

Loveridge's Angolan geckos, *Afroedura karroica bogerti* and *Pachydactylus scutatus angolensis* (Sauria, Gekkonidae): new distribution records, comments on type localities and taxonomic status

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Abstract

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In 1944 Loveridge described two new geckos from Angola, *Afroedura karroica bogerti* and *Pachydactylus scutatus angolensis*. The descriptions of both species have vague and confusing type localities and refinements are suggested based on early expedition reports, historical accounts from the region, and a review of cartographic material. Numerous new distribution records are reported for both species from expeditions undertaken from 1956–2016 by the authors or their colleagues. The taxonomic status of both species has changed, but new material from diverse habitats, altitudes and geological substrates indicates that further taxonomic adjustments are likely in order to reflect additional cryptic diversity.

Resumo

Em 1944, Loveridge descreveu duas espécies novas de Angola: *Afroedura karroica bogerti* e *Pachydactylus scutatus angolensis*. As descrições de ambas as espécies têm localidades-tipo vagas e confusas. Neste trabalho são sugeridos mais detalhes relativos a estas espécies, com base em relatórios de expedições, relatos históricos da região e revisão de material cartográfico. São relatados numerosos registros novos de distribuição para estas espécies, com base em expedições levadas a cabo entre 1956 e 2016 pelos autores ou colegas seus. A situação taxonômica das duas espécies alterou-se, mas material novo proveniente de habitats, altitudes, e substratos geológicos diversos, indicam que é provável que ocorram mais ajustes taxonômicos de forma a refletir uma diversidade críptica ainda maior.

Introduction

Studies on the herpetofauna of Angola have entered a new phase following increased collaboration on regional and national biodiversity surveys, multi-authored modern taxonomic reviews, and the emergence of young Angolan scientists (Branch 2016). Almost all recent surveys (e.g. Huntley 2009; Brooks 2012, 2013; Ceriaco et al. 2014, 2016; Ernst et al. 2014; Huntley and Francisco 2015; Conradie et al. 2016), have uncovered new national and regional distribution records (Branch and McCartney 1992; Branch and Conradie 2013; Conradie and Bourquin 2013; Ernst et al. 2014), as well as new species of amphibians (Conradie et al. 2012a, 2013) and reptiles (Conradie et al. 2012b; Stanley et al. 2016). However, problems arise when attempting to integrate these new findings with early literature and original species descriptions. Comparison is complicated by numerous factors, particularly the generally vague locality details for type material in early descriptions. It is not always obvious which localities or regions in these descriptions refer to modern towns in different parts of the country that have similar or identical names, and may be affected by the variant spellings of explorers and researchers. Exacerbating this is the loss of almost all of the material studied by José Vicente Barbosa du Bocage, the father of Angolan herpetology, in a fire that destroyed the Museu Bocage collections in 1978. As a consequence, many type specimens are no longer available and replacement 'topotypic' material requires confidence in the documentation of type localities. To illustrate these problems we consider two recent examples, *Afroedura karroica bogerti* Loveridge, 1944, and *Pachydactylus scutatus angolensis* Loveridge, 1944, where knowledge of the vague type localities given in the original description have become more defined following recent investigation and the integration of new and early observations. Both taxa are subsequently been elevated to specific status (see below).

Taxonomy

Angolan Flat Gecko (*Afroedura bogerti*)

History. The Angolan Flat Gecko (*Afroedura bogerti*) is a beautiful and zoogeographically interesting species. For many years knowledge of the species was based on a single specimen collected during the Vernay Angola Expedition (VAE) in 1925. Charles Bogert, after whom the gecko is named, was the Curator of Herpetology at the American Museum of Natural History (AMNH), and prepared a detailed report on the snakes collected by the VAE (Bogert 1940). He never published on the extensive lizard collections, but did draw Loveridge's attention to a specimen that he thought might be a new species, and for which a superb drawing had been prepared (fig. 1 in Loveridge 1944). Loveridge confirmed this assessment

and described the species in Bogert's honour. He considered it closely related to a South African species, *Oedura karroica* Hewitt, 1925, but did not consider the few African representatives of *Oedura* to be congeneric with Australian *Oedura* Gray, 1842, which had been based on the Australian species *Oedura marmorata* Gray, 1842. He therefore placed all African representatives of *Oedura* in a new genus, *Afroedura*, with his new subspecies, *Afroedura karroica bogerti* as the genotype.

Taxonomic status of *Afroedura bogerti*. Onderstall (1984) investigated relationships between *Afroedura* species, and on morphological grounds recognized three species groups. He examined material collected by WDH in 1971 and 1974, and based on its possession of two pairs of scancers per digit and a verticillate tail placed it in his 'transvaalica' group, along with *A. transvaalica* (Hewitt, 1925) and *A. loveridgei* Broadley, 1963. His 'africana' group, which included *A. karroica*, was characterized by having three pairs of scancers per digit and a verticillate tail, and he therefore elevated *A. bogerti* to a full species (Onderstall 1984). Based on material collected in 2009 from Tambor in the Iona National Park (see below), significant genetic divergence of *A. bogerti* from all other *Afroedura* (Jacobsen et al. 2014; Makhubo et al. 2015) confirmed its specific status. However, there remains confusion over its phylogenetic relationships. Jacobsen et al. (2014) and Makhubo et al. (2015) found that *A. bogerti* was part of the *A. transvaalica* group, although they differed in the latter group's relationships to other species groups. This association remains of zoogeographic interest as the range of *A. bogerti* is separated by nearly 2000 km from other members of the *A. transvaalica* group (sensu Jacobsen et al. 2014). However, among Angolan geckos it is easily recognized by its dorso-ventrally flattened body, smooth homogenous dorsal scalation, possessing 1-2 pairs of scancers under the fourth toe, and the verticillate tail.

Type locality of *Afroedura karroica bogerti*. In his description of *Afroedura k. bogerti*, Loveridge (1944) noted that the type specimen (AMNH 47841) was an adult male from Namba (Mombolo), Cuanza Sul Province, Angola, collected by Harry and Allan Chapman, between September and November 1925. Although the locality was not defined in more detail by Loveridge, Bogert (1940) had previously given general geographical co-ordinates for Mombolo (12°10'S, 14°50'E), but did not mention Namba. Crawford-Cabral and Mesquitela (1989) mapped the vertebrate collections recorded from Angola but overlooked Loveridge's (1944) two gecko descriptions. They did record Bogert's (1940) Mombolo (as 'Mombola') using the details given in his paper, and also listed Namba (Missão da Namba, 11°55' S, 14°51'E), approximately 27 km north of Bogert's Mombolo locality. It should be noted that the geographical co-ordinates listed for both these localities are relatively vague and provide only degrees and minutes.



Figure 1. A: (left) Photograph of the original “Titulo de Concessao” (28 January 1930) confirming William Chapman’s ownership of the farm that was purchased by the Kath-Brock family. **B:** (right) the farm map from the “Titulo de Concessao” showing ‘Alengo Sandula’ at middle of lower boundary.

There is no detailed history or route for the VAE, but a brief summary of the expedition is given in the Mammals of Angola (Hill and Carter 1941, p: 3). It records (salient comments abstracted):

Messrs. Herbert Lang and Rudyerd Boulton, collectors, went to Angola in April, 1925, and remained there for about three months. Landing at Lobito, near Catumbela, a few animals were secured here. The expedition went to Hanha Estate (not the Hanha usually given on maps), an oil palm plantation near the coast, some thirty-two kilometers north of Lobito. The party then went south by way of Huambo where they were joined by Messrs. A. S. Vernay, Alan and Charles Chapman..... At the end of August the expedition united at Capelongo and returned by way of Caconda to Huambo..... At Huambo the party again divided..... Boulton and Charles Chapman went to Namba in the Mombolo region.

The geographical locations of sites detailed in Hill and Carter (1941) are again relatively vague: i.e. Chipupe, near Cassongue (12°S, 15°E); Monte Victoria Verdun (12° 05'S, 15°E); and Namba (Mombolo) (11°35 S, 14°25' E).

Although Loveridge (1944) recorded that the type specimen of *A. k. bogerti* was collected during the VAE,

he specifically states that it was “collected by Harry and Allan Chapman, between September and November, 1925.” This was after the American members of the VAE had departed. This discrepancy is probably explained by a comment in Hill and Carter (1941, p: 5) where they note that their mammal material included “..... fifty mammals ... purchased from Mr. C. P. Chapman, collected at Chipupe, Namba, and Monte Victoria Verdun.”, and it is thus possible that Loveridge’s type specimen was obtained in the same way.

Many of these locations are discussed in the recently published ‘Reminiscences’ of William Chapman, the father of Charles, Harry and Alan Chapman (Stassen 2010). The latter two sons (note corrected spelling of Alan, not Allan) are the collectors of the type specimen of *A. k. bogerti* (Loveridge 1944). William Chapman was the son of the famous South African explorer James Chapman (Chapman 1868), and one of the original ‘Trek Boers’, who moved away from British rule in the Cape region, and eventually settled (1881–1928) in southern Angola.

Chapman notes “Ernst Meyer had selected a farm in the Mombolo country at the base of a mountain range called Namba” (Stassen 2010, p: 295). He later comments “The next day I crossed the Etala stream [a tributary of the Cuchem] with my wagon and went up to the small plain below the koppie on which I subsequently built my



Figure 2. The ruins of farm Monte Verde, surrounded by eucalyptus trees (middle distance), overlay those of William Chapman's farm Monte Victoria-Verdun. Viewed from an intrusive rock outcrop on the lower northern slopes of Sandula Hill.

house" (Stassen 2010, p: 297). He called it Monte Victoria-Verdun (Stassen 2010, p: 25 notes it was originally called Sandula, but see below).

It was noted (Stassen 2010, p: 13) that William Chapman:

..... liked the company of scientific explorers and quite a number of them were invited to stay for some time on his farm. As a result the type specimens of quite a few species of fauna and flora were recorded at Sandula, Namba or Chipepe, the farms of the Chapman clan near Mombolo.

A thorough examination of official detailed cartographic material supported by the historical accounts, allowed us to identify the possible location of Chapman's farm on topographic maps as "Fazenda Monte Verde", located on the northeastern slopes of the Lupangue mountains, close to the headwaters of the Etala stream, which drains between rock outcrops from the mountain. We were able to confirm this following a site visit (5-6 November 2016), and from inspection of the original "Titulo de Concessão", dated 28 January 1930 (Fig. 1A), that confirms the farm's ownership by William Chapman. The farm was purchased by the Kath-Brock family, who renamed it as Monte Verde. The original farm map attached to the title deed reveals that the "koppie" (hill) noted by Chapman was originally called Sandula (Fig. 1B). The brick farm buildings of the Brock family (12°10'09"S, 15°01'42"E, 1798m a.s.l.) were built on, and incorporate some of, the original Chapman house, but both are now derelict, whilst Sandula Hill (12°11'04"S, 15°01'41"E, 2242m a.s.l) is locally now called Monte Verde. This prominence is capped in granite outcrops, with intrusive rock outcrops on its lower slopes and is close to the farm site. These outcrops form suitable habitat for flat geckos (Fig. 2).

Stassen (2010, p25) notes "*Mombolo is a small village on the Benguela highlands in the Cuanza Sul district and is also called Omambolo, Nakamombolo or Makamombolo*". Although two small quimbos (villages) to the southwest of Chapman's farm have been identified in the cartographic material referenced as Mombolo, we consider that the name is more correctly associated with the general region to the south of *Missão da Namba*, as is shown in the *Carta de Angola* at the scale of 1/100 000, where the area immediately to the south of *Missão da Namba* is named Mombolo. This is an extensive grassy area named as the *Anhara do Mombolo*, and at the southern edge of which lies the present town of *Maka-Mombolo* (12°11'54"S, 14°52'06"E, 1760m asl) mentioned by Stassen (2010, p25). Local people refer to extensive flat natural grasslands as 'mombolos', areas suitable for planting staple crops. *Missão da Namba* is a Seventh-day Adventist church established by James Delmes Baker, who settled in the area in November 1928 (Anon, 2017).

The Lynes-Vincent bird expedition (1930–31) was a specialist trip for *Cisticola* species in Central and West Africa (Lynes and Sclater 1933, 1934). On 1 March 1931 the expedition visited "Chipepe (Mombolo loc. 5900ft)", identified in the official topographic maps as *Fazenda Quipepe* (11°59'30"S, 14°56'10"E), having driven 140 miles from Huambo, via Bailundo. The expedition then spent 2–8 March 1931 at "Namba (nr. Chipepe) 5700 ft. to 6700ft.", where they were assisted by "Herr Köster" (probably Paul Friedrich Heinrich Köster who married William Chapman's daughter Sarah, and who remained in the Mombolo region after the 'Trek Boers' moved to Namibia in 1928; Stassen 2010).

Although our studies and site visits give greater detail to the probable origin of the type specimen of *A. k. bogerti*, the exact location of its capture remains unknown,

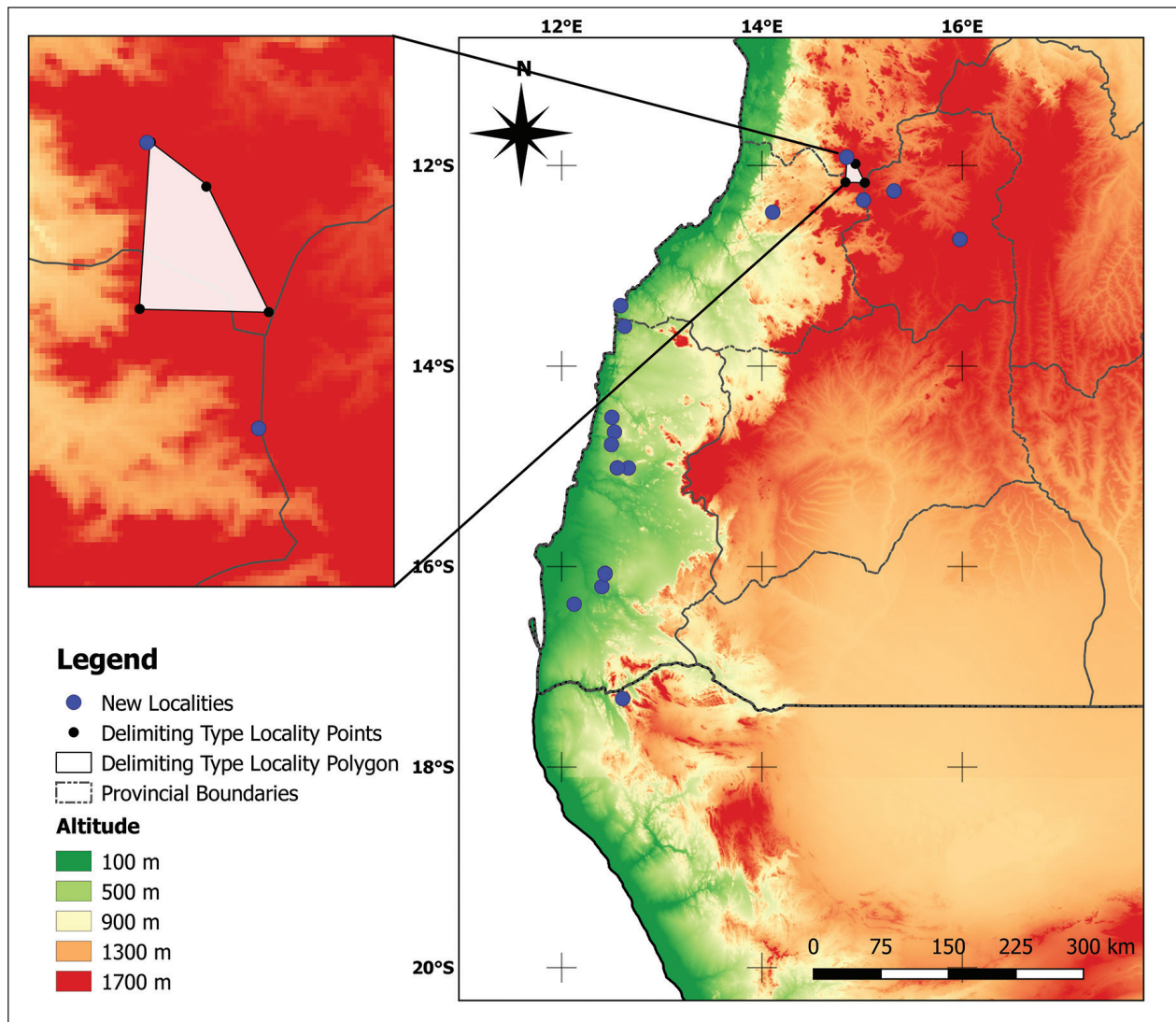


Figure 3. Geographical distribution of *Afroedura bogerti*. Insert (left) shows the polygon that encompasses the area from which the type specimen was collected. The problematic Namibian specimen is included.

and cannot be determined with greater accuracy based on existing knowledge. We conclude that the vague type locality, i.e. “Namba (Mombolo)” refers to a general area that probably corresponds to a polygon that can be delimited by the points (detailed above) of William Chapman’s farm (Monte Victoria-Verdun, later Monte Verde), Chiipepe/Quipepe, the farm of one of his sons, Missão da Namba, and Maka-Mombolo (Fig 3.). This is also adjacent to Mombolo (Missão da Namba, AO018, 11°55’S, 14°51’E), an Important Bird Area for the conservation of a number of Angolan birds (Birdlife 2016).

New distribution records for *Afroedura bogerti*. Following its discovery in 1925 the next specimen of this species was collected by Dr C. Koch on a Transvaal Museum Expedition to southwest Angola in September 1956. Collected near Caraculo (15°01’36.7”S, 12°39’07.57”E), this specimen (TM 24545) was not mentioned by FitzSimons (1959) in his description of new reptiles (e.g. *Pachydactylus caraculicus* and *Prosymna visseri*) collected during

Koch’s expedition. It did, however, direct subsequent searches when one of us (WDH) visited Angola (1971 and 1974) to specifically search for geckos of the genera *Pachydactylus*, *Rhoptropus* and *Afroedura*. These surveys obtained significant new *A. bogerti* material from various localities, including: TM 40263–68, 40279–95 (23 specimens), Caraculo, Namibe Province, 27 March 1971; TM 40508–20 (13 specimens), Tambor, Namibe Province, Angola (16°04’00.1”S, 12°26’59.9”E), 1 April 1971; TM 40536–37 (two specimens) Furnas (? – plotted as nearest rock outcrops to centre of quarter-degree square (QDS) 1612Ab in original field notes), Namibe Province (1612Ab, 16°23’30.0”S, 12°08’30.0”E), 1 April 1971; TM 41132–44 (13 specimens), turn off to Morro do Chapéu Armado, Namibe Province (14°31’42.8”S, 12°30’06.8”E), 18 April 1971; TM 41211–16 (six specimens), Lucira road, 5 km south of Catara River, Namibe Province (13°36’15.5”S, 12°38’44.0”E), 19 April 1971; TM 45366–68 (3 specimens), 10 km west of Soque, Huambo Province (12°21’45.2”S, 15°01’42.5”E), 10



Figure 4. Regional variation in colouration and habitus of *Afroedura bogerti* from Angola **A** Omauha Lodge, Namibe Province **B** 52 km N Caraculo, Namibe Province **C** Praia do Meva, Benguela Province (P Vaz Pinto). **D** Candumbo Rocks, Huambo Province (L Verburgt). All photos by WR Branch, except where noted.

May 1974; TM 45374, 1 km south Luimbale, Huambo Province (12°15'13.3"S, 15°19'00.8"E), 10 May 1974; TM 45381–98 (18 specimens), Candumbo Rocks, 16 km west of Vila Nova, Huambo Province (12°44'09.6"S, 15°58'27.8"E), 11 May 1974; TM 46587–90 (four specimens), 3 km west of Bocoio, Benguela Province (12°28'58.0"S, 14°06'24.8"E), 28 May 1974; TM 46631–34 (four specimens), Numba (= Namba), on track from Atome to Cassongue (vicinity of Missão da Namba), Cuanza Sul Province (11°55'01.9"S, 14°51'39.1"E), 29 May 1974.

Following a hiatus in field surveys to Angola during the protracted civil war (1975–2002), no additional material was added until international collaborative biodiversity surveys began in 2009. During the first of these (Huntley 2009) additional material was collected: PEM R17936–37 (two specimens), Omauha Lodge, 15 km south of Tambor, Namibe Province (16°12'02.2"S, 12°24'06.6"E, 341m), 18 January 2009; PEM R18041–42 (two specimens), CAS 248780–81 (two specimens donated by PEM), 0.5 km south of Tambor, Namibe Province (16°04'26.9"S, 12°25'59.8"E, 352m), 21 January 2009. Subsequent field work in the ProNamib region north of Namibe (2012, 2015) and in the Huambo region (2016) resulted in additional material from new localities: PEM R21595, Granite outcrops in sandy veld, 50 km E Namibe on main tar road to Leba, Namibe Province (15°00'56.1"S, 12°33'18.1"E, 516m a.s.l.), 8 December 2012; PEM R21596, small granite outcrops in succulent veld, 52 km N on tar road on road to Lucira from junction with Lubango-Namibe road, Namibe Province (14°39'29.0"S, 12°31'37.8"E, 586m a.s.l.);

AG 137-41 (to be accessioned into PEM collection), 5 specimens, 1 km east of Farm Mucongo, Namibe Province (14°47'01"S, 12°29'49"E, 314m a.s.l.), 7 November 2015; PEM R22488-89, 2 specimens, Praia do Meva (near Santa Maria), Benguela Province (13°23'48"S, 12°35'23"E, 10m a.s.l.), 28 December 2015; PEM R22490-91, 2 specimens, 1 km west Kandumbo on road to Boas Aguas, Huambo Province (12°44'10.1"S, 15°58'27.9"E, 1777m a.s.l.), 11 March 2016.

Currently Angolan *Afroedura bogerti* is known from approximately 15 localities that appear to fall into disjunct populations occurring above and below the Great Escarpment, and in diverse habitats and on different geological substrates. Colouration and scalation varies between the known populations of *A. bogerti* (Fig. 4) and preliminary morphological and genetic analysis corroborates the existence of cryptic diversity within the species (Branch et al. 2017). Molecular sequences for *A. bogerti* incorporated into recent phylogenies of the genus were based on tissues collected from lowland populations within the Angolan Namib region (Jacobsen et al. 2014, Tambor CAS 248780–81; Makhubo et al. 2015, Omauha Lodge, PEM R17936–37). A flat gecko, referred to as *Afroedura* cf. *bogerti*, was discovered in a rock crevice on the summit of the Otjihipa Mountains, northern Opuwo District, Namibia (approx. 17°18'18"S, 12°36'35"E, 1170m) in 1992 (Branch 1998; Griffin 2003). However, no voucher material is available in the State Museum, Windhoek (A.M. Bauer, pers. comm. May 2016), and the taxonomic status of the Namibian population cannot be assessed until further material becomes available.

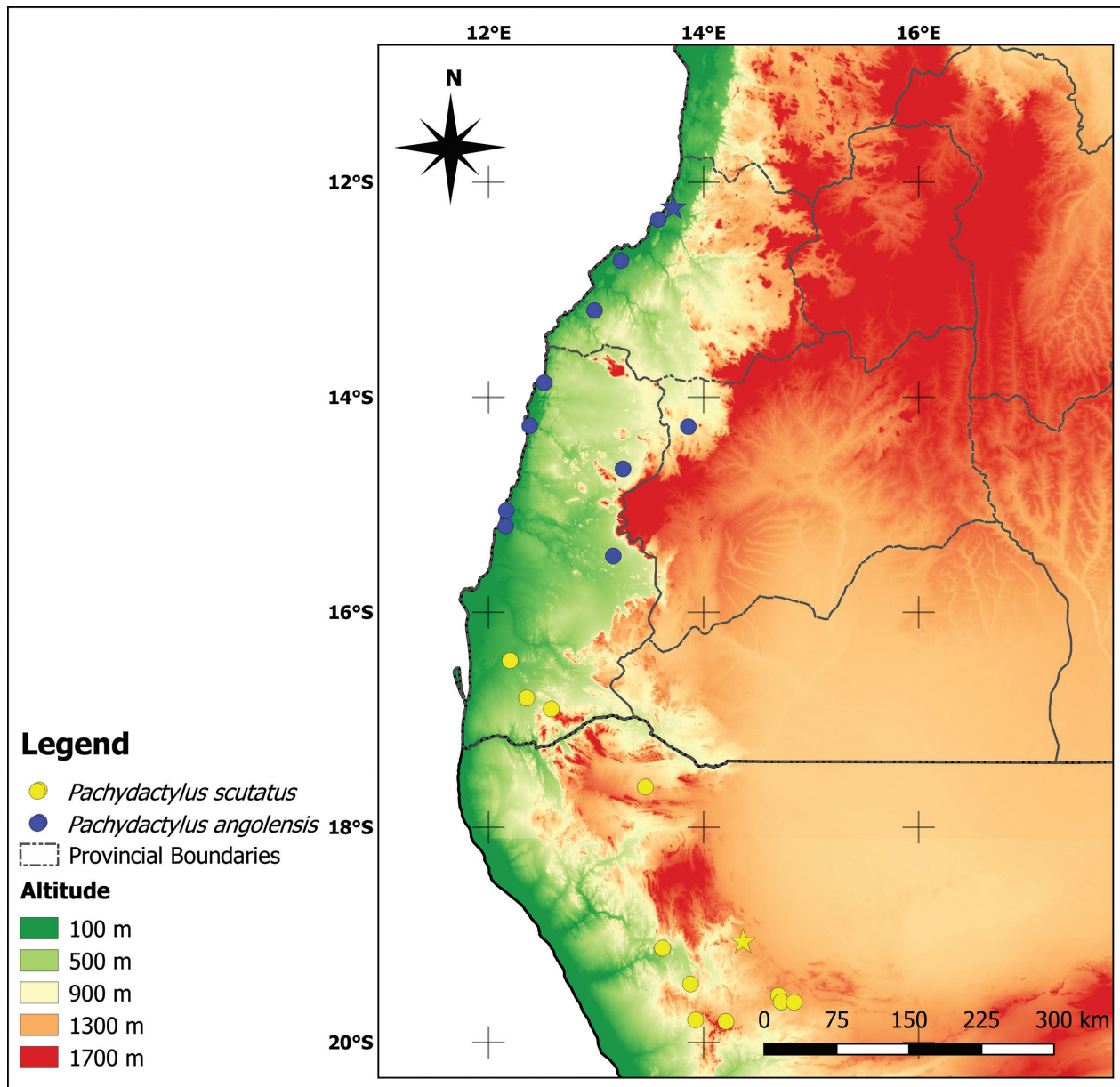


Figure 5. Distribution of *Pachydactylus angolensis* and *Pachydactylus scutatus* in Angola. Stars = type localities. For additional Namibian localities for *P. scutatus*, see Bauer et al. (2002).

Angolan Thick-toed Gecko (*Pachydactylus angolensis*)

History. In the same paper in which he described *Afroedura k. bogerti*, Loveridge also described the small terrestrial gecko *Pachydactylus scutatus angolensis* Loveridge, 1944. Loveridge’s (1944) description was based on three specimens. The holotype (AMNH 47874) was “an adult male from Hanha, Benguela Province, Angola, collected by Arthur Vernay, Herbert Lang and Rudyerd Boulton, May 17, 1925”. One of the two paratypes was also collected at the type locality but on 13 May 1925, and the other collected earlier “from Lobito Bay, Angola ... by Herbert Lang, April 24, 1925”. These dates, unlike those for *A. bogerti*, indicate that the geckos were actually collected during the VAE.

Taxonomic status of *Pachydactylus angolensis*. Bauer et al. (2002), in a review of Namibian *P. scutatus* Hewitt, 1927 (including the description of *P. parascutatus* Bauer, Lamb and Branch, 2002), elevated *P. angolensis* to a full species, noting the consistent nasal arrangement. A recent molecular phylogeny of the genus *Pachydactylus* (Heinicke et al. 2017) confirms the specific status of *P. angolensis*, but reveals its sister relationship to *P. cariculicus* not *P. scutatus*. With the elevation of *P. angolensis* to specific status, *P. scutatus* was considered to be restricted to Namibia north of the Brandberg. However, WDH (unpubl.) had already collected the first Angolan *P. scutatus* from Iona National Park (TM 40751), and others from Espinheira (TM 40615–18), when he visited the region in April 1971. Recent material from the latter locality has also been reported by Ceriaco et

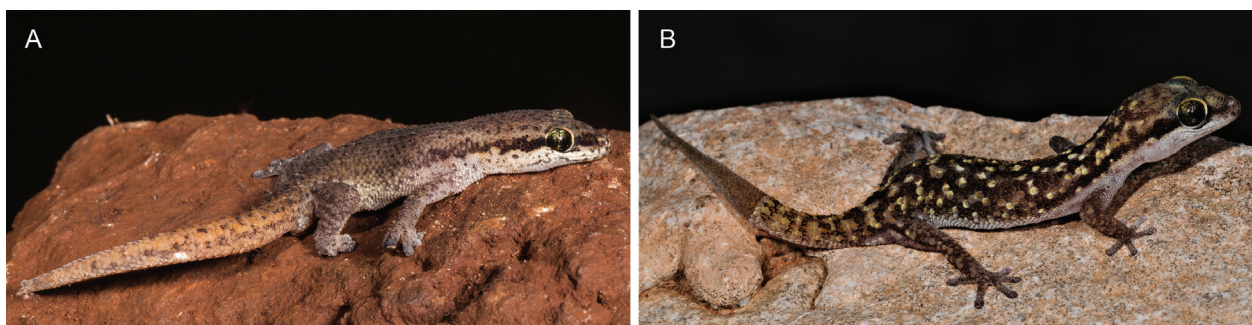


Figure 6. Regional variation in colouration of *Pachydactylus angolensis* from Angola. **A** *P. angolensis* – inland form (Serra da Tchivira: photo P. Vaz Pinto) **B** *P. angolensis* – coastal form (Chimalavera Regional Natural Park: photo WR Branch).

al. (2016). The TM geckos from Iona and Espinheira have the characteristic narrow and dark-edged white nape band illustrated in Boone and Barts (2006) which is not evident in *P. angolensis* or mentioned in its description (Loveridge 1944). Thick-toed geckos (*Pachydactylus*) are poorly represented in Angola, with only seven currently recognized species recorded; *P. cariculicus*, *P. scutatus*, *P. angolensis*, *P. punctatus*, *P. oreophilus*, *P. rangei* and *P. vanzyli*. This contrasts dramatically with *Pachydactylus* diversity in Namibia (38 species) and South Africa (30 species). *Pachydactylus angolensis* can be distinguished from most Angolan *Pachydactylus* (e.g. *P. cariculicus*, *P. punctatus*, *P. rangei* and *P. vanzyli*) by its keeled dorsal scalation, from *P. oreophilus* by its smaller size, and from *P. scutatus* by lacking a dark-edged white nape band and by the exclusion of the first upper labial and rostral from the nostril (*P. scutatus* has a well developed nape band, and both the first upper labial and rostral enter the nostril).

Type locality of *Pachydactylus scutatus angolensis*.

Angolan localities referenced under the toponym “Hanha” may cause confusion. Two main places are of concern, and both are situated in Benguela Province: Hanha do Norte (also Hanha Estate) and Hanha do Cubal. Bauer et al. (2002) noted that the holotype was “.. collected at Hanha (probably Hanha do Norte in quarter degree square 1213Bc; another locality, Hanha do Cubal, 1314Aa is also in the same province)”. The above assumption is here accepted, inasmuch as it avoided confusion between the two localities, and furthermore is corroborated by the fact that Hill and Carter (1941) had earlier noted that the VAE did not visit Hanha do Cubal, but rather the Hanha Estate oil palm plantation. Unfortunately, although the geographic description of Hill and Carter (1941) is basically correct, the co-ordinates they give (13°30' S, 14°30' E) are incorrect and refer to another Hanha toponym that lies south-east of the estate. It is indicated on a 1934 map of the region, and is now known as Cambondongolo (13°21'0”S, 14°24'0”E). To avoid further confusion we recommend that the type locality for *Pachydactylus scutatus angolensis* Loveridge, 1944 be restricted to - Hanha do Norte (12°14'42”S, 13°42'27”E), approximately 20 km north-east of Lobito, Benguela Province, Angola. This site is illustrated in fig. 1 of Hill and Carter (1941).

New distribution records for *Pachydactylus angolensis*.

Pachydactylus angolensis remains poorly-known from Angola. Additional material (Laurent 1964) was collected soon after the original description, and other specimens were collected from various localities in Namibe Province by Koch during his expedition in September 1956 (see above), including: Lungo (TM 24406), Lucira (TM 24445, 24449) and Bentiaba (TM 25454–55, 25459, 25476, 25478–79). These discoveries, and others from 24 km south of Benguela (TM 39110–11), stimulated WDH to collect more material in 1971 from Saco do Giraul (TM 40328–29), Lucira (TM 41172), 30 km north Dombe Grande (TM 41266), and in 1974 from Hanha (TM 46558). More recently Ceriaco et al. (2016) recorded a specimen from the Namibe-Lubango road, near Mangueriras (15°2'37”S, 13°9'36”E).

Recent collections of geckos currently attributed to *P. angolensis* are grouped into coastal and inland populations (Fig. 5), with coastal populations (<300m a.s.l.) usually associated with consolidated marine deposits, while inland populations (>600m a.s.l.) are found in granite or intrusive outcrops. Preliminary morphological investigation indicates variation in dorsal colouration and habitus (Fig. 6) between these populations that are indicative of further cryptic diversity in Angolan geckos, and will be investigated with integrative morphological and genetic studies (Branch in prep.).

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