

Monograph on
**Endemism in the
Highlands and Escarpments
of Angola and Namibia**



Angola Cave-Chat *Xenocopsychus ansorgei*
Photo: M Mills

Editors:

John M Mendelsohn
Brian J Huntley
Pedro Vaz Pinto

Published with support and funding from:

Ongava Research Centre (ORC)
Namibian Chamber of Environment (NCE)
Centro de Investigação em Biodiversidade
e Recursos Genéticos (CIBIO)
B2Gold Namibia
TotalEnergies

Language editor: Carole Roberts
Design and layout: Alice Jarvis

NJE Namibian Journal
of Environment

2023: Volume 8 www.nje.org.na

ISSN: 2026-8327 (online)

» [DOWNLOAD THE MONOGRAPH](#)

CONTENTS

Huntley BJ, Mendelsohn JM & Vaz Pinto P Preface to endemism on the highlands and escarpments of Angola and Namibia	i–iii
Huntley BJ, Mendelsohn JM & Vaz Pinto P The biological importance of the highlands of Angola and Namibia: Synopsis and conclusions.....	v–xiii

Geography of the highlands and escarpments

Jarvis AM The highlands and escarpments of Angola and Namibia: orientation maps.....	1–6
Mendelsohn JM & Huntley BJ Introducing the highlands and escarpments of Angola and Namibia	7–22
Miller RM Geology and landscape evolution of the highlands and escarpments of western Angola and Namibia.....	23–28
Huntley BJ Biomes and ecoregions of the highlands and escarpments of Angola and Namibia	29–41
Mendelsohn JM & Gomes AL The human environment in the highlands and escarpments of Angola and Namibia	43–51
Vaz Pinto P, Russo V & Veríssimo L The highlands in Angolan conservation areas	53–62

Diversity and endemism

Craven P & Kolberg H An overview of plant endemism on the highlands of Namibia	63–76
Goyder DJ, Gomes AL, Gonçalves FMP, Luís JC & Darbyshire I A botanical assessment of Mt Namba, Cuanza-Sul, Angola: an isolated mountain towards the northwestern limits of the Great Escarpment of southern Africa.....	77–92
Meller P, Lages F, Finckh M, Gomes A & Goyder D Diversity and endemism of geoxylc plants on the Angolan Planalto.....	93–109
Bruyns PV, Hanáček P & Klak C Diversity and endemism in the species-rich Ceropegieae (Apocynaceae) and <i>Euphorbia</i> in the highlands and escarpments of Angola and Namibia	111–134
Dexter KG, Swanepoel W, Loiseau O, Darbyshire I, Nanyeni L, Gonçalves FM, Chase F & Manzitto-Tripp EA High endemism of the genus <i>Petalidium</i> (Acanthaceae) in the highlands and escarpments of Angola and Namibia	135–147
Weeks A & Swanepoel W <i>Commiphora</i> of the highlands and escarpments of Angola and Namibia	149–159
Lautenschläger T, Aime MC, Clausnitzer V, Langer L, Meller P, Müller F, Nuss M, Teutloff N & Ernst R Green gem of the Northern Escarpment: biodiversity and endemism of the Serra do Pingano Forest Ecosystem.....	161–172
Kipping J, Clausnitzer V & Dijkstra K-DB The highlands and escarpment of Angola as an endemism hotspot for African dragonflies and damselflies (Insecta: Odonata).....	173–186
Gunter F, Jürgens N & Henschel JR Observations on the diversity of termites in Angola and Namibia.....	187–192
Mansell MW The Neuroptera of the highlands and escarpments of Angola and Namibia	193–196
Gomez K, Hawkes PG & Fisher BL Ant endemism in the highlands and escarpments of Angola and Namibia (Hymenoptera, Formicidae)	197–203
Gardiner AJ & Williams MC The endemic butterflies of Angola and Namibia and their evolutionary implications.....	205–230
Prendini L & Bird TL Endemism of Arachnida (Amblypygi, Scorpiones and Solifugae) in the highlands and escarpments of Angola and Namibia: current knowledge and future directions.....	231–244
Becker FS, Baptista NL, Vaz Pinto P, Ernst R & Conradie W The amphibians of the highlands and escarpments of Angola and Namibia.....	245–257
Bauer AM, Ceriáco LMP, Marques MP & Becker FS Highland reptiles of Angola and Namibia	259–276
Conradie W, Lobón-Rovira J, Becker FS, Schmitz A & Vaz Pinto P Flat gecko (<i>Afroedura</i>) diversity, endemism and speciation in the highlands and escarpments of Angola and Namibia.....	277–281
Skelton PH Fishes of the highlands and escarpments of Angola and Namibia.....	283–292
Mills MSL & Melo M Birds of the highlands and escarpments of Angola and Namibia: ornithological significance, avifaunal patterns and questions requiring further study	293–309
Palmeirim AF, Monadjem A, Vaz Pinto P, Taylor P, Svensson MS & Beja P Mammal endemism in the highlands and escarpments of Angola and Namibia.....	311–322
De Matos D, Zastrow J, Val A & Mendelsohn JM Caves and their fauna in the highlands and escarpments of Angola and Namibia	323–330

Flat gecko (*Afroedura*) diversity, endemism and speciation in the highlands and escarpments of Angola and Namibia

W Conradie^{1,2}, J Lobón-Rovira^{3,4,5,6}, FS Becker⁷, A Schmitz⁸, P Vaz Pinto^{3,6,9}

URL: <https://www.nje.org.na/index.php/nje/article/view/volume8-conradie>

Published online: 15th December 2023

¹ Port Elizabeth Museum (Bayworld), Humewood, South Africa; werner@bayworld.co.za

² Department of Nature Conservation Management, Natural Resource Science and Management Cluster, Faculty of Science, George Campus, Nelson Mandela University, George, South Africa

³ CIBIO-InBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Laboratório Associado, Universidade do Porto, Campus Agrário de Vairão, Vairão, Portugal

⁴ Faculdade de Ciências, Universidade do Porto, Porto, Portugal

⁵ Instituto Superior de Ciências da Educação da Huíla (ISCED-Huíla), Lubango, Angola

⁶ BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Campus de Vairão, Vairão, Portugal

⁷ National Museum of Namibia, Windhoek, Namibia

⁸ Natural History Museum of Geneva, Geneva, Switzerland

⁹ Fundação Kissama, Luanda, Angola

ABSTRACT

Nine species of African flat geckos (*Afroedura*) are known to be associated with the highlands and escarpments of Angola and Namibia (HEAN). Among these, the *Afroedura bogerti* group is the most speciose (with seven species) and endemic to the HEAN. Phylogenetically, it constitutes a young species group that speciated during the early Pleistocene (~1.91 mya). Although currently none of these species is regarded as threatened, their distribution falls largely outside protected areas which could compromise their future.

Keywords: *Afroedura*, Angola, diversity, endemism, flat gecko, Namibia, speciation

INTRODUCTION

African flat geckos of the genus *Afroedura* Loveridge, 1944 are medium to large (maximum snout–vent length is 83 mm) dorsoventrally flattened geckos with rupicolous (rock-living) habits. They occur from western Angola southwards to South Africa and along the eastern escarpment northwards to central Mozambique (Branch 1998, Jacobsen *et al.* 2014, Branch *et al.* 2021). They are typical highland species, found along the rocky mountainous areas of the escarpments, but apparently absent from most of the sandy lowlands in the interior of the continent.

Currently the genus comprises 34 species (Jacobsen *et al.* 2014, Branch *et al.* 2021, Conradie *et al.* 2022), many of them described in the last decade, from the northern provinces of South Africa (Jacobsen *et al.* 2014), central Mozambique (Branch *et al.* 2017) and northern Namibia and Angola (Branch *et al.* 2021, Conradie *et al.* 2022), and this number is expected to increase even further with the description of additional novel species (Makhubo *et al.* 2015, Busschau *et al.* 2019, Nicolau *et al.* 2023).

Most of the *Afroedura* species are restricted to South Africa and the eastern escarpment (Jacobsen *et al.* 2014), with only *A. africana*, *A. tirasensis* and the *A. bogerti* species group associated with the arid highlands and escarpments of Angola and Namibia

(HEAN). *Afroedura africana* and *A. tirasensis* are restricted to the arid western and central Namibian highlands. *Afroedura africana* shows a closer phylogenetic relationship to another arid-adapted South African species, *A. karrocia*, than to other species associated with the HEAN. High genetic divergence exists among material from the Erongo Mountains and may include undescribed cryptic taxa (Jacobsen *et al.* 2014, Bauer *et al.* 2023). *Afroedura tirasensis* has not been tested in a phylogenetic framework but is expected to be closely related to the *A. africana* group. For the remainder of this paper we will focus on the *A. bogerti* group, which has received more attention in the last few years.

THE AFROEDURA BOGERTI GROUP

Until recently *Afroedura bogerti* was the only species of *Afroedura* known to occur in Angola and adjacent northern Namibia (Marques *et al.* 2018), but a slew of new species descriptions (Branch *et al.* 2021, Conradie *et al.* 2022) has increased this number to six endemic species (*A. bogerti*, *A. donveae*, *A. praedicta*, *A. pundomontana*, *A. vazpintorum* and *A. wulfhaackei*) from Angola (Figure 1) and one from neighbouring Namibia (*A. otjihipa*; Figure 2).

These seven endemic species can be divided into two distinct groups based on morphological and molecular data: a northern group comprising three

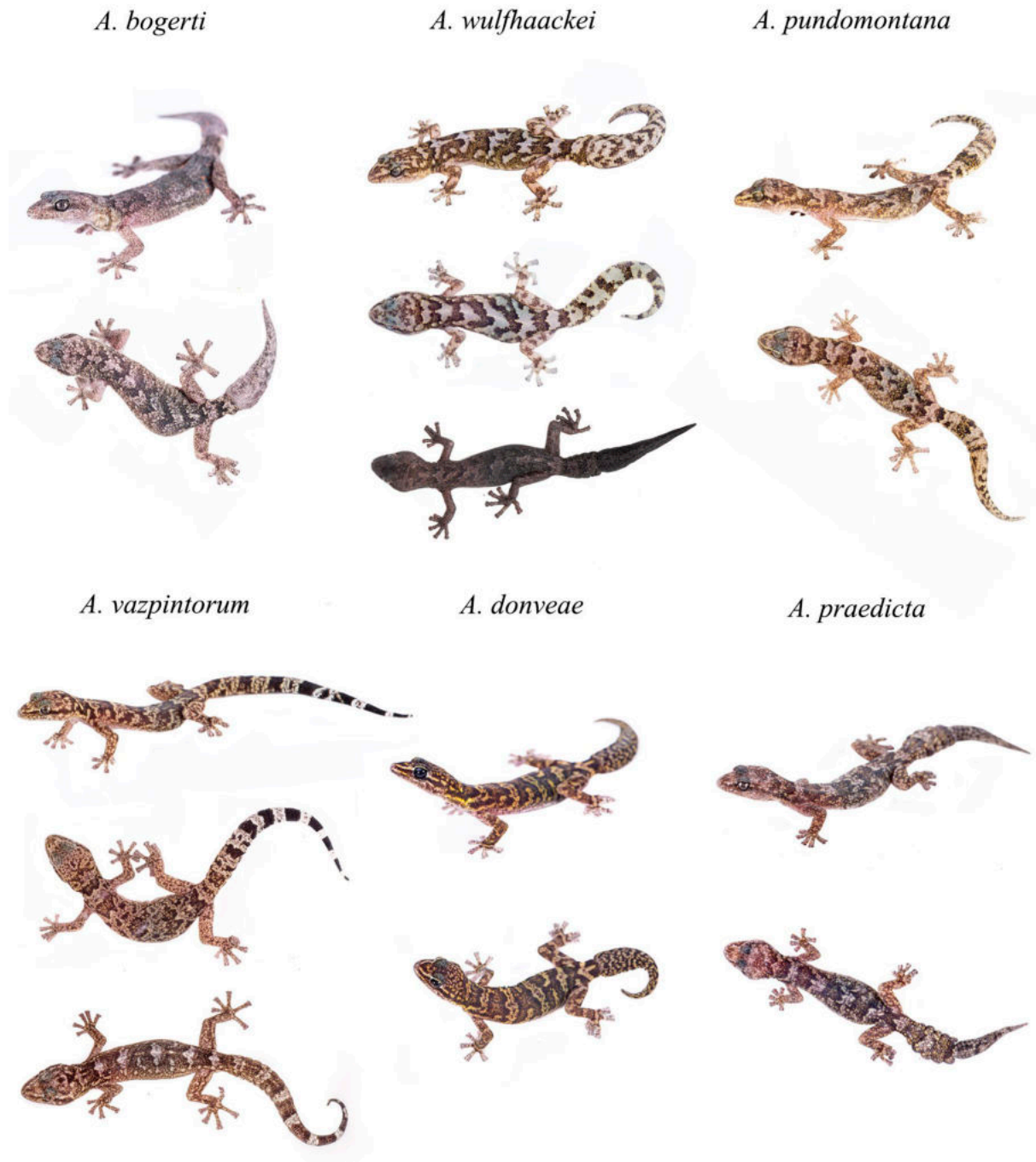


Figure 1: Collage of the different species of African flat geckos in the *Afroedura bogerti* group from Angola: *A. bogerti* from Namba, Cuanza-Sul Province; two specimens of *A. wulfhaackei* from Lépi (top) and one from Serra do Môco (bottom), Huambo Province; *A. pundomontana* from Bocoio, Benguela Province; two specimens of *A. vazpintorum* from Kapembawé, Benguela Province (top) and one from Tundavala, Huila Province (bottom); *A. donveae* from Omahua, Namibe Province; *A. praedicta* from Serra da Neve, Namibe Province. Photos: J Lobón-Rovira and P Vaz Pinto.

species which are found on the Angolan Planalto and associated escarpment (*A. bogerti*, *A. pundomontana* and *A. wulfhaackei*) and a southern group comprising four species present in the southwestern highlands and coastal plain (*A. donveae*, *A. otjihipa*, *A. praedicta* and *A. vazpintorum*). Predicted distributions and known localities are shown in Figure 3.

Northern group

Afroedura bogerti Loveridge, 1994 – Namba or Bogert’s flat gecko

This species is known only from the vicinity of Mt Namba in the southern part of Cuanza-Sul Province of Angola and is regarded as a strict highland-

associated species. It is a nocturnal, rupicolous species typically found sheltering in crevices and under exfoliating rock on larger granite outcrops in montane grasslands and associated scattered miombo and Afromontane forests at an elevation of 1,750–1,850 masl. Its International Union for Conservation of Nature (IUCN) assessment of Least Concern (Baptista *et al.* 2020) was made before the split of the species group and consequently its status needs reassessment. Although the species has a very restricted distribution, it is relatively common in suitable habitat and known to occur in degraded habitat (Branch *et al.* 2021). The removal of rock flakes for the construction of houses or other buildings may be a threat to this species.

***Afroedura pundomontana* Conradie *et al.*, 2022 – Bocoio flat gecko**

This species occurs at lower elevations than the other highland-associated species. It is restricted to elevations of 600–1,000 masl in Angola's Central Escarpment in central Benguela Province where it is found in low numbers on large granite rocky outcrops scattered among mixed escarpment woodlands. It has not been assessed for its threat status but could potentially trigger a threat category due to its limited distribution and the removal of rock flakes for the construction of houses and other buildings (Conradie *et al.* 2022).

***Afroedura wulphaackei* Branch *et al.*, 2021 – Huambo or Mombolo flat gecko**

This species occurs widely in the Angolan Planalto of Huambo Province, Angola, extending marginally into the Central Escarpment in the provinces of Benguela and Cuanza-Sul. It is mostly found sheltering in crevices and under exfoliating rock on larger granite outcrops at elevations of 1,750–2,055 masl. At least four genetically distinct, isolated populations have been identified (Branch *et al.* 2021, Conradie *et al.* 2022).

al. 2022). This species has not been assessed for its threat status, but its habitat might be threatened by the removal of rock flakes for building construction (Branch *et al.* 2021).

Southern group

***Afroedura donveae* Branch *et al.*, 2021 – Iona flat gecko**

Currently this species is only known from the arid coastal region of southwestern Namibe Province, Angola. It is typically found sheltering in crevices and under exfoliating rock on large granite outcrops scattered in the semidesert scrubland environment at low elevations of 340–355 masl. It is not regarded as a highland-associated species. Its threat status has not been assessed. Although it seems to have very restricted distribution, the population is probably stable and its habitat is not under threat.

***Afroedura otjihipa* Conradie *et al.*, 2022 – Otjihipa flat gecko**

Currently this species is only known from the Otjihipa Mountains in the Southern Escarpment, Namibia, where it occurs in small sandstone outcrops in arid woodland at elevations of 1,800–1,900 masl. While it is expected to occur more widely in suitable habitat, it has not been recovered from the dolomite ridges surrounding the type locality. Its threat status has not been assessed by the IUCN, but based on the remoteness and undisturbed habitat it occurs in, it is unlikely to trigger any threat status.

***Afroedura praedicta* Branch *et al.*, 2021 – Serra da Neve flat gecko**

This species is restricted to areas of higher elevation (1,900–2,000 masl) of the isolated Serra da Neve inselberg in northern Namibe Province. It is sympatric with another highland endemic, *Cordylus*



Figure 2: *Otjihipa flat gecko* (*Afroedura otjihipa*) from the Otjihipa Mountains in northern Namibia. Photo: F Becker.

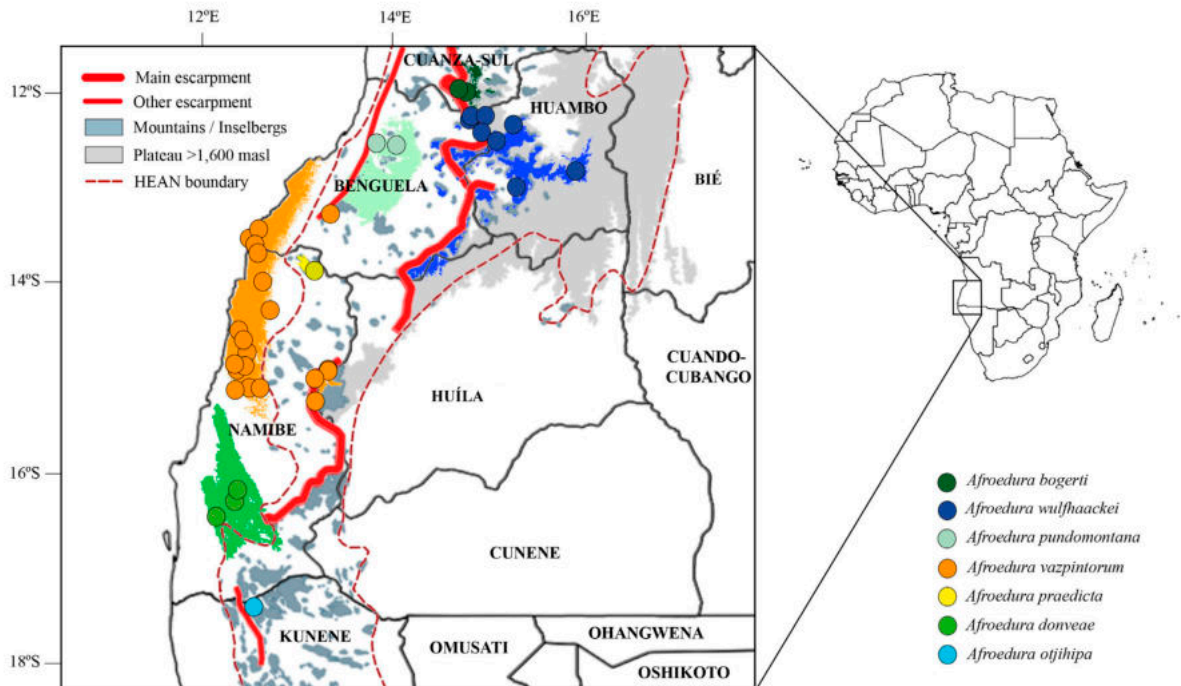


Figure 3: Predicted distributions and known localities of species of African flat geckos in the highlands and escarpments of Angola and Namibia (HEAN). Shaded areas indicate distributions (90% confidence interval based on Maxent predictive mapping, see Conradie *et al.* 2022) and points indicate known localities.

phonolithos. The conservation status of this species has not been assessed. Although it has a very restricted distribution, no plausible threats are known thus it might not trigger any threat status.

***Afroedura vazpintorum* Branch *et al.*, 2021 – coastal flat gecko**

This species is mostly associated with the low-lying (less than 500 masl) coastal semiarid environment of the Angolan Kaokoveld in Namibe and Benguela provinces. However, a possibly isolated highland population occurs on the Humpata Plateau, at elevations of 1,630–2,270 masl. This species has not been assessed for its threat status. It seems common and widely distributed and is probably not threatened.

DISCUSSION

Recent work by Conradie *et al.* (unpublished data) estimated the diversification between the northern and southern groups to have occurred somewhere between the late Pliocene and early Pleistocene (3.57–0.96 mya) based on a coalescent speciation model (stochastic models). Of particular interest is the diversification within the northern group, with *Afroedura bogerti* and *A. wulphaackei* currently represented by scattered populations on isolated mountains at high elevation across the Angolan Planalto, and *A. pundomontana* a bit further west on the escarpment. Although the strict Mt Namba endemic *A. bogerti* occurs in similar habitat and geographical proximity to some populations of

A. wulphaackei, it was found to be genetically closer to the escarpment species present at comparatively lower elevation, *A. pundomontana*. Morphological conservatism between sister taxa, together with habitat and ecological overlap found in this group, support the hypothesis that Angolan *Afroedura* have undergone allopatric speciation (vicariance) in the Angolan Planalto that could be associated with a non-adaptive radiation similar to those reported for other reptile radiations (e.g., Reaney *et al.* 2018). This speciation process could be driven by the substrate-specific character of this genus, leading to isolation during periods of climatological constraints.

On the other hand, the southern group seems to have followed a more complex pattern of speciation, with various populations isolated and specialised in different habitats and one widespread taxon. This is especially true in the case of *A. vazpintorum*, a species which is widespread across the coastal semiarid lowlands but is also present on top of the southern escarpment above 2,000 masl in typical montane environment. Genetic analysis revealed two deeply divergent mitochondrial lineages in *A. vazpintorum*, one exclusive to the southern highlands but the other present both above and below the escarpment (Branch *et al.* 2021, Conradie *et al.* 2022). These findings are consistent with a southern highland origin, followed by subsequent lowland colonisation and a more recent expansion on the coastal plain and secondary contact in the highlands. Although the ecological conditions are very different

on the southern highlands and semiarid coastal plain, various reptiles do occur in both regions including two representatives of the Gekkonidae, *Chondrodactylus fitzsimonsi* (Marques *et al.* 2018) and *Hemidactylus benguellensis* (Lobón-Rovira *et al.* 2021). The origin of remaining southern taxa, namely *A. donveae*, *A. otjihipa* and *A. praedicta*, is best explained by vicariance events but these are challenging to interpret with the available data. It is possible that Pleistocene climatic oscillations periodically promoted the expansion of *Afroedura* populations across the southern lowlands, followed by local extinctions when the climate became too dry, thus conferring a higher resilience on populations isolated on southern highlands and inselbergs; such dynamics may explain the origin and current distribution of southern taxa.

Overall, the speciation patterns found in Angolan *Afroedura* reveal an early split between central and southern highlands, with the former maintaining a close link with the western escarpment and the latter with the semiarid lowlands and various coastal inselbergs such as Serra da Neve or the Otjihipa Mountains. These patterns are likely to be of biogeographic significance, as they are remarkably similar to those observed for other lizards, such as *Cordylus* (Bates *et al.* 2023) and *Hemidactylus* (Lobón-Rovira *et al.* 2021), and for a rupicolous amphibian genus, *Poyntonophrynus* (Baptista *et al.* in review). These results establish the Angolan–Namibian highlands as an important biogeographic feature driving diversification processes in the HEAN, while underlining the Angolan Planalto, the western escarpment and various inselbergs as centres of endemism.

Further research is needed in this poorly known region of Africa. It is noteworthy that although the highlands and escarpments of Angola and Namibia are important for rupicolous species, they fall largely outside the currently designated protected areas and are therefore susceptible to the impacts of ongoing mining operations, human encroachment and related activities. The lack of a conservation strategy for these highlands could compromise the future of relict species and the still unknown diversity they support.

REFERENCES

- Baptista N, Bauer AM, Becker F, Conradie W, Ceriaco LMP (2020) *Afroedura bogerti*. The IUCN red list of threatened species 2020: e.T110186919A110186950. <https://doi.org/10.2305/IUCN.UK.2020-3.RLTS.T110186919A110186950.en>. [Accessed 14 June 2022].
- Baptista NL, Vaz Pinto P, Keates C, Lobón-Rovira J, Edwards E, Rödel M-O (in review) New species of *Poyntonophrynus* (Anura: Bufonidae) reflect poorly studied Angolan endemism centres. *Zookeys*.
- Bates MF, Lobón-Rovira J, Stanley EL, Branch WR, Vaz Pinto P (2023) A new species of green-eyed *Cordylus* Laurenti, 1768 from the west-central highlands of Angola, and the rediscovery of *Cordylus angolensis* (Bocage, 1895) (Squamata: Cordylidae). *Vertebrate Zoology* 73: 599–646. <https://doi.org/10.3897/vz.73.e95639>.
- Bauer AM, Ceriaco LMP, Marques MP, Becker FS (2023) Highland reptiles of southwestern Africa. In: Mendelsohn JM, Huntley BJ, Vaz Pinto P (eds) Monograph on endemism in the highlands and escarpments of Angola and Namibia. *Namibian Journal of Environment* 8: 259–276.
- Branch WR (1998) *Field guide to snakes and other reptiles of southern Africa*, 3rd ed. Struik, Cape Town.
- Branch WR, Guyton JA, Schmitz A, Barej MF, Naskrecki P, Farooq H *et al.* (2017) Description of a new flat gecko (Squamata: Gekkonidae: *Afroedura*) from Mount Gorongosa, Mozambique. *Zootaxa* 4324(1): 142–160. <https://doi.org/10.11646/zootaxa.4324.1.8>.
- Branch WR, Schmitz A, Lobón-Rovira J, Baptista NL, António T, Conradie W (2021) Rock island melody: A revision of the *Afroedura bogerti* Loveridge, 1944 group, with descriptions of four new endemic species from Angola. *Zoosystematics and Evolution* 97(1): 55–82. <https://doi.org/10.3897/zse.97.57202>.
- Busschau T, Conradie W, Daniels SR (2019) Evidence for cryptic diversification in a rupicolous forest-dwelling gecko (Gekkonidae: *Afroedura pondolia*) from a biodiversity hotspot. *Molecular Phylogenetics and Evolution* 139: 106549. <https://doi.org/10.1016/j.ympev.2019.106549>.
- Conradie W, Schmitz A, Lobón-Rovira J, Becker FS, Pinto PV, Hauptfleisch ML (2022) Rock island melody remastered: two new species in the *Afroedura bogerti* Loveridge, 1944 group from Angola and Namibia. *Zoosystematics and Evolution* 98(2): 435–453.
- Jacobsen NHG, Kuhn AL, Kuhn AL, Jackman TR, Bauer AM (2014) A phylogenetic analysis of the southern African gecko genus *Afroedura* Loveridge (Squamata: Gekkonidae), with the description of nine new species from Limpopo and Mpumalanga provinces of South Africa. *Zootaxa* 3846(4): 451. <https://doi.org/10.11646/zootaxa.3846.4.1>.
- Lobón-Rovira J, Conradie W, Iglesias DB, Ernst R, Verissimo L, Baptista N, Pinto PV (2021) Between sand, rocks and branches: an integrative taxonomic revision of Angolan *Hemidactylus* Goldfuss, 1820, with description of four new species. *Vertebrate Zoology* 71: 465–501. <https://doi.org/10.3897/vz.71.e64781>.
- Makhubo BG, Tolley KA, Bates MF (2015) Molecular phylogeny of the *Afroedura nivaria* (Reptilia: Gekkonidae) species complex in South Africa provides insight on cryptic speciation. *Molecular Phylogenetics and Evolution* 82: 31–42. <https://doi.org/10.1016/j.ympev.2014.09.025>.
- Marques MP, Ceriaco LMP, Blackburn DC, Bauer AM (2018) Diversity and distribution of the amphibians and terrestrial reptiles of Angola: atlas of historical and bibliographic records (1840–2017). *Proceedings of the California Academy of Sciences* 65(Suppl II): 1–501.
- Nicolau GK, Edwards S, Conradie W (2023) Hiding in the cracks: phylogenetics of the genus *Afroedura* (Squamata: Gekkonidae) in the Eastern Cape Province, South Africa. 15th Conference of the Herpetological Association of Africa, 16–19 January 2023, Hoedspruit, South Africa.
- Reaney AM, Saldarriaga-Córdoba M, Pincheira-Donoso D (2018) Macroevolutionary diversification with limited niche disparity in a species-rich lineage of cold-climate lizards. *BMC Evolutionary Biology* 18(1): 16. <https://doi.org/10.1186/s12862-018-1133-1>.