pattern of *N. intertexta* present even in a paratype of *N. broadleyi* (PEM R24157, Branch et al. 2019a). The recognition of species-specific patterns has confounded *Nucras* systematics since the time of Boulenger (1917, 1920). A possible, though purely speculative, interpretation could be that CAS 214642 represents mitochondrial introgression of *N. broadleyi* into *N. intertexta* in northern Namibia. Nuclear data for the Namibian sample would be needed to test this hypothesis. Alternatively, it might represent a new species allied to *N. broadleyi* or it could be conspecific with Angolan *N. broadleyi*. Under the last interpretation one would have to assume both that color pattern is very highly variable and that more (and more complete) sequence data would likely reveal less pronounced genetic distances between samples. If conspecific, this would represent a substantial range extension southward and would expand the extent of occurrence of *N. broadleyi* to over 117,000 km². Based

on the present evidence, given that we have only a single Namibian sample and very limited DNA sequence data, we refer this single sample to *N. aff. broadleyi*.

Discussion

The pattern of relationships retrieved here for *Nucras* was similar to other recent molecular results published by Edwards et al. (2013), Bauer et al. (2019), and Branch et al. (2019a). However, the recently described *N. broadleyi* was recovered as the sister species to the East African *N. boulengeri*, rather than as sister to the *N. tessellata/N. lalandii* clade (Branch et al. 2019a). All patterns of relationship within the main southern African clades, the *N. tessellata/N. lalandii* clade, and the *N. ornata/N. holubi* clade, are fully consistent with earlier findings, with the exception of the placement of *N. taeniolata*. This taxon, endemic to the Eastern Cape Province of South Africa, was previously recovered as the sister to *N. tessellata*, although with very shallow branch lengths subtending the species pair (Branch et al. 2019a; Edwards et al. 2013). Here we recover *N. taeniolata* embedded deeply within *N. tessellata*. Although two of our genetic markers (16S and ND4) overlap with these other studies and many of the same samples were used (see Table 1), our differing results may nonetheless reflect the differences in either genetic marker choice or taxon sampling, or both. The difference in the placement of *N. broadleyi* relative to Branch et al. (2019a) is likely due to the absence of any nuclear markers in our dataset.

The finding that *Nucras holubi* as currently construed is a species complex is novel, although results from Branch et al. (2019a) did show a deep divergence within the species. That the Namibian populations, here resurrected as *N. damarana*, should be specifically distinct is not surprising, given the large geographic disjunction from *N. holubi* in southeastern Africa. The



Fig. 6. *Nucras* aff. *broadleyi* (CAS 214642). (A) Whole body dorsum, (B) lateral view of head, and (C) dorsal view of head. Note the patterning resembling *Nucras intertexta* and the prominent occipital scale. Photos by M. Murdoch.



Fig. 7. Life photo of *Nucras* aff. *broadleyi* (CAS 214642) from 48 km west of Kamanjab on the road to Torra Bay (-19.65389, 14.35083), Kunene Region, Namibia. Photo by Randall Babb.

finding of two deeply divergent lineages of *N. holubi* in South Africa is unexpected. The two clades correspond to a clade north of the Soutpansberg and sister to *N. damarana*, and another clade represented by specimens from Limpopo Province south of the Soutpansberg plus a specimen from KwaZulu-Natal, at the extreme southeast of the species range (Burger 2014). Without much more extensive sampling, the ranges of these two lineages of *N. holubi* remain uncertain. The type locality given by Steindachner (1882) is “aus dem Thale des Krokodilflusses in Transvaal.” Based on Emil Holub’s travels (Holub 1881: 83), this would have been somewhere between the confluence of the Marico and Crocodile rivers and the junction of the Notwane River with the Limpopo River along what is today the Botswanan border with western Limpopo Province, South Africa. This location is well to the west of any of our samples and warrants further investigation, including topotypical genetic sampling and a careful morphological comparison of the types with specimens from throughout the range. In resurrecting *N. damarana*, we were able to identify several features that distinguish it from all *N. holubi sensu stricto*, but we did not attempt to distinguish among the latter.

The identification of a *Nucras* allied to *Nucras broadleyi* in northern Namibia was also surprising. The specimen was field identified as *N. intertexta*,

but was placed outside of all other southern African *Nucras* in preliminary analyses. The inclusion of *N. broadleyi* into our data set provided clear evidence that our specimen is most closely related to *N. broadleyi*, but there is a substantial difference in color pattern as well as a large genetic distance between our Namibian specimen and those reported by Branch et al. (2019a).

With the addition of our new data there are now four *Nucras* species recognized in Namibia: *N. tessellata* (widespread south of 22°N, except in the Namib), *N. intertexta* (widespread in central and western Namibia north of Windhoek, except in the Namib), *N. damarana* (endemic to northwestern Namibia), and *N. aff. broadleyi* (a single locality in the southern Kunene Region). Our single *N. aff. broadleyi* was found essentially in sympatry with *N. damarana* on the Kamanjab Plateau, where *N. intertexta* also occurs. Records of *N. intertexta* from northern Namibian localities should be reexamined given that our Namibian *N. broadleyi* demonstrates that specimens phenotypically similar to *N. intertexta* may, in fact, carry *N. broadleyi* DNA. Our record lies approximately 275 km south of the reported range of *N. broadleyi* (Branch et al. 2019a). While substantial, this alone should not rule out some connectedness of the Angolan and Namibian populations, given that

Nucras are relatively infrequently encountered and that the intervening region remains poorly explored herpetologically. A similar situation exists in the skink *Trachylepis laevis*, described from Angola (Boulenger 1907) and many decades later found as far south as the Kamanjab area (Bauer et al. 1993; Steyn and Mitchell 1965); and also in *Tomopterna ahli*, which was described as *T. damarensis* from Khorixas, southern Kunene Region and 15 years later was revealed to be as widespread as 538 km to the northwest in Namibe Province, Angola. Indeed, southwestern Angola shares a high herpetofaunal similarity with northwestern Namibia, and the Kunene Region in particular (Branch et al. 2019b; Marques et al. 2018).

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