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Is morphological-based taxonomy still effective in modern times? A response to Parrinha et al. (2025)

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Abstract. We reevaluate the recent species description of *Holaspis ngalangi* from Angola by Parrinha et al. (2025), which was based solely on variable morphological characters, through comparative analysis of specimens across the genus' range, including material previously examined but not reported by the original authors. Our analysis demonstrates that the proposed diagnostic traits of this species (precloacal scale morphology and ventral scale arrangement) are hypervariable within both *H. guentheri* and *H. laevis*, showing neither biogeographic nor morphological consistency. Notably, specimens from Angola's Dundo Museum, though examined by Parrinha et al. (2025), were omitted from their analysis despite exhibiting the same variable characteristics, strongly indicating these represent intraspecific variation rather than diagnostic species-lineage features. Consequently, we formally place *Holaspis ngalangi* Parrinha, Marques, Gonçalves, Tuitenko, Bauer & Ceríaco, 2025 as a junior synonym of *Holaspis guentheri* Gray, 1863, representing the second recent case of an Angolan reptile species description based solely on morphological data being synonymised within the last decade. These repeated cases highlight the inherent risks of morphology-only taxonomy, particularly when: (1) diagnostic characters show extensive overlap among taxa, and (2) multiple lines of evidence are not incorporated. Our findings also emphasize the critical need for robust, integrative species delimitation approaches in understudied regions like Angola, where high levels of cryptic diversity and phenotypic plasticity are likely to complicate taxonomic assessments.

Key words. Squamata, Lacertidae, *Holaspis*, integrative taxonomy, intraspecific variation, synonymy, Angola, good practice.

Introduction

The ongoing global biodiversity crisis has underscored the critical importance of accurately understanding global biological diversity. Notably, numerous studies have demonstrated that taxonomic identification provides a fundamental baseline for a wide range of scientific endeavours, including molecular and morphological research (e.g., Lis & Lis 2011), biogeographic and evolutionary studies (e.g., Falaschi et al. 2023, Luedtke et al. 2023), and, perhaps most crucially, the development and implementation of effective conservation strategies (e.g., Ebach 2011, Gascon et al. 2015, Lien et al. 2023). Without reliable taxonomy, efforts to assess species richness, track biodiversity loss, or prioritize conservation actions are severely compromised. Therefore, the description of species remains a cornerstone of biological sciences. Equally important is the identification and mitigation of taxonomic inflation, which can distort our understanding of biodiversity patterns and misguide resource allocation in conservation planning (Raposo et al. 2021, Lien et al. 2023).

In this context, the use of morphology-only taxonomy to describe species, here understood as the branch of traditional taxonomy that relies solely on morphological data as the unique source of evidence for making taxonomic decisions (i.e., naming, describing, and classifying

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organisms), has become a central topic of debate among taxonomists in the current molecular era, as they might overlook the intrinsic aspects of phenotypic diversity and/or the plasticity of the species (Alroy 2002, Fritz et al. 2007, Deichmann et al. 2017). Over the past century, advances in molecular techniques have revolutionized species delimitation, providing powerful tools for uncovering cryptic diversity and resolving complex taxonomic groups. Among these innovations are techniques such as museomics (i.e., the use of ancient DNA from historical specimens; e.g., McGuire et al. 2018, Raxworthy & Smith 2021, Zacho et al. 2021, Lalueza-Fox 2022), which have enabled molecular access to previously inaccessible, century-old material from natural history collections. As a result, traditional morphology-based approaches have come under increased scrutiny. Nevertheless, accurate morphology-based identification remains significantly important, emphasizing that it forms a critical foundation for any molecular studies (Lis & Lis 2011) and remains indispensable for practical taxonomy, particularly in regions or taxa where molecular data are sparse or unavailable (Lobón-Rovira et al. 2022, 2025).

Thus, in this new molecular era, "traditional taxonomy" has been relegated by most authors as a preliminary morphology-based identification in species inventories or for comparative morphological analyses, pending further validation. In this context, numerous researchers and scientific journals have argued that morphological data alone is insufficient for formal taxonomic decisions, particularly species descriptions. Thus, there is growing consensus that species delimitation should adopt an integrative approach, incorporating multiple lines of evidence (e.g., morphological, molecular, ecological, and behavioural data; de Queiroz 2007, Padial et al. 2010, Tolley et al. 2022) to make taxonomic decisions.

Recently, a new species of sawtail or gliding lizard, genus *Holaspis* Gray, 1863 (namely *Holaspis ngalangi*) was described from Angola based solely on morphological data (Parrinha et al. 2025). However, the absence of molecular, biogeographic, and detailed morphometric analyses has raised concerns, prompting this reevaluation. Until the species description by Parrinha et al. (2025), the genus *Holaspis* was considered to comprise two widely distributed species: *H. guentheri* Gray, 1863, and *H. laevis* Werner, 1896. While *H. laevis* is mostly restricted to the east of the Eastern Arc Rift System (occurring in Malawi, Mozambique, Kenya, and Tanzania) (Spawls et al. 2018) but also reported from Katanga in the Democratic Republic of Congo (de Witte 1933), *H. guentheri* is vastly distributed across Central Africa and extending westward into West Africa (Trape et al. 2012). These two species are easily distinguished based on the dorsal scalation arrangement and coloration: *Holaspis guentheri* has a pair of whitish or bluish dorsolateral stripes and two paravertebral stripes confined to most of the vertebral plates, while *H. laevis* lacks dorsolateral stripes (only paravertebral and lateral stripes) and the two paravertebral stripes are confined to the outer edges of the vertebral plates.

Holaspis guentheri was described based on a specimen sent by Andrew Smith to the British Museum of Natural History (BMNH, now the Natural History Museum of London), without any precise locality, which challenges any taxonomic treatment regarding this group due to its wide distribution. Nevertheless, Parrinha et al. (2025) described *H. ngalangi* as a putative sister species to *H. guentheri*, endemic to the Caconda region, Huíla Province, Angola, based on a single morphological difference between two Caconda specimens and the type material of *H. guentheri*. However, although the authors claimed to have examined "in person or through high resolution photographs" 210 *Holaspis* specimens from across its range, they provided no further details about this material, neither in the diagnosis, nor in subsequent comparisons in the species description. Furthermore, in their description, Parrinha et al. (2025) present an inadequately detailed comparative diagnosis with other *H. guentheri* material across its range, a particularly critical issue given this species' unknown type locality. Of particular concern was the lack of detailed comparison between *H. ngalangi* and other Angolan specimens that the authors assigned to *H. guentheri* (Parrinha et al. 2025: Supplementary Material 1, Ceríaco et al. 2020), including material collected from similar habitats (fide Laurent 1964: 56). However, a recent visit to the Dundo Museum by the authors of this work, and subsequent examination of available Angolan material revealed inconsistencies in the species description of *H. ngalangi*, which has motivated this work.

Material and methods

For this work we examined the characters detailed in the description of *H. ngalangi* (Parrinha et al. 2025), including examination of its holotype (BMNH 1906.8.24.57) and paratype (BMNH 1906.8.24.56), both collected at Caconda, Huila Province, Angola. Furthermore, we used the diagnostic characters used to describe *H. ngalangi* (Parrinha et al. 2025) and compared the types with additional specimens from Angola deposited at the Dundo Museum (MD), collected from Alto Cuilo and Alto Chicapa in northeastern Angola, localities with similar habitats (fide Laurent 1964: 56), as well as selected material from neighbouring regions of the Democratic Republic of the Congo (hereafter DRC) deposited at the Museum of Central Africa (RMCA), Belgium, and additional material from Cameroon, Gabon and Republic of Central Africa from the Port Elizabeth Museum (PEM), South Africa (Fig. 1). In total, we examined 32 specimens (5 from Angola, 1 from Cameroon, 23 from DRC, 2 from Gabon, and 1 from Republic of Central Africa), following the methodology outlined by Parrinha et al. (2025) who had already examined some of this material mentioned. The material examined by us is detailed in Table S1. Photographs of RMCA material here examined are available at the RMCA virtual repository (https://virtualcol.africamuseum.be/providence/pawtucket/index.php/MultiSearch/Index?search=holaspis).

Results

Detailed examination of *H. guentheri* and *H. laevis* specimens from across their range consistently confirmed the diagnostic features distinguishing these two species, particularly the presence of dorsolateral stripes present in *H. guentheri* versus respective absence in *H. laevis* (Gray 1863, Werner 1896). However, we observed significant morphological variation in the pholidosis of the cloacal region in both species, including differences in both the number and arrangement of precloacal plates as well as variation in the scale rows between the cloacal plates and ventral scales (Figs 2–5), characters that were previously used to diagnose the recently described *H. ngalangi*. This morphological variation includes, for instance, specimens with 1 to 3 precloacal plates or divided large precloacal plates, as well as the absence of rows of small scales between precloacal and ventral scales, or the presence of 1 to 5 rows of small scales between them (Fig. 2). Notably, this variation showed no discernible biogeographic pattern, as specimens from the same or nearby localities frequently exhibited different morphological states (Fig. 2).

Of particular interest were specimens of *H. guentheri* (MD 5313b, MD 5486b, PEM R26313, and BE_RMCA_Vert.R.916), which exhibited an uninterrupted series of paired, transversely enlarged scales connecting the anteriormost precloacal plate to a row of ventral scales (Figs 2, 5), a diagnostic trait of *H. ngalangi*. Critically, these specimens spanned Gabon, Angola, and DRC, indicating that the morphology ascribed to *H. ngalangi* occurs across a broader geographic and taxonomic range than previously recognized.

Among this variation, we found of special relevance the material from Dundo Museum (MD) which has been initially revised by Parrinha et al. (2025). Among these five specimens, the individuals MD 5313b from Alto Cuilo and MD 5486b from Alto Chicapa exhibited an uninterrupted series of paired, transversely enlarged scales connecting the anteriormost precloacal plate to a row of ventral scales, whereas other material with the same collecting information presents a variable scale arrangement on the cloacal section (Figs 4, 5).

Discussion

These results strongly indicate that the characters used to describe *Holaspis ngalangi* are not reliable diagnostic traits for *Holaspis*, as scalation in the cloacal region on this group exhibit high variability across species (in both *H. guentheri* and *H. laevis*) and across ranges, and show significant overlap between nominal species. Given this variation in scalation, the type material of *H. ngalangi* can be unequivocally assigned to *H. guentheri*, as it possesses the latter's key diagnostic character (Gray 1863): distinct dorsolateral stripes and paravertebral stripes confined to the vertebral plates.

Additionally, the description of *H. ngalangi* introduces further concerns. Parrinha et al. (2025) state that they examined 210 *Holaspis* specimens across the genus' range, including material from the Dundo Museum and the Royal Museum of Central Africa. However, they provide no specific data or comparative analysis of these specimens, a critical omission, given that their proposed diagnostic character is demonstrably hypervariable within the group. This raises questions about the rigor of their species delimitation process. These shortcomings could be interpreted in two ways: either the authors did not thoroughly examine the claimed material, or they selectively omitted conflicting data. Either scenario would reflect poor taxonomic practice, as it undermines the reproducibility and reliability of their conclusions. This issue is particularly critical for the material assigned to *H. guentheri* by the authors (from the MD collections), as these specimens exhibit clear morphological overlap between the two putative 'morphs.' While specimens MD 5313b and MD 5486b exhibit the morphological traits of *H. ngalangi*, others, such as MD5482, agreed with the holotype of *H. guentheri*. This

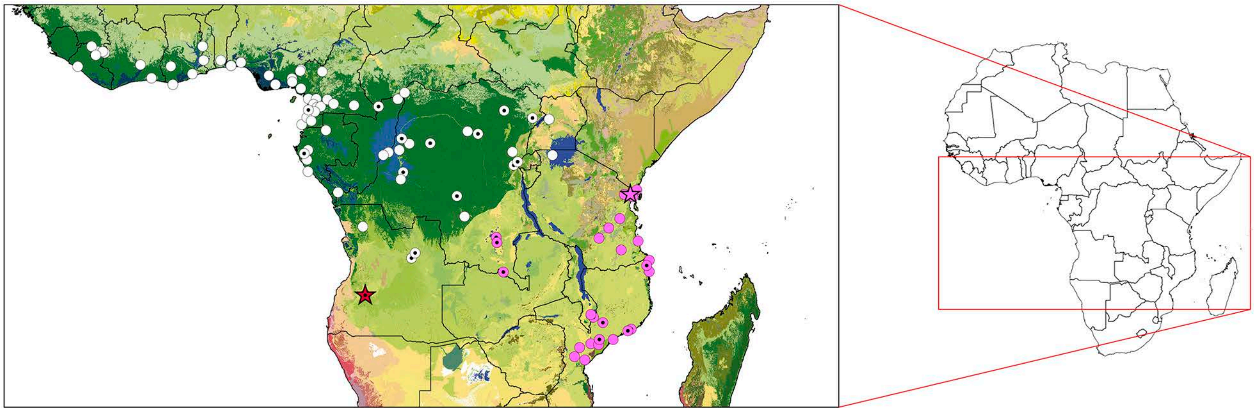

Figure 1. Geographical distribution of *Holaspis* in Africa based on Parrinha et al. (2025), museum records, and new records included in this work (Table S1), mapped against major vegetation divisions. White symbols depict records of *H. guentheri*; pink those of *H. laevis*; and red those of *H. ngalangi*. Stars indicate type localities. Black dots indicate specimens examined morphologically in this study.

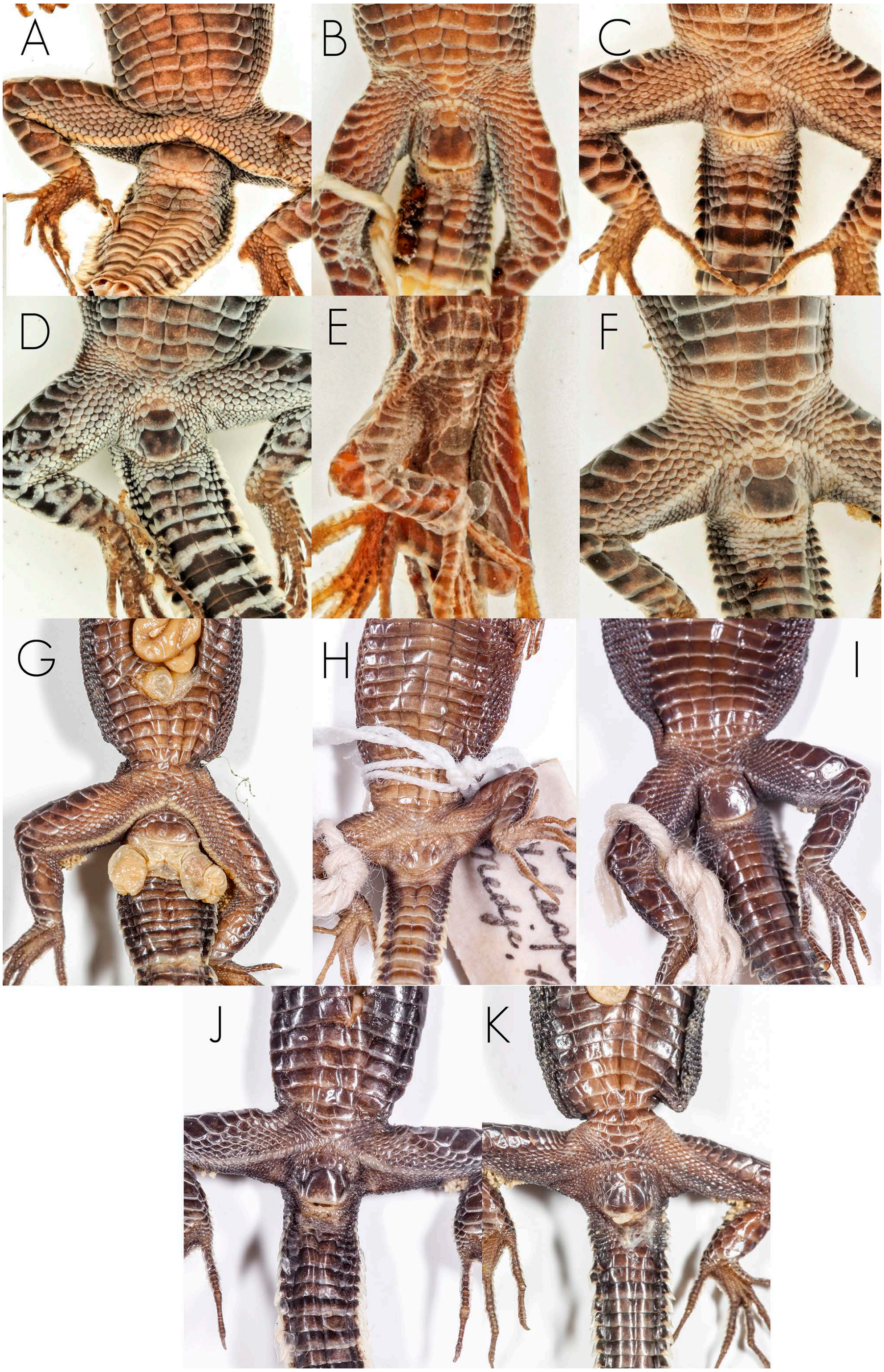

Figure 2. Graphical representation of morphological variation in the cloacal region of *Holaspis guentheri*: (A) BE_RMCA_Vert.R.1577 from Sankuru Province, DRC; (B) BE_RMCA_Vert.R.634 from Mai-Ndombe Province, DRC; (C) BE_RMCA_Vert.R.15688 from Tshopo Province, DRC; (D & F) BE_RMCA_Vert.1985.030.R.0060 & BE_RMCA_Vert.1985.030.R.0079 from Équateur Province, DRC; (E) BE_RMCA_Vert.R.916 from Bas-Congo Province, DRC; (G & K) PEM R24943 & PEM R26313 from Nyanga Province, Gabon; (H) PEM R13962 from Ituri Province, DRC; (I) PEM R13963 from South Region, Cameroon; (J) PEM R20432 from Sangha-Mbaere Region, Central African Republic. For precise localities see Table S1. Photos A–F: Jonathan Brecko.

distinction is particularly significant because the type locality of *H. guentheri* remains unknown (Loveridge 1936). Thus, such overlap directly contradicts the diagnostic distinctiveness claimed for *H. ngalangi* and further questions its validity. If the authors had thoroughly analysed this material, especially given its demonstrable intermediary, their conclusions might have been markedly different. Instead, the omission of these data suggests either insufficient examination or a failure to reconcile conflicting evidence, both of which erode confidence in taxonomic hypothesis of Parrinha et al. (2025). Consequently, with this current state of knowledge, we regard *Holaspis ngalangi* Parrinha, Marques, Gonçalves, Tuitenko, Bauer & Ceríaco, 2025 as a junior synonym of *Holaspis guentheri* Gray, 1863.

Finally, the extensive distribution of *H. guentheri*, spanning from Ivory Coast eastward across the Congo Basin to the Albertine Rift and southward to Angola, traversing the Congo-Guinean forests, warrants further investigation. Such a wide range may harbour multiple cryptic taxa, as reported by Lobón-Rovira et al. (2024) for the *Lygodactylus gutturalis* (Bocage, 1873) complex, a nominal species exhibiting a similar biogeographic pattern. Nevertheless, such taxonomic revision requires a cautious and comprehensive approach, incorporating genetic data from across its distributional range. Additionally, further scientific approaches, e.g., application of museomics, will likely be needed to clarify the geographic origin of the *H. guentheri* type (see Köhler et al. 2024 for a respective example). Consequently, future research may indeed reveal that Angolan populations present in Miombo woodlands, including the old material recovered from Caconda, Alto Cuílo and Alto Chicapa, represent an undescribed taxon, genetically separated from other miombo populations in Katanga (currently ascribed to *H. laevis*) and from rainforest populations of *H. guentheri*. However, given the significant issues identified in its original description and exemplified above, at the current state of knowledge we here propose to regard *H. ngalangi* as a non-valid taxon. This

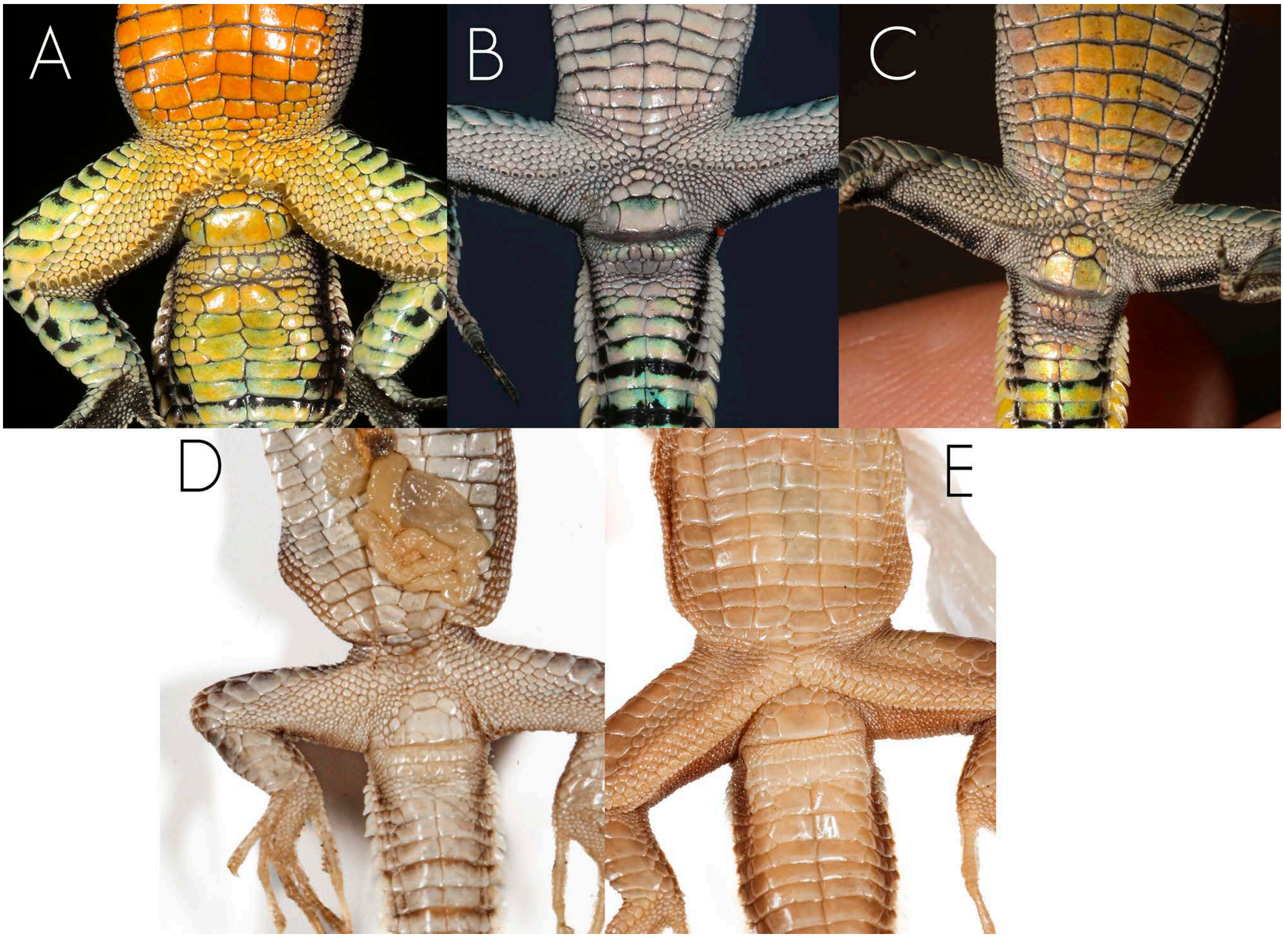

Figure 3. Graphical representation of morphological variation in the cloacal region of *Holaspis laevis* specimens: (A) PEM R21145 from Mount Mabu, Zambezia Province, Mozambique; (B) unvouchered specimen from near Quiterajo, Cabo Delgado Province, Mozambique; (C) unvouchered specimen from near Palma, Cabo Delgado Province, Mozambique; (D) PEM R13201 from near Nagonha River, Zambezia Province, Mozambique; (E) PEM R13289 from between Namagure and Moebase Zambezia Province, Mozambique. Photo C: Luke Verburgt.

recommendation is based on multiple indications against its validity, while acknowledging that any future claims of this taxon representing a new species would require a reevaluation and redescription.

In this regard, similar cases were the descriptions of *Hemidactylus vernayi* Ceríaco, Agarwal, Marques & Bauer, 2020 and *H. hannahsabinae* Ceríaco, Agarwal, Marques & Bauer, 2020 from Angola, both initially based on subtle or conflicting morphological diagnostic characters (Ceríaco et al. 2020). While *H. hannahsabinae* was subsequently synonymized following a thorough revision of Angolan *Hemidactylus*, genetic analyses confirmed *H. vernayi* as a valid taxon (Lobón-Rovira et al. 2021). This issue highlights a critical problem: such non-convincing practices risk promoting poor scientific standards by encouraging the premature description of divergent populations based on few or inconsistent lines of evidence, thus increasing taxonomic instability.

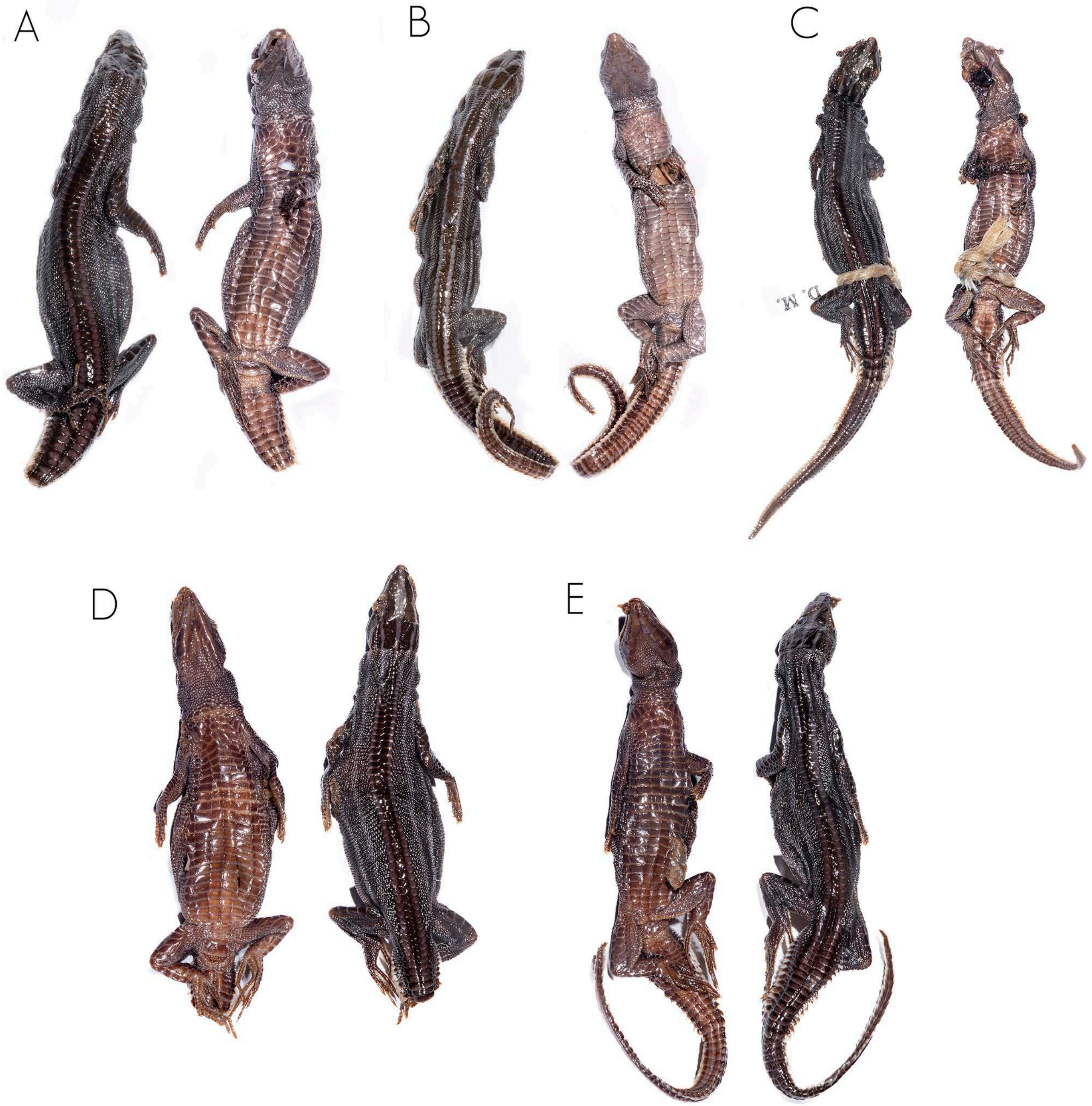

Figure 4. Unscaled photographs of dorsal and ventral views of specimens of *Holaspis guentheri* from Dundo Museum, Angola: (A) MD 5486a; (B) MD 5486b, and (C) MD 5468 from Alto Chicapa, Lunda-Norte Province, Angola; (D) MD 5313a, and (E) MD 5313b from Alto Cuilo, Lunda-Norte Province, Angola.

It must be noted that in modern taxonomy, describing species based solely on faint or subtle morphology characters and limited material remains a challenge, because of the lack of information about the intrinsic variability of the species, but also of the phenotypic plasticity. While such methodology to describe species can still be valid, they require robust and multiple lines of evidence (integrative taxonomy), such as consistent morphological distinctiveness (supported by morphometric analyses, e.g., PCA, MANOVA, or NMDS), or ecological divergence, rather than reliance on few or ambiguous diagnostic characters (Tolley et al. 2022, Lobón-Rovira et al. 2024, Wüster et al. 2024).

Nevertheless, it is important to emphasize the vital role of natural history museums in preserving type specimens and facilitating taxonomic revisions through accessible comparative material across different regions and temporal scales (Johnson et al. 2023). Morphology-based species descriptions may still be justified when compelling evidence suggests a putative species could be extinct, supported by multiple lines of evidence. However, such taxonomic decisions cannot rely solely on limited sampling efforts, such as those from a single expedition, or faint morphological evaluation. It is worth mentioning, that in Angola, where biodiversity remains understudied, fieldwork opportunities are rapidly expanding, as evidenced by the surge of scientific publications in the last decade across the territory (Ceríaco et al. 2018, Baptista et al. 2019, Conradie et al. 2021, 2022, 2023, Lobón-Rovira et al. 2022, 2025). There-

Figure 5. Detail photographs of the cloacal region (below) of specimens of *Holaspis guentheri* from Dundo Museum, Angola: (A) MD 5486a, (B) MD 5486b, and (C) MD 5468 from Alto Chicapa, Lunda-Norte Province, Angola; (D) MD 5313a and (E) MD 5313b from Alto Cuilo, Lunda-Norte Province, Angola.

fore, whenever possible, integrative approaches (e.g., combining morphology, molecular genetics, ecology, and/or behaviour) should remain the standard for robust species delimitation, as they provide greatest reliability.

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Supplementary data

The following data are available online:

Supplementary document S1. Examined material with Catalogue Numbers and geographic collecting information.