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- FISCHER, P. H. 1948. Données sur la résistance et de la vitalité des mollusques. *Journal de conchyliologie* **88** (3): 100–140.
- FISCHER, P. H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archives de zoologie expérimentale et générale* **74** (33): 627–634.
- KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Annals and Magazine of Natural History* (13) **2** (17): 309–320.
- KOHN, A. J. 1960b. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bulletin of the Bingham Oceanographic Collection, Yale University* **17** (4): 1–51.
- THIELE, J. 1910. Mollusca. B. Polyplacophora, Gastropoda marina, Bivalvia. In: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika ausgeführt in den Jahren 1903–1905* **4** (15). *Denkschriften der medizinisch-naturwissenschaftlichen Gesellschaft zu Jena* **16**: 269–270.

(continued inside back cover)

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PHYLLODACTYLUS PERINGUEYI
(REPTILIA, GEKKONIDAE)
ITS TAXONOMIC HISTORY, REDISCOVERY,
AND PHYLOGENETIC AFFINITIES

By
WILLIAM R. BRANCH
&
AARON M. BAUER

Cape Town

Kaapstad

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(With 5 figures and 1 table)

[MS accepted 20 August 1993]

ABSTRACT

The taxonomic status and provenance of the two syntypes of *Phyllodactylus peringueyi* are reviewed. A redescription of the species is given, based on the extant syntypes and new material referable to the species. The species is compared with all known geckos having *Phyllodactylus*-type toes. It is not referable to any other known species group and, on biogeographic grounds, it seems likely that *P. peringueyi* forms part of an endemic southern African radiation of leaf-toed geckos.

A lectotype and paralectotype are designated from the extant syntypes, which survive in poor condition. Of the two localities documented for the syntypes, i.e. Namaqualand and Chelsea Point, the first is considered doubtful. Many other specimens accessioned at the same time, and purportedly also collected by Péringuey from Namaqualand, represent species not known from that region and were probably inaccurately documented. There is no indication that the Chelsea Point locality is inaccurate, although no additional specimens have been collected from the region despite intensive searches. However, the species has recently been rediscovered 77 km west of Chelsea Point, in salt marshes of the Kromme River estuary, Eastern Cape.

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INTRODUCTION

The genus *Phyllodactylus* is a widespread and probably polyphyletic assemblage of small to moderate-sized geckos, with representatives world-wide. Recently, certain monophyletic groups have been recognized within *Phyllodactylus* sensu lato and have been accorded generic status (Dixon & Anderson 1973; Dixon & Kroll 1974; Kluge 1983; Cogger 1986). Species currently retained in *Phyllodactylus* are chiefly distributed throughout the New World, with the greatest diversity in the arid regions of the Pacific coast of Mexico and South America, and in Venezuela. The remaining Old World *Phyllodactylus* include two species in Thailand, one in the Mediterranean region, two on the island of Socotra, and five described species in southern Africa. *Phyllodactylus ansorgii*, endemic to Angola, is relatively poorly known but two of the South African species, *P. lineatus* and *P. porphyreus*, have been well collected and their distributions are well established, and a third, *P. microlepidotus*, is becoming so.

Since its description at the beginning of this century, the status and distribution of *Phyllodactylus peringueyi* Boulenger, 1910, have remained a persistent problem in South African herpetology. The two syntypes, which are believed to have been acquired 19 years apart, are catalogued as coming from two widely separated localities (Little Namaqualand and the Eastern Cape). Few southern African lizards have comparable distributions and these are common, widespread generalists with wide habitat tolerances (e.g. *Mabuya capensis* and *Agama atra*). No known geological or climatic events in the history of southern Africa are likely to have generated relict distributions matching the stated localities of the syntypes. In addition, the morphology of *P. peringueyi* is unlike that of any other South African gecko currently assigned to *Phyllodactylus*. Prior to this report, no new specimens had been discovered since the type description.

Although several authors have reviewed the problem posed by these enigmatic specimens (Hewitt 1937; FitzSimons 1943; McLachlan 1988), no new information regarding their identity has been available and, to date, no attempt to use any but the most superficial aspects of pholidosis in determining their affinities has been made. We present here the results of our studies on: the provenance and taxonomic history of the species; the condition and a fuller description of the syntype specimens; morphological variation in recently collected fresh material referable to the species; and a preliminary comparison of the species with all known congeners and species from allied leaf-toed genera.

MATERIALS AND METHODS

External features were examined using a binocular dissecting microscope, and osteological features revealed through the use of X-rays. Measurements were taken with Brown and Sharpe 'Digit-Cal Plus' digital calipers.

The syntypes of *Phyllodactylus peringueyi* and all fresh material referable to this species were examined (see Appendix). In addition, all known species of gekkonine geckos possessing '*Phyllodactylus*-type' toes (Russell & Bauer 1989)

were compared externally to address the specific distinctness of *P. peringueyi*. The species lists of Kluge (1983, 1991) served as a guide to the recognized taxa. Specimens of nearly all members of the genera *Paroedura*, *Asaccus*, *Ebenavia*, *Christinus* and *Urocotyledon*, in addition to those currently assigned to *Phyllodactylus* sensu stricto, were examined in the following collections: British Museum (Natural History) (BMNH), California Academy of Sciences (CAS), University of Kansas Museum of Natural History (KU), Academy of Natural Sciences of Philadelphia (ANSP), Louisiana State University Museum of Natural Sciences (LSU), United States National Museum (USNM), Field Museum of Natural History (FMNH), Museum für Naturkunde der Humboldt-Universität zu Berlin (ZMB), Port Elizabeth Museum (PEM), and South African Museum (SAM). Specimens of the following species were not examined, but were compared on the basis of published descriptions: *Phyllodactylus bordai*, *P. rutteni*, *P. transversalis*, *Paroedura homolorhinus*, *P. oviceps*, and *Urocotyledon weileri*. In addition, osteological comparisons were made using cleared-and-stained and dry skeletal material from the aforementioned institutions, as well as X-rays.

Historical information regarding the syntypes of *Phyllodactylus peringueyi* was derived from the surviving correspondence, registers, annual reports, and catalogues in the South African Museum, covering the period 1885–1910, during which time the specimens were acquired and described.

RESULTS AND DISCUSSION

Phyllodactylus peringueyi Boulenger, 1910

CONDITION OF THE SYNTYPES OF *PHYLLODACTYLUS PERINGUEYI*

The type description (Boulenger 1910) is based on two specimens, both of which are extant and housed in the herpetological collection of the South African Museum, Cape Town. They are now in only poor condition. Both were initially fixed in contorted positions, and numerous subsequent attempts to study their anatomy have resulted in considerable damage. This includes both incidental damage during dissections to determine internal features, and accidental damage in handling and during transit.

SAM-777. Snout–vent length, 23.5 mm; mid-body diameter, 4.5 mm. The skin is torn on the throat and in the middle of the belly, and has been cut around the margin of the lower jaw. The lower portion of the left forelimb, distal to the elbow, is absent (Fig. 1A). Similarly, only a tibia remains of the lower portion of the right hind limb. The right fore-limb is broken and torn at the elbow, although the lower part of the limb remains attached by a small skin flap. The specimen has no tail, this being lost distal to the hemipeneal pouches. The description of FitzSimons (1943) contains no comment on the tail. However, in the original description, Boulenger (1910) noted a total length of 45 mm (tail regenerated), but did not state which specimen was measured. A detached tail (11 mm) was found in the bottle containing the syntypes; it is likely to have come from *SAM-777*.

SAM-8628. Snout-vent length, 28.1 mm. Damage to this specimen is more extensive. Most of the tail is missing, leaving only the proximal 3 mm. The right fore-limb is broken just distal to mid-tibia, although the distal portion is attached by a skin flap (Fig. 1B). The thumb and terminal phalanges of the fourth finger are missing. The right hind limb is also broken just below the knee, with the lower portion of the limb attached by a skin flap. Only the third and fourth digits remain on the left fore-limb, and the middle digit of the left hind limb is truncated at the second phalanx. The skin over much of the dorsal surface of the skull, from the tip of the snout to the middle of the parietal region, has been removed. The right eyeball is punctured and the skin around the right margin of the lower jaw has been cut.

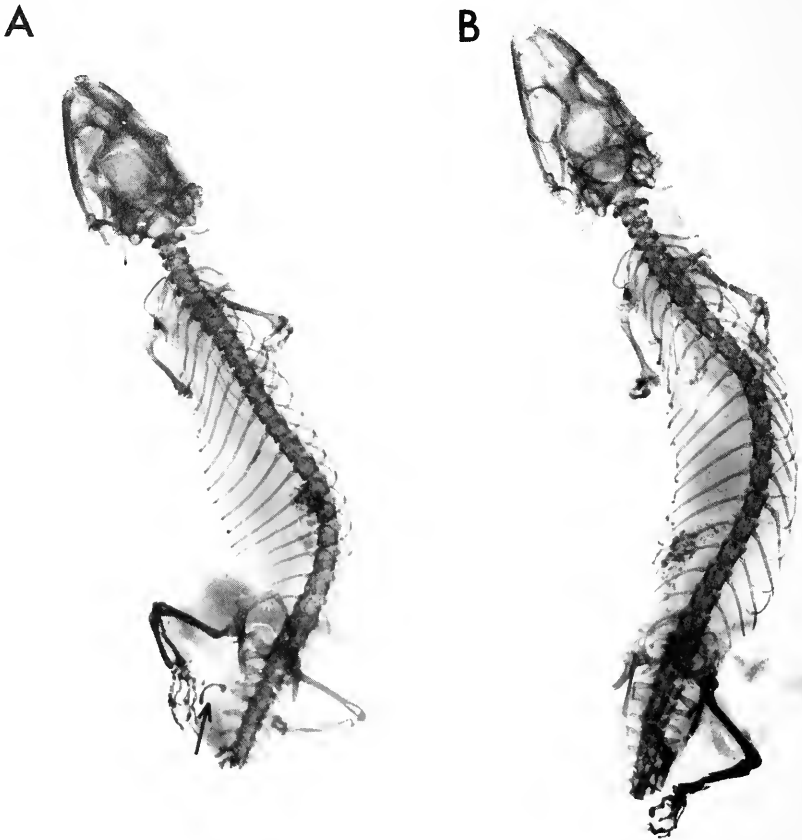


Fig. 1. Radiographs (dorsal views) of the syntypes of *Phyllodactylus peringueyi*. A. Lectotype SAM-777. B. Paralectotype SAM-8628. Note the reduced number of presacral vertebrae. The arrow in A indicates the cloacal bone in the male. The dark image of the hind limb is a result of over-exposure of the X-ray positive print to bring out details of the digits. Actual size of specimens: A. 23.5 mm SVL; B. 28.1 mm SVL.

DESIGNATION OF LECTOTYPE AND PARALECTOTYPE

Lectotype. We here designate the adult male, SAM-777, stated to have been collected by L. Péringuey in Little Namaqualand, Cape Province, South Africa, as the lectotype of the species.

Our reasons for this are as follows: it is in better condition, retaining large areas of skin covering the head; it is a male and thus displays a number of potentially useful sexually dimorphic features (e.g. cloacal bones); the detached tail most likely came from SAM-777 and this, therefore, is probably the specimen that formed the basis for measurements listed in the type description. Finally, although Boulenger (1910) did not designate a holotype, and none has been subsequently designated, the catalogue entry for SAM-777 has a pencilled entry 'type'.

Paralectotype. SAM-8628, an adult female, reputedly collected by A. Moorhouse at Chelsea Point, near Port Elizabeth, Cape Province, South Africa. FitzSimons (1943) was mistaken in describing SAM-8628 as a male.

Although we consider the stated locality for the lectotype to be mistaken and that for the paralectotype to be more acceptable, for reasons discussed below (see p. 23), we caution against acceptance of the published localities of both syntypes. The species appears to be restricted to the Eastern Cape (see p. 25).

REDISCOVERY OF THE SPECIES

Prior to this report, no new specimens of *P. peringueyi* have been collected since the original type description (Boulenger 1910). Due to its problematic status, the species was listed as 'Indeterminate' in the South African Red Data Book—Reptiles and Amphibians (McLachlan 1978; revised Branch 1988c), and even described as 'one of the herpetological mysteries of the region' in the most recent synopsis of the subcontinent's reptilian fauna (Branch 1988a: 211). Recently, whilst this manuscript was in preparation and after a preliminary synopsis of its findings had been presented (Branch & Bauer 1992), three specimens of a small, striped, leaf-toed gecko with keeled dorsal tubercles (Fig. 2), were collected in transitional salt-marsh/floodplain vegetation (including *Sarcocornia perennis*, *Chenolea diffusa* and *Iporobolus virginicus*) along the banks of the lower Kromme River (3424Bb Humansdorp; 34°07'15"S 24°45'30"E; alt. 1 m asl.). The specimens were referable to *P. peringueyi*. Fuller details of the species' rediscovery have been published elsewhere (Branch *et al.* 1992). Subsequent trips to the region have shown the species to be common along the banks of the lower Kromme River (see Fig. 5), but it has not been found in adjacent estuaries. It shelters under logs or in tussocks of thick vegetation, particularly *Restio* sp. In habitus, colour and preferred habitat of tussock vegetation, it shows a striking similarity to some Australian diplodactyline geckos, particularly *Crenadactylus ocellatus* and species of the *Diplodactylus michaelsoni* group. There are also intriguing similarities with the small Madagascan gecko *Ebenavia inunguis*. An analysis of the species' distribution and preferred habitat is in preparation (Branch in prep.).



Fig. 2. Péringuey's leaf-toed gecko (*Phyllodactylus peringueyi*): an adult male (PEM R6886) from Kaia da Balala, Kromme River, Humansdorp District, Eastern Cape.

REDESCRIPTION OF THE SPECIES

FitzSimons (1943) provided a description of the species, modified from that of Boulenger (1910). We have been able to determine a number of additional features that either extend or correct previous descriptions.

The head is flattened above; the snout is elongate and pointed, and almost twice the diameter of the eye and a little longer than the distance between the eye and the ear-opening (Fig. 3). The latter is small and rounded, whereas the eye has a vertical pupil. Head measurements of the syntypes are: length of head (tip of snout to rear of skull), 6.9 mm (SAM-777) and 7.3 mm (SAM-8628); width of head (at rear), 4.2 mm (both syntypes). Boulenger (1910) and FitzSimons (1943) described the head as being 1.5 times as long as broad, but the syntype measurements give a slightly higher ratio (1.65 and 1.73). Fresh material gives an even higher ratio (males, $n = 5$, range 1.78–1.97, mean 1.87; females, $n = 4$, range 1.78–1.93, mean 1.85), with no evidence of sexual dimorphism.

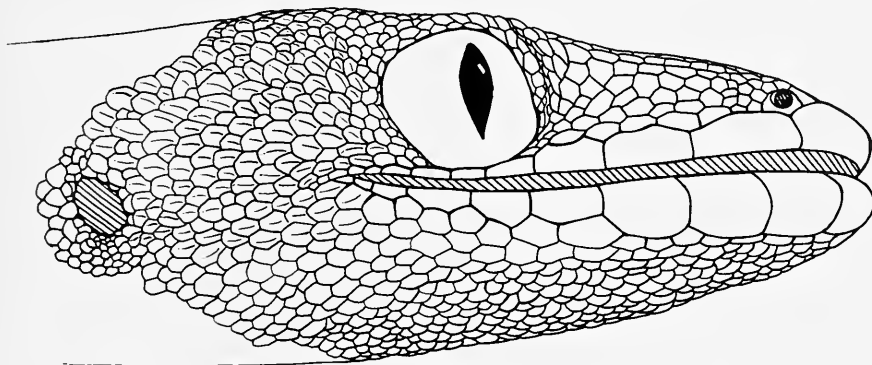


Fig. 3. Profile of *Phyllodactylus peringueyi* showing details of scalation (based on PEM R6908; lower Kromme River, Humansdorp District, Eastern Cape).

Boulenger (1910) and FitzSimons (1943) described the nostril as pierced between the rostral and four small nasal scales. However, in all fresh material, the nostril pierces a small nasal scale that is bordered by the rostral, first upper labial, two supranasal (the anterior larger and slightly wider than long), and by 2–3 small postnasal granules. Damage to the snout region of both syntypes makes it impossible to determine whether the original type description of the nasal condition is correct. The narrow borders of the nasal scale that surrounds the nostril make it easily overlooked.

The rostral is twice as broad as deep and lacks a median cleft. Boulenger (1910) noted that the granules on the snout were keeled, and FitzSimons (1943) added that they were larger and more strongly keeled than the scales on the back of the head. However, in fresh material the snout granules vary in the extent of their keeling and are equal to, or only slightly larger than, the scales on the crown of the head. The latter are also more irregular in outline. Other

details of head scalation include: 13–14 scales around ear; usually 13 scales between anterior margin of ear and posterior margin of eye; 9–11 scales between nostril and anterior margin of eye; 2 scales between upper labials and eye; 21–24 scales (excluding circumorbitals) between eyes across crown of head; 6–7 upper labials; 6–8 lower labials; no enlarged chin shields; 2–3 scales bordering the mental; 2–3 granules bordering rostral between anterior supranasals.

The body is rather elongate; the back is covered with coarse, more-or-less keeled granules, intermixed with numerous enlarged, longitudinally oval, strongly keeled tubercles. These are scattered, although they may form staggered irregular rows on the upper flanks. There are 13–14 tubercles across the back (11–12 in SAM-8628, which are also less prominently keeled). The gulars are small, rounded and granular, whereas the belly scales are smooth, flat, cycloid, imbricate, and at least twice the size of the gulars. The scales beneath the proximal portion of the tail are almost twice the size of those on the belly, and 16–18 scales border the anterior margin of the cloaca. There are no preanal pores. A large, semicircular scale, almost twice the size of adjacent scales, protrudes on each side of the tail base, just distal to the cloaca, forming a cloacal spur. It is present in both sexes, but is larger and more protruding in the male lectotype and other sexually mature males. The latter also have a distinctly swollen tail base due to the presence of the hemipenes.

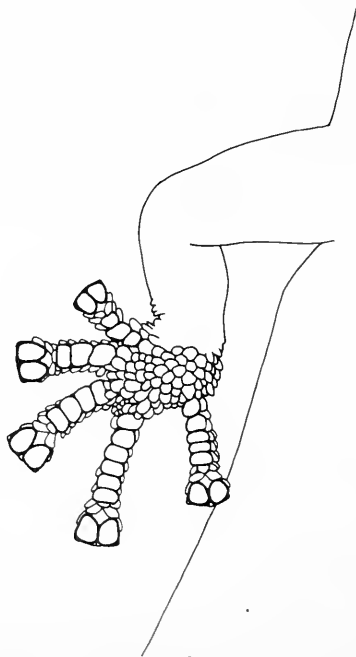


Fig. 4. Underside of right pes of *Phyllodactylus peringueyi* showing details of scalation (based on PEM R6886; Kaia de Balaia, Kromme River, Humansdorp District, Eastern Cape).

The limbs are short and pentadactyl (Fig. 4). The distal scanzors are rounded, moderately large, and medially divided, with a small claw between the paired distal expansions of each toe. The median row of subdigital scales is well developed and transversely enlarged, with 6–7 scales beneath the longest digit of the pes.

Colour

Superficially, there may appear to be sexual dichromatism; seven of eight adult males were boldly striped, whereas most females (five of seven) and all juveniles (two) and hatchlings (two) were uniformly coloured. However, captive specimens of both sexes readily change the intensity of the striped pattern, and gravid females may darken considerably. The correlation between coloration and activity and/or reproductive condition needs to be investigated further.

Striped phase (based on PEM R6886, an adult male). Body above with a light golden-brown vertebral stripe (1.4 mm wide, including 2–3 rows of dorsal tubercles with intervening granules) that extends from the back of the head to the beginning of the regenerated tail (in specimens with original tails, the stripe extends along the top of the tail for its full length). On each side this is edged by a thin black band (2 granules wide), which in turn is bordered by a broad (3–5 keeled tubercles wide) dark-brown dorsolateral band. Anteriorly, the latter is faintly divided by a very thin (1–2 granules wide) light-brown, longitudinal stripe that extends to the nostril, whereas posteriorly the band breaks up into fine, anastomosing stripes on the lower flanks. The dorsolateral bands fuse on the crown of the head at the level of the eyes; posteriorly they widen considerably and are most prominent over the hind limbs and tail base. The flanks are covered with a pale lateral 'band' that is composed of 3–4 faint, thin (one granule wide) brown stripes, separated by tan lines (also one granule wide) that occasionally anastomose. The band extends as a golden-brown stripe through the temporal region and eye, to the nostril. In some males the vertebral stripe lacks the black edge.

The iris is golden, coppery red, whereas the upper and lower labials are dirty cream, heavily stippled with dark spots. The throat has 4–6 vague, thin (one granule wide), dark-brown longitudinal stripes. The belly is also dirty cream with vestiges of thin dark stripes that radiate on to the lower surfaces of the hind limbs. The upper surfaces of both fore- and hind limbs are dirty golden brown, heavily stippled with dark spots.

Uniform phase (based on PEM R6908, an adult female). Head, body and upper surfaces of the limbs and tail uniform brown. There are faint vestiges of thin dark stripes on the flanks. The throat, belly and upper and lower labials are dirty cream with faint dark speckling.

Dimensions

Maximum snout–vent length: 28.3 mm females, 27.8 mm males. Unregenerated tails are approximately equal in length to that of the snout–vent; regenerated tails are usually smaller. Hatchlings measure 13–14 mm SVL, with a proportionately shorter tail (9–10 mm).

HISTORY OF THE SYNTYPES AND THEIR PROVENANCE

Cataloguing procedures and data recording in nineteenth-century herpetological collections were generally imprecise, and have generated several problems regarding type localities within *Phyllodactylus* (see Dixon & Huey 1970). However, the special circumstances at the South African Museum (SAM) have added exceptionally to the confusion surrounding *Phyllodactylus peringueyi*.

The lectotype, SAM-777, was acquired during the period that Péringuey himself was Assistant Director at the SAM. According to Summers (1975: 95), Péringuey had an '... incurable habit of trusting to his memory for the provenance of finds of all sorts', and once remarked 'I don't know what this Museum would do without my memory'. SAM-777, along with many reptiles supposedly collected in southern Namibia and the Western Cape, was not catalogued until 4-7 September, 1896, after the arrival of W. Sclater as Director at the South African Museum. At that time a large series of specimens (SAM-733 to 826, 835 to 892), all bearing the locality 'Namaqualand' and collector L. Péringuey, were accessioned.

The original entry in the herpetological catalogue, in the handwriting of Mr R. M. Lightfoot, general clerk and bookkeeper at the SAM, reads:

'SAM-777, *Phyllodactylus porphyreus* var. Namaqualand, 4 Sept 1886, L. Péringuey, in alc.'

A later note, in unidentified handwriting, adds:

'Now *P. peringueyi* Boulenger, type.'

'In 1885 Annual Report' has also been added in pencil by G. McLachlan, Curator of Herpetology, SAM, 1976-1989.

McLachlan believed that SAM-777, one of the *P. peringueyi* syntypes, was among the specimens listed in an appendix (in unknown handwriting) to the 1885 Annual Report of the SAM listing herpetological acquisitions for that year. These include seven species with the Namaqualand locality:

'*Chondrodactylus angulifer*, *Phyllodactylus* sp. nov. ?, *Phyllodactylus* sp. nov. ?, *Ptenopus garrulus*, *Pachydactylus formosus*, *Phyllodactylus lineatus* Gray, *Pachydactylus bibronii* and *Agama aculeata*.'

A register of specimens for 1885 (without localities or specimen numbers) lists, in Péringuey's handwriting:

'1 *Chondrodactylus angulifer*, 2 *Phyllodactylus lineatus* Gray, 4 *Pachydactylus formosus* Smith, 1 *Phyllodactylus* n. sp., 4 *Pachydactylus bibronii*, 1 *Pachydactylus* n. sp., 4 *Ptenopus garrulus*, *Agama aculeata*.'

The two lists differ only in that the report mentioned two specimens of a new species of *Phyllodactylus*, whereas the register gives one new *Phyllodactylus* and one new *Pachydactylus*. Whether the specimens were re-identified or incorrectly transcribed into the Annual Report from Péringuey's register is unknown.

The paralectotype is accessioned in the SAM herpetological catalogue as: 'SAM-8628 *Diplodactylus* sp. ? nov. Chelsea Point, nr. Port Elizabeth, 2 Dec 1904, A. C. Moorhouse, alc. Caught on beach, see letter 2/12/1904.'

Again, a later note adds 'Now *P. peringueyi* Boulenger.'

The 1904 SAM Annual Report notes, under thanks for recent acquisitions: 'Mr A. Moorhouse, for a new Lizard, of the family Geckonidae, and the genus *Diplodactylus*, found by him near Port Elizabeth. This is a specially interesting

form, as all the other species of the genus hitherto known have been obtained in Australia.'

Unfortunately, the letter from Moorhouse accompanying the specimen when it was donated to the SAM is not on file (M. Cherry pers. comm.). However, a letter from SAM Director W. Sclater to G. A. Boulenger at the British Museum, undated but bound between letters dated 30/11/1904 and 7/12/1904 in the SAM Letter Book for November 1897–October 1905, was located. In it Sclater asked Boulenger to identify a number of problematic specimens (several fish, a snake, and two geckos): 'I am sending you a small tube of things I cannot make (anything) of. The little *Phyllodactylus* from Algoa Bay seems quite different from (anything) we have. It appears to me to be (near) tuberculosus of your Catalogue . . . [SAM] 8628 Seashore on rocks of Algoa Bay, 12 miles from Port Elizabeth.'

THE ORIGIN OF THE SYNTYPES OF *PHYLLODACTYLUS PERINGUEYI*

In the description of *Phyllodactylus peringueyi*, Boulenger (1910: 494) provided the following details regarding the origins of the two syntypes: 'A male from Little Namaqualand (coll. Péringuey) and female from Port Elizabeth (coll. Moorhouse).' Distributions of African reptiles were poorly understood at the time, but it has since become clear that at least one of the localities is probably in error. Because Péringuey did not keep a written record of specimens accessioned, it was not until 1896, as many as 12 years after their collection, that specimens were catalogued. Many opportunities for mistakes in subsequent documentation of specimens may have occurred. This casts doubt especially on the 'Namaqualand' locality of the lectotype.

The term 'Namaqualand' was used by early workers in a much broader sense than it is today. As understood at the time of Péringuey, it probably included the area from Walvis Bay south to Clanwilliam in the Western Cape (approximately 1 100 km), and extended inland several hundred kilometres. Even in this broader context, however, many of Péringuey's SAM specimens, including several types, recorded from Namaqualand are likely to bear erroneous localities and should be viewed with extreme caution (Table 1).

The type of *Mabuya peringueyi* (= *Mabuya homalocephala peringueyi*) is catalogued as collected in Damaraland (although Boulenger (1888) gave the locality as Namaqualand in the type description). No other specimens of *Mabuya homalocephala* are known from north of the Orange River and the closest modern records are well to the south of Namaqualand, from the Cedarberg (Branch 1990a) and the Karoo National Park, Beaufort West (Branch & Braack 1989).

Similarly, neither of the snakes *Duberria lutrix* or *Crotaphopeltis hotamboeia*, supposedly obtained in Namaqualand by Péringuey, is found north of latitude 31°S. Despite its scientific name, *Pseudocordylus microlepidotus namaquensis* Hewitt, 1927, also based on Péringuey material, is not known from Namaqualand. It is restricted to the Nuweveldberg, which forms part of the inland escarpment mountains of the Cape (Branch & Braack 1989).

The most striking parallel with respect to *Phyllodactylus peringueyi*, is the case of SAM-799, also supposedly from Namaqualand. Although unidentified when accessioned, it was later identified as *Tetradactylus africanus* by

Boulenger (1910) and subsequently as *T. a. fitzsimonsi* by FitzSimons (1943). The latter author regarded the locality as unacceptable and noted (p. 298) that the 'specimen in question probably comes from Port Elizabeth'. Indeed, this subspecies is now known to be restricted to the environs of Port Elizabeth (Branch 1990b).

TABLE 1

South African Museum herpetological specimens catalogued from Namaqualand during the same period as *Phyllodactylus peringueyi* type specimens.

Species	SAM No.	Catalogue locality	Known distribution
<i>Phyllodactylus peringueyi</i>	777 (syntype)	Namaqualand	Kromme River estuary
<i>Duberria lurix</i>	770	Namaqualand	Southern Cape, Beaufort West
<i>Crotaphopeltis hotamboeia</i>	772	Namaqualand	Southern Cape, Beaufort West
<i>Agama atricollis</i>	849	Namaqualand	Northern Namibia and Transvaal lowveld
<i>Pseudocordylus microlepidotus namaquensis</i>	872 (type), 859, 864, 873	Namaqualand	Sutherland to Beaufort West
<i>Varanus albigularis</i>	875	Namaqualand	Eastern southern Africa and Central Namibia
<i>Pachydactylus fasciatus</i>	1052 (type) 1155	Namaqualand Natal	Northern Namibia
<i>Mabuya homalocephala peringueyi</i>	1054 (type)	Damaraland	No recent specimens
? (later identified as <i>Tetradactylus africanus</i> by Boulenger (1910) and updated to <i>T. a. fitzsimonsi</i> by FitzSimons (1943))	799	Namaqualand	Port Elizabeth

Similar locality problems plague other specimens associated with Péringuey. Another gecko, *Pachydactylus fasciatus*, was described by Boulenger (1888) from specimens supposedly collected by Péringuey from Namaqualand. Fitz-Simons (1943: 88) noted that '... there is a specimen (No. 1155) in the South African Museum, recorded from Natal; this specimen is identical to the cotype, (in structure, state of preservation etc.) and in all probability came from the same locality; its occurrence in Natal is otherwise unknown and beyond the bounds of possibility.' Even the Namaqualand locality 'between the mouth of the Orange River and Walfisch (Walvis) Bay' (Boulenger 1888: 136) is probably incorrect. The known distribution of *Pachydactylus fasciatus* is further north, with the southernmost confirmed record at Neu Barmen, near Windhoek. In addition, the species appears to be associated with the slopes of the inland escarpment rather than with coastal desert (Bauer & Branch 1991).

Nothing in the early SAM annual reports indicates that Péringuey ever visited Namibia, and a number of the specimens attributed to Péringuey in Boulenger's 1888 paper were, in reality, collected by Nightingale (e.g. *Oedura* (= *Afroedura*) *africana*, *Pythonodipsas carinata*, and *Vipera* (= *Bitis*) *peringueyi*) or Marloth (*Agama planiceps*) (Boulenger 1910). Nightingale donated a considerable amount of material (mainly entomological) to the SAM, mostly in 1886. It was shipped from Walvis Bay, although much would have been collected from further inland.

Although no additional specimens of *Phyllodactylus peringueyi* have ever been found around Port Elizabeth, there are no historical reasons to doubt the locality of the paralectotype supposedly collected there by Moorhouse in 1904. Moorhouse appeared on the Port Elizabeth voters roll for 1905–1907, and is there listed as a commercial traveller with Blaine and Co. (J. Bennie pers. comm.). His occupation raises the possibility that he may have collected specimens elsewhere on his travels, and SAM-8628 may have mistakenly been accessioned under Moorhouse's home address. However, this is unlikely as Chelsea Point, an uninhabited coastal landmark approximately 10 km due south of Port Elizabeth, is specifically listed.

Moorhouse was not a regular collector for the SAM and there is only one additional donation from him—a series of 44 specimens, including 3 species of frog, 8 species of lizard, and 13 species of snake (SAM-9021 to 9026, 9119 to 9146, 9149 to 9159). All the species are currently found in the Port Elizabeth region (Branch 1988a), adding circumstantial support to the correctness of the locality for the *P. peringueyi* paralectotype.

In addition to the problem of locality, there is a problem as to the date of collection of the syntypes. Hewitt (1937) noted that the nearly identical state of conservation of the specimens suggested that they had been collected and preserved at the same time. This does seem to be the case. *Phyllodactylus peringueyi* is so obviously different from other southern African geckos (due to its tubercular dorsal scalation) that it seems unlikely the Namaqualand specimen would not have been recognized as unusual and taken to Europe by Péringuey when he visited Boulenger in 1886–1887. It is therefore likely to have been acquired after 1888, not 1885 as listed. When Boulenger received the Chelsea Point specimen, after Sclater's letter in 1904, he immediately recognized its distinctiveness and described it as a new species (Boulenger 1910). It is therefore possible that Moorhouse collected both specimens, and that the reference in the 1885 specimen register to *Phyllodactylus* n. sp. does not refer to SAM-777.

There is no indication that Moorhouse collected more than a single specimen of *Phyllodactylus*. None the less, curatorial practice at the SAM at the time gave only one accession number to all specimens of a species collected at the same locality. It is most probable that more than one collection was forwarded to the SAM from Port Elizabeth.

THE DISTRIBUTION OF *PHYLLODACTYLUS PERINGUEYI* (Fig. 5)

All recent collections of *Phyllodactylus peringueyi* have been from transitional salt-marsh vegetation in the lower Kromme River. It has not been found in neighbouring estuaries or the adjacent coastline. If *P. peringueyi* was indeed collected at Chelsea Point, it is possible that it is now extinct there. The Port

Elizabeth region has been very well surveyed herpetologically, but no new specimens have been found. The senior author has been based in Port Elizabeth for over 12 years and has undertaken numerous extensive searches for the species. Chelsea Point is located on the south-western boundary of Cape Recife, an area that consists of shifting coastal dunes with scattered low sandstone outcrops and regions of calcrete pavement. It is naturally vegetated with a thick, dwarf heathland (fynbos), but is now heavily infested with introduced alien Australian *Acacia*. This was introduced at the turn of the century to control drifting sand dunes around the environs of the burgeoning city of Port Elizabeth. The dense stands of exotic *Acacia* now lead to extensive fires that may have resulted in the extinction of the species. These plants have been implicated in the reduction in numbers of the local berg adder, *Bitis atropos* (Branch 1988b). Alterations in fire regimes and afforestation with exotic timber plantations are believed to be responsible for the possible extinction of one other South African lizard, *Tetradactylus eastwoodae* (Jacobsen 1988).

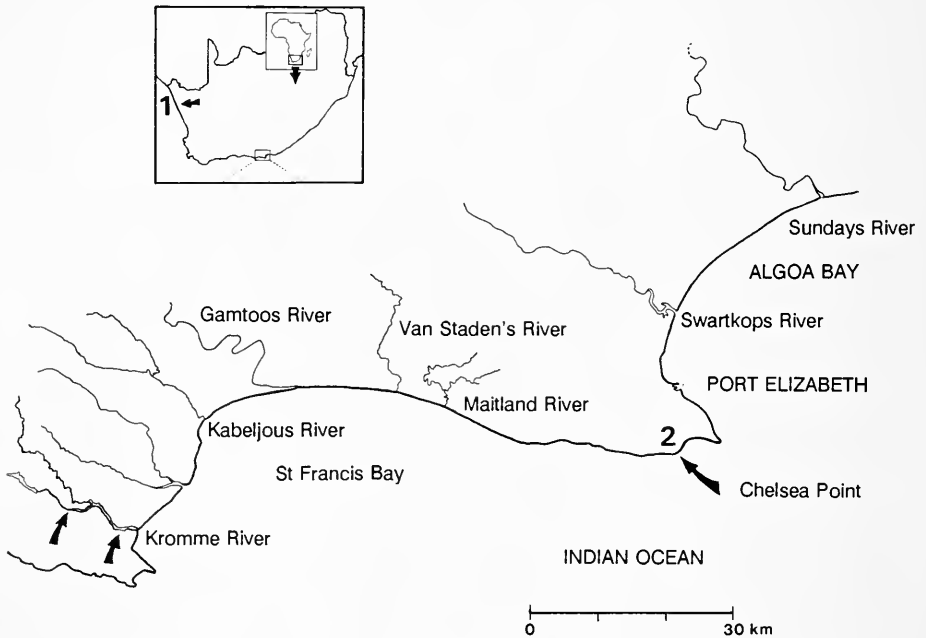


Fig. 5. Distribution of *Phyllodactylus peringueyi*. Listed collecting localities of the syntypes are shown by arrows: 1—Little Namaqualand, 2—Chelsea Point. The two arrows on the Kromme River in the larger map show the current limits of the range of *P. peringueyi* along the tidal reaches of the river.

The apparent restriction of *P. peringueyi* to the Kromme River estuary is biogeographically problematic. Such low-lying areas rarely harbour endemic species. Further, the vicissitudes of the estuarine environment suggest that the species may possess adaptations for coping with hypersalinity and even sporadic inundation. It is possible that the species has been introduced by human

agency or more probably by rafting. McLachlan (1988) noted that the Chelsea Point specimen had been found on the beach and suggested that the animal may have thus arrived as a result of overwater waif dispersal. Overwater transport has been implicated in other leaf-toed geckos. For example, the Galapagos species of *Phyllodactylus* appear to be derived from three overwater founder events, each originating from mainland western South America (Wright 1983). Other American *Phyllodactylus* are restricted to strand environments (Dixon & Huey 1970), although such forms have broader distributions than *P. peringueyi*.

RELATIONSHIPS OF *PHYLLODACTYLUS PERINGUEYI*

Hewitt (1937) listed a number of differences between *Phyllodactylus peringueyi* and other South African *Phyllodactylus* species, including: the markedly elongate snout; dark streak on the side of the head that passes through the eye; the broadly bell-shaped mental; the absence of chin shields or a median cleft in the rostral. He concluded (p. 206): 'It seems to agree best with the American group of species, and I do not accept it as South African.' This view was tentatively supported by FitzSimons (1943). Loveridge (1947) reported on Hewitt's statements without further comment of his own. The most recent review of *P. peringueyi* was provided by McLachlan (1988), who again questioned the origin of the specimens, although Dixon (*in* McLachlan 1988) has ruled out the specific identity of *P. peringueyi* with either American or Madagascan leaf-toed geckos, and our results confirm this.

Phyllodactylus peringueyi is a valid species that is morphologically distinct from all other described leaf-toed geckos. Specific identity with most other leaf-toed gecko species can easily be ruled out on the basis of external characters, and many species can be eliminated on the basis of size. The largest *P. peringueyi* has a SVL of 28.3 mm and radiographs clearly show that all long bone epiphyses are well ossified. Gravid females have SVLs of 26–28 mm, and the species is obviously a dwarf form. The greatly enlarged preanal scales typical of *P. gerrhopygus*, *P. heterurus* and *P. angustidigitatus* (Dixon & Huey 1970; Kroll & Dixon 1972) and the tuberculate condition of *P. leei* and *P. unctus* (Dixon 1964) are presumably apomorphic conditions within the genus; both conditions are lacking in *P. peringueyi*.

Because of the poor condition of the syntypes and the lack of published comparative data on other *Phyllodactylus* *sensu lato*, it has not been possible to determine the phylogenetic relationships of *P. peringueyi*. None the less, membership of the taxon in certain putatively monophyletic groups can be ruled out on the basis of the lack of one or more apomorphic traits. The nasal bones of *Phyllodactylus peringueyi* are paired and there is no evidence of a casque or other cranial ornamentation. The retention of the plesiomorphic condition for these features excludes *P. peringueyi* from membership in *Paroedura* (Dixon & Kroll 1974). Likewise, the presence of cloacal bones in males precludes close affinity with *Asaccus*, in which cloacal bones are entirely absent. The same criterion would remove the Socotran species, *P. riebeckii* and *P. trachyrhinus* from consideration as closest relatives (Kluge 1982). Further limitation of the affinities of the species is hindered by the lack of synapomorphic features diagnosing subunits within the remaining, polyphyletic assemblage currently subsumed within *Phyllodactylus* (Kluge 1983). Karyotypic and morphological

data obtained by Gordon (pers. comm.) have suggested a phylogeny for the South African *Phyllodactylus* species that tentatively links *P. peringueyi* to *P. porphyreus*, but the analysis included only the South African species. On biogeographic grounds it seems likely that *P. peringueyi* is part of an endemic southern African radiation of leaf-toed geckos. The monophyly of the group and the affinities of *P. peringueyi* within it will be assessed elsewhere in a broader phylogenetic analysis of African *Phyllodactylus* (Bauer & Branch, in prep.).

ACKNOWLEDGEMENTS

We are grateful to Mike Cherry (Department of Herpetology, South African Museum) for forwarding to us the syntypes of *Phyllodactylus peringueyi*, and for assistance with the early SAM catalogue and correspondence relating to the syntypes. Gordon Craig (Port Elizabeth) rediscovered the 'long-lost' *P. peringueyi*, and he and his family helped enthusiastically in searches for the species in the Kromme River estuary region. Gerald Haagner, Rob Hall, M. Burger and several other colleagues helped to collect fresh material. Murray Ralfe prepared the excellent head and foot line-drawings of this minute species. Harold Voris (FMNH), George Zug (USNM), Jens Vindum (CAS), Colin McCarthy and Nick Arnold (BMNH), David Good (LSU), John Cadle (ANSP) and William Duellman (KU) kindly loaned or permitted the examination of specimens in their care. Ken Tighe (USNM) kindly prepared the X-rays used in this study. Marcia Field (Villanova University) prepared the X-ray positive prints. Funding from Villanova University, the California Academy of Sciences, and the John Ellerman Trust at the University of Stellenbosch supported travel of AMB to South Africa.

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APPENDIX

Material of *Phyllodactylus peringueyi* examined:

SAM-777, Little Namaqualand, Cape Province, South Africa (lectotype).

SAM-8628, Chelsea Point, near Port Elizabeth, Cape Province, South Africa (paralectotype).

PEM R6886, 6916, 7210, Kaia da Balaia, Kromme River, Humansdorp, Cape Province South Africa (3424Bb; 34°07'15"S 24°45'30"E; alt. 1 m asl.).

PEM R6908-6915, region of road bridge at mouth of Kromme River (3424Bb; 34°08'15"S 24°48'50"E).

6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated: if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order. e.g.:

Family **Nuculanidae**

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierii Philippi, 1861: 87.

Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

semicolon separates more than one reference by the same author

full stop separates references by different authors

figures of plates are enclosed in parentheses to distinguish them from text-figures

dash, not comma, separates consecutive numbers.

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

7. SPECIAL HOUSE RULES

Capital initial letters

- (a) The Figures, Maps and Tables of the paper when referred to in the text
e.g. '... the Figure depicting *C. namacolus* . . .'; '... in *C. namacolus* (Fig. 10) . . .'
- (b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene
- (c) Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should preferably be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as

'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively. The generic name should not be abbreviated at the beginning of a sentence or paragraph.

Name of new genus or species is not to be included in the title; it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.



WILLIAM R. BRANCH
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PHYLLODACTYLUS PERINGUEYI
(REPTILIA, GEKKONIDAE)
ITS TAXONOMIC HISTORY, REDISCOVERY,
AND PHYLOGENETIC AFFINITIES