

Rock island melody: A revision of the *Afroedura bogerti* Loveridge, 1944 group, with descriptions of four new endemic species from Angola

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Abstract

Four new species of flat geckos in the *Afroedura bogerti* Loveridge, 1944 group are described from south-western and west-central Angola. The description of these new species significantly restricts the distribution range of typical *A. bogerti*, a morphologically very similar species, from which they differ genetically by 5.9–12% divergence for the mitochondrial 16S ribosomal RNA gene. Morphologically and genetically, Angolan *Afroedura* are divided into two main groups: a mostly south-western coastal group and a west-central inland/highland group. These two groups are further divisible into three and two subgroups respectively, all geographically isolated, differing by a combination of the following features: colouration, average adult size, number of mid-body scale rows, number of scale rows on dorsal and ventral surface of each tail verticil and if nostril scales are in contact or not. All five Angolan species are morphologically distinguishable and in agreement with the molecular results. An updated dichotomous key to the *Afroedura transvaalica* group is provided. The new discovery adds to a growing number of endemic Pro-Namib reptiles described from Angola in recent years.

Resumo

Aqui são descritas quatro novas espécies de osga-achatada, do grupo *Afroedura* Loveridge, 1944, do sudoeste e centro-oeste de Angola. A descrição destas novas espécies reduziu significativamente a área de distribuição da *A. bogerti* típica, uma espécie uma espécie morfológicamente muito semelhante às primeiras, da qual estas têm entre 5.9 e 12% de diferença genética para o gene mitocondrial 16S rRNA. Do ponto de vista morfológico e genético, as *Afroedura* de Angola dividem-se em dois grupos principais: o do sudoeste, maioritariamente das planícies costeiras e do norte, e o do planalto interior. Estes grupos podem ainda ser divididos em dois e três subgrupos, respectivamente, todos isolados geograficamente, e estes diferem entre si na combinação das seguintes características: coloração, tamanho médio dos adultos, número de fileiras de escamas na secção mediana do corpo, número de escamas dorsais e ventrais por cada anel caudal de escamas, escamas nasais em contacto ou não. É possível distinguir morfológicamente as cinco espécies de Angola, de forma concordante com os resultados da genética. Aqui apresentamos uma chave dicotómica actualizada para o grupo *Afroedura transvaalica*. Esta nova descoberta junta-se ao crescente número de répteis endémicos do Pro-Namibe descritos em Angola nos últimos anos.

† Deceased

Key Words

Biodiversity hotspot, cryptic species, endemism, Gekkonidae, Reptilia

Palavras-chave

Endemismo, espécies crípticas, Gekkonidae, hotspot de biodiversidade, Reptilia

Introduction

The current reptile diversity in Angola comprises about 300 species (Marques et al. 2018; Branch et al. 2019a; and subsequent descriptions listed below). New species are constantly being added (Conradie et al. 2012, 2020; Stanley et al. 2016; Marques et al. 2019a, b, 2020; Branch et al. 2019b; Ceriaco et al. 2020a, b, c; Hallerman et al. 2020) and more new species are expected in the country (Branch 2016; Branch and Tolley 2017; Branch et al. 2017a, b; Butler et al. 2019). As Angola is rebuilding after decades of civil war, more remote regions are becoming accessible to researchers, with the promise of additional cryptic species.

The Gekkonidae in Angola comprises eight genera, *Afroedura* (one species), *Afrogecko* (one species), *Chondrodactylus* (three species), *Hemidactylus* (eight species), *Kolekanos* (one species), *Lygodactylus* (five species), *Pachydactylus* (11 species) and *Rhoptropus* (seven species) (see Marques et al. 2018, 2020; Branch et al. 2019a; Ceriaco et al. 2020a, c). A total of 15 species of geckos are considered to be endemic to the country. This includes the monotypic *Kolekanos plumicaudus* (Haacke, 2008), the recently re-discovered *Afrogecko ansorgii* (Vaz Pinto et al. 2019), six species of *Hemidactylus* (Ceriaco et al. 2020a, c), three species of *Lygodactylus* (Marques et al. 2020), three species of *Rhoptropus* and *Pachydactylus angolensis* (Marques et al. 2018; Branch et al. 2019a). *Afroedura bogerti* is currently regarded as a near-endemic species as a specimen was also found in northern Namibia (Branch 1998; Griffin 2003).

Loveridge (1944) transferred African *Oedura* to the new genus *Afroedura* and described *A. karroica bogerti* from Angola after examining specimens collected during the 1925 Vernay Angolan Expedition. He designated this material as the type for the new genus and regarded it as part of the ‘*halli/karroica*’ group. Later, Onderstall (1984) investigated relationships between *Afroedura* species after examining material from south-western Angola collected by Wulf Haacke in the 1970s. He placed *A. k. bogerti* in the ‘*transvaalica*’ group, alongside *A. transvaalica* (Hewitt, 1925) and *A. loveridgei* (Broadley, 1963) and elevated *A. bogerti* to full species status, based on differences in numbers of paired scensors per digit and possession of a verticillate tail. Such findings were supported by recent phylogenetic studies, confirming that *A. bogerti* is part of the ‘*transvaalica*’ group (Jacobsen et al. 2014; Makhubo et

al. 2015; Branch et al. 2017a), with other species occurring to the east in Mozambique, Zimbabwe and South Africa. This relationship of the *A. bogerti* group to the ‘*transvaalica*’ group is of zoogeographic interest as it is separated from other members of the group by nearly 2000 km and occupies more arid and/or mesic environments.

Up to now, *Afroedura bogerti* was the only species of flat gecko known from Angola (Marques et al. 2018; Branch et al. 2017b). In a recent phylogenetic study, in which a new species from the ‘*transvaalica*’ group was described from central Mozambique (*Afroedura gorongosa*), cryptic diversity within Angolan *A. bogerti* populations was documented (Branch et al. 2017a) and this was elaborated on in more detail in a subsequent study (Branch et al. 2017b). Here we take the opportunity to investigate the Angolan *A. bogerti* group in detail and describe four new endemic species.

Materials and methods

Sampling

For the last decade (2009–2019), material of *Afroedura bogerti* was collected from south-western and west-central Angola (Fig. 1; see Branch et al. 2017a). Specimens were euthanised by oral application of benzocaine gel. After euthanasia, some geckos were fixed in 10% formalin and others in 95% ethanol, after which they were transferred to 70% ethanol for long-term storage at the Port Elizabeth Museum (PEM), South Africa, Museum für Naturkunde, Berlin, Germany (ZMB), Instituto Superior de Ciências da Educação da Huíla (ISCED, material listed here as NB), Huíla, Angola and Fundação Kissama (FKH), Luanda, Angola. Liver tissue or tail tips of newly-collected material was sampled and stored in 95–99% ethanol prior to fixation for further genetic analysis.

Molecular analyses

We used molecular methods to support the identified morphological groupings. Recent studies on the genus *Afroedura* (e.g. Branch et al. 2017a) have shown that the fast evolving 16S rRNA gene, with its hypervariable regions, perfectly resolves the different species within

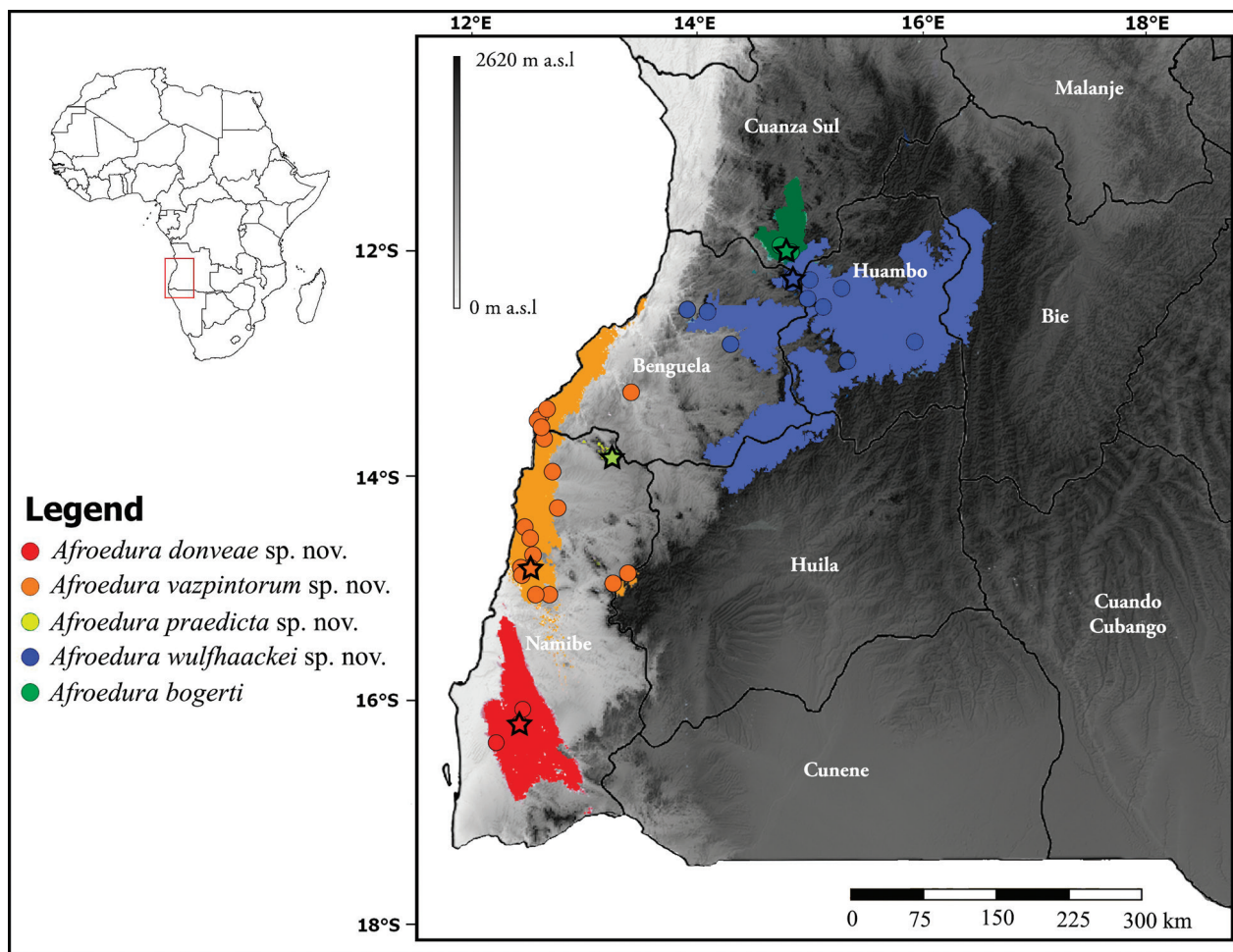


Figure 1. Digital elevation map showing the predicted distribution of the five newly-recognised species of *Afroedura* occurring in Angola (data for *A. wulphaackei* sp. nov. also contain the morphologically-indistinguishable *Afroedura* sp. 5–7 clades). Confirmed locality records are indicated by solid circles, with type localities indicated by stars. Coloured polygons indicate potential distribution areas with more than 90% of climatic habitat suitability.

this genus and even provides insights into the intraspecific structure of the different monophyletic lineages. Therefore, for our molecular comparisons, we combined newly-sequenced mitochondrial *16S* data for specimens from different *Afroedura* populations in Angola and complemented these with previously published (Branch et al. 2017a) sequences from GenBank. Total genomic DNA was extracted from tissue samples using the E.Z.N.A. Tissue DNA Kit (VWR/Omega bio-tek) and the Qiagen DNeasy Tissue Kit, following the manufacturer's protocols. A portion of the mitochondrial genome (*16S* rRNA gene) was PCR amplified and sequenced, following the methods described in Schmitz et al. (2005). All sequences have been deposited in GenBank (Table 1).

DNA sequences were aligned using the original chromatograph data in the programme BioEdit (Hall 1999) using ClustalX (Thompson et al. 1997) and the resulting alignment corrected manually. We sequenced 589 bp of the *16S* rRNA gene, including some fast-evolving, indel-rich loop regions. We deleted 6 bp that could not be unambiguously aligned, resulting in a total sequence length of 583 bp for each voucher. We used Bayesian

Inference (MrBayes v.3.26; Ronquist et al. 2012) and Maximum Likelihood (RAxML v.7.0.4; Stamatakis et al. 2006), using the rapid hill climbing algorithm and the GTR+G model of nucleotide substitution, following Stamatakis et al. (2006), to assess phylogenetic relationships. The best-fit model of sequence evolution for the Bayesian analysis was the TIM2+I+G model with values of $I = 0.5140$ and $G = 0.7180$, selected using jModeltest v.2.1.7 (Darriba et al. 2012) using the Bayesian Information Criterion (BIC).

Bootstrap analyses (BS) with 1000 pseudoreplicates were used to evaluate relative branch support in the ML analysis. We regarded tree topologies with bootstrap values of 70% or greater as supported (Huelsenbeck and Hillis 1993). Bayesian analyses were run for 10 million generations using four chains, sampling every 1000 generations, with the first 25% of trees discarded as burn-in. Stationarity, convergence and mixing of the parameters (ESS values) for the Bayes runs were checked in Tracer v.1.7.1 (Rambaut et al. 2018). Clades with posterior probabilities (PP) ≥ 0.95 were considered strongly supported. In total, sequences from 47 *Afroedura* specimens from Angola

Table 1. *Afroedura* specimens (field and museum numbers), generalised localities (see systematic accounts for full details) and GenBank accession numbers of vouchers used in this study.

Species	Locality	Sample Number	Museum Number	GenBank Number
<i>A. donveae</i> sp. nov.	Omauha Lodge	KTH09-196	PEM R17936	LM993776
		KTH09-197	PEM R17937	LM993777
		P9-284	NA	MW354008
		P9-285	NA	MW354009
<i>A. praedicta</i> sp. nov.	Serra da Neve	NB 853	ZMB 91607	MW354010
		NB 854	ISCED-NB 854	MW354011
		NB 855	ISCED-NB 855	MW354012
<i>A. vazpintorum</i> sp. nov.	50 km east Namibe on main tar road to Leba	ANG 289	PEM R21595	MF565454
	Meva Beach	"30"	PEM R22488	MF565455
	10.4 km south of Rio Mucungo on tar road to Bentiaba	samp 57/E260.13	PEM R24203	MF565458
		samp 58/E260.14	PEM R24204	MF565457
		samp 39/E260.12	NA	MF565459
	1 km east of Farm Mucungo	AG 137	PEM R24114	MF565460
		AG 138	PEM R24115	MF565463
		AG 141	PEM R24118	MF565462
	20 km south Bentiaba	samp 62/E260.15	PEM R24219	MF565456
	52 km north on tar road on road to Lucira	ANG 311	PEM R21596	MF565461
	Mariquita	P9-154	NA	MW354018
	approx. 18 km E Lucira	NB 834	ISCED-NB 834	MW354019
		NB 835	ISCED-NB 835	MW354020
	Carivo	P8-20	NA	MW354016
		P8-19	NA	MW354015
	Bimbe, Estação Zootecnica	NB 743	ISCED-NB 743	MW354017
		NB 745	ISCED-NB 745	MW354013
		NB 746	ISCED-NB 746	MW354014
<i>A. bogerti</i>	Farm Namba	samp 23/E260.1	PEM R24184	MF565467
		samp 24/E260.2	PEM R24185	MF565468
		samp 25/E260.3	PEM R24186	MF565466
	400 m north of Mission de Namba grounds	samp 27/E260.4	PEM R24187	MF565465
		samp 28/E260.5	NA	MF565464
	Namba	JLRZC0015	NA	MW354021
<i>A. wulphaackei</i> sp. nov.	5 km west of Maka-Mombolo	JLRZC0016	NA	MW354022
		samp 71/E260.17	PEM R24232	MF565477
		samp 72/E260.18	PEM R24233	MF565478
	Maka-Mombolo, north-east of Balombo	samp 73/E260.19	PEM R24234	MF565479
		samp 70/E260.16	PEM R24236	MF565476
		NB 817	ISCED-NB 817	MW354024
		NB 818	ISCED-NB 818	MW354025
		NB 819	ISCED-NB 819	MW354026
<i>A. sp. 5</i>	Farm Victoria-Verdun, 2 km S of Mt. Sandula	samp 33/E260.8	PEM R24191	MF565471
		samp 34/E260.9	PEM R24192	MF565469
		samp 31/E260.6	NA	MF565470
		P9-141	NA	MW354023
<i>A. sp. 6</i>	5 km southwest of Lepi	samp 37/E260.11	PEM R24201	MF565472
<i>A. sp. 7</i>	Candumbo Rocks Memorial	samp 35/E260.10	PEM R24200	MF565473
		WC-4037	PEM R22490	MF565474
		WC-4038	PEM R22491	MF565475

were included in the phylogenetic analysis (Table 1) to corroborate our morphological analyses. *Afroedura love-ridgei* (MF565446), shown by Branch et al. (2017a) to be a sister taxon, but still well outside the Angolan clade, was chosen as outgroup. Pairwise comparisons of uncorrected sequence divergences (p-distance) were computed in MEGA X (Kumar et al. 2018; Table 2).

Morphology

We examined material in the collections of the Port Elizabeth Museum (PEM), Ditsong National Museum of Natural History (formerly Transvaal Museum ~ TM), Museum für Naturkunde, Berlin, Germany (ZMB) and Instituto

Superior de Ciências da Educação da Huíla (ISCED), Huíla, Angola (see Material examined under systematic accounts). High quality photographs of the type specimen of *Afroedura bogerti* were also examined.

As with many other gecko genera, *Afroedura* is morphologically conservative, with few discrete differences. The following characters (detailed in Jacobsen 1992) were assessed: 1) presence or absence of internasal granules between the nasal scales; 2) number of postmental scales; 3) number of scales in contact in a straight line between the anterior corners of eyes across the crown of the head; 4) number of scales between upper edge of earhole and rear margin of eye, counted along the shortest distance between them; 5) number of scales between nostril and front edge of orbit, excluding postnasal; 6) number

of enlarged supralabials to the angle of the jaw at mid-orbital position; 7) number of enlarged infralabials to the angle of the jaw at mid-orbital position; 8) number of mid-body scale rows (MSR), counted at the widest part of the trunk; 9) number of scale rows on dorsal surface per tail whorl (counted 3–6 verticils, posterior to the cloaca); 10) number of scales rows on ventral surface per tail whorl (counted 3–6 verticils, posterior to the cloaca); and 11) number of precloacal pores in males.

The following measurements were taken in millimetres (mm) using a digital calliper (accuracy of 0.1 mm) with the aid of a Nikon SMZ1270 dissecting microscope: 1) snout-vent length (SVL – from the tip of the snout to the cloaca with the gecko flattened on its back), 2) tail length (TL, only original tails were measured); 3) head length (HL – tip of snout to retroarticular process of jaw); 4) head width (HW – widest point of head, approximately at the level of eyes); 5) snout length (SL – tip of snout to front of orbit); 6) eye diameter (ED – measured in horizontal orientation); 7) ear to eye length (EE – top edge of earhole to back of eye); 8) ear opening (EO – greatest length); and 9) internostril distance (IN – shortest distance between nostrils). All head measurements were taken on the right side of the head.

Measurements and scale counts were carried out mostly by WRB and WC incorporated newly-collected material to supplement the final dataset. Only adult material was used for additional comparative morphological analysis. Specimens were considered adult (sexually mature) at SVL > 38 mm (following Makhubo et al. 2015). Box-plots were created for all measurements and scale counts. Only the following measurements SVL, HL, HW, ED, EE and IN, number of scales rows on the dorsal surface per tail whorl, precloacal pores and MSR were included in morphological comparisons. The other measurements and scale counts were found not to be informative for further comparative analysis. These morphological data were tested for significant differences amongst species pairs using a Tukey multiple comparison of means test. Differences were considered significant at $P < 0.05$. All above-mentioned quantitative morphological comparisons were conducted using R v.3.4.1 (R Development Core Team 2014).

Potential distribution model

In order to identify potential distribution areas for Angolan *Afroedura*, a bioclimatic niche model was conducted using Maxent (Yang et al. 2013). The sampling area included a buffer of two degrees (~250 km) from the most peripheral observations of *Afroedura* species. Nineteen bioclimatic variables were obtained in WorldClim dataset (Fick and Hijmans 2017; <http://www.worldclim.org/>) at a spatial resolution of 30 arc-second (~1 km²). For those variables, we ran a correlation model to eliminate collinearity between variables in the sampled area and within sample points (Candau and Flemin 2005) and variables, with correlation coefficient ≥ 0.7 , were selected in order

to capture the bioclimatic range over the distribution of the species (Enriquez-Urzelai et al. 2019). Therefore, the variables included for the analysis were: mean diurnal temperature range (BIO1); maximum temperature of the warmest month (BIO5), minimum temperature of the coldest month (BIO6); annual precipitation (BIO12); precipitation seasonality (BIO15), precipitation of wettest quarter (BIO16). Given the small sample size for some species, we ran a cross-validation model using all the samples but leaving one out in each run, and hinge features with the regularisation parameters set to 2.5, to produce smoother response curves and reduce overfitting (Bittencourt-Silva et al. 2016; Briscoe et al. 2016). The final maps were generated selecting areas with more than 90% of habitat suitability for each species.

Results

Molecular analyses

Molecular analyses confirm that all Angolan *Afroedura* form a monophyletic clade, distinct from other members of the ‘*transvaalica*’ group (Branch et al. 2017a). The Angolan clade is resolved into eight genetically well-supported clades (Fig. 2), most of which show consistently large genetic differences between them (5.9–12%, Table 2) to a level that can be considered representative of species-level divergence (Table 2). While these values are lower than observed between other species of the ‘*transvaalica*’ group (Branch et al. 2017a), they are still surprisingly high for a local monophyletic radiation and indicative of recent and ongoing speciation in the genus *Afroedura* in Angola.

Two sister clades occur exclusively in the coastal region (except for the first subclade, see below) with a third related clade (*Afroedura* sp. 2) occurring a little further inland in the Serra da Neve mountain range (Fig. 1). The southernmost taxon within the identified coastal region (*Afroedura* sp. 1) is currently restricted to the arid Namib Desert region of south-western Angola and clusters with the species from Serra da Neve. Both clades are genetically well differentiated and show minimal internal genetic variation (> 0.8%, Table 2). The sister taxon to those two taxa (*Afroedura* sp. 3) is much more widely distributed across the semi-arid ‘Pro-Namib’ habitats of the coastal littoral north of Moçâmedes (= Namibe) (Fig. 1). Congruent with its much larger distribution, it also contains some clear, but consistent, genetic substructure (Fig. 2, Table 2). There are two well-supported major subclades within this taxon and the second, larger subclade shows some additional substructure. The first subclade contains two specimens from Bimbe (NB 745–6) on the Humpata plateau which are genetically quite distant from the rest of the coastal clade (~4.1%, Table 2). However, a third sample from the same locality (NB 743) groups well within the coastal clade. Follow-up analyses will be needed to resolve the status of this population which may prove to be not conspecific with *Afroedura* sp. 3.

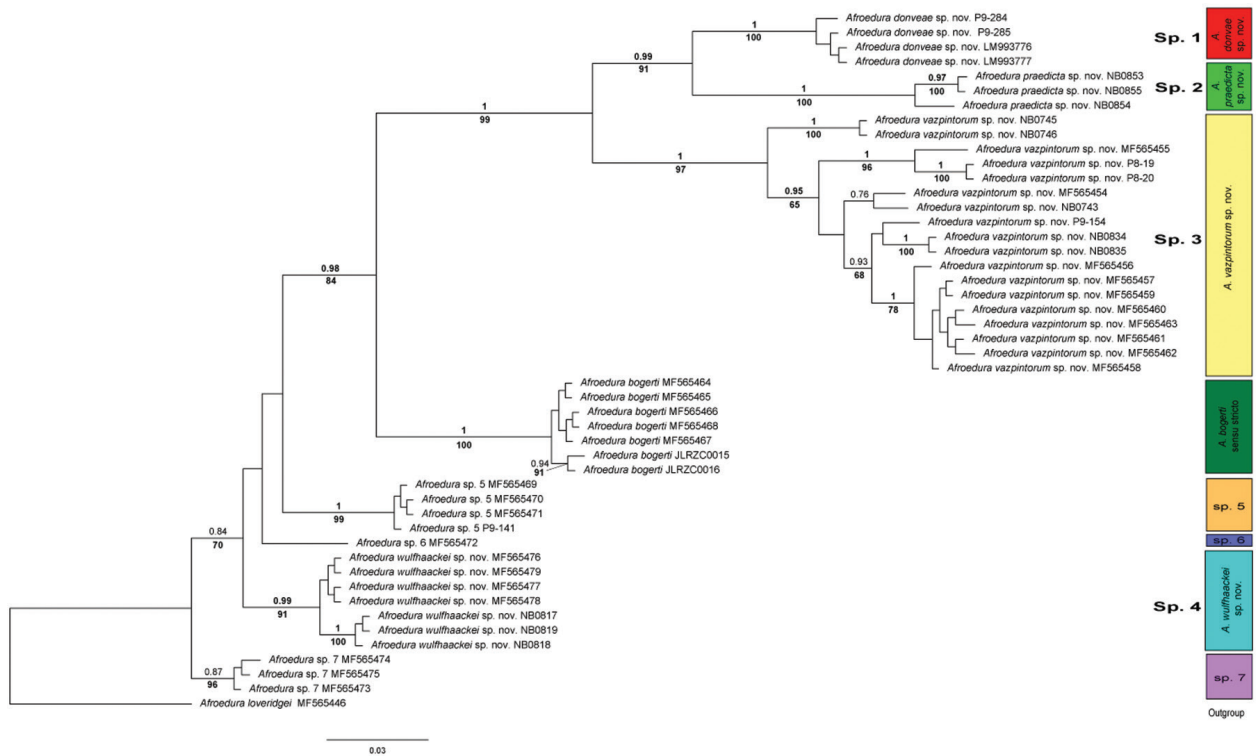


Figure 2. Phylogenetic tree topology for the *16S* gene (identical for Bayes and ML) using *Afroedura loveridgei* as outgroup. Support values for posterior probability and bootstraps are indicated by circles (ML: > 70% / PP: > 0.95).

Table 2. Summary of intra- and interclade uncorrected pairwise genetic distances for specimens of *Afroedura* clades compared to *A. loveridgei* for *16S* rRNA. Intraclade/intraspecific distances are marked in bold.

Species/Clade	Intraclade distances	Interclade/interspecific distances								
		<i>A. loveridgei</i>	<i>A. donveae</i> sp. nov.	<i>A. praedicta</i> sp. nov.	<i>A. vazpintorum</i> sp. nov.	<i>A. bogerti</i> sensu stricto	<i>A. sp.</i> 5	<i>A. sp.</i> 6	<i>A. sp.</i> 7	<i>A. wulphaackei</i> sp. nov.
<i>A. loveridgei</i>	–	–								
<i>A. donveae</i> sp. nov.	0.0015	0.1987	–							
<i>A. praedicta</i> sp. nov.	0.0077	0.1827	0.0654	–						
<i>A. vazpintorum</i> sp. nov.	0.0217	0.1890	0.0897	0.0870	–					
<i>A. bogerti</i> sensu stricto	0.0015	0.1757	0.1083	0.0908	0.1124	–				
<i>A. sp.</i> 5	0.0000	0.1588	0.1021	0.0988	0.1071	0.0634	–			
<i>A. sp.</i> 6	-	0.1667	0.1037	0.0976	0.1074	0.0650	0.0353	–		
<i>A. sp.</i> 7	0.0017	0.1478	0.1041	0.0953	0.1201	0.0722	0.0422	0.0378	–	
<i>A. wulphaackei</i> sp. nov.	0.0033	0.1518	0.0957	0.0893	0.1081	0.0592	0.0399	0.0327	0.0376	–

Five further, strongly supported, monophyletic clades occur above the Angolan escarpment and within the region of the putative type locality. The Namba population (here referred to as *A. bogerti* sensu stricto) is genetically well-differentiated from four southern highland clades (*Afroedura* sp. 4–7) and shows negligible internal genetic variation (> 0.15%, Table 2). The four remaining southern highland clades (*Afroedura* sp. 4–7), each of which is strongly supported, are genetically closely related (Table 2). This complex is very similar to the monophyletic clade *Afroedura* sp. 3 in having a comparatively-wide distribution (Fig. 1) and containing a surprising, but consistent, genetic substructure. The geographic and

taxonomic implications of these groupings require further analysis. The clades of *Afroedura* sp. 4–7 all show very low internal variation versus higher inter-clade variation. Genetic distances between *Afroedura* sp. 4–7 are about, on average, half as great as the shortest distances identified between the major clades identified in Angola (3.3–4.2% vs. 5.9–12.0%; Table 2).

Morphology

Results for the morphological analysis are summarised in Table 3 and Figure 3 and are discussed in more detail in

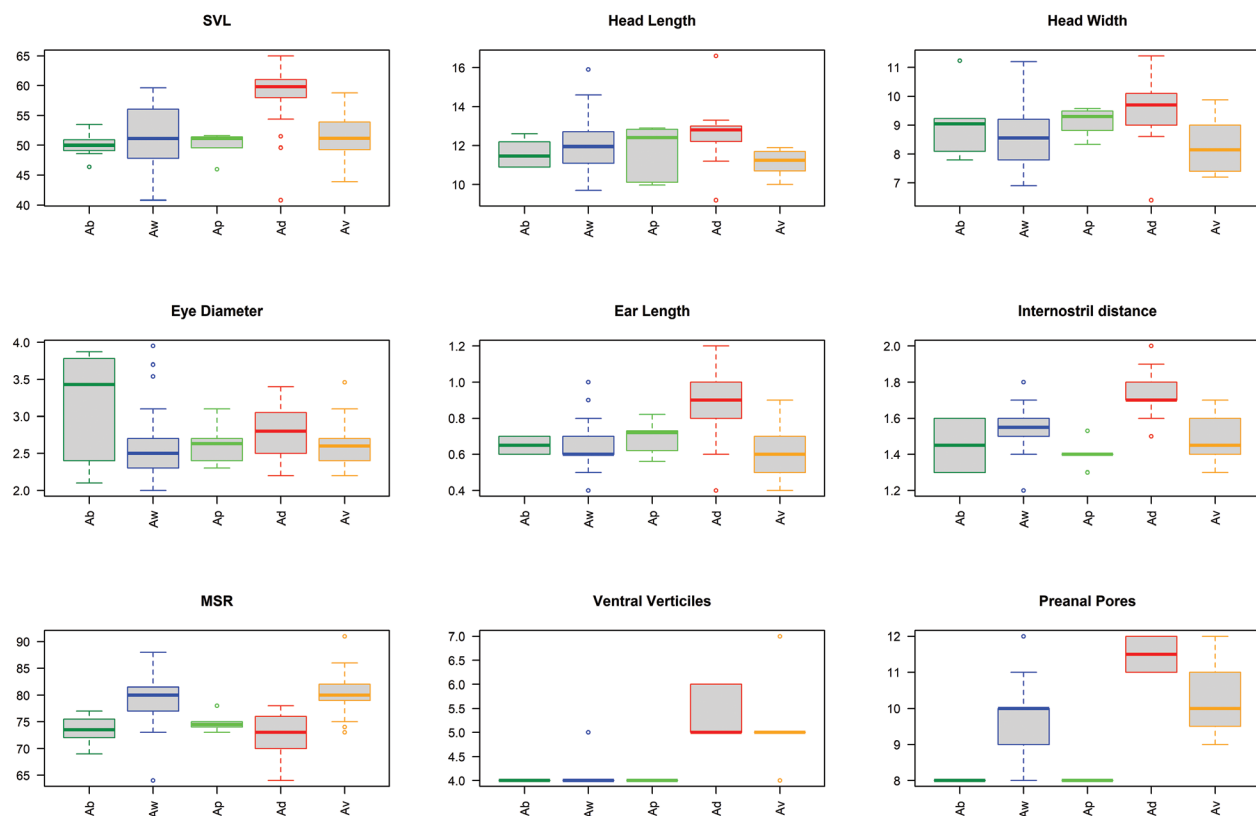


Figure 3. Summary boxplots (top whisker – maximum value; lower whisker – minimum value; dark horizontal line – median; box – 1st and 3rd quartile) comparing morphological features amongst the four species of *Afroedura* separated by sex: *Afroedura bogerti* (dark green – Ab; n = 9), *Afroedura wulphaackei* sp. nov. (including the morphologically-indistinguishable *Afroedura* sp. 5–7 clades; blue – Aw; n = 40), *Afroedura praedicta* sp. nov. (light green – Ap; n = 5), *Afroedura donveae* sp. nov. (red – Ad; n = 17), *Afroedura vazpintorum* sp. nov. (orange – Av; n = 48).

Table 3. Summary of morphological data for *Afroedura bogerti*, *A. wulphaackei* sp. nov. (including the members of the morphologically-indistinguishable *Afroedura* sp. 5–7 clades), *A. donveae* sp. nov., *A. vazpintorum* sp. nov. and *A. praedicta* sp. nov. Values are given as a range with mean values in parenthesis. M = male, F = female, n = sample size.

Character	<i>A. bogerti</i> (n = 9)	<i>A. wulphaackei</i> sp. nov. (n = 40)	<i>A. donveae</i> sp. nov. (n = 17)	<i>A. vazpintorum</i> sp. nov. (n = 48)	<i>A. praedicta</i> sp. nov. (n = 5)
Snout vent length (max)	M 50 mm F 54 mm	M 58 mm F 59 mm	M 59 mm F 65 mm	M 58 mm F 59 mm	M 52 mm F 51 mm
Head Length/Head Width	1.3 ± 0.09	1.4 ± 0.14	1.3 ± 0.09	1.3 ± 0.13	1.3 ± 0.14
Snout Length/Eye Distance	1.6 ± 0.34	1.9 ± 0.36	2.0 ± 0.19	1.8 ± 0.29	1.7 ± 0.19
Snout Length/Eye-Ear Distance	1.2 ± 0.07	1.2 ± 0.16	1.3 ± 0.30	1.2 ± 0.17	1.1 ± 0.09
Precloacal pores (males)	8	9–12 (9.7)	11–12 (11.5)	9–11 (10.2)	8 (8.0)
Ventral rows per tail verticil	4 (4.0)	4–5 (4.0)	5–6 (5.5)	5–7 (5.0)	4 (4.0)
Dorsal rows per tail verticil	5 (5.0)	5–6 (5.1)	6–7 (6.6)	6–7 (6.1)	5 (5.0)
Scales below 4 th toe	6–9 (6.9)	6–9 (7.4)	6–8 (7.7)	6–10 (8.0)	9–11 (9.6)
Mid-body scale rows	69–77 (73.5)	76–88 (79.3)	64–78 (72.8)	73–86 (80.3)	73–78 (74.8)
Scales between eyes	11–14 (12.4)	11–16 (13.7)	11–14 (11.0)	11–15 (13.1)	12–15 (13.5)
Scales: nostril to eye	8–12 (9.9)	8–11 (8.5)	8–11 (9.3)	7–11 (9.1)	9–10 (10.2)
Scales: ear to eye	14–16 (15.4)	15–18 (16.0)	11–14 (11.9)	13–17 (15.6)	13–16 (14.8)
Anterior nasals in contact	33%	68%	100%	100%	100%
Suptalabials	8–10 (8.4)	8–11 (8.2)	8–10 (9.0)	8–10 (8.8)	8–10 (9.2)
Infralabials	8–9 (8.3)	8–9 (8.4)	8–11 (9.3)	8–9 (9.1)	8–9 (8.5)

the species descriptions below. The Angolan material can be broadly divided into two main morphological groups: 1) south-western (mostly) coastal group: *Afroedura* sp. 1 and *Afroedura* sp. 3, defined by higher precloacal pores in males (10–12), higher numbers of scale rows on ventral and dorsal surface per tail verticil (5 and 6, respectively),

nasals always in contact and ventre immaculate, without pigmentation; 2) west-central inland/highland group: comprising species *Afroedura* sp. 4–7 and *A. bogerti* sensu stricto, defined by lower precloacal pores in males (8–10), lower numbers of scale rows on ventral and dorsal surface per tail verticil (4 and 5, respectively), nasals

Table 4. Tukey multiple comparisons of means of the four species combinations of Angolan *Afroedura* (values for *A. wulphaackei* sp. nov. include the members of the morphologically-indistinguishable *Afroedura* sp. 5–7 clades). Bold values indicate significant pairwise comparisons. SVL – snout-vent length; HL – head length; HW – head width; ED – eye-diameter; EE – ear-eye length; IN – internostri distance; MSR – mid-body scale rows.

Combinations	SVL	HL	HW	ED	EE	IN	Ventral verticil scale rows	Dorsal verticil scale rows	Preanal Pores	MSR
<i>A. bogerti</i> – <i>A. donveae</i>	P = 0.004	P = 0.273	P = 0.771	P = 0.262	P = 0.298	P = 0.031	P < 0.001	P < 0.001	P = 0.014	P = 0.988
<i>A. vazpintorum</i> – <i>A. donveae</i>	P < 0.001	P < 0.001	P < 0.001	P = 0.671	P < 0.001	P < 0.001	P = 0.035	P < 0.001	P = 0.103	P < 0.001
<i>A. wulphaackei</i> – <i>A. donveae</i>	P < 0.001	P = 0.264	P = 0.004	P = 0.642	P < 0.001	P < 0.001	P < 0.001	P < 0.000	P = 0.012	P < 0.001
<i>A. praedicta</i> – <i>A. donveae</i>	P = 0.015	P = 0.396	P = 0.840	P = 0.951	P = 0.139	P < 0.001	P < 0.001	P < 0.001	P < 0.001	P = 0.730
<i>A. vazpintorum</i> – <i>A. bogerti</i>	P = 0.932	P = 0.927	P = 0.424	P = 0.026	P = 0.992	P = 1.000	P < 0.001	P < 0.001	P = 0.168	P < 0.001
<i>A. wulphaackei</i> – <i>A. bogerti</i>	P = 0.942	P = 0.926	P = 0.767	P = 0.020	P = 1.000	P = 0.868	P = 1.000	P = 0.983	P = 0.381	P < 0.001
<i>A. praedicta</i> – <i>A. bogerti</i>	P = 1.000	P = 1.000	P = 1.000	P = 0.187	P = 1.000	P = 0.993	P = 1.000	P = 1.000	P = 1.000	P = 0.956
<i>A. wulphaackei</i> – <i>A. vazpintorum</i>	P = 1.000	P = 0.066	P = 0.839	P = 1.000	P = 0.769	P = 0.312	P < 0.001	P < 0.001	P = 0.676	P = 0.647
<i>A. praedicta</i> – <i>A. vazpintorum</i>	P = 0.980	P = 0.912	P = 0.462	P = 1.000	P = 0.777	P = 0.868	P < 0.001	P < 0.001	P = 0.007	P = 0.005
<i>A. praedicta</i> – <i>A. wulphaackei</i>	P = 0.984	P = 0.967	P = 0.782	P = 1.000	P = 0.987	P = 0.195	P = 1.000	P = 0.972	P = 0.048	P = 0.043

in contact (68% of specimens) or separated by smaller granules (33% of specimens) and ventre pigmented with fine black specks. Morphologically, we could not separate members of the *Afroedura* sp. 4–7 clades, which are supported by close phylogenetic relationships. For that reason, we grouped the morphological data of the four clades together. The south-western coastal group can be further divided into a southern and northern group, based on average adult SVL (57.6 vs. 51.3 mm) and overall colouration (see below). An isolated inland population on the Humpata plateau agrees with the northern lowland coastal group morphologically, with the exception of the darker pigmented ventre with an immaculate throat. The two west-central inland/highland groups are morphologically very similar and differ only in the average number of mid-body scale rows (73 vs. 79). An apparently isolated population on Serra da Neve (*Afroedura* sp. 2) agrees morphologically with this inland highland group in most aspects, but differs in that the nasals are always in contact (versus 33–68% of the time). The Tukey multiple comparisons of means showed significance differences amongst most pairwise comparisons and support the above morphological separation (Table 4).

Species descriptions

In summary, both genetics and morphology (particularly diagnostic features, such as the nasal condition [separated or in contact], colouration [ventral pigmentation], snout vent length, number of mid-body scale rows, number of pre-cloacal pores, number of dorsal and ventral scale rows per tail verticil), as well as geographical segregation, suggest that most of the major genetic clades recovered should be considered as separate species. We, therefore, take the opportunity here to provide an updated description for *A. bogerti* and describe the remaining clades as separate species. We apply the general lineage-based species concept, treating all populations that represent independent historical lineages supported by multiple different lines of evidence as listed above as separate species

(de Queiroz 1998). Except for the nominal form, no historical names are available for Angolan material (Uetz et al. 2020).

Afroedura bogerti Loveridge, 1944

Namba or Bogert's Flat Gecko

Osga-achadata da Namba, ou osga-achata de Bogert

Figures 5A, 6; Table 3

Note. The Namba Flat Gecko, *Afroedura bogerti* was described using a single male specimen collected by Harry and Alan Chapman in 1925 during the Vernay Expedition to Angola (Loveridge 1944; Branch et al. 2017b). According to Loveridge (1944), the specimen was collected at 'Namba (Mombolo)', even though Bogert (1940), in his list of Angolan localities, mentioned only 'Mombolo' and gave rough co-ordinates for it. The collectors were the sons of a famous South African farmer, William Chapman, who had hosted the scientific members of the Vernay Expedition on his properties. Within the Mombolo Region, William Chapman and his family had built or lived in three farms, Sandula (which he named Monte Victoria-Verdun and which later became Monte Verde), Chipepe (= Quipepe) and Namba (where a religious mission was subsequently established – Missão da Namba). Branch et al. (2017b) provided a detailed systematic review of *A. bogerti* in Angola and, noting the uncertainties regarding the exact localities of Chapman's material ascribed to Namba/Mombolo, restricted the type locality of the nominal form of *A. bogerti* to a polygon encompassing his three farms and the village of Maka-Mombolo. However, this created a taxonomical problem, as the specimens from Chapman's farms of Sandula and Namba represent two genetically-distinct clades. To resolve this issue, we re-instated the original type locality reference of 'Namba' and here restrict the type locality to the northern areas of Mombolo in the vicinity of Missão da Namba and, by default, the material from William Chapman's farm of Sandula represents an undescribed species.

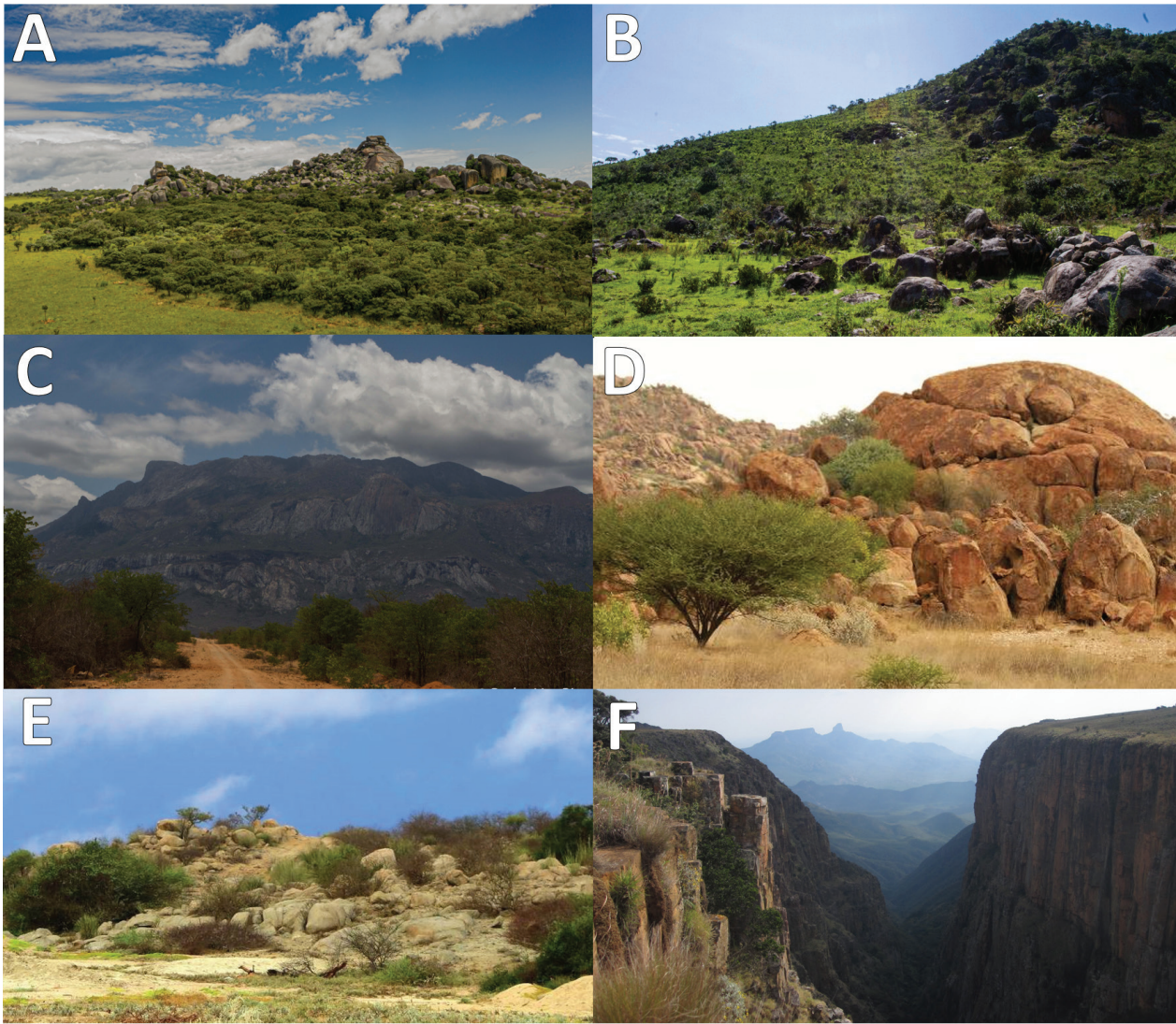


Figure 4. Typical habitat of Angolan *Afroedura*. **A.** Namba area (*A. bogerti*); **B.** Mt Sandula (*Afroedura* sp. 5); **C.** Serra da Neve (*A. praedicta* sp. nov.); **D.** Omauha Lodge (*A. donveae* sp. nov.); **E.** Farm Mucungo (*A. vazpintorum* sp. nov.); **F.** Bimbe (*A. vazpintorum* sp. nov.). Photos: **A.** Javier Lobón-Rovira; **B, D, E.** William R. Branch; **C.** Pedro Vaz Pinto; **F.** Ninda L. Baptista.

Synonym. *Afroedura karroica bogerti* – Loveridge 1944:1; *Afroedura bogerti* – Onderstall 1984:506, Jacobsen et al. 2014:467 (part), Branch et al. 2017b:157 (part), Marques et al. 2018: 177 (part), Branch et al. 2019a: 287 (part); *Afroedura bogerti* (clade 3) – Branch et al. 2017a:146–147.

Holotype. AMNH 47841, adult male, collected from Namba (Mombolo) (approx. -11.91417, 14.82083, 1827 m a.s.l.), Cuanza-Sul Province, Angola, by Harry and Allan (= Alan) Chapman, between September and November 1925 during the Vernay Expedition to Angola.

Additional material examined. *Females:* PEM R24185*, collected from granite bedrock and outcrops 200 m south of old farm paddock, Farm Namba (-11.91417, 14.82083, 1827 m a.s.l.), Cuanza-Sul Province, Angola, by William R. Branch, Pedro Vaz Pinto and Ninda L. Baptista on 3 November 2016;

PEM R24187*, collected from rocks 400 m north of Missão da Namba grounds (-11.91528, 14.84556, 1786 m a.s.l.), Cuanza-Sul Province, Angola, by William R. Branch, Pedro Vaz Pinto and Ninda L. Baptista on 4 November 2016; TM 46631–34, collected from Numba (= Namba) (approx. -11.91722, 14.84417, 1808 m a.s.l.), Cuanza-Sul Province, Angola, by Wulf Haacke on 29 June 1974. *Juveniles:* PEM R24184*, PEM R24186*, collected from granite bedrock and outcrops 200 m south of old farm paddock, Farm Namba (-11.91417, 14.82083, 1827 m a.s.l.), Cuanza-Sul Province, Angola, by William R. Branch, Pedro Vaz Pinto and Ninda L. Baptista on 3 November 2016. *genetically confirmed.

Additional non-vouchered genetic material. JL-RZC0015–6, collected from Namba (-11.88132, 14.76218, 1752 m a.s.l.), Cuanza-Sul Province, Angola, by Pedro Vaz Pinto and Javier Lobón-Rovira on 11 February 2020.

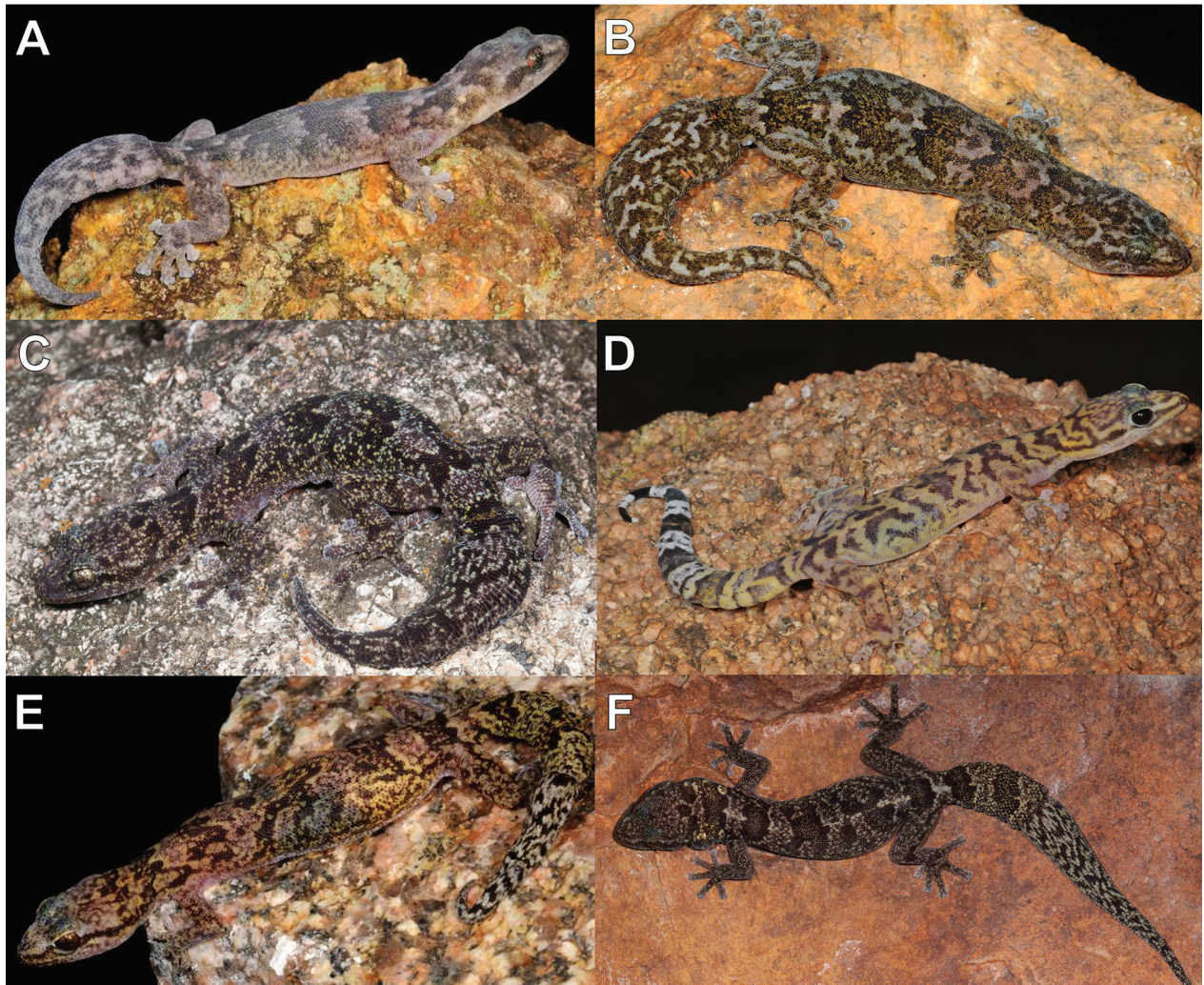


Figure 5. Live photos of Angolan flat geckos: **A.** *Afroedura bogerti* (PEM R24187); **B.** *Afroedura wulphaackei* sp. nov. (paratype PEM R24232); **C.** *Afroedura praedicta* sp. nov. (holotype NB 854); **D.** *Afroedura donveae* sp. nov. (holotype PEM R17937); **E.** *Afroedura vazpintorum* sp. nov. (holotype PEM R24118); **F.** *Afroedura vazpintorum* sp. nov. (NB 0745); Photos: **A, B, D, E.** William R. Branch; **C, F.** Pedro Vaz Pinto.

General description. (description based on the adult material listed above). Head and body dorsoventrally compressed; SVL 46.4–53.5 (mean 50.0) mm, HL 10.9–12.6 (mean 11.6) mm, HW 7.8–11.2 (mean 10.6) mm, broadest at posterior level of eye and 1.1–1.4 (mean 1.3) times longer than wide. Eyes large (2.1–4.3 [mean 2.8] mm wide), pupil vertical with indented margins; circumorbital scales small and smooth, elongate at upper anterior margins, upper posterior scales with small upward pointing spines. Snout rounded, 4.5–5.0 (mean 4.3) mm long, slightly longer than distance between eye and ear openings (3.6–4.3 [mean 3.6] mm). Scales on top of snout smooth, rounded, scales to the side larger than central ones, with no intervening minute granules. Scales on snout slightly subequal in size to those on back of head or nape. Scales on eyelids larger than those on the crown. Circumorbital scales are separated by a row of smaller scales from the large scales on eyelid. Nostril pierced between rostral, two to three nasal scales and the 1st supralabial; the supranasal being much larger

than the subequal postnasals and being separated from each other by one to two smaller scales. Nostrils slightly elevated. Rostral roughly rectangular, but with its upper edges elongated due to extensions into the nostril. Supralabials 8–10 (mean 8.4). Infralabials 8–9 (mean 8.3). A total of 11–14 (mean 12.4) scales across the crown at level of front of eyes. A total of 14–16 (mean 15.4) scales from front of ear to back of eye. Mid-body scale rows 69–77 (mean 73.5). Original tail slightly dorsoventrally flattened and distinctly verticillate, with obvious lateral constrictions that are not that distinct to the tip of tail; each verticil comprising 5 imbricate rows of scales dorsally and 4 imbricate scale rows ventrally and with ventral scales approximately twice the size of those on the dorsal surface. Limbs well developed, hindlimbs slightly longer than forelimbs. All digits with a large pair of distal scansors, separated by a large, curved claw and followed after a large gap by a smaller pair of scansors; infero-median row of digital scales enlarged transversely, particularly towards the scansors, where the ter-



Figure 6. Holotype of *Afroedura bogerti* (AMNH 47841) from Namba (Mombolo), Cuanza-Sul Province, Angola. Photos: Luis M.P. Ceriaco.

minal scale adjoining the first pair of scansors may be medially constricted, swollen and scansor-like, enlarged subdigital lamellae on 4th toe 6–9 (mean 6.9). Precloacal pores 8.

Colouration. *In life* (based on PEM R24187, Fig. 5A). Greyish above with six irregularly spaced darker grey crossbars from the occiput to the sacrum, central crossbars fused to form an X-shape; head with a dark grey band across the posterior edge of crown encompassing a small central pale spot; dark grey to black bar from nostril to the anterior margins of the ear opening; a vague, thin pale canthal stripe, extends on both sides from the nasal region to anterior margins of eye, continuing posteriorly of the eye to above the ear opening; upper and lower labials grey with diffuse yellow edges; lateral sides of the body with very faintly yellow-mustard scales scattered amongst more prominent darker grey scales; limbs greyish above with scattered darker grey markings with intervening faint yellow-mustard colouration; tail (regenerated) with irregular grey mottling; iris golden with a black narrow elliptic pupil with crenulated edge and black reticulation; ventre uniform greyish with scattered black specks; ventral limbs with scattered black specks, more prominent than on the ventrum. *In preservative* (based on PEM R24187): dorsum with six irregularly-spaced darker grey crossbars from the occiput to the sacrum with beige intervening blotches, central crossbars fused to form dark grey X-shape; ventre beige with numerous small scattered black specks on each

scale, more prominent anteriorly, laterally and posteriorly. *Variation:* Greyish to brownish above with five to six irregularly-spaced darker grey-brown W-shaped crossbars from the occiput to the sacrum, sometimes fused in the middle to form X-shapes, limbs and tail with grey blotches; ventre uniform greyish with scattered black specks. Juveniles with more sharply-defined pattern. The original description of the holotype (Fig. 6) was based on a preserved and bleached specimen: ‘Above, greyish; back with five or six obsolescent, irregularly W-shaped brown crossbars; limbs and tail immaculate. Below, whitish, uniform’ (Loveridge 1944). Examination of images of the holotype confirm the presence of fine brown coloured specks ventrally that indicates that the ventre was not immaculate as originally described.

Natural history and habitat (Fig. 4A). An exclusively rupicolous species sheltering in crevices and under flakes of exfoliating rock amongst large granite boulders during the day. Individuals were observed at night foraging in vertical rock faces of large granite boulders. The surrounding habitat was mostly montane grasslands and some cultivated fields, but also included stunted altitude miombo and some Afromontane forest elements in steeper gorges and between boulders. It should be noted that the southern face of Namba Mountain contains the most extensive and well-preserved Afromontane forest patches in Angola, recognised as an important biodiversity reservoir and regional hotspot (Mills et al. 2013).

Distribution and conservation. This species complex was previously considered to be widespread in granite boulders throughout south-western Angola (Branch et al. 2017b; Marques et al. 2018). Here, we show that it is restricted to the Namba Region in the southern parts of Cuanza-Sul Province, Angola (Fig. 1). Namba consists of a 25 km west-east orientated mountain range that climbs to an elevation of 2,420 m a.s.l. and towers southwards above the highland plateau of Mombolo. Our new series was collected at elevations of 1,750–1,850 m a.s.l., at the base of the south-facing slopes of the Namba Mountain chain, but the species probably occurs in suitable habitat higher up and possibly well above 2,000 m a.s.l. (Fig. 1). Considering the deep genetic divergence between this species and *Afroedura* present at the southern edge of Mombolo and the recognition of Namba as a biodiversity hotspot, it seems plausible for this species to have evolved in isolation on this mountain ‘island’. Nevertheless, *A. bogerti* may also extend its distribution further north into other poorly-studied mountain ranges in Cuanza-Sul Province (Fig. 1). The species seems to be relatively common in the Namba Mountains, but its biology remains poorly known.

***Afroedura wulfhaackei* sp. nov.**

<http://zoobank.org/681544BA-AA5F-473B-90BD-B2790838BC81>

Angolan Flat Gecko

Osga-achatada de Angola

Figures 5B, 7; Tables 3, 5

Note. The phylogenetic analysis identified four well-defined clades (*Afroedura* sp. 4–7) within the southern inland/highland major clade (see Results). Our data show that this southern major clade clearly represents at least one undescribed species of *Afroedura*. Despite comparatively-low genetic distances between the four clades recovered (Table 2), they were all retrieved separately in our phylogenetic analyses and, as our morphological examination failed to separate the four clades, we cannot assign them as separate species. Therefore, we decided to take a conservative approach and to describe only one of the clades as a new species for now and tentatively assign *Afroedura* sp. 5–7 to this species pending further work. Thus, we grouped the material according to these clades and selected the clade called here *Afroedura* sp. 4 (Fig. 2) as the name-bearing clade for our new species. Material from lower-altitude localities near Bocoio in Benguela Province groups morphologically with our new species, but needs to be tested in a phylogenetic framework.

Synonym. *Afroedura bogerti* – Branch et al. 2017b:157 (part); Marques et al. 2018: 177 (part); Branch et al. 2019a: 287 (part); *Afroedura bogerti* (clade 4) – Branch et al. 2017a:147.

Holotype. PEM R24234, adult male, collected 3 km north of Maka-Mombolo (-12.17056, 14.88167, 1756 m

a.s.l.), Benguela Province, Angola, by William R. Branch and Pedro Vaz Pinto on 15 November 2016.

Paratypes. PEM R24232–3, adult females, collected 3 km north of Maka-Mombolo (-12.17056, 14.88167, 1756 m a.s.l.), Benguela Province, Angola, by William R. Branch and Pedro Vaz Pinto on 15 November 2016; PEM R24236, adult male, collected above Maka-Mombolo, north-east of Balombo (-12.19833, 14.86833, 1857 m a.s.l.), Benguela Province, Angola, by William R. Branch and Pedro Vaz Pinto on 15 November 2016.

Additional referred material (not examined). NB 817–9, collected at Morro do Moco, camp near Canjonde (-12.42611, 15.14778, 1931 m a.s.l.), Huambo Province, Angola, by Pedro Vaz Pinto on 13 November 2017 (genetic samples included in this study).

Tentative referred additional material examined.

Afroedura sp. 5 (Males): PEM R24192–4, collected at William Chapman’s Farm Victoria-Verdun (Sandula), (-12.17194, 15.02667, 1834 m a.s.l.), Cuanza-Sul Province, Angola, by William R. Branch, Ninda L. Baptista and Pedro Vaz Pinto on 6 November 2016. *Afroedura* sp. 5 (Females): PEM R24190–1, PEM R24195–6, PEM R24199, collected at William Chapman’s Farm Victoria-Verdun (Sandula), (-12.17194, 15.02667, 1834 m a.s.l.), Cuanza-Sul Province, Angola, by William R. Branch, Ninda L. Baptista and Pedro Vaz Pinto on 6 November 2016. *Afroedura* sp. 5 (Juveniles): PEM R24197–8, collected at William Chapman’s Farm Victoria-Verdun (Sandula), (-12.17194, 15.02667, 1834 m a.s.l.), Cuanza-Sul Province, Angola, by William R. Branch, Ninda L. Baptista and Pedro Vaz Pinto on 6 November 2016. *Afroedura* sp. 6 (Males): PEM R24201, collected near Rio Chicanda, 5 km southwest of Lepi (-12.90861, 15.36472, 1534 m a.s.l.), Huambo Province, Angola, by William R. Branch, Ninda L. Baptista and Pedro Vaz Pinto on 8 November 2016. *Afroedura* sp. 7 (Males): TM 45382, TM 45387–8, TM 45392, TM 45396, collected at Candumbo Rocks, 16 km west of Vila Nova = Huambo (-12.73614, 15.97442, 1760 m a.s.l.), Huambo Province, Angola, by Wulf Haacke on 11 May 1971. *Afroedura* sp. 7 (Females): PEM R22490–1, collected 1 km west of Candumbo on road to Boas Águas (-12.73614, 15.97442, 1760 m a.s.l.), Huambo Province, Angola, by Luke Verburgt on 11 March 2016; TM 45383, TM 45390, TM 45393–4, TM 45397, collected at Candumbo Rocks, 16 km west of Vila Nova = Huambo (-12.73614, 15.97442, 1760 m a.s.l.), Huambo Province, Angola, by Wulf Haacke on 11 May 1971. *Afroedura* sp. 7 (Juveniles): PEM R24200, collected at Candumbo Rocks Memorial, 20 km east Humana to Cuito (-12.73722, 15.97333, 1750 m a.s.l.), Huambo Province, Angola, by William R. Branch, Ninda L. Baptista and Pedro Vaz Pinto on 7 November 2016; TM 45386, TM 45389, TM 45391, TM 45395, collected at Candumbo Rocks, 16 km west of Vila Nova = Huambo (-12.73614, 15.97442, 1760 m a.s.l.), Huambo Province, Angola, by

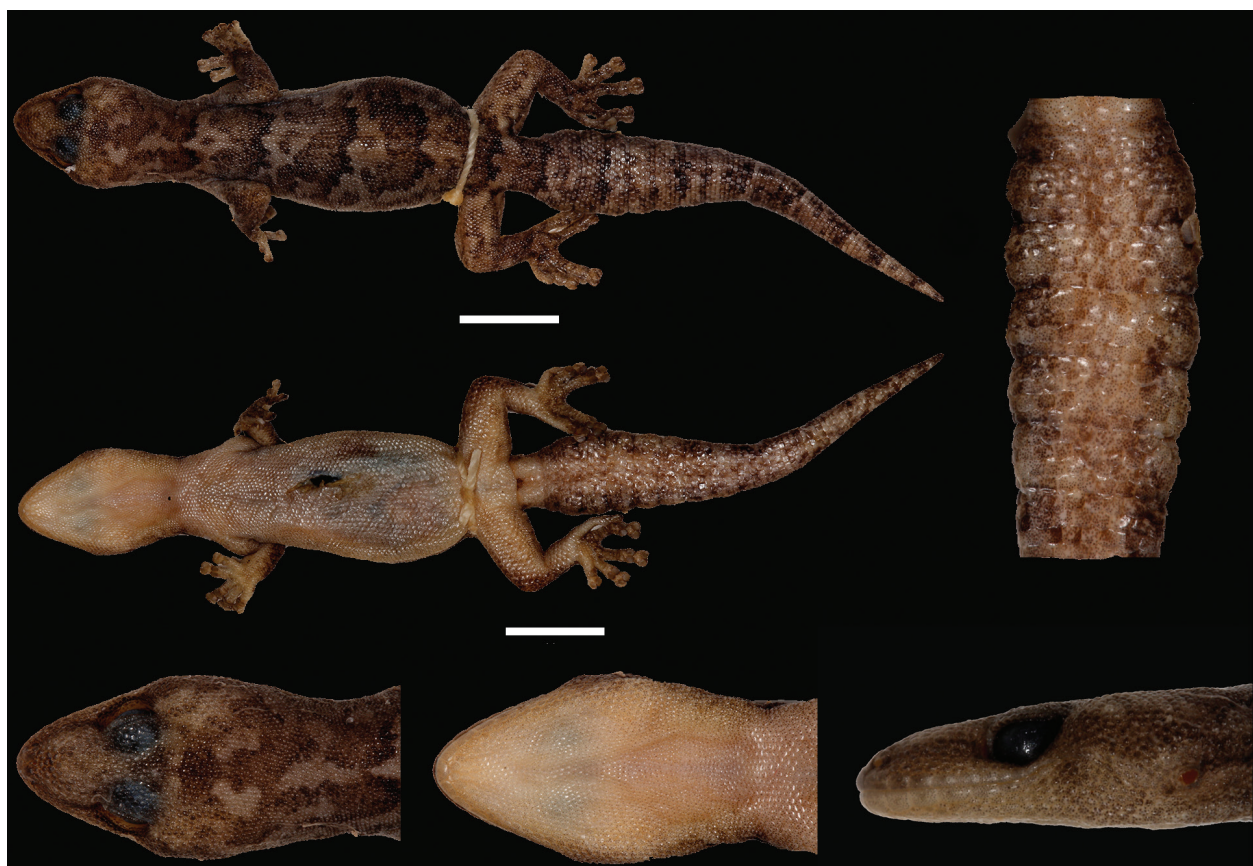


Figure 7. Holotype of *Afroedura wulfhaackei* sp. nov. (PEM R24234) from Maka-Mombolo, Benguela Province, Angola. Photos: Werner Conradie.

Wulf Haacke on 11 May 1971. *Unassigned clades (Females)*: TM 45374, collected 1 km south of Luimbale (-12.25367, 15.31694, 1591 m a.s.l.), Huambo Province, Angola, collected by Wulf Haacke on 10 May 1971; TM 45367–8, collected 10 km west of Soque (-12.34590, 15.01180, 1974 m a.s.l), Benguela Province, Angola, collected by Wulf Haacke on 10 May 1971; PEM R24743, collected at Morro do Pundo (-12.44389, 13.92250, 939 m a.s.l.), Benguela Province, Angola, by Pedro Vaz Pinto on 6 June 2018; TM 46587–8, TM 465890, collected 3 km west of Bocoio (-12.46605, 14.10694, 926 m a.s.l.), Benguela Province, Angola by Wulf Haacke on 25 May 1971. *Unassigned clades (Males)*: TM 45366 collected 10 km west of Soque (-12.34590, 15.01180, 1974 m a.s.l), Benguela Province, Angola, by Wulf Haacke on 10 May 1971, TM 46589, adult male, collected 3 km west of Bocoio (-12.46605, 14.10694, 926 m a.s.l.), Benguela Province, Angola, by Wulf Haacke on 25 May 1971.

Tentative referred additional material not examined. TM 45381, 45384–5, TM 45398, collected at Candumbo Rocks, about 25 km east of the city of Huambo (-12.73614, 15.97442, 1760 m a.s.l), Huambo Province, Angola, by Wulf Haacke on 11 May 1971 (placed in *Afroedura* sp. 7, based on same geographical area as genetically-assigned material); FKH 0239, collected at Monte Verde-Sandula (-12.17924, 15.03086, 2055 m

a.s.l.), Cuanza-Sul Province, Angola, by Pedro Vaz Pinto on 29 May 2019 (genetic sample included in this study placed it in *Afroedura* sp. 5).

Etymology. The new species is named in honour of Wulf Haacke, retired curator of the herpetology collection at the former Transvaal Museum (now Ditsong National Museum of Natural History). His herpetological expeditions to Angola in the early 1970s paved the way for this study and much of the material used in this study resulted from his expeditions. The name is constructed in the masculine singular genitive.

Diagnosis. A member of the greater ‘*transvaalica*’ group in possessing two pairs of enlarged scansors per digit and a strongly verticillate and flattened tail (Jacobsen et al. 2014). It is part of the *A. bogerti*-group which differs from other members of the ‘*transvaalica*’ group by having less than 88 mid-body scale rows (vs. 97–102 in *A. gorongosa*, 113–120 in *A. loveridgei*, 102–119 in *A. transvaalica*); by the rostral bordering the nostril (nostril excluded from rostral in *A. loveridgei*); by the anterior nasals being mostly in contact ~ 68% (separated by 1–3 granules in *A. gorongosa*; always in broad contact in *A. loveridgei*; usually in broad contact in *A. transvaalica* ~ 3–18%); and in having 11–16 scales between the anterior borders of the eyes (19–22 in *A. gorongosa*; 15–19 in *A. loveridgei*;

15–20 in *A. transvaalica*) (comparative data *vide* Branch et al. 2017a).

Afroedura wulfhaackei sp. nov. differs from other members of the *A. bogerti*-group by a combination of the following characters (see Tables 3, 4): 76–88 (mean 79.3) mid-body scale rows (69–77 [mean 73.5] in *A. bogerti*, 64–78 [mean 72.8] in *A. donveae* sp. nov., 73–86 [mean 80.3] in *A. vazpintorum* sp. nov., 73–78 [mean 74.8] in *A. praedicta* sp. nov.); by the anterior nasals being mostly (~68% of the time) in contact (~33% of the time in contact in *A. bogerti*; always in contact in *A. donveae* sp. nov., *A. vazpintorum* sp. nov. and *A. praedicta* sp. nov.); each verticil comprising 4–5 (mean 4.0) ventral and 5–6 (mean 5.1) dorsal rows of scales (4 and 5 in *A. bogerti* and *A. praedicta* sp. nov.; 5–6 [mean 5.5] and 6–7 [mean 6.6] in *A. donveae* sp. nov.; 5–6 [mean 5.0] and 6–7 [mean 6.1] *A. vazpintorum* sp. nov.); ventral surfaces greyish with scattered small black spots (similar to *A. bogerti* and *A. praedicta* sp. nov., immaculate in *A. donveae* sp. nov. and *A. vazpintorum* sp. nov.). *Afroedura wulfhaackei* sp. nov. differs more specifically from its sister highland species *A. bogerti* in having a higher number of mid-body scale counts (76–88 [mean 79.3] versus 69–77 [mean 73.5]) and differs from *A. praedicta* sp. nov. in that the nasals are separated by smaller granules (versus always in contact).

Holotype description. Adult male; SVL 51.4 mm; tail 47.1 mm (full original tail), with a small mid-ventral incision for the removal of liver sample. Measurements and meristic characters of holotype presented in Table 5. Head and body dorsoventrally compressed; HL 11.9 mm, HW 9.0 mm, broadest at posterior level of eye and 1.32 times longer than wide. Eye large (2.3 mm wide), pupil vertical with indented margins; circumorbital scales small and smooth, elongate at upper anterior margin, upper three posterior scales with small upward pointing spines. Snout rounded, 4.9 mm long, slightly longer than distance between eye and ear openings (4.0 mm). Scales on top of snout smooth, rounded, scales to the edge larger than central ones, with no intervening minute granules. Scales on snout slightly subequal in size to those on the back of head or the nape. Scales on eyelids larger than those on the crown, five scales deep from circumorbital scale to crown. Circumorbital scales are separated by a row of smaller scales from the larger scales on eyelids. Nostril pierced between rostral and three nasal scales; 1st supralabial narrowly excluded from nostril; the supranasal being much larger than the subequal postnasals and separated from each other by two smaller scales. Nostrils slightly elevated. Rostral roughly rectangular, but with its upper edges elongated due to extensions into the nostril. Eight supralabials on each side, the labial margin flexing upwards at the rictus (approx. mid-orbital position), with 3–4 minute scales proximal to the flexure. Ten infralabials on either side, with a small scale proximal to the flexure. At the lip, mental slightly narrower than adjacent infralabial, only three quarters the width of rostral and in contact with two distinctly elongate postmen-

tal scales. Scales on throat much smaller than those on belly; scales touching infralabials larger. Fifteen scales across the crown at level of front of eyes; 16 scales from ear to eye; 83 scales around mid-body. Ear opening deep, oblique and roughly oval, only half as high as wide (0.3 × 0.5 mm). Scales on dorsum smooth, non-overlapping, largest at mid-body, smaller on nape and tail base. Scales on ventrum flattened, not overlapping, more-or-less ovate at mid-ventrum, twice the size of lateral granules and 1.5 times those along the backbone. Original tail slightly dorsoventrally flattened and distinctly verticillate (11 verticils in total), with obvious lateral constrictions that are not that distinct to tip of tail; each verticil comprising 5 imbricate rows of scales dorsally and 4 imbricate scale rows ventrally and with ventral scales approximately twice the size of those on the dorsal surface. Limbs well developed, hindlimbs slightly longer than forelimbs, mite pockets (dermal crevices inhabited by small ectoparasitic mites) only present at anterior margin of hindlimbs. All digits with a large pair of distal scansors, separated by a large, curved claw and followed by a large gap (twice the length of terminal scansor) by a smaller pair of scansors; infero-median row of digital scales enlarged transversely, particularly towards the scansors, where the terminal scale adjoining the first pair of scansors may be medially constricted, swollen and scansor-like; enlarged subdigital lamellae on 4th toe 9. Precloacal pores 9.

Paratype variation (see Table 5 for more measurements and scale counts of type series). SVL varied from 49.1–55.7 mm; head length 1.34–1.45 times the head width; snout 1.99 times the diameter of eye. Supranasals always separated by smaller granules, usually with a single large granule in contact with the rostral between the

Table 5. Measurements (in mm) and scale counts for the type series of *Afroedura wulfhaackei* sp. nov.

Catalogue number	PEM R24234	PEM R24232	PEM R24233
Type Status	Holotype	Paratype	Paratype
Sex	Male	Female	Female
Snout vent length	51.4	49.1	55.7
Tail length	47.1	35.4	57.5
Tail condition	Original	Regenerated	Regenerated
Head length	11.9	10.9	12.3
Head width	9.0	7.5	8.5
Snout length	4.9	4.5	5.1
Eye distance	2.3	2.2	2.6
Eye-Ear distance	4.0	3.5	4.3
Precloacal pores (males)	9	–	–
Dorsal rows per tail verticil	5	–	5
Ventral rows per tail verticil	4	–	4
Scales below 4 th toe	9	8	7
Mid-body scale rows	83	82	76
Scales between eyes	15	13	14
Scales: nostril to eye	7	7	9
Scales: ear to eye	16	14	17
Anterior nasals in contact	No	No	No
Supralabials	9	7	9
Infralabials	8	9	8

supranasals, followed by 1–2 smaller granules in lateral contact; the first upper labial and rostral always enters the nostril and the width of the rostral at the lip margin is always wider than that of the mental; 2–3 postmental scales; supralabials 7–9; infralabials 8–9; scales between anterior edges of eyes 13–14; scales between nostril and anterior edge of orbit 7–9; scales between anterior edge of ear and rear margin of orbit 14–17; scales around mid-body 76–82; subdigital lamellae on 4th toe 7–8; dorsal scales per tail verticil 5; ventral scales per tail verticil 4. Precloacal pores 9.

Additional material variation. SVL 36.4–59.6 mm; original tail length 36.4–57.8 mm, 0.94 times SVL; head length 1.19–1.75 times head width; snout 1.91 times diameter of eye. The supranasals in contact in 22 specimens and separated by granules in eight specimens, usually with a single large granule in contact with the rostral between the supranasals, followed by 1–2 smaller granules in lateral contact; the first upper labial and rostral always enters the nostril and the width of the rostral at the lip margin is always wider than that of the mental; 2–4 postmental scales; supralabials 8–9; infralabials 8–9; scales between anterior edge of eye 12–16; scales between nostril and anterior edge of orbit 7–11; scales between anterior edge of ear and rear margin of orbit 15–18; scales around mid-body 75–88; subdigital lamellae on 4th toe 7–9; dorsal scales per tail verticil 5 (TM 45366, TM 46588 and PEM R24743 with 6); ventral scales per tail verticil 4 (TM 46588 with 5). Precloacal pores 9–12.

Colouration. *In life* (paratype PEM R24232, Fig. 5B): Greyish above with five irregularly-spaced darker cross-bars from the occiput to the sacrum, each crossbar consisting posteriorly out of three to four black scales wide forming a W-shape; anterior to W-shape are 8–10 scales deep with a mix of dark grey and mustard colours; each dark crossbar separated by light grey to beige blotches; head with irregular dark grey-mustard blotches on the crown with intervening light grey colouration; dark mustard to dark grey bar from nostril to the anterior margins of the ear opening; a vague, thin pale grey canthal stripe, extends on both sides from the nasal region to anterior margins of eye; upper and lower labials grey with diffuse mustard edges; lateral sides of the body with a mix of dark grey and yellow-mustard colouration; limbs greyish above with scattered darker grey markings with intervening yellow-mustard colouration; tail (regenerated) with irregular grey-mustard mottling; iris golden with a black narrow elliptic pupil with crenulated edge and black reticulation with light grey intervening blotches; ventrum uniform greyish with scattered black specks; ventral limbs with scattered black specks, more prominent than on the ventrum. *In preservative* (holotype PEM R24234, Fig. 7): Dorsum with five irregularly-spaced dark grey W-shaped crossbars from the occiput to the sacrum with beige intervening blotches; ventrum is beige with numerous small scattered black specks on each scale, more prominent pos-

teriorly. *Variation:* Greyish to brownish above with five to six irregularly-spaced darker grey-brown W-shaped cross-bars from the occiput to the sacrum, limbs and tail with grey blotches; ventrum uniform greyish with scattered black specks. Juveniles have sharper patterns and colours.

Natural history and habitat (Fig. 4B). An exclusively rupicolous species living in crevices between rocks or under flakes of exfoliating rocks in boulders at elevations of 920–2,055 m a.s.l. Specimens were collected in cracks of relatively small- to medium-sized boulders of carbonatitic origin surrounded by montane grassland. Some individuals were also found under flakes in large granite boulders and often in steep vertical rock faces and overhangs.

Distribution and conservation. This species is currently known from southern Cuanza-Sul, central Huambo and northern Benguela Provinces, Angola (Fig. 1). It appears to have a relatively large, but patchy, distribution on the Angolan highlands and may extend its range into neighbouring provinces. Although sometimes locally common, it appears to be absent from vast areas in-between, where the species would be expected to occur. Populations in isolated granite outcrops may be threatened by removal of rock flakes for construction of homes and other buildings.

Afroedura praedicta sp. nov.

<http://zoobank.org/FAECE4F2-AC75-4E57-8B78-D76FFA8C282D>

Serra da Neve Flat Gecko

Osga-achatada da Serra da Neve

Figures 5C, 8; Tables 3, 6

Holotype. NB 854, adult male, collected from Serra da Neve (–13.77354, 13.24825, 1944 m a.s.l.), Namibe Province, Angola, by Pedro Vaz Pinto, Ninda L. Baptista and Telmo António on 30 November 2017.

Paratypes. ZMB 91607 (NB 853), NB 855, adult males, collected from Serra da Neve (–13.77354, 13.24825, 1944 m a.s.l.), Namibe Province, Angola, by Pedro Vaz Pinto, Ninda L. Baptista and Telmo António on 30 November 2017. ZMB 91608 (NB 1053), NB 1054, adult females, collected from Serra da Neve (–13.77354, 13.24825, 1944 m a.s.l.), Namibe Province, Angola, by Pedro Vaz Pinto, Ninda L. Baptista and Telmo António on 30 November 2017. NB 1055, juvenile, collected from Serra da Neve (–13.77354, 13.24825, 1944 m a.s.l.), Namibe Province, Angola, by Pedro Vaz Pinto, Ninda L. Baptista and Telmo António on 30 November 2017.

Etymology. The specific epithet reflects the earlier prediction by WRB of the potential existence of an isolated population of *Afroedura* at Serra da Neve. We use the specific epithet “*praedicta*”, the Latin participle meaning predicted or anticipated, formed in the feminine genitive to match the gender of *Afroedura*.



Figure 8. Holotype of *Afroedura praedicta* sp. nov. (NB 854) from Serra da Neve, Namibe Province, Angola. Photos: Telmo António.

Diagnosis. A member of the greater ‘*transvaalica*’ group as it possesses two pairs of enlarged scansors per digit and a strongly verticillate and flattened tail (Jacobsen et al. 2014). Part of the *A. bogerti*-group which differs from other members of the ‘*transvaalica*’ group by having less than 78 mid-body scale rows (vs. 97–102 in *A. gorongosa*, 113–120 in *A. loveridgei*, 102–119 in *A. transvaalica*); by the rostral bordering the nostril (nostril excluded from rostral in *A. loveridgei*); by the anterior nasals always being in contact (separated by 1–3 granules in *A. gorongosa*; always in broad contact in *A. loveridgei*; usually in broad contact in *A. transvaalica* ~ 3–18%); and in having 12–15 scales between the anterior borders of the eyes (19–22 in *A. gorongosa*; 15–19 in *A. loveridgei*; 15–20 in *A. transvaalica*) (comparative data *vide* Branch et al. 2017a).

Afroedura praedicta sp. nov. differs from other members of the *A. bogerti*-group by a combination of the following characters (see Tables 3 and 4): 73–78 (mean 74.4 mid-body scale rows (69–77 [mean 73.5] in *A. bogerti*, 76–88 [mean 79.3] in *A. wulfhaackei* sp. nov., 64–78 [mean 72.8] in *A. donveae* sp. nov., 73–86 [mean 80.3] in *A. vazpintorum* sp. nov.); by the anterior nasals always being in contact (similar to *A. donveae* sp. nov. and *A. vazpintorum* sp. nov.; ~ 33% of the time in contact in *A. bogerti*; ~ 68% of the time in contact in *A. wulfhaackei* sp. nov.); each verticil having 4 ventral and 5 dorsal rows of scales (similar to the 4 and 5 in *A. bogerti*, 4–5 [mean

4.0] and 5–6 [mean 5.1] in *A. wulfhaackei* sp. nov.; but lower than the 5–6 (mean 5.5) ventral and 6–7 (mean 6.6) in *A. donveae* sp. nov. and 5–6 (mean 5.0) and 6–7 (mean 6.1) in *A. vazpintorum* sp. nov.); ventral surfaces grey with black specks on scales (similar to *A. bogerti* and *A. wulfhaackei* sp. nov.; immaculate in *A. donveae* sp. nov. and *A. vazpintorum* sp. nov.). *Afroedura praedicta* sp. nov. also differs from its sister highland species *A. bogerti* sp. nov. and *A. wulfhaackei* sp. nov. in that the nasals are always in direct contact (versus mostly separated).

Holotype description. Adult male; SVL 51.6 mm; tail 37.0 mm (regenerated tail, except for the first verticil), with a small mid-ventral horizontal incision for the removal of liver sample. Measurements and meristic characters of holotype presented in Table 6. Head and body dorsoventrally compressed; HL 12.9 mm, HW 7.9 mm, broadest at posterior level of eye and 1.6 times longer than wide. Eye large (2.6 mm wide), pupil vertical with indented margins; circumorbital scales small and smooth, elongated at upper anterior margin, the most upper posterior scale with very small upward pointing spines. Snout rounded, 5.0 mm long, slightly larger than the distance between eye and ear openings (4.2 mm). Scales on top of snout slightly granular and elevated, rounded, mostly equal in size, with no intervening minute granules. Scales on snout slightly subequal in size to those on back of

Table 6. Measurements (in mm) and scale counts for the type series of *Afroedura praedicta* sp. nov.

Catalogue number	NB 854	ZMB 91607	NB 855	ZMB 91608	NB 1054	NB 1055
Type status	Holotype	Paratype	Paratype	Paratype	Paratype	Paratype
Sex	Male	Male	Male	female	female	Juvenile
Snout vent length (max)	51.6	51.4	49.6	51.1	46.0	28.0
Head length	12.9	12.4	12.8	10.1	10.0	6.3
Tail length	37.0	29.2	–	43.4	–	22.1
Tail condition	Regenerated	Regenerated	Truncated	Regenerated	Truncated	Original
Head width	7.9	7.3	6.8	6.7	6.3	4.7
Snout length	5.0	4.8	4.8	4.2	4.3	2.5
Eye distance	2.6	2.7	3.1	2.4	2.3	1.8
Eye-ear distance	4.2	3.9	4.8	3.8	3.7	2.4
Precloacal pores (males)	8	8	8	–	–	–
Dorsal rows per tail verticil	4	4	–	4	–	4
Ventral rows per tail verticil	5	5	–	5	–	5
Scales below 4 th toe	9	11	10	9	–	9
Mid-body scale rows	74	75	74	75	73	78
Scales between eyes	12	13	12	14	15	15
Scales: nostril to eye	9	11	10	9	11	11
Scales: ear to eye	16	15	15	15	15	13
Anterior nasals in contact	Yes	Yes	Yes	Yes	Yes	Yes
Supralabials	8	10	8	10	9	10
Infralabials	9	9	9	8	8	8

head or nape, which in turn is irregular in size and mostly smooth. Scales on eyelids larger than those on the crown, six scales deep from circumorbital scales to crown. Circumorbital scales are separated by a row of smaller scales from the larger scales on eyelid. Nostril pierced between rostral, three nasal scales; 1st supralabial in contact with nostril; the supranasal being much larger than the subequal postnasals and are separated from each other by two smaller scales. Nostrils slightly elevated. Rostral roughly rectangular, but with its upper edges elongated due to extensions into the nostril. Eight supralabials on each side, the labial margin flexing upwards at the rictus (approx. mid-orbital position), with 2–3 minute scales proximal to the flexure. Nine infralabials on either side, with a small scale proximal to the flexure. At the lip, mental slightly narrower than adjacent infralabial, only three quarters the width of rostral and in contact with three distinctly elongate postmental scales. Scales on throat much smaller than those on belly; scales touching infralabials larger. Twelve scales across the crown at level of front of eye; 9 scales between nostril and front of eye; 16 scales from ear to eye; 74 scales around mid-body. Ear opening deep, oblique and roughly round, backward pointing, nearly equal as long as wide (0.7×0.6 mm). Scales on dorsum smooth, non-overlapping, largest at mid-body, smaller on nape and tail base. Scales on ventre flattened, not overlapping, more-or-less ovate at mid-ventrum and twice the size of lateral granules and 1.5 times those along backbone. Tail regenerated, except for the first verticil, with obvious lateral constriction before regenerated tail start; first verticil comprising 5 imbricate rows of scales dorsally and 4 imbricate scale rows ventrally and with ventral scales approximately twice the size of those on the dorsal surface. Limbs well developed, hindlimbs slightly longer than forelimbs, both without obvious mite pockets at posterior margin of limb insertions, mite pockets present at anterior margin of hindlimbs. All digits with a large pair of distal scansors, sep-

arated by a large, curved claw and followed after a large gap (twice the length of terminal scansor) by a smaller pair of scansors; infero-median row of digital scales enlarged transversely, particularly towards the scansors, where the terminal scale adjoining the first pair of scansors may be medially constricted, swollen and scansor-like; 9 enlarged scale rows under 4th toe. Precloacal pores 8.

Paratypes variation (see Table 6 for more measurements and scale counts of type series). SVL varied from 46.0–51.6 mm; head length 1.09–1.46 times head width; snout 1.71 times diameter of eye. The supranasals always in contact; the first supralabial enters the nostril (except for ZMB 91607 and NB 855) and rostral always enters the nostril and the width of the rostral at the lip margin is always wider than that of the mental; 2–3 postmental scales; supralabials 8–10, infralabials 8–9; scales between anterior edge of eye 13–15; scales between nostril and anterior edge of orbit 9–11; scales between ear and eye 13–16; scales around mid-body 73–78; subdigital lamellae on 4th toe 9–11; dorsal scales per tail verticil 5; ventral scales per tail verticil 4; precloacal pores 8.

Colouration. *In life* (holotype NB 854, Fig. 5C). Dark grey above with random yellow-olive scattered scales, with six irregularly-spaced, darker grey to black W-shaped crossbars, first one broken up into three blotches, each crossbar anteriorly bordered by a row of light white to yellow scales; head mostly grey with scattered darker grey and yellow scales, dark black bar from nostril to posterior of eye, continuing anteriorly of the eye to ear opening; no thin pale white canthal stripe; upper and lower labials dark grey with diffuse lighter grey edges; lateral sides of the body with a mix of dark grey and yellow blotches; limbs darker grey above with scattered yellow scales; tail (regenerated) with dark black blotches and irregular white to light grey mottling; iris dark brown

to golden with a narrow black elliptic pupil with crenulated edge and black reticulation; ventre uniform greyish with scattered black specks; ventral surface of limbs with scattered black specks, more prominent than on the ventrum. *In preservative* (holotype NB 854, Fig. 8): dorsum with five distinct, irregularly-spaced, dark grey W-shaped crossbars anteriorly, with beige intervening blotches, the posteriorly crossbar on the nape are broken up dark grey blotches; dorsally, the arms and legs are beige with irregular darker grey blotches; tail (regenerated part) with light grey to white mottling on darker grey to black background; dorsally, the head has mottled dark brown scales, dark grey bar running from the nasals through eye to anterior of the ear opening; supralabials dark brown-edged ventrally; infralabials scattered with dark brown markings dorsally; ventrum uniform greyish with scattered black specks; ventrally, limbs with scattered black specks, more prominent than on the ventrum. *Variation*: Similar colouration and patterning as the holotype (preserved) and paratype (life). Dorsal dark W-shaped crossbars number 5–6. Regenerated tails with fine dark brown to black mottling. Juveniles with more sharply-defined pattern and darker colouration.

Natural history and habitat (Fig. 4C). A rupicolous species found inside deep crevices and fractured rocks in large boulders of extrusive origin. All specimens were found on one site between 1,900–2,000 m a.s.l. The surrounding vegetation included altitude dwarf miombo and montane elements. Found in syntopy with *Cordylus pholidotos* at Serra da Neve.

Distribution and conservation. This species is known only from the alkaline mountain complex of Serra da Neve (Fig. 1).

Afroedura donveae sp. nov.

<http://zoobank.org/B2939E10-5F5D-45D0-9CBF-352D1D8A6B9A>

Iona Flat Gecko

Osga-achatada do Iona

Figures 5D, 9; Tables 3, 7

Synonym. *Afroedura bogerti* – Haacke 2008:6, Huntley 2009:84, Rösler 2000:57, Barts and Haacke 2010:39, Jacobsen et al. 2014:456 & 468 (part), Branch et al. 2017b:157 (part), Marques et al. 2018: 177 (part), Branch et al. 2019a: 287 (part); *Afroedura* cf. *bogerti* – Agarwal et al. 2017:649; *Afroedura bogerti* (clade 1) – Branch et al. 2017a:146.

Holotype. PEM R17937, adult female, collected from Omauha Lodge, 15 km south of Tambor (-16.20061, 12.40183, 341 m a.s.l.), Namibe Province, Angola, by William R. Branch, Werner Conradie, Krystal Tolley and John Measey on 18 January 2009.

Paratype. PEM R17936, collected from Omauha Lodge, 15 km South Tambor (-16.20061, 12.40183, 341 m a.s.l.), Na-

mibe Province, Angola, by William R. Branch, Werner Conradie, Krystal Tolley and John Measey on 18 January 2009.

Additional material examined. *Males*: TM 40508, TM 40512, TM 40516, TM 40518, collected from Tambor (-16.06667, 12.43333, 355 m a.s.l.), Namibe Province, Angola, by Wulf Haacke on 1 April 1971. *Females*: PEM R18041–2, collected 0.5 km south of Tambor (-16.07414, 12.43328, 352 m a.s.l.), Namibe Province, Angola, by William R. Branch, Krystal Tolley and John Measey on 23 January 2009; TM 40509–11, TM 40513–5, TM 40517, TM 40536–8, collected from Tambor (-16.06667, 12.43333, 355 m a.s.l.), Namibe Province, Angola, by Wulf Haacke on 1 April 1971.

Additional referred material (not examined). TM 40519–20, collected from Tambor (-16.06667, 12.43333, 355 m a.s.l.), Namibe Province, Angola, by Wulf Haacke on 1 April 1971; FKH 0341–2, collected from Omauha Lodge (-16.20061, 12.40183, 338 m a.s.l.), Namibe Province, Angola, by Pedro Vaz Pinto on 3 October 2019; CAS:HERP 263012–3, collected from Omauha (-16.19858, 12.40073, 338 m a.s.l.), Namibe Province, Angola, by Luis M.P. Ceriaco, Suzana Bandeira and Isham Agarwal on 25 and 27 November 2017; CAS:HERP 248780–1, collected 0.5 km south of Tambor (-16.07414, 12.43328, 352 m a.s.l.), Namibe Province, Angola, by William R. Branch, Krystal Tolley and John Measey on 23 January 2009.

Etymology. This gecko is named after Donvé Branch, WRB's wife, with the following personal quote: "This, the most beautiful of all the Angolan flat geckos, is named for my wife, Donvé Branch ('Dove') who bore the long periods I was away on fieldwork, and to whose nest I returned, and surrounded me with love until the end". The name is constructed in the feminine singular genitive.

Diagnosis. A member of the greater '*transvaalica*' group as it possesses two pairs of enlarged scansors per digit and a strongly verticillate and flattened tail (Jacobsen et al. 2014). Part of the *A. bogerti*-group which differs from other members of the '*transvaalica*' group by having less than 78 mid-body scale rows (vs. 97–102 in *A. gorongosa*, 113–120 in *A. loveridgei*, 102–119 in *A. transvaalica*); by the rostral bordering the nostril (nostril excluded from rostral in *A. loveridgei*); by the anterior nasals always in contact (separated by 1–3 granules in *A. gorongosa*; always in broad contact in *A. loveridgei*; usually in broad contact in *A. transvaalica* ~ 3–18%); and in having 11–14 scales between the anterior borders of the eyes (19–22 in *A. gorongosa*; 15–19 in *A. loveridgei*; 15–20 in *A. transvaalica*) (comparative data *vide* Branch et al. 2017a).

Afroedura donveae sp. nov. differs from other members of the *A. bogerti*-group by a combination of the following characters (see Tables 3, 4): 64–78 (mean 72.8) mid-body scale rows (69–77 [mean 73.5] in *A. bogerti*, 76–88 [mean 79.3] in *A. wulphaackei* sp. nov., 73–86 [mean 80.3] in *A. vazpintorum* sp. nov., 73–78 [mean 74.8] in *A. praedicta*



Figure 9. Holotype of *Afroedura donveae* sp. nov. (PEM R17937) from Omauha Lodge, 15 km south of Tambor, Namibe Province, Angola. Photos: Werner Conradie.

sp. nov.); by the anterior nasals always in contact (similar to *A. vazpintorum* and *A. praedicta* sp. nov.; in contact in ~33% of *A. bogerti*; in contact in ~68% of *A. wulfhaackei* sp. nov.); in each verticil having 5–6 (mean 5.5) ventral and 6–7 (mean 6.6) dorsal rows of scales (5–6 [mean 5.0] and 6–7 [mean 6.1] to *A. vazpintorum* sp. nov.; 4 and 5 in *A. bogerti* and *A. praedicta* sp. nov., 4–5 [mean 4.0] and 5–6 [mean 5.1] in *A. wulfhaackei* sp. nov.); ventral surfaces immaculate (similar to *A. vazpintorum* sp. nov.; greyish with black spots in *A. bogerti*, *A. wulfhaackei* sp. nov. and *A. praedicta* sp. nov.); larger average adult size 57.6 mm SVL (versus 50.0 mm in *A. bogerti*, 51.7 mm in *A. wulfhaackei* sp. nov., 51.3 mm in *A. vazpintorum* sp. nov.; 49.9 mm *A. praedicta* sp. nov.). *Afroedura donveae* sp. nov. differs more specifically from its sister lowland species *A. vazpintorum* sp. nov. in being larger (57.6 mm versus 51.3 mm average SVL) and having lower mid-body scale counts (64–78 [mean 72.8] versus 73–86 [mean 80.3]), higher numbers of precloacal pores (11–12 [mean 11.5] versus 9–11 [mean 10.2]), bolder colouration and distinct tail banding (versus duller colouration and less distinct tail banding).

Holotype description. Adult female: SVL 61.0 mm; tail 59.0 mm (full original tail), with a small mid-ventral incision for the removal of liver sample. Measurements and meristic characters of holotype presented in Table 7.

Head and body dorsoventrally compressed; HL 13.6 mm, HW 11.4 mm, broadest at posterior level of eye and 1.19 times longer than wide. Eyes large (3.4 mm wide), pupil vertical with indented margins; circumorbital scales small and smooth, elongated at upper anterior margin, upper three posterior scales with small upward pointing spines. Snout rounded, 5.6 mm long, longer than distance between eye and ear openings (4.5 mm). Scales on top of snout smooth, rounded, equal in size, with no intervening minute granules. Scales on snout slightly larger than those on back of head or nape. Scales on eyelids larger than those on the crown, 5 scales deep from circumorbital scale to crown. Nostril pierced between rostral, three nasal scales; 1st supralabial narrowly excluded from nostril; the supranasals are much larger than the subequal smaller postnasals, in broad contact with each other. Nostrils slightly elevated. Rostral roughly rectangular, but with its upper edges elongated due to extensions to the nostril. Nine supralabials on each side, the labial margin flexing upwards at the rictus (approx. mid-orbital position), with 1–2 minute scales proximal to the flexure. Ten infralabials on either side, with a small scale proximal to the flexure. At the lip, mental slightly narrower than adjacent infralabial, 63% of rostral and in contact with three distinctly elongated postmental scales. Scales on throat much smaller than those on belly, scales touching infralabials larger. Thirteen scales across the crown at level of

Table 7. Measurements (in mm) and scale counts for the type series of *Afroedura donveae* sp. nov.

Catalogue number	PEM R17937	PEM R17936
Type Status	Holotype	Paratype
Sex	Female	Female
Snout vent length	61.0	64.0
Tail length	59.0	38.0
Tail condition	Original	Regenerated
Head length	16.6	13.2
Head width	11.4	11.2
Snout length	5.6	5.5
Eye distance	3.4	3.1
Eye-Ear distance	4.4	4.4
Dorsal rows per tail verticil	6	-
Ventral rows per tail verticil	7	-
Scales below 4 th toe	8	7
Mid-body scale rows	74	68
Scales between eyes	13	12
Scales: nostril to eye	11	10
Scales: ear to eye	13	14
Anterior nasals in contact	Yes	Yes
Supralabials	8	8
Infralabials	10	10

front of eyes; 11 scales between nostril and front of eye; 13 scales from ear to eye; 74 scales around mid-body. Ear opening deep, oblique and roughly oval, only half as high as wide (0.4×0.9 mm). Scales on dorsum smooth, non-overlapping, largest at mid-body, smaller on nape and tail base. Scales on ventrum flattened, not overlapping, more-or-less ovate at mid-ventrum, twice the size of lateral granules and 1.5 times the size of scales along the dorsal mid-line. Original tail slightly dorsoventrally flattened and distinctly verticillate (16 whorls in total), with obvious lateral constrictions; each verticil comprising 7 rows of imbricate scales dorsally and 6 rows of imbricate scales ventrally, with ventral scales approximately twice the size of those on the dorsal surface. Limbs well-developed, hindlimbs slightly longer than forelimbs, both without obvious mite pockets at posterior margin of limb insertions; mite pockets present on anterior margin of hindlimbs. All digits with a large pair of distal scansors, separated by a large, curved claw and followed after a large gap (twice length of terminal scansor) by a smaller pair of scansors; infero-median row of digital scales enlarged transversely, particularly towards the scansors, where the terminal scale adjoining the first pair of scansors may be medially constricted, swollen and scansor-like; 8 enlarged scale rows under 4th toe.

Paratypes and additional examined material variation. SVL varied from 49.1–55.7 mm; original tail length 26.5–59.0 mm, 0.78 times SVL; head length 1.13–1.46 times head width; snout 1.99 times diameter of eye (see Table 7 for more measurements and scale counts of type series). Supranasals always in contact; the first upper labial and rostral always enters the nostril and the width of the rostral at the lip margin is always wider than that of the mental; 2–3 postmental scales (except PEM R18401 with only one); supralabials 8–10, infralabials 8–11; scales between anterior edges of eyes 10–13; scales be-

tween nostril and anterior edge of orbit 8–12; scales from ear to eye 11–14; scales around mid-body 64–78; subdigital lamellae on 4th toe 6–8; dorsal scales per tail verticil 6–7 (mean 6.6); ventral scales per tail verticil 5–6 (mean 5.5); precloacal pores 11–12.

Colouration. *In life* (holotype PEM R17937, Fig. 5D): Yellowish above, brighter anteriorly, with nine irregularly-shaped darker brown to black crossbars from the occiput to the sacrum, each separated by thinner (3–4 scales deep), light yellow crossbars; head with dark brown-black blotches on the crown with intervening pale yellow colouration; dark brown bar from nostril across the upper margins of the ear opening, connecting with dark brown lateral bar on the neck; a thin pale yellow canthal stripe extends on both sides from the nasal region to anterior margins of eye, continuing posteriorly from the eye on to the nape; upper and lower labials light grey with diffuse brown edges; lateral sides of the body with a mix of dark grey and yellow blotches; limbs yellowish above with scattered darker grey markings; tail (original) with irregular dark brown bars, separated by yellow bars anteriorly, posteriorly with black and white bars; iris dark black with irregular golden spots, a black, narrow, elliptical, crenulate-edged pupil with black reticulation; ventrum uniform beige with scattered brown specks on lateral edges only; ventrally, limbs with scattered brown spots. *In preservative* (holotype PEM R17937, Fig. 9): dorsum with nine irregularly spaced dark brown crossbars from the occiput to the sacrum with beige intervening blotches; dorsally, arms and legs darkly barred; tail with nine dark brown bars, bolder towards the tip; dorsally, head with mottled dark brown scales; a light beige canthal stripe from nostril to anterior corner of eyes, continuing from the posterior part of the eye to above the ear opening; dark brown bar running from the nasals above the ear opening to the neck; light beige stripe (one-scale-wide) from above the supralabials to the ear opening (two-scales-wide); supralabials ventrally dark brown-edged; infralabials with scattered dark brown markings dorsally; ventrum is mostly immaculate, with dark brown spots ventrally on the arms and legs; ventrally, tail with nine dark brown bars, bolder posteriorly. *Variation.* Similar colouration and patterning as to the holotype. Dorsal crossbars are often fused to form 2–3 dark brown, X-shaped crossbars. Original tails with 6–7 broad, dark brown to black bars, separated by light beige to white bars; some specimens with fine one-scale-wide black bar separating the lighter bars. Regenerated tails with fine dark brown mottling. Juveniles with more sharply-defined patterns.

Natural history and habitat (Fig. 4D). One or two elongated white eggs were laid on limestone rock, to which they adhere in captivity; eggs measure 12.9–14.7 mm (mean 13.8 mm) $\times$ 10.5–12.1 mm (mean 11.6 mm) ($n = 5$) and hatch after 88–92 days, with hatchlings measuring 30.2–30.9 mm SVL and 26.5–27.9 mm tail length ($n = 5$) (Barts and Haacke 2010). A rupicolous species living in

crevices between rocks and under flakes of exfoliating rock amongst larger granite boulders, at elevations of 340–355 m a.s.l. in the arid Namib Desert. It appears to be associated with large granite outcrops in semi-desert shrublands, along the drier fringes of the Pro-Namib. Vegetation includes *Senegalia* (= *Acacia*) *mellifera*, *Senegalia* spp., *Commiphora* sp., *Boscia foetida* and *Salvadora persica*.

Distribution and conservation. Currently known only from the south-western parts of Namibe Province in Angola, in granite formations around Tambor and on the right bank of the mid-Curoca River (Fig. 1). The species remains poorly known, but it is probably stable in numbers as the local habitat is currently not threatened. It likely occurs in Iona National Park.

***Afroedura vazpintorum* sp. nov.**

<http://zoobank.org/2F4BED05-22A1-4D23-AD46-3C5DCFF9BCC1>

Coastal Flat Gecko

Osga-achatada da planície costeira

Figures 5E, F, 10; Tables 3, 8

Synonym. *Afroedura bogerti* – Branch et al. 2017b:157 (part); Marques et al. 2018: 177 (part); Branch et al. 2019a: 287 (part); *Afroedura* cf. *bogerti* – Butler et al. 2019:231; *Afroedura bogerti* (clade 2) – Branch et al. 2017a:146; *Afroedura* sp. – Baptista et al. 2018:400.

Holotype. PEM R24118, adult female, collected 1 km east of Farm Mucungo (-14.78361, 12.49694, 314 m a.s.l.), Namibe Province, Angola, by William R. Branch, Ninda L. Baptista and Pedro Vaz Pinto on 7 November 2015.

Paratypes. *Males*: PEM R24114–5, collected 1 km east of Farm Mucungo (-14.78361, 12.49694, 314 m a.s.l.), Namibe Province, Angola, by William R. Branch, Ninda L. Baptista and Pedro Vaz Pinto on 7 November 2015. *Females*: PEM R24116–7, collected 1 km east of Farm Mucungo (-14.78361, 12.49694, 314 m a.s.l.), Namibe Province, Angola, by William R. Branch, Ninda L. Baptista and Pedro Vaz Pinto on 7 November 2015.

Additional material examined. *Males*: PEM R21596, collected 52 km north of Lubango-Namibe junction to Lucira (-14.65806, 12.52717, 586 m a.s.l.), Namibe Province, Angola, by William R. Branch on 8 December 2012; PEM R22489, collected from Praia do Meva (near Santa Maria) (-13.39667, 12.58972, 10 m a.s.l.), Benguela Province, Angola, by Pedro and Afonso Vaz Pinto on 28 December 2015; TM 40264–6, TM 40285, TM 40283, collected from Caraculo (-15.01667, 12.66667, 463 m a.s.l.), Namibe Province, Angola, by Wulf Haacke on 27 March 1971; TM 41137, TM 41141, TM 41144, collected from turn off to Morro do Chapéu Armado (-14.51185, 12.50190, 462 m a.s.l.), Namibe Province, Angola, by Wulf Haacke on 18 April 1971; NB 746,

collected from Bimbe, Estação Zootécnica (-14.915538 13.249479, 2268 m a.s.l.), Namibe Province, Angola, by Ninda L. Baptista and Pedro Vaz Pinto on 11 March 2018. *Females*: PEM R21595, collected 50 km east of Namibe on main tar road to Leba Pass (-15.01558, 12.55503, 516 m a.s.l.), Namibe Province, Angola, by William R. Branch on 8 December 2012; PEM R22488, collected from Praia do Meva (near Santa Maria) (-13.39667, 12.58972, 10 m a.s.l.), Benguela Province, Angola, by Pedro and Afonso Vaz Pinto on 28 December 2015; PEM R24203–4, collected 10.4 km south of Rio Mucungo on tar road to Bentiaba (-14.84194, 12.42778, 360 m a.s.l.), Namibe Province, Angola, by William R. Branch and Pedro Vaz Pinto on 11 November 2016; PEM R24219, collected approx. 20 km south of Bentiaba (-14.40278, 12.44972, 426 m a.s.l.), Namibe Province, Angola, by William R. Branch and Pedro Vaz Pinto on 12 November 2016; TM 40263, TM 40267–9, TM 40280–2, TM 40284, TM 40286–7, TM 40289–90, collected from Caraculo (-15.01667, 12.66667, 463 m a.s.l.), Namibe Province, Angola, by Wulf Haacke on 27 March 1971; TM 41132–6, TM 41138–9, TM 41142, collected from turn-off to Morro do Chapéu Armado (-14.51185, 12.50190, 462 m a.s.l.), Namibe Province, Angola, by Wulf Haacke on 18 April 1971; TM 41211–4, collected from Lucira road, 5 km south of Catara River (-13.60430, 12.62890, 341 m a.s.l.), Namibe Province, Angola, by Wulf Haacke on 19 April 1971; NB 744–5, collected from Bimbe, Estação Zootécnica (-14.915538 13.249479, 2268 m a.s.l.), Namibe Province, Angola, by Ninda L. Baptista and Pedro Vaz Pinto on 11 March 2018. *Juveniles*: TM 41215–6, collected from Lucira road, 5 km south of Catara River (-13.60430, 12.62890, 341 m a.s.l.), Namibe Province, Angola, by Wulf Haacke on 19 April 1971; NB 743, collected from Bimbe, Estação Zootécnica (-14.915538 13.249479, 2268 m a.s.l.), Namibe Province, Angola, by Ninda L. Baptista and Pedro Vaz Pinto on 11 March 2018.

Additional referred material (not examined). TM 24545, collected from Caraculo (-15.01667, 12.66667, 463 m a.s.l.), Namibe Province, Angola, by Charles Koch in September 1956; TM 40288, TM 40291–5, collected from Caraculo (-15.01667, 12.66667, 463 m a.s.l.), Namibe Province, Angola, by Wulf Haacke on 27 March 1971; TM 41140, TM 41143, collected from turn-off to Morro do Chapéu Armado (-14.51185, 12.50190, 462 m a.s.l.), Namibe Province, Angola, by Wulf Haacke on 18 April 1971; FKH 0248, collected from road to Praia do Furado (-14.78306, 12.41726, 403 m a.s.l.), Namibe Province, Angola, by Javier Lobón Rovira, Afonso and Pedro Vaz Pinto on 5 July 2019; P9-154, collected from Mariquita (-14.78355, 12.41783, 401 m a.s.l.), Namibe Province, Angola, by Javier Lobón Rovira, Afonso and Pedro Vaz Pinto on 5 July 2019; NB 834–5, collected approx. 18 km E of Lucira (-13.90749, 12.69201, 332 m a.s.l.), Namibe Province, Angola, by Pedro Vaz Pinto, Ninda L. Baptista and Telmo António on 28 November 2017; CAS:HERP 264666–80, 26467, 264704, collected from Mocongo (= Mucungo)



Figure 10. Holotype of *Afroedura vazpintorum* sp. nov. (PEM R24118) from 1 km east of Farm Mucungo, Namibe Province, Angola. Photos: Werner Conradie.

Farm (-14.7789, 12.48745, 309 m a.s.l.), Namibe Province, Angola, by Luis M.P. Ceriaco, Mariana Marques and Joyce Janota between 2–6 August 2018; NB 602, collected from Sta Maria (-13.49813, 12.60921, 332 m a.s.l.), Benguela Province, Angola, by Afonso and Pedro Vaz Pinto on 12 July 2017; FKH 0005–6, collected from Fazenda Carivo (-13.195467, 13.424319, 438 m a.s.l.), Benguela Province, Angola, by Pedro Vaz Pinto on 5 June 2018; CAS 263848–9, INBAC: AMB 10691, CAS 263878, collected from Tundavala (-14.82386, 13.38114, 1295 m a.s.l.), Huíla Province, Angola, by Mariana P. Marques, Luis M.P. Ceriaco, Suzana Bandeira, Matthew Heinicke, Brent Butler and Timóteo Júlio on 1 and 9 August 2017. All material referable to the new species based on geographical distribution and closeness to examined material.

Etymology. This species is named in honour of father and son, Pedro and Afonso Vaz Pinto, two enthusiastic Angolan naturalists with whom WRB spent a great deal of time in the field, to recognise their contributions in collecting and studying Angolan herpetofauna. The name is constructed in the masculine plural genitive.

Diagnosis. A member of the greater ‘*transvaalica*’ group as it possesses two pairs of enlarged scansors per digit and a strongly verticillate and flattened tail (Jacobsen et al. 2014). Part of the *A. bogerti*-group which differs from other members of the ‘*transvaalica*’ group by having less than 86 mid-body scale rows (vs. 97–102 in

A. gorongosa, 113–120 in *A. loveridgei*, 102–119 in *A. transvaalica*); by the rostral bordering the nostril (nostril excluded from rostral in *A. loveridgei*); by the anterior nasals always in contact (separated by 1–3 granules in *A. gorongosa*; always in broad contact in *A. loveridgei*; usually in broad contact in *A. transvaalica* ~ 3–18%); and in having 11–14 scales between the anterior borders of the eyes (19–22 in *A. gorongosa*; 15–19 in *A. loveridgei*; 15–20 in *A. transvaalica*) (comparative data *fide* Branch et al. 2017a).

Afroedura vazpintorum sp. nov. differs from other members of the *A. bogerti*-group by a combination of the following characters (see Tables 3, 4): 73–86 (mean 80.3) mid-body scale rows (69–77 [mean 73.5] in *A. bogerti*, 76–88 [mean 79.3] in *A. wulphaackei* sp. nov., 64–78 [mean 72.8] in *A. donveae* sp. nov., 73–78 [mean 74.8] in *A. praedicta* sp. nov.); by the anterior nasals always in contact (similar to *A. donveae* and *A. praedicta* sp. nov.; ~ 33% of the time in contact in *A. bogerti*; ~ 68% of the time in contact in *A. wulphaackei* sp. nov.); in each verticil having 5–6 (mean 5.0) ventral and 6–7 (mean 6.1) dorsal rows of scales (5–6 [mean 5.5] and 6–7 [mean 6.6] in *A. donveae* sp. nov.; 4 and 5 in *A. bogerti* and *A. praedicta* sp. nov., 4–5 [mean 4.0] and 5–6 [mean 5.1] in *A. wulphaackei* sp. nov.); ventral surfaces immaculate (similar to *A. donveae* sp. nov.; greyish with black spot in *A. bogerti*, *A. wulphaackei* sp. nov. and *A. praedicta* sp. nov.). *Afroedura vazpintorum* sp. nov. differs from its sister lowland species *A. donveae* sp. nov. in being smaller (51.3 versus

Table 8. Measurements (in mm) and scale counts for the type series of *Afroedura vazpintorum* sp. nov.

Catalogue number	PEM R24118	PEM R24114	PEM R24115	PEM R24116	PEM R24117
Type Status	Holotype	Paratype	Paratype	Paratype	Paratype
Sex	Female	Male	Male	Female	Female
Snout vent length	50.6	50.2	46.7	51.9	50.7
Tail length	44.5	27.0	22.7	34.1	24.7
Tail condition	Original	Regenerated	Regenerated	Regenerated	Regenerated
Head length	11.1	11.2	10.3	10.8	11.1
Head width	7.4	7.6	7.4	7.2	7.8
Snout length	4.3	4.4	4.0	4.4	4.4
Eye distance	2.5	2.7	2.3	2.5	2.6
Eye-Ear distance	4.1	3.9	3.9	4.2	3.9
Precloacal pores	-	12	10	-	-
Dorsal rows per tail verticil	5	-	5	5	7
Ventral rows per tail verticil	6	-	6	6	7
Scales below 4 th toe	9	7	8	7	7
Mid-body scale rows	73	81	79	83	74
Scales between eyes	11	14	14	11	13
Scales: nostril to eye	8	9	8	7	7
Scales: ear to eye	14	17	17	16	15
Anterior nasals in contact	Yes	Yes	Yes	Yes	Yes
Supralabials	9	8	8	9	8
Infralabials	8	9	8	9	9

57.6 mm average SVL), in having greater mid-body scale counts 73–86 (mean 80.3) versus 64–78 (mean 72.8), a lower number of precloacal pores (9–11 [mean 10.2] versus 11–12 [mean 11.5]), duller colouration and less distinct tail banding (versus bolder colouration and distinct tail banding).

Holotype description. Adult male; SVL 50.6 mm; tail 44.5 mm (partly regenerated tail); with a small mid-ventral incision for the removal of liver sample. Measurements and meristic characters of holotype presented in Table 8. Head and body dorsoventrally compressed; HL 11.1 mm, HW 7.4 mm, broadest at posterior level of eye and 1.5 times longer than wide. Eyes large (2.5 mm wide), pupil vertical with indented margins; circumorbital scales small and smooth, elongate at upper anterior margin, the most upper posterior scale with minute upward pointing spines. Snout rounded, 4.3 mm long, almost equal to distance between eye and ear openings (4.1 mm). Scales on top of snout slightly granular and elevated, rounded, mostly equal in size, with no intervening minute granules. Scales on snout slightly subequal in size to those on back of head or nape which, in turn, is irregular in size and mostly smooth. Scales on eyelids larger than those on the crown, 6 scales deep from circumorbital scales to crown. Circumorbital scales are separated by a row of smaller scales from the larger scales on eyelid. Nostril pierced between rostral, three nasal scales; 1st supralabial narrowly excluded from nostril; the supranasal being much larger than the subequal postnasals and being separated from each other by two smaller scales. Nostrils slightly elevated. Rostral roughly rectangular, but with its upper edges elongated due to extensions into the nostril. Nine supralabials on each side, the labial margin flexing upwards at the rictus (approx. mid-orbital position), with 2–3 minute scales proximal to the flexure. Eight infralabials on either side,

with a small scale proximal to the flexure. At the lip, mental slightly narrower than adjacent infralabial, only three quarters the width of rostral and in contact with three distinctly elongated postmental scales. Scales on throat much smaller than those on belly; scales touching infralabials larger. Eleven scales across the crown at level of front of eye; 8 scales between nostril and front of eye; 14 scales from ear to eye; 73 scales around mid-body. Ear opening deep, oblique and roughly oval, backward pointing, much taller than wide (0.6 × 0.1 mm). Scales on dorsum smooth, non-overlapping, largest at mid-body, smaller on nape and tail base. Scales on ventrum flattened, not overlapping, more-or-less ovate at mid-ventrum, twice the size of lateral granules and 1.5 times those along backbone. Original tail slightly dorsoventrally flattened and distinctly verticillate (7 whorls in total), with obvious lateral constrictions; each verticil comprising 6 imbricate rows of scales dorsally and 5 imbricate scale rows ventrally and ventral scales approximately twice the size of those on the dorsal surface. Limbs well developed, hindlimbs slightly longer than forelimbs, both without obvious mite pockets at posterior margin of limb insertions, mite pockets present at anterior margin of hindlimbs. All digits with a large pair of distal scansors, separated by a large, curved claw and followed after a large gap (twice the length of terminal scansor) by a smaller pair of scansors; infero-median row of digital scales enlarged transversely, particularly towards the scansors, where the terminal scale adjoining the first pair of scansors may be medially constricted, swollen and scansor-like; 9 enlarged scale rows under 4th toe. Precloacal pores 12.

Paratypes and additional material variation (see Table 8 for more measurements and scale counts of type series). SVL 43.9–58.8 mm; original tail length 42.3–67.0 mm, 0.94 times SVL; head length 1.07–1.61

times head width; snout 1.75 times diameter of eye. The supranasals are always in contact; the first upper labial and rostral always enter the nostril and the rostral at the lip margin is always wider than the mental; 2–3 postmental scales; supralabials 8–10, infralabials 8–9; scales between anterior edges of eyes 11–15; scales between nostril and anterior edge of orbit 7–11; scales between anterior edge of ear and rear margin of orbit 7–11; scales around mid-body 73–86; subdigital lamellae on 4th toe 6–10; dorsal scales per tail verticil 6–7 (mean 6.1); ventral scales per tail verticil 5–6 (mean 5.0); precloacal pores 9–12.

Colouration. *In life* (paratype PEM R24118, Fig. 5E). Light grey to yellow-olive above with six irregularly-spaced darker, brown to black, W-shaped crossbars from the occiput to the sacrum, central two broken up to form irregularly-shaped crossbars; each crossbar separated by yellow-olive to light grey blotches; head mostly light grey with scattered darker grey scales; dark brown band from nostril across the upper margins of the ear opening connecting with dark brown lateral bar on to the neck; a thin pale yellow canthal stripe extends on both sides from the nasal region to anterior margins of eye, continuing on to the nape; upper and lower labials light grey with diffuse dark brown edges; lateral sides of the body with a mix of dark grey and yellow blotches; limbs yellowish above with scattered darker grey markings; tail (original) with irregular dark brown bars separated by yellow bars; tail (regenerated) with black mottling on light grey background; iris dark brown with a black narrow elliptic pupil with crenulated edge and black reticulation; ventrum uniform beige with scattered brown specks on lateral edges of ventrum alone; ventrally, limbs with scattered brown spots. *In preservative* (holotype PEM R24118, Fig. 10): dorsum with three distinct, irregularly-spaced, dark brown W-shaped crossbars anteriorly, with beige intervening blotches, the posterior crossbars are broken up and irregularly spaced; dorsally, arms and legs darkly barred; tail (original part) with dark brown bars that are not well defined; tail (regenerated part) with dark brown mottling on beige background; dorsal head with mottled dark brown scales, light beige canthal stripe from nostril to anterior corner of eyes, continuing posterior to the eye to above the ear opening; dark brown band running from the nasals, above the ear opening, to the neck; light beige stripe (one-scale-wide) from above the supralabials to the ear opening

(two-scales-wide); supralabials dark brown edged ventrally; infralabials scattered with dark brown markings dorsally; ventrum mostly immaculate with dark brown spots ventrally on arms and legs. *Variation:* Similar colouration and patterning to the holotype (preserved) and paratype (as above, in life). Dorsal crossbars are often fused to form an X-shape or are irregular. When present, crossbars number 5–6. Coastal material is often very light in colouration and not as boldly patterned or brightly coloured compared to highland material. Original tails with 6–7 broad, dark brown to black bars, separated by light beige to white bars, some specimens with a fine one-scale-wide black bar splitting the lighter bars. Regenerated tails with fine dark brown to black mottling. Juveniles with more sharply defined patterns.

Natural history and habitat (Fig. 4E, F). This species was frequently observed at night in coastal areas hunting in small branches, bushes and small trees growing amongst rock crevices between large granite boulders. When disturbed, it quickly jumps to the rock faces and finds shelter under granite flakes. Mainly rupicolous, it is strongly associated with large granite boulders present throughout the semi-arid ecosystems of the Angolan Kaokoveld. Usually found in rocky habitats with succulent plants and dominated by acacia savannah (*Senegalia* spp.), preferring more wooded and less arid environments when compared to *A. donveae* sp. nov. Some specimens, referable to *A. vazpintorum* sp. nov., were found at high altitude near Bimbe, in crevices in pre-cambrian limestone formations, a rocky habitat framed by stunted Afromontane forest elements and surrounded by extensive montane grassland.

Distribution and conservation. Known from various localities in the coastal lowlands of Namibe and Benguela Provinces of Angola, stretching for about 250 km along the coast and up to 60 km inland, which is probably a fair reflection of the species' global range (Fig. 1). Occurs from near sea level to 500 m elevation. An apparently isolated population occurs on the Angolan highlands along the Humpata Plateau. This population occurs at a much higher elevation (above 2,000 m a.s.l.) and may warrant further phylogenetic analysis employing nuclear markers. The species seems common and widely distributed, mostly in relatively undisturbed habitat and, therefore, it is likely not threatened.

Updated key to the *Afroedura transvaalica*-group (updated from Branch et al. 2017a)

- | | | |
|---|---|------------------------|
| 1 | Mid-body scale rows more than 95 | 2 |
| – | Mid-body scale rows less than 95; occurs in northern Namibia and Angola | 4 |
| 2 | Rostral usually bordering nostril | 3 |
| – | Rostral usually excluded from nostril | <i>A. loveridgei</i> |
| 3 | Anterior nasals in contact (very rarely separated); scales around mid-body: South Africa 102–118 (mean 109), northern Zimbabwe 108–119 (average 114)..... | <i>A. transvaalica</i> |
| – | Anterior nasals separated by 1–3 granules; scales around mid-body 99–101 (average 100) | <i>A. gorongosa</i> |

4	Each tail verticil usually comprising 5 ventral and 6 dorsal rows of scales; anterior nasals always in contact; ventrum immaculate.....	5
–	Each tail verticil usually comprising 4 ventral and 5 dorsal rows of scales; anterior nasals not always in contact; ventrum greyish with small black specks.....	6
5	Mid-body scales 64–78 (mean 72.8); larger average adult size 57.1 mm SVL; precloacal pores 11–12 (mean 11.5) in males; bold colouration.....	<i>A. donveae</i> sp. nov.
–	Mid-body scales 73–86 (mean 80.3); smaller average adult size 48.6 mm SVL; precloacal pores 9–11 (mean 10.2) in males; dull colouration.....	<i>A. vazpintorum</i> sp. nov.
6	Anterior nasals always in contact.....	<i>A. praedicta</i> sp. nov.
–	Anterior nasals not always in contact.....	7
7	Mid-body scales 69–77 (mean 73.5).....	<i>A. bogerti</i>
–	Mid-body scales 76–88 (mean 79.3).....	<i>A. wulphaackei</i> sp. nov.

Discussion

When Loveridge (1947) provided the first syntheses of the genus *Afroedura*, he documented a total of only 12 species. When Onderstall (1984) reviewed the genus, he divided it into distinct morphological groups and described two new subspecies from South Africa and Eswatini (formerly Swaziland). Since then, Mouton and Mostert (1985) described a new endemic species from the Western Cape Province in South Africa, Jacobsen et al. (2014) formally added nine endemic species from the northern provinces of South Africa and elevated three subspecies to species status and Branch et al. (2017a) described a new endemic species from Gorongosa Mountains in central Mozambique, bringing the total number of species in the genus to 28. In the latter study, cryptic diversity within the Angolan *A. bogerti* group was documented and addressed in more detail afterwards (Branch et al. 2017b). Our study provides morphological evidence to support the genetic results, previously reported by Branch et al. (2017a, b) and describes four additional species in the genus, increasing the number of Angolan *Afroedura* species from one to five and to a total of 32 in Africa. Recent phylogenetic studies in South Africa have documented additional cryptic diversity in more widespread species (e.g. *A. amatolica*, *A. halli*, *A. nivaria* and *A. pondolia*) and new taxa are awaiting formal description (Makhubo et al. 2014; Busschau et al. 2019). More studies on the Angolan flat geckos are needed to understand their biology, natural history and true distribution and, thus, assess their conservation status.

The radiation within Angolan *Afroedura* seems to have followed a major split that separated the west-central highlands from a south-western group. Being a strictly rupicolous gekkonid genus that typically displays low dispersal mobility, populations could easily become isolated in suitable remaining habitat, thus leading to speciation events in these “rock islands” or inselbergs (Jacobsen et al. 2014; Branch et al. 2017a). All genetically-assigned specimens from the central Angolan highland group were collected at relatively high altitude in what is generally called the Angolan ancient massif or ancient plateau (Huntley 2019), mostly above 1,500 m a.s.l. So far, *A. bogerti*, *A. wulphaackei* sp. nov. and *Afroedura* sp.

5–7 were found to be restricted to different ancient mountain chains of heterogeneous geology or in isolated outcrops on the old plateau, which may explain the complex speciation patterns exhibited in a relatively-constricted area. In contrast, most of the landscape of south-western Angola has been actively transformed by tectonic forces in more recent geological times, as the coastal plain and southern escarpment have attained the current profile during the Pleistocene (Feio 1981). Exceptionally, Serra da Neve inselberg is an alkaline extrusion dating from the Cretaceous (Pereira 1977) and, therefore, pre-dating by far the rising of the southern escarpment. Thus, the existence of the new species, *A. praedicta* sp. nov., from the higher elevation on the Serra da Neve inselberg was half-expected, while *A. donveae* sp. nov. appears to have evolved in association with arid granitic landscapes of the Pro-Namib. Interestingly, *A. vazpintorum* sp. nov. is comparatively much more widely distributed across the Angolan Kaokoveld, but also linked to the highlands on the top of the southern escarpment at the Humpata Plateau, where an additional population was found. It is likely that the southern escarpment population represents a yet undescribed species and this will be investigated further in forthcoming efforts using a multi-gene approach with a more comprehensive series. The genetic distance indicated that, using only a *16S* marker is, on its own, a strong indication, but not enough to consider this isolated population as a formal species.

The obvious genetic (sub-)structure, identified between *A. wulphaackei* sp. nov. and the three morphologically-indistinguishable clades *Afroedura* sp. 5–7 and within *A. vazpintorum* sp. nov. (Fig. 2), seems surprising at first glance. However, both these species have a relatively-wide distribution area, when compared to the other known Angolan *Afroedura* species (Fig. 1) and, therefore, they are likely to occupy a broader range of niches, which may suggest they are undergoing a speciation process. Rupicolous species are known to require very specific suitable habitats and this often leads to a micro-fragmentation within their distribution range. These microhabitats are frequently separated from other suitable microhabitats by comparatively long distances, so these species could be considered as allopatric, which could conceivably lead to rapid speciation. This pattern has been reported from

other gecko species (Portik et al. 2013; Travers et al. 2014). As genetic changes can establish themselves well before any significant and consistent morphological differences develop between populations (see Branch et al. 2014), the lack of morphological differences between the detected morphologically-identical *Afroedura* sp. 5–7 clades and *A. wulfhaackei* sp. nov. as well as in *A. vazpintorum* sp. nov. can be considered as expected. The exact taxonomic status of *Afroedura* sp. 5–7, as being either conspecific with *A. wulfhaackei* sp. nov., representing additional taxa or even being hybrid populations, needs to be clarified using a multi-gene study and the morphological analyses of additional specimens from those populations.

Overall, the speciation pattern observed for Angolan *Afroedura* is similar to that of sympatric species of *Cordylus* (also rupicolous). Angolan *Cordylus* also include a central highland and a south-western group. The former group currently comprises a single species, *C. angolensis*, but it may, in fact, represent a species complex (Stanley et al. 2016; Bates et al. in prep.). On the other hand, the south-western group has, in recent years, been split into three species: *C. phonolithos* endemic to the Serra da Neve inselberg (Marques et al. 2019b), *C. namakuiyus* from the coastal Kaokoveld (Stanley et al. 2016) and *C. machadoi* from the higher elevations of the southern escarpment (Stanley et al. 2016). This parallel evolution highlights the importance of ‘rock islands’ as speciation sources for Angolan squamates.

A flat gecko discovered in a rock crevice on the summit of the Otjihipa Mountains, northern Opuwo District, Namibia (Branch 1998; Griffin 2003; Branch et al. 2017b) was referred to as *Afroedura* cf. *bogerti*. However, no voucher material is available at the National Museum of Namibia (A.M. Bauer, pers. comm. May 2016), nor have any recent specimens been collected to allow us to assign it to one of the species described here. There is also the possibility that it may represent yet another undescribed species. A specimen of *Cordylus* was also found in the Otjihepa and Baynes Mountains Region of northern Namibia and was assigned to *C. machadoi* (Branch 1998; Griffin 2003), but was recently shown to be more closely related to *C. namakuiyus* from south-western Angola (De-Boer et al. 2019). Recently, Bauer et al. (2020) recorded *Nucras* aff. *broadleyi*, a recently-described species from south-western Angola (Branch et al. 2019), in Cunene Province of Namibia. This parallel between Angolan and Namibian species, as well as the importance of the Cunene River as a barrier to gene flow, needs to be studied further.

In recent years, we have seen Angola embracing international collaboration that has led to an increase in biodiversity knowledge (Huntley 2009; Huntley and Francisco 2015; Brooks 2012, 2013; NGOWP 2017). This is especially true in the field of herpetology, with numerous new species of squamates being described in the last decade (Conradie et al. 2012, 2020; Stanley et al. 2016; Marques et al. 2019a, b, 2020; Branch et al. 2019; Ceriaco et al. 2020a, b, c; Hallerman et al. 2020; this study). Many of these new species descriptions apply to the more

arid regions below the Angolan escarpment, reinforcing this area as a regional biodiversity and endemism hotspot (Branch et al. 2019a) that requires effective protection.

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