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A new species of the *Pachydactylus weberi* group (Reptilia: Squamata: Gekkonidae) from the Orange River, with comments on its natural history

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Abstract. A new species of *Pachydactylus* belonging to the *P. weberi* group is described from the lower Orange River of South Africa and Namibia. The species shares the typical scalation features of this group (exclusion of the rostral from the nostril and presence of tubercular scales on the thighs) with 15 other southern African species but differs from all of these in its lack of a pale collar or nape band, even in the juveniles. The new species occupies cracks and crevices in boulders and cave walls. It has been successfully bred in captivity and preliminary data on hatchling size and incubation time are provided.

Key words. Squamata, Gekkonidae, *Pachydactylus*, new species, South Africa, Namibia, natural history, reproduction.

Introduction

The genus Pachydactylus and its close relatives Chondrodactylus, Colopus and Elasmodactylus account for the majority of gekkonid lizards in southern Africa, particularly in xeric areas of Namibia and the Northern Cape Province of South Africa. At present these genera together constitute a monophyletic group of at least 54 named species (BAUER & LAMB 2005, BAUER et al. in press). Within this lineage the most speciose subclade is the Pachydactylus serval/weberi group, with 19 recognized species (BAUER et al. in press). It achieves its greatest species richness from the Orange River to south central Namibia. This group had long proved difficult to deal with taxonomically (HEWITT 1935, FITZSIMONS 1943, LOVERIDGE 1947, McLachlan & Spence 1966), partly because of poor sampling, but also because of the great degree of morphological conservatism within the group as a whole. BAUER et al. (in press) revised this clade, resurrecting numerous forms from synonymy and describing eight new species, most of them allied more closely to P. weberi than to P. serval, and sharing with the former species the exclusion

of the rostral from the nostril and the presence of tubercular scales on the thighs. Four of the new species have distributions that are restricted to areas close to the Orange River. Two of these species are chiefly distributed along the lower Orange and the Fish River, in the Richtersveld and neighboring Namibia. The other two are less closely associated with the riverine corridor and are distributed north and south of the river, respectively. In addition to these species, BAUER et al. (in press) signaled the existence of two other, undescribed members of the P. weberi group. One of these, referred to as Pachydactylus sp. 1 by these authors, was known from a single locality on the lower Orange and from the area around Augrabies National Park, where its presence was first noted by VAN DER WALT (2000), who noted it as "Weber's Gecko" in a checklist to the reptiles of Augrabies. This is the easternmost locality for any member of the P. weberi group. Based on a cytochrome b mitochondrial gene tree, this new species was found to be genetically highly distinct from all other species sampled (BAUER et al. in press), but closest to P. robertsi, a poorly known species from the Karasberg in southeastern Namibia (BAUER et al. 2002). Here we

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present a formal description of this species and also provide information about its habitat and its reproduction in captivity.

Material and methods

Temperature and relative humidity were measured in the field using a thermohygrometer with sensor. Location was determined using a Meridian XL GPS (Magellan Systems Corporation).

Museum symbolic codes follow LEVITON et al. (1985), except for the National Museum of Namibia, Windhoek (formerly State Museum, Windhoek), for which we use the collection code employed by that institution (NMNW) in preference to SMW. Specimens were examined from the collections of the National Museum of Namibia (SMW), Flagship Institution of the North, Transvaal Museum (TM), University of Stellenbosch (USEC/H), and Zoologisches Forschungsmuseum Alexander Koenig (ZFMK). Comparisons were made with all other members of the Pachydactylus serval/weberi clade (see BAUER et al. in press for a list of specimens examined).

The following measurements were taken with Brown and Sharpe Digit-cal Plus digital calipers (to the nearest 0.1 mm): snout-vent length (SVL; from tip of snout to vent), trunk length (TrunkL; distance from axilla to groin measured from posterior edge of forelimb insertion to anterior edge of hindlimb insertion), head length (HeadL; distance between retroarticular process of jaw and snouttip), head width (HeadW; maximum width of head), head height (HeadH; maximum height of head, from occiput to underside of jaws), snout to eye distance (SnEye; distance between anteriormost point of eye and tip of snout), nares to eye distance (NarEye; distance between anteriormost point of eye and nostril), orbital diameter (OrbD; greatest diameter of orbit), eye to ear distance (Eye-Ear; distance from anterior edge of ear opening to posterior corner of eye), ear length (EarL; longest dimension of ear), interorbital distance (Interorb; shortest distance between left and right supraciliary scale rows), 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), and tail width (TailW; measured at widest point of tail). Unless otherwise stated, counts and measurements were made on right side of specimens.

A life color description was based on seven specimens (four adult males, two adult females, and one subadult male) using an RAL color register (German color norm, color register 840-HR and 841-GL).

Scale counts and external observations of morphology were made using a Nikon SMZ-1000 dissecting microscope. Preserved specimen photographs were taken with a Nikon CoolPix 990 digital camera. Radiographic observations were made using a Faxitron closed cabinet x-ray system.

Results

Pachydactylus atorquatus sp. n.

Holotype: TM 84939, adult male (Fig. 1); South Africa, Northern Cape Province, Augrabies National Park, Dassie Trail, in a sheltered depression on the plateau (28°35'15.6" S, 20°20'03.0" E, 619 m elevation); don. W.D. HAACKE, January 2004.

Paratypes: ZFMK 83354, adult female; same data as holotype. TM 85286, gravid



Fig. 1. Holotype of *Pachydactylus atorquatus* sp. n. (TM 84939) from Augrabies National Park, Northern Cape Province, South Africa. Scale bar = 20 mm. Photo by A.M. BAUER.



Fig. 2. Living adult male *Pachydactylus atorquatus* sp. n. with regenerated tail showing the more-or-less uniform dorsal coloration, lack of dorsal banding, and prominent tubercles. Photo by M. BARTS.



Fig. 3. Living adult male *Pachydactylus atorquatus* sp. n. Note the white stripe on snout and the continuation of pale tubercles along the length of the tail. Photo by M. BARTS.

female; South Africa, Northern Cape Province, Kenhardt District, Farm Zeekoe Steek, near Seekoeisteek River Camp, 0.7 km south of Orange River (28°29'17"S, 20°07'34"E); coll. M. BARTS, 22 October 2004. NMNW R 10494, adult male; Namibia, Karas Region, Karasburg District, Haib Mine at 28°41'49"S, 17°53'26"E); coll. M. GRIFFIN, 9 April 1997. Diagnosis: A large species, to 54.2 mm SVL (TM 84939), of the *Pachydactylus weberi* group. It may be distinguished from all other members of the *P. weberi* group by the combination of the following characters: nasal region moderately inflated (strongly so in *P. werneri*); rostral, but not first supralabial narrowly excluded from nostril (both excluded in *P. kobosensis*); dorsal scalation heteroge-

neous, with large, rounded to slightly oval, strongly keeled, juxtaposed tubercles arranged in 14 regular rows (partly imbricating in *P. robertsi*; tubercles in 20 or more rows in both P. robertsi and a new species from the Windhoek area); five undivided lamellae beneath digit IV of pes (typically six in P. acuminatus, P. kobosensis, P. tsodiloensis, and a new species from the Karasburg District of Namibia); tail to at least 114 % of SVL, annulate, bearing whorls of slightly 4-6 enlarged, strongly keeled tubercles, each separated from others in same row by a single lanceolate scale (caudal tubercles abutting in P. fasciatus); adult dorsal pattern gray-brown (dark, purplish-red in life) with no transverse body or nape bands (nape band only present in P. robertsi and a new species from the Windhoek area; nape and body bands present in all other members of the *P. weberi* group). Tips of tubercles on body and tail yellowish to bright white (Figs. 2-5). A broad off-white stripe from nostril to orbit, bounded below by a dark stripe passing through loreal region and continuing behind the orbit to the level of the occiput; a bright white stripe beneath orbit. Juvenile pattern (Figs. 4-5) similar to adult (with transverse body and/or nape bands in all other species).

Description of holotype: Adult male. Snoutvent length (SVL) 54.2 mm. Body weakly depressed, moderately long (TrunkL/SVL ratio 0.43). Head relatively short (HeadL/ SVL ratio 0.28), wide (HeadW/HeadL ratio 0.69), somewhat depressed (HeadH/HeadL ratio 0.41), clearly distinct from the neck. Lores and interorbital region weakly inflated. Snout long (Sn-Eye/HeadL ratio 0.39), longer than eye diameter (OrbD/Sn-Eye ratio 0.68); scales on snout and canthus enlarged relative to granular scales on crown, smooth, flattened to slightly domed; scales of interorbital and parietal regions strongly heterogeneous, with tiny granules interspersed with larger, domed to weakly conical, rounded to slightly oblong tubercles, each 30-100 % size of enlarged snout scales. Enlarged conical tubercles regularly scattered across parietal and temporal regions, less prominent on occiput. Eye moderate (OrbD/HeadL ratio 0.26); orbits without extra-brillar fringes; approximately 7 supraciliary scales at posterodorsal corner of orbit bearing very small spines; pupil vertical, with crenellated margins. Ear opening oval, large (EarL/HeadL ratio 0.11); eye to ear distance greater than diameter of eves (EveEar/OrbD ratio 1.15). Rostral approximately 40% as deep (0.8 mm) as wide (2.0), no rostral groove, contacted by two enlarged supranasals and first supralabials; nostrils oval, oriented dorsolaterally, each surrounded by two large postnasals, supranasal, and first supralabial; supranasals in contact anteriorly, separated by a single granule posteriorly; dorsal postnasals larger than ventral postnasals; nostril rims weakly inflated; one rows of scales separate orbit from supralabials; mental with nearly parallel sides, approximately 2.6 times deeper (2.3 mm) than wide (0.9 mm); no enlarged postmentals or chin shields. Enlarged supralabials to angle of jaws 11/11 (8/8 to midorbit); infralabials 8/9; interorbital scale rows at midpoint of orbit 22 (12 across narrowest point of frontal bone).

Dorsal tubercles large (8-10 times size of adjacent scales), largest on midflanks and smallest along dorsal midline and across shoulders, rounded to slightly oblong, with a pronounced median keel - higher and broader posteriorly, forming 14 regular longitudinal rows on trunk, grading into conical granular scales on lower flanks; each tubercle surrounded by a rosette of small, irregular, conical scales of variable size; ventral scales flattened, oval, subimbricate to imbricate, becoming somewhat larger posteriorly, largest on posterior abdomen and in precloacal region, approximately 33 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 sixth to one fourth size of ventral scales, increasing in size behind the angle of jaws. No preanal or femoral pores. Scales on palm, sole, and ventral surface of forelimb smooth,

	TM 84939	TM 85286	ZFMK 83354	NMNW R10494
	holotype	paratype	paratype	paratype
Sex	male	female	female	male
SVL	54.2	48.9	51.6	45.4
ForeaL	7.3	8.2	7.9	7.2
CrusL	9.3	8.3	9.5	7.9
TailL	35.1	55.6	16.0	43.2
(regen.)	31.4	38.8	broken	27.7
TailW	3.1	3.3	3.1	4.0
TrunkL	23.1	23.3	22.9	19.6
HeadL	15.3	14.6	15.5	13.5
HeadW	10.6	10.5	9.5	8.7
HeadH	6.3	6.0	5.5	5.3
OrbD	4.0	3.8	3.8	3.9
EyeEar	4.6	4.0	3.9	3.5
SnEye	5.9	5.9	5.7	5.0
NarEye	4.1	4.2	4.2	3.5
Interorb	4.4	3.9	4.0	4.1
EarL	1.8	1.1	1.2	1.1
Internar	1.7	1.3	1.2	1.0

A new species of the Pachydactylus weberi group

Tab. 1. Mensural data for the adult types of *Pachydactylus atorquatus*, sp. n. Abbreviations as in Materials and Methods. All measurements in mm.

flattened to granular; scales on ventral aspect of thighs enlarged, continuous with enlarged scales of precloacal region; scales on dorsal aspect of forelimb slightly domed to weakly conical, heterogeneous, subimbricate; scales on dorsum of thigh enlarged, conical, those on crus greatly enlarged.

Forelimbs short, stout (ForeaL/SVL ratio 0.13); hindlimbs short (CrusL/SVL ratio 0.17); digits relatively long, claws not visible; subdigital scansors, except for distalmost, entire, present only on distal portion of toes, approximately 1.5-2.0 times wider than more basal (non-scansorial) subdigital scales; interdigital webbing absent. Relative length of digits (manus): III>IV>V~II>I; (pes): IV>III~V>II>I. Subdigital scansors (excluding 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.

Regenerated tail sub-cylindrical, shorter than snout-vent length (TailL/SVL ratio 0.65); tail base with enlarged tubercles like those of body dorsum; regenerated portion with small, irregular, imbricating, smooth scales, much smaller on dorsum than on ventrum; some scales along ventral midline larger than adjacent scales; 2 small, smooth, dorsally-projecting postcloacal spurs on each side of hemipeneal bulge, anterior only slightly larger than posterior.

Coloration (in preservative): Dorsum a grayish brown, paler near limb insertions. Tubercles with tips or most of keel whit-



Fig. 4. Living juvenile *Pachydactylus atorquatus* sp. n. illustrating the sharp contrast between dorsal background coloration and the yellow and white tubercles and the lack of a nape band. Photo by M. BARTS.



Fig. 5. Head and forebody of living juvenile *Pachydactylus atorquatus* sp. n. Note the color pattern of the labial scales, iris, and ciliary scales. Photo by M. BARTS.

ish, most pronounced on lateral surfaces. Dorsum of head with intergranular spaces whitish. A broad white stripe between nostril and anterodorsal corner of orbit. Darker brown between white stripe and dorsal border of supralabials, on temporal region, and in circumauricular region, fading on nape. Infralabials and posterior supralabials cream colored with scattered brown pigment. Venter buff with scattered brown pigment around margins of flanks, throat, chin and limbs; palms, soles and digits mid-brown, midventral region of chest and anterior abdomen pearly white; tail venter dusky.

Coloration (in life). The background coloration of the head, body and limbs is purple-

red (RAL 3004). A white (RAL 9016) stripe approximately three scale rows in width extends between the nostrils and the anterior margin of the eyes. A white (RAL 9016) stripe extends from the fourth supralabial, beneath the eye, to the posterior border of the ear. The loreal area between these two white stripes is reddish-black (RAL 3009) and a thick stripe of this color continues behind the orbit to the end of the lateral surface of the head. The supraoculars are darker than the dorsum of the head and may be characterized as brilliant blue (RAL 5007). The ciliary scales are zinc yellow (RAL 1018) dorsally and white (RAL 9016) around the remainder of the eye. The iris is violet blue (RAL 5000) and the pupil is old rose (RAL 3014). The tubercular scales of the dorsum and flanks are golden yellow (RAL 1004) and in the outermost rows the tips of the tubercles are a distinctly lighter pale gray (RAL 7035). On the dorsal surfaces of the forelimbs the tubercular scales are also golden yellow, whereas on the dorsal surfaces of the hindlimbs only the tips of the tubercles are this color. The tubercles of the tail are signal white (RAL 9003). The ventral and subcaudal scales are cream white (RAL 9001) and the areas between the scales are white (RAL 9016). The subdigital lamellae are signal white (RAL 9003). Juveniles have essentially the same coloration as the adults, although the background coloration is somewhat lighter and the markings on the head are more distinct. A subadult male has a light blue (RAL 2012) sheen visible caudally on the otherwise homogeneous typical coloration. Coloration varies with time of day in Pachydactylus atorquatus, with animals having a darker coloration by night.

Variation: Variation in mensural characters of the holotype and adult paratypes are presented in Table 1. Paratypes similar to holotype except as noted. Female paratype TM 85286 is in poor condition, having died some time before being fixed and female paratype ZFMK 83354 is extremely soft and poorly fixed. Tubercles relatively prominent on occiput in TM 85286. Supralabial scales and



Fig. 6. Large boulder faces at Augrabies National Park. The crevices in such boulders are used as retreat sites by *Pachydactylus atorquatus* sp. nov. Photo by M. BARTS.



Fig. 7. Small cave at Augrabies National Park used by *Pachydactylus atorquatus* sp. n. Photo by M. BARTS.

infralabial scales 14/13, 12/11, 11/10 and 10/10, 10/10 and 8/8 in TM 85286, ZFMK 83354 and NMNW R10494, respectively.

Scansors of pes in NMNW R10494 4-4-5-5-5. Original portion of tail in paratypes consisting of segments each five dorsal scale rows long, encircled by enlarged, keeled tubercles with blunt, slightly flared, raised knobs posteriorly; six such tubercles in transverse series basally, decreasing to four at about one third of tail length; tubercles within a tansverse row typically separated by a single, narrow, lanceolate scale. Subcaudal scales rectangular (TM 85286) to cycloid (NMNW R10494), imbricating, largest in ventral midline. Tubercle tips on body dorsum bright white in NMNW R10494 and especially TM 85286, which also has bright white tips on conical flank scales and on the occipital and temporal tubercles.

Etymology: The specific epithet is Latin for "without a collar or necklace" and refers to the fact that the new species is the only member of the *Pachydactylus weberi* group that never possesses a pale nape band or collar. Although absent or faded in the adults of some other members of the group, a collar is present in hatchlings and juveniles of all other species in the group.

Distribution: This species appears to be limited to areas immediately adjacent to the Orange River in South Africa and Namibia. The holotype and two paratype specimens are all from the vicinity of Augrabies Falls, while the third paratype is from Haib Mine, approximately 250 airline km downriver.

Natural history: The habitat of *P. atorquatus* is in rocky terrain along the Orange River. At Augrabies National Park several specimens were observed in a 3 m deep, sheltered depression in the surface of a plateau (approx. 30×15 m surface area) about 15 m above the bank of the river. The species inhabits boulder crevices (Fig. 6) and cracks and crevices in cave walls (Fig. 7). One female and a subadult male were located in a cave measuring 680 cm wide by 520 cm deep. The height at the entrance was 82 cm, decreasing

by more than 40 % at the back. This cave was also occupied by rock hyrax (*Procavia capensis*) and in a smaller, neighboring cave the exuviae of a *Naja* sp. was found. In the latter cave, temperature and humidity measurements were made on 10h10 on a cloudy day (21 October 2004) one meter in front of the cave, at the cave entrance and 350 cm into the cave, yielding 28.8 °C with 30 % relative humidity (RH), 26.6 °C with 35 % RH, and 23.8 °C with 40 % RH, respectively.

A gravid female (paratype TM 85286) and a subadult male were found on a rocky slope of heavily eroded stone, approximately 15 m high, separated from the Orange River by a vineyard. The upper third of the slope was characterized by bare, smooth boulders. From the boulders to the foot of the slope, where the geckos were found active at night, the site was covered with small pieces of broken stone and remnants of larger pieces of boulders that had fallen from above.

The Haib Mine site is in a rocky area about 7 km north of the Orange River. The new species is sympatric with another new species of the *P. weberi* group at Haib Mine (BAUER et al. in press), but it is the only member of the group at Augrabies. It co-occurs with *P. montanus* and with *Chondrodactylus turneri laevigatus* (formerly *Pachydactylus*, see BAUER & LAMB 2005) in both areas and with *P. purcelli* and *P. haackei* (BARTS et al. 2005) at Augrabies.

Captive reproduction: On 3 May 2005 a clutch of fertilized eggs measuring 11.9×7.9 and 11.8×8.1 mm were laid. The young hatched on 1 July 2005, after 59 days. The SVL of the first hatchling was 21.2 mm and the TailL was 22.7 mm. The second hatchling had a size of 21.9 mm SVL + 22.6 mm TailL. A second clutch from another pair was laid on 31 July 2005, measuring 10.9×7.8 and 10.8×8.0 mm. The young from this clutch hatched on 4 and 5 August 2005, after 65 and 66 days and measured 21.9 mm SVL + 22.5 mm TailL and 21.1 mm SVL + 22.5 mm TailL, respectively.

Discussion

BAUER et al. (in press), using sequence data from the mitochondrial cytochrome b gene, demonstrated that P. atorquatus (as Pachydactylus sp. 1 or P. "Augrabies") is the sister species to P. robertsi among the species for which they had data. The new species shares with this form particularly large dorsal tubercles, but it is also strikingly similar in body form (although not color pattern) to the new species with which it is sympatric at Haib Mine, a species for which BAUER et al. (in press) lacked molecular data. These species, together with 13 others, constitute the Pachydactylus weberi group. Although many members of this group are allopatric with respect to each other (e. g., P. tsodiloensis, P. waterbergensis), the lower Orange River Valley region supports several sympatric species.

LAWRENCE (1929) first regarded southeastern Namibia, including the Karas Mountains and the area adjacent to the Orange River, as an area of reptile endemism, but knowledge of the herpetofauna of this region has progressed little since then. More recently, BAUER and BRANCH (2001 [2003]) and SCOTT et al. (2003) have emphasized the high level of lizard endemism in the Richtersveld, including the Orange River downstream from Vioolsdrif. BAUER (1999 [2000]) specifically suggested a role for the Orange River in the history of the Pachydactylus serval and weberi groups. The changing course of the Orange drainage since the Cretaceous (GOUDIE 2005) has provided ample opportunity both for speciation through local isolation and habitat fragmentation and for range expansion along the riverine corridor. However, until phylogenies for other groups of organisms with comparable distribution patterns are available for interpretation using analytical biogeographic methods, specific scenarios accounting for the spatial history of P. atorquatus and its relatives will remain speculative at best.

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