Zoosyst. Evol. 101 (2) 2025, 887–906 | DOI 10.3897/zse.101.136290

A needle in a haystack: Rediscovery and revised description of *Ichnotropis microlepidota* Marx, 1956, from the central highlands of Angola

Max Benito[1], Werner Conradie[2,3,4], Pedro Vaz Pinto[5,6,7,8], Javier Lobón-Rovira[5,6]

1 *Universidad Internacional Menéndez Pelayo, Calle de Isaac Peral 23, 28040 Madrid, Spain*
2 *Port Elizabeth Museum, 23 Beach Road, Humewood, Gqeberha, South Africa*
3 *School of Natural Resource Management, Nelson Mandela University (George Campus), George, South Africa*
4 *National Geographic Okavango Wilderness Project, Wild Bird Trust, Okavango, South Africa*
5 *CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Campus de Vairão, Universidade do Porto, 4485-661 Vairão, Portugal*
6 *BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Campus de Vairão, 4485-661 Vairão, Portugal*
7 *TwinLab CIBIO/ISCED, Instituto Superior de Ciências da Educação da Huíla, Rua Sarmento Rodrigues s/n, Lubango, Angola*
8 *Fundação Kissama, Rua 60 Casa 560, Lar do Patriota, Luanda, Angola*

https://zoobank.org/4DFDA337-6ADD-4AC4-AD3C-D50C6222C32D

Corresponding author: Javier Lobón-Rovira (j.lobon.rovira@cibio.up.pt)

Academic editor: Johannes Penner ♦ **Received** 3 September 2024 ♦ **Accepted** 21 February 2025 ♦ **Published** 25 April 2025

Abstract

Ichnotropis is a genus of small and elusive ground-dwelling lizards mostly distributed in the savannas and woodlands south of the Congo River. The genus comprises six nominal species and three subspecies; however, the phylogenetic hypothesis of this group and the taxonomical status of several taxa remain unresolved. Among these species, *Ichnotropis microlepidota* stands out, as it is only known from the type series since its discovery in the 1950s in the crop of a Chanting Goshawk in Mount Moco, in the central highlands of Angola. Consequently, due to the lack of a precise locality and its similar morphology to other species, the taxonomic status of this species has been debated by several authors. Thanks to the collection of new material across the Angolan territory, we take the opportunity to revise the group, using molecular and morphological techniques. Thus, we here provide the first phylogenetic hypothesis of the group in Angola and therefore a phylogenetic placement of *I. microlepidota*. As a result, we validate the taxonomic status of this elusive species and demonstrate that it represents a distinct taxon within the *bivittata* group, differing by 14.99% *16S* uncorrected p-distance from *I. bivittata*. Furthermore, we undertake an updated description of this species, providing additional external and internal (i.e., cranial osteology) morphological features that can be used to compare *I. microlepidota* with other members of the group. Finally, we identified two candidate new species from Angola and corroborated the importance of the central highlands of Angola as an important center of endemism in the western slope of Central Africa.

Key Words

Africa, CT scan, endemic, grasslands, herpetology, Lacertidae, Mount Moco

Introduction

Among reptiles, lizards have the highest proportion of species known only from their type localities, type series, or both combined, with several species known from a single specimen (Meiri et al. 2018). This is due to different factors, such as difficult-to-detect or elusive species (i.e., strictly fossorial species or canopy specialists), cryptic species that are challenging to identify or to distinguish from others in the field, or species that distribute across conflict zones and consequently are poorly surveyed or currently inaccessible (Tolley et al. 2016; Meiri et al. 2018).

Nonetheless, despite the growing number of recent rediscoveries (Rodrigues et al. 2013; Prates et al. 2017; Solano-Zavaleta et al. 2017; Wang et al. 2017; Baptista et al. 2020; Putra et al. 2020; Bates et al. 2023; Cowan et al. 2024), many species remain 'lost' and needs further investigation (Meiri et al. 2018; Lindken et al. 2024).

Notwithstanding, while Africa hosts nine out of the 34 biodiversity hotspots in the world, its biodiversity remains poorly known and understudied (Böhm et al. 2013; Deikumah et al. 2014; Tolley et al. 2016). This is mainly a consequence of political pressure and social instability in the continent, the difficult access to many areas, and the lack of resources in the territory (Rydén et al. 2020; Ogwu et al. 2022). All these situations have hampered scientific surveys in this still poorly explored continent. The case of Angola is remarkable. After the war of independence (1961–1975), it suffered nearly a 40-year-long civil war (1975–2002) that almost completely precluded any fieldwork or biodiversity research (Marques et al. 2018; Baptista et al. 2019).

The first herpetological surveys in Angola date from the 19th century during the colonial era, led mainly by European and western countries, like Portugal, England, the United States of America, or Germany (Marques et al. 2018; Baptista et al. 2019). In the last decade, political stabilization in Angola has motivated numerous expeditions to previously understudied or poorly explored areas across the country. Consequently, access to new material, coupled with the advancement of molecular techniques and morphological analysis, has led to the description of several new taxa (Conradie et al. 2012a, b, 2013, 2020, 2022a, b; Stanley et al. 2016; Ceríaco et al. 2018, 2020a, b, d, e, 2021, 2024; Branch et al. 2019a, b, c, 2021; Marques et al. 2019, 2020a, b, 2022b, 2023a, b, 2024a, b; Hallermann et al. 2020; Nielsen et al. 2020; Baptista et al. 2021, 2023; Lobón-Rovira et al. 2021b, 2022, 2024b; Parrinha et al. 2021; Wagner et al. 2021; Bates et al. 2023), several new species records (Marques et al. 2018, 2022a, 2023a, b, 2024a; Butler et al. 2019; Conradie et al. 2021, 2022b, 2023; Lobón-Rovira et al. 2022, 2024a, c) and some species rediscoveries (Branch et al. 2018; Baptista et al. 2020; Bates et al. 2023). However, some groups are better known than others, with some groups still poorly studied in Angola (e.g., *Ichnotropis*, *Agama* ~ Conradie, 2024, or *Leptopelis* ~ Baptista, 2024).

The family Lacertidae comprises ~370 species distributed in the more arid regions of Europe, Africa, and Asia (Uetz et al. 2025). Notably, southern Africa represents a high center for lacertid diversity (Branch 1998), which includes eight different genera, of which six are present in Angola: *Ichnotropis*, *Heliobolus*, *Holaspis*, *Meroles*, *Nucras*, and *Pedioplanis* (Branch et al. 2019a). In recent years, some of these genera have undergone taxonomic revisions in Angola (i.e., *Heliobolus* ~Marques et al. 2022b, *Nucras* ~Baptista et al. 2020; Branch et al. 2019a and *Pedioplanis* ~Conradie et al. 2012b; Parrinha et al. 2021). However, other groups like *Ichnotropis* have never been studied in detail, mainly due to the lack of fresh material and the highly problematic taxonomy of the group (van den Berg 2017).

Ichnotropis is a genus of small-sized African lizards (van den Berg 2017) with a wide distribution in the southern and eastern rim of the Congo River Basin, ranging from South Africa to Gabon in the west and northwards to the eastern coast of Tanzania. Exceptionally, *Ichnotropis chapini* Schmidt, 1919, has only been recorded from Adra, northern Democratic Republic of the Congo (DRC), close to the border with South Sudan, and seems to be isolated from all other *Ichnotropis* species (Schmidt 1919; Edwards et al. 2013; Engleder et al. 2013; van den Berg 2017). *Ichnotropis* lizards normally inhabit dry woodland savanna habitats, although they are also present in sandy deserts and even in relatively humid environments (van den Berg 2017).

This genus contains a total of six recognized species (*I. bivittata* Bocage, 1866, *I. capensis* (Smith, 1838), *I. chapini* Schmidt, 1919, *I. grandiceps* Broadley, 1967, *I. microlepidota* Marx, 1956, and *I. tanganicana* Boulenger, 1917) and several subspecies with questionable validity (e.g., *I. b. pallida* Laurent, 1964, *I. c. nigrescens* Laurent, 1952, and *I. c. overlaeti* Laurent, 1964). Six of these taxa have been recorded within Angolan territory (i.e., *I. b. bivittata*, *I. b. pallida*, *I. c. capensis*, *I. c. overlaeti*, *I. microlepidota*, and *I.* cf. *grandiceps*) (Marques et al. 2018; Conradie et al. 2022b). Not surprisingly, these elusive lizards have been poorly studied, with some of the species being only known from their type series, such as *I. microlepidota*, *I. tanganicana*, and *I. chapini* (van den Berg 2017). In addition, the lack of fresh material has prevented phylogenetic studies from exploring interspecific relationships of this group. Rarity in the observations of these lizards can be due to the fact that several sympatric species display a unique 'annual' reproductive strategy, in which their breeding cycles happen asynchronously, thus reducing competition between them (Broadley 1967, 1974, 1979; Jacobsen 1987) and potentially between juveniles and adults. Therefore, due to the above-mentioned elusive character of these lizards, information about their general ecology and biology in most of their representatives remains unknown or poorly understood.

Morphologically, the genus can be subdivided into two main groups, the *capensis* group, which only includes *I. capensis* and subspecies, and the *bivittata* group, which includes *I. bivittata*, *I. microlepidota*, and *I. tanganicana* (Boulenger 1921; Marx 1956; van den Berg 2017). *Ichnotropis chapini* is believed to be part of the *capensis* group (Schmidt 1919). The *capensis* group is characterized by having a more elongated and sharper snout than the species in the *bivittata* group (i.e., *I. bivittata*, *I. microlepidota*, and *I. tanganicana*), prefrontal scales usually not in contact with anterior supraocular scales, and well-defined head striations (Boulenger 1921; Marx 1956). On the other hand, the *bivittata* group normally has prefrontal scales in contact with the anterior supraocular, weakly defined head striations, and a much shorter and rounded snout (Boulenger 1921; Marx 1956). It is unclear to which of these groups *I. grandiceps* belongs, but it is considered closely related to *I. capensis* (Broadley 1967). Of all six recognized species, the taxonomic placement and validity of *I. microlepidota* has been the most controversial and discussed in recent years (Mayer 2013; Edwards et al. 2013; van den Berg 2017).

Ichnotropis microlepidota was described in 1956, when five specimens (FMNH 74283–74287) were removed from the crop of a Dark Chanting Goshawk (*Melierax metabates*) that was collected from the base of Mount Moco, Huambo Province, during a bird survey (Marx 1956). However, some authors have questioned the validity of this species and its distribution, suggesting that these specimens may have been transported by the goshawk from another locality (van den Berg 2017). Nevertheless, a series of apomorphic characters in *I. microlepidota*, which support its taxonomic recognition, including prefrontals in contact with anterior supraoculars, a row of smaller scales separating the supraciliaries from the supraoculars, and a more rounded snout, has motivated some authors to consider the species as related to the *bivitatta* group (Marx 1956; Edwards et al. 2013; van den Berg 2017). However, *I. microlepidota* differs from *I. bivitatta* by having smaller-sized dorsal scales, having more scales around midbody (43–50 vs. 32–39), and a lower number of subdigital lamellae under the fourth toe (16–17 vs. 19–21) (Marx 1956). It is noteworthy that prior to Marx's examination, Parker (1936) recorded a juvenile *Ichnotropis* from Mount Moco (1500–1900 m. a.s.l.), which he tentatively identified as *I. bivittata*, but noted some different characters (specifically, smaller scales and higher midbody scale rows [45–56]) that indicated it possibly being a distinct species from *I. bivittata*. Since then, no more individuals have been found. Therefore, the taxonomic status of *I. microlepidota* remains the subject of debate, as highlighted by Edwards et al. (2013), who suggested that resolution could only come through new material enabling a phylogenetic revision of this enigmatic genus.

The Central Highlands of Angola are represented by an archipelago of Afromontane forest pockets surrounded by montane grasslands with numerous peaks exceeding 2000 m. a.s.l. (Lobón-Rovira and Bauer 2021). Therefore, it is noteworthy to mention an *Ichnotropis* specimen photographed in Mount Namba that was documented in van den Berg (2020) as possibly being *I. microlepidota*. Although finally it could not be properly identified from the pictures, and the specimen was tentatively assigned to *I. bivittata*. This record should be taken into consideration due to Mount Namba having similar or identical habitat traits as Mount Moco and that they already share some endemic species (e.g., *Bitis heraldica* Boulenger, 1887 (Ceríaco et al. 2020c)).

With this work we aim to shed light on the taxonomic status of *I. microlepidota* and provide an updated phylogenetic hypothesis of this group in Angola. To achieve this goal, we implemented a robust phylogenetic analysis to revisit the taxonomic status of the different taxa recorded from Angola, based on the most complete molecular data, internal (3D osteological reconstruction of the skull), external morphological data, and distribution. This helped us to provide a phylogenetic placement of *I. microlepidota*, but also to corroborate if this species is part of the *bivittata* group as previously thought or, in contrast, if the species is more closely related to the *capensis* group.

Materials and methods

Sampling

Material of *Ichnotropis* spp. (specimens and tissue samples) has been collected across the Angolan territory between 2012 and 2021. Target sites included Mount Moco Special Reserve, Huambo Province, and Calandula (=Duque de Braganca), Malanje Province, for being the type localities of *I. microlepidota* and *I. bivittata*, respectively. In October 2020, an adult male, morphologically identified as *I. microlepidota*, was collected at Mount Moco (-12.4554, 15.1632). Nevertheless, despite the fact that we failed to collect fresh topotypic material of *I. bivittata*, additional material of *I. bivittata*, *I. capensis*, and *I.* cf. *grandiceps* was collected across the territory (Table 1) (Baptista et al. 2019; Conradie et al. 2023). The final dataset included 38 newly collected specimens of four Angolan *Ichnotropis* spp. (Table 1). Tissue samples and/or vouchers were collected. Vouchers were euthanized with an injection of tricaine methanesulphonate (MS222) (Conroy et al. 2009). After euthanasia, liver or muscle samples were collected for the phylogenetic analyses and stored in 95–99% ethanol. The individuals were fixed in 10% formalin, after which they were transferred to 70% ethanol for long-term storage in the Museu de História Natural e da Ciência—Universidade do Porto (MHNC-UP), Porth Elizabeth Museum (PEM), and Fundação Kissama Collection (FKH) herpetological collections. For each sample collected, the locality was recorded using the WGS84 coordinate datum.

Phylogenetic data

We extracted DNA from newly collected material using the EasySpin Genomic DNA Tissue Kit (Citomed, Portugal), following the manufacturer´s protocols. Concentrations were 5 µl PCR Master Mix, 0.4 µl of each primer, 3.2 µl H2O, and 1–3 µl DNA (DNA elution was adjusted to extraction results). Two mitochondrial genes, a partial mitochondrial ribosomal gene (*16S* rRNA; 511 bp) and a mitochondrial encoded gene *ND4* (802 bp), and two partial fragments of a nuclear gene (*RAG-1* ~985 bp and *c-mos* ~337 bp) were generated for most of the tissue samples detailed in Table 1. Primer and PCR reaction details are summarized in Table 2. The prepared PCR products were purified and sequenced at the Centre for Molecular Analysis (CTM-CIBIO, Porto, Portugal) and Macrogen Corp. (Amsterdam, Netherlands). Sequences were checked and edited using Geneious Prime v.2024.0.5 (http://www.geneious.com/) and aligned using the MUSCLE plugin for Geneious. All sequences have been deposited in GenBank (Table 1).

Table 1. List of material used for the phylogenetic analyses, including information on their catalog number, field number, country, localities, decimal geographic coordinates, and GenBank ascension numbers. Abbreviations: Aaron M. Bauer field numbers (AMB), California Academy of Sciences (CAS), Krystal Tolley field numbers (KTH, RSP, WP), Museu de História Natural e da Ciência - Universidade do Porto (MHNCUP), Ninda Baptista field numbers (NB), Pedro Vaz Pinto field numbers (P, L series), Port Elizabeth Museum (PEM), Stuart V. Nielsen field numbers (SVN), Thomas Branch field numbers (TB), Werner Conradie field numbers (WC, ANG). Missing data or unavailable information is indicated as Missing Data (–).

Species	Catalog No.	Field Number	Country	Locality	Latitude, Longitude	*16S*	*ND4*	*RAG1*	*C-mos*	Source
I. aff. grandiceps	PEM R23306	WC-3969	Angola	4 km upstream from Cuanavale River source	-13.5080, 18.8973	PV357715	PV412835	PV412862	PV390640	This work
I. aff. grandiceps	PEM R23420	WC-4816	Angola	Cuando River source	-13.0035, 19.1275	PV357716	PV412836	–	–	This work
I. aff. grandiceps	PEM R23362	WC-4056	Angola	drive to Cuanavale camp from Samanunga village	-13.0380, 18.8298	PV357717	PV412837	PV412863	–	This work
I. aff. grandiceps	PEM R23279	WC-3994	Angola	Cuanavale River source	-13.0903, 18.8940	PV357718	PV412838	PV412864	–	This work
I. b. bivittata	–	NB0675	Angola	Luando Integral Nature Reserve	-10.2772, 16.9533	PV357719	PV412839	PV412865	PV390641	This work
I. b. bivittata	–	P1-318	Angola	Cambau	-9.9633, 15.1706	PV357720	PV412840	PV412866	PV390642	This work
I. b. bivittata	PEM R23525	WC-4515	Angola	west of Cuito town on Aludungo rd.	-12.3278, 16.9067	PV357721	–	PV412867	–	This work
I. b. pallida	PEM R17934	KTH09-075	Angola	7 km East of Humpata	-14.9820, 13.4352	HF547775	HF547731	HF547694	–	Edwards et al. 2012
I. capensis	PEM R23530	WC-4585	Angola	Kembo River source	-13.1095, 19.0061	PV357722	PV412841	PV412868	PV390643	This work
I. capensis	PEM R23500	WC-4618	Angola	Kembo River source lake	-13.1360, 19.0453	PV357723	PV412842	PV412869	–	This work
I. capensis	PEM R20009	WC12-A191	Angola	HALO Cuito Cuanavale office	-15.1392, 19.1436	PV357724	PV412843	–	–	This work
I. capensis	PEM R20495	ANG-311	Angola	8.5 km north of Rito	-16.6232, 19.0535	PV357725	PV412844	–	–	This work
I. capensis	PEM R22069	L18	Angola	Gambos, Foster's farm	-15.8500, 14.6833	PV357726	PV412845	–	–	This work
I. capensis	–	NB0771	Angola	Bicuar National Park	-15.2435, 14.8915	PV357727	PV412846	PV412870	PV390644	This work
I. capensis	–	NB0772	Angola	Bicuar National Park	-15.2435, 14.8915	PV357728	PV412847	PV412871	PV390644	This work
I. capensis	–	NB0779	Angola	Bicuar National Park	-15.1048, 14.8403	PV357729	PV412848	PV412872	PV390644	This work
I. capensis	–	NB1116	Angola	Cusseque	-13.6851, 17.0795	PV357730	PV412849	–	PV390647	This work
I. capensis	PEM R27394	WC-6797	Angola	Quembo River bridge camp	-13.5275, 19.2806	PV357731	PV412850	PV412873	PV390648	This work
I. capensis	–	NB1123	Angola	Cusseque	-13.6782, 17.0832	PV357732	PV412851	–	PV390649	This work
I. capensis	–	NB1124	Angola	Cusseque	-13.6776, 17.0836	PV357733	PV412852	–	–	This work
I. capensis	–	NB1138	Angola	Cusseque	-13.6858, 17.0796	PV357734	–	–	–	This work
I. capensis	–	ABC2	Namibia	Katima Mulilo	-17.7000, 24.0000	JX962898	–	JX963023	JX962916	Engleder et al. 2013
I. capensis	CAS 209602	AMB 6007	South Africa	KwaZulu-Natal, Kosi Bay	-26.9400, 32.8200	DQ871149	–	DQ871207	–	Makokha et al. 2007
I. capensis	–	AMB 6001	Namibia	Road to Tsumkwe	-19.4600, 19.7200	DQ871148	–	DQ871206	–	Makokha et al. 2007
I. aff. capensis	PEM R19903	TB44	Angola	Camp Chiri, Miombo forest/camp	-9.3969, 20.4319	PV357735	PV412853	PV412874	–	This work
I. aff. capensis	PEM R23531	WC-4560	Angola	Sombanana village river	-12.3071, 18.6235	PV357736	PV412854	PV412875	–	This work
I. aff. capensis	MHNCUP-REP0984	P9-035	Angola	Mona Quimbundo – Tahal	-10.0583, 19.8056	PV357737	PV412855	–	–	This work
I. aff. capensis	PEM R19905	TB46	Angola	Camp Chiri, Miombo forest/camp	-9.3969, 20.4319	PV357738	PV412856	PV412876	–	This work
I. aff. capensis	–	P3-059	Angola	Cuemba	-12.1707, 18.2257	PV357739	PV412857	–	PV390650	This work
I. aff. capensis	PEM R23996	WC-6291	Angola	Lake Tchanssengwe	-12.4140, 18.6442	PV357740	PV412858	–	–	This work
I. aff. capensis	PEM R23409	WC-4557	Angola	Lungue Bungue River camp bridge crossing	-12.5835, 18.6660	PV357741	PV412859	PV412877	–	This work
I. microlepidota	MHNCUP-REP 0983	P0-044	Angola	Moco – Canjonde	-12.4554, 15.1632	PV357742	PV412860	PV412878	PV390651	This work

Species	Catalog No.	Field Number	Country	Locality	Latitude, Longitude	*16S*	*ND4*	*RAG1*	*C-mos*	Source
M. squamulosus	–	WP125	South Africa	Rooipoort Nature Reserve	-28.5937, 24.2100	HF547778	HF547738	HF547701	–	Edwards et al. 2012
M. squamulosus	–	RSP373	South Africa	Venetia Limpopo Reserve	-22.2661, 29.3329	HF547777	HF547737	HF547699	–	Edwards et al. 2012
M. squamulosus	PEM R19626	SVN362	South Africa	Lapalala Game Reserve, Landmanslust	-23.8759, 28.3061	HF547776	HF547736	HF547697	–	Edwards et al. 2012
M. squamulosus	–	ABH9	Tanzania	Laela	-8.7500, 32.1833	JX962897	–	EF632221	EF632266	Engleder et al. 2013
M. squamulosus	–	ABH3	Mozambique	unknown	–	JX962896	–	JX963022	JX962915	Engleder et al. 2013

Table 2. Primer details and PCR protocols used to generate sequences for this study. The PCR column denotes the number of repeated cycles/annealing temp (°C) used in the PCR.

Gene	Primer	Length (bp)	Reference	Sequence	PCR
16S	16S-L	511	Palumbi 1996	5'-CGCCTGTTTATCAAAAACAT-3'	40 / 54
	16S-H			5'-TGACTGCAGAGGGTGACGGGCGGTGTGT-3'	
c-mos	G73_69	337	Whiting et al. 2003	5'-GCGGTAAAGCAGGTGAAGAAA-3'	40 / 54
	G74_70			5'-TGAGCATCCAAAGTCTCCAATC-3'	
ND4	ND4 (ND4F)	802	Arévalo et al. 1994	5'-CACCTATGACTACCAAAAGCTCATGTAGAAGC-3'	40 / 58
	Leu (ND4R)			5'-CATTACTTTTACTTGGATTTGCACCA-3'	
RAG-1	f1aFw	985	Wiens et al. 2010	5'-CAGCTGYAGCCARTACCATAAAAT-3'	40 / 50–54
	r2Rv			5'-CTTTCTAGCAAAATTTCCATTCAT-3'	

Phylogenetic analyses

We used phylogenetic reconstructions to place *I. microlepidota* in an evolutionary context and to provide an updated phylogenetic hypothesis of the group for Angola. For these analyses, we combined the newly generated sequences and supplemented them with previously published sequence data of *Ichnotropis* spp. (i.e., Edwards et al. 2013; Engleder et al. 2013) downloaded from GenBank, using *Meroles squamulosus* as an outgroup (Table 1) for being a close-related member of the sister genus *Meroles* (Engleder et al. 2013). Phylogenetic analyses were run using Bayesian inference (BI) and maximum likelihood (ML) approaches using a concatenated dataset of the four genes. The partitioning schemes were assessed using PartitionFinder2 (Lanfear et al. 2017), and the best substitution model of sequence evolution was selected using ModelFinder in IQ-Tree v2.3.4 (Minh et al. 2021) with the Bayesian information criterion (BIC). We partitioned the combined dataset by gene, as suggested in PartitionFinder2. The best substitution models were TIM2+F+G4 (*16S*), TPM2u+F+I+G4 (*ND4*), K2P (*c-mos*), and K2P+G4 (*RAG-1*). Maximum likelihood (ML) analysis was performed in IQ-Tree v2.3.4 (Trifinopoulos et al. 2016) with four partitions of the concatenated dataset and 1000 bootstrap replicates following the ultrafast bootstrap approximation method (UFBoot) (Hoang et al. 2018). Bootstrap values of 95% or higher for the ML analysis were considered as strongly supported (Huelsenbeck and Hillis 1993). The Bayesian inference analysis was conducted with MrBayes v3.2.7 (Ronquist et al. 2012) on CIPRES (Miller et al. 2010) with four partitions of the concatenated dataset. The final BI analysis was run for 10×10^6 generations of the Metropolis coupled Markov chain Monte Carlo [(MC)3], sampled every 1000 generations. Convergence was assessed by examining the effective sample size (ESS) values using Tracer 1.7 (Rambaut et al. 2014), where all parameter values had ESS values > 200, and 25% of the trees generated were discarded as burn-in to generate a 50% majority rule consensus tree in MrBayes. We set the substitution model space with the option lset nst=mixed rates=invgamma. Bootstrap analyses (BS) with 1000 pseudoreplicates were used to evaluate relative branch support. Posterior probabilities (PP) were used to assess nodal support, and PP $\geq$ 0.95 was considered strongly supported. Finally, we used *16S* uncorrected pairwise sequence divergences (p-distance) to inspect intra- and interspecific variation, calculated in MEGA v.10.1.7 (Kumar et al. 2018).

External morphological data

For the external morphological analyses, we examined a total of 135 specimens of *Ichnotropis* from Angola, the Democratic Republic of the Congo (DRC), Namibia, and South Africa (Suppl. material 1: table S1). This material included 25 newly collected materials from Angola and 110 historical materials from across Africa deposited in the British Museum of Natural History, UK (BMNH), Field Museum of Natural History, USA (FMNH), the Royal Belgian Institute of Natural Sciences, Belgium (RBINS), the Royal Museum of Central Africa, Belgium (RMCA), and the Porth Elizabeth Museum, South Africa (PEM). Historical material from RBINS and RMCA, including the types of *I. c. overlaeti* and *I. c. nigrescens*, was included. We also included the type series of *I. microlepidota*, which is deposited in the Field Museum of Natural History (FMNH). In addition, we compared high-resolution images of the types.

We recorded morphometric measurements as follows: snout-vent length (SVL, from tip of snout to anterior cloaca opening), tail length (TL, from tip of tail to posterior cloaca opening), occipital-snout length (HL, from posterior end of occipital to tip of snout), head width (HW, at widest point), head height (HH, at highest point), snout to front of arm (S-FL, from tip of snout to anterior insertion of forelimb), snout to eye distance (SE, from tip of snout to anterior corner of eye), eye diameter (ED), eye to eye distance (EE, from anterior corner of eye to anterior corner of eye), tympanum width (Tymp-L, at its widest), fore limb length (FLL, from elbow to wrist), hind limb length (HLL, from knee to heel), inner limb length (IL, distance between inguinal and axillary regions), hind foot length (HFL, from ankle to tip of fourth toe excluding claw), lower jaw length (LJL, anterior edge of jaw bone to tip of lower jaw), fourth finger length (FFL, excluding claw), fourth toe length (FTL, excluding claw), anterior SO (length of anterior supraorbital scale), distance between anterior supraocular to second loreal (SO-L, measurement between the closest point of the anterior supraocular to the posterior edge of the second loreal), frontal scale width (FNW, at its widest point), frontal scale length (FNL). The meristic data collected was: number of upper labials (UL) for which we counted scales in anteriorly and posteriorly of the subocular, number of lower labials (LL), number of chin shields (including the number in direct contact), number of supraciliaries, longitudinal rows of ventral scales at midbody; transverse number of ventral scales (from line between posterior side of fore limbs to groin), scales around midbody (including ventral scales), number of granular scales separating supraorbital from the supraciliaries, rows of scales between anterior supraocular and second supraciliaries, number of scales separating anterior supraocular from posteriorly loreal, number of rows of scales between upper labials and temporal shield, number of subdigital lamellae from the base of the digit to tip of toe before the claw starts on the fourth toe and the number of femoral pores on the left and right side. We also examined if the occipital scale extended past the parietal scales, if there was contact between prefrontal scales and anterior supraocular, contact between supraoculars and supraciliaries, contact between frontonasal and supraciliaries, and if the anterior loreal scale was divided or not. All data was collected using a Leica LD2500 or Nikon SMZ1270 dissecting microscope, and measurements were taken in millimeters (mm) with a digital caliper (accuracy of 0.01 mm).

Morphological analyses

We used different datasets for the different analyses, defined as follows: Dataset 1, which included all specimens on which most morphological traits have been recorded (48 specimens), and Dataset 2, which included all the specimens (135 specimens; Suppl. material 1: table S1). First, to explore the main morphological differences among Angolan *Ichnotropis* species, we conducted two Principal Component Analyses (PCAs). The first analysis was performed using Dataset 1, while the second excluded the effect of head shape differences by removing head-related variables (HL, HW, and HH) from Dataset 1. These variables were size-corrected using SVL as a covariate, and the residuals were subsequently used in the PCAs. Following Branch et al. (2014), variables with communalities > 0.5 were retained in the PCA. A varimax rotation was applied, and principal components (PCs) with eigenvalues > 1.0 were extracted. The resulting PC scores were saved and used as input variables for a multivariate analysis of variance (MANOVA), with species as the fixed factor. Post-hoc pairwise comparisons were conducted using Tukey's HSD test to identify which variables explained the main morphological differences in the first two PCAs (Branch et al. 2014). Secondly, to explore other potential diagnostic characters between species, we tested the morphological variation in Dataset 2 across different taxa using permutational ANOVAs (PERMANOVAs) with the package RRPP (Collyer and Adams 2018) implemented in RStudio v.2023.09.1+494 (RStudio Team, 2022). Variables were size-corrected (SVL) and log-transformed prior to the analyses to mitigate the effects of size and multicollinearity. Finally, we used standard boxplots to visually represent those variables that showed significant differences between *I. microlepidota* and any other species.

Osteological data and comparisons

To identify potential diagnostic characters on the cranial elements of *Ichnotropis microlepidota*, we visually compare the high-resolution X-ray computed tomography (HRCT) scan of *I. microlepidota* (MHNCUP-REP0983) with material of *I. bivittata* (RCMA 14641, formerly the holotype of *I. c. nigrescens fide* Conradie et al. in prep.; and MCZ-R39726) (Suppl. material 1: table S2). HRCT was performed at the Royal Museum of Central Africa (RMCA) CT facilities and at Centro de Instrumentación Científica of Granada (CIC). The cranium of *Ichnotropis bivittata* (MCZ-R39726) was downloaded from the Morphosource platform (https://www.morphosource.org). Detailed parameters for each CT scan are defined in Suppl. material 1: table S2. All specimens were regarded as adults to avoid potential ontogeny variation of the skull elements. To guarantee we used adult specimens for the cranial comparisons, we checked the femoral pore development, as they are feebly visible or not completely developed in juveniles and subadults. The 3D segmentation models for the skulls were generated for articulated skulls using Avizo Lite 2019.1 (Thermo Fisher Scientific). To facilitate visualization, individual bone units of the cranium and jaws were colored following the same color palette as Lobón-Rovira and Bauer (2021). Bones not included in Lobón-Rovira and Bauer (2021) were included in the pallet and are defined in Suppl. material 1: table S3. Annotations were made manually in Adobe Photoshop v.25.7.0 (Adobe Systems Incorporated 2019). CT scan raw data (.tiff files) have been deposited in MorphoSource (www.morphosource.org; Suppl. material 1: table S2).

Results

Phylogenetic analyses

Both phylogenetic analyses (ML and BI) retrieved the same topology, although with different support strengths for some nodes. The phylogenetic analyses recovered five well-supported operational taxonomic units (OTUs) (Fig. 1) that are consistent with the pairwise comparisons of the *16S* uncorrected p-distances (4.57%–17.80%, Table 3).

The different phylogenetic reconstructions recovered a well-supported monophyletic group that includes individuals morphologically identified as *Ichnotropis* aff. *grandiceps.* This group clusters with a larger group (PP: 0.99, BS: 89%) that includes all the other members of the *Ichnotropis* genus (Fig. 1). The large clade includes two well-differentiated subclades, here identified as the *capensis* and *bivittata* groups (PP: 0.99, BS: 97%). The *capensis* group includes two well-supported subclades (PP: 1.00, BS: 100%) that differ genetically from each other by > 4.5% (*16S* uncorrected p-distance). The two main subclades recovered here in the *capensis* group represented a well-defined geographic distribution with one subclade (namely *I. capensis*) from central to the southern half of the Angolan territory, northeastern Namibia, and eastward to coastal South Africa, and a second subclade (namely *I.* aff. *capensis*) distributed in the northeastern half of the Angolan territory (Fig. 8). Within the *bivittata* group, the phylogenetic analyses retrieved two subclades that differ by a minimum of 14.83% (*16S* uncorrected p-distance, Table 3), including both subspecies of *I. bivittata* (namely, *I. b. bivittata* and *I. b. pallida*) and *I. microlepidota*, that were recovered as sister taxa (PP: 0.99, BS: 97%, Fig. 1). The two subspecies of *I. bivittata* differ by 4.03% (*16S* uncorrected p-distance, Table 3).

Morphological analyses

The results of the two PCAs explained a considerable portion of the variation in the three principal components in both analyses (69.5% and 68.65%, respectively). On the first PCA, the highest proportion of the variation in the PC1 is explained by the HL and S-FL, and in the PC2 by the HW and the Tymp_L (Suppl. material 1: table S4).

When we remove the HL, HW, and HH from the PCA analysis (PCA2; Suppl. material 1: table S4), the PC1 is explained by the S-FL and the HLL, and in the PC2 by the ED and the Tymp_L.

Nevertheless, in both analyses, the multivariate means on PC1 show no differences between the species (MANOVA PCA1 p value = 0.639; MANOVA PCA2 p value = 0.297) as shown in Fig. 2. The PC2 shows two main groupings exploring differently the morphospace (MANOVAs p value = 0.000). These results are supported by the *post hoc* pairwise comparison (Tukey's HSD) that does not show a significative difference in the PC1 (HL and S-FL) between species, but it does in several species pairs in the PC2 (e.g., HW and Tymp_L in *I. microlepidota–I.* aff. *capensis* $p < 0.05$) (Suppl. material 1: table S5).

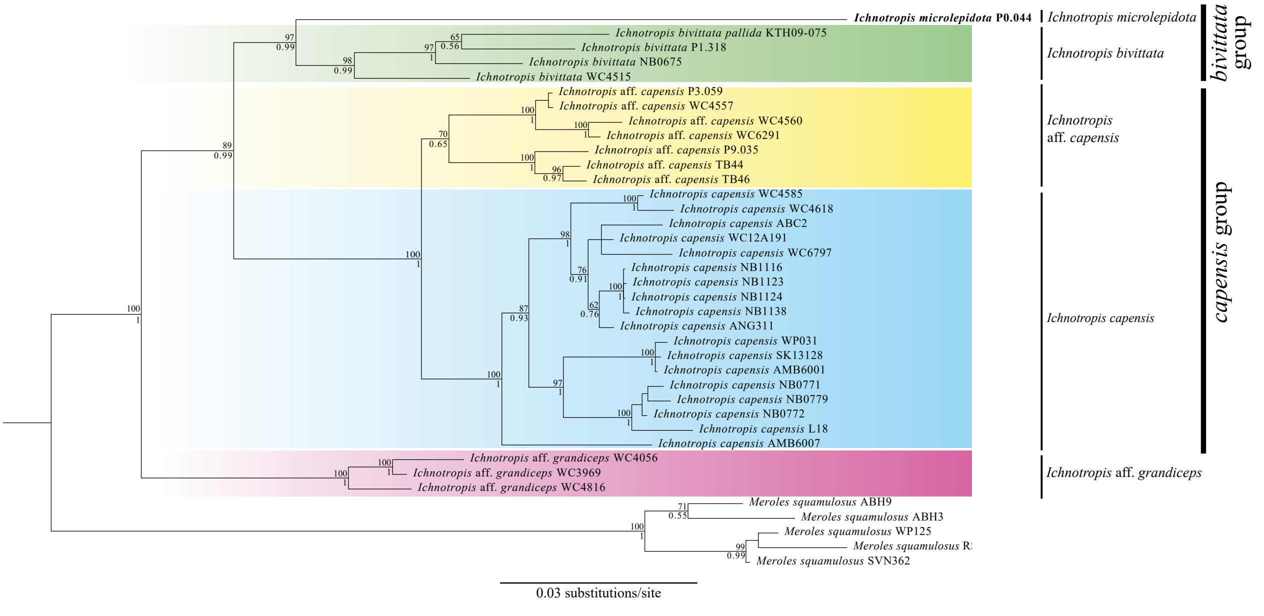

Figure 1. Bayesian inference tree based on concatenated dataset including 2635 bp of two mitochondrial (*16S*, *ND4*) and two nuclear-encoded (*C-mos*, *RAG1*) markers. Nodes are labeled with ML bootstrap values (BS) above and BI posterior probability (PP) below.

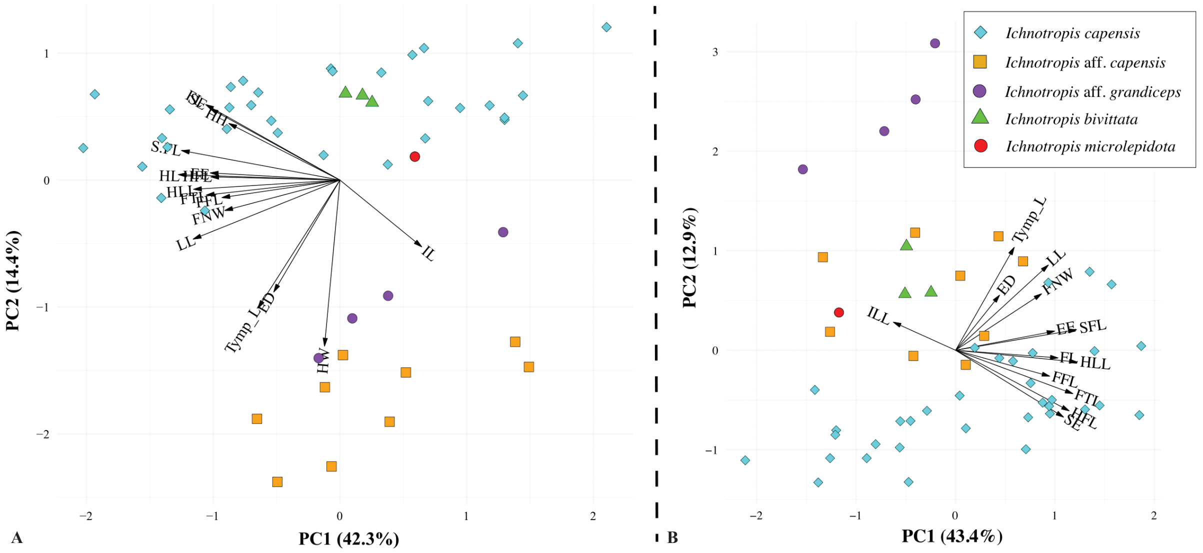

Figure 2. A. PCA plot of the first principal component (PC1) versus the second principal component (PC2) on Dataset 1 including all the morphological variables; **B.** PCA plot of the first principal component (PC1) versus the second principal component (PC2) of Dataset 1, excluding the three main morphological variables of the head (i.e., HL, HW, HH). Species are represented by different color and symbol included in the legend. For abbreviations see the Materials and Methods section. For loadings of all axes and explained variance, see Suppl. material 1: tables S4, S5.

Table 3. Percent sequence divergence for *16S* (uncorrected pairwise distances) between and within *Ichnotropis* species included on the phylogenetic analyses and *Meroles squamulosus*. Bold values on the diagonal depict mitochondrial divergence within species.

ID	1	2	3	4	5	6	7
1. *Ichnotropis microlepidota*	**n/c**						
2. *Ichnotropis bivittata bivittata*	14.83	**3.37**					
3. *Ichnotropis bivittata pallida*	15.50	4.03	**n/c**				
4. *Ichnotropis capensis*	16.23	8.50	9.13	**3.64**			
5. *Ichnotropis* aff. *grandiceps*	17.80	6.70	7.85	9.26	**1.30**		
6. *Ichnotropis* aff. *capensis*	15.88	6.76	7.68	4.57	8.72	**1.95**	
7. *Meroles squamulosus*	24.69	14.29	14.74	19.00	14.74	17.69	**3.25**

Despite the fact that the PERMANOVAs did not retrieve many additional significant results for the continuous measurements (Suppl. material 1: table S6), it recovers some additional significative differences not highlighted by the PCA analyses (Suppl. material 1: table S6). Thus, the main morphological differences between *I. microlepidota* and other *Ichnotropis* members are the SVL, three main head measurements (i.e., HL, HW, and HH), the S-FL, and the Tymp_L (Fig. 3, Suppl. material 1: table S6). For example, significant differences in head length (HL) have been found when compared to *I. capensis* (ANOVA: $F_{1,27}$ = 14.630; *p*-value = 0.001), *I.* aff. *grandiceps* (ANOVA: $F_{1,14}$ = 11.478; p-value = 0.008), and *I. bivittata* (ANOVA: $F_{1,21}$ = 10.335; *p*-value = 0.013), in the head width (HW) with *I.* aff. *grandiceps* (ANOVA: $F_{1,14}$ = 19.166; *p*-value = 0.000) and *I. capensis* (ANOVA: $F_{1,27}$ = 8.271; *p*-value = 0.037) and in the head height (HH) with *I.* aff. *grandiceps* (ANOVA: $F_{1,14}$ = 10.201; *p*-value = 0.015) (Fig. 3, Suppl. material 1: table S6). In addition, the results on the comparison of the meristic data show a marginal difference between *I. microlepidota* and the other members of the group (like midbody scales or lamellae under the fourth toe; Fig. 3), being exceptionally divergent when compared to *I.* aff. *grandiceps* in most of the meristic measurements (Fig. 3). Meristic comparison showed main differences in the midbody scale count, which is higher in *I. microlepidota* than in the other *Ichnotropis* species (43–50 vs. 32–39 in *I. bivittata*, 30–41 in *I. capensis*, 34–41 in *I.* aff. *Capensis*, and 43–48 in *I.* aff. *grandiceps*) and in the number of lamellae under the fourth toe, which conversely seems lower in *I. microlepidota* (16–19 vs. 18–20 in *I. bivittata*, 18–26 in *I. capensis*, 19–24 in *I.* aff. *capensis*, and 19–24 in *I.* aff. *grandiceps*) (Fig. 3). It is worth noticing that although not as high as in *I. microlepidota*, the number of scales around the midbody is also higher in *I.* aff. *grandiceps* than in the other species (excluding *I. microlepidota*).

The osteological comparison of the skulls of *I. microlepidota* and *I. bivittata* allows us to identify a few potential diagnostic characters between species. While the *I. microlepidota* cranium presents a more rounded shape in dorsolateral view, with a broader lateral profile and taller dorsoventral profile, the skull in both *I. bivittata* skulls presents a slenderer and more elongated overall shape (Fig. 4). In addition, the skull in *I. microlepidota* presents a shorter and more robust jugal bone than in the other two species, a broader and more longitudinally compressed

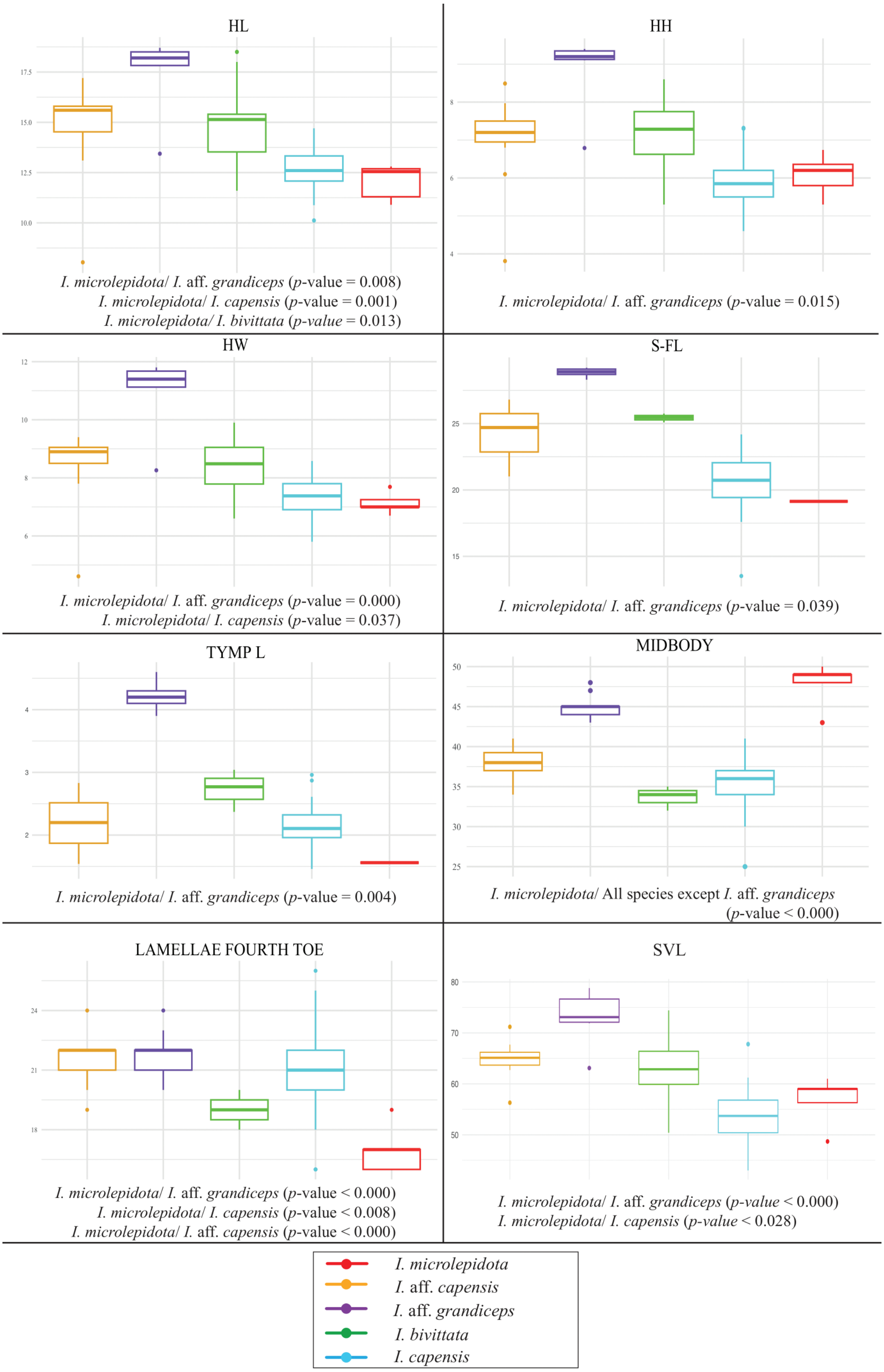

Figure 3. Boxplot (top whisker – maximum value; lower whisker – minimum value; bold horizontal line – median; box – 1st and 3rd quartile) displaying meristic measurements of *Ichnotropis* species. Different colors depict records of different species within *Ichnotropis*; see inset for color explanations. Significative values between *I. microlepidota* and other *Ichnotropis* species are highlighted under the graphics. For all ANOVA results see Suppl. material 1: table S6. For abbreviations see the Materials and Methods section.

maxilla and dentary bones in their lateral view, and a more downfacing and compressed premaxilla in its lateral view with a larger distance between the posterior ends of both pterygoid bones and jugals when compared to *I. bivittata*. Furthermore, the parietal bone is wider than longer in *I. microlepidota*, while in *I. bivittata*, the parietal presents a broader lateral profile. Finally, striation in the dorsal view of skulls seems to be more prominent in *I. microlepidota*, with a rougher-looking surface on almost all bones in the dorsal view of the skulls (Fig. 4).

Overall, due to the morphological and phylogenetic differences that support the taxonomic recognition of *I. microlepidota*, coupled with the lack of accurate morphological information about the species (e.g., coloration in life, osteology) and the taxonomic confusion around this taxon, we take the opportunity to provide an updated description (below) of *I. microlepidota*, aiming to provide an accurate description and comparison with other members of the group that could be useful for future taxonomic decisions on this group.

Ichnotropis microlepidota Marx, 1956

Figs 4–6, Table 4, Suppl. material 1: tables S1, S7

Holotype. FMNH 74285, adult male, collected at the foot of Mount Moco, Huambo Province, Angola, on 19 September 1954 by Gerd Heinrich.

Paratypes. FMNH 74283–84, adult females, with the same collecting information as the holotype; FMNH 74286–7, adult males, with the same collecting information as the holotype.

New additional material. MHNCUP-REP0983, adult male, collected at Mount Moco, Huambo Province, Angola (-12.4554, 15.1632), 2300 m a.s.l., on 18 October 2020 by Pedro Vaz Pinto.

Additional referred material. A juvenile specimen collected at Mount Moco, Huambo Province, Angola, 1500–1900 m a.s.l., in March 1934 by Karl Jordan (Parker 1936).

Updated description. Measurements and meristic data are summarized in Suppl. material 1: table S1. *Ichnotropis microlepidota* is a medium-sized lizard species (maximum SVL = 61.00 mm, mean 56.8 ± 4.8). 4 upper labials anteriorly to the subocular (mostly 2–3 posteriorly to the subocular), 7–8 (mostly 7) lower labials, and 5 pairs of chin shields, from which the first three pairs are in contact. Rostral with slight insertion between nasals. Single rhomboid frontonasal scale, slightly wider than longer. Undivided anterior loreal scale, which is smaller than the larger posterior loreal. Prefrontal scales longer than wider and in contact with supraoculars. Single row of scales between posterior loreal and anterior supraocular scales. Four supraciliaries on each side, which can be in contact or not with the anterior supraoculars. Three supraoculars, with the first (anterior one) being the largest,

Table 4. Summary of external morphological data of all species within the *Ichnotropis* genus. Measurements are shown in millimeters (mm) (average and standard deviations). Juveniles are excluded from these summary statistics. For individual measurements, see Suppl. material 1: table S8. Abbreviations are detailed in the Materials and Methods section. Missing data or unavailable information is indicated as not available (N/A).

Species	*I. bivittata*	*I. capensis*	*I.* aff. *capensis*	*I.* aff. *grandiceps*	*I. microlepidota*
N (males/females)	**(N = 10/6)**	**(N = 50/39)**	**(N = 9/3)**	**(N = 3/2)**	**(N = 3/2)**
SVL	62.4 ± 6.9	53.5 ± 4.9	65.3 ± 2.4	74.9 ± 3.1	56.8 ± 4.8
HL	14.9 ± 1.8	12.7 ± 0.9	15.2 ± 1.2	18.3 ± 0.4	11.8 ± 0.8
HW	8.4 ± 1	7.3 ± 0.6	8.8 ± 0.5	11.5 ± 0.3	7 ± 0.2
HH	7.2 ± 0.9	5.9 ± 0.6	7.2 ± 0.6	9.3 ± 0.1	5.9 ± 0.6
S-FL	25.4 ± 0.3	20.9 ± 1.7	24.4 ± 1.8	28.8 ± 0.4	19.14
SE	6.4 ± 0.1	6 ± 0.4	5.4 ± 0.9	6.4 ± 0.4	4.85
ED	2.9 ± 0.1	2.2 ± 0.4	3.7 ± 1.0	3.2 ± 0.3	2.62
EE	4.6 ± 0.1	4.2 ± 0.4	4.4 ± 1.1	3.2 ± 0.3	3.62
Tymp-L	2.7 ± 0.3	2.2 ± 0.3	2.2 ± 0.6	4.2 ± 0.3	1.56
FLL	7 ± 1.2	6.2 ± 0.7	7.5 ± 0.5	8.3 ± 0.6	5.45
HL	10.1 ± 1.5	10.6 ± 1.1	12.6 ± 1	13.4 ± 0.4	7.43
ILL	26.2 ± 4	25.1 ± 3.4	29.8 ± 1.4	36.3 ± 2.4	22.53
HFL	14.8 ± 1	16 ± 1.8	18.4 ± 1.8	16.4 ± 1.9	12
LJL	16.4 ± 0.9	13.4 ± 1.4	16.5 ± 1.9	21.6 ± 1.5	13.32
FFL	4 ± 0.4	3.9 ± 0.5	3.9 ± 0.6	5 ± 0.5	3.56
FTL	7.4 ± 0.6	8.4 ± 0.9	8.8 ± 1.2	9.8 ± 0.7	6.28
FNW	2 ± 0.3	1.8 ± 0.2	2.2 ± 0.1	2.6 ± 0.2	1.54
FNL	4.3 ± 0.6	2.3 ± 1	2.7 ± 1.1	2.1 ± 0.2	3.29
UL	4 ± 0	4.1 ± 0.2	4.1 ± 0.2	4.6 ± 0.5	4 ± 0
LL	6.3 ± 0.6	6.6 ± 0.6	6.2 ± 0.4	6.2 ± 0.3	7.6 ± 0.5
Chin shields	5 ± 0	5.2 ± 0.5	5 ± 0	4.9 ± 0.2	5 ± 0
SC	3 ± 0	3.9 ± 0.9	4 ± 0	5.1 ± 0.2	4 ± 0
Ventral plates longitudinal	24.8 ± 3.6	25.3 ± 2.4	28.4 ± 1.6	27.8 ± 1.8	25.4 ± 1.5
Ventral plates transverse	8.8 ± 1.1	8.8 ± 0.9	9.2 ± 0.4	10 ± 0	8.8 ± 1.1
Midbody	34 ± 1.2	35.5 ± 2.7	38.2 ± 1.9	44.8 ± 1.9	47.8 ± 2.8
Lamellae fourth toe	19.3 ± 1.2	21.3 ± 1.9	21.8 ± 1	21 21.2 ± 1.3	17 ± 1.2
FP	8.8 ± 0.9	10.1 ± 1.1	10.9 ± 0.8	12 12.2 ± 0.8	1 1.3 ± 0.8

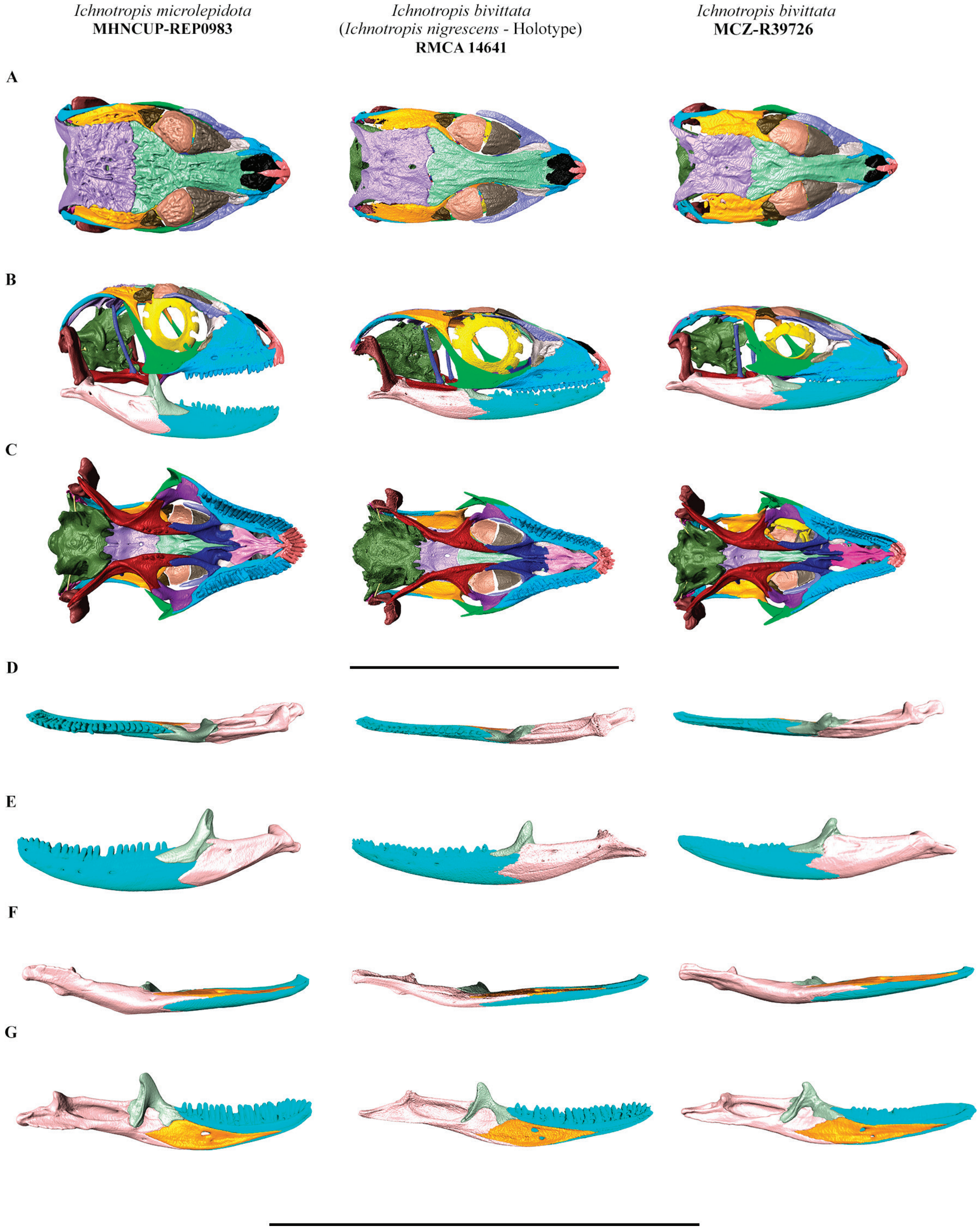

Figure 4. Comparative visualization of the skulls of *Ichnotropis microlepidota* (MHNCUP-REP0983) and *I. bivittata* (RMCA 14641; MCZ-R39726) (from left to right). Detail of the skull in **A.** Dorsal; **B.** Lateral, and **C.** Ventral views; and lower jaws in **D.** Dorsal; **E.** Lateral; **F.** Ventral, and **G.** Medial views. For the color palette, see Suppl. material 1: table S3. Scale bars: 10 mm.

followed by a slightly smaller second supraocular and a third one, which is the smallest. Eight rows of temporal scales between temporal shield and upper labials. Temporal shields half the length of parietals. Parietals twice as long than broad. Frontal scale 2–3 times longer than wide. Semicircular-shaped occipital scales slightly extending past the parietal scales. Head shields heavily striated. Dorsal scalation is composed of small, heavily keeled, rounded scales slightly elongated towards the back. High number of scales around the midbody (43–50, mean 47.8 ± 2.8). Middorsal scales slightly larger than dorsal scales and lack keeling towards the venter. Ventral pholidosis with large hexagonal scales that lack keeling. 23–27 ventral plates in the longitudinal section and between 8–10 in the transverse section. Tail scalation is formed by elongated and keeled scales pointing towards the tail tip and disposed in rings (Fig. 5). Subdigital lamellae 16–19. Femoral pores 9–12 per side.

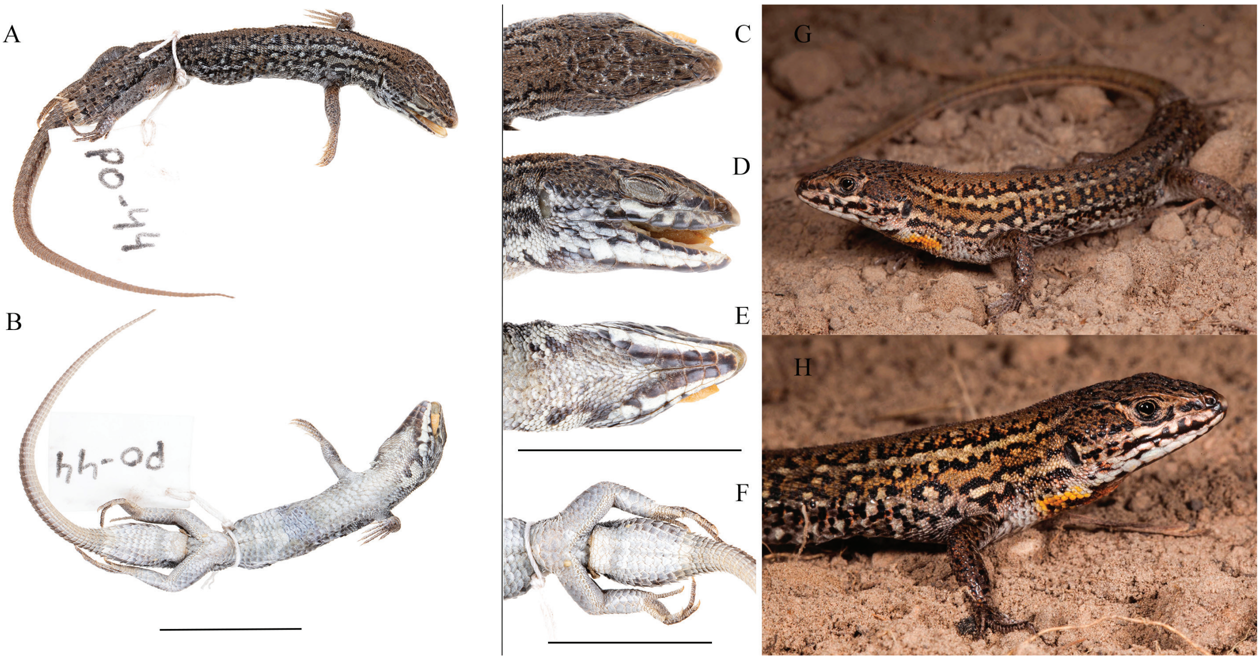

Figure 5. Specimen of *Ichnotropis microlepidota* (MHNCUP-REP0983) from Mount Moco, Huambo Province, Angola. (**A, B**) Dorsal and ventral view of the preserved specimen. Details of the head of the preserved specimen in (**C**) dorsal, (**D**) lateral, and (**E**) ventral view. (**F**) Detail of pelvic region and hind limbs. Scale bars represent 15 mm. In life pictures of the full body (**G**) and detail of the head (**H**). Photos by Max Benito and Pedro Vaz Pinto.

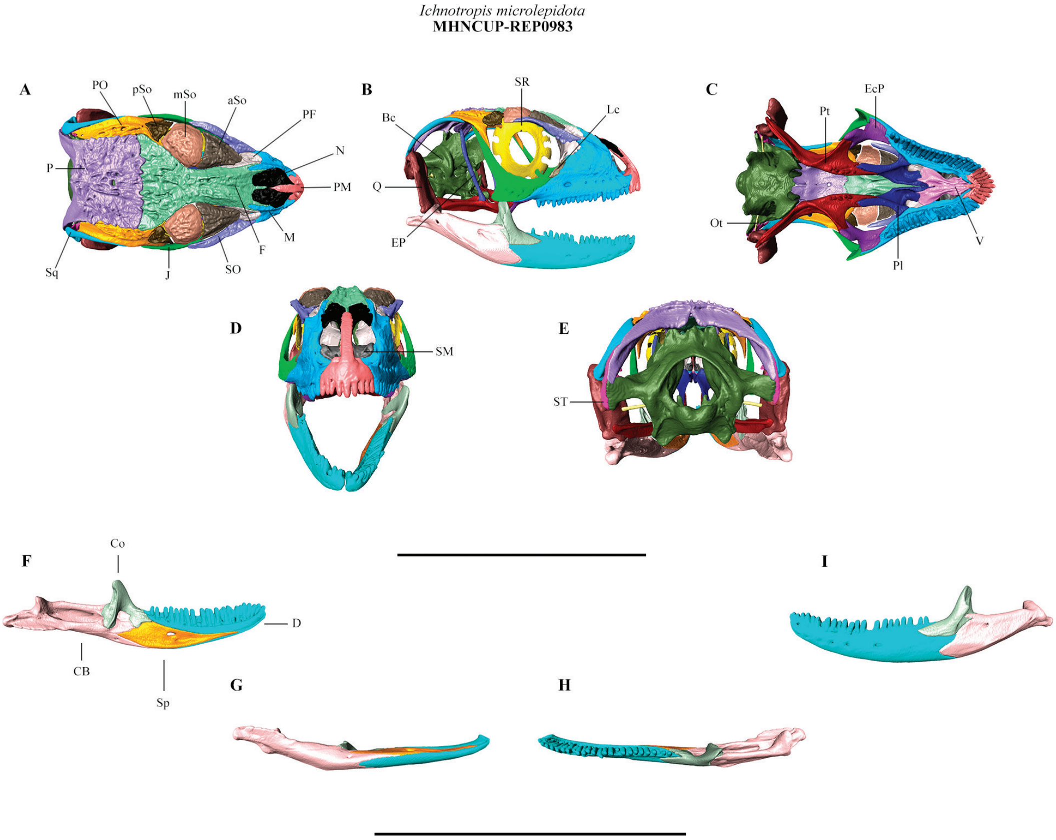

Figure 6. Detailed views in **A.** Dorsal; **B.** Lateral; **C.** Ventral; **D.** Frontal; **E.** Posterior of skull, and **F.** Medial; **G.** Ventral; **H.** Dorsal; **I.** Lateral view of the right jaw of *Ichnotropis microlepidota* (MHNCUP-REP0983). Abbreviations: aSo, anterior supraocular; Bc, braincase; Co, coronoid; CB, compound bone; D, dentary; EcP, ectopterygoid; EP, epipterygoid; F, frontal; J, jugal; Lc, lacrimal; M, maxilla; mSo, middle supraocupar; N, nasal; Ot, otostape; P, parietal; PF, prefrontal; Pl, palatine; PM, premaxilla; PO, postorbital; pSo, posterior supraocular; Pt, pretygoid; Q, quadrate; SM, septomaxilla; SO, supraorbital; Sp, splenial; Sq, squamosal; SR, sclerotic ring; ST, supratemporal; V, vomer. Scale bars represent 10 mm.

The cranium presents on its overall a rounded shape on its lateral and dorsal view (Fig. 6A, B). Frontal and parietal bones fused and separated by the fronto-parietal suture (Fig. 6A). Both bones are heavily striated in their dorsal view. Pineal foramen present in the medial section of the parietal bone. Postorbital bones prominent, in tight contact with the postocular, frontal, parietal, and squamosal bones. Supratemporal bone present, located as a splinter of a bone between the squamosal and the posterolateral process of the parietal (Fig. 6E). Nasal bones paired (Fig. 6D). Lacrimal bone present and unfused with the maxilla (Fig. 6B). A large jugal bone present in contact with the lacrimal bone, ectopterygoid, and postorbital bone. Braincase elements fused. Otostapes unperforated. The sclerotic rings comprise 14 ossicles with similar shape and size. Vomer bones paired (Fig. 6C). A robust lower jaw with a high and prominent coronoid bone (Fig. 6F–I). Compound bone and surangular bones fused. Splenial bone large in contact with compound bone, coronoid, and dentary. Nine premaxillary tooth loci, 20 maxillary tooth loci, and 22–23 dentary tooth loci.

Comparative diagnosis. This species can be differentiated from *I. bivittata* by having higher number of scales around the midbody (43–50 vs. 32–39 in *I. bivittata*) and a lower number of subdigital lamellae under the fourth toe (16–19 vs. 18–20 in *I. bivittata*). Furthermore, *I. bivittata* presents narrowly yellow-spaced spots above the front limbs, while *I. microlepidota* lacks this dorsolateral spotting. Furthermore, *I. microlepidota* presents anterior suboculars, which can be in contact or not with the supraciliaries, while in *I. bivittata*, they are always separated. Moreover, it differs from the *capensis* group by having a more rounded and shorter snout, prefrontals in contact with the anterior supraoculars, a higher number of scales around the midbody (43–50 vs. 30–41 in *I. capensis* and 34–41 in *I.* aff. *capensis*), a lower number of subdigital lamellae under the fourth toe (16–19 vs. 18–26 in *I. capensis* and 19–24 in *I.* aff. *capensis*), and for lacking a lateral orange band in adult males, which is highly conspicuous in adult males from the *capensis* group. It also differs from *I.* aff. *grandiceps* in the number of lamellae under the fourth toe (16–19 vs. 19–24 in *I.* aff. *grandiceps*) and for the same orange band in adult males as in the *capensis* and *bivittata* groups. In addition, *I. microlepidota* can be differentiated from *I. bivittata* based on a few osteological characters as follows: broader cranium dorsoventrally, with a taller dorsoventral profile, a shorter and more robust jugal bone, a more downfacing and laterally compressed premaxilla, and longitudinally compressed maxilla and dentary bones in *I. microlepidota versus* a narrower and shorter cranial profile in I. *bivittata*. The skull of *I. bivittata* presents an overall rounded shape in its lateral and dorsal view. Parietal and frontal bones separated by the fronto-parietal suture, and both with low striation in their dorsal view. The pineal foramen situated in the medial to anterior section of the parietal. Elongated jugal bones in their lateral view, in contact with lacrimal bone, ectopterygoid, and the postorbital bone. Otostapes unperforated. The sclerotic rings comprise 14 ossicles with similar shape and size. Nasal and vomer bones paired. An elongated lower jaw formed by coronoid, dentary, splenial, and fused compound bones, all of them in contact. Nine premaxillary tooth loci, 20 maxillary tooth loci, and 23 dentary tooth loci. (Fig. 4).

Coloration in life (Fig. 5G–H). The dorsal pattern consists of a light brown dorsal band that reaches from behind the head to the posterior limbs, surrounded by two discontinuous bands consisting of black blotches. The pattern on the lateral side of the body consists of two light cream to yellow bands from ear opening height extending towards the back. Between them, a row of consecutive pairs of white ocelli surrounded by external black sections. Under the lower lateral band, another row of continuous single ocelli. The head is brown on top, sprinkled with black markings on most of the scales. Mouth opening is surrounded by a black coloration, which turns white to the upper part of the upper labials and to the lower part of the lower labials. The first row of chin shields is fully black, and rows 2–5 are half white (towards the outside) and half black. The gular coloration consists of a light orange color, some black scales, and two conspicuous bright yellow-orange speckles under the posterior end of both lower jaws. Ventral coloration is immaculate white.

Variation. Meristic and morphometric data are summarized in Suppl. material 1: table S1. The new individual of *I. microlepidota* (MHNCUP-REP0983) has a smaller snout-vent length when compared to the type series (Suppl. material 1: table S1). Sexual dimorphism appears in the head height (HH), higher in males than in females (6.2 ± 0.5 vs. 5.3 ± 0), in the head length (HL), longer in males (12.1 ± 1 vs. 11.5 ± 0.2), in the scales around the midbody, higher in females (49–50 vs. 43–49), and in the number of ventral scales in transversal view, higher in males (8–10 vs. 8). In addition, the newly collected material presents a proportionally larger HH (Suppl. material 1: table S1) when compared to the type series, probably a consequence of the decomposition stage of the type series when they were found.

Distribution and habitat. *Ichnotropis microlepidota* represents a micro-endemic Angolan species only known to occur at Mount Moco, Huambo Province (Fig. 8). The type series (holotype and paratypes) were found in the crop of a goshawk, which was collected at the base of Mount Moco. However, the locality may lack precision given that the bird could have captured the lizard elsewhere. The habitats at Mount Moco include open montane and fire-prone grasslands with scattered bushes and trees, rocky outcrops, and remnants of Afromontane forest in deep gullies (Fig. 7). The montane grasslands start at around 1800 m a.s.l. but are most prominent above 2100 m a.s.l. and are formed by a thick layer of grass and small bushes as well as many rocks underneath. The grass species present in those grasslands are *Festuca* spp., *Monocymbium ceresiiforme*, *Themeda triandra*, *Tristachya inamoena*, *Tristachya bequertii*, *Hyparrhenia andongensis*,

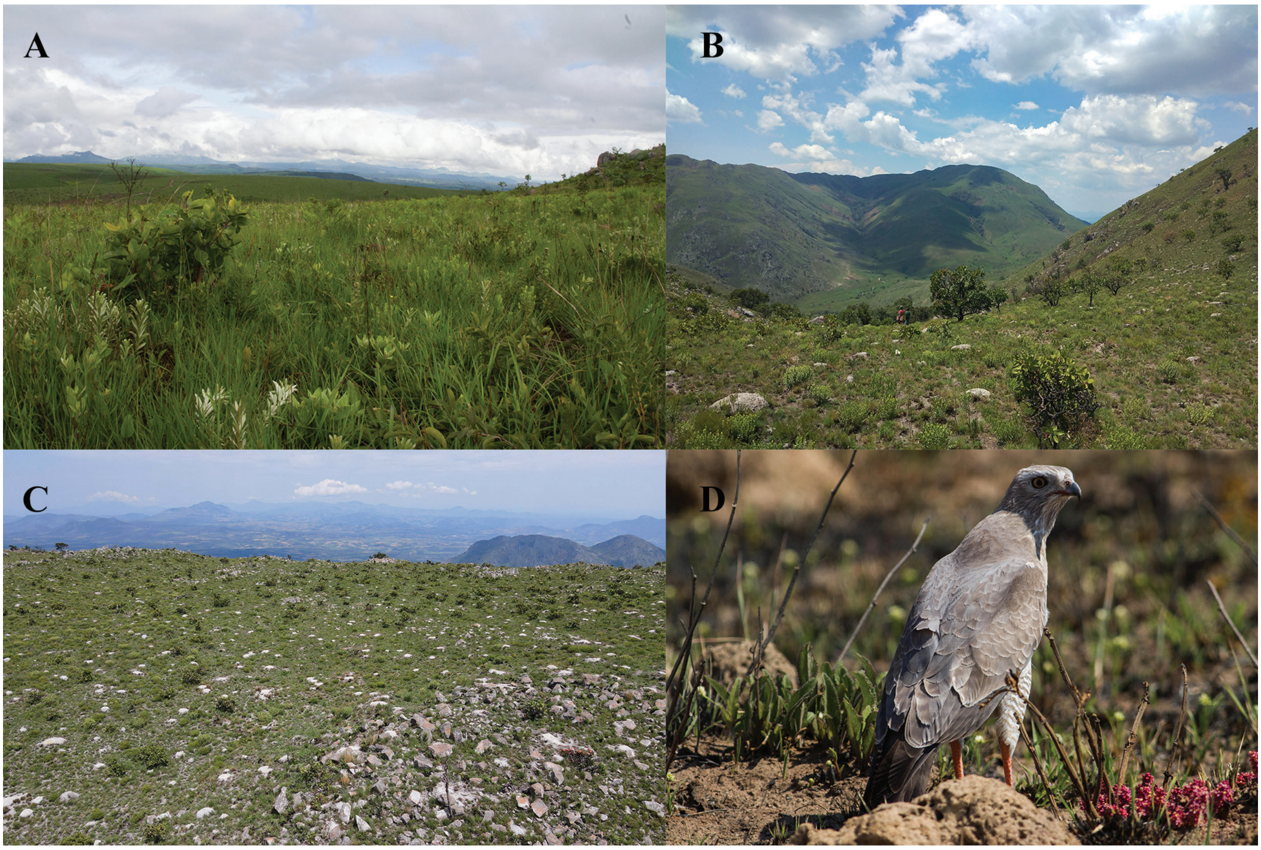

Figure 7. A–C. Habitat of *Ichnotropis microlepidota* in Mount Moco, Huambo Province; **D.** Dark Chanting Goshawk (*Melierax metabates*) from Mount Moco. Photos by Pedro Vaz Pinto.

and *Hyparrhenia quarrei*, among others (Mills et al. 2011). Shrub cover usually includes species such as *Cliffortia* spp., *Erica* spp., *Philippia benguelensis*, *Protea trichophylla*, *Stoebe vulgaris*, and *Xerophyta* spp., although the last ones mainly appear in rocky outcrops (Mills et al. 2011).

Natural history. *Ichnotropis microlepidota* is a ground-dwelling lizard with diurnal habits. The specimen reported here (MHNCUP-REP0983) was found during the day on top of an exposed small rock in open montane grassland habitat, with thick vegetation cover. Few reptile species were observed in the area, but at least one Viperidae species has been previously recorded in the region and same habitat, namely the endemic *Bitis heraldica*, which may prey on *Ichnotropis microlepidota*. Other reptile species recorded nearby but associated with rocky or wetland habitat included *Crotaphopeltis hotamboeia*, *Cordylus momboloensis*, *Trachylepis albopunctata*, *Trachylepis sulcata*, *Panaspis cabindae*, *Agama* cf. *schacki*, and *Afroedura wulfhaackei*.

Conservation status. The species is listed as Data Deficient (DD) on the IUCN Red List (Ceríaco et al. 2020c). This is a consequence of the lack of information about the distribution of this species and the specific threats that menace the sites where it occurs. Even with the collection of this new individual of *I. microlepidota* (MHNCUP-REP0983), this information is still incomplete, and therefore, it is likely that this species will remain listed as Data Deficient (DD).

Discussion

Although most lacertid genera in Angola have been recently revised and several new species have been described (Conradie et al. 2012b; Branch et al. 2019b; Baptista et al. 2020; Parrinha et al. 2021; Marques et al. 2022b), *Ichnotropis* has been neglected as a consequence of the lack of fresh material to evaluate the species relationships in a phylogenetic context. Therefore, the relationships between the genus members and the taxonomical status of some of them, such as *I. microlepidota*, have been the subject of debate. The access to newly collected topotypical material from Mount Moco and additional fresh material from different sites across the Angolan territory has allowed us to verify the taxonomic status of the species, but also to better assess the relationships of *I. microlepidota* with other members of this group, providing the first phylogenetic placement of *I. microlepidota.*

Morphologically, the new material of *I. microlepidota* (MHNCUP-REP0983) from Mount Moco agreed with the original description of *I. microlepidota* (Marx 1956). In addition, the genetic information has allowed us to demonstrate that *I. microlepidota* represents a distinct taxon within the *bivittata* group, which conforms a monophyletic clade containing *I. bivittata* and *I. microlepidota* as sister species. Although the nodal support within this group is sufficient, further sampling efforts are needed to obtain new fresh material within the group to provide a larger and more robust phylogenetic hypothesis.

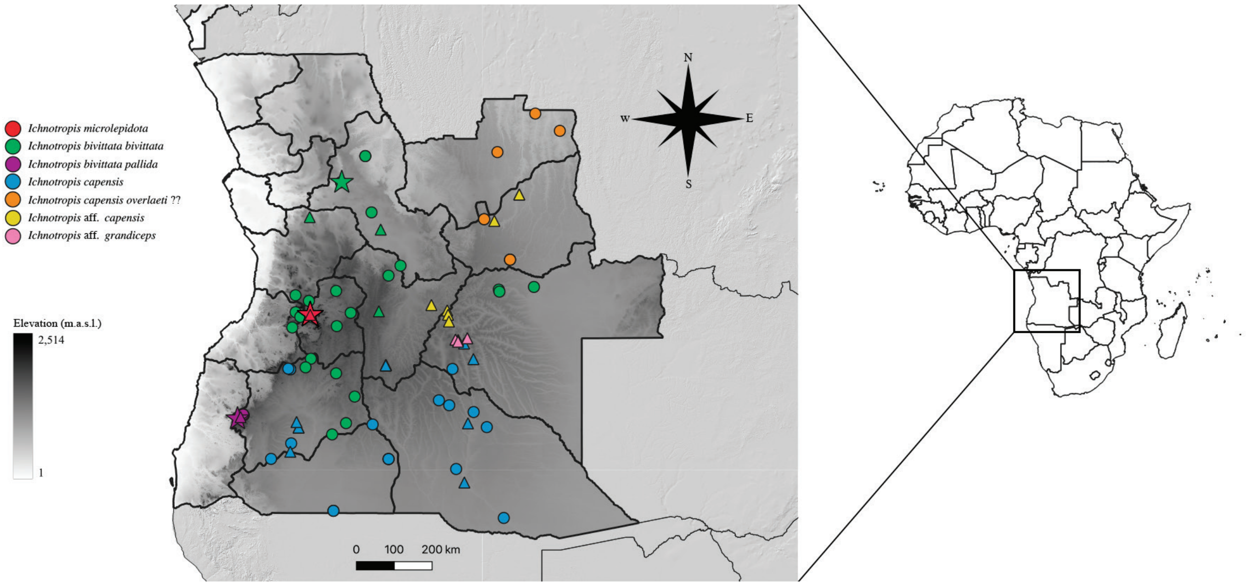

Figure 8. Geographic distribution of *Ichnotropis* within Angolan territory, on a greyscale elevation map (Fick and Hijmans 2017). Different colors depict records of different species within *Ichnotropis*; see the inset for color explanations. Circles represent historical records, triangles denote newly collected material, and start denotes type localities.

The phylogenetic reconstruction recovered three main groups among Angolan *Ichnotropis*, including five different taxa (*I.* aff. *grandiceps*, *I. capensis*, *I.* aff. *capensis*, *I. bivittata*, and *I. microlepidota*). Even though the two subspecies of *I. bivittata* show relevant mitochondrial distances in the *16S* gene (4.03%), we cannot confirm whether the *I. b. pallida* subspecies represents a valid species or not due to the lack of sufficient genetic and morphological material for this work. Therefore, further sampling is recommended to clarify the taxonomy of this subspecies. Moreover, we failed to retrieve any genetic lineage that can be ascribed to *I. c. overlaeti* (see below regarding the status of this subspecies) in Angola (Marques et al. 2018). On the other hand, our phylogenetic and morphological analyses retrieve a highly divergent clade within the *capensis* group that represents a candidate new species (namely, *I.* aff. *capensis*). In addition, detailed examination of the type series of *I. c. overlaeti* and *I. c. nigrescens* challenges the validity of these two subspecies and places them in the *bivittata* group. Thus, the taxonomic status of this candidate new species cannot be resolved in this work due to taxonomic inconsistencies found in the original description and the detailed examination of the type series of *I. c. overlaeti* and *I. c. nigrescens*. Consequently, a detailed revision of this entire group is still needed to shed light on the taxonomy of all *Ichnotropis*.

External morphology seems to be very conserved among *Ichnotropis* species, and few characters are reliable enough to identify species. However, the new material has allowed us to provide unequivocal diagnostic character between *I. microlepidota* and other *Ichnotropis* species in terms of scalation, coloration, and morphometry. In addition, we identified some diagnostic characters on the skull between *I. microlepidota* and I. *bivittata*. However, previous works have already shown that lizard species can display significant intraspecific osteological variation (e.g., Lobón-Rovira 2024a), and therefore the cranial diagnostic characters here proposed must be taken with caution due to the low series used for this osteological comparison. In addition, despite the fact that morphology is very conserved in this group, *I. microlepidota* can be easily distinguished morphologically and genetically from *I. bivittata* (the only species occurring in sympatry), and therefore guarantees the taxonomic status of this species.

Color polymorphism is known for being highly prevalent among and within Lacertidae. This has led to dismissing coloration as a reliable diagnostic character to use to distinguish between different taxa (Brock et al. 2022). However, the large series of material examined in this work have allowed us to assess coloration features that we consider worth mentioning, which could be useful when identifying *I. microlepidota* from other *Ichnotropis* species (namely, the lack of a red/orange lateral band in adult males and the presence of consecutive rows of black encircled white ocelli). Moreover, the narrowly spaced yellow spots above the forelimbs present in *I. bivittata* and absent in *I. microlepidota* are a key coloration feature to take into consideration to differentiate the two species. These spots are the reason for finally identifying the doubtful individual in van den Berg (2020) as *I. bivittata* and not *I. microlepidota*.

The results of this work represent another example of the importance of the central highlands as the main center of endemism in southwestern Africa for amphibians and reptiles (Bauer et al. 2023; Lobón-Rovira 2024a) as well as underline the importance of Mount Moco as an important conservation area (Gonçalves et al. 2019; Branch et al. 2021; Lobón-Rovira et al. 2021a; Conradie et al. 2022c; Baptista et al. 2023; Bates et al. 2023).

In addition, we consider that this elusive species might exist in other areas with similar habitat traits, such as Mount Namba, and consequently we highlight the importance of further surveys on the central highlands aiming to shed light on the distribution and conservation status of this still poorly known endemic lizard.

It must be highlighted that the conservation status of this species remains unclear due to the lack of data about its distribution and relative abundance (Ceríaco et al. 2020c). However, the grassland habitat in Mount Moco is highly threatened by intentionally provoked bushfires to create suitable land portions for agriculture and livestock, which affects possible suitable habitat for this species (Cáceres et al. 2013). Furthermore, montane grasslands seem to play a crucial role in complicating the detectability of this species and others in this area, which are also rarely found in surveys, such as the Angolan adder (*Bitis heraldica*) (Ceríaco et al. 2020d). Consequently, this highlights again the importance of continuing fieldwork in these remote and poorly explored areas of Angola to shed light on the conservation status of this endemic species.

To conclude, this work demonstrates the taxonomic status of a poorly known and endemic Angolan species but also provides the first revision of this group in Africa. We here provide crucial genetic material for key species of this group (i.e., *I. microlepidota*) that can help to solve future taxonomic questions on this group. Therefore, this work can help to better understand the evolutionary history of elusive ground lizards and serve as a foundation for future studies in this group.

Acknowledgements

Work supported by National Funds through FCT-Fundação para a Ciência e a Tecnologia in the scope of the project LA/P/0048/2020. This work was only possible due to the institutional collaboration with the Ministry of Environment of the Republic of Angola (MINAMB), and in particular, the support received by Dr. Miguel Xavier, Director of Instituto Nacional de Biodiversidade e Conservação (INBC). We also acknowledge the remarkable logistical assistance of Fundaçao Kissama, especially Vlady Russo. JLR is currently supported by Associação BIOPOLIS CIBIO Base FUI 2020–2023 - UIDB1 50027 i2020. We thank CTM staff (especially Susana Lopes, Sofia Mourão, and Patrícia Ribeiro) at CIBIO for their tireless work and support in the lab. This work was partially supported by the Synthesis+ BE-TAF Project 2022 Grant obtained by JLR. We thank Garin Cael and Olivier Pauwels, from RMCA and RBINS, respectively, for their kind support providing relevant material deposited in their respective herpetological museums. WC thanks the Wild Bird Trust, which administrates the National Geographic Okavango Wilderness Project (2015–2019 National Geographic Society grant), and Chris Brooks, who organized the SAREP Aquatic Biodiversity Survey of the upper Angola Catchments of the Cubango-Okavango River Basin (May 2012) and the lower Cuito and Cuando River basins (April 2013). Material was collected and exported under the following export permits issued by the Angolan Ministry of Environment Institute of Biodiversity (MINAMB): 31/GGPCC/2016, 151/INBAC/MINAMB/2019). WC further thanks Chad Keates for processing the samples collected by him.

References

Baptista NL (2024) Conservation biogeography of Angolan amphibians. [PhD Thesis]. Porto: Faculdade de Ciências da Universidade do Porto.

Baptista NL, Conradie W, Vaz Pinto P, Branch WR (2019) The amphibians of Angola: Early studies and the current state of knowledge. In: Huntley BJ, Russo V, Lages F, Ferrand N (Eds) Biodiversity of Angola. Science & Conservation: A Modern Synthesis. Springer, Cham, 24–281.

Baptista NL, Tolley KA, Bluhm M, Finckh M, Branch WR (2020) Rediscovery, range extension, habitat and phylogenetic relation of the endemic Scaled Sandveld Lizard *Nucras scalaris* Laurent, 1964 (Sauria: Lacertidae) in the central Angolan plateau. African Journal of Herpetology 69(1): 12–28. https://doi.org/10.1080/21564574.2020.1778108

Baptista NL, Pinto PV, Keates C, Edwards S, Roedel MO, Conradie W (2021) A new species of red toad, *Schismaderma* Smith, 1849 (Anura: Bufonidae), from central Angola. Zootaxa 5081(3): 301–332. https://doi.org/10.11646/zootaxa.5081.3.1

Baptista NL, Pinto PV, Keates C, Lobón-Rovira J, Edwards S, Rödel MO (2023) Two new *Poyntonophrynus* species (Anura: Bufonidae) highlight the importance of Angolan centers of endemism. Vertebrate Zoology 73: 991–1031. https://doi.org/10.3897/vz.73.e103935

Bates MF, Lobón-Rovira J, Stanley EL, Branch WR, Pinto PV (2023) A new species of green-eyed *Cordylus* Laurenti, 1768 from the west-central highlands of Angola, and the rediscovery of *Cordylus angolensis* (Bocage, 1895) (Squamata: Cordylidae). Vertebrate Zoology 73: 599–646. https://doi.org/10.3897/vz.73.e95639

Bauer AM, Ceríaco LMP, Marques MP, Becker FS (2023) Highland reptiles of Angola and Namibia. Namibian Journal of Environment 8: 259–276.

Bocage JVB (1866) Lista dos reptis das possessões portuguezas d`Africa occidental que existem no Museu de Lisboa. - Jornal de Sciencias Mathematicas, Physicas e Naturaes, Academia Real das Sciencias de Lisboa 1(1): 37–56.

Böhm M, Collen B, Baillie JEM, Bowles P, Chanson J, Cox N, Hammerson G, Hoffmann M, Livingstone SR, Ram M, Rhodin AGJ, Stuart SN, van Dijk PP, Young BE et al. (2013) The conservation status of the world’s reptiles. Biological Conservation 157: 372–385. https://doi.org/10.1016/j.biocon.2012.07.015

Boulenger GA (1887) Catalogue of the lizards in the British Museum (Natural History). Vol. III. Lacertidae. - London, 1887: I-XII + 1–118.

Boulenger GA (1917) XXII.—Descriptions of new lizards of the family Lacertidæ. Annals and Magazine of Natural History 19(111): 277–279. https://doi.org/10.1080/00222931709486935

Boulenger GA (1921) Monograph of the Lacertidae. Vol. II. - British Museum (Natural History). Department of Zoology, London, 451 pp.

Branch WR (1998) Field guide to snakes and other reptiles of southern Africa, Struik Publishers, Cape Town, South Africa, 160–176.

Branch WR, Bayliss J, Tolley KA (2014) Pygmy chameleons of the *Rhampholeon platyceps* complex (Squamata: Chamaeleonidae): Description of four new species from isolated 'sky islands' of northern Mozambique. Zootaxa 3814(1): 1–36. https://doi.org/10.11646/zootaxa.3814.1.1

Branch WR, Baptista N, Pinto PV (2018) Angolan amphisbaenians: rediscovery of *Monopeltis luandae* Gans 1976, with comments on the type locality of *Monopeltis perplexus* Gans 1976 (Sauria: Amphisbaenidae). Herpetology Notes 11: 603–606.

Branch WR, Conradie W, Vaz Pinto P, Tolley K (2019a) Another Angolan Namib endemic species: a new *Nucras* Gray, 1838 (Squamata: Lacertidae) from south-western Angola. Amphibian & Reptile Conservation 12(2): 85–95. https://zenodo.org/doi/10.5281/zenodo.3731976

Branch WR, Baptista N, Keates C, Edwards S (2019b) Rediscovery, taxonomic status, and phylogenetic relationships of two rare and endemic snakes (Serpentes: Psammophiinae) from the south-western Angolan plateau. Zootaxa 4590(3): 342–366. https://doi.org/10.11646/zootaxa.4590.3.2

Branch WR, Baptista N, Pinto PV, Conradie W (2019c) The reptiles of Angola – history, diversity, endemism and hotspots. In: Huntley BJ, Ferrand N (Eds) Biodiversity of Angola. Science & Conservation: A Modern Synthesis. Springer, Cham, 283–326.

Branch WR, Schmitz A, Lobón-Rovira J, Baptista NL, António T, Conradie W (2021) Rock island melody: A revision of the *Afroedura bogerti* Loveridge, 1944 group, with descriptions of four new endemic species from Angola. Zoosystematics and Evolution 97(1): 55–82. https://doi.org/10.3897/zse.97.57202

Broadley DG (1967) The life cycles of two sympatric species of *Ichnotropis* (Sauria: Lacertidae). Zoologica Africana 3(1): 1–2. https://doi.org/10.1080/00445096.1965.11447347

Broadley DG (1974) Field studies on 'annual lizards' of the genus Ichnotropis. The Rhodesia science news 8, 309 pp.

Broadley DG (1979) A field study of two sympatric "annual" lizards (genus Ichnotropis) in Rhodesia. South African Journal of Zoology 14(3): 133–138. https://doi.org/10.1080/02541858.1979.11447662

Brock KM, McTavish EJ, Edwards DL (2021) Color polymorphism is a driver of diversification in the lizard family Lacertidae. Systematic Biology 71(1): 24–39. https://doi.org/10.1093/sysbio/syab046

Butler BO, Ceríaco LM, Marques MP, Bandeira S, Júlio T, Heinicke M P, Bauer AM (2019) Herpetological survey of Huíla Province, southwest Angola, including first records from Bicuar National Park. Herpetological Review 50(2): 225–240.

Cáceres A, Santos P, Tchalo F, Mills M, Melo M (2013) Human use of natural resources and the conservation of the afromontane forest in Mount Moco, Angola. Journal of Sustainable Development in Africa 15(3): 91–101.

Ceríaco LM, Marques MP, Bandeira S, Agarwal I, Stanley EL, Bauer AM, Heinicke MP, Blackburn DC (2018) A new earless species of *Poyntonophrynus* (Anura, Bufonidae) from the Serra da Neve inselberg, Namibe province, Angola. ZooKeys 780: 109–136. https://doi.org/10.3897/zookeys.780.25859

Ceríaco LM, Agarwal I, Marques MP, Bauer AM (2020a) A review of the genus *Hemidactylus* Goldfuss, 1820 (Squamata: Gekkonidae) from Angola, with the description of two new species. Zootaxa 4746(1): 1–71. https://doi.org/10.11646/zootaxa.4746.1.1

Ceríaco LMP, Heinicke MP, Parker K, Marques MP, Bauer AM (2020b) A review of the African snake-eyed skinks (Scincidae: *Panaspis*) from Angola, with the description of a new species. Zootaxa 4747(1): 77–112. https://doi.org/10.11646/zootaxa.4747.1.3

Ceríaco LMP, Baptista NL, Conradie W (2020c) *Ichnotropis microlepidota*. The IUCN Red List of Threatened Species 2020: e. T44929734A44929746. [Accessed on 27 July 2024]

Ceríaco LM, Tolley KA, Marques MP, Heinicke MP, Bauer AM (2020d) 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(1): 108–118. https://doi.org/10.1080/21564574.2020.1782484

Ceríaco LMP, Agarwal I, Marques MP, Bauer AM (2020e) A correction to a recent review of the genus *Hemidactylus* Goldfuss, 1820 (Squamata: Gekkonidae) from Angola, with the description of two additional species. Zootaxa 4861(1): 92–106. https://doi.org/10.11646/zootaxa.4861.1.6

Ceríaco LM, Santos BS, Marques MP, Bauer AM, Tiutenko A (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(1–4): 18–48.

Ceríaco LM, Marques MP, Parrinha D, Tiutenko A, Weinell JL, Butler BO, Bauer AM (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. https://doi.org/10.1206/0003-0090.465.1.1

Collyer ML, Adams DC (2018) RRPP: An r package for fitting linear models to high-dimensional data using residual randomization. Methods in Ecology and Evolution 9(7): 1772–1779. https://doi.org/10.1111/2041-210X.13029

Conradie W (2024) Herpetofaunal diversity and affiliations of the unexplored south-eastern Angola. [PhD Thesis]. South Africa: Nelson Mandela University, 640 pp.

Conradie W, Branch WR, Measey GJ, Tolley KA (2012a) A new species of *Hyperolius* Rapp, 1842 (Anura: Hyperoliidae) from the Serra da Chela mountains, southwestern Angola. Zootaxa 3269(1): 1–17. https://doi.org/10.11646/zootaxa.3269.1.1

Conradie W, Measey GJ, Branch WR, Tolley KA (2012b) Revised phylogeny of African sand lizards (*Pedioplanis*), with the description of two new species from south-western Angola. African Journal of Herpetology 61(2): 91–112. https://doi.org/10.1080/21564574.2012.676079

Conradie W, Branch WR, Tolley KA (2013) Fifty shades of grey: giving colour to the poorly known Angolan Ashy reed frog (Hyperoliidae: *Hyperolius cinereus*), with the description of a new species. Zootaxa 3635(3): 201–223. https://doi.org/10.11646/zootaxa.3635.3.1

Conradie W, Deepak V, Keates C, Gower DJ (2020) Kissing cousins: a review of the African genus *Limnophis* Günther, 1865 (Colubridae: Natricinae), with the description of a new species from north-eastern Angola. African Journal of Herpetology 69(1): 79–107. https://doi.org/10.1080/21564574.2020.1782483

Conradie W, Baptista NL, Verburgt L, Keates C, Harvey J, Julio T, Neef G (2021) Contributions to the herpetofauna of the Angolan Okavango-Cuando-Zambezi river drainages. Part 1: Serpentes (snakes).

Conradie W, Keates C, Baptista NL, Lobón-Rovira J (2022a) Taxonomical review of *Prosymna angolensis* Boulenger, 1915 (Elapoidea, Prosymnidae) with the description of two new species. ZooKeys 1121: 97–143. https://doi.org/10.3897/zookeys.1121.85693

Conradie W, Keates C, Verburgt L, Baptista NL, Harvey J, Julio T, Neef G (2022b) Contributions to the herpetofauna of the Angolan Okavango-Cuando-Zambezi River drainages. Part 2: Lizards (Sauria), chelonians, and crocodiles.

Conradie W, Schmitz A, Lobón-Rovira J, Becker FS, Vaz Pinto P, Hauptfleisch ML (2022c) Rock island melody remastered: two new species in the *Afroedura bogerti* Loveridge, 1944 group from Angola and Namibia. Zoosystematics and Evolution 98(2): 435–453. https://doi.org/10.3897/zse.98.86299

Conradie W, Keates C, Verburgt L, Baptista NL, Harvey J (2023) Contributions to the herpetofauna of the Angolan Okavango-Cuando-Zambezi river drainages. Part 3: Amphibians.

Conroy CJ, Papenfuss T, Parker J, Hahn NE (2009) Use of Tricaine Methanesulfonate (MS222) for Euthanasia of Reptiles. Journal of the American Association for Laboratory Animal Science 48: 28–32.

Cowan O, Conradie W, Keates C, Telford NS, Petford M, Egan V, Tolley KA (2024) Lost lizards: The importance of targeted surveys in filling knowledge gaps for reptile conservation in South Africa. Journal for Nature Conservation 84: 126790. https://doi.org/10.1016/j.jnc.2024.126790

Deikumah JP, McAlpine CA, Maron M (2014) Biogeographical and taxonomic biases in tropical forest fragmentation research. Conservation Biology 28(6): 1522–1531. https://doi.org/10.1111/cobi.12348

Edwards S, Branch WR, Vanhooydonck B, Herrel A, Measey GJ, Tolley KA (2013) Taxonomic adjustments in the systematics of the southern African lacertid lizards (Sauria: Lacertidae). Zootaxa 3669(2): 101–114. https://doi.org/10.11646/Zootaxa.3669.2.1

Engleder A, Haring E, Kirchhof S, Mayer W (2013) Multiple nuclear and mitochondrial DNA sequences provide new insights into the phylogeny of South African Lacertids (Lacertidae, Eremiadinae). Journal of Zoological Systematics and Evolutionary Research 51(2): 132–143. https://doi.org/10.1111/jzs.12012

Fick SE, Hijmans RJ (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37(12): 4302–4315. https://doi.org/10.1002/joc.5086

Gonçalves FM, Braine D, Bauer AM, Valério H, Marques MP, Ceríaco LM (2019) Rediscovery of the poorly known Angolan Adder, *Bitis heraldica* (Bocage, 1889) (Serpentes: Viperidae): New records, live photographs and first case history of envenomation. Herpetological Review 50(2): 241–246.

Hallermann J, Ceríaco LMP, Schmitz A, Ernst R, Conradie W, Verburgt L, Marques MP, Bauer AM (2020) A review of the Angolan House snakes, genus *Boaedon* Duméril, Bibron and Duméril (1854) (Serpentes: Lamprophiidae), with description of three new species in the *Boaedon fuliginosus* (Boie, 1827) species complex. African Journal of Herpetology 69(1): 29–78. https://doi.org/10.1080/21564574.2020.1777470

Hoang DT, Chernomor O, Von Haeseler A, Minh BQ, Vinh LS (2018) UFBoot2: improving the ultrafast bootstrap approximation. Molecular Biology and Evolution 35(2): 518–522. https://doi.org/10.1093/molbev/msx281

Huelsenbeck JP, Hillis DM (1993) Success of phylogenetic methods in the four-taxon case. Systematic Biology 42(3): 247–264. https://doi.org/10.1093/sysbio/42.3.247

Jacobsen NHG (1987) Notes on Reproduction in Ichnotropis squamulosa and Interspecific competition with Ichnotropis capensis in the Transvaal. The Journal of the Herpetological Association of Africa 33: 51–63.

Kumar S, Stecher G, Li M, Knyaz C, Tamura K (2018) MEGA X: Molecular evolutionary genetics analysis across computing platforms. Molecular Biology and Evolution 35: 1547–1549. https://doi.org/10.1093/molbev/msy096

Lanfear R, Frandsen PB, Wright AM, Senfeld T, Calcott B (2017) PartitionFinder 2: new methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. Molecular Biology and Evolution 34(3): 772–773.

Laurent RF (1952) Batraciens et reptiles récemment acquis par le Musée du Congo Belge. Revue Zoologique et Botanique Africaine 45(3, 4): 198–203.

Laurent RF (1964) Reptiles et Amphibiens de l'Angola (Troisième contribution). Publicações culturais da Companhia de Diamantes de Angola 67: 11–165.

Lindken T, Anderson CV, Ariano-Sánchez D, Barki G, Biggs C, Bowles P, Chaitanya R, Cronin DT, Jähnig SC, Jeshcke JM, Kennerley RJ, Lacher T, Swandby JL, Liu C, Long B, Mallon DP, Martin GM, Meiri S, Pasachnik S, Reynoso VH, Stanford CB, Stephenson PJ, Tolley K, Carvajal OT, Waldien DL, Woinarski J, Evans T (2024) What factors influence the rediscovery of lost tetrapod species?. Global Change Biology 30(1): e17107. https://doi.org/10.1111/gcb.17107

Lobón-Rovira J (2024a) Inferring the evolutionary trends in Southern Africa geckos: from wide to local perspective. Ph.D. Thesis. University of Porto, Porto, 524 pp.

Lobón-Rovira J, Bauer AM (2021) Bone-by-bone: A detailed skull description of the White-headed dwarf gecko *Lygodactylus picturatus* (Peters, 1870). African Journal of Herpetology 70(2): 75–94. https://doi.org/10.1080/21564574.2021.1980120

Lobón-Rovira J, Conradie W, Buckley Iglesias D, Ernst R, Veríssimo L, Baptista NL, Pinto PV (2021) Between sand, rocks and branches: An integrative taxonomic revision of Angolan *Hemidactylus* Goldfuss, 1820, with description of four new species. Vertebrate Zoology 71: 465–501. https://doi.org/10.3897/vz.71.e64781

Lobón-Rovira J, Conradie W, Baptista NL, Pinto PV (2022) A new species of feather-tailed leaf-toed gecko, *Kolekanos* Heinicke, Daza, Greenbaum, Jackman & Bauer, 2014 (Squamata, Gekkonidae) from the poorly explored savannah of western Angola. ZooKeys 1127: 91–116. https://doi.org/10.3897/zookeys.1127.84942

Lobón-Rovira J, Bauer AM, Pinto PV, Trape JF, Conradie W, Kusamba C, Júlio T, Cael G, Stanley EL, Hughes DF, Behangana M, Masudi FM, Pauwels OP, Greenbaum E (2024b) Integrative revision of the *Lygodactylus gutturalis* (Bocage, 1873) complex unveils extensive cryptic diversity and traces its evolutionary history. Zoological Journal of the Linnean Society 201(2): 447–492. https://doi.org/10.1093/zoolinnean/zlad123

Lobón-Rovira J, Baptista NL, Clark T, Verburgt L, Jongsma G, Conradie W, Veríssimo L, Pinto PV (2024c) Filling the gaps: herpetological checklist of Mayombe National Park and Cabinda Province (Angola) shed light on one of the most unexplored corners of tropical Central Africa. African Journal of Herpetology 2025: 1–59.

Makokha JS, Bauer, AM, Mayer W, Matthee CA (2007) Nuclear and mtDNA-based phylogeny of southern African sand lizards, Pedioplanis (Sauria: Lacertidae). Molecular Phylogenetics and Evolution 44(2): 622-633. https://doi.org/10.1016/j.ympev.2007.04.021

Marques MP, Ceríaco LM, Blackburn DC, Bauer AM (2018) Diversity and distribution of the amphibians and terrestrial reptiles of Angola: atlas of historical and bibliographic records (1840–2017). California Academy of Sciences.

Marques MP, Ceriaco LM, Stanley EL, Bandeira S, Agarwal I, Bauer AM (2019) A new species of girdled lizard (Squamata: Cordylidae) from the Serra da Neve Inselberg, Namibe Province, southwestern Angola. Zootaxa 4668(4): 503–524. https://doi.org/10.11646/zootaxa.4668.4.4

Marques MP, Ceriaco LM, Buehler MD, Bandeira S, Janota JM, Bauer AM (2020a) Description of a new long-tailed skink (Scincidae: *Trachylepis*) from Angola and the Democratic Republic of the Congo. Zootaxa 4568(1): 51–68. https://doi.org/10.11646/zootaxa.4568.1.3

Marques MP, Ceríaco LM, Buehler MD, Bandeira S, Janota JM, Bauer AM (2020b) A revision of the Dwarf Geckos, genus *Lygodactylus* (Squamata: Gekkonidae), from Angola, with the description of three new species. Zootaxa 4583(3): 301–352. https://doi.org/10.11646/zootaxa.5555.3.1

Marques MP, Parrinha D, Santos BS, Bandeira S, Butler BO, Sousa ACA, Bauer AM, Wagner P (2022a) All in all it's just another branch in the tree: A new species of *Acanthocercus* Fitzinger, 1843 (Squamata: Agamidae), from Angola. Zootaxa 5099(2): 221–243. https://doi.org/10.11646/zootaxa.5099.2.4

Marques MP, Ceríaco LM, Heinicke MP, Chehouri RM, Conradie W, Tolley A, Bauer AM (2022b) The Angolan bushveld lizards, genus *Heliobolus* Fitzinger, 1843 (Squamata: Lacertidae): Integrative taxonomy and the description of two new species. Vertebrate Zoology 72: 745–769. https://doi.org/10.3897/vz.72.e85269

Marques MP, Parrinha D, Ceríaco LM, Brennan IG, Heinicke MP, Bauer AM (2023a) A new species of thick-toed gecko (*Pachydactylus*) from Serra da Neve and surrounding rocky areas of southwestern Angola (Squamata: Gekkonidae). Vertebrate Zoology 73: 325–343. https://doi.org/10.3897/vz.73.e101329

Marques MP, Parrinha D, Tiutenko A, Lopes-Lima M, Bauer AM, Ceríaco LM (2023b) A new species of African legless skink, genus *Acontias* Cuvier, 1816 "1817" (Squamata: Scincidae) from Serra da Neve inselberg, south-western Angola. African Journal of Herpetology 72(2): 145–162. https://doi.org/10.1080/21564574.2023.2246487

Marques MP, Parrinha D, Lopes-Lima M, Tiutenko A, Bauer AM, Ceríaco LM (2024a) An island in a sea of sand: a first checklist of the herpetofauna of the Serra da Neve inselberg, southwestern Angola. ZooKeys 1201: 167–217. https://doi.org/10.3897/zookeys.1201.120750

Marques MP, Parrinha D, Lopes-Lima M, Tiutenko A, Bauer AM, Ceríaco LM (2024b) A treasure trove of endemics: two new species of snake-eyed skinks of the genus Panaspis Cope, 1868 (Squamata, Scincidae) from the Serra da Neve Inselberg, southwestern Angola. Evolutionary Systematics 8: 167–182. https://doi.org/10.3897/evolsyst.8.121103

Marx H (1956) A new lacertid lizard from Angola. Publication (Chicago Natural History Museum), 802 pp.

Mayer W (2013) Kommentierte Lacertiden-Liste für Europa, Afrika, den Nahen Osten inklusive der Arabischen Halbinsel und Asien. Lacertidae (Eidechsen Online) 7: 81–141.

Meiri S, Bauer AM, Allison A, Castro-Herrera F, Chirio L, Colli G, Das I, Doan TM, Glaw F, Grismer LL, Hoogmoed M, Kraus F, LeBreton M, Meirte D, Nagy ZT, Nogueira CC, Oliver P, Pauwels OSG, Pincheira-Donoso D, Shea G, Sindaco R, Tallowin OJS, Torres-Carvajal O, Trape JF, Uetz P, Wagner P, Wang Y, Ziegler T, Roll U (2018) Extinct, obscure or imaginary: the lizard species with the smallest ranges. Diversity and Distributions 24(2): 262–273. https://doi.org/10.1111/ddi.12678

Miller MA, Pfeiffer W, Schwartz T (2010) Creating the CIPRES science gateway for inference of large phylogenetic trees. In: Gateway Computing Environments Workshop 2010: 1–8.

Mills MS, Olmos F, Melo M, Dean WRJ (2011) Mount Moco: its importance to the conservation of Swierstra's Francolin *Pternistis swierstrai* and the Afromontane avifauna of Angola. Bird Conservation International 21(2): 119–133. https://doi.org/10.1017/S0959270910000493

Minh BQ, Dang CC, Vinh LS, Lanfear R (2021) QMaker: fast and accurate method to estimate empirical models of protein evolution. Systematic Biology 70(5): 1046–1060. https://doi.org/10.1093/sysbio/syab010

Nielsen SV, Conradie W, Ceríaco LMP, Bauer AM, Heinicke MP, Stanley EL, Blackburn DC (2020) A new species of Rain Frog (Brevicipitidae, *Breviceps*) endemic to Angola. ZooKeys 979: 133–160. https://doi.org/10.3897/zookeys.979.56863

Ogwu MC, Izah SC, Iyiola AO (2022) An Overview of the Potentials, Threats and Conservation of Biodiversity in Africa. In: Chibueze Izah S (Eds) Biodiversity in Africa: Potentials, Threats and Conservation. Sustainable Development and Biodiversity 29. Springer, Singapore.

Palumbi SR (1996) The polymerase chain reaction. In: Hillis D, Moritz C, Mable B (Eds) Molecular Systematics. 2nd edn. Sunderland: Sinauer Associates, 205–247.

Parker HW (1936) Dr. Karl Jordan's expedition to South-West Africa and Angola: herpetological collection. Novitates Zoologicae 40: 115–146.

Parrinha D, Marques MP, Heinicke MP, Khalid F, Parker KL, Tolley KA, Childers JL, Conradie W, Bauer AM, Ceríaco LM (2021) A revision of Angolan species in the genus *Pedioplanis* Fitzinger (Squamata: Lacertidae), with the description of a new species. Zootaxa 5032(1): 1–46. https://doi.org/10.11646/zootaxa.5032.1.1

Prates I, Melo-Sampaio PR, de Oliveira Drummond L, Teixeira Jr M, Rodrigues MT, Carnaval AC (2017) Biogeographic links between southern Atlantic Forest and western South America: rediscovery, re-description, and phylogenetic relationships of two rare montane anole lizards from Brazil. Molecular Phylogenetics and Evolution 113: 49–58. https://doi.org/10.1016/j.ympev.2017.05.009

Putra CA, Amarasinghe AT, Hikmatullah D, Scali S, Brinkman J, Manthey U, Ineich I (2020) Rediscovery of Modigliani's nose-horned lizard, *Harpesaurus modiglianii* Vinciguerra, 1933 (Reptilia: Agamidae) after 129 years without any observation. *Taprobanica:* The Journal of Asian Biodiversity 9(1): 3–11. https://doi.org/10.47605/tapro.v9i1.216

Rambaut A, Suchard MA, Xie D, Drummond AJ (2014) Tracer Version 1.6. http://beast.bio.ed.ac.uk/Tracer

Rodrigues MT, Teixeira Jr M, Dal Vechio F, Amaro RC, Nisa C, Camacho A, Damasceno R, Roscito J, Nunes PMS, Recoder RS (2013) Rediscovery of the earless microteiid lizard *Anotosaura collaris* Amaral, 1933 (Squamata: Gymnophthalmidae): a redescription complemented by osteological, hemipenial, molecular, karyological, physiological and ecological data. Zootaxa 3731(3): 345–370. https://doi.org/10.11646/zootaxa.3731.3.5

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Hohna S, Larget B, Liu L, Suchard MA, Huelsenback JP (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61: 539–542. https://doi.org/10.1093/sysbio/sys029

RStudio Team (2022) RStudio: Integrated Development Environment for R. RStudio, PBC, Boston, MA. http://www.rstudio.com

Rydén O, Zizka A, Jagers SC, Lindberg SI, Antonelli A (2020) Linking democracy and biodiversity conservation: Empirical evidence and research gaps. Ambio 49: 419–433. https://doi.org/10.1007/s13280-019-01210-0

Schmidt KP (1919) Contributions to the herpetology of the Belgian Congo based on the collection of the American Museum Congo Expedition, 1909–1915 (39). American Museum of Natural History.

Smith A (1838) Contributions to the Natural History of Southern Africa. Art. VIII. Magazine of natural history, London 2(14): 92–94.

Solano-Zavaleta I, De la Luz NMC, Clause AG (2017) Solving a 50-year mystery: Rediscovery of Mesaspis antauges (Squamata: Anguidae). Zootaxa 4303(4): 559–572. https://doi.org/10.11646/zootaxa.4303.4.7

Stanley EL, Ceríaco LM, Bandeira S, Valerio H, Bates MF, Branch WR (2016) A review of *Cordylus machadoi* (Squamata: Cordylidae) in southwestern Angola, with the description of a new species from the Pro-Namib desert. Zootaxa 4061(3): 201–226. https://doi.org/10.11646/zootaxa.4061.3.1

Trifinopoulos J, Nguyen LT, von Haeseler A, Minh BQ (2016) W-IQ-TREE: A fast online phylogenetic tool for maximum likelihood analysis. Nucleic Acids Research 44: 232–235. https://doi.org/10.1093/nar/gkw256

Tolley KA, Alexander GJ, Branch WR, Bowles P, Maritz B (2016) Conservation status and threats for African reptiles. Biological Conservation 204: 63–71. https://doi.org/10.1016/j.biocon.2016.04.006

Uetz P, Freed P, Aguilar R, Reyes, F, Kudera J, Hosek J (2025) The Reptile Database. http://www.reptile-database.org [accessed 01/03/2025]

van den Berg MP (2017) An annotated bibliographic history of *Ichnotropis* Peters, 1854 (Reptilia, Lacertidae) with remarks on the validity of some of the including species. Lacertidae (Eidechsen Online) 4: 60–138.

van den Berg MP (2020) Could this be the first live image of *Ichnotropis microlepidota*? Lacertidae (Eidechsen Online) 2: 14–18.

Wagner P, Butler BO, Ceríaco LM, Bauer AM (2021) A new species of the *Acanthocercus atricollis* complex (Squamata: Agamidae). Salamandra 57(4).

Wang K, Ren J, Jiang K, Yuan Z, Siler CD (2017) Rediscovery of the enigmatic Mountain Dragon, *Japalura yulongensis* (Reptilia: Sauria: Agamidae), with notes on its natural history and conservation. Zootaxa 4318(2): 351–363. https://doi.org/10.11646/zootaxa.4318.2.8

Whiting AS, Bauer AM, Sites Jr JW (2003) Phylogenetic relationships and limb loss in sub-Saharan African scincine lizards (Squamata: Scincidae). Molecular phylogenetics and evolution 29(3): 582–598. https://doi.org/10.1016/S1055-7903(03)00142-8

Wiens JJ, Kuczynski CA, Townsend T, Reeder TW, Mulcahy DG, Sites Jr JW (2010) Combining phylogenomics and fossils in higher-level squamate reptile phylogeny: molecular data change the placement of fossil taxa. Systematic Biology 59(6): 674–688. https://doi.org/10.1093/sysbio/syq048

Supplementary material 1

Morphological measurements of all individuals

Authors: Max Benito, Werner Conradie, Pedro Vaz Pinto, Javier Lobón-Rovira

Data type: docx

Explanation note: Information on the individuals used for the skull segmentations; color pallete used in the skull segmentations for bones not included in Lobón-Rovira and Bauer (2021); Principal component analysis (PCA) loadings, ANOVA analysis results; list of individuals used for the genetic work and distribution (map), with information about their museum and field numbers, localities, coordinates and source.

Link: https://doi.org/10.3897/zse.101.136290.suppl1