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A treasure trove of endemics: two new species of snake-eyed skinks of the genus *Panaspis* Cope, 1868 (Squamata, Scincidae) from the Serra da Neve Inselberg, southwestern Angola

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Abstract

Four species of the genus *Panaspis* – *P. cabindae*, *P. wahlbergii*, *P. maculicollis* and *P. mocamedensis* – are currently known from Angola. The analysis of recently collected specimens from Serra da Neve Inselberg, an isolated mountain located in northern Namibe Province, revealed unexpected taxonomic diversity in the group. Using an integrative taxonomy approach based on morphological and DNA sequence data, with both mitochondrial (16S) and nuclear (RAG-1) genes, we were able to distinguish two distinct populations, described here as two new species, *Panaspis ericae* **sp. nov.** and *P. mundavambo* **sp. nov.** Both species are assumed to be endemic to the inselberg. This reinforces our notion of southwestern Angola as a hotspot of skink diversity, and highlights the urgent need for the conservation of Serra da Neve.

Key Words

Reptiles, integrative taxonomy, Africa, herpetofauna, cryptic species

Introduction

African snake-eyed skinks of the genus *Panaspis* Cope, 1868, are represented in Angola by four different species: *Panaspis* aff. *breviceps* (Peters, 1873), in the escarpment areas of Kwanza Sul and Kwanza Norte provinces; *P. cabindae* (Bocage, 1866), extending from central Africa to the central highlands of Angola; *P. maculicollis* Jacobsen & Broadley, 2000, in the south-eastern province of Cuando-Cubango; *P. mocamedensis* Ceríaco, Heinicke, Parker, Marques & Bauer, 2020, in the southwestern province of Namibe; and *P. wahlbergii* (Smith, 1849), on the central plateau of Angola (Ceríaco et al. 2020). The systematic placement of the genus has been a matter of debate for decades (Fuhn 1969, 1972; Perret 1973, 1975; Greer 1974; Schmitz et al. 2005; Jesus et al. 2007), until the recent molecular phylogeny by Medina et al. (2016) provided a much-needed clarification. In the last decade, several new species of *Panaspis* have been described from sub-Saharan Africa: *P. thomensis* Ceríaco, Soares, Marques, Bastos-Silveira, Scheinberg, Harris, Brehm & Jesus, 2018, from São Tomé Island, in the Gulf of Guinea (Soares et al. 2018); *P. namibiana* Ceríaco, Branch & Bauer, 2018, from Central Namibia (Ceríaco et al. 2018a); *P. tsavoensis* Kilunda, Conradie, Wasonga, Jin, Peng, Murphy, Malonza & Che, 2019, from southern Kenya (Kilunda et al. 2019); *P. mocamedensis* from southwestern Angola (Ceríaco et al. 2020) and *P. annettesabinae* Colston, Pyron & Bauer, 2020 from central Ethiopia (Colston et al. 2020).

Despite this progress, further cryptic diversity awaiting formal description is expected in the genus. Such cryptic diversity has already been documented by Medina et al. (2016), and further field workers in biodiverse but poorly explored areas, and more are likely to be discovered. One such case deals with two putative new species we recently collected on the Serra da Neve Inselberg in northern Namibe Province, southwestern Angola. Serra da Neve is an isolated mountain of subvolcanic origin with a basal area of approximately 630 km^2 and is the second highest peak of Angola at 2489 m (Pereira 1977). Serra da Neve lies in what Mendelsohn and Huntley (2023) define as “the southern escarpment landscape”, an area ranging from the Coporolo River in Benguela Province, Angola, to the Huab River in Kunene Region, Namibia. The inselberg is covered by a Miombo forest habitat, contrasting with the surrounding lowland habitats, which are mainly dominated by Namibian woodland savanna and arid areas of Namib Desert (Grandvaux-Barbosa 1970). Recent fieldwork at Serra da Neve revealed an impressive number of strictly endemic species, such as a bufonid frog of the genus *Poyntonophrynus* (Ceríaco et al. 2018), three geckos (genera *Lygodactylus*, *Afroedura*, and *Rhoptropus*; Branch et al. 2020; Marques et al. 2020; Parrinha et al. 2024), one cordylid lizard of the genus *Cordylus* (Marques et al. 2019), and a legless skink of the genus *Acontias* (Marques et al. 2023a). Moreover, near or regional endemics also occur in the inselberg and its surroundings (Marques et al. 2024). Ceríaco et al. (2020) reported the presence of *P. cabindae* on the southern slopes of the inselberg, at the locality of Mamué (-13.8015, 13.1206). During a recent survey of the inselberg, several *Panaspis* specimens were collected both at the top of the mountain and in the surrounding lowlands. Some of these are representatives of two putative new species. Building on the data provided by Medina et al. (2016) and Ceríaco et al. (2020), we here provide an integrative approach to the revision of Serra da Neve’s *Panaspis* and describe two new taxa. Biogeographic and conservation considerations are also provided.

Materials and methods

Newly collected specimens were euthanized with MS-222 following standard practices (Simmons 2015), fixed in 10% buffered formalin in the field and subsequently transferred to 70% ethanol for long-term storage. Liver tissue was removed before formalin fixation and preserved in 95% ethanol. The specimens were deposited in the collections of the Museu Nacional de História Natural e da Ciência da Universidade de Lisboa, Lisboa, Portugal (**MUNHAC**). For mensural and meristic comparisons, we used the datasets presented by Ceríaco et al. (2018, 2020) which included Angolan and Namibian *Panaspis* specimens deposited in the collections at American Museum of Natural History (**AMNH**), New York, New York, USA; California Academy of Sciences (**CAS**), San Francisco, California, USA; Carnegie Museum of Natural History (**CM**), Pittsburgh, Pennsylvania, USA; Field Museum of Natural History (**FMNH**), Chicago, Illinois, USA; Museum for Comparative Zoology (**MCZ**), Harvard University, Cambridge, Massachusetts, USA; Florida Museum of Natural History (**FLMNH**), Gainsville, USA; Natural History Museum of Los Angeles County (**LACM**), Los Angeles, California, USA; University of Texas El-Paso Herpetological collection (**UTEP**), El-Paso, Texas, USA; Port Elizabeth Museum/Bayworld (**PEM**), Port Elizabeth, South Africa; Iziko South African Museum, Cape Town, South Africa (**SAM**); Ditsong National Museum of Natural History (**TM**), Pretoria, South Africa; National Museum of Namibia (formerly Staatsmusem Windhoek), Windhoek, Namibia (**SMW**); Instituto de Investigação Científica Tropical (**IICT**), Lisbon, Portugal; Museu de História Natural e da Ciência da Universidade do Porto (**MHNC-UP**), Porto, Portugal; Muséum national d’Histoire naturelle (**MNHN**), Paris, France; Naturhistorisches Museum (**NHMW**), Wien, Austria; Senckenberg Forschungsnstitut und Naturmuseum, Frankfurt am Main, Germany (**SMF**); and the Natural History Museum (**BMNH**), London, United Kingdom.

Molecular methods

DNA was extracted from tissue samples of newly collected specimens using the Spin Column Animal Genomic DNA Miniprep Kit from Biobasic (Markham, Ontario, Canada), following the manufacturer’s instructions. The mitochondrial 16S rRNA and the nuclear Recombination Activating Protein 1 (RAG1) genes were then amplified following Ceríaco et al. (2020) with the following primers 16S (16SA 5’-CGCCTGTTTATCAAAAACAT-3’; 16SB 5’-CCGGTCTGAACTCAGATCACGT-3’ Palumbi et al. 1996) and RAG1 (RAG1f700 5’-GGAGACATGGACACAATCCATCCTAC-3’; RAG1r700 5’-TTTGTACTGAGATGGATCTTTTTGCA-3’; Bauer et al. 2007). Briefly, genes were amplified in 25 µL PCRs, with an initial denaturing temperature of 95 °C for 2 min, followed by denaturation at 95 °C for 35 seconds (s), annealing at 50 °C for 35 s, and extension at 72 °C for 95 s with 4 s added to the extension per cycle for 32 or 34 cycles (for the mitochondrial or nuclear gene, respectively).The mitochondrial 16S rRNA and the nuclear Recombination Activating Protein 1 (RAG1) genes were then amplified and sequenced for subsequent phylogenetic analyses.

The successful amplifications underwent enzymatic purification and were then sequenced using the BigDye Terminator v3.1 Cycle sequencing protocol (Applied Biosystems, Waltham, MA, USA) with an automated Sequencer ABI3500xl Genetic Analyzer at the Centre for Molecular Analysis (CTM) in the Research Centre in Biodiversity and Genetic Resources (CIBIO), Vairão, Portugal. Two datasets, 16S and RAG1, were created using MAFFT software (version 7.304, Katoh and Standley 2013), which included newly sequenced individuals (refer to Table 1 for GenBank Accession numbers) and all previously available sequences of the same genes from Medina et al. (2016) and Ceriaco et al. (2020). The 16S and RAG1 datasets were then concatenated into a single dataset with 1,319 nucleotides (nt) (16S = 671 nt; RAG1 = 648 nt) for phylogenetic analyses. The outgroup used was a combination of those employed by Medina et al. (2016) and Ceriaco et al. (2020) (Table 1). Each partition was tested for substitution saturation using DAMBE 7 (Xia 2018) following the method of Xia et al. (2003). Little saturation was found, even under the assumption of an asymmetric tree ($p < 0.001$). Incongruence Length Difference (ILD) tests were conducted to investigate incongruence between the two concatenated genes (Farris et al. 1994). The tests showed no significant phylogenetic conflict between the 16S and RAG1 ($p = 0.95$). Pairwise sequence divergences (uncorrected *p*-distance) of 16S sequences were calculated using MEGA X. Phylogenies were estimated using Maximum Likelihood (ML) and Bayesian Inference (BI) methods in IQ-TREE v. 2.2.0 (Minh et al. 2020) and Mr Bayes v. 3.2.7a (Ronquist et al. 2012), respectively. The best-fitting nucleotide substitution models for each partition of the subsequent analyses were selected using JModelTest 2.1.10 (Darriba et al. 2012) under the corrected Akaike Information Criterion. The dataset was partitioned by gene and run using the GTR + I + G model for the 16S and GTR + G for the RAG1 partitions. BI analyses were performed using program-generated trees and four Markov chains with default incremental heating. Two independent runs of 15×10^6 generations were sampled at 1,000-generation intervals, resulting in a total of 15,000 trees. A burn-in of 10% was determined by assessing the convergence of log-likelihood and parameter values using Tracer v. 1.7.1 (Rambaut et al. 2018). Phylogenetic analyses were conducted for ML. An initial tree search was followed by 10 independent runs and 10,000 ultrafast bootstrap replicates. Maximum likelihood trees were constructed also for the RAG1 and 16S datasets alone, using IQ-TREE the same parameters as above. The haplotype network reconstruction of the RAG1 dataset was conducted in TCS 1.21 (Clement et al. 2000) with a statistical parsimony limit of 95%.

Morphological methods

Specimens were measured with a digital caliper to the nearest 0.1 mm. Lepidosis was examined under a stereo-microscope. Scale nomenclature, scale counts and measurements used in the description follow Broadley (2000), Jacobsen and Broadley (2000), Soares et al. (2018) and Ceríaco et al. (2018, 2020). We measured the following 23 characters: snout–vent length (SVL), from snout to vent; tail length (TL), from anal plate to tip of tail, measured only in specimens with complete original tails; head length (HL), from tip of snout to anterior tympanum border; head height (HH), from the base of the maxilla to top of head; head width (HW), at the widest part of the maxilla; eye-diameter (ED); eye-tympanum distance (ET); eye-snout distance (ES), from the front of the eye to the tip of the snout; length of the arm (LA); length of the forearm (LFA); length of the leg (LL); length of the foreleg (LFL); distance between limbs (LD), minimum distance between the insertion of the anterior and posterior limbs; number of scale rows at midbody (MSR); number of paravertebral scales (SAD), from the nuchal (excluded from count) to base of the tail; number of scales ventrally (SAV), from the mental (excluded from count) to the anal plate (excluded); number of subdigital scales under Finger-IV (LUFF); number of subdigital scales under Toe-IV (LUFT); number of supralabials (SL), with those widened in subocular position indicated between brackets; number of supraciliaries (SC); nature of contact between parietals (CP); nature of contact between frontoparietals (CFP); nature of contact between prefrontals (CPF); nature of contact between prefrontal and preoculars (CPF/PO). Finally, coloration pattern was reported, and high-resolution photographs of preserved specimens taken. These data were compared with relevant literature on the group (Perret 1973, 1975; Jacobsen and Broadley 2000; Ceríaco et al. 2018a, 2020; Soares et al. 2018; Colston et al. 2020) and comparative material of congeners occurring in Angola and Nambia, namely *P. cabindae*, *P. wahlbergii*, *P. maculicollis*, *P. mocamedensis* and *P. namibiana*. All new specimens examined in this study are listed in the type and additional material sections of each species' taxonomic account. Locality data are reported in the form of decimal degrees and use the WGS 84 map datum. Older (non-GPS) records are mostly derived from Marques et al. (2018) and have been georeferenced using GEOLocate web application (https://www.geo-locate.org). Elevations are all reported as meters above sea level.

Species concept

We adopt de Queiroz (1999) General Lineage Concept (GLC) which defines a species as a single, independent metapopulation lineage, diagnosable by multiple lines of evidence/criteria suggesting evolutionary independence. In order to fullfill the criteria of the GLC, we adopted an congruent integrative approach (*sensu* Padial et al. 2010) combining the results of the above mentioned mtDNA, nuclear DNA and morphological characters.

Table 1. Specimens used for genetic analysis and corresponding GenBank accession numbers for genes used in the study. See Materials and Methods section for collection abbreviations. Institution and field number acronyms not cited in the Material and Methods were retrieved from Medina et al. (2016) suppl. material.

Species	**Collection number**	**Field number**	**Locality**	**Genbank**	
				16S	**RAG1**
Panaspis annettesabinae	ZMNH H2019,2176	TJC264	ETHIOPIA: Oromia Region, 8 km SW of Bedele on the Metu-Bedele rd, Buno Bedele zone	KU23675	–
Panaspis africanus	MUNHAC/MB03-001133	UMRTGGPR-698 / PR357	SÃO TOMÉ AND PRÍNCIPE: Príncipe Island, Montalegre	EU164475	DQ675337
Panaspis breviceps	ZFMK 87662	MM 105	CAMEROON: Mawne	KU236786	KU298714
Panaspis breviceps	ZFMK 87663	MM 106	CAMEROON: Mawne	KU236787	KU298715
Panaspis cabindae	PEM R19467	ANG 21	ANGOLA: Lunda Norte Prov., Lagoa Carumbo	KU236741	KU298690
Panaspis cabindae	Uncatalogued	PM 049	DRC: Luango-Nzambi, Bas-Congo	KU236750	KU298697
Panaspis cabindae	Uncatalogued	PM 050	DRC: Luango-Nzambi, Bas-Congo	KU236751	KU298698
Panaspis cabindae	PEM R21594	WRB 810	ANGOLA: Bengo Prov., Riverine Forest, Bengo	KU236765	KU298705
Panaspis cabindae	PEM R20256	WRB 804	ANGOLA: Zaire Prov., Soyo	KU236768	KU298708
Panaspis cabindae	CAS 263553	AMB 10315	ANGOLA: Namibe Prov., Mamué	MN846689	MN850709
Panaspis cabindae	FLMNH 187242	–	ANGOLA: Namibe Prov., Mamué	MN846690	MN850710
Panaspis cabindae	MUNHAC/MB03-001088	–	ANGOLA: Malanje Prov., Laúca Dam	MN846698	MN850711
Panaspis cabindae	MUNHAC/MB03-001091	–	ANGOLA: Malanje Prov., Laúca Dam	MN846699	MN850712
Panaspis ericae **sp. nov.**	MUNHAC/MB03-001525	LMPC 3209	ANGOLA: Namibe Prov. Serra da Neve, Catchi	PP810194	PP816726
Panaspis ericae **sp. nov.**	MUNHAC/MB03-001526	LMPC 3210	ANGOLA: Namibe Prov. Serra da Neve, Catchi	PP810195	PP816727
Panaspis ericae **sp. nov.**	MUNHAC/MB03-001528	LMPC 3275	ANGOLA: Namibe Prov. Serra da Neve, Catchi, base camp headquarters	PP810196	PP816728
Panaspis ericae **sp. nov.**	MUNHAC/MB03-001529	LMPC 3282	ANGOLA: Namibe Prov. Serra da Neve base, 2 km N of Maylowe	PP810197	PP816729
Panaspis ericae **sp. nov.**	MUNHAC/MB03-001530	LMPC 3354	ANGOLA: Namibe Prov. Serra da Neve base, 2 km N of Maylowe	PP810198	PP816730
Panaspis ericae **sp. nov.**	MUNHAC/MB03-001531	LMPC 3355	ANGOLA: Namibe Prov. Serra da Neve base, 2 km N of Maylowe	PP810199	PP816731
Panaspis ericae **sp. nov.**	MUNHAC/MB03-001534	LMPC 3395	ANGOLA: Namibe Prov. Serra da Neve base, 2 km N of Maylowe	PP810200	PP816732
Panaspis sp. Katanga 1	UTEP 21175	ELI 295	DRC: Katanga, Mulongo	KU236729	KU298685
Panaspis sp. Katanga 1	UTEP 21174	ELI 294	DRC: Katanga, Mulongo	KU236730	KU298686
Panaspis sp. Katanga 2	–	JHK 26	DRC: Katanga, Kisanfu Camp	KU236726	KU298682
Panaspis sp. Katanga 2	PEM R17454	WRB 575	DRC: S Katanga, Kalakundi Copper Mine	KU236736	KU298689
Panaspis sp. Katanga 2	–	WRBNimb083	ZAMBIA: NW Zambia	KU236742	KU298691
Panaspis sp. Limpopo	–	MCZ-A 27176	SOUTH AFRICA: Limpopo Prov., Hoedspruit	KU236743	KU298692
Panaspis maculicollis	CAS 234099	MCZF 38733	SOUTH AFRICA: Limpopo Prov., Farm Vrienden	KU236720	KU298678
Panaspis maculicollis	CAS 234188	MCZF 38848	SOUTH AFRICA: Limpopo Prov., Farm Nooitgedacht	KU236728	KU298684
Panaspis maculicollis	CAS 234135	MCZF 38790	SOUTH AFRICA: Limpopo Prov., Farm Vrienden	KU236747	KU298694
Panaspis maculicollis	Uncatalogued	MBUR 02843	SOUTH AFRICA: Limpopo Prov., Phalaborwa	KU236748	KU298695
Panaspis maculicollis	Uncatalogued	MBUR 02848	SOUTH AFRICA: Limpopo Prov., Phalaborwa	KU236749	KU298696
Panaspis maculicollis	PEM R20475	ANG 421	ANGOLA: Cuando Cubango Prov., Benero Campsite, near Jamba	KU236770	KU298711
Panaspis mocamedensis	MUNHAC/MB03-001532	LMPC 3381	ANGOLA: Namibe Prov. Serra da Neve base, 2 km N of Maylowe	PP810201	PP816733
Panaspis mocamedensis	MUNHAC/MB03-001533	LMPC 3382	ANGOLA: Namibe Prov. Serra da Neve base, 2 km N of Maylowe	PP810202	PP816734
Panaspis mundavambo **sp. nov.**	MUNHAC/MB03-001527	LMPC 3242	ANGOLA: Namibe Prov. Serra da Neve, near Catchi, MPLA cabin	PP810203	PP816735
Panaspis sp. Malawi	PEM R20247	WRB 568	MALAWI: Mt. Mulanje, Sombani Trail	KU236732	KU298687
Panaspis sp. Mozambique 1	–	SVN 693	MOZAMBIQUE: Gorongosa National Park	KU236754	KU298699
Panaspis sp. Mozambique 1	PEM R20561	WC 1251	MOZAMBIQUE: Sofala Prov, Chemba, Ecofarm	KU236764	KU298704
Panaspis sp. Mozambique 1	PEM R20591	WRB 886	MOZAMBIQUE: Tete Prov., Ruoni Hill S	KU236769	KU298710
Panaspis sp. Mozambique 4	PEM R20569	WRB 855	MOZAMBIQUE: Cabo Delgado Prov., Balama, Syran graphite mine	KU236766	KU298706
Panaspis sp. Mozambique 4	PEM R20576	WRB 856	MOZAMBIQUE: Cabo Delgado Prov., Balama, Syran graphite mine	KU236767	KU298707
Panaspis namibiana	MCZ R183767	AMB 7634	NAMIBIA: Sesfontein	KU236727	KU298683
Panaspis sp. Tanzania 1	–	WRB 0026	TANZANIA: Arusha	KU236718	KU298676
Panaspis sp. Tanzania 1	–	WRB 0021	TANZANIA: Arusha	KU236719	KU298677
Panaspis sp. Tanzania 2	PEM R20799	WRB 573	TANZANIA: Serengeti, Klein’s Camp	KU236735	KU298688
Panaspis togoensis	TCWC 94557	TJH 2629	BENIN: Dogo Forest	KU236758	KU298701
Panaspis wahlbergii	CAS 234209	MCZF 38868	SOUTH AFRICA: Limpopo Prov.	KU236721	KU298679
Panaspis wahlbergii	MCZ R184443	AMB 8293	SOUTH AFRICA: Limpopo Prov.	KU236722	KU298680
Panaspis wahlbergii	CAS 234194	MCZF 38852	SOUTH AFRICA: Limpopo Prov.	KU236724	KU298681
Panaspis wahlbergii	TM 84299	–	SOUTH AFRICA: Limpopo, Groblersdal	KU236746	KU298693
Panaspis wahlbergii	NMB R10286	SVN 742	MOZAMBIQUE: Sofala Prov., Beira	KU236755	KU298700
Panaspis wahlbergii	TCWC 95563	TJH 3213	SOUTH AFRICA: Northern Cape, Kimberley	KU236759	KU298702
Panaspis wahlbergii	TCWC 95588	TJH 3253	SOUTH AFRICA: Northern Cape, Kimberley	KU236760	KU298703
Panaspis wahlbergii	PEM R21298	WC 2721	SOUTH AFRICA: Mpumalanga, Doornkop Reserve	KU236781	KU298712
Panaspis wahlbergii	PEM R21297	WC 2723	SOUTH AFRICA: Mpumalanga, Doornkop Reserve	KU236782	KU298713
Outgroup					
Broadleysaurus major	–	–	–	AJ416922	HM161157
Cordylus marunguensis	UTEP 20374	EBG 2993	DRC: Katanga, Pepa	JQ389803	KU298675
Lacertaspis gemmiventris	CAS 207858	RCD 13255	EQUATORIAL GUINEA: Bioko Island	KU236792	KU298719
Lacertaspis gemmiventris	CAS 207854	RCD 13251	EQUATORIAL GUINEA: Bioko Island	KU236793	KU298720
Lacertaspis rohdei	ZFMK 75382	–	CAMEROON: Mt. Nlonako	KU236790	KU298717
Leptosiaphos blochmanni	UTEP 21177	EBG 1610	DRC: South Kivu, Bichaka	KU236798	KU298722
Leptosiaphos koutoui	MNHN 2001.0697	–	CAMEROON: Meiganga, Adamaoua Plateau	KU236789	KU298716
Leptosiaphos sp.	ZFMK 75381	–	CAMEROON: Mt. Nlonako	KU236791	KU298718
Leptosiaphos sp.	ZFMK 69552	–	CAMEROON: Mt. Nlonako	KU236794	KU298721
Mochlus afer	ZFMK 54317	E56.17	KENYA: Kiyawetanga	KU705386	KU841442
Plestiodon inexpectatus	KU 8232	–	–	AY217990	AY662632
Trachylepis sulcata	ZFMK 66424	–	NAMIBIA: Kaokoland Region, Ongongo waterfall	KC345403	HQ829808
Typhlosaurus braini	CAS 214581	AMB 6340	NAMIBIA: Erongo Region, Rooibank	HQ180025	HQ180106
Typhlosaurus braini	CAS 214579	AMB 6338	NAMIBIA: Erongo Region, Rooibank	HQ180128	HQ180137

Results

Serra da Neve *Panaspis* included in our phylogenetic analysis belong to four mitochondrial and nuclear lineages, of which two are attributable to already known species, while the other two are not (Fig. 1). Serra da Neve representatives of *P. cabindae* were previously included in the dataset of Ceríaco et al. (2020). Besides *P. cabindae*, our analysis provides genetic verification for three other species of *Panaspis* at the Serra da Neve inselberg. Of these additional species, two specimens (MUNHAC/MB03-001532, 001533) from the base of Serra da Neve, near the village of Maylowe (-13.8280, 13.2625) unambiguously represent *P. mocamedensis*; six other specimens, morphologically very similar to *P. cabindae* and collected both near Maylowe (MUNHAC/MB03-001529, 001530, 001531, 001534; Fig. 2) and at the top of the inselberg, near Catchi village (MUNHAC/MB03-001525, 001526, 001528) are phylogenetically related to the clade containing *P. cabindae* and the Gulf of Guinea insular species; and a third form, represented by a single specimen (MUNHAC/MB03-001527) collected in riverine area near Catchi (-13.7618, 13.2514), phylogenetically is sister to *P. annettesabinae* from Ethiopia. Serra da Neve samples are genetically distinct, displaying respectively 5.3% and 2.9% pairwise 16S sequence divergence from their closest relatives (Table 2).

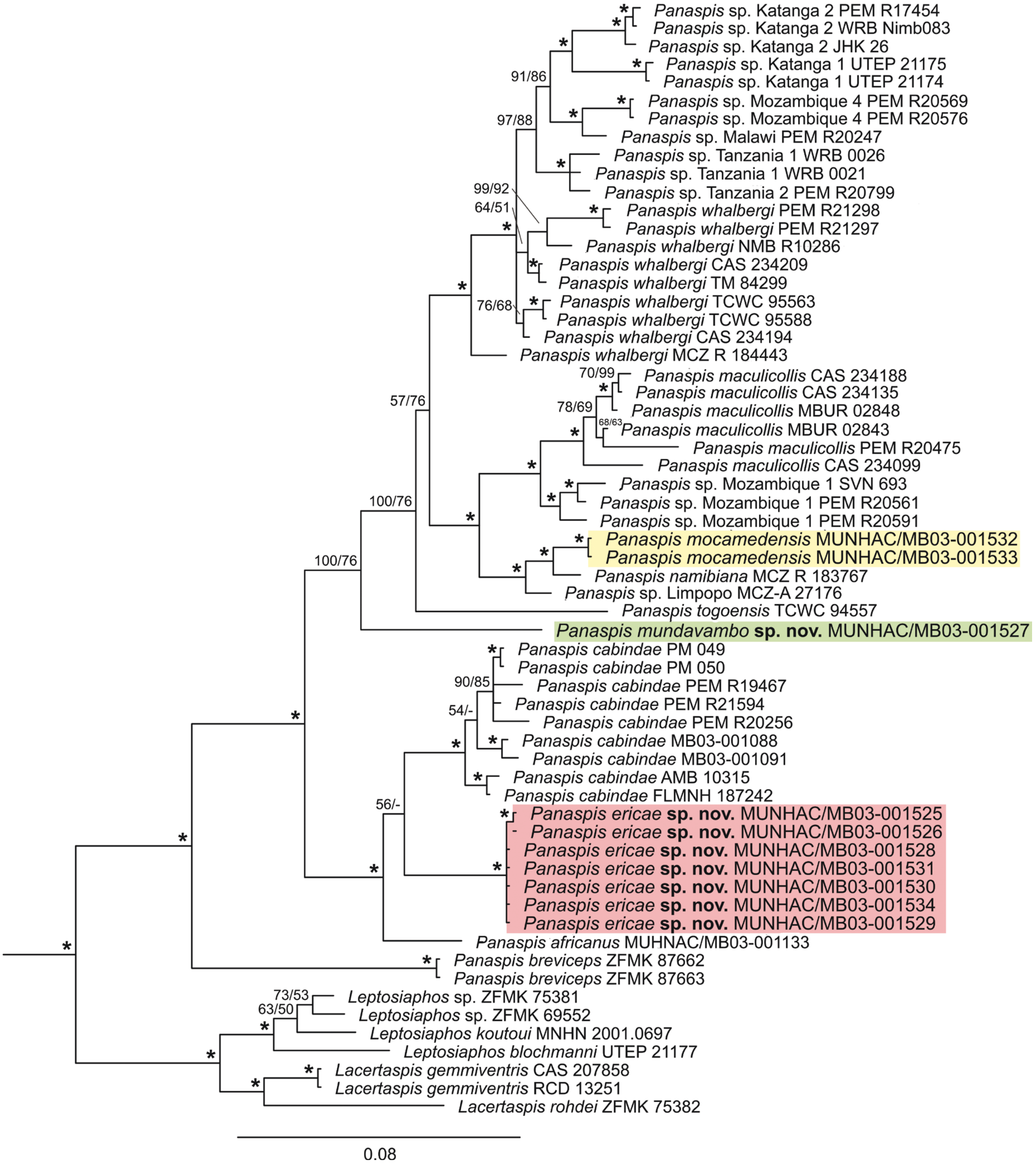

Figure 1. Bayesian Inference (BI) phylogenetic tree inferred from the concatenated 16S and RAG1 dataset. Support values above the branches are BI per cent posterior probabilities/ Maximum Likelihood ultrafast bootstraps. Support values > 0.95 for both phylogenetic analyses are indicated by an asterisk. The most divergent external outgroup sequences were deleted for clarity.

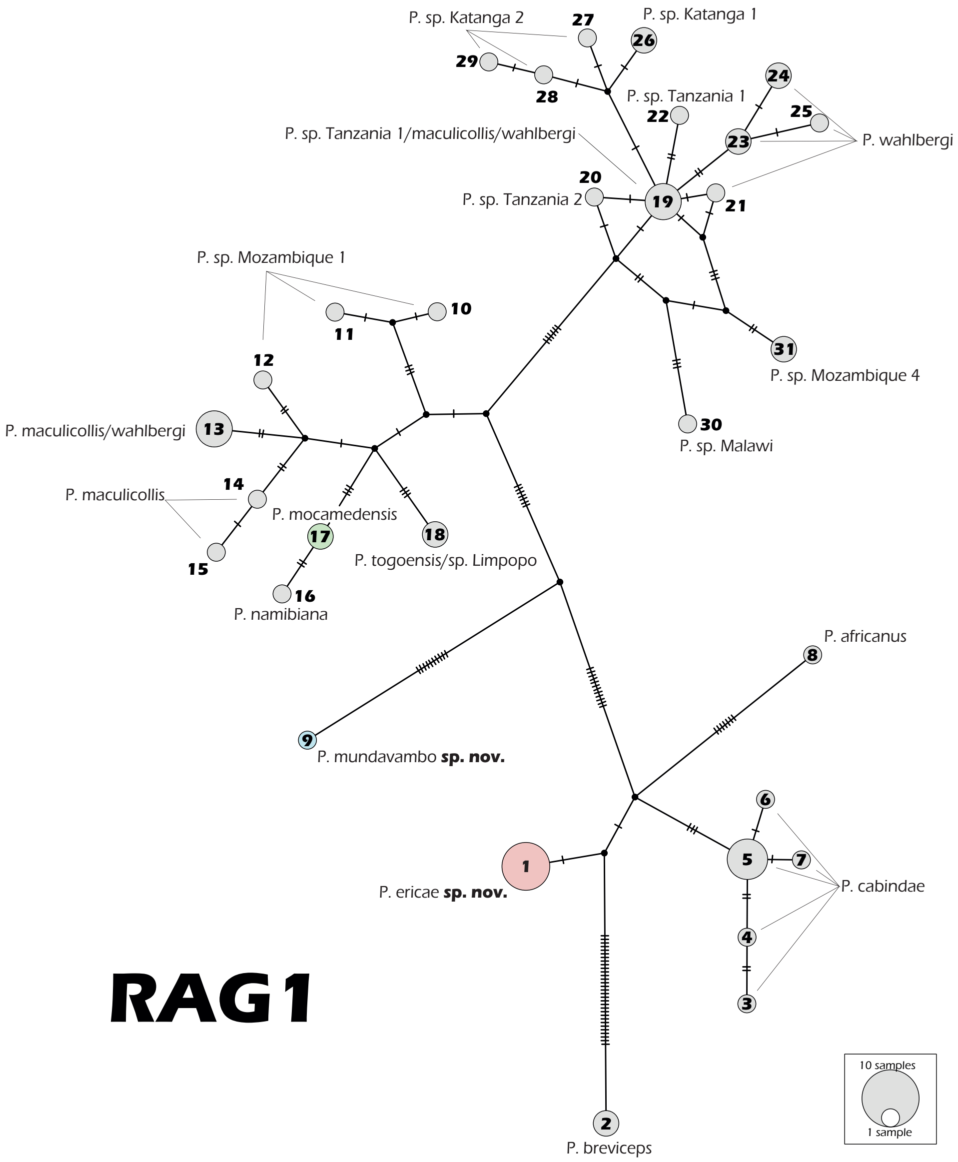

Figure 2. RAG1 haplotype (TCS) network showing the relationships of all *Panaspis* sequences (see Appendix 1). Circle size is proportional to observed haplotype frequencies, each dash indicates a nucleotide substitution. Coloured circles represent newly sequenced species.

Table 2. Uncorrected *p*-distance of the 16S RNA gene fragment between *Panaspis* taxa and respective nearest neighbour.

Taxon	Mean *p*-distance (16S) % (nearest neighbour)
Panaspis mocamedensis	**2.1** (*Panaspis* sp. Namibia)
Panaspis ericae **sp. nov.**	**5.3** (*Panaspis cabindae*)
Panaspis mundavambo **sp. nov.**	**2.9** (*Panaspis annettesabinae*)
Panaspis africanus	**4.5** (*Panaspis cabindae*)
Panaspis breviceps	**6.0** (*Panaspis togoensis*)
Panaspis cabindae	**4.5** (*Panaspis africanus*)
Panaspis sp. Katanga 1	**3.8** (*Panaspis* sp. Malawi)
Panaspis sp. Katanga 2	**3.7** (*Panaspis* sp. Malawi)
Panaspis sp. Limpopo	**1.2** (*Panaspis* sp. Namibia)
Panaspis maculicollis	**3.3** (*Panaspis* sp. Mozambique 1)
Panaspis sp. Malawi	**1.9** (*Panaspis* sp. Mozambique 4)
Panaspis sp. Mozambique 1	**3.3** (*Panaspis maculicollis*)
Panaspis sp. Mozambique 4	**1.9** (*Panaspis* sp. Malawi)
Panaspis namibiana Namibia	**1.2** (*Panaspis* sp. Limpopo)
Panaspis sp. Tanzania 1	**0.7** (*Panaspis* sp. Tanzania 2)
Panaspis sp. Tanzania 2	**0.7** (*Panaspis* sp. Tanzania 1)
Panaspis togoensis	**6.0** (*Panaspis breviceps*)
Panaspis wahlbergii	**2.6** (*Panaspis* sp. Malawi)

These values fall within the usual recognized species-level divergence for the genus (Ceríaco et al. 2020). The haplotype network of RAG1 shows a significant divergence between the newly described and previously sequenced species. Additionally, while some *Panaspis* species, namely *P. maculicollis*, *P. wahlbergii*, and *Panaspis* Tanzania 1, share haplotypes, the newly sequenced species do not have any common haplotypes with other species (Fig. 2).

The four taxa of *Panaspis* occurring in the Serra da Neve Inselberg differ from each other and other Angolan and African species in several consistent morphological characters. Mensural and meristic data for the studied species are presented in Table 3. A combination of molecular and morphological data allows us to recognize the existence of four species of *Panaspis* in the Serra da Neve inselberg, two of which are here described as new species. Detailed diagnoses for the two new species are given in the taxonomic accounts below.

Table 3. Comparison between the different species of *Panaspis* occurring in Angola and neighboring Namibia. Data from Jacobsen and Broadley (2000), Ceríaco et al. (2018, 2020) and this paper.

	***Panaspis* aff. *breviceps* (*n* = 3) (data from Ceríaco et al. (2020))**	***Panaspis cabindae* (*n* = 44) (data from Ceríaco et al. (2020))**	***Panaspis maculicollis* (data from Jacobsen and Broadley 2000 – non-Angolan material)**	***Panaspis wahlbergii* (*n* = 4) (data from Ceríaco et al. (2020))**	***Panaspis mocamedensis* (*n* = 6) (data from Ceríaco et al. (2020) and the two specimens collected from this study**	***Panaspis namibiana* (*n* = 11) (data from Ceríaco et al. (2018a) – Namibian material)**	***Panaspis mundavambo* sp. nov. (*n* = 1)**	***Panaspis ericae* sp. nov. (*n* = 6)**
Maximum SVL	56.9 mm	38.4 mm	43 mm	38.7 mm	36.7 mm	42.6 mm	35.8	35.2
Maximum TL	-	51.6 mm	-	39 mm	39.3 mm	55.7 mm	51.7	44.8
Condition of the eye	Movable lower eyelids	Pre-ablepharine	Ablepharine	Ablepharine	Ablepharine	Ablepharine	Ablepharine	Pre-ablepharine
Presence of supranasals	Yes	Yes	No	No	No	No	No	Yes
Scales across Venter	52–61	53–62	-	56–62	56–61	56–67	54	55–60
Midbody Scale Rows	32–34	23–26	22–28	25–26	23–24	22–26	24	23–26
Scales across Dorsum	56–61	54–62	-	56–61	56–60	57–68	53	53–58
Lamellae under 4th finger	9–10	7–11	-	9–10	9–10	8–12	8	8–10
Lamellae under 4th finger	12–13	13–17	13–17	13–16	14–16	13–16	13	13–15
Frontoparietal scales condition	Separated, but in median contact	Separated, but in median contact	Fused	Fused	Fused	Fused	Fused	Separated, but in median contact
Presence of a white ventrolateral stripe	no	no	no	yes	no	no	no	no

Systematic accounts

Panaspis ericae sp. nov.

https://zoobank.org/DF1D1955-945C-44BF-B4FB-5E33548C9EEF

Figs 3–8

Remarks. This new species belongs to the clade containing both *P. cabindae* and the Gulf of Guinea Oceanic Island taxa, *P. africanus*, *P. thomensis* and *P. annobonensis*. The phylogenetic relationship between *P. cabindae* and the island taxa had already been highlighted by Medina et al. (2016), Soares et al. (2018) and Ceríaco et al. (2020). The discovery of an additional taxa belonging to this Central-African clade is interesting, especially in the biogeographic context of the Serra da Neve inselberg. While most of the taxa occurring in the inselberg and its surroundings belong to here called "southern African" clades, the presence of other Central African associated species such as *P. cabindae* and *Bitis gabonica* (Marques et al. 2024) denotes a past connectivity between Serra da Neve and the north-south humid/highland corridors that allow taxa from Central Africa to expand to southern regions such as Namibe Province.

Figure 3. Live photo of the holotype of *Panaspis ericae* sp. nov. (MUNHAC/MB03-001525) from vicinity of Catchi, Serra da Neve. Photo by Arthur Tiutenko.

Type materials. ***Holotype.*** MUNHAC/MB03-001525 (field number LMPC 3209; Fig. 3), unsexed adult, from the rock outcrops near Catchi, Serra da Neve (-13.7653, 13.2571, 1645 m), Namibe Province, Republic of Angola, collected by Mariana P. Marques, Diogo Parrinha, Arthur Tiutenko and Luis M.P. Ceríaco on 29 October 2022.

Paratypes. MUNHAC/MB03-001526 (field number LMPC 3210), same data as holotype; MUNHAC/MB03-001528 (field number LMPC 3275) from the basecamp near Catchi (-13.7627, 13.2562, 1597 m), Namibe Province, Republic of Angola, collected on 1 November 2022; MUNHAC/MB03-001529 - 001531 (field numbers LMPC 3282, 3354, 3355; Fig. 4) from 2 km N of Maylowe, near a dry riverbed (-13.8265, 13.2601, 720 m), Namibe Province, Republic of Angola, collected between 3 and 5 November 2022. All specimens were collected by the same collectors as the holotype.

Additional material. 2 km N of Maylowe, near dry riverbed [-13.8265, 13.2601, 720 m] (MUNHAC/MB03-001534).

Diagnosis. *Panaspis ericae* sp. nov. can be distinguished from other member of the genus by the following combination of characteristics: 1) presence of supranasals; 2) pre-ablepharine eye (as defined by Greer 1974); 3) frontoparietals not fused, in broad contact with each other; 4) dorsum coppery-brown, with a dorsolateral light stripe extending to tail, followed by dark brown flanks; 5) absence of dark spots on middorsal region; 5) absence of rows of light spots on the neck; 6) absence of a white ventrolateral stripe; 7) 23 to 26 midbody scales rows.

Figure 4. Live photo of the paratype of *Panaspis ericae* sp. nov. (MUNHAC/MB03-001531) from vicinity of Maylowe, Serra da Neve. Photo by Arthur Tiutenko.

Figure 5. Preserved holotype of *Panaspis ericae* sp. nov. (MUNHAC/MB03-001525). Photos by Diogo Parrinha.

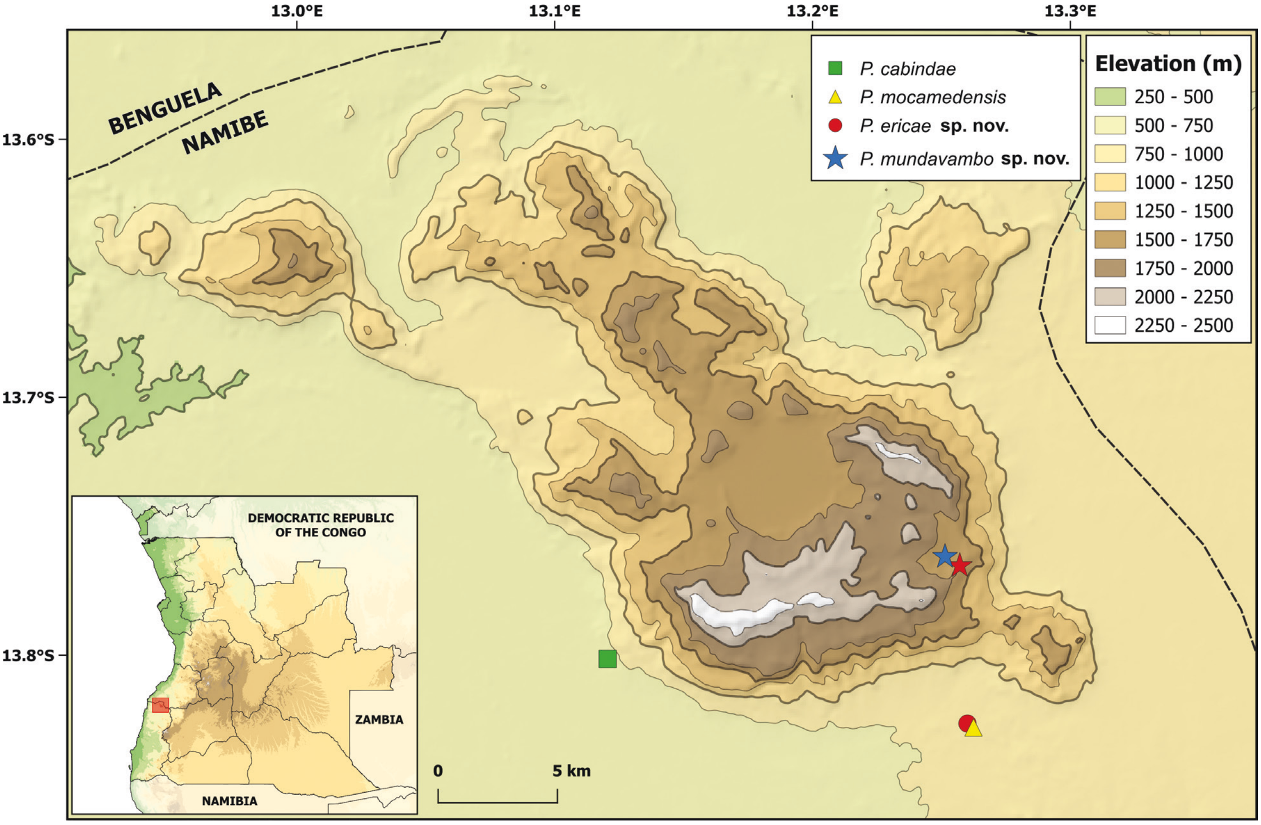

Figure 6. Topographic map of the Serra da Neve Inselberg with collection localities of *Panaspis* species in the region. Stars represent the type localities of the newly described species.

Figure 7. Miombo woodlands near the type locality of *P. ericae* sp. nov., in Catchi, Serra da Neve. Photo by Arthur Tiutenko.

Figure 8. Dry riverbed in mopane woodlands and its associated leaflitter in the base of Serra da Neve, near Maylowe, where some of the paratypes of *Panaspis ericae* sp. nov., were collected. Photo by Arthur Tiutenko.

Description of the holotype. Unsexed adult in good condition. Arrangement and relative size of head, body and tail scalation typical for *Panaspis*. Robust, cylindrical body with well-developed pentadactyl limbs. Fore- and hind-limbs do not overlap when adpressed against the body. SVL 32.6 mm, TL 44.8 mm. Head length 6.1 mm, with relatively acuminate snout (HL 148% HW). Other relevant measurements are presented in Table 4. Rostral wider than high, and visible from above. Nasals widely separated behind rostral by frontonasal. Frontonasal flat anteriorly, wider than long. Nostrils small, set posteriorly in the nasals bordering the postnasal; supranasals present. Prefrontals separated from each other, contacting loreals, first supraciliary, first supraocular, frontonasal and frontal. Two loreals, subequal in size; two preoculars, inferior slightly larger. Frontal length shorter than distance between anterior tip of frontal and tip of snout; frontal in contact with prefrontals and frontonasal anteriorly, and with first supraoculars and frontoparietals posteriorly. Frontoparietals fused, in contact with each other, the frontal, supraoculars, parietals and interparietal. Frontoparietal plus interparietal length about 1.5 times the length of the frontal. Interparietal diamond shaped, posterior edge more acuminate, with visible parietal foramen in the center; parietals about the same width as that of the frontoparietals and contacting each other behind interparietal. A pair of large, broad nuchals collectively bordered by a total of eight dorsals. Supraoculars three. Supraciliaries four (left side) and five (right side), first higher than broad, last wider than high. Pretemporals two. Tympanum visible, ear opening wider than high, approximately one-fourth the height of the eye. Supralabials seven, the fifth being the subocular. Pre-ablepharine eye. Infralabials six. Postmental bordering seven scales (mental, two primary chin-shields, and two infralabials on each side). Ventral scales smooth. MSR 25, SAD 57, SAV 58. Scales on palms and soles smooth. Relative length of digits of manus III>IV>II>VI>I; relative length of digits of pes IV>III>II=V>I; tips missing on digits III of right pes, II of left pes, and digit 4 of right manus. LUFF 10 (left side); LUFT 14 (right and left side). Tail long, robust and tapering smoothly.

In preservative, dorsal aspect of head, dorsum and tail coppery brown; tail slightly lighter. A light dorsolateral stripe runs from posterior edge of eye through tail (becoming mostly indistinct on distal half of tail), bordered below by a thin black line. Flanks, face and sides of tail uniformly dark to greyish brown, slightly lighter on tail. Labials greyish white, with dark spots. Scales individually stippled with black, especially on top of head; some irregularly scattered dark spots on head and tail, but not on flanks or middorsal region. Ventrum greyish white; underside of tail creamy white.

Variation. Variaton in scalation and body measurements of the type series of *Panaspis ericae* sp. nov. is reported in Table 4. The majority of the paratypes agree entirely with the holotype, with few minor variations. In MUNHAC/MB03-001528 the prefrontals are in single point contact instead of separated. Paratype MUNHAC/MB03-001529 has an intrusive scale between parietals and nuchals. All paratypes generally agree with the holotype in terms of coloration.

Comparison with other Southwestern African Panaspis and related forms. As the molecular data provide evidence of the independence of the *P. ericae* sp. nov. lineage from all other taxa, we here restrict our morphological comparisons to those named congeners occurring in Namibia and Angola and its sister taxa from the Gulf of Guinea Oceanic Islands (*P. africanus*, *P. thomensis* and *P. annobonensis*). *P. ericae* sp. nov. can immediately be distinguished from *P. maculicollis*, *P. wahlbergii*, *P. mocamedensis* and *P. mundavambo* sp. nov. by having its frontoparietal scales not fused and in median contact, while on the latter taxa the frontoparietals are fused. It can also be easily distinguished from *P.* aff. *breviceps* by the condition of the eye (pre-ablepharine *versus* completely movable lower eyelids in *P.* aff. *breviceps*) and a considerably lower number of midbody scale rows (23–26 *versus* 32–34 in *P.* aff *breviceps*). Similarly, it can also be easily distinguished from the Gulf of Guinea Oceanic Island species, *P. africanus*, *P. thomensis* and *P. annobonensis* by the eyelid condition (pre-ablepharine in *P. ericae* sp. nov. *versus* completely movable lower eyelids in the latter taxa). *P. ericae* sp. nov. is morphologically very similar to *P. cabindae*, with which it was originally confused in the field. Due to the extreme morphological conservatism of the genus, the morphological differences between these two species are subtle. However, since the two species are truly cryptic we followed Rheindt et al. (2023) and present a molecular diagnosis of the species. *Panaspis ericae* sp. nov, differs from its closest relative *P. cabindae* by a total of 23 fixed single nucleotide substitutions plus one insertion in the 16S rRNA alignment and by 11 fixed single nucleotide substitutions in the RAG1 alignment (see Appendix 2). The main molecular diagnostic feature between both species is the base nucleotide composition at positions 112, 114, 131, 150, 167, 208, 209, 219, 229, 231, 232, 282, 288, 295, 304, 315, 317, 318, 320, 322, 324, 325, 334, and 336 of the 16S rRNA gene alignment and positions 6, 15, 183, 215, 234, 354, 366, 519, 521, 568, and 570 of the RAG1 gene alignment.

Distribution. The newly described species is currently only known from the Serra da Neve Inselberg in northern Namibe Province, southwestern Angola (Fig. 6). Given the isolation of the inselberg and the stark contrast with its surrounding habitat, the newly described species is assumed to be endemic to Serra da Neve.

Habitat and natural history notes. In the highlands of Serra da Neve, at about 1600 m above sea level, specimens were collected under leaf litter in an area dominated by dense Miombo woodlands (MB03-001525, 001526, 001528) (Fig. 7; Grandvaux-Barbosa 1970; Huntley 2023). On the other hand, the specimens collected in the lowlands of the inselberg, at about 720 m above sea level, were found near a dry riverbed in an area dominated by dense mopane woodland in sandy soils with abundant leaf litter (MUNHAC/MB03-001529, 001530, 001531, 001534) (Fig. 8) The species, as most *Panaspis*, seems to be a leaf-litter dweller. Its occurrence in both the base and top of Serra da Neve in two different habitats (miombo in the more humid highlands and mopane in the arid lowlands) indicates some ecological adaptability. It occurs in sympatry with *Panaspis mocamedensis* near Maylowe, preferring denser woodlands with more shade and leaf litter, especially associated with riparian areas, while *P. mocamedensis* occurs in the more open and arid woodlands. Paratypes MUNHAC/MB03-001530 and 001528 were gravid. Paratypes MUNHAC/MB03-001530 and 001531 were collected on a pitfall trap.

Etymology. The specific epithet "*ericae*" is formed in the genitive singular and is feminine. It is given in honor of Erica Tavares (1997–), an Angolan biologist and conservationist. Through her work in the Angolan environmental platform "Eco Angola" (of which Erica is a co-founder), Erica has revolutionized the Angolan conservation and ecological discourse, providing opportunities for members of the Angolan civil society, students, and young researchers to learn, debate and contribute to environmental causes. We suggest "Erica's Snake-Eyed Skink" and "Lagartixa da Manta-Morta de Erica" as the English and Portuguese common names, respectively, for this species.

Table 4. Measurements (in mm) and scale counts of the holotype and paratypes of *Panaspis ericae* sp. nov. and *Panaspis mundavambo* sp. nov. Abbreviations are the same as those described in Materials and methods.

Taxon	*Panaspis ericae* sp. nov.						*Panaspis mundavambo* sp. nov.
Specimen ID.	**MUNHAC/MB03-1525 (Holotype)**	**MUNHAC/MB03-1526 (Paratype)**	**MUNHAC/MB03-1528 (Paratype)**	**MUNHAC/MB03-1529 (Paratype)**	**MUNHAC/MB03-1530 (Paratype)**	**MUNHAC/MB03-1531 (Paratype)**	**MUNHAC/MB03-1527 (Holotype)**
SEX	Unsexed	Unsexed	Female	Unsexed	Female	Unsexed	Unsexed
SVL	32.6	35.2	34.7	31.0	34.4	29.3	35.6
TL	44.8	_	_	43.8	36.2	_	51.7 (missing tail tip)
HL	6.1	6.0	5.7	5.5	5.5	5.2	6.6
HH	2.6	2.5	2.8	2.4	2.2	2.5	4.2
HW	4.1	4.2	3.8	4.0	3.9	3.6	5.1
LA	2.5	2.5	2.3	2.4	2.2	2.1	2.8
LFA	2.0	1.7	1.7	2	1.9	1.7	2.5
LL	3.6	3.5	2.9	2.8	3.0	2.9	4.0
LFL	2.9	3.0	2.3	2.2	2.4	2.1	3.4
LD	17.3	20.8	20.3	17.8	19.9	16.4	19.4
ED	1.1	1.1	1.0	1.0	0.9	1.1	0.9
ET	2.2	2.0	2.0	2.3	2.1	2.2	2.3
ES	2.5	2.5	2.1	2.4	2.9	2.1	2.9
MSR	25	25	24	25	26	23	24
SAV	58	57	57	57	60	55	54
SAD	57	55	56	53	58	54	53
LUFT	14	15	13	15	15	13	13
LUFF	10	9	9	19	9	8	8
SC	4	5	4	5	5	4	5
SL(SO)	7(5)	6(5)	7(5)	7(5)	7(5)	7(5)	7(5)
CP	Contact	Contact	Contact	Contact	Contact	Contact	Contact
CFP	Contact	Contact	Contact	Contact	Contact	Contact	Fused
CPF	Separated	Separated	Single Point Contact	Single Point Contact	Separated	Separated	Separated

Panaspis mundavambo sp. nov.

https://zoobank.org/BFE63A66-529B-421D-8617-E78DDF44E9EE

Figs 6, 9, 10

Holotype. MUNHAC/MB03-1527 (field number LMPC 3242), unsexed adult, from the MPLA post near Catchi, Serra da Neve (-13.7618, 13.2514, 1614 m), Namibe Province, Republic of Angola, collected by Mariana P. Marques, Diogo Parrinha, Arthur Tiutenko and Luis M.P. Ceríaco on 31 October 2022 (Fig. 9).

Diagnosis. *Panaspis mundavambo* sp. nov. can be distinguished from other members of the genus by the following combination of characters: 1) absence of supranasals; 2) ablepharine eye (as defined by Greer 1974); 3) frontoparietals fused; 4) dorsum coppery-brown, with a thin dorsolateral light stripe extending from above eye to base of tail, most distinct on anterior third of its length; flanks dark brown; 5) absence of rows of light spots on the neck; 6) presence of series of black spots on middorsal region; 7) absence of a white ventrolateral stripe; 8) 24 midbody scales rows.

Description of the holotype. Unsexed adult in good condition, but the tail missing the tip. Arrangement and relative size of head, body and tail scalation typical for *Panaspis*. Robust, cylindrical body with well-developed pentadactyl limbs. Fore- and hind-limbs do not overlap when adpressed against the body. SVL 35.6 mm; tail incomplete, measuring 51.7 mm. Head length 6.6 mm, with relatively short snout (HL 129% HW). Other relevant measurements are presented in Table 4. Rostral wider than high, and visible from above. Nasals widely separated behind rostral by frontonasal. Frontonasal rounded anteriorly, wider than long. Nostrils small, set posteriorly in the nasals bordering the postnasal; supranasals absent. Prefrontals separated from each other, contacting loreals, first supraocular, first supraciliary, frontal and frontonasal. Two loreals, anterior one higher than broad, posterior one subquadrangular; preocular divided diagonally into two subtriangular scales on right side, and horizontally on left side into a small superior scale and a larger inferior one. Frontal length shorter than distance between anterior tip of frontal and tip of snout; frontal in contact with frontonasal and prefrontals anteriorly, and first supraocular posteriorly. Frontoparietals fused, in contact supraoculars; parietals and interparietal. Frontoparietal plus interparietal length twice the length of the frontal. Interparietal subtriangular, anterior margin wider and rounded, slightly acuminate posteriorly, with visible parietal foramen in the center; parietals about the same width as fused frontoparietals, in broad contact with each other behind interparietal. A pair of large, broad nuchals collectively bordered by a total of eight dorsals. Supraoculars three. Supraciliaries four, first higher than broad and last wider than high. Pretemporals two. Tympanum visible, ear opening wider than high, approximately one-fifth the height of the eye. Supralabials seven, the fifth being the subocular. Ablepharine eye. Infralabials six. Postmental bordering seven scales (mental, two primary chin-shields, and two infralabials on each side). Ventral scales smooth. MSR 24, SAD 53, SAV 54. Scales on palms and soles smooth. Relative length of digits of manus III>IV>II=V>I; relative length of digits of pes IV>III>II=V>I; toe V of right pes missing. LUFF scales eight; LUFT scales 13 on right side and 12 on left side. Tail long, robust and tapering smoothly.

In preservative, ground color of dorsum and upper side of head coppery brown; tail lighter, golden brown. A thin, light dorsolateral stripe extends from supraocular area to base of tail, being most distinct on anterior third of its length and faint posteriorly; below, a dark brown lateral band extends from snout to base of tail, darker on face, neck and axilla, lighter and less distinct from middorsal coloration posteriorly. Dorsal scales individually stippled with black, especially on dorsal aspect of head; labials greyish white, with individual black spots; pale and black spots scattered on lateral sides of neck. Middorsal region with black spots, forming somewhat longitudinal series. Venter uniformly greyish to blueish white; underside of tail slightly orange; palms and soles brownish.

Comparison with other Southwestern African Panaspis and related forms. As the molecular data provide evidence of the independence of the *P. mundavambo* sp. nov. lineage from all other taxa, we here restrict our morphological comparisons to those named congeners occurring in Namibia and Angola and its sister taxon *P. annettesabinae*. *P. mundavambo* sp. nov. can immediately be distinguished from *P. cabindae. P. ericae* sp. nov. and *P.* aff. *breviceps*, by not having supranasals (*versus* present in *P. cabindae*, *P. ericae* sp. nov. and *P.* aff. *breviceps*), by having an ablepharine eye (*versus* pre-ablepharine eye in *P. cabindae* and *P. ericae* sp. nov., and completely movable lower eyelids in *P.* aff. *breviceps*), and by having the frontoparietals fused (*versus* divided in *P. cabindae*, *P. ericae* sp. nov. and i *P.* aff. *breviceps*). In comparison with *P. wahlbergii*, *P. mundavambo* sp. nov. can be distinguished by its coloration, namely by the presence of longitudinal series of dark spots on the middorsal region and the lack of a ventrolateral white stripe (*versus* the absence of middorsal dark spots and presence of white ventrolateral stripe in *P. wahlbergii*), and by having an overall lower number of scales across venter (54 *versus* 56–62 in *P. wahlbergii*), midbody scales rows (24 *versus* 25–26 in *P. wahlbergii*), scales across dorsum (53 *versus* 56–61 in *P. wahlbergii*) and lamellae under the fourth finger (8 *versus* 9–10 in *P. wahlbergii*). *Panaspis mundavambo* sp. nov. can be distinguished from *P. maculicollis* by the presence of longitudinal series of dark spots on middorsal region (*versus* no dark spots on middorsal region in *P. maculicollis*), and a lower number of lamellae under fourth finger (8 *versus* 13–17). *P. mundavambo* sp. nov. can be distinguished from *P. namibiana* by having a lower count of scales across venter (54 in *P. versus* 56–67 in *P. namibiana*) and dorsum (53 *versus* 57–68 in *P. namibiana*). *P. mundavambo* sp. nov. can be distinguished from *P. mocamedensis* by the presence of series of black spots on middorsal region (*versus* black spots absent in *P. mocamedensis*), and by having a smaller count of scales across venter (54 in *P. versus* 56–61 in *P. mocamedensis*), across dorsum (53 *versus* 56–60 in *P. mocamedensis*) and smaller number of lamellae under the fourth finger (8 *versus* 9–10 in *P. mocamedensis*). Comparing *P. mundavambo* sp. nov. with its sister taxon, *P. annettesabinae* from Ethiopia, the newly described species has prefrontal scales separated from each other (*versus* in contact in *P. annettesabinae*), a smaller count of scales across venter

Figure 9. Preserved holotype of *Panaspis mundavambo* sp. nov. (MUNHAC/MB03-1527). Photos by Diogo Parrinha.

Figure 10. Type locality of *P. mundavambo* sp. nov. from a riparian gallery near Catchi, Serra da Neve. Photo by Luis M.P. Ceríaco.

(54 *versus* 68 in *P. annettesabinae*), smaller number of scales across dorsum (53 *versus* 62 in *P. annettesabinae*).

Distribution. The newly described species is currently only known from single locality on the Serra da Neve Inselberg, southwestern Angola (Fig. 6). Given the isolation of the inselberg and the stark contrast with its surrounding habitat, the newly described species is assume to be locally restricted, although it may occur elsewhere in Angola (W. Conradie, pers. comm.).

Habitat and natural history notes. The holotype was collected under a log in an area dominated by woodlands at about 1600 m above sea level (Grandvaux-Barbosa 1970; Huntley 2023). Very little is known about its ecology and natural history. It seems to be associated with riparian areas (Fig. 10). It occurs close to *P. ericae* sp. nov.. The single collected specimen was found in denser woodlands near a riparian gallery, while *P. ericae* sp. nov. was found in slightly more open miombo that dominates the landscape.

Etymology. The specific epithet "*mundavambo*" refers to the Mukwando (local tribe) name for Serra da Neve Inselberg (Opunda Mundavambo), to which the species is endemic, and is applied here as a substantive in apposition. We propose the English vernacular name "Serra da Neve Snake-Eyed Skink" and the Portuguese vernacular name of "Lagartixa da Manta-Morta da Serra da Neve".

Discussion

The discovery of two new species of *Panaspis* on Serra da Neve is unexpected, as is the inselberg's capacity for harboring a total of four species of such cryptic andecologically conservative group of animals. *Panaspis*, also known as leaf-litter skinks, are generally ground dwellers who inhabit areas of leaf-litter and forest floors preying on termites and other small invertebrates (MPM pres. Obs.). While our data are extremely limited to make any kind of robust ecological inference, it appears that the type of soil and habitat may ecologically partition the niche of the four taxa: *P. mundavambo* sp. nov. may be restricted to high elevation riparian galleries, while *P. cabindae* occurs in lowland humid and forested areas. *P ericae* sp. nov. was found both in miombo and mopane habitats, but in the latter, it was found only in dry riverbeds, while *P. mocamedensis* in leaf-litter outside these. This ecological partition needs attention and Serra da Neve *Panaspis* may become an interesting case study for anyone wanting to focus on these types of ecological questions.

Besides this surprising intrageneric diversity in such a small area, the discovery of these two new species recovers recurring patterns regarding the Serra da Neve herpetofauna. In just the last five years, one toad (Ceríaco et al. 2018b) and four reptile strictly endemic species (Marques et al. 2019, 2020, 2023a; Branch et al. 2021), one strictly endemic gecko in the process of description (Parrinha et al. in prep.), and four other lizard species (Parrinha et al. 2021; Marques et al. 2022, 2023b; Ceríaco et al. 2024) have been described from the inselberg and its surroundings. These discoveries demonstrate that Serra da Neve is a biodiversity hotspot, particularly interesting for the large proportion of endemic species per area. Therefore, the description of these two additional species of *Panaspis* fits into the recent history of discovery in the inselberg, which is likely to continue yielding new taxonomic discoveries. Biogeographically, these two new species also share common trends with other recently described species. It has been shown that some of the Serra da Neve endemic taxa have closely related species in the Eastern African highlands, as is the case for *Acontias mukwando* and *Lygodactylus baptistai* (Marques et al. 2020, 2023b), a pattern also seen in the newly described *P. mundavambo* sp. nov. On the other hand, *P. ericae* sp. nov. belongs to a more Central African lineage, composed of species such as *P. cabindae* and the Gulf of Guinea Oceanic Islands taxa. The presence of *P. mocamedensis* at the base of Serra da Neve ties the *Panaspis* fauna to the more southwestern Angolan endemic fauna. Serra da Neve is thus an interesting biogeographic melting pot, which ultimately contributes to its rich and unique biodiversity. Interestingly though, *P. wahlbergii* has not been recorded in the inselberg, despite being common in the neighboring Huila escarpment and plateau (Ceríaco et al. 2020).

This new addition to the known endemic fauna of Serra da Neve is another example of the conservation importance of this inselberg, a fact that has already been noted by several authors (Pinto et al. 2023; Marques et al. 2024). As the two new species appear to be endemic to Serra da Neve, and therefore their areas of occurrence do not exceed 630 km^2 (assuming that both of the species are homogeneously distributed across the inselberg), both are of conservation interest. Nevertheless, the currently available data do not allow us to conduct a full-scale conservation assessment and therefore we suggest that a status of Data Deficient (DD) is warranted for both species (IUCN Standards and Petitions Committee 2019). More work is needed to uncover the true biodiversity of Serra da Neve and ensure its protection for future generations.

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References

Bauer AM, Ceríaco LMP, Marques MP, Becker FS (2023) Highland reptiles of Angola and Namibia. Namibian Journal of Environment 8: 259–276.

Branch WR, Schmitz A, Lobón-Rovira J, Baptista NL, António T, Conradie W (2021) Rock Island Melody: A revision of the *Afroedura bogerti* Loveridge, 1944 group, with descriptions of four new endemic species from Angola. Zoosystematic and Evolution 97: 55–82. https://doi.org/10.3897/zse.97.57202

Ceríaco LMP, Branch WR, Bauer AM (2018a) A new species of African snake-eyed skink (Scincidae: *Panaspis*) from central and northern Namibia. Zootaxa 4527(1): 140–150. http://doi.org/10.11646/zootaxa.4527.1.12

Ceríaco LMP, Marques MP, Bandeira S, Agarwal I, Stanley EL, Bauer AM, Heinicke MP, Blackburn DC (2018b) A new earless species of *Poyntonophrynus* (Anura, Bufonidae) from the Serra da Neve Inselberg, Namibe Province, Angola. ZooKeys 780: 109–136. http://doi.org/10.3897/zookeys.780.25859

Ceríaco LMP, Heinicke MP, Parker KL, Marques MP, Bauer AM (2020) A review of the African snake-eyed skinks (Scincidae: *Panaspis*) from Angola, with the description of a new species. *Zootaxa* 4747(1): 77–112. https://doi.org/10.11646/zootaxa.4747.1.3

Ceríaco LMP, Marques MP, Tiutenko A, Weinell JL, Butler BO, Bauer AM (2024) The *Trachylepis* (Squamata: Scincidae) of Angola: An integrative taxonomic review with the description of seven new species. Bulletin of the American Museum of Natural History 465: 1–153. https://doi.org/10.5531/sd.sp.65

Clement M, Posada D, Crandall, KA (2000) TCS: a computer program to estimate gene genealogies. Molecular Ecolology 9: 1657–1659. https://doi.org/10.1046/j.1365-294x.2000.01020.x

Colston TJ, Pyron RA, Bauer AM (2020) A new species of African snake-eyed skink (Scincidae: *Panaspis*) from Ethiopia. Zootaxa 4779(2): 190–200. https://doi.org/10.11646/zootaxa.4779.2.2

Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest2: more models, new heuristics and high-performance computing. Nature Methods 9: 772. https://doi.org/10.1038/nmeth.2109

de Queiroz K (1999) The general lineage concept of species, species criteria, and the process of speciation. In: Howard DJ, Berlocher SH (Eds) Endless Forms: Species and Speciation. Oxford University Press, New York, USA, 57–75.

Fuhn IE (1969) The “polyphyletic” origin of the genus *Ablepharus* (Reptilia, Scincidae): a case of parallel evolution. Journal of Zoological Systematics and Evolutionary Research 7(1): 67–76. https://doi.org/10.1111/j.1439-0469.1969.tb00849.x

Fuhn IE (1972) Révision du phylum forestier du genre *Panaspis* Cope (Reptilia, Scincidae, Lygosominae). Revue Roumaine de Biologie, série de Zoologie 17(4) : 257–272.

Grandvaux-Barbosa LA (1970) *Carta Fitogeográfica de Angola*. Instituto de Investigação Científica de Angola, Luanda, 323 pp.

Greer AE (1974) The generic relationships of the scincid lizard genus *Leiolopisma* and its relatives. Australian Journal of Zoology 31: 1–67. https://doi.org/10.1071/AJZS031

Huntley BJ (2023) Biomes and ecoregions of the highlands and escarpment of Angola and Namibia. Namibian Journal of Environment 8: 29–41.

IUCN Standards and Petitions Committee (2019) Guidelines for Using the IUCN Red List Categories and Criteria. Version 14. http://www.iucnredlist.org/documents/RedListGuidelines.pdf

Jacobsen NHG, Broadley DG (2000) A new species of *Panaspis* Cope (Reptilia: Scincidae) from southern Africa. African Journal of Herpetology 49(1): 61–71. https://doi.org/10.1080/21564574.2000.9650017

Jesus J, Harris DJ, Brehm A (2007) Relationships of *Afroablepharus* Greer, 1974 skinks from the Gulf of Guinea islands based on mitochondrial and nuclear DNA: Patterns of colonization and comments on taxonomy. Molecular Phylogenetics and Evolution 45(3): 904–914. https://doi.org/10.1080/21564574.2017.1413015

Katoh K, Standley D.M. (2013) MAFFT Multiple Sequence Alignment Software Version 7: Improvements in Performance and Usability. Molecular Biology and Evolution 30(4): 772–780. https://doi.org/10.1093/molbev/mst010

Kilunda FK, Conradie W, Wasonga DV, Jin J-Q, Peng M-S, Murphy RW, Malonza PK, Che J (2019) Revalidation and resurrection of *Panaspis massaiensis* (Angel, 1924) and the description of a new species of *Panaspis* Cope (Squamata: Scincidae) from south-eastern Kenya. Zootaxa 4706(2): 255–274. https://doi.org/10.11646/zootaxa.4706.2.3

Marques MP, Ceríaco LMP, Blackburn DC, Bauer AM (2018) Diversity and distribution of the amphibians and terrestrial reptiles of Angola – Atlas of historical and bibliographic records (1840–2017). Proceedings of the California Academy of Sciences Series 4, 65(supplement 2): 1–501.

Marques MP, Ceríaco LMP, Stanley EL, Bandeira S, Agarwal I, Bauer AM (2019) A new species of girdled lizard (Squamata: Cordylidae) from Serra da Neve inselberg, Namibe province, southwestern Angola. Zootaxa 4668(4): 503–524. http://dx.doi.org/10.11646/zootaxa.4668.4.4

Marques MP, Ceríaco LMP, Buehler MD, Bandeira SA, Janota JM, Bauer AM (2020) A revision of the dwarf geckos, genus *Lygodactylus* (Squamata: Gekkonidae), from Angola, with the description of three new species. Zootaxa 4853: 301–352. https://doi.org/10.11646/zootaxa.4853.3.1

Marques MP, Ceríaco LMP, Heinicke MP, Chehouri RM, Conradie W, Tolley KA, Bauer AM (2022) The Angolan bushveld lizards, genus *Heliobolus* Fitzinger, 1843 (Squamata: Lacertidae): Integrative taxonomy and the description of two new species. Vertebrate Zoology 72: 745–769. https://doi.org/10.3897/vz.72.e85269

Marques MP, Parrinha D, Tiutenko A, Lopes-Lima M, Bauer AMB, Ceríaco LMP (2023a) A new species of African legless-skink, genus *Acontias* Cuvier, 1818 “1817” (Squamata: Scincidae) from Serra da Neve inselberg, southwestern Angola. African Journal of Herpetology. https://doi.org/10.1080/21564574.2023.2246487

Marques MP, Parrinha D, Ceríaco LMP, Brennan IG, Heinicke MP, Bauer AM (2023b) A new species of thick-toed gecko (*Pachydactylus*) from Serra da Neve and surrounding rocky areas of southwestern Angola. Vertebrate Zoology 73: 325–343. https://doi.org/10.3897/vz.73.e101329

Marques MP, Parrinha D, Lopes-Lima M, Tiutenko A, Bauer AM, Ceríaco LMP (2024) An island in a sea of sand: a first checklist of the herpetofauna of the Serra da Neve inselberg, southwestern Angola. ZooKeys 1201: 167–217. https://doi.org/10.3897/zookeys.1201.120750

Medina MF, Bauer AM, Branch WR, Schmitz A, Conradie W, Nagy ZT, Hibbitts TJ, Ernst R, Portik DM, Nielsen SV, Colston TJ, Kusamba C, Behangana M, Rödel M-O (2016) Molecular phylogeny of *Panaspis* and *Afroablepharus* skinks (Squamata: Scincidae) in the savannas of sub-Saharan Africa. Molecular Phylogenetics and Evolution 100: 409–423. https://doi.org/10.1016/j.ympev.2016.04.026

Mendelsohn JM, Huntley BJ (2023) Introducing the highlands and escarpments of Angola and Namibia. Namibian Journal of Environment 8: 7–22.

Minh BQ, Nguyen MAT, Von Haeseler A (2013) Ultrafast approximation for phylogenetic bootstrap. Molecular Biology and Evolution 30: 1188–1195. https://doi.org/10.1093/molbev/mst024

Padial JM, Miralles A, De la Riva I, Vences M (2010) The integrative future of taxonomy. Frontiers in Zoology 7: 16. https://doi.org/10.1186/1742-9994-7-16

Parrinha D, Marques MP, Heinicke MP, Khalid F, Parker KL, Tolley KA, Childers JL, Conradie W, Bauer AM, Ceríaco LMP (2021) A revision of the genus *Pedioplanis* Fitzinger (Squamata: Lacertidae) from Angola, with the description of a new species. Zootaxa 5032(1): 1–46. https://doi.org/10.11646/zootaxa.5032.1.1

Pereira E (1977) Serra da Neve (Angola) – Nota sobre a geomorfologia da região e idade das aplanações. Boletim da Sociedade Geologica de Portugal 20: 277–282.

Perret JL (1973) Contribution à l’étude des *Panaspis* (Reptilia, Scincidae) d’Afrique occidentale avec la description de deux espèces nouvelles. Revue Suisse de Zoologie 80 : 595–630. https://doi.org/10.5962/bhl.part.75958

Perret JL (1975) La differentiation dans le genre *Panaspis* Cope (Reptilia: Scincidae). Bulletin de la Société Neuchâteloise des Sciences Naturelles 98 : 5–16.

Pinto PV, Russo V, Veríssimo L (2023) The highlands in Angolan conservation areas. Namibian Journal of Environment 8: 53–62.

Rheindt F, Bouchard P, Pyle RL, Welter-Schultes F, Aescht E, Ahyong ST, Ballerio A, Bourgoin T, Ceríaco LMP, Dmitriev D, Evenhuis N, Grygier MJ, Harvey MS, Kottelat M, Kluge N, Krell F-T, Kojima J, Kullander SO, Lucinda P, Lyal CHC, Scioscia CL, Whitmore D, Yanega D, Zhang Z-Q, Zhou H-Z, Pape T (2023) Tightening the requirements for species diagnoses would help integrate DNA-based descriptions in taxonomic practice. PLoS Biology 21(8): e3002251. https://doi.org/10.1371/journal.pbio.3002251

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61(3): 539–42. https://doi.org/10.1093/sysbio/sys029

Schmitz A, Ineich I, Chirio L (2005) Molecular review of the genus *Panaspis sensu lato* (Reptilia: Scincidae) in Cameroon, with special reference to the status of the proposed subgenera. Zootaxa 863: 1–28. http://doi.org/10.11646/zootaxa.863.1.1

Simmons JE (2015) Herpetological collections and collections management. 3rd edn. Society for the Study of Amphibians and Reptiles: Herpetological Circular 42.

Soares LB, Ceríaco LMP, Marques MP, Bastos-Silveira C, Scheinberg LA, Harris DJ, Brehm A, Jesus J (2018) Review of the leaf-litter skinks (Scincidae: *Panaspis*) from the Gulf of Guinea oceanic islands, with the description of a new species. African Journal of Herpetology. https://doi.org/10.1080/21564574.2017.1413015

Xia X (2018) DAMBE7: New and Improved Tools for Data Analysis in Molecular Biology and Evolution. Molecular *Biology* and *Evolution* 35(6): 1550–1552. https://doi.org/10.1093/molbev/msy073

Xia X, Xie Z, Salemi M, Chen L, Wang Y (2003) An index of substitution saturation and its application. Molecular Phylogenetics and Evolution 26(1) :1–7. https://doi.org/10.1016/s1055-7903(02)00326-3

Appendix 1

Table A1. RAG1 haplotype (TCS) network showing the relationships of all *Panaspis* sequences.

SPECIES	COLLECTION NUMBER	RAG1 HAPLOTYPE
Panaspis ericae **sp. nov.**	LMPC-3209	1
Panaspis ericae **sp. nov.**	LMPC-3210	1
Panaspis ericae **sp. nov.**	LMPC-3275	1
Panaspis ericae **sp. nov.**	LMPC-3282	1
Panaspis ericae **sp. nov.**	LMPC-3354	1
Panaspis ericae **sp. nov.**	LMPC-3355	1
Panaspis ericae **sp. nov.**	LMPC-3395	1
Panaspis mundavambo **sp. nov.**	LMPC-3242	9
Panaspis mocamedensis	LMPC-3381	17
Panaspis mocamedensis	LMPC-3382	17
Panaspis africanus	–	8
Panaspis breviceps	ZFMK 87662	2
Panaspis breviceps	ZFMK 87663	2
Panaspis cabindae	PEM R19467	5
Panaspis cabindae	Uncatalogued	5
Panaspis cabindae	Uncatalogued	5
Panaspis cabindae	PEM R21594	6
Panaspis cabindae	PEM R20256	5
Panaspis cabindae	AMB 10315	3
Panaspis cabindae	FLMNH 187242	4
Panaspis cabindae	MB03-001088	5
Panaspis cabindae	MB03-001091	7
Panaspis sp. Katanga 1	UTEP 21175	26
Panaspis sp. Katanga 1	UTEP 21174	26
Panaspis sp. Katanga 2	–	27
Panaspis sp. Katanga 2	PEM R17454	29
Panaspis sp. Katanga 2	–	28
Panaspis sp. Limpopo	–	18
Panaspis maculicollis	CAS 234099	19
Panaspis maculicollis	CAS 234188	13
Panaspis maculicollis	CAS 234135	13
Panaspis maculicollis	Uncatalogued	14
Panaspis maculicollis	Uncatalogued	13
Panaspis maculicollis	PEM R20475	15
Panaspis sp. Malawi	PEM R20247	30
Panaspis sp. Mozambique 1	–	10
Panaspis sp. Mozambique 1	PEM R20561	11
Panaspis sp. Mozambique 1	PEM R20591	12
Panaspis sp. Mozambique 4	PEM R20569	31
Panaspis sp. Mozambique 4	PEM R20576	31
Panaspis namibiana	MCZ R183767	16
Panaspis sp. Tanzania 1	–	22
Panaspis sp. Tanzania 1	–	19
Panaspis sp. Tanzania 2	PEM R20799	20
Panaspis togoensis	TCWC 94557	18
Panaspis wahlbergii	CAS 234209	24
Panaspis wahlbergii	MCZR 184443	13
Panaspis wahlbergii	CAS 234194	19
Panaspis wahlbergii	TM 84299	24
Panaspis wahlbergii	NMB R10286	23
Panaspis wahlbergii	TCWC 95563	21
Panaspis wahlbergii	TCWC 95588	19
Panaspis wahlbergii	PEM R21298	25
Panaspis wahlbergii	PEM R21297	23
Broadleysaurus major	–	–
Cordylus marunguensis	UTEP 20374	–
Lacertaspis gemmiventris	CAS 207858	–
Lacertaspis gemmiventris	CAS 207854	–
Lacertaspis rohdei	ZFMK 75382	–
Leptosiaphos blochmanni	UTEP 21177	–
Leptosiaphos koutoui	MNHN 2001.0697	–
Leptosiaphos sp.	ZFMK 75381	–
Leptosiaphos sp.	ZFMK 69552	–
Mochlus afer	ZFMK 54317	–
Plestiodon inexpectatus	–	–
Trachylepis sulcata	–	–
Typhlosaurus braini	CAS 214581	–
Typhlosaurus braini	CAS 214579	–

Appendix 2

Fixed nucleotide differences of 16S rRNA and RAG1 gene sequences of *P. ericae* sp. nov. compared to the sequence alignment of *P. cabindae* (del = deletion; ins = insertion mutation).

Panaspis ericae sp. nov.

16S rRNA: 112C, 114G, 131C, 150T, 167A, 208T, 209 ins T, 219A, 229C, 231C, 232T, 282A, 288A, 295T, 304C, 315G, 317T, 318G, 320T, 322C, 324C, 325C, 334C, 336T.

RAG1: 6T, 15G, 183A, 215A, 234T, 354A, 366A, 519T, 521C, 568C, 570G.

Panaspis cabindae

16S rRNA: 112T, 114A, 131T, 150C, 167G, 208A, 209 del, 219G, 229A/G, 231A, 232C, 282G, 288C, 295A, 304A, 315T/A, 317A, 318C, 320C, 322G, 324A, 325T, 334A, 336G.

RAG1: 6G, 15C, 183G, 215G, 234C, 354G, 366G, 519C, 521T, 568A, 570A.