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A new species of thick-toed gecko (*Pachydactylus*) from Serra da Neve and surrounding rocky areas of southwestern Angola (Squamata: Gekkonidae)

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Abstract

Several specimens of *Pachydactylus angolensis*, a poorly known Angolan endemic gecko, have recently been collected in southern Angola, considerably increasing its known distribution range. Previous observations led to the hypothesis that two different morphological forms exist in the country—a coastal form and an inland form. Based on the morphological examination of historical and recently collected specimens, as well as on newly generated molecular data, we conducted a taxonomic revision of this putative species complex. The results support the separation of these two forms as two different species. The coastal form belongs to the nominotypic population, while the inland form is here described as a new species, *Pachydactylus maiatoi* **sp. nov.**. A brief comment on the biogeographical implications of this discovery is also provided.

Keywords

Africa, biogeography, integrative taxonomy, reptiles, type specimens

Resumo

Vários espécimes de *Pachydactylus angolensis*, uma osga endémica de Angola, rara e pouco conhecida, foram recentemente coletados no sul de Angola, aumentando consideravelmente a sua área de distribuição conhecida. Observações anteriores levantaram a hipótese da existência de duas formas morfológicas distintas no país — uma forma costeira e outra das regiões interiores. Com base

na observação morfológica de espécimes históricos e recentes, bem como dados moleculares gerados recentemente, levou-se a cabo a revisão taxonómica deste putativo complexo de espécies. Os resultados suportam a separação destas duas formas em duas espécies diferentes. A forma costeira pertence à população nominotípica, enquanto a forma das regiões interiores é aqui descrita como uma nova espécie, *Pachydactylus maiatoi* **sp. nov.**. Apresentam-se ainda as implicações biogeográficas desta nova descoberta.

Palavras-chave

África, biogeografia, espécimes tipo, répteis, taxonomia integrativa

Introduction

The genus *Pachydactylus* Wiegmann, 1834 is represented in Angola by 10 species (Marques et al. 2018; Branch et al. 2019b; Lobón-Rovira et al. 2022), namely *P. angolensis* Loveridge, 1944, *P. caraculicus* FitzSimons, 1959, *P. parascutatus* Bauer, Lamb & Branch, 2002, *P.* cf. *punctatus* Peters, 1854, *P.* cf. *oreophilus* McLachlan & Spence, 1976, *P. rangei* (Anderson, 1908), *P. scherzi* (Mertens, 1954), *P.* cf. *rugosus* Smith, 1849, *P. wahlbergii* (Peters, 1869), and *P. vanzyli* (Steyn & Haacke, 1966). Laurent (1964) considered *Pachydactylus amoenoides* Hewitt, 1935 as a distinct species from *P. punctatus* based on their sympatry in southern regions of Angola (Marques et al. 2018). Bauer and Branch (1995) synonymized *P. amoenoides* with *P. punctatus*, although the taxonomic status of *P. amoenoides* is currently being reviewed (Bauer et al. unpublished). Currently the genus accommodates 57 recognized species (Uetz et al. 2022) across its southern African distribution and together with its close relatives *Chondrodactylus* Peters, 1870 and *Elasmodactylus* Boulenger, 1895, it comprises the most successful and diverse radiation of lizards in southern Africa (Heinicke et al. 2017). Recent species-level phylogenies have provided important insights about the diversification of the genus and defined several species groups (Bauer 1999; Bauer and Lamb 2005; Heinicke et al. 2017). Of special interest for this study is the "northwestern group" to which all but four of the species of *Pachydactylus* occurring in Angola (*P. rangei, P. vanzyli*, *P.* cf. *rugosus* and *P. wahlbergii*) belong. The members of this "northwestern group" as defined by Bauer (1999), Bauer and Lamb (2005) and most recently by Heinicke et al. (2017) are restricted to northern Namibia and southwestern Angola, with the exception of the *P. punctatus* species complex which extends to South Africa, Botswana, Mozambique, Malawi, Zambia and the Democratic Republic of the Congo (Heinicke et al. 2011). The group comprises the *P. punctatus* species complex, *P. scherzi*, *P. caraculicus*, *P. angolensis*, *P. parascutatus, P. scutatus* Hewitt, 1927, *P. gaiasensis* Steyn & Michell, 1967, the *P. oreophilus* species complex, *P. sansteynae* Steyn & Michell, 1967, *P. otaviensis* Bauer, Lamb & Branch, 2006, *P. boehmei* Bauer, 2010, *P. maraisi* Heinicke, Adderly, Bauer & Jackman, 2011, and *P. bicolor* Hewitt, 1926 (Heinicke et al. 2017).

Despite a considerable number of *Pachydactylus* species being described in recent decades (Bauer et al. 2002, 2006a, 2006b; Branch et al. 2011; Heinicke et al. 2011), undescribed cryptic diversity remains (Bauer and Branch 1995; Heinz 2011; Branch et al. 2017). Part of this diversity is found in some populations of taxa that either occur or are endemic to Angola. This is the case of *P.* cf. *oreophilus* and *P.* cf. *rugosus*, whose Angolan and some northern Namibian populations are already known to represent putative new species (Bauer et al. unpublished; Lobón-Róvira et al. 2022), or even the case of the *P. punctatus* species complex, signaled long ago as a species complex by Bauer and Branch (1995) and Heinz (2011), and whose Angolan populations are currently being evaluated and described as new (Marques et al. unpublished). This also seems to be the case of the Angolan endemic *P. angolensis*. The taxon was described by Loveridge (1944) as *Pachydactylus scutatus angolensis*, based on three specimens collected in coastal regions of Benguela Province by Arthur Vernay, Herbert Lang and Rudyerd Boulton in 1925 during the American Museum of Natural History Vernay-Lang Angolan Expedition. In their review of the *Pachydactylus scutatus* group, Bauer et al. (2002) re-examined the type specimens and elevated *P. s. angolensis* to a full species, closely allied to *P. scutatus*. Bauer and Lamb's (2005) phylogeny of southern African *Pachydactylus* did not include *P. angolensis* due to the lack of genetic material at the time but suggested that the species should belong to the "northwestern clade" of the genus, which was later confirmed by Heinicke et al. (2011). Heinicke et al. (2017) found that *P. angolensis* was sister to *P. caraculicus*, instead of being closely related to *P. scutatus* as supposed before. The holotype is from Hanha, a small town 6 km inland from the coast and on the border of the Cacubi river [–12.2450°, 13.7075°], whereas the two paratypes were collected approximately 20 km south, at Lobito Bay [–12.3500°, 13.5500°]. Additional details regarding the type locality of *P. angolensis* were provided by Branch et al. (2017), who noted the historical confusion between Hanha do Norte and Hanha do Cubal, two geographically proximate localities bearing a similar name, as already noted by Bauer et al. (2002). The authors confirmed Bauer et al.' (2002) assumption that Hanha do Norte is the correct type locality for this species (Branch et al. 2017). The type series is still present in the collections of the American Museum of Natural History (AMNH), New York, which holds the holotype

Figure 1. Holotype (AMNH R47874) of *P. angolensis*, from Hanha, Benguela Province, Angola. Photo by Luis M.P. Ceríaco.

and one paratype, AMNH R47874 (Fig. 1) and AMNH R47872, respectively, and in the collections of the Museum of Comparative Zoology (MCZ), Massachusetts, which is the repository of the remaining paratype (MCZ R46856).

Subsequent records were given by Laurent (1964), who reported on four specimens from the "environs de Moçamedes", one of which was collected in the coastal region of "Praia das Conchas" [–15.1333°, 12.1167°], while the other three were collected by the side of the road that connects Sá da Bandeira (now Lubango) to Moçâmedes (precise locality impossible to georeference). These specimens are still extant in the collections of the Museu Regional do Dundo (MD), in Lunda Norte Province, under the catalogue number MD 1931 (Ceríaco et al. 2020c).

Further specimens of this species were collected by Charles Koch, on an expedition to southwest Angola in September 1956, as well as Wulf D. Haacke in 1971 and 1974. Koch's and Haacke's specimens were deposited in the Transvaal Museum (TM; today Ditsong National Museum of Natural History) but these records were only published much later by Bauer (2010), Ceríaco et al. (2016), and Branch et al. (2017). These included specimens collected in Namibe Province, namely in São Nicolau, Bentiaba [–14.2667°, 12.3833°], Lucira [–13.8667°, 12.5333°], Lungo [–14.3167°, 13.2000°], São Nicolau [–14.2577°, 12.3969°] and Saco do Giraul [–15.0688°, 12.1422°], and from Benguela Province, namely Hanha, 20 km north of Lobito [–12.2585°, 13.6734°], Benguela, 24 km south [–12.6975°, 13.2522°], and 30 km north of Dombe Grande [–12.7309°, 13.2302°].

Due to the violent civil war that afflicted Angola from 1975 to 2002, decades passed without the sighting or the collection of additional specimens of this species in Angola. Between 2013 and 2019 several specimens of this species were collected in both Namibe and Benguela provinces by our team. In December 2013 a juvenile specimen was collected during the California Academy of Sciences (CAS), Villanova University (VU) and Instituto Nacional da Biodiversidade e Áreas de Conservação (INBAC) joint expedition to southwestern Angola. This specimen (CAS 254887), reported by Ceríaco et al. (2016), was collected in a rocky outcrop, covered with vegetation, in the south side of the Namibe-Lubango road, 2 km East (by road) of Mangueiras [–15.0436°, 13.1600°]. This was the most inland record for the species. Two years later, during a subsequent expedition to the southwestern regions of Benguela Province, a total of ten specimens, agreeing with the topotypical and coastal coloration pattern, were collected in the Chimalavera Regional Natural Park (Fig. 2).

Approximately 180 km southeast of Chimalavera, in August 2018, two of the authors of this study (MPM and LMPC) collected an additional specimen of *P. angolensis* under some rocks near the old Portuguese fort of the coastal town of Bentiaba [–14.2733°, 12.3850°] (Fig. 3).

At around the same time, during surveys further inland in Namibe Province — mostly in the Serra da Neve inselberg and the surrounding regions of Maungo — additional specimens resembling *P. angolensis* were collected. These were, however, morphologically different from all the remaining coastal material collected so far, having a duller dorsal coloration without the presence of any kind

Figure 2. A Life photo of a juvenile *Pachydactylus angolensis* from Chimalavera Regional Natural Park (CAS 266480). **B** General view of the habitat in Chimalavera Regional Natural Park. Photos by Luis M.P. Ceríaco.

of scattered white spots (as reported by Loveridge (1944) in the original description), a character present in all other coastal specimens. Branch et al. (2017) reported a similar observation between the coastal and inland populations of *P. angolensis*, which they labeled as the "coastal form" and the "inland form". Besides the records of the specimens available in the TM (cited above), Branch et al. (2017) provided reference to two photo-vouchers, one from Chimalavera to illustrate the "coastal form" and another from Serra da Tchivira [–14.3167°, 13.8833°] to illustrate the "inland form".

Together with the review of the existing historical specimens of *P. angolensis*, these newly collected specimens from several localities across southwestern Angola

Figure 3. A Life photo of *Pachydactylus angolensis* from Bentiaba (CAS 264237). **B** General view of the old Portuguese fort at Bentiaba and its surrounding habitat. Photos by Luis M.P. Ceríaco.

allowed us to investigate the taxonomic identity of these two forms in Angola. Based on a combination of morphological, meristic, and coloration characters and DNA sequence data, we found evidence that supports the recognition of the "coastal" and "inland" forms of *P. angolensis* as two different taxa. We adopt the general lineage species concept (de Queiroz 1999) and recognize the "inland form" of *P. angolensis* as a separate and previously undescribed species.

In order to stabilize the taxonomy and to provide an improved estimate of the distribution of the genus in southern Africa, we describe the inland form as a new species and provide additional data on the distribution and ecology of these two taxa. Presumptive specimens of

P. angolensis from far northern Namibia have been determined to be *P. parascutatus* (Marques et al. 2018).

Materials and Methods

Newly collected specimens for this study were euthanized with MS-222 following an approved IACUC protocol (Villanova University #1866), fixed in 10% buffered formalin in the field, and transferred to 70% ethanol for long-term storage at the conclusion of field work. Liver tissue was removed before formalin fixation and preserved in either RNAlater and transferred to 95% ethanol or directly in 95% ethanol for long-term storage. For mensural and meristic comparisons, we examined other Angolan and Namibian *Pachydactylus* specimens (including the type series of *P. angolensis*), deposited in the collections of the American Museum of Natural History (**AMNH**), New York, U.S.A.; the California Academy of Sciences (**CAS**), San Francisco, U.S.A.; the Museum of Comparative Zoology (**MCZ**), Harvard University, Cambridge, Massachusetts, U.S.A.; the Museu Nacional de História Natural e da Ciência da Universidade de Lisboa (**MUHNAC**), Lisboa, Portugal; the Museu Regional do Dundo (**MD**), Dundo, Angola; the Instituto Nacional da Biodiversidade e Áreas de Conservação (**INBAC**), Kilamba-Kiaxi, Angola; and the Ditsong National Museum of Natural History (**TM**), Pretoria, Gauteng, South Africa.

Phylogenetic methods

Taxon sampling includes 16 specimens of *Pachydactylus angolensis* sensu lato from across their coastal and inland range in Angola, along with six specimens of their presumed sister species *P. caraculicus*. Additional sampling includes specimens representing all species in the "northwestern group" of *Pachydactylus*, as well as exemplars of other species groups of *Pachydactylus* (Heinicke et al. 2017). *Chondrodactylus bibronii* was included to root the tree. All samples, along with locality data, voucher information, and GenBank accession numbers can be found in Table 1. Genomic DNA was isolated from ethanol-preserved tissues using Qiagen DNeasy blood and tissue kits. We chose to target mitochondrial and nuclear loci that have proven useful in assessing inter- and intraspecific relationships among gekkotans, including *Pachydactylus*, providing us the opportunity to take advantage of preexisting sequence data. For samples unique to this study, segments of the mitochondrial locus ND2 (NADH dehydrogenase subunit 2; 1041 bp), and nuclear locus RAG1 (recombination activating gene 1; 1038 bp) were amplified under standard protocols (Heinicke et al. 2017) in 25 µL reactions with published primer pairs (see Table 2). Amplified products were visualized on 1.5% agarose gels and purified using AMPure magnetic bead system (Agencourt Bioscience). Sequencing reactions used ABI Prism BigDyeTerminator (Applied Biosystems), and product was purified using Agencourt CleanSeq magnetic bead system (Agencourt Bioscience). Sequencing was carried out on an automated ABI 3730 for electrophoresis, and electropherograms were imported into Geneious 9.0 for assembly and subsequent alignment via MAFFT. We inspected all alignments by eye, and made adjustments as needed to ensure that 3-nucleotide alignment gaps corresponded to single codon deletions. To estimate the phylogenetic relationships among samples we used IQTree multicore version 2.2 (Nguyen et al. 2014). Initial partitioning was by locus and codon position, with the program allowed to identify the best partitioning scheme (Lanfear et al. 2012) under the Bayesian Information Criterion and best-fitting model of molecular evolution identified using ModelFinder (Kalyaanamoorthy et al. 2017). Branch support was assessed using 1000 ultrafast bootstraps (Minh et al. 2013). We also calculated uncorrected between-species mean sequence distances (p-distance) for the ND2 alignment using MEGA 11 (Tamura et al. 2021).

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 Loveridge (1944), Bauer et al. (2006a, 2006b) and Heinicke et al. (2011). We measured the following 15 features: snout-vent length (**SVL**), from tip of snout to vent; crus length (**CrusL**), from base of heel to knee; tail length (**TailL**), from vent to tip of unregenerated tail; tail width (**TailW**), measured at base of tail; axilla to groin length (**TrunkL**); head length (**HeadL**), distance from retroarticular process of the jaw to snout-tip; head width (**HeadW**), measured at angle of jaws; head depth (**HeadH**), measured from the base of the lower jaw to the top of head; ear length (**EarL**), longest dimension of ear; forearm length (**ForeaL**), from base of palm to elbow; orbital diameter (**OrbD**); nostril to eye distance (**NarEye**), distance between anteriormost point of eye and nostril; snout to eye distance (**SnEye**), distance between anteriormost point of eye and tip of snout; eye to ear distance (**EyeEar**), distance from anterior edge of ear opening to posterior corner of eye; interorbital distance (**Interorb**), shortest distance between left and right superciliary scale rows (Table 3, 4).

Coloration pattern was reported, and high-resolution photographs of preserved specimens taken. These data were compared with relevant literature on the group (Loveridge 1944, 1947; Laurent 1964; Bauer and Branch 1995; Bauer et al. 2002, 2006a, 2006b; Branch et al. 2011; Heinicke et al. 2011) and comparative material of congeners occurring in southern Angola, namely *P. angolensis*, *P. caraculicus*, *P.* cf. *orephilus*, *P. scutatus*, *P. scherzi*, *P. rangei*, *P.* cf. *rugosus* and members of the *P. punctatus* species complex. All specimens examined in this study are listed in Table 1.

Table 1. Specimens used for morphometric and genetic analyses and corresponding GenBank accession numbers for genes used in the study. Locality data and elevation are reported in the form of decimal degrees and use the WGS 84 map datum and meters above sea level, respectively. See Materials and Methods section for collection abbreviations. Catalog and field number acronyms not cited in the Material and Methods section as follows: LSUMZ H, Genetic Resources, Louisiana State University Museum of Zoology, Baton Rouge, Louisiana, USA; NMZB, Natural History Museum of Zimbabwe, Bulawayo, Zimbabwe; AMB, Aaron M. Bauer field numbers; JET, James Titus-McQuillan field numbers; JVV, Jens V. Vindum field numbers; LMPC, Luis M.P. Ceríaco field numbers; NMB, National Museum Bloemfontein, Bloemfontein, South Africa; NMNW: National Museum of Namibia, Windhoek, Namibia; PEM, Port Elizabeth Museum, Bayworld, Gqeberha, South Africa. All genotyped specimens of *Pachydactylus maiatoi* **sp. nov.** are part of the type series. Newly generated sequences are denoted with an asterisk (*).

Species	Specimen ID		Locality	Coordinates	Elevation	GenBank Accession Number	
	Field No.	Museum No.				ND2	RAG-1
Pachydactylus angolensis Loveridge, 1944	n/a	AMNH R47874	Angola: Benguela, Hanha	–12.2450°, 13.7075°	24	—	—
	n/a	AMNH R47872	Angola: Benguela, Lobito Bay	–12.3500°, 13.5500°	7	—	—
	AMB 9961	CAS 266474	Angola: Benguela, Chimalavera National Park, camp	–12.9337°, 13.1699°	252	OQ680165*	OQ680144*
	AMB 9962	CAS 266475	Angola: Benguela, Chimalavera National Park, camp	–12.9337°, 13.1699°	252	OQ680166*	OQ680145*
	AMB 9979	CAS 266476	Angola: Benguela, Chimalavera National Park, camp	–12.9337°, 13.1699°	252	OQ680167*	OQ680146*
	AMB 9980	CAS 266477	Angola: Benguela, Chimalavera National Park, camp	–12.9337°, 13.1699°	252	OQ680168*	OQ680147*
	AMB 10002	CAS 266478	Angola: Benguela, Chimalavera National Park, camp	–12.9337°, 13.1699°	252	OQ680174*	OQ680148*
	AMB 10003	CAS 266479	Angola: Benguela, Chimalavera National Park, camp	–12.9337°, 13.1699°	252	OQ680169*	OQ680149*
	AMB 10004	CAS 266480	Angola: Benguela, Chimalavera National Park, camp	–12.9337°, 13.1699°	252	OQ680170*	OQ680150*
	AMB 10034	CAS 266481	Angola: Benguela, Chimalavera National Park, waterhole	–12.7917°, 13.1274°	207	OQ680173*	—
	AMB 10024	CAS 266482	Angola: Benguela, Dombe Grande, Cuio rd	–12.9781°, 13.0739°	69	OQ680171*	—
	AMB 10025	CAS 266483	Angola: Benguela, Dombe Grande, Cuio rd	–12.9781°, 13.0739°	69	OQ680172*	OQ680151*
	n/a	MD 1931a	Angola: Namibe, Praia das Conchas	–15.1333°, 12.1167°	16	—	—
	n/a	MD 1931b	Angola: Namibe, environs de Moçamedes (Moçâmedes surroundings)	—	—	—	—
	n/a	MD 1931c	Angola: Namibe, environs de Moçamedes (Moçâmedes surroundings)	—	—	—	—
	n/a	MD 1931d	Angola: Namibe, environs de Moçamedes (Moçâmedes surroundings)	—	—	—	—
	n/a	TM 25454	Angola: Namibe, San Nicolau (=São Nicolau)	–14.2577°, 12.3969°	22	—	—
	n/a	TM 25455	Angola: Namibe, San Nicolau (=São Nicolau)	–14.2577°, 12.3969°	22	—	—
	n/a	TM 40329	Angola: Namibe, Saco de Giraul	–15.0688°, 12.1422°	38	—	—
	n/a	TM 39111	Angola: Benguela, 24 km S	–12.6975°, 13.2522°	98	—	—
	n/a	TM 41266	Angola: Benguela, 30 km N of Dombe Grande	–12.7309°, 13.2302°	86	—	—
	n/a	TM 46558	Angola: Benguela, Hanha, 20 km N of Lobito	–12.2585°, 13.6734°	82	—	—
	AMB 9863	CAS 264237	Angola: Namibe, Bentiaba fort	–14.2733°, 12.3850°	51	—	—
Pachydactylus austeni Hewitt, 1923	AMB 3295	LSUMZ H1629	South Africa: Northern Cape, Port Nolloth	–29.2519°, 16.8697°	14	KY224250	JQ945321
Pachydactylus bicolor Hewitt, 1926	AMB 7631	NMNW (pending)	Namibia: 2 km S Erwee	–19.7048°, 14.3143°	1182	JN543870	JN543911
Pachydactylus boehmei Bauer, 2010	MCZ FS-A38529	MCZ R 184883	Namibia: Farm Uisib	–19.5516°, 17.2364°	1400	JN543906	JN543947

Species	Specimen ID		Locality	Coordinates	Elevation	GenBank Accession Number	
	Field No.	Museum No.				ND2	RAG-1
Pachydactylus capensis (Smith, 1846)	AMB 8361	MCZ R 184499	South Africa: Limpopo, Kgama	–24.0516°, 28.4342°	1267	HQ165962	HQ165992
Pachydactylus caraculicus FitzSimons, 1959	AMB 10347	CAS (pending)	Angola: Namibe, N'Dolondolo	–13.8133°, 13.1362°	681	OQ680175*	OQ680152*
	AMB 10622	CAS (pending)	Angola: Namibe, Virei	–16.1196°, 12.8346°	522	OQ680176*	OQ680153*
	AMB 10626	CAS (pending)	Angola: Namibe, between Copopolo and Tchitundulo, outcrop near camp	–16.0913°, 12.8357°	564	OQ680177*	OQ680154*
	JET157	n/a	Angola: Namibe, 52 km N on road to Lucira from jct. with Lubango-Namibe road	–14.65806°, 12.52717°	586	OQ680178*	OQ680155*
	JET158	n/a	Angola: Namibe, 52 km N on road to Lucira from jct. with Lubango-Namibe road	–14.65806°, 12.52717°	586	OQ680179*	OQ680156*
	MCZ FS-A38952	MCZ R 185767	Namibia: 32 km S of Epupa Falls on Okangwati Rd.	–17.2358°, 13.2292°	975	JN543889	JN543933
Pachydactylus gaiasensis Steyn & Mitchell, 1967	AMB 7596	MCZ R 184169	Namibia: 22.4 km N. Ugab River Crossing on Gai-As Rd.	–20.7816°, 14.1086°	520	JN543891	KM073533
Pachydactylus geitje (Sparrman, 1778)	n/a	PEM R11226	South Africa: Farm Gunsfontein	–32.5664°, 20.6811°	1548	JN543887	JN543931
Pachydactylus kladeroderma Branch, Bauer & Good, 1996	n/a	PEM R1253	South Africa: Western Cape	—	—	KY224251	JQ945323
Pachydactylus kochii FitzSimons, 1959	AMB 6326	CAS 214803	Namibia: 59 km N Swakopmund	–22.1992°, 14.3267°	9	KY224212	KY224311
Pachydactylus labialis FitzSimons, 1938	MCZ FS-A38412	MCZ R 184758	South Africa: Northern Cape, Port Nolloth Dump	–29.2558°, 16.9131°	26	KY224227	KY224325
Pachydactylus maiatoi **sp. nov.**	AMB 10284	CAS 266484	Angola: Namibe, N'Dolondolo	–13.8133°, 13.1362°	681	OQ680180*	—
	AMB 10345	CAS 266485	Angola: Namibe, N'Dolondolo	–13.8133°, 13.1362°	681	OQ680181*	—
	JVV 8564	CAS 254887	Angola: Namibe, Namibe-Lubango rd, 2 km E of Mangueiras	–15.0436°, 13.1600°	625	KY224217	OQ680164*
	AMB 10216	CAS 266486	Angola: Namibe, Serra da Neve base camp	–13.7770°, 13.2591°	1488	OQ680182*	—
	LMPC 1182	MB03-001246	Angola: Namibe, Serra da Neve, Maylowe village	–13.8355°, 13.2755°	798	—	—
	AMB 11349	CAS 264256	Angola: Namibe, Maungo	–14.5383°, 12.7474°	363	—	—
	AMB 11402	CAS 264267	Angola: Namibe, Maungo, abandoned health post	–14.5397°, 12.7447°	368	—	—
Pachydactylus maraisi Heinicke, Adderly, Bauer & Jackman, 2011	JV 1856	NMNW (pending)	Namibia: 2.7 km S of Wlotzkasbaken	–22.4314°, 14.4612°	8.8	JN543871	JN543912
Pachydactylus mariquensis Smith, 1849	n/a	NMB R10936	South Africa: N. Cape, along N10 from Britstown to Prieska	–30.1925°, 23.0957°	1042	JN569157	JN569190
Pachydactylus oreophilus McLachlan & Spence, 1967	AMB 10449	pending accession	Angola: Namibe, Omahua	–16.1986°, 12.4007°	340	OQ680183*	OQ680157*
	MCZ FS-A38962	MCZ R 185769	Namibia: N of Okangwati	–17.2900°, 13.1586°	1180	JN543892	JN543936
Pachydactylus otaviensis Bauer, Lamb and Branch 2006	MCZ FS-A38512	MCZ R 184867	Namibia: Farm Varianto	–19.3794°, 17.7408°	1530	JN543893	JN543937
Pachydactylus parascutatus Bauer, Lamb and Branch 2002	AMB 6512	CAS 214750	Namibia: 8 km W Sesfontein	–19.1681°, 13.5675°	523	JN543894	JN543938

Species	Specimen ID		Locality	Coordinates	Elevation	GenBank Accession Number	
	Field No.	Museum No.				ND2	RAG-1
	AMB 10464	pending accession	Angola: Namibe, Omahua	−16.1986°, 12.4007°	340	OQ680184*	OQ680158*
Pachydactylus punctatus Peters, 1854	AMB 10036	INBAC/AMB 10036	Angola: Benguela, Chimalavera Nature Reserve, waterhole	−12.7917°, 13.1274°	207	OQ680185*	OQ680159*
	MCZ F-28699	MCZ R193175	Namibia: Farm Omandumba	−21.5391°, 15.5456°	2215	OQ680186*	OQ680160*
	—	PEM R12461	South Africa: Northern Cape, Riuchtersveld, Sendelingsdrift	−28.1233°, 16.8934°	698	KY224233	KY224331
Pachydactylus rangei (Andersson, 1908)	AMB 10436	CAS 263008	Angola: Namibe, Curoca River	−16.2653°, 12.3209°	190	OQ680187*	OQ680161*
Pachydactylus rugosus Smith, 1849	AMB 5050	CAS 201905	South Africa: Northern Cape, Richtersveld National Park, Sendelingsdrif dump	−28.0980°, 16.8778°	718	KY224252	JQ945325
Pachydactylus sansteynae Steyn & Mitchell, 1967	AMB 6350	CAS 214589	Namibia: 1 km S Huab Bridge	−20.9008°, 13.5336°	29	JN543898	KY224334
Pachydactylus scherzi Mertens, 1954	JVV 8387	CAS 254810	Angola: Namibe, Iona National Park, Espinheira	−16.7858°, 12.3547°	456	OQ680188*	OQ680162*
	MCZ FS-A38577	MCZ R 184938	Namibia: W. Side of Grootberg Pass	−19.8400°, 14.1136°	1380	KY224236	KY224335
Pachydactylus scutatus Hewitt, 1927	JVV 8451	CAS 254826	Angola: Namibe, Espinheira	−16.7977°, 12.3542°	474	OQ680189*	OQ680163*
	MCZ Z-37843	NMNW 11150	Namibia: Windpoort farm	−19.3501°, 15.4833°	1182	JN543901	JN543943
Pachydactylus serval Werner, 1910	n/a	MCZ R 185989	Namibia: Brukkaros Mountain, S Slope	−25.8969°, 17.7772°	1096	HQ165956	HQ165986
Pachydactylus wahlbergii (Peters, 1869)	n/a	NMZB 16974	Zambia: Southern Province, Kazungula District, Kalamba Station	−17.8838°, 26.2137°	573	JN569158	JN569191
Pachydactylus weberi Roux, 1907	n/a	PEM R12449	South Africa: Northern Cape, 1.4 km S of Garies	−30.5749°, 17.9965°	222	HQ165960	HQ165990
Chondrodactylus bibroni (Smith, 1846)	AMB 4853	CAS 201841	South Africa: Northern Cape, 28 km E Pofadder	−29.0214°, 19.6517°	795	JN543886	JN543930

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 Branch et al. (2017) and have been georeferenced using the GEOLocate web application (https://www.geo-locate.org). Elevations are all reported as meters above sea level.

Results

Phylogenetic relationships

The final concatenated alignment includes 51 terminals and 2079 nucleotide sites. The best partitioning scheme includes four partitions, with the three ND2 codon positions treated as three separate partitions and the full RAG1 alignment grouped as a fourth partition. The following best-fitting models of evolution were used in the analysis: GTR + F + I + Γ (ND2 1^{st} position); TIM3 + F + I + Γ (ND2 2^{nd} position); TIM + F + Γ (ND2 3^{rd} position); HKY + F + Γ (RAG1). The phylogeny (Fig. 4) recovers a strongly supported (99% bootstrap) monophyletic northwestern clade lowercase of *Pachydactylus* that includes both the coastal and inland "*angolensis*" taxa. These two species are recovered as each other's closest relatives with maximum (100% bootstrap) support. Interrelationships of species within the northwestern clade lowercase are similar to those recovered by Heinicke et al. (2017), but the position of the coastal + inland *angolensis* clade differs. Our results suggest that this clade is neither most closely related to *P. scutatus* (Loveridge 1944; Bauer 2002) nor to *P. caraculicus* (Heinicke et al. 2017). Instead, coastal + inland is recovered as most closely related to *P. oreophilus* with 90% bootstrap support. The differing position compared to the molecular analysis in Heinicke et al. (2017) is apparently due to a single RAG1 sequence (Genbank accession KY224316) misattributed to *P. angolensis* (= inland taxon) in Heinicke et al. (2017) but identical to *P. caraculicus* according to our denser sampling here. We interpret this sequence as most likely representing a sequencing contaminant. All of the new RAG1 sequences of coastal and inland taxa generated for this study instead match the pattern of the concate-

Table 2. List of primers used for PCR in this study.

Gene	Primer	Sequence	Source	Use
ND2	ND2 f17	5'-TGACAAAAAATTGCNCC-3'	Macey et al. (2000)	Sequencing
ND2	CO1 R1	5'-AGRGTGCCAATGTCTTTGTGRTT-3'	Macey et al. (1997)	Amplification and Sequencing
ND2	CO1 R8	5'-GCTATGTCTGGGGCTCCAATTAT-3'	Weisrock et al. (2001)	Amplification and Sequencing
tRNATrp	Trp R3	5'-TTTAGGGCTTTGAAGGC-3'	Greenbaum et al. (2007)	Sequencing
tRNAMet	Met F1	5'-AAGCTTTCGGGCCCATACC-3'	Macey et al. (1997)	Amplification and Sequencing
RAG1	RAG1 g396	5'-TCTGAATGGAAATTCAAGCTGTT-3'	Groth and Barrowclough (1999)	Amplification and Sequencing
RAG1	RAG1 g397	5'-AAAGGTGGCCGACCGAGGCAGCATC-3'	Groth and Barrowclough (1999)	Amplification and Sequencing
RAG1	RAG1 f700	5'-GGAGACATGGACACAATCCATCCTAC-3'	Bauer et al. (2007)	Sequencing
RAG1	RAG1 r700	5'-TTTGTACTGAGATGGATCTTTTTGCA-3'	Bauer et al. (2007)	Sequencing

Table 3. Morphological and meristic comparisons between *Pachydactylus angolensis* and *P. maiatoi* **sp. nov.**. Data presented as "mean [minimum–maximum]", measurements are presented in millimeters (mm). Abbreviations are those described in Materials and Methods section.

	P. angolensis **("coastal form") (*n* = 18)**	***P. maiatoi*** **sp. nov. ("inland form") (*n* = 7)**
SVL	34.2 [21.9–40.8]	32.1 [17.8–40.5]
TL	30.2 [17.9–39.6]	27.1 [31.5–22.6]
ForeaL	4.2 [2.6–5.2]	3.8 [1.7–4.8]
CrusL	4.9 [3.1–6.4]	4.9 [2.7–6.2]
TailW	2.6 [1.3–3.2]	3.0 [4.0–1.9]
TrunkL	15.2 [9.7–18.3]	15.4 [8.8–20.5]
HeadL	10.0 [7.2–11.7]	9.6 [5.8–11.8]
HeadW	5.9 [4.1–19]	6.2 [3.6–7.5]
HeadH	3.8 [2.4–4.7]	3.6 [2.9–4.4]
OrbD	2.2 [1.4–2.8]	2.2 [1.5–2.7]
EyeEar	2.6 [1.8–3.5]	2.5 [1.5–2.5]
SnEye	3.4 [2.3–4.1]	3.6 [2.7–4.2]
NarEye	2.4 [1.3–3.3]	2.3 [1–3.0]
InterOrb	2.6 [1.2–3.4]	2.5 [1.3–3.3]
EarL	0.6 [0.4–0.7]	0.6 [0.3–0.9]

Table 4. Mensural (in mm) counts of the holotype and paratypes of *Pachydactylus maiatoi* **sp. nov.**. Abbreviations are the same as those described in the Materials and Methods section.

	CAS 266485	**CAS 266486**	**CAS 266484**	**CAS 254887**	**CAS 264256**	**CAS 264267**	**MB03-001246**
	Holotype	**Paratype**	**Paratype**	**Paratype**	**Paratype**	**Paratype**	**Paratype**
Sex	♂	juvenile/♂	♀	♂	♂	♂	♂
SVL	36.1	17.8	37.8	23.4	40.5	36.1	32.7
ForeaL	4.7	1.7	4.3	3.2	3.9	4.8	4.1
CrusL	5.5	2.7	5.6	3.5	6.2	5.4	5.4
TailL (total)	4.0	—	—	22.7	27.9	10.3	—
TailL (regen)	23.7	—	—	—	3.6	4.6	2.7
TailW	4.0	—	—	1.9	3.1	3.4	2.7
TrunkL	16.3	8.8	18.5	10.0	20.5	15.9	17.7
HeadL	10.3	5.9	11	7.5	11.2	11.8	9.6
HeadW	6.9	3.6	7.5	4.5	7.5	6.8	6.6
HeadH	3.8	2.9	3.7	3.1	4.4	4.2	3.2
OrbD	2.3	1.5	2.2	2.0	2.2	2.7	2.3
EyeEar	3.2	1.5	2.8	1.8	3.1	2.8	2.7
SnEye	4.1	2.7	3.9	2.8	4.2	3.9	3.9
NarEye	2.7	1.0	2.9	1.7	2.7	3.0	2.5
InterOrb	3.3	1.8	3.1	2.3	3.0	2.8	1.3
EarL	0.3	0.4	0.6	0.3	0.6	0.6	0.8

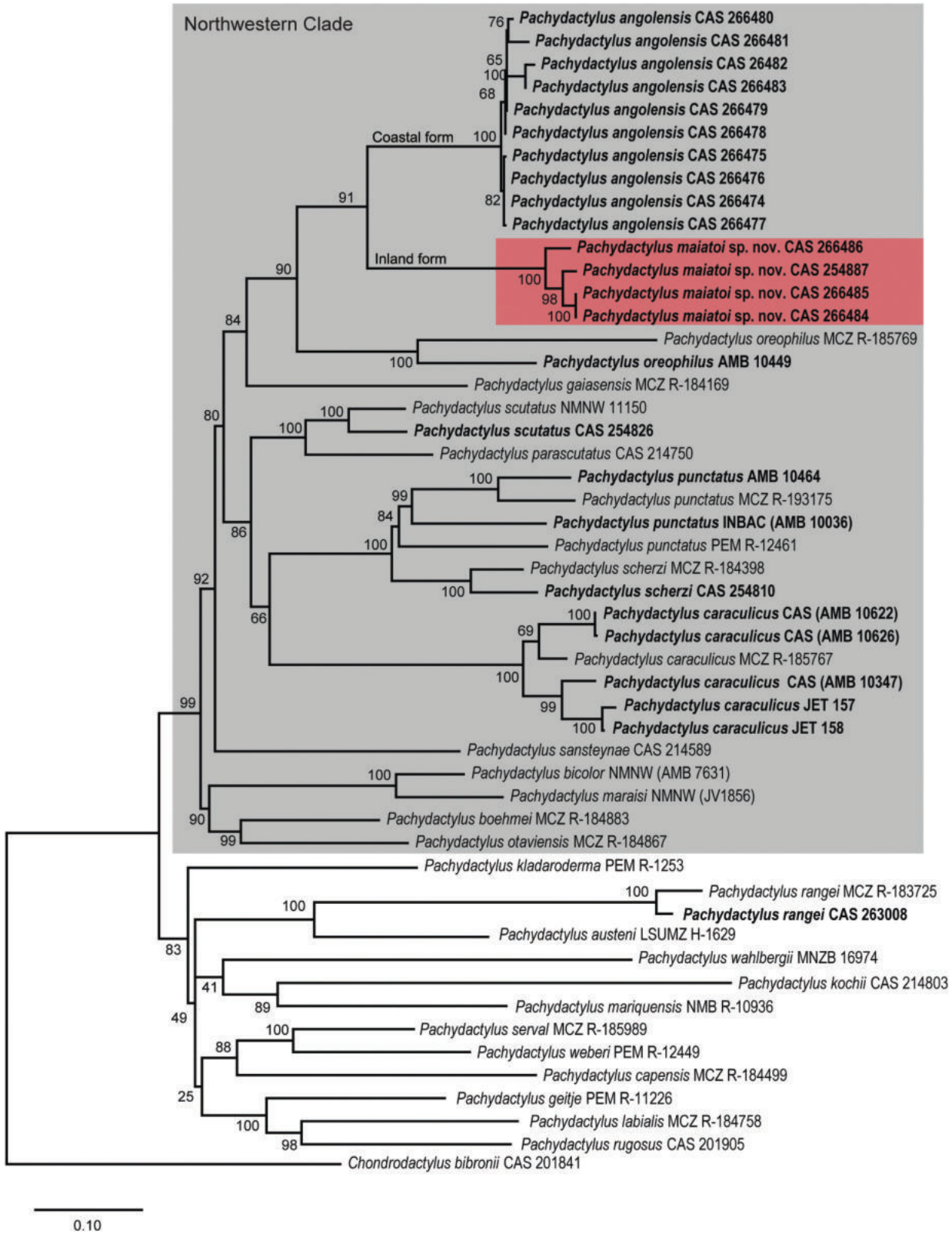

Figure 4. Maximum likelihood phylogeny of *Pachydactylus* based on a concatenated dataset of ND2 and RAG1 sequences. The tree is rooted with an exemplar of the closely related genus *Chondrodactylus*. Samples from Angola are shown in bold. Bootstrap support values are shown at nodes.

nated phylogeny when analyzed as an individual locus (Fig. 4).

The genetic distinctiveness of the inland from the coastal form is substantial, far greater than that between some other species pairs within the northwestern clade lowercase. The uncorrected mean ND2 sequence distance between the two species is 21%. In comparison, the uncorrected mean ND2 distance between *P. bicolor* and *P. maraisi* is 16%, that between *P. scutatus* and *P. parascutatus* is 17%, and that between *P. punctatus* and *P. scherzi* is 18%.

Systematics

(Reptilia: Squamata: Gekkonidae)

Pachydactylus maiatoi sp. nov.

https://zoobank.org/0C35D42A-405C-4C72-89C2-5C670FFF7FCA

Figs 5–9; Tables 3, 4

Pachydactylus angolensis – Ceríaco et al. (2016: 25)
Pachydactylus angolensis "inland form" – Branch et al. (2017: 164)
Pachydactylus angolensis [partim] – Marques et al. (2018: 192)

Holotype. An adult male (CAS 266485, field no. AMB 10345), collected in N'Dolondolo [–13.8133°, 13.1362°, 681 m a.s.l.], Namibe Province, Angola, by Luis M.P. Ceríaco, Suzana A. Bandeira, and Ishan Agarwal on 22 November 2016.

Paratypes. Six specimens: one adult male (CAS 254887, field no. JVV 8564), collected in Namibe-Lubango rd, 2 km E of Mangueiras [–15.0436°, 13.1600°, 625 m a.s.l.], Namibe Province, Angola, by Luis M.P. Ceríaco, Hilária Valério, Suzana A. Bandeira, Sango de Sá, Arianna L. Kuhn, Edward L. Stanley, and Jens V. Vindum on 5 December 2013; one adult female (CAS 266484, field no. AMB 10284) with the same data as the holotype; one juvenile (CAS 266486, field no. AMB 10216) collected in Serra da Neve, base camp [–13.7770°, 13.2591°, 1488 m a.s.l.], Namibe Province, Angola, by Luis M.P. Ceríaco, Suzana A. Bandeira, and Ishan Agarwal on 18 November 2016; one adult male (CAS 264256, field no. AMB 11349) collected in Maungo [–14.5383°, 12.7474°, 363 m a.s.l.], Namibe Province, Angola, by Mariana P. Marques, Luis M.P. Ceríaco and Joyce M. Janota on 7 August 2018; one adult male (CAS 264267, field no. AMB 11402) collected in Maungo, abandoned health post [–14.5397°, 12.7447°, 368 m a.s.l.], Namibe Province, Angola, by Mariana P. Marques, Luis M.P. Ceríaco and Joyce M. Janota on 9 August 2018; one adult male (MUHNAC/MB03-001246, field no. LMPC 1182) collected in Serra da Neve, Maylowe village [–13.8355°, 13.2755°, 798 m a.s.l.], Namibe Province, Angola, by Mariana P. Marques, Luis M.P. Ceríaco, and Joyce M. Janota on 26 February 2019.

Additional material. Namibe Province: Serra da Neve, rocky area near Catchi village [–13.7642°, 13.2573°, 1614 m a.s.l.] (MUHNAC/MB03-001247); Serra da Neve base, 2 km N of Maylowe [–13.8280°, 13.2625°, 820 m a.sl.] (MUHNAC/MB03-001248); Lungo [–14.3167°, 13.2000°, 749 m a.s.l.] (imprecise locality) (TM 24406).

Diagnosis. A small, rupiculous *Pachydactylus* with a depressed body form. SVL at least 40.5 mm (Table 3, 4). Dorsum with enlarged, keeled dorsal scales. OrbD slightly greater than EyeEar. Rostral and supralabials excluded from the nostril rim. Lack of contact between the nostril and both the first supralabial and rostral. Tail indistinctly segmented with juxtaposed to subimbricate scalation. Dorsal pattern almost uniform beige to dark brown, sometimes with small and very diffuse whitish spots, with a dark mask in the lateral side of the head terminating above or just anterior to the ear. Labials white. Venter cream with brown spots on limbs and tail. Tail lighter than the dorsum. Forelimbs and hindlimbs moderately short and stout, interdigital webbing absent, free digits with four (4) subdigital, undivided lamellae.

Comparison with other *Pachydactylus* species. From other members of the "northwestern clade" of *Pachydactylus* (fide Heinicke et al. 2017) it may be easily differentiated from *P. bicolor*, *P. maraisi*, *P. punctatus*, *P. scherzi*, and *P. caraculicus* by its enlarged, keeled dorsal scales (versus atuberculate or smooth scales in the latter). It can be differentiated from most other member of the northwestern group (*P. scutatus*, *P. parascutatus*, *P. boehmei*, *P. gaiasensis, P. oreophilus*, *P. sansteynae*) by the lack of contact between the nostril and both the first supralabial and the rostral (in contact in all the latter). It can be distinguished from *P. otaviensis*, endemic to the Otavi highlands in Namibia, by not having the first supralabial in contact with the nostril (versus in contact in *P. otaviensis*) and by having a homogeneous cream to brown dorsal coloration pattern (versus consisting of three pale bands on the nape, just posterior to adpressed elbow, and posterior trunk, anterior to lumbar region in *P. otaviensis*). Regarding its sister species, *P. angolensis*, the newly described species consistently differs in terms of its coloration, with *P. angolensis* presenting scattered large white spots and orange blotches in its light brown dorsum, while in *P. maiatoi* **sp. nov.** the dorsum is generally homogenously cream to dark brown, although some specimens may present small and very diffuse whitish spots.

Regarding the other species of *Pachydactylus* occurring in Angola but not belonging to the "northwestern group", *P. maiatoi* **sp. nov.** differs from *P. vanzyli* by the presence of four (4) subdigital undivided lamellae on fourth toe (versus two (2) in the latter), from *P. rangei* and *P. wahlbergii* by having enlarged, keeled dorsal scales (versus atuberculate and very smooth skin). It can be further distinguished from *P. vanzyli* and *P. rangei* by its free digits (versus webbed digits of pes or both manus and pes in the latter), and its general color (pinkish in *P. rangei* versus cream to brown in *P. maiatoi* **sp. nov.**). *Pachydactylus rangei* only occurs in dunes and in very sandy regions including dry river beds, whereas the new species is rupiculous. It differs from *P.* cf. *rugosus* by its much less spiny appearance and by its dorsal coloration pattern (mostly homogeneous cream to brown in *P. maiatoi* **sp. nov.** versus cream bands on brown dorsum in *P.* cf. *rugosus*).

Description of Holotype. Adult male. SVL 36.1 mm (Fig. 5; Table 3). Body moderately depressed, elongate (TrunkL/SVL 0.45). Head short (HeadL/SVL 0.28), moderately wide (HeadW/HeadL 0.66), depressed (HeadH/HeadL 0.38), slightly distinct from neck. Lores inflated; interorbital region flat. Snout slightly acuminate and con-

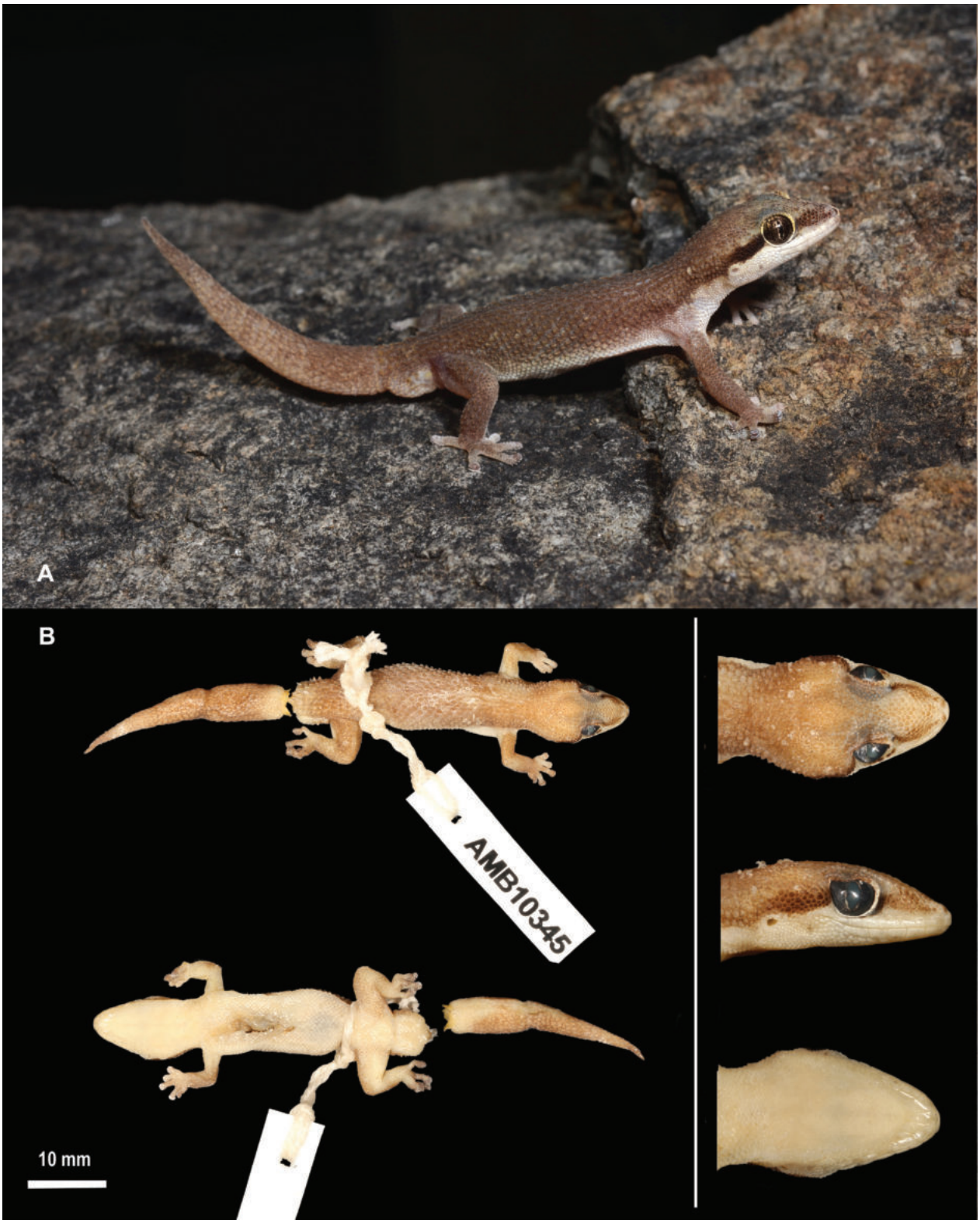

Figure 5. Photos of the holotype (CAS 266485) of *P. maiatoi* **sp. nov.**, (**A**) life and (**B**) preserved, from N'Dolondolo, Namibe Province, Angola. Photo by Luis M.P. Ceríaco.

vex, and moderately long (SnEye/HeadL 0.39), longer than eye diameter (OrbD/SnEye 0.57); scales on snout and canthus large, smooth, flattened, heterogeneous in size and shape; scales of interorbital and parietal regions heterogeneous, regularly scattered with tiny granules interspersed with larger conical to rounded tubercles. Eye small (OrbD/HeadL 0.22), with 10–12 superciliaries and posterodorsal corner of orbit bearing very small spines; pupil vertical, with crenellated margins; Ear-opening small, horizontally ovoid (EarL/HeadL 0.06). Eye to ear distance higher than the diameter of eye (EyeEar/OrbD 1.39). Rostral approximately 50% as deep as wide, no rostral groove, contacted by two enlarged supranasals and first supralabials; nostrils oval, each surrounded by

Figure 6. Life photo of one the paratypes (CAS 264267) of *P. maiatoi* **sp. nov.**, from Maungo, Namibe Province, Angola. Photo by Luis M.P. Ceríaco.

Figure 7. Juvenile paratype (CAS 254887) of *Pachydactylus maiatoi* **sp. nov.**. Photo by Luis M.P. Ceríaco.

two postnasals, supranasal, without contact with the first supralabial or rostral; supranasals in contact; one row of scales separates orbit from supralabials; mental elongate, deeper than wide; no enlarged postmentals or chin shields. Enlarged supralabials (left/right) counted to rictus 7/8 (6 to mid-orbit); infralabials 6/7; interorbital scale rows between superciliary rows at midpoint of orbit 19 (8 across narrowest point of frontal bone).Dorsal tubercles large (about ten times the size of adjacent scales), largest dorsolaterally and smallest along dorsal midline rounded, with a pronounced median keel, forming 16 regular longitudinal rows on trunk, grading into posteriorly-directed, conical scales on lower flanks; each tubercle surrounded by an irregular rosette of about 3 to 7 small domed to conical scales; ventral scales flattened, rounded to oval, subimbricate to imbricate, mostly homogeneous, largest on precloacal region, approximately 30 between lowest conical granular rows on flank at midbody; chin granules approximately one fifth the size of ventral scales, increasing in size rather abruptly between gular region and chest.

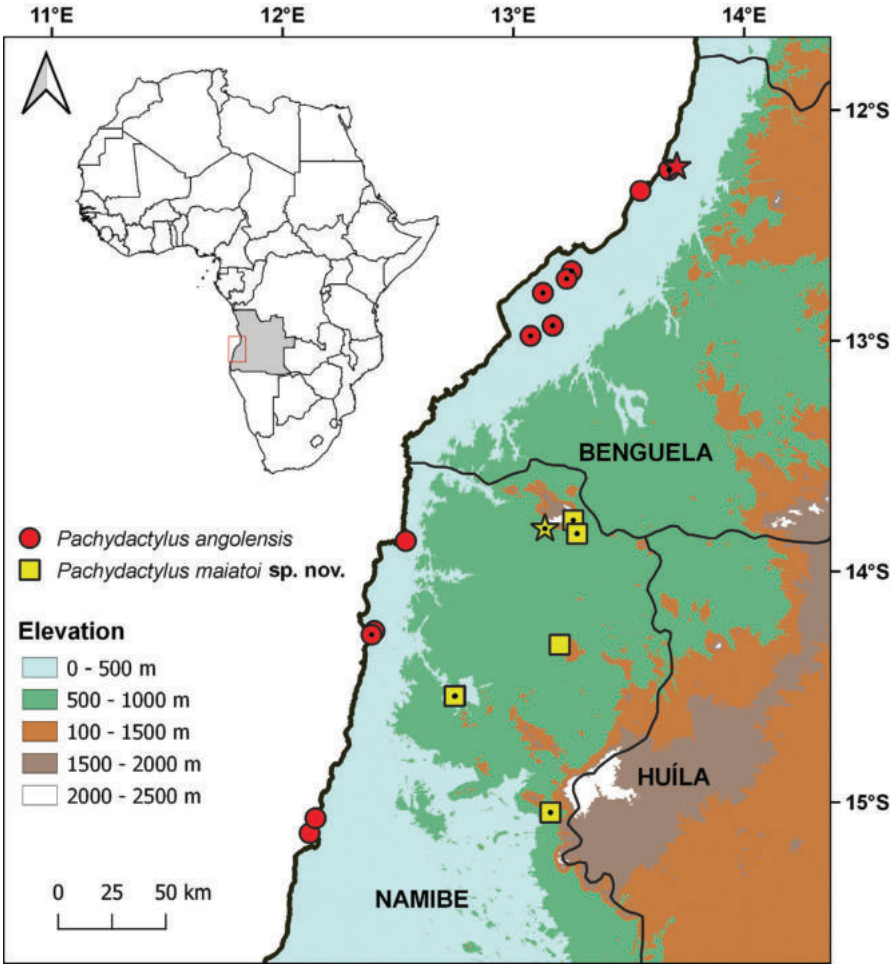

Figure 8. Distribution of *Pachydactylus angolensis* and *Pachydactylus maiatoi* **sp. nov.** in Angola. Stars represent the respective type localities; dotted symbols denote localities represented in the phylogenetic analysis.

No precloacal or femoral pores. Scales on palm, sole, and ventral surface of forelimb smooth, granular; scales on dorsal aspect of forelimb small, smooth, heterogeneous, subimbricate; scales on preaxial and ventral aspects of thighs somewhat enlarged, smooth, imbricate; scales on dorsum of thigh non-tuberculate, heterogeneous, small to large, flattened to conical; scales on dorsum of crus small, conical, with scattered large (about eight times the size of adjacent scales), keeled round tubercles. Forelimbs short, stout (ForeaL/SVL 0.13); hindlimbs short (CrusL/SVL 0.15); digits short; subdigital scansors, except for distal-most, entire, present only on distal portion of toes, approximately 1.5 times wider than more basal (non-scansorial) subdigital scales; interdigital webbing absent. Relative length of digits (manus): III ~ IV > V > II > I; (pes): IV > III > V > II > I. Subdigital scansors (excluding small distal divided scansor) I (3), II (3), III (3), IV (3), V (3) — manus; I (4), II (4), III (4), IV (4), V (3) — pes. Tail sub-cylindrical, fully regenerated; weakly depressed; postcloacal spurs present.

Coloration of the Holotype. Dorsum almost homogeneous brown with small and diffuse whitish spots (Fig. 5). Dark facial band extending from snout, through the eye and becoming more evident from the posterior part of the eye to right above the ear opening, stopping before the ear opening. Top of head beige slightly lighter than the dorsum. Supralabials and infralabials completely white. Limbs of the same color of the dorsum but digits paler. Venter cream with brown spots on limbs and tail. Tail lighter than the dorsum. Life coloration (Fig. 5A) is similar to that in preservative (Fig. 5B).

Variation. Variation in mensural and meristic characters of the holotype and adult paratypes are presented in Table 3. All paratypes agree entirely with the holotype and have a similar coloration pattern, only varying the tone of the coloration — from beige (e.g., CAS 254887, 264267; 266484, 266486) to darker brown (e.g., CAS 264256; MB03-001246). Some specimens (CAS 254887, 266484) present very faded brown spots on venter region. The juvenile paratype (CAS 254887, SVL 23.4 mm, Fig. 7) has similar coloration to that of adults, but the tail presents very vague darker bands.

Distribution and habitat. *Pachydactylus maiatoi* **sp. nov.** appears to be restricted to southwestern Angola, namely in the inland regions of northern Namibe Province and along the highlands associated with the Angolan escarpment (Fig. 8). Individuals were collected under rocks in areas with sparse vegetation, but always associated to inselbergs (Fig. 9). It is expected that the species also occurs in neighboring areas of Benguela Province, but so far, no records of the species have been found in that province. The new species has a rupiculous habitat, while *P. angolensis*, as observed by the authors, is terres-

Figure 9. A Type locality of *Pachydactylus maiatoi* **sp. nov.**, N'Dolondolo, Serra da Neve inselberg, northern Namibe Province. Photo by Ishan Agarwal. **B** Collecting locality of the paratype (CAS 264267) in Maungo region, central Namibe Province. Photo by Luis M. P. Ceríaco.

trial with a habitat preference similar to that of *P. punctatus*.

Conservation. *Pachydactylus angolensis* as previously construed was evaluated as a stable species of Least Concern (Ceríaco et al. 2020d). Although only *Pachydactylus angolensis* sensu stricto is represented in a formal conservation area (i.e. Chimalavera Regional Natural Park), both species are relatively widespread in regions that are subject to minimal habitat transformation. Following the IUCN Red List criteria and guidelines (IUCN Standards and Petitions Committee 2019), and using the GeoCAT:

geospatial conservation assessment tool (Bachman et al. 2011), we estimated an extent of occurrence of around 13.700 km² for *Pachydactylus maiatoi* **sp. nov.** and 18.500 km² for *P. angolensis*, which classify both species as Vulnerable (VU) based on their extent of occurrence. However, further research on the extent of occurrence, population trends and ecology of these species is fundamental for a formal assessment of their conservation status.

Etymology. The species is named after the Angolan biologist Francisco Maiato Gonçalves (Huambo, 1982–), a researcher and curator of the Herbarium of Lubango (ISCED), and vice-dean for Research and International Affairs at the University Mandume Ya Ndemufayo, Huíla Province, Angola. Francisco Maiato Gonçalves represents a new generation of Angolan researchers and a driving force in the study and conservation of southern Angolan biodiversity. The specific epithet is a patronym in the masculine genitive singular. We propose the English common name of Maiato's thick-toed gecko and the Portuguese common name of osga-de-dedos-grossos-de-Maiato.

Discussion

Southwestern Angola has been recognized by several authors as a hotspot of diversity for reptiles, especially associated with arid and hyper-arid habitats (Ceríaco et al. 2016; Marques et al. 2018; Branch et al. 2019b). This is particularly true for lizards, as suggested by the description of several endemic or near-endemic species in the last decade, including six lacertids (Conradie et al. 2012; Branch et al. 2019a; Parrinha et al. 2021; Marques et al. 2022), six gekkonids (Ceríaco et al. 2020b; Marques et al. 2020; Branch et al. 2021; Lobón-Rovira et al. 2022a), one scincid (Ceríaco et al. 2020a) and two cordylids (Stanley et al 2016; Marques et al. 2019). Gekkonids are particularly diverse in the region, with more than half of Angolan species recorded in Iona National Park alone (Lobón-Rovira et al. 2022b). The description of *Pachydactylus maiatoi* **sp. nov.** represents the most recent addition to the gekkonid fauna of Angola, raising the number of Angolan *Pachydactylus* to 11, and to a total of 58 recognized species in the genus. However, this number is expected to rise with further works on the taxonomy of Angolan *Pachydactylus*, as cryptic diversity identified in other groups within the genus awaits formal description. This is especially true for the *P.* cf. *punctatus* group, for which an ongoing revision is being prepared (Bauer et al. unpublished).

While these discoveries highlight the significance of southwestern Angola as a hotspot of diversity and endemism, considerable areas remain largely unexplored in terms of biodiversity and require further surveys and research efforts. The study of the Angolan radiation of *Pachydactylus* represents yet another contribution to the overall knowledge of biogeographic patterns in southwestern Angola. While the region supports endemic lizards that are generally widespread (e.g., *Pedioplanis haackei* Conradie, Measey, Branch & Tolley, 2012), it also hosts more geographically restricted endemics, like *Pedioplanis huntleyi* Conradie, Measey, Branch & Tolley, 2012 in the mountainous areas of southeastern Namibe Province, and several recently described species known only from the Serra da Neve inselberg (e.g., *Lygodactylus baptistai* Marques et al., 2020, *Afroedura praedicta* Branch et al., 2021, *Cordylus phonolithos* Marques et al., 2019). *Pachydactylus angolensis* as currently construed joins other gekkonids (e.g., *Hemidactylus vernayi* Ceríaco, Agarwal, Marques & Bauer, 2020*, Bauerius ansorgii* (Boulenger, 1907)) and lacertids (e.g., *Pedioplanis benguelensis* (Bocage, 1867)) in a group of lizards endemic to the coastal areas of Namibe and Benguela provinces. This narrow, low elevation (< 500 m a.s.l.) coastal belt between Moçâmedes and Benguela experiences cooler temperatures and less precipitation than the central plains to the east, and has been suggested to be particularly affected by fog and low clouds resulting from the cooling effect of the upwelling Benguela Current (Huntley 2019), an important source of water in the arid and hyper-arid habitats of southwestern Africa. Although no detailed data on the occurrence and effects of fog is available for Angola, previous authors have suggested that it plays an important role in the ecology of the arid savannas of coastal Angola (Pinto et al. 2019). The diversity and distribution of endemic lizards in southwestern Angola suggests the existence of complex biogeographical patterns resulting from the interaction between climate and topography, which shall be investigated elsewhere.

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