

Original article

A long-known new species of gecko allied to *Pachydactylus bicolor* (Squamata: Gekkonidae) from the central Namibian coast

MATTHEW P. HEINICKE¹, LAUREN M. ADDERLY,
AARON M. BAUER & TODD R. JACKMAN

Department of Biology, Villanova University, Mendel Hall, 800 Lancaster Avenue, Villanova, Pennsylvania 19085, USA

Abstract.—A new species of the ‘northwestern clade’ of *Pachydactylus* is described from the coast of central Namibia. It has long been considered a population of the widespread species *Pachydactylus bicolor*, from which it differs in body proportions, in having at least six adhesive lamellae on some digits and in having juxtaposed to subimbricate, rather than strongly imbricate, scales on the original tail. Additionally, the new species is unique in maintaining, as an adult, a more-or-less uniform colour pattern of white flecks on a dark brown background, with no evident underlying banded pattern. Molecular phylogenetic analyses of all species of the ‘northwestern clade’ of *Pachydactylus*, using RAG1 and ND2 nucleotide sequences, confirm the placement of the new species as the closest relative of *P. bicolor*, with genetic distances between *P. bicolor* and the new species similar to those observed between other pairs of species in *Pachydactylus*. Phylogenetic relationships of the new species and *P. bicolor* to other members of the northwestern clade are discussed.

Key words.—Gekkonidae, *Pachydactylus*, Namibia, new species, fog belt, phylogeny

INTRODUCTION

More than 50 species of *Pachydactylus* are currently recognised (Bauer & Lamb 2005; Bauer, Barts *et al.* 2006; Bauer, Lamb *et al.* 2006; Bauer 2010; Branch *et al.* 2011), making it the dominant group of nocturnal geckos in southern Africa. While the range of the genus extends as far as Angola and Mozambique, the greatest diversity occurs in the arid zones of Namibia and the adjacent Northern Cape Province of South Africa. A minimum of 36 species of *Pachydactylus* occur in the Republic of Namibia alone, the majority of which are endemic (Branch 1998; Bauer, Lamb *et al.* 2002; Bauer, Pauwels *et al.* 2002; Bauer 2010; Branch *et al.* 2011). Twelve of these species comprise the morphologically diverse, rupicolous ‘northwestern clade’ (*sensu* Bauer & Lamb 2005; Bauer 2010: *P. angolensis*, *P. bicolor*, *P. boehmei*, *P. caraculicus*, *P. gaiasensis*, *P. oreophilus*, *P. otaviensis*, *P. parascutatus*, *P. punctatus*, *P. sansteynae*, *P. scherzi*, and *P. scutatus*). As the informal clade name implies, the group is largely restricted to northern Namibia and adjacent Angola, with a single

¹Corresponding author. Email: matthew.heinicke@villanova.edu

Online Supplementary Material is available for this article which can be accessed via the online version of this journal available at www.tandf.co.uk/journals/THER

species, *P. punctatus* Peters, 1854, extending southwards into South Africa, north to Katanga Province in the Democratic Republic of Congo, and east to the Indian Ocean coast of Mozambique (Bauer & Branch 1995). Excluding *P. punctatus*, the member of the clade with the widest distribution is *P. bicolor* (Hewitt 1926).

Pachydactylus punctatus bicolor was described by Hewitt (1926) from 'Kaross, in the Kaokoveld, S.W.A.' [= Kaross, Opuwo District, Kunene Region, Namibia] on the basis of two specimens (both catalogued under South African Museum 17297, now apparently missing; pers. com., D. Hamerton, May 2011). As is evident from the description, the accompanying photograph, and the specific epithet, the description was based on the distinctively patterned juvenile form, which has a mostly black body and a pale, ashy to whitish marking on the nape and similar or yellowish bands across the sacrum and tail base. Lawrence (in Hewitt 1926) also noted the species from Warmbad and Caimaais, both near Sesfontein. Subsequent early citations to the taxon (Hewitt 1927; Lawrence 1929, 1936) provided neither new localities nor any biological data. FitzSimons (1938) reported on a large series of material from the more southerly localities of Kamanjab, Paderburn [Paderborn], Huab and near Karub. Recognising that Hewitt's description was based exclusively on juveniles, he provided a re-description and elevated *bicolor* to specific status. All subsequent authors have considered *Pachydactylus bicolor* as a full species and additional published localities (FitzSimons 1943; Loveridge 1947; Mertens 1955) extended the known southern distribution of the species to near the Swakop River and filled in records across northern Namibia (the record from Chamaeis in south coastal Namibia reported by Mertens [1955] is certainly an error for Caimaais). Mertens (1971) published the first record from a coastal locality: 20 miles north of Swakopmund. Visser (1984) and Branch (1988, 1998), incorporating data from numerous major collections, indicated a continuous distribution from central Namibia north to the Kaokoveld.

Fitzsimons (1938, 1943) provided the first evidence of ontogenetic colour change in *Pachydactylus bicolor*. The juvenile colouration has been interpreted as being aposematic (Van den Elzen 1983) and has been likened to that of juvenile *Heliobolus lugubris*, which have been regarded as mimics of oospister beetles (Huey and Pianka 1977; Schmidt 2004). Barts and Kowalski (2006) documented the ontogenetic transition from juvenile to adult. FitzSimons (1938) noted some variation in colour pattern across localities (e.g., specimens from near Karub were 'very pale'). Visser (1984) figured specimens from populations at Karibib and Spitskoppie [= Spitzkop], the former showing a darker colour phase and the latter a light phase. Branch (1988) had suggested that there are discrete subadult and adult colour patterns. However, the variation he illustrated can be observed in a single individual, as *P. bicolor* can change from the paler pattern described by FitzSimons (1938) to a darker pattern in which a chocolate wash obscures the underlying banding and emphasises the yellowish to whitish punctations in the pattern (Fig. 1A,B) (Bauer *et al.* 1993; Bauer & Lamb 2001) through the influence of temperature, light, or background (Barts & Kowalski 2006). However, even at its darkest, the typical adult pattern is generally still evident. Physiological colour change in geckos in response to background matching is common (Vetter and Brodie 1977; Bauer, Pauwels *et al.* 2002), and at least in *Hemidactylus turcicus*, it has been demonstrated that the 'default' colouration is pale, with melanophores concentrated (Zaidan & Wiesbusch 2007). In preserved

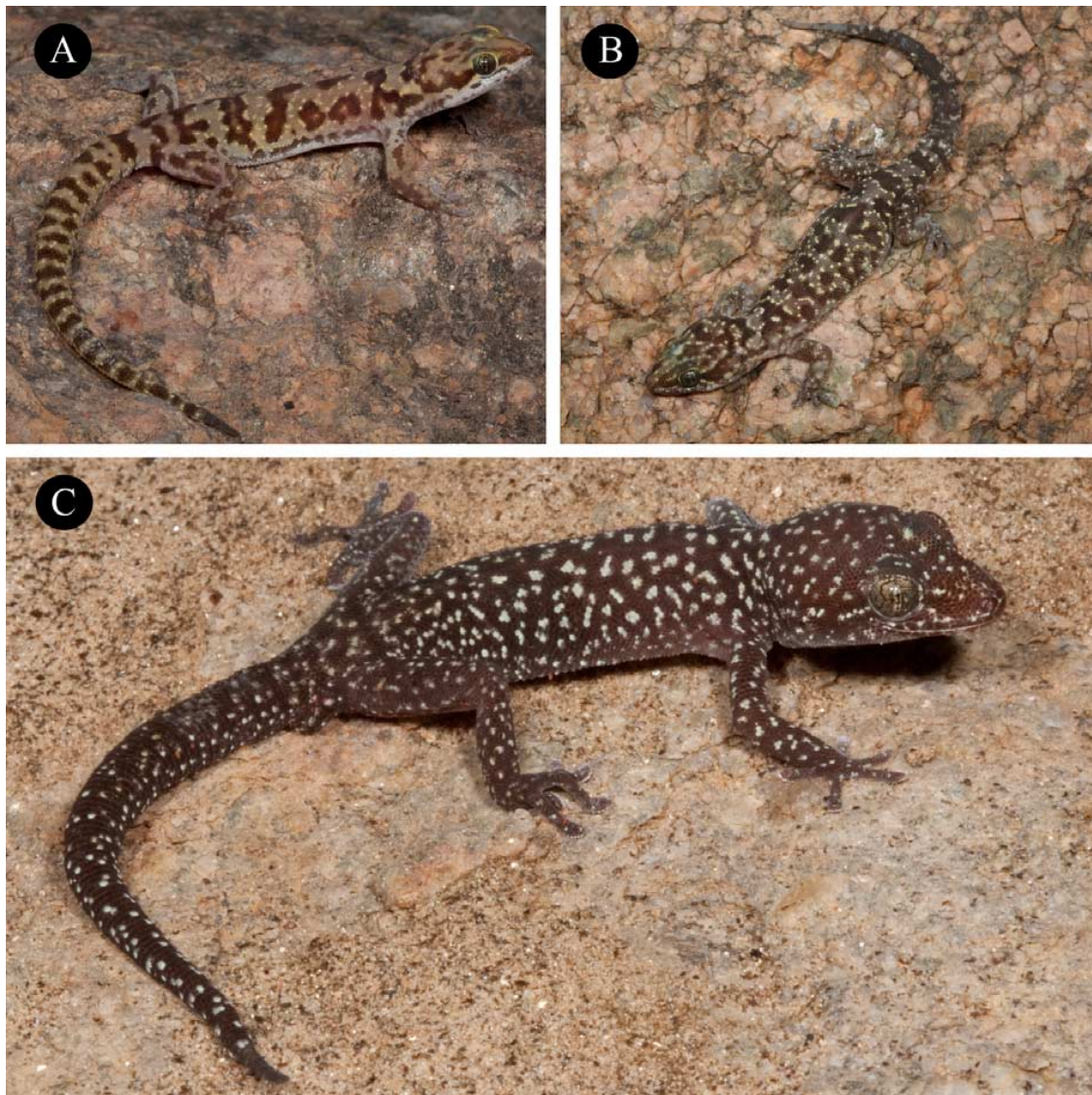


Figure 1. Photos of typical *Pachydaetylus bicolor* from Kamanjab, Namibia depicting (A) light and (B) dark physiological colour phases; note that when in dark phase, white flecks become more noticeable but dark markings are still obvious. (C) Photo of *Pachydaetylus maraisi* sp. n., male paratype (MCZ R184218); note lack of darker markings underlying dark ground colour. Note: Photos by J. Marais.

specimens of *P. bicolor* only the lighter colouration is seen, arguing that this is likewise the resting state in this species.

An exception is seen in coastal populations of *P. bicolor* (Fig. 1C). These geckos resemble the darker colour phase of more inland specimens of *P. bicolor*, but in life they apparently never change to a significantly paler pattern and no clear underlying banded pattern is visible through the dark brown dorsal colouration (although the intensity and contrast of the brown dorsum and white spots are physiologically variable), and in preservative they do not blanch to a paler form. Series of photos showing the coastal form were presented by Hebbard (2004) and Barts and Kowalski (2006). This difference is striking enough that Branch (1998) mistakenly identified a photograph of this species as *P. sansteyni* [= *P. sansteynae*]. Although overall body form and the similarities between the coastal form's colour and the dark phase of inland *P. bicolor* clearly demonstrate the link between these populations, the limited

ability to change colour in the former may be taxonomically significant and so we undertook a more detailed comparison of inland versus coastal populations heretofore referred to *Pachydactylus bicolor*. Based on evidence from both external morphology and genetic data, we recognise the coastal populations of *P. bicolor* as a new species, described below.

MATERIALS AND METHODS

Morphology

The following measurements were taken with Brown and Sharpe Digit-cal Plus digital calipers (to the nearest 0.1 mm) as per Bauer, Lamb *et al.* (2006): snout–vent length (SVL; from tip of snout to vent), crus length (CrusL; from base of heel to knee); tail length (TailL; from vent to tip of unregenerated tail), tail width (TailW; measured at base of tail); axilla to groin length (TrunkL); head length (HeadL; distance from retroarticular process of the jaw to snout-tip), head width (HeadW; measured at angle of jaws), head depth (HeadD; maximum height of head, from occiput to throat), ear length (EarL; longest dimension of ear); forearm length (ForeaL; from base of palm to elbow); orbital diameter (OrbD), nostril to eye distance (NarEye; distance between anteriormost point of eye and nostril), snout to eye distance (SnEye; distance between anteriormost point of eye and tip of snout), eye to ear distance (EyeEar; distance from anterior edge of ear opening to posterior corner of eye), and interorbital distance (Interorb; shortest distance between left and right superciliary scale rows).

Scale counts and external observations of morphology were made using a Nikon SMZ-1000 dissecting microscope. Comparisons were made with museum material of *Pachydactylus bicolor sensu stricto* (see Appendix 1) and representatives of members of the ‘northwestern clade’ of *Pachydactylus* (*sensu* Bauer & Lamb 2005; Bauer, Lamb *et al.* 2006). Standard codes for museum collections follow Leviton *et al.* (1985): California Academy of Sciences, San Francisco (CAS), Museum of Comparative Zoology, Harvard University, Cambridge, USA (MCZ), Museum of Vertebrate Zoology, University of California, Berkeley (MVZ), National Museum of Namibia, Windhoek (NMN), Bayworld (=Port Elizabeth Museum), Port Elizabeth (PEM), South African Museum, Cape Town (SAM), Ditsong (=Transvaal Museum), Pretoria (TM). Field collection codes are Aaron M. Bauer (AMB), Jon Boone (JB), and Jens Vindum (JV).

Molecular Phylogeny

Qiagen DNeasy blood and tissue kits were used to extract DNA from samples of eight individuals of the coastal ‘*P. bicolor*’, 14 individuals of the inland form of *P. bicolor*, 19 individuals representing all other species in the northwestern clade, 4 individuals from 4 additional *Pachydactylus* species, and 1 individual of *Chondrodactylus bibronii* (see Online Supplementary Material for localities and GenBank numbers). After DNA isolation, PCR reactions were performed in 25 μ L volumes, using the primers L4437 and H5540 for amplification of a portion of the mitochondrial gene ND2 (Macey *et al.* 1997) and the primers RAG1F700,

RAG1R700, R13, and R18 for amplification of the nuclear gene RAG1 (Bauer *et al.* 2007; Groth & Barrowclough 1999). Purification of PCR products was via the Agencourt AMPure system, followed by cycle sequencing and pre-electrophoresis purification using the Agencourt CleanSeq system. Capillary electrophoresis was performed on an ABI 3700 sequencer. New sequences were deposited in GenBank (accession numbers JN543869–JN543948).

Resulting sequences were inspected in BioEdit (Hall 1999) to detect call errors and, for the RAG1 data, polymorphic sites. Alignment was performed by eye. The final aligned dataset measured 1595 bases: 557 bp of ND2 and 1 038 bp of RAG1. Prior to analysis, sequences were translated to amino acids in Molecular Evolutionary Genetics Analysis (MEGA) software (Tamura *et al.* 2007), which confirmed the data contained no stop codons or indels. Maximum likelihood (ML) and maximum parsimony (MP) analyses were performed on the complete dataset. Analyses were also performed separately on the ND2 and RAG1 alignments to confirm no strong topological conflict exists between the loci. Best-fitting models for each gene were identified using jModelTest 0.1 (Posada 2008) as GTR + I + G for ND2 and TrN + G for RAG1. ML analyses were performed using RAxML 7.2.6 (Stamatakis 2006). The data were partitioned by gene for the combined analysis, and unpartitioned for the ND2 and RAG1 single-gene analyses. Because RAxML employs only GTR models, and only a single model per analysis, the GTR + I + G model was used for the combined and ND2 analyses, and GTR + G for the RAG1 analysis. MP analyses were performed using MEGA (Tamura *et al.* 2007), using close-neighbour interchange searches on 10 random-addition trees. Nodal support was assessed for all ML and MP analyses via bootstrapping (1000 replicates per analysis).

RESULTS

Pachydactylus maraisi sp. n.

Holotype.—CAS 193888 (Fig. 2): adult female; Namibia, Erongo Region, Swakopmund District, Hentiesbaai Road, 2.7 km S Wlotzkasbaken, coll. A.M. Bauer,

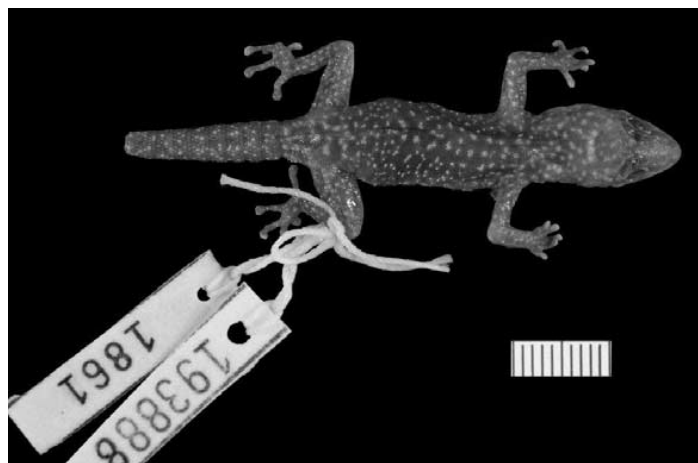


Figure 2. Holotype of *Pachydactylus maraisi* sp. n., CAS 193888.
Note: Scale bar = 10 mm.

H.E. Robeck, D. King, and J.V. Vindum, 25 June 1993. (Note that this specimen will be donated to the National Museum of Namibia.)

Paratypes.—CAS 193885 (adult female), CAS 193886 (adult male), CAS 193887 (adult female), CAS 193889 (adult male) JV1852 (adult male), JV1855 (adult male), JV1856 (subadult female), JV1860 (adult male); same data as holotype. MCZ R184218 (adult male), MCZ R184219 (adult female), MCZ R184220 (adult female), and MCZ R184225 (adult female); Namibia, Erongo Region, Swakopmund District, Hentiesbaai Road, 2.7 km S Wlotzkasbaken, coll. A.M. Bauer, T. Lamb, G. Shea, A.P. Russell, T. Gamble, A. Cottone, H. Jamniczky, R. Babb, P. Moler, and J. Marais, 11 June 2005. (Note that JV1852, 1855–56, and 1860 will be donated to the National Museum of Namibia.)

Additional material examined.—MCZ A38233–34; same data as holotype. CAS 214576; Namibia, Erongo Region, Swakopmund District, 29.0 km N of Swakopmund (22°25'38''S, 14°27'53''E). TM 24966; Namibia, Erongo Region, Swakopmund District, Mile 66. NMN 175; Namibia, Erongo Region, Swakopmund District, Wlotzkasbaken. NMN 1725, TM 55323; Namibia, Erongo Region, Swakopmund District, Swakopmund.

Diagnosis.—SVL to at least 40.9 mm. A small, rupicolous *Pachydactylus* with a depressed body form. Dorsum atuberculate, with smooth, flat, round granules, grading to subimbricate scales on flanks. OrbD smaller than EyeEar. Rostral excluded from nostril rim. Enlarged conical scales restricted to dorsal side of crus. Tail indistinctly segmented with juxtaposed to subimbricate scalation. Dorsal pattern uniform dark brown with numerous white flecks throughout.

Pachydactylus maraisi is most similar to other members of the 'northwestern clade' of *Pachydactylus*. Within this clade, *Pachydactylus maraisi* can be readily distinguished from *P. angolensis*, *P. boehmei*, *P. gatasensis*, *P. oreophilus*, *P. otaviensis*, *P. parascutatus*, *P. sansteynae*, and *P. scutatus* by its lack of enlarged, keeled dorsal scales or tubercles (present in others). From *P. bicolor*, *P. caraculicus*, and *P. scherzi*, *P. maraisi* differs in colour pattern, lacking transverse bands or blotches (Fig. 1C, 2) (present in other species). In addition, *P. caraculicus* differs from *P. maraisi* in having subimbricate dorsal scales, some of which are keeled, having imbricate scales on the tail (juxtaposed to subimbricate in *P. maraisi*), having fewer adhesive lamellae (three or four per digit, vs. five to seven in *P. maraisi*), and, in males, having only two scales per cloacal spur (four to five in *P. maraisi*). *Pachydactylus punctatus* and *P. scherzi* differ from *P. maraisi* in body shape, being noticeably rounder in cross section with weakly convex snouts, having fewer adhesive lamellae (three or four per digit), having the first supralabial sometimes participating in nostril rim, having an unsegmented tail, and having three granules separating the dorsal postnasals. The most similar species to *P. maraisi* is *P. bicolor*, but *P. bicolor* (in addition to colouration differences) has a more robust, thickset appearance, with noticeably shorter limbs and digits (CrusL/SVL ratio mean 0.18 in 13 measured *P. maraisi*, 0.16 in 16 measured *P. bicolor*; *t*-test $p = 0.002$), has fewer adhesive lamellae (up to 5 per digit; always 6 on at least some digits in *P. maraisi*), and has imbricate scalation on the tail.

Description of holotype.—Adult female. SVL 38.8 mm. Body relatively depressed, elongate (TrunkL/SVL ratio 0.42). Head elongate, large (HeadL/SVL ratio 0.29), relatively wide (HeadW/HeadL ratio 0.73), somewhat depressed (HeadH/HeadL

ratio 0.48), distinct from neck. Lores inflated; interorbital region slightly concave. Snout short (SnEye/HeadL ratio 0.41), longer than eye diameter (OrbD/SnEye ratio 0.65); scales on snout slightly enlarged, smooth, flattened, roughly hexagonal; scales on snout up to twice as large as those of interorbital region and parietal table. Eye moderately large (OrbD/HeadL ratio 0.24); orbits without extra-brillar fringes; superciliary scales not bearing spines; pupil vertical, with crenulated margins. Ear opening oval, small (EarL/HeadL ratio 0.08); eye to ear distance greater than diameter of eyes (EyeEar/OrbD ratio 1.3). Rostral approximately 50% as deep (0.7 mm) as wide (1.4 mm); no rostral groove; contacted by two enlarged supranasals and first supralabials; nostrils circular, each surrounded by two postnasals and one supranasal; supranasals in broad contact; dorsal postnasals separated by two granules from one another; nostril rims quite inflated; one row of scales separates orbit from supralabials; mental trapezoidal, significantly wider anteriorly than posteriorly, approximately twice as deep (1.4 mm) as wide (0.7 mm, measured from centre of scale); no enlarged postmentals or chin shields. Enlarged supralabials to mid-orbit 7 (L) and 8 (R), with an additional 4 (L) and 2 (R) small, non-granular scales beyond mid-orbit, followed by several granular scales along labial margin to rictus; 8 enlarged infralabials; 22 interorbital scale rows between superciliary scale rows (at midpoint of orbit), 8 across narrowest point of frontal bone.

Dorsal scales granular, smooth, flat, round with little variation in size; flank scales as on dorsum but subimbricate; ventral scales flattened, subimbricate to imbricate, becoming somewhat larger posteriorly, round to hexagonal in shape; gular scales granular, less than one-half size of ventral scales of chest, increasing abruptly in size on throat. No precloacal or femoral pores. Scales on palm, sole, and ventral surface of forelimb small, smooth, granular, juxtaposed; scales on ventral aspect of hindlimbs smooth, juxtaposed to subimbricate; scales on dorsal aspect of forelimb smooth, flat granules; scales on dorsum of thigh somewhat enlarged, smooth, flat granules; scalation on crus heterogeneous, with large conical tubercles separated by smaller round granules.

Forelimbs moderately short, stout; forearm short (ForeaL/SVL ratio 0.16); hindlimbs relatively short, tibia moderately short (CrusL/SVL ratio 0.19); digits relatively short, claws short, needle-like, only visible on some digits of pes; subdigital scansors, except for distalmost, entire, present only on distal portion of toes, approximately 1.5 times wider than more basal (non-scansorial) subdigital lamellae; interdigital webbing absent. Relative length of digits (manus): III > IV > V > II > I; (pes): IV > III > V > II > I. Subdigital scansors, (manus; R/L when varying): I (5), II (5/6), III (6), IV (6), V (5/6); (pes) I (6), II (6), III (6), IV (6/7), V (6). Tail sub-cylindrical, weakly depressed; original TailL unknown (but slightly longer than SVL based on paratype with original tail, see **Variation**); tail constricted basally, then expanded before tapering towards break, segmented but not distinctly so; each segment with four to five rows of scales dorsally and three ventrally; caudal scales smooth and flat, juxtaposed to subimbricate dorsally, grading to subimbricate ventrally; four small postcloacal spurs on each side of tailbase, non-overlapping, arranged in a slightly angled row from anterodorsal to posteroventral.

Colouration.—In preservative (Fig. 2): ground colour of dorsum uniformly medium/dark chocolate brown, becoming slightly lighter on head. Small white flecks, each one to several granules in extent, are more-or-less uniformly distributed across the

entire dorsum, including dorsal aspects of head, limbs, and tail. Otherwise, no visible bands, blotches, spots, or other markings dorsally. Venter uniformly cream-coloured, becoming somewhat more yellow in gular region and slightly darker on tail.

In life (Fig. 1C): as in preservative, but brown dorsal ground colour more vibrant and generally darker and white spots brighter. Some unevenness in background colour evident at cold temperatures, resulting in a somewhat mottled appearance, with white spots more diffuse. Somewhat darker brown barring on tail sometimes visible. Iris a silvery cream.

Variation.—Variation in mensural characters of the holotype and paratypes are presented in Table 1. All paratypes share with the holotype the same colour pattern and configuration of the scales of the nasal region, except in CAS 193889 a granule occurs above the contact between the supranasals, which is absent in other individuals. Juvenile colouration is as in *P. bicolor*. Number of subdigital adhesive lamellae, as well as labial scale numbers, varied across the type series and are also presented in Table 1. Regardless of this variation, one or more digits always have at least six adhesive lamellae. The male paratypes (CAS 193886, CAS 193889, JV 1852, JV 1855, JV 1860, MCZ R184218) have weakly differentiated (though more prominent than in the female holotype) precloacal spurs, each bearing a single row of five (rarely, four) enlarged, compressed, white scales, at least three of which are directed dorsally (Fig. 1C). In paratypes with fully regenerated tails (CAS 193885, CAS 193886, CAS 193887, JV 1856), the colour pattern of the original tail is maintained, but segmentation is lost. Length of regenerated tail about equal to SVL. Only one paratype had a full-length unbroken tail (MCZ R184225), somewhat longer than SVL (TailL/SVL ratio 1.12).

Etymology.—Named for our friend and colleague Johan Marais, collector of some individuals of the type series, and in recognition of his contributions to both academic and popular herpetology in southern Africa. The epithet is formed in the masculine genitive.

Distribution.—The species is known from a few localities immediately adjacent to the Namibian coast between Swakopmund and Cape Cross (Fig. 3), with the majority of known specimens from near the fishing village of Wlotzkasbaken. The range of *Pachydactylus maraisi* is complementary to that of *P. bicolor*, which occurs broadly in suitably rocky inland localities throughout northwestern Namibia (Bauer *et al.* 1993; Branch 1998; Barts & Kowalski 2006). The range of *P. maraisi* as confirmed by museum vouchered localities extends for less than 50 km along the coast, however, all suitable rocky outcrops along the coast should be investigated for additional populations.

Natural history.—*Pachydactylus maraisi* occurs on grey to black dolerite (troctolite) boulders on sand that occur in a strip on the Namibian coastline between Swakopmund and Cape Cross (Fig. 4) (Barts & Kowalski 2006). By day, *P. maraisi* occupies narrow vertical to horizontal cracks in the boulders, usually near the tops of the boulders, but occasionally only a few cm above the sand. During sunny periods they sometimes partially emerge, exposing part of the body at the very edge of the crack they are inhabiting. Like its congeners, *P. maraisi* has a clutch size of two eggs. At least some individuals are infested by trombiculid mites (Fig. 1C), although we have not noted any cases of severe infestation.

Table 1. Mensural and labial scale data (measurements in mm) for the type series of *Pachydactylus maraisi* sp. n.

Sex	CAS 193888*		CAS 193885		CAS 193886		CAS 193887		CAS 193889		JV 1852		JV 1855		JV 1856		JV 1860		MVZ R184218		MVZ R184219		MVZ R184220		MVZ R184225				
	Female	Female	Female	Female	Male	Male	Male	Female	Male	Male	Male	Male	Male	Male	Female	Female	Male	Male	Male	Male	Female	Female	Male	Male	Female	Female	Male	Male	
SVL	38.8	39.2	36.6	40.9	35.5	38.2	38.1	38.1	38.1	38.1	38.1	38.2	38.1	38.1	29.0	29.0	38.0	38.0	38.0	34.1	34.1	39.7	39.7	34.4	34.4	33.0	33.0	34.4	34.4
Foreal	6.3	5.6	5.6	6.3	5.6	5.6	5.9	6.3	5.6	5.6	5.6	5.6	5.9	4.8	4.8	5.7	5.7	5.7	5.1	5.1	6.0	6.0	5.9	5.9	4.5	4.5	5.9	5.9	
CrusL	7.2	6.5	6.8	7.2	6.4	6.5	6.6	7.2	6.4	6.4	6.5	6.5	6.6	6.0	6.0	6.4	6.4	6.4	6.2	6.2	6.7	6.7	6.9	6.9	5.9	5.9	6.9	6.9	
TailL (total)	18.7(b)	36.1	35.0	39.0	8.3(b)	14.5(b)	2.6(b)	39.0	8.3(b)	8.3(b)	14.5(b)	14.5(b)	2.6(b)	30.7	30.7	6.3(b)	6.3(b)	6.3(b)	36.0	36.0	9.7(b)	9.7(b)	11.0(b)	11.0(b)	37.0	37.0	11.0(b)	11.0(b)	
TailL (regen.)	-	29.3	31.0	32.9	-	-	-	32.9	-	-	-	-	-	27.2	27.2	-	-	-	3.1	3.1	-	-	-	-	-	-	-	-	
TailW	3.9	4.0	4.6	4.4	3.3	4.2	3.9	4.4	3.3	3.3	4.2	4.2	3.9	2.7	2.7	4.5	4.5	4.5	2.5	2.5	2.7	2.7	2.6	2.6	1.9	1.9	2.6	2.6	
TrunkL	16.2	15.0	14.8	17.6	15.1	14.2	15.3	17.6	15.1	15.1	14.2	14.2	15.3	11.3	11.3	14.9	14.9	14.9	14.5	14.5	17.3	17.3	15.0	15.0	14.0	14.0	15.0	15.0	
HeadL	11.3	10.9	11.1	11.3	10.0	11.1	1.7	11.3	10.0	10.0	11.1	11.1	1.7	8.8	8.8	10.8	10.8	10.8	10.3	10.3	11.2	11.2	11.0	11.0	9.5	9.5	11.0	11.0	
HeadW	8.3	7.8	8.4	8.6	7.5	8.8	8.4	8.6	7.5	7.5	8.8	8.8	8.4	6.8	6.8	7.8	7.8	7.8	7.2	7.2	8.2	8.2	7.2	7.2	6.5	6.5	7.2	7.2	
HeadD	4.0	3.3	3.4	4.0	3.4	3.8	3.8	4.0	3.4	3.4	3.8	3.8	3.8	3.0	3.0	4.1	4.1	4.1	3.3	3.3	3.5	3.5	3.0	3.0	2.7	2.7	3.0	3.0	
OrbD	2.7	2.9	2.9	2.9	2.5	2.8	2.7	2.9	2.5	2.5	2.8	2.8	2.7	2.7	2.7	2.8	2.8	2.8	2.6	2.6	3.0	3.0	2.7	2.7	2.6	2.6	2.7	2.7	
EyeEar	3.6	3.4	3.5	3.7	3.6	3.7	3.7	3.7	3.6	3.6	3.7	3.7	3.7	2.9	2.9	3.6	3.6	3.6	3.0	3.0	3.4	3.4	2.9	2.9	2.6	2.6	2.9	2.9	
SnEye	4.6	4.6	4.4	4.7	3.9	4.3	4.0	4.7	3.9	3.9	4.3	4.3	4.0	3.4	3.4	4.1	4.1	4.1	3.7	3.7	3.8	3.8	3.5	3.5	3.4	3.4	3.5	3.5	
NarEye	3.5	3.6	3.6	3.6	3.2	3.3	3.4	3.6	3.2	3.2	3.3	3.3	3.4	3.0	3.0	3.1	3.1	3.1	3.0	3.0	3.1	3.1	2.9	2.9	2.5	2.5	2.9	2.9	
Interorb	3.3	2.9	3.1	3.5	3.1	3.3	3.2	3.5	3.1	3.1	3.3	3.3	3.2	2.7	2.7	2.9	2.9	2.9	2.2	2.2	2.2	2.2	2.4	2.4	2.2	2.2	2.4	2.4	
EarL	0.9	0.8	1.1	1.0	0.9	0.8	0.8	1.0	0.9	0.9	0.8	0.8	0.8	0.6	0.6	0.9	0.9	0.9	0.6	0.6	0.9	0.9	0.7	0.7	0.5	0.5	0.7	0.7	
Internar	1.1	1.0	1.2	1.2	1.0	1.0	1.1	1.2	1.0	1.0	1.0	1.0	1.1	0.9	0.9	1.1	1.1	1.1	0.9	0.9	1.0	1.0	0.9	0.9	0.8	0.8	0.9	0.9	
Supralab. (L/R)	8/8	9/9	9/8	10/9	9/9	9/9	9/8	9/9	9/9	9/9	9/9	9/9	9/8	9/9	9/9	9/10	9/10	9/10	9/9	9/9	9/9	9/9	8/8	8/8	8/8	8/8	9/9	9/9	
Infralab. (L/R)	8/8	8/8	8/8	9/9	8/8	8/8	8/7	9/9	8/8	8/8	8/8	8/8	8/7	8/8	8/8	8/8	8/8	8/8	8/9	8/9	7/8	7/8	8/8	8/8	8/8	9/9	9/9		

Notes: Abbreviations as in Materials and Methods; *holotype.

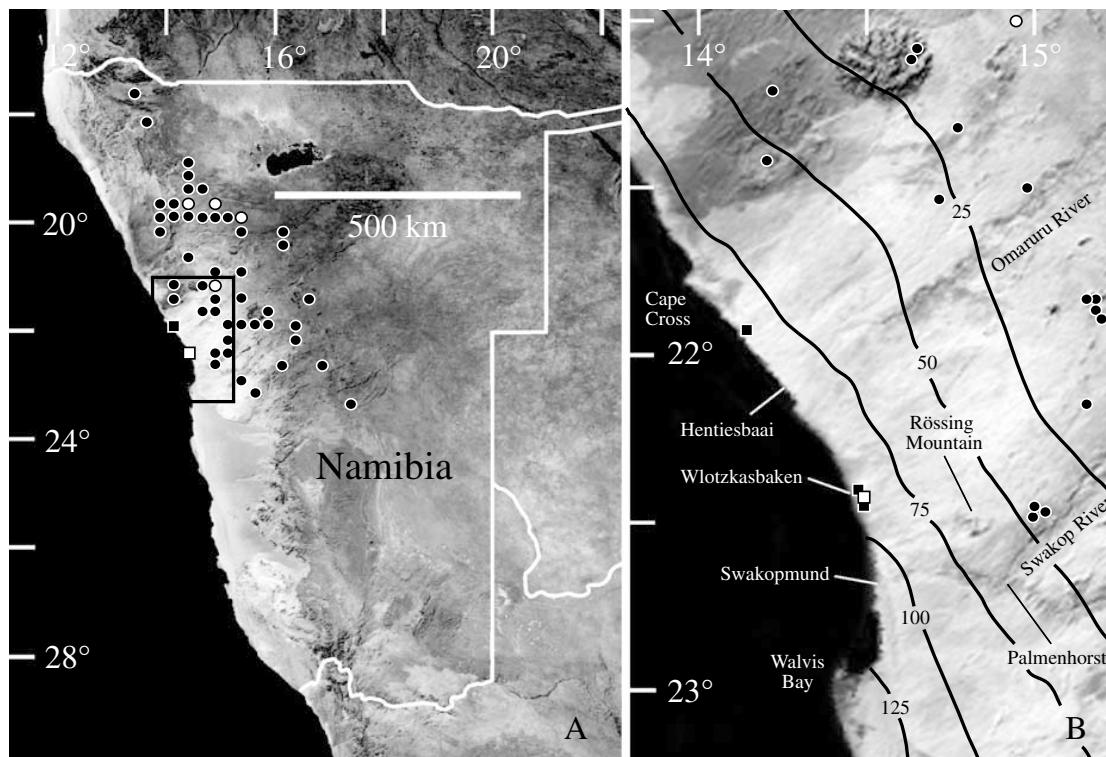


Figure 3. (A) Map of Namibia, depicting quarter-degree squares with records of *Pachydactylus bicolor* (circles) and *P. maraisi* (squares); localities included in molecular phylogenetic analyses are coloured white, while localities based on museum records are coloured black; the holotype and paratype localities of *P. maraisi* are within the white square. (B) Close-up of distributions in west-central Namibia, with geographic features mentioned in the text indicated; isopleths correspond to numbers of fog days; locality records are based on the following collections: CAS, MCZ, MVZ, NMN, PEM, SAM, TM.

The new species is part of a very simple gecko community in the dolerite boulder fields that includes only *Rhoptropus bradfieldi* and *Chondrodactylus* aff. *fitzsimonsi* among climbing geckos, as well as the terrestrial *Rhoptropus afer*, *Ptenopus carpi*, and *Colopus kochi*. *Chondrodactylus turneri laevigatus* may also co-occur, but a review of *Chondrodactylus* specimens from the type locality reveals them to be allied to *C. fitzsimonsi*.

Conservation status.—The entire confirmed range of *Pachydactylus maraisi* falls within the boundaries of Dorob National Park, proclaimed in December 2010. Although the settlement of Wlotzkasbaken is excluded from the park, areas to the east of the coast road, including the dolerite boulder fields, lie within its jurisdiction. Although the type locality is easily accessible, as are certain other localities likely to support the species, nominal protection is now provided by the park. The species has a small area of occupancy (possibly as little as 20 km², although further survey work may expand this), but there are no data relevant to assessing habitat decline or population fluctuation. If the area of occupancy of *P. maraisi* is no more than 20 km², then the species would qualify as ‘Vulnerable’ under IUCN criterion D. However, as all suitable habitat has not been thoroughly documented and additional study may reveal additional occupied areas or potential threats, we recommend a status of ‘Data Deficient’ under the IUCN red list criteria.



Figure 4. Habitat of *Pachydactylus maraisi* sp. n. on the Namibia coast – dolerite boulders on sand at the type locality, 2.7 km S Wlotzkasbaken.

Phylogeny.—The combined phylogeny of ND2 and RAG1 sequence data strongly supports a sister relationship between *Pachydactylus maraisi* and *P. bicolor* (ML/MP bootstrap 100/98; Fig. 5). Single-gene analyses also strongly support this relationship (not shown). Elsewhere in the phylogeny of northwestern clade species, strong support was recovered for sister relationships between *P. otaviensis* and *P. boehmei*, between *P. scherzi* and *P. punctatus*, and among *P. scutatus*, *P. parascutatus*, and *P. angolensis*. Deeper relationships within the northwestern clade received only moderate to poor support, however, so the closest relatives of *P. maraisi* and *P. bicolor* are unresolved. Uncorrected pairwise ND2 genetic distances between these species range from 12 to 17%. These distances were similar to those between other included pairs of related species, such as *P. punctatus* and *P. scherzi* (15%), or *P. serval* and *P. weberi* (17%). Similarly, uncorrected pairwise RAG1 genetic distances between *P. maraisi* and *P. bicolor* are about 1.0% – approximately the same as those between other species pairs (0.8–1.3%). This degree of divergence, while small, resulted in four to five amino acid differences between *P. maraisi* and *P. bicolor* RAG1 sequences.

DISCUSSION

Although comprised almost entirely of small to mid-size rock-dwelling species, the northwestern clade of *Pachydactylus* does encompass a fairly wide range of morphological diversity as compared with the more morphologically conservative *serval/weberi* clade (Bauer, Lamb *et al.* 2006), most notably in body size and proportion and dorsal scalation. Thus, several rough morphotypes within the northwestern clade can be identified. *Pachydactylus gaiasensis* and *P. oreophilus* are significantly larger than other members of the northwestern clade (SVL up to 68 mm in *P. gaiasensis*). *Pachydactylus angolensis*, *boehmei*, *otaviensis*, *parascutatus*, and *scutatus* are small-bodied with heavily keeled dorsal scalation. *Pachydactylus sansteynae* is intermediate between these species and those species without keeled dorsal tubercles, which include *P. maraisi*, *P. bicolor*, *P. caraculicus*, *P. punctatus*, and

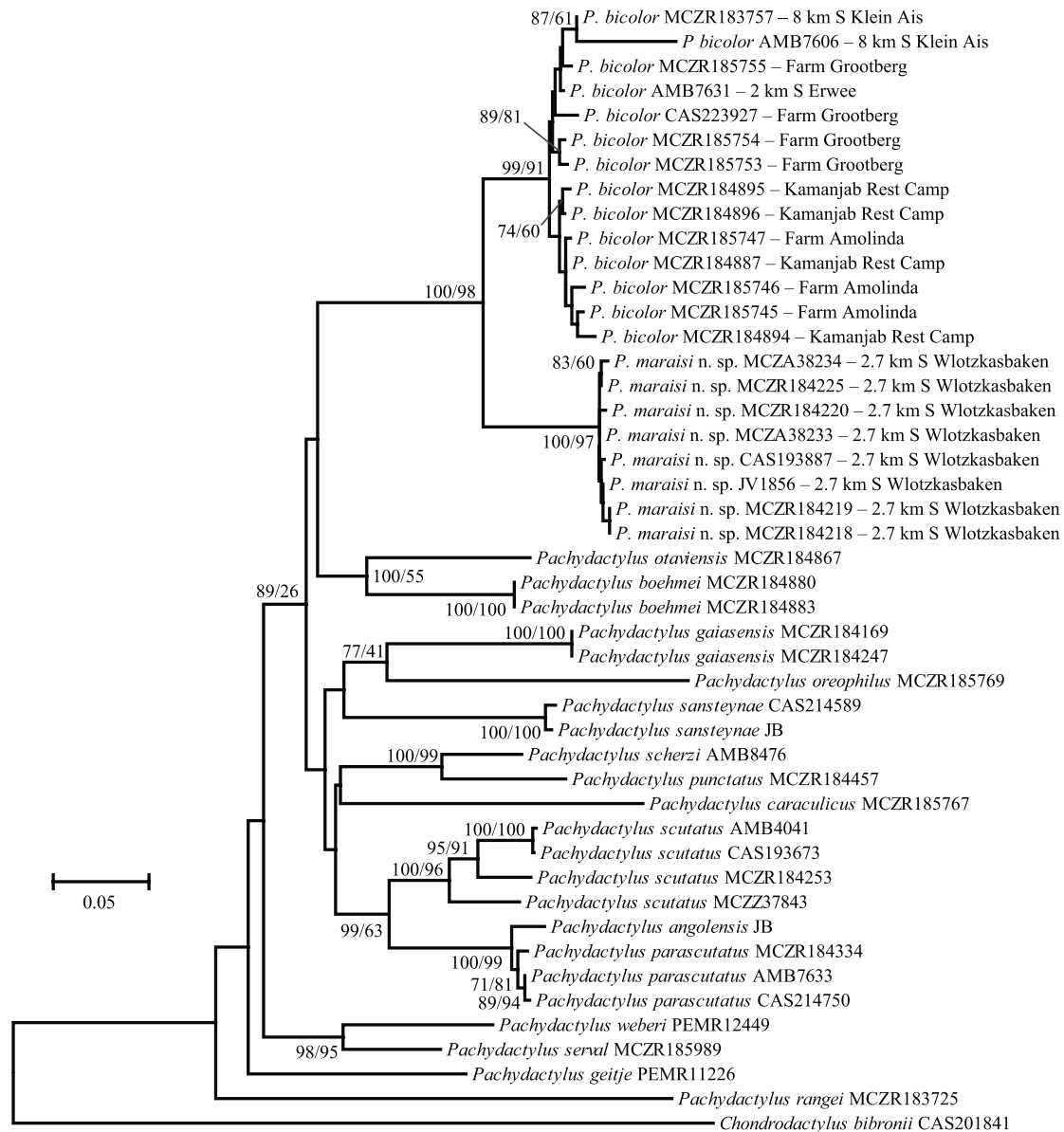


Figure 5. Phylogeny of the ‘northwestern clade’ of *Pachydactylus*, based on a ML analysis of RAG1 and ND2 sequences (1595 bp).

Notes: Support values (ML bootstrap/MP bootstrap) are indicated at nodes; values are not given for nodes receiving poor support (bootstrap values < 70 for both ML and MP methods).

P. scherzi. These small-bodied, smooth-scaled species can be further divided among the more terrestrial species with short snouts and bodies round in cross-section (*P. punctatus* and *P. scherzi*), and more flattened, longer-snouted crevice-dwelling species (*P. maraisi*, *P. bicolor*, *P. caraculicus*).

Some of these rough morphotypes are reflected in relationships recovered in molecular phylogenetic analyses. Bauer and Lamb (2005) initially recovered *Pachydactylus bicolor* as part of a larger northwestern clade that included *P. scherzi*+*P. punctatus*, *P. oreophilus*+*P. gaisensis*, *P. scutatus*+*P. parascutatus*, *P. sansteynae*, with *P. caraculicus* as *P. bicolor*’s closest relative. Although not included in their phylogeny, they also suggested that *P. angolensis* was a member of this clade based on similarities to *P. parascutatus* (Bauer, Lamb *et al.* 2002). Bauer,

Lamb *et al.* (2006) suggested that *P. otaviensis* was a member of the *weberi* group as was another unnamed species from the Otavi Highlands region. Both of these taxa have subsequently been identified as additional members of the northwestern clade (Bauer 2010). Phylogenetic analyses performed for the present study largely conform to the results of Bauer and Lamb (2005), which is unsurprising given that both included RAG1 data in their sequence data sets. The major differences between Bauer and Lamb (2005) and the analyses performed for this study are that this analysis did not provide significant support for the placement of *P. caraculicus*, but did include the species *P. angolensis*, *P. boehmei*, and *P. otaviensis*. Considering the relationships outlined previously, most of the morphotypes seemingly represent monophyletic groups, with the probable exception of the small-bodied, heavily keeled species (divided between a *boehmei/otaviensis* clade and an *angolensis/parascutatus/scutatus* clade).

Confirmation of the distinctiveness of *Pachydactylus maraisi* further reinforces both the diversity of *Pachydactylus* in Namibia and the range-restricted nature of many of these species. Within just the northwestern clade, *P. maraisi* joins *P. gaiasensis*, *P. boehmei*, and *P. otaviensis* in being extremely range restricted, whereas only *P. bicolor*, *P. punctatus*, *P. scutatus*, *P. oreophilus*, and to a lesser extent *P. caraculicus*, might be considered widespread. The high diversity of *Pachydactylus* in Namibia and the restricted ranges of many species are probably both associated with substrate specificity promoting cladogenesis, with lineages restricted to particular substrate types becoming allopatrically isolated by the ebb and flow of Namib sands (Bauer 1999). In addition, recognition of *P. maraisi* highlights the fact that even low-diversity areas, such as the coastal boulder community favored by *P. maraisi*, can be important in harboring endemic biotic elements (Simmons *et al.* 1998).

With respect to adult colour pattern *P. maraisi* and *P. bicolor* share essentially the same pattern elements, and the pale spots that are so evident in the former species are more subtle elements of that of the latter. *Pachydactylus maraisi* differs chiefly in that its default dorsal background colouration (that also assumed by the animal after death) is a darker, more uniform brown and in its restricted ability to lighten physiologically. These traits may be adaptations for life in the fog belt of coastal southwestern Africa, which also harbours other endemic herpetofaunal elements (e.g. *Breviceps macrops*; Channing & Wahlberg 2011). The central coast of Namibia, north of Swakopmund, receives more than 75 fog days per year (Fig 3B; Atlas of Namibia Project, produced by the SFB 389 'ACACIA' E1 subproject conducted by the University of Cologne — http://www.uni-koeln.de/sfb389/e/e1/download/atlas_namibia/index_e.htm), potentially placing a constraint on the ability of ectothermic animals to reach preferred body temperatures. Melanism of diurnal lizards has been associated with the cool, sometimes fogbound, coastal climates of the southwestern Cape (Mouton & Oelofsen 1988; Mouton *et al.* 2002; Daniels *et al.* 2004) and the Namibian coast near Lüderitz (Portik *et al.* 2010). Coastal populations of *Rhoptropus bradfieldi* that occupy the same boulder fields as *P. maraisi* are also melanistic (Bauer & Lamb 2001), presumably providing thermal advantage to these diurnal geckos. Unlike these heliotherms, *P. maraisi* is chiefly nocturnal and thigmothermic; however, dark colouration may still provide some benefit as these lizards will take advantage of sunny periods to partly expose themselves (see **Natural history**). Whether the darker colouration of *P. maraisi* does provide a significant thermal benefit remains to be seen. Thus far, the diagnostic traits of the species have

only been identified in coastal populations. However, the effects of the fog extend far inland and it is possible that *P. maraisi* may also penetrate further than currently recognised, especially as potentially suitable rocky substrates are scattered inland between the Swakop and Omaruru valleys. Although specimens examined from east of Rössing Mountain appear to be typical *P. bicolor* (Fig. 3B), a specimen resembling *P. maraisi* was photographed between Rössing and Palmenhorst (M. Barts, pers. com., June 2011), suggesting that near-coastal populations may require further study.

ACKNOWLEDGEMENTS

We thank the Namibian authorities for permission to collect and export specimens. Johan Marais, Randy Babb, Paul Moler, Jens Vindum, Hedi Roebuck, David King, Trip Lamb, Glenn Shea, Anthony P. Russell, Tony Gamble, Amanda Cottone, and Heather Jamniczky provided field companionship and assistance, Eli Greenbaum assisted in the laboratory, and Jens Vindum (CAS), José Rosado (MCZ), Denise Hamerton (SAM), Laretta Mahlengu (TM), and Bill Branch (PEM) provided access to specimens and data. Mirko Barts kindly provided information on his field and captive experiences with *P. maraisi*. Funding was provided by grant DEB-0844523 from the National Science Foundation, USA.

REFERENCES

- BARTS, M. & T. KOWALSKI. 2006. Die Dickfingergeckos des südlichen Afrikas. Teil V: *Pachydactylus bicolor* Hewitt, 1926. *Sauria* 28(1): 5–10.
- BAUER, A.M. 1999. Evolutionary scenarios in the *Pachydactylus* group geckos of southern Africa: new hypotheses. *Afr. J. Herpetol.* 48: 53–62.
- BAUER, A.M. 2010. A new species of *Pachydactylus* (Squamata: Gekkonidae) from the Otavi Highlands of northern Namibia. *Bonn. Zool. Bull.* 57: 257–266.
- BAUER, A.M., M. BARTS & F. HULBERT. 2006. A new species of the *Pachydactylus weberi* group (Reptilia: Squamata: Gekkonidae) from the Orange River, with comments on its natural history. *Salamandra* 42: 83–92.
- BAUER, A.M. & W.R. BRANCH. 1995. Geographic variation in western populations of the *Pachydactylus punctatus* complex (Reptilia: Gekkonidae). *Trop. Zool.* 8: 69–84.
- BAUER, A.M., W.R. BRANCH & W.D. HAACKE. 1993. The herpetofauna of the Kamanjab area and adjacent Damaraland, Namibia. *Madoqua* 18: 117–145.
- BAUER, A.M., A. DE SILVA, E. GREENBAUM & T.R. JACKMAN. 2007. A new species of day gecko from high elevation in Sri Lanka, with a preliminary phylogeny of Sri Lankan *Cnemaspis* (Reptilia: Squamata: Gekkonidae). *Mitt. Mus. Naturk. Berlin, Zool. Reihe* 83(S1): 22–32.
- BAUER, A.M. & T. LAMB. 2001. A reconsideration of the systematic status of *Rhoptropus bradfieldi diporus* Haacke 1965. *Afr. J. Herpetol.* 50: 71–78.
- BAUER, A.M. & T. LAMB. 2005. Phylogenetic relationships of southern African geckos in the *Pachydactylus* group (Squamata: Gekkonidae). *Afr. J. Herpetol.* 54: 105–129.
- BAUER, A.M., T. LAMB & W.R. BRANCH. 2002. A revision of *Pachydactylus scutatus* (Reptilia: Squamata: Gekkonidae) with the description of a new species from northern Namibia. *Proc. Cal. Acad. Sci.* 53: 23–36.
- BAUER, A.M., T. LAMB & W.R. BRANCH. 2006. A revision of the *Pachydactylus serval* and *P. weberi* groups (Reptilia: Squamata: Gekkonidae) of southern Africa, with the description of eight new species. *Proc. Cal. Acad. Sci.* 57: 595–709.
- BAUER, A.M., O.S.G. PAUWELS & L. CHANHOME. 2002. A new species of cave-dwelling *Cyrtodactylus* (Squamata: Gekkonidae) from Thailand. *Nat. Hist. J. Chulalongkorn Univ.* 2(2): 19–29.

- BRANCH, W.R. 1988. Field Guide to the Snakes and Other Reptiles of Southern Africa. Struik Publishers, Cape Town.
- BRANCH, W.R. 1998. Field Guide to the Snakes and Other Reptiles of Southern Africa. Third edition. Struik Publishers, Cape Town.
- BRANCH, W.R., A.M. BAUER, T.R. JACKMAN & M.P. HEINICKE. 2011. A new species of the *Pachydactylus weberi* complex (Reptilia: Squamata: Gekkonidae) from the NamibRand Reserve, southern Namibia. *Breviora* 524: 1–15.
- CHANNING, A. & K. WAHLBERG. 2011. Distribution and conservation status of the desert rain frog *Breviceps macrops*. *Afr. J. Herpetol.* 60(2).
- DANIELS, S.R., P.LEF.N. MOUTON & D.A. DU TOIT. 2004. Molecular data suggest that melanistic ectotherms at the south-western tip of Africa are the products of Miocene climatic events: evidence from cordylid lizards. *J. Zool., London* 263: 373–383.
- FITZSIMONS, V.F. 1938. Transvaal Museum expedition to south-west Africa and Little Namaqualand, May to August 1937. Reptiles and amphibians. *Ann. Trans. Mus.* 19: 153–209.
- FITZSIMONS, V. F. 1943. The lizards of South Africa. *Mem. Trans. Mus.* 1: 1–528.
- GROTH, J.G. & G.F. BARROWCLOUGH. 1999. Basal divergences in birds and the phylogenetic utility of the nuclear RAG-1 gene. *Mol. Phylo. Evol.* 12: 115–123.
- HALL, T.A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nuc. Acids Symp. Ser.* 41: 95–98.
- HEBBARD, S. 2004. A Close-up View of the Namib and Some of its Fascinating Reptiles. S. Hebbard, Swakopmund.
- HEWITT, J. 1926. Some new or little-known reptiles and batrachians from South Africa. *Ann. S. Af. Mus.* 20: 473–490.
- HEWITT, J. 1927. Further descriptions of reptiles and batrachians from South Africa. *Rec. Albany Mus.* 3: 371–415.
- HUEY, R.B. & E.R. PIANKA. 1977. Natural selection for juvenile lizards mimicking noxious beetles. *Science* 195: 201–203.
- LAWRENCE, R.F. 1929. The reptiles of S.W.A. *J. S. W. Afr. Sci. Soc.* 2: 13–27.
- LAWRENCE, R.F. 1936. The prostigmatic mites of South African lizards. *Parasitology* 28: 1–39.
- LEVITON, A.E., R.H. GIBBS, E. HEAL & C.E. DAWSON. 1985. Standards in herpetology and ichthyology: part 1, standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia* 1985: 802–832.
- LOVERIDGE, A. 1947. Revision of the African lizards of the family Gekkonidae. *Bull. Mus. Comp. Zool.* 98: 1–469.
- MACEY, J.R., A. LARSON, N.B. ANANJEVA, Z. FANG & T.J. PAPPENFUSS. 1997. Two novel gene orders and the role of light-strand replication in rearrangement of the vertebrate mitochondrial genome. *Mol. Biol. Evol.* 14: 91–104.
- MERTENS, R. 1955. Die Amphibien und Reptilien Südwestafrikas, aus den Ergebnissen einer im Jahre 1952 ausgeführten Reise. *Abh. Senckenberg. Naturf. Ges.* 490: 1–172.
- MERTENS, R. 1971. Die Herpetofauna Südwest-Afrikas. *Abh. Senckenberg. Naturf. Ges.* 529: 1–110.
- MOUTON, P.LEF.N., C.J. NIEUWOUTD, N.C. BADENHORST & A.F. FLEMMING. 2002. Melanistic *Cordylus polyzonus* (Sauria: Cordylidae) populations in the western Cape, South Africa: relics or ecotypes? *J. Herpetol.* 36: 526–531.
- MOUTON, P.LEF.N. & B.W. OELOFSEN. 1988. A model explaining patterns of geographical character variation in *Cordylus cordylus* (Reptilia: Cordylidae) in the south-western Cape, South Africa. *S. Afr. J. Zool.* 23: 20–31.
- PORTIK, D., A.M. BAUER & T.R. JACKMAN. 2010. The phylogenetic affinities of *Trachylepis sulcata nigra* and the intraspecific evolution of coastal melanism in the western rock skink. *Afr. Zool.* 45: 147–159.
- POSADA, D. 2008. jModel Test: phylogenetic model averaging. *Mol. Biol. Evol.* 25: 1253–1256.
- SCHMIDT, A.D. 2004. Die Mimikry zwischen Eidechsen und Laufkäfern [Mimicry between lizards and ground beetles]. Edition Chimaira, Frankfurt am Main.
- SIMMONS, R.E., M. GRIFFIN, R.E. GRIFFIN, E. MARAIS & H. KOLBERG. 1998. Endemism in Namibia: patterns, processes and predictions. *Biodiv. Conserv.* 7: 513–530.
- STAMATAKIS, A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22: 2688–2690.
- TAMURA, K., J. DUDLEY, M. NEI & S. KUMAR. 2007. MEGA 4: molecular evolutionary genetics analysis (MEGA) software version 4.0. *Mol. Biol. Evol.* 24: 1596–1599.

- VAN DEN ELZEN, P. 1983. Zur Herpetofauna des Brandberges, Südwest-Afrika. Bonn. Zool. Beitr. 34: 293–309.
- VETTER, R.S. & E.D. BRODIE. 1977. Background color selection and antipredator behavior of the flying gecko, *Ptychozoon kuhli*. Herpetologica 33: 464–467.
- VISSER, J. 1984. Noord-Transvaal se tier en Suidwes se tweekleur! Landbouweekblad, 11 May: 36–37, 39.
- Z Aidan, F. & P.L. WIEBUSCH. 2007. Effects of temperature and illumination on background matching in Mediterranean geckos (*Hemidactylus turcicus*). Texas J. Sci. 59: 127–136.

Received: 2 July 2011; Final acceptance: 9 August 2011

Appendix 1. Comparative Specimens Examined

See the following references for lists of *P. angolensis*, *P. boehmei*, *P. caraculicus*, *P. gaisensis*, *P. oreophilus*, *P. otaviensis*, *P. parascutatus*, *P. punctatus*, *P. sansteynae*, *P. scherzi*, and *P. scutatus* examined: Bauer (2010), Bauer & Branch (1995), Bauer, Lamb et al. (2002) Bauer, Barts et al. (2006), Bauer, Lamb et al. (2006).

P. bicolor: **Namibia: Erongo Region: Karibib District:** 47 mi E Hentiesbaai: CAS 126210; 20 km W Karibib: MCZ R163282–83; 8 km S Klein Ais (21°00′09″S, 14°55′03″E): MCZ R183757, AMB 7606; Black Range 72: SAM ZR46609; 5 km S Gross Spitzkoppe: SAM ZR46626–27; Spitzkoppe: PEM R4880–1, 4885, 6470, 6479–80, 12674, 12680, NMN 177, 4674; Okomitundu 24: SAM ZR46607–08; Mooirivier 360: SAM ZR46541; Uitdraai 35: SAM ZR 46553; Pforte: SAM ZR46643–44; Amieb: SAM ZR44582, NMN 1804; Usakos: PEM R15751; Erongo: PEM R12662–65; Karibib: PEM R12676, 4 km W Usakos: TM 55075; 12681; Wilhelmstal: PEM R15752; Emeritus: NMN 3252; **Omaruru District:** Brandberg: PEM R12675, TM 25813, 53921, 79285, NMN 169, 172–73, 179; Okombahe: TM 52054; Uis: NMN 170, 176, 180; Uis-Hentiesbaai Rd. at Brandberg West Turnoff: TM 55941; Water Bank Station: TM 17466, 20734–35; Liebig's Ranch: TM 17469; 16 km NE Ozondati: TM 52769; Otjongoro: NMN 1797, 8024, 8030, 8042, 8045; **Swakopmund District:** Messum Crater (21°26′25.8″, 14°13′12.9″): CAS 214814; 3 km S Bloedkoppie: TM 49878–80; Bloedkoppie: NMN 1379; Ganab Waterhole: TM 56999; **Kunene Region: Khorixas District:** 2 km S Erwee (19°43′00″S, 14°18′44″E): AMB 7631; Tevrede 643: SAM ZR46952–53, 46958; Makukous Spring: TM 49309; Farm Twyfelfontein: TM 49423–24; Farm Wereldsend: TM 57713; Farm Onverwag: TM 64756; Farm Humor: TM 5279395; Farm Palmwag: TM 68549; Torrabaai Rd, 81 km W of Kamanjab; Torrabaai Rd, 63.4 km W of Kamanjab (19°41′00″S, 14°19′10″E): CAS 223912–15; Torrabaai Rd, 58 km W of Kamanjab (19°39′20″S, 14°21′10″E): CAS 223927–28; Torrabaai Rd, 56.7 km W of Franken entrance: CAS 176284–85; Torrabaai Rd, 37.8 km W of Franken entrance: CAS 176292–93; Kamanjab-Torrabaai Rd, Grootberg Pass (19°50.584′S, 14°07.696′E): CAS 193675; Kamanjab-Torrabaai Rd, 59.3 km W of Kamanjab (19°39.100′S, 14°21.335′E): CAS 193680, AMB 4052; Torrabaai Rd, 48 km W of Kamanjab, (19°39′14″S, 14°21′03″E): CAS 214661–63; Torrabaai Rd, 68 km W of Kamanjab, (19°43′00″S, 14°18′40″E): CAS 214681–89; Torrabaai Rd, 74.2 km W of Kamanjab (19°45′40″S, 14°17′03″E): CAS 214693–96; E side of Road 3706, 19.3 km N of entrance to Palmwag: CAS 175344; Torrabaai Rd, 108.9 km W of Kamanjab: CAS 176101–08; Torrabaai Rd, 101.7 km W of Kamanjab: CAS 176116–19; Torrabaai Rd, 95.9 km W of Kamanjab:

CAS 176126–31; Torrabaai Rd, 44 km W of Kamanjab: CAS 176151; Hentiesbaai-Uis Rd, 24 km W of Hwy C35 (21°18'17''S, 14°35'14''E): CAS 206959, AMB 5935; 25 km E of Grootberg Pass: CAS 206960, AMB 5936; ~60 km W. Kamanjab on Torrabaai Rd. (19°40'57''S, 14°19'09''E): MCZ R184919; 31.9 km E Grootberg Pass (19°40'57''S, 14°19'09''E): MCZ R184197–98; 62.8 km W Kamanjab Rest Camp on Rd. to Grootberg Pass (19°40'56''S, 14°19'08''E): MCZ R185753–55; 67.5 km W Kamanjab on Torrabaai Rd. (19°43'00''S, 14°18'44''E): MCZ R183766; Hobatere Lodge, 2.5 km from main gate (19°18'07''S, 14°27'26''E): MCZ R184934–35; 52 km N Palmwag on Sesfontein Rd (19°27'28''S, 13°52'41''E): AMB 5946 **Opuwo District:** Kowares: SAM ZR17470, PEM R12666–73, 12836–7; Kamanjab-Ruacana Rd, 98.4 km N of Kamanjab: CAS 193719; Opuwo-Okangwati Rd, Otjivize (17°37.188 S, 13°27.535 E): CAS 193731; Opuwo: TM 24500–01; **Outjo District:** 17 mi S of Outjo: CAS 85944; Otjitambi: SAM ZR19908; SE of Otjovasondu: PEM R12679, 12682–85; Hirabis South: NMN 174; Farm Franken: CAS 175347–53, 175360–74, 176066–68, 176176–77; Farm Franken, Haus Franken: CAS 176261–62; Farm Franken, vic. Haus Franken: CAS 176278; 62.0 km E Kamanjab, Farm Amolinda (19°48'29''S, 15°22'46''E): MCZ R185745–47; Kamanjab Rest Camp, 3 km W Kamanjab (19°37'48''S, 14°48'57''E): MCZ R184887, 184894–97; Farm Lobshorn (19°45'S, 14°44'E): AMB 4028; Kamanjab: PEM R12686, TM 17203–08, 17238–42, 17244–45, 17263–64; 6 mi. N Kamanjab: PEM R12687–91; Farm Paderborn: TM 17319; Farm Huab, 261: TM 17343–45, 17359, NMN 168; Farm Tutara, 55: TM 28200–08; Farm Oenitzaub: TM 48630–31; Peet Alberts: TM 48638–39; **Otjozondjupa Region:** **Okahandja District:** Farm Ozombusomasse: TM 68319–21.