SALAMANDRA **61**(1): 53–69
15 February 2025 | ISSN 0036–3375

SALAMANDRA
German Journal of Herpetology

The genus *Holaspis* (Squamata: Lacertidae) in Angola: a tale of forgotten specimens and disappearing forests, with the description of a new species

Diogo Parrinha[1,2,3], Mariana P. Marques[1,2,3,4], Francisco M. P. Gonçalves[5,6], Arthur Tiutenko[7], Aaron M. Bauer[8] & Luis M .P. Ceríaco[1,3,4,9]

[1] CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Campus de Vairão, Universidade do Porto, 4485-661 Vairão, Portugal

[2] Departamento de Biologia, Faculdade de Ciências da Universidade do Porto, Rua do Campo Alegre 1021, 4169-007 Porto, Portugal

[3] BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Campus de Vairão, 4485-661, Vairão, Portugal

[4] Carnegie Museum of Natural History, Section of Amphibians and Reptiles, 4400 Forbes Avenue, Pittsburgh PA 15213, USA

[5] Herbário do Lubango, ISCED-Huíla, Rua Sarmento Rodrigues S/N, Lubango, Angola

[6] Universidade Mandume Ya Ndemufayo, Avenida Hoji Ya Henda No. 30, Lubango, Angola

[7] Friedrich-Alexander-Universität Erlangen-Nürnberg, Erlangen, Germany

[8] Department of Biology and Center for Biodiversity and Ecosystem Stewardship, Villanova University, Villanova, PA 19085, USA

[9] Departamento de Vertebrados, Museu Nacional, Universidade Federal do Rio de Janeiro, Quinta da Boavista, São Cristóvão, 20940-040 Rio de Janeiro, Brasil

Corresponding author: Diogo Parrinha, e-mail: parrinha.diogo45@gmail.com

Manuscript received: 27 March 2024
Accepted: 15 November 2024 by Philipp Wagner

Abstract. The members of the Afrotropical lacertid genus *Holaspis* are strikingly specialized lizards, adapted for gliding in forest canopies, with serrated blue tails. Two species are currently recognized within the genus: *Holaspis guentheri* from West and Central Africa, and *Holaspis laevis* from East Africa. The currently known southern limits of *H. guentheri* are in the northern Angolan Guineo-Congolian habitats, which are remnants of forests connecting the country to West/Central Africa. The oldest record of the species in Angola, dating back to the 19th century, is based on a currently lost specimen collected by José d'Anchieta near Caconda, southwest Angola. Caconda is situated on the Angolan Central Plateau, which is part of the Great Escarpment of southern Africa. The loss of Anchieta's specimen and its geographic context led most authors to disregard it, leaving its taxonomic identity dubious until now. The rediscovery of two additional specimens from Caconda, collected by William John Ansorge in the early 20th century and deposited in the Natural History Museum, London, allowed us to confirm the presence of the genus in the region, prompting targeted surveys and examination of additional material. Our surveys failed to locate any *Holaspis* near Caconda, with alarming rates of deforestation in the region raising the possibility that this population may already be extinct. The reexamination of the extant Caconda specimens and comparison with *H. guentheri* and *H. laevis* revealed consistent morphological differences that suggests that the Caconda population may represent a distinct taxonomic unit. Here we describe the *Holaspis* from Caconda as a new species, presumably endemic to the Angolan Central Plateau. These findings and their implications are discussed in the biogeographical context of the highlands of western Angola, a recognized hotspot of diversity and endemism for several taxonomic groups.

Key words. Taxonomy, biogeography, natural history collections, deforestation, highlands.

Introduction

The lacertid genus *Holaspis* Gray, 1863 (Squamata: Lacertidae), represented by strikingly specialized lizards adapted for arboreal habits and gliding in forest canopies, with flattened bodies and serrated blue tails, is currently represented by only two species (Arnold 1989, 2002, Greenbaum et al. 2011). The genus and its type species, *Holaspis guentheri* Gray, 1863, were described by Gray (1863) based on a juvenile specimen (BMNH 1946.8.7.31; Fig. 1) without any locality data, purchased in Paris and donated by Andrew Smith to the collections of the British Museum (currently the Natural History Museum, London). Subsequent records of *H. guentheri* allowed the identification of its geographic

range in the forests of tropical Africa, from Sierra Leone to Tanzania (Müller 1885, Matschie 1892, Boulenger 1887). Werner (1895) subsequently described the subspecies *H. guentheri laevis* Werner, 1895 from East Africa. The type specimen of *H. guentheri laevis* (BMNH 1946.8.7.25, originally 95.4.8.4; Fig. 2) is an adult female from the Usambara Mountains, Tanzania labeled as the type of "*Holaspis muelleri* n. sp." (pers. obs.), presumably an early working name intended to honor Dr. August Müller, who was director of the "Linnaea" in Berlin and sent the specimen to Werner for identification (Werner 1895).

Most authors regarded *H. laevis* as a synonym of *H. guentheri*, recording additional material from central and eastern Africa (Tornier 1897, Schmidt 1919, Boulenger 1921, Barbour & Loveridge 1928, Cott 1934, de Witte & Laurent 1942, Loveridge 1951, de Witte 1953), until Loveridge (1953) revived *H. g. laevis* as a valid subspecies, distinguished from typical *H. g. guentheri* based on dorsal coloration pattern. Subsequent authors followed Loveridge's opinion, and new records were published for both *H. g. guentheri* (Angel et al. 1954, Laurent 1964, Dunger 1967) and *H. g. laevis* (Loveridge 1955, Broadley 1963). Broadley (2000) considered both *H. guentheri* and *H. laevis* as valid species, an opinion that was followed by other authors (Ineich 2003, Broadley & Cotterill 2004, Ullenbruch et al. 2010, Böhme et al. 2011, Pauwels & Itam 2013, Malonza & Bauer 2014, Conradie et al. 2016, Malonza et al. 2018, Pauwels et al. 2018). *Holaspis guentheri* is restricted to West/Central Africa, from Sierra Leone to the Great Lakes region of Uganda and Tanzania and southwards to northern Angola (Trape et al. 2012, Marques et al. 2018, Spawls et al. 2018), while *H. laevis* occurs in East Africa, from central Mozambique to southeastern Kenya and as far inland as the Katanga region of the Democratic Republic of the Congo (Broadley & Cotterill 2004, Spawls et al. 2018, Pietersen et al. 2021).

Northern Angola has been regarded as the southwestern limit of *H. guentheri* (Boulenger 1921, Arnold 1989, 2002), even if Angolan records are scarce. Even though no specimens from Angola were known at the time, when Bocage (1895) published his major opus on Angolan herpetofauna, he included the species in his listing of the species present, transcribing the original description of the species by Gray (1863). Bocage's expectation was certainly based on his knowledge of habitat continuity between West and Central Africa and northern Angola, which is the southern limit of the Guineo-Congolian habitats where the species is found.

The oldest available record of this species in the country dates to the late 19th century and was based on a specimen collected by the Portuguese naturalist and explorer José Alberto d'Anchieta (1832–1897). Anchieta collected zoological material in Angola for more than three decades, spending most of this time based in Caconda, in the northern highlands of present-day Huíla Province (Banha de Andrade 1985). He died in September 1897 while exploring the neighboring regions of Caconda, in what would be his last field expedition (Banha de Andrade 1985). The specimens collected by Anchieta during his last expedition were posthumously shipped to the Lisbon Museum (currently Museu Nacional de História Natural e da Ciência, Universidade de Lisboa) and contained reptiles and amphibians that were examined and published by Ferreira (1897). Among other specimens, Ferreira (1897) reported a specimen of

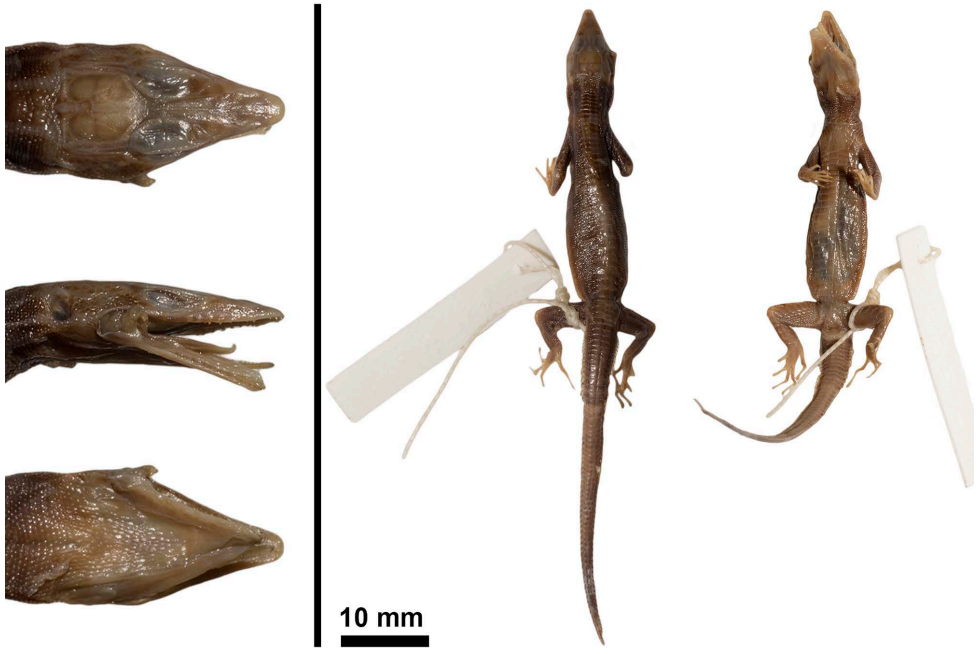

Figure 1. Preserved holotype of *Holaspis guentheri* (BMNH 1946.8.7.31). Photos by Diogo Parrinha.

H. guentheri collected by the late explorer in 1897 at "Rio Cuce", Huíla Province. This was the first vouchered record of the species for Angola and the southernmost record for the genus. Acknowledging its rarity, Ferreira (1897) provided a detailed description of this specimen. Nearly a decade later, in 1905 two additional specimens were collected in the Caconda region by the British explorer William John Ansorge (1850–1913). Ansorge's specimens were deposited in the collections of the British Museum of Natural History and later reported by Boulenger (1921).

Although not directly citing Ferreira (1897) nor Boulenger (1921), other authors were aware of these records, as they acknowledged the occurrence of *H. guentheri* in Angola (e.g. Barbour & Loveridge 1928, Loveridge 1953). Approximately four decades later, Laurent (1964) provided the next records of the species in Angola based on specimens collected in Alto Cuílo (MD 5313 [two specimens]) and Alto Chicapa (MD 5482, 5468 and 5486 [two specimens]) in Lunda Sul Province, northeastern Angola. These specimens are still extant (although maintained in suboptimal conditions) in the collections of Museu Regional do Dundo, Angola (Ceríaco et al. 2020a; pers. obs.).

With few exceptions (e.g., Monard 1937), the specimens collected by Anchieta and Ansorge in the Caconda region were apparently ignored or disregarded by modern authors who have dealt with both the Angolan herpetofauna and the genus *Holaspis* (Marques et al. 2018, Branch et al. 2019). The identity of the specimens reported by Ferreira (1897) and Boulenger (1921) from Huíla Province were considered dubious (Marques et al. 2018), as the recorded localities in the Central Plateau are separated by more than 500 km from the nearest generally accepted record of the species (Laurent 1964, Ernst et al. 2020). Anchieta's specimen was lost in the fire that destroyed the zoological collections of the Lisbon Museum in 1978, thus precluding any further revision of its identity. This led Marques et al. (2018) to interpret Ferreira's (1897) record as a case of misidentification, suggesting that Anchieta's specimen might have been a *Cordylosaurus subtesselatus* (Smith, 1844), considering the similar blue color pattern and geographic context.

The most recent record of *H. guentheri* in Angola was based on a specimen from Serra Pingano in Uíge Province, northwestern Angola and deposited in the Senckenberg Natural History Collections in Dresden (Ernst 2015, Ernst et al. 2020). The authors reported this as the third record of the species for the country, although none of the earlier records are cited (Ernst et al. 2020). Branch et al. (2019) acknowledged only the records from northern Angola (Laurent 1964, Ernst 2015), not commenting on those from Caconda provided by Ferreira (1897) and Boulenger (1921). More recently, another specimen of *H. guentheri* was observed in the Angolan exclave of Cabinda and made publicly available through the citizen science platform iNaturalist (Ferreira 2022).

A recent visit to the collections of the Natural History Museum, London allowed us to examine the two surviving specimens collected in Caconda by Ansorge in 1905. The examination of these specimens, together with the previous record by Ferreira (1897), unambiguously confirm the existence of an apparently isolated population of a species of the genus *Holaspis* in the Caconda region, in the highlands of northern Huíla Province. This prompted surveys in forested areas near Caconda during November 2023, although

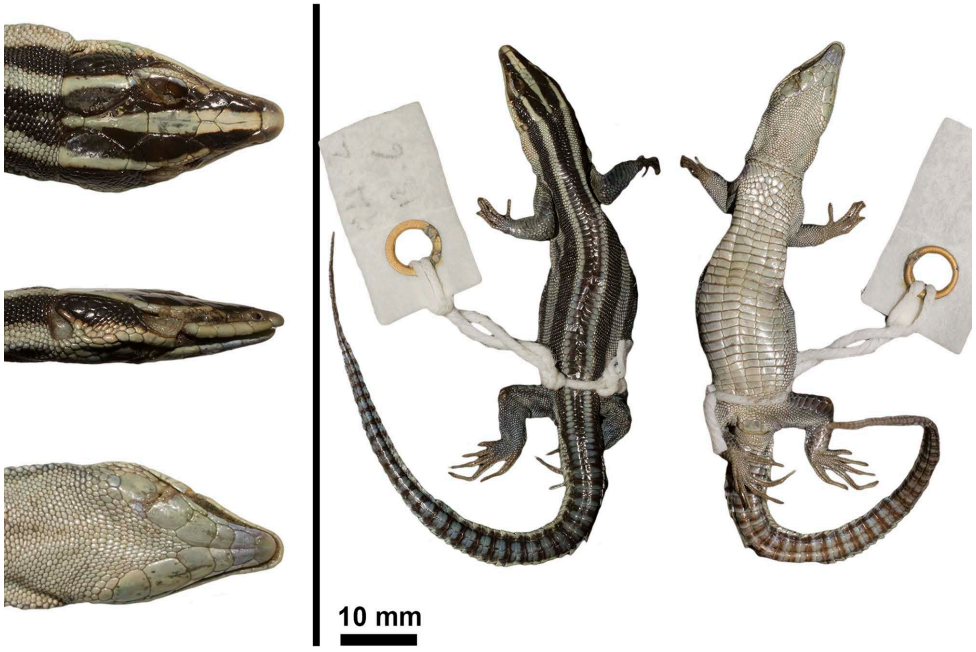

Figure 2. Preserved holotype of *Holaspis laevis* (BMNH 1946.8.7.25). Photos by Diogo Parrinha.

unsuccessful. The elusive habits of the genus, closely associated with forest canopies, and the alarming rate of deforestation observed in the region likely contributed to our lack of success. Based on morphological evidence, we recognize the Caconda population as a new species of *Holaspis,* apparently endemic to the Angolan Central Plateau, which we describe herein. An updated key to the genus *Holaspis* is also provided, as well as additional morphological data and photos of the types of *H. guentheri* and *H. laevis*.

Materials and methods

Material examined

For mensural and meristic comparisons, we examined 28 specimens of *Holaspis* including the two specimens collected by Ansorge in Caconda (BMNH 1906.8.24.56–57), and the type specimens of *Holaspis guentheri* (BMNH 1946.8.7.31) and *Holaspis laevis* (BMNH 1946.8.7.25). Additional material was examined in person or through high resolution photographs (specimens not measured or scale counted). A total of 210 specimens were examined for this study, which are deposited in the collections of the Natural History Museum, London, UK (BMNH); the Muséum national d'Histoire naturelle, Paris, France (MNHN); Institut royal des Sciences naturelles de Belgique, Bruxelles, Belgium (IRSNB); the Naturhistorisches Museum Basel, Basel, Switzerland (NMB); the Zoological Research Museum Alexander Koenig, Bonn, Germany (ZFMK); the Musée royal de l'Afrique centrale, Tervuren, Belgium (RMCA); the Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark (ZMUC); the American Museum of Natural History, NY, USA (AMNH); the Florida Museum of Natural History, University of Florida, FL, USA (UF); the Carnegie Museum of Natural History, PA, USA (CM); the National Museum of Natural History, Smithsonian Institution, Washington DC, USA (USNM); the California Academy of Sciences, CA, USA (CAS); the Museum of Comparative Zoology, Harvard University, MA, USA (MCZ); and the Museu Regional do Dundo, Dundo, Angola (MD). A complete list of the material examined is provided as supplementary material. Historical localities were georeferenced using the web application GeoLocate (https://www.geo-locate.org/default.html). Coordinates are presented in decimal degrees and use the WGS-84 map datum, and elevations are presented as meters above sea level.

Morphological analysis

Specimens were measured using a digital caliper to the nearest 0.1 mm and lepidosis was observed with the help of a stereomicroscope. Scale counts and measurements follow those used in earlier *Holaspis* descriptions and diagnoses (Gray 1863, Werner 1895, Boulenger 1921), and abbreviations were standardized following Darko et al. (2022). The following 20 mensural and meristic characters were recorded: snout–vent length (SVL), measured from tip of snout to vent; tail length (TAL), from vent to tip of tail, measured only in specimens with complete, original tails; forearm length (FLL), from elbow to base of palm; crus length (HLL), from knee to base of heel; trunk length (AGD), corresponding to the distance between axilla and groin; head length (HL), measured from tip of snout to posterior margin of retroarticular process of jaw; head width (HW), maximum width of head; head height (HH), maximum height of head from occiput to underside of jaw; collar–snout length (CSL), measured between median collar plate and tip of snout; number of supralabials anterior to subocular (SL); number of infralabials (IL); number of supracilliaries (SCl); number of collar plates (CP); number of longitudinal rows of ventral scales (LVSR), between collar (excluded) and last complete row of enlarged ventral plates (included); transverse rows of ventral scales (TVSR); number of gular scales in a straight line between median collar plate (excluded) and symphysis of chin shields (GS); number of subdigital lamellae under fourth finger (LF4) and fourth toe (LT4); number of femoral pores on each leg (FP); and the number of chin shields (CS). The general shape and arrangement of precloacal scales and the type of contact between head shields were also noted, as well as coloration pattern.

Study area

Locality data for historical collections is usually vague, making it difficult to retrace and geolocate the collecting localities with confidence and accuracy. In order to narrow down the potential localities where Anchieta and Ansorge collected the *Holaspis* specimens, we reviewed existing information on the itineraries and collections gathered by these two naturalists (Chapin, undated; Azevedo Pinho 1897, Banha de Andrade 1985). On a report dated 5 November 1897, the chief of the Caconda outpost, lieutenant António d'Azevedo Pinho provided an official record of Anchieta's death to the Portuguese authorities (Azevedo Pinho 1897). Written in a late 19th century Portuguese style, Azevedo Pinho (1897) reports that: "Anchieta, although old and tired, wanted to work (…). Anchieta, trying to get some additional zoological results, ordered a wagon from Europe (…) and in the end of July he left towards Cusse [= Cusse River] and Quando [= Cuando River]; I still had the pleasure of seeing him (…) in the beginning of August when he came to Caconda to collect his salary, and he told me "I'm happy, I will do something more before old Bocage dies, after this survey he will be happy". He spent two days and left again, and after approximately a month someone told me that Anchieta was sick. A few days later, around 10 of 14th September, a soldier told me "The Senhor Doutor just arrived but dead". (…) After confirming his death, I started to question his sons and other people about the circumstances of his death, and what I could conclude, according to what I was told, was that José d'Anchieta became sick at old Martins Gomes Pereira's libata [= house], but as usual didn't care about the sickness and continued working under sun

and rain. When he got worse, he wanted to leave and was able to travel up to Quicambe [= Chicambe village], where, as usual, he rested in his typóia [= litter]. At around 10 pm his son went to check on him and found his father dead. The son then drove the body directly to Caconda. This is all I know. The products of his last survey are in this fortress, waiting to be dispatched as soon as I can get some carriers, it is a box containing some specimens." [translated from the original Portuguese version by the authors]

No field journals or letters on the itinerary of Ansorge's expeditions in Angola are known to exist. However, a manuscript produced by the north American ornithologist James Chapin (1889–1964) with notes on the places surveyed by the explorer supports the fact that Ansorge collected in Caconda on 28 December 1905 (Chapin, undated). This is the collecting date that is mentioned on the label of the BMNH specimens. Caconda lies at about 1600 m above sea level in the northern area of southwest Angola, as defined by Mendelsohn & Mendelsohn (2018), and is part of the Angolan Plateau in the broader context of the Great Escarpment of southern Africa (Mendelsohn & Huntley 2023). In the 19th century, the region of Caconda was probably covered by primary Miombo woodlands dominated by *Brachystegia* spp. and *Julbernardia paniculata* (Grandvaux-Barbosa 1970, Huntley 2023), with vegetation described as "exuberantly copious and varied" by Anchieta (Banha de Andrade 1985). Nowadays, Caconda and its surroundings are greatly transformed by human activities, with woodlands being continuously degraded by subsistence agriculture (pers. obs.). A recent vegetation survey in Huíla Province with focus on woody species found that the dominant vegetation in Caconda, Caluquembe and Chicomba belongs to *Combretum-Pericopsis* communities, which are normally associated with Miombo key-species, and indicate that the primary vegetation type in those areas were typical Miombo woodlands (Chisingui et al. 2018). The *Combretum* communities are generally considered as pioneer species, which normally become established after disturbances, while *Pericopsis* are hardwood species, usually left in the fields by local people because of its useful characteristics, such as its value as construction material (Gonçalves et al. 2017; pers. obs.).

The town of Caconda [-13.7371°, 15.0614°, 1674 m a.s.l.], and the villages of Cusse [-13.5174°, 15.1893°, 1759 m a.s.l.] and Chicambe [-13.7826°, 15.3653°, 1540 m a.s.l.] form a polygon of approximately 400 km² in northern Huíla Province (Fig. 3). Cusse and Chicambe lie, respectively, about 27 km north and 30 km west of Caconda in a straight line, with a distance of circa 33 km between Cusse and Chicambe. The Cuando River (not to be confused with the larger south-

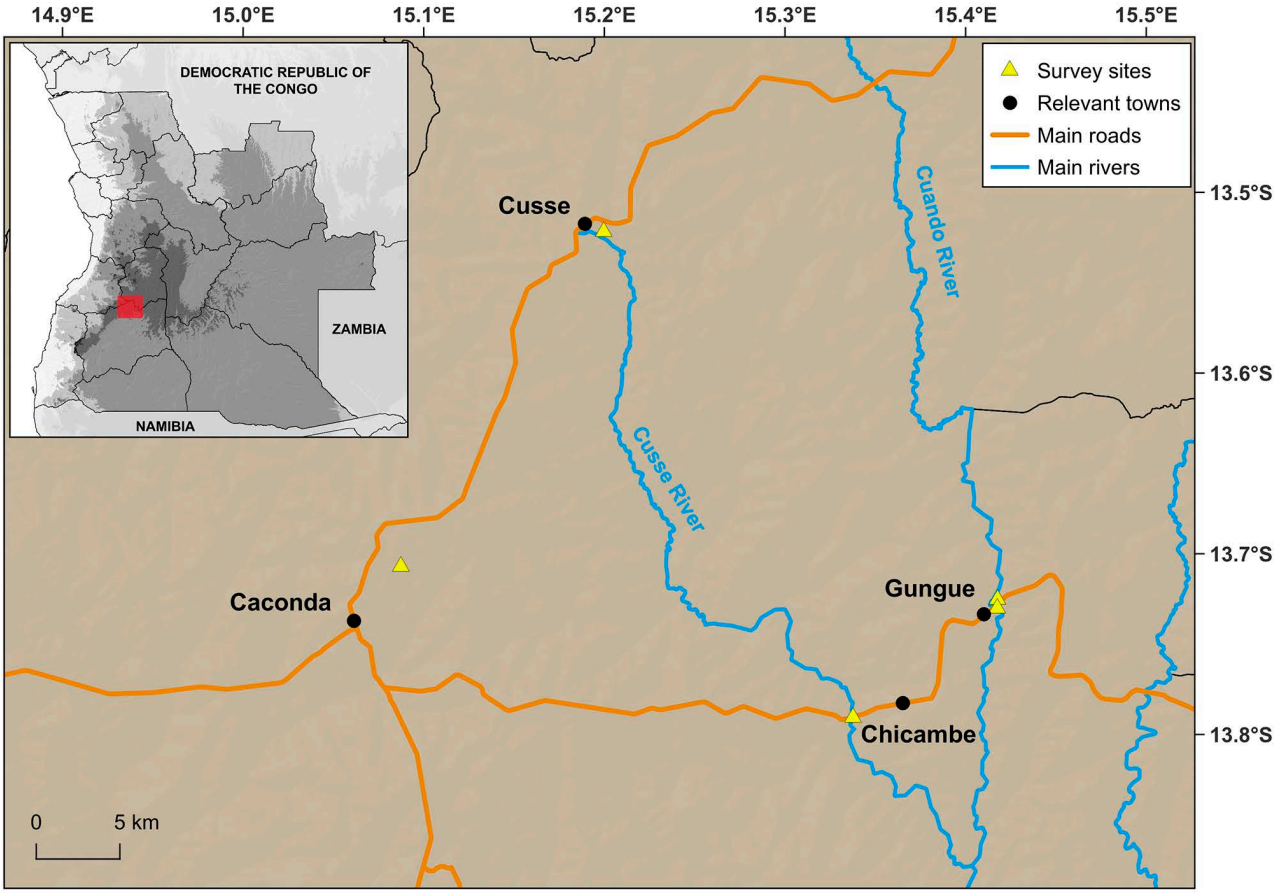

Figure 3. Map of the Caconda region in Angola, showing survey sites, relevant towns, roads, and rivers.

eastern Angolan Cuando River, which flows through the Linyanti Swamp on its way to the Zambezi River) arises in Huambo Province and flows southwards through Gungue village [-13.7335°, 15.4102°, 1536 m a.s.l.], about 10 km northeast of Chicambe, continuing southwards to merge with the Cunene River near Cachicala village. The Cusse River arises near Cusse village and flows southwards near Chicambe to meet the Cuando River further south (Fig. 3).

Based on the available information on the itineraries of Anchieta and Ansorge and the typology of habitats used by the genus *Holaspis* (e.g. Schmidt 1919, Laurent 1964, Ernst et al. 2020), we selected five sampling sites in the region of Caconda with potential suitable habitats for *Holaspis* (Fig. 3). Site 1 is located in the graveyard of the Missão Católica de Caconda, about 5 km north of the town [-13.7070°, 15.0874°, 1658 m a.s.l.]. Even though the surroundings of the area are highly disturbed, a small area of Miombo is present in the surroundings of the Mission's graveyard (Fig. 4A). Similarly, Site 2 is located in an informal graveyard near Cusse village and the source of the Cusse River [-13.5217°, 15.1997°, 1728 m a.s.l.], where there is a small patch of Miombo with herbaceous cover on the

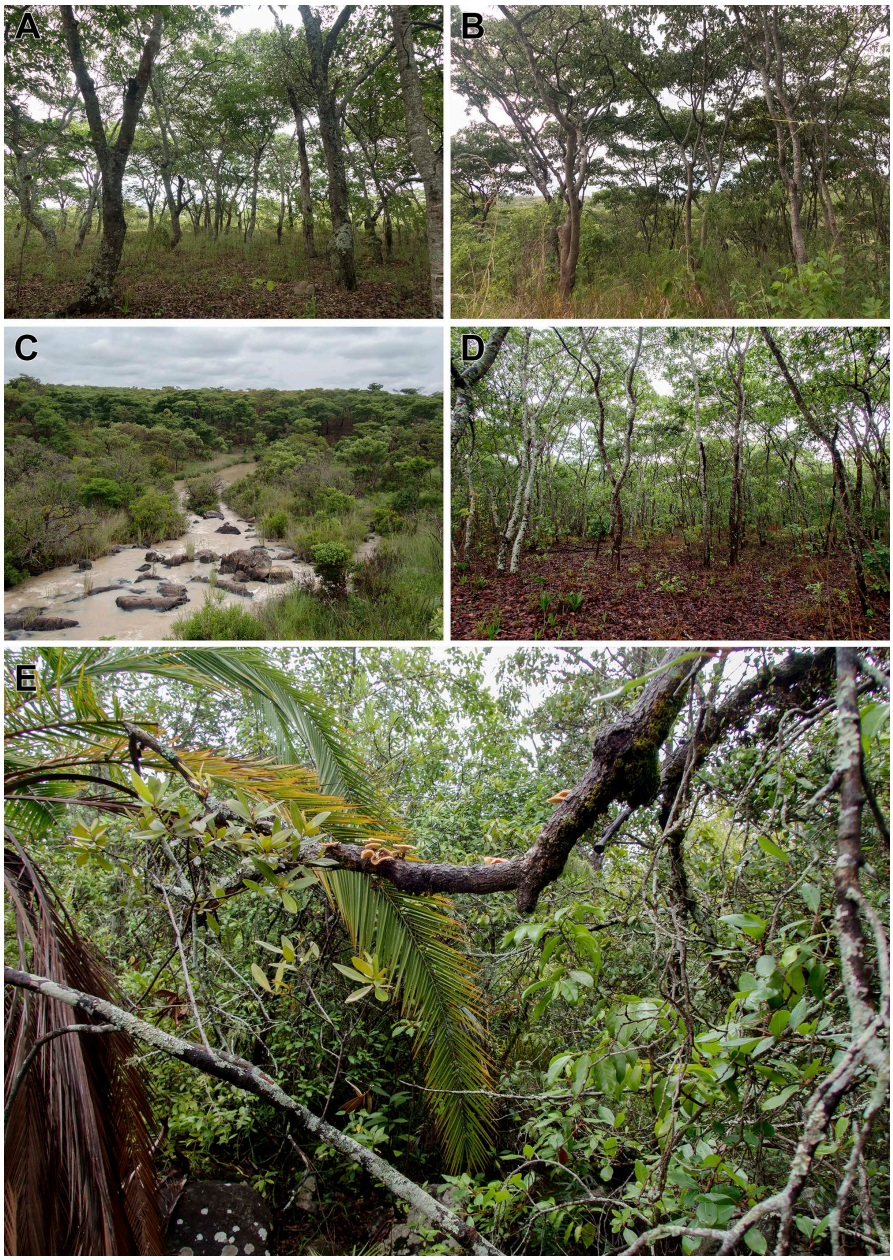

Figure 4. Habitats at the survey sites in the region of Caconda, Angola: (A) Missão Católica de Caconda, graveyard (Site 1); (B) Cusse, graveyard (Site 2); (C) Cusse River near Chicambe (Site 3); (D) Gungue, Miombo (Site 4); (E) Cuando River near Gungue (Site 5). Photos by Diogo Parrinha.

slopes of a rock outcrop (Fig. 4B). Further south along the Cusse River, near Chicambe village, at Site 3 [-13.7906°, 15.3377°, 1478 m a.s.l.], the river flows wider and is surrounded by a mosaic of isolated Miombo patches, typically dominated by *Brachystegia bohemii,* agricultural land and deforested areas, devoid of most of its original riparian gallery (Fig. 4C). Further east, the surroundings of Gungue village are also characterized by a mosaic of isolated Miombo patches, agricultural land and deforested areas. In contrast to the more open Miombo surveyed near Caconda and Cusse, the Miombo patch surveyed at Site 4 near Gungue village [-13.7253°, 15.4177°, 1539 m a.s.l.] is characterized by a denser Miombo with more shade, less herbaceous cover, and more leaf litter (Fig. 4D). The woodlands here are denser, with dominant tree species such as *Brachystegia bohemii*, *Erythrina abyssinica*, *Pterocarpus angolensis*, *Lannea discolor* and other woody species. The herbaceous layer becomes more interesting with characteristic Afromontane elements like *Xerophyta* cf. *concolor*, and orchids growing on rock outcrops where we documented other Afromontane taxa such as *Lindernia crassifolia*, *L. linearlifolia* and *Impatiens assurgens*, also known from Serra da Namba further north in Cuanza-Sul Province (Goyder et al. 2023). Site 5 is located on the Cuando River near Gungue [-13.7302°, 15.4176°, 1509 m a.s.l.], where there can still be found stretches of preserved riverine forest, dominated by species like *Ficus sur*. The habitat here is notably more humid, with denser vegetation and a profusion of mosses and epiphytic plants associated with the subtropical riparian gallery (Fig. 4E).

Nomenclatural acts

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new names contained herein are available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The LSID (Life Science Identifier) for this publication is: urn:lsid:zoobank.org:pub: 5E014E82-C84D-4028-B82C-EFFBEAAB68F6. The electronic edition of this work was published in a journal with an ISSN, and has been archived and is available from the following digital repositories: salamandra-journal.com, zenodo.org.

Results

Our recent surveys that targeted forested areas in the region of Caconda failed to find any *Holaspis*. The examination of the existing specimens from the Caconda region and their comparison with available specimens of *Holaspis* revealed morphological differences in the arrangement of precloacal scales, which unambiguously differentiate the southern Angolan specimens from the two currently recognized species in the genus. The arrangement that distinguishes the Caconda specimens from the two recognized species of *Holaspis* was not observed in any of the additional 205 specimens for which this character was examined. No significant meristic differences were found between taxa, but the number of pale dorsal stripes, identical to that found on *H. guentheri*, also distinguished the Caconda specimens from *H. laevis*. Operating under the General Lineage species concept (De Queiroz 1999), these results provide sufficient evidence to consider the Caconda population as a distinct species. Morphological data for *Holaspis* species is presented in Table 1. The new species is described and diagnosed in the taxonomic account below. An updated key to the species of the genus *Holaspis* is provided below.

Taxonomy

***Holaspis ngalangi* sp. n.**

(Figs 5–6)

ZooBank LSID: urn:lsid:zoobank.org:act:7A42D5C1-CD02-46F6-8ECD-AA7BFDC87BA8
Holaspis guentheri: Ferreira (1897: 242); Boulenger (1921: 377) [part]; Monard (1937: 73)
Cordylosaurus subtessellatus [?]: Marques et al. (2018: 229) [part]

Remarks: This new species of *Holaspis* is known only from three specimens collected in the late 19th and early 20th centuries near Caconda, Huíla Province. The first known specimen of this species was collected by Anchieta in 1897 at "Rio Cuce" and reported by Ferreira (1897), but was lost in the fire that destroyed the collections of the Lisbon Museum in 1978. Two additional specimens were collected in Caconda by Ansorge in 1905 and sent to the British Museum of Natural History. These were reported by Boulenger (1921) as *Holaspis guentheri* and are the only surviving representatives of the genus in the Angolan Central Plateau. The re-examination of these specimens and other comparative material (210 specimens in total, see supplementary material) revealed consistent morphological differences that allow the distinction of the Caconda specimens from the two recognized species of the genus.

Holotype: BMNH 1906.8.24.57, an adult female from Caconda [georeferenced to -13.7371°, 15.0614°, 1674 m a.s.l.], Huíla Province, Angola, collected by William John Ansorge on 28 December 1905 (Fig. 5).

Paratype: BMNH 1906.8.24.56, an adult female with the same collecting data as the holotype (Fig. 6).

Description of the holotype: Well preserved, adult female with complete original tail (Fig. 5). SVL 47.2 mm; TL 57.8 mm. Body depressed, with well-developed pentadactyl limbs; tail slightly longer than SVL (TL/SVL 1.22). Head moderately sized (HL/SVL 0.19), depressed and distinct from neck. Other relevant measurements are provided in Table 2. Rostral wider than high, visible

Table 1. Mensural and meristic data for the studied species. Abbreviations are listed in the Materials and methods. Data presented as "mean [min–max]".

	Holaspis guentheri (n = 15)	*Holaspis laevis* (n = 11)	*Holaspis ngalangi* sp. n. (n = 2)
SVL (max.)	52.2	51.1	47.2
TAL (max.)	63.3	69.4	57.8
TAL/SVL	1.2 [1.0–1.3]	1.4 [1.3–1.5]	1.2
FLL	5.6 [4.2–8.5]	5 [3.6–6.6]	5.1 [5.0–5.3]
HLL	6.6 [5.1–7.6]	6.2 [4.6–7.9]	6.5 [6.4–6.6]
AGD	22.1 [13.9–26.9]	19.8 [14.4–25.5]	23.4 [22.0–24.8]
HL	10.9 [9.1–12.7]	11 [8.8–14.1]	9.8 [9.6–10.0]
HW	5.7 [4.7–6.8]	6.4 [5.0–8.1]	5.9 [5.8–6.0]
HH	3.1 [2.1–3.8]	3.3 [2.8–4.8]	3.4 [3.2–3.6]
CSL	15.2 [12.7–17]	15.4 [11.7–19.5]	15.3 [14.7–16]
SL	4 [4–5]	4 [4–5]	4
IL	6 [5–7]	6 [5–6]	7 [6–7]
SCl	7 [5–8]	7 [6–8]	7
CP	9 [7–11]	10 [8–13]	10
LVSR	6	6	6
TVSR	26 [23–28]	28 [25–38]	29 [28–30]
GS	30 [27–35]	31 [27–39]	29 [27–30]
LF4	12 [10–14]	14 [12–15]	11 [10–11]
LT4	18 [15–20]	21 [18–23]	18 [17–19]
FP	21 [18–24]	21 [17–24]	19 [18–19]

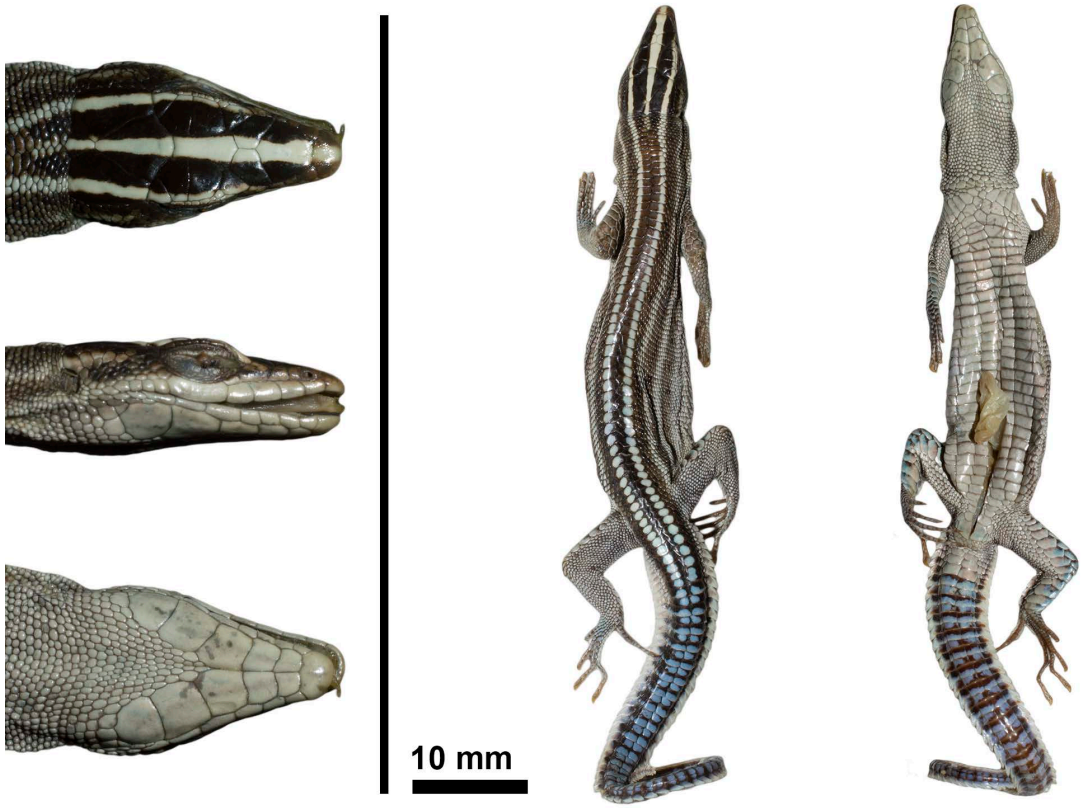

Figure 5. Preserved holotype of *Holaspis ngalangi* sp. n. (BMNH 1906.8.24.57). Photos by Diogo Parrinha.

Table 2. Mensural and meristic data for the type specimens of *Holaspis ngalangi* sp. n., *Holaspis guentheri* and *Holaspis laevis*. Abbreviations are listed in the Materials and methods. When asymmetrical, values are given as (left/right). Asterisks (*) denote incomplete tails.

	Holaspis guentheri	*Holaspis laevis*	*Holaspis ngalangi* sp. n.	
	BMNH 1946.8.7.31 (Holotype)	BMNH 1946.8.7.25 (Holotype)	BMNH 1906.8.24.57 (Holotype)	BMNH 1906.8.24.56 (Paratype)
Sex	F	F	F	F
SVL	37.6	47.5	47.2	46.9
TAL	34.3*	68.3	57.8	38.2*
TAL/SVL	–	1.4	1.2	–
FLL	4.2	5.0	5.3	5.0
HLL	5.2	6.4	6.4	6.6
AGD	18.9	23.7	22.0	24.8
HL	9.9	11.0	9.6	10.0
HW	4.7	6.9	5.8	6.0
HH	2.1	3.1	3.6	3.2
CSL	12.8	16.1	16.0	14.7
SL	5/4	5/4	4	4
IL	7	6	6/7	7/6
SCl	7	8	7	7
CP	9	9	10	10
LVSR	6	30	30	6
TVSR	26	6	6	28
GS	30	39	30	27
LF4	13	14	11	10
LT4	16	22	19	17
FP	23/22	22	20/19	18/18

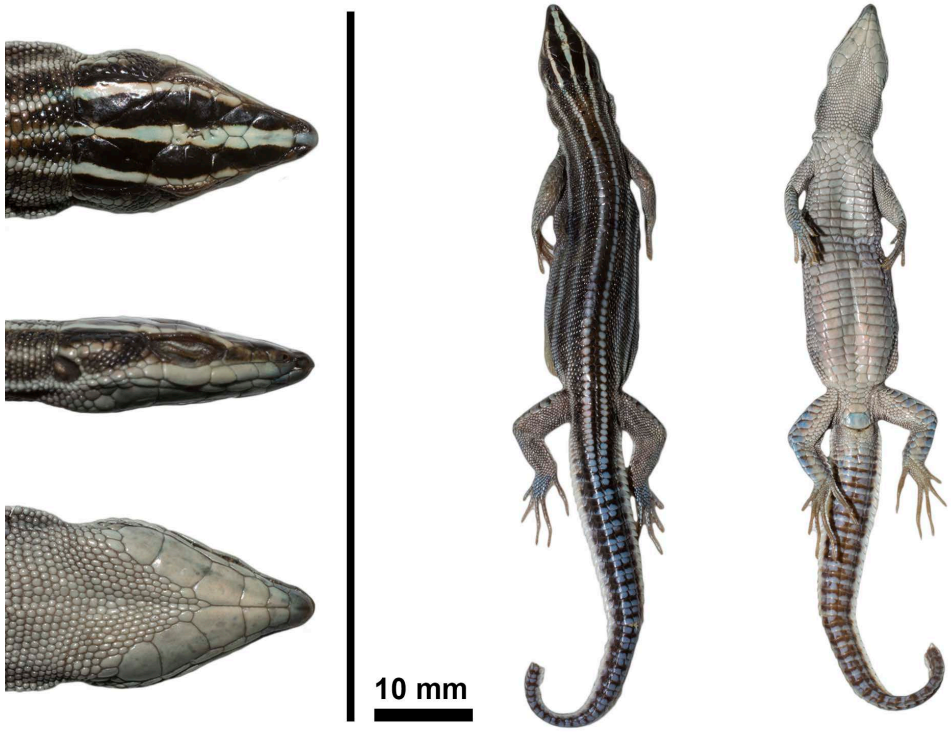

Figure 6. Preserved paratype of *Holaspis ngalangi* sp. n. (BMNH 1906.8.24.56). Photos by Diogo Parrinha.

from above, and nearly as deep as it is wide. Frontonasal large, as long as broad, in contact with rostral anteriorly, prefrontals posteriorly, and nasals and anterior loreal on each side; prefrontals in median contact with each other, frontonasal, loreals, first preocular and frontal. Frontal longer than wide, its length shorter than distance between anterior edge of frontal and tip of snout, in contact with prefrontals, interparietal, and first three supraoculars on each side. Frontoparietals fused with interparietal, forming a large subtriangular scale in contact with occipital, parietals, frontal and last two supraoculars on each side. Parietals longer than broad, separated from each other; occipital small and subtriangular, slightly longer than broad. Four supraoculars on each side, second and third larger. Supracilliaries 7, separated from second and third supraoculars by a row of small granules. Nostril pierced posteriorly on nasal scale so that it effectively borders postnasal. Two loreals, posterior one largest. Subocular bordering lip, about three times as wide as high; 4 supralabials anterior to subocular. Lower eyelid scaly, with 3 somewhat enlarged, semi-transparent scales in the middle of right side; a single enlarged, semi-transparent scale on left side. Temporals small and granular, those immediately behind eye slightly larger; ear opening rounded to vertically ovoid; tympanic shield positioned on dorsal superior edge of ear opening, slightly wider than high, preceded by other enlarged scales between corner of eye, parietals and temporal granules. Infralabials 6/7 (left/right); mental slightly wider than long, in contact with first infralabial on each side and first pair of chin shields. Five pairs of chin shields, first three in broad median contact. Collar distinct, covered with 10 enlarged plates; gular scales small and granular, 30 in a straight line between median collar plate and symphysis of chin shields. Ventral scales smooth and slightly imbricate, subrectangular, in 6 longitudinal and 30 transverse rows; those on first row posterior to collar irregularly shaped and mostly higher than broad; scales on outer rows narrower, subquadrangular. Anal plate greatly enlarged, slightly wider than high, surrounded by a semicircle of enlarged precloacal scales, the one on anterior position largest and transversely enlarged. Three pairs of transversely enlarged scales connect the last row of ventral scales and anteriormost precloacal. A series of 20/19 (left/right) femoral pores on each leg, separated by a pair of poreless, transversely enlarged scales in the middle. A vertebral series of paired, transversely enlarged plates, starts a short distance behind occipital and runs to tip of tail; otherwise, dorsal scales small and granular. A row of enlarged plates covers the anterior aspect of limbs; foreleg covered below by transversely enlarged plates, with four curved scales protruding posteriorly. Scales on palms and soles small, smooth, and granular, anteriormost row enlarged; toes III, IV and V fringed with serrated scales on basal half, distal half angled; LF4 11; LT4 19. Tail strongly depressed, covered with pairs of transversely enlarged plates along midline above and below; subtriangular lateral scales curved backwards form a serrated fringe along the edges of tail.

In preservative, background coloration on dorsum and top of head black; three pale longitudinal stripes on top of head, yellowish to greenish white: median one starting on tip of snout and fading a short distance behind occipital; on each side, another stripe starts on first supraocular and extends to nape, where both stripes become closer and restricted to the enlarged vertebral plates, sometimes reduced to series of spots posteriorly. Four additional pale stripes on dorsum and flanks: a pair of dorsolateral stripes starting behind eyes and a pair of lateral stripes starting behind lips, both extending to hindlimb insertion. Limbs blueish grey above; hands and feet blue. Ventral parts creamy white; outer edges of hindlimbs light blue; anal plate with a subtle blue tinge. Tail black with two series of blue spots or streaks above and below, each spot on an enlarged plate, more irregularly defined below; blue spots more uniform on basal portion of tail, alternating between slightly wider and narrower rows posteriorly. Serrated fringes greyish to creamy white on basal portion of tail, light blue posteriorly.

Variation: The paratype (Fig. 6) agrees almost entirely with the holotype in terms of scalation and coloration. Mensural and meristic data for the holotype and paratype are presented in Table 2.

Definition: *Holaspis ngalangi* sp. n. is defined by the following combination of characters: 1) Head, body and tail strongly depressed, with serrated fringes on hindlimbs and tail; 2) frontoparietals fused with interparietal; 3) two series of transversely enlarged vertebral plates along dorsum and tail; 4) dorsum black with three pairs of pale stripes, with paravertebral stripes confined to enlarged dorsal plates; 5) an uninterrupted series of paired, transversely enlarged scales between ventral and precloacal scales (see Fig. 7).

Diagnosis: *Holaspis ngalangi* sp. n. can be readily distinguished from both of its congeners, *H. guentheri* and *H. laevis*, by the presence of an uninterrupted series of paired, transversely enlarged scales between the last row of ventral scales and anteriormost precloacal scale (versus last ventral scales and anteriormost precloacal scale separated by at least one row of small granular scales in *H. guentheri* and *H. laevis*; see Fig. 7); it can be further distinguished from *H. laevis* by having a pair of dorsolateral stripes (versus only paravertebral and lateral stripes in *H. laevis*) and a pair of paravertebral stripes confined to enlarged dorsal plates (versus paravertebral stripes not confined to enlarged dorsal plates in *H. laevis*).

Distribution: The species is only known from Caconda and the Cusse River, in northern Huíla Province, Angola (Fig. 8). It is likely endemic to this region of the Angolan Plateau.

Habitat and natural history notes: Nothing is known about its natural history, as no field notes were provided by any of

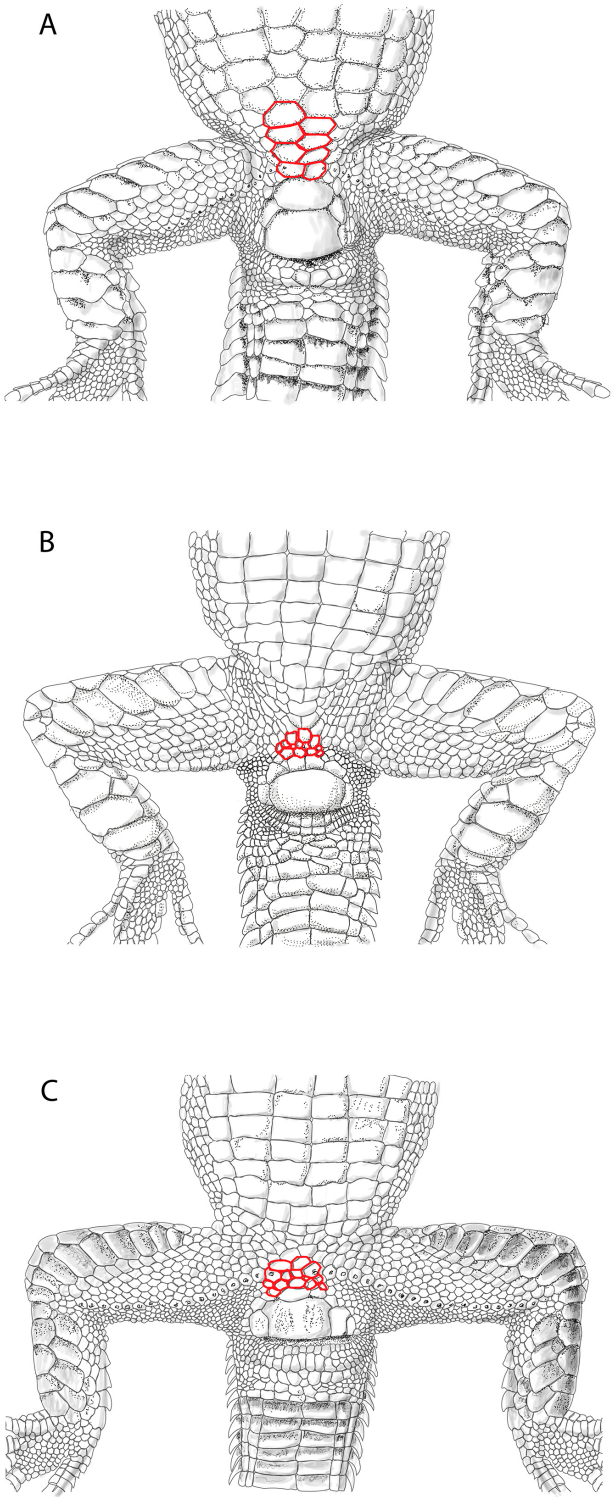

Figure 7. Drawings showing differences in the arrangement of scales between cloacal and ventral regions in *Holaspis* species: (A) paratype of *Holaspis ngalangi* sp. n. (BMNH 1906.8.24.57); (B) holotype of *Holaspis guentheri* (BMNH 1946.8.7.31); (C) holotype of *Holaspis laevis* (BMNH 1946.8.7.25). Drawings by Arthur Tiutenko.

the collectors, and it has not been recorded for more than 100 years. *Holaspis ngalangi* sp. n., like its congeners, is presumably an arboreal species, jumping and gliding between the branches of the forest canopy (Fig. 9).

Conservation status: Considering that the new species likely has the same ecological requirements as the other species on the genus (i.e., well preserved forests), the current rate of deforestation in Angola, and especially in the Angolan Central Plateau, where the Caconda region lies, poses serious threats to its survival (Fig. 9). The Angolan Central Plateau, which comprises Huambo, Bié and Huíla provinces, has been one of the most deforested areas in the continent (Cabral et al. 2011, Schneibel et al. 2016, 2017, Chiteculo et al. 2018, 2019, Mendelsohn & Mendelsohn 2018, Leite et al. 2018, Mendelsohn 2019, Catarino et al. 2020, Miapia et al. 2021, Powell et al. 2023). The current deforestation pattern has reached its peak in the last decades, but it has been an ongoing process since the late 19th century (Mendelsohn & Mendelsohn 2018, Mendelsohn 2019, Powell et el. 2023). The situation in the Caconda area is especially worrisome (Mendelsohn & Mendelsohn 2018, Mendelsohn 2019, Mendelsohn & Gomes 2023). During surveys in the area by our team since 2017, we have been able to observe the progression of deforestation activities (Fig. 10). The few observed areas with remaining healthy Miombo forests where the species might occur were very limited and sparse, usually associated with rock outcrops and steep slopes that render the terrain inaccessible and unsuitable for agriculture, or those associated with religious sites such as missions and graveyards. No specimens were observed during our surveys and no records other than those collected in the late 19th and early 20th centuries exist. The fact that Anchieta was based in the Caconda region for more than two decades and only collected one specimen suggests that the species was already rare in the late 19th century, especially considering that the region was covered by extensive forests at the time (Anchieta in Banha de Andrade 1985). This leads to the possibility that the species may already be extinct due to deforestation, or that it survives only in relict populations confined to the denser and more humid forests associated with riparian galleries. Nevertheless, our current data does not allow us to infer any IUCN Red List category other than Data Deficient (DD), which means that further surveys in the area are fundamental to assess the status of its populations, if still extant.

Etymology: The specific epithet "*ngalangi*" is a noun in apposition and is given in honor of the Ovimbundu Kingdom of Ngalangi, which dominated northern Huila Province and had its capital in present day Caconda. The Kingdom of Ngalangi was dismantled by the Portuguese during the Portuguese-Ovimbundu wars in the late 1760s. We suggest "Ngalangi Gliding Lizard" and "Lagartixa Planadora Galangue" as the English and Portuguese common names, respectively.

Updated key to the genus *Holaspis*

1a. Dorsum black with three pairs of pale longitudinal stripes; paravertebral stripes confined to enlarged dorsal plates 2

1b. Dorsum black with two pairs of pale longitudinal stripes; paravertebral stripes not confined to enlarged dorsal plates ..... *Holaspis laevis*

2a. Ventral and precloacal scales separated by at least one row of small granular scales .... *Holaspis guentheri*

2b. Last row of ventral scales and anteriormost precloacal scale connected by an uninterrupted series of paired, transversely enlarged scales .. *Holaspis ngalangi* sp. n.

Discussion

The description of *Holaspis ngalangi* sp. n. raises the number of *Holaspis* species occurring in Angola to two, and the total number of species in this highly specialized genus to three. The fact that the only known specimens of this new species were collected more than 100 years ago and remained forgotten until now highlights the importance of natural history collections for the description of biodiversity (Ceríaco 2015, Ceríaco et al. 2021, Ceríaco & Passos 2023, Major et al. 2023). The role of natural history collections assumes relevance in cases where historical material is used to describe new species which are potentially already extinct (Ceríaco & Passos 2023, Major et al. 2023).

Considering the lack of success in recent targeted surveys and the alarming rate of habitat loss in the region, it is possible that *Holaspis ngalangi* sp. n. is already extinct, similar to some other recently described reptiles (Ceríaco & Passos 2023, Major et al. 2023), although anecdotal reports from local villagers raise the possibility that the species is still extant in the Caconda region, likely confined to relict populations in isolated forest patches. The negative results of our surveys are probably due to a combination of factors, namely the low total search days, the elusive habits of the genus, closely associated with forest canopies, and the striking rate of deforestation in the region. The fact that Anchieta was only able to collect a single specimen, in the last days of his life, after more than 20 years of exploring the region suggests that *Holaspis ngalangi* sp. n. was already a rare species (or at least difficult to observe/collect) in the 19th century. Considering its probable dependence on well preserved woodlands, habitat loss in the Central Plateau represents a serious threat to any remaining populations of the species. This region of Angola has one of the highest deforestation rates, with increasing population density leading to the loss of woodlands to fire, crops, firewood and charcoal (Mendelsohn & Mendelsohn 2018, Mendelsohn 2019, Mendelsohn & Gomes 2023). Despite the existence of several areas of conservation interest with high levels of biodiversity and endemism in the central highlands of Angola, no formal conservation area has been designated to date (Marques et al. 2018, Huntley et al. 2019, Vaz Pinto et al. 2023). Without formal protection, woodlands and forests in the Central Plateau and Escarpment become increasingly diminished, with negative effects on biodiversity.

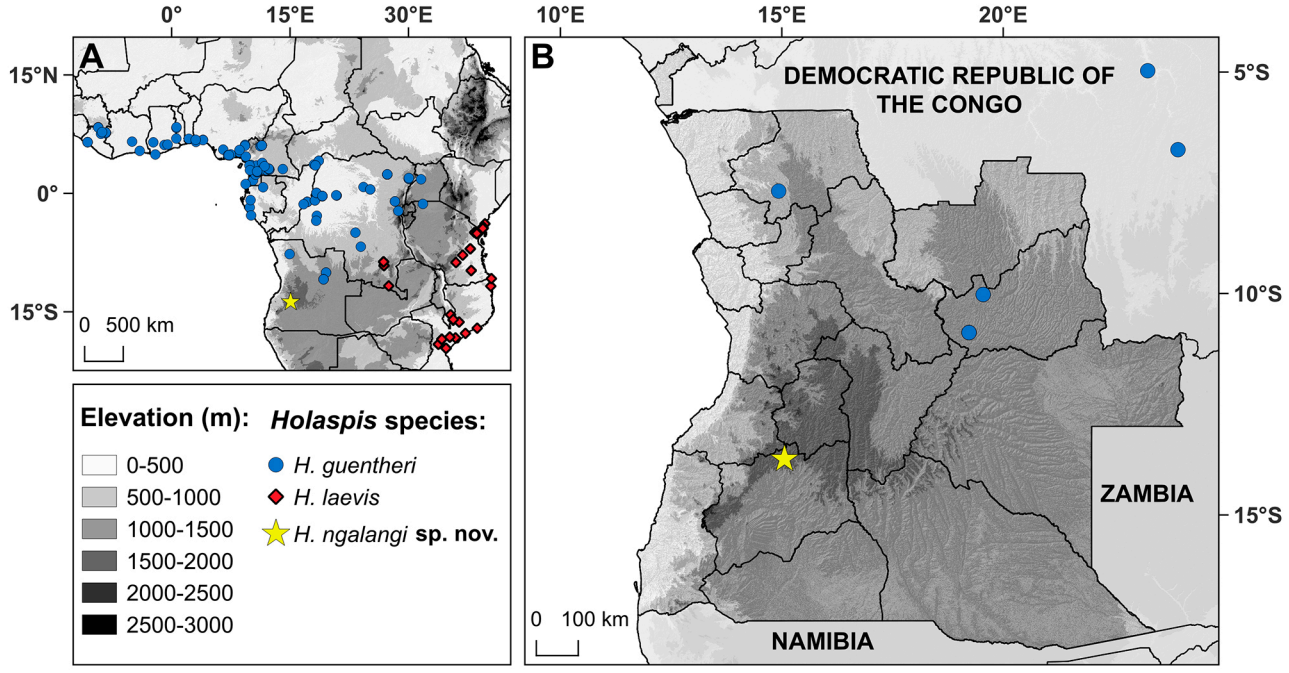

Figure 8. Maps showing the distribution of the genus *Holaspis* in Africa (A) and Angola (B).

With a clear distinction between West/Central and East African taxa, the biogeographic patterns observed in the genus *Holaspis* generally agree with those found in other Afrotropical lizards (Wagner et al. 2008, 2009, Greenbaum et al. 2011). The discovery of a new *Holaspis* species in the Angolan Central Plateau contributes to the growing body of knowledge on the biogeographical context of Angola's herpetofauna. The Angolan section of the Great Escarpment of southern Africa has already been noted as a hotspot of diversity and endemism for reptiles (Marques et al. 2018, Branch et al. 2019, Bauer et al. 2023), amphibians (Marques et al. 2018, Baptista et al. 2019, Becker et al. 2023), birds (Mills & Melo 2023) and mammals (Palmeirim et al. 2023). Caconda is located on the Angolan Central Plateau, bordering the Central Escarpment and Marginal Mountain Chain and their numerous inselbergs (Mendelsohn & Huntley 2023), where there is a confluence of reptile species with different biogeographic affinities. Some areas, especially those associated with riverine galleries and the Escarpment forests, present a southern continuity of ecological conditions for species with Guineo-Congolian affinities, such as *Panaspis cabindae* (Bocage, 1866), *Trachylepis maculilabris* (Gray, 1845) and *T. albilabris* (Hallowell, 1857) (Ceríaco et al. 2020b, 2024). On the other hand, species with Zambezian affinities are also found in the region, such as *T. attenboroughi* Ceríaco, Marques, Parrinha, Tiutenko, Weinell, Butler & Bauer, 2024 and *T. wahlbergii* (Peters, 1870) (Ceríaco et al. 2024). Among the endemic herpetofauna of the region, many species are affiliated with southern African taxa, such as *Afroedura wulfhaackei* Branch, Schmitz, Lobón-Rovira, Baptista, António & Conradie, 2021, *Cordylus angolensis* (Bocage, 1895) and *T. ansorgii* (Boulenger, 1907) (Bates et al. 2023, Conradie et al. 2023, Ceríaco et al. 2024), but we can also find local endemics with Central African affinities, as is the case of *Bitis heraldica* (Bocage, 1889) (Ceríaco et al. 2020c). Such biogeographic patterns generally also apply to other vertebrate groups, such as rodents, carnivores, ungulates, and birds (Rodrigues et al. 2015, Krásová et al. 2021, Mills & Mello 2023).

The interaction between climate and topography has played a significant role in the shaping of current patterns of reptile diversity and distribution in the region. Historical climatic shifts and consequent contraction of tropical forests have been hypothesized to be a driver of cladogenesis in Afrotropical lizards (Wagner et al. 2009, Greenbaum et al. 2011), and likely played a role in the evolution

Figure 9. Illustration of *Holaspis ngalangi* sp. n. in its putative habitat, with threats such as deforestation represented in the background. Drawing by Arthur Tiutenko.

Figure 10. Threats to *Holaspis ngalangi* sp. n. near Gungue village. (A) deforested area next to remaining patch of Miombo; (B) local villager chopping wood for personal use. Photos by Diogo Parrinha.

and isolation of *Holaspis ngalangi* sp. n.. This is a more general pattern that also applies in the case of the *Bitis* subgenus *Macrocerastes* and the divergence of the Afromontane endemic *B. heraldica* (Ceríaco et al. 2020c). Although Caconda lies in the wet Miombo woodland ecoregion (Huntley 2023), *Combretum collinum-Pericopsis angolensis* tree communities in the region contrast with typical Miombo associations of adjacent areas and are more similar to those found in East African Miombo woodlands (Chisingui et al. 2018). Furthermore, the vegetation from the woodlands that we sampled near Gungue village, bordering the Cuando River, shows some Afromontane elements previously recorded from Serra da Namba in Cuanza-Sul Province (Goyder et al. 2023). While targeted surveys and the collection of new material are fundamental for a proper assessment of the conservation status of *H. ngalangi* sp. n., its phylogenetic placement and the evolutionary history of the genus, further faunal and botanical surveys in the region may provide additional insights into the biogeography of the highlands of western Angola.

Acknowledgements

We thank the following curators, collections managers and technicians for providing access and photographs of specimens deposited in the collections at their care: Jeffrey Streicher and Patrick Campbell (BMNH); Olivier Pauwels (IRSNB); Ilunga André (MD); David Kizirian and Lauren Vonnahme (AMNH); David C. Blackburn and Coleman Sheehy III (UF); Esther Langan and Christina Keating-Sami (USNM); Erica Ely and Lauren Scheinberg (CAS); David Marques (NMB); Claudia Koch and Morris Flecks (ZFMK); Stevie Kennedy-Gold, Matthew Gage and Joe Martinez (MCZ); Annemarie Ohler, Stéphane Grosjean, Mathilde Aladini and Jérôme Courtois (MNHN); Garin Cael and Jonathan Brecko (RMCA); Mark Scherz and Daniel Johansson (ZMUC). Isabel Saluhana, a local teacher at Cusse village, is acknowledged here for her kind welcoming and valuable comments on the presence of forests in the region. Instituto Superior de Ciências da Educação da Huíla (ISCED) and Universidade Mandume Ya Ndemufayo (UMN), as well as the local authorities in Caconda, Cusse and Gungue are thanked for the logistical support. Philipp Wagner and an anonymous reviewer are thanked for providing relevant comments during the review process. Field work was supported by the US National Science Foundation (NSF grant DEB 2146654) and BIOPOLIS/CIBIO-InBIO (UIDP/50027/2020). Diogo Parrinha is currently supported by Fundação para a Ciência e Tecnologia (FCT grant 2021.05238.BD).

References

Angel, F., J. Guibé & M. Lamotte (1954): La reserve naturelle intégrale du mont Nimba. Fascicule II. Lézards. – Mémoires de l'Institut Français d'Afrique Noire, **40**: 371–379.

Arnold, E. N. (1989): Systematics and adaptative radiation of Equatorial African lizards assigned to the genera *Adolfus*, *Bedriagaia*, *Gastropholis*, *Holaspis* and *Lacerta* (Reptilia: Lacetidae). – Journal of Natural History, **23**: 525–555.

Arnold, E. N. (2002): *Holaspis*, a lizard that glided by accident: mosaics of cooption and adaptation on a tropical forest lacertid (Reptilia, Lacertidae). – Bulletin of the Natural History Museum of London, Zoology, **68**: 155–163.

Azevedo Pinho, A. (1897): Carta dando noticia da morte de Anchieta. – Arquivo Histórico Ultramarino, Lisboa. [Unpublished document]

Banha de Andrade, A. A. (1985): O Naturalista José de Anchieta. – Instituto de Investigação Científica Tropical, Centro de Estudos de História e Cartografia Antiga, Lisboa.

Baptista, N., W. Conradie, P. Vaz Pinto & W. R. Branch (2019): The amphibians of Angola: early studies and current state of knowledge. – pp. 243–281 in: Huntley, B. J., V. Russo, F. Lages & N. Ferrand (eds): Biodiversity of Angola: Science & Conservation, a modern synthesis. – Springer, Cham.

Barbour, T. & A. Loveridge (1928): A comparative study of the herpetological faunae of the Uluguru and Usambara mountains, Tanganyika Territory with descriptions of new species. – Memoirs of the Museum of Comparative Zoology, **50**: 84–265.

Bates, M. F., J. Lobón-Rovira, E. L. Stanley, W. R. Branch & P. Vaz Pinto (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.

Bauer, A. M., L. M. P. Ceríaco, M. P. Marques & F. S. Becker (2023): Highland reptiles of Angola and Namibia. – pp. 259–276 in: Mendelsohn, J., B. J. Huntley & P. Vaz Pinto (eds): Monograph on endemism in the highlands and escarpments of Angola and Namibia. – Namibian Journal of Environment, **8**.

Becker, F. S., N. Baptista, P. Vaz Pinto, R. Ernst & W. Conradie (2023): The amphibians of the highlands and escarpments of Angola and Namibia. – pp. 245–257 in: Mendelsohn, J., B. J. Huntley & P. Vaz Pinto (eds): Monograph on endemism in the highlands and escarpments of Angola and Namibia. – Namibian Journal of Environment, **8**.

Bocage, J. V. B. (1895): Herpétologie d'Angola et du Congo. – Ministério da Marinha e das Colónias, Lisboa.

Böhme, W., M.-O. Rödel, C. Brede & P. Wagner (2011): The reptiles (Testudines, Squamata, Crocodylia) of the forested southeast of the Republic of Guinea (Guinée forestière), with a country-wide checklist. – Bonn zoological Bulletin, **60**: 35–61.

Boulenger, G. A. (1887): Catalogue of the lizards in the British Museum (Natural History). Volume III. Lacertidae, Gerrhosauridae, Scincidae, Anelytropidae, Dibamidae, Chamaeleontidae. – Trustees of the British Museum (Natural History), London.

Boulenger, G. A. (1921): Monograph of the Lacertidae. Volume 2. – Trustees of the British Museum (Natural History), London.

Branch, W. R., P. Vaz Pinto, N. Baptista & W. Conradie (2019): The reptiles of Angola: history, diversity, endemism and hotspots. – pp. 283–334 in: Huntley, B. J., V. Russo, F. Lages & N. Ferrand (eds): Biodiversity of Angola: Science & Conservation, a modern synthesis. – Springer, Cham.

Broadley, D. G. (1963): An expedition to Tete and South Nyasaland. – Journal of the Herpetological Association of Rhodesia, **20**: 18–26.

Broadley, D. G. (2000): Geographical distribution. *Holaspis laevis* (Werner, 1895). – African Herp News, **35**: 13–14.

Broadley, D. G. & F. D. P. Cotterill (2004): The reptiles of southeast Katanga, an overlooked "hot spot". – African Journal of Herpetology, **53**: 35–61.

Cabral, A. I. R., M. J. Vasconcelos, D. Oom & R. Sardinha (2011): Spatial dynamics and quantification of deforestation in the central-plateau woodlands of Angola (1990–2009). – Applied Geography, **31**: 1185–1193.

Catarino, S., M. M. Romeiras, R. Figueira, V. Aubard, J. M. N. Silva & J. M. C. Pereira (2020): Spatial and temporal trends of burnt area in Angola: implications for natural vegetation and protected area management. – Diversity, **12**: 307.

Ceríaco, L. M. P. (2015): Lost in the middle of the sea, found in the back of the shelf: A new giant species of *Trachylepis* (Squamata: Scincidae) from Tinhosa Grande islet, Gulf of Guinea. – Zootaxa, **3973**: 511–527.

Ceríaco, L. M. P., M. P. Heinicke, K. L. Parker, M. P. Marques & A. M. Bauer (2020b): A review of the African snake-eyed skinks (Scincidae: *Panaspis*) from Angola, with the description of a new species. – Zootaxa, **4747**: 77–112.

Ceríaco, L. M. P., M. P. Marques, A. Ilunga, E. Afonso, D. Blackburn & A. M. Bauer (2020a): Illustrated type catalogue of the "lost" herpetological collections of the Museu do Dundo, Angola. – Bulletin of the Museum of Comparative Zoology, **162**: 379–440.

Ceríaco, L. M. P., M. P. Marques, D. Parrinha, A. Tiutenko, J. L. Weinell, B. O. Butler & A. M. Bauer (2024): The *Trachylepis* (Squamata: Scincidae) of Angola: an integrative taxonomic review with the description of seven new species. – Bulletin of the American Museum of Natural History, **465**: 1–153.

Ceríaco, L. M. P. & P. Passos (2023): Historical natural history collections allow the description of a new and presumably extinct species of dwarf gecko (Squamata: Gekkonidae: *Lygodactylus* Gray, 1864) from Fernando de Noronha Island, Brazil. – Anais da Academia Brasileira de Ciências, **95**: e20230222.

Ceríaco, L. M. P., B. S. Santos, M. P. Marques, A. M. Bauer & A. Tiutenko (2021): Citizen Science meets specimens in old formalin filled jars: a new species of Banded Rubber Frog, genus *Phrynomantis* (Anura, Phrynomeridae) from Angola. – Alytes, **38**: 18–48.

Ceríaco, L. M. P., K. A. Tolley, M. P. Marques, M. P. Heinicke & A. M. Bauer (2020c): A dwarf among Giants: phylogenetic position of the elusive Angolan Adder (*Bitis heraldica*) and biogeographic affinities of Angolan Afromontane regions. – African Journal of Herpetology, **69**: 108–118.

Chapin, J. P. (undated): Ansorge, William J.: summary of itineraries in Angola, 1903–1910. – Records of the American Geographical Society, New York. [Unpublished document]

Chisingui, A. V., F. M. P. Gonçalves, J. J. Tchamba, J. Camôngua Luís, M. F. F. Rafael & J. L. M. Alexandre (2018): Vegetation survey of the woodlands of Huíla Province. – pp. 426–437 in: Revermann, R., K. M. Krewenka, U. Schmiedel, J. M. Olwoch, J. Helmschrot & N. Jürgens (eds): Climate change and adaptive land management in southern Africa – assessments, changes, challenges, and solutions. – Biodiversity & Ecology, **6**. – Klaus Hess Publishers, Göttingen & Windhoek.

Chiteculo, V., A. Abdollahnejad, D. Panagiotidis, P. Surovy & R. P. Sharma (2019): Defining deforestation patterns using satellite images from 2000 and 2017: assessment of forest management in Miombo forest – a case study of Huambo Province in Angola. – Sustainability, **11**: 98.

Chiteculo, V., B. Lojka, P. Surovy, V. Verner, D. Panagiotidis & J. Woitsch (2018): Value chain of charcoal production and implications for forest degradation: case study of Bié Province, Angola. – Environments, **5**: 113.

Conradie, W., G. B. Bittencourt-Silva, H. M. Engelbrecht, S. P. Loader, M. Menegon, C. Nanvonamuquitxo, M. Scott & K. A. Tolley (2016): Exploration into the hidden world of Mozambique's sky island forests: new discoveries of reptiles and amphibians. – Zoosystematics and Evolution, **92**: 163–180.

Conradie, W., J. Lobón-Rovira, F. S. Becker, A. Schmitz & P. Vaz Pinto (2023): Flat gecko (*Afroedura*) diversity, endemism and speciation in the highlands and escarpments of Angola and Namibia. – pp. 277–281 in: Mendelsohn, J., B. J. Huntley & P. Vaz Pinto (eds): Monograph on endemism in the highlands and escarpments of Angola and Namibia. – Namibian Journal of Environment, **8**.

Cott, H. B. (1934): The Zoological Society's Expedition to the Zambesi, 1927. 5. On a collection of lizards, mainly from Portuguese East Africa, with descriptions of new species of *Zonurus*, *Monopeltis*, and *Chirindia*. – Proceedings of the Zoological Society of London, **1934**: 145–173.

Darko, Y.A., O. Voss & P. Uetz (2022): A dictionary of abbreviations used in reptile descriptions. – Zootaxa, **5219**: 421–432.

De Queiroz, K. (1999): The general lineage concept of species, species criteria, and the process of speciation. – pp. 57–75 in: Howard, D. J. & S. H. Berlocher (eds): Endless forms: species and speciation. – Oxford University Press, New York.

De Witte, G. F. (1953): Exploration du Parc National de l'Upemba. Mission G.F. de Witte en collaboration avec W. Adam, A. Janssens, L. Van Meel et R. Verheyen (1946–1949). Fascicule 6. Reptiles. – Institut des Parcs Nationaux du Congo Belge, Bruxelles.

De Witte, G. F. & R. Laurent (1942): Liste des Lacertidae du Congo belge et description d'une espèce nouvelle. – Revue de Zoologie et de Botanique Africaines, **36**: 165–180.

Dunger, G. T. (1967): The Lizards and Snakes of Nigeria. Part 2: the lacertids of Nigeria. – The Nigerian Field, **32**: 117–131.

Ernst, R. (2015): A rapid assessment of the herpetofauna of the Serra do Pingano ecosystem in Uíge Province, northern Angola. Instituto Nacional da Biodiversidade e Áreas de Conservação, Ministério do Ambiente, Luanda. [Unpublished document]

Ernst, R., T. Lautenschläger, M. F. Branquima & M. Hölting (2020): At the edge of extinction: a first herpetological assessment of the proposed Serra do Pingano rainforest national Park in Uíge Province, northern Angola. – Zoosystematics and Evolution, **96**: 237–262.

Ferreira, J. B. (1897): Lista dos reptis e amphibios que fazem parte da ultima remessa de J. d'Anchieta. – Jornal de Sciencias Mathematicas, Phyisicas e Naturaes, **2**: 129–137.

Ferreira, R. (2022): iNaturalist observation. – https://www.inaturalist.org/observations/109576310, accessed on 5 March 2024.

Gonçalves, F. M. P., R. Revermann, A. L. Gomes, M. P. M. Aidar, M. Finckh & N. Jürgens (2017): Tree species diversity and composition of Miombo woodlands in South-Central Angola: a chronosequence of forest recovery after shifting cultivation. – International Journal of Forestry Research, **2017**: 6202093.

Goyder, D. J., A. L. Gomes, F. M. P. Gonçalves, J. C. Luís & I. Darbyshire (2023): A botanical assessment of Mt Namba, Cuanza-Sul, Angola: an isolated mountain towards the northwestern limits of the Great Escarpment of southern Africa. – pp. 77–92 in: Mendelsohn, J., B. J. Huntley & P. Vaz Pinto (eds): Monograph on endemism in the highlands and escarpments of Angola and Namibia. – Namibian Journal of Environment, **8**.

Grandvaux-Barbosa, L. A. (1970): Carta fitogeográfica de Angola. – Instituto de Investigação Científica de Angola, Luanda.

Gray, J. E. (1863): Descriptions of two new genera of lizards (*Holaspis* and *Poriodogastar*, A. Smith, MS.). – Proceedings of the Zoological Society of London, **1863**: 152–155 + pls. 10–11.

Greenbaum, E., C. O. Villanueva, C. Kusamba, M. M. Aristote & W. R. Branch (2011): A molecular phylogeny of Equatorial African Lacertidae, with the description of a new genus and species from eastern Democratic Republic of the Congo. – Zoological Journal of the Linnean Society, **163**: 913–942.

Huntley, B. J. (2023): Ecology of Angola: terrestrial biomes and ecoregions. – Springer, Cham.

Huntley, B. J., P. Beja, P. Vaz Pinto, V. Russo, L. Veríssimo & M. Morais (2019): Biodiversity conservation: history, protected areas and hotspots. – pp. 495–512 in: Huntley, B. J., V. Russo, F. Lages & N. Ferrand (eds): Biodiversity of Angola: Science & Conservation, a modern synthesis. – Springer, Cham.

Ineich, I. (2003): Contribution à la connaissance de la biodiversité des régions afro-montagnardes: les reptiles du mont Nimba. – pp. 597–637 in: Lamotte, M. & R. Roy (eds): Le peuplement animal du mont Nimba (Guinée, Côte d'Ivoire, Liberia). – Mémoires du Muséum national d'Histoire naturelle, **190.**

Krásová, J., O. Mikula, J. Bryja, N. L. Baptista, T. António, T. Aghová & R. Šumbera (2021): Biogeography of Angolan rodents: The first glimpse based on phylogenetic evidence. – Diversity and Distributions, **27**: 2571–2583.

Laurent, R. F. (1964): Reptiles et amphibiens de l'Angola (Troisème contribution). – Publicações Culturais da Companhia de Diamantes de Angola, **67**: 1–165.

Leite, A., A. Cáceres, M. Melo, M. S. L. Mills & A. T. Monteiro (2018): Reducing emissions from deforestation and forest degradation in Angola: insights from the scarp forest conservation 'hotspot'. – Land Degradation & Development, **29**: 4291–4300.

Loveridge, A. (1951): On reptiles and amphibians from Tanganyika Territory collected by C. J. P. Ionides. – Bulletin of the Museum of Comparative Zoology, **106**: 175–204.

Loveridge, A. (1953): Zoological results of a fifth expedition to East Africa III. Reptiles from Nyasaland and Tete. – Bulletin of the Museum of Comparative Zoology, **91**: 235–373.

Loveridge, A. (1955): On a second collection of reptiles and amphibians taken in Tanganyika Territory by C. J. P. Ionides, Esq.. – Journal of the East African Natural History Society, **22**: 169–198.

Major, T., P. Renk, J. Reissing, J. L. A. Paijmans, E. Morris, M. Hofreiter, A. Barlow, D. G. Broadley & W. Wüster (2023): Museum DNA reveals a new, potentially extinct species of rinkhals (Serpentes: Elapidae: *Hemachatus*) from the Eastern Highlands of Zimbabwe. – PLoS ONE, **18**: e0291432.

Malonza, P. K. & A. M. Bauer (2014): A new species of arboreal forest-dwelling gecko (*Hemidactylus*: Squamata: Gekkonidae) from coastal Kenya, East Africa. – Zootaxa, **3786**: 192–200.

Malonza, P. K., D. M. Mulwa, J. O. Nyamache & G. Jones (2018): Biogeography of the Shimba Hills ecosystem herpetofauna in Kenya. – Zoological Research, **39**: 97–104.

Marques, M. P., L. M. P. Ceríaco, D. C. Blackburn & A. M. Bauer (2018): Diversity and distribution of the amphibians and terrestrial of Angola. Atlas of Historical and Bibliographic records (1840–2017). – Proceedings of the California Academy of Sciences, Series 5, **65** (Supplement II): 1–501 + Appendix.

Matschie, P. (1892): Über eine kleine Sammlung von Säugethieren und Reptilien, welche Herr L. Conradt aus Usambara (Deutsch Ostafrika) heimgebracht hat. – Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin, **1892**: 101–110.

Mendelsohn, J. M. (2019): Landscape changes in Angola. – pp. 123–140 in: Huntley, B. J., V. Russo, F. Lages & N. Ferrand (eds): Biodiversity of Angola: Science & Conservation, a modern synthesis. – Springer, Cham.

Mendelsohn, J. M. & A. L. Gomes (2023): The human environment in the highlands and escarpments of Angola and Namibia. – pp. 43–51 in: Mendelsohn, J., B. J. Huntley & P. Vaz Pinto (eds): Monograph on endemism in the highlands and escarpments of Angola and Namibia. – Namibian Journal of Environment, **8**.

Mendelsohn, J. M. & B. J. Huntley (2023): Introducing the highlands and escarpments of Angola and Namibia. – pp. 7–22 in: Mendelsohn, J., B. J. Huntley & P. Vaz Pinto (eds): Monograph on endemism in the highlands and escarpments of Angola and Namibia. – Namibian Journal of Environment, **8**.

Mendelsohn, J. & S. Mendelsohn (2018): South West Angola. – Arte & Ciência, Porto.

Miapia, L. M., D. Ariza-Mateos, V. Lacerda-Quartín & G. Palacios-Rodríguez (2021): Deforestation and biomass production in Miombo forest in Huambo (Angola): a balance between local and global needs. – Forests, **12**: 1557.

Mills, M. & M. Melo (2023): Birds of the highlands and escarpments of Angola and Namibia: ornithological significance, avifaunal patterns and questions requiring further study. – pp. 293–309 in: Mendelsohn, J., B. J. Huntley & P. Vaz Pinto (eds): Monograph on endemism in the highlands and escarpments of Angola and Namibia. – Namibian Journal of Environment, **8**.

Monard, A. (1937): Contribution à l'Herpétologie d'Angola. – Arquivos do Museu Bocage, **8**: 19–154.

Müller, F. (1885): Vierter Nachtrag zum Katalog der herpetologischen Sammlung des Basler Museums. – Verhandlungen der Naturforschenden Gesellschaft in Basel, **7**: 668–717.

Palmeirim, A. F., A. Monadjem, P. Vaz Pinto, P. Taylor, M. S. Svensson & P. Beja (2023): Mammal endemism in the highlands and escarpments of Angola and Namibia. – pp. 311–322 in: Mendelsohn, J., B. J. Huntley & P. Vaz Pinto (eds): Monograph on endemism in the highlands and escarpments of Angola and Namibia. – Namibian Journal of Environment, **8**.

Pauwels, O. S. G., L. Bahaa-el-din, J.-L. Albert, P. Carlino, F. Giannuzzi, L. Chirio, J.-F. Gillet, E. Poirier & T. Stévart (2018): Miscellanea Herpetologica Gabonica XIV. – Bulletin of the Chicago Herpetological Society, **53**: 185–190.

Pauwels, O. S. G. & S. Itam (2013): *Holaspis guentheri* (Günther's gliding lizard) predation. – Herpetological Review, **44**: 674–675.

Pietersen, D., L. Verburgt & J. Davies (2021): Snakes and other reptiles of Zambia and Malawi. – Struik Nature, Cape Town.

Powell, L. L., P. Vaz Pinto, M. S. L. Mills, N. L. Baptista, K. Costa, K.-D. B. Dijkstra, A. L. Gomes, P. Guedes, T. Júlio, A. Monadjem, A. F. Palmeirim, V. Russo & M. Melo (2023): The last Afromontane forests in Angola are threatened by fires. – Nature Ecology & Evolution, **7**: 628–629.

Rodrigues, P., R. Figueira, P. Vaz Pinto, M. B. Araújo & P. Beja (2015): A biogeographical regionalization of Angolan mammals. – Mammal Review, **45**: 103–116.

Schmidt, K. P. (1919): Contributions of the herpetology of the Belgian Congo based on the collection of the American Museum Congo Expeditions, 1909–1915. Part 1, turtles, crocodiles, lizards and chameleons. – Bulletin of the American Museum of Natural History, **39**: 385–624 + pls. 7–32.

Schneibel, A., M. Stellmes, A. Order, D. Frantz, B. Kowalski, E. Hass & J. Hill (2017): Assessment of spatio-temporal changes of smallholder cultivation patterns in the Angolan Miombo belt using segmentation of Landsat time series. – Remote Sensing of Environment, **195**: 118–129.

Schneibel, A., M. Stellmes, A. Röder, M. Finckh, R. Revermann, D. Frantz & J. Hill (2016): Evaluating the trade-off between food and timber resulting from the conversion of Miombo forests to agricultural land using multi-temporal Landsat data. – Science of the Total Environment, **548–549**: 390–401.

Spawls, S., K. Howell, H. Hinkel & M. Menegon (2018): Field guide to east African reptiles. 2nd edition. – Bloomsbury, London, New Delhi, New York, Sydney.

Tornier, G. (1897): Die Kriechthiere Deutsch-Ost-Afrikas. Beitrage zur Systematik und Descendenzlehre. – Geographisce Verlagsbuchhandlung Dietrich Reimer, Berlin.

Trape, J.-F., S. Trape & L. Chirio (2012): Lézards, crocodiles et tortues d'Afrique occidentale et du Sahara. – IRD Éditions, Marseille.

Ullenbruch, K., O. Grell & W. Böhme (2010): Reptiles from southern Benin, West Africa, with the description of a new *Hemidactylus* (Gekkonidae), and a country-wide checklist. – Bonn zoological Bulletin, **57**: 31–54.

Vaz Pinto, P., V. Russo & L. Veríssimo (2023): The highlands in Angolan conservation areas. – pp. 53–62 in: Mendelsohn, J., B. J. Huntley & P. Vaz Pinto (eds): Monograph on endemism in the highlands and escarpments of Angola and Namibia. – Namibian Journal of Environment, **8**.

Wagner, P., W. Böhme, O. S. G. Pauwels & A. Schmitz (2009): A review of the African red-flanked skinks of the *Lygosoma fernandi* (Burton, 1836) species group (Squamata: Scincidae) and the role of climate change in their speciation. – Zootaxa, **2050**: 1–30.

Wagner, P., J. Köhler, A. Schmitz & W. Böhme (2008): The biogeographical assignment of a west Kenyan rain forest remnant: further evidence from analysis of its reptile fauna. – Journal of Biogeography, **35**: 1349–1361.

Werner, F. (1895): Ueber einige Reptilien aus Usambara (Deutsch-Ostafrika). – Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien, **45**: 190–194.