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A new species of *Pachydactylus* (Squamata: Gekkonidae) from the Otavi Highlands of northern Namibia

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Abstract. A new species of the "northwestern clade" of *Pachydactylus* is described from the Otavi Highlands of northeastern Namibia. It is distinguishable from all other members of this clade and from the superficially similar members of the *Pachydactylus serval/weberi* group on the basis of its inclusion of the rostral in the nostril rim, the possession of a maximum of only four undivided scansors beneath the digits of the pes, is 16 rows of strongly keeled, rounded, juxtaposed dorsal trunk tubercles, its projecting, keeled, lanceolate caudal tubercles, and its complex dorsal trunk patterning. Its probable closest relative is *P. otaviensis*, also form the Otavi Highlands. These are the only known endemic reptiles from this dolomitic area and their existence points both to an unappreciated area of diversity and endemism in northeastern Namibia and to the need for additional herpetological work in even well-known parts of the country.

Key words. Gekkonidae, *Pachydactylus*, Namibia, new species.

INTRODUCTION

Pachydactylus Wiegmann, 1834 is the most species-rich genus of geckos in southern Africa, with more than 50 species currently recognized (Bauer & Lamb 2005; Bauer et al. 2006a, 2006b; Branch et al. 2010). Although all parts of the subcontinent are inhabited by members of this group, the arid zones of Namibia the adjacent portions of the Northern Cape Province of South Africa have the highest diversity. A minimum of 35 species of *Pachydactylus* occur in the Republic of Namibia alone, the majority of which are endemic (Branch 1998; Bauer et al. 2002, 2006a; Branch et al. 2010). Most of these fall into one of two species-rich clades that have been previously identified: the *Pachydactylus serval/weberi* group and the "northwestern clade" of *Pachydactylus* (*sensu* Bauer & Lamb 2005). Most species in both clades are relatively small-bodied, rupicolous species. Most members of the *P. serval/weberi* group are restricted to southern Namibia and the Northern Cape, with the greatest richness along the lower Orange River Valley and in the Karasberg Mountains, where up to five members of the group occur sympatrically. However, five members assigned to the group have been found north of 21°S latitude: *P. fasciatus* Boulenger, 1888 – widely distributed in northwestern Namibia east of the Namib and north of the Swakop River, *P. waterbergensis* Bauer & Lamb, 2003 – endemic to the immediate vicinity of the Waterberg Plateau. *P. tsodiloensis* Haacke, 1966 – in the Tsodilo Hills of northwestern Botswana, and *P. otaviensis* Bauer, Lamb & Branch, 2006 and an undescribed species ('*Pachydactylus* sp. 2', Bauer et al. 2006a) – both from the Otavi Highlands (Otaviberge) of northeastern Namibia. Bauer & Lamb (2005) and Bauer et al. (2006a) used molecular phylogenetic data to confirm that the first three of these species comprise a monophyletic group that is sister to the rest of the *P. serval/weberi* group. However, recent multi-gene phylogenetic analyses incorporating all but one of the recognized species of *Pachydactylus* (Heinicke, Jackman & Bauer, unpublished) have demonstrated that *P. otaviensis* is not a member of the *P. serval/weberi* clade (these phylogenetic results will be presented in their entirety elsewhere), but rather part of the "northwestern clade", which otherwise comprises ten morphologically diverse species that are widely distributed in Namibia and southern Angola, with a single species, *P. punctatus* Peters, 1854, extending southwards into South Africa and east to the Indian Ocean coast of Mozambique (Bauer & Branch 1995).

Excluding *P. punctatus*, *P. otaviensis* has the easternmost distribution of any member of the "northwestern clade", being known only from the farms Uithoek and Varianto, both in the Tsumeb District, Oshikoto Region in the eastern Otavi Highlands (quarter degree square 1917Bc; Fig. 1). A second species from the Otavi Highlands was sig-

Table 1. Mensural and labial scale data for the type series of *Pachydactylus boehmei* sp.n. Abbreviations as in Materials and Methods, all measurements in mm.

	Holotype	Paratypes			
	MCZ R184884	MCZ R184880	MCZ R184881	MCZ R184882	MCZ R184883
Sex	female	female	female	male	female
SVL	44.4	43.21	44.0	35.4	34.8
ForeaL	6.6	6.8	6.6	5.4	4.7
CrusL	7.9	7.9	8.6	5.5	5.9
TailL (total)	44.5	6.9	39.0	35.8	30.3
TailL (regen.)	–	BR	33.4	–	21.6
TailW	4,8	4.7	4.7	3.9	3.5
TrunkL	21.0	18.8	19.0	15.6	13.8
HeadL	13.7	14.1	13.0	11.5	12.0
HeadW	8.3	8.3	9.0	6.9	7.2
HeadD	5.0	5.3	5.3	3.8	4.0
OrbD	3.5	3.8	3.8	2.8	3.3
EyeEar	3.4	3.7	3.2	2.9	2.5
SnEye	4.9	5.0	4.7	4.2	4.2
NarEye	3.7	3.9	3.6	2.9	3.0
Interorb	4.4	4.3	3.9	3.6	3.0
EarL	1.0	0.9	1.0	0.7	0.7
Internar	1.4	1.1	1.3	1.0	1.2
Supralab. (L/R)	10/9	11/10	10/10	9/9	10/10
Infralab. (L/R)	7/7	8/8	7/8	8/8	9/8

naled by Bauer et al. (2006a) as "*Pachydactylus* sp. 2", but was not described as it was known only from one juvenile and one hatchling, making meaningful comparisons with other species difficult. However, Bauer et al. (2006a) noted that it exhibited some features shared with the *P. weberi* complex *sensu stricto* and others with the *P. serval* complex, and that it possessed a unique and diagnostic juvenile color pattern. Subsequent field work on the Farm Uisib has yielded a series of adult specimens of this species, permitting its description. Ongoing molecular phylogenetic work verifies that it too is, in fact, correctly assigned to the "northwestern clade" of *Pachydactlyus*.

MATERIALS AND METHODS

The following measurements were taken with Brown and Sharpe Digit-cal Plus digital calipers (to the nearest 0.1 mm) as per Bauer et al. (2006a): 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 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); 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 (see Appendix) representing all species in the *Pachydactylus serval/weberi* group and the "northwestern clade" of *Pachydactylus* (*sensu* Bauer & Lamb 2005; Bauer et al. 2006a). Standard codes for museum collections follow Leviton et al. (1985) except as noted (*): California Academy of Sciences, San Francisco (CAS), Museum of Comparative Zoology, Harvard University, Cambridge, USA (MCZ), National Museum of Namibia, Windhoek (NMN*), Naturmuseum und Forschungsinstitut Senckenberg, Frankfurt am Main (SMF), South African Museum, Cape Town (SAM), Transvaal Museum, Pretoria (TM), Zoologisches Forschungsmuseum Alexander Koenig, Bonn (ZFMK).

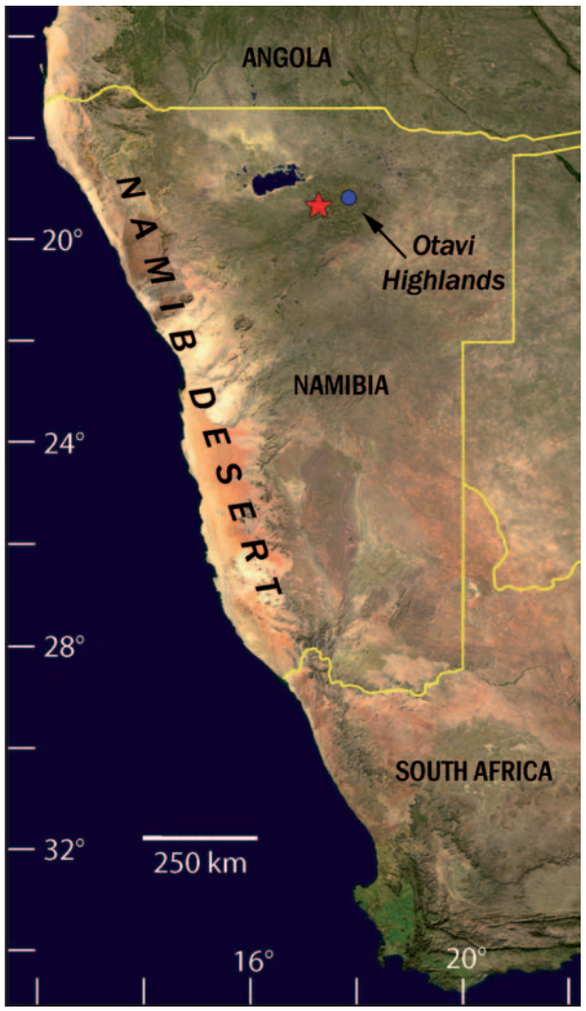

Fig. 1. Map of Namibia and surrounding countries illustrating the type locality of *Pachydactylus boehmei* sp. n. (red star) and of the related *P. otaviensis* (blue circle) in the Otavi Highlands of northeastern Namibia. Satellite image from NASA MODIS sensor (available at http://visibleearth.nasa.gov).

RESULTS

***Pachydactylus boehmei* sp. n.**
Pachydactylus sp. 2 Bauer, Lamb & Branch (Bauer et al. 2006a: 684)

Holotype. MCZ R184884 (Figs 2–3): adult male; Namibia, Otjozondjupa Region, Grootfontein District, Farm Uisib, 19°33'06"S, 17°14'11"E, 1400 m a.s.l. coll. A.M. Bauer, J. Marais, T. Jackman, and W.R. Branch, 15 September 2006.

Paratypes. MCZ R184880–81 (adult females), 184883 (subadult/adult female), MCZ R184882 (subadult/adult male), same data as holotype.

Additional material. TM 84999, 85005; Namibia, Otjozondjupa Region, Grootfontein District, Farm Uisib (19°33'08"S, 17°14'07"E).

Diagnosis. Snout-vent length to at least 44.4 mm. A moderate-sized *Pachydactylus* with a depressed body form. Trunk with 16 rows of enlarged, keeled tubercles, grading into prominent conical scales on flanks (Figs 2–4). Orbital diameter as great as eye-ear distance. Rostral participating in nostril rim. Dorsal surface of thighs and shanks covered by enlarged conical to keeled scales. Tail with keeled lanceolate tubercles restricted to one scale row per tail segment. Dorsal pattern with an occipital-nuchal loop, a "V"-shaped band on posterior of neck, a transverse bar anterior to hindlimb insertion, and a series of oval markings or fusions thereof on the trunk (Figs 2–5).

Among its congeners *P. boehmei* sp n. is superficially similar to some members of the *P. weberi* group, but can be distinguished from these by its inclusion of the rostral in the nostril rim and the possession of a maximum of only four undivided scansors beneath the digits of the pes (versus at least five on some digits). Among other members of the "northwestern clade" of *Pachydactylus* it may be differentiated from *P. bicolor* Hewitt, 1926, *P. punctatus*, *P. scherzi* Mertens, 1954, and *P. caraculicus* FitzSimons, 1959 by its tuberculate (versus atuberculate) dorsum, from *P. angolensis* Loveridge, 1944 by its inclusion of the rostral and first supralabial in the nostril border (versus both excluded), from *P. oreophilus* McLachlan & Spence, 1967 by its smaller size (maximum SVL < 45 mm versus 57 mm), and lower number of subdigital lamellae (4 versus 5–6 undivided lamellae), from *P. gaiasensis* Steyn & Mitchell, 1967 by its smaller size (maximum SVL < 45 mm versus 68 mm), lower number of subdigital lamellae (4 versus 5–7 undivided lamellae), longer tail (slightly longer than SVL versus less than SVL), and lack of a vertebral stripe, from *P. sansteynae* Steyn & Mitchell, 1967 by its much larger dorsal tubercles (4–10 times larger than other dorsal scales versus less than twice size of dorsal granules) and presence (versus absence) of tubercles on the parietal region, from *P. parascutatus* Bauer, Lamb & Branch, 2002 by its larger size (to 44.4 mm versus < 40 mm SVL) and presence of a pale dorsal collar (versus no collar), and from *P. scutatus* Hewitt, 1927 by is juxtaposed (versus imbricating) keeled dorsal scales, enlarged conical (versus small and granular) flank scales, projecting lanceolate (versus flattened and rounded to oval) caudal tubercles, and its complex dorsal trunk patterning (versus patternless or with small, scattered dark markings. *Pachydactylus boehmei* sp n. is most similar to the geographically proximal *P. otaviensis*, but may be distinguished from this form by its inclusion (versus exclusion) of the rostral in the nostril rim, the presence of 4 (versus 5) lamellae beneath digit IV of the pes, 16 (versus 18) longitudi-

Fig. 2. Holotype of *Pachydactylus boehmei* sp. n., MCZ R184884. Scale bar = 10 mm.

nal rows of keeled dorsal tubercles, and differences in color pattern.

Description of holotype. Adult female. Snout-vent length (SVL) 44.4 mm. Body relatively depressed, elongate (TrunkL/SVL ratio 0.46). Head elongate, large (HeadL/SVL ratio 0.31), relatively narrow (HeadW/HeadL ratio 0.61), depressed (HeadH/HeadL ratio 0.36), distinct from neck. Lores inflated; interorbital region flat. Snout short (SnEye/HeadL ratio 0.36, longer than eye diameter (OrbD/SnEye ratio 0.71); scales on snout enlarged, smooth, slightly domed, roughly hexagonal; scales on snout much larger than those of interorbital region and parietal table. Eye moderately large (OrbD/HeadL ratio 0.25); orbits without extra-brillar fringes; posterior superciliary scales bearing five small spines; pupil vertical, with crenelated margins. Ear opening oval, small (EarL/HeadL ratio 0.07), round; eye to ear distance approximately equal to diameter of eyes (Eye-Ear/OrbD ratio 0.97). Rostral approximately 50% as deep (0.9 mm) as wide (1.9); no rostral groove; contacted by two enlarged supranasals and first supralabials; nostrils oval, each surrounded by two postnasals, one supranasal, first supralabial, and rostral; supranasals in broad contact; dorsal postnasals separated by two granules from one another; nostril rims weakly inflated; 1–2 rows of scales separate orbit from supralabials; mental rectangular, only slightly wider anteriorly than posteriorly, approximately 1.6 times deeper (1.8 mm) than wide (1.1 mm); no enlarged postmentals or chin shields. Enlarged supralabials to angle of jaws 9(R)–10(L), 8 to mid-orbit, several granular scales along labial margin to rictus; enlarged infralabials 7; interorbital scale rows between superciliary scale rows (at midpoint of orbit) 30, 8 across narrowest point of frontal bone.

Enlarged conical tubercles present from posterior border of orbit and occiput posteriorly; dorsal trunk tubercles large (4–10 times size of adjacent scales), rounded, with a strongly developed median keel, forming approximately 16 longitudinal rows; tubercles largest on dorsolateral surfaces of trunk, smaller along vertebral midline, and grading into enlarged conical scales on flanks; each enlarged tubercle surrounded by rosette of smaller pyramidal scales, some also keeled, larger keeled tubercles typically separated from one another by a single smaller scale; ventral scales flattened, subimbricate, becoming somewhat larger posteriorly, approximately 40 between lowest tubercular rows at midbody; non-tuberculate scales on dorsum at midbody similar in size to those on ventrum at same level; gular granules 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 heterogeneous, with midsized conical to keeled tubercles intermixed with smaller granular to conical scales; scales on dorsum of thigh and crus greatly enlarged, conical and keeled, in contact with each other or narrowly separated by much smaller interscales.

Forelimbs moderately short, stout; forearm short (ForeaL/SVL ratio 0.15); hindlimbs relatively short, tibia moderately short (CrusL/SVL ratio 0.18); digits relatively short, claws minute, stylet-like, visible only with difficul-

Fig. 3. Life photo of holotype of *Pachydactylus boehmei* sp. n. Photo by Johan Marais.

ty on some digits of the 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 scales; interdigital webbing absent. Relative length of digits (manus): III > IV > II > V > I; (pes): IV > III > V > II > I. Subdigital scansors, exclusive of divided distalmost scansor (manus): I (4), II (4), III (4), IV (4), V (4); (pes) I (4), II (4), III (4), IV (4), V (4).

Tail sub-cylindrical, clearly depressed; original tail approximately snout-vent length (TailL/SVL ratio 1.00); tail constricted basally, then expanded before tapering towards tip, distinctly segmented; each segment with 5 rows of scales dorsally and 3 ventrally, dorsal caudal , tail segment; caudal tubercles heterogeneous, medial tubercles more-or-less recumbent, lateral tubercles projecting, up to 8 keeled tubercles per row basally, decreasing to 4 on distal caudal segments; subcaudal scales smooth, imbricating, oval to rectangular; no enlarged postcloacal spurs on side of tail-base.

Coloration. In preservative (Fig. 2): Ground color of dorsum straw to yellowish brown with mid-brown markings. A broad "V"-shaped nape band and a transverse band anterior to hindlimb insertion. Trunk bearing a series if irregular oval markings, darker on their edges than at their centers, 3 (left) and 4 (right) markings in paravertebral position, 6 on upper left flank, last fused with transverse band, 2 on upper right flank followed by an irregular longitudinal marking representing the fusion of several oval markings. An additional pair of small dark markings at anterior face of hindlimb insertion and an additional cross-band on dorsum of posterior sacrum.

Head with a pale stripe from nostril to anterodorsal rim of orbit. Dark stripe along loreal region to mid-anterior of orbit, continuing from midposterior of orbit, above ear, to meet contralateral stripe to form a complete loop between the occiput and nape. Crown mottled, a triangular brown marking with apex at supranasals scales extending back to anterodorsal orbital rim. Labial scales pale with diffuse speckling; grayish vertical markings on lateral edges of rostral.

Limbs mottled with irregular markings. Tail with alternating irregular bands of grayish-brown and mid-brown, 20 dark bands including tail tip; most caudal tubercles cream to beige. Body venter beige, soles and palms grayish, tail venter grayish-brown with irregular darker gray-brown markings scattered along length of tail.

In life (Fig. 3): Background color of dorsum a pale pinkish-gray. Labial scales, canthal stripe, and nape whitish. Dark markings yellowish-to mid brown, darkest on head and occiput. Venter white.

Variation. Variation in mensural characters of the holotype and paratypes are presented in Table 1. All paratypes share with the holotype the same number of longitudinal rows of dorsal tubercles, number of subdigital lamellae, and configuration of the scales of the nasal region. Labial scale numbers varied across the type series and are also presented in Table 1. The male paratype, MCZ R184882 has prominent precloacal spurs (Fig. 4A), each bearing two rows of enlarged, compressed, dorsally-directed scales. Those of the dorsal row (5 scales on both sides) larger than those of ventral row (5 scales left, 6 scales

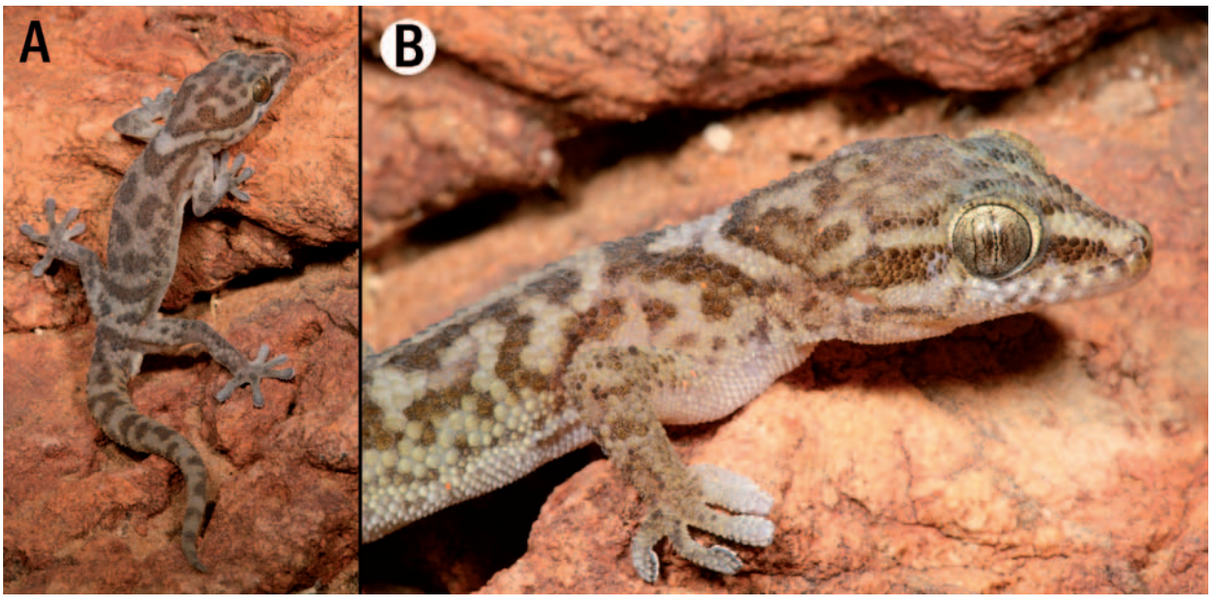

Fig. 4. Life photos of paratypes of *P. boehmei* sp. n. (A) MCZ R184882, male – note the raised precloacal spur visible lateral to the tail base. (B) MCZ R184880, female – note the transition from rounded, keeled dorsal tubercles to enlarged conical flank scales. Photos by Johan Marais.

right). Color pattern variable amongst paratypes (Figs 4–5). Dark occipital and nape bands thinner in MCZ R184880, R184882 than in holotype. Dorsal oval patterns largely replaced by coalescent blotches and lines except in MCZ R184881. Dorsal pattern weakly contrasting in MCZ R184883.

Etymology. Named for Prof. Dr. Wolfgang Böhme (born 21 November 1944), my longtime friend and colleague and a leading contributor to African herpetology. It is a privilege to apply this patronym to a species of one of the continent's dominant genera on the occasion of his nominal retirement from his position at the Museum Alexander Koenig. The epithet is formed in the masculine genitive.

Distribution. The species is known only from Farm Uisib in the Grootfontein District of northeastern Namibia (Fig. 1). This lies in the western portion of the Otaviberge or Otavi Highlands, 15 km northwest of the town of Otavi. The distribution of *P. boehmei* sp n. in the region is unknown and the closely related *P. otaviensis* occurs only 50 km to the northeast. These two geckos are relatively isolated from other members of the "northwestern clade" of *Pachydactylus* except the ubiquitous *P. punctatus*; the nearest known localities for *P. bicolor* and *P. scutatus* being more than 200 km distant. Other rock-dwelling congeners in other clades are also quite remote, with *P. waterbergensis* approximately 125 km to the south and *P. tsodiloensis* almost 400 km to the north-northeast. The Otavi Highlands as a whole has been poorly explored herpetologically and may harbor other isolated populations and/or endemic species of lizards. A number of endemic invertebrates and fish are already known from the Otavi-Tsumeb-Grootfontein area (Barnard et al. 1998).

Natural history. The area where *P. boehmei* sp n. occurs is characterized as mountain savanna and karstveld (Giess 1971). The type series was collected in broadleaf savanna on rocky dolomite hills (Fig. 6). Specimens collected by the author and colleagues were moving on rock faces or were found in large crevices or cracks between 22:30 and 00:30. The two Transvaal Museum specimens (see Additional material) referred to this species were collected in the course of searching for scorpions (E. Scott & L. Prendini, pers. comm.). Barnards Namib day gecko, *Rhoptropus barnardi* Hewitt, 1926, was also collected at Farm Uisib, which is one of the easternmost localities for any member of its genus. Other species observed at the type locality were the widespread *Chondrodactylus turneri* (Gray, 1864), *Trachylepis sulcata* (Peters, 1867), and *T. punctulata* (Bocage, 1872). *Lygodactylus capensis* (Smith, 1849) was collected at the nearby Uisib farmhouse (19º33'11"S, 17º13'00"E).

Two enlarged eggs are visible through the ventral body wall of the holotype collected in mid-September, suggesting spring breeding and hatching late in the year, corresponding to the rainy season. Trombiculid mites were found on the specimens, most notably in between the

Fig. 5. Paratype series of *Pachydactylus boehmei* sp. n. showing variation in the dorsal color pattern and degree of pattern boldness. Scale bar = 10 mm.

scales of the tail base. In the male paratype, MCZ 184882, the infestation of mites around the tail base and scales of the precloacal spurs was particularly severe.

Phylogenetic affinities. *Pachydactylus boehmei* sp n. is similar in habitus to the other small-bodied, tuberculate members of the "northwestern clade". It is superficially most similar to the neighboring species *P. otaviensis*, although the latter species lacks the rostral-nostril contact that is typical for most members of the clade. Preliminary molecular results suggest that these two species are indeed sister taxa.

Conservation status. *Pachydactytlus boehmei* sp n. does not occur in any protected areas. At its type locality it is undisturbed and the jagged, rocky terrain precludes human encroachment into its specific habitat. However, depending upon the extent of its actual range it may be under some threat from local mining activity in some places. Until such time as the species' distribution and threats can be evaluated more fully, I recommend that it be considered Data Defficient under the IUCN threat category system.

DISCUSSION

The discovery of this apparently range-restricted species highlights Namibia's high biodiversity and endemism (Maggs et al. 1998). M. Griffin (1998) identified 55 reptile species as being strictly or primarily endemic to Namibia, but recent discoveries, particularly in *Pachydactylus* (Bauer et al. 2002, 2006a; Bauer & Lamb 2003) have increased this to approximately 70. The "northwestern clade" of *Pachydactylus* is particularly diverse along the Northern Namibian Escarpment (*sensu* Irish 2002), which corresponds roughly to the Kaokoveld center of Floral Endemism (Volk 1966; van Wyk & Smith 2001) and is recognized as a regional center of endemism for reptiles in general (Crowe 1990; Simmons et al. 1998; Griffin 2000). The Otavi Highlands have also been ranked as an area of high biodiversity importance (Irish 2002), but like the Waterberg to the south, the relatively low relief (a maximum of 2155 m in surrounding plains of 1200–1500 m) and accessibility to surrounding areas that promotes diversity also decreases the prospects for long-term isolation and, consequently, endemism. Thus, it is somewhat surprising that two species of *Pachydactylus*,

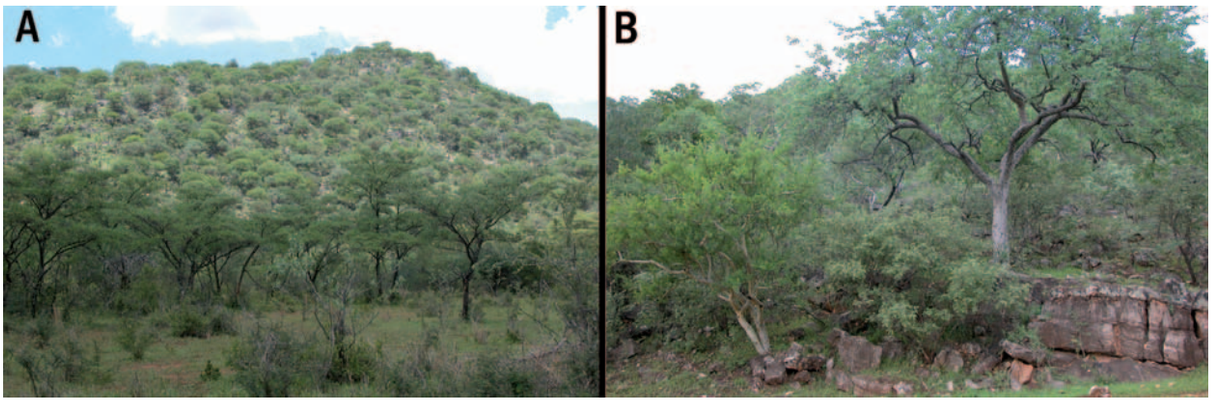

Fig. 6. Habitat of *Pachydactylus boehmei* sp. n. in the Otavi Highlands: (A) View of typical dolomite hill. (B) Broken dolomite providing cracks and fissures as retreat sites for geckos. Photos by Elizabeth Scott.

P. otaviensis and *P. boehmei* sp n., appear to be restricted to this region. Bauer (1999 [2000]) emphasized the role of substrate specificity as a cladogeneic agent in *Pachydactylus* and it seems likely that dependence on microhabitats provided by the dolomite outcrops of the Otaviberge has isolated these species from rest of the "northwestern clade". Other groups of organisms that respond similarly to historical ecological conditions should be expected to show similar patterns of endemism and indeed this is the case in scorpions (R.E. Griffin 1998), which include many substrate specific rupicolous species, such as the bothriurid *Lisposoma josehermana* Lamoral, 1979, which is largely restricted to the Otavi Highlands (Prendini 2003, 2005).

Despite over 50 years of relatively intense study (e.g., Mertens 1955, 1971; Haacke 1965; van den Elzen 1978; Bauer et al. 1993; Griffin, 2000, 2003), novel herpetological taxa continue to be discovered in Namibia on a regular basis. That *Pachydactylus boehmei* sp n. occurs in a densely-populated (by Namibian standards) agricultural district with excellent road access demonstrates that even "well known" parts of the country remain understudied.

Acknowledgements. I thank the many colleagues and students who have accompanied me on trips to Namibia, and in particular Johan Marais, Todd Jackman and Bill Branch, who participated on the field trip on which the types of *P. boehmei* were collected. I am also grateful to Andre Schoeman and his family, who made us welcome at Farm Uisib, and to the Ministry of the Environment and Mike Griffin, who have supported my work in Namibia for more than 20 years. Specimens were collected under Namibian Research/Collecting Permit 1068/2006. For access to comparative material I thank José Rosado, Jonathan Losos and James Hanken (MCZ), Lauretta Mahlengu and Wulf Haacke (TM), Jens Vindum (California Academy of Sciences), Mathilda Awases (NMN), Wolfgang Böhme (ZFMK), and Gunther Köhler (SMF). Photos were kindly provided by Johan Marais and Elizabeth Scott. This research was funded by the National Science Foundation of the United States through grants DEB 0515909 and DEB 0844523 to the author. Finally, I thank Philipp Wagner for inviting me to submit this manuscript, and Wolfgang Böhme, whose illustrious career has provided the opportunity to present these data.

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APPENDIX

Comparative specimens examined

See Bauer et al. (2006ab) for a list of *P. weberi* group, *P. otaviensis*, and *P. sansteynae* specimens examined, Bauer & Branch (1995) for a list of *P. punctatus* and *P. scherzi* examined, and Bauer et al. (2002) for a list of *P. angolensis*, *P. scutatus* and *P. parascutatus* examined. Only specimens not included in these publications are listed below. For localities without precise coordinates quarter degree square (QDS) references have been provided when possible. Each single degree square is subdivided into four quarter degrees, designated A–D (A=NW quadrant, B=NE quadrant, C=SW quadrant, D=SE quadrant). Each quarter degree is in turn divided into four similarly designated divisions, yielding a basic unit one sixteenth of a degree square, or one quarter of a degree on a side (e.g., 1915Ac represents the unit bounded by 19°15'S and 19°30'S and 15°00'S and 15°15E). All QDS references in this paper refer to degrees South and East.

P. angolensis: **Angola: Namibe Province:** San Nicolau (1412Ab): TM 25454–55, 25459, 25476, 25478–79; Saco de Giraul: TM 40328–30, TM 46558; Lucira (1312Dc): TM 41172, 24406, 24445, 24449; Lungo: TM 24406; **Benguela Province**: Hanha, 20 km N of Lobito (1213Ab); 24 km S Benguela: TM 39110–11; 30 km N of Dombe Grande: TM 41266.

P. bicolor: **Namibia: Erongo Region: Karibib District:** 47 mi E Hentiesbaai: CAS 126210; 20 km W Karibib: MCZ R163282–83; **Swakopmund District:** 29.0 km N of Swakopmund (22°25'38"S, 14°27'53"E): CAS 214576; 31.1 km N Swakopmund on Hentiesbaai Rd. (22°25'42"S, 14°27'43"E): MCZ R184218–20, 184225; Messum Crater (21°26'25.8"S, 14°13'12.9"E): CAS 214814; **Kunene Region: Khorixas District:** 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; Torra Bay Rd, 48 km W of Kamanjab, (19°39'14"S, 14°21'03"E): CAS 214661–63; Torra Bay Rd, 68 km W of Kamanjab, (19°43'00"S, 14°18'40"E): CAS 21468–89; Torra Bay 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; 25 km E of Grootberg Pass: CAS 206960; ~60 km W. Kamanjab on Torra Bay 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; **Opuwo District:** 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; **Outjo District:** 17 mi S of Outjo: CAS 85944; 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.

P. caraculicus: **Angola: Namibe Province:** 36 mi. northwest of Mocamedes [Namibe]: CAS 85959; **Namibia: Kunene Region: Opuwo District:** Okangwati-Epupa Rd, 43.4 km N of Okangwati: CAS 193799; 193804–05; 41.9 km N. of Okanguati on Epupa Falls Rd: CAS 206980; 32 km S Epupa Falls on Okangwati Rd. (17°14´09”S, 13°13´45”): MCZ R185767.

P. gaiasensis: **Namibia: Kunene Region: Khorixas District:** vic. Gai-as (20°47’18”S, 14°06’44”): CAS 214626–28; 22.4 km N Ugab River on road to Gai-as (20°46’59”S, 14°06’31”, 520 m a.s.l.): AMB 7568-69 (NMN), MCZ R184169-70, R184248; Gai-As (20°46’45”S, 14°04’30”E, 520 m): AMB 8484 (NMN), MCZ Z-37873 (NMN), MCZ R184181, R184192–93; Gai-As (20°46´46´´S,14°04´29´´E): MCZ R185967–75, 185979–80; “False Gai-As” (20°47’14.9”S, 14°06’44.6”E): MCZ Z-37853–54 (NMN), MCZ R184185, R184187; 7 km E Gai-as (20°47’S, 14°07’E): TM 68962–66; Messem Crater, 21 26.430 S, 14 13.215 E : CAS 214800; Messum Mts. (2114Ac): TM 56346; Farm Twyfelfontein: TM 42182; near Gai-as, ~20 mi N Brandberg: TM 32868–80 [paratypes].

P. oreophilus: **Angola: Namibe Province:** Caraculo (15°01’S, 12°40’E): TM 24519–25, 24452; 20 km W Virei: TM 41011–15; Tambor: TM 40532–34; 6 km S Rio Coroca towards Iona: TM 40575–76; Mutiambo River on road to Lucira: TM 41088; Furnas: TM 40561–62; Namibe 7 km from Iona towards Oncocau, Iona Reserve: TM 40762; Assuñcao: TM 40152; Saiona River, 25 km NW Cainde: TM 40976–77; **Benguela Province:** 35 km S Dombe Grande towards Lucira: TM 41246; **Namibia: Kunene Region: Opuwo District:** near Purros (18°46’S, 12°59E); TM 68465–67; Hoanib River (19°18’S, 13°15’E): TM 64185; Hoanib River, 44 km E Mudorib River (19°18’S, 13°15’E): TM 56889; Epupa Falls (16°59’S, 13°17’E): TM 38771–72, 71579; 6 km S Ohnborimbonga (1712Bb): TM 49084–85; Marienfluß, 40 mls S Kunene: TM 32532; near Otjinende, Kaokoveld (1712Db): TM 49219; Epupa (1613Cc): TM 47775; N Okangwati on Epupa Falls Rd. (17°17´24´´S, 13°09´31´´E): MCZ R185769; Paracamp, Sesfontein (19°07´52´´S, 13°35´17´´E): MCZ R-184945–47; Paracamp, Sesfontein (19°07´55”S, 13°35´20”E): MCZ R184290; ca 2 km N of Sesfontein, Para Camp (19°07’28”S, 13°35’29”E): CAS 214736, 214754; ca 4 km N of Sesfontein, Para Campsite (19°07’56”S, 13° 35’18”E): CAS 223919–22.

P. otaviensis: **Namibia: Oshikoto Region: Tsumeb District:** Farm Varianto (19°22´46”S, 17°44´27”E): MCZ R184867.

P. parascutatus: **Namibia: Kunene Region: Opuwo District:** Mudorib River, 12 km from Hoanib River (19°23’S, 13°17’E): TM 68488–92; Okamungodona, 15 km W Orawanji (18°49’S, 13°39’E): TM 71519–21; Otunungwa, Kaokoveld: TM 32401–03; Kharu-gaiseb River (19°45’S, 13°25’E): TM 68517–18; Bottom of Van Zyl’s Pass (1712Da): TM 71497; 37 km N Sesfontein towards Kaoko Otavi (1813Dc): TM 48876–77; Otjiu, Kaokoveld: TM 32358; 32858–59; 18 miles SW Orupembe: TM 31494; Otjinungwa, Kaokoveld: TM 32860; 4 km NW Etenga towards Omborombongo (1712Bd): TM 49060; Nangolo Flats (1712Ad): TM 24322; Otjiunongua (1712Ab): TM 32546; Sesfontein (19°07’S, 13°37’E): TM 79078; Ongongo/Kaoko: ZFMK 66434.

P. scutatus: Angola: Namibe Province: Iona, Iona Reserve: TM 40751; Espinheira, Iona Reserve: TM 40615–18; 6 km S Rio Coroca, Iona: TM 40577; Namibia: Erongo Region: Omaruru District: Ugab River Bridge near Brandberg W. Mine: TM 36463; Ugab River (20°58’S, 14°12’E): TM 49708; Tsisab Gorge, Brandberg (2114Ba): TM 79286; Brandberg: SMF 58564; Sraussenhöhle an der Jochmannswald, Brandberg: SMF 45658; Kunene Region: Khorixas District: Farm Palmwag (19°53’S, 13°53’E): TM 56865; Farm Paderborn (1914Dd): TM 17302; Kamanjab (1914Db): TM 17209, 17270, 36372; Damaraland (20°30’S, 13°49’E): TM 68754; Farm Huab (1914Db): TM 17338; Farm Palmfontein (part of Grootberg): TM 36465; Farm Blauwpoort (2014cb): TM 49419; Agab Spring (20°05’S, 13°50’E): TM 56936; Opuwo District: Epupa Falls (16°59’S, 13°17’E): TM 71352–53; Otjiu, Kaokoveld: TM 32539.

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