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The *Nucras* (Squamata: Lacertidae) of the eastern Zambezi River Basin, with the description of a new species from Zambia

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Abstract

The *Nucras* of the eastern Zambezi River basin region, comprising Zambia, Malawi and central Mozambique have been poorly studied. We re-evaluated the type specimens of *Lacerta cameranoi* Bedriaga, 1886 and *L. tessellata pseudotessellata* Bedriaga, 1886, both collected at Tete, Mozambique by Wilhelm Peters in the 1840s. Both are assignable to *N. ornata*, the most widespread *Nucras* in the region. However, an additional specimen collected from Tete is referrable to *N. holubi*, filling a collecting gap for this species between central Zimbabwe and southern Malawi. *Nucras* records from northeastern Zambia include several *N. boulengeri*, two photo-vouchered records, one unidentifiable and the other an enigmatic form not consistent with any known species, and a new species from Senga Hill, Northern Province. The new species, *Nucras margaritae* **sp. nov.**, is known only from its holotype. It is morphologically similar to *N. ornata*, from which it is separated by 620 airline km, but is deeply genetically divergent from all congeners and is sister to the clade comprising *N. holubi*, *N. ornata*, *N. damarana* and *N. intertexta*. At least five species of *Nucras*, four currently named, inhabit the greater eastern Zambezi River basin.

Key words: systematics, taxonomy, Mozambique, Malawi, type specimens, *Nucras ornata*, *Nucras holubi*, *Nucras margaritae* sp. nov.

Introduction

Sub-Saharan African lacertids are members of a group identified by Arnold (1989, 1991), based on morphological data, as “advanced lacertids,” a monophyletic group equivalent to the currently recognized Tribe Eremiadini (Hipsley *et al*. 2009). The Eremiadini are divided into a primarily “Ethiopian” clade and a primarily “Saharo-Eurasian” clade. The Ethiopian clade comprises a chiefly southern African lineage and a more northern lineage, the latter having its greatest diversity in and near the Horn of Africa (Mayer & Pavlicev 2007; Hipsley *et al*. 2009; Greenbaum *et al*. 2011; Kapli *et al*. 2011; Edwards *et al*. 2013a, b; Engleder *et al*. 2013). Within this northern group, however, two genera have distributions that extend well into southern Africa, *Heliobolus* Fitzinger, 1843 and *Nucras* Gray, 1838. *Nucras* was erected as a subgenus of *Eremias* to accommodate the South African species *Lacerta lalandii* Milne-Edwards, 1829 and was subsequently treated as a full genus by Gray (1845). Although allocations to several other new or existing genera were employed in ensuing years (see Bedriaga 1886 and synonymies in Boulenger 1917, 1920; Broadley 1972), the application of the generic name has been stable since Boulenger (1887).

However, the recognition and delimitation of species within *Nucras* has been anything but stable. Boulenger (1887) initially recognized only two species, *N. delalandii* (Duméril & Bibron, 1839) and *N. tessellata* (Smith, 1838). In his subsequent revisions, he (Boulenger 1917, 1920) divided the latter into *N. intertexta* (Smith, 1838),

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within which he included "var. *holubi*" (Steindachner, 1882)—itself with eight different infrasubspecific forms, and *N. tessellata*, which encompassed taxa now recognized as *N. livida* (Smith, 1838), *N. taeniolata* (Smith, 1838) and *N. ornata* (Gray, 1864). Two nominal taxa, *Lacerta cameranoi* and *Lacerta tessellata pseudotessellata,* both described by Bedriaga (1886) from Tete, Mozambique, were included by Boulenger in the synonymies of *N. intertexta holubi* and *N. tessellata*, respectively. Cott (1934) resurrected the name *L. cameranoi* for what he considered to be a subspecific form of *N. intertexta* from Mozambique and Nyasaland (Malawi) and Parker (1936) described *N. damarana* as a subspecies of *N. intertexta* from northern South-West Africa (Namibia). FitzSimons (1943) treated both *N. damarana* and *N. holubi* as valid subspecies of *N. intertexta* but followed Boulenger in considering *N. ornata* and *N. pseudotessellata* as synonyms of *N. tessellata*, and *N. cameranoi* as a synonym of *N. intertexta holubi.* Later, Loveridge (1953) transferred *N. cameranoi* to the synonymy of *N. intertexta ornata,* which he recognized as subspecifically valid (although he made no mention of *N. pseudotessellata*).

Broadley (1972) conducted a major revision of the *Nucras tessellata* group, which included all the southern African taxa then known, except *N. lalandii*. He recognized *N. tessellata tessellata* (with *N. elegans* as a synonym), *N. t. livida*, *N. taeniolata taeniolata*, *N. taeniolata ornata* (with *holubi* as a recognizable infrasubspecific variety, and *N. pseudotessellata, N. cameranoi* and *N. damarana* as synonyms), along with an unnamed Angolan subspecies. In the same work, Broadley also described *Nucras caesicaudata* and recognized *N. intertexta*, with only *N. ocellata* as a synonym. Subsequent revisionary work has sorted out some of the confusion within the group, with Jacobsen (1989) raising *N. ornata* to a full species, Bates (1996) elevating *N. holubi* to specific status, Branch *et al*. (2019) describing Broadley's unnamed Angolan subspecies as *Nucras broadleyi* Branch, Conradie, Vaz Pinto & Tolley, 2019, and Bauer *et al*. (2020) resurrecting *Nucras damarana* as a full species. *Nucras aurantiaca* Bauer, Childers, Broeckhoven & Mouton, 2019 was also described as a new species allied to *N. tessellata*.

Although the phylogenetic position, distribution, and biology of the southern African (and, more recently, the Angolan) forms of *Nucras* have been studied (Edwards *et al*. 2013b; Bauer *et al*. 2019, 2020; Branch *et al*. 2019; Baptista *et al*. 2020), knowledge of *Nucras* in the eastern part of the Zambezi River basin (eastern Zambia, Malawi, central Mozambique) has lagged behind. Three species of *Nucras* are currently recognized from the region based on vouchered specimens (Pietersen *et al*. 2021). The first, the chiefly East African *N. boulengeri* (Spawls *et al*. 2018), is known from a single record from Isoka in the northwest of Zambia (PEM R7147; Broadley 1971; Haagner *et al*. 2000; Pietersen *et al*. 2021) and two recent records from the Niassa Special Reserve in northern Mozambique (Buruwate & Lloyd-Jones 2024); this species will not be considered further. The second species, *N. ornata*, is widespread in southern parts of central Zambia, as well as southern Malawi and parts of central and northern Mozambique, extending southwards to northeastern South Africa and Eswatini (Broadley 1971, 1972; Burger 2014; Pietersen *et al*. 2021; Burger & Tolley 2023b; but see Alexander & Tolley 2021b). Finally, *Nucras holubi* is known only from east of Masasa, Malawi (NMZB 13978–79; Burger 2014; Pietersen *et al*. 2021; Burger & Tolley 2023a) but appears to be absent from Zambia. Its occurrence in west central Mozambique is unresolved, as records from Tete, Manhica and Sofala provinces have not been critically reevaluated since the separation of *N. holubi* from *N. ornata*. This same issue clouds the identity of *Lacerta tessellata pseudotessellata* and *L. cameranoi*, both based on material from Tete. These names were assigned to the synonymy of *N. taeniolata ornata* by Broadley (1972), but he did not examine the types and the status of these nominal taxa has not been re-evaluated in light of the current taxonomy.

In addition to vouchered material of the taxa discussed above, Broadley and Berry (2009) presented a photograph of an unidentified species from near the Manze-Luangwa confluence in South Luangwa National Park, Zambia, which was distinguished from *N. ornata* and *N. holubi* by its distinctive color pattern. It remains a mystery as no specimens have yet been collected. More recently, a virtual record in the *Reptile Atlas of Africa* (https://vmus.adu.org.za/?vm=ReptileMAP-180710 [although this site is currently inaccessible]) dated 2021-05-03 from Chama, Chama District, Muchinga Province, Zambia (-11.2172, 33.1599) was interpreted by Alexander & Tolley (2021b) to be *N. ornata* (*fide* D. Pietersen, pers. comm.). If correct, this would extend the known range of *N. ornata* by at least 220 km from the nearest Malawian record and more than 500 km from the closest vouchered record in Zambia. While the image is clearly a *Nucras*, it is not possible to unambiguously determine the identity of the species.

Zambian *Nucras* records in general are relatively few in number (Broadley 1971, 1972; D. Pietersen, *in litt*.). A specimen of *Nucras* from northeastern Zambia recently collected by one of us (MB) is both morphologically and genetically distinctive and is herein described as a new species. We also take this opportunity to re-evaluate the identity of Bedriaga's *Lacerta cameranoi* and *L. tessellata pseudotessellata*, as these nominal taxa, as well as *N. ornata* and *N. holubi*, must be accounted for in establishing the identity of the new species.

Materials and Methods

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 (crus + manus length, from elbow to tip of 4th finger), 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), Ear (maximum height of ear opening). Details of pholidosis, including head scalation, as well as femoral pore disposition, were also recorded. Subdigital lamellae were counted from digital base to the first lamella proximal to the claw sheath. Comparisons were made with all other species of *Nucras* based on material listed in the Appendix and with literature sources, especially Broadley (1972) as adjusted for subsequent taxonomic changes (e.g., Jacobsen 1989; Bates 1996). Through the courtesy of Shiela Broadley (Natural History Museum of Zimbabwe, Bulawayo) we also used data from museum specimens recorded by the late Donald G. Broadley, and measurements and photographs of Mozambican Nucras were provided by Frank Tillack (Museum für Naturkunde, Berlin).

Standard symbolic codes for institutions referred to in this paper (including Figure 1 and Appendix) follow Sabaj (2020) except as noted: CAS—California Academy of Sciences, San Francisco, California, USA; JPT—private collection of J. P. Tello, Maputo, Mozambique; MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; NHMUK—Natural History Museum, London, United Kingdom (previously BMNH); NMB—National Museum, Bloemfontein, Free State province, South Africa; NMZB—Natural History Museum, Museum of Zimbabwe, Bulawayo, Zimbabwe (including NMZB-UM = former Umtali Museum collections); NMZL—Livingstone Museum, Livingstone, Zambia; PEM—Port Elizabeth Museum (Bayworld), Gqeberha, Eastern Cape province, South Africa; ZMB—Museum für Naturkunde, Berlin, Germany. In addition, the following field number series are used: LMH (Vincent Egan), MB and MBUR (Marius Burger), NB (Ninda Baptista), HZ (Michael Cunningham), RBH (Raymond B. Huey).

To determine the phylogenetic placement of the undescribed Zambian individual, sequence data from the new specimen (NMB R11574: ND2—GenBank no. MG846514; 16S—GenBank no. MG846600) were added to an existing molecular dataset of 66 *Nucras* spp. that has been previously published (see Bauer *et al*. 2020: Table 2 for localities and GenBank accession numbers). To this we also added data from *Nucras scalaris* Laurent, 1964 (Baptista *et al.* 2020; 16S—MT431951). The complete dataset thus includes mitochondrial (mtDNA) sequence data from 12 of the 13 currently described *Nucras* species and from six eremiadine outgroup taxa: *Australolacerta australis* (Hewitt, 1926), *Heliobolus lugubris* (Smith, 1838), *Meroles knoxii* (Milne-Edwards, 1829), *M. suborbitalis* (Peters, 1870), *Pedioplanis laticeps* (Smith, 1845), and *P. namaquensis* (Duméril & Bibron, 1839). Genomic DNA was extracted from muscle tissue that had been stored in 95% EtOH using the Qiagen DNAeasy Kit. De novo sequence data was generated for two of the three mtDNA markers, ND2 and 16S, using the PCR primer pairs METF1 (ND2-Forward: 5′-AAGCTTTCGGGCCCATACC-3′) (Macey *et al.* 1997) and CO1R1(ND2-Reverse: 5′-AGRGTGCCAATGTCTTTGTGRTT-3′) (Arèvalo *et al.* 1994), and 16Sa-l (16S-Forward: 5′-CGCCTGTTTATCAAAAACAT-3′) and 16S-H (16S-Reverse: 5′-CCGGTCTGAACTCAGATCACGT-3′) (Palumbi *et al*. 1991). PCR products were visualized using 1.5% agarose gels before being purified with the AMPure magnetic bead solution kit (Agencourt Bioscience, Beverley, MA, USA). Cycle sequencing was performed using the BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, CA, USA) and then purified using the CleanSeq magnetic bead kit (Agencourt Bioscience, Beverley, MA, USA). Sequences were analyzed on an ABI 3730xl DNA analyzer and subsequently assessed in Geneious v6.1.5. An initial sequence alignment was constructed using MUSCLE v3.8.31 and then manually adjusted by eye.

We calculated uncorrected pairwise distances between samples for ND2 and 16S using the function ‘dist.dna’ in the package *ape* v5.0 (Paradis & Schliep 2019) in RStudio v.2023.9.1.494 (R Core Team 2023). Phylogenetic trees were constructed using 1,686 base pairs (bp) derived from three mitochondrial markers (16S, ND2, and ND4). ND4 was unavailable for the new species but was included in order to incorporate data from a prior study (Edwards 2013b) for the resolution of broader intrageneric relationships. Variable and parsimony-informative sites were assessed using the ‘seg.sites’ and ‘pis’ functions from the *ape* package v.5.0 (Paradis & Schliep 2019) and *ips* v.0.0.11 package (Heibl 2019), respectively. Maximum likelihood (ML) phylogenetic analyses were performed using IQ-TREE v2.2.0.3 (Minh *et al*. 2020), while Bayesian inference (BI) analyses were implemented through the CIPRES Science Gateway v3.3 (Miller *et al*. 2010) using MrBayes v3.2.7a (Ronquist *et al*. 2012). Initial analyses were performed on individual genes before generating a concatenated mtDNA alignment used for the final analyses.

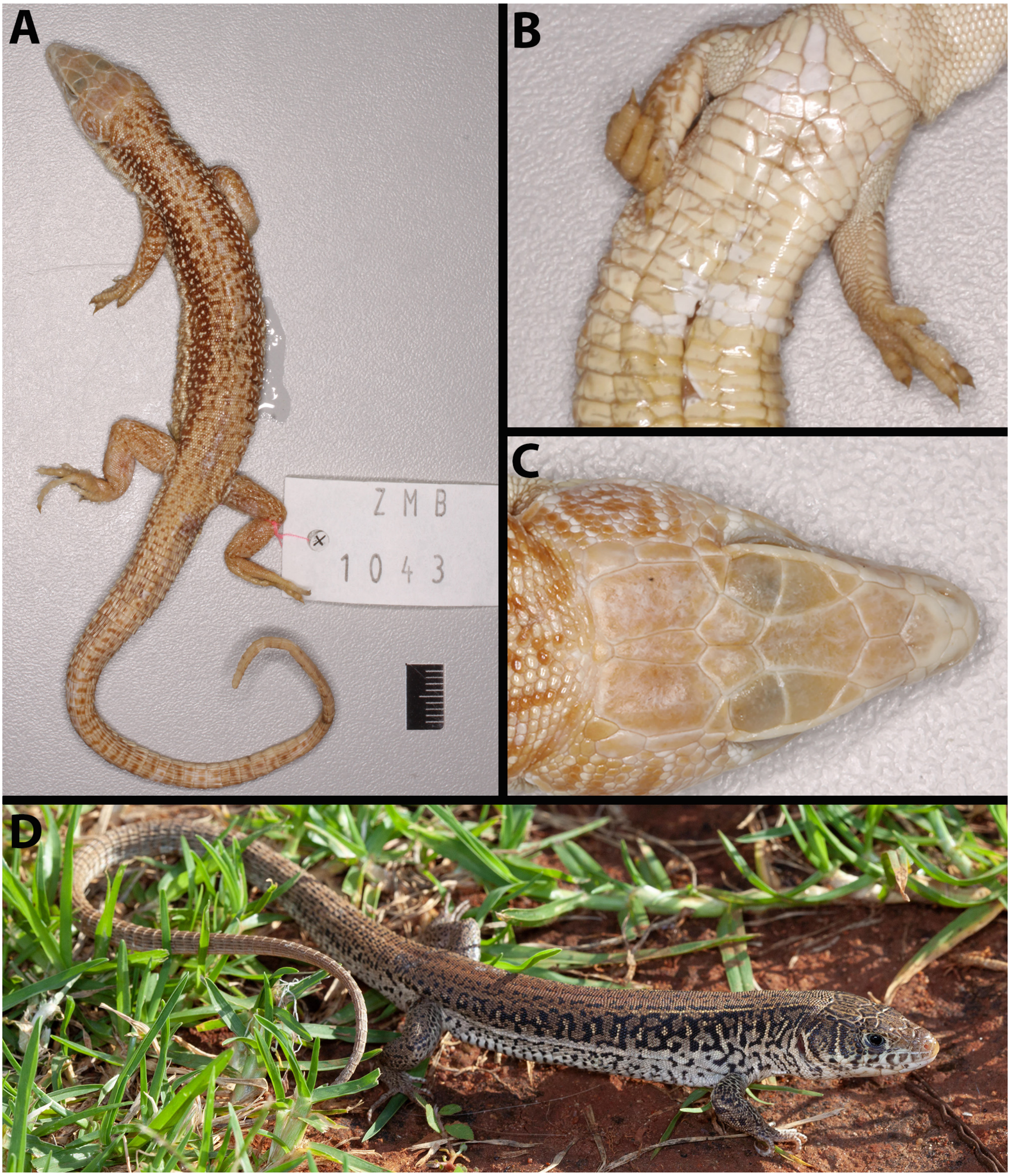

FIGURE 1. A. Dorsal view of ZMB 1043, holotype of *Lacerta cameranoi* Bedriaga, 1886. Photo by Frank Tillack. Scale bar = 10 mm. B. Ventral view of ZMB 1043 showing the anomalous hypertrophied digits considered diagnostic by Bedriaga. C. Dorsal view of head of ZMB 1043; note the absence of a parietal foramen. D. *Nucras ornata* from the Lebombo Mts, Eswatini, showing reduction of striping and dark patterning on the flanks. Photo © Johan Marais.

We used PartitionFinder v2.1.1 (Lanfear *et al*. 2017) to determine the optimal partitioning scheme and best substitution model for each partition based on the Bayesian Information Criterion (BIC). This analysis identified five partitions for the concatenated mtDNA dataset: (1) the first codon position of ND2, (2) the second codon position of ND2 and first codon position of ND4, (3) the third codon position of ND2 and the second codon position of ND4, (4) the third codon position of ND4, and (5) the entire 16S gene. All ML partitions were analyzed under the GTR+I+Γ model of evolution with 1,000 rapid nonparametric bootstrap (BS) replicates. The BI analysis employed the same partitioning scheme and all partitions were analyzed using the GTR+Γ model of evolution. The BI analysis consisted of two independent runs of 50 million generations each, with sampling every 10,000 generations. Convergence of the Markov chains (n = 4) was assessed visually using Tracer v1.7.1 (Rambaut *et al*. 2018), and the first 25% of trees were discarded as burn-in.

Results

The status of *Lacerta tessellata pseudotessellata* and *Lacerta cameranoi*

Bedriaga (1886) described *L. tessellata pseudotessellata* and *Lacerta cameranoi* on the basis of a single specimen each from material housed in the Zoological Museum of Berlin (now Museum für Naturkunde) collected by Wilhelm Peters at Tete, central Mozambique, where he spent the period from December 1844 to September 1845 (Bauer *et al.* 1995). Peters (1854) referred the specimens to *L.*[*acerta*] *Delalandii* without comment, but in his *Reise nach Mossambique* (Peters 1882) he assigned them to *Lacerta tessellata*, following the taxonomy of Duméril & Bibron (1839). Peters (1882) recognized two color varieties. The first corresponds to Variété C of Duméril & Bibron (1839) and to *Teira ornata* of Gray (1864). This he regarded as most closely resembling his younger specimens, with three dorsal white stripes extending to the tail base and a series of white, vertically oriented markings continuing from the side of the head well onto the flanks. In the adults of this variety the white stripes were more indistinct. Peters' second variety lacked the white dorsal stripes entirely, had a darker ground coloration and bore the lateral vertical markings only on the head and neck, with the markings forming spots and dots more posteriorly. Peters did not mention the number of specimens he had collected, but Lichtenstein & von Martens (1856) listed six *Lacerta Delalandii* from "Tette" in the *Nomenclator Reptilium et Amphibiorum*, corresponding to six specimens listed in the ZMB specimen registers (see below), four of which are extant in Berlin today.

Bedriaga (1886) examined the Berlin material in the context of his monographic revision of the Lacertidae. The holotypes of *L. tessellata pseudotessellata* and *Lacerta cameranoi* were cited by number in the descriptions, but were not recorded as types in the register of the Berlin collection and were consequently overlooked by Bauer & Günther (1995) in their type catalogue of Berlin lacertids. Originally, both specimens were catalogued as ZMB 1043, but one has since been reregistered as ZMB 71093. Based on Bedriaga's quite detailed descriptions, ZMB 1043 (Fig. 1) corresponds to the holotype of *L. cameranoi* and ZMB 71093 (Fig. 2) to that of *L. t. pseudotessellata*. Bedriaga's descriptions were lengthy, but emphasized putative diagnostic features that, in the context of broader sampling, likely reflect individual variation. For example, *L. t. pseudotessellata* was distinguished by the configuration of its precloacal shields and *L. cameranoi* by its thick digits, an anomalous condition (Fig. 1B). Both specimens show typical coloration patterns for *N. ornata* (Figs. 1D, 2D). ZMB 1043 corresponds to Peters' second variety, with no trace of the dorsal stripes remaining and quite dark flanks bearing many small white flecks (Fig. 1A), a common pattern in larger *N. ornata* (Fig. 1D) reflecting the fragmentation of the vertical flank markings that are usually present in younger specimens. It retains the vertical barring on the head and neck.

ZMB 71093 exhibits dorsal stripes on the front half of the body and retains the distinct vertical barring to approximately midbody as well (Figs. 2A, 2C). This corresponds to Peters' first variety and is typical of many *N. ornata* throughout the range of the species (Fig. 2D). Both specimens also lack a parietal foramen (Figs. 1C, 2B) and are relatively large (SVL + TL = 82 mm + 120 mm and 75 mm + 130 mm, respectively, as reported by Bedriaga; 83 mm + 129 mm and 76 mm + 129 mm, respectively as measured currently, F. Tillack, pers. comm., 4 January 2024). Both specimens also have eight or nine transversely enlarged preaxial plates on the forearms. Based on these characteristics, we are confident that both of Bedriaga's nomina, *Lacerta cameranoi* and *L. t. pseudotessellata* are correctly placed in the synonymy of *Nucras ornata*, as proposed by Broadley (1972). The occurrence of this species at Tete is also confirmed by additional vouchered specimens (MCZ R50999–51002; NMZB-UM 9283) and a 2014 photo vouchered record (https://www.inaturalist.org/observations/793096).

Two additional *Nucras* specimens collected by Peters at Tete also survive in Berlin, ZMB 1044 (originally three specimens under this number) and ZMB 1045. ZMB 1045 (Fig. 3A) is a juvenile specimen (34.2 mm SVL) in poor condition; nonetheless, it is a clear match to Peters' (1882) description of the boldly patterned variety that he believed was Gray's *Teira ornata*. It is, in fact, quite similar to the holotype of *Teira ornata* (NHMUK 1946.8.6.75, originally 64.1.9.30; Fig. 3B), which is also a juvenile and exhibits the typical strong patterning of this life stage (Fig. 3C). This specimen has the published type locality of "South-Eastern Africa" (entered in the Natural History Museum re-registration catalogue as "Zambesi") and was collected by John Kirk on the Zambezi Expedition (1858–1863). Unfortunately, the exact locality of its collection is uncertain. Kirk spent extended periods at Tete and in the Shire Highlands in what is today Malawi, but he also collected specimens below Tete on the Lower Zambezi, including near Sena (Senna) and the mouth of the Shire River. Further, during the early part of the expedition, he was stationed in the Zambezi Delta and at several points during the expedition he returned to the river mouth (Heinz *et al*. 2021). Other biological specimens returned by Kirk have the localities Quellimane (now Quelimane) and Gorongoza (Günther 1864; Hill 1922; Dritsas 2005). Broadley (1972) restricted the type locality to "Zambezi River," which is consistent with Kirk's known areas of activity.

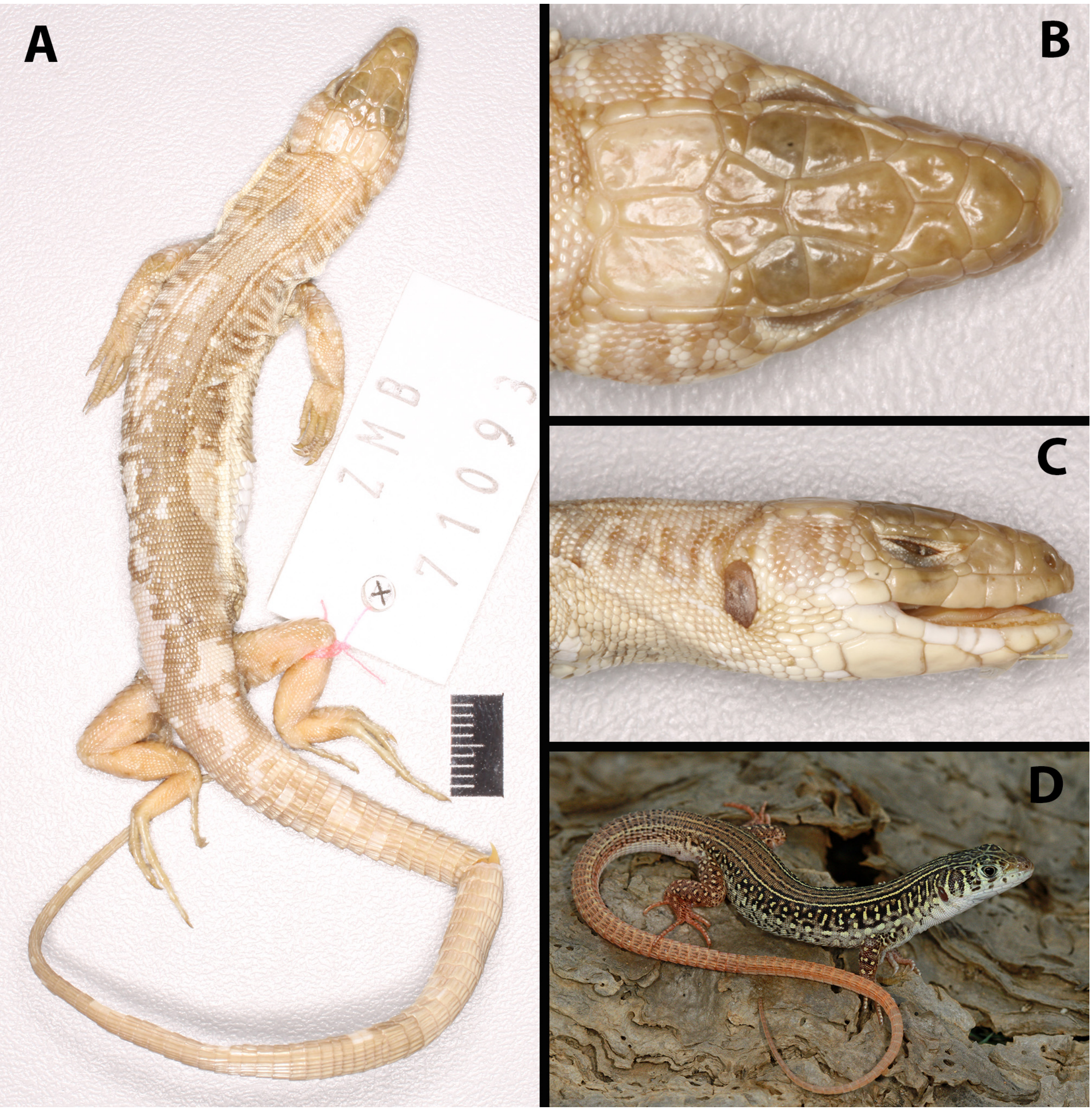

FIGURE 2. A. Dorsal view of ZMB 71093, holotype of *Lacerta tessellata pseudotessellata* Bedriaga, 1886. Scale bar = 10 mm. B. Dorsal view of head of ZMB 71093; note the absence of a parietal foramen. C. Lateral view of head of ZMB 71093 showing prominent vertical markings that continue beyond the midpoint of the trunk. Photos A–C by Frank Tillack. D. *Nucras ornata* from Mugugu Dam, Eswatini, showing bold patterning on anterior of body. Photo © Luke Kemp.

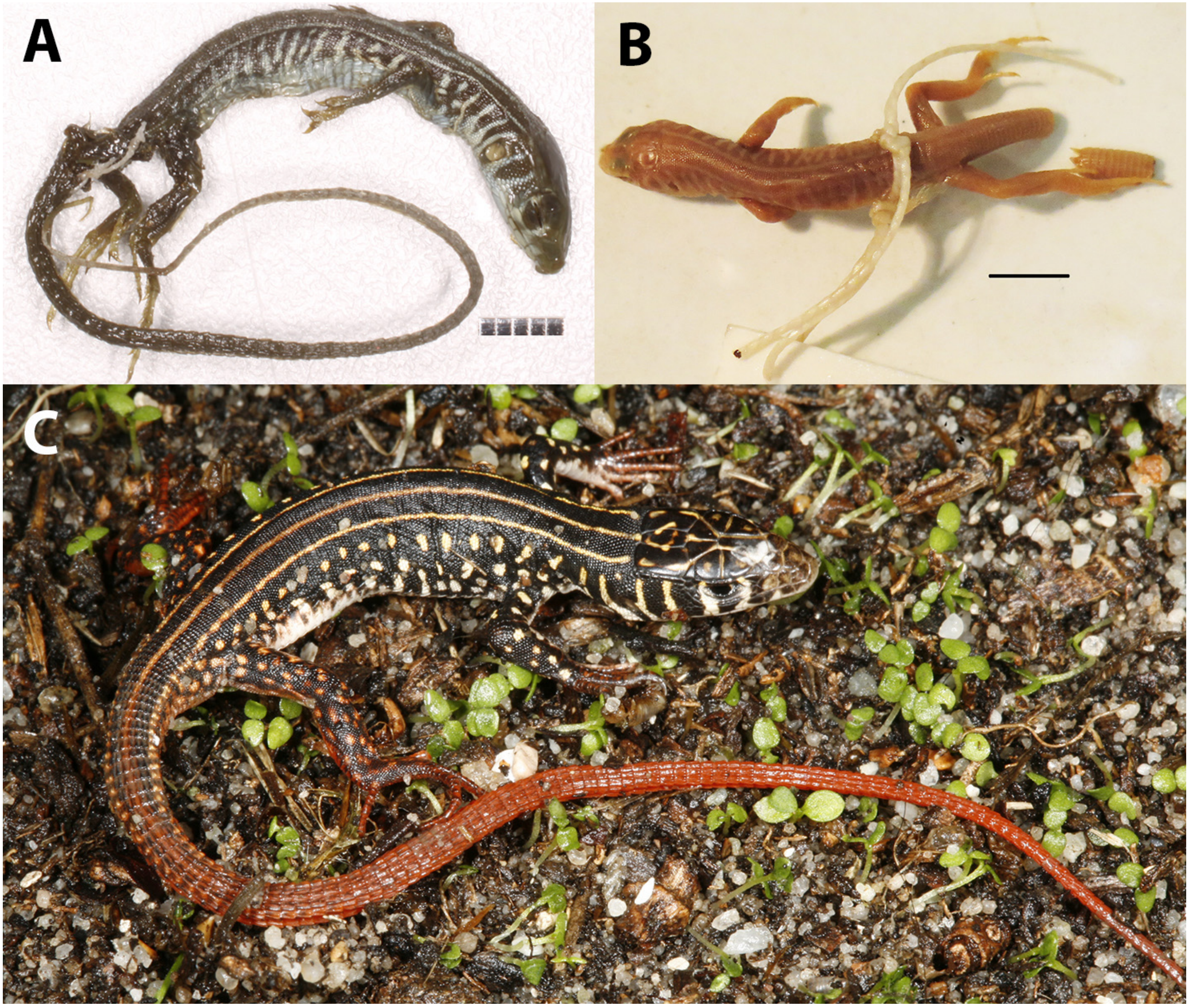

FIGURE 3. Juvenile *Nucras ornata*. A. ZMB 1045 from Tete, Mozambique, collected with the types of *L. cameranoi* and *L. t. pseudotessellata*. Photo by Frank Tillack. Scale bar = 5 mm. B. Holotype of *Teira ornata* Gray, 1864. Photo by A.M. Bauer. Scale bar = 5 mm. C. Living juvenile *N. ornata* from the Lebombo Mts, KwaZulu-Natal province, South Africa. Photo by M. Burger.

ZMB 1044 (Fig. 4A), with SVL of 62.5 mm, on the other hand, has a rather different pattern, with three pale dorsal stripes extending onto the tail, but lacking pale vertical elements on the head, neck and flanks. Instead, this specimen exhibits two longitudinal series of discrete round to oval spots along the flanks, the upper with the spots all separated from one another and the lower mostly fused. This pattern is typical of *Nucras holubi* (Steindachner, 1882) (Fig. 4B) and this specimen also has a small, but clearly visible, parietal window, another feature distinguishing *N. holubi* from *N. ornata* (Pietersen *et al*. 2021; although not completely diagnostically reliable, pers. obs.). This specimen provides confirmation that the two species occur in sympatry at Tete (Fig. 5) and strongly suggests that the distribution of *N. holubi* in Zimbabwe is continuous with that in southern Malawi via a corridor through Tete Province, Mozambique. This intermediate record bridges the gap between the previously reported continuous distribution, extending from the northern Eastern Cape province of South Africa to the Zimbabwean Midlands (Alexander & Tolley 2021a; see also photo vouchered record https://www.inaturalist.org/observations/51621578), more than 290 km southwest of Tete, and the isolated Malawian record from near Masasa (NMZB-UM 13978–79), more than 240 km northeast of Tete (Fig. 5).

FIGURE 4. *Nucras holubi*. A. ZMB 1044 from Tete, Mozambique, collected with the types of *L. cameranoi* and *L. t. pseudotessellata*. Photo by Frank Tillack. Scale bar = 10 mm. B. *Nucras holubi* from Alldays, Limpopo province, South Africa. Photo © Johan Marais.

Phylogeny

Final alignments were as follows: ND2—403 bp (246 variable, 216 parsimony informative); ND4—732 bp (462 variable, 301 parsimony informative); 16S—551 bp (264 variable, 181 parsimony informative). The tree topologies derived from the BI and ML analyses were generally well-supported, with no observed conflicts. Both analyses identified three major clades (Clades A–C, Fig 6); however, in the BI analysis, the arrangement of these clades was not well-resolved, with lower posterior probability (PP) support values at deeper nodes. Clade A is sister to Clade B + Clade C (BS = 100%). Clade A includes *Nucras scalaris,* which is weakly supported as the sister to (*N. boulengeri* + *N. broadleyi sensu lato*) (BS = 77%, PP = 0.51). Within *N. broadleyi sensu lato*, *N. broadleyi sensu stricto* (PEM R24157 and PEM R24005) from Angola is sister to *N.* aff. *broadleyi* (CAS 214642) from northern Namibia (BS = 89%, PP = 0.64). Clade B includes a single Zambian specimen (NMB R11574), which represents a highly genetically distinct lineage (uncorrected p-distances, as percentages, from all other *Nucras* spp.: ND2, 17.73–23.68, mean 20.59; 16S, 13.35–20.26, mean = 16.49) resolved as sister (BS = 97%, PP = 0.73) to ((*N. holubi* + *N. damarana*) (*N. ornata* + *N. intertexta*)) (BS = 97–100%, PP = 0.67–0.99). In Clade C, *N. lalandii* is deeply divergent from all other congeners (BS = 96%, PP = 0.99). Among remaining species, *N. aurantiaca* is sister to (*N. livida* + (*N. tessellata* + *N. taeniolata*)) (BS = 82–99%, PP = 0.75–1.0). The two specimens representing *N. taeniolata* (PEM R18080 and HZ251) are nested within the *N. tessellata* clade, but their precise placement within the clade remains unresolved (BS = 50%, PP = 0.63).

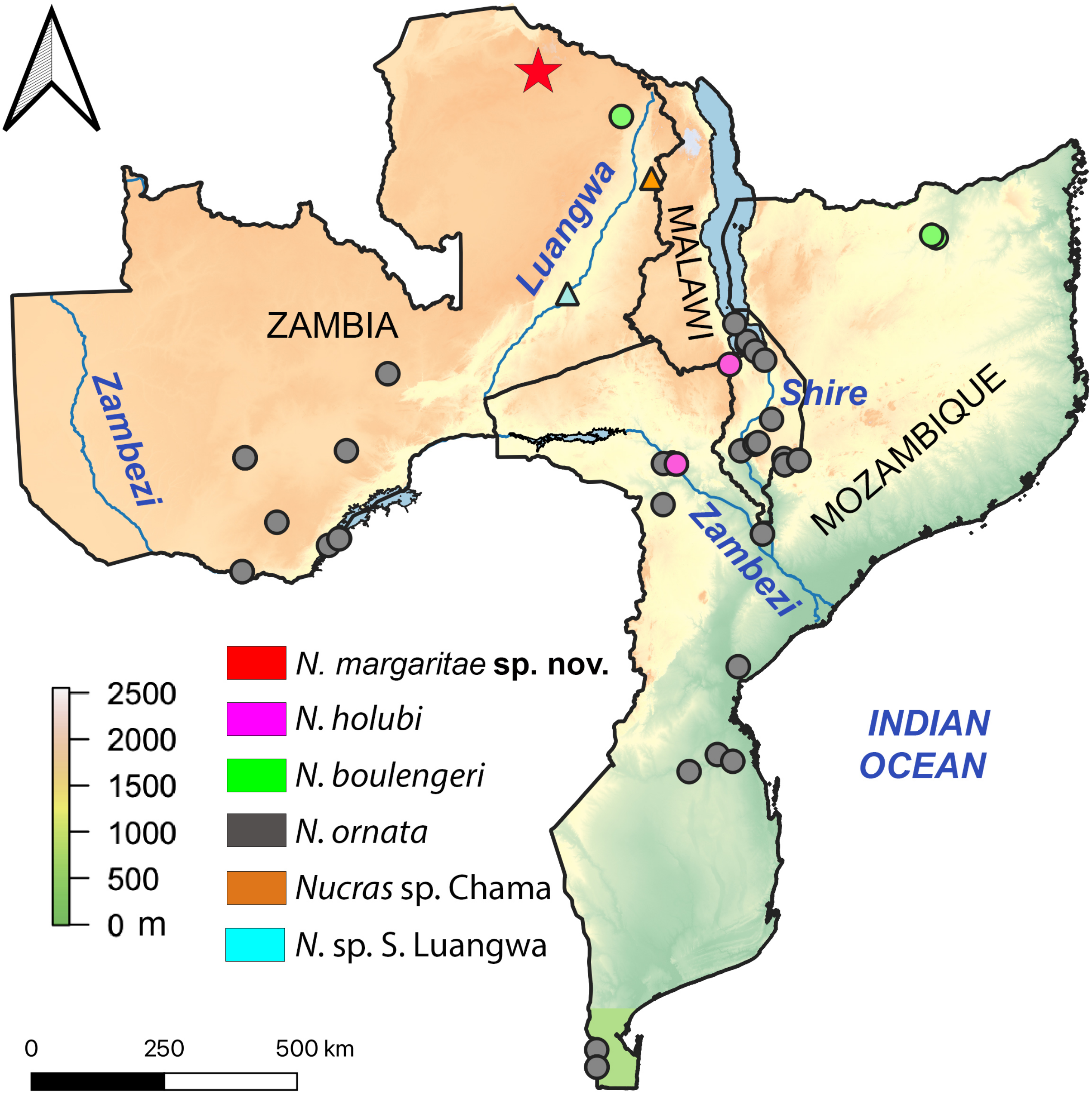

FIGURE 5. Map of Zambia, Malawi and Mozambique showing the known localities for *Nucras* spp. The red star indicates the type locality of *Nucras margaritae* **sp. nov.** The overlapping pink and gray dots mark Tete, the type locality of *Lacerta cameranoi* and *L. tessellata pseudotessellata*. Cartography by Jonathan DeBoer.

Nucras margaritae **sp. nov.**
(Figs. 7–8)

Holotype: NMB (National Museum, Bloemfontein) R11574 (field number MBUR [Marius Burger] 01427), adult female (confirmed by epiphyseal fusion in long bones in radiographs). Zambia, Northern Province, 5.3 km WSW of Senga Hill, -9.386°, 31.19683°, 1650 m elevation. (see Distribution below). Collected by Marius Burger, 27 November 2005.

Diagnosis: A moderately sized (SVL to at least 65 mm) *Nucras* distinguished from all congeners by having 46–48 dorsal scale rows across midbody, enlarged plates on the preaxial face of the forearm (Fig. 7B), two granules between the supraocular and supraciliary scales on each side (Fig. 8B), a tiny parietal window evident in interparietal scale (Figs. 7C–D), 26 subdigital lamellae under digit IV of the pes, 28 femoral pores (14 on each side with a diastema of two poreless scales medially), nape and forebody bearing three pale stripes, no stripes on flanks, distinct barring on lateral surface of head and neck (Fig. 8B), and flanks bearing more-or-less vertically oriented pale spots surrounded by thick black borders (Figs. 7A, 8A).

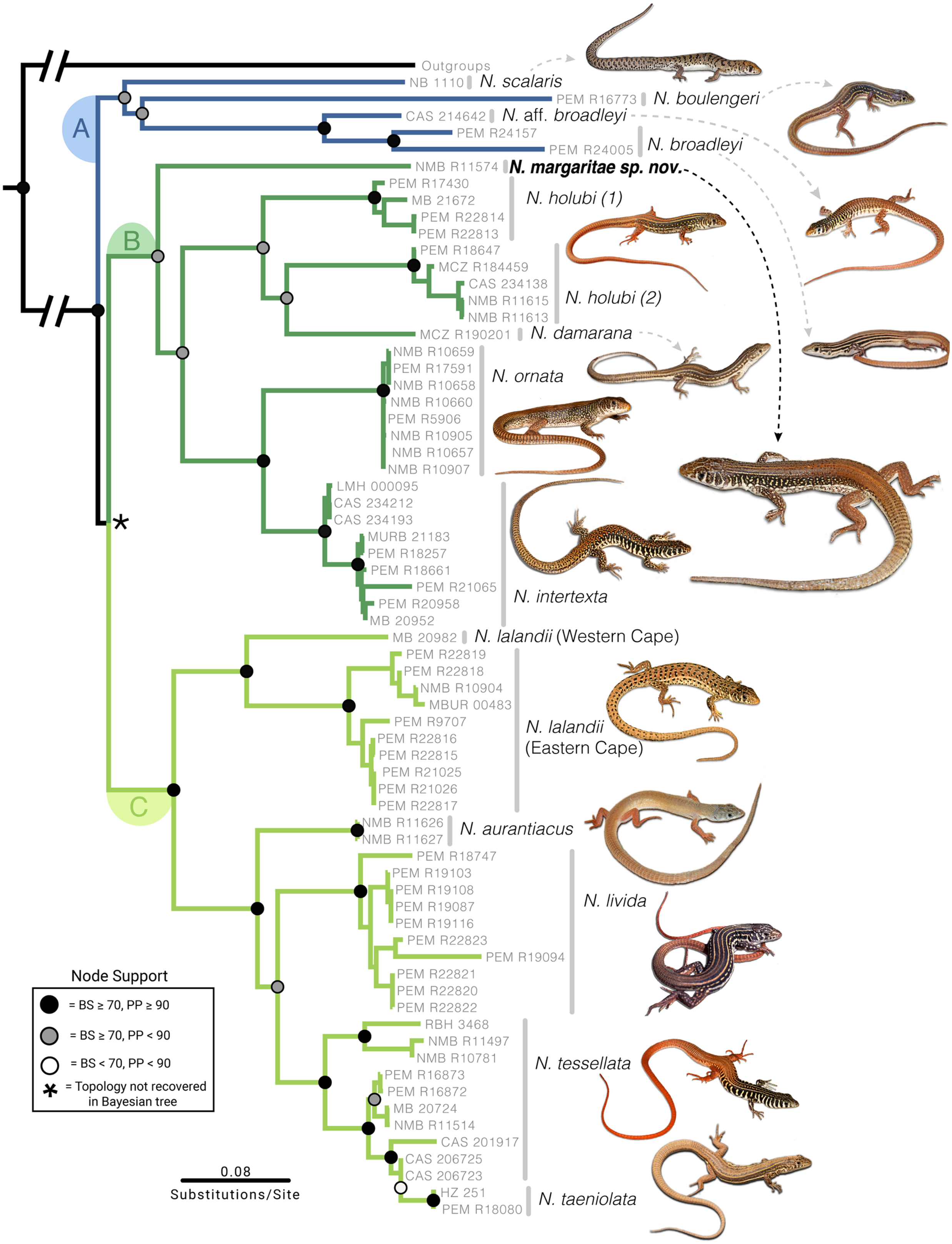

FIGURE 6. Maximum likelihood tree showing relationships of *Nucras margaritae* **sp. nov.** to its congeners. Bayesian posterior probabilities and ML bootstrap values are indicated. A, B and C refer to more inclusive clades discussed in the text. Figure by J.L. Childers.

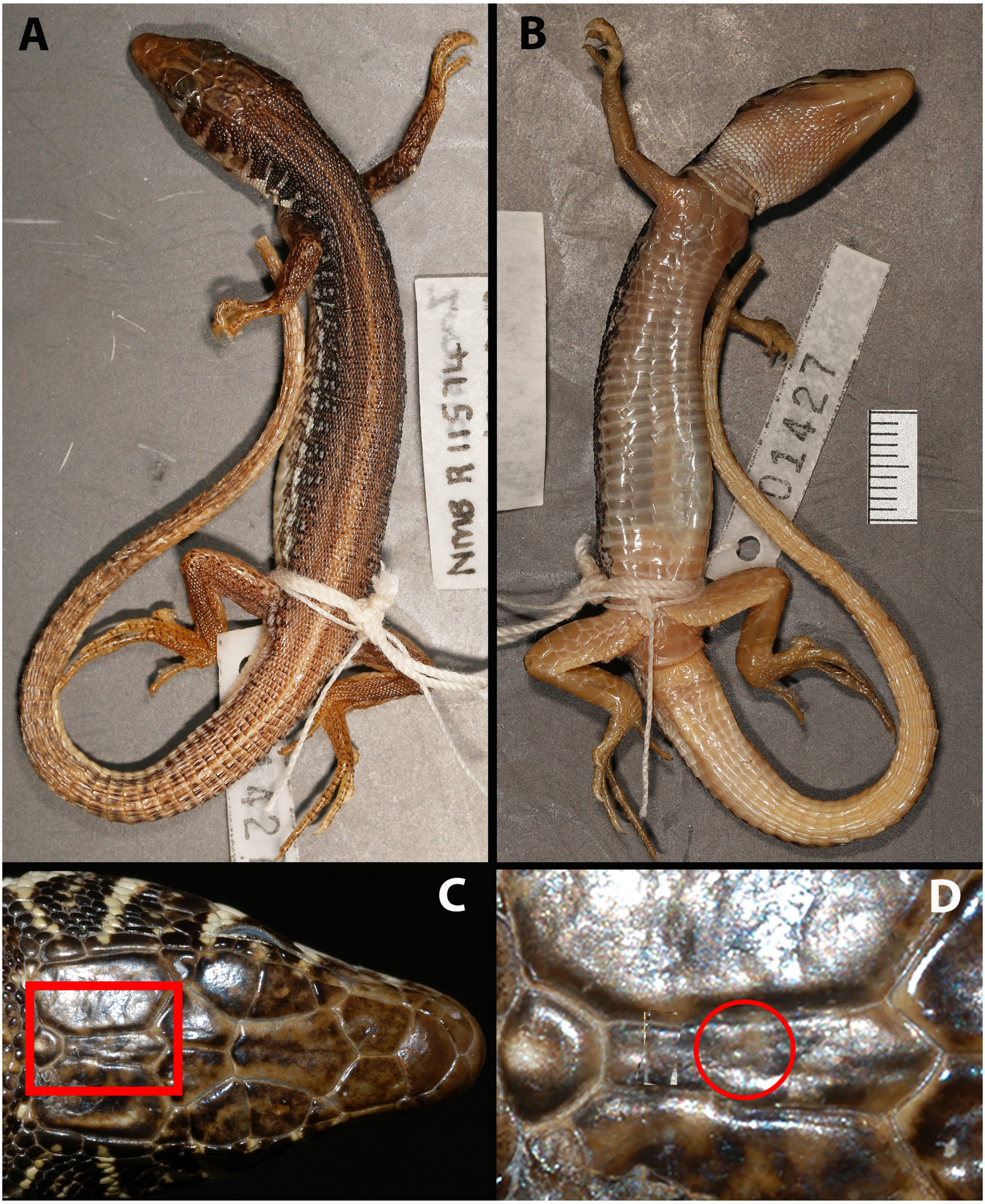

FIGURE 7. Holotype (NMB R11574) of *Nucras margaritae* **sp. nov.** A. Dorsal view of preserved specimen. B. Ventral view of preserved specimen. C. Dorsum of head of holotype in life, red rectangle corresponds to magnified image in D. D. Close-up of interparietal scale of holotype. The minute parietal window is the "dimple" visible in the center of the red circle. Photos A–B by Justin Bernstein, photos C–D by M. Burger.

Nucras margaritae **sp. nov.** differs from *N. lalandii* in having enlarged plates on the preaxial face of the forearm, from *N. boulengeri* in having more (26 *versus* 24) subdigital lamellae under digit IV of the pes and granules present between the supraocular and supraciliary scale rows; from *N. scalaris* and *N. aurantiaca* in having a color pattern with longitudinal elements (*versus* crossbands only and a more-or-less uniform/patternless dorsum, respectively); and from *N. intertexta* in lacking pale dorsal spots or reticulations. In having three pale dorsal stripes on the nape, *N. margaritae* **sp. nov.** is distinguished from *N. tessellata* (usually two or four stripes on nape), *N. livida* (six stripes on nape), *N. broadleyi* (four stripes on nape), and *N. taeniolata* (four or five stripes on nape). It shares three stripes on the nape with *N. caesicaudata*, *N. holubi, N. damarana*, and *N. ornata* (although the vertebral stripe may be lacking in the last of these), but differs from *N. caesicaudata* in having fewer pale stripes on the body dorsum (three *versus* seven), lacking a bright blue tail, and in its larger body size (65 *versus* 57 mm maximum SVL). *Nucras margaritae* **sp. nov.** is most similar to *N. ornata, N. damarana*, and *N. holubi*. *Nucras margaritae* **sp. nov.** differs from *N. holubi* and *N. damarana* in possessing a distinct barring pattern on the temporal region and neck and having the pale markings of the anterior flank arranged vertically (*versus* lateral pattern of neck and trunk comprising pale spots in one or two more-or-less horizontal rows). It differs from *N. ornata* in possessing a visible parietal window (Figs. 7C–D) in the interparietal scale (usually absent in *N. ornata*, including northern specimens; D.G. Broadley, unpubl. data—the consistency of this character in *N. margaritae* **sp. nov.** can only be evaluated when more specimens are available), and in its smaller size (65 *versus* 95 mm maximum SVL). The head also appears to be more depressed, but due to variation in the position of fixation we were not able to confirm this impression. Broadley (1972) considered that variation in several scale characters, including the number of transverse rows of ventral scales, was uninformative in the *N. tessellata* group, but his comparisons were confounded by the fact that his taxonomy resulted in the lumping of some now-accepted species. It may or may not be of note that the holotype of *N. margaritae* **sp. nov.** has 29 transverse rows of ventral scales between the collar and groin. While this falls within the range of *N. ornata* from Zambia, Malawi and Mozambique (n = 39; range 28–35; mean 31.3), only three individuals had a count below 30, and among 107 specimens of "*N. ornata*" from Zimbabwe (Broadley's concept of *N. ornata* included *N. holubi* as well), the mean was 31.1. Of course, the reliability of putative diagnostic features in *N. margaritae* **sp. nov.**, as for all taxa known from a single individual, must be considered tentative until such time as variability in the species can be assessed.

Finally, *N. margaritae* **sp. nov.** can be excluded as the undescribed species illustrated by Broadley and Berry (2004), as the only photograph of the latter species reveals four pale stripes on the nape and on the sides of the neck, and a pale-yellow longitudinal stripe extending to the shoulder, where it breaks up into a series of spots. Moreover, the photographed individual lacks any trace of barring on the neck and temporal region.

Description: Measurements: SVL 65.2 mm, TrW 9.6 mm, TailL (regenerated) 77.4 mm, TailW 6.2 mm, AGL 34.7 mm, HumL 6.2 mm, ForeaL 13.8 mm, FemL 11.4 mm, CrusL 11.2 mm, PesL 16.2 mm, HeadL 16.4 mm, HeadW 9.2 mm, HeadD 8.0 mm, CSn 21.1 mm, OrbD 3.4 mm, NEye 4.8 mm, EyeE 5.5 mm, EarH 3.5 mm., EarW 1.5 mm.

The holotype is intact and in good condition except that the distal portion of the regenerated tail had been taken for tissue. Body moderately slender and elongate (AGL/SVL 0.53), trunk shorter than hind limbs (AGL/[FemL + CrusL + PesL] 0.89), regenerated tail longer than SVL (TailL/SVL 1.19), moderately slender and tapering. Limbs short, pes longer than shank or femur (PesL/FemL 1.42; PesL/CrusL 1.47). Head large (HeadL/SVL ratio 0.25), distinct from neck, slightly elongate (HeadW/HeadL 0.56), not strongly depressed (HeadD/HeadL 0.49). Snout blunt, short (NEye/HeadL 0.29), less than 1.5 times eye diameter (NEye/OrbD 1.41). Eye relatively large (OrbD/HeadL ratio 0.21); lower eyelid scaly, with four large translucent/semi-opaque scales surrounded by a rim of small granules. Margin of eyelids pigmented dark brown. Eye to ear distance more than 1.5 times diameter of eye (EyeE/OrbD 1.62).

Ear opening vertical, much higher than wide (EarH/EarW 2.33), 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, 2.5 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 8/8, increasing in size posteriorly to the fifth, which is largest and in subocular position. Infralabials 7/7, all much longer than high.

Nostrils semicircular, surrounded by enlarged supranasal and bordered posteriorly by two postnasals, each approximately a quarter the size of supranasal. Two loreal scales, anterior trapezoidal, bordering posterior loreal, postnasals, second and third (point contact only) supralabials, and, narrowly, both prefrontal and frontonasal; posterior loreal seven-sided, posterior face much higher than anterior, 4–6 times larger than anterior loreal (Fig. 8B), and bordering the prefrontal, first supraciliary, three preocular scales, supralabials three and four (and in point contact with supralabial five on the left side). Supranasals in contact with one another posteriorly; frontonasal roughly hexagonal, wider than long, with lateral apices projecting posteriorly, gabled anteriorly; prefrontals in broad contact medially. Frontal scale approximately 1.5 times wider anteriorly than posteriorly, lateral terminus of frontal-frontoparietal suture lies posterior to border between second and third supraoculars. Four supraocular scales, second and third much larger than first and fourth; seven supraciliary scales, smallest at midorbit, where there are two small granules separating the supraoculars from the main row of supraciliaries. Parietals six-sided, much longer than wide, with slight forward projection wedging between frontoparietal and fourth supraciliary. Interparietal scale narrow and elongate, separating posterior-most portion of frontoparietals from one another and completely separating left and right parietals; parietal window present but tiny; occipital scale very small, pentagonal, narrower anteriorly than posteriorly, only about 4–5 times size of nuchal granules (Fig. 7C). 2/2 supratemporal scales, anterior narrow and elongate, posterior less than half the size of anterior, but much larger than scales of cheek region.

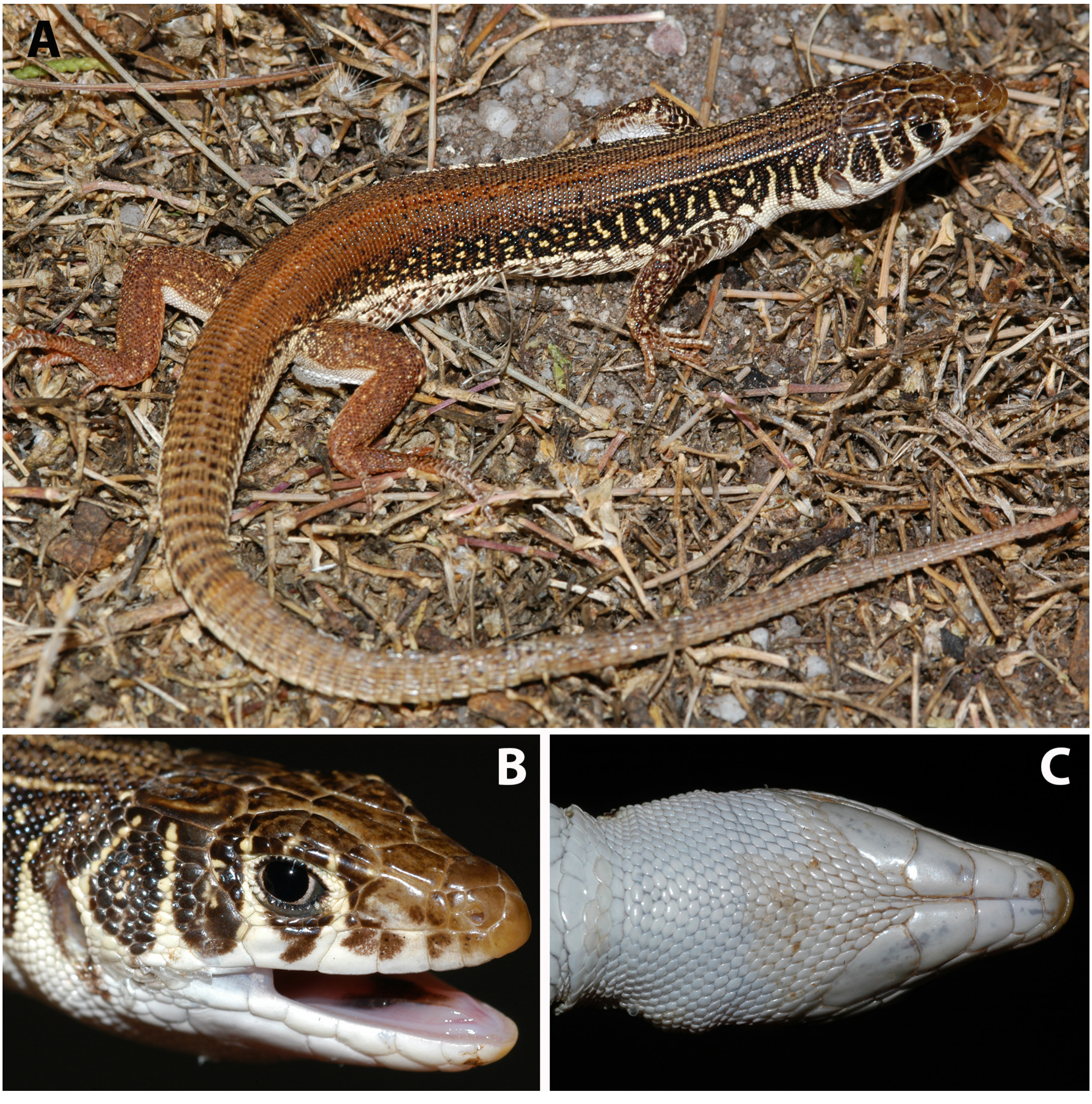

FIGURE 8. Holotype of *Nucras margaritae* **sp. nov.** in life. A. Whole body showing color pattern. B. Oblique view of head illustrating dorsal and lateral head scalation. C. Ventral view of head and throat. Photos by M. Burger.

Mental roughly semicircular, broader than deep, much wider than rostral, bordered posteriorly by a pair of small chin shields in midline contact with one another and bordering first and second infralabials (Fig. 8C). Second set of chin shields larger and also in contact with each other medially and second and third infralabials laterally; third pair larger still, in point contact with each other anteriorly but otherwise separated from one another by a narrow longitudinal row of throat scales. Fourth pair of chin shields 1.5 times as large as third and widely separated from one another, bordering infralabials four through six. A relatively indistinct gular fold present, scales anterior to this roughly hexagonal and becoming longitudinally elongate and angled medially at approximately the level of the angle of the jaws; scales between gular fold and collar enlarged and rectangular. Collar border comprising a series of enlarged scales, the largest in median position and rhomboidal in shape, decreasing in size laterally and anteriorly.

Dorsal pholidosis homogeneous, comprising 46–48 longitudinal rows of small granules (Figs. 7A, 8A), becoming slightly larger and more flattened on flanks. Six longitudinal rows of transversely widened ventral plates plus one ventrolateral row of smaller plates on each side (= 8 longitudinal ventral rows *sensu* Broadley 1972; Fig. 7B), and 29 transverse rows of ventral plates between collar and groin.

Femoral pores extending to knee, 14 on each thigh, with left and right series separated by a diastema of two small poreless scales (Fig. 7B). Scales in row immediately posterior to femoral pore row oval, approximately one-half size of pore-bearing scales. Scales of rows anterior to pores much larger, two (distal) to four (middle and proximal) rows between pore-bearing scales and enlarged preaxial plates. Large, roughly semicircular patch of precloacal plates anterior to cloaca, constituent scales extremely large, largest bordering posterior margin medially, bordered laterally by one plate on each side, each half the size of the median plate, and anteriorly by two scales, each slightly larger than the lateral plates; a semi-circular series of much smaller scales bordering the precloacal plates laterally and anteriorly.

Preaxial surface of forelimb with a series of seven transversely enlarged scales; postaxial surface covered by smaller, flattened, juxtaposed scales (Fig. 7B). 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 8-12-20-26-11/8-10-19-26-12.

Posterior 38.0 mm of tail regenerated. Original tail portion with approximately 35 elongate rectangular scales per whorl at level of knee of adpressed hindlimb. Basal portion of tail with two rows of dorsal scales for each ventral row, although becoming 1:1 at level of crus of adpressed limb. Basal portion of tail with most scales smooth and only scattered keeled scales, rapidly transitioning to keeled dorsal scales, and with most of the tail with all scales keeled. Scales of regenerated portion of tail similar, but more irregular in shape.

Coloration (in life) (based on life photographs; Figs. 7C–D; 8A–C). Dorsum mid-brown becoming increasingly orangey-brown towards the sacrum, with three pale dorsal stripes. A thicker (1.5–2 granules wide) vertebral stripe grades from light brown at occiput to orange-brown at level of shoulder and becomes brighter from mid-trunk posteriorly and is bordered by narrow (maximum one granule wide) black stripes from the occiput to mid-trunk and thereafter to tail base by scattered black flecks. A pair of thinner (one granule wide) cream-colored dorsolateral stripes bordered by thicker (1–1.5 granules wide) black stripes extend from occiput to mid-trunk, where they fade out, with only a single broken line of black granules extending towards the sacrum. Flanks below dorsolateral stripe bearing a series of irregular, fragmented, more-or-less vertically oriented yellowish-cream markings, each 1–2 scales in width and surrounded by a black border of 1–2 scales in width. These markings are largely confluent, but with small interstitial areas mid-brown, like dorsum; markings more fragmented posterior to the level of midbody.

Dorsum of head mid- to light brown with darker brown markings on all head shields posterior to prefrontals; suture zones of shields generally lighter. Side of head and neck dominated by alternating white to cream (ventral to dorsal) colored vertical bars and much wider dark brown markings. Anterior-most white bar just anterior to eye, second just behind eye, another in temporal region and one bordering anterior margin of ear. Three additional bars between posterior border of ear and level of collar. Ventral portions of anterior white bars confluent with predominantly white coloration of supralabials and jaw joint region. More posterior bars confluent with white of venter. Dark brown spaces between bars with irregular central cream centers, except anterior-most, which runs through eye. Iris black. Venter white with some irregular brown markings on lateral-most ventral plates and adjacent ventrolateral granules. Chin and throat immaculate white except for several faded gray markings on chin shields.

Forelimbs mottled mid- and dark brown with scattered irregular cream markings on dorsal and preaxial surfaces, white below. Dorsum of manual digits whitish. Hindlimbs mottled orangey-brown with small, scattered cream and dark brown markings, some just a single scale in extent although larger proximally, on dorsal and preaxial surfaces; venter white.

Tail dorsum orangey brown basally with narrow, transverse, brown paravertebral markings becoming more prominent posteriorly to form distinct rings alternating with straw-colored inter-spaces. Tail base bearing a narrow ventrolateral pattern of cream to pale-yellowish spots with dark brown margins, confluent with similar flank markings. Regenerated portion of tail grayish-brown with indistinct darker markings on dorsum.

Coloration (in preservative). Coppery above, with cream areas in life a pearl gray and white areas with a brownish tint, especially on venter (Figs. 7A–B).

Etymology: The specific epithet is a matronym honoring our friend and colleague Margarita Metallinou (1985–2015), whose untimely passing during fieldwork in Zambia was a great loss to systematic herpetology and to all who knew her (Carranza & Bauer 2016).

Distribution and Natural History: *Nucras margaritae* **sp. nov.** is presently only known from the type locality near Senga Hill in northeastern Zambia (Fig. 5). The distribution map for *Nucras ornata* in Alexander & Tolley (2021b) shows the distribution for that species to extend to Chama in northeastern Zambia. As noted above, however, the Chama record is based on a photograph that cannot be identified to species. It may be another record of *N. margaritae*, **sp. nov.** or, as treated by Alexander & Tolley (2021b), a northern extension of *N. ornata*. Alternatively, it could represent yet another unnamed lineage.

The holotype of *N. margaritae* **sp. nov.** was found under a stone on sand in degraded Miombo Woodland (Fig. 9) with scattered stones and rocky protrusions. Other lizards found at the same locality include *Mochlus sundevallii* (Smith, 1849) and *Lygodactylus* cf. *angularis* Günther, 1893.

Conservation: The status of *Nucras margaritae* **sp. nov.** must be considered as Data Deficient. Senga Hill does not fall within Zambia's protected area network but is close to Nsumbu National Park and it is likely that this species may occur there. If the unidentified *Nucras* from Chama is referrable to *N. margaritae* **sp. nov.**, then this species would likely occur in the adjacent North Luangwa and Luambe National Parks as well.

Discussion

Edwards *et al*. (2013b), in the context of an ecomorphological study, presented the first phylogenetic tree for *Nucras*, incorporating eight species, including all of those then recognized as occurring in southern Africa (except the rare *N. caesicaudata* Broadley, 1972), as well as the East African *N. boulengeri*, which was recovered as sister to all remaining congeners. Subsequent studies have recognized new species from southwestern Angola (*N. broadleyi*; Branch *et al*. 2019) and from the Strandveld of the Western Cape province of South Africa (*N. aurantiaca;* Bauer *et al.* 2019). In addition, the northern Namibian taxon *N. damarana* has been resurrected from the synonymy of *N. holubi* (Bauer *et al.* 2020) and the Angolan endemic species, *N. scalaris*, previously known only from its type material, has been rediscovered and its known range expanded (Baptista *et al*. 2020). As a consequence, molecular phylogenetic sampling includes 12 *Nucras* species (Bauer *et al*. 2019, 2020; Baptista *et al*. 2020; although no single previous phylogeny has included all of these), leaving only *N. caesicaudata* uninvestigated.

The tree topology retrieved by our ML analysis is, unsurprisingly given that the same data were used, fully consistent with that found by Bauer *et al.* (2019, 2020). It is also consistent, based on a partly overlapping set of molecular markers, for those taxa sampled in common, with that of Edwards *et al*. (2013b) and, for relationships within our Clades B and C, with those of Branch *et al.* (2019) and Baptista *et al.* (2020). The phylogenetic placement of *N. margaritae* **sp. nov.**, for which ND4 data were lacking, remained consistent whether the entire dataset was analyzed or if ND4 was excluded. Differences in the placement of taxa within our poorly supported Clade A, compared to the last two studies, are likely attributable to the absence of nuclear gene sampling in our analysis. Our finding that both *N. holubi* and *N. tessellata* are paraphyletic (see also Bauer *et al.* 2020) has not been corroborated by other studies, possibly owing to their smaller sample sizes for these taxa.

Our results support the recognition of *Nucras margaritae* **sp. nov.** as a species that is clearly morphologically distinguishable from all its congeners except *N. ornata*, from which it differs by only subtle features (presence of a parietal window and considerably smaller size). It is, nonetheless, clearly very deeply genetically divergent from all congeners, including *N. ornata* from South Africa (KwaZulu-Natal and Mpumalanga provinces). There remains the issue that our genetic sampling of *N. ornata* is from the southern part of its distribution, whereas its type locality is from the north (Zambezi River). However, the minimum divergence of 17.73% (ND2) and 13.35% (16S) of *N. margaritae* **sp. nov.** from any other congener is incompatible with the interpretation that it might represent simply a northern extension of *N. ornata*, as these values far exceed p-distances that might be expected as a result of intraspecific isolation by distance. The locality of *N. margaritae* **sp. nov.** is separated by approximately 620 airline km from the nearest vouchered record of *N. ornata*, and between 790 km (Tete) and 1,180 km (Zambezi Delta) from the restricted *N. ornata* type locality of "Zambezi River." Further, Senga Hill lies in the Central Zambezian Wet Miombo Woodlands ecoregion, whereas *N. ornata* localities in the eastern Zambezi region fall mostly within the Dry Miombo Woodlands ecoregion or adjacent mixed woodlands (Regional Centre for Mapping of Resource for Development; https://opendata.rcmrd.org/datasets/africa-ecoregions/).

FIGURE 9. Degraded miombo woodland habitat at type locality of *Nucras margaritae* **sp. nov.** near Senga Hill, Northern Province, Zambia. Photo by M. Burger.

Our examination of the type material of both *L. tessellata pseudotessellata* and *Lacerta cameranoi* confirms Broadley's (1972) assumption that these are junior synonyms of *N. ornata.* In addition to being fully consistent with *N. ornata* with respect to diagnostic features and coloration, both have the type locality of Tete, well within the known range of *N. ornata* and, indeed, one of the likely points of collection of its type, based on known movements of its collector (Heinz *et al*. 2021). This excludes the possibility that one of these largely forgotten nomina could apply to our Senga Hill specimen.

Thus, we consider the genus *Nucras* to be represented in the greater eastern Zambezi region by a minimum of four species: (1) the widespread *N. ornata*, present throughout the Shire and Zambezi valleys and extending through Zimbabwe and into northeastern South Africa and Eswatini; (2) *N. holubi*, primarily distributed further south, but confirmed from one locality in Malawi and from Tete in the Mozambique pedicle, the latter on the basis of ZMB 1044, collected by Wilhelm Peters 180 years ago; (3) *N. margaritae* **sp. nov.**, represented by a single specimen from near Senga Hill, Zambia, and described here; (4) *N. boulengeri*, a more northerly distributed species known from northernmost Mozambique and far northeastern Zambia; and (5) the "mystery" species known only from a photograph (Broadley & Berry 2009) from South Luangwa National Park, Zambia. Although the last of these is distinctive enough in pattern to exclude it being one of the four named species from the region, a second photo-vouchered specimen from Chama is not identifiable and cannot, on the basis of existing evidence, be excluded from representing one of the first three listed species.

The conservative morphology of most *Nucras* species, and their similar, often intergrading color patterns, have long posed a problem for systematists. Boulenger (1917, 1920) and Broadley (1972) came to very different conclusions regarding the systematics of these lacertids, but molecular data has been largely responsible for establishing a relatively stable pattern of relationships and species boundaries that differs substantially from both of these earlier workers. Resolution is still required for several problems in South Africa, most notably the polyphyly of *N. holubi* in Limpopo province and the validity of *N. taeniolata* in the Eastern Cape province. In the eastern Zambezi River Basin, limited collection in northern Mozambique and northeastern Zambia remains a hindrance to the clarification of distributional ranges and patterns of intraspecific variation in both genetics and morphology.

Acknowledgements

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Appendix

Comparative material from eastern Zambezi region (Malawi, Mozambique and Zambia). Unmarked = data from D.G. Broadley data sheets. * = photographs and measurements provided by Frank Tillack; ** = specimens examined. For extralimital comparative material examined see Bauer *et al.* (2019, 2020); additional data for Zimbabwean material of *N. ornata* and *N. holubi* derived from D.G. Broadley data sheets based on material listed in Broadley (1972) as "*Nucras taeniolata ornata*

Nucras ornata

Malawi: NHMUK 77.7.2.2–3**; MCZ 50986**, 50998**; NMZB-UM 4159, 18456, 24123–29; TM 21424–25. **Mozambique:** NHMUK 1946.8.6.75** (type of *Teira ornata*), 1933.7.1.87–88**; JPT 1595; MCZ 50999**, 51001–02**; NMZB 7588, 9283; NMZB-UM 22020, 28542, 30537–40; ZMB 1043* (type of *Lacerta cameranoi*), 1045*, 71093* (type of *Lacerta tessellata pseudotessellata*). **Zambia:** NMZB 2206–10, NMZB-UM 18056, 19884, 20851, 23397; NMZL 129.

Nucras holubi

Malawi: NMZB 13978–9. **Mozambique:** ZMB 1044*.