

A review of the Namaqua gecko, *Pachydactylus namaquensis* (Reptilia: Gekkonidae) from southern Africa, with the description of two new species

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An analysis of morphological and allozyme variation in the Namaqua gecko, *Pachydactylus namaquensis* from southern Africa is presented. Three separately evolving lineages, well defined by morphology and allozyme variation, are identified. The isolated southern population, occurring on the southern escarpment and Cape Fold Mountains surrounding the western Little Karoo, is named *P. kladaroderma* sp. nov., and is characterized by a slit-like ear opening, low number of granules bordering the mental (3-6) and mental and adjacent infralabials (5-13), the frequent (79%) occurrence of the supralabial entering the nostril, and its drab brown base colouration. A northern population, occurring in southern Namibia and the Richtersveld is named *P. haackei* sp. nov., and is characterized by its more rounded or squared ear opening; high number of granules bordering the mental and adjacent infralabials (11-19), the general exclusion of the supralabial from the nostril (only 3.7% entry), and brighter, lighter colouration. It is further differentiated from *P. kladaroderma* on the basis of fixed differences at 11 allozyme loci. Both new species differ from *P. namaquensis*, which is mainly restricted to Little Namaqualand, but is sympatric with *P. haackei* in the Lower Orange River region, by their more heterogenous dorsal scalation, smaller cloacal spurs, lack of spine-like tubercles on the lateral surfaces of the tail, and more fragile skin. The type locality of *P. namaquensis* is restricted to 'the vicinity of Springbok, Little Namaqualand, Northern Cape Province, South Africa'.

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The lizard fauna of southern Africa is one of the most diverse and speciose in the world (Bauer 1993) and yet it remains relatively poorly known. In an analysis of terrestrial vertebrate diversity and endemism in southern Africa, Crowe (1990) found that the southern and western parts of the subcontinent constitute the area of highest regional endemism. He reported that lizards exhibit moderate to high levels of localized endemism throughout southern Africa, with up to 43% specific endemism in the western arid zones of Namibia and the Cape. The western arid regions are an epicentre of speciation (Poynton & Broadley 1978), particularly for geckos. Of the 76 gecko species in southern Africa, 35 are in the genus *Pachydactylus* or in genera that make *Pachydactylus sensu stricto* paraphyletic (Branch 1988; Bauer 1990; Bauer & Branch 1995). Members of the lineage occur throughout the subcontinent, generally are abundant, have restricted ranges, and show a great range of microhabitat specializations. Eight representatives of this group have been found in sympatry in the Karoo National Park, South Africa (Branch & Braack 1989), and 11 are broadly sympatric in the area between Kamanjab and the Skeleton Coast National Park in northern Namibia (Bauer, Branch & Haacke 1993). In both areas, the majority of species occur in rocky habitats where they occupy cracks and surfaces of different types, or they are terrestrial.

Attempted revisions within *Pachydactylus sensu stricto* have met with limited success (Hewitt 1927; FitzSimons 1943; Loveridge 1947; McLachlan & Spence 1966; McLachlan 1979). Several species groups have been recognized on the basis of superficial similarities of habitus and scalation,

although the recognition of such groups in the absence of a phylogenetic hypothesis may be imprudent. A non-phylogenetic alpha-level taxonomic revision of *Pachydactylus sensu stricto* is currently in progress (McLachlan, pers. comm.), but the only formal 'groups' so far defined in the literature are the *P. weberi* and *P. serval* groups of McLachlan & Spence (1966) and the *P. capensis* complex of Broadley (1977; see also Jacobsen 1989). More recently an analysis of morphological variation in the *Pachydactylus punctatus* complex (Bauer & Branch 1995) has revealed significant differences between populations above and below the western escarpment in Namibia, and has led to the recognition of two species. Bauer & Branch (1995) also suggested that subtle differences in the lowland western species, *P. scherzi*, might reveal further species if larger samples became available and/or molecular methods could be employed.

At the end of the last century, Sclater (1898) described a large new gecko 'obtained in Namaqualand', naming it after its locality and placing it in the genus *Elasmodactylus*, recently erected by Boulenger (1894) for *tuberculosis* from Tanzania, and now known from Zaire, Zambia and adjacent areas. Subsequently, *Elasmodactylus namaquensis* was transferred to the genus *Pachydactylus* Wiegmann 1834 by Methuen & Hewitt (1914). They noted that justification for the recognition of *Elasmodactylus* as distinct from *Pachydactylus*, i.e., the presence of claws on the toes in the former, is an inconstant character. Subsequent workers (Haacke 1976; Joger 1980, 1984, 1985; Bauer & Good 1995) have demonstrated that females of the *Pachydactylus*-group genera generally possess claws on digits I and V of the pes. Joger (1985)

argued for the revival of *Elasmodactylus* for *tuberculosis*, but this was based on the retention of plesiomorphic characters such as the presence of preanal pores and a partly divided rostral, which he regarded as having transformed in the putatively monophyletic group (*Pachydactylus* proper + *Chondrodactylus* + *Palmatogecko* + *Colopus* + *Kaokogecko* + *Rhoptropus*). With respect to *P. namaquensis*, Joger (1985) suggested that it was reasonably closely related to *P. bibronii* and reported an immunological distance of about 22%, corresponding to a divergence time of 20 million years. Joger's (1985) material was supposedly derived from 'Kharkamas, Namibia' (presumably Karkams, Little Namaqualand, South Africa).

Methuen & Hewitt (1914) noted the first Namibian specimens to be referred to *Pachydactylus namaquensis* from the Great Karasberg Mountains, and additional specimens from Namaqualand were later recorded by Hewitt (1932) and FitzSimons (1938). In his monographic revision of the subcontinent's lizards, FitzSimons (1943) summarized museum records for the species, including a new southern record from the Witteberg, south of Matjiesfontein, that he later reported on in more detail (FitzSimons 1946). Haacke (1965) extended the northern limit with a record from Farm Tiras, Bethanie District, Namibia. More recent range extensions referred to the species have occurred in the south, including the Nuweveldberge in the escarpment mountains of the central Karoo (Branch & Braack 1989; Branch 1990), the eastern Langeberg Mountains in the Cape Fold Mountains (Boycott 1990), and the western Little Karoo (Burger 1993). The distribution of *Pachydactylus namaquensis*, as understood and illustrated in Visser (1984) and Branch (1988), is disjunct, with a gap of approximately 370 km separating the southern population from the closest record (Garies) of the Namaqualand and Namibian populations.

Morphological variation within *Pachydactylus namaquensis* has never been evaluated. Field observations and the examination of specimens from throughout its range indicate that there is significant variation within the taxon as presently construed. In addition, the application of allozyme analysis in the determination of cryptic, morphologically-conservative species is increasing (Brody, Mouton & Grant 1993; Channing, Hendricks & Dawood 1994; Branch, Bauer & Good 1995). Noting the isolated and possible relictual nature of a population of *P. namaquensis* in the escarpment mountains of the Nuweveldberge, Branch & Braack (1989) recommended that the taxonomic status of the southern population be investigated. When comparing Garies and Karasberg material, Hewitt (1932) also noted in passing that Namibian material may deserve subspecific recognition, but gave no potentially diagnostic features. We here present an analysis of morphological and allozyme variation in *P. namaquensis*, with the recognition and description of two new species. The discovery of cryptic species subsumed within *P. namaquensis* also necessitates a reappraisal of morphological and distributional limits for the species, and of natural history observations attributed to it.

Materials and methods

Fresh material was collected during numerous field trips to the northern, central and southern Cape region, and deposited

in the Port Elizabeth Museum (PEM). This was supplemented with additional material and localities obtained from the following museums: J. Ellerman Museum, Stellenbosch (JEM), South African Museum, Cape Town (SAM); Transvaal Museum, Pretoria (TM), California Academy of Sciences, San Francisco (CAS), Museum of Vertebrate Zoology, Berkeley (MVZ), United States National Museum of Natural History, Washington (USNM), and American Museum of Natural History (AMNH). Description of scutellation follows FitzSimons (1943), and data were obtained at $\times 8$ or $\times 40$ magnification with a Carl Zeiss dissecting microscope. Cleared and double stained specimens and radiographs prepared in a Faxitron cabinet X-ray system were used to examine osteological features. The following details were recorded.

Scalation: Scales entering the nostril (recorded separately for both sides of the head); number of granules separating nasorostrals (if they were in contact behind the rostral, even if separated posteriorly by a granule(s), they were recorded as being in contact); number of granules bordering mental and adjacent infralabials; the number of supra- and infralabials (including small scales at the rictus); dorso-lateral body tubercles (objective description of the degree of tuberculation is difficult; the size of tubercles in the dorso-lateral region relative to the size of surrounding granules, and the average number of granules surrounding 10 enlarged tubercles were recorded); caudal tubercles (presence or absence of enlarged spine-like tubercles on the lateral surfaces of the tail); cloacal spurs (size and number of enlarged, flattened tubercles on the ventro-lateral surface of the tail base); shape of ear opening (in non-distorted heads); claws (on the fingers and toes); skin tears (including fresh and healed damage).

Morphometrics: The following measurements were recorded to the nearest 0.01 mm with Brown and Sharpe digital calipers: snout-vent length; original tail length (partially or fully regenerated tails were noted); head width (at widest point); head length (from middle of ear aperture to tip of snout); eye diameter; snout (from anterior margin of eye to tip of snout); ear to eye (from posterior margin of eye to anterior margin of ear); pad length (from proximal margin of first enlarged scansor to distal tip of scansor, on 4th toe); pad width (widest point of enlarged scansors under 4th toe). Ordination comparisons were conducted using the SAS computer package (SAS Institute 1994) to determine whether samples were distinguishable in multivariate space. Discriminant function analyses were conducted with CANDISC and DISCRIM. These techniques require that no characters be missing from the data matrix, and many specimens had to be excluded from analysis. Specimens with regenerated or missing tails were therefore analysed separately.

Allozymes: Tissue samples were obtained from seven southern populations from the Great and Little Karoo, and one from the Richtersveld population. Voucher specimens are listed in Table 1. Livers were dissected from freshly killed specimens and maintained either in liquid nitrogen or in ultra-cold freezers (-76°C). Liver tissue from each specimen was homogenized with approximately equal parts tissue and deionized water. The samples were then subjected to horizontal starch gel electrophoresis using standard techniques

Table 1 Voucher specimens for allozyme study

Population	No.	Mus. No.
<i>Pachydactylus kladaroderma</i>		
1 Molteno Pass, Karoo Nat. Pk	10	PEM R11193-5, R11197-8, R11201, CAS 198285
Sakrivier, Nuweveldberg	1	PEM R11199
2 Komsberg Pass	3	PEM R11234-6
3 Sutherland	3	PEM R11212-3, CAS 198301
4 Verlatekloof	2	PEM R11224-5
5 Anysberg Nature Reserve	2	CAS 195395-96
6 Sewenweekspoor	1	PEM R11240
7 Huisrivier Pass	1	PEM R11246
<i>Pachydactylus haackei</i>		
8 12.6 km E. Sendelingsdrift, Richtersveld Nat. Pk	2	CAS 193362-3
Hottentotsparadys, 8.7 km E. Helskloof Gate, RNP	1	CAS 193445
20 km E. Sendelingsdrift, RNP	2	CAS 186341-2
22 km E. Sendelingsdrift, RNP	1	CAS 186350

Table 2 Buffer systems and loci scored in allozyme analysis of the *Pachydactylus kladaroderma* and *P. haackei*. Buffer systems are described by Selander *et al.* (1971) and Ayala *et al.* (1972). Buffer system abbreviations: A = LiOH (pH 8.2), B = Poulik (pH 8.7), C = Tris-citrate (pH 8.0), D = Tris-citrate (pH 8.0) with NADP

Enzyme	Enzyme Commission number	Locus	Buffer system
Aspartate aminotransferase	2.6.1.1	Aat	A
Alcohol dehydrogenase	1.1.1.1	Adh	D
Adenylate kinase	2.7.4.3	Ak-1,2	C
Fumarase	4.2.1.2	Fum	B
Glucose-6-phosphate dehydrogenase	5.3.1.9	Gd	D
Glucose dehydrogenase	1.1.1.47	Gdh	A
L-glutamate dehydrogenase	1.4.1.3	Glud	C
Isocitrate dehydrogenase (2 loci)	1.1.1.42	Icdh-1,2	D
L-lactate dehydrogenase (2 loci)	1.1.1.27	Ldh-1,2	C
Malate dehydrogenase (2 loci)	1.1.1.37	Mdh-1,2	C
Malic enzyme	1.1.1.40	Me	D
Dipeptidase (3 loci)	3.4.13.11	Pep-1,2,3	B
Tripeptide aminopeptidase	3.4.11.4	Pep-4	B
Proline peptidase	3.4.13.9	Pep-5	B
Phosphogluconate dehydrogenase	1.1.1.44	Pgdh	D
Phosphoglucomutase	5.4.2.2	Pgm	A
Pyruvate kinase	2.7.1.40	Pk	D
Superoxide dismutase	1.15.1.1	Sod	B

(Selander, Smith, Yang, Johnson & Gentry 1971; Harris & Hopkinson 1976; Hillis & Moritz 1990). Twenty-three loci were scored using the buffer systems listed in Table 2. Nei (1978) genetic distances were calculated using the BIOSYS computer package (Swofford & Selander 1981).

Results and Discussion

The morphological and allozyme features discussed below reveal the presence of three separately evolving lineages that can be distinguished from each other by a mosaic of features. No available names exist for two of these lineages, and for convenience they are here first described, then the character variation used to determine species limits is discussed. We also present a redescription of *P. namaquensis*, correcting knowledge of its distribution and natural history. An abbreviated synonymy, listing only first use of major synonyms and current name, is given for each species.

Pachydactylus namaquensis Figure 1a (Namaqua thick-toed gecko)

Elasmodactylus namaquensis Sclater, 1898. *Ann. S. Afr. Mus.* 1: 109, pl. V, fig. 2.

Pachydactylus namaquensis Methuen & Hewitt, 1914.

Redescription of holotype: Differences in the paratype (PT) are shown in brackets; measurements of types are given in Table 3. SAM 935; adult female (PT, same number; adult female). Head depressed, slightly longer than broad and distinct from neck; snout obtusely rounded and 1.26 times the ear to eye distance (PT 1.37), and 1.88 times the eye diameter (PT 1.85); ear opening obliquely rounded, height less than twice width, enlarged lobules or tympanic shields absent; eye relatively large, ringed by small ciliary granules that are only slightly larger on the upper edge, and with a vertical pupil that constricts to two pinhole openings in preserved specimens; rostral broader than wide, with a scalloped dorsal edge and lateral 'horns' that project into the nostrils; nasal region distinctly raised, with nostril directed upwards and bordered by three nasals and extensions of the rostral and first supralabial; suture of supranasal and rostral rounded to form a scallop into the dorsal margin of the rostral; supranasals in contact anteriorly (PT, separated by a single granule); mental rectangular, narrower than rostral, more than 1.5 times longer than broad, and bordered by 10 granules (PT, 7); no enlarged chin shields; 22 granules border the mental and adjacent infralabials (PT 16); supralabials 12 on right, 11 on left (PT, 11/11); infralabials 10 on right, 11 on left (PT 11/11). Scales on snout and between eyes small and granular, larger on loreal and canthal region; crown of head covered with small granules with no scattered tubercles; chin and throat covered with small, flattened granules. Back covered with granules that are larger than those on crown, intermixed with enlarged tubercles that may be flattened or faintly keeled, and longitudinally oval or rounded, and are denser and more rounded on the sides of the body and absent along backbone; dorsal tubercles twice size of surrounding granules and ringed by 10–12 granules; tubercles on thighs rounded and subconical. Belly covered with flattened, smooth, imbricate scales, that are enlarged on underside of thighs.

Body stout; limbs short; digits moderate, with distal expansions well developed and subdigital lamellae arranged as follows: fingers I and II, 10 lamellae each; fingers III to V, 11 lamellae each; toe I, 10 lamellae, toe II, 11 lamellae, toe III, 12 lamellae; toes IV and V, 13 lamellae. The last (most distal) lamella of each digit is paired; all toes have obvious claws, but these are absent on the fingers. The median row of sub-

Table 3 Morphometric data for the type series of species within the *Pachydactylus namaquensis* complex. (NM = not measured)

Mus. No.	Sex	SVL	Tail	Eye	HW	HL	Snout	Ear-Eye
<i>Pachydactylus namaquensis</i>								
Holotype								
SAM 935	F	77.02	65.55	4.65	16.86	19.8	8.62	6.28
Paratype								
SAM 935	F	84.67	Lost	4.91	18.17	20.85	9.24	7.34
<i>Pachydactylus kladarodemra</i>								
Holotype								
PEM R11195	F	79.66	69.34	3.77	17.18	20.85	9.40	6.41
Paratypes								
CAS 198288	F	77.67	NM	5.19	16.84	19.49	7.60	6.12
CAS 198301	F	71.93	NM	4.94	15.08	18.73	7.50	5.30
CAS 186392	F	70.69	59.56	5.49	16.26	18.84	7.39	5.64
LSUMZ 56974	F	66.62	NM	5.14	14.84	17.87	7.67	5.39
PEM R11193	F	71.85	54.00	3.70	15.44	18.52	7.88	6.09
PEM R11194	M	72.16	56.00	4.05	16.94	20.71	8.44	6.40
PEM R11197	M	78.63	Lost	3.80	17.23	20.94	9.17	6.37
PEM R11198	F	54.74	43.91	2.99	13.34	15.13	6.31	5.00
PEM R11199	F	54.21	17.0(R)	2.66	3.26	14.89	6.17	4.34
PEM R11200	M	82.15	60.0(R)	4.29	19.60	22.68	9.94	7.40
PEM R4370	Juv	51.07	40.03	3.17	11.87	13.35	6.13	4.00
PEM R4660	F	73.42	12(R)	3.89	16.54	18.82	8.21	5.95
PEM R6544	M	77.17	76.30	NM	NM	NM	NM	NM
<i>Pachydactylus haackei</i>								
Holotype								
PEM R 9282	F	83.47	76.08	4.19	18.36	19.38	8.55	7.02
Paratypes								
CAS 193362	F	84.11	77.42	5.65	17.12	20.60	8.65	6.64
PEM R10941	M	78.11	Lost	3.57	18.00	19.42	8.23	6.59
PEM R7305	M	66.36	Lost	4.52	15.71	17.56	7.44	5.98
PEM R7358	F	63.42	66.01	4.53	15.00	17.79	6.97	5.15
PEM R7359	Juv	43.43	44.27	3.29	10.84	12.92	5.29	4.07
PEM R7606	M	84.84	73(R)	4.87	18.58	22.24	9.05	7.29
PEM R9283	F	72.37	74.52	3.73	17.28	18.05	7.34	6.31
PEM R9284	F	80.90	60.8(R)	3.86	18.14	19.19	8.01	6.76
AMNH 141230	F	77	54	4.79	16.6	19.7	8.2	6.3

digital scales on the basal portion of digits 2–3 times width of adjacent granules and occasionally divided. Original tail (65.55 mm) distinctly smaller than snout-vent length (SVL 1.17 times tail length; PT, tail lost), very broad basally and tapering rapidly; segmented, distinctly so on sides, each segment above with 6–7 rows of scales including towards the distal border of the segment a transverse row of 6–8 enlarged, pointed tubercles, of which the lateral ones are the largest and are extended into prominent spines (Figure 1b); below the scales are large and imbricate, arranged in three rows on the proximal segments, reducing to two rows at midlength, and to a single series of enlarged subcaudals (without eschuchen scales) distally. An oblique row of four large, flattened tubercles occurs on the tail base on either side of the vent.

Colouration: Faded in types; based on PEM preserved material. Dorsum light tan, heavily patterned with vague dark brown blotches that are more conspicuous on the tail, forming a series of 6–7 irregular bands; in life a Kliprand specimen (illustrated by Visser 1984) shows four paired subrectangular pale blotches along the backbone, and these are also evident in a Garies specimen (Figure 1a); ventrum cream, lighter beneath the head, throat, chest and lower surfaces of the limbs and tail.

Diagnosis: This species may be diagnosed from the majority of *Pachydactylus* species by its large size (maximum SVL 84.7 mm), and scattered dorsal tubercles. It may be diagnosed from the large *P. bibronii* and *P. laevigatus* by the entry of the rostral into the nostril and the lack of skull co-ossification,



A



B

Figure 1 Dorsal views of *Pachydactylus namaquensis* (Garies, CAS 167642): (A) whole animal, (B) close up of original tail base showing enlarged lateral spines.

and from *P. tetensis* by the absence of preanal pores in males. It differs from *P. kladaroderma* and *P. haackei* (described below) by the larger dorsal tubercles, larger cloacal spurs,

spine-like tubercles on the lateral surfaces of the tail, and less fragile skin. It is further differentiated from *P. haackei* in possessing a narrow parietal process of the postfrontal bone.

Distribution: Restricted to the mountains of Namaqualand, from near Leliefontein in the Kamiesberge (3018Ac) in the south, to Nicodaemus and Kuboes, in the Vandersterberge, Richtersveld National Park (Figure 4). A single specimen (SAM 43639), labelled Namuskluft Inselberg (2716Dd) at the southern end of the Huib-Hoch Plateau is the northern record for the species, and the only known Namibian record. A specimen of *P. haackei* (SAM 43637; see below) with the same locality and collecting data, indicates sympatry between the two species. Possible sympatry between the two species also occurs in the Vandersterberge in the Richtersveld, where the two species have been collected only 3 km apart.

Natural history: Attribution of fragile skin to the species (Visser 1984; Branch 1988) stems from FitzSimons' (1943) general observations in his species account, but which now seem to have been based on confusion with other species. The most detailed histological and biomechanical investigation of the phenomenon (Bauer, Russell & Shadwick 1993) was undertaken on voucher specimens now referred to another species (see below), and also included an illustration of a torn skin in a specimen of *P. haackei*. The phenomenon appears to occur in *P. namaquensis*, but with a much reduced (30%) incidence. We cannot confirm from personal observation that this species is also active during the day. Previous comments on the topic attributed to the species may have been based on confusion with other species. Lawrence (1936) described a new species of prostigmatic mite (*Geckobia namaquensis*) from Garies material.

Remarks: There is confusion over the number of types, date of publication, and type locality of *P. namaquensis*. The type description was published in the first issue of the SAM Annals. Reprints are dated 1898, whereas the volume is usually dated 1899. The volume was issued in three parts between June 1898 and December 1899. Sclater's description of *Elasmodactylus namaquensis*, and a new frog (*Heleophryne purcelli*) and snake (*Grayia lubrica*; = *Lycodonorphus laevisissimus*), appeared in the first issue, and all should therefore be correctly dated as 1898. This was correctly recorded by Loveridge (1947), but both Methuen & Hewitt (1914) and FitzSimons (1938, 1943) incorrectly list the date of description of *Elasmodactylus namaquensis* as 1899.

The type locality is given only as 'Namaqualand' by Sclater (1898), but this was amended, possibly by mistake and certainly without comment, to 'Little Namaqualand' by Boulenger (1910), and this change was followed by FitzSimons (1938, 1943). Sclater (1898) specifically designated a single type (SAM 935), noting only in passing that there '... exists in the Museum a second specimen, of which, however, the history is unfortunately unknown'. Methuen & Hewitt (1914) appear to have been the first to consider the second specimen as a second type, whereas FitzSimons (1943) listed simply 'Types in the South African Museum'. Loveridge (1947), on the other hand, referred to a type and paratype. Currently, two specimens are stored in the South African Museum under the number SAM 935, where both are catalogued as types. Both

are females; the largest specimen (A, SVL 84.7 mm) lacks a tail; that in the smaller specimen (B, SVL 77.0 mm) is unre-generated but detached. Both specimens conform to the scutellation details given in the type description, with the exception that neither has 10 supra- and infralabials on both sides (supralabials 11 on both sides in A, 11 and 10 in B; infralabials 11 on both sides in A and B) and the nasorostrals are separated by a granule in A, and are in contact in B (Sclater made no mention of the nasorostral condition in the type description). The type SVL is given as 80 mm, and the illustration of the type shows an attached, original tail (Sclater, 1898). The smaller specimen has an intact tail and appears closer to the type description. We here recognize it as the holotype of *Pachydactylus namaquensis*; the larger specimen is the paratype.

During the last century Namaqualand was poorly defined and could have been construed as extending from the Nuweveldberg to southern Namibia. The vague type locality could therefore encompass all three species determined above. W. C. Sculley, who collected the types of *P. namaquensis*, was the last magistrate and Civil Commissioner for the northern border of the Cape Colony and Namaqualand, and he spent most of his time based in Springbok and Bushmanland (McLachlan, pers. comm., 3 May 1995). Snakes collected by Sculley, and listed by Sclater as being collected in Namaqualand, include *Psammophis crucifer* and the wide-ranging *Pseudaspis cana*. The former is rare in Namaqualand, where it has a restricted distribution and is known from only four localities (Broadley 1983). These include two coastal localities, Hondeklipbaai (3017Ad) and Kleinsee (2917Ca), outside of the range of any of the '*P. namaquensis*' groups. However, the remaining two localities, Steinkopf and Springbok, both occur within the range of *P. namaquensis*. Both of Sclater's extant types (see above), and the excellent illustration in dorsal view in the type description, are obviously referable to specimens from the Namaqualand region. They have well differentiated dorsal scalation, with enlarged, faintly keeled tubercles more than twice the size of the surrounding granules; spine-like lateral tubercles on the tail; although female they have an arc of four enlarged cloacal spurs; the supralabial enters the nostril; and there are 10 and 7 (holotype and paratype, respectively) granules bordering the mental, and 22 and 16 granules bordering the mental and adjacent infralabials.

It clearly remains undesirable for the type of *P. namaquensis* to retain a type locality as vague as 'Namaqualand', and we here take the opportunity to restrict the type locality to the vicinity of Springbok, Namaqualand, Northern Cape Province, South Africa. Our reasons for this are: (a) in their morphological attributes the types are referable to *P. namaquensis*, which is the only species of the group occurring in the region; (b) the captor of the type, W.C. Sculley, was frequently based in Springbok at the time that the type was acquired; and (c) other reptiles collected by Sculley are found around Springbok, particularly *Psammophis crucifer*, which is poorly known elsewhere in Little Namaqualand and unknown from Great Namaqualand.

Pachydactylus kladaroderma n. sp. Figures 2a and 3. (Fragile thick-toed gecko)

Pachydactylus namaquensis FitzSimons, 1943 (in part).

Type Material: Holotype: PEM R11195, adult female, collected by W.R. Branch, G.V. Haagner, A.M. Bauer, and C. Weatherby, 8 February 1995.

Type locality: 'Dolerite Towers', Moltene Pass, Nuweveldberge, Karoo National Park (32°15'09"S, 22°34'07"E, 1077m; 3222Bc) Western Cape Province.

Paratypes: Thirteen specimens: PEM R11193-94, CAS 198285, same details as holotype; PEM R6544, type locality, collector G.V. and A. Haagner, and A. Vlok, 10 October 1991; PEM R11197-98; CAS 198286, roadside cutting, Moltene Pass, Nuweveldberge, Karoo National Park (32°12'34"S, 22°33'35"E, 1164 m; 3222Ba); PEM R11200, CAS 198288, LSUMZ 56974, top of Moltene Pass, Nuweveldberge (32°10'24"S, 22°32'55"E; 1682 m); PEM R11199, Sak Rivier, Nuweveldberge (32°03'56"S, 22°27'01"E, 1504 m; 3222Ab); same date and collectors as holotype; PEM R4370, R4660, Karoo National Park (3222Ad, 3222Bc), W.R. Branch, October 1984.

Additional material: 32 specimens (see Appendix).

Etymology: From the Greek *kladarios* (easily broken) and *derma* (skin), with reference to the fragile skin exhibited by this species and several other species of *Pachydactylus* to which it may be closely related (see general discussion).

Description: Holotype: PEM R11195, adult female. Head depressed, slightly longer than broad and distinct from neck; snout obtusely rounded and 1.43 times the ear to eye distance, and 2.23 times the eye diameter; ear opening an oblique,



Figure 2 Dorsal views of: (A) *Pachydactylus kladaroderma* sp. nov. (Anysberg, CAS 195395) and (B) *Pachydactylus haackei* sp. nov. (Richtersveld National Park, CAS 193362).



Figure 3 Lateral view of live holotype (PEM R11195) of *Pachydactylus kladaroderma*.

elongate (height more than twice width), rounded slot that lacks enlarged lobules of tympanic shields; eye relatively large, ringed by small ciliary granules that are only slightly larger on the upper edge, and with a vertical pupil that constricts to two pinhole openings in preserved specimens; rostral broader than wide, with a scalloped dorsal edge and lateral projections into the nostrils; nasal region distinctly raised, with nostril directed upwards and bordered by three nasals and extensions of the rostral and first supralabial; suture of supranasal and rostral rounded to form a scallop into the dorsal margin of the rostral; supranasals separated by a single granule; mental rectangular, narrower than rostral, more than 1.5 times longer than broad, and bordered by five granules; no enlarged chin shields, infralabials bordered by granules that are largest bordering the first infralabial on each side; eight granules border the mental and adjacent infralabials; supralabials 12; infralabials 12. Scales on snout and between eyes small and granular, larger on loreal and canthal region; crown of head covered with small granules with no scattered tubercles; chin and throat covered with small, flattened granules. Back covered with granules that are larger than those on crown, intermixed with enlarged tubercles that may be flattened or faintly keeled, and longitudinally oval or rounded, and are denser and more rounded on the sides of the body and absent along backbone; tubercles on thighs rounded and subconical. Belly covered with flattened, smooth, imbricate scales, that are enlarged on underside of thighs.

Body stout; limbs short; digits moderate, with distal expansions well developed and subdigital lamellae arranged as follows: fingers I and II, 10 lamellae each; fingers III to V, 11 lamellae each; toe I, 10 lamellae, toe II, 11 lamellae, toe III, 12 lamellae; toes IV and V, 13 lamellae. The last (most distal) lamella of each digit is paired; all toes have obvious claws, but these are absent on the fingers. The median row of subdigital scales on the basal portion of digits 2–3 times width of adjacent granules and occasionally divided. Original tail (69.34 mm) slightly smaller than snout-vent length, very broad basally and tapering rapidly; segmented, distinctly so on sides, each segment above with 6–7 rows of scales includ-

ing towards the distal border of the segment a transverse row of 6–8 enlarged, pointed tubercles, of which the lateral ones are the largest, but not extended into spines; below the scales are large and imbricate, arranged in three rows on the proximal segments, reducing to two rows at midlength, and to a single series of enlarged subcaudals (without eschuchen scales) distally. An oblique row of three enlarged, flattened tubercles occurs on the tail base on either side of the vent. Meristics for holotype and paratype series are shown in Table 3.

Colouration: Dark grey-brown dorsally, with vague blotches that are more conspicuous on the tail, forming a series of six irregular bands, that are wider distally; ventrum grey, lighter beneath the head, throat, chest and lower surfaces of the limbs and tail.

Diagnosis: This species may be diagnosed from the majority of *Pachydactylus* species by its large size (maximum SVL 85.9 mm), scattered dorsal tubercles, and fragile skin. It may be diagnosed from *P. bibronii* and *P. laevigatus* by the entry of the rostral into the nostril and the absence of co-ossified skin on the head, and from *P. tetensis* by the absence of pre-anal pores in males. It differs from *P. namaquensis* and *P. haackei* by: its more slit-like ear opening (round or squared in *P. namaquensis* and *P. haackei*); low number of granules bordering the mental (3–6), and mental and adjacent infralabials (5–13); the frequent (79%) occurrence of the supralabial entering the nostril; and its drab brown base colouration. It is further differentiated from *P. haackei* on the basis of the 11 fixed allozyme loci differences discussed below, in having a narrow parietal process of the postfrontal bone, and by having relatively broader pads on the 4th toe, and from *P. namaquensis* by the more heterogenous dorsal scalation, smaller cloacal spurs, lack of spine-like tubercles on the lateral surfaces of the tail, and more fragile skin.

Distribution: Restricted to the southern escarpment mountains and Cape Fold Mountains (Figure 4). It extends in an arc from the Aasvoëlberge, at the eastern end of the Nuweveldberge (3122Dd), along the escarpment edge to Verlatekloof

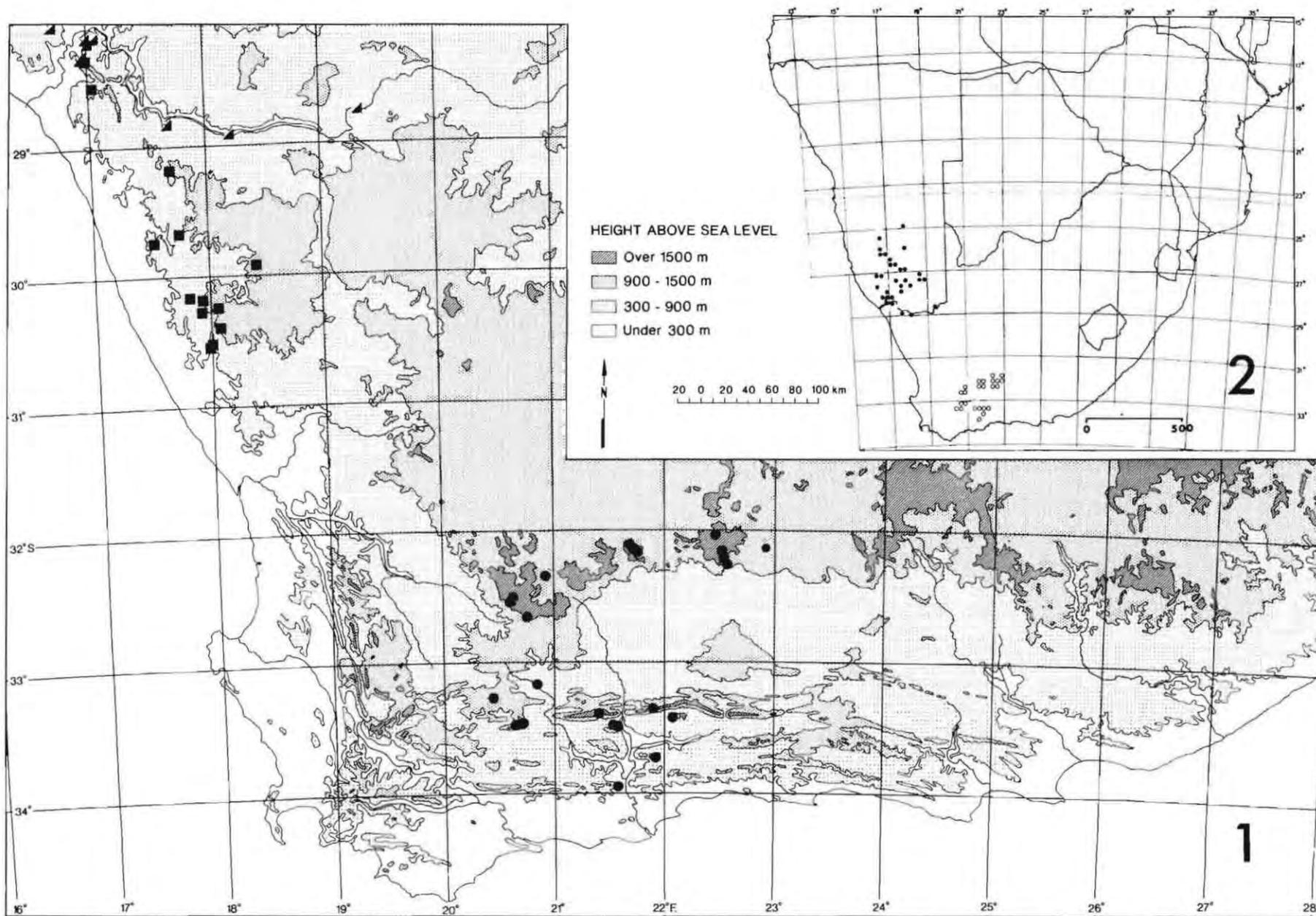


Figure 4 Distribution of species in the *Pachydactylus namaquensis* complex. Map 1. *Pachydactylus kladaroderma* (solid circles); *Pachydactylus namaquensis* (solid squares; a single Namibian record, Namuskluft Inselberg (2716Dd), is not shown); and *Pachydactylus haackei* (half triangles; most Namibian records are shown in Map 2). Map 2 (insert). *Pachydactylus haackei* (solid circles); *Pachydactylus kladaroderma* (open circles).

Pass at the southern tip of the Roggeveldberge, and south, via the Witteberg near Matjiesfontein, to the central Cape Fold Mountains surrounding the western Little Karoo (Branch & Bauer 1995). It may be expected to extend north along the Roggeveldberge, possibly to the Hantamberge. The southern record is on the northern slopes of the Langeberge, at Farm Bergfontein, Riversdale (3321Dc), although Visser (1984) noted a vague locality in the Langeberge near Albertina. It has been collected as high as 1682 m a.s.l in the Nuweveldberge, and at 750 m a.s.l in the plains around Anysberg.

Natural history: A histological and biomechanical investigation of fragile skin in the species (as *P. namaquensis*) was undertaken by Bauer, Russell & Shadwick (1993). Specimens in the Nuweveldberge have been collected sharing large horizontal cracks in metamorphosed sandstones and shales with *Pachydactylus bibronii*, *P. oculus* and *Mabuya sulcata*. All specimens have been collected on large rock outcrops, often in relatively moist habitats (veld types follow Acocks, 1975), eg. central upper Karoo (Molteno Pass), mountain renosterveld (Verlatekloof Pass, Komsberg Pass), succulent mountain scrub (Huisrivier Pass), karroid broken veld (Anysberg), and false fynbos (Gamka Mountain Nature Reserve, Langeberge, and Seweweekspoort). A paratype (PEM R6544) was collected whilst active on the road at the type locality in the early evening (19h00), and another was active at 22h00 (Huisrivier Pass). Three of four specimens collected at the type locality (including the holotype), were sitting on roadside rockfaces, in exposed, but shaded positions up to 20 cm from retreats, at 14h00 on a clear, hot day. Other geckos active during the day in similarly exposed positions, sometimes in full sun, were also observed at Verlatekloof Pass (07h50), Komsberg Pass (10h30), and Gamka Mountain Nature Reserve (12h15). Their drab, mottled colour pattern imparts an effective camouflage, and geckos remain immobile when first observed, but run quickly into shelter if approached too closely. Within the Cape Fold Mountains the species has mutually exclusive distributions with two other large geckos; *Afroedura hawequensis*, described from the Hawekwa Mountains near Paarl (Mouton & Mostert 1985), is restricted to mountain isolates in the south-western Cape, from Villersdorp to Bainskloof (Mouton, et al. 1987); a large, as yet undescribed *Phyllodactylus* species occurs at high altitude in rock cracks on the eastern Cape Fold Mountains, and has been collected within 6 km of a single juvenile *P. kladaroderma* (Branch & Bauer 1995). The latter was collected at lower altitude on the northern slopes of the Swartberg, but may occasionally occur syntopically with the Swartberg *Phyllodactylus*.

Pachydactylus haackei n. sp. Figure 2 (Haacke's thick-toed gecko)

Pachydactylus namaquensis Methuen & Hewitt, 1914 (in part).

Type Material: Holotype: PEM R9282, adult female, collected 30 June 1994 by W.R. Branch, R. Shine, P. Harlow and J. Webb.

Type locality: Farm Kuchanas, Great Karasberg, southern Namibia (27°02'S, 18°43'E; 2718Ba).

Paratypes: Nine specimens: PEM R9283-4, 10941, same

details as holotype; PEM R7606, adult female, 1.3 km SE towards Nichodaemus from the top of Helskloof Pass, Richtersveld National Park (28°20'37"S, 16°59'01"E; 2816Bd; alt. 677 m), collected W.R. Branch and R. Hall, 15 September 1992; PEM R7358-9, juvenile and subadult, 'Akkedis Drive', Richtersveld National Park (28°10'35"S, 17°01'13"E; 2817Aa), W.R. Branch and R. Hall, 1 September 1992; CAS 193362, adult female, 12.6 km E of Sendelingsdrift, Richtersveld National Park (28°08'S, 16°58'E; 2816Bb), A.M. Bauer, J. Vindum, H. Robeck and D. King, 29 June 1993; PEM R7305, adult male (tail lost), north-west of Koeroedals, Richtersveld National Park (2817Ac); AMNH 141230, 20 km E Ai-Ais Hot Springs, Ai-Ais and Fish River Canyon Reserve (27°38'S, 16°20'E), D. Frost and A. Channing, 21 September 1994.

Additional material: 48 specimens (see Appendix).

Etymology: Named after Wulf D. Haacke, Curator of Herpetology, Transvaal Museum (Pretoria), in acknowledgement of his long association with the geckos of the western arid regions of southern Africa.

Description: Holotype: PEM R9282, adult female. Head depressed, slightly longer than broad and distinct from neck; snout obtusely rounded, swollen in the canthal region, and 1.22 times the ear to eye distance, and 2.04 times the eye diameter; ear opening an oblique oval (height less than twice width), that lacks enlarged lobules of tympanic shields; eye relatively large, ringed by small ciliary granules that are only slightly larger on the upper edge, and with a vertical pupil that constricts to two pinhole openings in preserved specimens; rostral broader than wide, with a scalloped dorsal edge and lateral projections into the nostrils; nasal region distinctly raised, with nostril directed upwards and bordered by three nasals and extension of the rostral; first supralabial excluded from nostril by contact between rostral and postnasal; suture of supranasal and rostral rounded to form a scallop into the dorsal margin of the rostral; supranasals separated by a single granule; mental rectangular, narrower than rostral, more than 1.5 times longer than broad, and bordered by six granules; no enlarged chin shields, infralabials bordered by granules; 15 granules border the mental and adjacent infralabials; supralabials 12; infralabials 11. Scales on snout and between eyes small and granular (a slight skin tear occurs in the midline), larger on loreal and canthal region; crown of head covered with small granules with no scattered tubercles; chin and throat covered with small, flattened granules. Back covered with granules that are larger than those on crown, intermixed with enlarged tubercles that are rarely more than twice surrounding granules, that may be faintly keeled, and longitudinally oval or rounded, and are denser and more rounded on the sides of the body and absent along backbone; tubercles on thighs rounded and subconical. Belly covered with flattened, smooth, imbricate scales, that are enlarged on underside of thighs.

Body stout; limbs short; digits moderate, with distal expansions well developed and subdigital lamellae arranged as follows: fingers I, III, IV and V, 11 lamellae each, finger IV with 12 lamellae; toe I, 10 lamellae, toe II, 11 lamellae, toe III, IV and V with 13 lamellae. The last (most distal) lamella of each digit is paired; all fingers and toes lack claws. The median

row of subdigital scales on the distal portion of digits 2–3 times width of adjacent granules and occasionally divided. Tail (76.1 mm, last 13 mm regenerated) slightly shorter than snout-vent length, very broad basally and tapering rapidly; segmented, distinctly so on sides, each segment above with 5–7 rows of scales including towards the distal border of the segment a transverse row of 6–8 enlarged, pointed tubercles, of which the lateral ones are the largest but are not extended into spines; below the scales are large and imbricate, reducing to one row at midlength, and becoming irregular distally. An oblique row of three to four enlarged, flattened tubercles occurs on the tail base on either side of the vent. Meristics for the type series are shown in Table 3.

Colouration: Pink-grey dorsally, with vague blotches that are more conspicuous on the tail, forming a series of seven irregular bands, that are wider distally; ventrum cream, lighter beneath the head, throat, chest and lower surfaces of the limbs and tail, and with vague dark reticulation on sides.

Diagnosis: This species may be diagnosed from the majority of *Pachydactylus* species by its large size (maximum SVL 84.8 mm), scattered dorsal tubercles, and fragile skin. It may be diagnosed from *P. bibronii* and *P. laevigatus* by the entry of the rostral into the nostril and absence of co-ossification of the skin on the head, and from *P. tetensis* by the absence of preanal pores in males. It differs from *P. kladaroderma* by its more round or squared ear opening (slit-like in *P. kladaroderma*); high number of granules bordering the mental and adjacent infralabials (11–19); the general exclusion of the supralabial from the nostril (only 3.7% entry); and brighter, paler colouration. It is further differentiated from *P. kladaroderma* on the basis of the 11 fixed allozyme loci differences discussed below, and from *P. namaquensis* by the more heterogenous dorsal scalation, smaller cloacal spurs, lack of spine-like tubercles on the lateral surfaces of the tail, and more fragile skin. From both *P. namaquensis* and *P. kladaroderma* it differs in having a more robust parietal process of the post-frontal bone, narrower pads on the 4th toe, and an original tail that is subequal to or longer than the snout-vent length.

Distribution: Centered mainly in southern Namibia, extending as far north as Farm Duwisib, Maltahohe District (2516Bc). In the south it is found in the rocky mountains along the lower Orange River, extending inland to Onseepkans and west to the Vandersterberg in the Richtersveld (Figure 4). The altitude record appears to be between 5000–6000 ft (944–1133 m); FitzSimons (1938) recorded a specimen from this general altitude from Brukkaros Mountain, and a large female was collected at 1087 m a.s.l. on the summit of the Aurusberg (Branch 1994).

Natural history: The species is rupicolous, and possibly communal (at least in winter). Diurnal activity away from rock cracks has not definitely been observed for this northern species, as FitzSimons' observations (1938) of such activity may refer to true *P. namaquensis*. The holotype and a series of three other paratypes (2 females, 1 male; PEM R9282-4, R10941), collected in mid-winter (30 June), were all sheltering together in a large crack beneath an exfoliating slab on a gneiss outcrop in the foothills of the Great Karasberg. Sharing the same crack were two *Pachydactylus bibronii* and two

Agama aculeata adults. Another paratype (PEM R7606) was collected in a rock crack on an exfoliating granite outcrop in Nama Succulent Karoo vegetation, with large clumps of *Aloe pearsoni*, *Euphorbia mauritanica*, *Tylecodon paniculata* and small clumps of *Aloe melanocantha*, *Gasteria pillansi* and *Stapelia garipeensis*. It was collected in association with a number of other rupicolous lizards, including *Platysaurus capensis*, *Mabuya sulcata*, *Mabuya variegata*, *Pachydactylus bibronii*, and *Pachydactylus weberi*. Two of the paratypes (PEM R7358-9) were collected on a small granite koppie bordering a dry river bed, with *Aloe dichotoma* and *Pachypodium namaquensis* vegetation, and in association with *Cordylus polyzonus*, *Platysaurus capensis*, *Pedioplanis inornata*, *Mabuya variegata*, *M. sulcata*, and *Pachydactylus weberi*. Haacke (1965) recorded this species (as *P. namaquensis*) as occurring with *P. laevigatus* and *Afroedura africana tirasensis* on granite boulders in the Bethanie District, Namibia. FitzSimons (1938) recorded communal egg sites in rock cracks at Barby, and another was found on the Aurusberg (Branch 1994). An egg size of approximately 16 mm was recorded by FitzSimons (1938). Like *P. kladaroderma*, *P. haackei* has an exceptionally fragile skin and an illustration of the phenomenon in a Richtersveld specimen is included in Bauer, Russell & Shadwick (1993).

Key to the species in the *Pachydactylus namaquensis* complex

- 1 Enlarged, spine-like scales along lateral margins of tail; cloacal spines large; dorsal tubercles enlarged, twice diameter of surrounding granules
 *P. namaquensis*
 Lateral margin of tail with only slightly enlarged scales; cloacal spines small; dorsal tubercles heterogenous, rarely twice diameter of surrounding granules
 2
- 2 Ear opening slit-like; 5-13 granules bordering mental and adjacent infralabials; first supralabial usually entering the nostril; original tail shorter than snout vent length
 *P. kladaroderma* n. sp.
 Ear opening rounded; 11-19 granules bordering mental and adjacent infralabials; first supralabial rarely entering the nostril; original tail longer than snout vent length
 *P. haackei* n. sp.

Character variation

Scalation: The rostral always enters the nostril in *P. namaquensis* and *P. haackei*, and is excluded from only 7.7% of nostrils in *P. kladaroderma* (owing to contact of the nasorostral and 1st supralabial). In contrast the first supralabial usually enters the nostril in *P. kladaroderma* (79.34%), is mostly excluded in *P. namaquensis* (34% entry), and rarely enters in *P. haackei* (3.7%). The nasorostrals are in contact in the holotype of *Pachydactylus namaquensis* and separated by a granule in the paratype. The nasorostral condition was variable; they were in contact in 56% of *P. namaquensis*, but in only 28.26% and 27.27% in *P. kladaroderma* and *P. haackei*, respectively. Although FitzSimons (1943) recorded that 1–4 small granules may separate the anterior nasorostrals, in only

three cases were the nasorostrals separated by more than a single granule during this study. This discrepancy may arise from different methodologies, as FitzSimons may have counted all granules (including those in longitudinal series) separating the nasorostrals. Hewitt's (1932) claim that Garies material (*P. namaquensis*) has increased numbers of granules separating the nasorostrals relative to Karasberg material (*P. haackei*) is not upheld.

Slater (1898) and FitzSimons (1943) noted the absence of chin-shields and that the throat was covered in small granules, but they did not count the granules bordering the mental and adjacent infralabials. This is unfortunate, as it is an informative character (Figure 5). The holotype of *P. namaquensis* has 10 granules bordering the mental and 22 granules bordering the mental and adjacent infralabials (7 and 16, respectively in the paratype). Fewer granules border both the mental (3–6, mean 4.7), and mental and adjacent infralabials (5–13, mean 10.36) in *P. kladaroderma*, than either *P. namaquensis* (mental, 7–11, mean 8.28; mental + LL, 13–21, mean 16.48) or *P. haackei* (mental 3–10, mean 6.52; mental + LL, 11–19, mean 14.49). Generally higher counts were obtained for the number of supra- and infralabials during this study than previously recorded (e.g. Slater 1898; FitzSimons 1943), probably because of the inclusion of small scales in the rictal region. There were no significant differences in either supra- or infralabial counts between the groups.

Both the holotype and paratype of *P. namaquensis* have enlarged dorsal tubercles, that are well keeled, greater than twice the size of surrounding granules, and ringed by 10–12 granules. This condition categorized *P. namaquensis*. *P. kladaroderma* and *P. haackei* had more heterogeneous dorsal scalation, the distinction between tubercles and granules being less defined, the former rarely being more than twice the size of granules, only feebly keeled, and ringed by only 8–11 granules. The illustration of the type (Slater 1898) shows greatly enlarged and spine-like lateral tubercles on the tail base. This is confirmed in both types and in all *P. namaquensis* specimens ($n = 14$; Figure 1b) with, at least in part, original tails, including adults and juveniles, and both sexes.

Original tails in *P. kladaroderma* ($n = 27$) and *P. haackei* ($n = 24$) usually had a horizontal series of 6–8 enlarged tubercles on each tail annulus, and although these were slightly larger in *P. kladaroderma* than *P. haackei* those on the sides were never spine-like, or greater than twice the size of the dorsal tubercles on the tail. Enlarged cloacal tubercles were present in all groups, but subject to some variation and complicated by sexual dimorphism, as cloacal spurs were larger in males than females in all groups. They were strongly developed in most specimens (96%) of *P. namaquensis*, where they numbered from 3–5 and in mature males often formed a prominent arc on the ventral surface of the tail base. The types of *P. namaquensis*, which are both female, have four medium-sized spurs on either side of the tail base. In *P. kladaroderma* large cloacal spurs were infrequent (22.22%), and only present in mature males (where they never reached the degree of development seen in *P. namaquensis*). Enlarged spurs were rare (1.88%) in *P. haackei*, where they were usually smaller in both sexes and restricted to the ventro-lateral surfaces of the tail base.

Slater (1898) noted that the ear opening was oval in the type of *P. namaquensis*. Although individually variable in all groups, the ear opening has a greater tendency to be slit-shaped, sloping at a gentle angle from the vertical, in *P. kladaroderma* (76.8%) than in either *P. namaquensis* (18%) and *P. haackei* (7.5%), where it ranged from oval, rounded to squarish in outline. Slater (1898) initially placed *namaquensis* in the genus *Elasmodactylus* because of the presence of claws on the toes in the type. In both female types claws are very obvious on all the hind toes. Subsequent workers (Haacke 1976; Joger 1980, 1984, 1985; Bauer & Good 1995) have demonstrated that females of the *Pachydactylus*-group genera also generally possess claws on digits I and V of the pes. Claws were only found on the hind limbs, and were variably present in all three groups. They were present in: 43.33% ($n = 43$) of *P. kladaroderma*; 81.81% ($n = 20$) of *P. namaquensis*; and 52.94% ($n = 26$) of *P. haackei*. Claws appeared more frequently in females than males, but in all groups a few males had claws: *P. kladaroderma*: claws present in 73.33%

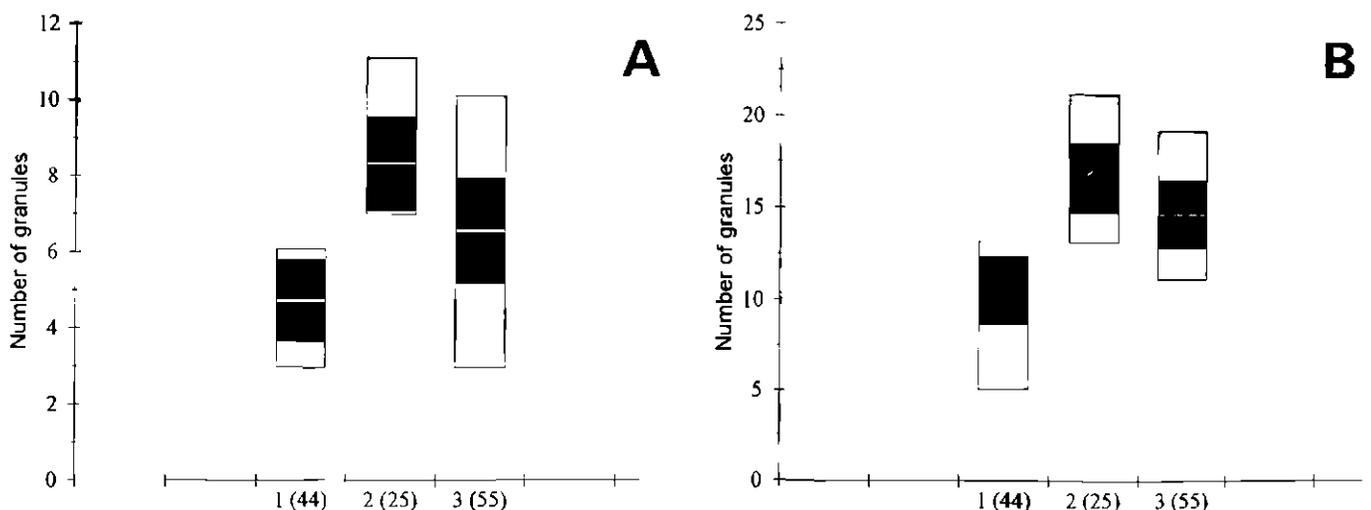


Figure 5 Number of granules bordering the mental (A), and mental and first supralabial (B) in the *Pachydactylus namaquensis* complex. Whisker bars display range, mean and one standard deviation around the mean. 1. *Pachydactylus kladaroderma*; 2. *Pachydactylus namaquensis*, and *Pachydactylus haackei* ($n =$ number of specimens).

females ($n = 15$), 9.09% of males ($n = 11$); *P. namaquensis*: claws present in 100% females ($n = 8$), 33% of males ($n = 3$); and *P. haackei*: claws present in 61.53% females ($n = 13$), 40% of males ($n = 5$). The variability in the presence of claws in the groups remains unexplained. Investigation was only performed at $\times 40$ magnification, and small claws hidden within the terminal scales may have been overlooked. The 'presence' or 'absence' of claws may then be simply a reflection of the degree of development of the claws. It remains evident, however, that claws on the hind toes in *P. namaquensis* are significantly more fully developed, either in size or presence, than in either *P. kladaroderma* or *P. haackei*.

The presence of body scars and fresh skin tears was not evenly distributed among the groups, being found in 58% of *P. kladaroderma*, 70% of *P. haackei*, and only 30% of *P. namaquensis*. Neither of the two types of *P. namaquensis* have torn skin.

Morphometrics: For discriminant function analysis all eight morphometric characters examined were adjusted for overall body size differences by dividing by snout-vent length. Of the 128 specimens used in the analysis only 38 had complete morphometric information. A further 68 specimens had complete information except for tail length. For this reason, all analyses were conducted twice: once for 106 specimens (38 *P. kladaroderma*, 23 *P. namaquensis*, 45 *P. haackei*) but excluding tail length, and once for 38 specimens (14 *P. kladaroderma*, 9 *P. namaquensis*, and 15 *P. haackei*) with all measurements included. The remaining 22 specimens were not considered further.

Post-hoc identification of specimens into taxa by discriminant function analysis (DISCRIM procedure; SAS 1994) was fairly good when tail data were excluded; 84.2% of *P. kladaroderma*, 95.7% of *P. namaquensis*, and 91.1% of *P. haackei* were properly identified. One to three specimens of each taxon were misclassified as each of the other two groups

except that no *P. namaquensis* were misclassified as *P. haackei*. A plot of canonical axes 1 and 2 from the CANDISC procedure in SAS (SAS 1994) is illustrated in Figure 6a, where the lack of complete discrimination is seen in the partial overlap of the polygons. Plots of axes 1 and 2 from a canonical analysis of the reduced set of specimens for which tail data was available are shown in Figure 6b. In this case, the *P. haackei* polygon does not overlap either that of *P. kladaroderma* or *P. namaquensis*, suggesting a more complete discrimination of the groups. Discrimination was, in fact, complete among all specimens, and the post-hoc classification by discriminant function analysis of these data yields 100% correct identification of the specimens.

After conducting Bartlett's test to insure equivalent variances in the ratio data resulting by division of the variables by snout-vent length, analyses of variance (ANOVA) were conducted to determine the most important single morphometric variables for discriminating among the three groups. Only tail length and head length showed significant results ($p = 0.0001$ and 0.020 , respectively). Post-hoc Scheffe's tests further showed that the significant differences in these variables occurred between *P. kladaroderma* and *P. haackei* in both characters, and between *P. namaquensis* and *P. haackei* in tail length. *P. haackei* has a significantly longer tail than either of the other species and a significantly shorter head than *P. namaquensis*.

Allozymes: Eight of the 23 loci scored in this analysis were monomorphic in all populations (Adh, Ak, Ldh1, Mdh1, Mdh2, Me, Pep4, and Sod). The distribution of alleles at the other 15 loci is presented in Table 4. Of the 15 variable loci, *P. haackei* and *P. kladaroderma* were fixed for alternative alleles or allele combinations at 11 (Aat, Fum, Gd, Gdh, Glud, Icdh2, Pep2, Pep3, Pep5, Pgdh, and Pk). At the remaining four loci (Icdh1, Ldh2, Pep1, and Pgm) one or more *P. kladaroderma* populations were heterozygous for a *P.*

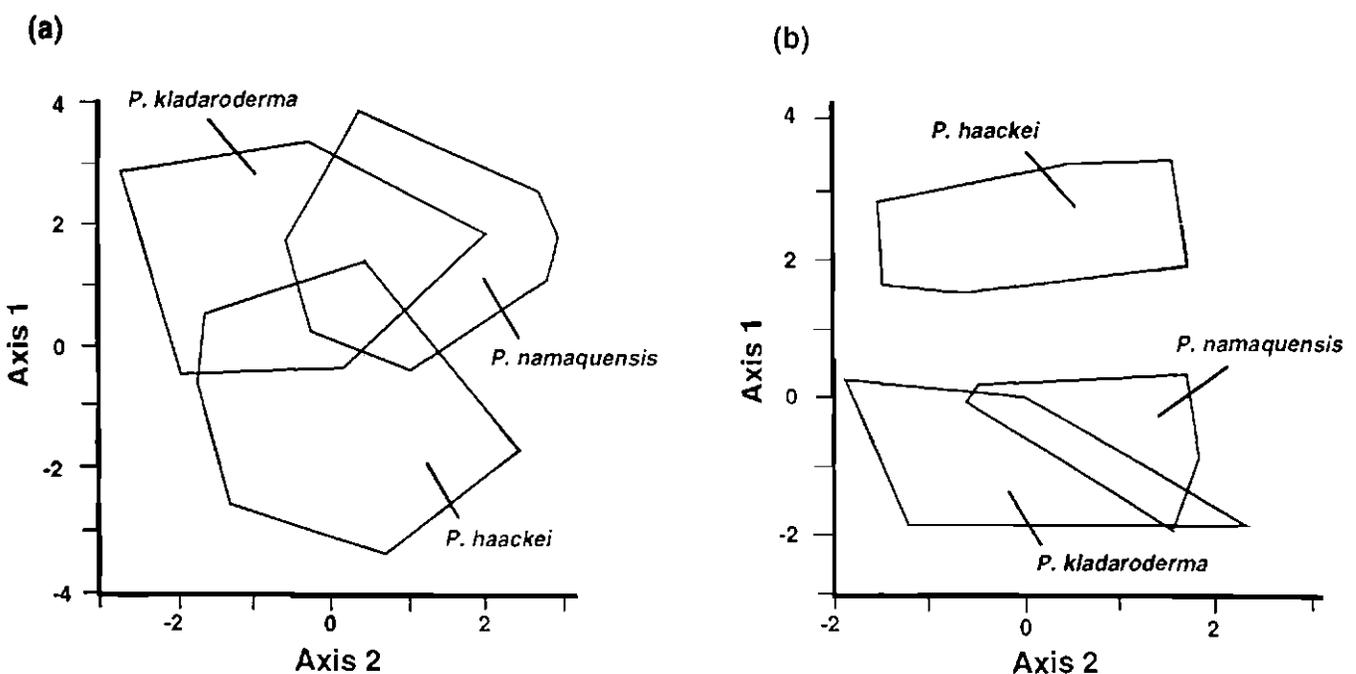


Figure 6 Discriminate Function Analysis. Plots of canonical axes 1 and 2 for data sets lacking (A) and including (B) tail data for the *Pachydactylus namaquensis* complex.

Table 4 Distribution of alleles at the 15 loci that are variable within *Pachydactylus kladaroderma* and *P. haackei*. Adh, Ak, Ldh1, Mdh1, Mdh2, Me, Pep4 and Sod were monomorphic in all populations. Mol = Molteno Pass; Kom = Komsberg Pass; Suth = Sutherland; Ver = Verlaterskloof Pass; Any = Anysberg; Sew = Seweweekspoort; Huis = Huisrivier Pass

	<i>P. kladaroderma</i>							
	<i>P. haackei</i>	Mol	Kom	Suth	Ver	Any	Sew	Huis
Aat	a	b	b	b	b	b	b	b
Fum	a	b	b	b	b	b	b	b
Gd	a	b	b	b	b	b	b	b
Gdh	a	b	b	b	b	b	b	b
Glud	a	b	b	b	b	b	b	b
Icdh1	a	a(0.69) b(0.31)	b	b	b	b	b	b
Icdh2	a	b(0.36) c(0.64)	b	b	b	b	b	b
Ldh2	a	a(0.27) b(0.73)	a	a(0.83) b(0.17)	a	a	a	a
Pep1	a(0.83) b(0.17)	c	c	b(0.83) c(0.17)	c	b(0.75) c(0.25)	c	c
Pep2	a	b	b	b	b	b	b	b
Pep3	a	b	b	b	b	b	b	b
Pep5	a	b	b	b	b	b	b	b
Pgdh	a	b	b	b	b	b	b	b
Pgm	a	a(0.64) b(0.36)	a	a(0.67) b(0.33)	a(0.50) b(0.50)	a	a	a
Pk	a	b	b	b	b	b	b	b

haackei allele. Nei (1978) genetic distances were much greater (DN=0.833-0.873) between *P. haackei* and *P. kladaroderma* than among the populations of *P. kladaroderma* (DN=0-0.083) (Table 5).

General discussion

Allozyme differentiation in the absence of a test of sympatry cannot be taken as irrefutable evidence for species-level dis-

tinction, but the magnitude of the genetic difference between *P. kladaroderma* and *P. haackei* provides very strong circumstantial evidence for their specific distinctness. Good (1988) found that the lizard genera *Elgaria* and *Ophisaurus*, representing two distinct subfamilies of the family Anguillidae, were fixed for different alleles at only seven of 22 loci; *P. kladaroderma* and *P. haackei* differ at 11 of 23 loci.

Isolation by distance is the rule in non-vagile terrestrial organisms, so that populations that are geographically closer should be more genetically similar than populations that are farther apart. *P. haackei* is genetically much more distinct from any population of *P. kladaroderma* than are any of those populations to each other. However, *P. haackei* is also geographically much farther away. If the *P. haackei* to *P. kladaroderma* genetic distance simply represents the differentiation that would be expected within *P. kladaroderma* populations at that great a geographic distance, the allozyme differences between the two forms cannot be considered evidence for species status. To test this, geographic and genetic distances within *P. kladaroderma* populations were compared. Genetic differentiation per unit distance in this group ranges from zero to 0.255 Nei (1978) distance units per 100 km but there is no significant relationship ($p < 0.05$) between genetic and geographic distance among the populations. The mean genetic/geographic distance ratio for all comparisons was 0.041 Nei units per 100 km. The geographic distances from the *P. haackei* sample to the seven *P. kladaroderma* samples range from 582 to 724 km. The mean within-*P. kladaroderma* divergence value would suggest that the genetic distance expected at that distance should be 0.239-0.297. The actual values are 0.833-0.873. Perhaps even more telling is the fact that there are no fixed allele differences among any of the populations of *P. kladaroderma*, including the population showing the largest genetic/geographic distance ratios in comparisons to other populations (Sutherland). There are 11-12 fixed differences between these populations and *P. haackei*. No frozen tissues of *P. namaquensis* were available for comparison with the new taxa. Genetic distances between all three taxa is presently under study (Branch, Bauer & Good, in prep.).

Few comparable studies on genetic distance have been published for other southern African reptiles. Brody *et al.*

Table 5 Nei (1978) genetic distances among populations *Pachydactylus kladaroderma* and *P. haackei*. Mol = Molteno Pass; Kom = Komsberg Pass; Suth = Sutherland; Ver = Verlaterskloof Pass; Any = Anysberg; Sew = Seweweekspoort; Hus = Huisrivier Pass

	<i>P. kladaroderma</i>							
	<i>P. haackei</i>	Mol	Kom	Suth	Ver	Any	Sew	Huis
<i>P. haackei</i>	-							
Mol	0.839	-						
Kom	0.833	0.045	-					
Suth	0.873	0.083	0.056	-				
Ver	0.873	0.034	0.011	0.045	-			
Any	0.844	0.080	0.033	0.022	0.044	-		
Sew	0.833	0.045	0	0.056	0.011	0.033	-	
Hus	0.833	0.045	0	0.056	0.011	0.033	0	-

(1993) recorded Nei distances less than 0.27, with most lower than 0.2, between members of the *C. cordylus* complex, including *C. cordylus*, *C. oelofseni*, *C. niger*, *C. peersi* and *C. macropholis*. The latter two species are well defined rupicolous and terrestrial species, respectively, and yet have a genetic distance of only 0.1 ± 0.053 . Likewise, a Nei's distance of 0.25 was calculated between northern and southern sand sea populations of the Namib lacertid *Meroles anchietae* (Gordon & Griffin 1989). Distances between gekkonid taxa tend to be greater than seen in other lizard groups. Good & Bauer (1995) found Nei's distances of 0.571 to 0.833 between species of Madagascan *Phelsuma* and 0.833 to 1.190 between these and the southern African species *Phelsuma ocellata*. Within the day geckos of the Namib, genetic distances ranged from 0.182 between the sister taxa *Rhoptropus barnardi* and *R. biporosus* to 1.037 between *R. afer* and *R. boultoni* (Bauer & Good 1995). This range of distances is comparable to those determined between *P. kladaroderma* and *P. haackei* in this study. Support that the genetic differentiation between *P. kladaroderma* and *P. haackei* clearly suggests species-level differentiation is also illustrated when other within-*Pachydactylus* allozyme analyses are compared. The distinct species *P. bicolor*, *P. serval*, and *P. weberi* show only 4–8 fixed differences across the same 23 loci (Good & Bauer, unpubl.).

Genetic distance data may be used in conjunction with accurately dated geological events in order to calibrate a molecular clock (Maxson, Sarich & Wilson 1975; Sarich, 1977). These are only truly meaningful, however, if the divergence seen is in fact related to the dated events and if the taxa under study have evolved at equal rates since their separation (Murphy 1983). Nonetheless, empirical evidence suggests that comparable rates of allozyme evolution exist for many vertebrates. For lizards, a range of calibrations ranging from 8.4–26 MY per Nei's (1978) genetic distance unit have been calculated (Murphy & Papenfuss 1980; Murphy 1983; Wright 1983; Good 1988). Based on this range of values, the greatest divergence within the sampled populations of *P. kladaroderma* would correspond to a 0.74–2.2 MY time scale. The distance between *P. kladaroderma* populations and *P. haackei*, on the other hand, would correspond to a 7.4–22.7 MY divergence. Although the time scale derived from the genetic distance data is approximate at best, it does suggest a divergence of *P. haackei* and *P. kladaroderma* that may be related to Miocene events, with Pleistocene to Recent events being associated with separation between populations of the latter species.

It is likely that cladogenic events within the *P. namaquensis-kladaroderma-haackei* group are reflections of vicariant events that resulted in the fragmentation of the Cape Fold Mountains. The fragmentation of the Cape Folds is seen in the distribution of many amphibian and reptile taxa including *Phyllodactylus* (Branch, et al. 1995) and *Arthroleptella* (Channing, et al. 1994). Dating of specific events in the geological evolution of the Cape Folds remains obscure. However, there have been three main periods of orogenic activity in the region. Initial downwarping of the continental margins in the Jurassic and Cretaceous produced the great eastern and western escarpments in southern Africa and initiated the central basin of the Kalahari (Dingle, Siesser & Newton 1993). This was followed by periods of uplift during the Oligocene-

Miocene and Pliocene-Pleistocene, to yield the existing topography of the southern and western areas of the Cape (Axelrod & Raven 1978).

In the absence of a thorough revision of the genus *Pachydactylus*, it is not possible to evaluate the relationships of the three taxa discussed herein with any certainty. However, the fact that all were previously subsumed under the one name *Pachydactylus namaquensis* certainly suggests that these species are each other's closest relatives. Phenetically, *P. namaquensis* and *P. kladaroderma* are more similar to each other than either is to *P. haackei*, but this need not indicate sister status for this pair. All of the taxa express a number of features that are otherwise rare among *Pachydactylus*. Perhaps most striking of these is the ability to undergo regional integumentary loss as an escape mechanism. In these and other fragile-skinned geckos, a combination of a bi-layered dermis and preformed zones of weakness in the outer layer of the skin permit the loss of large patches of skin in response to imposed tensile forces (Bauer & Russell 1992). This ability is also seen in *Pachydactylus scutatus*, although it has probably evolved independently (Bauer, Russell & Shadwick 1993). This condition, however, is also seen in *P. tetensis* and in *P. tuberculosus*. Like members of the *P. namaquensis* group, these are both very large members of the genus and they appear to share a number of osteological features and scalation characteristics with them. Loveridge (1953) suggested that *P. tetensis* was both a descendent of *P. tuberculosus* and the ancestor of *P. namaquensis*.

The large genetic distance between *Pachydactylus haackei* and *P. kladaroderma* suggests that these two taxa diverged 13–23 mya. If indeed *P. tetensis* and *P. tuberculosus* are allied to these forms, it would seem likely that they are even more distantly related. It is possible that this group of large, skin-shedding geckos may represent relict forms of an early subdivision within the genus as a whole. These taxa have distributions peripheral to the genus as a whole, occupying the southern and western margins of the escarpment and the northern and eastern rim of the range of the genus. Patterns of relationship within this putatively monophyletic group and between it and other *Pachydactylus* are presently under study.

The recognition of two new large species of *Pachydactylus* raises some interesting points. First, it highlights the extent to which the southern African lizard fauna remains unknown, and suggests that detailed studies of other lizards may reveal that specific level variation may be subsumed within single taxa as presently construed. This has increasingly been the case among southern African geckos (e.g., Bauer & Branch 1995; Branch, et al. 1995). Secondly, the near sympatry of *P. haackei* and *P. namaquensis* raises the question of what, if anything, serves to segregate these morphologically very similar geckos. A comparable situation occurs in the northern Cape and western Namibia, where *P. bibronii* and *P. laevigatus* occur in sympatry. Clearly, much basic biological research remains to be done on southern African lizards, even in areas that have been 'well known' for long periods.

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Appendix 1 Specimens examined. AMNH = American Museum of Natural History; CAS = California Academy of Sciences, LSUMZ = Louisiana State University Museum of Natural Science, MCZ = Museum of Vertebrate Zoology; PEM = Port Elizabeth Museum; USNM = United States National Museum of Natural History. Localities are followed by quarter-degree coordinates in parentheses. H = holotype, P = paratype.

Pachydactylus haackei

Namibia: Farm Duwisib, Maltahohe, 25°17'S, 16°34'E (2516Bc) – TM 48391; Farm Barby, 25°50'S, 16°35'E (2516Dc) – TM 17596, 17606, 17608; Brukkaros Mountain, 25°52'S, 17°47' (2517Dd) – TM 17789; Farm Tiras, 26°10'S, 16°36'E (2616Ba) – TM 28284; 50 km S. of Helmeringhausen, 26°16'S, 17°02'E (2617Ac) – TM 28363-7; 32 km E. Goageb, 26°47'S, 17°32'E (2617Dc) – TM 17729; Seeheim, W. Keetmanshoop, 26°49'S, 17°48'E (2617Dd) – TM 22294-5; Farm, Luderitz, 27°12'S, 16°28'E (2716Ab) – TM 53195-6; Farm, Churuthabis, Bethanic, 27°27'S, 17°26'E (2717Ad) – TM 53219; Farm Horloog, Keetmanshoop, 27°25'S, 17°57'E (2717Bd) – TM 41850-1; Fish River Canyon, 27°35'S, 17°37'E (2717Da) – TM 27276-7, 36389, 50064, 50080, 50534, 54440; Narudas Sd, 27°14'S, 18°45'E (2718Bc) – TM 3098; west rim of Fish River Canyon, MVZ 144836-40; 6.4 km W. of Klein Karas, 27°32'S, 18°01'E (2718Ca) – TM 27988; Kraikluft, Great Karas Mountains – TM 3100-1; Aurusberg summit, Sperrgebiet, 27°38'S, 16°20'E (2716Cb) – PEM R7446; 20 km E. Ai-Ais Hot Springs, Ai-Ais and Fish River Canyon Reserve (27°38'S, 16°20'E) – AMNH 141229-30 (P); Namuskluft Inselberg (2716Dd) – SAM 43637; Farm Kuchanas, Great Karasberg, 27°02'S, 18°43'E (2718Ba) – PEM R9282 (H), R 9283-4 (P), 10941 (P); Dassiefontein (2718Bc) – SAM 46713; Obib Mountain (2816Ba) – SAM 44430; PEM R10546-7.

Northern Cape Province, South Africa: 12.6 km E. of Sendelingsdrift, Richtersveld National Park (2816Bb) – CAS 193362 (P), CAS 193363; Hottentotsparadys, 8.7 km E. of Helskloof gate, Richtersveld National Park (2816Bd) – CAS 193445; Helskloof Pass, Richtersveld National Park (2816Bd) – PEM R7606 (P); ca. 20 km E. of Sendelingsdrift, Richtersveld National Park (2817Aa) – CAS 186341-2; ca. 22 km. E. of Sendelingsdrift, Richtersveld National Park (2817Aa) – CAS 186348-50, 189016; north-west of Koeroedals, Richtersveld National Park (2817Ac) – PEM R7305 (P); Ploegberg, Richtersveld (2817Ca) – TM 52585; Richtersveld National Park, 28°10'35"S, 17°01'13"E (2817Aa) – PEM R7350, 7358-9 (P); 23.5 km E of Sendelingsdrift, Richtersveld National Park (2817Aa) – CAS 193640; 6 km S Vioolsdrift, 28°49'S, 17°41'E (2817Dc) – TM 27961; Mt Slater (?), Goodhouse (2818Bd) – PEM R10551; Goodhouse, 28°54'S, 18°14'E (2818Cc) – TM 17861-2; Onseepkans (2819Cd) – PEM R2430.

Pachydactylus namaquensis

Namibia: Namuskluft Inselberg (2716Dd) – SAM 43639.

Northern Cape Province, South Africa: NW slopes Nicodaemus, Richtersveld National Park, 28°21'15"S, 16°59'33"E (2816Bd) – PEM R7635; Koubos, Richtersveld, 28°26'S, 16°58'E (2816Bd) – PEM R10548; Namaqualand (here restricted to vicinity of Springbok) – SAM 935 (H); Klipfontein, 29°13'S, 17°40'E (2917Ba) – TM 17900-2, 17904, 17908; Sandhoogte, Eselsfontein, 29°41'S, 17°45'E (2917Da) – TM 65858; 6 km from Komaggas towards Springbok, 29°45'S, 17°31'E (2917Dc) – TM 34164; Gamocp, 29°54'S, 18°25'E (2918Cd) – TM 54698; Kamieskroon,

30°12'S, 17°56'E (3017Bb) – CAS 186367, TM 13714-5; between Kamieskroon and Springbok – USNM 162431-2; Kamiesberg Pass, 30°11'S, 17°49'E (3017Bb) – TM 35211; 6 km SW Kamieskroon, 30°17'S, 17°54'E (3017Bd) – TM 34048; Garies, 30°34'S, 17°59'E (3017Db) – TM 18143, PEM R10549; 4.6 km N. of Garies (3017Db) – CAS 167642; between Garies and Kamiesberg (3018Ac) – PEM R9540-3; 7 km NW Leliefontein, Kamiesberg, 30°15'S, 18°03'E (3018Ac) – TM 35191-2.

Pachydactylus kladaroderma

Western Cape Province, South Africa: Dunedin (3122Cd) – SAM 44862; Brandersberg, Aasvoëlberg, 30 km W. Three Sisters (3122Dd) – PEM R4894; Karoo National Park (3222Ad, 3222Bc) – PEM R3823, 4309, 4370 (P), 4532, 4660 (P); Molteno Pass, Karoo National Park, 32°14'S, 22°35'E (3222Ba) – PEM R6544 (P); Dolerite pillars, Molteno Pass, Karoo National Park, 32°15'09"S, 22°34'07"E, 1077 m (3222Bc) – PEM R11193-4 (P), P11195 (H); CAS 198285 (P); Beaufort West (3222Bc) – PEM R10550; roadside cutting, middle plateau, Molteno Pass, Karoo National Park, 32°12'34"S, 22°33'35"E, 1164 m (3222Ba) – PEM R11197-98 (P); CAS 198286 (P); top of Molteno Pass, 32°10'24"S, 2°32'55"E; 1682 m (3222Ab) – PEM R11200 (P), CAS 198288, LSUMZ 56974 (P); Sakrivier, Nuweveldberge, 32°03'56"S, 22°27'01"E, 1504 m (3222Ab) – PEM R11199

(P); top of Oukloof Pass, 32°08'50"S, 21°44'18"E, 1543 m (3221BA) – PEM R11211; Oukloof Pass, Fraserberg District, 32°09'S, 21°46'E (3221Bb) – TM 36193-4; Farm Vaalpunt, 25 km NE Sutherland, 32°22'17"S, 20°56'12"E, 1438 m (3220Bd) – PEM R11212-13, CAS 198301; Farm Verlatekloof, Sutherland, 32°32'S, 20°36'E (3220Da) – TM 55488; top of Verlatekloof Pass, Roggeveld Mountains, Sutherland District, 32°31'34"S, 20°38'08"E, 1535 m (3220Da) – PEM R11224-25); Farm Komsberg, Komsberg Pass, Roggeveldberg, 32°40'53"S, 20°45'44"E, 1627 m (3220Db) – PEM R11234-36); Laingsburg, 33°11'S, 20°51'E (3320Bd) – TM 36019; N slopes Witteberg, Laingsburg (3320Bc) – TM 19526; 2 km W of entrance to Anysberg Nature Reserve 33°44'S 20°27'E (3320Bc) – CAS 186392-4; Anysberg Nature Reserve 33°27'49"S 20°44'30"E (3320Bc) – CAS 195395-6; Prinspoort, Anysberg Nature Reserve (3320Bc) – PEM R6098; 5.9 km W. of Huisrivier Pass, Calitzdorp District, 33°29'S 21°33'E (3321Bc) – PEM R7061; Huisrivierpass, 33°29'46"S, 21°35'00"E, 528 m (3321Dc) – PEM R11246; Kliphuisvlei, Groot Swartberg, 33°21'S, 21°54'E (3321Bd) – PEM R8198; 2 km into northern part of Sevenweekspoort, 33°23'12"S, 21°24'33"E, 1000 m (3321Ad) – PEM R11240; 4.7 km along east-west ridge running south of Synganskop, Gamka Mountain Nature Reserve, 33°44'30"S, 21°54'30"E (3321Db) – PEM R6755, 6801; Farm Bergfontein, Riversdale, 33°58'S, 21°35'E (3321Dc) – TM 54809.