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Rediscovery, range extension, habitat and phylogenetic relation of the endemic Scaled Sandveld Lizard *Nucras scalaris* Laurent, 1964 (Sauria: Lacertidae) in the central Angolan plateau

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**ABSTRACT**

The Scaled Sandveld Lizard *Nucras scalaris* Laurent, 1964 is a poorly known lacertid endemic to north-eastern Angola and is only known from the type series collected more than half a century ago. The original description provided a comprehensive morphological description, but there was a lack of information regarding its evolutionary relationships and habitat associations. A recent discovery of *N. scalaris* from Cusseque, Bié Province, on the central Angolan plateau provided the opportunity to address some knowledge gaps of this species. A phylogenetic analysis confirmed its distinctiveness at the species level. Despite a limited dataset, the analysis suggests that *N. scalaris* is sister to *N. broadleyi* rather than *N. lalandii*, the latter having been assumed to be the sister species, because of morphological similarity between them. The new record of *N. scalaris* represents a range extension of more than 350 km to the southwest and extends the elevation range to 1570 m above sea level, compared to previous known localities at about 1300 m above sea level (Alto Cuílo and Alto Chicapa, in Lunda Sul Province). The specimen also provides new information on live coloration, as well as the habitat association of grassy shrubland that is dominated by geoxylic sufrutices (the so-called ‘underground forests’) characteristic of the Angolan Miombo Woodlands. This new information raises the question whether poor survey data have led to an under-estimation of faunal diversity in this peculiar and overlooked vegetation type, and reinforces the need for further surveys which could highlight the importance of this habitat.
RESUMO
O Lagarto-da-areia-de-laurent *Nucras scalaris* Laurent, 1964 é um lacertídeo endémico do nordeste de Angola sobre o qual se sabe muito pouco, sendo apenas conhecido da série tipo, colhida há mais de meio século. A descrição original da espécie fornece bastante detalhe a nível morfológico, mas até agora não havia nenhuma informação acerca das relações filogenéticas ou do habitat a que a espécie está associada. Uma redescoberta recente do lagarto no Cusseque, na província do Bié, no planalto central de Angola, permitiu preencher algumas das lacunas de conhecimento que existiam relativamente a esta espécie. Uma análise filogenética confirmou que *N. scalaris* é distinto a nível específico de todos os outros *Nucras*. Embora os nossos dados sejam limitados, *N. scalaris* parece ser a espécie-irmã de *N. broadleyi* e não de *N. lalandii*, como se pensava anteriormente, devido a semelhanças morfológicas entre ambas. O novo registo de *N. scalaris* representa uma extensão da sua área de ocorrência de mais de 350 km para sudoeste, e de um aumento de altitude para 1570 m acima do nível do mar quando comparado com as localidades de onde era conhecido anteriormente a cerca de 1300 m acima do nível do mar (Alto Cuilo e Alto Chicapa, na província da Lunda Sul). Está agora disponível mais informação sobre a coloração do animal vivo, e a espécie parece estar associada ao ongote, as ‘florestas subterrâneas’ características da Mata de Miombo Angolana. Esta descoberta levanta a questão sobre se a escassez de levantamentos terão levado a subestimar a diversidade faunística associada a este tipo de vegetação peculiar e negligenciado, e reforça a necessidade de mais levantamentos que possam realçar a importância deste habitat.

PALAVRAS-CHAVE
Mata de Miombo Angolana; Província do Bié; geóxilas; Anharas de Ongote; Reptilia; florestas subterrâneas

Introduction

The genus *Nucras* Gray, 1838 (Squamata: Sauria: Lacertidae) contains twelve species that occur across southern and eastern Africa (Bauer et al. 2019; Branch et al. 2019b). In southern Africa, *Nucras* are distributed mainly in the arid and mesic savanna on sandy soils, although some species enter fynbos, montane grassland and Karoo scrub (Branch 1998; Alexander and Marais 2007). Two endemic species of *Nucras* are currently known to occur in Angola (Marques et al. 2018; Branch et al. 2019b; Branch et al. 2019c): *Nucras scalaris* Laurent, 1964, from the northeast, and *Nucras broadleyi* Branch, Conradie, Vaz Pinto and Tolley, 2019 from the southwest. *Nucras broadleyi* is within the larger *N. tessellata + lalandii* species complex that occurs in the arid regions of southern Africa, although it is the most genetically distinct and geographically distant species in that complex (Branch et al. 2019b). Very little information exists about the Scaled (or Laurent’s) Sandveld Lizard, *N. scalaris* from Angola. It is only known from the type series of four specimens, three males (no. 5401, 5481 and 5485) and one female (no. 5346) collected in June/July 1954 from the type locality Alto Chicapa, and from Alto Cuilo, both in Lunda Sul Province of north-eastern Angola (Figure 1). The type specimens are in the collection at the Museu Regional do Dundo, Angola, except for paratype no. 5485, which is deposited in the Museum of Comparative Zoology, Harvard (accession no. MCZ Herp R74121).
Laurent (1964) provides a detailed description of the species, which resembles *N. lalandii* (Milne-Edwards, 1829) from south-eastern Africa, but has consistent morphological differences that place it as a separate taxon. Features distinguishing *N. scalaris* from *N. lalandii* are a larger number of dorsal midbody scale rows (41–49 v 34–42, respectively), a larger

![Map of Angola showing ecoregions according to Burgess et al. (2004).](image)

**Figure 1.** Map of Angola showing ecoregions according to Burgess et al. (2004). Records of the *Nucras scalaris* type series depicted in red, and the new record in orange.

Laurent (1964) provides a detailed description of the species, which resembles *N. lalandii* (Milne-Edwards, 1829) from south-eastern Africa, but has consistent morphological differences that place it as a separate taxon. Features distinguishing *N. scalaris* from *N. lalandii* are a larger number of dorsal midbody scale rows (41–49 v 34–42, respectively), a larger
number of lamellae under the fourth toe (21–27 v 16–22), the existence of enlarged scales under the forearm in *N. scalaris* (absent in *N. lalandii*), and the dorsal coloration consisting of fewer transversal bars that are more complete and regular in *N. scalaris* than in *N. lalandii* (Laurent 1964). Until now, no information was available about the evolutionary relationships or habitat associations of *N. scalaris* although it has been regarded as the sister species to *N. lalandii*, because of their morphological similarity (Laurent 1964).

Here, we report on the first record of this species since the original description more than 50 years ago and provide live photographs and details on habitat for the first time. In addition, we included *Nucras scalaris* in a phylogenetic analysis, to assess whether *N. scalaris* does represent a separate species, if it might be within the *N. lalandii + tessellata* complex, and/or whether it is a sister species to *N. lalandii*. Lacertids, including *Nucras*, are considered to be labile in their morphology, with their similarities linked to ecology rather than shared ancestry (e.g. Edwards et al. 2012; Edwards et al. 2013). Thus, the similar morphological features between *N. scalaris* and *N. lalandii* might not reflect a recent common ancestor, and *N. scalaris* might be more closely related to geographically proximate species, such as *N. broadleyi*. Notably, *Nucras scalaris* and *N. lalandii* are currently separated by at least 1 700 km. For these two species to have shared a recent common ancestor, a major vicariance event would be necessary to explain that relationship. An alternative, and possibly more likely scenario would be that *N. scalaris* diverged from species that are geographically closer to it than *N. lalandii*.

**Materials and methods**

**Study area and sampling**

Within the Southern African Science Service Centre for Climate Change and Adaptive Land Management (SASSCAL) project, biodiversity monitoring and surveys have been carried out across Angola (Baptista et al. 2018; Jürgens et al. 2018; Baptista et al. 2019). During herpetological surveys in the Cusseque observatory (approximately −13.683 °S, 17.085 °E; 1 572 m above sea level) in the Municipality of Chitembo, Bié Province (Figure 1), an adult female *Nucras scalaris* was captured on 14 June 2018. The observatory is located in the upper valley of the Cusseque River, on the southern slopes of the central Angolan plateau. In Cusseque, vegetation varies from closed miombo woodlands to different types of grasslands and peatlands (Revermann et al. 2013). The climate is semi-humid, with a pronounced rainy season between November and April (Weber 2013). The lizard was caught in a pitfall trap set along a drift fence placed on an open sandy strip. In the ecotone, this sandy strip separates peatlands in a small tributary of Cusseque River (downslope), from geoxyllic suffrutex-dominated grassy shrublands (‘underground forests’ locally called ‘Anharas de Ongote’) and open miombo woodlands (upslope) (Figure 2).

These grassy shrublands and woodlands grow on pasmmo-ferralitic soils, with a sandy topsoil of several decimetres depth overlaying a strongly weathered, batholithic substrate. During the rainy season, precipitation infiltrates in the sandy soils and percolates between sand and underlying batholithic substrates into the peatlands. The greyish-white sandy strip (Figures 2B and 2C), where the pitfall trap was placed, corresponds to the zone where interflow waters seep out during strong rains and flows into the adjacent peatlands.
The downslope peatlands are dominated by tuft grasses (e.g. *Monocymbium ceresiiforme*, *Tristachya huillensis*), sedges and bracken (*Pteridium* sp.), and are used for shifting, small-scale, dry season local farming. For most of the year the soils of the peatland are water saturated, drying out only for a short period at the end of the dry season. The lizard was collected and euthanized by hypothermia and then freezing (Lillywhite et al. 2017), preserved in 70% ethanol, and deposited in the herpetological collection in Instituto Superior de Ciências da Educação da Huíla (ISCED-Huíla), Lubango, Angola, with the following accession no. NB1110. Tissue for DNA extraction was collected after preservation.

**Morphological analysis**

Measurements of the specimen were taken with a digital calliper to the nearest 0.1 mm following Laurent (1964), Edwards et al. (2013) and Branch et al. (2019b). These included: snout-vent length (SVL): tip of snout to anterior edge of cloaca, tail length: tip of tail to posterior edge of cloaca, total length: combined SVL and tail length, head length: from anterior edge of occipital/parietal scale to tip of snout, head width: width of head (just behind eye), head height: height of head at the posterior part of the cranium, snout length: from anterior corner of eye to tip of snout, foot length: from distal tip of fourth toe to back of heel, eye length: horizontal diameter of eye, ear-eye length: from posterior
corner of eye to anterior edge of ear opening. Laurent (1964) used several body ratios in the original description of *N. scalaris*, but Broadley (1972) discussed their use in the genus *Nucras*, concluding that there was too much overlap in these features, precluding their usefulness for species identification. Accordingly, we opted to only use full measurements in the present study. Characterisation of scalation and other features followed Laurent (1964), Broadley (1972) and Branch et al. (2019b) for upper labials: anterior and posterior to subocular, lower labials, indicating the position of the largest, dorsal midbody scale rows, transverse rows of ventrals, longitudinal rows of ventrals, supraciliaries, granules between supraciliaries and supraoculars, number of subdigital lamellae under 4th toe, number of scales in collar, presence or absence of enlarged scales under forearm, the presence of interparietal and whether it was in contact with occipital, number of femoral pores. All counts were performed on both left and right sides. This new material was compared with the detailed description of historical type material of the species provided in literature and with information taken from the photographs available in MCZBASE (2020) (Table 1).

**Phylogenetic analysis**

To examine whether *N. scalaris* is within the *N. tessellata* + *lalandii* complex, we placed the recently collected *N. scalaris* individual in a phylogenetic context using data downloaded from GenBank (*ND4*, *16S* rRNA and *RAG1* genes) for a final dataset that included 10 of the 12 described species (Table 2), and an outgroup with three species (*Australolacerta australis*, *Ichnotropis capensis*, *Meroles suborbitalis*). The only tissue sample in existence of *N. scalaris* is muscle that was excised from the whole specimen previously preserved in 70% ethanol. DNA template was extracted from this tissue using multiple methods (NaCl, phenol/chloroform, Qiagen Micro kit, Qiagen DNeasy kit, Zymo extraction kit), but each yield a poor-quality degraded (100–500 bp) template (concentration <10 µg µl⁻¹, A260/280 > 2.2 and A260/230 > 1.8). We made numerous attempts to sequence all three genes with multiple different primer combinations and PCR conditions, including trials for internal primers, but only the *16S* rRNA gene amplified.

Amplification of 431 base pairs (bp) of the *16S* rRNA gene was carried out with primers 16Sa and 16Sb (Palumbi 1996) with the PCR profile: denaturation for 4 min at 95 °C, followed by 35 cycles of denaturation (94 °C, 45 s), annealing (52 °C, 45 s), and extension (72 °C, 1 min) and a final extension at 72 °C for 10 min. PCR product was inspected through electrophoresis on a 0.8% agarose gel. Sanger sequencing was carried out at Macrogen (Amsterdam, Netherlands) using the forward primer for three separate PCR products to ensure sequence consensus of this problematic sample. The new sequence was aligned in Geneious v.11 (Kearse et al. 2012) with the data downloaded from GenBank.

Phylogenetic analyses were run using maximum likelihood and Bayesian approaches on a dataset of 41 taxa, including the outgroup for a total of 2016 base pairs (Table 2). In addition, a *16S*-only tree was run for the same group of taxa following the same analysis protocols as the full dataset. The Bayesian analysis was run using MrBayes 3.2.6 (Huelsenbeck and Ronquist 2001) at the Cyberinfrastructure for Phylogenetic Research (CIPRES) Science Gateway v3.3 (Miller et al. 2010). Data were partitioned by marker, with a final alignment containing 893 bp for *RAG1*, 678 bp for *ND4* and 446 bp for *16S* (exclusions made for 36 bases of hypervariable region as aligned to the outgroup taxa). jModelTest v.1 (Posada 2008) was used to assess the evolutionary model that best fitted
Table 1. Morphometric, meristic, coloration and habitat data for *Nucras scalaris* (newly collected specimen, data from Laurent 1964 and MCZBASE 2020), *Nucras broadleyi* (data from Branch et al. 2019b), and *Nucras lalandii* (data from FitzSimons 1943; Laurent 1964; Branch 1998; Edwards et al. 2013). All measurements in mm. N/A – not available in literature.

<table>
<thead>
<tr>
<th></th>
<th>NB11110 (left/right)</th>
<th><em>Nucras scalaris</em></th>
<th><em>Nucras broadleyi</em></th>
<th><em>Nucras lalandii</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Snout-vent length</td>
<td>88.7</td>
<td>83–88</td>
<td>36–74</td>
<td>75–110</td>
</tr>
<tr>
<td>Tail</td>
<td>165</td>
<td>141–182</td>
<td>90–144+</td>
<td>N/A</td>
</tr>
<tr>
<td>Total length</td>
<td>253.7</td>
<td>229–265</td>
<td>130–218</td>
<td>N/A</td>
</tr>
<tr>
<td>Head length</td>
<td>16</td>
<td>N/A</td>
<td>9.5–13.8</td>
<td>15.8 ± 1.9</td>
</tr>
<tr>
<td>Head width</td>
<td>10.9</td>
<td>N/A</td>
<td>5.9–6.4</td>
<td>10.0 ± 1.6</td>
</tr>
<tr>
<td>Head height</td>
<td>9.3</td>
<td>N/A</td>
<td>N/A</td>
<td>8.4 ± 1.2</td>
</tr>
<tr>
<td>Snout length</td>
<td>6.1</td>
<td>N/A</td>
<td>3.8–4.9</td>
<td>N/A</td>
</tr>
<tr>
<td>Foot length</td>
<td>12.4</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>Eye length</td>
<td>3.5</td>
<td>N/A</td>
<td>2.1–2.4</td>
<td>N/A</td>
</tr>
<tr>
<td>Ear-eye length</td>
<td>6.6</td>
<td>N/A</td>
<td>3.5–4.2</td>
<td>N/A</td>
</tr>
<tr>
<td>Upper labials</td>
<td>4(2)/4(2)</td>
<td>4(2)/N/A</td>
<td>4(2)</td>
<td>6*</td>
</tr>
<tr>
<td>Lower labials</td>
<td>6(3)/6(3)</td>
<td>6–8*</td>
<td>6(3)</td>
<td>5–7</td>
</tr>
<tr>
<td>Dorsal midbody scale rows</td>
<td>38</td>
<td>41–49</td>
<td>38–50</td>
<td>34–42</td>
</tr>
<tr>
<td>Ventral (transverse rows)</td>
<td>8</td>
<td>8</td>
<td>8</td>
<td>8</td>
</tr>
<tr>
<td>Ventral (longitudinal rows)</td>
<td>31</td>
<td>30–35</td>
<td>27–33</td>
<td>32–38</td>
</tr>
<tr>
<td>Supraciliaries</td>
<td>7/6</td>
<td>6–8</td>
<td>5–7</td>
<td>5–7</td>
</tr>
<tr>
<td>Granules between supraciliaries and supraoculars</td>
<td>1/1</td>
<td>1–3</td>
<td>0–6</td>
<td>1–3</td>
</tr>
<tr>
<td>Femoral pores</td>
<td>11/11</td>
<td>11–14</td>
<td>12–16</td>
<td>10–15</td>
</tr>
<tr>
<td>Number of scales in collar</td>
<td>8</td>
<td>9–11</td>
<td>7</td>
<td>7–14</td>
</tr>
<tr>
<td>Interparietal Y/N</td>
<td>In contact</td>
<td>In contact</td>
<td>Majority in contact.</td>
<td>Usually in contact</td>
</tr>
<tr>
<td>Interparietal contact with occipital?</td>
<td></td>
<td>except for one specimen</td>
<td>Varying from separate to broad contact</td>
<td>behind with a small occipital thus separating parietals. Exceptionally not reaching occipital, and parietals in contact</td>
</tr>
<tr>
<td>Enlarged scales under forearm?</td>
<td>Present</td>
<td>Present</td>
<td>Present</td>
<td>Absent</td>
</tr>
<tr>
<td>Dorsal coloration pattern</td>
<td>12 complete and regular transversal bars</td>
<td>12–13 complete and regular transversal bars</td>
<td>Longitudinal stripes; pale longitudinal stripes broken up posteriorly with flanks spotted and broken paravertebral stripes</td>
<td>Incomplete and irregular transversal bars</td>
</tr>
<tr>
<td>Habitat</td>
<td>Geoxyl suffrutex dominated grassy shrubland on sandy soils within Angolan Miombo Woodlands</td>
<td>N/A</td>
<td>Mopane woodlands, dry savannas, and semi-desert shrublands</td>
<td>Montane and temperate grassland.</td>
</tr>
</tbody>
</table>

Each of the partitions using the Akaike’s Information Criterion Corrected (AIC), and this was incorporated into the Bayesian analysis (16S and ND4, nst = 6 + G (GTR + G); RAG1, nst = 2 + G (HKY + G)). The Markov Chain Monte Carlo (MCMC) was run for 20 million generations twice in parallel, with a burn-in of 10%. A ML analysis was run using RAxML (Stamatakis 2014) through the CIPRES portal. The dataset was partitioned by marker applying the GTR+I+G model for each partition with 1,000 bootstrap replicates. For all analyses, Tracer v1.6 (Rambaut et al. 2014) was used to verify that the effective sample size (ESS)
was above 200 for all parameters. Finally, pairwise uncorrected net p-distances between *N. scalaris* and other members of the genus were estimated for 16S using MEGA v.7 (Kumar et al. 2016) with no missing data in the alignment.

### Results

**Morphology**

Meristic and scalation data are summarized in Table 1. The new specimen (NB1110) has a serpentiform shape, with an elongated and cylindrical body, a thick and long tail (186% of SVL), and short limbs (Figures 3A and 3B). Nostrils oriented laterally in a
short (68% longer than wide) and tall head (85% wider than tall), rounded snout (Figures 4B and 4C). Six upper labials, four anterior to subocular and two posterior to subocular; and six lower labials with the third being the largest. Seven and six supraciliaries on the left and right side, respectively, and one granule between supraciliaries and supraoculars on both sides. Its dorsal scalation consists of small oval or rounded granular scales, smooth, juxtaposed and more elongated in the front, imbricated and less elongated and polygonal in the back. Anterodorsal surface of the forearm has two series of scales larger than the adjacent scales; one or two series of plates clearly larger than the adjacent scales on the proximal part of the inferior surface of the forearm (Figure 4F); dorsal surface of the tibia covered on granular scales; large scales on the ventral surface of the tibia. Tail scales keeled, forming regular elongated rings, pointing obtusely to the back; middorsal scales barely larger than adjacent, ventral scales slightly larger than dorsal scales and more weakly keeled, but sharper. It has a conspicuous dorsal coloration pattern, consisting of a series of twelve continuous dark transversal bars in the trunk, and over forty interrupted bars in the tail (Figure 3A). The colouration and body shape are essentially identical to the plate showing the *N. scalaris* paratype (Ang. 5481, see Laurent (1964), p 58, Figure 17), although the tail is considerably thicker in NB1110. The new specimen is also morphologically identical to Ang. 5485 (MCZ Herp R-74121) from the type series, as concluded after comparison with photographs available in the Museum of Comparative Zoology on-line database (MCZBASE 2020). Ventral coloration is plain white (Figure 4A). The specimen is assigned to *N. scalaris* based on strong morphological agreement with the species’ original description (Laurent 1964) in meristic, morphometric and coloration features (Table 1). The only exceptions to this are the collar formed by eight scales and 38 midbody scale rows with ranges of 9–11 and 41–49, respectively (Laurent 1964; Figure 4D). These small discrepancies are expected given that the species was described from only four specimens, and intra-specific variation probably has not been fully captured.

Figure 3. Live *Nucras scalaris*, adult female (NB1110) from Cusseque, Bié Province, Angola. (A) Dorsal view of lizard in pitfall trap where it was captured, note coloration consisting of conspicuous transversal bands and long and thick tail. (B) Lateral view. Photo credit: A,B: M Bluhm.
Phylogenetic analyses

Similar to previous phylogenetic analyses (e.g. Edwards et al. 2013; Bauer et al. 2019; Branch et al. 2019), there were two main clades of *Nucras* (excluding *N. boulengeri*). The *N. tessellata* + *lalandii* species complex are all from southern Africa, either endemic to the arid or semi-arid regions of South Africa (*N. lalandii*, *N. livida* and *N. taeniolata*) or Namibia, Botswana and South Africa (*N. tessellata*). There is a separate, well-supported clade with species (*N. intertexta*, *N. ornata* and *N. holubi*) from the more mesic east (southern Zimbabwe and Mozambique, and north-western South Africa). Finally, there is a separate, distinct lineage with one species (*N. boulengeri*) from East Africa that is sister to all other *Nucras*.

The new specimen of *N. scalaris* is confirmed as a separate taxon, because it does not fall within any of the other *Nucras* species for either the three gene or the 16S phylogeny (Figure 5; Supplementary material Figure S1). Furthermore, pairwise uncorrected net 16S p-distances between *N. scalaris* and other *Nucras* were 7–12% (Table 3) further substantiating its species status. The three gene analysis supports *Nucras scalaris* as being within the larger *N. tessellata* + *lalandii* + *broadleyi* complex from arid southern Africa. The phylogeny suggests there is a sister relationship between *N. scalaris* and *N. broadleyi*. Although the node is well-supported by the Bayesian analysis (0.97 pp), the maximum likelihood bootstrap value is moderate (66%).

It should be noted that the 16S-only analysis has essentially no support at deeper internal nodes, resulting in a large polytomy for the major clades (Supplementary material Figure S1). Regardless, each of the terminal clades (i.e. species) are well-supported and
N. scalaris remains a separate taxon in this 16S topology. The sister relationship between N. scalaris and N. broadleyi does not receive support in the 16S-only analysis, although N. scalaris also does not appear to be sister to N. lalandii.

Habitat and ecology

The geoxyllic suffrutex-dominated grassy shrublands (‘underground forests’) are likely to be the main habitat of Nucras scalaris. Between August and December, these grassy
Table 3. Pairwise uncorrected net p-distances for species of *Nucras* for the 16S gene, with intra-specific values on the diagonal. Intra-specific values were not estimated (na) for species with only one individual in the dataset.

<table>
<thead>
<tr>
<th></th>
<th>N. scalaris</th>
<th>N. broadleyi</th>
<th>N. boulengeri</th>
<th>N. holubi</th>
<th>N. intertexta</th>
<th>N. lalandii</th>
<th>N. livida</th>
<th>N. ornata</th>
<th>N. taeniolata</th>
<th>N. tessellata</th>
</tr>
</thead>
<tbody>
<tr>
<td>N. scalaris</td>
<td>na</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>N. broadleyi</td>
<td>0.086</td>
<td>0.047</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>N. boulengeri</td>
<td>0.119</td>
<td>0.095</td>
<td>na</td>
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shrublands are dominated by geoxylic sufrutices, such as *Brachystegia russelliae*, *Cryptosepalum exfoliatum* ssp. *sufruticans*, *Syzygium guineense* ssp. *huillense*, *Euclea crispa* and *Combretum platypetalum*, forming a dense covering at about 30 to 50 cm above the ground. From the end of December to the start of the dry season, the inflorescences of typical savanna grasses, such as *Tristachya nodiglumis*, *Aristida* spec. div., and *Ctenium concinnum* dominate, forming a more open layer at about 1–1.5 m height lasting four to six months. Man-made fires run through the grassland in July or August, leaving bare soil for a few weeks before the geoxyles begin to resprout.

In this heterogeneous habitat, additional structure is provided by multi-stemmed shrubs and a scattering of larger trees, such as *Monotes africana*, *Protea gaguedii*, *Swartia madagascariensis*, *Strychnos cocculoides*, *Burkea africana*, and *Ochna pulchra*. The habitat also includes burnt tree stumps and a considerable amount of deadwood. There are biogenous structures, such as termite mounds of 1–1.5 m height (Figure 2D) and lines of mole hills (ca 20–30 cm high) made by Mechow’s mole-rats (*Fukomys mechowii*). These structures interrupt the geoxylic matrix and provide open spots where lizards can bask. Given there are ample termite mounts in this habitat, these insects probably are an important prey item for *N. scalaris*.

**Discussion**

The new *Nucras* specimen from the central Angolan plateau morphologically fits the description of *Nucras scalaris*, making this the first record since the original description more than half a century ago. Although the genetic data are limited, we confirm that *N. scalaris* is a separate species that falls within the larger clade containing both *N. broadleyi* and the *N. tessellata + lalandii* complex. It is likely that *N. scalaris* is sister to *N. broadleyi* not *N. lalandii*, but this is based on a single gene and one individual. Although the relationship received moderate to good support in the three gene phylogeny, it was not supported in the 16S-only analysis. Therefore, confirmation of this relationship will have to be verified through additional samples for phylogenetic analyses.

A morphometric and meristic comparison among *N. scalaris*, *N. broadleyi* and *N. lalandii* show overlap between several characters (Table 1). The presence of enlarged scales on the surface of the arm (Figure 4F) that distinguishes *N. scalaris* from *N. lalandii*, does not distinguish *N. scalaris* from *N. broadleyi*. However, a number of morphological features can distinguish these two species. The dorsal coloration is cream with twelve transversal and continuous dark brown bands in *N. scalaris* (Figure 3) versus a dorsum with a series of longitudinal pale stripes and bright orange tail in *N. broadleyi* (Branch et al. 2019b). Furthermore, *Nucras scalaris* has a much larger and robust body than *N. broadleyi*. These species occupy different habitats, because *N. scalaris* is associated with the ‘underground forests’ in the Angolan Miombo Woodlands in the plateau in central and north-eastern Angola, whereas *N. broadleyi* inhabits mopane woodlands, dry savannas, and semi-desert shrublands from southwestern Angola (Branch et al. 2019b).

Although Sandveld lizards are thought to be relatively abundant, they are rarely observed (Branch 1998; van der Meer et al. 2010; Branch et al. 2019b). Unlike other lacertids, they tend to avoid the open spaces where detectability would be high, making them difficult to record. It is interesting to note that all specimens of *N. scalaris* were recorded in the dry season (July 1954 and June 2018). However, the few records collected to date does
not allow for an assessment whether lizards are more active in the dry season, or whether the very limited sampling has resulted in a bias, because of random events. However, only one specimen of *N. scalaris* was captured in a pitfall trap from a trap line that was left for four days in the dry season. During the same period, we commonly caught other lizards, such as *Panaspis*, *Trachylepis* and *Ichnotropis*. Active searches in the wet season (March 2019), 25 km north of the type locality, did not produce any additional records of *N. scalaris* (Vaz Pinto, pers. comm.), nor did targeted surveys in Cusseque during the late dry season in September 2019. Other lizards recorded in Cusseque include *Acanthocercus* sp., *Agama aculeata*, *Gerrhosaurus bulsi-multilineatus* complex, *Ichnotropis capensis*, *Panaspis* sp., *Trachylepis binotata*, *Sepsina angolensis*, and *Zygaspis quadrifrons*. Consequently, although other species appear to be relatively easy to record in the same area, *N. scalaris* does not appear to be abundant.

All three known localities for *N. scalaris*, Alto Chicapa, Alto Cuílo and Cusseque, are located in the broad Angolan Miombo Woodlands Ecoregion (Burgess et al. 2004). The characterization of this ecoregion does not include the open geoxylic suffrutex-dominated grassy shrubland (‘underground forests’), although it is an extensive and locally important habitat type in this area (Barbosa 1970). Indeed, it is the typical vegetation type across vast areas of the Angolan plateau (Zigelski et al. 2019), including Alto Cuílo and Alto Chicapa (Vaz Pinto, pers. comm.). Overall, these findings provide another piece to the puzzle regarding the biogeography of Angolan reptiles, an area of work that has been previously highlighted as crucial (see Branch et al. 2019c). If the distribution of this species is limited to the Angolan plateau, its status as an Angolan endemic would be reinforced. It will be important, however, to understand whether this perceived endemism is the result of under-sampling or a poor appreciation of the ecology of the species, or whether it is truly an Angolan endemic.

This new record extends the distribution of *Nucras scalaris* to Bié Province, approximately 380 km southwest of the previously known range (Figure 1) and increases the known elevation of occurrence from 1 300 m to 1 570 m above sea level. The record also corresponds with the first instance of any Sandveld lizard associated with ‘underground forest’ habitats. The cylindrical and elongated body shape possibly reflect a propensity to shelter within and beneath the short and dense vegetation (Figures 2C and 2D), which might explain why the species is seldom encountered. Although the ecology and life history of *N. scalaris* is still relatively unknown, we can infer that termites are probably an important prey item for *N. scalaris*, as with other species of Sandveld lizards (Branch 1998; Alexander and Marais 2007; van der Meer et al. 2010). Despite there being many unknowns regarding this species, the single specimen has advanced our knowledge of this poorly known Angolan endemic reptile. The finding has also prompted the species to be removed from the IUCN Red List Data Deficient category and allowed for a full assessment to be carried out. The species has now been evaluated as Least Concern given the large range extension covering an area that is not currently under any major concerning threats (Baptista et al. forthcoming). However very little is still known about this species’ real distribution, ecology and abundance, and additional studies might provide a more precise assessment.

The discovery of this species in the ‘underground forest’ begs the question whether other undocumented species diversity could be associated with this peculiar and often overlooked vegetation type. The new record of *N. scalaris* adds to a recent series of
rediscoveries of endemic Angolan herpetofauna, including frogs (Conradie et al. 2013; Baptista et al. 2018), lizards (Stanley et al. 2016; Vaz Pinto et al. 2019), amphisbaenians (Branch et al. 2018) and snakes (Branch et al. 2019a; Gonçalves et al. 2019). These discoveries are progressively contributing to our understanding of these poorly known species, as well as providing a more comprehensive understanding of Angolan herpetofauna and biogeography.

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