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A NEW SPECIES OF ROCK-DWELLING *PHYLLODACTYLUS*
(SQUAMATA: GEKKONIDAE) FROM THE RICHTERSVELD, SOUTH
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The South African members of the gekkonid genus *Phyllodactylus* include *P. porphyreus* (Daudin), *P. microlepidotus* FitzSimons, *P. peringueyi* Boulenger, a large new species from the Swartberg Mountains (Haacke, in prep.), and at least five small, secretive species, all of which until recently were subsumed under the name *P. lineatus* Gray. The *P. lineatus* group is distributed along the coastal regions and Cape Fold Mountains from southern Namibia around the Cape to the region of Grahamstown in the Eastern Cape (Visser, 1984; Branch, 1988a). Morphological and allozyme analyses of these forms (Branch et al., 1995) have revealed a pattern of affinities related to the geography of the region. *Phyllodactylus lineatus* (*sensu stricto*) is restricted chiefly to areas below 250 m elevation in an arc from extreme southwestern Namibia to the Oliphants River in the Karoo and is associated primarily with bark or vegetation. The remaining taxa in the group, in contrast, are chiefly rock-dwellers. Two of them, *P. essexi* Hewitt (1925) from the Eastern Cape and *P. rupicolus* FitzSimons (1938) from northern Little Namaqualand, had been recognized at least subspecifically in the past. Two other species, *P. hewitti* and *P. hexaporus*, distributed more widely in the

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Cape Fold Mountains, have long been known from large series but were not recognized taxonomically until recently (Branch et al., 1995). In the course of reviewing the genus in southern Africa we discovered an additional species of small rock-dwelling *Phyllodactylus* that had only once before been reported in the literature (as *P. lineatus rupicolus*; Haacke, 1970) and that has been collected from only a few localities. The new species is in some ways similar to *P. rupicolus*, its geographically nearest neighbor among the rock-living leaf-toed geckos, but it is clearly distinct in several features from that species and all other members of the genus.

MATERIALS AND METHODS

Geckos were collected under permits issued by the Directorate of Nature Conservation of the Cape Province and the Director of National Parks. All material has been accessioned into the collections of the California Academy of Sciences (CAS), the Port Elizabeth Museum (PEM), or the Museum of Natural Science, Louisiana State University (LSUMZ). AMB numbers in the discussion below are field numbers of as yet uncatalogued specimens in the PEM collection. In addition, previously collected specimens in the Transvaal Museum (TM) were included in the comparative material. All measurements were made to the nearest 0.01 mm using Sharpe & Brown Digi-Cal digital calipers. Specimens of the new taxon were compared to specimens of all Old World species of the genus *Phyllodactylus*, as well as to representative New World *Phyllodactylus* and representative leaf-toed geckos of the genera *Asaccus*, *Christinus*, *Ebenavia*, *Paraoedura*, and *Urocyttarus*.

Tissues from the new species were compared with those from representatives of other southern African *Phyllodactylus* (*P. essexi*, *P. hewitti*, *P. lineatus*, *P. rupicolus*, *P. microlepidotus*, *P. peringueyi*, *P. porphyreus*, and the undescribed Swartberg gecko) at 24 allozyme loci. Samples of liver tissues dissected from freshly killed specimens were homogenized in deionized water, stored in liquid nitrogen or in an ultracold freezer, and subjected to horizontal starch-gel electrophoresis using standard techniques (Selander et al., 1971; Harris and Hopkinson, 1976; Hillis and Moritz, 1990). Nei (1978) genetic distances and a UPGMA (unweighted pair-group arithmetic average clustering) phenogram based on those distances were calculated using BIOSYS (Swofford and Selander, 1981).

Phyllodactylus gemmulus new species (Figs. 1-2)

HOLOTYPE.--CAS 193645, an adult male, collected 29 June 1993, 22.6 km by road E Sendelingsdrif (Park Headquarters), Richtersveld National Park,

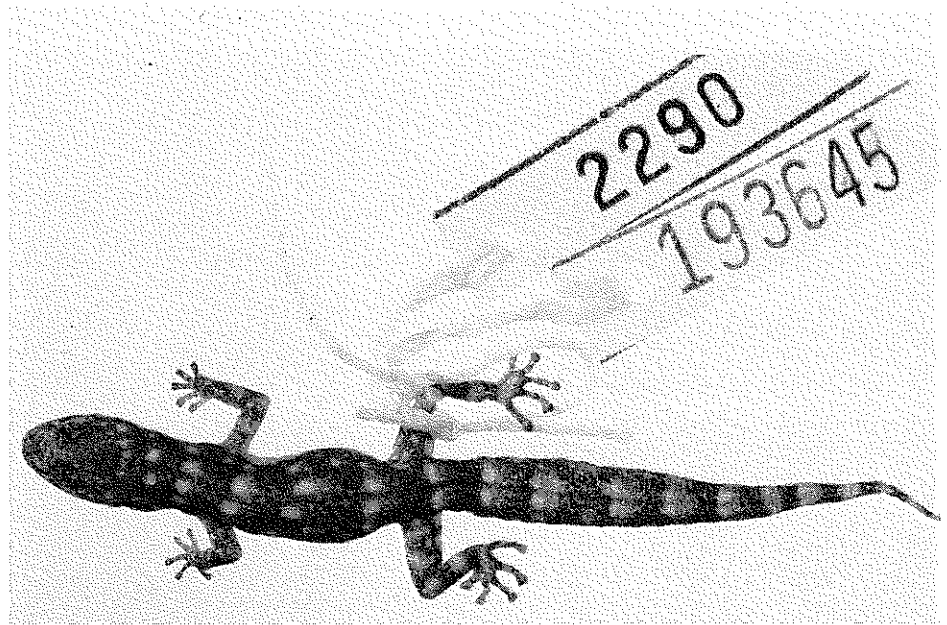


Figure 1. Holotype of *Phyllodactylus gemmulus*, CAS 193645, from the Richtersveld National Park, Northern Cape Province, South Africa. Note the relatively elongate body.

Northern Cape Province, South Africa, by A. M. Bauer, J. V. Vindum, H. Robeck, and D. King.

PARATYPES.--(all localities in quarter degree square 2816Bb [unless otherwise noted], Richtersveld National Park, Northern Cape Province, South Africa) CAS 186352, ca. 22 km E Sendelingsdrif; CAS 193364, 12.6 km E Sendelingsdrif; CAS 193641-42, 23.5 km E Sendelingsdrif; LSUMZ 57323, 6.5 km E rd. turning to Pokkiespram, 28°09'51"S, 17°01'30"E (quarter degree square 2817Aa); PEM 7786-93, Swartpoort, 28°08'10"S, 16°59'34"E; PEM 7372-73, 7378-80, Richtersveld National Park, 28°08'02"S, 16°59'34"E; PEM 9209, near road turning to Pokkiespram, 28°08'13"S, 16°58'14"E.

OTHER SPECIMENS.--AMB 4697, CAS 200080, LSUMZ 57322, 15.4 km E road turning to Pokkiespram, Richtersveld National Park, Northern Cape Province, South Africa, 28°09'48"S, 17°01'10"E (2817Aa); CAS 200090, 6.5 km E road turning to Pokkiespram, Richtersveld National Park, Northern Cape Province, South Africa, 28°08'18"S, 16°58'59"E (2816Bb); AMB 4743, CAS 200095, 0.9 km S N. end Brown Pass, Richtersveld National Park, Northern Cape Province, South Africa, 28°07'35"S, 17°00'45"E (2817Aa); AMB 4688, 8.3 km E road turning to Pokkiespram, Richtersveld National Park, Northern Cape Province, South Africa, 28°07'53"S, 16°59'51"E (2816Bb); TM 35398-400, Macmillan's Pass, NE Rosh Pinah, Namibia, 27°56'S, 16°54'E (2716Dd); PEM 10974-79, Stinkfontein, Northern Cape Province, South Africa, 28°46'S, 17°17'E (2817Cd); TM 27935-36, 10 km E Eksteenfontein, Northern Cape Province, South Africa, 28°52'S, 17°21'E (2817Cd).

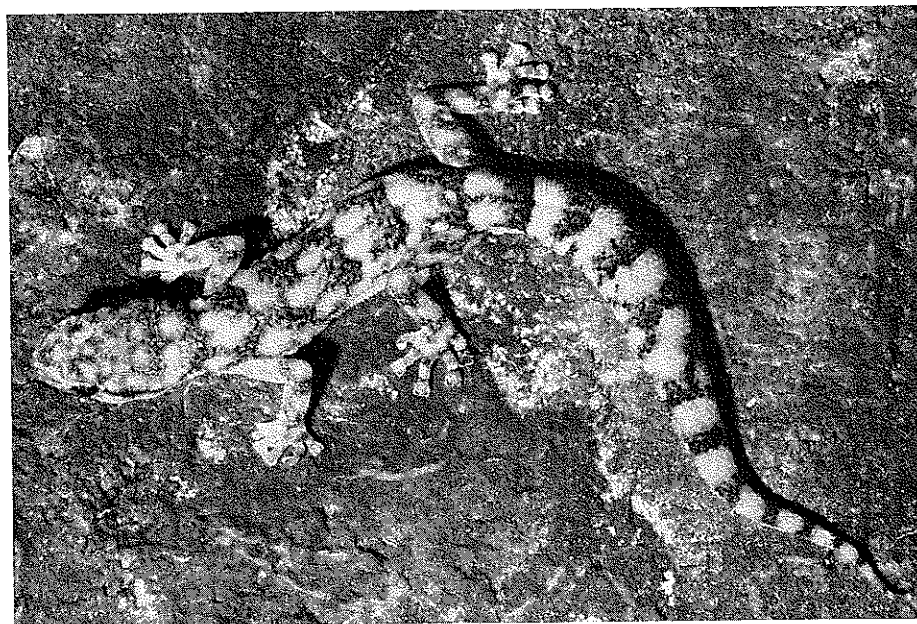


Figure 2. Living specimen of *Phyllodactylus gemmulus* illustrating flattened body posture and typical color pattern.

DIAGNOSIS.--A small species of the *P. lineatus* group, having an adult snout-vent length (SVL) of 23-30 mm and distinguished from other species in the genus and species group by the following combination of characteristics: head depressed; dorsal body scalation homogeneous; midbody scale rows 70-86; 4 preanal pores in males; dorsal color pattern with transverse rows of large yellow spots on a brown or mottled background. *Phyllodactylus gemmulus* differs from *P. microlepidotus*, *P. porphyreus*, and an undescribed species from the Swartberg Mountains by its smaller size, and from the last species and *P. peringueyi* by its homogeneous body scalation. It is distinguished from *P. lineatus* and several related forms (resurrected or described by Branch et al., 1995) by its elongate trunk and its color pattern of large, diffuse yellow spots (small pale spots may be found in other species and small orange spots are seen in *P. rupicolus* from Namaqualand). It is distinguished from *P. hexaporus* and from *P. lineatus* by its lower number of preanal pores, and from all members of the group except *P. lineatus* by a relatively low number of midbody scale rows. *Phyllodactylus gemmulus* is also distinguished by four unique allozyme alleles (see below).

DESCRIPTION OF HOLOTYPE.--Snout-vent length 23.6 mm; tail length 30.7 mm; head length 7.1 mm; head width 4.6 mm; snout length 3.0 mm; orbital width 1.4 mm; ear to eye distance 2.3 mm. Head depressed, 1.6 times longer than broad, distinct from neck; snout obtusely rounded, 1.3 times ear-to-

eye distance and 2.1 times eye diameter; ear opening small, slightly oblique and rounded, lacking enlarged lobules or tympanic shields; eye relatively large, ringed by small ciliary granules with a vertical pupil constricted to two pinhole openings in preserved specimens; rostral sub-pentagonal, broader than wide with a median cleft above; nostril directed upward and pierced between rostral, first supralabial, and three nasal scales; anteriormost nasal largest; supranasals separated by three small granules; mental subpentagonal, as broad as or a little broader behind than adjoining infralabials; a median pair of enlarged chinshields in contact with mental, and considerably larger than granules behind; chinshields bordered by six convex granules; throat covered with granules, these granules smaller posteriorly; supralabials 10; infralabials 8. Scales on snout granular and convex, the largest being larger than those on back, much larger than the small convex to slightly flattened granules on back of head. Body elongate and dorsoventrally flattened. Limbs of moderate length; digits depressed in their basal part, with three rows of scales inferiorly, the median series moderately enlarged transversely; digital expansions rounded, slightly broader than basal portion and each bearing a pair of subrectangular adhesive scansors below; minute claws on all digits of manus and pes. Four preanal pores. Upper surface of body and limbs covered with uniform, smooth, flat granules, these granules larger than or subequal to those on crown. Eighty-four scales around midbody. Belly covered with flattened, smooth, imbricate scales, much larger than scales on back. Tail original, 130% of SVL, slightly flattened dorsoventrally, tapering, covered above with regular transverse rows of uniform, smooth, subimbricate, subrectangular scales (the scales much larger than scales on the back), and below with scales much larger than those above and even larger than those of the belly. An oblique row of three enlarged, flattened tubercles at the base of the tail on either side of the vent.

COLOR IN PRESERVATIVE (Fig. 1).--Body mottled brown above, with a longitudinal series of five more-or-less paired, dorsolateral, pale yellow spots; small blotches on flanks that may be aligned with dorsolateral series to form irregular transverse series. Top of snout and crown mottled light brown; vague dark brown stripe extending from nostril through upper eye onto temporal region and side of neck. Belly cream, with dark stipples on lateral scales; these stipples more extensive below limbs and on throat (forming scattered flecks). Upper surface of limbs blotched, irregularly on forelimbs, more distinctly on hind limbs, with a series of three pale yellow blotches on mid-femur, knee, and mid-shank. Tail with 12 pale bands above, each 2-3 scales wide. Subcaudal region cream-colored with mottled brown infusions.

COLOR IN LIFE (Fig. 2).--Similar to preserved color except dorsal spots and those on femora beige or pale pink, containing smaller canary yellow spots displaced anteriorly; pale spots on head also yellow; anterior margins of light bands on tail with two small canary yellow spots or a thin yellow band.

VARIATION.--The paratypes range from 19.1 to 29.9 mm SVL. Chinshields number 1-4 (usually 2-3) and are bordered by 4-8 granules (mean 6). Two of 19 paratypes have four scales between the nostrils, all others have five, as does the holotype. There are 1-3 nasorostrals, 9-12 (mean 11) scales from the anterior border of the orbit to the nostril, 13-18 (mean 16.5) scales across the crown between the orbits, 7-10 supralabials, and 6-9 infralabials. Preanal pores are present only in males; there are almost invariably four, although five were observed in one individual. Scales around midbody number 70-86 (mean 77.5). The color pattern is always dominated by the large yellow dorsal spots, but these may coalesce, especially in larger individuals. Regenerated tails lack the distinct banding of the original. In some paratypes the dorsal spots are less regular in outline and alignment, and they may form a vague scalloped pattern similar to that seen in other small African leaf-toed geckos such as *P. lineatus* and *P. rupicolus*.

ETYMOLOGY.--From the Latin *gemmula*, a small jewel or gem, referring to the small size and bright (for the genus) dorsal coloration of the species. The name also alludes to the fact that the species occurs in an area noted for its alluvial diamond deposits.

NATURAL HISTORY.--The holotype and all of the paratypes were collected during daylight hours beneath flakes on granite boulders (Fig. 3) in areas dominated by *Pachypodium*, *Aloe*, and plants of the families Mesembryanthemaceae and Crassulaceae. The Richtersveld National Park is known to harbor seven amphibian and 54 reptile species, of which 15 are geckos (Branch and Bauer, unpublished). Among the more common lizard species found in the same habitat with *Phyllodactylus gemmulus* are *Pachydactylus weberi*, *Pachydactylus* n. sp. (*P. namaquensis* group), *Pachydactylus laevigatus*, *Phelsuma ocellata*, and *Platysaurus capensis*. The first of these may be found in the same cracks occupied by *P. gemmulus*. No *P. gemmulus* were observed to be active during daylight, but when exposed the animals are alert and seek cover immediately. Although diet was not analyzed, this species almost certainly feeds exclusively on arthropods, as do most small geckos (Loveridge, 1947).

ALLOZYME COMPARISONS.--Allozyme comparisons with other members of the *P. lineatus* group (*sensu* Branch et al., 1995) indicate a range of 5-11 fixed differences (out of 24 loci investigated) between *P. gemmulus* and the four putative taxa with which it was compared. Of these, the greatest similarity (five fixed differences) was seen with respect to *P. lineatus*. The number of fixed differences between *P. gemmulus* and other southern African *Phyllodactylus* range from 15 (*P. microlepidotus*) to 22 (*P. peringueyi*). *Phyllodactylus gemmulus* exhibits unique alleles at the Gpi-1, Pep-3, Pgm-1, and Pk loci.

Nei's (1978) genetic distances from *P. gemmulus* to other members of the *P. lineatus* group range from 0.35 (distance to *P. lineatus*) to 0.69 (distance to *P.*



Figure 3. Typical habitat of *Phyllodactylus gemmulus* in northeastern region of the Richtersveld National Park. Geckos were collected under exfoliating granite on the exposed boulders.

essexii). In contrast, distances between all other pairs in the group range from 0.18 to 0.41. Although genetic distance data alone cannot be used as unambiguous indication of specific status, the values found in comparisons of *P. gemmulus* with other small African *Phyllodactylus* are at least as large as distances between many other species pairs in the group and comparable to specific-level differences found in the gekkonid genera *Phelsuma*, *Rhoptropus*, and *Pachydactylus* (Branch et al. 1995; Good and Bauer, 1995; Bauer and Good, 1996), and are greater than those reported between species of *Cordylus* from the southwestern Cape region (Brody et al., 1993).

UPGMA clustering suggests that *P. gemmulus* is the most dissimilar member of the *P. lineatus* group. A phylogenetic tree based on allozyme data is poorly resolved, but it unambiguously supports sister-group status of *P. gemmulus* with *P. lineatus* (a comprehensive review of the phylogeny of African *Phyllodactylus* is in preparation). Nei's distances from *P. gemmulus* to other southern African members of the genus range from 1.10 (*P. microlepidotus*) to 2.49 (*P. peringueyi*). This is comparable to allozyme distances to a variety of supposedly unrelated leaf-toed geckos from around the world.

DISCUSSION

The type series of *P. gemmulus* was collected in rocky areas of the Richtersveld National Park, chiefly in Halfmens Pass and Brown Pass (Fig. 4). The park occupies the northern portion of the Richtersveld, an arid montane area of approximately 8000 km² bordered by the bend of the Orange River in the north and Anenous Pass in the south. The area receives winter (May-September) rainfall of 50-300 mm per annum. The limits of distribution of the species within this region are difficult to assess. The animals are small and easily overlooked and the terrain is rugged, with relatively poor access, but the range may nevertheless be rather restricted. In the course of a review of all of the *Phyllodactylus* material in South African museums, only 11 specimens from three localities other than our own were identified. The specimens from Macmillan's Pass near Rosh Pinah indicate that the Orange River is not an effective barrier for this species and establish the occurrence of *P. gemmulus* in Namibia. It should also be looked for in Ai-Ais Nature Reserve on the Namibian side of the Orange River. It is unlikely that the species ranges to the west of the Richtersveld National Park boundary in South Africa or into the Diamond Area (Diamantgebied) in Namibia. These areas are parts of the Namib Desert and suitable rocky habitat is generally unavailable. This is especially true to the west of Rosh Pinah, where the Obib Dunes form an absolute barrier to rock-dwelling forms. This has been confirmed by recent collecting in the Sperrgebiet that has revealed only *P. lineatus*. The few known localities lie west of the approximate boundary between the more mesic Succulent Karoo Division of the Greater Cape Floral Zone and the xeric Eastern Gariep District of the Namib Subdomain (Jürgens, 1991). The southern and eastern boundaries of the range are more problematic, but south of Eksteenfontein there is a shift to more open habitat without the rocky microhabitats characteristic of the Richtersveld. It is unknown if *P. gemmulus* extends south and west of the main body of the Richtersveld into the Kristalberge or Nababiepsberge.

The Richtersveld is an area with plant endemism at approximately 50% at the species level (van Jaarsveld, 1981). In addition, an endemic toad has been described from the Richtersveld National Park (Branch and Braack, 1996). The area also harbors *Phelsuma ocellata*, the only southwest African member of a chiefly Malagasy group of geckos (Good and Bauer, 1995). The Richtersveld and adjacent Little Namaqualand have been singled out as one of seven herpetologically "sensitive areas" in South Africa owing to the occurrence of at least 13 rare, vulnerable, restricted, or peripheral amphibians and reptiles (Branch 1988b). Recent descriptions of new taxa (e.g., Branch and Braack, 1996; this study) serve to further highlight the distinctiveness of the region.

Most southern African members of the genus *Phyllodactylus* have limited distributional ranges associated with particular highland areas

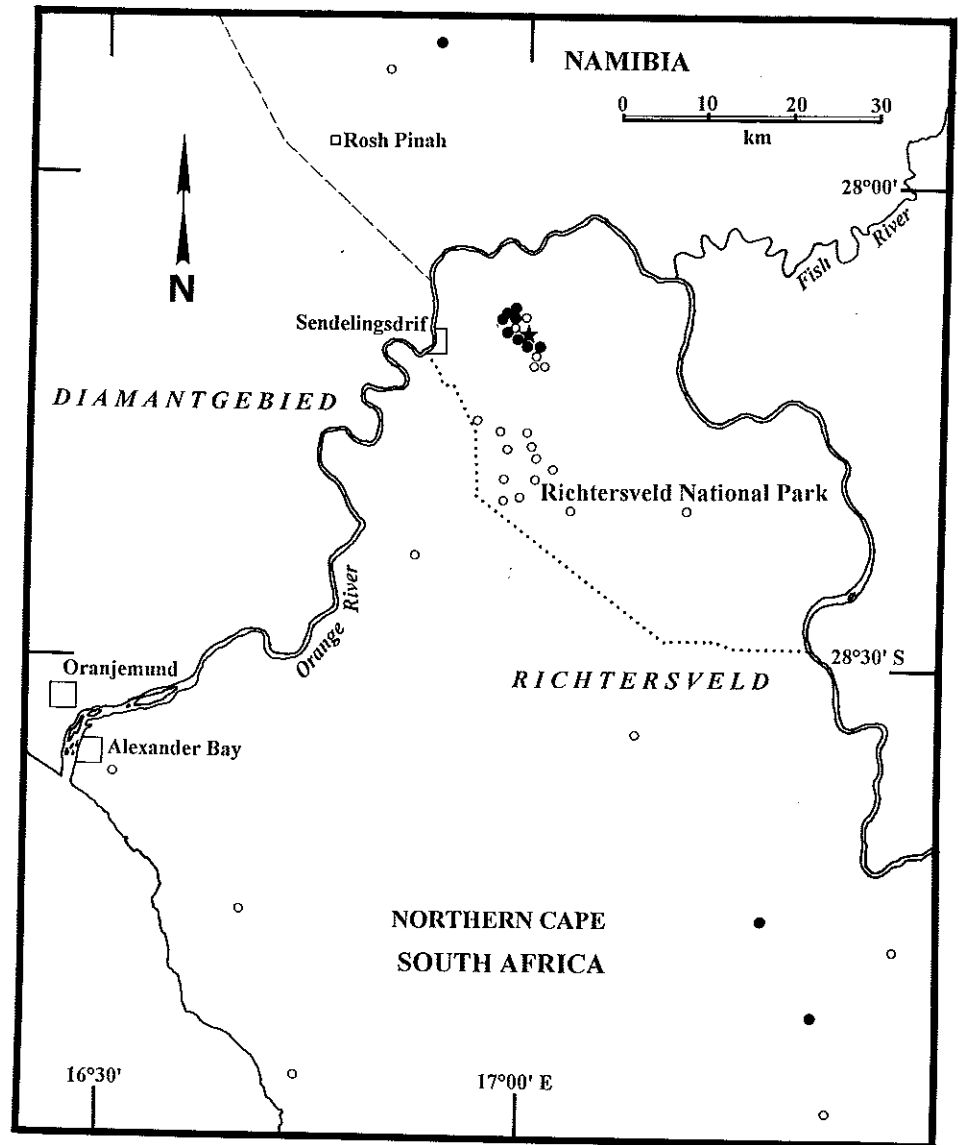


Figure 4. Distribution of *Phyllodactylus gemmulus* (solid circles) in the Richtersveld region of the Northern Cape Province and adjacent Namibia. The holotype locality is marked by a solid star. Known localities of the only sympatric congener, *P. lineatus*, are shown as smaller open circles. Open squares mark the named towns and mines. The dashed line marks the boundary of the Namibian Diamond Area and the dotted line marks the southern boundary of the Richtersveld National Park. See Fig. 5 for a more general map of the region.

(Branch et al., 1995). Exceptions are: *P. lineatus*, which is broadly distributed at low elevations (generally below 250 m) from southern Namibia to the Karoo (with few known localities in the eastern part of the range); *P. porphyreus*, which is broadly distributed in coastal southern and western areas of the Cape (with outlier populations into Namaqualand); and *P. peringueyi*, which is limited to a small area of estuarine vegetation in the eastern Cape (Branch and Bauer, 1994). Of these forms, only *P. lineatus* overlaps the distribution of *P. gemmulus* (Figs. 4-5). The two taxa have been recorded within 100 m of one another but segregate on the basis of habitat preference. In the Richtersveld, *P. gemmulus* is entirely restricted to rocky areas, whereas *P. lineatus* is encountered most often under bark, in piles of dried leaves or wood, or in dry, hollow plant stems. Specimens of *P. lineatus* from the Aurusberg in Namibia, the northernmost population known, appear to be completely typical in both habitat and morphology (Branch, 1994), and there is no evidence of intergradation with *P. gemmulus* in any area where the two co-occur. The only other member of the *P. lineatus* group that approaches the distribution of *P. gemmulus* is *P. rupicolus*. This recently resurrected taxon (Branch et al., 1995) is also a rock-living form and ranges from Bitterfontein in the south to Steinkop in the north, with all known localities above 300 m. The northernmost locality of the latter species is approximately 60 km southeast of the southernmost known locality for *P. gemmulus* and is separated from it by the gap of Anenous Pass (Fig. 5).

It appears likely that cladogenesis within the *P. lineatus* group is related to vicariant events associated with the montane blocks on which the species (except *P. lineatus* itself) occur. Although leaf-toed geckos occupy a wide variety of habitat types (Carillo de Espinoza et al., 1990; Bauer and Russell, 1991), leaf-toed morphology has probably evolved in association with rocky habits (Russell and Bauer, 1989). Most southern African geckos exhibit some level of substrate specificity. This specificity has resulted in limited vagility and, coupled with a complex geologic and climatic history, has resulted in high levels of cladogenesis and regional endemism (Bauer, 1993). Comparisons among other members of the *P. lineatus* group (Branch et al., 1995) suggest that cladogenic events beginning in the Miocene and extending through the Pleistocene may have resulted in the observed diversity in this group. Candidate events include Miocene orogenic activity and more recent climatic changes that have affected vegetation. A detailed scenario of the origin of *P. gemmulus*, however, must await a well-supported hypothesis of relationships among African *Phyllodactylus* as a whole.

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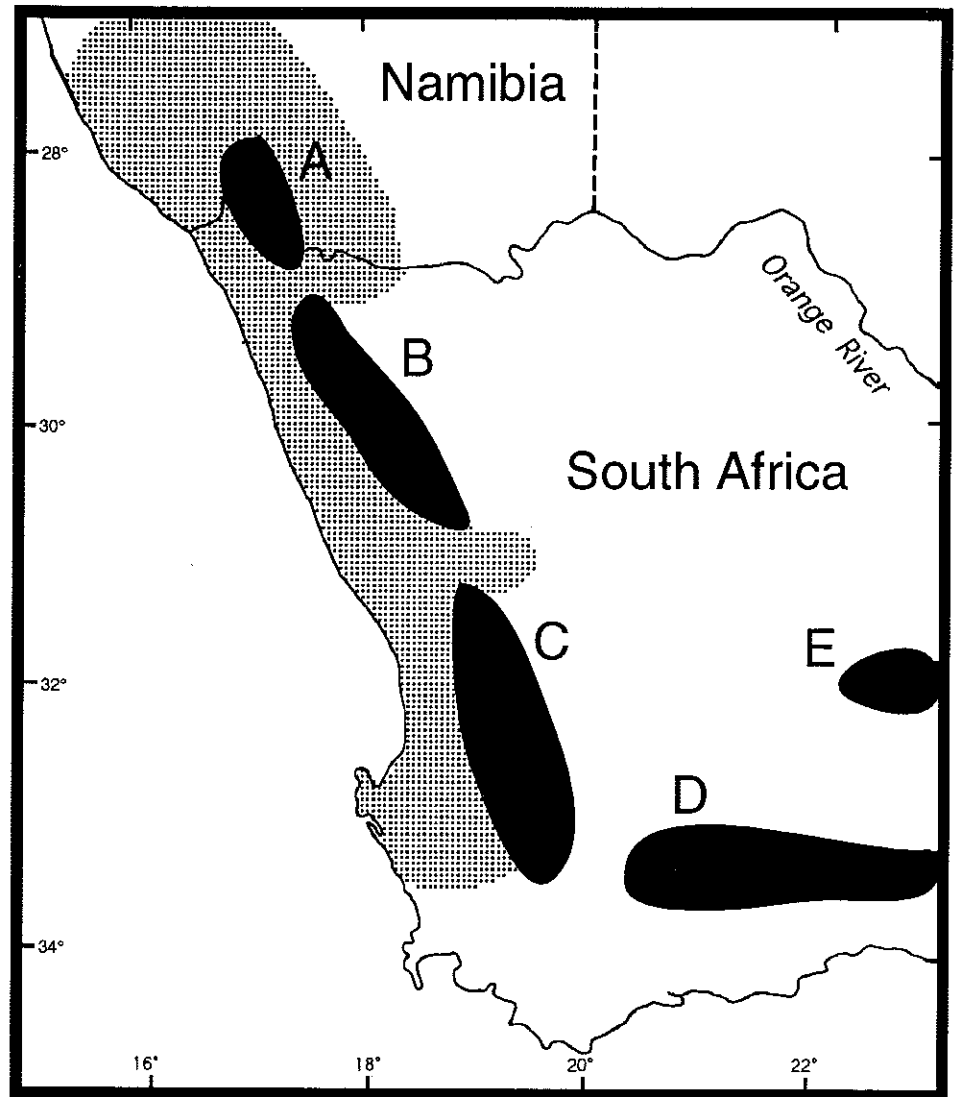


Figure 5. Distribution of small *Phyllodactylus* (*P. lineatus* group) in western South Africa and adjacent Namibia. Shaded area indicates the approximate distribution of *P. lineatus* (isolated localities to the east of the main range are not illustrated). This species occurs in sympatry or near-sympatry with other members of the genus at the edges of upland areas and in valleys extending through areas of high relief (not shown). Black areas indicate the approximate ranges of rock-dwelling species of the *P. lineatus* group. A marks the range of *P. gemmulus*, and B-E the ranges of the other rock-dwelling forms (B=*P. rupicolus*, C=*P. hexaporus*, D=*P. hewitti*, E=*P. cf. hewitti* [population under investigation]; see Branch et al., 1995, for distributional details). The gap between areas A and B is in the vicinity of Anenous Pass.

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