



Molecular analysis confirms *Agama picticauda* invasion on Western Indian Ocean islands

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Abstract The Western Indian Ocean biodiversity hotspot hosts a remarkable array of endemic species, but invasive alien species increasingly threaten its unique ecosystems. Lizards of the West African *Agama agama* species group are successful colonizers, with recent introductions to Grande Comore (Comoros Archipelago) and Reunion Island. Systematic revisions within the native range of the *A. agama* species group have left many of the introduced populations without clear identity. We used molecular

methods to determine the identities of the *Agama* species introduced to Grande Comore and Reunion Island, define their respective likely origin, and assess body size characteristics for each island population. We identified *Agama picticauda* as the species present on both islands with likely origins in two distinct Western African regions. Agamas from Reunion Island had longer and wider heads with greater body weight than Grande Comore individuals. Sexual size dimorphism on both islands was driven by weight, with males being heavier than females. We provide foundations for further research on the ecology and impacts of *A. picticauda* on Western Indian Ocean

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islands and to aid in the development of targeted management strategies for controlling this invasive reptile.

Keywords Body size · Comoros · Invasive alien species · Phylogenetics · Range expansion · Reunion Island

Introduction

The unique biodiversity of islands faces substantial threats from invasive alien-species (IAS) introductions (Fernández-Palacios et al. 2021). Island biota often evolve in isolation, making them particularly vulnerable to non-native species, that can outcompete, prey on, or introduce diseases to native species (Myers et al. 2000). The cumulative impact of these invasions can disrupt ecological processes, reduce biodiversity, and lead to the collapse of native ecosystems, making IAS one of the leading causes of species extinction on islands (Fernández-Palacios et al. 2021). Increased international trade and human movement have accelerated the spread of IAS over the recent past, causing IAS records to rise exponentially worldwide (Mormul et al. 2022). IAS management is critical for preserving native biodiversity, protecting ecosystem integrity, and maintaining ecological balance, but relies on detailed knowledge of invasive-species biology and behaviour. Precise species identification is therefore crucial for understanding introduction pathways and specific threats as well as developing targeted, effective management actions.

Lizards of the West African *Agama agama* species group are successful colonizers that greatly profit from globalisation. Introductions have been recorded to many areas around the world, including numerous island nations (Kraus 2009; Wagner et al. 2012), and further spread is expected (van den Burg et al. 2024). However, recent systematic revision within the native range of the *A. agama* species group have left many

of these introduced populations without clear identity (Mediannikov et al. 2012; Leaché et al. 2014, 2017; Nuñez et al. 2016), which also affects populations on the islands in the Western Indian Ocean. In the Comoros Archipelago, the introduction to Grande Comore most likely dates to 1998 (Meirte 2004) with a likely introduction pathway through parcel service (Wagner et al. 2009). The Grande Comore population was originally referred to as *A. agama*, but it exhibits a relatively small adult body size compared to other continental *A. agama* populations, warranting further investigation of its identity (Wagner et al. 2009). On Reunion Island, the first individuals were recorded in 1995 at the main maritime port area, introduced through container shipments (Guillermot et al. 1998). The taxon was initially identified as *A. agama* (Guillermot et al. 1998) and later assigned to the subspecies *A. a. africana* (Probst et al. 2002). Given the rapid spread of agamas on these two islands (Nature Océan Indien 2023; KC Webster pers obs) and the threat they pose to the islands' unique biodiversity, population assessments have become increasingly urgent. Here, we use molecular analysis to determine *Agama* species identity on Grande Comore and Reunion Island, identify their places of origin, and assess morphological differences between the two island populations.

Materials and methods

Field sampling

Sampling of *Agama* spp. on Grande Comore and Reunion Island was conducted in June to August 2022 (Fig. 1). The lizards were captured by hand using lasso noosing or modified versions of commercially available mammal glue traps. Body measurements were taken using callipers for head dimensions (to the nearest 0.01 mm), rulers for snout-vent length (to the nearest 1 mm) and Pesola scales for weight (to the nearest 0.5 g). Due to the non-native and invasive status of agamas, all captured individuals were chemically euthanised using either an overdose of Tricaine Methanesulfonate (MS222) injected into the abdomen or an overdose of Lidocaine applied to the mouth. Mechanical euthanasia was also implemented on Grand Comore, which combined decapitation and blunt force trauma

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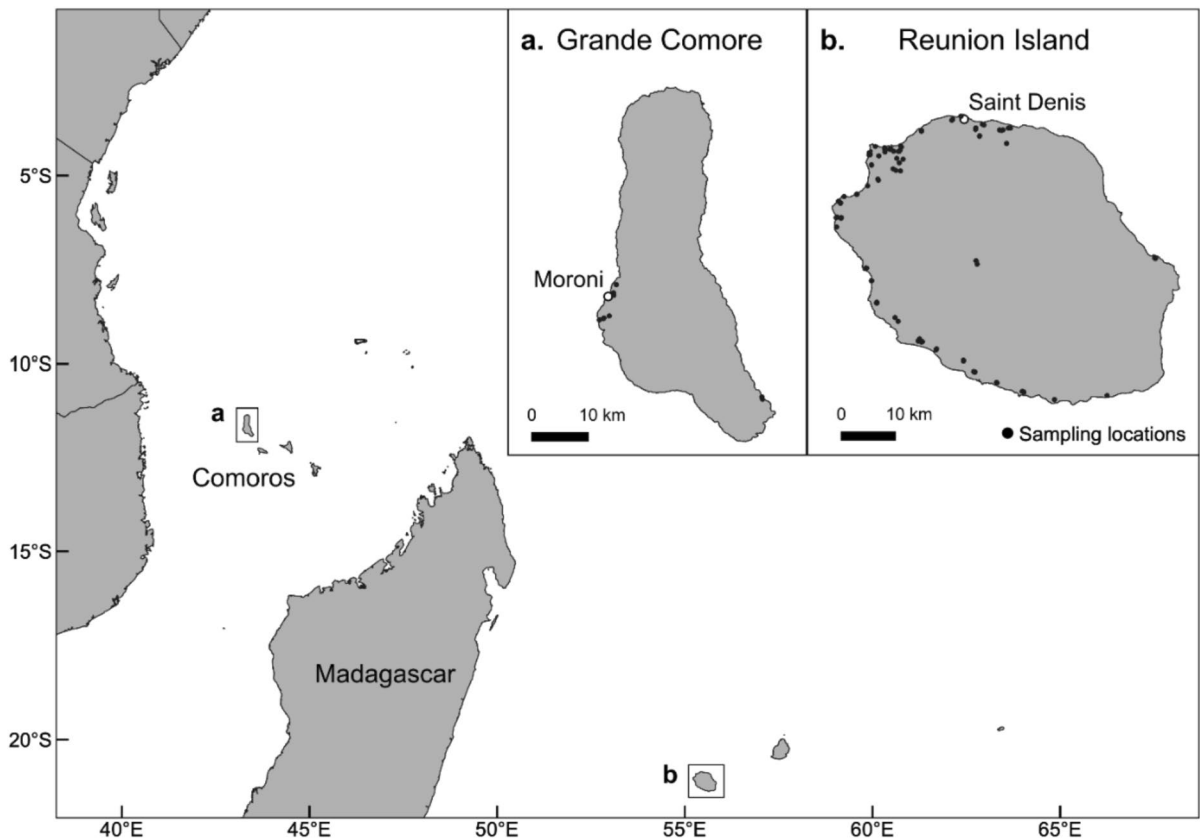


Fig. 1 Sampling locations of *Agama* spp. for molecular dataset on a) Grande Comore and b) Reunion Island in the Western Indian Ocean. Capital cities are labelled

applied to the head to destroy the central nervous system. Sex was determined by examining the presence of femoral pores and hemipenial bulges and confirmed through dissection to identify reproductive organs. Gravid females were recorded, and the number of eggs counted. A tail or tongue muscle tissue sample was collected from each individual and stored in 95% ethanol at room temperature until DNA extraction. We sampled 218 *Agama* spp. for the molecular analysis, consisting of 31 individuals from Grande Comore and 187 individuals from Reunion Island. Supplemental tissue samples from the same individuals were deposited at the Museum of Southwestern Biology, Albuquerque, New Mexico, USA. Additional data on morphological traits were collected from 21 females and 24 males in Grande Comore during June 2024 fieldwork and are included in the morphological analysis.

Molecular analysis

Out of 218 samples, we successfully sequenced 206 *Agama* vouchers from Grande Comore and Reunion Island. We used the fast-evolving 16S rRNA gene with its hypervariable regions, which perfectly resolves the different species within this genus (Mediannikov et al. 2012; Leaché et al. 2014). For comparisons, we combined our newly sequenced mitochondrial 16S data with previously published sequences from GenBank (Leaché et al. 2014). Total genomic DNA was extracted from tissue samples using the E.Z.N.A. Tissue DNA Kit (VWR/Omega BioTek) 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 are deposited in GenBank (Supplementary Information Table S1).

DNA sequences were aligned using the original chromatograph data in the programme Geneious Prime (version 2024.0.5; <https://www.geneious.com>) and manual corrections as well as follow-up direct sequence comparisons were done with the program BioEdit (Hall 1999). We sequenced 507 bp of the 16S rRNA gene, including some fast-evolving, indel-rich loop regions for each voucher that could be unambiguously aligned. We used MEGA11 (Tamura et al. 2021) to calculate the uncorrected genetic distances within and between the different geographic clades using the “between group mean” and the “within group mean” distance analyses with the pairwise deletion option set for each analysis. Phylogenetic analysis was conducted using Bayesian Inference (BI) methods. The BI analysis was conducted with MrBayes version 3.2.6 using the TrN+I+G model with 10 million generations, sampling every 1000 generations, with the first 25% of samples discarded as burn-in. The best-fit model of sequence evolution for the Bayesian analysis was selected using jModel-test v.2.1.7 (Darriba et al. 2012) using the Bayesian Information Criterion (BIC). We used *Pseudotrapelus sinaitus* (GenBank accession number KU097432) as an outgroup.

Morphological analysis

In the absence of prior data for these populations, we defined the adult size threshold based on the smallest gravid female measured in our dataset (SVL = 82.4 mm). To avoid skewed data, we removed all non-adults (juveniles and subadults, n = 53) from the analysis. Furthermore, adults with missing data (n = 7) were also excluded, resulting in a final morphological dataset of 203 *Agama*, comprising of 61 and 142 individuals from Grande Comore and Reunion Island, respectively. We used principal component analysis (PCA) to explore differences between islands and sexes in three morphological traits adjusted for body size, defined as snout-vent length (SVL). These were head length (HL), head width (HW), and body weight (Weight). Morphological traits often scale differently by body size in males and females and between populations (Balakrishna et al. 2021). Therefore, we adjusted morphological variables to remove the effect of size by transforming each variable as

$$Z = Y_i(\overline{SVL}/SVL_i)^b$$

following Villamil et. Al. (2017). Z represents the transformed value of the variable Y, which is the variable affected by size. The exponent b is the slope of the linear regression between log(Y) and log(SVL). The transformation scales individuals to the same size and adjusts their shape according to allometry (Lleonart et al. 2000). To check that no size effect persisted after transformation, a student’s t-test was used to evaluate slopes of linear regression between each transformed variable and SVL. Under a successful size correction, a slope of zero is expected.

PCA was performed on the scaled values and Euclidean distance matrix using the vegan package version 2.6–6.1 unconstrained redundancy analysis (Okanasen et al. 2018). We performed permutational multivariate analysis of variance (PERMANOVA) based on the Euclidean distance matrix to identify differences in morphological traits between islands and sexes. All analyses were run in R 4.3.1 (R Core Team 2023).

Results

Molecular analysis

Our phylogenetic analysis, which included all 206 newly generated sequences (see Supplementary Information Table S1), consistently placed all sampled individuals from Grande Comore and Reunion Islands within the clade corresponding to *A. picticauda* (Fig. 2). This clustering of our new vouchers with reference sequences of *A. picticauda* from other geographic regions was strongly supported by high posterior probabilities (BI), thus verifying that all individuals from Grande Comore and Reunion Island are *Agama picticauda*. Also, subsequent manual comparison of the alignment and the different haplotypes within *A. picticauda* showed that consistent variation exists between different populations: we found well separated sub-clades within *A. picticauda* with a principal separation between West African- and Central African populations and another less-pronounced split within the West Africa Ghana grouping (1.26%). The *A. picticauda* individuals from Grande Comore nearly all shared a single haplotype,

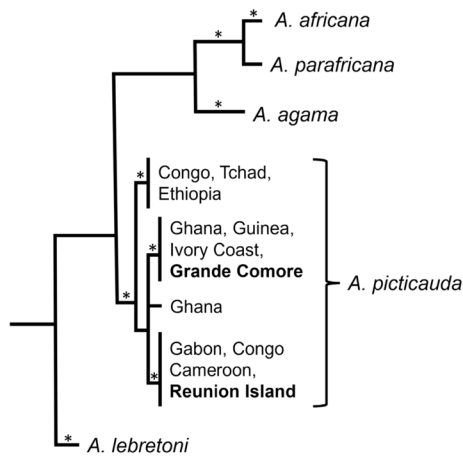


Fig. 2 Evolutionary relationships of introduced populations of *Agama* using Bayesian analyses and a reference dataset of Leaché et al. (2014). The nodes marked with an asterisk (*) show significant support values (≥ 0.95)

with only 4 individuals showing a single-point mutation each. The same situation was true for the individuals from Reunion Island, with nearly all sharing the same haplotype, and with only a few isolated single-point mutations in a few of the specimens. In contrast, based on our MEGA11 distance analyses we found a divergence of 1.29% between the haplotypes from the two islands (Table 1). The Grande Comore haplotypes fell into the West African clade, whereas the Reunion Island haplotypes fell into the Central Africa clade, supporting a likely different origin of both populations. Our phylogenetic comparison with published reference sequences of *A. picticauda* from different West African countries (Fig. 2) indicate that the origin of the Grande Comore *A. picticauda* likely lies in the region of Ivory Coast, Ghana and Guinea, whereas the origin of the Reunion Island individuals likely lies in the region of Cameroon, Congo and Gabon.

Table 1 Estimates of evolutionary divergence over sequence pairs between groups

	Outgroup	Reunion Island	Grande Comore	Central Africa	West Africa
Outgroup	–	0.0399	0.0444	0.0419	0.0432
Reunion Island	0.0006	–	0.0129	0.0003	0.0096
Grande Comore	0.0006		–	0.0138	0.0072
Central Africa	0.0000			–	0.0098
West Africa	0.0071				–

Morphological analysis

The final morphological dataset consisted of 108 females and 95 males. Descriptive statistics of morphological data are summarised in Supplementary Information Table S2. Variation in body size-adjusted morphological traits was mostly accounted for in the first two principal components. The first two axes of the PCA explained 79.8% of the variance in the dataset (Fig. 3), with axis 1 capturing the geographical variation between the Grande Comore population and the Reunion Island population, and axis 2 capturing the variation between sexes mainly for the Reunion Island population. *Agama picticauda* specimens from Reunion Island were overall larger than Grande Comore individuals, with longer and wider heads and greater mass ($F_{1,199} = 65.90$, $p < 0.001$). For the two populations combined sexual size dimorphism was pronounced in weight, with males being heavier than females ($F_{1,199} = 44.61$, $p < 0.001$). This pattern was consistent for each island population (Grande Comore: $F_{1,59} = 12.59$, $p < 0.001$; Reunion Island: $F_{1,140} = 27.32$, $p < 0.001$).

Discussion

Our molecular analysis identified *Agama picticauda* as the *Agama* species present on Grande Comore and Reunion Island. Aligning with previous data from Leaché et al. (2014), the Grande Comore population likely originated from the Ivory Coast/Ghana/Guinea region, whereas the Reunion Island population likely originated from the Cameroon/Congo/Gabon region, confirming independent introductions to these two islands. We found no variation within the sampled individuals of both islands, pointing to a single introduction event or possibly multiple introductions from a small source population.

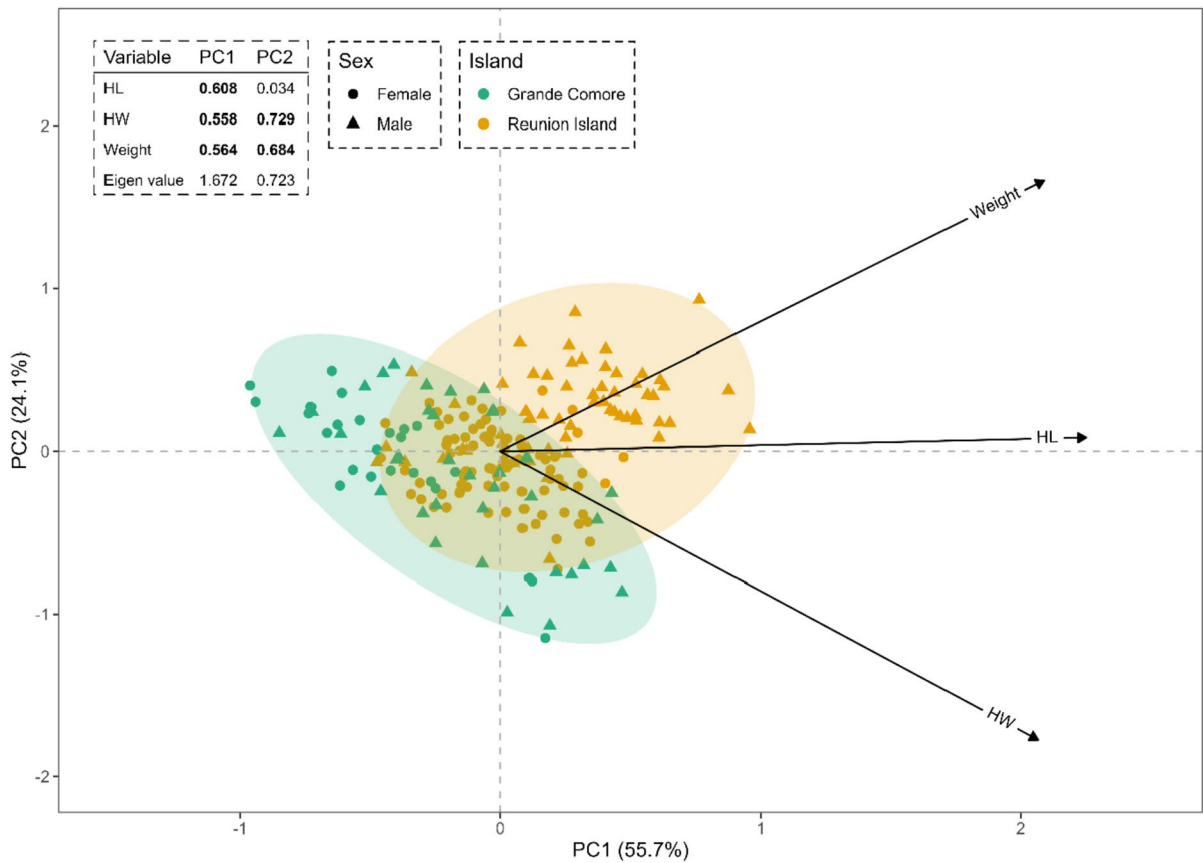


Fig. 3 Results from principal component analysis (PCA) of the relationships of body-size adjusted morphological traits between islands and sex in *Agama picticauda* as described by the first two principal components. Points represent individuals, with color depicting the island and shape depicting the sex. Black arrows represent the strength (arrow length) and direc-

tion of the variables. Ellipses represent 1 *SD* from the centroid of each island group. The inset shows principal components and factor scores (unrotated). Morphological traits (factors) with an eigen value of greater than ± 0.4 are in bold. HL = head length, HW = head width

Florida holds the first reported introduction of *Agama* spp. Outside of their native range in 1976 (Nuñez et al. 2016). Molecular analysis identified Florida's population as *A. picticauda* with four haplotypes originating in the broad region of Western Africa, indicating several independent introductions, most likely through released individuals from the pet trade (Nuñez et al. 2016). Anecdotal evidence suggests the Grande Comore population might have been founded by released pets as well; however, accidental introduction through commercial transport of goods is more likely (Wagner et al. 2009). On Reunion Island, the first individuals were found in the main maritime port area where container shipments arrive regularly from western Africa, indicating their introduction via

trade (Guillermet et al. 1998). Our results underscore the necessity of managing trade-related IAS risks and emphasize the importance of implementing biosecurity measures, including stricter pre-border and border policies and controls.

Morphological differences between the island populations are pronounced, with Reunion Island individuals being overall larger, with longer and wider heads and greater weight compared to Grande Comore individuals, thus confirming previously found relatively small adult sizes on Grande Comore (Wagner et al. 2009). Interestingly, individuals from Ghana, a possible country of origin for the Grande Comore population, display larger mean SVL in both, females and males than does the Grande Comore population

(Supplementary Information Table S2, Krishnan et al. 2019). *Agama picticauda* exhibits sexual size dimorphism with females smaller than males (van den Burg et al. 2024), which we also observed in our island populations. Our findings provide a foundation for further research on the biology and ecology of these two *A. picticauda* populations so as to elucidate their evolution and adaptations, and assess the colonization risk posed by these continental invaders.

Agama picticauda is known to be aggressively territorial (Yeboah 1982) and prey on a variety of arthropods and reptiles (Henigan et al. 2019; Ofori et al. 2023), presenting a possible threat to the unique biodiversity on both islands. In particular, *Oplurus cuvieri comorensis* an endemic lizard of conservation concern on Grande Comore is predicted to be negatively impacted by the spread of *A. picticauda* through predation and habitat competition (Hawllitschek et al. 2011; Vences and Hawllitschek 2011). On Reunion Island, *A. picticauda* has rapidly spread across all coastal areas, and the first stable, reproducing populations at higher elevation were recorded as of 2022 (Cilaos, 1200 m asl.; Nature Océan Indien 2023). The Critically Endangered *Phelsuma inexpectata* on Reunion Island relies heavily on urban gardens for habitat (Sanchez 2021), and the spread of *A. picticauda* could possibly drive these small, fragmented gecko populations to extinction through predation and possible disease transmission. Research is urgently needed to assess the impacts of *A. picticauda* on the biodiversity of both islands, which remain unquantified.

Despite the high number of invasions of alien reptiles on islands (Capinha et al. 2017), efforts to eradicate established populations remain limited (Spatz et al. 2022). From Reunion Island, *A. picticauda* could potentially invade Mauritius, while its presence on Grande Comore risks spreading to neighbouring islands in the Comoros archipelago. On Reunion Island, an Invasive Species Strategy and Action Plan for *A. picticauda* has been established through a collaborative effort between governmental and non-governmental organisations to mitigate the spread and associated risks of this invasive reptile (Nature Océan Indien 2023). Similar initiatives are urgently needed in the Comoros. Overall, biosecurity across the Western Indian Ocean islands must be strengthened through improved regulations, stricter quarantine protocols, enhanced monitoring, the

development of effective control tools, and capacity-building and awareness initiatives.

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Author contributions All authors contributed to the study conception and design. Data collection was performed by Markus A. Roesch, Kathleen C. Webster, Nicolas Huet, Oliver Hawllitschek, Youssef Mohamed, Sohan Sauroy-Toucouère. Data analysis was performed by Markus A. Roesch, Andreas Schmitz. The first draft of the manuscript was written by Markus A. Roesch and Andreas Schmitz. All authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Declarations

Conflict of interest The authors have no competing interests to disclose.

Ethical approval Animal capture, handling and euthanasia was performed under order no. 2023-605 SG/SCOPP/BCPE in accordance with article L411.8 of the Environment Code on the territory of Reunion Island. Research activities on Grand Comore and export of samples were permitted by the Centre national de documentation et de recherche scientifique in Moroni, Grand Comore following animal processing methods approved by the University of New Mexico Institutional Animal Care and Use Committee in protocol ##22-201298-MC. Access and benefit-sharing was approved in accordance with Article 17, paragraph 2, of the Nagoya Protocol and accessible under the reference number TREL2206915S/624.

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References

- Balakrishna S, Amdekar MS, Thaker M (2021) Morphological divergence, tail loss, and predation risk in urban lizards. *Urban Ecosyst* 24(6):1391–1398. <https://doi.org/10.1007/s11252-021-01122-6>
- Capinha C, Seebens H, Cassey P et al (2017) Diversity, biogeography and the global flows of alien amphibians and reptiles. *Divers Distrib* 23(11):1313–1322. <https://doi.org/10.1111/ddi.12617>
- Darriba D, Taboada GL, Doallo R, Posada D (2012) jModel-Test 2: more models, new heuristics and parallel computing. *Nat Methods* 9:1–772. <https://doi.org/10.1038/nmeth.2109>
- Fernández-Palacios JM, Kreft H, Irl SD et al (2021) Scientists' warning—The outstanding biodiversity of islands is in peril. *Glob Ecol Conserv* 31:e01847. <https://doi.org/10.1016/j.gecco.2021.e01847>
- Guillemet C, Couteyen S, Probst JM (1998) Une nouvelle espèce de reptile naturalisée à La Réunion, l'Agame des colons *Agama agama* (Linnaeus). *Bull Phaethon* 8:67–69
- Hall TA (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symp* 41:95–98
- Hawlitshchek O, Brückmann B, Berger J, Green K, Glaw F (2011) Integrating field surveys and remote sensing data to study distribution, habitat use and conservation status of the herpetofauna of the Comoro Islands. *Zookeys* 144:21–78. <https://doi.org/10.3897/zookeys.144.1648>
- Henigan LE, Blais CR, Dzikowski NT, Romagosa CM, Claunch NM (2019) *Agama picticauda* (Peters's Rock Agama). *Cannibalism Nat History Notes Herpetol Rev* 50:132–133
- Kraus F (2009) Alien reptiles and amphibians: a scientific compendium and analysis. Springer, Netherlands, Dordrecht. <https://doi.org/10.1007/978-1-4020-8946-6>
- Krishnan S, Ofori-Boateng C, Fujita MK, Leaché AD (2019) Geographic variation in West African *Agama picticauda*: insights from genetics, morphology and ecology. *Afr J Herpetol* 68(1):33–49. <https://doi.org/10.1080/21564574.2018.1509139>
- Leaché AD, Wagner P, Linkem CW et al (2014) A hybrid phylogenetic–phylogenomic approach for species tree estimation in African *Agama* lizards with applications to biogeography, character evolution, and diversification. *Mol Phylogenet Evol* 79:215–230. <https://doi.org/10.1016/j.ympev.2014.06.013>
- Leaché AD, Grummer JA, Miller M et al (2017) Bayesian inference of species diffusion in the West African *Agama agama* species group (Reptilia, Agamidae). *Syst Biodivers* 15(3):192–203. <https://doi.org/10.1080/14772000.2016.1238018>
- Lleonart J, Salat J, Torres GJ (2000) Removing allometric effects of body size in morphological analysis. *J Theor Biol* 205(1):85–93. <https://doi.org/10.1006/jtbi.2000.2043>
- Mediannikov O, Trape S, Trape JF (2012) A molecular study of the genus *Agama* (*Squamata Agamidae*) in West Africa, with description of two new species and a review of the taxonomy, geographic distribution, and ecology of currently recognized species. *Russ J Herpetol* 19(2):115–142
- Meirte D (2004) Les Reptiles. In: M. Louette, M., Meirte, D., Jocque, R. (ed) *La faune terrestre de l'Archipel des Comores*, Musée royal de l'Afrique centrale, Tervuren, Belgium, pp. 209–210.
- Mormul RP, Vieira DS, Bailly D et al (2022) Invasive alien species records are exponentially rising across the Earth. *Biol Invasions* 24(10):3249–3261. <https://doi.org/10.1007/s10530-022-02843-1>
- Myers JH, Simberloff D, Kuris AM, Carey JR (2000) Eradication revisited: dealing with exotic species. *Trends Ecol Evol* 15(8):316–320. [https://doi.org/10.1016/S0169-5347\(00\)01914-5](https://doi.org/10.1016/S0169-5347(00)01914-5)
- Nature Océan Indien (2023) Plan Opérationnel de Lutte contre l'Agame des roches à La Réunion. 2024 - 2028. Éd. Chloé Bernet, Steven Calesse, Sébastien Dervin, Marion Neymeyer, Markus Roesch & Jérémie Souchet. Association Nature Océan Indien pour l'Office Français de la Biodiversité et le Département de La Réunion. 58 pp + annexes.
- Núñez LP, Krysko KL, Avery ML (2016) Confirmation of introduced *Agama picticauda* in Florida based on molecular analyses. *Bull Florida Museum Nat Hist* 54:138–146
- Ofori BY, Martey P, Anderson RS et al (2023) The costs of living in the city: influence of urbanization on the trophic niche and body condition of the African rainbow lizard *Agama picticauda*. *Eur J Wildl Res* 69(6):114. <https://doi.org/10.1007/s10344-023-01743-6>
- Okanagan J, Blanchet FG, Friendly M, et al (2018) vegan: Community Ecology Package (2.5- 3).
- Probst JM, Abhaya K, Turpin A, Deso G (2002) Détermination de la sous-espèce d'Agame des colons *Agama agama* récemment naturalisée à La Réunion. *Bull Phaethon* 15:48
- R Core Team (2023) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Sanchez M (2021) *Phelsuma inexpectata*. The IUCN Red List of Threatened Species 2021: e.T17450049A17450059. <https://doi.org/10.2305/IUCN.UK.2021-2.RLTS.T17450049A17450059.en>
- Schmitz A, Brandley MC, Mausfeld P et al (2005) Opening the black box: phylogenetics and morphological evolution of the Malagasy fossorial lizards of the subfamily “Scincinae.” *Mol Phylogenet Evol* 34:118–133. <https://doi.org/10.1016/j.ympev.2004.08.016>
- Spatz DR, Holmes ND, Will DJ et al (2022) The global contribution of invasive vertebrate eradication as a key island

- restoration tool. *Sci Rep* 12(1):13391. <https://doi.org/10.1038/s41598-022-14982-5>
- Tamura A, Stecher G, Kumar S (2021) MEGA11: molecular evolutionary genetics analysis version 11. *Mol Phylogenet Evol* 38:3022–3027. <https://doi.org/10.1093/molbev/msab120>
- van den Burg MP, Wasilewski JA, Thorpe RS et al (2024) The threat of Peters's Rock Agama (*Agama picticauda*) to reptile diversity across the Lesser Antilles. *Anim Conserv* 27(1):1–4. <https://doi.org/10.1111/acv.12889>
- Vences M, Hawlitschek O (2011) *Oplurus cuvieri*. The IUCN Red List of Threatened Species. 2011: e.T172763A6913310. <https://doi.org/10.2305/IUCN.UK.2011-2.RLTS.T172763A6913310.en>
- Villamil J, Camargo A, Maneyro R (2017) Morphological variation and sexual dimorphism in *Liolaemus wiegmanni* (Duméril & Bibron, 1837) (Squamata Liolaemidae) from Uruguay. *Acta Herpetol.* https://doi.org/10.13128/Acta_Herpetol-18188
- Wagner P, Glaw F, Glaw K, Böhme W (2009) Studies on African Agama IV: first record of *Agama agama* (Sauria: Agamidae) from Madagascar and identity of the alien population on Grande Comore Island. *Herpetol Notes* 2:73–77
- Wagner P, Bauer AM, Wilms TM, Barts M, Böhme W (2012) Miscellanea accrodontia: notes on nomenclature, taxonomy and distribution. *Russ J Herpetol* 19(2):177–189
- Yeboah S (1982) Observations on territory of the rainbow lizard *Agama agama*. *African J Ecol* 20(3):187–192. <https://doi.org/10.1111/j.1365-2028.1982.tb00289.x>

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