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A NEW SPECIES OF THE *PACHYDACTYLUS WEBERI* COMPLEX (REPTILIA: SQUAMATA: GEKKONIDAE) FROM THE NAMIBRAND RESERVE, SOUTHERN NAMIBIA

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ABSTRACT. A new species of gecko of the *Pachydactylus weberi* complex is described from the NamibRand Reserve in southern Namibia. It is morphologically well differentiated from all other members of this group, in lacking thigh tubercles, and can further be distinguished by its small size (< 45 mm snout–vent length), participation of the first supralabial in the nostril rim, snout scales much larger than interorbital scales, and three body bands in juveniles and adults. It has a distinctive, bold, contrasting hatchling coloration that superficially resembles that of *P. mclachlani*, from which it is distinguished both morphologically and genetically. DNA sequence data from two nuclear genes (RAG-1, PDC) and the ND2 mitochondrial gene plus its five flanking tRNAs (2,975 bp) reveal that this new species is most closely related, among the taxa sampled, to *P. monicae* from the lower Orange River valley.

KEY WORDS: Namibia; Gekkonidae; Pachydactylus; new species; ontogenetic color change

INTRODUCTION

Geckos constitute a substantial proportion of the herpetological diversity of southern Africa, with more than 120 species currently recorded and at least 16 additional species awaiting description. *Pachydactylus* is the most species-rich lizard genus in southern Africa, with at least 50 species known from the subcontinent (Branch, 1998; Bauer, Barts, and Hulbert 2006; Bauer, Lamb, and Branch, 2006). Only one species (*P. katan*-

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ganus of the Democratic Republic of Congo) is entirely extralimital to the subcontinent (Bauer and Lamb, 2002; Broadley, 2003). At least 35 species of Pachydactylus are known to occur in the Republic of Namibia, of which 18 are endemic (Branch, 1998; Bauer et al., 2002; Bauer, Lamb, and Branch, 2006). Although most species of Pachydactylus are morphologically distinct, for many years, species boundaries within the small, rupicolous species of the P. serval and P. weberi complexes were especially problematic. Relationships within these speciose groups were finally teased apart by detailed morphological and molecular studies, resulting in the recognition of 22 species (Bauer, Barts, and Hulbert, 2006; Bauer, Lamb, and Branch, 2006), although one of these, P. otaviensis, is now known to belong to another clade (Bauer, 2010).

Despite intensive scientific investigation of the Namibian gecko fauna during the last few decades, new species remain to be described. Shortly after publication of a monographic review of the Pachydactylus serval and P. weberi complexes (Bauer, Lamb, and Branch, 2006), a photograph of an unusual hatchling gecko was sent to the senior author for identification. It was found at Sossusvlei Mountain Lodge (now Sossusvlei Desert Lodge) in the northern section of the Namib-Rand Nature Reserve near the eastern edge of the Namib dunefields at the base of the Nubib Mountains. It was very similar in color pattern to the hatchling of P. mclachlani, a species known only from the Karas Region, southern Namibia, approximately 300 km to the southeast. This hatchling thus either represented another novelty or a considerable range extension for P. mclachlani. Subsequent visits to the Sossusvlei Desert Lodge resulted in the collection of a series of specimens of this unusual gecko. Investigation of its morphology and phylogenetic relationships confirm that it represents yet another new species of the *Pachydactylus weberi* complex, which we describe 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, and Branch (2006): snout-vent length (SVL; from tip of snout to vent), forearm length (ForeaL; from base of palm to elbow), crus length (CrusL; from base of heel to knee), tail length (TailL; from vent to tip of tail), tail width (TailW; measured at base of tail), axilla to groin length (TrunkL; measured from posterior margin of forelimb insertion to anterior margin of hindlimb insertion), head length (HeadL; distance retroarticular process of the jaw and 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), orbital diameter (OrbD; measured at midorbit), 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 with the use of a Nikon SMZ-1000 dissecting microscope. Comparisons were made with museum material representing all species in the *Pachydactylus serval* and *P. weberi* groups (*sensu* Bauer and Lamb, 2005; Bauer, Lamb, and Branch 2006). See Bauer, Lamb, and Branch (2006) for a complete list of specimens examined. Standard codes for museum collections follow Leviton *et al.* (1985).

	Museum		GenBan	k Accession	Numbers
Taxon	Voucher	Locality	ND2	RAG-1	PDC
P. capensis P. fasciatus	MCZ R-184499 CAS 223931	South Africa: Limpopo, Kgama Namibia: Torrabaai Rd., 58 km W of Kamaniab (19°39'20''S, 14°21'10''E)	HQ165962 n/a	HQ165992 HQ165979	HQ165977 HQ165964
	MCZ R-185759	Namibia: 58 km W of Kamanjab Rest Camp on road to Grootberg Pass (19°38'57"S, 14°24'33"E)	HQ165949	HQ165978	HQ165963
P. serval	MCZ R-185997	Namibia: Brukkaros Mountain, S slope (25°53'49"S, 17°46'38"E)	HQ165957	HQ165987	HQ165972
	MCZ R-185989	Namibia: Brukkaros Mountain, S slope (25°53'49"S, 17°46'38"E)	HQ165956	HQ165986	HQ165971
P. purcelli	CAS 198295	South Africa: Western Cape, Farm Oukloof (32°11′36″S, 21°55′38″E)	HQ165955	HQ165985	HQ165970
	PEM R16895	South Africa: Northern Cape, Farm Kleinbegin (28°54′53″S, 21°40′14″E)	HQ165954	HQ165984	HQ165969
P. mclachlani	MCZ R-186000	Namibia: Farm Narudas (27°22'12"S, 18°51'29"E)	HQ165951	HQ165981	HQ165966
	MCZ R-185094	Namibia: 6.7 km NW of Aroab on road to Keetmanshoop (26°46'46"S, 19°35'17"E)	HQ165950	HQ165980	HQ165965
P. weberi	CAS 206824	South Africa: Northern Cape, Brandberg, Farms Kourootje and Kap Vley (29°49'52"S, 17°22'35"E)	HQ165961	HQ165991	HQ165976
	PEM R12449	South Africa: Northern Cape, 1.4 km S of Garies	HQ165960	HQ165990	HQ165975
P. monicae	LSUMZ 57343	South Africa: Northern Cape, Richtersveld National Park, Sendelingsdrif	HQ165953	HQ165983	HQ165968
	CAS 193418	South Africa: Northern Cape, Richtersveld National Park, Sendelingsdrif	HQ165952	HQ165982	HQ165967
P. etultra n. sp.	MCZ R-184977	Namibia: Sossusvlei Mountain Lodge (24°47'2"S, 15°53'22"E)	HQ165958	HQ165988	HQ165973
	MCZ R-184978	Namibia: Sossusvlei Mountain Lodge (24°47′2″S, 15°53′22″E)	HQ165959	HQ165989	HQ165974

Table 1. Specimens of $P_{ACHYDACTYLUS}$ used in molecular phylogenetic analyses. All sequences are new to this study.^a

^aAbbreviations for museum numbers are as follows: CAS = California Academy of Sciences, LSUMZ = Louisiana State University Museum of Natural Science, MCZ = Museum of Comparative Zoology (Harvard University), PEM = Port Elizabeth Museum.

Molecular Phylogenetics. Sequences were obtained from tissue samples representing two individuals of the new species, plus two each of six other species of the Pachydactylus serval and P. weberi complexes (Table 1): P. fasciatus, P. mclachlani, P. monicae, P. purcelli, P. serval, and P. weberi. Pachydac*tylus capensis*, a representative of the probable sister group of this clade (Bauer and Lamb, 2005), was chosen as the outgroup. The sequence data set includes the complete mitochondrial NADH dehydrogenase subunit 2 gene plus five adjacent tRNAs (ND2; 1,542 bp aligned), along with portions of the nuclear protein-coding genes phosducin (PDC; 395 bp aligned) and recombination activating gene 1 (RAG-1; 1,038 bp aligned).

Genomic DNA was isolated from ethanolpreserved tissue samples with a Qiagen DNeasy blood and tissue kit. Polymerase chain reaction was then performed on isolated DNA in 25-µL reactions with the published primers L4437, L4882b, ND2F101, ND2R102, H5540, H5934, H6159, PHOF2, PHOR1, RAG1F700, RAG1R700, RAG13, and RAG18 (Macey et al., 1997, 2000; Groth and Barrowclough, 1999; Weisrock et al., 2001; Greenbaum et al., 2007; Bauer et al., 2007). One novel primer was also used: ND2F106 (5'-ACAGGATTYATACCAAA-ATG-3'). Reaction conditions were as follows: denaturation at 95°C (2 min), then 32-34 cycles of denaturation at 95°C (35 s), annealing at 50°C (35 s), and extension at 72°C (initially 150 s, with 4 s added per cycle). Annealing temperature was lowered for poorvielding samples. The AMPure magnetic bead system (Agencourt Bioscience) was used to purify amplified DNA fragments. The sequencing reaction employed dye-terminator chemistry with cycle sequencing, followed by purification via the CleanSeq magnetic bead system (Agencourt Bioscience). An ABI 3700 sequencer was used for electrophoresis and analysis. Resulting chromatograms were inspected by eye and compared against their reverse complements in BioEdit (Hall, 1999) to detect call errors, with sequences translated to check for premature stop codons. Initial alignments were performed with Clustal W (Thompson et al., 1994) and manually corrected to take into account codon deletions and tRNA secondary structure. The separate gene sequences were then concatenated into a single data set for analyses.

Maximum likelihood and parsimony methods were used for phylogenetic reconstruction. All three gene regions were concatenated for the analyses. Both analyses treated gaps as missing data and employed pairwise deletion. PhyML (Guindon and Gascuel, 2003) and jModelTest 0.1.1 (Posada, 2008) were used to estimate parameters for all standard models of evolution. The Akaike Information Criterion (AIC) was used to identify the best fitting model of evolution (GTR + Γ) for use in the likelihood analysis. The likelihood analysis was performed in PhyML version 2.2.4 with a BIONJ starting tree, the gamma parameter fixed to the previously estimated value, and empirical base frequency estimates. The parsimony analysis was performed in MEGA 4 (Kumar et al., 2008) with the use of a min-mini heuristic search (search level 10). For both analyses, branch support was assessed by running 1,000 bootstrap replicates.

DESCRIPTION OF NEW SPECIES

Pachydactylus etultra Branch, Bauer, Jackman, and Heinicke, new species Sossus Gecko Figures 1–3; Table 2

Holotype. MCZ R184980 (field no. MCZ A38619), adult female, Republic of Namibia, Hardap Region, Maltahöhe District, Namib-Rand Nature Reserve, Sossusvlei Desert Lodge, 24°46′45.3″S, 15°53′17.8″E (quarter-degree unit 2415DD), 896 m elevation, 21 September 2006, W.R. Branch and P. Dunning.

Paratypes. Nine specimens, all from same locality as holotype; MCZ R184977–79, 184981–82 (four adult females and an adult male; see Table 2), 21 September 2006, W.R. Branch, A.M. Bauer, J. Marais, & T. Jackman; PEM R17293 (hatchling), 20 April 2007, W.R. Branch; PEM R17294 (subadult), 21 April 2007, W.R. Branch; PEM R17295 (adult male) and PEM R17287 (adult female), 22 April 2007, W.R. Branch, D. Branch, & V. Swanepoel.



Figure 1. Preserved holotype of *Pachydactylus etultra*, new species (MCZ R184980). Scale bar = 10 mm.

Diagnosis. A dorsoventrally flattened species (Figs. 1, 2A) typical of the P. weberi complex (sensu Bauer, Lamb, and Branch, 2006), in having the rostral excluded from the nostril (Figs. 2B, C), but distinguished from all other species in the complex in lacking thigh tubercles (Fig. 2D). It can be further distinguished from members of the P. weberi complex by a combination of the following characters: rupicolous (terrestrial in *P. fasciatus*); the first supralabial narrowly enters the nostril (excluded in *P. kobosensis*) (Fig. 2C); snout rounded and nasal region moderately inflated (snout pointed and nasal region strongly inflated in *P. werneri*); scales on snout larger than interorbital tubercles (equal in size in P. monicae) (Fig. 2B); digits not long (digits long in *P. werneri*) (Fig. 2C); body slender, caudal tubercles within a tail whorl well separated (body large and robust, caudal tubercles within a tail whorl abut in *P. fasciatus*); size small, SVL < 45 mm (maximum SVL \geq 49 mm in all other members of the complex, except P. robertsi, P. reconditus, P. monicae, P. mclachlani, and P. visseri); dorsal scalation heterogeneous (largely homogeneous in *P. kobosensis*), with

the entire dorsum of trunk equally tuberculate (anterior third of dorsum typically less strongly tuberculate than posterior in P. acuminatus); three body bands (including nape and sacral bands) present in juveniles (Fig. 3B) and adults, although sometimes obscured in the latter (all bands, including nape, absent in P. atorquatus; only nape band present in juveniles and adults of P. robertsi and P. reconditus; four body bands in *P. werneri*; and five or more body bands in P. visseri, P. tsodiloensis, and P. waterbergensis); bands narrow and straight-edged, lost or obscured in adults (body bands broad and retained in adults in P. goodi, bands broad and wavy-edged in P. weberi).

Description of Holotype. Adult female. SVL 44.5 mm (Figs. 1, 2A, B). Body moderately depressed, elongate (TrunkL/SVL 0.41). Head short (HeadL/SVL 0.25), moderately wide (HeadW/HeadL 0.68), depressed (HeadD/HeadL 0.37), distinct from neck, which is inflated because of enlarged endolymphatic sacs. Lores inflated, interorbital region flat. Snout moderately long (SnEye/HeadL 0.39), much longer than eye diameter (OrbD/SnEye 0.59); scales on snout



Figure 2. Life views of *Pachydactylus etultra*: adult female holotype (MCZ R184980) illustrating the depressed habitus and characteristic coloration (A) and enlarged scales of the snout and participation of the first supralabial in the nostril rim (B). Adult female paratype (PEM R17287) showing the typical somewhat inflated circumnasal scales and short digits (C), small dorsal tubercles, and atuberculate thighs (D) of this species. Photographs by W. R. Branch.



Figure 3. Life views of *Pachydactylus etultra*: hatchling paratype (PEM R17293) showing the characteristic boldly contrasting pattern (A). Subadult paratype (PEM R17294) showing the fading of the dark dorsal background, leaving darker margins to the body bands (B). Photographs by W. R. Branch.

and canthus large, smooth, flattened, heterogeneous in size and shape; scales of interorbital and parietal regions strongly heterogeneous, with tiny granules interspersed with larger, domed to conical, rounded tubercles, each about one-quarter the size of largest snout scales. Enlarged conical tubercles regularly scattered across occipital and temporal regions. Eye small (OrbD/HeadL 0.23); orbits without extrabrillar fringes; 4–5 superciliaries at posterodorsal corner of orbit bearing very small spines; pupil vertical, with crenellated margins. Ear opening oval, horizontal, small (EarL/HeadL 0.07); eye to ear distance approximately equal to diameter of eye (EyeEar/OrbD 1.04). Rostral approximately 55% as deep (0.6 mm) as wide (1.1), no rostral groove, contacted by two enlarged supranasals and first supralabials; nostrils

	MCZ	MCZ	MCZ	MCZ	MCZ	MCZ	PEM	PEM	PEM	PEM
	R 184980	R 184977	R 184978	R184979	R184981	R184982	R17293	R 17294	R 17295	R 17287
	Holotype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype
Sex	Female	Female	Female	Male	Female	Female	Hatchling	Subadult	Male	Female
SVL	44.5	34.1	39.2	39.1	41.0	41.1	17.3	25.7	38.5	39.1
ForeaL	5.2	4.9	6.3	5.4	5.4	5.8	2.0	3.4	5.8	5.2
CrusL	6.7	5.8	6.9	7.1	6.8	6.4	2.6	4.5	6.2	6.2
TailL (total)	40.4	2.6^{*}	42.3	15.2	19.7	41.6	15.1	13.2	31.8^{*}	12.5*
TailL				5.7	9.0			5.5		
(regenerated)										
TailW	3.7	1.6	2.9	3.2	3.1	3.1	1.3	2.2	3.8	3.2
TrunkL	18.3	14.2	16.7	15.6	16.9	16.4	7.7	11.9	15.9	19.3
HeadL	11.2	9.4	11.9	10.0	11.4	10.6	5.6	7.2	10.7	10.6
HeadW	7.7	6.6	6.4	7.1	7.0	7.0	3.8	5.4	7.2	7.1
HeadD	4.1	3.3	3.3	3.3	3.6	3.5	1.9	3.3	3.9	3.7
OrbD	2.6	2.6	2.6	2.7	2.5	2.9	1.6	1.9	2.5	2.5
EyeEar	2.7	2.5	2.7	2.7	2.5	3.1	1.0	1.8	2.7	2.6
SnEye	4.4	4.0	4.3	4.4	4.3	4.2	2.1	3.1	4.1	4.0
NarEye	3.1	2.9	3.1	3.3	3.0	3.3		2.2	3.4	3.3
Interorb	3.5	2.5	2.7	3.3	3.3	3.3	2.1	2.4	3.6	3.2
EarL	0.8	0.7	0.8	0.6	0.9	0.8		0.6	1.0	1.0
^a Abbreviation:	s as in Materi	als and Metho	ds; all measure	ements in mm	; * = broken	tail.				

Table 2. Mensural data for the type series of $Pachydactylus\ etultra$, Sp. nov.^a

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oval, oriented dorsolaterally, each surrounded by two postnasals, supranasal, and narrowly by first supralabial; supranasals in broad contact; dorsal postnasal slightly larger than ventral postnasal, separated by a single granule; nostril rims moderately inflated; 1-2 rows of scales separate orbit from supralabials; mental elongate with nearly parallel sides, 2.25 times deeper (1.8 mm) than wide (0.8 mm); no enlarged postmentals or chin shields. Enlarged supralabials (left/right) counted to rictus 13/13 (8/8 to midorbit); infralabials 10/10; interorbital scale rows between superciliary rows at midpoint of orbit 25 (11 across narrowest point of frontal bone).

Dorsal tubercles large (about six times the size of adjacent scales), largest dorsolaterally and smallest along dorsal midline and on anterior one third of trunk, rounded, with a pronounced median keel, forming 14 regular longitudinal rows on trunk, grading into posteriorly directed, conical scales on lower flanks; each tubercle surrounded by a regular rosette of about 10 small domed to conical scales; ventral scales flattened, rounded to oval, subimbricate to imbricate, becoming larger posteriorly, largest on posterior abdomen and in precloacal region, approximately 40 between lowest conical granular rows on flank at midbody; tubercular scales on dorsum at midbody much larger than ventral scales at same level; chin granules approximately one fourth size of ventral scales, increasing in size rather abruptly between gular region and chest. No preanal or femoral pores. Scales on palm, sole, and ventral surface of forelimb smooth, granular; scales on dorsal aspect of forelimb small, smooth, heterogeneous, subimbricate; scales on preaxial and ventral aspects of thighs somewhat enlarged, smooth, imbricate; scales on dorsum of thigh nontuberculate, heterogeneous, small to large, flattened to conical; scales on dorsum of crus small, conical, with scattered large (about five times the size of adjacent scales), smooth conical tubercles.

Forelimbs short, stout (ForeaL/SVL 0.12); hindlimbs short (CrusL/SVL 0.15); digits short, minute stylet-like claws visible under magnification on all digits except digit I of manus; subdigital scansors, except for distalmost, entire, present only on distal portion of toes, approximately 1.3 times wider than more basal (nonscansorial) subdigital scales; interdigital webbing absent. Relative length of digits (manus): III \sim IV > V > II > I; (pes): IV > III > V > II > I. Subdigital scansors (excluding small distal divided scansor) I (4), II (4), III (4), IV (4), V (4) manus; I (4), II (5), III (5), IV (5), V (5)—pes.

Tail subcylindrical, weakly depressed; original tail somewhat shorter than SVL (TailL/SVL 0.91) to somewhat longer than SVL for original tails (on the basis of MCZ R184982 and 184978); tail smoothly tapering, with distinct whorls of scales; dorsal caudal scales oval to rectangular, heterogeneous in size, subcaudal scales 3-4 times size of dorsal caudals, subimbricate, squarish, becoming elongate on distal portion of tail; 4-5 transverse rows of scales per whorl dorsally, 3 ventrally, dorsal scales of posteriormost row of each whorl enlarged, weakly keeled, separated from adjacent keeled scales by a single, somewhat smaller scale, posterior half of tail without keels on, or small interscales between, enlarged dorsal scales. midventral caudal scales enlarged relative to adjacent scales (6-8 times size of dorsal caudal scales); no postcloacal spurs.

Coloration of Holotype (in alcohol). Dorsum beige to brownish-yellow with three transverse bands bordered by thinner midbrown edges (Fig. 1). Nuchal band extending from posteroventral border of orbit, through ear, and across nape. Anterior trunk band of same width, anterior to midbody, at level of elbow of adpressed forelimb. A third, much broader pale band from anterior to hindlimb insertion to anterior sacrum is less conspicuous than the anterior bands, and several mid-brown tubercles are enclosed in its pale center. Dark anterior border of nape band passes through ventral portion of orbit to nostril; a diffuse, thick cream stripe from anterodorsal margin of each orbit to posterior margin of ipsilateral nostril. Top of head beige with a darker snout and frontal region; relatively symmetrical midbrown markings at midparietal table and on occiput. Supralabials brown, with areas of reduced pigment, especially around sutures and on posterior scales. Infralabials paler, with central regions of some scales deeply speckled, much lighter pigment on others, especially mental and first infralabials. Limbs mottled, lacking a discrete pattern; digits pale. Tail with alternating light (beige) and dark (midbrown) bands of approximately equal width. Life coloration (Fig. 2A) is similar to that in preservative, but the background color is a pale lavender.

Variation. Variation in mensural characters of the holotype and adult paratypes are presented in Table 2. All paratypes are similar in scalation to holotype but have more strongly developed keels on the dorsal caudal scales. Male paratypes also lack precloacal and femoral pores.

The hatchling paratype (PEM R17293, SVL 17.3 mm) has similar coloration to that of hatchling *P. mclachlani*, with a blackish dorsum, wavy-edged bright white trunk band, and ashy white nape band that extends forward along the jawline to the eye (Fig. 3A). As with *P. mclachlani* juveniles, the upper surfaces of the fore- and hindlimbs are ashy gray with a brown infusion, whereas the top of the head is golden brown. A conspicuous pale white eye ring, heavily infused with golden orange, is along its upper edge. The tail is bright orange with 8–9 vague darker bands, subequal in width

to the lighter orange interspaces; it lacks the enlarged golden tubercles present in subadults and adults. Unlike P. mclachlani hatchlings, there is an extra ashy white sacral band, followed behind by a dark brown band at the level of the hindlimb insertion. Additionally, there are a number of scattered white blotches, including a transverse bar almost midway between the chest and sacral white bands, and two small white spots on either side of the forelimb insertion. An additional juvenile (not collected, but photographed by Miles Paul) has very similar coloration, but the postsacral band is darker, with only a single, slightly off-center spot between the chest and sacral bands.

In life, the subadult paratype (PEM R17294) had an intermediate coloration between that of the adult and hatchling paratypes (Fig. 3B). The body color was a pale golden tan with thin dark brown bands bordering the dirty cream nape, chest, and sacral bands; the enlarged body tubercles were golden on the flanks, darker on the dorsum. The crown was golden orange with darker enlarged tubercles; the extension of the nape band onto the snout was white only below the eye, and the pale eye ring was golden. The upper surfaces of the limbs matched the background color of the dorsum, although the limbs were paler at their junction with the body; the upper surfaces of the digits were gravish, and the ventrum and undersurfaces of the head and limbs was dirty cream; the tail was diffuse golden brown, with little evidence of banding, and was highlighted with rings of golden tubercles.

Distribution. This species is currently known with certainty only from the type locality and is therefore another Namibian endemic. Suitable habitat occurs extensively on rocky mountain slopes of the Nubib Mountains in the NamibRand Nature Reserve (Figs. 4, 5), and the species probably



Figure 4. General habitat at the type locality of *Pachydactylus etultra*. View facing southeast toward the Nubib Mountains. Photograph by W. R. Branch.

has a wider distribution in the region. Several specimens from the Maltahöhe District assigned by Bauer, Lamb, and Branch (2006) to *P. acuminatus* might in fact be referable to *P. etultra*. These include a specimen from Sesriem (SAM 44623) and two (SAM 45524, 44528) from Tsaris Pass, respectively, 35 and 55 km from the type locality. A questionable record of *P. acuminatus* from the Amichab Mountains (but without precise locality; see Bauer, Lamb, and Branch 2006) in the southern Swakopmund District (TM 32136) could also belong to this form and should be re-examined.

Habitat and Natural History. Some specimens were collected on rocky slopes at night, where they were active on and between rock faces. Other specimens were collected around the lodge accommodation, some climbing on rocks composing the boundary walls and chalets. One of the two known hatchlings was collected on gravel on a path, whereas the other was found on the floor of a chalet, both within the lodge complex. Pachydactylus etultra is the only member of the P. weberi species complex found in the region, but the more distantly related congeners P. rugosus and P. punctatus are expected to be present (Branch 1998).



Figure 5. Map of western southern Africa indicating the type locality of *Pachydactylus etultra* in the northern part of the NamibRand Nature Reserve, as well as the distribution of all other species of the *Pachydactylus weberi* group. Distributions of other species based on Bauer, Barts, and Hulbert (2006) and Bauer, Lamb, and Branch (2006). Satellite image from NASA MODIS sensor (available at http://visibleearth.nasa.gov).

Conservation. Several members of the *P. weberi* and *P. serval* complexes have relatively restricted distributions, but only one species is considered threatened (*P. goodi,* Vulnerable, Bauer, in press). *Pachydactylus etultra* is common at the type locality in a well-protected conservancy and with large regions of similar habitat in the region. It is therefore unlikely to be of conservation concern. However, further surveys are re-

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Figure 6. Maximum likelihood phylogeny of *Pachydactylus serval* and *P. weberi* group species, rooted with *P. capensis.* Bootstrap values (ML/MP) are indicated at nodes. Support values are not shown for intraspecific relationships, but all are 100.

quired to assess the species' full range and habitat requirements, and it should be treated as Data Deficient until such information is available.

Etymology. The specific epithet honors "&Beyond" (previously CC Africa), an ecotourism venture that has won many awards for the conservation of African wildlife and the upliftment of local people. The first specimen of this new species was brought to our attention by Peter Dunning, then lodge manager of the CC Africa Sossusvlei Mountain Lodge within the NamibRand Private Reserve, the area in which all specimens have been found. The name is a noun in apposition and is a literal Latin translation of "and" (*et*) "beyond" (*ultra*).

Phylogenetic Relationships. The final alignment (2,975 bp) included 837 variable and 635 parsimony-informative sites. A single most parsimonious tree was found, with a length of 1,721 steps. The best likelihood tree had a $-\ln L$ score of 11,725.40071. Both phylogenies displayed identical topologies (Fig. 6). Pachydactylus etultra is recovered with significant support (maximum likelihood/maximum parsimony [ML/MP] boot-

strap 100/98) as a close relative of *P. monicae* from the lower Orange River valley (Fig. 5), whereas other between-species branches received nonsignificant support. Both *P. mclachlani*, the most superficially similar species to *P. etultra*, and *P. serval*, which shares a similar juvenile pattern, fall well outside the *etultra* + *monicae* grouping.

DISCUSSION

Despite more than 50 years of relatively intense herpetological study in Namibia (e.g., Mertens, 1955, 1971; Bauer et al., 1993; Bauer and Branch, 1995; Branch et al., 1996; Griffin, 2000, 2003), knowledge of gecko diversity in Namibia continues to increase. Eleven new species of Pachydactylus have been described from Namibia in the first decade of this century (Bauer et al., 2002; Bauer and Lamb, 2003; Bauer, Lamb, and Branch, 2006; Bauer, 2010). This reflects greater access to remote areas and richer specimen resources on which to base taxonomic decisions, as well as the availability of molecular phylogenetic methods to assess relationships.

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The phylogeny presented here is preliminary and incomplete, but it does demonstrate that *P. etultra* does not form a monophyletic group with the phenetically similar P. mclachlani or with other species with which it shares a similar hatchling color pattern. Its closest affinity among sampled taxa is with P. monicae, a recently described species that occurs along the lower Orange River and in the valleys of the Fish and Hoolog Rivers. The type locality of P. etultra lies approximately 360 km NNW of the closest P. monicae locality near Rosh Pinah (Bauer, Lamb, and Branch, 2006). It is much nearer localities for P. acuminatus (not genetically sampled here), which occurs from Aus in the south to Duwisib (only 85 km from Sossusvlei Desert Lodge) in the north (Fig. 5). A more detailed multigene phylogenetic analysis of the P. serval and P. weberi groups, including P. etultra, as well as P. acuminatus, P. visseri, P. mclachlani, and P. goodi, all taxa not investigated in the cytochrome bbased analysis of Bauer, Lamb, and Branch (2006), is in preparation.

The unusual boldly banded black and white body coloration of hatchling P. etultra is similar to that of a number of other Pachydactylus, including P. mclachlani, P. carinatus, P. serval, P. bicolor, P. gaiasensis, and P. oreophilus. Whereas P. mclachlani is relatively closely allied to P. etultra, the other species are either members of the P. serval complex (P. serval and P. carinatus) or of a separate northern Namibian clade (P. bicolor, P. gaiasensis, and P. oreophilus; Bauer and Lamb, 2005). Although the species vary in size and habitat, they are all mainly rupicolous. A similar striking black and white-banded hatchling pattern occurs in the Bushveld lizard (Heliobolus lugubris), a small terrestrial lacertid common in savanna habitats, where it is postulated (Huey and Pianka, 1977; Schmidt, 2004) that this bold hatchling color mimics the coloration of the highly distasteful predacious ground beetles or "oogpisters" (*Anthia* sp., Carabidae). Although it is possible that a similar form of Batesian mimicry could be involved with the boldly patterned *Pachydactylus* hatchlings, protecting them from predation in the first few months of life as they disperse from their natal oviposition sites, the pattern might simply be cryptic and disruptive.

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LITERATURE CITED

BAUER, A. M. 2010. A new species of *Pachydactylus* (Squamata: Gekkonidae) from the Otavi Highlands of northern Namibia. *Bonn Zoological Bulletin* 57: 257–266. —. In press. *Pachydactylus goodi*: species account, *In* M. F. Bates, M. Burger, W. R. Branch, A. M. Bauer, J. Marais, G. J. Alexander, and M. S. de Villiers eds. *Atlas and Red Data Book of the Reptiles of South Africa, Lesotho and Swaziland.* Pretoria, South African National Biodiversity Institute.

- , AND W. R. BRANCH. 1995. Geographic variation in western populations of the *Pachydactylus punctatus* complex (Reptilia: Gekkonidae). *Tropical Zoology* 8: 69–84.
 - —, AND T. LAMB. 2002. Phylogenetic relationships among members of the *Pachydactylus capensis* group of southern African geckos. *African Zoology* **37:** 209–220.
 - —, AND —, 2003. A new species of the *Pachydactylus weberi* group (Reptilia: Squamata: Gekkonidae) from the Waterberg Plateau, Namibia. *Cimbebasia* **19:** 1–12.
- _____, AND ______. 2005. Phylogenetic relationships of southern African geckos in the *Pachydactylus* Group (Squamata: Gekkonidae). *African Journal* of Herpetology **54**: 105–129.
 - —, W. R. BRANCH, AND W. D. HAACKE. 1993. The herpetofauna of the Kamanjab area and adjacent Damaraland, Namibia. *Madoqua* **18**: 117–145.
 - —, T. LAMB, AND W. R. BRANCH. 2002. A revision of *Pachydactylus scutatus* (Reptilia: Squamata: Gekkonidae) with the description of a new species from northern Namibia. *Proceedings of the California Academy of Sciences* **53**: 23–36.
 - —, M. BARTS, AND F. HULBERT. 2006. A new species of the *Pachydactylus weberi* group (Reptila: Squamata: Gekkonidae) from the Orange River, with comments on its natural history. *Salamandra* 42: 83–92.
- —, T. LAMB, AND 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. *Proceedings of the California Academy of Sciences* **57:** 595–709.
- —, A. DE SILVA, E. GREENBAUM, AND 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). *Mitteilungen aus dem Museum für Naturkunde in Berlin. Zoologische Reihe* 83(Supplement): 22–32.
- BRANCH, W. R. 1998. Field Guide to the Snakes and Other Reptiles of Southern Africa, 3rd ed. Cape Town, Struik Publishers.
 - —, A. M. BAUER, AND D. A. GOOD. 1996. A review of the Namaqua gecko, *Pachydactylus namaquensis* (Reptilia: Gekkonidae) from southern Africa, with

the description of two new species. *South African Journal of Zoology* **31:** 53–69.

- BROADLEY, D. G. 2003. Pachydactylus katanganus de Witte 1953, a species endemic to the Upemba National Park (Sauria: Gekkonidae). African Journal of Herpetology 52: 69–70.
- GREENBAUM, E., A. M. BAUER, T. R. JACKMAN, M. VENCES, AND F. GLAW. 2007. A phylogeny of the enigmatic Madagascan geckos of the genus *Uroplatus* (Squamata: Gekkonidae). *Zootaxa* 1493: 41–51.
- GRIFFIN, M. 2000. The species diversity, distribution and conservation of Namibian reptiles: a review. Namibia Wissenschaftliche Gesellschaft Journal 48: 116–141.
- 2003. Annotated Checklist and Provisional National Conservation Status of Namibian Reptiles. Windhoek, Namibia Scientific Society.
- GROTH, J. G., AND G. F. BARROWCLOUGH. 1999. Basal divergences in birds and the phylogenetic utility of the nuclear RAG-1 gene. *Molecular Phylogenetics* and Evolution 12: 115–123.
- GUINDON, S., AND O. GASCUEL. 2003. A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. *Systematic Biology* **52**: 696– 704.
- HALL, T. A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symposium Series 41: 95–98.
- HUEY, R. B., AND E. R. PIANKA. 1977. Natural selection for juvenile lizards mimicking noxious beetles. *Science* 195: 201–203.
- KUMAR, S., J. DUDLEY, M. NEI, AND K. TAMURA. 2008. MEGA: a biologist-centric software for evolutionary analysis of DNA and protein sequences. *Briefings in Bioinformatics* 9: 299–306.
- LEVITON, A. E., R. H. GIBBS, E. HEAL, AND 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.
- MACEY, J. R., A. LARSON, N. B. ANANJEVA, Z. FANG, AND T. J. PAPENFUSS. 1997. Two novel gene orders and the role of light-strand replication in rearrangement of the vertebrate mitochondrial genome. *Molecular Biology and Evolution* 14: 91–104.
- —, J. A. SCHULTE, A. LARSON, N. B. ANANJEVA, Y. WANG, R. PETHIYAGODA, N. RASTEGAR-POUYANI, AND T. J. PAPENFUSS. 2000. Evaluating trans-Tethys migration: an example using acrodont lizard phylogenetics. *Systematic Biology* **49**: 233–256.
- MERTENS, R. 1955. Die Amphibien und Reptilien Südwestafrikas, aus den Ergebnissen einer im Jahre 1952 ausgeführten Reise. Abhandlungen der Senck-

enbergischen naturforschenden Gesellschaft **490:** 1–172.

- 1971. Die Herpetofauna Südwest-Afrikas. Abhandlungen der Senckenbergischen naturforschenden Gesellschaft 529: 1–110.
- POSADA, D. 2008. jModelTest: phylogenetic model averaging. *Molecular Biology and Evolution* 25: 1253–1256.
- SCHMIDT, A. D. 2004. *Mimikry zwischen Laufkäfern und Eidechsen*. Frankfurt am Main, Edition Chimaira.
- THOMPSON, J. D., D. G. HIGGINS, AND T. J. GIBSON. 1994. CLUSTAL W: improving the sensitivity of pro-

gressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acids Research* **22**: 4673–4680.

WEISROCK, D. W., J. R. MACEY, I. H. UGURTAS, A. LARSON, AND T. J. PAPENFUSS. 2001. Molecular phylogenetics and historical biogeography among salamandrids of the "true" salamander clade: rapid branching of numerous highly divergent lineages in *Mertensiella luschani* associated with the rise of Anatolia. *Molecular Phylogenetics and Evolution* 18: 450–464.