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A revision of Angolan species in the genus *Pedioplanis* Fitzinger (Squamata: Lacertidae), with the description of a new species

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Abstract

The genus *Pedioplanis* reaches its northernmost limit in western Angola, where it is represented by three species, *Pedioplanis benguelensis*, *P. haackei* and *P. huntleyi*. The taxonomic status of *P. benguelensis* remains problematic, mainly due to the vague original description and the loss of the original type material. Here we provide a revision of the Angolan representatives of the genus, with the description of a new species, *Pedioplanis serodioi* **sp. nov.**, from the lowlands of southwestern Angola. Phylogenetic analyses using a combination of mitochondrial (*16S* and *ND2*) and nuclear (*RAG-1*) markers, as well as morphological data, support the recognition of the new species. For purposes of nomenclatural stability, we designate a neotype for *P. benguelensis* and provide motivation to correct the spelling of the specific epithet to "*benguelensis*". The clarification of the status of *P. benguelensis* and the description of a new species contribute to a better understanding of the taxonomy and biogeography of the genus *Pedioplanis*, as well as the general biogeographic context of southwestern Angola, adding to the growing evidence in favor of the recognition of this region as a hotspot of lizard diversity and endemism. An updated key to the genus is also provided.

Key words: Reptiles, lizards, Africa, Kaokoveld, endemism, taxonomy, neotype

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Resumo

O género *Pedioplanis* atinge o seu limite setentrional em Angola, onde é representado por três espécies, *Pedioplanis benguelensis*, *P. haackei* e *P. huntleyi*. O estatuto taxonómico de *P. benguelensis* permanece problemático, sobretudo devido à falta de detalhe na descrição original e à perda do material típico original. É aqui apresentada uma revisão dos representantes angolanos do género, com a descrição de uma nova espécie, *Pedioplanis serodioi* **sp. nov.**, das terras baixas do sudoeste de Angola. Análise filogenética utilizando uma combinação de genes mitocondriais (*16S* e *ND2*) e nucleares (*RAG-1*), bem como dados morfológicos, suportam o reconhecimento desta nova espécie. Tendo em vista a estabilidade nomenclatural, é designado um neótipo para *P. benguelensis*, bem como motivação para corrigir a ortografia do epíteto específico para "*benguelensis*". A clarificação do estatuto de *P. benguelensis* e a descrição de uma nova espécie contribuem para uma melhor compreensão da taxonomia e biogeografia do género *Pedioplanis*, assim como o contexto biogeográfico do sudoeste de Angola, acrescentando às evidências crescentes a favor do reconhecimento desta região como *hotspot* de diversidade e endemismo de lagartos. É também apresentada uma chave dicotómica actualizada para o género.

Palavras-chave: Répteis, lagartos, África, Kaokoveld, endemismo, taxonomia, neótipo

Introduction

Located in a transition zone between west-central Africa and southern Africa, Angola is one of the largest countries on the continent and hosts an extraordinary diversity of biomes and habitats, ranging from tropical and subtropical moist broadleaf forests in the north to deserts and xeric shrublands in the south (Marques *et al.* 2018; Huntley 2019). As a reflection of the diverse climate and landscape, more than 100 species of amphibians and nearly 300 species of reptiles have been recorded from Angola (Marques *et al.* 2018; Baptista *et al.* 2019b; Branch *et al.* 2019c). Several decades of armed conflict rendered travel and access to remote localities impractical and dangerous to carry out research, but new field surveys conducted in recent post-war years have resulted in the description of more than 30 new species of reptiles and amphibians (Conradie *et al.* 2012a, 2012b, 2013; 2020a; Stanley *et al.* 2016; Ceríaco *et al.* 2018; 2020a, 2020b, 2020c, 2021; Branch *et al.* 2019b, 2021; Marques *et al.* 2019a, 2019b, 2020; Hallermann *et al*. 2020; Nielsen *et al.* 2020; Lobón-Rovira *et al.* 2021), the rediscovery of several rare and poorly known species (*e.g.*, Branch *et al.* 2018, 2019a; Gonçalves *et al.* 2019; Vaz Pinto *et al.* 2019; Baptista *et al.* 2020) and the first records of species previously unknown for the country (*e.g.*, Branch & Conradie 2013; Ceríaco *et al.* 2016; Conradie & Bourquin 2013; Conradie *et al.* 2016, 2020b; Baptista *et al.* 2019a; Ernst *et al.* 2020). Among the reptiles described in the past two decades are several lizard species endemic or near-endemic to southwestern Angola (Haacke 2008; Conradie *et al.* 2012b; Stanley *et al.* 2016; Branch *et al.* 2019b, 2021; Marques *et al.* 2019, 2020; Ceríaco *et al.* 2020b), highlighting the importance of this region as a lizard hotspot and center of endemism.

The lacertid genus *Pedioplanis* Fitzinger, 1843, whose members are commonly referred to as Sand Lizards, comprises 15 currently recognized species and three subspecies, endemic to southwestern Africa (Branch 1998; Uetz *et al.* 2021; Childers *et al.* 2021). Most species currently allocated to *Pedioplanis* were originally described within the genus *Eremias* Wiegmann, 1834, and later assigned to the subgenus *Mesalina* Gray, 1838 by Boulenger (1918, 1921). The generic name *Pedioplanis* has been widely used by most authors since Baletto (1968) suggested its application for southern African members of *Mesalina*. The genus *Pedioplanis* reaches its northern limit in western Angola, which is home to a considerable diversity of lacertids (Marques *et al.* 2018; Branch *et al.* 2019b). Of these lacertids, *Pedioplanis* is one of the most diverse genera in the region. Currently, three species are recognized from Angola—*Pedioplanis benguelensis* (Bocage, 1867), *P. haackei* Conradie, Measey, Branch & Tolley, 2012 and *P. huntleyi* Conradie, Measey, Branch & Tolley, 2012.

Angolan *Pedioplanis* have historically been assigned to *P. benguelensis*, *P. namaquensis* (Duméril & Bibron, 1839) and *P. undata* (Smith, 1838). The first records of representatives of the genus in the country were provided by the Portuguese zoologist José Vicente Barbosa du Bocage, with the description of *Eremias benguelensis* based on specimens collected by the explorer José Alberto d'Anchieta from "Benguella" in western Angola (Bocage 1867a, 1867b). Subsequently, Boulenger (1887) synonymized *E. benguelensis* with *E. namaquensis*, a decision that was later followed by Bocage (1895). Bocage's (1895) decision to accept Boulenger's (1887) interpretation was later reinforced by the exclusion of *E. benguelensis* from the type catalogue of the Lisbon Museum (Bocage 1897). However, Boulenger (1918, 1921) later recognized *E. benguelensis* as a valid species and assigned additional

Angolan specimens to *E. undata*, providing the first record of the latter species for the country. Most authors followed Boulenger (1918, 1921) in regarding *P. benguelensis* as a valid species (Parker 1936; Monard 1937; Mertens 1954, 1971; Szczerbak 1975; Arnold 1989, 1991; Mayer 1989), and some even considered it to extend into northern Namibia (Branch 1998; Conradie *et al.* 2012b; Herrmann & Branch 2013). On the other hand, Laurent (1964) followed Boulenger (1921) in assigning Angolan specimens to *E. undata undata* but considered *E. benguelensis* to be a variety or synonym of *E. namaquensis*.

In the first molecular phylogeny of the genus, Makokha *et al.* (2007) uncovered cryptic diversity in Namibian and South African species, but Angolan material was unavailable and the status of *P. benguelensis* remained unresolved, with most authors accepting the presence of *P. benguelensis*, *P. namaquensis* and *P. undata* in Angola (Branch 1998; Makokha *et al.* 2007; Haacke 2008). The uncertainty surrounding the status of Angolan populations of *Pedioplanis* was due in part to the loss of original type material and exacerbated by the long period of armed conflict that prevented the collection of fresh material for analysis.

In a revised phylogeny of the genus, Conradie *et al.* (2012b) uncovered a previously unknown clade of Angolan *Pedioplanis* with at least five distinct lineages, one of which was assigned to *P. benguelensis*, two were described as new species (*P. haackei* and *P. huntleyi*), while the remaining two, each represented by a single specimen collected between Moçâmedes and the Leba escarpment, were provisionally unassigned. Given the lack of topotypic material, the authors followed Boulenger's (1918, 1921) morphological diagnosis and conservatively assigned newly collected specimens from Namibe Province to *P. benguelensis*, providing the first molecular data for the species. More recently, Childers *et al.* (2021) provided a comprehensive phylogeny of the *P. undata* species complex, with the description of two new species from Namibia (*P. branchi* Childers, Kirchhof & Bauer, 2021 and *P. mayeri* Childers, Kirchhof & Bauer, 2021). All *Pedioplanis* species currently known to occur in Angola are endemic or near-endemic, and there is no support for the presence of *P. namaquensis* or *P. undata* in the country (Conradie *et al.* 2012b; Marques *et al.* 2018; Childers *et al.* 2021).

As part of ongoing research on the herpetofauna of Angola, we examined morphological data collected from specimens housed in natural history collections and expanded on previous phylogenetic analyses to present a comprehensive review of Angolan members of the genus *Pedioplanis*. The collection of new material during recent herpetological surveys in Benguela and Namibe provinces, including the type locality region, allowed for a reassessment of the taxonomic status and diagnosis of *P. benguelensis*. Specimens collected in the coastal areas of southwestern Angola present a combination of morphological characters that differentiate them from populations assigned to *P. benguelensis* by previous authors (Boulenger 1921; Conradie *et al.* 2012b), and all remaining congeners in the region. The distinctiveness of these populations is supported by phylogenetic data. In this paper we describe a new species of *Pedioplanis* from Angola and provide updated diagnoses and distribution data for all currently recognized *Pedioplanis* which occur in the country. A redefinition and designation of a neotype for *P. benguelensis* are provided, along with an updated key to the genus.

Materials and methods

Material examined. New material was collected in Angola under permitted fieldwork carried out over several expeditions that took place between 2012 and 2019. Newly collected specimens were preserved in 10% buffered formalin in the field and subsequently transferred to 70–75% ethanol for long-term preservation. Liver tissue was removed before formalin fixation and preserved in 95–99% ethanol for phylogenetic analysis. For mensural and meristic comparison, we examined Angolan *Pedioplanis* specimens deposited in the collections of the California Academy of Sciences (CAS), San Francisco, California, USA; Ditsong National Museum of Natural History (TM) (formerly Transvaal Museum, Northern Flagship Institution), Pretoria, South Africa; Museu de História Natural e da Ciência da Universidade do Porto (MHNC-UP), Porto, Portugal; Museu Regional do Dundo (MD), Dundo, Lunda Norte, Angola; and Port Elizabeth Museum (PEM), at Bayworld, Port Elizabeth, South Africa. The material housed in the Natural History Museum (BMNH), London, UK was not examined by the authors but was considered for the production of distribution maps, as the morphological data provided by Boulenger (1921) is sufficiently detailed to allow the comparison with current data and the reassignment of these specimens to one of the currently recognized species. All specimens examined in this study are listed in the taxonomic accounts below. An asterisk following the catalog number denotes genotyped specimens. Locality data are presented in decimal degrees using the WGS 84

datum system. Historical records (non-GPS) were derived from Marques *et al.* (2018) and georeferenced using the GEOLocate web application (https://www.geo-locate.org). Elevational data are reported in meters above sea level (a.s.l.).

Molecular methods. We constructed a multi-locus DNA sequence dataset to estimate phylogenetic relationships among *Pedioplanis*. The dataset used fragments of the mitochondrial genes *16S* (580 bp) and *ND2* (968 bp) and the nuclear gene *RAG-1* (1314 bp), which maximized overlap with *Pedioplanis* sequence data from previous studies (Makhoka *et al.* 2007; Conradie *et al.* 2012b; Childers *et al.* 2021). New sequences were generated for 120 *Pedioplanis* specimens from Angola and 36 from elsewhere in Africa (Table 1). Seventy-six additional specimens (21 Angolan) were incorporated from available GenBank sequences. The phylogenetic dataset includes multiple specimens of all recognized *Pedioplanis* species as well as specimens of the African lacertid genera *Australolacerta, Heliobolus, Ichnotropis, Meroles*, and *Nucras* as outgroup taxa (Table 1).

DNA was extracted from ethanol-preserved tissue samples using Qiagen DNeasy tissue kits following the manufacturer's protocol. We amplified target DNA regions in 25 µl PCR reactions using NEB *Taq* polymerase and the primers listed in Table 2. The following cycling conditions were used: 95 °C initial denaturation (150 s), followed by 40 cycles of denaturation at 95 °C (30 s), annealing at 50–55 °C (30 s) and extension at 72 °C (60 s), with a 72 °C final extension (150 s). Amplified PCR products were purified using Axygen AxyPrep magnetic beads, with these products sequenced by the University of Michigan Advanced Genomics Core, at Villanova University, or at Macrogen (Amsterdam). MEGA-X (Kumar *et al.* 2018) was used for chromatogram inspection and assembly of contigs. We used ClustalX (Larkin *et al.* 2007) under default parameters, implemented in MEGA-X, to generate alignments of each gene. We also used MEGA-X to calculate uncorrected *ND2* sequence divergences among all pairs of individuals in the dataset, applying the pairwise deletion option for alignment gaps or missing data.

The individual gene alignments were concatenated for phylogenetic analyses. We used PartitionFinder 2.1.1 (Lanfear *et al.* 2017) to identify the best-fitting partitioning scheme and models of evolution under the corrected Akaike Information Criterion using a greedy search algorithm. Each gene and codon position of the protein-coding genes (*ND2* and *RAG-1*) were considered as potential sets in the partitioning scheme. The best-scoring scheme used for phylogenetic analyses included six subsets and the following models of evolution: *16S* (GTR+I+G); *ND2* position 1 (TVM+I+G); *ND2* position 2 (TVM+I+G); *ND2* position 3 (GTR+G); *RAG-1* position 1 + position 2 (TIM+I+G); *RAG-1* position 3 (TrNef+I+G). The primary maximum likelihood (ML) analysis was performed using IQ-TREE 2.1.2 (Nguyen *et al.* 2015). Branch support for the analysis was estimated using 1000 ultrafast bootstrap replicates (Hoang *et al.* 2018). Additional ML phylogenetic analyses were run separately for each of the genes to assess if there was discordance among the datasets.

Morphological methods. For mensural and meristic comparisons, morphological data was recorded for 211 *Pedioplanis* specimens from Angola, representing the three species known to occur in the country plus a fourth one that is described herein. Scale nomenclature, scale counts and measurements follow Conradie *et al.* (2012b). The following mensural and meristic characters were recorded: snout–vent length (SVL), measured from the tip of the snout to the anterior edge of the cloaca; tail length (TL), from the vent to the tip of the tail, measured only in specimens with complete, original tails; head length (HL), from the anterior edge of the occipital scale to the tip of the snout; head width (HW), measured behind the eyes, where the head is widest; inter-limb length (ILL), corresponding to the distance between the insertion of the anterior and posterior limbs; body length (BL), from the anterior edge of the cloaca to the collar; collar-snout length (CSL), from the median collar plate to the tip of the snout; length of the forelimb (LFL), from the elbow to the wrist; length of the hindlimb (LHL), measured from knee to heel; number of supralabials anterior to the subocular (SL); number of infralabials (IL); number of supraciliaries (SC); number of small granules anterior to the supraoculars (GrSO); presence and shape of tympanic shield; rows of small granules between supraoculars and supraciliaries (GrRows); number of enlarged transparent scales on the lower eyelid (Eye); number of longitudinal (LVSR) and transverse (TVSR) rows of ventral scales; number of femoral pores (FP); number of collar plates (CP); number of gular scales (GS), in a straight line from the symphysis of the chin shields to the median collar plate; and the number of subdigital lamellae under the fourth toe (LUFT). Comparisons were made with all other described species of *Pedioplanis*, based mainly on literature sources (Boulenger 1921; Mayer 1989; Branch 1998; Conradie *et al.* 2012b; Kirchhof *et al.* 2017; Childers *et al.* 2021).

TABLE 1. GenBank accession numbers of *Pedioplanis* and outgroup specimens/samples used in phylogenetic analyses. Sample abbreviations not listed in the material examined section are as follows: ABE (Werner Mayer field collection), AG and ANG (William R. Branch field collection), AMB (Aaron M. Bauer field collection), DDT (Dahne Du Toit field collection), JSM (Jane S. Makokha field collection), KTH (Krystal A. Tolley field collection), MBUR (Marius Burger field collection), MCZ (Museum of Comparative Zoology, Harvard University), MCZ FS (Museum of Comparative Zoology, Harvard University field series), MH and CF (Michael Cunningham field collection), NHMW (Natural History Museum, Vienna), NMNW (National Museum of Namibia, Windhoek), SK (Sebastian Kirchhof field collection), WC (Werner Conradie field collection), ZMB (Museum für Naturkunde, Berlin).

Species	Catalog Number	Field/tissue Number	Country, Province/Region, locality	16S	ND2	RAG1
Australolacerta australis	—	—	South Africa, Western Cape, Zuurberg Private Nature Reserve	DQ871152	DQ871094	DQ871208
Heliobolus lugubris	MCZ R184277	—	Namibia, Kamanjab	DQ871141	DQ871083	DQ871199
Ichnotropis capensis	CAS 209602	AMB 6067	South Africa, KwaZulu-Natal, Kosi Bay	DQ871149	DQ871091	DQ871207
Meroles suborbitalis	CAS 206735	AMB 5589	South Africa, Northern Cape, Groenriviermond	DQ871147	DQ871089	DQ871205
Nucras tessellata	CAS 206723	AMB 5582	South Africa, Northern Cape, Groenriviermond	DQ871143	DQ871085	DQ871201
P. benguelensis	CAS 266244	AMB 10012	Angola, Benguela, Chimalavera Nature Reserve	MZ708843	MZ712592	—
P. benguelensis	CAS 266245	AMB 10013	Angola, Benguela, Chimalavera Nature Reserve	MZ708844	MZ712593	MZ712671
P. benguelensis	CAS 266246	AMB 10018	Angola, Benguela, Chimalavera Nature Reserve	MZ708845	MZ712594	—
P. benguelensis	CAS 266237	AMB 9964	Angola, Benguela, Chimalavera Nature Reserve	MZ708846	—	MZ712672
P. benguelensis	CAS 266238	AMB 9965	Angola, Benguela, Chimalavera Nature Reserve	MZ708847	MZ712595	—
P. benguelensis	CAS 266239	AMB 9966	Angola, Benguela, Chimalavera Nature Reserve	MZ708848	MZ712596	—
P. benguelensis	CAS 266240	AMB 9968	Angola, Benguela, Chimalavera Nature Reserve	MZ708849	MZ712597	—
P. benguelensis	CAS 266241	AMB 9983	Angola, Benguela, Chimalavera Nature Reserve	MZ708850	MZ712598	MZ712673
P. benguelensis	CAS 266242	AMB 9984	Angola, Benguela, Chimalavera Nature Reserve	MZ708851	MZ712599	MZ712674
P. benguelensis	CAS 266243	AMB 9985	Angola, Benguela, Chimalavera Nature Reserve	MZ708852	MZ712600	MZ712675
P. benguelensis	CAS 266247	AMB 10026	Angola, Benguela, Dombe Grande-Cuio	MZ708853	MZ712601	—
P. benguelensis	PEM R24110	AG 92	Angola, Benguela, nr. Meva fishing village	MZ708854	—	MZ712676
P. benguelensis	PEM R25195	—	Angola, Cuanza-Sul, Sumbe	MZ708855	—	—
P. benguelensis	PEM R25196	—	Angola, Cuanza-Sul, Sumbe	MZ708856	MZ712602	MZ712677
P. benguelensis	PEM R18540	MBUR 2144	Angola, Namibe, 31.5 km E of Moçâmedes	HE794015	HE795001	HE796668
P. benguelensis	PEM R21665	ANG 305	Angola, Namibe, Moçâmedes-Bentiaba rd.	MZ708857	MZ712603	MZ712678
P. benguelensis	PEM R21666	ANG 308	Angola, Namibe, Moçâmedes-Bentiaba rd.	MZ708858	MZ712604	MZ712679
P. benguelensis	PEM R24142	AG 155	Angola, Namibe, Mucungo farm	MZ708859	MZ712605	MZ712680
P. benguelensis	PEM R21648	WC-1846	Angola, Namibe, N Moçâmedes	MZ708860	MZ712606	MZ712681
P. benguelensis	PEM R21649	WC-1847	Angola, Namibe, N Moçâmedes	MZ708861	MZ712607	MZ712682

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TABLE 1. (continued)

Species	Catalog Number	Field/tissue Number	Country, Province/Region, locality	16S	ND2	RAG1
P. benguelensis	PEM R21650	WC-1804	Angola, Namibe, N Moçâmedes	MZ708862	MZ712608	MZ712683
P. benguelensis	PEM R21651	WC-1852	Angola, Namibe, N Moçâmedes	MZ708863	MZ712609	MZ712684
P. benguelensis	PEM R21652	WC-1853	Angola, Namibe, N Moçâmedes	MZ708864	MZ712610	MZ712685
P. benguelensis	PEM R21658	WC-1798	Angola, Namibe, N Moçâmedes	MZ708865	MZ712611	MZ712686
P. benguelensis	PEM R24076	AG 86	Angola, Namibe, nr. Lucira	MZ708866	MZ712612	—
P. breviceps	MCZ R184255	—	Namibia, Kunene, Gai-As	—	MW822935	MW823395
P. breviceps	MCZ R184265	—	Namibia, Kunene, Gai-As	DQ871117	DQ871059	DQ871175
P. breviceps	NMNW 10871	—	Namibia, Kunene, Gai-As	—	MW823053	MW823401
P. breviceps	NMNW 10946	—	Namibia, Kunene, Gai-As	—	MW823269	MW823387
P. breviceps	NMNW 10947	—	Namibia, Kunene, Gai-As	DQ871118	DQ871060	DQ871176
P. breviceps	NHMW 35356.1	—	Namibia, Kunene, Gai-As	DQ871116	DQ871058	DQ871174
P. breviceps	NMNW 10869	—	Namibia, Kunene, nr. Gai-As	DQ871119	DQ871061	DQ871177
P. breviceps	MCZ R184312	—	Namibia, Kunene, Orupembe-Munutum rd. jct.	—	MW823042	MW823404
P. breviceps	ZMB 89326	—	Namibia, Erongo, Wuestenquell-Swakopmund	—	MW823047	MW823398
P. burchelli	PEM R17256	—	South Africa, Eastern Cape, Grahamstown	—	DQ925375	—
P. burchelli	PEM R16929	—	South Africa, Eastern Cape, Indwe	—	MW823257	MW823311
P. burchelli	—	KTH-346	South Africa, Free State, Qwa Qwa	DQ871123	DQ871065	DQ871181
P. burchelli	PEM R17260	—	South Africa, Western Cape, Beaufort West	—	EU723564	—
P. burchelli	—	MH0334	South Africa, Western Cape, Cederberg	DQ871120	DQ871062	DQ871178
P. burchelli	—	CF169	South Africa, Western Cape, Kouebokkeveld	DQ871121	DQ871063	DQ871179
P. burchelli	—	KTH-137	South Africa, Western Cape, nr. Ceres	DQ871122	DQ871064	DQ871180
P. gaerdesi	CAS 214745	AMB 6507	Namibia, Kunene, 29 Km W Sesfontein	DQ871133	DQ871075	DQ871191
P. gaerdesi	MCZ R184167	—	Namibia, Kunene, 33.2 Km E Ugab Crossing	DQ871132	DQ871074	DQ871190
P. gaerdesi	NMNW 9342	—	Namibia, Kunene, 52 km N Palmwag	—	MW823162	MW823406
P. gaerdesi	MCZ R185887	—	Namibia, Kunene, Gai-As	—	MW823167	MW823546
P. gaerdesi	—	ABE448	Namibia, Kunene, Palmwag	DQ871134	DQ871076	DQ871192
P. gaerdesi	NHMW 35371.12	—	Namibia, Kunene, Purros	DQ871135	DQ871077	DQ871193
P. gaerdesi	CAS 214599	AMB 6361	Namibia, Erongo, Arandis Mine	—	MW823144	MW823545
P. gaerdesi	ZMB 89330	—	Namibia, Otjozondjupa, Waterberg	—	MW823164	MW823544

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TABLE 1. (continued)

Species	Catalog Number	Field/tissue Number	Country, Province/Region, locality	16S	ND2	RAG1
P. gaerdesi	NMNW 10962	—	Namibia, Para Camp	—	MW823161	MW823447
P. haackei	PEM R21661	WC-1841	Angola, Huila, 13 km N Quilengues	MZ708867	MZ712613	MZ712687
P. haackei	PEM R18471	MBUR 2208	Angola, Namibe, 10 km S Lake Arco	HE793998	HE795009	HE796675
P. haackei	PEM R18472	MBUR 2209	Angola, Namibe, 10 km S Lake Arco	HE793996	HE795010	HE796676
P. haackei	—	AG 84	Angola, Namibe, 17 km W Chichamba	MZ708868	MZ712614	MZ712688
P. haackei	PEM R18474	MBUR 2305	Angola, Namibe, 20 km N Omauha	HE793999	HE795014	HE796678
P. haackei	—	AG 69	Angola, Namibe, 3 km E Chicambi	MZ708869	MZ712615	MZ712689
P. haackei	—	AG 70	Angola, Namibe, 3 km E Chicambi	MZ708870	MZ712616	MZ712690
P. haackei	—	AG 71	Angola, Namibe, 3 km E Chicambi	—	MZ712617	MZ712691
P. haackei	PEM R21664	ANG 288	Angola, Namibe, 7.8 km W Leba Pass	MZ708871	MZ712618	MZ712692
P. haackei	PEM R18460	MBUR 2132	Angola, Namibe, 7.8 km W Leba Pass	—	HE795000	HE796667
P. haackei	CAS 264769	AMB 10367	Angola, Namibe, Caraculo	MZ708872	MZ712619	MZ712693
P. haackei	PEM R24057	AG 59	Angola, Namibe, Catara river valley	MZ708873	MZ712620	MZ712694
P. haackei	PEM R24061	AG 65	Angola, Namibe, Catara river valley	MZ708874	MZ712621	MZ712695
P. haackei	PEM R24062	AG 73	Angola, Namibe, Catara river valley	MZ708875	MZ712622	—
P. haackei	CAS 264805	AMB 10588	Angola, Namibe, Chipumpo-Virulundo	MZ708876	MZ712623	MZ712696
P. haackei	CAS 264774	AMB 10384	Angola, Namibe, Curoca-Omauha	MZ708877	MZ712624	MZ712697
P. haackei	CAS 264775	AMB 10385	Angola, Namibe, Curoca-Omauha	MZ708878	MZ712625	MZ712698
P. haackei	CAS 264777	AMB 10390	Angola, Namibe, Curoca-Omauha	MZ708879	MZ712626	MZ712699
P. haackei	CAS 264778	AMB 10391	Angola, Namibe, Curoca-Omauha	MZ708880	MZ712627	MZ712700
P. haackei	CAS 264779	AMB 10392	Angola, Namibe, Curoca-Omauha	MZ708881	MZ712628	MZ712701
P. haackei	CAS 254835	JVV 8515	Angola, Namibe, Iona National Park	KU662315	MW823070	MW823438
P. haackei	CAS 254840	JVV 8510	Angola, Namibe, Iona National Park	KU662314	MW823069	MW823440
P. haackei	CAS 254860	JVV 8491	Angola, Namibe, Iona National Park	KU662318	MW823066	MW823441
P. haackei	PEM R18461	MBUR 2158	Angola, Namibe, Lake Arco	HE793993	HE795004	HE796671
P. haackei	PEM R18475	MBUR 2307	Angola, Namibe, Lake Arco-Espinheira rd.	HE794000	HE795015	HE796679
P. haackei	PEM R24103	AG 99	Angola, Namibe, Lucira Dam	MZ708882	MZ712629	MZ712702
P. haackei	PEM R21662	ANG 258	Angola, Namibe, Moçâmedes-Bentiaba rd.	MZ708883	MZ712630	MZ712703

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TABLE 1. (continued)

Species	Catalog Number	Field/tissue Number	Country, Province/Region, locality	16S	ND2	RAG1
P. haackei	PEM R21663	ANG 307	Angola, Namibe, Moçâmedes-Bentiaba rd.	MZ708884	MZ712631	MZ712704
P. haackei	CAS 254951	JVV 8313	Angola, Namibe, Namibe Nature Reserve	KU662316	MW823068	MW823442
P. haackei	CAS 254953	JVV 8316	Angola, Namibe, Namibe Nature Reserve	KU662313	MW823065	MW823436
P. haackei	CAS 264781	AMB 10419	Angola, Namibe, nr. Curoca river	MZ708885	MZ712632	MZ712705
P. haackei	CAS 264806	AMB 10634	Angola, Namibe, nr. Curoca river	MZ708886	—	—
P. haackei	CAS 264807	AMB 10635	Angola, Namibe, nr. Curoca river	MZ708887	MZ712633	MZ712706
P. haackei	CAS 264808	AMB 10636	Angola, Namibe, nr. Curoca river	MZ708888	MZ712634	MZ712707
P. haackei	CAS 264810	AMB 10638	Angola, Namibe, nr. Curoca river	MZ708889	—	MZ712708
P. haackei	—	AG 98	Angola, Namibe, nr. Lucira	MZ708890	MZ712635	MZ712709
P. haackei	CAS 254763	JVV 8702	Angola, Namibe, NW Pico Azevedo	KU662317	MW823071	MW823457
P. haackei	CAS 254764	JVV 8703	Angola, Namibe, NW Pico Azevedo	—	MW823067	MW823439
P. haackei	CAS 254767	JVV 8708	Angola, Namibe, NW Pico Azevedo	KU662312	MW823064	MW823437
P. haackei	CAS 264780	AMB 10417	Angola, Namibe, Omauha	MZ708891	MZ712636	—
P. haackei	CAS 264784	AMB 10456	Angola, Namibe, Omauha	MZ708892	MZ712637	—
P. haackei	CAS 264785	AMB 10457	Angola, Namibe, Omauha	MZ708893	—	MZ712710
P. haackei	CAS 264786	AMB 10458	Angola, Namibe, Omauha	MZ708894	—	MZ712711
P. haackei	CAS 264787	AMB 10459	Angola, Namibe, Omauha	MZ708895	—	MZ712712
P. haackei	CAS 264788	AMB 10460	Angola, Namibe, Omauha	MZ708896	—	MZ712713
P. haackei	CAS 264789	AMB 10461	Angola, Namibe, Omauha	MZ708897	MZ712638	MZ712714
P. haackei	CAS 264790	AMB 10462	Angola, Namibe, Omauha	MZ708898	MZ712639	MZ712715
P. haackei	INBAC/AMB 10416	AMB 10416	Angola, Namibe, Omauha	MZ708899	MZ712640	MZ712716
P. haackei	CAS 264791	AMB 10470	Angola, Namibe, Omauha-Virei	MZ708900	MZ712641	MZ712717
P. haackei	PEM R18464	MBUR 2180	Angola, Namibe, rd. to Tambor	HE793997	HE795006	—
P. haackei	PEM R18465	MBUR 2189	Angola, Namibe, rd. to Tambor	HE793994	HE795007	HE796673
P. haackei	PEM R18469	MBUR 2200	Angola, Namibe, rd. to Tambor	HE793995	HE795008	HE796674
P. haackei	INBAC/AMB 10393	AMB 10393	Angola, Namibe, Tambor	MZ708901	MZ712642	MZ712718
P. haackei	CAS 264757	AMB 10266	Angola, Namibe, vic. N'Dolondolo	MZ708902	MZ712643	MZ712719
P. haackei	CAS 264758	AMB 10267	Angola, Namibe, vic. N'Dolondolo	MZ708903	—	MZ712720
P. haackei	CAS 264759	AMB 10268	Angola, Namibe, vic. N'Dolondolo	MZ708904	—	MZ712721

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TABLE 1. (continued)

Species	Catalog Number	Field/tissue Number	Country, Province/Region, locality	16S	ND2	RAG1
P. haackei	CAS 264760	AMB 10269	Angola, Namibe, vic. N'Dolondolo	MZ708905	MZ712644	MZ712722
P. haackei	CAS 264761	AMB 10270	Angola, Namibe, vic. N'Dolondolo	MZ708906	—	MZ712723
P. haackei	CAS 264762	AMB 10275	Angola, Namibe, vic. N'Dolondolo	MZ708907	—	—
P. haackei	CAS 264763	AMB 10290	Angola, Namibe, vic. N'Dolondolo	MZ708908	—	MZ712724
P. haackei	CAS 264764	AMB 10291	Angola, Namibe, vic. N'Dolondolo	MZ708909	—	—
P. haackei	CAS 264765	AMB 10292	Angola, Namibe, vic. N'Dolondolo	MZ708910	—	—
P. haackei	CAS 264794	AMB 10551	Angola, Namibe, Virei-Virulundo	MZ708911	MZ712645	MZ712725
P. haackei	CAS 264795	AMB 10552	Angola, Namibe, Virei-Virulundo	MZ708912	MZ712646	—
P. haackei	CAS 264796	AMB 10553	Angola, Namibe, Virei-Virulundo	MZ708913	MZ712647	MZ712726
P. haackei	CAS 264797	AMB 10554	Angola, Namibe, Virei-Virulundo	MZ708914	MZ712648	MZ712727
P. haackei	CAS 264798	AMB 10555	Angola, Namibe, Virei-Virulundo	MZ708915	—	—
P. haackei	CAS 264799	AMB 10556	Angola, Namibe, Virei-Virulundo	MZ708916	—	—
P. haackei	CAS 264800	AMB 10557	Angola, Namibe, Virei-Virulundo	MZ708917	—	MZ712728
P. haackei	CAS 264801	AMB 10558	Angola, Namibe, Virei-Virulundo	MZ708918	—	MZ712729
P. haackei	CAS 264803	AMB 10560	Angola, Namibe, Virei-Virulundo	—	MZ712649	MZ712730
P. huntleyi	PEM R18490	WC09-041	Angola, Cunene, 26 km SE Onconcua	HE794004	HE795020	HE796682
P. huntleyi	PEM R18487	WC09-029	Angola, Namibe, 14 km W Moimba	HE794001	HE795018	HE796681
P. huntleyi	PEM R18485	WC09-021	Angola, Namibe, 16 km E Iona	HE794003	HE795017	—
P. huntleyi	PEM R18484	WC09-018	Angola, Namibe, 8 km NE Iona	HE794006	HE795016	HE796680
P. huntleyi	CAS 254864	JVV 8497	Angola, Namibe, Iona National Park	KU662311	MW823063	MW823405
P. huntleyi	CAS 264811	AMB 10646	Angola, Namibe, nr. Virulundo	MZ708919	—	MZ712731
P. huntleyi	CAS 264812	AMB 10647	Angola, Namibe, nr. Virulundo	MZ708920	—	MZ712732
P. huntleyi	CAS 264813	AMB 10648	Angola, Namibe, nr. Virulundo	MZ708921	—	MZ712733
P. huntleyi	INBAC/AMB 10632	AMB 10632	Angola, Namibe, nr. Virulundo	MZ708922	—	MZ712734
P. huntleyi	INBAC/AMB 10645	AMB 10645	Angola, Namibe, nr. Virulundo	MZ708923	MZ712650	—
P. huntleyi	PEM R18478	MBUR 02250	Angola, Namibe, rd. to Oncocua	HE794005	HE795011	—
P. huntleyi	PEM R18479	MBUR 02276	Angola, Namibe, rd. to Oncocua	HE794002	HE795012	HE796677
P. husabensis	ZMB 83404	—	Namibia, Erongo, Farm Friedhelm Sack	—	MW823057	MW823528
P. husabensis	—	SK516.2013	Namibia, Erongo, Ida Camp	—	MW823056	MW823534

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TABLE 1. (continued)

Species	Catalog Number	Field/tissue Number	Country, Province/Region, locality	16S	ND2	RAG1
P. husabensis	—	SK558.2013	Namibia, Erongo, Khan	—	MW823275	MW823533
P. husabensis	—	SK645.2013	Namibia, Erongo, Khan	—	MW823059	MW823539
P. husabensis	ZMB 83403	SK45.2013	Namibia, Erongo, Khan	—	MW823272	MW823536
P. husabensis	PEM R18139	—	Namibia, Erongo, Langer Heinrich	HE794008	HE795021	—
P. husabensis	MCZ R184164	—	Namibia, Erongo, Swakop River	DQ871139	DQ871081	DQ871197
P. husabensis	PEM R18140	—	Namibia, Erongo, Tinkas mountains	HE794007	HE795022	—
P. husabensis	—	ABE473	Namibia, Ukub W	DQ871138	DQ871080	DQ871196
P. branchi	NHMW 35340.5	—	Namibia, Erongo, Rossing	DQ871130	DQ871072	DQ871188
P. branchi	CAS 214789	AMB 6552	Namibia, Erongo, S Karibib	DQ871128	DQ871070	DQ871186
P. branchi	PEM R18127	—	Namibia, Erongo, Tinkas mountains	HE794009	HE795023	—
P. branchi	—	ABE472	Namibia, Erongo, Tsaobis Leopard Park	DQ871131	DQ871073	DQ871189
P. branchi	—	ABE458	Namibia, Erongo, Usakos	DQ871129	DQ871071	DQ871187
P. inornata	MCZ R193371	—	Namibia, Hardap, 43 km N Mariental	—	MW823199	MW823508
P. inornata	—	MCZ FS-A28289	Namibia, Hardap, Farm Weltevrede	—	MW823227	MW823510
P. inornata	MCZ R193104	—	Namibia, Hardap, Farm Weltevrede	—	MW823221	MW823516
P. inornata	NHMW 35340.9	—	Namibia, Karas, Fish River Canyon	DQ871137	DQ871079	DQ871195
P. inornata	MCZ R184767	—	South Africa, Northern Cape, 9 km N Lekkersing	—	MW823196	MW823501
P. inornata	—	KTH-595	South Africa, Northern Cape, Farm Kuthula	DQ871140	DQ871082	DQ871198
P. inornata	PEM R12444	—	South Africa, Northern Cape, Richtersveld	DQ871136	DQ871078	DQ871194
P. laticeps	ZMB 82782	—	Namibia, Karas, Aussenkehr Canyon	MN015332	MW822934	—
P. laticeps	ZMB 82783	—	Namibia, Karas, Aussenkehr Canyon	—	MW822933	—
P. laticeps	PEM R17212	—	South Africa, Western Cape, Anysberg Nature Reserve	DQ871125	DQ871067	DQ871183
P. laticeps	PEM R17214	—	South Africa, Western Cape, Anysberg Nature Reserve	DQ871124	DQ871066	DQ871182
P. laticeps	—	JSM021	South Africa, Western Cape, Anysberg Nature Reserve	DQ871126	DQ871068	DQ871184
P. laticeps	—	KTH-222	South Africa, Western Cape, Tankwa Karoo	DQ871127	DQ871069	DQ871185
P. lineoocellata	MCZ R183775	—	Namibia, Kunene, 76.2 Km E Ugab Crossing	DQ871105	DQ871047	DQ871163
P. lineoocellata	MCZ R188266	—	Namibia, Hardap, 28 km SW Gochas	—	MW823027	MW823380
P. lineoocellata	MCZ R193343	—	Namibia, Hardap, 35 km S Gochas	—	MW823005	MW823340
P. lineoocellata	NHMW 35360.1	—	Namibia, Hardap, Aranos	DQ871106	DQ871048	DQ871164

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TABLE 1. (continued)

Species	Catalog Number	Field/tissue Number	Country, Province/Region, locality	16S	ND2	RAG1
P. lineoocellata	CAS 223974	AMB 6862	Namibia, Karas, 45 Km N Helmeringhausen	DQ871104	DQ871046	DQ871162
P. lineoocellata	NHMW 35385.2	—	Namibia, Karas, Luderitz	DQ871103	DQ871045	DQ871161
P. lineoocellata	ZMB 89346	—	Namibia, Karas, Sperrgebiet	—	MW822962	MW823367
P. lineoocellata	MCZ R184524	—	South Africa, Limpopo, Kgama	DQ871108	DQ871050	DQ871166
P. lineoocellata	PEM R17357	—	South Africa, Limpopo, Kgama	—	MW822938	MW823343
P. lineoocellata	—	MBUR 531	South Africa, Northern Cape	—	MW822954	MW823320
P. lineoocellata	—	MH0336	South Africa, Western Cape, Cederberg	DQ871107	DQ871049	DQ871165
P. lineoocellata	—	DDT09	South Africa, Western Cape, Matjiesrivier Nature Reserve	DQ871109	DQ871051	DQ871167
P. namaquensis	NMNW 10549	—	Namibia, Kunene, 17 Km E Ugab crossing	DQ871098	DQ871040	DQ871156
P. namaquensis	—	ABE54	Namibia, Kunene, Otjondeka	DQ871102	DQ871044	DQ871160
P. namaquensis	NMNW 10547	—	Namibia, Erongo, rd. to Uis	DQ871097	DQ871039	DQ871155
P. namaquensis	CAS 214784	AMB 6549	Namibia, Erongo, S Karibib	DQ871095	DQ871037	DQ871153
P. namaquensis	NHMW 35351.20	—	Namibia, Erongo, Trekkopje	DQ871096	DQ871038	DQ871154
P. namaquensis	MCZ R193356	—	Namibia, Hardap, 90 km S Mariental	—	MZ712651	MZ712735
P. namaquensis	CAS 200033	AMB 4558	South Africa, Northern Cape, Richtersveld	DQ871101	DQ871043	DQ871159
P. namaquensis	CAS 200105	AMB 4775	South Africa, Northern Cape, Richtersveld	DQ871100	DQ871042	DQ871158
P. namaquensis	PEM R11967	—	South Africa, Northern Cape, Richtersveld	DQ871099	DQ871041	DQ871157
P. rubens	NHMW 35341.8	—	Namibia, Otjozondjupa, Waterberg	DQ871110	DQ871052	DQ871168
P. rubens	ZMB 84748	—	Namibia, Otjozondjupa, Waterberg	—	MW823121	MW823450
P. rubens	ZMB 89351	—	Namibia, Otjozondjupa, Waterberg	—	MW823120	MW823451
P. serodioi **sp. nov.**	INBAC/AMB 9967	AMB 9967	Angola, Benguela, Chimalavera Nature Reserve	—	MZ712652	—
P. serodioi **sp. nov.**	PEM R21659	WC-1807	Angola, Benguela, rd. to Cubal	MZ708924	MZ712653	MZ712736
P. serodioi **sp. nov.**	PEM R24006	AG 19	Angola, Namibe, 10 km W Lola	MZ708925	—	MZ712737
P. serodioi **sp. nov.**	PEM R24007	AG 20	Angola, Namibe, 10 km W Lola	MZ708926	—	MZ712738
P. serodioi **sp. nov.**	PEM R24010	AG 23	Angola, Namibe, 10 km W Lola	MZ708927	MZ712654	—
P. serodioi **sp. nov.**	PEM R27733	AG 36	Angola, Namibe, 20 km SW Camacuio	MZ708928	MZ712655	MZ712739
P. serodioi **sp. nov.**	PEM R18459	WC09-033	Angola, Namibe, 3 km E Moimba	HE794014	HE795019	—
P. serodioi **sp. nov.**	PEM R24032	AG 29	Angola, Namibe, 30 km W Lola	MZ708929	MZ712656	—
P. serodioi **sp. nov.**	PEM R24033	AG 35	Angola, Namibe, 30 km W Lola	MZ708930	—	—

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TABLE 1. (continued)

Species	Catalog Number	Field/tissue Number	Country, Province/Region, locality	16S	ND2	RAG1
P. serodioi **sp. nov.**	PEM R24034	AG 30	Angola, Namibe, 30 km W Lola	MZ708931	MZ712657	MZ712740
P. serodioi **sp. nov.**	PEM R24035	AG 31	Angola, Namibe, 30 km W Lola	MZ708932	MZ712658	MZ712741
P. serodioi **sp. nov.**	PEM R18454	MBUR 2300	Angola, Namibe, 47 km E Moçâmedes	HE794013	HE795013	—
P. serodioi **sp. nov.**	PEM R21653	ANG 297	Angola, Namibe, 50 km E Moçâmedes	MZ708933	MZ712659	—
P. serodioi **sp. nov.**	PEM R21654	ANG 298	Angola, Namibe, 50 km E Moçâmedes	MZ708934	MZ712660	MZ712742
P. serodioi **sp. nov.**	PEM R21655	ANG 268	Angola, Namibe, 50 km E Moçâmedes	MZ708935	MZ712661	—
P. serodioi **sp. nov.**	PEM R21656	ANG 269	Angola, Namibe, 50 km E Moçâmedes	—	MZ712662	—
P. serodioi **sp. nov.**	PEM R21657	ANG 270	Angola, Namibe, 50 km E Moçâmedes	MZ708936	MZ712663	MZ712743
P. serodioi **sp. nov.**	PEM R18449	MBUR 2146	Angola, Namibe, 50 km E Moçâmedes	HE794010	HE795002	HE796669
P. serodioi **sp. nov.**	PEM R18450	MBUR 2147	Angola, Namibe, 50 km E Moçâmedes	HE794011	HE795003	HE796670
P. serodioi **sp. nov.**	CAS 264752	AMB 10181	Angola, Namibe, Bibala Crossroad	MZ708937	—	MZ712744
P. serodioi **sp. nov.**	CAS 264753	AMB 10182	Angola, Namibe, Bibala Crossroad	MZ708938	MZ712664	MZ712745
P. serodioi **sp. nov.**	CAS 264767	AMB 10364	Angola, Namibe, Bibala Crossroad	MZ708939	—	—
P. serodioi **sp. nov.**	CAS 264768	AMB 10365	Angola, Namibe, Bibala Crossroad	MZ708940	—	MZ712746
P. serodioi **sp. nov.**	CAS 264754	AMB 10183	Angola, Namibe, Camacuio	MZ708941	MZ712665	MZ712747
P. serodioi **sp. nov.**	CAS 264755	AMB 10184	Angola, Namibe, Camacuio	MZ708942	—	MZ712748
P. serodioi **sp. nov.**	CAS 264766	AMB 10334	Angola, Namibe, N'Dolondolo	MZ708943	MZ712666	MZ712749
P. serodioi **sp. nov.**	PEM R24050	AG 38	Angola, Namibe, nr. Camacuio	MZ708944	MZ712667	MZ712750
P. serodioi **sp. nov.**	PEM R24051	AG 39	Angola, Namibe, nr. Camacuio	MZ708945	MZ712668	MZ712751
P. serodioi **sp. nov.**	PEM R24052	AG 40	Angola, Namibe, nr. Camacuio	MZ708946	MZ712669	MZ712752
P. serodioi **sp. nov.**	CAS 254896	JVV 8578	Angola, Namibe, nr. Caraculo	KU662320	MW823250	MW823384
P. serodioi **sp. nov.**	CAS 254906	JVV 8598	Angola, Namibe, nr. Caraculo	KU662321	MW823249	MW823385
P. serodioi **sp. nov.**	CAS 254909	JVV 8601	Angola, Namibe, nr. Caraculo	KU662319	MW823248	MW823383
P. serodioi **sp. nov.**	PEM R18453	MBUR 2165	Angola, Namibe, rd. to Tambor	HE794012	HE795005	HE796672
P. mayeri	NHMW 35339.13	—	Namibia, Kunene	DQ871112	DQ871054	DQ871170
P. mayeri	CAS 214643	AMB 6406	Namibia, Kunene, 59 Km W Kamanjab	DQ871113	DQ871055	DQ871171

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TABLE 1. (continued)

Species	Catalog Number	Field/tissue Number	Country, Province/Region, locality	16S	ND2	RAG1
P. mayeri	—	ABE451	Namibia, Kunene, Palmwag	DQ871114	DQ871056	DQ871172
P. mayeri	NHMW 35339.5	—	Namibia, Erongo, Uis	DQ871111	DQ871053	DQ871169
P. mayeri	NHMW 35339.25		Namibia, Khomas, Nauchas	DQ871115	DQ871057	DQ871173
P. undata	—	SK54.2013	Namibia, Erongo, vic. Amichab Mountain	—	MW823125	MW823512
P. undata	MCZ R193376	—	Namibia, Hardap, Rehoboth	—	MZ712670	MZ712753
P. undata	NMNW 11084	—	Namibia, Otjozondjupa, SW Farm Namases	—	MW823136	MW823458
P. undata	MCZ R184791	—	South Africa, Northern Cape, 31 km E Upington	—	MW823197	MW823506

TABLE 2. List of PCR primers used in this study.

Gene	Primer	Sequence	Direction	Source
16S	16S-A	5'-CGCCTGTTTATCAAAAACAT-3'	Forward	Palumbi *et al.* (1996)
16S	16S-B	5'-CCGGTCTGAACTCAGATCACGT-3'	Reverse	Palumbi *et al.* (1996)
ND2	L4437a	5'-AAGCTTTCGGGCCCATACC-3'	Forward	Macey *et al.* (1997)
ND2	H5540	5'-TTTAGGGCTTTGAAGGC-3'	Reverse	Macey *et al.* (1997)
ND2	vMet2	5'-GCTAAACAAGCTTTCGGGCCCATACC-3'	Forward	Cunningham and Cherry (2004)
ND2	vTrp	5'-CTCCTGCTTAGGGCTTTGAAGGC-3'	Reverse	Cunningham and Cherry (2004)
RAG-1	RAG1-PedF1	5'-ACAGCAGTGTGCAAGTAAGAGAT-3'	Forward	This study
RAG-1	RAG1-PedF2	5'-GGYGAYRTTGACACAATCCATCCTAT-3'	Forward	This study
RAG-1	RAG1-PedR1	5'-GTACTGAGGTGTATCTTGTTGCA-3'	Reverse	This study
RAG-1	RAG1-PedR2	5'-CAGCAAAAGCTTTCACTTGAAGT-3'	Reverse	This study
RAG-1	R13	5'-TCTGAATGGAAATTCAAGCTGTT-3'	Forward	Groth and Barrowclough (1999)
RAG-1	R18	5'-GATGCTGCCTCGGTCGGCCACCTTT-3'	Reverse	Groth and Barrowclough (1999)
RAG-1	RAGfo	5'-GAAAAGGGCTACATCCTGG-3'	Forward	Mayer and Pavlicev (2007)
RAG-1	RAG-R1	5'-AAAATCTGCCTTCCTGTTATTG-3'	Reverse	Mayer and Pavlicev (2007)

Results

Phylogenetic relationships. Interspecific relationships in *Pedioplanis* (Fig. 1) are consistent with other molecular phylogenetic studies of *Pedioplanis* (Makokha *et al.* 2007; Conradie *et al.* 2012b; Childers *et al.* 2021) for the described species. The deepest divergence in *Pedioplanis* is between a clade that is near-endemic to South Africa (*P. burchelli* (Duméril & Bibron, 1839) + *P. laticeps* (Smith, 1845)) and all other *Pedioplanis*. Of the remaining species, many have widespread distributions across southwestern Africa, with others being more restricted to Namibia or Angola. Angolan *Pedioplanis* consist of four species, each of which is morphologically diagnosable (see below). *Pedioplanis haackei* and *P. huntleyi* were previously described by Conradie *et al.* (2012b). A species previously labeled as *P.* sp. 1 we recognize herein as *P. benguelensis* based on a larger sample size permitting us to document the coastal geographic range and morphological characteristics of this clade. The final Angolan species, from Namibe and Benguela provinces, has previously been labeled as *P. benguelensis* but we recognize here as a new species, which is described below. Sequencing for the same markers used here of 339 *Pedioplanis* samples from Namibia, including many from the Kunene Region bordering Angola, has failed to document any of the Angolan clades (Childers *et al.* 2021), suggesting that all four Angolan species are endemic. Three Angolan species (*P. benguelensis*, *P. haackei*, *P. huntleyi*) form a clade that is most closely related to the Namibian *P. undata* complex (*P. mayeri, P. rubens* (Mertens, 1954)*, P. inornata* (Roux, 1907)*, P. undata, P. branchi, P. gaerdesi* (Mertens, 1954)). This larger grouping is, in turn, sister to the Namibian species *P. husabensis* Berger-Dell'Mour & Mayer, 1989 and the new Angolan species that is described herein.

Angolan *Pedioplanis* species are all genetically distinct from one another and from non-Angolan species. The four Angolan species have uncorrected pairwise *ND2* sequence divergences of at least 10% from all non-Angolan congeners. The most closely related pair of Angolan species, *P. haackei* and *P. huntleyi*, have pairwise *ND2* divergences of 6–9% (Table 3). Some intraspecific phylogeographic structure exists within the Angolan species. In *P. benguelensis*, pairwise *ND2* divergences are a maximum of 4.2%. The two identifiable genetic groupings of *P. benguelensis* include a paraphyletic clade of southern samples distributed in coastal Namibe Province and a well-supported northern subclade distributed as far north as Cuanza-Sul Province. *Pedioplanis haackei* is divided into two reciprocally monophyletic subclades (average pairwise *ND2* divergence 4.5%). These subclades also have a

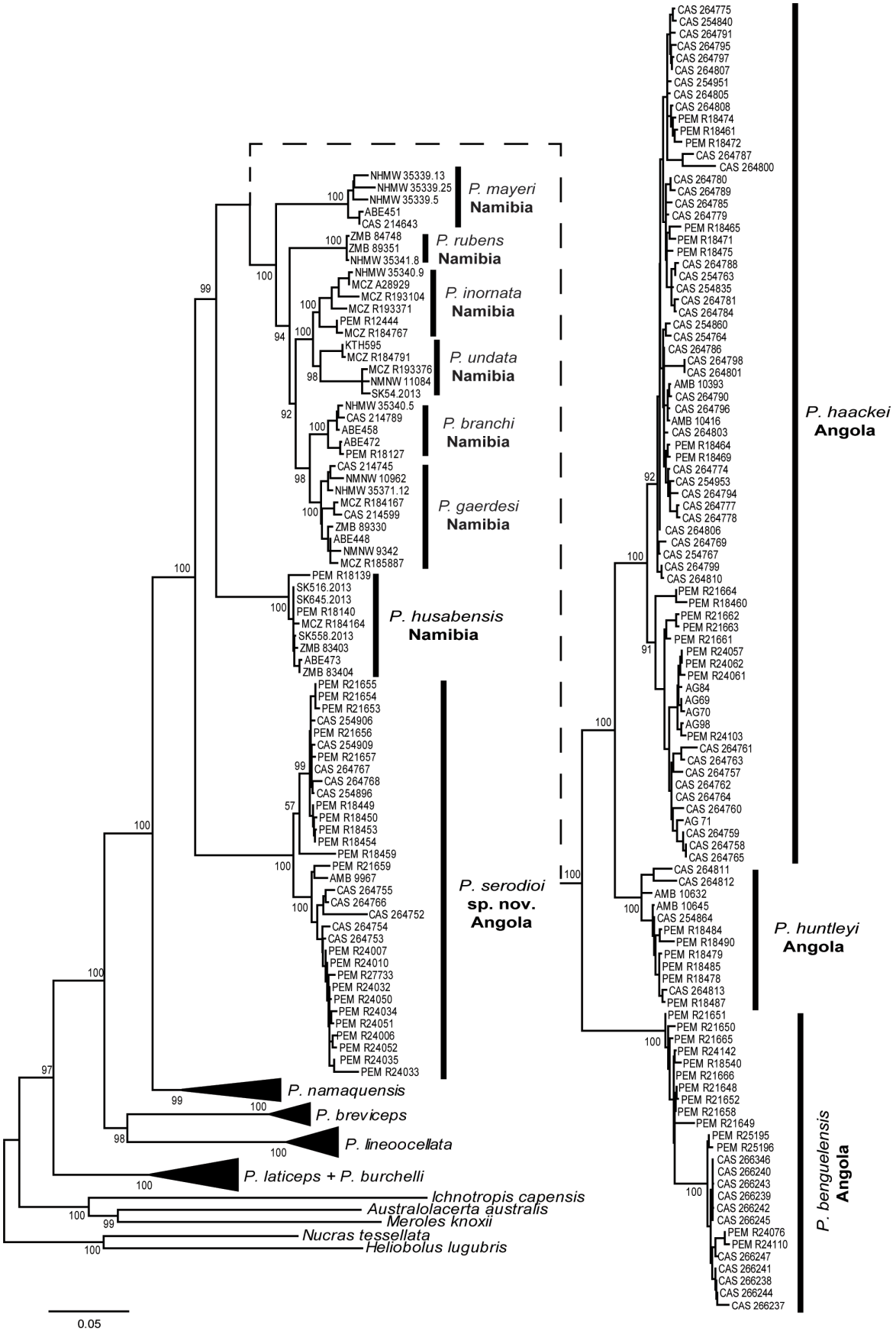

FIGURE 1. Maximum likelihood phylogeny of *Pedioplanis* based on the concatenated multi-locus dataset. Black triangles indicate multiple sampled specimens. Bootstrap support values are provided at major nodes.

TABLE 3. Uncorrected pairwise *ND2* sequence divergences among *Pedioplanis* species. Reported values are minimum to maximum ranges for all individual pairwise comparisons of each taxon pair. Angolan taxa are indicated in bold.

	1	2	3	4	5	**6**	**7**	8
1. *benguelensis*	0.00–0.04							
2. *branchi*	0.13–0.15	0.00–0.03						
3. *breviceps*	0.17–0.25	0.17–0.22	0.00–0.09					
4. *burchelli*	0.20–0.26	0.22–0.24	0.18–0.24	0.01–0.12				
5. *gaerdesi*	0.12–0.15	0.04–0.06	0.17–0.23	0.21–0.25	0.00–0.03			
6. *haackei*	0.12–0.18	0.11–0.15	0.17–0.31	0.21–0.29	0.10–0.17	0.00–0.07		
7. *huntleyi*	0.12–0.14	0.12–0.14	0.18–0.23	0.21–0.24	0.11–0.13	0.06–0.09	0.00–0.02	
8. *husabensis*	0.15–0.18	0.13–0.15	0.17–0.22	0.20–0.24	0.11–0.15	0.13–0.19	0.13–0.16	0.00–0.03
9. *inornata*	0.14–0.16	0.06–0.08	0.18–0.24	0.21–0.25	0.05–0.09	0.11–0.17	0.13–0.15	0.11–0.15
10. *laticeps*	0.21–0.25	0.21–0.23	0.19–0.26	0.14–0.19	0.21–0.24	0.18–0.30	0.22–0.25	0.20–0.22
11. *lineoocellata*	0.19–0.25	0.19–0.24	0.19–0.24	0.22–0.27	0.20–0.24	0.20–0.28	0.21–0.24	0.19–0.23
12. *mayeri*	0.15–0.18	0.11–0.13	0.20–0.23	0.22–0.25	0.11–0.13	0.13–0.20	0.13–0.16	0.13–0.17
13. *namaquensis*	0.18–0.21	0.16–0.19	0.18–0.23	0.19–0.23	0.16–0.19	0.16–0.25	0.17–0.22	0.16–0.18
14. *rubens*	0.13–0.15	0.07–0.09	0.16–0.23	0.20–0.24	0.06–0.09	0.10–0.20	0.12–0.15	0.11–0.13
15. *serodioi* sp. nov.	0.16–0.20	0.17–0.19	0.20–0.25	0.22–0.27	0.16–0.18	0.15–0.25	0.15–0.18	0.16–0.19
16. *undata*	0.14–0.16	0.08–0.09	0.19–0.24	0.22–0.25	0.07–0.09	0.12–0.17	0.13–0.16	0.13–0.14

.....continued on the next page

TABLE 3. (Continued)

	9	10	11	12	13	14	**15**	16
1. *benguelensis*								
2. *branchi*								
3. *breviceps*								
4. *burchelli*								
5. *gaerdesi*								
6. *haackei*								
7. *huntleyi*								
8. *husabensis*								
9. *inornata*	0.02–0.05							
10. *laticeps*	0.22–0.25	0.00–0.14						
11. *lineoocellata*	0.19–0.25	0.21–0.28	0.00–0.09					
12. *mayeri*	0.11–0.13	0.21–0.24	0.21–0.25	0.01–0.05				
13. *namaquensis*	0.17–0.19	0.20–0.25	0.18–0.22	0.18–0.21	0.00–0.16			
14. *rubens*	0.07–0.08	0.20–0.24	0.19–0.25	0.10–0.12	0.16–0.18	0.00–0.01		
15. *serodioi* sp. nov.	0.16–0.19	0.23–0.26	0.19–0.23	0.18–0.20	0.17–0.21	0.17–0.20	0.00–0.07	
16. *undata*	0.06–0.09	0.21–0.24	0.20–0.25	0.11–0.15	0.17–0.20	0.07–0.10	0.18–0.21	0.00–0.08

north/south division, with the division between subclades occurring at approximately -15° latitude. *Pedioplanis huntleyi* has the most restricted distribution among Angolan *Pedioplanis* and little genetic structure, with the deepest intraspecific divergence separating samples from the same locality. The most genetically variable Angolan *Pedioplanis* is the new species described below, with a maximum of 6.5% pairwise *ND2* divergence. There are three genetically identifiable subclades in the dataset, one of which is represented by a single sample, but these also have broad geographic overlap and lack obvious diagnostic morphological differences.

Morphology. Mensural and meristic data for the studied species are presented in Table 4. The four *Pedioplanis* species occurring in Angola differ from each other and from other congeners from neighboring regions in several morphological characters and can be identified through the key presented in this paper. Detailed diagnoses for each species are provided in the taxonomic accounts below.

TABLE 4. General comparison between the species of *Pedioplanis* occurring in Angola. Data presented as "mean (standard deviation) [minimum–maximum]". Mensural characters are presented in mm. Abbreviations are described in the Materials and Methods.

	P. benguelensis (n = 42)	***P. haackei*** (n = 84)	***P. huntleyi*** (n = 22)	***P. serodioi* sp. nov.** (n = 63)
SVL	48.3 (7) [26–58.1]	45.9 (5) [31.7–59.3]	54.6 (3) [47.5–58.9]	43.5 (4.4) [25–50.2]
TL	125.9 (18.7) [89–153.9]	106.4 (13.6) [85.7–135.7]	121.4 (20.3) [85.5–158.7]	92.5 (11.9) [69–111]
TL/SVL	2.4 (0.2) [1.9–2.7]	2.3 (0.2) [1.7–2.9]	2.2 (0.3) [1.6–2.7]	2.1 (0.3) [1.5–2.6]
ILL	22.4 (3.1) [14.8–27.5]	20.9 (3.2) [13.8–29.3]	25.2 (1.7) [21.8–28]	21 (2.7) [10.7–25.3]
BL	30.2 (4.2) [21.5–36.8]	28.7 (3.8) [19.6–39.5]	34.8 (2.3) [29.6–38.6]	27.8 (3.4) [15.5–35.4]
CSL	18.3 (2.1) [14–21.6]	17.1 (2) [10.2–22.9]	20 (1.6) [17.4–22.7]	15.7 (1.8) [9.7–20.1]
HL	11.7 (1) [9.1–13.5]	10.9 (1.2) [7.7–14]	12.9 (1.3) [10.8–14.8]	10.5 (1.1) [6.6–12.9]
HW	6.8 (1) [5–8.8]	6.5 (0.7) [5–8.9]	7.9 (0.8) [6.5–9.3]	6.1 (0.8) [4.2–7.9]
LFL	6.4 (0.8) [4.2–8.3]	6.3 (0.8) [4.3–8.4]	7.2 (0.6) [6.4–8.2]	5.2 (0.5) [4–6.4]
LHL	9.9 (1.2) [6.7–12.3]	10 (1.1) [6.8–12.1]	12 (1.4) [9.8–16.3]	8.7 (0.9) [5.5–10.6]
SL	5 (0.4) [4–6]	4.9 (0.5) [4–6]	4.9 (0.5) [4–6]	4.1 (0.5) [3–6]
IL	6.2 (0.4) [6–7]	6.1 (0.4) [5–8]	6 (0.7) [4–7]	6.1 (0.4) [5–7]
SC	6 (0.5) [4–7]	6 (0.3) [5–7]	5.9 (0.3) [5–6]	5.9 (0.4) [5–7]
GrSO	16.2 (4) [9–26]	15.1 (4.1) [7–28]	9.5 (2.1) [6–13]	12.4 (3.6) [6–24]
GrRows	2 (0.4) [1–3]	1.9 (0.4) [1–3]	1.4 (0.5) [1–2]	1.3 (0.5) [1–2]
Eye	2 (0.2) [1–3]	2 (0) [2–2]	2 (0.2) [1–2]	1 (0.1) [1–2]
LVSR	10 (0) [10–10]	10 (0.2) [9–11]	10 (0) [10–10]	10 (0) [10–10]
TVSR	28.6 (1.3) [27–32]	27.7 (1.7) [20–31]	28.6 (1) [26–30]	27.2 (1.5) [23–31]
CP	10.9 (1.9) [7–14]	8.7 (1.4) [6–12]	8.5 (1.2) [6–10]	8.3 (1.9) [5–17]
GS	28.7 (2.3) [24–35]	28.2 (2.1) [23–37]	30 (2.3) [26–34]	27.6 (2.2) [22–32]
FP	13.6 (1) [11–16]	13.3 (1.3) [11–17]	12.9 (0.9) [12–15]	12.6 (1.2) [10–17]
LUFT	26.8 (1.6) [23–30]	27.1 (2.1) [22–32]	26.5 (2.2) [20–29]	25.2 (2) [22–32]

Systematics

(Reptilia: Squamata: Lacertidae)

Pedioplanis benguelensis (Bocage, 1867)

(Figs. 2–4)

Eremias Benguellensis: Bocage (1867a: 221)
Eremias benguelensis: Bocage (1867b: 229)
Eremias namaquensis: Boulenger (1887: 91) [part]; Bocage (1895: 31) [part]
Eremias undata: Boulenger (1921: 283) [part]

Pedioplanis sp. 1: Conradie *et al.* (2012b: 95)
Pedioplanis benguellensis: Ceríaco *et al.* (2016: 56) [part]; Marques *et al.* (2018: 222) [part]; Branch *et al.* (2019b: 92; 2019c: 306) [part]

Bocage (1867a) briefly mentioned three specimens of a new species *"Eremias benguellensis"*, collected by Anchieta in "Benguella" [= Benguela, Benguela Province], referring to a "diagnosis elsewhere". In a subsequent paper that appeared immediately after in the same issue of the *Jornal de Sciencias Mathematicas, Physicas e Naturaes,* Bocage (1867b) provided a morphological description of "*Eremias benguelensis*", spelling the specific epithet with a single "l". The correct spelling of the name "*benguelensis*" has not been established to date, with both spellings being used by different authors over the years. The lack of a diagnosis in Bocage's (1867a) first paper could lead one to consider it a *nomen nudum* under Article 12 of the *International Code of Zoological Nomenclature*, however, the fact that both papers were simultaneously published in the same issue raises ambiguity. Considering this, the Principle of the First Reviser should be applied and, therefore, under Article 24.2 of the *Code*, Boulenger (1887) would act as First Reviser and establish "*benguelensis"* as the valid spelling.

In the morphological description of *Eremias benguelensis,* Bocage (1867b) seemingly describes only one specimen and makes no reference to a type series, even though he provides a range of ventral scales. In an annotated type catalogue of the lacertids in the Museum für Naturkunde (ZMB), Berlin, Germany, Bauer & Günther (1995) note that the ZMB catalogue lists a syntype (ZMB 7762) of *Eremias benguelensis* collected in "Maconjo" and donated by Bocage, which could not be located by the authors and was considered lost. The locality "Maconjo" could not be located by Bauer & Günther (1995) and has been tentatively interpreted as "Fazenda Mucungo, Namibe Province" by Marques *et al.* (2018). However, Vaz Pinto *et al.* (2019) noted the existence of two historical collecting localities bearing the name "Maconjo" in Angola: one near Capangombe in Namibe Province, where Anchieta was known to collect; and another in Benguela Province, visited by William John Ansorge between 1903 and 1905, that these authors restricted to the "vicinity of the streams Conjo, Conjo Pequeno, and Cocumba (12º52'S, 13º21'E, 355 m asl), 20 km south of Uche, Benguela Province" (Vaz Pinto et al. 2019). Considering this, if a specimen bearing the locality "Maconjo" was indeed donated by Bocage to the ZMB, it most likely would have been collected by Anchieta in Namibe Province, near Capangombe. However, this specimen could not have been part of the original type series, as the description of *Eremias benguelensis* was published before Anchieta sent the first batch of specimens from Maconjo to Bocage in early October 1867 (Banha de Andrade 1985), and reference to that specific locality was only made in Bocage (1873). Nevertheless, this putative syntype has not since been located in the ZMB collections (Bauer & Günther 1995; LMPC pers. obs.) and its status could not be verified.

Boulenger (1887) referred *E. benguelensis* to the synonymy of *E. namaquensis* without providing any justification or record of Angolan specimens, and this was followed by Bocage (1895), who referred his previous records to the synonymy of this species. However, Bocage's (1895) interpretation of "*namaquensis*" could have included up to three distinct taxa, as his material at hand comprised specimens from "Benguella" and "Catumbella", which likely represented true *P. benguelensis*, and specimens from "l'intérieur de Mossamedes" and "Capangombe", which probably represented a different taxon. Except for a specimen collected by Anchieta in Capangombe (MHNCUP/REP 0231, Fig. 11, see below), this material was lost in the fire that engulfed and destroyed all the collections of Museu Bocage in 1978 (Marques *et al.* 2018), making it impossible to ascertain the taxonomic identity of these specimens.

Based on material collected by Ansorge and deposited in the collections of the BMNH, Boulenger was the first author to recognize the existence of two distinct species in Angola, recovering *E. benguelensis* as a valid species, diagnosed by the presence of a "large transparent disc formed of a single black-edged scale" on the lower eyelid (Boulenger 1918), and assigning specimens characterized by a "lower eyelid with a transparent disc formed of 2 (…) larger black-edged scales", from "Maconjo" and "Huxe", in Benguela Province, to *Eremias undata* (Boulenger 1921). However, even though Bocage (1867b) mentioned a "transparent disc" on the lower eyelid, he did not mention the number of scales it comprised. The interpretation of this character can be ambiguous, considering that Bocage might have ignored the taxonomic value of this character, as did Laurent (1964) when he included both specimens with one and two transparent scales on the lower eyelid in the material he assigned to *Eremias undata*. Additional specimens conforming to Boulenger's (1921) description of *E. undata* were collected by Wulf Haacke in Benguela and Namibe provinces during the 1970s and are deposited in the collections of the Ditsong National Museum of Natural History. Specimens conforming to Boulenger's (1921) description of *Eremias undata*, with two transparent scales on the lower eyelid, were also collected by Conradie et al (2012b). Boulenger's (1918, 1921)

diagnosis of *E. benguelensis* based on the condition of the lower eyelid was accepted by subsequent authors (*e.g.,* Parker 1936; Monard 1937; Mertens 1971; Szczerbak 1975; Mayer 1989; Arnold 1991; Branch 1998), leading Conradie *et al.* (2012b) to assign newly collected material from Namibe Province to this species.

During recent surveys, additional material was collected in the coastal areas of Benguela Province, in the vicinity of the original type locality of "Benguella", which allowed for a reassessment of the status and diagnosis of *P. benguelensis*. As the original type material was lost in the fire that destroyed the collections of Museu Bocage on 18 March 1978, and the putative syntype identified by Bauer & Günther (1995) could not be located in the ZMB collections, the allocation of the name *P. benguelensis* to a specific taxonomic unit within the various lineages of Angolan *Pedioplanis* remains problematic. This situation is exacerbated by the lack of details provided by Bocage (1867a, 1867b) in the original descriptions, and the differences in subsequent interpretations by Boulenger (1887, 1918, 1921), Bocage (1895), Laurent (1964) and Conradie *et al.* (2012b). For the purpose of taxonomic and nomenclatural stability we consider it necessary to designate a neotype for this species.

Our results indicate that at least two species of *Pedioplanis* occur near Benguela, and Bocage's (1867b) vague description could apply to either of them. The only known surviving specimen that was presumably examined by Bocage (MHNCUP/REP 0231) has a single transparent scale on the lower eyelid, agreeing with Boulenger's (1918, 1921) diagnosis of *P. benguelensis*. However, while the material cited by Bocage (1867a) from Benguela was shipped by Anchieta in September 1866, the first batch of specimens from Capangombe was only shipped in July 1867 and reptiles from this locality were only cited in Bocage (1873). Therefore, this specimen could not have been part of the original type series, and was never unambiguously referred to *P. benguelensis*. Furthermore, it is likely that Bocage's (1867a) original material comprised more than one taxon, and Boulenger's (1918, 1921) decision to allocate the name *P. benguelensis* to his specimens with a single transparent scale on the lower eyelid was based on his own interpretation of Bocage's vague description, as we found no evidence suggesting that he ever examined Bocage's original material.

Instead of being consistent with Boulenger's (1918, 1921) interpretation, we believe Bocage's (1867b) original description of coloration—"ligne médiane d'une raie longitudinale noiratre (…) De chaque côté de cette raie dorsale une autre raie plus large noire, bordée en dessou de blanc"—is the most informative portion of his description and is more consistent with the coastal populations with two transparent scales on the lower eyelid, treated by Boulenger (1921) as *Eremias undata*. While these specimens display three distinct and well-defined dark dorsal stripes (see Diagnosis below), those with a single transparent scale on the lower eyelid most often show an indistinct vertebral stripe and broken dorsolateral stripes (see description below). Furthermore, we considered the proximity to the type locality as a main factor for the name allocation decision. Even though both species are sympatric in the vicinity of Benguela, what we designate as *P. benguelensis* sensu stricto has a coastal distribution centered in Benguela, while *P. benguelensis* sensu Boulenger (1918, 1921) is widely distributed in inland Benguela and Namibe provinces, with records from the coastal areas being scarce. Considering that Anchieta's first exploration of Benguela was mostly limited to coastal areas (Banha de Andrade 1985), we believe that he would be more likely to have collected the former rather than the latter. A designation of a neotype for *Pedioplanis benguelensis* (Bocage 1867) and an updated diagnosis for the species are provided below.

Diagnosis. *Pedioplanis benguelensis* is a boldly striped and medium-sized Sand Lizard, with an average SVL of 48 mm (max 58 mm) and a tail roughly two and a half times the SVL (Fig. 2). It can be distinguished from other species of the genus in Angola and Namibia by the following combination of characters: (1) lower eyelid with two enlarged transparent scales (rarely one—PEM R24110, or three—CAS 266239), with two to four smaller ones below; (2) five (rarely four or six) supralabials anterior to the subocular and usually three posteriorly; (3) two (sometimes one or three) rows of small granules between the supraoculars and supraciliaries; (4) a group of 9–26 (>13 in 75% of specimens) small granules preceding the supraoculars; (5) ventral scales in ten longitudinal rows; (6) presence of three bold black stripes extending from the back of the head to the base of the tail. The background coloration of the dorsum is brownish, with black stripes intercalated with thinner yellowish lines. The vertebral stripe splits at the neck, and in rare cases may be entirely divided into two thinner lines. Dorsolateral stripes are bold and well-defined. On the flanks there is a dark lateral stripe that starts behind the eye and extends to the hindlimb insertion, usually faint and reticulated, and often with a series of yellow spots along its lower edge. There may also be a thin and irregular line or series of streaks of reddish to black coloration, starting behind the labials and extending to the hindlimb insertion. The hindlimbs and the tail are greyish to reddish brown, with the legs often covered above by more or less distinct pale circles surrounded by dark pigmentation. The underparts are white, sometimes reddish at the base of the tail and hindlimbs.

Comparison with other *Pedioplanis* species. *Pedioplanis benguelensis* is readily distinguished from *P. burchelli*, *P. laticeps*, *P. breviceps* (Sternfeld, 1911), *P. namaquensis* and *P. husabensis* by the presence of two enlarged transparent scales on the lower eyelid (*versus* eight or more opaque to semi-transparent scales in the remaining species); from *P. lineoocellata* (Duméril & Bibron, 1839) by the presence of an enlarged tympanic shield (*versus* no enlarged tympanic shield in *P. lineoocellata*); from *P. inornata*, *P. rubens*, *P. gaerdesi* and *P. branchi* by the presence of distinct dorsal stripes (*versus* no stripes in *P. inornata*, *P. rubens*, *P. gaerdesi* and *P. branchi*); and from *P. undata* by a higher number of granules anterior to the supraoculars (usually >13 in *P. benguelensis versus* <14 in *P. undata*). *Pedioplanis benguelensis* is identical in most morphological characters to *P. mayeri*, from which it can be distinguished based on a greater maximum number of granules anterior to the supraocular (9–26 in *P. benguelensis versus* 9–16 in *P. mayeri*) and geographic location (*P. benguelensis* restricted to Angola *versus P. mayeri* restricted to Namibia). Regarding Angolan congeners, *P. benguelensis* is distinguished from *P. haackei* by dorsal color pattern (dark stripes distinct all the way to the tail in *P. benguelensis versus* mostly fading posteriorly in *P. haackei*); and from *P. huntleyi* by a higher number of granules anterior to the supraoculars (usually >13 in *P. benguelensis versus* <12 in *P. huntleyi*), usually two rows of granules between supraoculars and supraciliaries (*versus* usually one in *P. huntleyi*) and dorsal color pattern (dark stripes distinct all the way to the tail in *P. benguelensis versus* faded posteriorly in *P. huntleyi*). It is distinguished from an undescribed species by the presence of two enlarged transparent scales on the lower eyelid (*versus* one, see description below).

Neotype. CAS 266242 (field number AMB 9984; Fig. 3), adult male from Chimalavera Nature Reserve, vicinity of Main Camp [-12.83377°, 13.16991°, 293 m], Benguela Province. Collected by Luis M.P. Ceríaco, David C. Blackburn and Aaron M. Bauer on 11 December 2015. This specimen was selected as neotype because it was collected in the same biogeographic region and in the vicinity of the original type locality (< 35 km distant), has associated genetic data, and its morphological characters closely match the original description.

Additional material. 49 specimens: **Benguela Province:** 5 km inland from Meva beach [-13.47778°, 12.59222°, 244 m] (PEM R24225); Chimalavera Nature Reserve, vicinity of Main Camp [-12.83377°, 13.16991°, 293 m] (CAS 266237*–266241*, 266243*–266246*); Dombe Grande-Cuio road [-12.97805°, 13.07391°, 130 m] (CAS 266247*); pass into Meva Bay [-13.42278°, 12.57083°, 103 m] (PEM R24101, 24102); near Benguela [-12.63556°, 13.31500°, 64 m] (PEM R22070); road to Benguela, S of Dombe Grande [-13.02000°, 13.08806°, 280 m] (PEM R24741, 24742); small canyon near Meva fishing village [-13.41556°, 12.57639°, 30 m] (PEM R24110*, 24111, 27735, 27736); 10 km N of Lobito [-12.33478°, 13.65085°, 301 m] (TM 46575); 35 km S of Dombe Grande [-13.27569°, 12.94866°, 362 m] (TM 41254); Cimo, Equimina River [-13.333333°, 12.933333°, 268 m] (TM 41245); **Cuanza-Sul Province:** Sumbe [-11.20026°, 13.84186°, 11 m] (PEM R25195*, 25196*); **Namibe Province:** 10.4 km S of Makonga River, on tar road to Bentiaba [-14.84194°, 12.427778°, 370 m] (PEM R24209, 24210); 10 km SE of Lucira [-13.93139°, 12.59444°, 546 m] (PEM R24076*); road to Bentiaba, 25 km N of junction with Lubango-Namibe road [-14.85292°, 12.42481°, 430 m] (PEM R21665*, 21666*); sand road towards Chapeu Armando [-14.51972°, 12.44028°, 471 m] (PEM R24147); 2 km S of Chapéu Armado [-14.46917°, 12.33750°, 23 m] (PEM R24138); Mucungo farm [-14.79528°, 12.49500°, 342 m] (PEM R24142*), [-14.77890°, 12.48745°, 305 m] (CAS 266250); Bentiaba Fort [-14.27329°, 12.38505°, 51 m] (CAS 266254); dirt tracks N of Moçâmedes [-14.93503°, 12.26406°, 167 m] (PEM R21648*–21650*); small ridges N of Moçâmedes [-14.92408°, 12.37192°, 314 m] (PEM R21651*, 21652*); 31.5 km E of Namibe [-15.01686°, 12.39003°, 310 m] (PEM R18540*); 12 km S of Bentiaba [-14.34642°, 12.41838°, 248 m] (TM 41148, 41149); Bentiaba [-14.26667°, 12.38333°, 11 m] (TM 25464); Lucira [-13.86667°, 12.53333°, 51 m] (TM 41191); Lucira road, 5 km S of Catara River [-13.60194°, 12.62888°, 331 m] (TM 41198, 41201, 41229); coastal tracks 11 km N of Namibe, 1 km before old bridge across Giraul River [-15.08906°, 12.17014°, 58 m] (PEM R21658*).

The following specimens were tentatively assigned to this species based on a combination of morphological characters and geographic location (11 specimens): **Benguela Province:** Cimo, Equimina River [-13.33333°, 12.93333°, 268 m] (TM 41244); **Namibe Province:** 10 km SE of Lucira [-13.93139°, 12.59444°, 546 m] (PEM R24077); road to Bentiaba, 5 km S of Makonga River [-14.79750°, 12.43389°, 394 m] (PEM R24216, 24217); 2 km S of Chapéu Armado [-14.46917°, 12.33750°, 23 m] (PEM R24139); 2 km inland from Mucuio Bay [-14.89611°, 12.23722°, 110 m] (PEM R24155); Bentiaba [-14.26667°, 12.38333°, 11 m] (TM 25466, 43965); Lucira road, 5 km S of Catara River [-13.60194°, 12.62888°, 331 m] (TM 41228, 41232, 41233).

FIGURE 2. Live specimens of *P. benguelensis*. Above: PEM R24101, female found on a limestone ridge at the top of a pass into Meva Bay, Benguela Province. Below: PEM R21651*, male found on small ridges of sandstone boulders and limestone north of Moçâmedes, Namibe Province. Photos by William R. Branch.

FIGURE 3. Neotype male of *Pedioplanis benguelensis* (Bocage, 1867) (CAS 266242, field number AMB 9984). Photos by Luis M.P. Ceríaco.

Description of the Neotype. The neotype is an adult male with a complete original tail (Fig. 3). SVL 57.4 mm; TL 144.1 mm. Body relatively stout (SVL/HL 4.35), with hindlimbs longer than forelimbs and tail length two and a half times the SVL (TL/SVL 2.51). Moderately sized head (HL/SVL 0.23), distinct from the neck. Other relevant measurements are presented in Table 5. Rostral wider than high, visible from above. Nostril pierced between three scales; supranasals slightly swollen and in broad contact with each other behind rostral; infranasal in contact with rostral, first supralabial and anterior loreal; postnasal small and subquadrangular, placed between the supranasal, infranasal, anterior loreal and frontonasal. Frontonasal slightly longer than wide, rounded anteriorly and slightly acuminate posteriorly. Prefrontals in broad contact with each other, the loreals, frontonasal and frontal. Two loreals, posterior largest. Frontal longer than wide, narrower posteriorly, in contact with prefrontals anteriorly, supraoculars laterally and frontoparietals posteriorly. Paired frontoparietals in broad median contact, touching the frontal and posterior supraocular anteriorly, and the parietals and interparietal posteriorly. Interparietal pentagonal, longer than broad. Occipital small, wider than long, in broad contact with interparietal, its posterior margin slightly wider than the anterior. Parietals longer than wide, in contact with frontoparietals, interparietal and occipital. Two rounded supraoculars in contact with each other and the frontal, preceded by a group of 14 (right side) and 13 (left side) small granules, those in contact with the frontal and prefrontal largest. Two rows of small granules between supraoculars and supraciliaries. Supraciliaries six (right side) and seven (left side), first longest. Temporal scales small and granular. One narrow and elongated tympanic shield at the anterodorsal edge of ear opening. Subocular bordering lip, upper margin wider than lower. Five supralabials anterior to subocular and three posteriorly. Lower eyelid with two black edged, enlarged transparent scales, with two smaller ones below. Infralabials six. Mental wider than long, in contact with first infralabials and first pair of chin shields. Four pairs of chin shields, first three in median contact and fourth largest. Gular scales 31, in a straight line between the symphysis of the chin shields and median collar plate. Collar free, comprising seven enlarged plates. Ventral scales smooth, in ten longitudinal and 28 transverse rows; outer scales smaller than others; those on the first complete transverse row posterior to collar notably longer than others. Precloacal scales irregular and subequal, central ones largest. Fifteen femoral pores on each leg. Lamel-

lae under fourth toe 27. Dorsal scales small and granular, larger towards ventral scales. Upper forelimbs covered above by large hexagonal plates; forearm covered above by slightly imbricate and keeled scales, larger than dorsal scales, and below by enlarged plates. Hindlimbs covered above by slightly imbricate and keeled scales, larger than dorsal scales, and below by enlarged plates. Scales on tail diagonally keeled, except for those on ventral side of basal portion, which are smooth.

Coloration (in preservative). Head and limbs brownish; hindlimbs covered above with pale circles surrounded by black speckling. Dorsum with three bold and well-defined dark stripes intercalated with four thinner white to yellowish lines, extending from the back of the head to the base of the tail. The black vertebral stripe splits at the nape towards parietals. Flanks with a reticulated black stripe extending from the back of the eye to the hindlimb insertion, with a series of pale spots running along its lower edge. Tail brown above, with some black keeled scales. Moderate greyish speckling on the labials and flanks. Venter white.

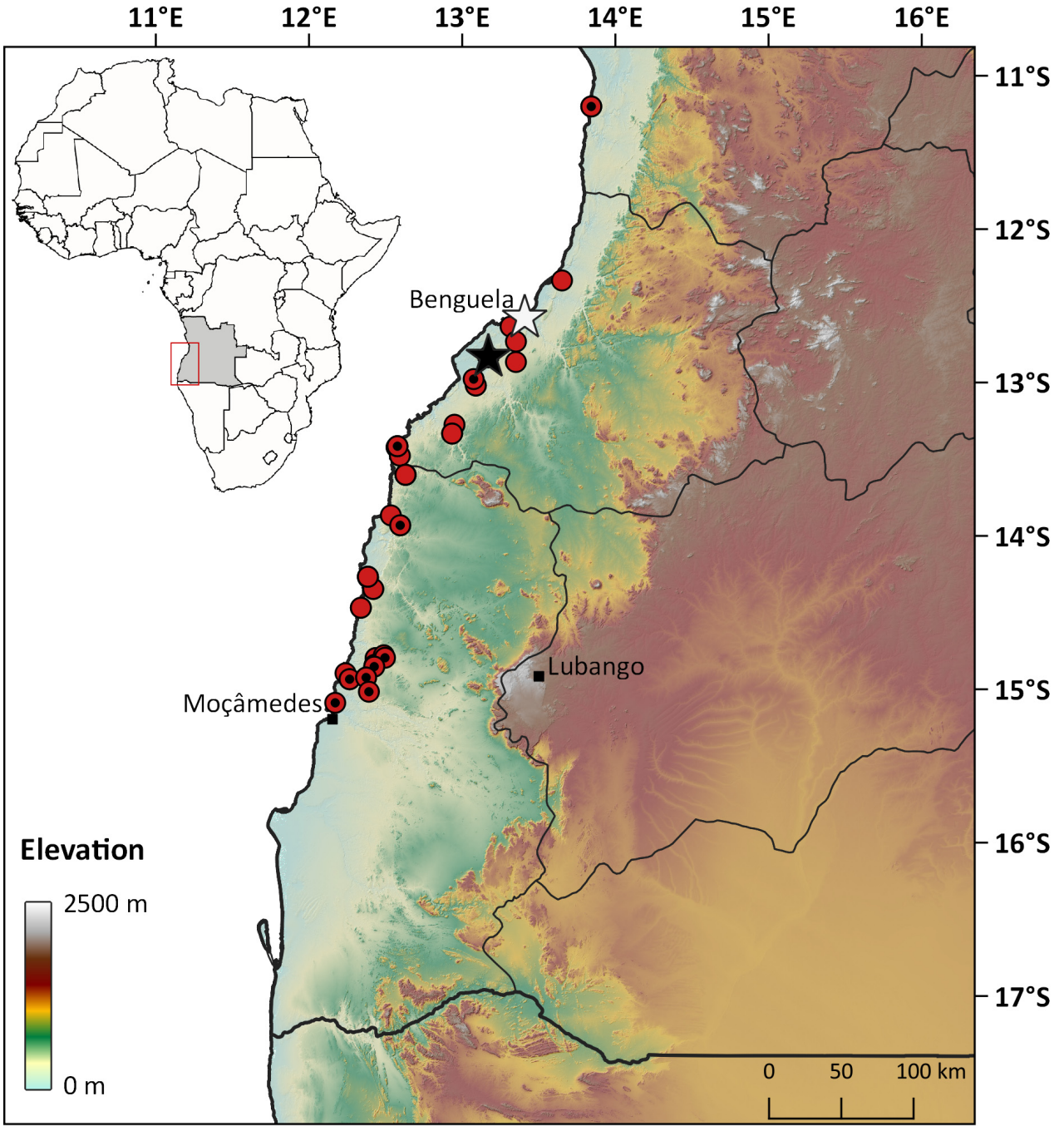

FIGURE 4. Geographic distribution of *Pedioplanis benguelensis* based on museum vouchers. Localities represented in the phylogenetic analysis are indicated with a black center. White star denotes the original type locality and black star represents the neotype locality. Major cities are represented by a black square.

Distribution and habitat. Known records of *P. benguelensis* are restricted to lower elevation areas (below 546 m) in coastal Angola, as far as 30 km inland from the coastline, from Moçâmedes, Namibe Province, northwards to Sumbe, Cuanza-Sul Province (Fig. 4). It is sympatric with an undescribed species in most of coastal Benguela Province and northern Namibe Province, and *P. haackei* in the littoral of northern Namibe Province. This species inhabits the xeric coastal areas of southwestern Angola, which are characterized by sublittoral steppes with bushes and herbage, mostly belonging to the plant genera *Senegalia, Commiphora*, *Colophospermum*, *Aristida*, *Schmidtia* and *Setaria* (Grandvaux-Barbosa 1970; Fig. 5).

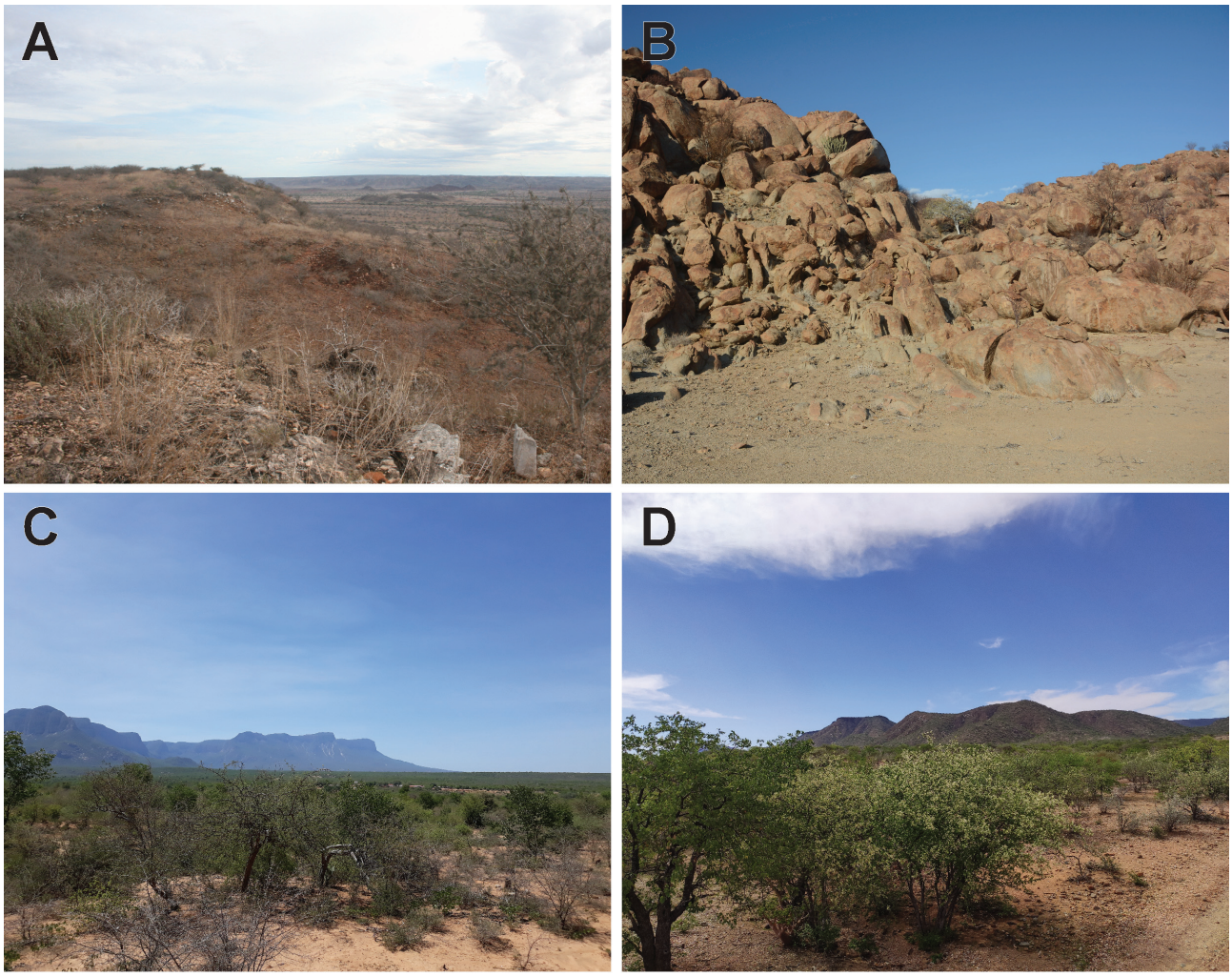

FIGURE 5. Typical habitats of Angolan *Pedioplanis*. **A.** Dry coastal savanna with sparse vegetation at Chimalavera Natural Regional Park, Benguela Province (*P. benguelensis*). Photo by Luis M.P. Ceríaco. **B.** Rocky outcrops near Omauha Lodge, Namibe Province (*P. haackei*). Photo by Ishan Agarwal. **C.** Mopane dominated shrubland near Capangombe, Namibe Province (*P. serodioi* **sp. nov.**). Photo by Luis M.P. Ceríaco. **D.** Mopane shrubland near Oncocua, Cunene Province (*P. huntleyi*). Photo by Luis M.P. Ceríaco.

Pedioplanis haackei Conradie, Measey, Branch and Tolley, 2012
(Figs. 6–7)

Eremias undata undata: Laurent (1964: 60) [part]
Pedioplanis undata: Haacke (2008: 6)
Pedioplanis sp. 2: Conradie *et al.* (2012b: 95)
Pedioplanis haackei: Conradie *et al.* (2012b: 101); Ceríaco *et al.* (2016: 37; 2018: 113) [part]; Marques *et al.* (2018: 223; 2019b: 504); Branch *et al.* (2019b: 92; 2019c: 296)
Pedioplanis sp.: Ceríaco *et al.* (2020: 401) [part]

This species was formally described by Conradie *et al.* (2012b) based on specimens collected between Lake Arco and Espinheira, in Namibe Province. It is possible that Bocage's (1895) records of *Eremias namaquensis* from "Capangombe" and "l'intérieur de Mossamedes" included representatives of this species, but the loss of this material precludes any confident conclusion. Specimens from Moçâmedes and Munhino in Namibe Province, and Quilengues in Huíla Province, collected by António de Barros Machado in 1949, were later reported by Laurent (1964) as *Eremias undata undata* and are still deposited in the collections of the Museu Regional do Dundo. Additional specimens were collected in Namibe Province by Wulf Haacke in the 1970s, deposited in the collections of the Ditsong National Museum of Natural History and later reported as *Pedioplanis undata* (Haacke 2008). New material reported by Ceríaco *et al.* (2016) and in this paper considerably expand the known distribution area of *Pedioplanis haackei*. A specimen collected by Conradie *et al.* (2012b) near the bottom of the Leba escarpment (PEM R18460*, field number MBUR 02132) was provisionally treated by the authors as a separate lineage, *Pedioplanis* sp. 2. Our analysis, however, shows that this specimen belongs to a northern clade of *P. haackei*, and we interpret this as an indication of intraspecific genetic structure rather than a distinct taxon.

Diagnosis: A small *Pedioplanis* with an average SVL of 45 mm (max 59 mm), with a tail length roughly two and a half times the SVL (Fig. 6). It can be distinguished from other species of the genus in Angola and neighboring regions by the following combination of characters: (1) lower eyelid with two enlarged transparent scales, often with a row of smaller ones below; (2) five (rarely four or six) supralabials anterior to the subocular and two to three posteriorly; (3) two (rarely one or three) rows of small granules between the supraoculars and supraciliaries; (4) a group of 7–28 (>12 in 75% of specimens) small granules anterior to the supraoculars; (5) ventral scales in ten (rarely nine or 11) longitudinal rows; (6) variable color pattern, usually with three dark dorsal stripes faded posteriorly. Among Angolan *Pedioplanis*, this species seems to be the most variable in terms of color pattern. The dorsum is greyish brown anteriorly and pale brown to brick red posteriorly, usually with dark stripes starting at the back of the head and fading between midbody and two-thirds along the back. The vertebral stripe splits or widens at the neck, or may be entirely split into two thinner stripes, with a greyish interspace. Dorsolateral stripes are usually wider and more distinct than the vertebral one. On the flanks there is a dark lateral stripe that starts behind the eye and usually fades posteriorly, often faint and reticulated, with a series of yellow to blueish circles running along its lower edge. However, the extension and distinctiveness of dorsal stripes is quite variable, being completely absent in some specimens, and extending nearly to the base of the tail in others. Hind limbs and tail reddish-brown to brick red, with the hindlimbs sometimes covered above by faint pale circles. White ventrally, sometimes reddish at the base of the tail.

Comparison with other *Pedioplanis* species. *Pedioplanis haackei* is readily distinguished from *P. burchelli*, *P. laticeps*, *P. breviceps*, *P. namaquensis* and *P. husabensis* by the presence of two enlarged transparent scales on the lower eyelid (*versus* eight or more opaque to semi-transparent scales in other species); from *P. lineoocellata* by the presence of an enlarged tympanic shield (*versus* no enlarged tympanic shield in *P. lineoocellata*); from *P. inornata*, *P. rubens*, *P. gaerdesi* and *P. branchi* by the presence of dorsal stripes (*versus* no stripes in *P. inornata*, *P. rubens, P. gaerdesi* and *P. branchi*); from *P. undata* by color pattern (bold anterior dorsal striping that fades posteriorly in *P. haackei versus* dorsal striping bold or not, may be reduced with pale longitudinal elements or even a single middorsal stripe restricted to the nape in *P. undata*) and a greater maximum number of granules anterior to the supraoculars (7–28 in *P. haackei versus* 8–13 in *P. undata*); and from *P. mayeri* by color pattern (dorsal stripes usually faded posteriorly in *P. haackei versus* bold and distinct all the way to the tail in *P. mayeri*), and a greater maximum number of granules anterior to the supraocular (7–28 in *P. haackei versus* 9–16 in *P. mayeri*). It can be further distinguished from *P. undata* and *P. mayeri* by geographic location (*P. haackei* restricted to Angola *versus P. mayeri* and *P. undata* restricted to Namibia). With respect to Angolan congeners, *P. haackei* is distinguished from *P. benguelensis* by color pattern (posterior dorsum usually reddish with faded stripes in *P. haackei versus* bold stripes all the way to the tail in *P. benguelensis*); it is distinguished from *P. huntleyi* by a smaller average SVL (mean 45 mm in *P. haackei versus* 54 mm in *P. huntleyi*), a higher number of granules anterior to the supraoculars (usually >11 in *P. haackei versus* <12 in *P. huntleyi*) and two rows of granules between supraoculars and supraciliaries (*versus* one in *P. huntleyi*). It is distinguished from an undescribed species by the presence of two transparent scales on the lower eyelid (*versus* one, see description below).

Holotype: PEM R18465*, an adult male collected along the road to Tambor, Namibe Province [-15.87606°, 12.20583°, 196 m], by William R. Branch, G. John Measey, Werner Conradie and Krystal A. Tolley on 19 January 2009.

FIGURE 6. Live specimens of *Pedioplanis haackei*. Above: CAS 266123 from the base of Serra da Neve, Namibe Province, with typical coloration. Photo by Luis M.P. Ceríaco. Below: CAS 264795 from Virei-Virulundo, Namibe Province, with indistinct dorsal stripes. Photo by Ishan Agarwal.

Additional material. 121 specimens: **Benguela Province:** 2 km from Lucira-Benguela road, towards Cape Santa Maria [-13.51167°, 12.62833°, 285 m] (PEM R24087); **Huíla Province:** 13 km N of Quilengues, on road to Benguela [-13.97247°, 14.04717°, 936 m] (PEM R21661*); **Namibe Province:** 10 km S of Lake Arco [-15.83044°, 12.14125°, 121 m] (PEM R18470, 18471*, 18472*); on the road to Benguela, 2 km N of turning to Lucira [-13.90528°, 12.54417°, 312 m] (AG 98*); road to Bentiaba, 52 km N of junction with Lubango-Namibe road [-14.65806°, 12.52717°, 586 m] (PEM R21662*, 21663*); 5 km along fence leading to Baptista farm [-16.05847°, 12.42597°, 343 m] (PEM R18468); Humpata-Namibe road, 7.8 km from bottom of Leba pass [-15.04467°, 13.15947°, 642 m] (PEM R18460*, 21664*); along road to Tambor [-15.88778°, 12.36417°, 300 m] (PEM R18464*), [-15.87606°, 12.20583°, 196 m] (PEM R18466–18467); base of Serra da Neve, on dirt road to Quilengues [-13.81594°, 13.32644°, 892 m] (MHNC-UP/REP 645); base of Serra da Neve, on dirt road to the top of the mountain [-13.83424°, 13.27669°, 803 m] (MHNC-UP/REP 634-635, CAS 266123); Catara River valley [-13.62417°, 12.83556°, 454 m] (PEM R24057*, 24058, 24059, 24060, 24061*, 24062*); Caraculo [-15.01651°, 12.64251°, 487 m] (CAS 264769*); Chipumpo-Virulundo [-16.19125°, 12.85595°, 539 m] (CAS 264805*); Curoca-Omahua [-15.81918°, 12.14273°, 100 m] (CAS 264774*, 264775*, 264776), [-15.95026°, 12.49531°, 394 m] (CAS 264777*–264779*); dry river valley, approximately 10 km S of turning to Lucira [-13.96389°, 12.53222°, 137 m] (PEM R24223, 24224); Lucira Dam [-13.87889°, 12.56556°, 339 m] (PEM R24103*, 24104); Mucungo farm [-14.78111°, 12.48983°, 296 m] (MHNCUP/REP 633), [-14.77890°, 12.48745°, 305 m] (CAS 266248); Munhino [-14.92000°, 13.00000°, 393 m] (MD 1918b); near Virulundo [-16.28523°, 12.94192°, 718 m] (CAS 264806*–264808*, 264810*); near Curoca River [-16.24468°, 12.34068°, 265 m] (CAS 264781*); off road 20 km N of Omauha Lodge [-16.07414°, 12.43328°, 352 m] (PEM R18474*); Omauha-Virei [-16.14506°, 12.59460°, 538 m] (CAS 264791*); Omauha Lodge [-16.19858°, 12.40073°, 340 m] (CAS 264780*, 264784*–264790*, MHNC-UP/REP 644, INBAC/AMB 10416*), [-16.20033°, 12.40003°, 343 m] (CAS 254835*); Omauha Lodge, N of entrance to Iona National Park [-15.99694°, 12.40694°, 301 m] (PEM R18473); Red Canyons near Lake Arco [-15.74597°, 12.13989°, 81 m] (PEM R18461*, 18462, 18463); road from Lake Arco to Espinheira [-15.91356°, 12.39519°, 319 m] (PEM R18475*); road to Tambor [-15.88119°, 12.22267°, 192 m] (PEM R18469*); sandstone hill near Piambo [-14.65833°, 12.36944°, 365 m] (PEM R22041); vicinity of N'Dolondolo [-13.80866°, 13.13521°, 731 m] (CAS 264757*, 264765*); Virei-Virulundo [-16.31018°, 12.79597°, 471 m] (CAS 264794*, 264801*, 264803*); 10 km E of Munhino [-14.87821°, 13.13195°, 566 m] (TM 46726); 12 km N of Furnas [-15.02513°, 12.18828°, 69 m] (TM 40570); 12 km N of Tambor [-15.96780°, 12.39581°, 262 m] (TM 40496); 23 km W of Virei [-15.66886°, 12.74089°, 397 m] (TM 41025); 30 km N of Tambor [-15.89287°, 12.37609°, 312 m] (TM 40489–40491); 35 km S of Moçâmedes [-15.48000°, 12.21000°, 150 m] (MD 1946); 3 km E of Chicambi village [-13.89556°, 12.78222°, 612 m] (AG 69*–71*); 5 km (by road) NW of Pico Azevedo [-15.47547°, 12.46219°, 408 m] (CAS 254763*, 254764*), [-15.47600°, 12.46150°, 399 m] (CAS 254767*); 60 km (by road) E of Tômbua [-15.87760°, 12.21668°, 189 m] (TM 40451–40453); Assunção [-14.86667°, 13.10000°, 505 m] (TM 40181); 17 km W of Chicamba village [-13.91722°, 12.68111°, 531 m] (AG 84*); Inamangando farm [-14.05114°, 12.42733°, 24 m] (TM 41157, 41158); Iona National Park, N of Tambor [-15.99539°, 12.40647°, 306 m] (CAS 254840*); Iona National Park, Curoca river crossing [-16.30000°, 12.43333°, 198 m] (TM 40580); Lungo [-14.66667°, 13.25000°, 679 m] (TM 24397, 24398, 24400); Moçâmedes [-15.16667°, 12.16667°, 6 m] (TM 22844–22845); Pediva Hot Springs, S side of the river [-16.29381°, 12.56033°, 235 m] (CAS 254860*); Pico Azevedo [-15.53400°, 12.49197°, 359 m] (CAS 254939); Namibe Nature Reserve [-15.77292°, 12.33269°, 262 m] (CAS 254951*, 254953*); Saiona River [-15.40000°, 13.20000°, 534 m] (TM 40983–40985); Tambor [-16.13556°, 12.42972°, 379 m] (TM 40501, 40502), [-16.06710°, 12.42970°, 348 m] (INBAC/AMB 10393*).

The following specimens were tentatively assigned to this species based on a combination of morphological characters and geographic location (10 specimens): **Benguela Province:** 2 km turning on Cape Santa Maria from Lucira-Benguela coastal road [-13.51167°, 12.62833°, 285 m] (PEM R24086, 24088); **Namibe Province:** 13.6 km S of Mucungo Farm [-14.85528°, 12.42889°, 400 m] (PEM R24153); 1 km SE of Mucungo Farm [-14.78667°, 12.49611°, 303 m] (PEM R24133–24135); 8.8 km S of Mucungo Farm [-14.80167°, 12.41917°, 579 m] (PEM R24160); Catara River valley [-13.62278°, 12.80750°, 454 m] (PEM R27734); Lucira [-13.86667°, 12.53333°, 51 m] (TM 24430, 41190).

Distribution and habitat. *Pedioplanis haackei* occurs over most of Namibe Province north of -16º latitude, extending marginally into southern Benguela Province, and northwestern Huíla Province below 1000 m (Fig. 7). It is absent from the more xeric areas of southwestern Namibe Province, as well as southeastern Namibe Province,

where it is replaced by *P. huntleyi*, with both species occurring in sympatry near Virulundo and Pediva Hot Springs. *Pedioplanis haackei* is sympatric with *P. benguelensis* in coastal areas, and with the undescribed species in several localities along most of its range. This species inhabits a vast area covering different habitat types, from more xeric areas to areas dominated by Mopane woodlands (Grandvaux-Barbosa 1970; Fig. 5).

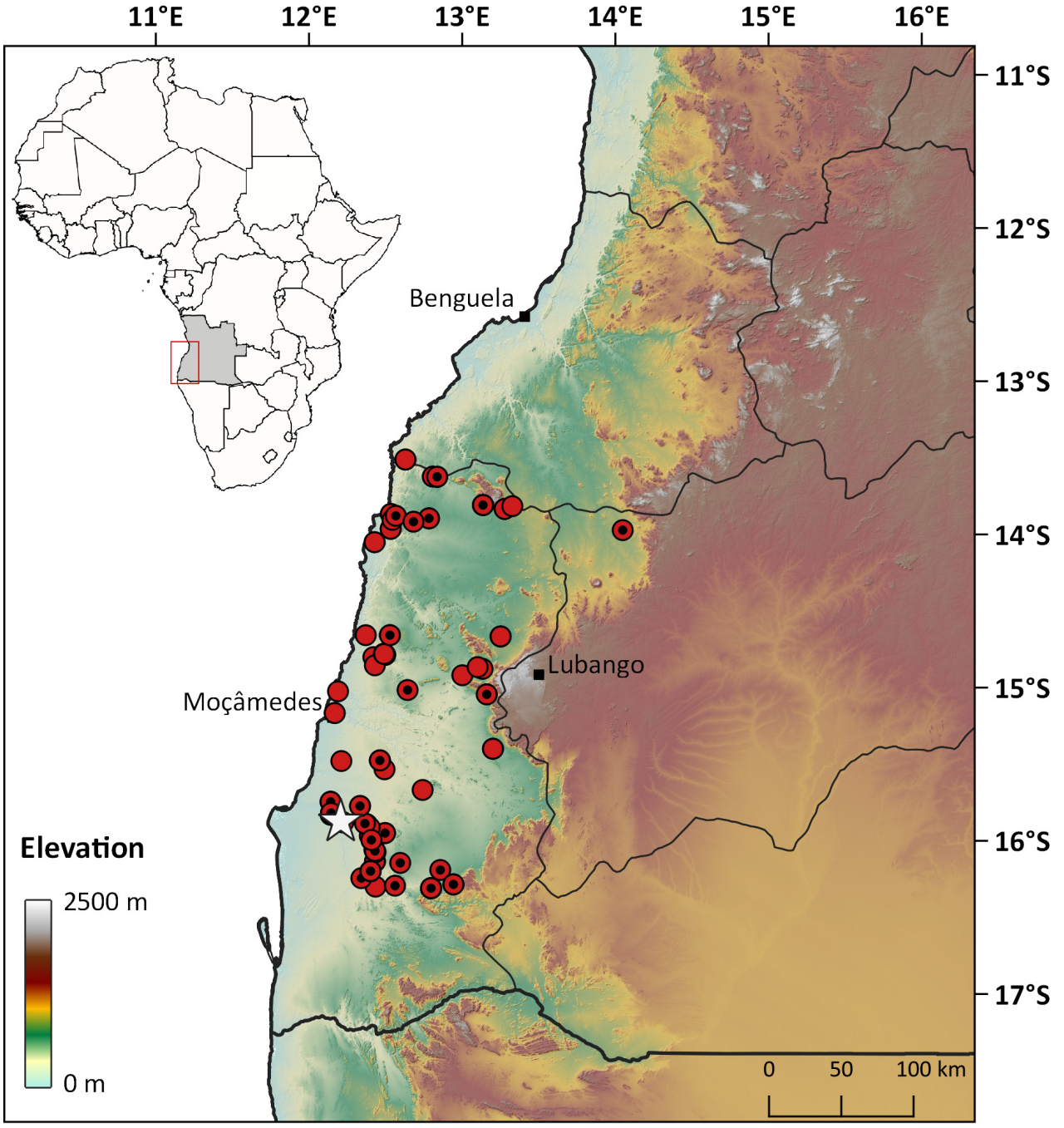

FIGURE 7. Geographic distribution of *Pedioplanis haackei* based on museum vouchers. Localities represented in the phylogenetic analysis are indicated with a black center. White star denotes the type locality. Major cities are represented by a black square.

***Pedioplanis huntleyi* Conradie, Measey, Branch and Tolley, 2012**
(Figs. 8–9)

Pedioplanis huntleyi: Conradie *et al.* (2012b: 105); Ceríaco *et al.* (2016: 56; 2018: 113); Marques *et al.* (2018: 224; 2019b: 504); Branch *et al.* (2019b: 92; 2019c: 296)
Pedioplanis haackei: Ceríaco *et al.* (2016: 37) [part]

Conradie *et al.* (2012b) described *Pedioplanis huntleyi* based on specimens collected in the southeastern areas of Namibe Province and western regions of Cunene Province. Additional material reported by Ceríaco *et al.* (2016) (CAS 254864*, as *P. haackei*) and in this study document a northward extension of the known distribution range of *Pedioplanis huntleyi*. There are no taxonomic or nomenclatural issues with this species.

Diagnosis: A rather large *Pedioplanis*, with an average SVL of 55 mm (max 59 mm) and a tail length two and a half times the SVL (Fig. 8). It can be distinguished from other species of the genus in Angola and neighboring regions by the following combination of characters: (1) lower eyelid with two enlarged transparent scales, usually with a row of smaller ones below; (2) five (rarely four or six) supralabials anterior to the subocular and three posteriorly; (3) one (sometimes two) row of small granules between the supraoculars and supraciliaries; (4) supraoculars preceded by a group of 6–13 (<12 in 75% of specimens) small granules; (5) ventral scales in ten longitudinal rows; (6) three dark dorsal stripes faded posteriorly. Coloration similar to *P. haackei*, but less variable. Dorsum greyish brown anteriorly and reddish-brown to brick red posteriorly, with three dark stripes starting behind the head and fading between midbody and two-thirds along the back. The vertebral stripe splits or widens at the neck and is often more faded than the dorsolateral stripes. On the flanks there is a dark lateral stripe that starts behind the eye and usually fades posteriorly, often faint and reticulated, with a series of yellow to blueish circles running along its lower edge. Hind limbs and tail reddish-brown to brick red, with the hindlimbs sometimes covered above by faint pale circles. White ventrally, sometimes reddish at the base of the tail.

FIGURE 8. Live specimen of *Pedioplanis huntleyi* (MHNC-UP/REP 643) from the vicinity of Elola village, Cunene Province. Photo by Luis M.P. Ceríaco.

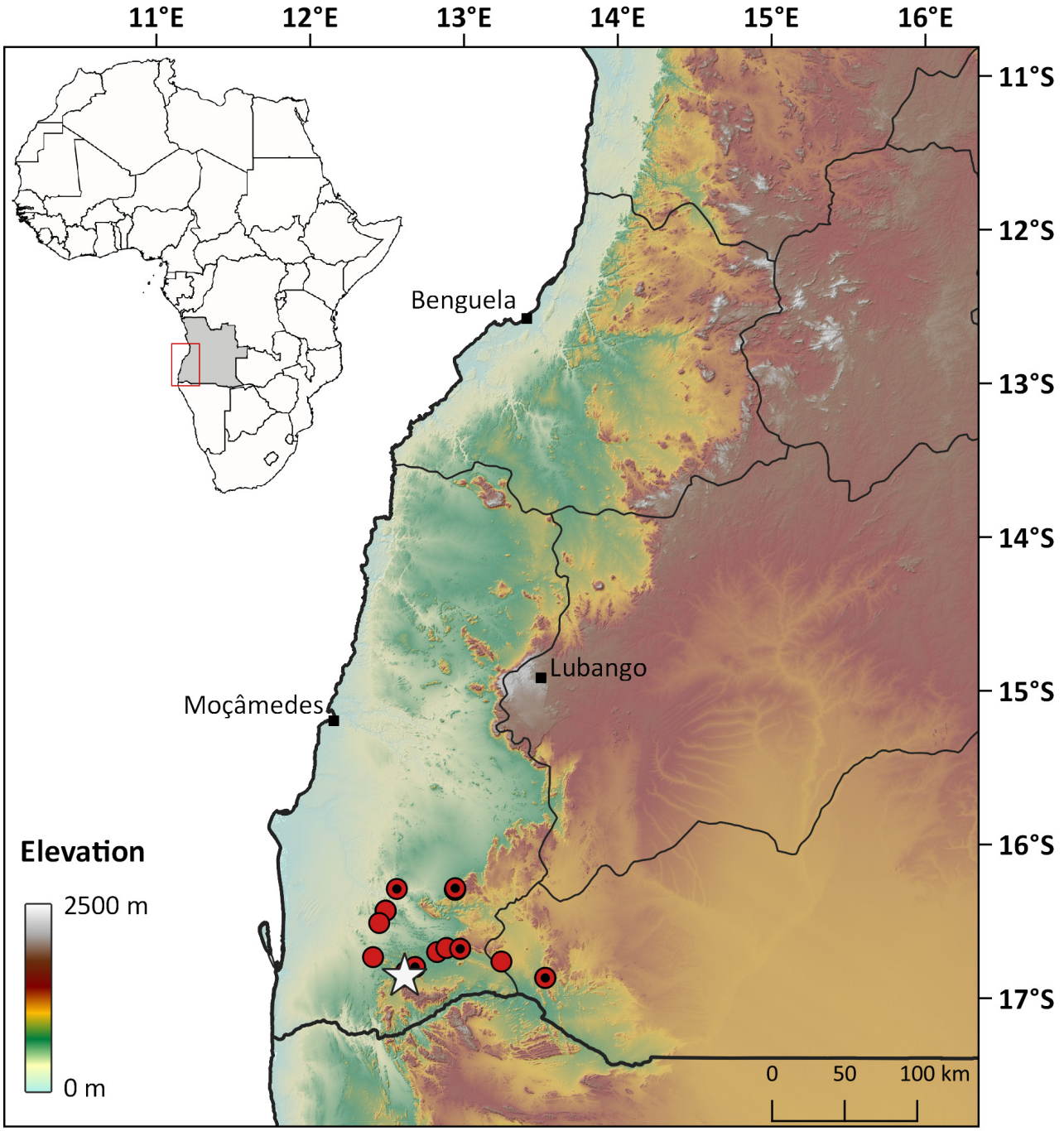

FIGURE 9. Geographic distribution of *Pedioplanis huntleyi* based on museum vouchers. Localities represented in the phylogenetic analysis are indicated with a black center. White star denotes the type locality. Major cities are represented by a black square.

Comparison with other *Pedioplanis* species. *Pedioplanis huntleyi* is readily distinguished from *P. burchelli*, *P. laticeps*, *P. breviceps*, *P. namaquensis* and *P. husabensis* by the presence two enlarged transparent scales on the lower eyelid (*versus* eight or more opaque to semi-transparent scales in other species); from *P. lineoocellata* by the presence of an enlarged tympanic shield (*versus* no enlarged tympanic shield in *P. lineoocellata*); from *P. inornata*, *P. rubens, P. gaerdesi* and *P. branchi* by the presence of dorsal stripes (*versus* no stripes in *P. inornata, P. rubens, P. gaerdesi* and *P. branchi*). *P. huntleyi* is identical in most morphological characters to *P. undata* and *P. mayeri*, from which it can be distinguished based on color pattern (dorsal stripes always faded posteriorly in *P. huntleyi versus* usually bold and distinct all the way to the tail in *P. mayeri* and bold or faded in *P. undata*) and geographic location (*P. huntleyi* restricted to Angola *versus P. mayeri* and *P. undata* restricted to Namibia). With respect to other Angolan

species, *P. huntleyi* can be distinguished from *P. benguelensis* by a lower number of granules anterior to the supraoculars (usually <12 in *P. huntleyi versus* >13 in *P. benguelensis*), one row of granules between the supraoculars and supraciliaries (*versus* two in *P. benguelensis*) and color pattern (dorsal stripes faded posteriorly in *P. huntleyi versus* distinct all the way to the tail in *P. benguelensis*); it is distinguished from *P. haackei* by a larger SVL (average 54 mm in *P. huntleyi* versus 45 mm in *P. haackei*), a lower number of granules anterior to the supraoculars (usually <11 in *P. huntleyi versus* >12 in *P. haackei*) and one row of granules between the supraoculars and supraciliaries (*versus* two in *P. haackei*). It is distinguished from an undescribed species by the presence of two transparent scales on the lower eyelid (*versus* one, see description below).

Holotype: PEM R18479*, an adult male collected on the road to Oncocua, 7 km from Iona, Namibe Province [-16.85831°, 12.61275°, 803 m], by Werner Conradie, Eduardo Traguedo, Krystal A. Tolley and William R. Branch on 21 January 2009.

Additional material. 26 specimens: **Cunene Province:** 26 km SE of Oncocua [-16.86889°, 13.52750°, 846 m] (PEM R18483, 18489, 18490*); NE of Elola village [-16.76251°, 13.24230°, 892 m] (MHNC-UP/REP 643); **Namibe Province:** 14 km W of Moimba [-16.67944°, 12.97389°, 684 m] (PEM R18481, 18487*); 23 km W of Moimba [-16.67444°, 12.88500°, 602 m] (PEM R18482, 18488); 16 km E of Iona [-16.79806°, 12.68056°, 785 m] (PEM R18480, 18485*); 26 km E of Iona [-16.70056°, 12.82417°, 623 m] (PEM R18486); 8 km NE of Iona [-16.82917°, 12.62111°, 743 m] (PEM R18484*); Iona National Park [-16.43150°, 12.48930°, 431 m] (MHNC-UP/REP 640–642), [-16.85972°, 12.61111°, 811 m] (TM 40739); Iona National Park, 50 km S of Curoca River [-16.73367°, 12.40757°, 472 m] (TM 40596); near Virulundo [-16.28523°, 12.94192°, 718 m] (INBAC/AMB 10632*), [-16.29485°, 12.94075°, 759 m] (CAS 264811*–264813*, INBAC/AMB 10645*); road to Espinheira, 40 km S of Omauha Lodge [-16.51164°, 12.44761°, 371 m] (PEM R18476); road to Oncocua, 7 km from Iona [-16.85834°, 12.61275°, 803 m] (PEM R18477, 18478*); Pediva Hot Springs, south side of the river [-16.29000°, 12.56219°, 270 m] (CAS 254864*).

Distribution and habitat. Known records of *Pedioplanis huntleyi* are restricted to southwestern Angola south of -16° latitude, from eastern Iona National Park in Namibe Province eastwards to the Oncocua region in Cunene Province, between 270 and 892 m (Fig. 9). This species is sympatric with *P. haackei* in some localities along the northern limits of its range. This species inhabits xeric areas dominated by Mopane forests (*Colophospermum mopane*) (Grandvaux-Barbosa 1970; Fig. 5).

Pedioplanis serodioi **sp. nov.**

(Figs. 10–13)

Eremias benguelensis: Boulenger (1918: 5; 1921: 287); Parker (1936: 134); Mertens (1954: 177)
Eremias benguellensis: Monard (1937: 72); Mertens (1971: 59)
Eremias undata undata: Laurent (1964: 60) [part]
Mesalina benguelensis: Szczerbak (1975: 24)
Pedioplanis benguelensis: Arnold (1989: 213); Mayer (1989: 135)
Pedioplanis benguellensis: Arnold (1991: 785); Branch (1998: 173); Conradie *et al.* (2012b: 95); Ceríaco *et al.* (2016: 37); Marques *et al.* (2018: 222) [part]
Pedioplanis sp.: Ceríaco *et al.* (2020: 401) [part]

The first records of this species were probably those provided by Bocage (1895) as *Eremias namaquensis* from "Capangombe par M. d'Anchieta" and "l'intérieur de Mossamedes par MM. Capello et Ivens". However, earlier records as *Eremias benguelensis* from "Benguella" (Bocage 1867a, 1867b) could have also represented this taxon. Nevertheless, the loss of these specimens precludes any further inferences regarding their taxonomic identity. The only exception is a specimen collected by Anchieta in Capangombe (MHNCUP/REP 0231, Fig. 11) and still deposited in the collections of MHNC-UP, which represents the first confirmed record of this species.

Boulenger's (1918, 1921) diagnosis of "*benguelensis*" was characterized by the presence of a single transparent scale on the lower eyelid, which was present in his specimens from "Huxe" [= Uche, Benguela Province] and "Ponang Kuma" [= Dongoena, Cunene Province], collected by Ansorge. Boulenger's (1918, 1921) diagnosis was followed by most authors (*e.g.,* Monard 1937; Szczerbak 1975; Mayer 1989; Branch 1998) and Parker (1936) reported a specimen (BMNH 1936.8.1.514) from "Catengue", Benguela Province, collected during the Karl Jordan's expedition to South-West Africa and Angola and deposited in the collections of the Natural History Museum, Lon-

don. Laurent (1964) reported additional Angolan material under the name *Eremias undata undata*, including among his records two specimens with a single transparent scale on the lower eyelid, collected by Barros Machado in Munhino, Namibe Province (MD 1918a), and Quilengues, Huíla Province (MD 1970-1).

Following Boulenger's (1918, 1921) diagnosis and the lack of topotypic comparative material, Conradie *et al.* (2012b) conservatively assigned specimens collected in central and southeastern Namibe Province to *P. benguelensis*, providing the first molecular data for this species. Three additional specimens conforming to Boulenger's (1918, 1921) diagnosis of *P. benguelensis* were collected by Ceríaco *et al.* (2016) near Caraculo, Namibe Province. The collection of true *P. benguelensis* from the coastal areas of Benguela Province allowed for a reassessment of Angolan populations assigned to this species. Our analysis revealed species-level phylogenetic distance as well as consistent morphological differences from all named species of *Pedioplanis*. Based on the evidence produced in this study, we here describe a new species of Angolan *Pedioplanis* characterized by the presence of a single transparent scale on the lower eyelid (see *P. benguelensis* account for discussion on the name allocation decision).

Diagnosis: *Pedioplanis serodioi* **sp. nov.** is a rather small *Pedioplanis*, with an average SVL of 44 mm (max 50 mm) and a tail length roughly twice the SVL (Fig. 10). It can be distinguished from other *Pedioplanis* species in Angola and neighboring regions by the following combination of characters: (1) lower eyelid with a single black-edged, enlarged transparent scale; (2) four (rarely three, five or six) supralabials anterior to the subocular and two (rarely three) posteriorly; (3) One (sometimes two) row of small granules between the supraoculars and supraciliaries; (4) a group of 6–24 (<15 in 75% of specimens) small granules preceding the supraoculars; (5) ventral scales in ten longitudinal rows; (6) a pair of irregularly edged dorsolateral stripes or series of spots and a faint or absent vertebral stripe. The dorsum is greyish brown to pale grey, often with extensive black speckling throughout. There may be a thin, dark vertebral stripe, but this is usually faint and indistinct, or reduced to irregular black streaks. A pair of irregularly edged, black dorsolateral stripes extend from the back of the head to the base of the tail, often broken into series of black spots on a reddish-brown background. A pale line separates the dorsolateral stripes from a lateral stripe that starts behind the eye and extends to the base of the tail, often faint and reticulated, with a series of yellow spots running along its lower edge. There is often a reddish stripe extending from the posterior labials to the hindlimb insertion, up to four scales wide, continuous or broken into series of streaks. The hindlimbs are often covered above by pale circles surrounded by black pigmentation. Venter white.

Comparison with other *Pedioplanis* species. *Pedioplanis serodioi* **sp. nov.** is distinguished from *P. gaerdesi* by the number of supralabials anterior to the subocular (usually four in *P. serodioi* **sp. nov.** *versus* five to six in *P. gaerdesi*) and color pattern (dark dorsolateral stripes or series of spots in *P. serodioi* **sp. nov.** *versus* no dorsal stripes in *P. gaerdesi*); and from all the remaining species of the genus by consistently possessing a single transparent scale on the lower eyelid (*versus* two or more scales in other species). Regarding Angolan congeners, it can be further distinguished from *P. benguelensis* by a lower number of supralabials anterior to the subocular (usually four in *P. serodioi* **sp. nov.** *versus* five in *P. benguelensis*), one row of granules between supraoculars and supraciliaries (*versus* two in *P. benguelensis*), fewer granules anterior to the supraoculars (usually <15 in *P. serodioi* **sp. nov.** *versus* >13 in *P. benguelensis*) and color pattern (dorsolateral stripes often broken and vertebral stripe indistinct in *P. serodioi* **sp. nov.** *versus* all stripes distinct and well-defined in *P. benguelensis*); from *P. haackei* by the presence of one row of granules between supraoculars and supraciliaries (*versus* two in *P. haackei*), fewer granules anterior to the supraoculars (usually <15 in *P. serodioi* **sp. nov.** *versus* >11 in *P. haackei*) and color pattern (dorsolateral stripes often broken and vertebral stripe indistinct in *P. serodioi* **sp. nov.** *versus* dorsal stripes continuous and faded posteriorly in *P. haackei*); and from *P. huntleyi* by a smaller SVL (average 43 mm in *P. serodioi* **sp. nov.** *versus* 54 mm in *P. huntleyi*), a lower number of supralabials anterior to the subocular (four in *P. serodioi* **sp. nov.** *versus* five in *P. huntleyi*) and color pattern (dorsolateral stripes often broken and vertebral stripe indistinct in *P. serodioi* **sp. nov.** *versus* dorsal stripes continuous and faded posteriorly in *P. huntleyi*).

Holotype. CAS 254906 (field number JVV 8598, Fig. 12), adult male collected on the north side of the road from Namibe to Lubango, road marker 59, 1.8 km West (by road) of Caraculo [-15.01888°, 12.64014°, 491 m], Namibe Province, by Luis M.P. Ceríaco, E.L. Stanley, Arianna L. Kuhn, Jens V. Vindum, Sango de Sá, Suzana Bandeira and Hilária Valério on 6 December 2013.

Paratypes. 11 specimens: CAS 254909* (field number JVV 8601), with the same collecting data as the holotype. CAS 264752* (field number AMB 10181) from Bibala Crossroad [-14.74398°, 13.32852°, 863 m], collected by Luis M.P. Ceríaco, Suzanna Bandeira and Ishan Agarwal on 18 November 2016. CAS 264767* and CAS 264768* (field numbers AMB 10364 and 10365, respectively) from Bibala Crossroad [-14.74398°, 13.32852°, 863 m],

FIGURE 10. Live specimens of *Pedioplanis serodioi* **sp. nov.**. Above: PEM R24010*, male found 10 km west of Lola, on the road to Camacuio, Namibe Province. Photo by William R. Branch. Below: female paratype (CAS 264752) from Bibala Cross-road, Namibe Province. Photo by Ishan Agarwal.

collected by Luis M.P. Ceríaco, Suzanna Bandeira and Ishan Agarwal on 23 November 2016. CAS 264754* (field number AMB 10183) from Camacuio [-14.11365°, 13.24320°, 670 m], collected by Luis M.P. Ceríaco, Suzanna Bandeira and Ishan Agarwal on 18 November 2016. CAS 264766* (field number AMB 10334) from N'Dolondolo [-13.81328°, 13.13618°, 681 m], collected by Luis M.P. Ceríaco, Suzanna Bandeira and Ishan Agarwal on 22 November 2016. MHNCUP/REP 0231, collected by José d'Anchieta in Capangombe [-14.93309°, 12.96477°, 422 m]. PEM R18449* and 18450* (field numbers MBUR 02146 and 02147, respectively), collected by Werner Conradie, William R. Branch, Krystal A. Tolley, G. John Measey among rocks and boulders by roadside 50 km E of Namibe [-15.01661°, 12.55650°, 516 m] on 18 January 2009. PEM R18453* (field number MBUR 02165), collected by Dirk Bellstedt among rocks and boulders by roadside 50 km E of Namibe [-15.01958°, 12.52458°, 550 m] on 18 January 2009. PEM R18459* (field number WC09-33) from east of Moimba [-16.71833°, 13.12194°, 834 m], collected by Werner Conradie on 24 January 2009.

Additional material. 70 specimens: **Benguela Province:** Chimalavera Nature Reserve, vicinity of Main Camp [-12.83377°, 13.16991°, 293 m] (INBAC/AMB 9967*); Catengue [-13.06222°, 13.75611°, 586 m] (PEM R27699, 27700); 7 km east of Catengue, on road to Cubal [-12.99942°, 13.79856°, 814 m] (PEM R21659*, 21660); 30 km SSW of Benguela [-12.74389°, 13.15167°, 55 m] (PEM R 22071, 22072); 2 km turning on Cape Santa Maria from Lucira-Benguela coastal road [-13.51167°, 12.62833°, 285 m] (PEM R 24089); Maconjo, near Benguela-Catengue road [-12.85472°, 13.39472°, 399 m] (PEM R27701); 15 km E of Lobito [-12.37056°, 13.72833°, 252 m] (PEM R27702); **Namibe Province:** Capangombe [-15.09738°, 13.13909°, 542 m] (CAS 264240); base of Serra da Neve, on dirt road to the top of the mountain [-13.83424°, 13.27669°, 803 m] (MHNC-UP/REP 636, CAS 266122); base of Serra da Neve, on dirt road to Quilengues [-13.81594°, 13.32644°, 892 m] (MHNC-UP/REP 637, 638); base of Serra da Neve, Malowe village [-13.83549°, 13.27547°, 798 m] (MHNC-UP/REP 639, 646); Munhino [-14.96667°, 12.96667°, 393 m] (MD 1918a); 50 km E of Moçâmedes on main road to Leba [-15.01558°, 12.55503°, 516 m] (PEM R21653*, 21654*, 21655*, 21656*, 21657*); Camacuio [-14.11365°, 13.24320°, 670 m] (CAS 264755*); 10 km W of Lola, road northwest to Camacuio [-14.29028°, 13.53056°, 802 m] (PEM R24006*, 24007*, 24008, 24009, 24010*, 24011, 24012); 30 km W of Lola, road northwest to Camacuio [-14.27583°, 13.45806°, 791 m] (PEM R24032*–24035*); just before Camacuio [-14.14333°, 13.27556°, 712 m] (PEM R24050*–24052*); 50 km E of Namibe by roadside [-15.01661°, 12.55650°, 516 m] (PEM R18451, 18452); approximately 20 km S of Bentiaba [-14.40278°, 12.44972°, 426 m] (PEM R24220); approximately 20 km SW of Camacuio [-14.21472°, 13.40556°, 803 m] (PEM R27733*); road between Namibe and Humpata 47km E of Namibe [-15.01942°, 12.52881°, 527 m] (PEM R18454*, 18455–18458); road north of Bibala towards Lola [-14.41611°, 13.56472°, 920 m] (PEM R24026–24027); Bibala Crossroad [-14.74398°, 13.32852°, 863 m] (CAS 264753); Namibe-Lubango road, 1.8 km W (by road) of Caraculo [-15.01888°, 12.64014°, 491 m] (CAS 254896*); Caraculo [-15.01667°, 12.66667°, 463 m] (TM 40211); 14 km NE of Caraculo [-14.91304°, 12.73356°, 446 m] (TM 40210, 40254–40262); Leba Pass bottom [-15.04108°, 13.19029°, 696 m] (TM 46756); Lungo [-14.66667°, 13.25°, 679 m] (TM 24399); 10 km E of Munhino [-14.87821°, 13.13195°, 566 m] (TM 46727–46728); Pico do Azevedo [-15.55000°, 12.51667°, 347 m] (TM 41071, 41072); **Huíla Province:** 15 km N of Quilengues [-13.94208°, 14.04557°, 927 m] (MD 1970-1); between Chingoroi and Quilengues [-13.87278°, 13.96528°, 926 m] (PEM R22068).

Description of the Holotype. The holotype is an adult male with a complete original tail (Fig. 12). SVL 48 mm; TL 104 mm. Body relatively stout (SVL/HL 4.29), with hindlimbs longer than forelimbs and tail 2.16 times as long as the SVL. Moderately sized head (HL/SVL 0.23), distinct from the neck. Other relevant measurements are presented in Table 5. Rostral wider than high, visible from above. Nostril pierced between three scales; supranasals slightly swollen and in broad contact with one another behind rostral; infranasal in contact with rostral, first supralabial and anterior loreal; postnasal small and subquadrangular, placed between supranasal, infranasal, anterior loreal and frontonasal. Frontonasal hexagonal, as long as it is wide. Prefrontals in broad contact with each other, the loreals, frontonasal and frontal. Two loreals, posterior largest. Frontal longer than wide, narrower posteriorly, in contact with prefrontals anteriorly, supraoculars laterally and frontoparietals posteriorly. Paired frontoparietals in broad median contact, touching frontal and posterior supraocular anteriorly, and the parietals and interparietal posteriorly. Interparietal longer than broad, rounded anteriorly, its posterior margin much narrower than the anterior. Occipital small and slightly wider than it is long, posterior margin more than twice as wide as anterior, in broad contact with interparietal. Parietals longer than wide, in contact with frontoparietals, interparietal and occipital. Two rounded supraoculars in contact with each other and the frontal, preceded by a group of 14 (right side) and 13 (left side) small granules, those in contact with the frontal and prefrontal largest. One row of small granules between

anterior supraocular and supraciliaries, increasing to two rows posterior to supraocular suture. Supraciliaries six, the first longest. Temporal scales small and granular. One narrow and elongated tympanic shield at anterodorsal edge of the ear opening. Subocular bordering lip, upper margin much wider than lower. Five (right side) and four (left side) supralabials anterior to subocular and two posterior to subocular. Lower eyelid with a single black-edged, enlarged transparent scale. Infralabials six. Mental wider than long, in contact with first infralabials and first pair of chin shields. Four pairs of chin shields, first three in median contact and fourth largest. Gular scales 26, in a straight line between symphysis of the chin shields and median collar plate. Collar free, comprising six enlarged plates. Ventral scales smooth, in nine longitudinal and 27 transverse rows; outer scales smaller than others; first complete transverse row posterior to collar notably longer than others. Precloacal scales irregular and subequal, with a single scale larger than the other in the center. Femoral pores 13 on each leg. Lamellae under fourth toe 23. Dorsal scales small and granular, larger towards the ventral scales. Upper forelimb covered above by large hexagonal plates; forearm covered above by slightly imbricate and keeled scales, larger than dorsal scales, and below by enlarged plates. Hindlimbs covered above by slightly imbricate and keeled scales, larger than dorsal scales, and below by enlarged plates. Scales on tail diagonally keeled, except for those on ventral side of basal portion, which are smooth.

Coloration (in preservative). Dorsum pale greyish with some black speckling, especially on the limbs and tail; hindlimbs covered above by pale circles surrounded by black pigmentation. There is a barely distinct, greyish vertebral stripe that splits at the neck, as well as a pair of dorsolateral series of black spots extending to the base of the tail. Lateral stripe somewhat faint and reticulated, with a series of pale circles running along its lower edge. Tail greyish above, with some black speckling and dark keeled scales. White ventrally.

Variation in the type series. Variation in scalation and measurements among the type series of *Pedioplanis serodioi* **sp. nov.** is reported in Table 5. Except for minor differences in scalation and color pattern, all paratypes generally agree with the holotype. The prefrontals are separated by a small azygous scale in MHNCUP/REP 0231, CAS 254909, CAS 264766, PEM R18453 and PEM R18459, while in CAS 264768 and CAS 264752 there are two longitudinally aligned scales between the prefrontals. Unlike the holotype, dorsolateral stripes are continuous, but irregularly outlined, in CAS 254909, CAS 264752, CAS 264768, CAS 264766, PEM R18453, and indistinct in MHNCUP/REP 0231. The remaining paratypes agree with the holotype in having broken (at least partially) dorsolateral stripes.

FIGURE 11. Paratype of *Pedioplanis serodioi* **sp. nov.** (MHNCUP/REP 0231), collected by Anchieta from Capangombe, Namibe Province. Photos by Bruna Santos.

Table 5. Mensural (in mm) and meristic data relative to the type series of *Pedioplanis serodioi* **sp. nov.** and the neotype of *P. benguelensis*.

Species	***P. benguelensis***	***P. serodioi* sp. nov.**											
Catalog number	**CAS 266242 (neotype)**	**CAS 254906 (holotype)**	**CAS 254909 (paratype)**	**CAS 264752 (paratype)**	**CAS 264767 (paratype)**	**CAS 264768 (paratype)**	**CAS 264754 (paratype)**	**CAS 264766 (paratype)**	**MHNCUP/ REP 0231 (paratype)**	**PEM R18449 (paratype)**	**PEM R18450 (paratype)**	**PEM R18453 (paratype)**	**PEM R18459 (paratype)**
Sex	M	M	-	F	F	F	M	M	-	M	F	M	M
SVL	57.4	48.1	38.9	46.2	48.3	47.7	45.5	42.7	50.2	41.91	43.7	43.2	43.9
TL	144.1	104.1	89.8	-	-	86.2	103.3	-	83.6	-	-	-	-
TL/SVL	2.5	2.2	2.3	-	-	1.8	2.3	-	1.7	-	-	-	-
HL/SVL	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.3	0.2	0.3	0.3
SVL/HL	4.3	4.3	4.2	5.2	4.8	4.8	4.5	4.3	4.4	3.9	4.3	3.9	3.9
ILL	24.5	19.4	17.3	21.4	23.2	23.3	20.3	17.4	25.2	21.3	21.7	21.1	21.1
BL	36	28.6	23.9	31.2	31.4	31.9	28.2	27.1	33.2	25.4	28.9	26.4	27.6
CSL	21.6	19.8	14.7	15.2	16.6	15.6	17.4	15.8	16.8	15.2	16.1	17.3	16
HL	13.2	11.2	9.4	9	10	9.9	10.2	9.9	11.3	10.7	10.3	11	11.3
HW	8.8	7.4	6.1	6.9	7.1	6.8	7.2	7.3	7.6	6.1	6.2	6.9	6.3
LFL	7	5.6	5.1	4.9	5.9	5.8	6.4	5.6	5.7	5.1	5	5.4	5.5
LHL	11.1	9.7	7.8	8	8.8	8.4	9.9	8.9	9.3	9.2	8.4	8.5	9.3
SL	5/5	5/4	4/4	4/4	4/4	4/4	4/4	4/5	4/4	4/4	4/4	4/4	4/4
IL	6/6	6/6	6/6	6/6	6/6	7/7	6/6	6/6	6/6	6/6	6/6	6/6	7/6
SC	6/7	6/6	6/6	6/6	6/7	7/6	6/5	6/6	6/6	6/6	6/6	6/6	6/6
GrSO	15/13	14/13	10/12	14/11	8/9	13/10	13/11	17/17	10/11	6/8	7/7	17/18	6/7
GrRows	2	1	1	1	2	1	1	1	1	1	1	1	1
Eye	2	1	1	1	1	1	1	1	1	1	1	1	1
LVSR	10	10	10	10	10	10	10	10	10	10	10	10	10
TVSR	28	27	27	27	24	25	25	26	28	26	28	26	29
CP	7	6	6	6	8	7	7	7	6	9	8	8	9
GS	31	26	29	31	28	28	31	29	27	24	29	29	27
FP	15/15	13/13	13/13	12/12	13/16	12/11	13/12	14/14	13/13	13	12	11	12
LUFT	27	23	23	25	26	23	23	23	22	23	27	22	27

FIGURE 12. Holotype of *Pedioplanis serodioi* **sp. nov.** (CAS 254906*, field number JVV 8598). Photos by Luis M.P. Ceríaco.

Distribution and habitat. *Pedioplanis serodioi* **sp. nov.** has a broad distribution in the low elevation areas of southwestern Angola, from central Benguela Province to western Cunene Province, except for the more xeric areas of southwestern Namibe Province (Fig. 13). Voucher specimens from northern Namibia deposited in the Ditsong National Museum of Natural History (TM 38789–95 from Okjivakandu; TM 33292 and 38903 from Opuwo; TM 38868, 38870–71 from Otjiwise) are provisionally referred to *Pedioplanis* cf. *serodioi* **sp. nov.** based on the presence of a single transparent scale on the lower eyelid and dorsal coloration, but the identity of these populations is pending genetic confirmation (see Discussion). The current gaps in the distribution of *P. serodioi* **sp. nov.** are likely an artifact of incomplete sampling, and further surveys in southern Angola and adjacent northern Namibia shall improve our knowledge of the distribution range of this species. At 1121 m above sea level, the specimens collected by Ansorge in "Ponang Kuma" [= Dongoena, Cunene Province] (Boulenger 1921) represent the highest elevation recorded for any Angolan *Pedioplanis*. It occurs sympatrically with all other Angolan congeners in several localities across its range. This species inhabits a vast area covering different habitat types, from more xeric areas to areas dominated by Mopane woodlands (Grandvaux-Barbosa 1970; Fig. 5).

Etymology. The species is named after the Angolan scholar João Manuel Serôdio de Almeida (1943–present), professor of the Biology Department of the Faculty of Sciences of Agostinho Neto University, Luanda, Angola. João Serôdio has had a pivotal role in scientific research and biodiversity conservation in Angola, as manager of several conservation areas, Vice-Minister for the Environment (1997–2000) and by training several generations of Angolan biologists. Prof. Serôdio has been a strong supporter and advocate of the present herpetological research in Angola. The name is formed in the genitive masculine singular. We propose the English common name of Serôdio's Sand Lizard, and the Portuguese common name of Lagartixa da Areia de Serôdio.

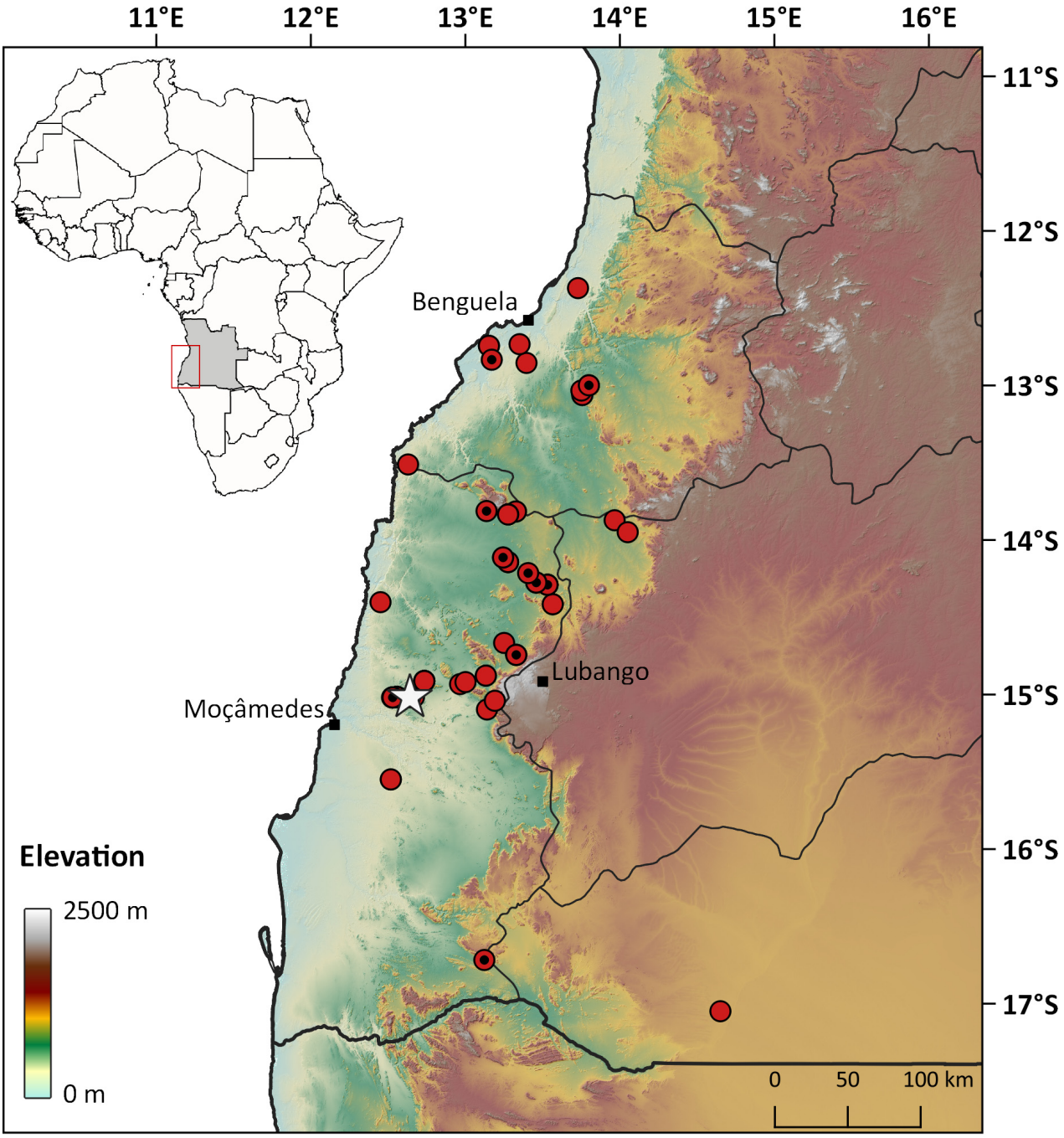

FIGURE 13. Geographic distribution of *Pedioplanis serodioi* **sp. nov.** based on museum vouchers. Localities represented in the phylogenetic analysis are indicated with a black center. White star denotes the type locality. Major cities are represented by a black square.

Discussion

Over the past decade, there have been significant discoveries and descriptions of many new species of vertebrates in Angola, including 22 new species of lizards (Conradie *et al.* 2012b; Stanley *et al.* 2016; Ceríaco *et al.* 2020a, 2020b, 2020c; Branch *et al.* 2019b, 2021; Marques *et al.* 2019a, 2019b, 2020; Lobón-Rovira *et al.* 2021) five new species of snakes (Conradie *et al.* 2020a; Hallermann *et al.* 2020) and five new species of amphibians (Conradie et al. 2012a, 2013; Ceríaco et al. 2018, 2021; Nielsen *et al.* 2020). Along with several other species awaiting formal description, this represents a significant increase in the number of species recorded for the country, emphasizing

that the biodiversity of Angola has been significantly underestimated, and that biodiversity surveys are essential for delivering much-needed foundational knowledge.

The present work represents a new contribution to the growing body of knowledge on Angola's biodiversity and biogeographical context. The arid and semi-arid regions associated with the Namib Desert in southwestern Africa, from southern Angola to western South Africa, constitute a known hotspot of reptile diversity, especially for lizards (Lewin *et al.* 2016). The lizard families Gekkonidae, Lacertidae and Scincidae are particularly speciose in Namibia (Herrmann and Branch 2013), with several species' distributions extending across the Cunene River to their northern limits in the low elevation areas of southwestern Angola, as is the case of *Pachydactylus rangei* (Andersson, 1908) and *Meroles anchietae* (Bocage, 1867) (Marques *et al.* 2018). Furthermore, southwestern Angola has been recognized as an area of relevance in terms of reptile endemism (Marques *et al.* 2018; Branch *et al.* 2019c). This is especially true for lizards, as suggested by the recent description of several endemic or near-endemic species, including the gekkonids *Kolekanos plumicaudus* (Haacke, 2008), *Lygodactylus baptistai* Marques, Ceríaco, Buehler, Bandeira, Janota & Bauer 2020, *Afroedura donveae* Branch, Schmitz, Lobón-Rovira, Baptista, António & Conradie 2021, *A. vazpintorum* Branch, Schmitz, Lobón-Rovira, Baptista, António & Conradie 2021 and *A. praedicta* Branch, Schmitz, Lobón-Rovira, Baptista, António & Conradie 2021; the scincid *Panaspis mocamedensis* Ceríaco, Heinicke, Parker, Marques & Bauer, 2020; the cordylids *Cordylus namakuyus* Stanley, Ceríaco, Bandeira, Valerio, Bates & Branch, 2016 and *C. phonolithos* Marques, Ceríaco, Stanley, Bandeira, Agarwal & Bauer, 2019; and the lacertids *Nucras broadleyi* Branch, Conradie, Vaz Pinto & Tolley, 2019, *Pedioplanis haackei* and *P. huntleyi*. *Pedioplanis serodioi* **sp. nov.** is the 23rd lizard species to be described from Angola in the past decade and represents the fourth addition to the lacertid fauna of southwestern Angola, stressing the significance of this region as a hotspot of lizard diversity and endemism.

Since Makohka *et al.* (2007) presented the first molecular phylogeny of the genus *Pedioplanis* four new species have been described, two from Angola (Conradie *et al.* 2012b) and the other two from Namibia (Childers *et al.* 2021). Furthermore, cryptic diversity has also been documented in *P. namaquensis* (Makohka *et al.* 2007; Childers 2016). The present study raises the number of *Pedioplanis* species in Angola to four, and to a total of 16 species in the genus. With four species, all of which are endemic or near-endemic according to our current knowledge, Angola now supports *Pedioplanis* diversity comparable to South Africa, with five species, two of which are near-endemic (Bates *et al.* 2014). However, it is still considerably low when compared to Namibia, where the genus reaches its peak diversity with 12 species, seven of which are endemic (Herrmann & Branch 2013; Childers *et al.* 2021).

The study of the Angolan radiation of *Pedioplanis*, among other lacertids, represents a contribution to the understanding of the complex biogeographic patterns shaping lizard diversity in the Pro-Namib. At -11º latitude, the records of *P. benguelensis* from Sumbe, Cuanza-Sul Province reported here represent the northernmost record for any species in the genus. The distribution range of this species follows a narrow coastal belt that occurs mostly between Moçâmedes and Benguela, a region where coastal fog and low clouds resulting from upwelling of the cold Benguela Current have been suggested to be most pronounced (Huntley 2019). Namib coastal fogs have been shown to influence vegetation structure (Juergens *et al.* 2013), and several animal species opportunistically or obligately exploit fog-derived moisture as a resource (Mitchell *et al.* 2020), but the knowledge on the effects of fog on desert ecology in Angola is still very limited. Nevertheless, Vaz Pinto *et al.* (2019) suggested that it may play a role in the overall shaping of ecological conditions in the coastal savannas inhabited by *Pedioplanis benguelensis* and *Afrogecko ansorgii* (Boulenger, 1907). Further research is needed to better understand the role of past climatic changes and putative biogeographic barriers in the dispersal and diversification of Angolan *Pedioplanis*.

A juvenile specimen of "*Eremias namaquensis*" was reported by Bocage (1895) among the material sent to him by Anchieta from Caconda, Huíla Province. If verified, this record would represent a considerable extension to the genus' elevational range in Angola, being the only known record from the highlands of Huíla Province. However, considering the currently known distribution of the genus in the country, it is unlikely to occur above the Angolan escarpment, and this may be a case of misidentification or mislabeling, as suggested in similar cases (Branch *et al.* 2019b). A considerable number of *Pedioplanis* specimens were also collected during the Vernay Angola Expedition in 1925 and deposited in the collections of the American Museum of Natural History, New York, USA. Bogert (1940) published an account of the snakes collected during this expedition and some lizard groups were recently examined (Stanley *et al.* 2016; Ceríaco *et al*. 2020a). However, there is no published account of the *Pedioplanis* material collected during this expedition, which could possibly expand our knowledge on the distribution of the genus in the country.

Recent fieldwork in Namibia produced no evidence for the presence of any of the Angolan *Pedioplanis* south of the Cunene River, suggesting that all four species are Angolan endemic (Childers *et al.* 2021). However, as noted by Conradie *et al.* (2012b), the Ditsong National Museum of Natural History holds a series of specimens from northern Namibia ("Okjivakandu", "Opuwo" and "Otjiwise") that conform to *P. serodioi* **sp. nov.** in color pattern and the condition of the lower eyelid with a single transparent scale, a feature known only from *P. gaerdesi* and *P. serodioi* **sp. nov.** If genetically confirmed, these records would expand the known distribution of *P. serodioi* **sp. nov.** into adjacent Namibia, as suggested by previous authors (Branch 1998; Conradie *et al.* 2012b; Herrmann & Branch 2013). Similar cases have been documented, where specimens from northern Namibia have been provisionally referred to species known only from southwestern Angola, such as *Afroedura* cf. *bogerti* (Branch *et al.* 2021) and *Nucras* aff. *broadleyi* (Bauer *et al.* 2020). However, further surveys and research are needed to clarify the status of those populations.

All of the Angolan *Pedioplanis* have large ranges which extend into regions that have minimal habitat transformation, and parts of their ranges are included in gazetted conservation areas (*i.e.*, Chimalavera Natural Regional Park, Namibe Partial Reserve and Iona National Park). Therefore, following the IUCN Red List criteria and guidelines (IUCN 2001), it would be likely that the status of Least Concern would be appropriate for each of the Angolan *Pedioplanis*. Nevertheless, research that allows for a better estimation of geographical distribution, natural history and ecology would be beneficial for their future assessment under the IUCN categories and criteria. As far as we know, none of the *Pedioplanis* species occurring in Angola are exploited by local populations or occur in the pet trade.

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Updated key to the species of the genus *Pedioplanis*

1a) Enlarged and elongated tympanic shield present . . . **2**
1b) Tympanic shield small or absent . . . **12**
2a) Lower eyelid with 1–2 enlarged transparent scales . . . **3**
2b) Lower eyelid opaque to semi-transparent with 10–12 slightly enlarged scales; ventral scales in 12–14 longitudinal rows; dorsum usually striped . . . ***P. namaquensis***
3a) Dorsum uniform or irregularly spotted . . . **4**
3b) Dorsum with longitudinal stripes or series of spots . . . **7**
4a) Lower eyelid with 1–2 enlarged transparent scales; tail nearly three times the snout–vent length; dorsum uniform or speckled; pale spots on the flanks . . . ***P. gaerdesi***
4b) Lower eyelid with 2 enlarged transparent scales; tail length just over two times the snout–vent length . . . **5**
5a) Dorsum uniform reddish; faint greyish band on the flanks but no lateral spots . . . ***P. rubens***
5b) Dorsum greyish to reddish, uniform or with pale to dark mottling; pale spots on the flanks . . . **6**
6a) Lateral spots green; average adult snout–vent length 47 mm (range 42–56 mm) . . . ***P. inornata***
6b) Lateral spots yellow; average adult snout–vent length 44 mm (range 40– 49 mm) . . . ***P. branchi***
7a) Lower eyelid with single enlarged, transparent scale; usually 4 supralabials anterior to subocular; 1 row of granules between supraoculars and supraciliaries; dorsum greyish with dark dorsolateral stripes or series of spots . . . ***P. serodioi* sp. nov.**
7b) Lower eyelid with 2 enlarged transparent scales, often with a row of smaller ones below . . . **8**
8a) Restricted to Angola . . . **9**
8b) Restricted to Namibia . . . **11**
9a) Dorsal stripes bold and distinct all the way to the tail; restricted to coastal areas . . . ***P. benguelensis***
9b) Dorsal stripes faded posteriorly . . . **10**
10a) Usually less than 11 small granules anterior to supraoculars; one row of granules between supraoculars and supraciliaries; average snout–vent length 54 mm . . . ***P. huntleyi***
10b) Usually more than 12 small granules anterior to supraoculars; two rows of granules between supraoculars and supraciliaries; average snout–vent length 45 mm . . . ***P. haackei***
11a) Dorsal stripes bold or faded; small granules anterior to supraoculars 8–13; femoral pores on a single leg 11–14 (central Namibia) . . . ***P. undata***
11b) Dorsal stripes usually bold; small granules anterior to supraoculars 9–16; femoral pores on a single leg 12–16 (northern and central Namibia) . . . ***P. mayeri***
12a) Lower eyelid with 2 enlarged transparent scales; 3–4 protruding lobes on ear opening; ventral scales in 12–14 longitudinal rows . . . ***P. lineoocellata***
12b) Lower eyelid with 8 or more opaque to semi-transparent scales . . . **13**
13a) Lower eyelid with 8 slightly enlarged scales disposed in two horizontal rows; usually 5–6 supralabials anterior to subocular; small tympanic shield present; dorsum irregularly spotted . . . ***P. husabensis***
13b) Lower eyelid with 12 or more opaque to semi-transparent scales . . . **14**
14a) Ventral scales in 12 longitudinal rows; usually 4 supralabials anterior to subocular; juveniles and females longitudinally striped; adult males uniform or irregularly spotted; restricted to Namibia . . . ***P. breviceps***
14b) Ventral scales in 12–18 longitudinal rows; restricted to South Africa . . . **15**
15a) Ventral scales in 16–18 longitudinal rows; interior nasals usually separated; usually 15 or more small granules anterior to supraoculars; 5 pairs of chin shields . . . ***P. laticeps***
15b) Ventral scales in 12–16 longitudinal rows; interior nasals usually in contact; usually 15 or less small granules anterior to supraoculars; 4 pairs of chin shields . . . ***P. burchelli***

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