A Revision of *Pachydactylus scutatus* (Reptilia: Squamata: Gekkonidae) with the Description of a New Species from Northern Namibia

by

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A review of taxa previously synonymized with *Pachydactylus scutatus* (Gekkonidae) reveals that both *P. angolensis* and *P. robertsi* should be regarded as specifically distinct. Although the former species appears to be closely related to *P. scutatus*, the latter is probably more closely allied to the *P. weberi* complex. A new member of the *P. scutatus* group is described from the Kaokoveld of northern Namibia. Both diagnostic morphological features and DNA sequence divergence observed for the cytochrome *b* gene support the distinctiveness of the new taxon.

The genus *Pachydactylus* is the most speciose group of geckos in southern Africa. At least 34 species are currently recognized (Kluge 2001), 20 of which occur in Namibia (Branch 1998; Griffin 2000). Although the genus is well represented throughout Namibia, the country's rocky, arid northwest is especially species rich (Bauer et al. 1993; Griffin 2000). The last complete revisions of *Pachydactylus* (FitzSimons 1943; Loveridge 1947) were conducted before many taxa from this region were first collected. Increased field work in northwestern Namibia from the 1960s onwards resulted in the discovery of species previously known only from Angola (e.g., *Pachydactylus caraculicus*; Haacke 1970) and in the description of several new taxa including *Pachydactylus oreophilus* (McLachlan and Spence 1967), *P. gaiasensis*, and *P. sansteyni* (Steyn and Mitchell 1967). Subsequent revisions and systematic analyses of subgroups of *Pachydactylus* (e.g., McLachlan and Spence 1966; Broadley 1977; Bauer and Branch 1995; Branch et al. 1996; Lamb and Bauer 2000, in press) have not addressed the phylogeny or taxonomy of the northern Namibian species.

One of the most distinctive geckos of northern Namibia, *Pachydactylus scutatus*, was described from Kowaris [= Kowares] near Etosha by Hewitt (1927), who considered it closely related to *P. montanus* (a synonym of *P. serval*). FitzSimons (1938) reported additional specimens from Kamanjab, Paderborn, and Huab, all to the south of the type locality. In the same paper, FitzSimons also described *Pachydactylus robertsi* from a unique holotype from Farm Kraikluft in the Great Karas Mountains. FitzSimons noted that *P. robertsi* superficially resembled *P. scutatus*, but could be distinguished by nostril position, dorsal and caudal scalation, and head color.

Subsequently, Loveridge (1944) described *P. scutatus angolensis* from Hanha and Lobito Bay in Benguella Province, Angola. He also re-evaluated the status of *P. robertsi*, reducing it to a subspecies

of *P. scutatus*, even though he had never examined specimens of either *P. scutatus* or *P. robertsi*. He regarded all three forms as "a further development of the scaly-backed *P. p. punctatus*" and based his subspecific asignments on the continuity of variation in dorsal keeling among them. Although Loveridge's taxonomy has received broad support (e.g., Loveridge 1947; Mertens 1955; Wermuth 1965; Kluge 1993, 2001; Rösler 2000), some recent herpetological works dealing with Namibian *Pachydactylus* (e.g., Branch 1998; Bauer 1999[2000]) have not recognized subspecies within *P. scutatus*.

Mertens (1955), Van den Elzen (1983), and Bauer and colleagues (1993) reported numerous additional localities for *Pachydactylus scutatus*, but *P. robertsi* remains known only from the unique holotype, and only four additional specimens of *P. s. angolensis*, all from near Namibe, Angola [Quarter Degree Square (QDS) 1512Aa: 15° latitude, 12° longitude, upper case letters identify quadrants, lower case letters quadrants within quadrant], have been reported in the literature (Laurent 1964). Laurent (1964) provided some scale counts for these specimens but, unfortunately, none that are informative within the *P. scutatus* group. These specimens, catalogued in the Dundo collection in Angola, are not currently accessible, and ongoing civil strife in Angola precludes the collection of fresh material. Due in part to the paucity of material, a critical evaluation of the affinities and validity of the non-nominate members of the *P. scutatus* group has yet to be undertaken. Indeed, the only published statement concerning phylogenetic relationships within this group is that of FitzSimons (1959), who believed that *Pachydactylus caraculicus* was perhaps both geographically and phylogenetically intermediate between *P. s. angolensis* and *P. s. scutatus*. This interpretation was challenged by Laurent (1964), who noted that *P. s. angolensis* occurs in sympatry with *P. caraculicus* in southern Angola and, therefore, must be specifically distinct.

As part of a major revision of *Pachydactylus* and related geckos, we re-examined the types of *P. robertsi* and *P. s. angolensis* in light of current knowledge of the distribution and morphological variation of *P. s. scutatus*. We also collected additional specimens of of the *P. scutatus* group from the Kaokoveld and adjacent parts of the Kunene Region of Northern Namibia for DNA sequence analysis to determine if morphological variation within the group is reflected by genetic divergence. We here present a revision of the *P. scutatus* group, which entails the revalidation of *P. robertsi* and *P. angolensis* as full species, as well as the description of a new taxon from extreme northwestern Namibia.

MATERIAL AND METHODS

The following measurements were taken with Brown and Sharpe Digit-cal Plus digital calipers (to the nearest 0.01 mm): snout-vent length (SVL; from tip of snout to vent), tibia length (TBL; from base of heel to knee); tail length (TL; from vent to tip of unregenerated tail), tail width (TW; measured at base of tail); head length (HL; distance between posterior edge of last supralabial and snout-tip), head width (HW; measured at angle of jaws), head depth (HD; maximum height of head, from occiput to throat), ear length (EL; longest dimension of ear); forearm length (FA; from base of palm to elbow); eye diameter (ED; greatest diameter of orbit), eye to nostril distance (E-N; distance between anteriormost point of eye and nostril), eye to snout distance (E-S; distance between anteriormost point of eye and tip of snout), eye to ear distance (E-E; distance from anterior edge of ear opening to posterior corner of eye), and interorbital distance (IO; shortest distance between medial rims of left and right orbits).

Scale counts and external observations of morphology were made using a Nikon SMZ-10 dissecting microscope. Radiographic observations were made using a Faxitron closed cabinet X-ray system. Comparisons were made with museum material, as well as original published descriptions and descriptions provided in broader faunal and taxonomic treatments. Standard codes for museum collections follow Leviton et al. (1985).

DNA sequence analysis was also conducted to determine whether morphological features distinguishing the new form from *P. scutatus* and other congeners were complemented by substantive genetic divergence. Tissue samples from nine specimens (six members of the *P. scutatus* group and three representing two other congeners) were processed at field collection sites and preserved in a saturated salt-DMSO buffer (Amos and Hoelzel 1991). Genomic DNA was extracted from liver using the Qiagen QIAamp DNA Mini kit. Portions of the mitochondrial cytochrome *b* (cyt *b*) gene were used to assess sequence variation among specimens. The primers L14724 and H15149 (Meyer et al. 1990) were used to amplify a 400 bp segment of the cyt *b* gene; 50 µl reactions were amplified for 32 cycles at 92°C for 45 sec, 55°C for 35 sec, and 72°C for 1 min. Amplification products were purified over Centri-sep columns and served as templates in cycle-sequencing reactions employing dye-labeled terminators (PRISM kit, Applied Biosystems, Inc.). PRISM reaction products were analyzed on an Applied Biosystems 373A automated DNA sequencer. Forward and reverse sequences were generated for each sample and their complementarity confirmed using the Sequence Navigator software (Applied Biosystems, Inc.). Sequences were aligned using the CLUSTAL X program, applying default settings (Thompson et al. 1997). Pairwise sequence divergence estimates were derived using the Hasegawa-Kishino-Yano model (HKY85; Hasegawa et al. 1985), which assumes different evolutionary rates for transitions and transversions and unequal base frequencies.

SYSTEMATICS

Examination of the types of *P. robertsi* and *P. scutatus angolensis* in light of current understanding of the geographic range and morphological variation of typical *P. scutatus* suggests that both taxa should be considered specifically distinct. FitzSimons (1938) and subsequent workers recognized the affinity of *P. robertsi* to *P. scutatus* on the basis of enlarged dorsal scales and a distinct, white nuchal collar.

The unique type of *P. robertsi* (Fig. 1) possesses moderately well-developed keels on enlarged, weakly imbricate dorsal scales. Although the dorsal scales superficially resemble those of *P. scutatus*, most other characteristics indicate an affinity with the *Pachydactylus weberi* complex (including *P. weberi sensu stricto* and several taxa currently accorded subspecific status or regarded as synonyms of *P. weberi*). In particular, the exclusion of the rostral, but not the first supralabial, from the nostril typifies *P. weberi*, and the degree of dorsal scale keeling falls within the range of Namibian specimens of this species. In addition to scalation, similarities in the nuchal collar of *P. robertsi* have been considered evidence for its affinities with *P. scutatus*. However, adults of many members of the *P. weberi* group commonly retain elements of the juvenile pattern, which most frequently consists of three bands: one on the neck, one near mid-body and one in the sacral region. In *P. robertsi* and certain *P.* cf. *weberi*, especially those from central Namibia (e.g., Windhoek: TM 32834, 328383; Klein Windhoek: TM 28781; Horebis Nord, Karibib District: TM 33650), only the anterior band is retained. The white collar in *P. scutatus* is usually one scale width thick (Fig. 5), whereas in *P. robertsi* it spans 2–3 scales and is situated somewhat more posteriorly on the neck (Fig. 1).

The assignment of *P. robertsi* to the *P. weberi* complex also makes sense geographically. At the time of the description of *P. robertsi*, *P. scutatus* was known from only four localities. Based on modern collections, the range of *P. scutatus* is strictly limited to the region from the Brandberg to the north and west, more than 700 km from the *P. robertsi* type locality. *Pachydactylus robertsi* is quite distinctive from typical *P. weberi* from Little Namaqualand, but its relationships within the broader context of the *P. weberi* complex as a whole remain unresolved. At present we regard *P. robertsi* as a distinctive species allied to *P. weberi* and tentatively restricted to the Great Karas Mountains. This taxon will be considered in more detail in a revision of the *P. weberi* complex (Bauer et al., in prep.).

Pachydactylus s. angolensis (Fig. 2) is clearly more similar to *P. s. scutatus* than is *P. robertsi*. Loveridge (1944, 1947) noted the exclusion of both the first supralabial and rostral scales from the

nostril in this form. This condition, the chief di-
agnostic feature employed in the taxon descrip-
tion, presumably also characterizes the four
additional specimens reported on by Laurent
(1964), who noted nothing to the contrary.
Loveridge's types were collected at Hanha
(probably Hanha do Norte in quarter degree
square 1213Bc another locality, Hanha do
Cubal, 1314Aa is also in the same province) and
Lobito Bay (1213Bc), both in Benguela Prov-
ince. Laurent's (1964) material was from the
"environs de Moçâmedes" (now Namibe,
Namibe Province), approximately 335 km south
of the type locality. The rostral/supralabial scale
condition has not been recorded in any of the
typical *P. scutatus* examined by us or reported in
the literature. As this character appears to be
constant, we regard it as diagnostic evidence for
the recognition of *P. angolensis* as distinct from
P. scutatus. These taxa also differ in color pat-
tern and dorsal and caudal scalation (outlined in
the morphological comparisons section of the
Discussion below).

The occurrence of *P. angolensis* in coastal
and near coastal localities also suggests ecologi-
cal differences from *P. scutatus*. Laurent's
(1964) specimens were collected from crevices
in friable rock along the roadside from Sá de

FIGURE 1. Holotype of *Pachydactylus robertsi* (TM 17854).
Note the position and width of the nuchal collar. Scale
bar = 10 mm.

Bandeira to Namibe and under rocks on the littoral plateau of "das Conchas" beach, whereas typical *P.
scutatus* are usually associated with rock flakes on exfoliating boulders (FitzSimons 1938; Bauer et al.
1993). On the basis of its distinctive scalation, coloration, and ecology, we regard *Pachydactylus
angolensis* as a valid species, probably closely allied to *P. scutatus*. At present all known specimens
are from lowland, near coastal localities in Namibe and Benguela provinces, southwestern Angola.
The southernmost locality, Namibe (1512Aa), is approximately 250–280 km northwest of the north-
ernmost localities of *P. scutatus* (Otjivize, 1713Cb and Epupa, 1613Cd), but the intervening area has
been poorly collected and the true extent of the distribution of *P. angolensis* remains uncertain.

Even upon the removal of *P. robertsi* and *P. angolensis* from synonymy with *P. scutatus*, signifi-
cant morphological variation among populations of *P. scutatus* remains. Specimens we collected near
Sesfontein, as well as museum material from Kaoko Otavi and Orupembe, are especially distinctive.
Based upon detailed comparisons with *P. scutatus* and *P. angolensis*, we here recognize and describe
a third member of the *P. scutatus* group.

REPTILIA: SQUAMATA: GEKKONIDAE

***Pachydactylus parascutatus* sp. nov.**
Fig. 3, Pl. 1

HOLOTYPE. — National Museum of Namibia (SMW) R 9454 (previously California Academy
of Sciences [CAS] 214755; Field Number AMB 6518) (adult female), from the vicinity of Para Camp,
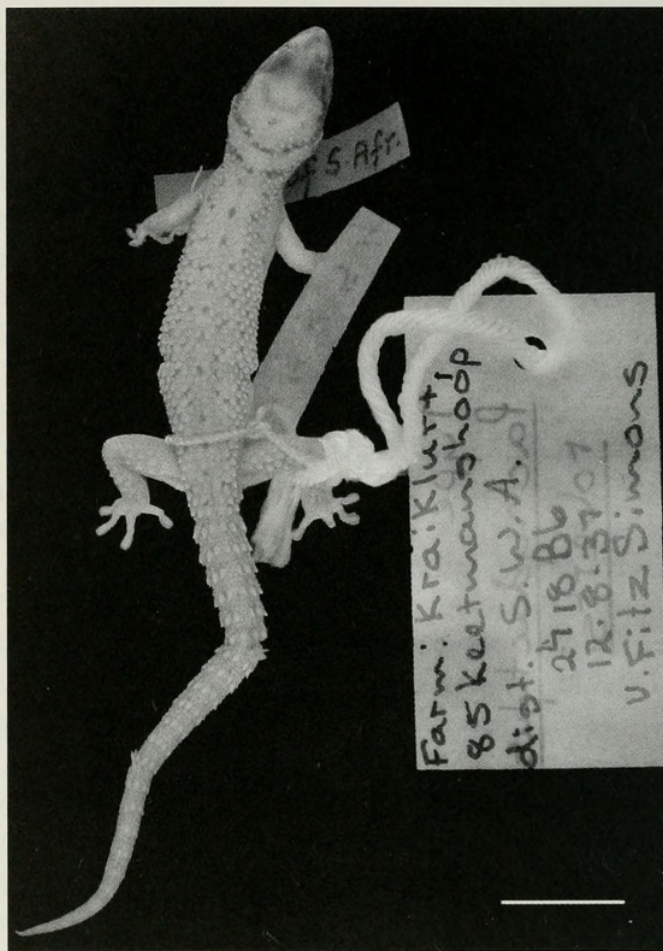
2 km north of Sesfontein, Opuwo District, Kunene Region, Namibia (19°07'28"S, 13°35'29"E), collected by R. D. Babb, A. M. Bauer, T. Lamb, W. R. Branch, P. Moler, V. Schneider, S. Lochetto, and A. Meeker, 3 June 2000.

PARATYPES. — CAS 214735 (Field number AMB 6498; adult male), same locality and collectors as holotype, collected 2 June 2000; CAS 214750 (Field number AMB 6512; adult female), Purros Rd., ca. 8 km west of Sesfontein, Opuwo District, Kunene Region, Namibia (19°10'05"S, 13°34'03"E), collected by R. D. Babb, A. M. Bauer, T. Lamb, W. R. Branch, P. Moler, V. Schneider, S. Lochetto, and A. Meeker, 3 June 2000; SMW R 182 (adult male), Kaoko Otavi, Opuwo District, Kunene Region, Namibia, collected by W. Steyn, 8 October 1965; SMW R 184 (adult female), 20 km west of Orupembe, Opuwo District, Kunene Region, Namibia, collected by W. Steyn, 6 October 1965.

ADDITIONAL MATERIAL EXAMINED. — CAS 214749 (Field number AMB 6511; juvenile), 27 km, Purros Rd., ca. 27 km W of Sesfontein, Opuwo

FIGURE 2. Holotype of *Pachydactylus angolensis* (AMNH R 47874). Scale bar = 10 mm.

District (19°03'16"S, 13°30'08"E), collected by R. D. Babb, A. M. Bauer, T. Lamb, W. R. Branch, P. Moler, V. Schneider, S. Lochetto, and A. Meeker, 3 June 2000.

ETYMOLOGY. — The specific epithet reflects the similarity of the new species to *P. scutatus* and also commemorates the type locality near "Para Camp," a rustic camp site operated by villagers near the town of Sesfontein.

DIAGNOSIS. — Snout-vent length to 38.40 mm (largest female paratype); body sub-cylindrical, not depressed; most dorsal scales large, rounded, strongly keeled, juxtaposed or weakly imbricate, in approximately 14 rows; ventral scales subimbricate, scales on dorsum of forelimb and granules between larger dorsal scales unkeeled; nostril surrounded by two postnasals, supranasal, rostral and first supralabial; enlarged scansorial lamellae under digit IV of pes 4–5; adult dorsal pattern with numerous dark brown markings, without distinct white nuchal collar; original tail more-or-less banded; venter buff with light brown speckling.

DESCRIPTION (based on holotype). — Adult female (Fig. 3, Pl. 1). Snout-vent length 35.25 mm. Body sub-cylindrical, not markedly depressed, elongate (A-G/SVL ratio 0.44). Head elongate, large (HL/SVL ratio 0.29), moderately wide (HW/SVL ratio 0.19), somewhat depressed (HD/HL ratio 0.36), distinct from neck. Lores and interorbital region inflated. Snout short (E-S/HW ratio 0.57), longer than eye diameter (ED/E-S ratio 0.63); scales on snout and forehead flattened, round to oval; scales on snout much larger than those of parietal table. Eye relatively small (ED/HL ratio 0.23); orbits without extra-brillar fringes; posterior supracilliary scales bearing small spines; pupil vertical,with crenelated margins. Ear opening oval, small (EL/HL ratio 0.07), greatest diameter horizontal; eye to ear distance greater than diameter of eyes (E-E/ED ratio 1.09). An irregular series of flattened to
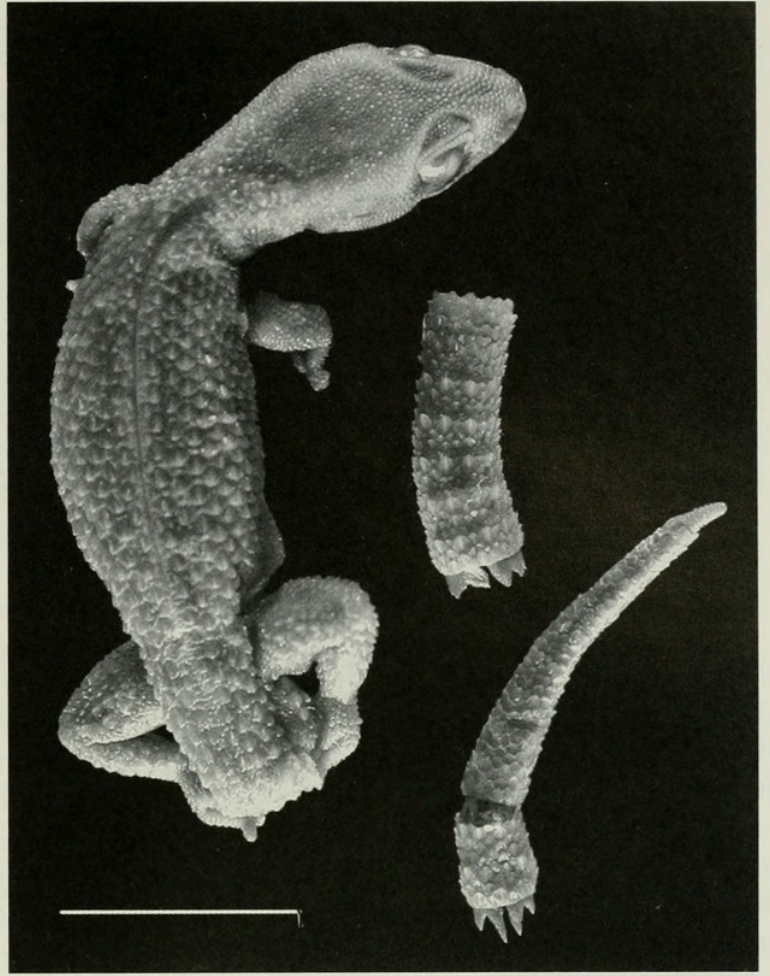
weakly conical tubercles between posterior border of orbit and occiput. Rostral approximately half as deep as wide; no rostral groove; contacted by two enlarged supranasals and first supralabials; nostrils rounded, each surrounded by two postnasals, supranasal, rostral, and first supralabial; supranasals in broad contact anteriorly, separated posteriorly by a single small granule; dorsal postnasals separated by two granules anteriorly and three posteriorly; one row of scales separate orbit from supralabials. Mental rectangular, approximately three times deeper than wide; no enlarged postmentals or chin shields.

Scales grade from granular on parietal region to a mixture of granules and enlarged conical tubercles on occiput, becoming keeled on nape; dorsal body scales large, rounded, flattened, with a pronounced median keel, forming approximately 14 rows; a single granular scale present in the space formed at the junction of four adjacent keeled tubercles (Fig. 4A); scales decreasing sharply in size on flanks, becoming smooth, subimbricate; ventral scales flattened, subimbricate, becoming somewhat larger posteriorly; scales on dorsum at mid-body much larger than those on ventrum at same level; chin granules approximately one third to one half size of ventral scales, increasing gradually in size on throat. No preanal or femoral pores; no preanal groove. Scales on palm and sole smooth, rounded; scales on ventral aspect of hind limbs and dorsal aspect of forelimbs imbricate, not keeled; those on dorsal aspect of distal thigh and crus greatly enlarged, keeled to mucronate.

Forelimbs moderately short, stout; forearm short (FA/SVL ratio 0.11); hindlimbs relatively short, tibia short (TBL/SVL ratio 0.15); digits moderately short, minute claws present on digits II and III of the pes only; subdigital scansors, except for distalmost, entire, present only on distal portion of toes, 1.5–2.0 times wider than more basal (non-scansorial) subdigital scales; interdigital webbing absent. Relative length of digits (manus; measurements in mm in parentheses): IV (1.71) > III (1.70) > II (1.68) > V (1.60) > I (1.49); (pes): IV (3.02) > III (2.61) > V (2.50) > II (1.95) > I (1.08). Subdigital scansors (manus): I (3), II (4), III (3), IV (3), V (3); (pes) I (4), II (5), III (5), IV (5), V (5).

Tail cylindrical; partially regenerated tail longer than snout-vent length (TL/SVL ratio 1.13); tail relatively thick, tapering, with distinct whorls of scales; each transverse row of enlarged, keeled tubercles separated by two rows of smaller scales; smaller scale rows continuous around tail; each row of enlarged tubercles replaced ventrally by two rows of smaller scales; each row of keeled dorsal caudal tubercles more-or-less continuous, interrupted occasionally by isolated small granules; corresponding to two rows of ventral scales; subcaudal scales pointed posteriorly, imbricating; two somewhat enlarged, smooth, conical postcloacal spurs on each side of tailbase.

Scutellation. Supralabials to angle of jaws 8; infralabials 7; interorbital scale rows (at midpoint of orbit) 19 (8 across narrowest point of frontal bone); midbody scale rows at belly to lowest row of keeled dorsal tubercles 37.

Osteology. Premaxillary teeth 9; phalangeal formulae 3-3-4-5-3 for manus and 3-3-4-5-4 for pes; presacral vertebrae 26, including three anterior cervical (without ribs) and one lumbar; sacral vertebrae 2; 5 pygal and 8.5 post pygal caudal vertebrae to point of regeneration; no cloacal bones present. Endolymphatic sacs enlarged, filled with calcium.

Coloration (in life; Pl. 1). Ground color of dorsum beige to yellowish brown with relatively regularly arranged mid-brown, roughly diamond-shaped markings; flanks with a pale rosy flush from underlying tissue; original tail with a series of darker markings at each pair of smaller dorsal scale rows, form-
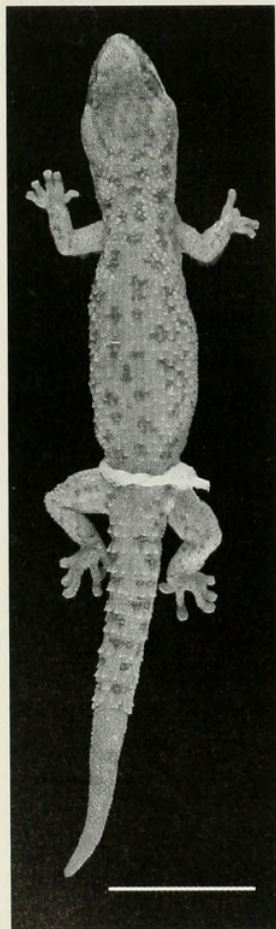
FIGURE 3. Holotype of *P. parascutatus*, sp. nov. (SMW R 9454) from Para Camp, 2 km north of Sesfontein, Opuwo District, Namibia. Scale bar = 10 mm.
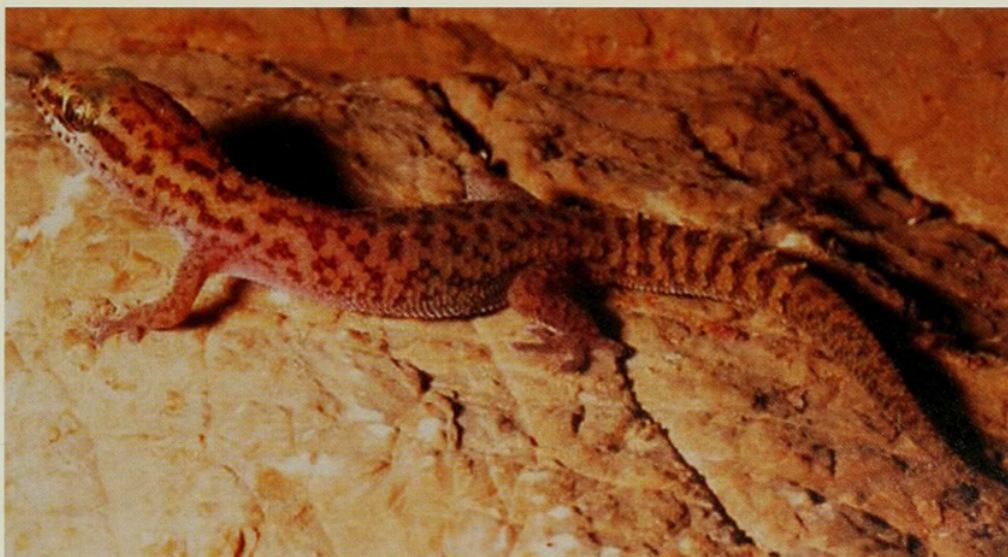
PLATE 1. Holotype of *Pachydactylus parascutatus* sp. nov. in life.

ing incomplete bands on some tail segments; dorsal surfaces of limbs mottled with scattered brown markings similar to those of dorsum. A thick, brown line from nostril, across canthus rostralis, to orbit, continuing posteriorly to approximately level of occiput, breaking up into markings that merge with dorsal pattern; bordered above by a thick whitish line, most distinct between nostril and anterodorsal corner of orbit. A series of three weakly defined, mid-brown, concentric semicircles extending posteriorly from frontoparietal suture, posterior border of orbit and occiput, respectively. Labial scales whitish; anterior supralabials and all infralabials bearing mid-brown markings. Venter buff with light specklings of brown pigment on all but midventral scales of chest and abdomen, densest on underside of tail and thighs.

VARIATION. — The adult paratypes (Table 1) are similar to the holotype in most respects, but differ in the following ways: CAS 214750 – dorsal pattern bolder, forming more regular longitudinal markings, especially on nape and shoulders; CAS 214735 – band from eye continues on left side beyond shoulder, dorsal markings fused, but still irregular, hemipeneial bulge present, two large white pointed cloacal spurs on each side of vent; SMW R 182—more strongly patterned than holotype with darker brown markings, three clocal spurs per side, precloacal scales larger than abdominal scales; SMW R 184—lacking distinct white canthal stripe, head markings more diffuse, virtually no ventral speckling (perhaps an artifact of blanching in preservative), four cloacal spurs per side. In the single juvenile specimen examined (CAS 214749), the white canthal lines continue behind the orbits, fusing on the nape to form a distinctive V-shaped collar as in *P. scutatus*. Males possess a single pair of crescentic cloacal bones, similar to those of *P. scutatus* and *P. angolensis*, and have prominent hemipenial bulges and somewhat enlarged cloacal spurs. We could find no evidence of even minute claws in either of the male specimens examined.

DISTRIBUTION. — The specimens examined are derived from a small area in the Kaokoveld north of the Hoanib River. All localities are relatively arid, but the two eastern areas, near Sesfontein and Kaoko Otavi are characterized by open mopane woodland or savanna, whereas the locality to the west of Orupembe is dominated by grasses and other herbaceous plants and is considered part of the northern Namib proper (Giess 1971). The species thus occurs in two adjacent floral domains or biomes (Jürgens 1991; Irish 1994). PEM R1964–5 from "Sesfontein" appear to be typical *P. scutatus*. Although this locality, if accurate, would imply sympatry with *P. parascutatus*, it is probable that it is imprecise and that the specimens may have been derived from some distance to the south of Sesfontein itself, within the accepted range of typical *P. scutatus*. Typical *P. scutatus* are also known from at least two localities (Otjivize and Epupa) to the north of *P. parascutatus*. In order to determine
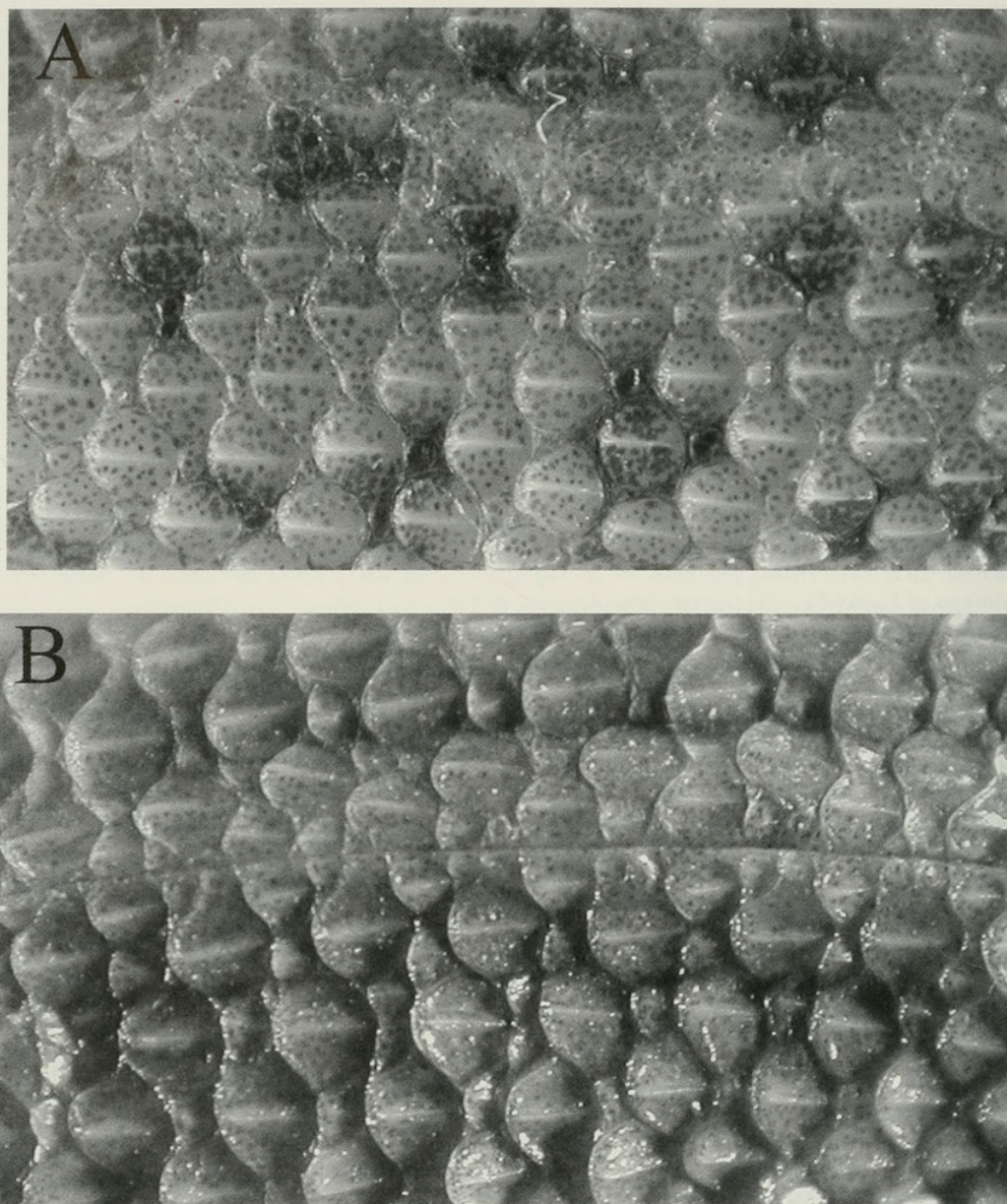
FIGURE 4. Mid-dorsal back scalation of A) *Pachydactylus parascutatus* and B) *P. angolensis*. Note the small, mostly granular scales at the junction of each quartet of keeled imbricate scales in A in comparison to their larger, often keeled counterparts in B.

whether *P. parascutatus* actually occurs in strict sympatry with either *P. scutatus* or *P. angolensis*, all older museum material should be re-examined and additional collecting should be conducted in the area from Sesfontein north to the Kunene River and into southern Angola.

NATURAL HISTORY. — The holotype was collected at night (approximately 20 hr) active on the surface of limestone rocks on a hillside. CAS 214735 was collected on the same hillside. CAS 214750 was collected by day amongst rubble beneath a large, flat slab of sandstone near the top of a steep slope beneath an overhanging cliff. CAS 214749 was collected by day from a vertical crevice between two large flat pieces of sandstone. In contrast *Pachydactylus scutatus* typically shelters under rock flakes on exfoliating boulders (FitzSimons 1938; Bauer et al. 1993), or occasionally in deeper rock cracks. The fact that *P. scutatus* have been taken in pitfall traps (SMW R 7972, 8002, 8032), however, suggests that this species may also be active terrestrially and not as strictly rupicolous as generally believed. Based on the capture conditions of the types of *P. parascutatus*, the microhabitat preference of this species appears intermediate between *P. scutatus* and *P. angolensis*, which has been taken from crevices in friable rocks and from under stones on the ground (Laurent 1964).

TABLE 1. Mensural data for the type series of *Pachydactylus parascutatus*, sp. nov. Abbreviations as in Materials and Methods, all measurements in mm.

	Holotype	Paratypes			
	SMW R 9454	CAS 214735	CAS 214750	SMW R 182	SMW R 184
Sex	Female	Male	Female	Male	Female
SVL	35.25	33.58	37.10	34.56	38.40
FA	4.02	4.96	5.13	4.70	4.48
TBL	5.43	4.96	5.40	5.61	5.84
TL (total)	26.30	9.67	33.89	25.16	3.63
TL (regen.)	12.86	tail broken	20.02	13.17	tail broken
TW	3.23	2.92	3.37	3.59	3.86
A-G	15.41	14.07	17.04	13.44	16.95
HL	10.31	9.84	11.78	9.99	9.84
HW	6.43	5.83	6.05	6.23	6.59
HD	3.76	3.04	3.61	4.02	3.37
ED	2.32	2.06	2.40	2.42	2.38
E-E	2.52	2.51	2.51	2.90	2.89
E-S	3.68	3.62	3.69	3.97	3.63
E-N	3.12	2.65	2.56	2.41	2.32
IO	2.88	2.79	2.79	3.30	2.70
EL	0.72	0.67	0.84	0.62	0.64

Like that of *P. scutatus*, the skin of *P. parascutatus* is fragile and easily damaged by handling (Bauer and Russell 1992; Bauer et al. 1993). The skin of the flank and limbs of several paratypes (CAS 214735, 214750) were damaged in collection. Fragile skin in these forms is a manifestation of regional integumentary loss, an antipredator escape strategy that has been proposed as useful against certain types of lizard predators, such as snakes and other lizards (Bauer et al. 1989, 1993; Bauer and Russell 1992).

Other reptiles collected at Para Camp, Sesfontein, were *Pachydactylus oreophilus*, *P. turneri*, *Rhoptropus barnardi*, *Leptotyphlops occidentalis*, *Prosymna visseri*, and *Pythonodipsas carinata*. *Psammophis trigrammus* was collected at one of the paratype localities.

DISCUSSION

MORPHOLOGICAL COMPARISONS. — The relatively small body size (to 38.40 mm) of *P. parascutatus* easily distinguishes it from *P. tuberculosus*, *P. tetensis*, and all members of the *P. bibronii*, and *P. namaquensis* groups. These are basal members of the genus (Lamb and Bauer 2002), all of which exceed 100 mm in adult SVL and possess 10 or more lamellae beneath the fourth toes of the pes (vs. 4–5 in *P. parascutatus*). Among "small-bodied" *Pachydactylus*, the combination of enlarged, contiguous, keeled dorsal scales and the entry of both the first supralabial and the rostral into the nostril occurs only in the *P. scutatus* group. Some members of the *P. weberi* complex (only one species currently recognized [Branch 1998], but currently under revision) have variably developed keels and, although the first supralabial typically enters the nostril, the rostral is usually excluded. Only in the case of *P. robertsi* (see above) do the dorsal scales approach the width of those of *P. parascutatus*, but the rostral is excluded from the nostril in *P. robertsi*.

Within the *Pachydactylus scutatus* group, *P. parascutatus* differs from *P. angolensis* in the condition of the nasal scales (both rostral and supralabial excluded from nostril in *P. angolensis*). In addition, in *P. angolensis* the small scales lying at the junction of each quartet of larger dorsal scales are frequently keeled (Fig. 4B). These small scales are flat or granular in the new species (Fig. 4A). The large dorsal scales are relatively strongly imbricate in *P. angolensis*, but weakly so or juxtaposed in *P.*

parascutatus. In addition, the former species has keeled scales on the dorsal surface of the forelimb (vs. smooth) and small, sometimes keeled scales separating the enlarged caudal tubercles (vs. no or few small intervening granules). *Pachydactylus angolensis* also has keeling on the rows of smaller caudal scales (between tubercular whorls), whereas such keeling is weak or altogether absent in *P. parascutatus*. The dorsal pattern may also be diagnostic. Loveridge (1944) described the types of *P. angolensis* as grayish to reddish brown and noted the presence of white spots on the dorsum. At the time of Loveridge's description, the types had already been in preservative for 19 years, and the life colors were clearly highly modified. The pattern of the holotype today is at best weakly discernable. However, although similar head patterning is evident, there is no evidence of the dark dorsal markings typical of *P. parascutatus*. A paratype of *P. angolensis* (MCZ 49856) exhibits no evidence of a neck band and possesses remnants of broken transverse bands formed by pale scales on the dorsum.

    Pachydactylus parascutatus shares with *P. scutatus* the same snout scalation pattern and is very similar in most aspects of body scalation. It differs from this form chiefly in color pattern. Adult *P. parascutatus* lack the well-defined nuchal collar that typifies *P. scutatus* (Fig. 5). However, this collar is evident in the single juvenile specimen (CAS 214749) of *P. parascutatus* that we examined. Even in this specimen, however, the collar lacks the dark edging characteristic of *P. scutatus*. In *P. parascutatus* the light head markings are less well defined than in *P. scutatus*, where they are often immaculate and bold. In addition, most *P. scutatus* exhibit a uniform or very weakly patterned dorsum (Fig. 5A; although dark scattered markings do occur in some specimens, e.g., SMW R 5183 and CAS
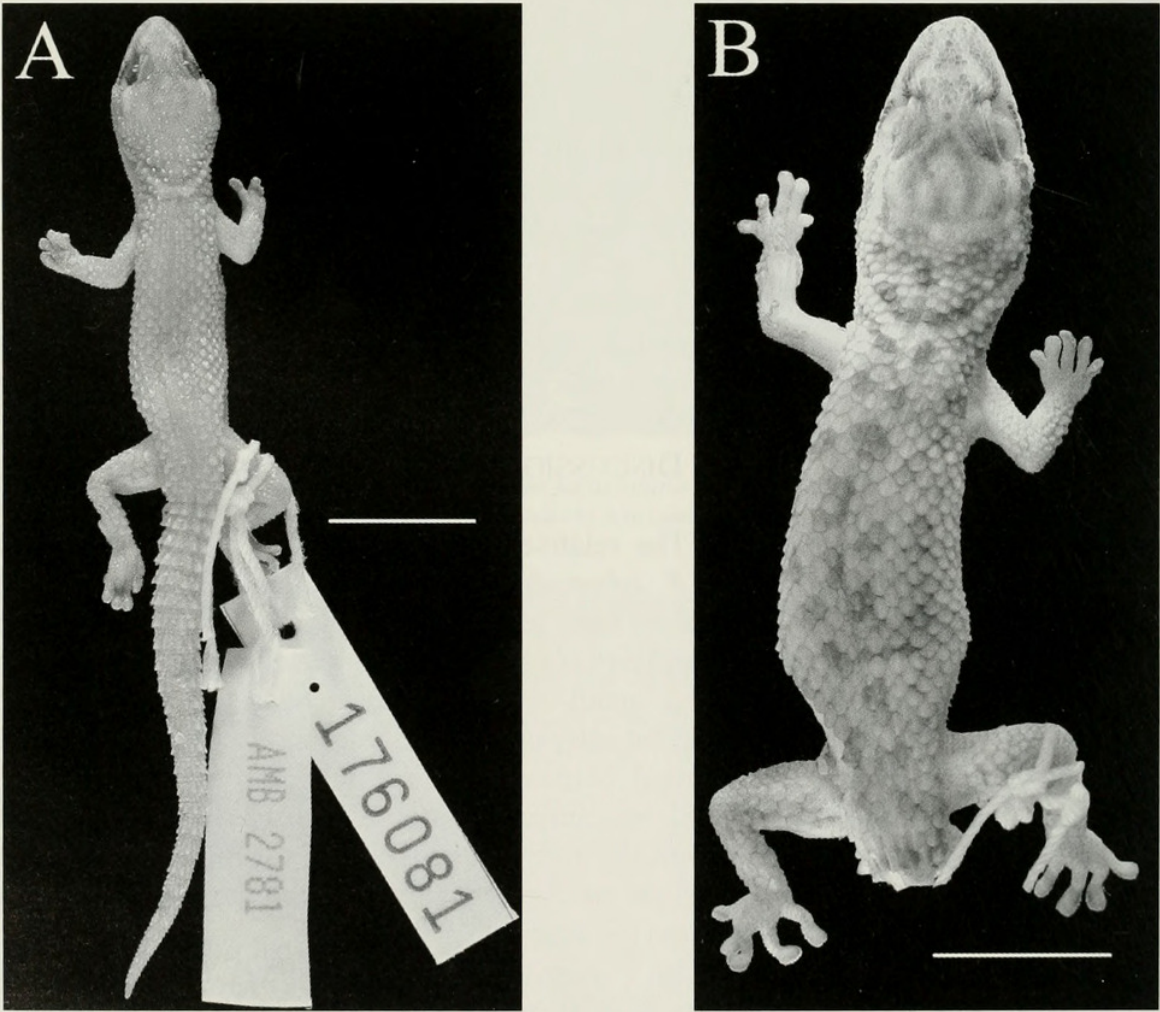

FIGURE 5. *Pachydactylus scutatus* from A) Farm Franken, Outjo District, Kunene Region, Namibia (CAS 176081) near the type locality of Kowares and B) 19°37′27″S, 14°43′19″E, Khorixas District, Kunene Region, Namibia. The unpatterned dorsum of A is the most common pattern. B is a particularly heavily patterned individual. Compare the position and width of the nuchal collars of these specimens with the type of *P. angolensis* (Fig. 1). Scale bars = 10 mm.

TABLE 2. Pairwise sequence divergence estimates for *Pachydactylus parascutatus* and representative congeners derived using the Hasegawa-Kishino-Yano model (Hasegawa et al. 1985).

Species	Specimen	1	2	3	4	5	6	7	8
1 *P. sansteyni*	CAS 214589	—							
2 *P. sansteyni*	CAS 214767	0.00000	—						
3 *P. parascutatus*	SMW R 9454	0.22466	0.22466	—					
4 *P. parascutatus*	CAS 214735	0.22466	0.22466	0.00000	—				
5 *P. parascutatus*	CAS 214750	0.21688	0.21688	0.00538	0.00538	—			
6 *P. parascutatus*	CAS 214749	0.21688	0.21688	0.00538	0.00538	0.00000	—		
7 *P. scutatus*	CAS 193673	0.28113	0.28113	0.18739	0.18739	0.18749	0.18749	—	
8 *P. scutatus*	AMB 5943	0.28100	0.28100	0.20284	0.20284	0.20296	0.20296	0.04488	—
9 *P. weberi*	CAS 206754	0.26117	0.26117	0.20631	0.20631	0.20255	0.20255	0.25972	0.23425

193673; Fig. 5B; see also Branch 1998, plate 85) with a unicolor or diffusely-patterned tail, whereas *P. parascutatus* are relatively heavily patterned, with dark marks over most of the dorsum and a distinctly banded tail. *Pachydactylus scutatus* also appear to grow to much larger sizes than the new species. Branch (1998) recorded a maximum size of 42 mm SVL for *P. scutatus*, but the largest specimens we examined attained sizes of approximately 47 mm SVL, in comparison to a maximum of less than 39 mm in *P. parascutatus*. Radiographs of specimens of *P. scutatus* of 33–38 mm SVL reveal that they are juveniles or subadults, with poor ossification of the limb joints, whereas *P. parascuatus* in this size range are adults. The largest of the types of *P. angolensis* measures 42 mm SVL. *Pachydactylus scutatus* also has a somewhat more flattened or depressed habitus than the new species.

MOLECULAR COMPARISONS. — Pairwise comparisons between *Pachydactylus parascutatus* and *P. scutatus* yielded genetic distance values for cyt *b* in the range of 17.6–20.3%, whereas intraspecific comparisons reveal differences of 0.0–0.5% among *P. parascutatus* (maximum geographic distance between samples approximately 25 km) and 5% between *P. scutatus* from across a 35 km distance (Table 2). These interspecific comparison values are only slightly less than those between *P. parascutatus* and *P. sansteyni* (21.7–22.5%), another Kaokoveld regional endemic species, and *P. weberi* (20.3–20.6%), another strongly keeled member of the genus. Like most interspecific comparisons in *Pachydactylus*, these values are in the middle to higher end of divergence values reported for reptile (and other vertebrate) congeners with respect to cyt *b* sequence divergence (Johns and Avise 1998). A higher order molecular phylogeny of *Pachydactylus* (Lamb and Bauer 2002) reveals that *P. parascutatus* is the sister species of *P. scutatus* and that these two species (and presumably *P. angolensis*, for which tissues are unavailable) are members of a monophyletic group that also includes the northern Namibian endemics *P. oreophilous* and *P. gaiasensis*.

BIOGEOGRAPHY. — The removal of *Pachydactylus robertsi* from the *P. scutatus* group eliminates the need to explain the enigmatic disjunction of more than 700 km that previously characterized the geographic distribution of this group. The *P. scutatus* group as recognized here is endemic to the region of northwestern Namibia and southwestern Angola, an area first identified as a center of reptile

endemism by Steyn and Mitchell (1965) based on the distribution of the skink *Mabuya laevis*. Bauer et al. (2001) regarded this species and numerous others (e.g., *Pedioplanis benguellensis*, *Pachydactylus caraculicus*, *P. fitzsimonsi*, *Sepsina alberti*, *Hemirhagerrhis viperina*, *Lycophidion hellmichi*, *Coluber zebrinus*, *Prosymna visseri*) as elements of a significant trans-Kunene mopaneveld area of endemism. *Pachydactylus scutatus* as presently defined is largely restricted to the numerous koppies scattered across the northern Namibian mopaneveld. *Pachydactylus parascutatus* appears to be distributed on the western periphery of the mopaneveld and into the largely treeless areas of the northern Pronamib. This distribution, as currently understood, is similar to that of the geckos *Pachydactylus oreophilus* and *Rhoptropus biporosus*. The recognition of a new species in this region further emphasizes the significance of northwestern Namibia as a center of reptile diversity (Simmons et al. 1998; Griffin 2000) and highlights the degree to which members of the genus *Pachydactylus* have radiated in the western arid zone of southern Africa (Bauer 1999[2000]).

ACKNOWLEDGMENTS

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SPECIMENS EXAMINED

Museum acronymys follow Leviton et al. (1985). Specimens for which molecular data were obtained are marked with an asterisk (*).

Pachydactylus angolensis: Angola: AMNH R-47874 (holotype), MCZ 49856 (paratype), Hanha.

Pachydactylus parascutatus: Namibia, Kunene Region: CAS 214735* (paratype), SMW R 9454* (formerly CAS 214755; holotype), vic. Para Camp, 2 km N Sesfontein, Opuwo District (19°07'28"S, 13°35'29"E); CAS 214749*, Purros Rd., ca. 27 km W of Sesfontein, Opuwo District (19°03'16"S, 13°30'08"E); CAS 214750* (paratype), Purros Rd., ca. 8 km W Sesfontein, Opuwo District (19°10'05"S, 13°34'03"E); SMW R 182 (paratype), Kaoko Otavi, Opuwo District (1815Bc); SMW R 184 (paratype), 20 km W of Orupembe, Opuwo District (1812Ab).

Pachydactylus robertsi: Namibia, Karas District: TM 17854 (holotype), Farm Kraikluft, Great Karas Mountains, Great Namaqualand.

Pachydactylus sansteyni: Namibia, Kunene District: CAS 214589*, Skeleton Coast National Park, ca. 1 km S of Huab River Bridge, Khorixas District (20°54'03"S, 13°32'01"E); CAS 214767*, Skeleton Coast National Park, N bank of Huab River at Huab River Bridge, Khorixas District (20°54'04"S, 13°31'30"E); SMW R 1623–5, 1637 (paratypes), 1626 (holotype), Kuidas (2013 Da); SMW R 7690, 20 mi. N of Ugab river Mouth on Coast, Khorixas District.

Pachydactylus scutatus: Namibia, Kunene Region: CAS 176081, Farm Franken, Outjo District; CAS 176112, Torrabaai Rd., 70.9 km W of Kamanjab, Khorixas District; CAS 193672–3*, Kamanjab-Torrabaai Rd., Khorixas District (19°37'27"S, 14°43'19"E); CAS 193733, Otjivize, Opuwo-Okangwati Rd., Opuwo District (17°37'11"S, 13°27'32"E); AMB 5943*,CAS 206961, Sesfontein Rd., 25.3 km N Palmwag, Khorixas District; AMB 5945, Sesfontein Rd., 52 km N Palmwag, Khorixas District (19°27'28"S, 13°52'41"E); SMW R 181, Numas Valley, Brandberg; SMW R 183, Kamanjab, Outjo District; SMW R 185 Brandberg (2114Ba); SMW R 5183, Ugab River at rd. 76 (20°52'S, 14°57'E);. SMW R 5722, Palmwag (19°47'S, 13°55'E); SMW R 7972, 8002, 8032, Otjongoro, Omaruru District (20°53'S, 15°38'E).

Pachydactylus weberi: South Africa, Northern Cape Province: CAS 206754*, South Africa, Northern Cape Province, Kleinsee, Nature Reserve (29°38'49"S, 17°05'02"E); Namibia, Erongo Region: TM 33650, Horebis Nord, Karibib District; Namibia, Khomas Region: TM 32834, 32838, Windhoek; TM 28781, Klein Windhoek.