

A new species of Namib Day Gecko (Gekkonidae: *Rhoptropus* Peters, 1869) from the Serra da Neve inselberg, southwestern Angola

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
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Abstract

The genus *Rhoptropus* comprises nine recognized species of diurnal geckos endemic to the arid regions of Angola and Namibia. Seven species occur in Angola, including the widespread *R. boultoni* and the poorly known Angolan endemics *R. benguellensis* and *R. montanus*, formerly recognized as subspecies of *R. boultoni*. While *R. benguellensis* is relatively widespread in the Angolan Escarpment highlands, *R. montanus* is geographically restricted to the Huíla Plateau. Recent fieldwork on the Serra da Neve inselberg, a herpetological diversity hotspot in southwestern Angola, revealed the presence of an undescribed species of *Rhoptropus* at an elevation of approximately 1600 m. An integrative taxonomic approach combining coloration, morphological and molecular data supports the recognition of this population as a distinct taxonomic unit with affinities to *R. montanus*, which we describe herein as *Rhoptropus nivimontanus* **sp. nov.** The discovery of a new species of *Rhoptropus* endemic to Serra da Neve is discussed in the biogeographic context of the region.

Key words: Africa, endemism, escarpment, systematics, taxonomy

Introduction

Namib Day Geckos of the genus *Rhoptropus* Peters, 1869 are part of the *Pachydactylus* group radiation, the most diverse clade of geckos in sub-Saharan Africa (Bauer & Good 1996; Bauer & Lamb 2005; Kuhn 2016; Heinicke *et al.* 2017a). The genus consists of nine currently recognized species of diurnal and mostly rupicolous geckos occurring in the arid regions of western Namibia and southwestern Angola (Kuhn 2016; Heinicke *et al.* 2017a; Uetz *et al.* 2023). Seven species are known to occur in Angola—*Rhoptropus afer* Peters, 1869; *R. barnardi* Hewitt, 1926; *R. biporosus* FitzSimons, 1957; *R. boultoni* Schmidt, 1933; *R. benguellensis* Mertens, 1938; *R. montanus* Laurent, 1964; and *R. taeniosictus* Laurent, 1964—of which the last three are endemic to the country (Marques *et al.* 2018).

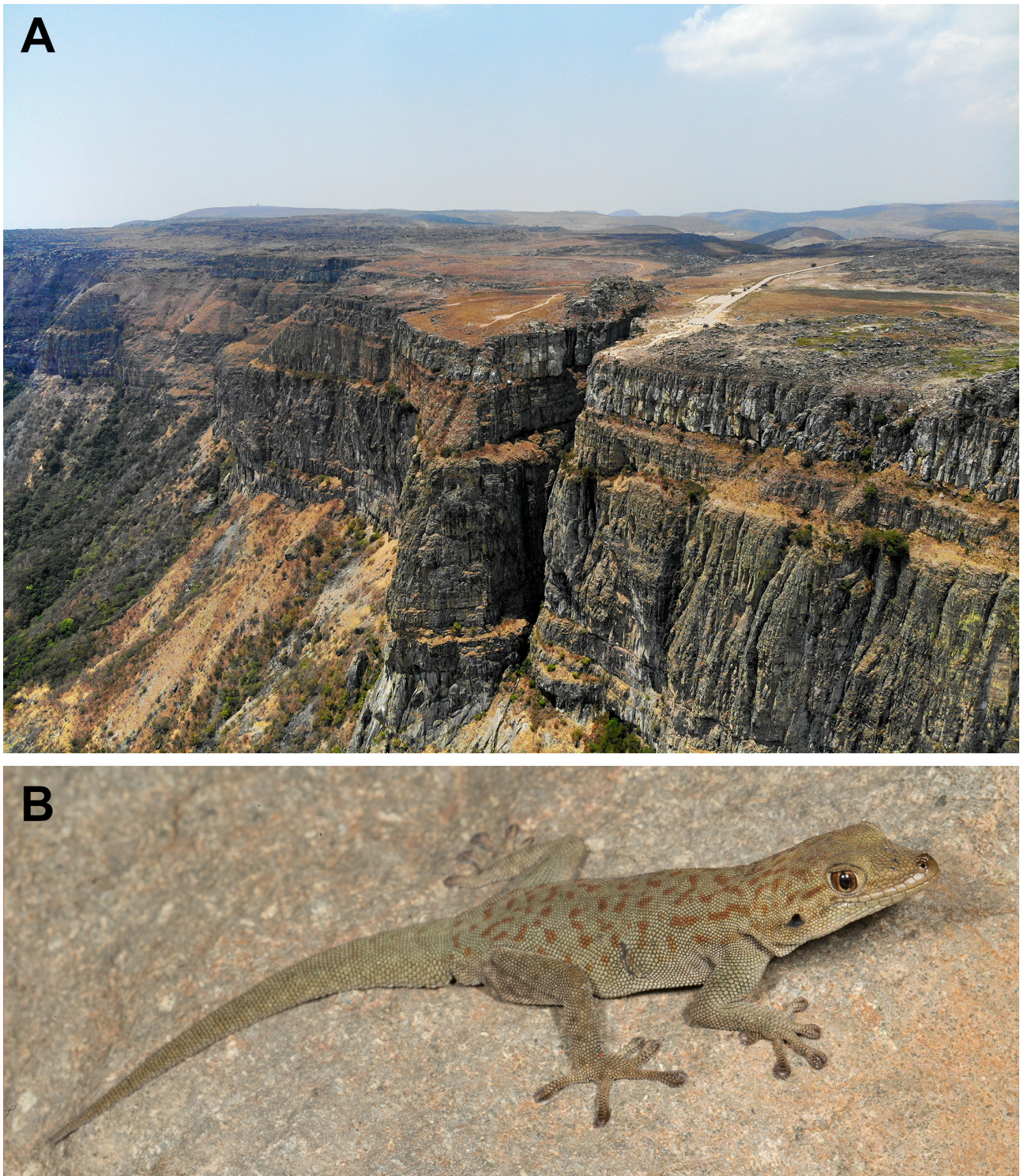


FIGURE 1. A. Habitat of *Rhothropus montanus* at Tundavala; B. Live specimen of *R. montanus* (CAS 267263) from Tundavala, Huíla Province. Photos by LMPC.

Rhothropus boultoni, the largest species of the genus, was described by Schmidt (1933) based on specimens collected by the Pulitzer Angola Expedition at Pico Azevedo, Namibe Province. It is one of the most widespread species in the genus, reaching its northern limit in the arid shrublands and savannas of southwestern Angola (Marques *et al.* 2018) and extending southward to the northern Erongo Region of Namibia (Kuhn 2016). Three subspecies of *R. boultoni* were formerly recognized—nominotypical *R. b. boultoni*, and the Angolan endemics *R. b. benguellensis* and *R. b. montanus* (Mertens 1938; Laurent 1964). Mertens (1938) described *benguellensis* as a subspecies of *R.*

boultoni from Cubal in inland Benguela Province, and additional records are scarce (e.g., Hellmich 1957; Laurent 1964). *Rhoptropus montanus* was described by Laurent (1964) as a highland form of *R. boultoni* from the Humpata Plateau in Huíla Province (Fig. 1). For decades this taxon remained known only from the holotype (MD 1854a), which is still extant but poorly preserved in the collections of Museu Regional do Dundo, Lunda Norte Province, Angola (Ceriaco *et al.* 2020). These three taxa, henceforth referred to as the *boultoni* “group”, differ from other congeners in being generally robust *Rhoptropus* with a dark dorsal coloration covered by an irregular orange to red pattern, instead of the more complex dorsal pattern typical of other members of the genus, including different shades of brown and grey overlayed by black and pale spots.

The taxonomic history of the genus is complex and marked by frequent misidentifications and misapplication of names, mostly due to the morphological conservatism of the genus and the lack of comparative material (Bauer & Good 1996). The long period of war and political instability that affected Angola hindered the collection of new material, preventing significant advances in the taxonomy and biogeography of *Rhoptropus*, particularly the Angolan endemics *R. taeniostictus*, *R. benguellensis* and *R. montanus*, known only from few published records. Large series of these species were collected mostly by Wulf Haacke during the 1970s and are deposited in the collections of the Ditsong National Museum of Natural History (formerly Transvaal Museum) in South Africa, but a complete account of this material was never published.

New material collected during recent fieldwork in Angola allowed the identification of undescribed cryptic diversity associated with *R. barnardi* and *R. biporosus*, and the validation of poorly known species (Ceriaco *et al.* 2016; Kuhn 2016; Butler *et al.* 2019), paving the way for the preparation of a comprehensive phylogeny (Bauer *et al.* in prep.) and a taxonomic revision (Parrinha *et al.* in prep.) of the genus. While recent phylogenetic works validate the specific status of *R. boultoni*, *R. benguellensis* and *R. montanus*, contrary to previous postulations, no support was found for close relationships between these taxa (Kuhn 2016; Heinicke *et al.* 2017a; Butler *et al.* 2019).

During a recent expedition to the Serra da Neve inselberg in northern Namibe Province, we collected three specimens of a putatively undescribed species of *Rhoptropus*, reported by Marques *et al.* (2024a) as *Rhoptropus* aff. *montanus* (Fig. 2). Although similar to *R. montanus* in general habitus and most meristic characters, the Serra da Neve specimens differ from *R. montanus* and all other congeners in color pattern. The substrate specificity of members of the genus and the ecological isolation of the inselberg further support the hypothesis that the Serra da Neve specimens represent an undescribed species of *Rhoptropus* (Bauer 1999; Marques *et al.* 2024a). With six strictly endemic reptile species, Serra da Neve is the region in southwestern Africa with the greatest number of strict endemics per unit area (Marques *et al.* 2024a, 2024b). Based on morphological and molecular data, we recognize the Serra da Neve montane *Rhoptropus* as a distinct species, which we describe herein. We provide additional data and comments on the distribution of the *boultoni* “group” in Angola and discuss these results in the biogeographic context of the region.

Materials and Methods

Material examined. Specimens collected for this study were fixed in 10% buffered formalin in the field and transferred to 70% ethanol for long term preservation. Liver tissue was removed before formalin fixation and preserved in 95% ethanol. For mensural and meristic comparisons, we examined 33 specimens representing the putative new species and the members of the *boultoni* “group”—*Rhoptropus boultoni*, *R. benguellensis* and *R. montanus*—including the holotypes of *R. boultoni* (CM 5634) and *R. montanus* (MD 1854a). Additional material was examined only for identification purposes through morphological characters, but no complete measurements were recorded from these specimens and, therefore, they were not included in the morphological comparisons. Specimens consulted for this study are housed in the collections of the California Academy of Sciences (CAS), San Francisco, USA; the Carnegie Museum of Natural History (CM), Pittsburgh, USA; the Museum of Comparative Zoology (MCZ), Harvard University, Cambridge, USA; the Muséum national d’Histoire naturelle (MNHN), Paris, France; the Museu Nacional de História Natural e da Ciência da Universidade de Lisboa (MUHNAC), Lisbon, Portugal; the Museu Regional do Dundo (MD), Dundo, Angola; the Ditsong National Museum of Natural History (TM, formerly Transvaal Museum), Pretoria, South Africa; and the reference collection of the Instituto Nacional da Biodiversidade e Áreas de Conservação (INBAC), Ministério do Ambiente, Luanda, Angola. A complete list of material examined is provided as supplementary data (<https://doi.org/10.6084/m9.figshare.27854292>). Locality data

are presented in the form of decimal degrees and use the WGS-84 map datum, and elevations are reported in meters above sea level. Older records were derived from Marques *et al.* (2018) or georeferenced using the GEOLocate web tool (<https://www.geo-locate.org>).

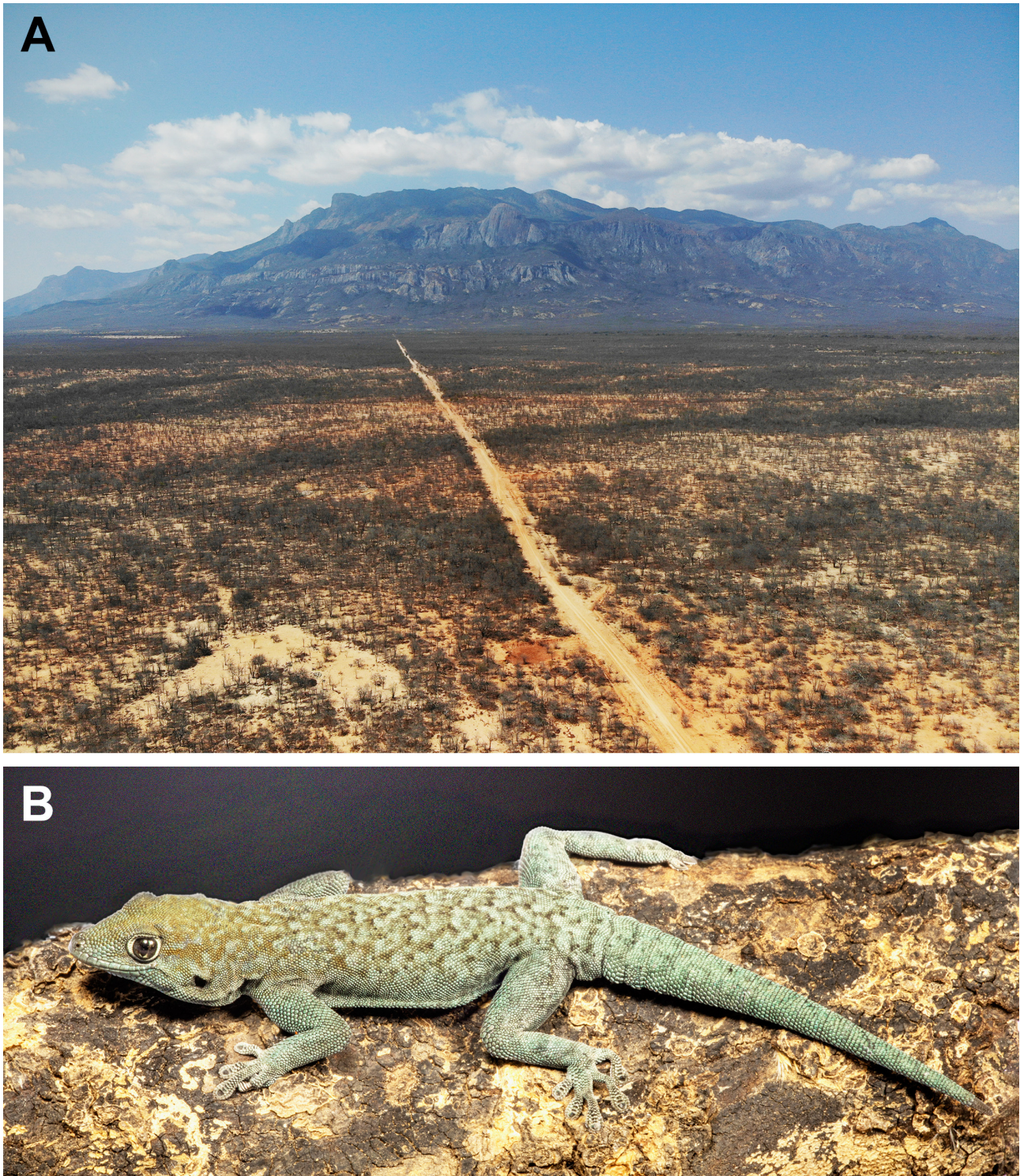


FIGURE 2. **A.** Serra da Neve Inselberg and surrounding lowlands; **B.** Live holotype of *Rhoptropus nivimontanus* **sp. nov.** (MUHNAC/MB03-1706) from the highlands of Serra da Neve, Namibe Province. Photos by LMPC (**A**) and AT (**B**).

Morphological data collection. Specimens were measured with a digital caliper to the nearest 0.1 mm and lepidosis was observed with the help of a stereomicroscope. Scale counts and measurements follow those used in earlier *Rhoptropus* descriptions (e.g., Schmidt 1933; Mertens 1938; Laurent 1964), and abbreviations were

standardized following Darko *et al.* (2022). The following 26 mensural and meristic characters were recorded: snout-vent length (SVL), measured from tip of snout to vent; tail length (TAL), from vent to tip of tail, measured only in specimens with complete original tails; tail width (TW), measured at base of tail, immediately posterior to post-cloacal swelling; forearm length (FLL), from elbow to base of palm; crus length (CL), from knee to base of heel; trunk length (AGD), corresponding to the distance between axilla and groin; body width (BW), maximum width of body; head length (HL), measured from tip of snout to posterior margin of retroarticular process of jaw; head width (HW), measured at widest position; head height (HH), maximum height of head from occiput to underside of jaw; eye diameter (ED), greatest horizontal diameter of eyeball; eye-ear distance (EE), from anterior edge of ear opening to posterior edge of eye; eye-snout distance (ES), from anterior margin of eye to tip of snout; eye-nostril distance (EN), from anterior margin of eye to nostril; internarial distance (IN), corresponding to minimum distance between nostrils; inter-orbital distance (IOD), measured across narrowest point of frontal bone; number of supralabials (SL); number of infralabials (IL); number of circumnasal scales (CN); number of internasal scales in contact with rostral (INS); number of enlarged subdigital scales under fourth finger (SF4) and fourth toe (ST4); number of distal subdigital lamellae under fourth finger (LF4) and fourth toe (LT4); number of precloacal pores (PCP); number of dorsal scales across midbody (DSR). The following qualitative characters were also noted: orientation of nostrils and degree of nasal swellings; sharpness of rostrum and snout profile; relative size and arrangement of chin shields and gular scales; relative size and arrangement of subcaudal scales; general habitus and limb proportions. Color pattern was recorded, and high-resolution photographs of live and preserved specimens were taken.

Phylogenetic analysis. Sampling for the molecular phylogenetic analysis was designed to produce a comparative data set consisting of sequences from the three Serra da Neve specimens, series of individuals for *Rhoptropus boultoni* “group” species (*R. benguellensis*, *R. boultoni*, and *R. montanus*), and individual exemplars of all other *Rhoptropus* species (Table 1). Seven species of the closely related genera *Chondrodactylus*, *Elasmodactylus*, and *Pachydactylus* plus the more distantly related *Goggia* were included as outgroups (Gamble *et al.* 2012; Heinicke *et al.* 2017a, 2017b). Regions of the 16S ribosomal RNA (525 bp) and protein-coding genes ND2 (1,041 bp) and RAG1 (1,038 bp) were used in analyses to maximize compatibility with available sequences from previous studies (Lamb & Bauer 2001; Kuhn 2016; Heinicke *et al.* 2017a, 2017b; Lobón-Rovira *et al.* 2022). For new samples, genomic DNA was isolated using Qiagen DNeasy kits following manufacturer’s protocols. Extracted DNA was used in PCR reactions with the following primer pairs: 16SA/16SB for 16S (Palumbi 1996), L4437/H5540 and L4882b/H5934 for ND2 (Macey *et al.* 1997, 2000), and R13/RAG1R700 and RAG1F700/R18 for RAG1 (Growth & Barrowclough 1999; Bauer *et al.* 2007). Amplified PCR fragments were purified followed by Sanger sequencing. Sequence electropherograms were imported to MEGA 11 (Tamura *et al.* 2021) for inspection, assembly, and alignment. Sequence alignments implemented in MEGA 11 used MUSCLE (Edgar 2004) under default parameters. Alignment gaps in the protein-coding ND2 sequences were manually corrected to conform to codon positions, and both ND2 and RAG1 sequences were translated to confirm that sequences did not contain premature stop codons. Individual gene alignments incorporated both new sequences and published sequences obtained from GenBank. 16S and RAG1 sequences were successfully obtained for the Serra da Neve population. Although ND2 data are not available for the Serra da Neve samples, we retained the gene in our study due to its broad availability across other *Rhoptropus*. Accession numbers of all sequences included in the study are listed in Table 1.

Phylogenetic analyses using the Maximum likelihood (ML) criterion were conducted using IQTree 2.2 (Nguyen *et al.* 2014). The three single-gene alignments were used to construct preliminary phylogenies under the GTR+I+G model of evolution to confirm that no strongly conflicting signal existed among the genes. Following this confirmation, the three alignments were concatenated for the final phylogenetic analysis. The concatenated alignment includes one terminal per sample for *Rhoptropus benguellensis*, *R. boultoni*, *R. montanus*, and *R. sp.* (Serra da Neve), and one terminal per species for other taxa, generating a final data set with 53 terminals and 2,604 alignment positions. Seven partitions were initially defined in the data set: 16S, ND2 codon position 1, 2, 3, and RAG1 codon position 1, 2, 3. ModelFinder was used to identify the best grouping of partitions and models of evolution under the Bayesian Information Criterion (Lanfear *et al.* 2012; Kalyaanamoorthy *et al.* 2017). Based on this, the three RAG1 codon positions were grouped into a single partition and the following models of evolution were applied for the final combined ML analysis: TIM2+F+I+G (16S); GTR+F+I+G (ND2 codon position 1; ND2 codon position 2; ND2 codon position 3); HKY+F+G (RAG1). Branch support for the ML analysis was assessed using 1000 ultrafast bootstrap replicates (Minh *et al.* 2013). We also calculated uncorrected pairwise distances for the mitochondrial gene with the most complete species sampling, 16S, in MEGA11.

TABLE 1. Specimens used for genetic analysis and corresponding GenBank accession numbers. New sequences have accession numbers PQ594933–PQ594945 and PQ613920–PQ613978. Sample codes not listed in the material examined are as follows: SBH (S. Blair Hedges tissue collection); MBUR (Marius Burger field number); AMB (Aaron M Bauer field number); WC (Werner Conradie field number); P (field number *vide* Lobón-Rovira *et al.* 2022); MCZ FS (Museum of Comparative Zoology field series); NMNW (National Museum of Namibia, Windhoek).

| Species | Sample Number | Locality | 16S | ND2 | RAG1 |
|------------------------------------|------------------|---|----------|----------|----------|
| <i>Chondrodactylus fitzsimonsi</i> | CAS 206981 | Namibia: Kunene, Okanguati Road | AF449109 | OK563286 | OK563485 |
| <i>Elasmodactylus tetensis</i> | CAS 261795 | Zimbabwe: Mashonaland East, N bank Rwenya River | AY026934 | | |
| | PEM R-5540 | Mozambique: Niassa, Niassa Game Reserve | | KY224213 | KY224312 |
| <i>Goggia lineata</i> | SBH 267107 | n/a | AY763274 | | |
| | CAS 193625 | South Africa: Northern Cape, Richtersveld NP | | MF154728 | MF154850 |
| <i>Pachydactylus namaquensis</i> | CAS 206923 | South Africa: Northern Cape, Steinkopf | AF449107 | | DQ275444 |
| | MBUR 01770 | South Africa: Western Cape, Rooiberg | | KY224230 | |
| <i>Pachydactylus punctatus</i> | n/a | n/a | AB612270 | AB612270 | |
| | PEM R-12461 | South Africa: Northern Cape, Sendelingsdrift | | | KY224331 |
| <i>Pachydactylus rangei</i> | CAS 214780 | Namibia: Erongo, Rooibank | AY123375 | | DQ275417 |
| | MCZ R-183725 | Namibia: Erongo, Swakop River | | JN543907 | |
| <i>Pachydactylus rugosus</i> | CAS 201905 | South Africa: Northern Cape, Richtersveld NP | AF449113 | KY224252 | JQ945325 |
| <i>Pachydactylus weberi</i> | CAS 206754 | South Africa: Northern Cape, Kleinsee | AF449115 | PQ613951 | DQ275430 |
| <i>Rhoptropus afer</i> | CAS 206949 | Namibia: Erongo, 17.3 km E Hentiesbaai | AY026931 | | DQ275453 |
| | MCZ R-183711 | Namibia: Erongo, Rössing Mountain | | KY224254 | |
| <i>Rhoptropus barnardi</i> | AMB 5938 | Namibia: Kunene, Palmwag Lodge | AY026929 | | |
| | CAS 214658 | Namibia: Kunene, Torra Bay Road | | KY224243 | KY224341 |
| <i>Rhoptropus benguellensis</i> | MUHNAC/MB03-1800 | Angola: Benguela, Dembi | PQ594937 | | PQ613923 |
| | MUHNAC/MB03-1801 | Angola: Benguela, Dembi | PQ594938 | PQ613959 | PQ613924 |
| | WC1834 | Angola: Kwanza Sul, 3.5 km W Conde | | KY224246 | KY224346 |
| | MUHNAC/MB03-1337 | Angola: Kwanza Sul, AH Lauca | | PQ613960 | PQ613920 |
| | MUHNAC/MB03-1336 | Angola: Kwanza Sul, AH Lauca | PQ594935 | PQ613961 | PQ613921 |
| | MUHNAC/MB03-1338 | Angola: Kwanza Sul, AH Lauca | PQ594936 | PQ613962 | PQ613922 |
| <i>Rhoptropus biporosus</i> | CAS 193822 | Namibia: Kunene, 37 km W Orupembe | AY026928 | | |
| | CAS 224030 | Namibia: Kunene, 18.3 km W Orupembe | | KY224244 | KY224342 |

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TABLE 1. (Continued)

| Species | Sample Number | Locality | 16S | ND2 | RAG1 |
|--------------------------------|---------------|--|----------|----------|----------|
| <i>Rhoptropus boultoni</i> | CAS 264698 | Angola: Namibe, Bentiaba river near Maungo | PQ594939 | PQ613963 | PQ613925 |
| | CAS 206975 | Namibia: Kunene, 1 km N Skeleton Coast Park entry | AY026930 | | DQ275454 |
| | CAS 214713 | Namibia: Kunene, Twyfelfontein | | KY224256 | EF534810 |
| | CAS 254892 | Angola: Namibe, 2 km E Mangueiras | | PQ613971 | PQ613926 |
| | CAS 254902 | Angola: Namibe, 1.8 km W Caraculo | | PQ613978 | PQ613927 |
| | CAS 267479 | Angola: Namibe, Vipungos | PQ594940 | | |
| | P9.252 | Angola: Namibe, Iona NP, Cunene River Baptista Camp | ON006705 | | |
| | P1.123 | Angola: Namibe, Iona NP, Serra Cafema | ON006704 | | |
| | P9.277 | Angola: Namibe, Iona NP, Omauha | ON006708 | | |
| | P9.262 | Angola: Namibe, Iona NP, 5km NE of Cunene Camp | ON006707 | | |
| | CAS 254752 | Angola: Namibe, Iona NP, 3.4 km SW Espinheira | | PQ613974 | PQ613928 |
| | CAS 254795 | Angola: Namibe, Iona NP, Espinheira | | PQ613975 | PQ613929 |
| | CAS 254834 | Angola: Namibe, Iona NP, Omauha Lodge | | PQ613976 | PQ613930 |
| | CAS 254849 | Angola: Namibe, Iona NP, Rio Curoca crossing | | PQ613973 | PQ613931 |
| | CAS 254857 | Angola: Namibe, Iona NP, Rio Curoca | | PQ613977 | PQ613932 |
| | CAS 254921 | Angola: Namibe, Pico Azevedo | | PQ613972 | PQ613933 |
| | MCZ R-193218 | Namibia: Kunene, Farm Omburo Ost | | PQ613967 | PQ613934 |
| | MCZ R-184196 | Namibia: Kunene, 27.8 km E Grootberg Pass | | PQ613968 | PQ613935 |
| | MCZ FS-A38211 | Namibia: Kunene, ~10 km N Reddrum | | PQ613966 | PQ613936 |
| | MCZ FS-A27688 | Namibia: Kunene, ridge adjacent to Epupa Falls camp | | PQ613965 | PQ613937 |
| | MCZ R-184208 | Namibia: Kunene, near Kunene River | | PQ613964 | PQ613938 |
| | MCZ R-185749 | Namibia: Kunene, 62 km E Kamanjab, Farm Amolinda | | PQ613969 | PQ613939 |
| | MCZ R-185959 | Namibia: Kunene, Farm Otijitambi | | PQ613970 | PQ613940 |

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TABLE 1. (Continued)

| Species | Sample Number | Locality | 16S | ND2 | RAG1 |
|--|--------------------------|---|----------|----------|----------|
| <i>Rhoptropus bradfieldi</i> | n/a | Namibia: Erongo, Hentiesbaai Road | AY026932 | | |
| | NMNW (MCZ FS- A38226) | Namibia | | KY224245 | KY224343 |
| <i>Rhoptropus diporus</i> | CAS 214605 | Namibia: Kunene, near Gai-as | AY026933 | | |
| | CAS 214604 | Namibia: Kunene, near Gai-as | | KM073692 | KM073536 |
| <i>Rhoptropus montanus</i> | CAS 254866 | Angola: Namibe, Leba Pass overlook | | PQ613952 | PQ613942 |
| | CAS 254867 | Angola: Namibe, Leba Pass overlook | PQ594941 | PQ613953 | PQ613941 |
| | CAS 254868 | Angola: Namibe, Leba Pass overlook | PQ594942 | PQ613954 | PQ613943 |
| | CAS 254869 | Angola: Namibe, Leba Pass overlook | | PQ613955 | PQ613944 |
| | CAS 254870 | Angola: Namibe, Leba Pass overlook | PQ594943 | PQ613956 | PQ613945 |
| | CAS 254871 | Angola: Namibe, Leba Pass overlook | | PQ613957 | PQ613946 |
| | CAS 254872 | Angola: Namibe, Leba Pass overlook | PQ594944 | PQ613958 | PQ613947 |
| <i>Rhoptropus nivimontanus</i> sp. nov. | MUHNAC/MB03-1706 | Angola: Namibe, Serra da Neve | | | PQ613948 |
| | MUHNAC/MB03-1707 | Angola: Namibe, Serra da Neve | PQ594933 | | PQ613949 |
| | MUHNAC/MB03-1708 | Angola: Namibe, Serra da Neve | PQ594934 | | PQ613950 |
| <i>Rhoptropus taeniostictus</i> | CAS 254908 | Angola: Namibe, Namibe- Lubango Road | | KY224248 | KY224248 |
| | CAS 267514 | Angola: Namibe, Caraculo | PQ594945 | | |

Results

Despite being superficially similar to the members of the *boultoni* “group” (i.e., *R. boultoni*, *R. benguellensis* and *R. montanus*), the specimens collected at Serra da Neve have a greenish blue coloration, distinct from all other species in the genus, and can be further diagnosed based on meristic characters (Table 2). The new species is morphologically most similar to *R. montanus* in general habitus and meristic characters (Table 2).

Our phylogenetic analyses support the recognition of the Serra da Neve population as a distinct evolutionary lineage, whose closest relative is *R. montanus*, another montane endemic from the Angolan Escarpment (Fig. 3). The phylogeny also recovers several patterns of relationship within *Rhoptropus* that were strongly supported in Heinicke *et al.* (2017a), including a close relationship among *R. bradfieldi* and *R. diporus* and a clade formed by *R. barnardi*, *R. benguellensis*, and *R. biporosus*. The phylogeny also matches previous studies in not recovering a monophyletic “*boultoni*” complex (Kuhn 2016; Heinicke *et al.* 2017a). Instead, *R. benguellensis*, *R. boultoni*, *R. montanus*, and the Serra da Neve population are part of a larger strongly supported clade that also includes *R. barnardi*, *R. biporosus*, and *R. taeniostictus*, together encompassing all but one of the Angolan *Rhoptropus*. A phylogeny constructed using only 16S and RAG1 data recovers identical patterns of relationship among *Rhoptropus* species.

Our results indicate that the montane *Rhoptropus* from Serra da Neve represents a genetically divergent lineage. It differs from *R. montanus* by an average pairwise distance of 11.2% for the mitochondrial 16S sequences, greater than pairwise 16S distances for the other two sister-species pairs in *Rhoptropus* (2.8% for *R. bradfieldi*/*R. diporus* and 9.8% for *R. barnardi*/*R. biporosus*) and greater than the highest pairwise distance among the well-sampled and geographically widespread *R. boultoni* specimens (9.8%). It can be distinguished from all other members of the

genus based on coloration pattern and meristic characters. Furthermore, the isolation and biogeographic context of the inselberg further support the recognition of this population as a distinct taxon. Based on the evidence presented herein and following de Queiroz’s (1999) general lineage species concept, we describe the Serra da Neve montane *Rhoptropus* as a new species.

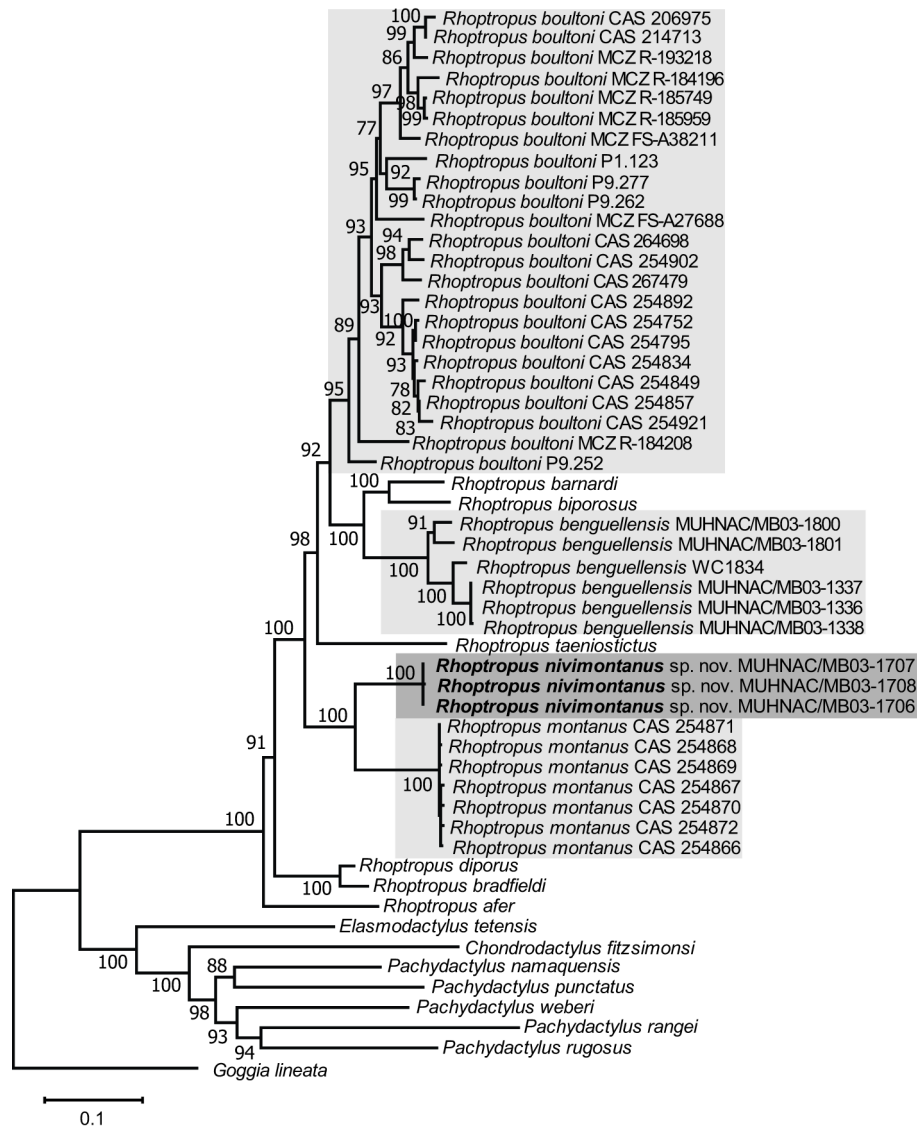


FIGURE 3. Phylogeny of *Rhoptropus* based on a maximum likelihood analysis of the concatenated 16S/ND2/RAG1 nucleotide sequence data set. Bootstrap support values are indicated at nodes. Shading indicates samples belonging to the non-monophyletic *boultoni* “group”, including *R. nivimontanus* **sp. nov.**

TABLE 2. Morphological comparison between *Rhoptropus nivimontanus* **sp. nov.** and members of the *boultoni* “group”. Data for *R. boultoni* recorded from both Angolan and Namibian specimens. Abbreviations are those described in the materials and methods. Mensural characters are presented in millimeters; data presented as “mean [min.–max.]”.

| | <i>Rhoptropus benguellensis</i> (n=8) | <i>Rhoptropus boultoni</i> (n=13) | <i>Rhoptropus montanus</i> (n=9) | <i>Rhoptropus nivimontanus</i> sp. nov. (n=3) |
|----------|--|--------------------------------------|-------------------------------------|---|
| max. SVL | 52.4 | 73.9 | 57 | 55.3 |
| SL | 10 [9–11] | 12 [11–13] | 11 [10–11] | 10 [9–11] |
| IL | 8 [6–8] | 9 [7–10] | 8 [8–9] | 8 [8–8] |
| INS | 1 [1–1] | 1 [1–1] | 2 [1–2] | 2 [2–2] |

.....continued on the next page

TABLE 2. (Continued)

| | <i>Rhoptropus benguellensis</i> (n=8) | <i>Rhoptropus boultoni</i> (n=13) | <i>Rhoptropus montanus</i> (n=9) | <i>Rhoptropus nivimontanus</i> sp. nov. (n=3) |
|---------|--|--------------------------------------|-------------------------------------|---|
| SF4 | 10 [9–11] | 10 [8–12] | 9 [9–10] | 9 [8–10] |
| LF4 | 8 [7–8] | 10 [8–12] | 8 [7–8] | 8 [8–8] |
| SF4+LF4 | 18 [17–19] | 20 [18–23] | 17 [16–18] | 17 [16–18] |
| ST4 | 12 [11–13] | 13 [10–15] | 10 [9–12] | 11 [10–11] |
| LT4 | 8 [8–9] | 11 [9–13] | 9 [8–10] | 9 [8–9] |
| ST4+LT4 | 20 [19–22] | 24 [20–27] | 19 [17–20] | 19 [19–20] |
| PCP | 6 [2–7] | 5 [3–6] | 5 [5–6] | 7 [7–7] |
| DSR | 67 [61–74] | 80 [74–87] | 58 [54–61] | 63 [62–65] |
| CS | Present | Present | Present | Present |
| SC | Enlarged single | Enlarged single | Enlarged pairs/single | Enlarged single |

Systematics

(Reptilia: Squamata: Gekkonidae)

Rhoptropus nivimontanus sp. nov.

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(Figs. 4–8)

Rhoptropus aff. *montanus*: Marques *et al.* (2024a: 189)

Holotype. MUHNAC/MB03-1706 (field number LMPC 3120), an adult male collected by Mariana P. Marques, Luis M.P. Ceriaco, Diogo Parrinha and Arthur Tiutenko near Catchi village, Serra da Neve [−13.7618°, 13.2514°, 1614 m], Namibe Province, Angola, on 27 October 2022.

Paratypes. An adult female (MUHNAC/MB03-1707, field number LMPC 3121) and a juvenile (MUHNAC/MB03-1708, field number LMPC 3145), with the same collecting data as the holotype.

Diagnosis. A medium sized *Rhoptropus* with a maximum SVL of 55 mm (MUHNAC/MB03-1707), body stout, partly regenerated tail about the same length as SVL (Figs. 4, 5). Head wide, with rounded snout. Nasal swellings separated by 2 INS; SL 9–11; IL 8. A well-defined row of enlarged chin shields behind infralabials. Dorsal scales irregularly granular, 62–65 across midbody. Precloacal scales slightly enlarged, bearing 7 pores in males. Digits relatively stout, with 16–18 subdigital scales and lamellae under fourth finger (8–10 SF4 + 8 LF4) and 19 under fourth toe (10–11 ST4 + 8–9 LT4). Tail distinctly segmented, wider at the base and smoothly tapering. Subcaudals transversely enlarged, disposed in a single row with three scales per tail segment. Dorsum greenish blue with a somewhat irregular, yellowish green pattern covering top of head, becoming darker and more reticulated from shoulders to base of tail, interspersed with scattered black speckles; ventral parts light blue.

Rhoptropus nivimontanus sp. nov. differs from all its congeners in its blue and green coloration without any reddish pattern, pale or black spots on dorsum (*versus* dorsum pale brown to black with reddish or black pattern in other species). It further differs from *R. boultoni* by having fewer dorsal scales across midbody (62–65 *versus* 74–87); 2 internasal scales (*versus* 1), and fewer subdigital scales and lamellae under fourth finger (16–18 *versus* 18–23) and fourth toe (19–20 *versus* 20–27); from *R. benguellensis* by having a blue ventrum (*versus* creamy white) and 2 internasal scales (*versus* 1); and from its sister species, *R. montanus*, by having more dorsal scales across midbody (62–65 *versus* 54–61). The male also has more precloacal pores than males of *R. montanus* (7 vs. 5–6).

Description of the holotype. Mensural and meristic characters for the holotype are presented in Table 3. Adult male with a nearly complete, original tail (Figs. 4–5). Body robust (AGD/SVL 0.41). Head moderately long (HL/SVL 0.29), wide (HW/HL 0.73), weakly depressed (HH/HL 0.36), distinct from neck. Snout medium (ES/HL 0.43), rounded, with blunt profile. Canthus rostralis not prominent; shallow depression present immediately behind nasal swellings. Eye small (ED/HL 0.17), its diameter shorter than distance from eye to tip of snout (ED/ES 0.39). Supraciliaries small and slightly pointed; no supraciliary dermal fold present. Ear opening vertically ovoid, situated below eye level, smaller than eye diameter (EH/ED 0.56), with small dermal fold extending from superior margin;

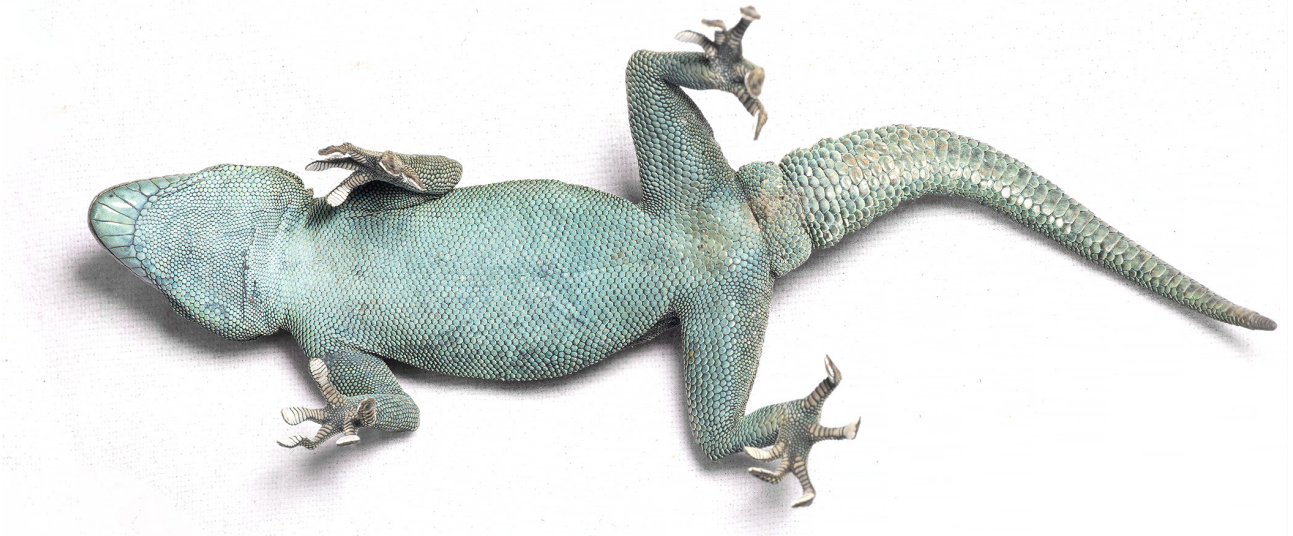
A**B**

FIGURE 4. Dorsal (A) and ventral (B) views of the holotype of *Rhoptropus nivimontanus* **sp. nov.** in life (MUHNAC/MB03-1706). Photos by AT.

distance from eye to ear greater than eye diameter (EE/ED 1.71). Rostral wider than deep, with small backwards prolongation between nasal swellings, in contact with first supralabial and two nasals at each side, and two internasal scales. Nostril situated between three weakly swollen circumnasal scales, oriented dorsally; nasal swellings separated by two INS, followed posteriorly by three smaller scales. Scales on snout larger than those on dorsum and occiput; largest located in front of eye, slightly conical and keeled. Mental greatly elongated and tapering to a point posteriorly, in contact with first infralabial on each side and median chin shield posteriorly. A well-defined row of enlarged chin shields is present, bordering mental and first three infralabials on each side, extending obliquely backwards

along gular region. Gular scales irregular in size, those immediately posterior to chin shields slightly larger than those on throat. SL 11/10 (R/L); IL 8/8 (R/L), first two greatly elongated; small intrusive scale present between IL III and IV on left side. Dorsal scales small and granular, rounded, with weak tendency to become larger towards flanks, 65 across midbody. Ventral scales larger than dorsals, smooth, rounded to sub-hexagonal, slightly imbricate on chest. Precloacal scales slightly enlarged, rounded to sub-hexagonal, bearing 7 continuous pores disposed in a chevron. Limbs long and stout (FLL/SVL 0.15, CL/SVL 0.18); scales on limbs smooth and juxtaposed; those on anterior and ventral aspect of hindlimbs distinctly larger, as well as those on anterior aspect of forearm; scales on palms and soles small and rounded. Digits relatively stout, wider on distal portion; covered above with somewhat enlarged scales distally; clawless or with small triangular scale in place of claw. Ventral surface of digits covered with enlarged scales along the midline (non-scansorial), followed by undivided (except for distalmost) transverse lamellae under distal expansion. Fourth finger of right manus with 10 enlarged scales along midline and 8 transverse lamellae on distal expansion; fourth toe of right pes with 11 enlarged scales along midline and 9 transverse lamellae on distal expansion. Relative length of digits III>IV>II>I=V (right manus); III=IV>V>II>I (right pes). Tail slightly shorter than SVL (TAL/SVL 0.84), last 2 mm regenerated, weakly depressed, wider at base, tapering to point. Tail segmented, with distinct lateral constrictions between proximal segments, less conspicuous distally; dorsal surface covered with smooth, granular scales disposed in rows, slightly larger than dorsals; subcaudal scales irregularly enlarged in first 3 segments, fourth segment with 3 pairs of enlarged scales on midventral section and following segments with a single row of transversely enlarged scales, disposed in 3 scales per tail segment. Regenerated portion of tail unsegmented, with a single row of enlarged scales along midventral section.

TABLE 3. Mensural and meristic data for the type series of *Rhoptropus nivimontanus* **sp. nov.**. Abbreviations are the ones listed in the materials and methods.

| | MUHNAC/MB03-1706 | MUHNAC/MB03-1707 | MUHNAC/MB03-1708 |
|---------|----------------------------|------------------|------------------|
| | Holotype | Paratype | Paratype |
| Sex | Male | Female | Juvenile |
| SVL | 52.4 | 55.3 | 31.7 |
| AGD | 21.5 | 21.2 | 12 |
| BW | 13.6 | 15 | 7.8 |
| TAL | 44 (last 2 mm regenerated) | - | - |
| TW | 6.2 | 6.3 | 2.8 |
| FLL | 7.6 | 8.1 | 4.7 |
| CL | 9.7 | 9.9 | 5.9 |
| HL | 15 | 16.3 | 9.7 |
| HH | 5.4 | 5.4 | 3.5 |
| HW | 11 | 11.6 | 7.1 |
| ED | 2.5 | 2.7 | 1.8 |
| EN | 4.8 | 5.1 | 2.9 |
| ES | 6.4 | 6.6 | 4 |
| EE | 4.3 | 4.1 | 2.4 |
| IN | 1.4 | 1.4 | 0.8 |
| IOD | 1.4 | 1.7 | 1 |
| PCP | 7 | - | - |
| SL | 11 | 11 | 9 |
| IL | 8 | 8 | 8 |
| CN | 3 | 3 | 3 |
| INS | 2 | 2 | 2 |
| SF4+LF4 | 10+8 | 9+8 | 8+8 |
| ST4+LT4 | 11+9 | 10+9 | 11+8 |
| DSR | 65 | 62 | 63 |

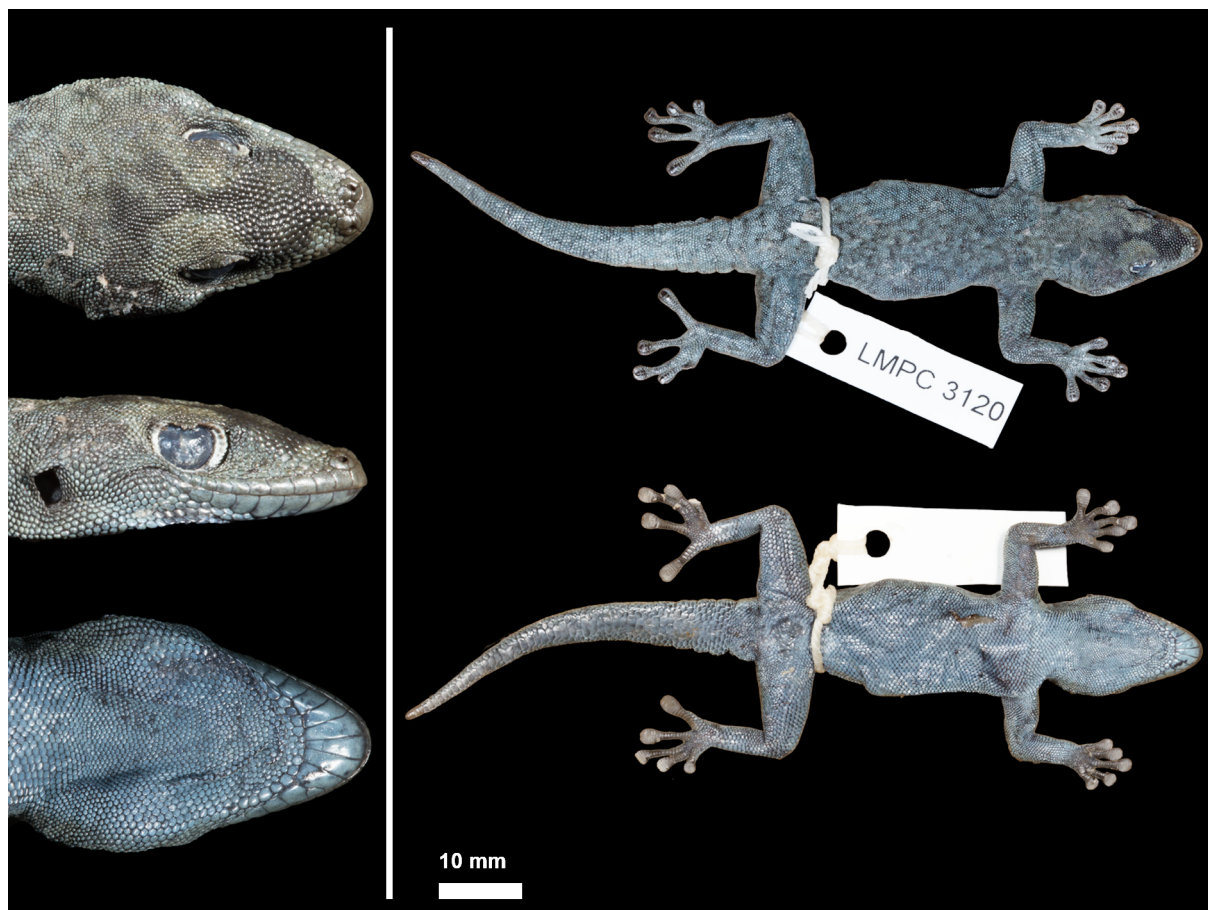


FIGURE 5. Preserved holotype of *Rhoptropus nivimontanus* **sp. nov.** (MUHNAC/MB03-1706). Photos by DP.

Coloration in life (Fig. 4): Dorsum greenish blue; a light yellowish green hue begins behind the nasal swellings and extends through interorbital region to occiput, where it is more distinct; green pattern becomes progressively darker and more reticulated from shoulders towards base of tail, interspersed with scattered black speckles. Limbs mostly homogeneous, with faint and irregular dark shades on hindlimbs; enlarged scales over distal expansion of digits black centered. Ventral parts light blue, slightly darker on precloacal and subcaudal regions.

Coloration in preservative (Fig. 5): Dorsum dark greyish blue; green pattern on dorsum reduced to dull dark brown; on dorsal aspect of head, light green pattern replaced by a distinct black patch, starting behind internasal granules and between postnasal depressions, extending through forehead and interorbital region above frontal bone and fading at occiput. Ventral parts blue.

Variation. Mensural and meristic variation among the type series is presented in Table 3. Both paratypes agree entirely with the holotype in terms of coloration. Female paratype MUHNAC/MB03-1707 lacking precloacal pores or pits; mostly clawless, bearing minute claws on digits I and V of left pes. Tail broken in both paratypes prior to collection, after first (MUHNAC/MB03-1708) and third (MUHNAC/MB03-1707) postpygal tail segments.

Distribution. *Rhoptropus nivimontanus* **sp. nov.** is only known from the type locality near Catchi village, in the highlands of the Serra da Neve inselberg, Namibe Province, Angola (Fig. 6). Considering the substrate specificity of the genus and the ecological isolation of the inselberg, it is assumed to be endemic to higher elevation areas of Serra da Neve.

Habitat and natural history notes. Very little is known about the ecology and natural history of *R. nivimontanus* **sp. nov.** The type series was collected at roughly 1600 m above sea level in an area dominated by Miombo woodlands on the highlands of the inselberg (Huntley 2023; Marques *et al.* 2024a). Specimens were found in a riparian area with denser vegetation and barely any granite outcrops (Fig. 7), in contrast to surrounding woodlands in the inselberg occupied by congener *R. aff. barnardi*. It was observed together with *Lygodactylus nyaneka* Marques, Ceriaco, Buehler, Bandeira, Janota & Bauer, 2020 on tree branches, suggesting more arboreal rather than rupicolous habits.

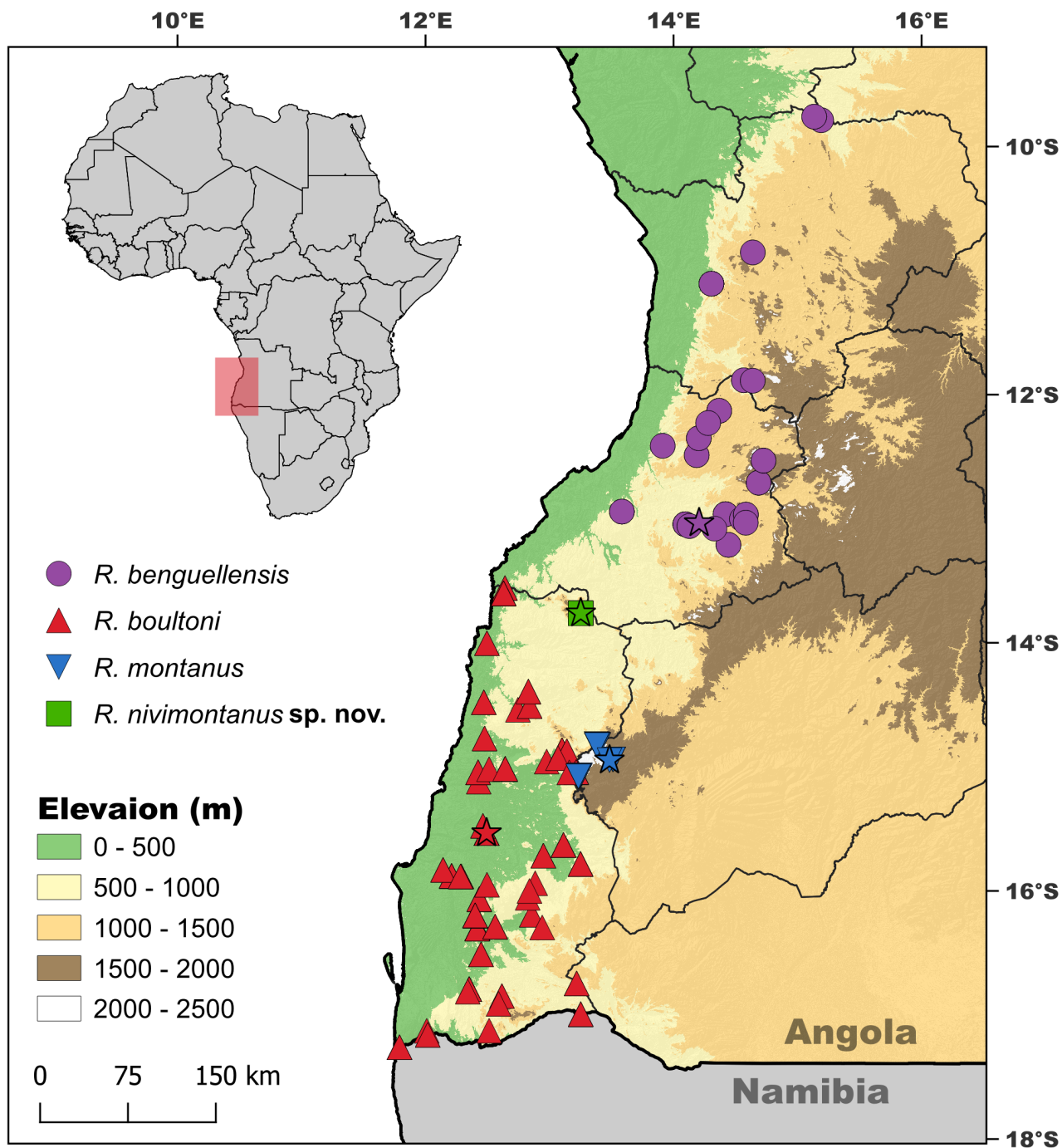


FIGURE 6. Distribution of *Rhoptropus nivimontanus* sp. nov. and the *boultoni* “group” in Angola. Stars represent the respective type localities.

Etymology. The specific epithet “*nivimontanus*” is formed by the combination of the Latin words “*nivis*” (genitive singular of *nix*, i.e., snow) and “*montanus*” (nominative adjectival of *mons*, i.e., pertaining to mountains) (Brown 1956). It is given in reference to the species’ endemic distribution in the Serra da Neve inselberg, whose Portuguese name directly translates to “Mountain of the Snow”. We suggest the English and Portuguese common names “Serra da Neve Day Gecko” and “Osga Diurna da Serra da Neve”, respectively.



FIGURE 7. Habitat of *Rhothropus nivimontanus* **sp. nov.** at the type locality near Catchi village, on the highlands of Serra da Neve, Namibe Province. Photo by LMPC.

Conservation. *Rhothropus nivimontanus* **sp. nov.** is known only from three specimens and is apparently endemic to the Serra da Neve inselberg. Assuming that the species is homogeneously distributed throughout the inselberg, we estimated an extent of occurrence of approximately 630 km² using the GeoCAT Geospatial Conservation Assessment Tool (Bachman *et al.* 2011). Despite its remoteness, the landscape near human settlements is visibly transformed, with large deforested areas dedicated to agriculture or cattle pastures (Fig. 8; Marques *et al.* 2024a). Considering the apparent association of *R. nivimontanus* **sp. nov.** with arboreal habitats and riparian areas, it might become particularly vulnerable to deforestation, an alarming cause of habitat loss in the highlands of the Angolan Central Plateau (Mendelsohn 2019). Currently available data does not allow for an unambiguous assessment of the conservation status of *R. nivimontanus* **sp. nov.** While we recommend the status of Data Deficient for this species, further surveys targeted at Serra da Neve and other inselbergs in the region, and a formal conservation assessment are warranted, especially considering the susceptibility of montane species to climate change (Sinervo *et al.* 2010; Moreira *et al.* 2023).

Discussion

Southwestern Angola is a hotspot of diversity and endemism for reptiles, where climate interacts with the escarpment to create a heterogeneous landscape (Marques *et al.* 2018; Branch *et al.* 2019; Bauer *et al.* 2023; Huntley 2023). The description of *Rhothropus nivimontanus* **sp. nov.** raises the total number of recognized species in the genus to ten, and those occurring in Angola to eight, four of which are endemic. However, these numbers are expected to rise, as cryptic diversity linked to *Rhothropus barnardi* and *R. biporosus* is being formally described (Parrinha *et al.* in prep.). Additionally, *R. nivimontanus* **sp. nov.** represents the seventh endemic reptile described from Serra da Neve (Marques *et al.* 2018, 2024a).

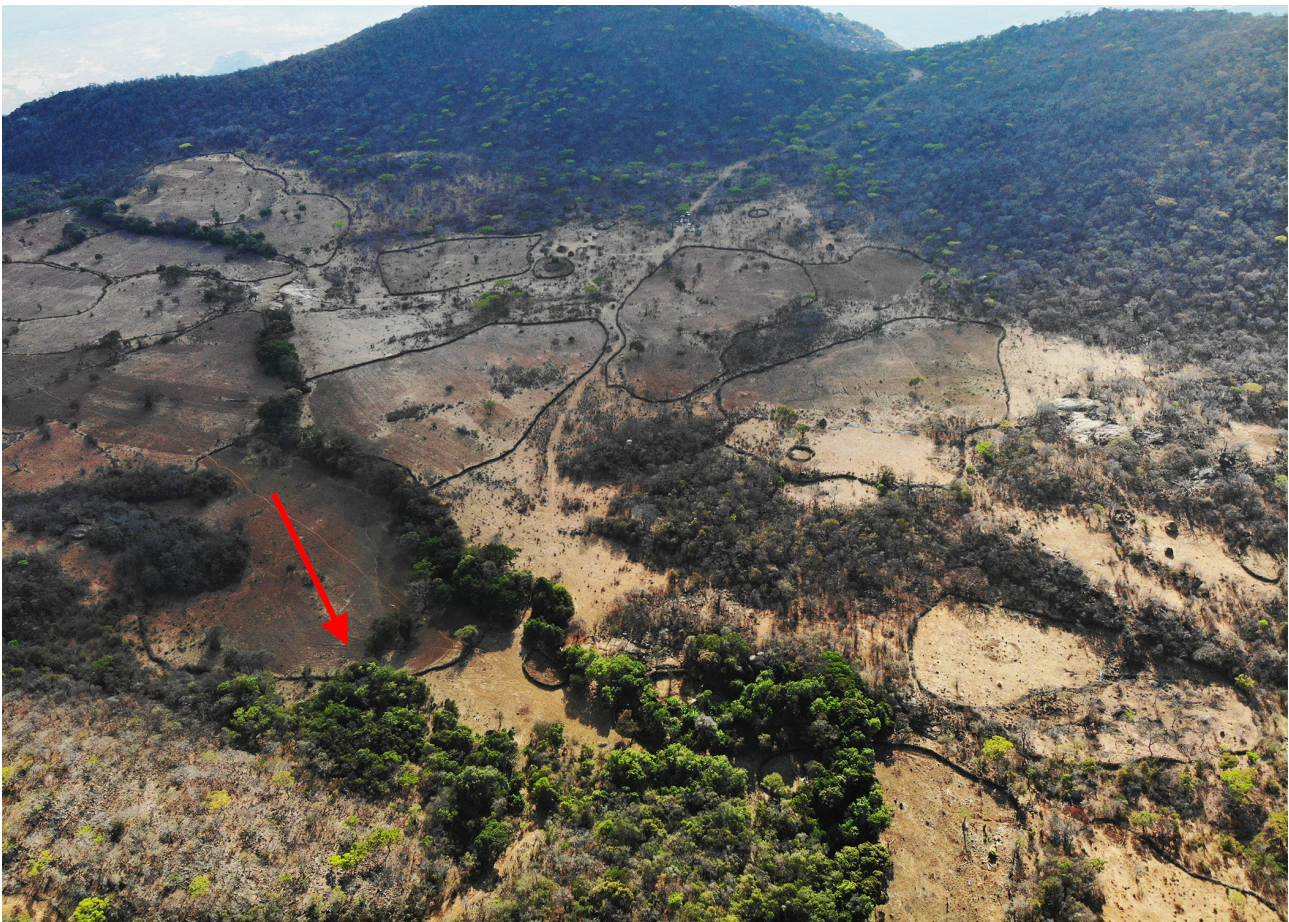


FIGURE 8. General view of Catchi village and plateau, with riparian gallery and type locality of *Rhoptropus nivimontanus* **sp. nov.** in foreground (red arrow). Photo by LMPC.

The discovery of *Rhoptropus nivimontanus* **sp. nov.** also contributes to our knowledge on the natural history of the genus. Although *Rhoptropus* are generally considered a group of arid adapted geckos from the xeric habitats of the Namib Desert, both *R. benguellensis* and *R. nivimontanus* **sp. nov.** occur in more mesic and densely vegetated areas associated with the escarpment, often in close proximity to flowing rivers. While most members of the genus are strictly rupicolous, *R. boultoni* is known to utilize Baobab trees as an alternative substrate even when similar sized boulders are present (*pers. obs.*). *Rhoptropus nivimontanus* **sp. nov.** seems to be the most arboreal member of the genus, an observation supported by the notorious lack of rock outcrops at the type locality.

Even though it is still poorly explored, the inselberg has been recognized for its herpetological diversity, with one amphibian (*Poyntonophrynus pachnodes* Ceriaco, Marques, Bandeira, Agarwal, Stanley, Heinicke, Blackburn & Bauer, 2018), one cordylid (*Cordylus phonolithos* Marques, Ceriaco, Stanley, Bandeira, Agarwal & Bauer, 2019), two gekkonids (*Lygodactylus baptistai* Marques, Ceriaco, Buehler, Bandeira, Janota & Bauer, 2020 and *Afroedura praedicta* Branch, Schmitz, Lobón-Rovira, Baptista, António & Conradie, 2021) and two scincids (*Acontias mukwando* Marques, Parrinha, Tiutenko, Lopes-Lima, Bauer & Ceriaco, 2023 and *Panaspis ericae* Marques, Parrinha, Lopes-Lima, Tiutenko, Bauer & Ceriaco, 2024) strictly endemic to Serra da Neve (Ceriaco *et al.* 2018; Marques *et al.* 2019, 2020, 2023, 2024b; Branch *et al.* 2021). With approximately one endemic species per 100 km², Serra da Neve makes an important contribution to the regional herpetological diversity of southwestern Angola being one of the most endemic-rich areas in southwestern Africa (Marques *et al.* 2024a).

The Serra da Neve inselberg is part of the Southern Escarpment as defined by Mendelsohn & Huntley (2023), extending from the “Coporolo River in Benguela Province to the Huab River in Namibia”. In contrast to the surrounding arid lowlands dominated by Mopane woodlands, the highlands of the inselberg are dominated by more mesic Miombo woodlands, similar to the vegetation found in the Central Escarpment and further inland in

the highlands of the Angolan Plateau (Huntley 2023; Mendelsohn & Huntley 2023; Marques *et al.* 2024a). This ecological isolation contributes to the high degree of endemism and biogeographic patterns observed in the inselberg fauna, with affinities to southern, central, and eastern Africa (Marques *et al.* 2024a). The phylogenetic placement of *Rhoptropus nivimontanus* **sp. nov.** as sister species to *R. montanus* is in line with patterns observed in other taxa, where the inselberg endemics are more closely related to species from the highlands of the Angolan Escarpment—as is the case of *Cordylus phonolithos* (Marques *et al.* 2019; Bates *et al.* 2023), or East African mountains—*Acontias mukwando* and *Lygodactylus baptistai* (Marques *et al.* 2020, 2023)—rather than to congeners from the surrounding arid lowlands. On the other hand, the occurrence of endemic species with central African affinities such as *Panaspis ericae* further reinforces the biogeographic importance of the inselberg (Marques *et al.* 2024b).

The Great Escarpment of Angola is a recognized hotspot of reptile diversity, particularly for rupicolous lizards, with several endemic species in different sections of the escarpment (Bauer *et al.* 2023; Conradie *et al.* 2023). Even though no formal conservation action has been taken to date, both Serra da Neve and the Humpata Plateau, among other areas of the escarpment, have been signaled as key areas for conservation due to the high diversity and endemism of herpetological taxa (Vaz Pinto *et al.* 2023; Marques *et al.* 2024a). Three species of Angolan *Rhoptropus* are closely associated with different sections of the escarpment as defined by Mendelsohn & Huntley (2023)—*R. montanus* from the Humpata Plateau in the Marginal Mountain Chain; *R. nivimontanus* **sp. nov.** from the Serra da Neve inselberg in the Southern Escarpment; and *R. benguellensis* on the Central Escarpment. Despite the morphological similarities and geographic association with the escarpment, *R. benguellensis* is not closely related to the more circumscribed montane endemics *R. montanus* and *R. nivimontanus* **sp. nov.**. The biogeographic and evolutionary significance of these findings can only be adequately contextualized in a comprehensive phylogeny of the genus *Rhoptropus* that also broadly samples populations in Namibia (Bauer *et al.* in prep.).

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