Vertebrate Zoology 75, 2025, 627–672 | DOI 10.3897/vz.75.e167366

SENCKENBERG
world of biodiversity

Systematics of African rough-scaled lizards, with description of two new species from eastern Angola (Squamata: Lacertidae: *Ichnotropis* Peters, 1854)

Werner Conradie[1,2,3], Chad Keates[3,4,5], Eli Greenbaum[6], Javier Lobón-Rovira[7,8], Krystal A. Tolley[9], Max Benito[10], Pedro Vaz Pinto[7,8,11], Reuben V. van Breda[12], Luke Verburgt[3,13,14]

1 *Port Elizabeth Museum (Bayworld), Beach Road, Humewood, Gqeberha, 6013, South Africa*
2 *Department of Conservation Management, Natural Resource Science and Management Cluster, Faculty of Science, George Campus, Nelson Mandela University, George, 6529, South Africa*
3 *National Geographic Okavango Wilderness Project, Wild Bird Trust, Santon, 2196, South Africa*
4 *South African Institute for Aquatic Biodiversity, Makhanda, 6140, South Africa*
5 *Ft. Lauderdale Research and Education Center, University of Florida, Davie, FL 33314, USA*
6 *Department of Biological Sciences, University of Texas at El Paso, El Paso, TX 79968, USA*
7 *CIBIO, Centro de Investigacao em Biodiversidade e Recursos Geneticos, InBIO Laboratorio Associado, Campus de Vairao, Universidade do Porto, 4485-661 Vairao, Portugal*
8 *BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Campus de Vairao, 4485-661 Vairao, Portugal*
9 *Department of Zoology, University of Johannesburg, Auckland Park, Johannesburg, 2006, South Africa*
10 *Universidad Internacional Menéndez Pelayo, Calle de Isaac Peral 23, 28040 Madrid, Spain*
11 *Fundação Kissama, Rua 60 Casa 560, Lar do Patriota, Luanda, Angola*
12 *Unit for Environmental Sciences and Management, North-West University, Potchefstroom, 2531, South Africa*
13 *Enviro-Insight CC, Unit 8 Oppidraai Office Park, Pretoria, 0050, South Africa*
14 *Department of Zoology and Entomology, University of Pretoria, Pretoria, 0001, South Africa*

https://zoobank.org/F811EE38-D26A-4C49-A863-D2800F54BA7B

Corresponding author: Werner Conradie (werner@bayworld.co.za)

Academic editor Uwe Fritz | **Received** 13 July 2025 | **Accepted** 3 October 2025 | **Published** 21 November 2025

Citation: Conradie W, Keates C, Greenbaum E, Lobón-Rovira J, Tolley KA, Benito M, Vaz Pinto P, van Breda RV, Verburgt L (2025) Systematics of African rough-scaled lizards, with description of two new species from eastern Angola (Squamata: Lacertidae: *Ichnotropis* Peters, 1854). Vertebrate Zoology 75: 627–672. https://doi.org/10.3897/vz.75.e167366

Abstract

Ichnotropis is a genus of medium-sized lacertids endemic to sub-Saharan Africa, characterised by rough head shields. The genus currently comprises six nominal species distributed across much of southern, central, and eastern Africa. Some species are apparently active at only certain times of the year, resulting in limited specimen collections and severely hampering research. This scarcity of material has historically made comprehensive systematic reviews of the genus difficult and has led to the description of numerous regional morphological variants as distinct species or subspecies. Material collected in recent years has enabled us to provide a new phylogenetic hypothesis of *Ichnotropis* using two mitochondrial genes (16S and ND4) and two nuclear genes (c-mos and RAG-1). Our phylogenetic dataset includes 56 individuals representing five of the six currently recognised species (excluding *I. chapini*). Additionally, the broad geographical sampling of the widespread *I. capensis* group has allowed us to explore the taxonomic status of several species and subspecies within the group. As a result, we demonstrate the monophyly of *Ichnotropis* in relation to other African lacertids and present the most comprehensive phylogeny of the genus to date. We also provide the first phylogenetic placements for *I. tanganicana* and *I. grandiceps*, which allows us to validate their taxonomic statuses. Furthermore, we recovered a new cryptic species closely related to *I. grandiceps*, and identified several well-supported clades within the *I. capensis* group, all corroborated by multi-locus species delimitation analyses. One of these clades is described herein as a new species, while the remaining taxa of interest are discussed and highlighted for future investigation. Based on our findings, we recommend the following taxonomic revisions: *Ichnotropis longipes* and *I. macrolepidota* should remain synonyms of *I. capensis*; *I. bivittata pallida* and *I. capensis nigrescens* are treated as a junior synonyms of *I. bivittata*; and *I. overlaeti* is considered a junior synonym of *I. tanganicana*. Although we could not determine the phylogenetic placement of *I. chapini* due to the lack of genetic material, its head morphology and scalation support its reassignment to the *I. bivittata* group. Thus, it is retained as a valid species pending the availability of new material for further taxonomic actions. In conclusion, this study resolves several long-standing taxonomic issues within one of Africa's most understudied lacertid genera and lays a solid foundation for future research on the genus *Ichnotropis*.

Keywords

Africa, cryptic species, reptiles, sub-Sahara, taxonomy

Introduction

The family Lacertidae comprises 388 recognised species and numerous subspecies distributed across Africa, Europe, and Asia (Uetz et al. 2025). Although the main species hotspot can be found in the Palearctic, particularly in arid zones such as northern Africa and the Arabian Peninsula, substantial diversity also occurs farther south. Central and southern Africa—spanning much of sub-Saharan Africa, from south of the Congo River Basin to the southernmost tip of the continent—harbours at least 65 recognised species across 11 genera (Uetz et al. 2025). This accounts for approximately 17% of global lacertid diversity, underscoring the region's significance as a centre of endemism and evolutionary diversification within the family. Despite its richness, the lacertid fauna of central and southern Africa remains comparatively understudied (Tolley et al. 2016), highlighting a gap in our knowledge on the family's biogeography and evolutionary history.

In recent years, several phylogenetic studies have attempted to address this gap by focussing on central and southern African lacertid genera, including *Adolfus* (Greenbaum et al. 2011, 2018), *Pedioplanis* (Makokha et al. 2007; Conradie et al. 2012; Childers et al. 2021; Parrinha et al. 2021), *Meroles* (Edwards et al. 2012, 2013a), *Nucras* (Edwards et al. 2013b; Branch et al. 2019; Bauer et al. 2019, 2020, 2025; Baptista et al. 2020), and *Heliobolus* (Marques et al. 2022a). Some of these and other studies have also focused on alpha taxonomy (Greenbaum et al. 2011; Edwards et al. 2013a; Englender et al. 2013; Wagner et al. 2014). Collectively, these studies have improved our knowledge of lacertid systematics and diversity, resulting in the description of multiple new species. Despite this progress, detailed phylogenetic and phylogeographic studies are still lacking for certain genera, such as *Holaspis*, *Ichnotropis*, *Latastia*, and *Tropidosaura*.

The African lacertid genus *Ichnotropis* Peters, 1854 comprises several small to medium-sized, rough-scaled, terrestrial species that inhabit mesic to xeric savannas in central and southern Africa (Branch 1998; Spawls et al. 2018; Pietersen et al. 2021; Benito et al. 2025). Interestingly, the genus includes several sympatric species that are presumed to have an annual reproductive strategy, in which they breed asynchronously, and this might be a strategy to reduce interspecific competition (Broadley 1967a, 1974, 1979; Jacobsen 1987). However, our knowledge of this ecological phenomenon is hampered by the lack of robust ecological studies on this genus.

Knowledge of the genus is based largely on the work of Boulenger (1921) and subsequent species descriptions by de Witte and Laurent (1942), Laurent (1952), Marx (1956) and Broadley (1967b), as well as a recent comprehensive synthesis of the genus provided by van den Berg (2017). Six species are currently recognised as valid: *Ichnotropis bivittata* Bocage, 1866; *Ichnotropis capensis* (Smith, 1838); *Ichnotropis chapini* Schmidt, 1919; *Ichnotropis grandiceps* Broadley, 1967; *Ichnotropis microlepidota* Marx, 1956; and *Ichnotropis tanganicana* Boulenger, 1917. Furthermore, the subspecies, *I. bivittata pallida* Laurent, 1964 is considered to be valid, while additional species or subspecies (i.e., *I. capensis nigrescens* Laurent, 1952; *I. macrolepidota* Peters, 1864; *I. longipes* Boulenger, 1902; *I. overlaeti* de Witte & Laurent, 1942) have been described but are currently not considered valid, or are controversial (Uetz et al. 2025). Confusion therefore persists in the literature regarding the number of accepted species, their diagnostic characteristics, and synonyms (van den Berg 2017). Thus, in the absence of a strong phylogenetic framework for *Ichnotropis* that can be used to clarify species boundaries, and a detailed morphological revision, this confusion is likely to continue.

In recent years, collections of *Ichnotropis* across its range have improved, particularly due to a concerted effort to carry out biodiversity surveys in under-sampled regions such as Angola (Conradie et al. 2016, 2022a; Benito et al. 2025), the Democratic Republic of the Congo (DRC) (Keates 2024) and Zambia (Pietersen et al. 2017). This has allowed for validation of the taxonomic status of some described species within a phylogenetic framework in the current study, as well as providing a more informed knowledge baseline regarding the diversity and evolution of this group in central and southern Africa. Through this process, we aim to stabilise the taxonomy of the group and lay a foundation for future work.

Material and Methods

Sampling

Over the past decade, multiple new *Ichnotropis* specimens were collected across central and southern Africa, especially from Angola, Democratic Republic of the Congo (**DRC**), Mozambique, South Africa and Zambia (Table 1). Initial species identifications were based on key diagnostic features (e.g., dorsolateral colouration, head scalation, supraocular–supraciliar-prefrontal contacts) reported in the literature (Boulenger 1921; Marx 1956; Broadley 1967b; van Berg 2017), supplemented by examination of type and topotypic or near-topotypic material (see Morphology below), and by considering geographic proximity to the respective type localities. DNA samples were collected from either liver, muscle or tail tips and preserved in 99% ethanol after which voucher specimens were fixed in 10% formalin and transferred to 70% ethanol for long-term storage at the Port Elizabeth Museum (**PEM**, South Africa), the Colecção Herpetológica do Lubango (**CHL**, Angola), the National Museum Namibia (**NMNW**, Namibia), the Museu de História Natural e da Ciência–Universidade do Porto (**MHNC-UP**, Portugal), the Museo delle Scienze di Trento (**MUSE**, Italy), and the Fundação Kissama Collection (**FKH**, Angola). Representative material was also deposited with the Ministry of Environment, Luanda, Angola (**MINAMB**), and the Museu de História Natural de Maputo, Mozambique (**MHNM**). For all newly collected specimens, geographic coordinates were recorded in decimal degrees (WGS84 datum, four decimal places) using a handheld GPS, and elevation in meters above sea level (a.s.l.).

DNA extraction, amplification and sequencing

DNA was isolated from tissue samples using a standard salt extraction method (Aljanabi and Martinez 1997). Standard Polymerase Chain Reaction (**PCR**) procedures were utilised to amplify one partial mitochondrial ribosomal gene (16S rRNA [**16S**]), one partial mitochondrial gene (NADH-dehydrogenase subunit 4 [**ND4**]), and two partial nuclear genes (oocyte maturation factor [**c-mos**], recombination activating gene 1 [**RAG-1**]). Each amplification was conducted with a PCR mixture of 25 μl total volume, containing 12.5 μL Taq DNA Polymerase 2x Master Mix (Ampliqon; 3 mM $MgCl_2$, 0.4 mM dNTPs and Ampliqon Taq DNA polymerase), 2 μl forward primer (10 μM), 2 μl reverse primer (10 μM), and 8.5 μl of extracted genomic DNA (20–50 ng/μl) and water combined. The cycling profile for all the genes was as follows: Initial denaturation step at 94°C for 5 min, followed by 30–37 cycles of 94°C for 30 s, 42–58°C for 45 s, and 72°C for 45 s, with a final extension at 72°C for 8 min. The cycling profile for the genes differed only in the annealing temperature and the number of cycles (Table S1). The prepared PCR products were sent to Macrogen Corporation in Amsterdam, The Netherlands, for purification and sequencing with forward primers.

Phylogenetic analyses

For the phylogenetic analyses, 46 *Ichnotropis* individuals were sequenced, supplemented with sequences from 10 individuals available from GenBank. Six *Meroles squamulosus* individuals were used as outgroup taxa (Table 1). For each gene, new sequences were checked and edited using BioEdit Sequence Alignment Editor v.7.2.5 (Hall 1999), and then aligned with the GenBank sequences in MEGA v.7.0.27 (Tamura et al. 2013), using the ClustalW v.1.6 alignment algorithm with default settings for alignment parameters (Thompson et al. 1994). Single gene maximum likelihood (**ML**) trees were created in IQ-TREE v.2.1.3 (Nguyen et al. 2015) to visually check the placement of sequences and compare topologies. DAMBE v.7.3.1 (Xia 2018) was used to test for saturation using the individual as well as combined first and second codon positions of each protein-coding gene. As none of the genes were found to be saturated, the genes were not partitioned by codons. In addition, congruence between individual gene datasets, as well as between mitochondrial and nuclear datasets, were tested using 100 replicates of the partition-homogeneity test (**PHT**) (Farris et al. 1994, 1995) in PAUP* v.4.0a169 (Swofford 2003). All gene-tree combinations were congruent, allowing for the creation of a concatenated dataset of 2128 base pairs for further phylogenetic analyses, with the individual gene alignments joined using SequenceMatrix v.1.8.2 (Vaidya et al. 2011).

The optimal partition scheme and best-fitting models of molecular evolution were selected using ModelFinder implemented in IQ-TREE (Chernomor et al. 2016; Minh et al. 2021). The following settings were used: -p partition file (each partition has its own evolution rate), a greedy strategy and the FreeRate heterogeneity model excluded (only invariable sites and Gamma rate heterogeneity considered) (Chernomor et al. 2016; Kalyaanamoorthy et al. 2017). As MrBayes is not able to implement all the IQ-TREE models, the -mset mrbayes command was used to ensure that only models that were compatible with MrBayes were selected. The best-fitting model schemes selected for each dataset were as follows: 16S: GTR+G, ND4: GTR+I+G, c-mos+RAG-1: HKY+G.

Maximum likelihood phylogenies were generated in IQ-TREE, using a random starting tree and the best-fitting model schemes selected for each dataset (as selected above). The ultrafast bootstrap approximation (UFBoot) method (Hoang et al. 2018) was implemented using 5000 replicates and a minimum correlation coefficient of 0.99. To ensure accuracy, the analysis was run twice to confirm that independent ML searches recovered the same topologies.

Bayesian inference (**BI**) was run using MrBayes v.3.2.7a (Ronquist et al. 2012) on the CIPRES Science Gateway XSEDE (http://www.phylo.org; Miller et al. 2010) using the gene-partitioned scheme and model selection identified by ModelFinder implemented in IQ-

Table 1. Material used for the phylogenetic analyses, including sample number, museum catalogue number, country, locality, geographic coordinates, and GenBank/ENA accession numbers. Abbreviations: Aaron M. Bauer field numbers (AMB), British Museum of Natural History (BMNH), California Academy of Sciences (CAS), Colecção Herpetológica do Lubango (CHL), Chad Keates field series (CKD), Enviro-Insight (EI), Fundação Kissama Collection (FKH). Krystal Tolley field numbers (KTH, RSP, WP), Marius Burger field numbers (MBUR), Museu de História Natural e da Ciência - Universidade do Porto (MHNCUP), Ninda Baptista field numbers (NB), Museu de História Natural de Maputo (MHNM), National Museum Namibia (NMNW), Museo delle Scienze di Trento (MUSE), Pedro Vaz Pinto field numbers (P, L series), Port Elizabeth Museum (PEM), Reuben V. van Breda field numbers (RE), Sebastian Kirchof field numbers (SK), Stuart V. Nielsen field numbers (SVN), Thomas Branch field numbers (TB), Werner Conradie field numbers (WC, ANG), William R. Branch field numbers (WRB). Missing data or unavailable information is indicated as NA.

Sample No.	Museum catalogue No.	Species	Country	Locality	Latitude	Longitude	16S	ND4	RAG-1	c-mos
WC-4515	PEM R23530	*Ichnotropis b. bivittata*	Angola	West of Cuito town on Aludungo road	−12.3278	16.9067	PV357721	OZ347967	PV412867	
NB0675	CHL0675	*Ichnotropis b. bivittata*	Angola	Luando Integral Nature Reserve	−10.2772	16.9533	PV357719	PV412839	PV412865	PV390641
P1-318	FKH-0833	*Ichnotropis b. bivittata*	Angola	Cambau	−10.1048	15.2182	PV357720	PV412840	PV412866	PV390642
KTH09-075	PEM R17934	*Ichnotropis b. pallida*	Angola	7 km East of Humpata	−14.9820	13.4352	HF547775	HF547731	HF547694	
ABC2	NA	*Ichnotropis capensis*	Namibia	Katima Mulilo	−17.5066	24.2688	JX962898		JX963023	JX962916
AMB-6001	NMNW	*Ichnotropis capensis*	Namibia	Road to Tsumkwe	−19.4600	19.7200	DQ871148	HF547732	DQ871206	
AMB-6067	CAS 209602	*Ichnotropis capensis*	South Africa	Kosi Bay, KwaZulu-Natal	−26.9400	32.8200	DQ871149	HF547733	DQ871207	
ANG-311	PEM R20495	*Ichnotropis capensis*	Angola	8.5 km North of Rito	−16.6232	19.0535	PV357725	PV412844	OZ347936	
BMNH 2019. 2745	BMNH 2019. 2745	*Ichnotropis capensis*	Zambia	Sioma Ngwezi National Park	−16.8987	23.5985	MK464418			
BMNH 2019. 2746	BMNH 2019. 2746	*Ichnotropis capensis*	Zambia	Chavuma Farm	−13.0701	22.9288	MK464417			
BMNH 2019. 2747	BMNH 2019. 2747	*Ichnotropis capensis*	Zambia	Lukwakwa	−12.6608	24.4370	MK464416			
BMNH 2019. 2750	BMNH 2019. 2750	*Ichnotropis capensis*	Zambia	Nanzila Plains, Kafue National Park	−16.2814	25.9168	MK464415			
BOX23-C02	PEM R24748	*Ichnotropis capensis*	South Africa	Tembe Elephant Park, KwaZulu-Natal	−27.0217	32.4583	OZ347416	OZ347968		
EI-0437	NA	*Ichnotropis capensis*	South Africa	Lepalale, Limpopo	−23.6391	27.5981		OZ347969	OZ347937	OZ347957
EI-0443	PEM R25370	*Ichnotropis capensis*	South Africa	Lepalale, Limpopo	−23.6391	27.5981		OZ347970		OZ347958
EI-0444	PEM R25371	*Ichnotropis capensis*	South Africa	Lepalale, Limpopo	−23.6391	27.5981	OZ347417	OZ347971	OZ347938	OZ347959
L-18	PEM R22069	*Ichnotropis capensis*	Angola	Gambos, Foster‘s farm	−15.8500	14.6833	PV357726	PV412845	OZ347939	
MOZ14-356	NHNM	*Ichnotropis capensis*	Mozambique	Chizavane, Zona Braza Lodge	−25.0137	34.0376	OZ347418	OZ347972	OZ347940	
MOZ14-357	PEM R21112	*Ichnotropis capensis*	Mozambique	Chizavane, Zona Braza Lodge	−25.0137	34.0376	OZ347419	OZ347973	OZ347941	
MOZ14-358	PEM R21113	*Ichnotropis capensis*	Mozambique	Chizavane, Zona Braza Lodge	−25.0137	34.0376	OZ347420	OZ347974	OZ347942	OZ347960
NB0771	CHL0771	*Ichnotropis capensis*	Angola	Bicuar National Park	−15.2435	14.8915	PV357727	PV412846	PV412870	PV390644
NB0772	CHL0772	*Ichnotropis capensis*	Angola	Bicuar National Park	−15.2435	14.8915	PV357728	PV412847	PV412871	PV390644
NB0779	CHL0779	*Ichnotropis capensis*	Angola	Bicuar National Park	−15.1049	14.8403	PV357729	PV412848	PV412872	PV390644
NB1116	CHL1116	*Ichnotropis capensis*	Angola	Cusseque	−13.6851	17.0795	PV357730	PV412849	OZ347943	PV390647
NB1123	CHL1123	*Ichnotropis capensis*	Angola	Cusseque	−13.6782	17.0832	PV357732	PV412851		PV390649
NB1124	CHL1124	*Ichnotropis capensis*	Angola	Cusseque	−13.6782	17.0832	PV357733	PV412852		
NB1138	CHL1138	*Ichnotropis capensis*	Angola	Cusseque	-13.6782	17.0832	PV357734			
PEM R15556	PEM R15556	*Ichnotropis capensis*	Mozambique	7 km North of Chibuto	−24.6231	33.5661		OZ347975		
RE211206B1	NMNW R11561	*Ichnotropis capensis*	Namibia	Khaudum	−18.2876	20.9897	OZ347421	OZ347976	OZ347944	
RE211206B3	NMNW R11562	*Ichnotropis capensis*	Namibia	Khaudum	−18.2876	20.9897		OZ347977	OZ347945	
SK13128	NA	*Ichnotropis capensis*	Namibia	Naye-Naye	−19.9235	20.6976	MN015330	MN030223		

Sample No.	Museum catalogue No.	Species	Country	Locality	Latitude	Longitude	16S	ND4	RAG-1	c-mos
WC-3660	PEM R22021	*Ichnotropis capensis*	Zambia	Ngonye Falls	−16.6736	23.5969	OZ347422	OZ347978	OZ347946	OZ347961
WC-6797	PEM R27394	*Ichnotropis capensis*	Angola	Quembo River bridge camp	−13.5275	19.2806	PV357731	PV412850	PV412873	PV390648
WC12-A191	PEM R20009	*Ichnotropis capensis*	Angola	HALO Cuito Cuanavale office	−15.1392	19.1436	PV357724	PV412843	OZ347947	
WP031	NA	*Ichnotropis capensis*	Namibia	50 km North of Gobabis	−22.0000	19.1400		HF547734	HF547695	
WRB INH2	NA	*Ichnotropis capensis*	Mozambique	Inhassoro	−21.7143	35.2103	OZ347423	OZ347979	OZ347948	
WC-4585	PEM R23525	*Ichnotropis capensis*	Angola	Quembo River source	−13.1095	19.0061	PV357722	PV412841	PV412868	PV390643
WC-4618	PEM R23500	*Ichnotropis capensis*	Angola	Quembo River source	−13.1360	19.0453	PV357723	PV412842	PV412869	
RE211206D1	NMNW R12212	*Ichnotropis grandiceps*	Namibia	Khaudum	−18.2876	20.9897	OZ347424	OZ347980		
P3-059	MHNCUP-REP 0983	*Ichnotropis longicorpa* **sp. nov.**	Angola	Cuemba	−12.1707	18.2257	PV357739	PV412857		OZ347962
P9-035	MHNCUP-REP 0984	*Ichnotropis longicorpa* **sp. nov.**	Angola	Mona Quimbundo	−10.0583	19.8056	PV357737	PV412855	OZ347949	OZ347963
TB-44	PEM R19903	*Ichnotropis longicorpa* **sp. nov.**	Angola	Camp Chiri, Miombo forest/camp	−9.3969	20.4319	PV357735	PV412853	PV412874	
TB-46	PEM R19905	*Ichnotropis longicorpa* **sp. nov.**	Angola	Camp Chiri, Miombo forest/camp	−9.3969	20.4319	PV357738	PV412856	PV412876	
WC-4557	PEM R23409	*Ichnotropis longicorpa* **sp. nov.**	Angola	Lungwebungu River camp bridge crossing	−12.5835	18.6660	PV357741	PV412859	PV412877	
WC-4560	PEM R23531	*Ichnotropis longicorpa* **sp. nov.**	Angola	Sombanana village river	−12.3071	18.6235	PV357736	PV412854	PV412875	OZ347964
WC-6291	PEM R23996	*Ichnotropis longicorpa* **sp. nov.**	Angola	Lake Tchanssengwe	−12.4140	18.6442	PV357740	PV412858	OZ347950	
P0-44	MHNCUP-REP 0983	*Ichnotropis microlepidota*	Angola	Serra do Moco – Canjonde	−12.4261	15.1478	PV357742	PV412860	PV412878	PV390651
WC-3969	PEM R23306	*Ichnotropis robusta* **sp. nov.**	Angola	4 km upstream from Cuanavale River source	−13.0508	18.8973	PV357715	PV412835	PV412862	PV390640
WC-3994	PEM R23279	*Ichnotropis robusta* **sp. nov.**	Angola	Cuanavale River source	−13.0903	18.8940	PV357718	PV412838	PV412864	
WC-4056	PEM R23362	*Ichnotropis robusta* **sp. nov.**	Angola	drive to Cuanavale River Camp from Samanunga village	−13.0380	18.8298	OZ347425	OZ347981	OZ347951	
WC-4816	PEM R23420	*Ichnotropis robusta* **sp. nov.**	Angola	Cuando River source	−13.0035	19.1275	PV357716	PV41283		
CKD-457	PEM R28456	*Ichnotropis tanganicana*	DRC	Upemba National Park	−9.0442	26.9966	OZ347426	OZ347982	OZ347952	
CKD-432	PEM R28448	*Ichnotropis tanganicana*	DRC	Upemba National Park	−9.0442	26.9966	OZ347427	OZ347983	OZ347953	OZ347965
CKD-433	PEM R28449	*Ichnotropis tanganicana*	DRC	Upemba National Park	−9.0442	26.9966	OZ347428	OZ347984	OZ347954	OZ347966
CKD-442	PEM R28452	*Ichnotropis tanganicana*	DRC	Upemba National Park	−9.0442	26.9966	OZ347429	OZ347985	OZ347955	
MTSN 9947	MUSE-VER 09947	*Ichnotropis tanganicana*	DRC	Kindingi, West of Kabobo Plateau	−5.2626	28.9076	OZ347430		OZ347956	
ABH3		*Meroles squamulosus*	Mozambique	unknown			JX962896		EF632221	EF632266
ABH9		*Meroles squamulosus*	Tanzania	Laela	−8.7500	32.1833	JX962897		JX963022	JX962915
MBUR00872		*Meroles squamulosus*	South Africa	Cleveland, Limpopo	−24.0219	31.1991	LT745784	LT745812	LT745838	
RSP373		*Meroles squamulosus*	South Africa	Venetia Limpopo Reserve, Limpopo	−22.2661	29.3329	HF547777	HF547737	HF547699	
SVN362	PEM R19626	*Meroles squamulosus*	South Africa	Lapalala Game Reserve, Limpopo Landmanslust, Limpopo	−23.8759	28.3061	HF547776	HF547736	HF547697	
WP125		*Meroles squamulosus*	South Africa	Rooipoort Nature Reserve Northern Cape	−28.5937	24.2100	HF547778	HF547738	HF547701	

TREE. Two parallel runs of the MCMC were run for 20 million generations, each with four independent chains, and trees were sampled every 1000 generations using BEAGLE (Ayres et al. 2019). A burn-in of 20% was used to generate the consensus tree. Tracer v.1.7.2 (Rambaut et al. 2018) was used to assess the effective sample size (**ESS**) for the run parameters. The ESS values were found to be above 200, indicating that the burn-in was adequate. Both the ML and BI trees were generated using FigTree v.1.4.4 (Rambaut 2018). Nodes with bootstrap support (**BS**) ≥ 95% for ML analyses as well as posterior probabilities (**PP**) ≥ 0.95 for the BI analyses (Huelsenbeck and Rannala 2004) were regarded as well supported.

Species delimitation analyses were performed to explore species boundaries and elucidate whether there was potential cryptic diversification within *Ichnotropis*. Mitochondrial genes (16S, ND4) were combined for species delimitation analyses, excluding the outgroup taxa, and the sequences were trimmed to 1134 bp to minimise missing data in the datasets. Several different delimitation analyses were run: Automatic Barcode Gap Discovery (**ABGD**), Assemble Species by Automatic Partitioning (**ASAP**), Poisson Tree Processes (**PTP**), Multi-rate Poisson Tree Process (**mPTP**), and Bayesian Poisson Tree Processes (**bPTP**). Alignments were prepared and uploaded onto the ABGD Web Interface (https://bioinfo.mnhn.fr/abi/public/abgd/abgdweb.html, web version 22 May 2023) and the ASAP Web Interface (https://bioinfo.mnhn.fr/abi/public/asap/asapweb.html, web version 22 May 2023) as FASTA files. For ABGD, the following settings were used: Standard pairwise distance (p distance) metrics, minimum barcode gap width (1), intraspecific divergence minimum (0.001) and maximum (0.1) (Puillandre et al. 2012). For ASAP, the Simple Distance (p distance) substitution model was used (Puillandre et al. 2021). Multi-locus ML phylogenies were created for the two concatenated mitochondrial genes in IQ-TREE as outlined above. The phylogenies were rendered as unrooted nexus files and uploaded onto the bPTP web server (http://species.h-its.org/ptp; Zhang et al. 2013) for the PTP and bPTP analyses, and the mPTP analysis was conducted using the web server at http://mptp.h-its.org/#/tree (Kapli et al. 2016).

Uncorrected pairwise distances (p distances) were estimated in MEGA X (Kumar et al. 2018) for mitochondrial genes (16S, ND4). Sequences were trimmed to minimise missing data in the datasets and p distances were estimated using uniform rates, pairwise deletion of remaining data, and 500 bootstrap replicates.

Morphology

We examined all newly collected material in the collections of the National Museum of Namibia (NMNW), Windhoek, Namibia, and Port Elizabeth Museum (PEM). Additional morphological data were gathered from the following museum collections: PEM, Ditsong National Museum of Natural History, Pretoria (**TM**); Musée Royal de l'Afrique Centrale, Tervuren, Belgium (**RMCA**); and Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium (**IRSNB**). The morphological dataset was further supplemented with data from primary literature (Boulenger 1921; Loveridge 1933; de Witte and Laurent 1942; Laurent 1952, 1964; Broadley 1967b; Haacke 1970) and unpublished data of D.G. Broadley and W.R. Branch. The final dataset incorporates morphological data from the type specimens of: *Ichnotropis bivittata*, *I. capensis nigrescens*, *I. chapini*, *I. macrolepidota*, *I. microlepidota*, and *I. overlaeti*. Additionally, high-resolution images of the type specimens of *I. longipes* and *I. tanganicana* were consulted, as well as key specimens in the Dundo Museum, Angola (**DM**) and Museum of Comparative Zoology, USA (**MCZ**). List of material examined can be found in the Appendix. This represents all the relevant type material, except for the type of *Ichnotropis capensis*, which remains unaccounted for in the Natural History Museum, London (**BMNH**). The available material enables us to confidently assign our specimens to known species and to make informed taxonomic decisions.

Scale nomenclature, scale counts, and measurements used in the descriptions follow previous studies on African Lacertidae (Conradie et al. 2012; Branch et al. 2019; Parrinha et al. 2021; Benito et al. 2025), and were adjusted as needed to address the morphology of *Ichnotropis*. The following measurements were taken in millimetres (mm) using a digital calliper (accuracy of 0.01 mm) with the aid of a Nikon SMZ1270 microscope: Snout–vent length (**SVL**, tip of the snout to the posterior edge of the cloaca); tail length (**TAIL**, tip of tail to posterior edge of the cloaca, measured only for specimens with complete original tails); total length (**TL**, combined SVL and tail length); head length (**HL**, from the anterior edge of the occipital scale to the tip of the snout); head width (**HW**, widest part of head –usually measured just behind the eye); head height (**HH**, measured just behind the eyes); snout to front of arm (**S-FL**, from tip of snout to anterior insertion of forelimb); eye diameter (**ED**, from top anterior to the posterior edge of eye); snout to eye distance (**SE**, from tip of snout to anterior edge of eye); eye-to-eye distance (**EE**, from anterior edge of one eye to anterior edge of the other eye); tympanum length (**Tymp-L**, at its widest part vertically); lower jaw length (**LJL**, anterior edge of the jaw bone to tip of lower jaw); inter-limb length (**ILL**, distance between axillary and inguinal regions); forelimb length (**FLL**, from elbow to wrist); hind limb length (**HLL**, from knee to heel); hind foot length (**HFL**, from ankle to tip of fourth toe, excluding claw); fourth finger length (**FFL**, excluding claw), fourth toe length (**FTL**, excluding claw), length of anterior supraocular scale (**SO**), 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), and frontal scale length (**FNL**). All measurements, except for EE, FNW, FNL, were taken on the right side of the body.

The following scalation details were recorded with the aid of a dissecting microscope: Number of supralabials (**SL**, anterior to the subocular); number of infralabials (**IL**); the number and condition of the nasal scales; the number and condition of the loreals; scalation condition of the lower eyelids; number of supraciliaries (**SC**); the condition of temporal scales and the elongate temporal plate (scales between parietals and temporal scales); the degree of head striations (ridges) present on the dorsal head; the condition of the tympanum opening and the tympanic shield; the condition of the frontonasals (**FN**), prefrontals (**PF**, whether the PF is in contact with anterior SO and if the PF is in contact with 1st SC), frontal (**F**), interparietal (**IP**), parietals (**P**) and occipital scales (**O**); number of supraoculars (**SO**) [note: for this study we restrict the supraoculars to the two larger scales and refer to the cluster of 1–4 smaller scales posterior to the 2nd SO as the post-supraoculars]; number of smaller scales in front of the anterior SO, touching frontal, prefrontal and 1st SC; number of granules in contact with the two large SO and SC; number of paired chin shields (**CS**, and the number in contact); midbody scale rows (**MSR**); longitudinal ventral scale rows (**LVSR**, counted midway between fore- and hind limbs); transverse rows of ventrals (**TVSR**, counted from the axilla to the groin); femoral pores (right/left); and subdigital lamellae under the 4th toe (**LUFT**).

To investigate the morphological variation between *Ichnotropis* species and to compare them with previously published material (Benito et al. 2025), two separate principal component analyses (**PCA**) were run on adult specimens. We considered specimens to be adults if the SVL was larger than 40 mm, as that was the smallest size at which we could clearly observe the hemipenal bulge in males. First, a PCA was performed on the full dataset, which included all measurement variables (Dataset 1). The initial analysis revealed that head-related measurements (HH, HL, HW) accounted for most of the variation. To determine whether other variables contributed notable variation, a second PCA was run on a reduced dataset that excluded these head measurements (Dataset 2). All the variables were first size-corrected using a linear regression with body size (SVL) as the covariate, and the residuals were used as input variables for the PCA. Variables with communalities > 0.5 were retained in the analysis, a varimax rotation was applied, and vectors with eigenvalues > 1.0 were extracted (Tabachnick and Fidel 2019). The resulting principal component (PC) scores were saved and subsequently used as input for a multivariate analysis of variance (**MANOVA**), with species as the fixed factor. Differences between species were evaluated post hoc using Tukey's HSD test. All analyses were conducted in RStudio v.2023.09.1+494 (RStudio Team 2022).

In order to explore other potential diagnostic characters between species, we tested the morphological variation in Dataset 1 and 2 across different taxa using permutational ANOVAs (**PERMANOVA**s) 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, standard boxplots were used to visually represent the variables that were significantly different between species.

Mapping

To enable production of contemporary geographic distribution maps for all *Ichnotropis* species, observation locations were sourced from published datasets (e.g., van den Berg 2017; Marques et al. 2018), museum databases (PEM, TM, RMCA, IRSNB), and other citizen science repositories (http://www.inaturalist.org; http://vmus.adu.org.za [records were download before the website shut down]). Each record obtained from online sources was checked for diagnostic features mentioned in this study to confirm species identifications. Those which could not be confidently identified were excluded from the mapping exercise. However, historical specimens that were not examined, or for which identification could not be verified, were tentatively mapped based on their initial identification in the original publication or museum catalogue. The online GeoNames gazetteer (http://www.geonames.org) or the GEOLocate Web Application (https://www.geo-locate.org/web/WebGeoref.aspx) was used to georeference all historical data lacking precise location information. Finally, all valid observation records were mapped using QGIS v.3.2 (http://qgis.org). Data used for mapping can be found at: https://doi.org/10.6084/m9.figshare.30285421.

Results

Phylogenetic analyses

Both maximum likelihood and Bayesian inference analyses recovered identical topologies for the concatenated dataset (Figs 1, S1, S2), with strong support at most major nodes. Although the mitochondrial and nuclear gene trees produce different topology in the placement of *I. microlepidota*, these differences were not considered to represent strong phylogenetic conflict (see Figs S3, S4). Our phylogenetic results recovered four distinct clades within *Ichnotropis*.

Ichnotropis tanganicana was consistently supported as sister to all other congeners in all analyses, from which it is highly divergent (Table 2). All species delimitation methods supported its distinct species status and further subdivided it into two lineages (Fig. 1).

Ichnotropis microlepidota was recovered as sister to the *I. bivittata* clade, though this relationship was not strongly supported in the BI analysis. Nevertheless, all species delimitation analyses favoured its specific status, with notably high pairwise p distances for 16S and ND4 genes (Table 2). The *I. bivittata* clade contained only four samples and amongst them, topotypic material of *I. b. pallida* (KTH09-075), which exhibited high intraspecific variation. This sample differed markedly from other *I. b. bivittata* samples, with divergence values comparable to those in the *I. capensis* group, but lower than between other species (Table 2). Additionally, all species delimitation analyses—except mPTP—

Table 2. Mean sequence divergences (uncorrected p distances) between *Ichnotropis* species for 16S and ND4 genes, given as percentages. The numbers in the diagonal grey boxes represent the mean intraspecific sequence divergences and standard errors, numbers below the diagonal grey boxes represent the mean interspecific sequence divergences, while numbers above the diagonal grey boxes represent standard errors of the interspecific sequence divergences. n/c – was not possible to estimate sequence divergences.

	16S	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
1	*I. capensis* sensu lato	3.0 ± 0.5	0.9	1.5	1.4	1.4	1.4	1.7	1.6
2	*I. longicorpa* **sp. nov.**	5.9	2.6 ± 0.8	1.5	1.4	1.3	1.2	1.6	1.6
3	*I. robusta* **sp. nov.**	11.2	12.0	0.2 ± 0.2	1.1	1.4	1.3	1.7	1.5
4	*I. grandiceps*	11.5	11.8	6.3	n/c	1.4	1.3	1.7	1.6
5	*I. b. pallida*	11.6	10.5	9.9	10.3	n/c	0.9	1.7	1.5
6	*I. b. bivittata*	11.5	9.8	8.8	9.3	5.4	3.8 ± 0.8	1.6	1.4
7	*I. microlepidota*	16.4	16.1	16.4	16.1	14.4	13.9	n/c	1.8
8	*I. tanganicana*	15.8	14.5	12.9	13.8	13.1	12.2	18.4	1.8 ± 0.4
	ND4								
1	*I. capensis sensu lato*	7.7 ± 0.6	0.8	1.3	1.3	1.4	1.1	1.3	1.2
2	*I. longicorpa* **sp. nov.**	12.3	6.6 ± 0.6	1.3	1.3	1.4	1.1	1.3	1.2
3	*I. robusta* **sp. nov.**	22.1	19.6	1.4 ± 0.3	1.3	1.6	1.2	1.5	1.4
4	*I. grandiceps*	22.3	20.4	15.3	n/c	1.6	1.2	1.5	1.4
5	*I. b. pallida*	21.5	20.6	22.3	20.7	n/c	1.1	1.6	1.7
6	*I. b. bivittata*	19.2	17.6	20.0	19.6	12.8	9.4 ± 0.9	1.3	1.3
7	*I. microlepidota*	24.0	21.6	24.4	24.4	22.6	20.6	n/c	1.4
8	*I. tanganicana*	19.1	18.0	21.7	21.8	22.7	19.4	21.2	0.1 ± 0.1

identified each *I. bivittata* lineage as a candidate species (Fig. 1).

Ichnotropis grandiceps was recovered as a sister taxon to the *I. capensis* group. Furthermore, newly collected material from Angola was recovered as a distinct lineage, sister to a sample from Namibia (RE211206D1) collected from near the type locality of *I. grandiceps*, and with high divergence in both mitochondrial markers (Table 2). All delimitation analyses supported the distinctiveness of the Angolan lineage as a candidate new species (Fig. 1).

Within the *I. capensis* group, high levels of intraspecific variation were detected, with three major clades (Clades 1–3) returned in the phylogenetic analysis. Species delimitation analyses recovered between three and seven candidate species among these clades, which do not necessarily agree with the three major clades. Sequence divergence among Clade 1 with Clades 2 and 3 (collectively referred to as *I. capensis* sensu lato) was >5% for 16S and ~12% for ND4 (Table 2), comparable to species-level thresholds amongst other African Lacertidae (~2–12% 16S and 7–23% ND4; Conradie et al. 2012; Edwards et al. 2013a; Branch et al. 2019; Parrinha et al. 2021). Furthermore, *I. capensis* sensu lato was consistently supported as distinct across all species delimitation methods. It should be noted that the intra-specific variation within *I. capensis* sensu lato, while surprisingly high, was not comparable with species level divergence (Fig. 1; Table 2). Overall, we propose that the genetic evidence, taken with other evidence (see below) suggests that each of these groups can be considered separately evolving metapopulations under the general lineage concept of species (de Queiroz 1998; see below).

Morphology

The two PCAs produced similar results despite analysing different subsets of original variables. In PCA1 (Dataset 1), PC1 (37.3%) and PC2 (13.11%) together explained 50.41% of the total variation, with PC1 primarily correlated to head-related variables (HL and SE) and PC2 correlated to limb measurements (FTL and HFL; Fig. 2; Table S2). Similarly, in PCA2 (Dataset 2), PC1 (36.24%) and PC2 (11.41%) accounted for 47.65% of the total variation, in which PC1 is also correlated with head morphology (SE and LJL), while PC2 correlated to the same variable as in previous analysis, suggesting consistent underlying morphological patterns regardless of variable inclusion. The MANOVA showed significant differences between the species for only PC2 (P = 0.000) in both PCAs, and for PC1 of PCA2 (P = 0.007; Table S2). Post hoc pairwise comparisons (Tukey's HSD) revealed no signif-

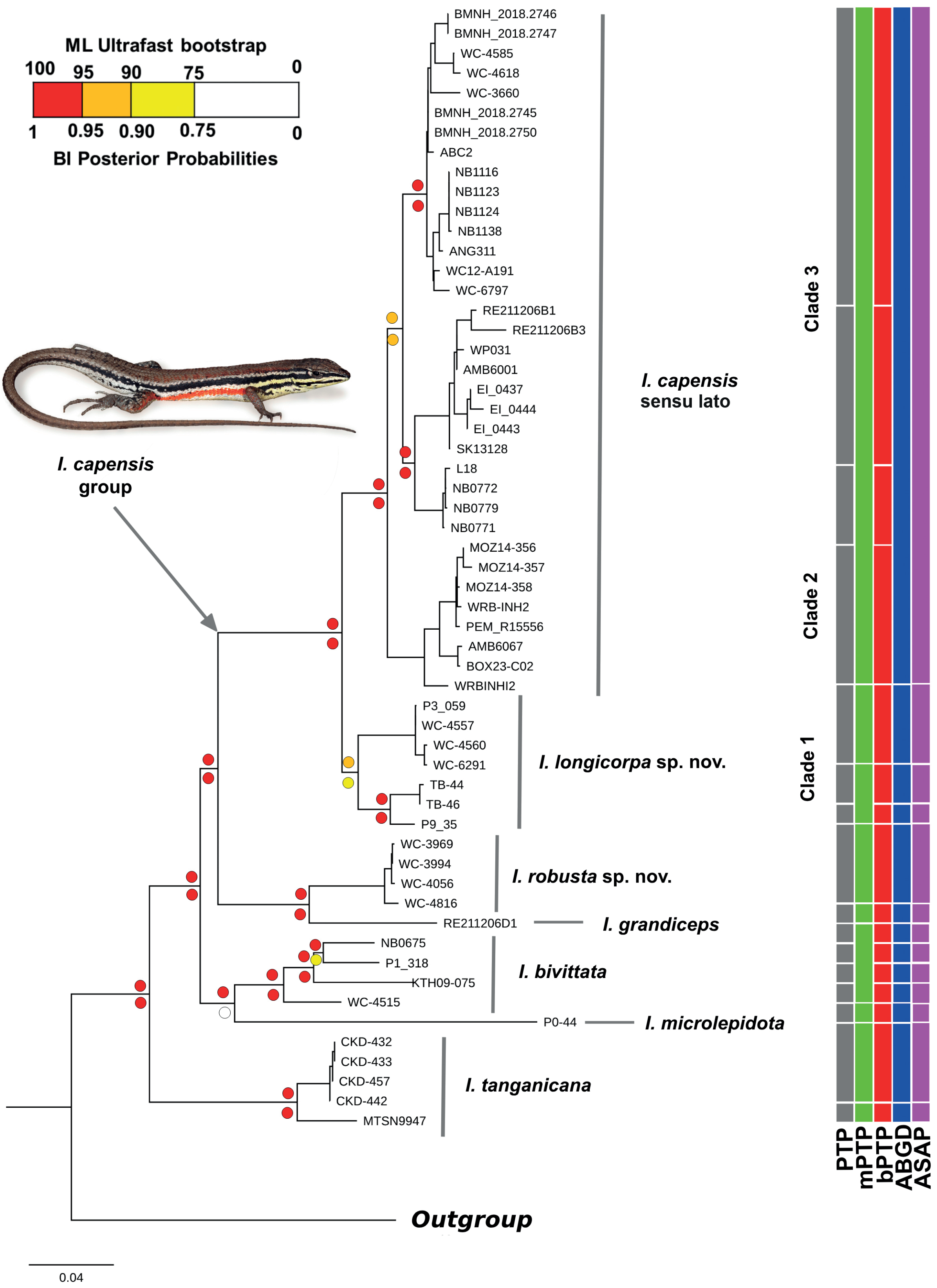

Figure 1. IQ-TREE maximum likelihood consensus phylogeny for *Ichnotropis* with likelihood bootstrap support values (above) and Bayesian posterior probabilities (below) indicated at each node (see key in top left). The coloured bars to the right of the phylogeny summarise the results for each of the species delimitation analyses. Inset image: *I. capensis* sensu stricto. The scale bar represents substitutions/site.

icant differences between species for PC1 (P > 0.05), but significant differences were detected for PC2 in both analyses (Table S3). The main differences detected were between species of different groups (e.g., *I. bivittata* versus *I. capensis*; *I. capensis* versus *I. grandiceps*) but not within the different groups (Table S3).

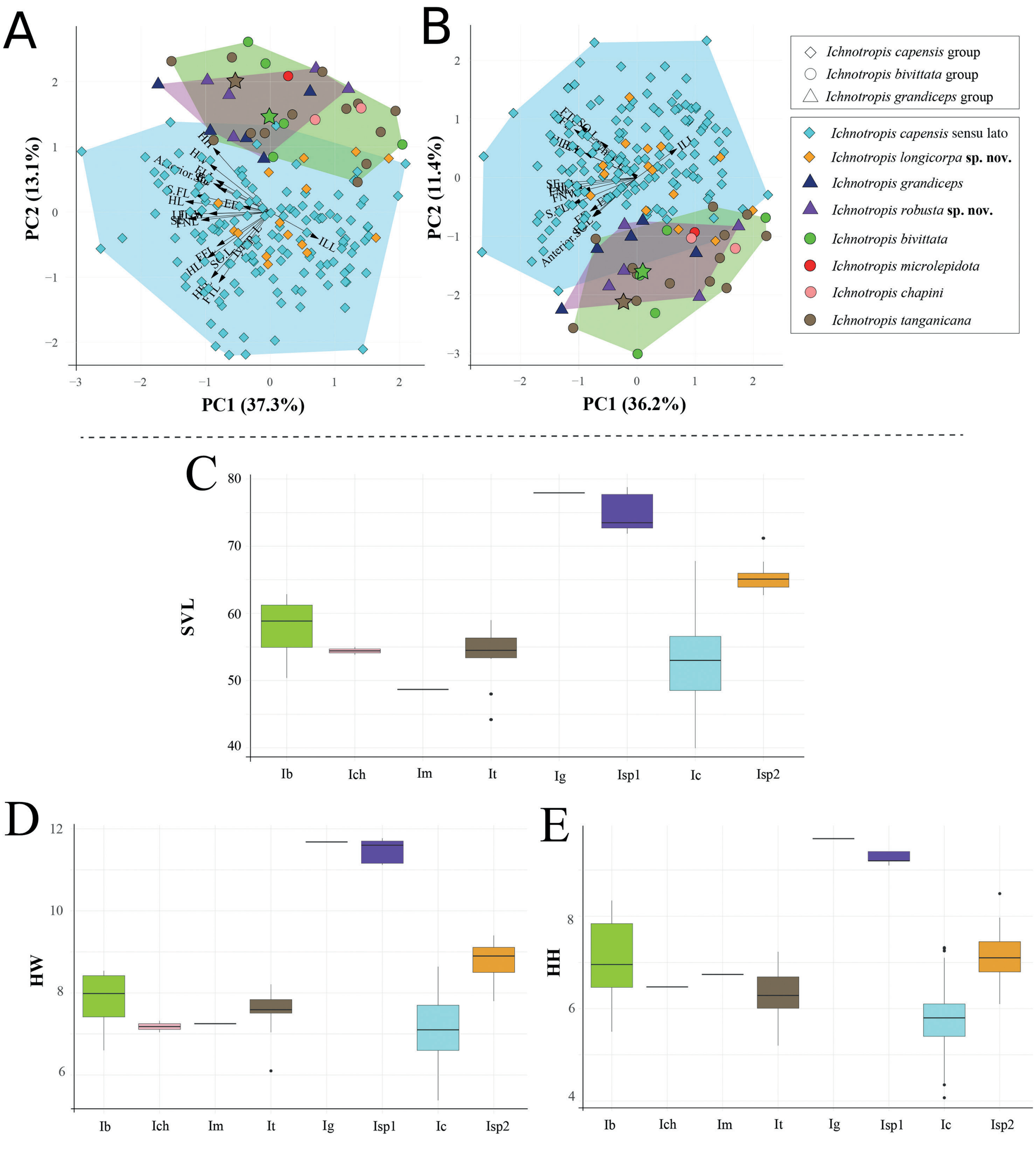

Figure 2. Above: Scatterplots of the first two principal components for *Ichnotropis*, based on the full Dataset 1 (**A**) and reduced Dataset 2 (**B**). Arrows indicate the loadings of morphological variables (see Materials and Methods for abbreviations). The green star marks the holotype of *Ichnotropis capensis nigrescens* (BE_RMCA_Vert.R.14641), and the brown star marks the holotype of *Ichnotropis overlaeti* (BE_RMCA_Vert.R.9691). Below: Box plots showing **C** snout–vent length (SVL), **D** head width (HW), and **E** head height (HH). Species are represented by different colours, and species groups are enclosed by polygons, as indicated in the legend.

In addition, the PERMANOVA analysis revealed additional significant differences not captured by the MANOVA of the principal components, primarily in snout–vent length (SVL) and two head measurements (head width, HW; head height, HH; Table S4). Notably, the new candidate species sister to *I. grandiceps* exhibited key morphological divergence, differing significantly in HW compared to *I. bivittata* (ANOVA: F = 10.445, P = 0.030), *I. capensis* (F = 17.514, P = 0.001), and the candidate species sister to *I. capensis* (F = 16.096, P = 0.002). Differences in HH were also detected between *I. grandiceps* and *I. capensis* (F = 16.483, P = 0.001), as well as between *I. grandiceps* and the candidate species sister to *I. capensis* (F = 13.388, P = 0.007). Additionally, *I. capensis* differed from *I. microlepidota* (F = 9.443, P = 0.048) and the candidate species sister to *I. grandiceps* (F = 10.452, P = 0.030) in HH.

The morphological analyses suggest overall, that the genus *Ichnotropis* can be divided into three distinct morphological groups based on head morphology and

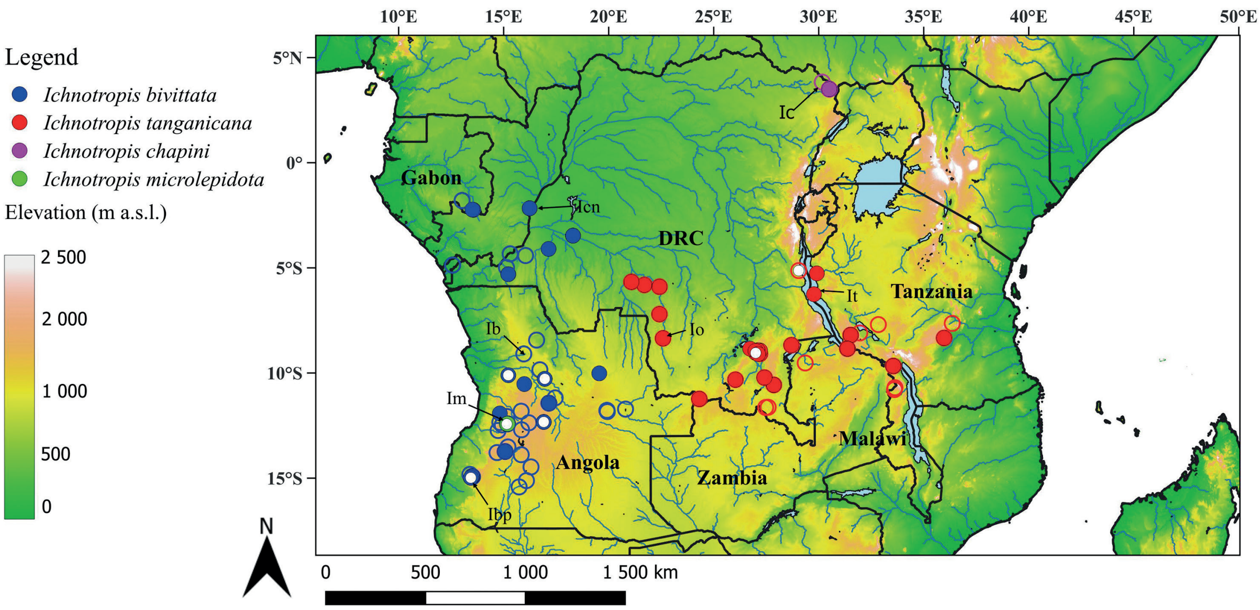

Figure 3. Records of specimens from the *Ichnotropis bivittata* group, based on all literature records (open circles), examined material (closed circles) and genetically analysed material (white centres). Respective type localities are indicated by arrows: Ib – *I. bivittata*, Ibp – *I. bivittata pallida*, Ic – *I. chapini*, Im – *I. microlepidota*, Icn – *I. capensis nigrescens*, Io – *I. overlaeti* and It – *I. tanganicana*.

scalation. These groupings provide a useful framework for species identification and can be used to support the species hypotheses from the phylogenetic analyses: The *I. bivittata*, *I. grandiceps*, and *I. capensis* groups. The *I. bivittata* group can be defined morphologically based on a more rounded snout, the prefrontal scale mostly in contact with the anterior large supraocular (89% in contact, n = 86), and with irregular strongly developed head striations. The *I. grandiceps* group can be defined by a robust but pointed snout, a prefrontal scale that is always separated from the anterior large supraocular, and a head with weakly developed striations. The *I. capensis* group can be defined by a narrower and pointed snout, the prefrontal mostly separated from the anterior supraocular (96%, n = 288), with prominent and evenly spaced head striations. These morphological groupings are in part supported by the phylogenetic analyses, except for *I. tanganicana*, which forms its own monotypic clade.

Colouration in *Ichnotropis* is very variable depending on breeding season, ontogeny, and habitat. However, based on the breeding colouration of males, *Ichnotropis* can be divided into the same three morphological groups described above. The *I. bivittata* group has scattered blue or yellow-orange or black-edged white spots on the lower flanks of the body, between the limbs. The ventral scales are often uniform grey, but can have scattered black speckles. The *I. grandiceps* group is characterised by a uniform brick red-brown dorsum with scattered darker brown speckles. The gular region and flanks can be light yellow in the breeding season. The *I. capensis* group shows the most variation in dorsal colouration, but is most often characterised by dark black stripes on the flanks with a continuous orange line on the lower flanks between the legs. The gular region and flanks can be light yellow in the breeding season.

Systematics

Based on the morphological differences (head shape and scalation) and the distinct dorsal colouration differences observed among the adult breeding male material examined, combined with the above-mentioned genetic evidence (species delimitation and p distance analyses), the new material of *I.* cf. *grandiceps* and *I. capensis* Clade 1 from eastern Angola are described below as new species. Our approach to delimitation follows the general lineage-based species concept, which is based on multiple different lines of evidence (morphology, colouration, genetics) supporting independent evolving metapopulation lineages (de Queiroz 1998). No historical names are available for these new species, thus leaving no outstanding taxonomic or nomenclatural concerns. While the species delimitation analyses suggested the presence of additional putative species, we were unable to identify consistent morphological characters to justify their recognition at this time. Additionally, we also provide a systematic review of the other *Ichnotropis* species, discussing their taxonomy, morphology and distribution.

Reptilia: Squamata: Lacertidae

The *Ichnotropis bivittata* group

The phylogenetic analyses recovered the *I. bivittata* group that includes *I. bivittata* (including *I. b. pallida*), *I. chapini* and *I. microlepidota*. However, based on the morphological similarities, we also consider the independent *I. tanganicana* lineage to be part of the *I. bivittata* group as it shares the following morphological features with all other members of the *I. bivittata* group: Short, rounded head; prefrontal largely in contact with the anterior supraocular; well-defined head striations; and a series of dorsolateral markings, which appear as yellow spots in *I. bivittata*, blue spots in *I. tanganicana*, or black-edged white spots in *I. microlepidota*. This group is restricted to the more mesic savannas of central Africa from central Angola to northern DRC and eastern Tanzania (Fig. 3).

Ichnotropis bivittata Bocage, 1866

Angolan rough-scaled lizard

Figures 4–7; Table 3

Taxonomic note. Bocage (1866) described *Ichnotropis bivittatus* (= *bivittata*) based on a series of specimens collected from Duque de Bragança [= Calandula], Malanje Province, Angola, despite Günther (based on material that Bocage had sent to him) considering them to be the same as *I. capensis*. Boulenger (1887) followed Günther and did not consider *I. bivittata* to be a valid species. This prompted Bocage (1895) to relegate *I. bivittata* into the synonymy of *I. capensis*. It was not until Boulenger (1921) reviewed the family Lacertidae that *I. bivittata* was reinstated as a valid species. This taxonomic revision was followed by most subsequent authors, except for a brief period when *I. bivittata* was regarded as a subspecies of *I. capensis* (Laurent 1952; Hellmich 1957; Manaças 1963; Robertson et al. 1963). The above confusion led to much of the historical Angolan material being incorrectly assigned to *I. capensis* (Marques et al. 2018).

When Laurent (1964) described the subspecies *I. b. pallida* he distinguished it from the nominotypical form based on its duller dorsal colouration and differences in head scalation—specifically, its less pronounced keeled head striations, distinct interparietal shape, and small frontoparietals that were separated by the interparietal (see Ceríaco et al. 2020a: fig. 30). However, colouration in *Ichnotropis*, as in many lacertids, is highly variable and influenced by factors such as substrate, age and sex, rendering it an unreliable taxonomic character—except when comparing adult breeding male material, where it can provide useful diagnostic insights. Furthermore, the head scalation observed in the holotype appears to be aberrant, as the scalation differs from a topotypic specimen from Humpata (PEM R17934; Fig. 7). Specifically, the configuration where the frontoparietals are separated by the interparietal, which in turn is in contact with the frontal, has not been observed in any other *Ichnotropis* specimens examined in this study, including the topotypic Humpata specimen. Although phylogenetic analyses reveal notable divergence between the Humpata specimen and other *I. bivittata* samples, further research is necessary before making definitive taxonomic decisions regarding the validity of *I. b. pallida*. Therefore, we currently treat *I. b. pallida* as a junior synonym of *I. bivittata*.

In the same paper, Laurent (1952) described *Ichnotropis capensis nigrescens* based on two specimens exhibiting darker ventral surfaces. Notably, the paratype (BE_RMCA_Vert.R.1869), originating from Luluabourg [= Kananga, Kasaï-Central Province, DRC], had previously been designated as a paratype in the description of *Ichnotropis overlaeti* by de Witte and Laurent (1942). The initial classification of *nigrescens* as a subspecies of *I. capensis* was guided by Boulenger's (1921) key, which emphasised the separation of the prefrontal from the anterior supraocular. Subsequently, Loveridge (1933) synonymised this subspecies with *I. capensis*. Upon examining the type specimens, along with two additional specimens housed at RMCA (BE_RMCA_Vert.R.15925 and BE_RMCA_Vert.R.16240) from Ndwa Village near Bolobo—proximate to the holotype's locality—it was observed that they possess a short and rounded snout, a character consistent with members of the *I. bivittata* group (see Fig. 2). Consequently, these specimens are transferred to the *I. bivittata* group instead of *I. capensis*. Specifically, the holotype (BE_RMCA_Vert.R.14671) and the two additional specimens are assigned to *I. bivittata* sensu lato based on the presence of closely spaced pale spots (possibly yellow in life) above the forelimb, whereas the Kananga paratype (BE_RMCA_Vert.R.1869) is reassigned to *I. tanganicana*, based on shared morphological (supraocular in contact with supraciliaries) and colouration characteristics detailed in the species account below (evenly spaced white dorsolateral spots; described as being blue by de Witte and Laurent 1942). Given the substantial sequence divergence observed in our limited *I. bivittata* material, the name *nigrescens* may be applied to northern populations, particularly those from the Republic of the Congo, DRC and Gabon, should future studies support the recognition of a distinct species in this region.

Synonymy. *Ichnotropis capensis nigrescens* Laurent, 1952: 201 (new synonymy); *Ichnotropis bivittata pallida* Laurent, 1964: 64 (new synonymy).

Syntypes. BMNH 1946.9.3.47–48 (1866.6.11.3–4), ZMB 5827 [additional syntypes in Lisbon Museum were probably destroyed by a fire in 1978], collected from Duque de Bragança [= Calandula], Malanje Province, Angola by F.A.P. Bayão.

General description. A medium-sized lacertid with a rounded snout and strongly striated head scales. Nostril pierced between three nasals; the supranasals in broad contact behind the rostral; single frontonasal as broad as long; paired prefrontal scales in broad contact medially; prefrontal mostly in contact with the anterior supraocular (separate in BE_RMCA_Vert.R.40 [*I. overlaeti* paratype], BE_RMCA_Vert.R.14641 [*I. capensis nigrescens* holotype] and NMZB-UM 16358), separated from the first supraciliary by a smaller scale (rarely in contact); two large supraoculars, which are separated from the supraciliaries by one row (or rarely two rows anteriorly) of small scales (7–9) and preceded by a cluster of 2–5 smaller scales; 1–3 smaller post-supraocular scales; paired frontoparietal scales in broad contact; two parietals separated by an interparietal; occipital scale not reaching much past parietals;

Figure 4. Photographs in life of *Ichnotropis bivittata* depicting the closely spaced yellow spots just posterior to the forelimbs. Specimens photographed at **A** Cuito town (PEM R23530), Angola; **B** Cambau (FKH-0833), Angola; **C** Cangandala National Park, Angola; **D** Luando Reserve (CHL0675), Angola; and **E** Humpata (PEM R17934 – *I. b. pallida*), Angola. Photographs: A – Werner Conradie; B, C, D – Pedro Vaz Pinto; E – William R. Branch.

two loreal scales present, the anterior one smaller than the posterior; posterior loreal is separated from the anterior supraocular by two smaller scales; subocular in contact with lip; 3–6 (mostly 4) supralabials anterior to the subocular and two posteriorly; 6–9 (mostly 6) infralabials; 5 (rarely 6) chin shields, with the anterior three (rarely four)

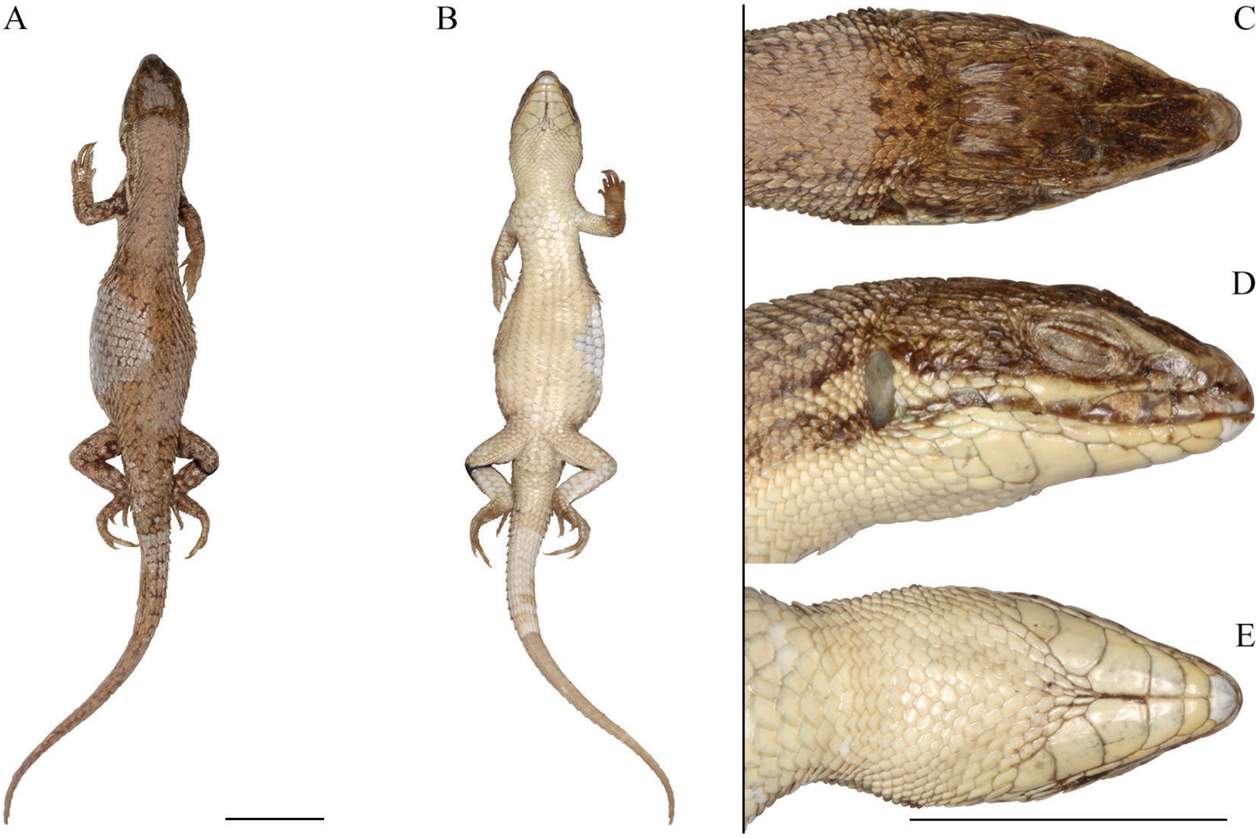

Figure 5. Syntype (ZMB 5827) of *Ichnotropis bivittata* from Duque de Bragança [= Calandula], Malanje Province, Angola. Photographs of body in **A** dorsal and **B** ventral views, and head in **C** dorsal, **D** lateral and **E** ventral views. Scale bars represent 10 mm. Photographs: Frank Tillack.

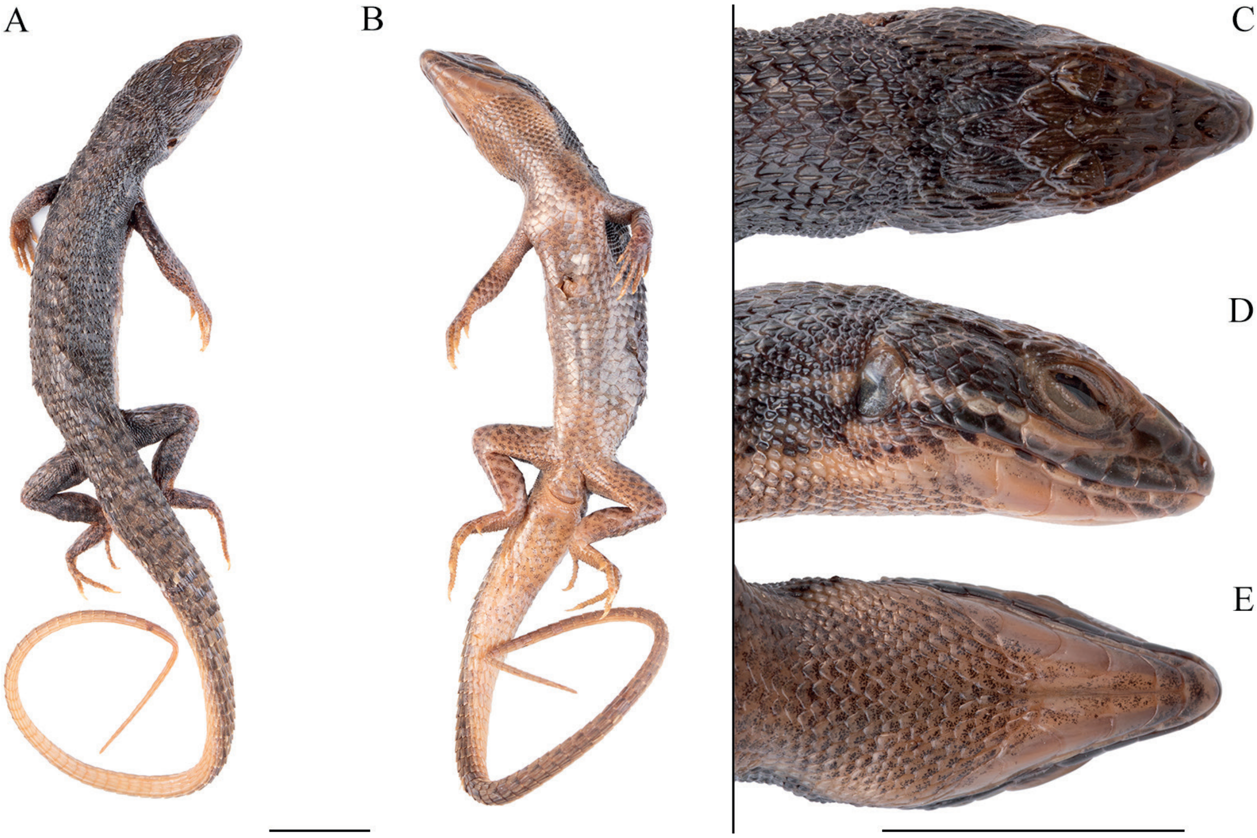

Figure 6. Holotype (BE_RMCA_Vert.R.14641) of *Ichnotropis capensis nigrescens* from Bolobo, Democratic Republic of the Congo. Photographs of body in **A** dorsal and **B** ventral views, and head in **C** dorsal, **D** lateral and **E** ventral views. Scale bars represent 10 mm. Photographs: Max Benito.

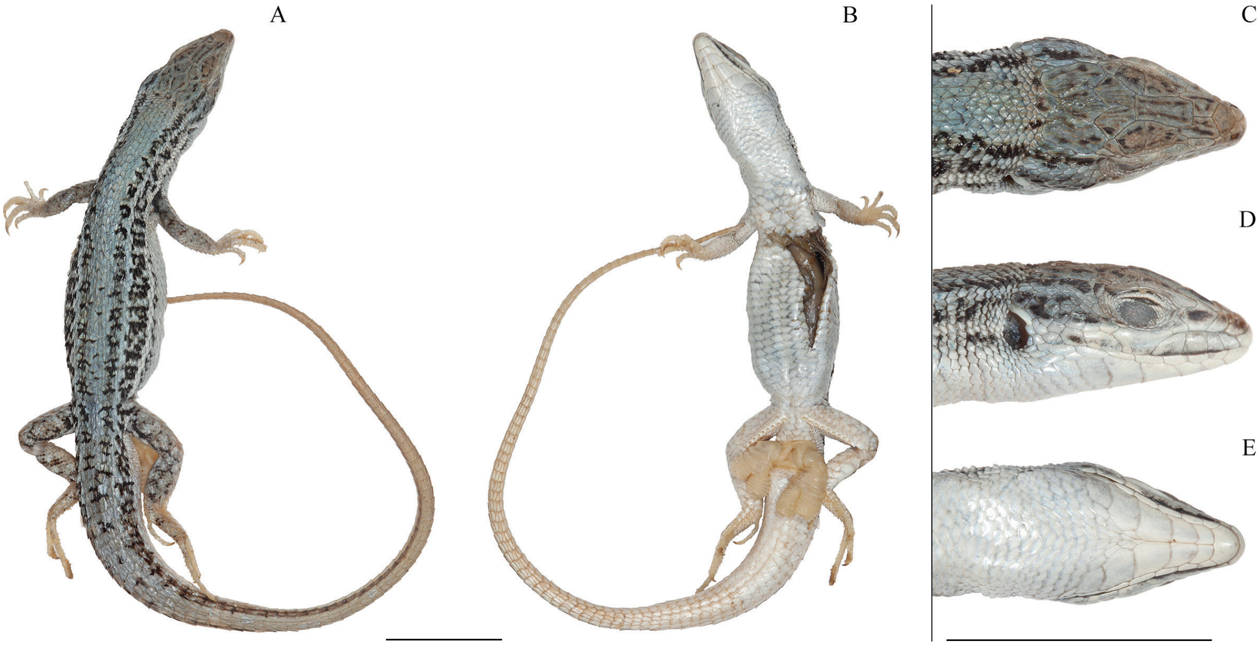

Figure 7. Topotypic (PEM R17934) *Ichnotropis bivittata pallida* from Humpata, Huila Province, Angola. Photographs of body in **A** dorsal and **B** ventral views, and head in **C** dorsal, **D** lateral and **E** ventral views. Scale bars represent 10 mm. Photographs: Werner Conradie.

in broad contact; 3–4 (mostly 4) supraciliaries; 29–40 midbody scale rows; 8–10 longitudinal rows of enlarged ventral plates; 22–31 transverse ventral scale rows; 17–24 subdigital lamellae under the 4th toe; 10–14 femoral pores per thigh. Size: Adult specimens varied from 42.2–75.0 mm (mean: 63.2 mm) SVL and 85.0–156 mm (mean: 109.7mm) TAIL. Largest female: 71 mm SVL (FMNH 74288 – Serra do Moco, Angola); largest male: 75 mm SVL (NMZB-UM 16358 – Chitau, Angola). Colouration (Fig. 4): The dorsal side of the head, body and tail varies from brown to coppery red, sometimes with dark brown to black paired blotches. The flanks are dark brown to black, typically with two pale dorsolateral stripes. The upper stripe, usually two scales wide, originates behind the eye and extends onto the tail. The lower stripe begins anteriorly at the supralabials, tracing posteriorly through the ear, over the arm, and to the groin, though it may not be distinctly defined at midbody. Between these two stripes lies a broad band of coppery brown to black scales, interspersed with scattered black markings. Beneath the lower pale stripe there are scattered brown to black markings, sometimes accompanied by orange spots or blotches that extend onto the venter. During the breeding season, males exhibit more prominent orange flanks (extending onto the lower side of the tail), while the white stripes and lateral sides of the head become vividly yellow anteriorly. Diagnostic narrowly-spaced yellow or orange spots above the arm extend backwards for about a third of the body in both sexes. Dorsal tail with scattered white specks and black bars. The venter is typically plain white, although some individuals may have a grey venter or scattered fine grey to black specks.

Distribution. *Ichnotropis bivittata* is known from Angola's central plateau, with its range extending northward into western DRC, the Republic of the Congo, and southeastern Gabon (Fig. 3). Laurent (1964) reported both *I. overlaeti* de Witte & Laurent, 1942 and *I. bivittata* occurring sympatrically at Alto Cuilo, Lunda-Sul Province, Angola. During a recent field expedition to Alto Cuilo, the presence of *I. bivittata* was confirmed, and re-examination of historical DM (Dundo Museum) material attributed to *I. overlaeti* revealed it to be rather assignable to *I. capensis* sensu lato, based on a narrower and sharper head profile, the prefrontal in contact with the anterior supraocular and absence of any dorsolateral spots. In the present study, we also document the occurrence of *I.* aff. *capensis*—herein described as a new species—from Mona Quimbundo, approximately 62 km east of Alto Cuilo. These findings indicate that three distinct *Ichnotropis* species occur in the Miombo woodland of northeastern Angola. Historical records of *I. bivittata* from eastern Angola (Manaças 1963) require re-evaluation, as they may be referable to the *I. capensis* group or possibly to *I. tanganicana*.

Habitat and Natural History. *Ichnotropis bivittata* inhabits wet Miombo woodlands, preferring open, sandy areas suitable for thermoregulation and foraging. It is a diurnal, terrestrial species and an active forager, primarily preying on small arthropods such as ants, beetles, and termites (Pietersen et al. 2021). Activity peaks during warmer periods and declines in cooler or wetter conditions.

Table 3. Summary of morphological data for the *Ichnotropis bivittata* group. Measurements are all shown in millimetres (mm). Values are given as a range, with mean ± standard deviation in parenthesis. Juveniles were excluded from the measurements, but were included in the scalation data. For abbreviations see Materials and Methods section. n = sample size.

Characters	*I. bivittata*	*I. chapini*	*I. microlepidota*	*I. tanganicana*
	n = 39	n = 3	n = 6	n = 32
SVL	42.2–75.0 (63.2 ± 8.33)	53.8–58.0 (55.6 ± 2.15)	48.7–52.0 (50.4 ± 1.45)	41.0–60.0 (53.9 ± 4.21)
TAIL	85–156 (109.7 ± 15.47)	77	69.8	55.6–107.9 (81.7 ± 12.15)
HL	12.1–15.3 (13.6 ± 1.22)	11.7–12.9 (12.2 ± 0.64)	12.6	11.2–14.2 (12.6 ± 0.79)
HW	6.0–9.9 (8.3 ± 1.08)	7.0 –8.7 (7.7 ± 0.89)	6.7–7.3 (7.0 ± 0.20)	6.1–8.7 (7.6 ± 0.51)
HH	5.4–8.7 (7.2 ± 0.90)	6.5	5.3–6.7 (5.9 ± 0.62)	5.2–8.4 (6.8 ± 0.71)
ED	4.1–4.7 (4.4 ± 0.29)	4.2–5.2 (4.7 ± 0.70)	3.6	3.9–4.5 (4.2 ± 0.18)
SE	3.9–6.8 (5.6 ± 0.90)	4.9–5.9 (5.4 ± 0.53)	4.3–5.2 (4.7 ± 0.37)	5.1–6.6 (5.8 ± 0.36)
LL	14.2–17.2 (15.6 ± 1.6)	11.5 –13.8 (12.7 ± 1.63)	13.3	12.3–16.0 (13.8 ± 1.02)
IL	23.6–33.9 (26.7 ± 3.31)	24.3–33.0 (28.8 ± 4.33)	22.5	19.4–29.4 (24.8 ± 3.0)
FLL	5.8–9.4 (7.5 ± 1.13)	6.1–6.9 (6.5 ± 0.52)	5.4	4.7–8.7 (6.5 ± 0.80)
HLL	9.0–12.4 (10.4 ± 1.28)	9.2–9.5 (9.3 ± 0.23)	7.4	7.9–10.7 (9.2 ± 0.79)
TAIL/SVL	1.3–2.4 (1.8 ± 0.28)	1.3	1.4	1.2–2.0 (1.6 ± 0.23)
HL/SVL	0.2 (0.2 ± 0.01)	0.2 (0.2 ± 0.02)	0.3	0.2–0.3 (0.2 ± 0.02)
ES/HL	0.4–0.5 (0.4 ± 0.02)	0.4–0.5 (0.4 ± 0.02)	0.4	0.4–0.5 (0.5 ± 0.01)
HW/HL	0.5–0.7 (0.6 ± 0.05)	0.3–0.7 (0.6 ± 0.10)	0.6	0.6 (0.6 ± 0.03)
MSR	29–40	34–35	43–50	28–42
LVSR	8–10	8–10	8 –10	8–10
TVSR	22–31	24–25	26–30	20–27
SL	3–6 (mostly 4)	4–5 (mostly 4)	4	3–5 (mostly 4)
IL	6–9 (mostly 6)	6–7 (mostly 6)	6–8 (mostly 7)	5–7 (mostly 6)
SC	3–4 (mostly 4)	3–5 (mostly 4)	4	4–5 (mostly 4)
LUFT	17–24	18–20	16–19	17–22
Femoral pores	10–14	8–9	10–13	10–15

Ichnotropis chapini Schmidt, 1919

Chapin's rough-scaled lizard

Figure 8; Table 3

Taxonomic note. When *I. chapini* was described, it was differentiated from its congeners based on the presence of an anterior supraloreal, thus having two anterior loreal scales (Schmidt 1919). However, additional material collected from Adra in northeastern DRC does not possess any anterior supraloreal (de Witte 1933; Laurent 1952). Despite the limited material available, the scalation observed in the type specimen appears to be anomalous. This is further supported by the fact that we have only recorded this condition (an anterior supraloreal) once for all of the other *Ichnotropis* specimens examined (n = 432). As in the previous species, *I. chapini* was assigned to the *I. capensis* group based on the observation that the prefrontal is separated from the anterior supraocular (Boulenger 1921). Examination of high-resolution photographs of the holotype (Fig. 8) and physical examination of additional material from RMCA showed that this species belongs to the *I. bivittata* group, based on the more rounded head (Fig. 2). This species also seems geographically well isolated from other species in the genus, but this might just be an effect of under-sampling. The seasonality of *Ichnotropis* species makes them hard to observe outside or the breeding season. Consequently, coupled with the absence of any modern material and thus molecular data, we retain this species as valid until more data become available.

Holotype. AMNH 10674, adult female, collected from Aba, Haut-Uele Province, DRC in July 1911.

General description. A medium-sized lacertid with a robust, rounded snout. Head scalation moderately striated. Nostril pierced between three nasals; the supranasals are in broad contact behind the rostral; single frontonasal, as broad as long; paired prefrontal scales in broad contact medially; prefrontal not in contact with anterior supraocular and separated from the supraciliaries by a smaller scale; two large supraoculars, which are separated from the supraciliaries by one row of small scales (6–8) and preceded by a cluster of 2–3 (3 median) smaller scales; one post-supraocular scale; two loreal scales present, which are separated from the anterior supraocular by two scales (except in the holotype, where the anterior loreal is divided to form a supraloreal on both sides and on the left side of BE_RMCA_Vert.R.3657); subocular in contact with lip; 4–5 (mostly 4) supralabials in front of subocular; 6–7 (mostly 6) infralabials; five chin shields, with the anterior 2–3 in broad contact (in the holotype only the first two chin shields are in contact, while in BE_RMCA_Vert.R.3657 the third chin shield is in narrow

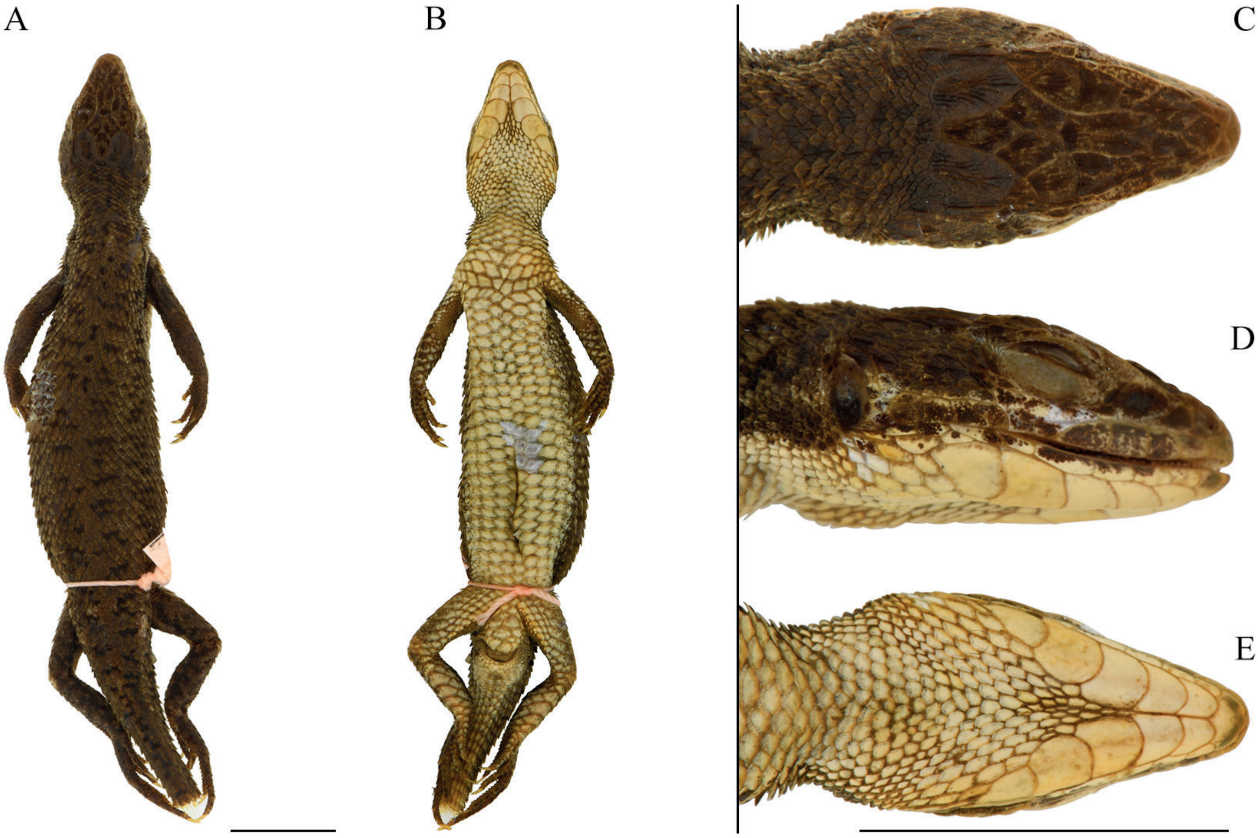

Figure 8. Holotype (AMNH 10674) of *Ichnotropis chapini* from Aba, Haut-Uele Province, Democratic Republic of the Congo. Photographs of body in **A** dorsal and **B** ventral views, and head in **C** dorsal, **D** lateral and **E** ventral views. Scale bars represent 10 mm. Photographs: Lauren Vonnahme.

contact anteriorly); 3–5 (mostly 4) supraciliaries; 34–35 midbody scale rows; 8–10 longitudinal rows of enlarged ventral plates; 24–25 transverse ventral scale rows;18–20 subdigital lamellae under 4th toe; 8–9 femoral pores per thigh. Size: Adult specimens varied from 53.8–58.0 mm (median: 55.0 mm) SVL and 77 mm TAIL (all specimens' tails missing or truncated; this measurement is based on Schmidt 1919). Largest female: 58 mm SVL (AMNH 10674 – holotype); largest male: 55.0 mm SVL (BE_RMCA_Vert.R.3656 – Adra, DRC). Colouration (based on preserved specimens; Fig. 8): Dorsal surface uniformly greyish brown, with scattered darker brown to black scales. A distinct lateral white stripe originates at the subocular region, bordered both dorsally and ventrally by narrow black lines; this stripe extends over the forelimbs but does not reach the hind limbs in females (AMNH 10674 and BE_RMCA_Vert.R.3657), but reaches the hind limbs in the male (BE_RMCA_Vert.R.3656). A second faint dorsolateral line is present above the lower white stripe, and only extends to just posterior of the forearms in females, while in the male this stripe is more prominent and extends to just above the hind limbs. Between these lines are a series of transverse black spots in the females, each spanning 2–3 scales in width and approximately half a scale in length, located at the tips of the scales. In the male the space between the two white stripes forms a prominent black band with scattered black scales. This band extends onto the temporal and snout area. Dorsally, two similar series of transverse black markings flank the vertebral region, extending laterally to the dorsolateral stripe. Ventral scales and chin shields are white with subtle grey margins. The two outermost ventral rows are punctuated with small brown dots in females, but form a continuous narrow black band between the limbs in the male and extends onto the supralabials. Supralabials and infralabials are irregularly mottled with light and dark pigmentation. Limbs greyish brown dorsally, transitioning to a lighter tone on the ventral surfaces.

Distribution. Only known from northeastern DRC in the vicinity of Aba (Fig. 3). Given this locality's proximity to the border with South Sudan (< 10 km), it is likely to occur in the latter country.

Habitat and Natural History. Very little is known about this species, but it is expected to have similar habitat requirements to other *Ichnotropis* species.

Ichnotropis microlepidota Marx, 1956

Mount Moco rough-scaled lizard

Figures 9, 10; Table 3

Taxonomic note. Described based on five specimens retrieved from the crop of a Dark Chanting Goshawk (*Melierax metabates*) at the base of Serra do Moco (the geographical feature of Serra do Moco which includes the highest peak in Angola at 2620 m a.s.l., is often colloquially referred to as Mount Moco) (Marx 1956). Parker (1936) was actually the first to document this species as *I. bivittata* from Serra do Moco and alluded to its smaller dorsal scales. Remarkably, these smaller dorsal scales were one of the main diagnostic features when *I. microlepidota* was described. However, its taxonomic status has been disputed in the past (Mayer 2013) because of its resemblance to *I. bivittata* and the lack of precise locality data, given that the type series was found in the crop of a dark chanting goshawk (Marx 1956). No additional specimens were collected until PVP collected a topotypic specimen in October 2020 at Serra do Moco (Benito et al. 2025). Thanks to this new material, Benito et al. (2025) provided the first phylogenetic placement of the species, validating its taxonomic status and demonstrating that this species belongs to the *I. bivittata* group.

Holotype. FMNH 74285, adult male, collected from the 'foot of Mount Moco' [= Serra do Moco], Huambo Province, Angola, by Gerd Heinrich on 19 September 1954.

Paratypes. FMNH 74283–84 (females), FMNH 74286–87 (males); same collection details as holotype.

Figure 9. Photographs in life of *Ichnotropis microlepidota* (MHNCUP-REP0983) from Serra do Moco, Huambo Province, Angola (adapted from Benito et al. 2025). Photographs in **A** dorsolateral view of the full body and **B** lateral view of the head. Photographs: Pedro Vaz Pinto.

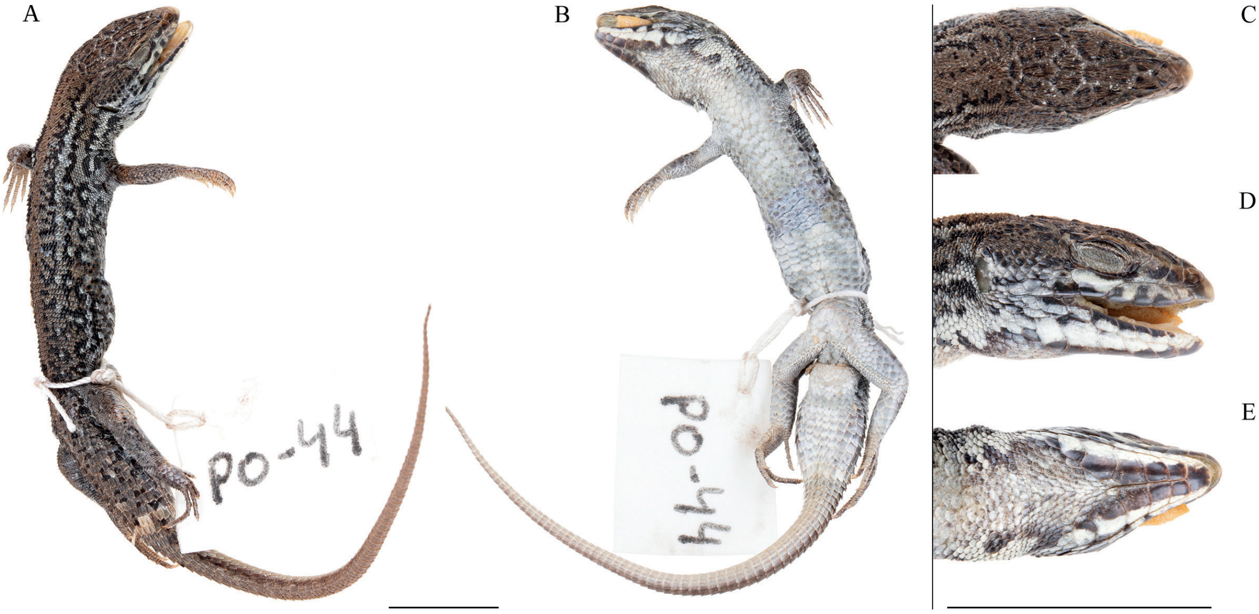

Figure 10. *Ichnotropis microlepidota* (MHNCUP-REP0983) specimen from Serra do Moco, Huambo Province, Angola (adapted from Benito et al. 2025). Photographs of body in **A** dorsal and **B** ventral views, and head in **C** dorsal, **D** lateral and **E** ventral views. Scale bars represent 10 mm. Photographs: Max Benito.

Additional material. MHNCUP-REP0983, adult male, collected at Serra do Moco, Huambo Province, Angola (−12.4554°, 15.1632°, 2300 m a.s.l.), on 18 October 2020 by Pedro Vaz Pinto (Benito et al. 2025); juvenile specimen collected at Serra do Moco, Huambo Province, Angola, 1500–1900 m a.s.l., in March 1934 by Karl Jordan (Parker 1936).

General description. A medium-sized, robust lacertid with a rounded snout and strongly striated and keeled head scales. Nostril pierced between three nasals; the supranasals are in broad contact behind the rostral; single frontonasal, as broad as long; paired prefrontal scales in broad contact medially; prefrontal in contact with the anterior supraocular and either in contact or narrowly separated from supraciliaries by a smaller scale; two large supraoculars, preceded by a single scale (documented by Marx 1956 as a small supraocular); the anterior supraocular is in broad or narrow contact with the 1st supraciliary anteriorly; the posterior part of the anterior supraocular and the posterior supraocular are separated from the supraciliaries by one row of small scales (6); one post-supraocular scale; two loreal scales present, which are separated from the anterior supraocular by one scale; subocular in contact with lip; four supralabials in front of subocular; 6–8 infralabials (mostly seven); five chin shields, with the anterior three pairs in broad contact; four supraciliaries (Marx 1956 recorded five, but he included the posterior loreal); 43–50 midbody scale rows; 8–10 longitudinal rows of enlarged ventral plates; 26–30 transverse ventral scale rows; 16–19 subdigital lamellae under the 4th toe; 10–13 femoral pores per thigh. Size: Adult specimens varied from 48.7–52.0 mm (mean: 50.4 mm) SVL and 69.8 mm TAIL (only one specimen with intact tail). Largest female: 51 mm SVL (FMNH 74283); largest male: 52 mm SVL (FMNH74285, 74286). Colouration (Fig. 9): The dorsal pattern features a light brown central band extending from just behind the head to the hind limbs. This band is bordered on each side by two broken rows of black blotches. Along the lateral sides of the body, two cream to yellow longitudinal stripes run from the level of the ear openings posteriorly to the hind limbs. Between these stripes lie a series of paired white ocelli, each bordered externally by black rings. Below the lower lateral stripe there is a continuous row of single white ocelli. The dorsal surface of the head is brown, mottled with black speckling across most scales. The mouth is bordered in black, which fades to white along the upper portion of the supralabials and the lower portion of the infralabials. The first row of chin shields is entirely black, while rows two through five are bicoloured—black medially and white laterally. The throat (gular region) is pale red-orange, interspersed with black scales and marked by two distinct bright yellow-orange spots located beneath the posterior ends of the lower jaws. The ventral surface is uniformly white

Distribution. Currently only known from the slopes of Serra do Moco, in the central Angolan highlands (Fig. 3).

Habitat and Natural History. The specimens from the type series were preyed upon by a dark chanting goshawk (*Melierax melabates*) (Marx 1956). The specimen collected by PVP (MHNCUP-REP0983) was found during the day on top of an exposed small rock in open montane grassland, with thick vegetation cover at 2300 m a.s.l. (Benito et al. 2025). The montane habitat in Serra do Moco is mainly formed by a thick layer of grass and small bushes as well as many rocks underneath. This type of habitat is likely to hinder the species detectability.

Ichnotropis tanganicana Boulenger, 1917

Tanzanian rough-scaled lizard

Figures 11–13; Table 3

Taxonomic note. This species was described from the ‘East Coast [of] Lake Tanganyika’ in modern-day Tanzania based on a single subadult specimen that was collected in 1896. When Boulenger (1917) described *I. tanganicana*, he ascribed the holotype to a subadult male. However, after our examination of high-resolution photographs of the type specimen it was not possible to sex it, so we regarded it as an unsexed subadult specimen. Since its description, no additional material has been documented. However, due to the vague description provided by Boulenger (1917), the taxonomic status of this species has been questioned by some authors (Mayer 2013). On the other hand, based on some diagnosable head scalation features (i.e., supraoculars in contact with supraciliaries), this species was preliminary retained as valid in subsequent years (Spawls et al. 2002, 2018; van den Berg 2017; Uetz et al. 2025).

In this study, an adult female specimen collected from the mid-elevation Miombo woodlands west of the Kabobo Plateau, DRC (MTSN 9947; Fig. 11E) agreed with the description of *I. tanganicana* based on the supraocular arrangement, (i.e., anterior supraocular in direct contact with the supraciliaries), and the colouration (bronzy olive dorsum with three fine black stripes on nape). However, Boulenger (1917), in his description of the type specimen after 20 years of preservation, did not document the unique, evenly-spaced blue dorsolateral spots observed in the new DRC specimen (Fig. 11E). Based on this new information about the dorsal colouration, we revisited the literature, examined known museum specimens (previously ascribed to *I. bivittata* in eastern DRC and adjacent Zambia and Tanzania) and consulted online citizen science platforms.

Of special interest is the case of the first specimens of *I. bivittata* from Ipemi, Udzungwa Mountains, Tanzania, documented by Loveridge (1933). He states that, in comparison to the type, he regards his specimens as conspecific with *I. bivittata* and distinct from *I. tanganicana*, of which he also examined the type. However, he provides no further details. In his description of the specimens’ colour, he offered a detailed account of the colouration as follows: ‘…series of blotches which is rather more black

Figure 11. Photographs in life of *Ichnotropis tanganicana* from across its range, depicting the evenly spaced dorsolateral blue spots. Photographs from **A** Rukwa, Tanzania; **B** Cambua, Democratic Republic of the Congo; **C** Rumphi, Malawi (https://www.inaturalist.org/observations/146895735); **D** Nyika National Park, Malawi (https://www.inaturalist.org/observations/146684850); **E** Kindingi, Lake Tanganyika (MTSN 9947), Democratic Republic of the Congo; and **F** Upemba National Park, Democratic Republic of the Congo (https://www.inaturalist.org/observations/249778421). Photographs: David Lloyd-Jones; B – Colin Tilbury, C – Marc Henrion, D – Tim Brammer, E – Wandege Muninga, D – Naftali Honig.

than chestnut-brown having the appearance of ocelli by reason of a blueish-white central spot in each …'. Examination of high resolution images of the two Ipemi specimens in the Museum of Comparative Zoology (MCZ R30836–7) confirmed the presence of the unique blue lateral spots (although faded to white in preservative) and the dorsal colouration, but the supraoculars were not in contact with the supraciliaries, as reported in the type specimen (BMNH 1946.9.3.49) of *I. tanganicana*. This difference might have been the reason why Loveridge (1933) considered his material to be conspecific with *I. bivittata* rather than *I. tanganicana*.

Additionally, de Witte and Laurent (1952) again mentioned these unique dorsolateral blue spots in the colour description of *I. overlaeti*: "… from this place it is sometimes replaced by a series of small blue spots more or less bordered with black, extending to the base of the hind limbs; blue spots are also present on the upper band, between the front and hind limbs." (translation from French to English). When we examined the type specimens of *I. overlaeti* at the RMCA (Fig. 13), we not only confirmed the remnants of blue lateral spots and the nape colouration, but we also confirmed the presence of contact between the supraoculars and the supraciliary scales, in agreement

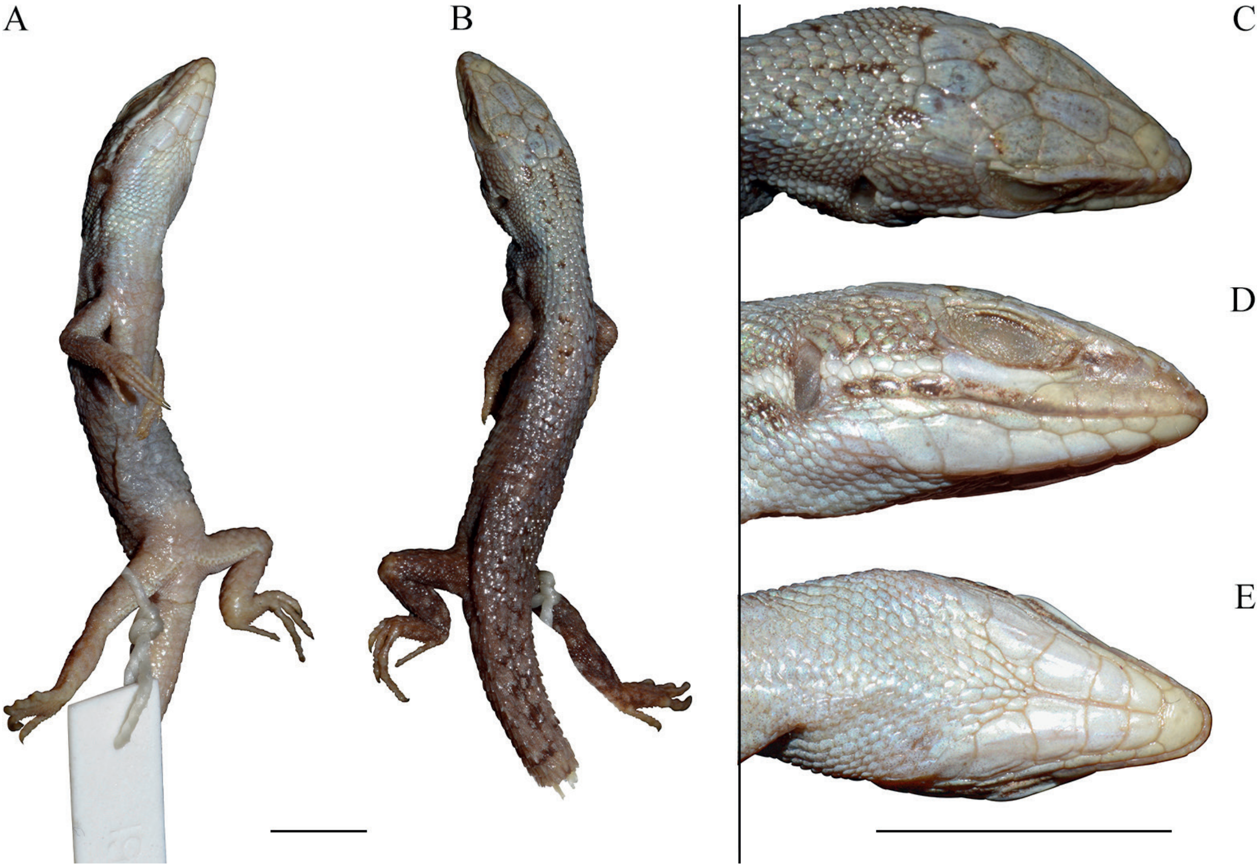

Figure 12. Holotype (BMNH 1946.9.3.49) of *Ichnotropis tanganicana* from 'East coast of Lake Tanganyika', Tanzania. Photographs of body in **A** ventral and **B** dorsal views, and head in **C** dorsal, **D** lateral and **E** ventral views. Photographs: Patrick Campbell.

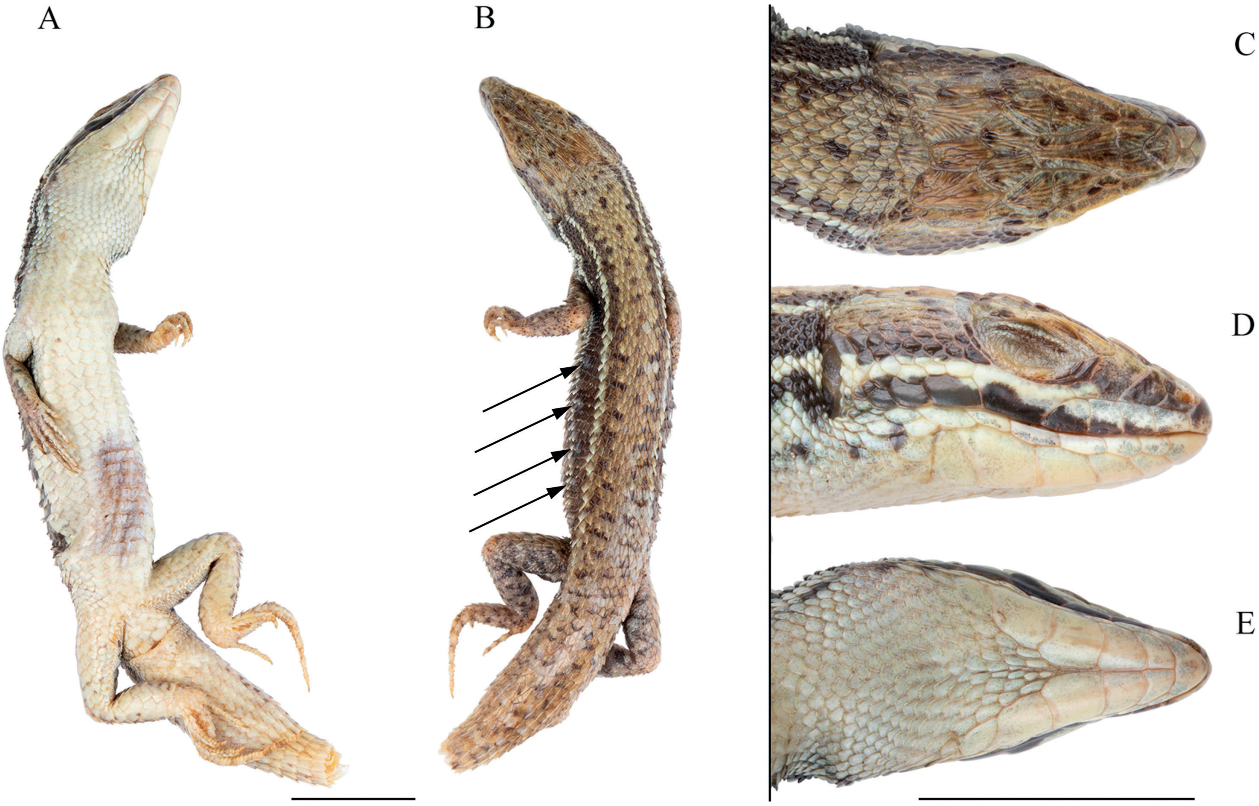

Figure 13. Holotype (BE_RMCA_Vert.R.9691) of *Ichnotropis overlaeti* from Kapanga, Haut-Katanga Province, Democratic Republic of the Congo. Photographs of body in **A** ventral and **B** dorsal (note the evenly spaced white dorsolateral spots indicated by the arrows) views, and head in **C** dorsal, **D** lateral and **E** ventral views. Scale bars represent 10 mm. Photographs: Max Benito.

with *I. tanganicana*. Nevertheless, this feature was only present in the holotype (BE_RMCA_Vert.R.9691) and one of the original paratypes (BE_RMCA_Vert.R.1869, later used as a paratype for *I. nigrescens*). However, the other paratype material conformed morphologically to either *I. bivittata* (see above) or *I. capensis* sensu lato (see below).

Other published sources showing photographs of *I. bivittata* (sic) with blue spots include de Witte (1933: plate 2, fig. 1) from southeastern DRC, Spawls et al. (2018: 202, bottom right) from southwestern Tanzania, and Phadima et al. (2024: 22; also on iNaturalist 146895735) from northwestern Malawi. Additional records were also found on iNaturalist (191773297, 146684850, 147210660, 87417155) and ReptileMap (169500) from DRC, Malawi and Zambia

Based on the combined evidence, all the above material can thus be confidently assigned to *I. tanganicana*. We therefore take this opportunity to expand on the original description of *I. tanganicana* and synonymise *I. overlaeti* with *I. tanganicana*.

Synonymy. *Ichnotropis overlaeti* de Witte & Laurent, 1942: 173 (new synonymy).

Holotype. BMNH 1946.9.3.49 (96.5.14.14), collected from 'East Coast [of] Lake Tanganyika', Tanzania, presented to the museum by Mr. WH. Nutt in 1896.

General description. A medium-sized lacertid with a robust, rounded snout. Head scalation weakly to moderately striated. Nostril pierced between three nasals; the supranasals are in broad contact behind the rostral; single frontonasal, as broad as long; paired prefrontal scales in broad contact medially; prefrontal mostly in contact with the anterior supraocular (n = 29 in contact, seven not in contact; three in contact on one side only) and separated from supraciliaries by a smaller scale; two large supraoculars, which are either in direct contact (n = 15) or separated (n = 18) from the supraciliaries by a series of small scales; those that are not in contact are separated by one row of small scales (3–9) and preceded by a cluster of 1–6 (1.7 average) smaller scales; one post-supraocular scale; two loreal scales present, which are separated from the anterior supraocular by two scales; subocular in contact with lip; 3–5 (mostly 4) supralabials in front of subocular; 5–7 (mostly six) infralabials; five chin shields, with the anterior three in broad contact; 4–5 (mostly four) supraciliaries; 28–42 (average: 36.0) midbody scale rows; 8–10 (average: 8.4) longitudinal rows of enlarged ventral plates; 20–27 (average: 22.8) transverse ventral scale rows; 17–22 subdigital lamellae under the 4th toe; 10–15 femoral pores per thigh. Size: Adult specimens varied from 41.0–60.0 mm (mean: 53.9 mm) SVL and 55.6–107.9 mm (mean: 81.7 mm) TAIL. Largest female: 60 mm SVL (NMZB-UM 24433 – Misuku Hills, Malawi); largest male: 56 mm SVL (NMZB-UM 24432 – Misuku Hills, Malawi). Colouration (Fig. 11): The top of the head and the anterior part of the body are coppery red, sometimes with three clearly defined black stripes on the nape. The anterior part of the dorsum is grey with scattered brown paired blotches with black edging, extending onto the tail. The flanks are dark brown to black, typically with interrupted white dorsolateral stripes. The upper stripe originates behind the eye and extends onto the neck and then breaks up into smaller white blotches. The lower stripe begins anteriorly at the supralabials, tracing posteriorly through the ear and over the arm, breaking into smaller white blotches on the anterior third of the body. Between these two stripes lies a broad dark brown to black band. Diagnostic, evenly-spaced green to blue spots start above the arm and extend posteriorly to the groin in both sexes. Beneath the lower interrupted white stripe/blotches lies another narrow band of brown to black scales, sometimes accompanied by orange spots or blotches extending onto the venter. During the breeding season, males exhibit more prominent orange flanks, while the lower white stripe and lateral head become vivid yellow anteriorly. The specimen from the DRC (MTSN 9947) exhibits a bright orange lower jaw. The venter is typically plain white but can have light grey colouration.

Distribution. Known from western Tanzania, south to northern Malawi, and eastward to northern Zambia and southern DRC (Fig. 3).

Habitat and Natural History. The Lukwati specimen was discovered in grassland adjacent to *Brachystegia* woodland. This specimen exhibited peculiar leg-tucking behaviour, wherein it raised its body and folded its legs to the sides (Spawls et al. 2018; Lloyd-Jones pers. comm.). A gravid female was observed laying eggs in January (iNaturalist 146684850). Shelled eggs in the oviducts of one specimen measured 13.5 mm × 6.5 mm (Robertson et al. 1963). Stomach contents were documented to contain Acrididae, Mantidae, Isoptera, and Araneae (Robertson et al. 1963).

The *Ichnotropis grandiceps* group

Phylogenetically and morphologically, the *I. grandiceps* group includes *I. grandiceps* and a candidate new species from Angola described here, which share the following morphological features: Robust, broad and depressed head; the prefrontal always separated from the anterior supraocular; weak head striations; and uniform brown to red dorsum. This group is restricted to the Kalahari Basin, from central Angola to northern Namibia (Fig. 14).

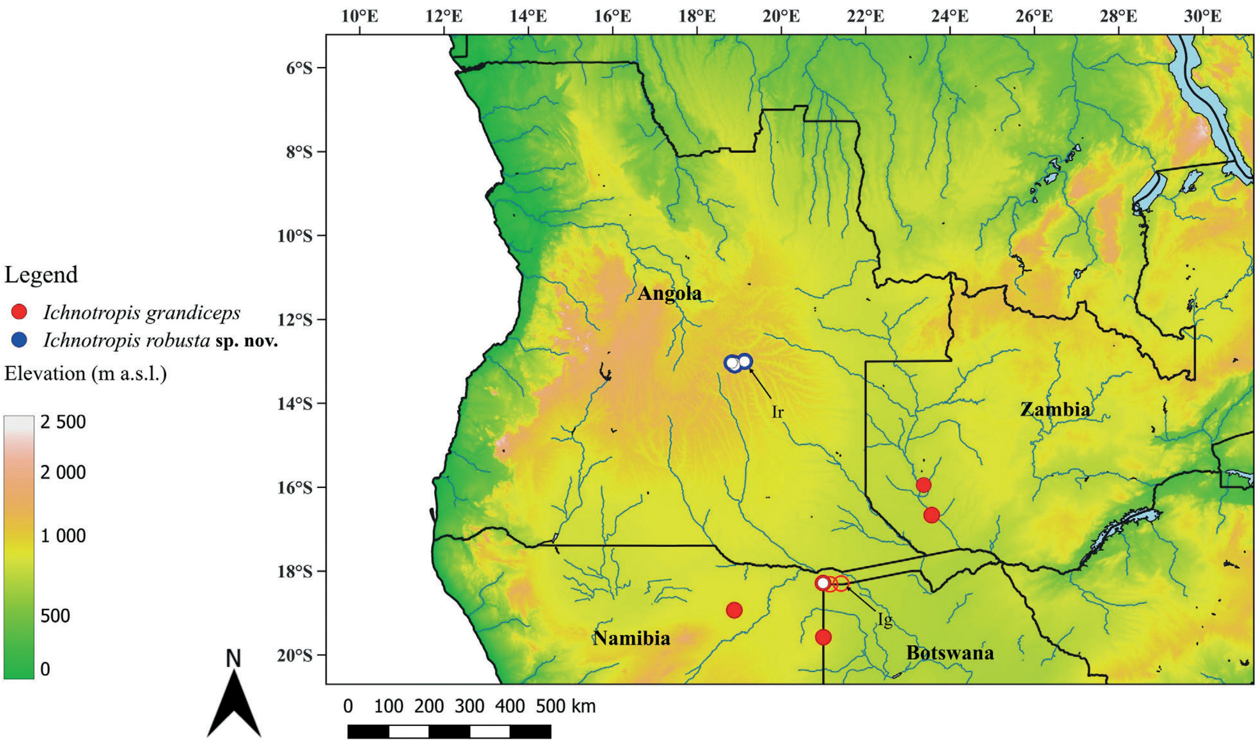

Figure 14. Records of the *Ichnotropis grandiceps* group, based on all literature records (open circles), examined material (closed circles) and genetically analysed material (white centres). Respective type localities are indicated by arrows: Ig – *I. grandiceps*, and Ir – *I. robusta* **sp. nov.**

Ichnotropis grandiceps Broadley, 1967

Zambezi rough-scaled lizard

Figures 15, 16; Table 4

Taxonomic note. This is the most recently described species of *Ichnotropis*. It was described from the western Zambezi Region in north-eastern Namibia, based on only three specimens, and was distinguished from sympatric *I. capensis* based on its larger size, rounded head and dorsal colouration (Broadley 1967b). This is a rarely documented species and it is only known from the type series, four additional specimens collected from north-eastern Namibia (Haacke 1970), one specimen from Khaudum, Namibia (van Breda 2023), and one specimen from western Zambia (Pietersen et al. 2017). Conradie et al. (2022a) tentatively assigned material from eastern Angola to this species based on shared morphology, but phylogenetic analyses (see Results) recover it as a separate sister lineage, which represents a candidate new species described below.

Holotype. USNM 163989, an adult male, collected '25 miles west of Mohembo, Botswana, on the border of the Caprivi Strip (South West Africa)', Namibia by T.N. Liversedge and S.W. Goussard on 20 May 1967.

Paratypes. NMZB-UM 16278 (male) and USNM 163990 (juvenile); same collection details as holotype.

General description. A large, robust lacertid with a pointed snout. Head scalation weakly striated. Nostril pierced between three nasals; the supranasals are in broad contact behind the rostral; single frontonasal, as broad as long; paired prefrontal scales in broad contact medially; prefrontal separated from the anterior supraocular by a smaller scale (except on the right-side of TM 86237) and separated from supraciliaries by a smaller scale (except on the right-side of TM 38309); two large supraoculars, which are separated from the supraciliaries by one row of small scales (5–9) and preceded by a cluster of smaller scales (3–7); 2–3 post-supraocular scales; two loreal scales present, which are separated from the anterior supraocular by two scales; subocular in contact with lip; 4–5 (mostly five) supralabials in front of subocular; 5–7 (mostly six) infralabials; five chin shields, with the anterior three in broad contact; 4–5 (mostly five) supraciliaries; 44–47 (average: 45.6) midbody scale rows; 10 longitudinal rows of enlarged ventral plates; 27–31 (average: 28.3) transverse ventral scale rows; 20–26 subdigital lamellae under the 4th toe; 8–14 femoral pores per thigh. Size: Adult specimens varied from 57.2–77.9 mm (mean: 65.6 mm) SVL and 103.4–148.0 mm (mean: 124.9 mm) TAIL. Largest female: 77.9 mm SVL (RE211206D1/NMNW R12212 – Khaudum, Namibia); largest male: 70 mm SVL (USNM 163989 – 40 km W of Mohembo, Botswana). Colouration (in preservative; Fig. 16): Above pale grey-brown, with darker stippling and a few scattered dark black spots on the body and tail. A poorly defined dark brown dorsolateral band extends from the neck to the groin, where it breaks up into a line of lateral spots on the tail. Sides of the head and lower flanks white. Venter white. In juveniles or subadults (Fig. 15), the dark brown lateral band is replaced by a mustard-coloured band (Pietersen et al. 2017).

Figure 15. Photographs in life of juvenile *Ichnotropis grandiceps*. Specimens photographed from **A** Ngonye Falls (TM 86237), Zambia and **B** Chitokoloki, Zambia. Photographs: A – Darren Pietersen; B – Frank Willems.

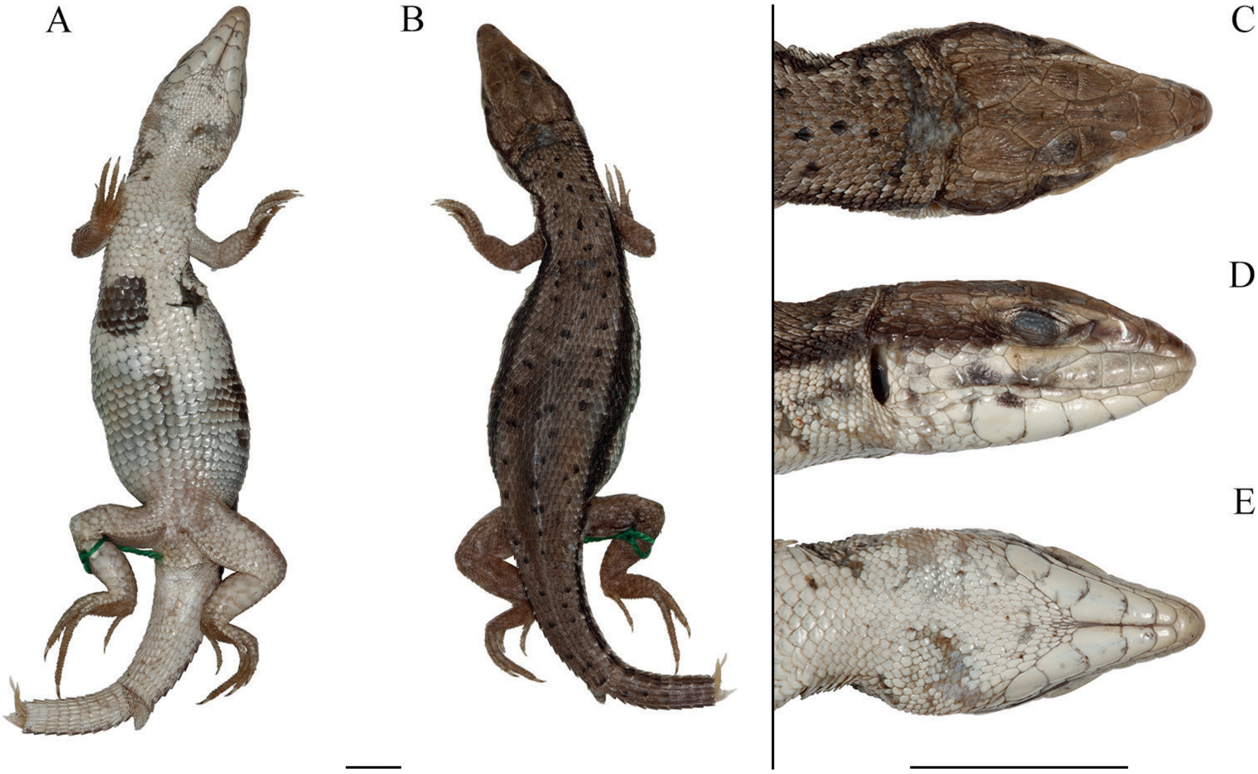

Figure 16. *Ichnotropis grandiceps* (RE211206D1/NMNW R12212) specimen from Khaudum, Namibia. Photographs of body in **A** ventral and **B** dorsal views, and head in **C** dorsal, **D** lateral and **E** ventral views. Photographs: Werner Conradie.

Table 4. Summary of morphological data for the *Ichnotropis grandiceps* group. Measurements are presented in millimetres (mm). Values are given as a range with mean ± standard deviation in parenthesis. Data for adults and subadults are presented separately. For abbreviations, see the Materials and Methods section. n = sample size.

Characters	***I. grandiceps***	***I. grandiceps***	***I. robusta* sp. nov.**	***I. robusta* sp. nov.**
	n = 6 (adults)	n = 4 (subadults)	n = 5 (adults)	n = 11 (subadults)
SVL	57.2–77.9 (65.6 ± 7.52)	57.2–77.9 (65.6 ± 7.52)	71.9–78.8 (74.9 ± 3.12)	35.6–51.1 (44.6 ± 5.33)
TAIL	103.4–148.0 (124.9 ± 16.21)	38.5–50.2 (44.9 ± 5.97)	121.0–140.0 (133.0 ± 8.29)	68.0–100.9 (88.2 ± 11.76)
HL	12.7–18.2 (16.0 ± 2.11	9.9–13.5 (12.0 ± 4.558)	17.8–18.7 (18.3 ± 0.39)	9.5–04.7 (11.9 ± 1.60)
HW	7.7–12.0 (9.3 ± 1.97)	5.8–7.9 (6.9 ± 1.08)	11.1–11.8 (11.5 ± 0.31)	5.6–8.5 (7.2 ± 1.07)
HH	6.4–9.7 (7.8 ± 1.39)	5.4–6.8 (6.2 ± 0.72)	9.1–9.4 (9.3 ± 0.13)	5.8–6.8 (6.4 ± 0.41)
ED	4.9–6.0 (5.2 ± 0.50)	3.0–4.6 (4.0 ± 0.90)	2.9–3.8 (3.2 ± 0.42)	2.3–2.7 (2.6 ± 0.16)
SE	6.3–8.2 (7.0 ± 0.85)	4.6–6.0 (5.5 ± 0.73)	6.1–8.4 (8.3 ± 0.12)	5.4–6.0 (5.6 ± 0.25)

Characters	*I. grandiceps*	*I. grandiceps*	*I. robusta* sp. nov.	*I. robusta* sp. nov.
LL	14.3–18.3 (16.1 ± 1.99)	10.5–15.0 (13.3 ± 1.96)	20.5–24.2 (21.6 ± 1.53)	1.1–17.0 (13.8 ± 1.90)
IL	24.8–38.9 (30.4 ± 5.99)	19.4–38.9 (26.1 ± 6.9)	33.4–40.1 (36.3 ± 2.38)	18.2–26.0 (22.0 ± 2.77)
FLL	6.9–9.4 (7.8 ± 1.11)	4.2–6.5 (5.3 ± 1.15)	7.2–8.6 (8.3 ± 0.62)	3.8–6.4 (5.1 ± 0.89)
HLL	10.6–13.7 (11.8 ± 1.35)	7.0–9.0 (8.3 ± 1.13)	12.8– 13.9 (13.4 ± 0.44)	6.5– 10.5 (8.7 ± 1.35)
TAIL/SVL	1.3–2.2 (1.9 ± 0.34)	2.0 (2.0 ± 0.02)	1.6–1.9 (1.8 ± 0.17)	1.8–2.1 (2.0 ± 0.09)
HL/SVL	0.2–0.3 (0.2 ± 0.01)	0.3 (0.3 ± 0.01)	0.2–0.3 (0.2 ± 0.01)	0.3 (0.3 ± 0.01)
ES/HL	0.4–0.5 (0.5 ± 0.03)	0.4–0.5 (0.5 ± 0.02)	0.4–0.5 (0.5 ± 0.01)	0.4–0.5 (0.4 ± 0.00)
HW/HL	0.5–0.7 (0.6 ± 0.05)	0.5–0.6 (0.6 ± 0.04)	0.6–0.7 (0.6 ± 0.02)	0.6–0.7 (0.6 ± 0.03)
MSR	44–47		43–48	
LVSR	10		9–10	
TVSR	27–31		26–33	
SL	4–5 (mostly 5)		4–6 (mostly 5)	
IL	5–7 (mostly 6)		5–7 (mostly 6)	
SC	4–5 (mostly 5)		4–5 (mostly 5)	
LUFT	20–26		20–26	
Femoral pores	8–14		8–14	

Distribution. Known from northeastern Namibia and adjacent Botswana, and from western Zambia (Fig. 13). The apparent gap in distribution between northeastern Namibia/Botswana and western Zambia likely reflects a lack of sampling, and the species' range is believed to be more continuous.

Habitat and Natural History. Ontogenetic colour differences have been observed between juveniles and adults (this study). Found in sympatry with *I. capensis* sensu lato. Associated with *Baikiaea* woodland on deep Kalahari alluvial sands and hard lime-rich soils in open woodland (Haacke 1970; Pietersen et al. 2021).

Ichnotropis robusta sp. nov.

Robust rough-scaled lizard

https://zoobank.org/1E069D01-1F86-488F-9025-DEBDB47BEA00

Figures 17, 18; Tables 4, 5

Chresonymy.

Ichnotropis cf. *grandiceps* – Conradie et al. (2022a: 198); *Ichnotropis* aff. *grandiceps* – Benito et al. (2025: 893).

Holotype. PEM R23420 (field number WC-4816), adult male, collected from Cuando River source (–13.0035°, 19.1275°, 1343 m a.s.l.), Moxico Province, Angola by Werner Conradie and James Harvey on 21 November 2016.

Paratypes. 4 specimens: a) PEM R23361 (field number WC-4063) and PEM R23362 (field number WC-4056), adult females, collected on the road between Cuanavale River source camp and Samanunga village (–13.0380°, 18.8298°, 1605 m a.s.l.), Moxico Province, Angola by Werner Conradie and Luke Verburgt on 13 March 2016; b) PEM R23421, adult male, same collection details as holotype; c) PEM R23482 (field number WC-4804), adult male, collected from Cuando River source, trap 4 (–13.0016°, 19.1296°, 1372 m a.s.l.), Moxico Province, Angola by Werner Conradie and James Harvey on 15 November 2016.

Additional juvenile material. 12 specimens: a) PEM R23279–80; INBAC (no number), collected from Cuanavale River source lake (–13.0933°, 18.8940°, 1367 m a.s.l.), Moxico Province, Angola by Werner Conradie on 1 March 2016; b) PEM R23299–300, grassland west of Cuanavale River source en route to Samanunga village (–13.0751°, 18.8848°, 1366 m a.s.l.), Moxico Province, Angola by Werner Conradie and Luke Verburgt on 16 March 2016; c) PEM R23303–9, trap 4 km upstream from Cuanavale River source lake (–13.0508°, 18.8973°, 1380 m a.s.l.), Moxico Province, Angola by Werner Conradie from 28 February to 15 March 2016.

Etymology. The species name *robusta* is the feminine form of the Latin adjective robustus, meaning 'robust' or 'sturdy', in reference to the large, heavy-built adults of this species.

Diagnosis. Assigned to *Ichnotropis* due to the absence of a well-defined collar, digits not serrated or fringed, subdigital lamellae keeled, and subocular bordering the lip. A large *Ichnotropis* with a single frontonasal; subocular bordering the lip; a single anterior loreal; feebly developed head shield striations; prefrontals well separated from the anterior supraocular; and supraciliaries separated from the supraoculars by a series of smaller scales.

The new species can be distinguished from other *Ichnotropis* species based on a combination of the following characters: Prefrontals well separated from the anterior supraocular (versus mostly in contact in *I. bivittata*, *I. microlepidota* and *I. tanganicana*); high number of midbody scale rows (43–48 versus 25–42 in *I. capensis* sensu lato); large, robust head and rounded snout (versus small depressed head and pointed snout in *I. capensis* sensu lato); four (46%) to five (50%) supralabials anterior to the subocular (versus mostly four in *I. capensis* sensu lato); distinctive large trapeziform occipital wedged between the parietals, not protruding past parietals (versus occipital usually extending posteriorly, well beyond the level of the parietals in *I. capensis* sensu lato).

The new species resembles *I. grandiceps* in its large size, robust, rounded head; prefrontals well separated from anterior subocular; high midbody scale rows (43–48 versus 44–47) and genetic similarity. Due to the lack of comparative adult material of *I. grandiceps*, no clear morphological and colouration differences could be observed between the two species. However, the two species exhibit clear differences in habitat preferences. All *I. grandiceps* material have either been found in drier Zambezian Baikiaea woodlands or Combretum-Vachellia bushveld (Broadley 1967b; Haacke 1970; Pietersen et al. 2017) at lower elevations (less than 1000 m a.s.l.), while the new species is associated with the higher elevations (above 1300 m a.s.l.) of the Angolan Plateau, which consists of moister Angolan Miombo woodland.

In the phylogenetic analysis, the uncorrected p distances show that the new species differs by >6.7% for 16S and >16.3% for ND4 sequence divergence from other *Ichnotropis* species (Table 2).

Holotype description (Fig. 18). Adult male measuring 73.5 mm SVL and 96 mm TAIL (regenerated). Body moderately depressed; head not depressed, 1.7 times as long as broad (HL 18.9/HW 11.1 mm), its length equivalent to 25.7% of snout–vent length, expanded in the temporal region and very distinct from the neck. Adpressed hind limb reaches the anterior ear opening. The foot length is almost equal to the head length (FL 18.3/HL 18.9 mm).

Upper head shields very feebly striated and keeled; nostril pierced between three nasals, the supranasals in broad contact behind the rostral; frontonasal slightly broader than long (2.6 × 2.4 mm); prefrontals much longer than broad (4.3 × 1.7 mm), in broad contact medially, not reaching the anterior supraoculars (separated by a small keeled scale), and separated from the anterior loreal by a small keeled scale; frontal twice as long as its maximum width between the posterior tips of the prefrontals (6.2 × 3.0 mm), rounded anteriorly and strongly narrowed posteriorly; frontoparietals longer than broad; parietals longer than broad (5.4 × 2.8 mm), extending posteriorly, widely separated by a large interparietal and occipital, the latter small and its posterior margin level with the posterior borders of the parietals; an elongate keeled upper temporal shield borders the parietal; two supraoculars, the anterior supraocular longer than its distance from posterior loreal (2.3 mm vs. 1.8 mm), and in contact with posterior half of frontal; the second is smaller, separated from the supraciliaries by nine (right)/eight (left) small keeled scales (except the 4th supraciliary on the left side, which is in narrow contact with the second supraocular); two post-supraocular scales; five supraciliaries, the first two much longer than the others and forming a long oblique suture. Lower nasal in contact with the rostral, first supralabial and anterior loreal; postnasal small, in contact with the other two nasals, frontonasal, and anterior loreal; two loreals, the posterior one much larger; four supralabials anterior to the subocular, whose lower border on the lip is much shorter (2.5×) than the upper; three supralabials posterior to the subocular; temporal scales strongly keeled; a narrow tympanic shield on the upper anterior edge of the vertically elongate ear opening; lower eyelid scaly with a median series of vertically elongate scales. Six infralabials; four (right) and five (left) large chin shields, the first two (right) and three (left) in median contact; gular scales imbricate; no collar.

Dorsal scales rhomboid, strongly keeled and imbricate, lateral scales smaller and feebly keeled, passing gradually into the smooth, rounded ventral plates, which are broader than long; 44 scales around the middle of the body; ventral plates in 10 longitudinal and 29 transverse rows between fore- and hind limbs; preanal scales irregular; scales on upper surfaces of limbs rhomboid, strongly keeled, and imbricate; 12 femoral pores on each side; subdigital lamellae pluricarinate and spinulose, 21 under the 4th toe; caudal scales strongly keeled above and below, except those just posterior to the vent, which are smooth.

Colouration. (In life, breeding colouration; similar to Fig. 17A): Above uniform reddish-brown, with small black spots on the lower body and anterior third of tail; dorsolateral bands as in preserved colouration, but more vivid; gular, chin shields and posterior section of white dorsolateral band bright yellow to anterior of the forelimb insertion, fading to just behind the arm; front limbs brick red dorsally, hind limbs dark grey anteriorly and brick red posteriorly; venter (except gular) white. Colouration (in preservative; Fig. 18): Above pale grey-brown, with a few scattered dark brown to black spots (not covering more than one scale) on lower body and upper tail; a well-defined broad (covering 3–4 scales at midbody) black dorsolateral band extends from the tip of the snout to the groin; below this black dorsolateral band is a second narrow white band (covering 1–2 scales at midbody) which also extends from the tip of the snout to the groin; below this white band is another narrow black band extending from the mental, along the edge of the jaw (edge of supra- and infralabials), to just behind the forelimb insertion, where it fades to fine specks towards the groin. Limbs dorsally brown and ventrally white; venter white.

Paratype variation. The paratypes are in general agreement with the holotype in most regards, differing only in: Two large supraoculars, which are separated from the supraciliaries by a single row of smaller scales (7–10) and preceded by a cluster of smaller scales (3–5) (except in PEM R23482, the 1st supraciliary is in narrow contact with the anterior supraocular on the right side); 1–3 post-supraocular scales; large occipital scale that separates the two interparietals and extends well past their posterior edge; two loreal scales present, which are separated from the anterior supraocular by 1–2 scales; 4–5 (mostly 5) supralabials in front of the subocular; 6–7 (mostly 6) infralabials; five chin shields, with the anterior three in broad contact; five supraciliaries; 43–48 (average: 45.0) midbody scale rows; 26–30 (average: 27.8)

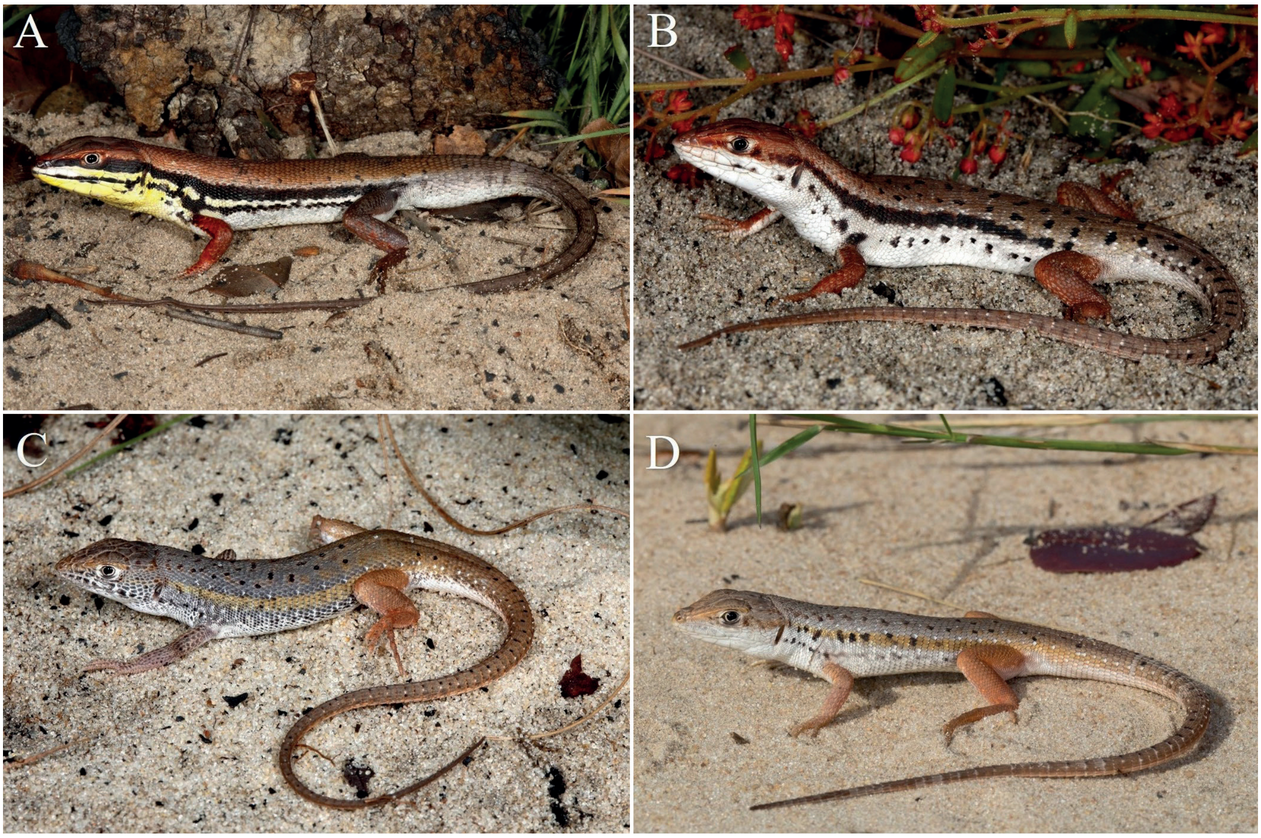

Figure 17. Photographs in life of *Ichnotropis robusta* **sp. nov.** Photographs of **A** adult male (PEM R23482) from Cuando River source, Angola; **B** adult female (PEM R23362) from the road between Cuanavale River source camp and Samanunga village, Angola; **C** juvenile (PEM R23304) from 4 km upstream of Cuanavale River source lake, Angola; and **D** juvenile (PEM R23300) from the road between Cuanavale River source camp and Samanunga village, Angola. Photographs: A, B, C – Werner Conradie; D – Luke Verburgt.

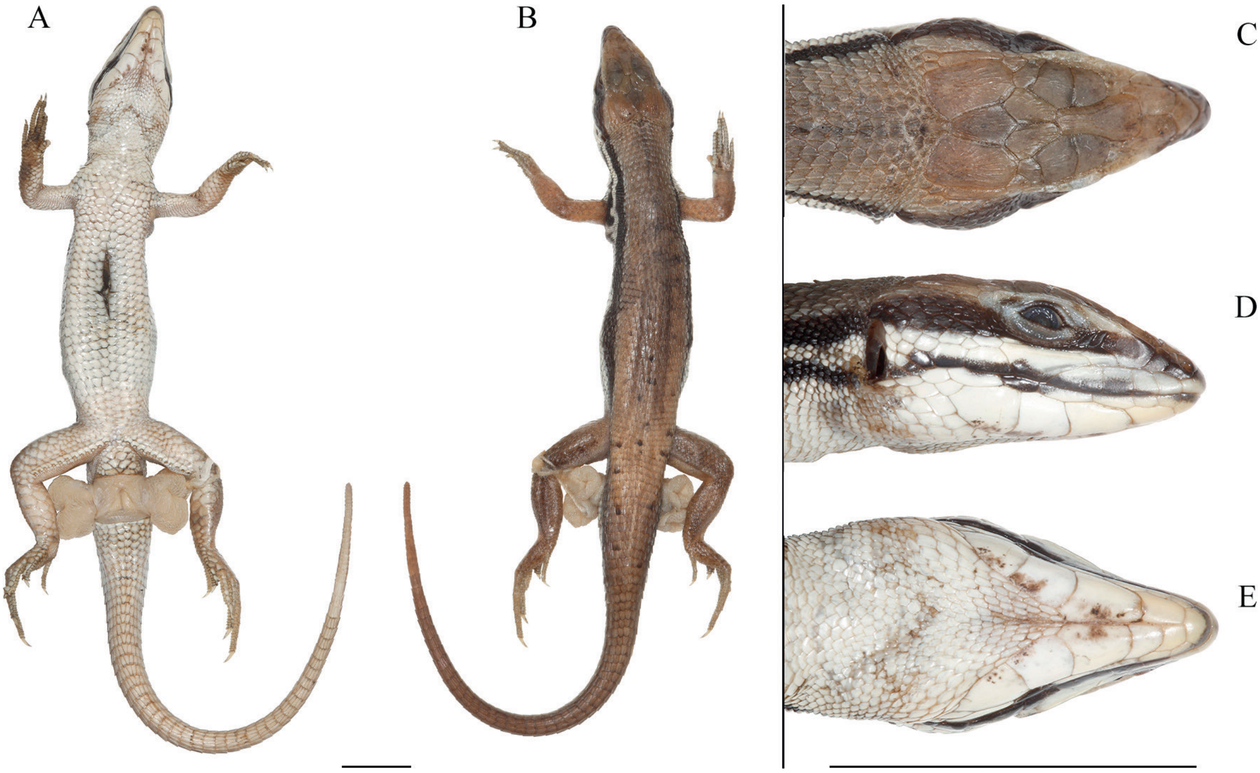

Figure 18. Holotype (PEM R23420) of *Ichnotropis robusta* **sp. nov.** from Cuando River source, Moxico Province, Angola. Photographs of body in **A** ventral and **B** dorsal views, and head in **C** dorsal, **D** lateral and **E** ventral views. Scale bars represent 10 mm. Photographs: Werner Conradie.

Table 5. Measurements (in mm) and scale counts for the type series of *Ichnotropis robusta* **sp. nov.** Scale counts given as Right/Left. For abbreviations, see the Materials and Methods section. t = truncated.

Catalogue No.	**PEM R23420**	**PEM R23482**	**PEM R23421**	**PEM R23362**	**PEM R23361**
Type status	Holotype	Paratype	Paratype	Paratype	Paratype
Sex	Male	Male	Male	Female	Female
SVL	73.5	71.9	72.7	77.7	78.8
TAIL	96t	135.0	140.0	121.0	136.0
HL	18.7	18.5	17.9	17.8	18.5
HW	11.1	11.8	11.7	11.2	11.6
HH	9.2	9.1	9.2	9.4	9.4
ED	2.9	3.8	3.1	3.0	3.1
SE	8.1	8.4	8.2	8.2	8.3
LL	21.3	21.5	20.6	20.5	24.2
IL	36.3	33.4	35.8	36.0	40.1
FLL	8.3	8.6	8.6	8.5	7.2
HLL	13.8	13.3	13.1	12.8	13.4
TAIL/SVL	—	1.9	1.9	1.6	1.7
HL/SVL	0.3	0.3	0.2	0.2	0.2
ES/HL	0.4	0.5	0.5	0.5	0.4
HW/HL	0.6	0.6	0.7	0.6	0.6
MSR	44	44	45	43	48
LVSR	10	10	10	10	10
TVSR	29	26	26	28	30
SL	4/4	4/4	5/5	5/4	5/5
IL	6/6	7/6	7/6	6/6	6/6
SC	5/6	5/5	5/5	5/5	5/5
LUFT	21	22	20	20	23
Femoral Pores	12/12	13/12	14/14	12/11	12/12

transverse ventral scale rows; 20–23 subdigital lamellae under the 4th toe; 11–14 femoral pores per thigh. Size: Adult specimens varied from 71.9–78.8 mm (mean: 75.3 mm) SVL and 121–140.0 mm (mean: 133.0 mm) TAIL. Largest female: 78.8 mm SVL + 136 mm TAIL (PEM R23361); largest male: 73.5 mm SVL + 96.0 mm truncated tail (Holotype). Colouration (Fig. 17B): Females with numerous scattered black scales on back and tail, scattered white scales along the upper edge of the dorsolateral dark brown band, continuing onto the tail. Lower dorsolateral black band broken from behind the head to the tail.

Additional juvenile material variation. Prefrontal separated from the anterior supraocular by 1–2 smaller scales (in contact in PEM R23300 and R23299 – both sides; PEM R23309 – left side only) and separated from supraciliaries by a smaller scale (except PEM R23305 and PEM R23299); two large supraoculars, which are separated from the supraciliaries by one row (two in PEM R23280 and R23303) of small scales (7–10) and preceded by a cluster of smaller scales (2–7) (except in PEM R23300, where the 1st supraciliary is in narrow contact with the anterior supraocular on the right side; in narrow contact on the left side in PEM R23306; in PEM R23307, the 2nd and 3rd supraciliaries are in contact with the posterior supraocular on the right and anterior supraocular on the left); 1–2 post-supraocular scales; two loreal scales present, which are separated from the anterior supraocular by 1–2 scales; subocular in contact with the lip; 4–6 (mostly five) supralabials in front of the subocular; 6–7 (mostly six) infralabials; five chin shields, with the anterior three in broad contact; 5–6 (mostly five) supraciliaries; 43–47 (average: 45.0) midbody scale rows; 9–10 longitudinal rows of enlarged ventral plates; 30–33 (average: 32.4) transverse ventral scale rows; 20–25 subdigital lamellae under the 4th toe; 11–13 femoral pores per thigh. Size: Juvenile specimens varied from 35.6–51.1 mm (mean: 44.6 mm) SVL and 68.0–100.9 mm (mean: 88.2 mm) TAIL. Colouration (Fig. 17C, D): In juveniles, the dorsum is grey anteriorly and orange posteriorly, with scattered black and white specks, and a narrow mustard coloured dorsolateral band. The dorsum of the tail is orange with scattered black and white scales. The venter is white.

Distribution. Only recorded from the headwaters of the Okavango (Cuito and Cuanavale Rivers) and Cuando Rivers in central Angola (Fig. 14).

Habitat and Natural History. Ontogenetic colour differences have been observed between juveniles and adults. Breeding colouration males and gravid females were collected in November 2016, while non-breeding females and juveniles were found in February–March 2016. Juveniles were only observed on sandier areas around the source of the Cuanavale River, while two adult females were found on the elevated grassland ridges surrounding the river. Found in sympatry with *I. capensis* sensu lato.

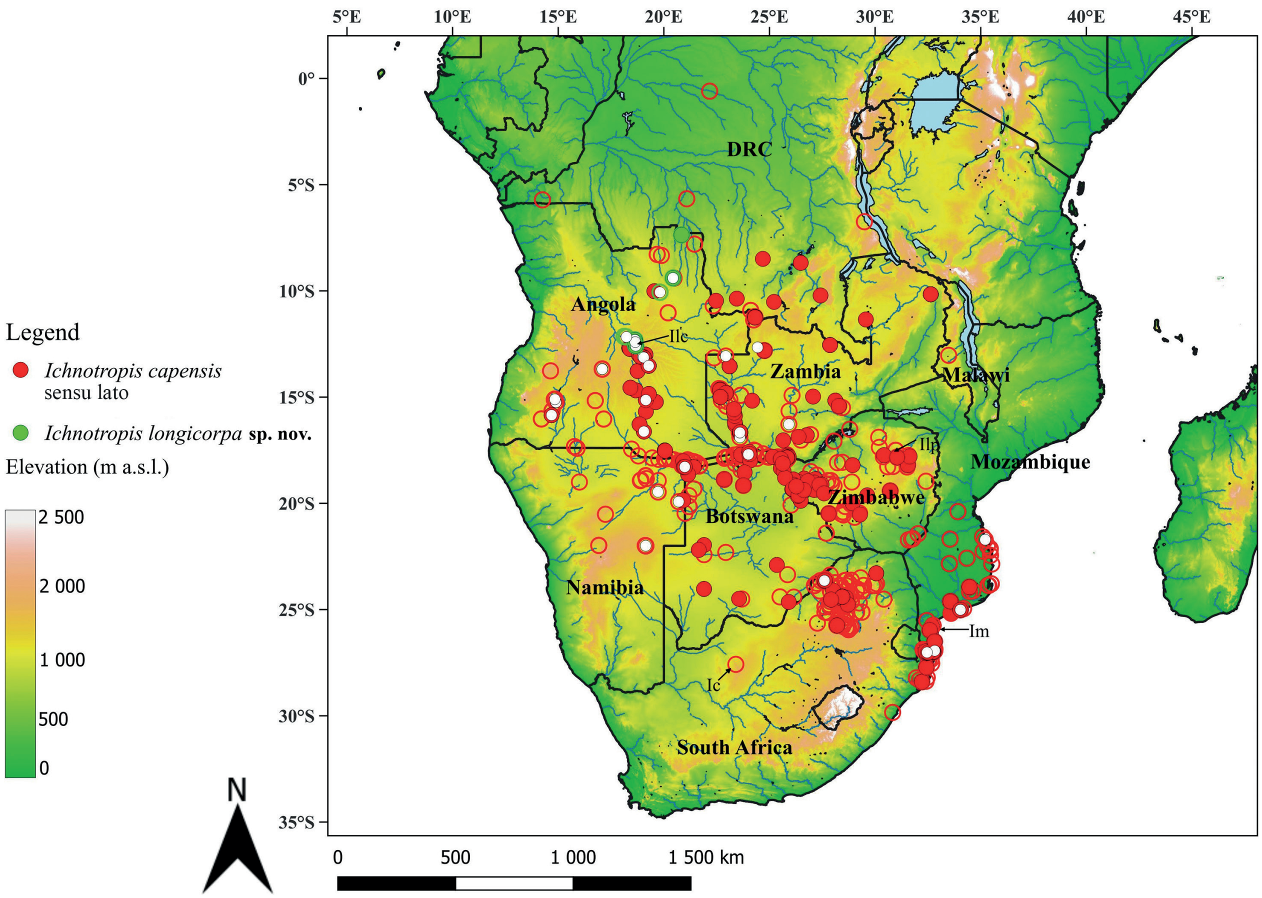

Figure 19. Geographic records of the *Ichnotropis capensis* group, based on all literature records (open circles), examined material (closed circles) and genetically analysed material (white centres). Respective type localities are indicated by arrows: Ic – *I. capensis*, Ilc – *I. longicorpa* **sp. nov.**, Ilp – *I. longipes*, and Im – *I. macrolepidota*.

The *Ichnotropis capensis* group

Based on the phylogenetic reconstructions and the morphological data, the *I. capensis* group includes *I. capensis* sensu lato and a candidate new species (described below) from central Angola, which share the following morphological features: A more slender build (compared to the other two groups), the prefrontal mostly separated from the anterior supraocular, and a narrow, flattened head with distinct evenly spaced head striations. This group is restricted to the Kalahari Basin from the central Angolan plateau to northern Namibia, eastward to the east coast of Mozambique and South Africa (Fig. 19).

Ichnotropis capensis (Smith, 1838) sensu lato

Cape rough-scaled lizard

Figures 20–23; Table 6

Taxonomic note. *Ichnotropis capensis* was originally described from the “sandy deserts around Latakoo”, which corresponds to the present-day Kuruman area in the Northern Cape province, South Africa. Since its original description, no additional specimens have been collected from the type locality or proximate areas. The nearest known record today is from Giya Camp in southern Botswana, approximately 340 km north of the type locality. This gap in distribution may be due to limited sampling effort in the region (Tolley et al. 2023), or alternatively, it may reflect uncertainty or inaccuracy in the locality information provided by Smith (1838), who was traveling extensively across the northern provinces of South Africa at the time. Due to the uncertainty surrounding the type locality and the fact that the type specimen remains unaccounted for in the BMNH (P. Campbell, pers. comm. 23 January 2024), the designation of a neotype is recommended to further stabilise the taxonomic status of *Ichnotropis capensis*. However, we refrain from taking this action at present, because we lack comparative material from the southern and eastern parts of the species’ distribution, including areas near the type locality of *Ichnotropis longipes* (Mazoë and the region between Umtali and Marandellas). Although we have examined photographs of the *I. longipes* type specimens (all subadults), we choose not to assign this name to any of the remaining *I. capensis* clades until additional material becomes available and a neotype for *I. capensis* can be designated.

Jacobsen et al. (2010) noted the presence of disjunct populations of *Ichnotropis capensis* between the east coast of southern Africa and the interior. Populations from the eastern coastal regions of South Africa and adjacent Mozambique form a distinct monophyletic clade

Figure 20. Photographs in life of *Ichnotropis capensis* sensu lato from **A** Cuando River source, Angola (adult male), **B** Cuanavale River source, Angola (adult female), **C** Xai-Xai, Mozambique (adult male), **D** Ngonye Falls, Zambia (adult female), **E** Zambezi Region, Namibia (adult male), **F** Kosi Bay, South Africa (adult male). Photographs: A–D – Werner Conradie; E, F – William R. Branch.

that differs genetically by 4.1–6.4% 16S uncorrected p distance from other *I. capensis* populations. Although this coastal material could be referred to *Ichnotropis macrolepidota* Peters, 1854—originally described from Lourenço Marques (now Maputo), Mozambique—our analysis indicates that the observed genetic differences fall within the expected range of intraspecific variation and likely reflect geographic separation between populations. This was further supported by the lack of clear morphological or geographical separation. As such, we consider *Ichnotropis macrolepidota* a junior synonym of *I. capensis*. Nevertheless, if future studies demonstrate that the eastern coastal populations represent a distinct operational taxonomic unit (OTU), the name *I. macrolepidota* should be resurrected for it.

Synonymy. *Algyra capensis* Smith, 1838: 94; *Tropidosaura Dumerelii* Smith, 1849: appendix 7; *Ichnotropis macrolepidota* Peters, 1854: 617; *Ichnotropis longipes* Boulenger, 1902: 17.

Type. BMNH 1865.5.4.56, collected from the ‘Sandy deserts around Latakoo’ [= Kuruman], Northern Cape, South Africa by Andrew Smith.

General description. A medium-sized lacertid with a narrow and depressed snout. Head scalation strongly striated. Nostril pierced between three nasals; the supranasals are in broad contact behind the rostral; single frontonasal, as broad as long; paired prefrontal scales in broad contact medially; prefrontal separated from the

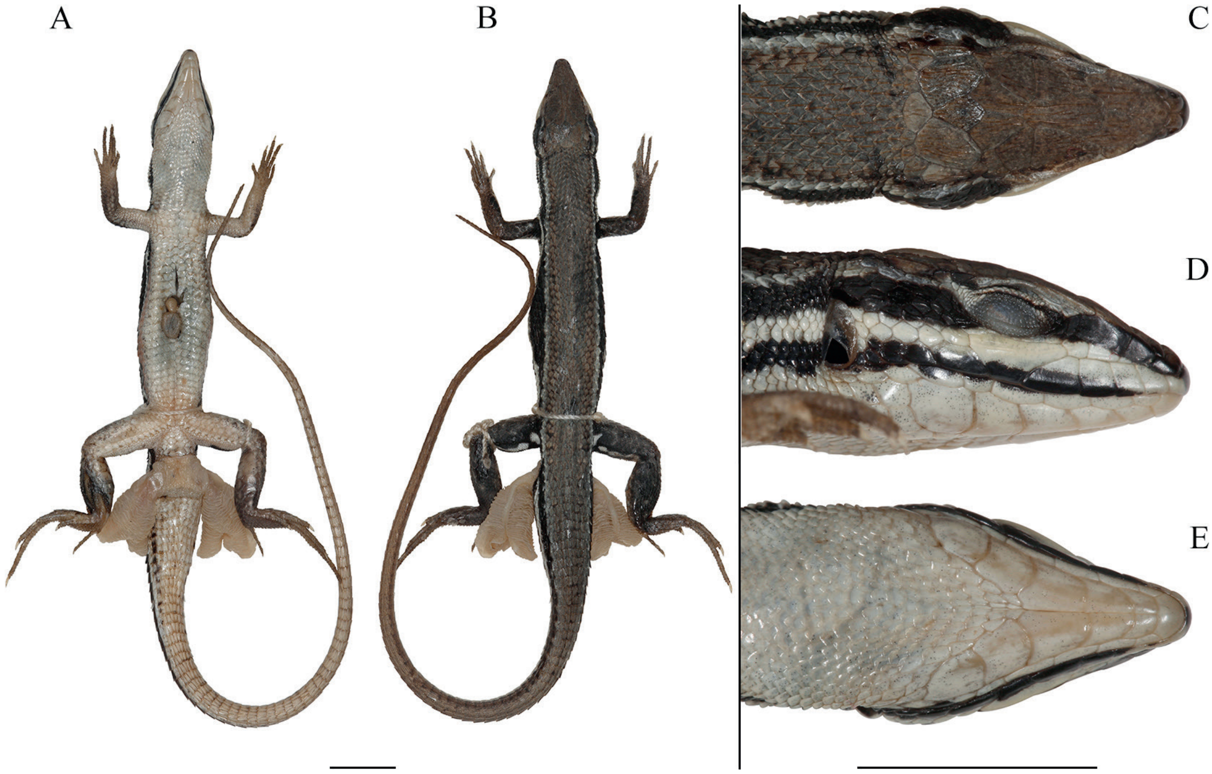

Figure 21. *Ichnotropis capensis* sensu lato (PEM R27396) from middle Quembo River bridge camp, Moxico Province, Angola. Photographs of body in **A** ventral and **B** dorsal views, and head in **C** dorsal, **D** lateral and **E** ventral views. Scale bars represent 10 mm. Photographs: Werner Conradie.

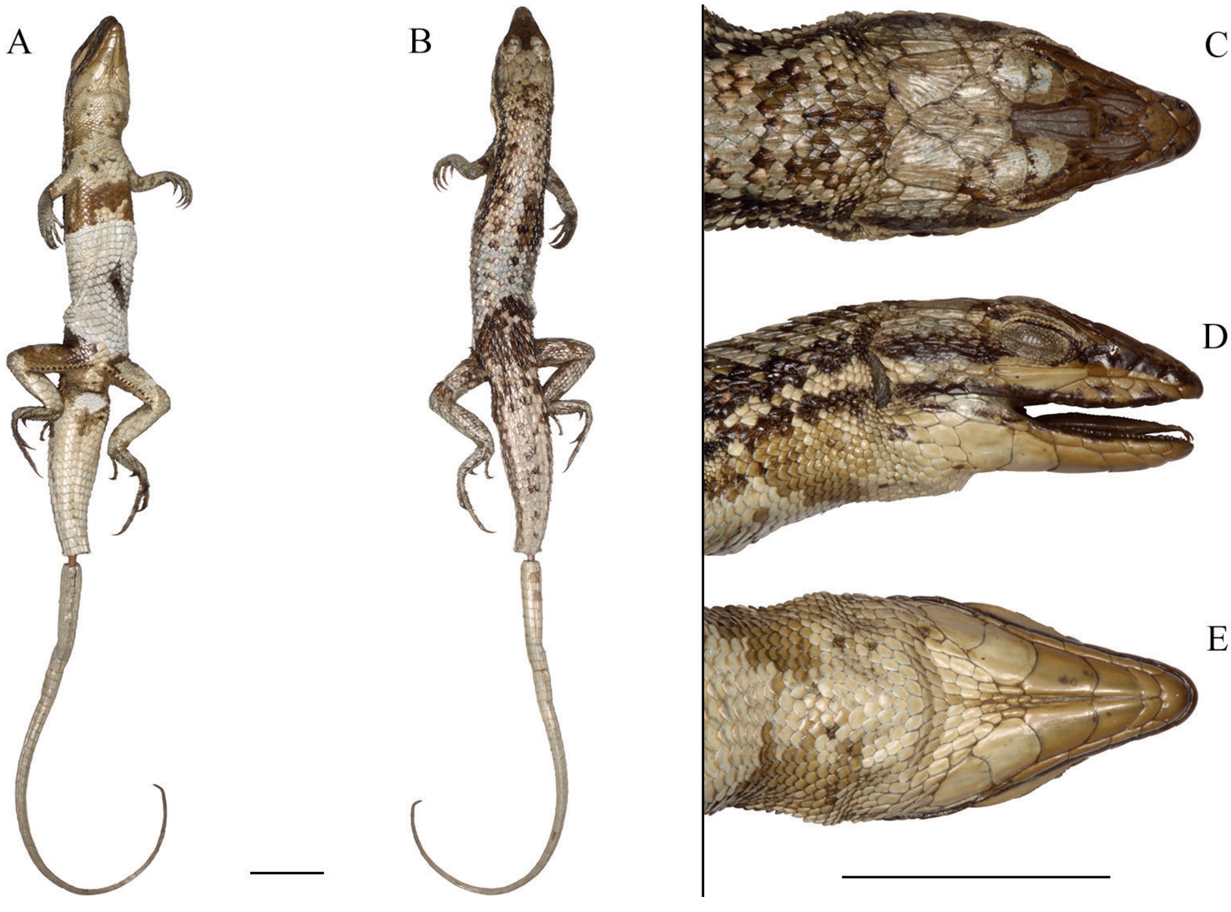

Figure 22. Syntype (ZMB 6123) of *Ichnotropis macrolepidota* from Lourenço Marques [= Maputo], Mozambique. Photographs of body in **A** ventral and **B** dorsal views, and head in **C** dorsal, **D** lateral and **E** ventral views. Scale bars represent 10 mm. Photographs: Frank Tillack.

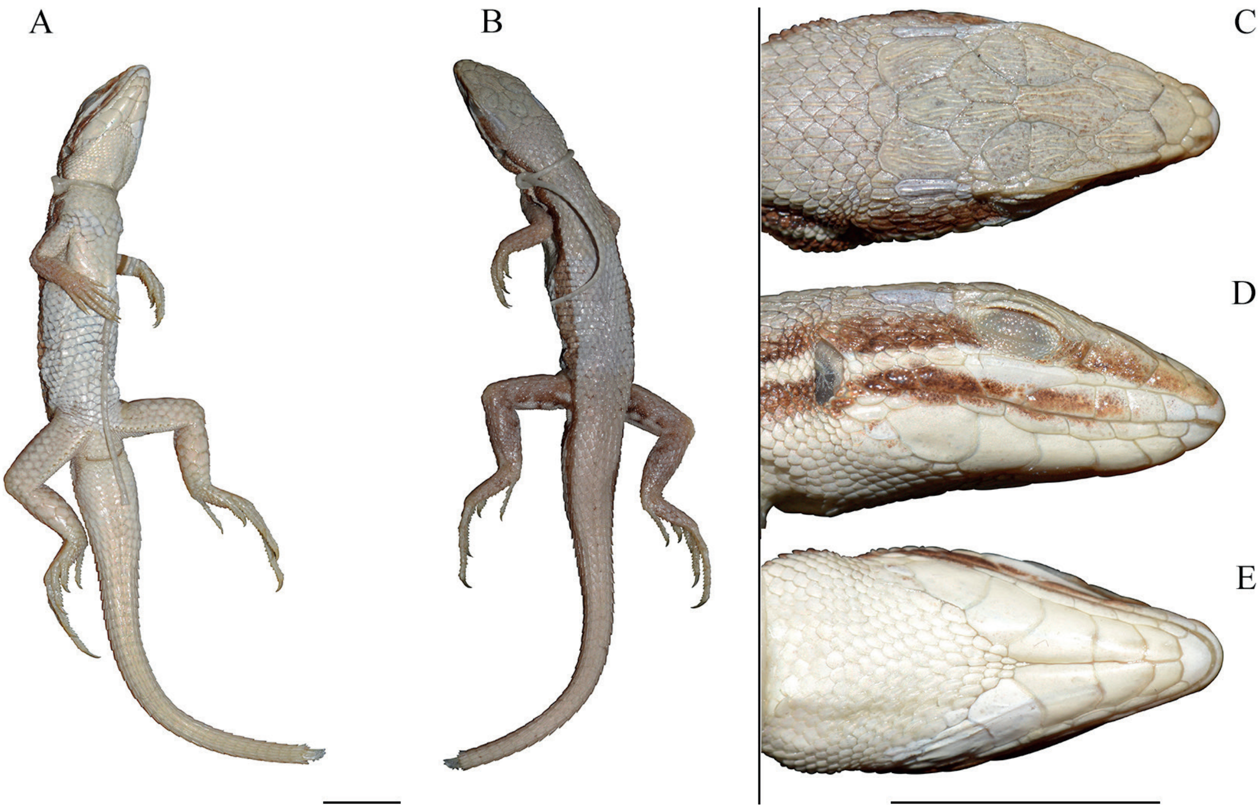

Figure 23. Syntype (BMNH 1946.8.4.23) of *Ichnotropis longipes* from Mazoë, Zimbabwe. Photographs of body in **A** ventral and **B** dorsal views, and head in **C** dorsal, **D** lateral and **E** ventral views. Scale bars represent 10 mm. Photographs: Patrick Campbell.

anterior supraocular (only in contact in 15 out of 245 specimens examined) and separated from supraciliaries by a smaller scale; two large supraoculars, which are separated from the supraciliaries by one (very rarely two) row of small scales (4–9) and preceded by a cluster of 3–10 smaller scales; two loreal scales present, which are separated from the anterior supraocular by 2–3 scales; 1–2 post-supraoculars; subocular in contact with the lip; 3–6 (mostly four) supralabials in front of the subocular; 5–8 (mostly six) infralabials; five chin shields, with the anterior three in broad contact; 3–5 (mostly four) supraciliaries; 25–42 (average: 36.7) midbody scale rows; 8–10 (average: 8.8) longitudinal rows of enlarged ventral plates; 20–31 (average: 25.8) transverse ventral scale rows; 16–26 (average: 21.6) subdigital lamellae under the 4th toe; 6–15 femoral pores per thigh. Size: Adult specimens varied from 40.0–67.8 mm (mean: 54.6 mm) SVL and 69.5–149.0 mm (mean: 110.4 mm) TAIL. Largest female: 65 mm SVL (NMZB-UM 9228 – Umtali, Zimbabwe); largest male: 67.8 mm SVL (BE_RMCA_Vert.R.7785 – Dilolo, DRC). Colouration (Fig. 20): In males, the flanks feature a striking, broad black longitudinal band that originates at the tip of the snout, passes through the eye, and extends posteriorly well beyond the hind limbs, gradually fading towards the tip of the tail. This black band is bordered by two distinct white stripes: The upper stripe begins just behind the eye, while the lower stripe originates at the rostral plate, crosses the tympanum, and runs parallel to the black band along the length of the body. Below the lower white stripe, a vivid reddish-orange stripe is especially prominent on the anterior flanks. A secondary short black line also originates at the snout, runs across the supralabials along the side of the head, and terminates anterior to the insertion of the forelimbs. The main black band on the flank is often scattered with small white spots, particularly towards the posterior end of the body. In breeding males, the white stripes on the head and neck, as well as the gular region, become infused with a bright yellow hue. The dorsal surface is a rich reddish-brown, adorned with scattered dark brown speckling. Females exhibit a more subdued colouration, with an overall grey-brown tone that is lighter on the ventral side. A single, less pronounced dark black stripe originates at the snout, passes through the eye, and continues along the flanks, gradually fading towards the tail. Juveniles and subadults are often grey in colouration with a white dorsolateral stripe. The venter is mostly white, but some specimens exhibit grey colouration with scattered black specks.

Distribution. Widespread, occurring across several countries in southern Africa, including Angola, Namibia, Botswana, Zambia, Zimbabwe, Mozambique, and parts of South Africa and Malawi (Fig. 19). Historical records from north-eastern Angola and DRC assigned to *I. capensis* or *I. overlaeti* need to be re-evaluated in light of this study and might be assignable to either *I. tanganicana*, *I. bivittata* or *I. longicorpa* **sp. nov.** (see new species description below).

Habitat and Natural History. This species prefers arid to mesic savanna habitats. It is a diurnal lizard, actively

Table 6. Summary of morphological data for the *Ichnotropis capensis* group. Measurements are in millimetres (mm). Values are given as a range with mean ± standard deviation in parenthesis. Juveniles were excluded from the measurements, but were included in the scalation data. For abbreviations, see the Materials and Methods section. n = sample size.

Characters	*I. capensis* sensu lato	*I. longicorpa* sp. nov.
	n = 256	n = 12
SVL	40.0–67.8 (54.8 ± 5.11)	62.7–71.2 (66.4 ± 2.37)
TAIL	69.5–149.0 (110.4 ± 17.89)	117–160 (137.5 ± 15.94)
HL	10.1–14.7 (12.7 ± 0.97)	13.1–17.2 (15.1 ± 1.16)
HW	5.6–8.6 (7.2 ± 0.67)	7.8–9.4 (8.7 ± 0.46)
HH	4.5–7.5 (5.9 ± 0.62)	6.1–8.5 (7.4 ± 0.61)
ED	3.9–6.3 (4.5 ± 0.52)	2.4–5.9 (4.4 ± 0.98)
SE	4.0–7.0 (5.2 ± 0.77)	6.0–7.3 (6.9 ± 0.40)
LL	12.5–16.4 (14.2 ± 1.18)	14.4–18.7 (17.8 ± 1.27)
IL	18.5–31.6 (25.5 ± 3.29)	27.4–31.6 (28.7 ± 1.42)
FLL	5.0–8.2 (6.2 ± 0.70)	6.8–8.4 (7.5 ± 0.46)
HLL	7.4–13.2 (10.5 ± 1.25)	10.6–13.5 (12.3 ± 0.96)
TAIL/SVL	1.2–2.7 (2.0 ± 0.28)	1.9–2.4 (2.2 ± 0.22)
HL/SVL	0.2–0.3 (0.2 ± 0.01)	0.2–0.3 (0.2 ± 0.01)
ES/HL	0.4–0.5 (0.5 ± 0.02)	0.4–0.5 (0.4 ± 0.02)
HW/HL	0.2–0.7 (0.6 ± 0.06)	0.5–0.6 (0.6 ± 0.03)
MSR	25–42	34–41
LVSR	8–10	9–10
TVSR	20–31	25–31
SL	3–6 (mostly 4)	4–5 (mostly 4)
IL	5–8 (mostly 6)	6–7 (mostly 6)
SC	3–5	4
LUFT	16–26	19–24
Femoral pores	6–15	10–13

foraging for small invertebrates such as termites, spiders, beetles, and grasshoppers. Females lay up to nine eggs per clutch, typically during the summer months from October to November. The eggs measure approximately 5.5–7.0 mm by 8.5–9.5 mm. The incubation period ranges from 56 to 77 days, with hatchlings emerging between January and March. Females may produce up to two clutches within a single breeding season.

Ichnotropis longicorpa sp. nov.

Long-bodied rough-scaled lizard

https://zoobank.org/2D3A7A69-E837-4542-89C3-D4CC18A2A160

Figures 24, 25; Tables 6, 7

Chresonymy.

Ichnotropis capensis overlaeti – Laurent (1950: 12, in part); *Ichnotropis capensis* – Conradie et al. (2022a: 198, in part); *Ichnotropis* aff. *capensis* – Benito et al. (2025: 893).

Holotype. PEM R23410 (field number WC-4558), adult male, collected from Lungwebungu River camp bridge crossing, (–12.5835°, 18.6660°, 1304 m a.s.l.), Moxico Province, Angola by Werner Conradie and Luke Verburgt on 22 October 2016.

Paratypes. 6 specimens: a) PEM R23409 (field number WC-4557), adult male, same collection details as holotype; b) PEM R23502 (field number WC-4522), and PEM R23531 (field number WC-4560), adult male and female respectively, collected from Sombanana Village (–12.3108°, 18.6239°, 1403 m a.s.l.), Moxico Province, Angola by Werner Conradie and Luke Verburgt on 9 October 2016; c) PEM R23505–7 (field number WC-4543, WC-4562 and WC-4563, respectively), adult males, collected from Lake Tchanssengwe (–12.4102°, 18.6348°, 1414 m a.s.l.), Moxico Province, Angola by Werner Conradie and Luke Verburgt on 21 October 2016.

Additional material. 9 specimens: a) PEM R19903 (field number TB 44) and PEM R19905 (field number TB 46), adult female and male respectively, collected from Camp Chiri, Miombo forest/camp (–9.3969°, 20.4319°, 1004 m a.s.l.), Lunda-Sul Province, Angola by Tom Branch on 24 October 2008; b) PEM R23977 (field number WC-6267), juvenile, collected from near Lungwebungu Trap 2 (–12.5820°, 18.6656°, 1208 m a.s.l.), Moxico Province, Angola by Werner Conradie and Alex Rebelo on 22 April 2018; c) PEM R23986 (field number WC-6266), juvenile, collected from Lungwebungu Trap 1 (–12.5801°, 18.6674°, 1298 m a.s.l.), Moxico Province, Angola by Werner Conradie and Alex Rebelo on 22 April 2018; d) PEM R23996–7 (field numbers WC-6291 and WC-6292, respectively), juveniles, collected from Lake Tchanssengwe (–12.4140°, 18.6442°, 1393 m a.s.l.), Moxico Prov-

Figure 24. Photographs in life of *Ichnotropis longicorpa* **sp. nov.** Photographs of **A** adult male (PEM R23410) from Lungwebungu River camp bridge crossing, Angola, and **B** adult female (PEM R23531) from Sombanana village, Angola. Photographs: Werner Conradie.

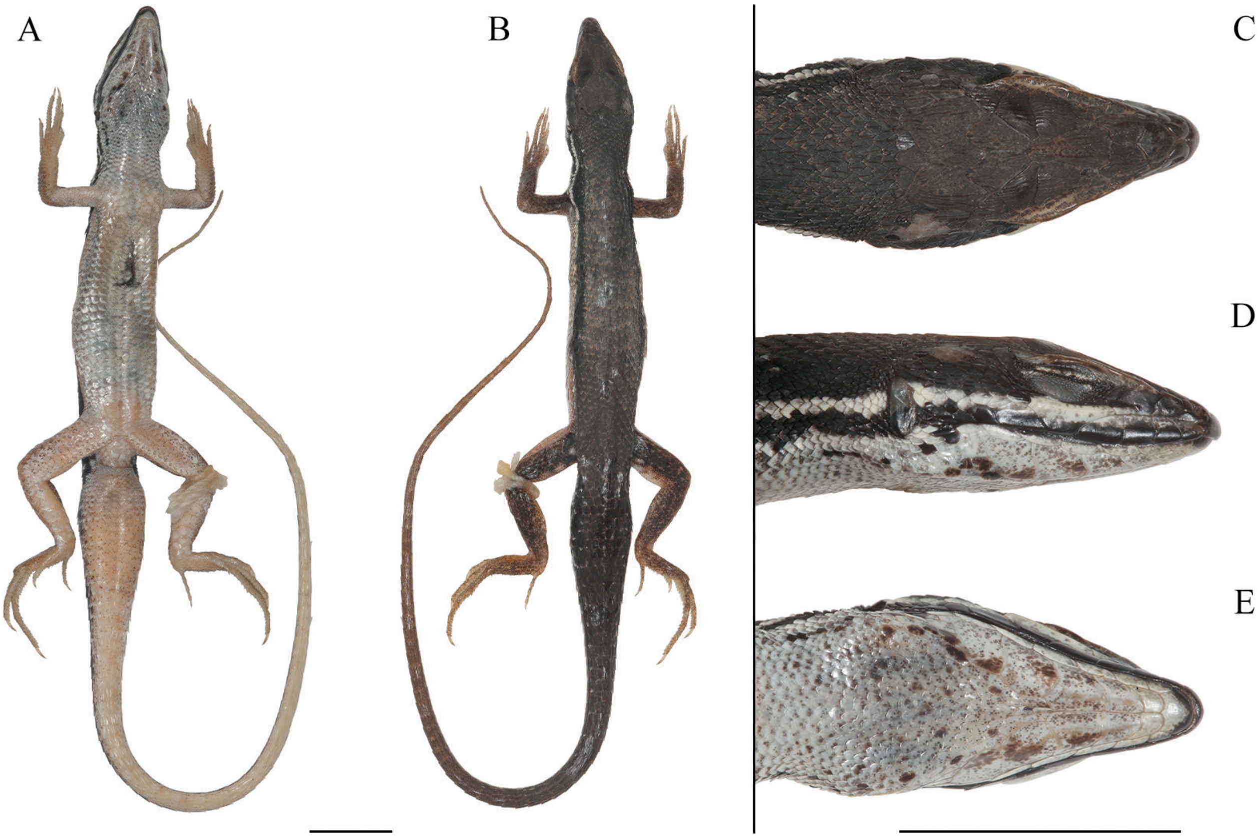

Figure 25. Holotype (PEM R23410) of *Ichnotropis longicorpa* **sp. nov.** from Lungwebungu River camp bridge crossing, Moxico Province, Angola. Photographs of body in **A** ventral and **B** dorsal views, and head in **C** dorsal, **D** lateral and **E** ventral views. Scale bars represent 10 mm. Photographs: Werner Conradie.

ince, Angola by Werner Conradie and Alex Rebelo on 23 April 2018; e) BE_RMCA_Vert.R.17490, 17492 (adult males) and BE_RMCA_Vert.R.17491 (adult female), collected from the Dundo region, Lunda-Norte Province, Angola by Barros Machado on 14 December 1947.

Etymology. The species name *longicorpa* is the feminine form of the Latin adjective longicorpus, derived from longus (long) and corpus (body), referring to this species' elongate body.

Diagnosis. Assigned to *Ichnotropis* due to the absence of a well-defined collar, digits not serrated or fringed, subdigital lamellae keeled, and subocular bordering the lip. A slender *Ichnotropis* with a single frontonasal; subocular bordering the lip; a single anterior loreal; feebly developed head shield striations, prefrontals well separated from the anterior supraocular; and supraciliaries separated from the supraoculars by a series of smaller scales.

The new species can be distinguished from other *Ichnotropis* species based on a combination of the following

Table 7. Measurements (in mm) and scale counts for the type series of *Ichnotropis longicorpa* **sp. nov.** Scale counts are given as Right/Left. For abbreviations, see the Materials and Methods section. t = truncated.

Catalogue No.	**PEM R23410**	**PEM R23409**	**PEM R23502**	**PEM R23505**	**PEM R23506**	**PEM R23507**	**PEM R23531**
Type Status	Holotype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype
Sex	Male	Male	Male	Male	Male	Male	Female
SVL	67.7	63.0	64.3	63.9	65.4	66.2	63.1
TAIL	160.0	146.0	149.0	92t	127.0	148.0	117.0
HL	15.6	15.8	15.6	14.7	15.3	15.8	13.1
HW	8.5	8.6	9.4	8.9	8.9	9.2	7.8
HH	7.1	7.3	7.5	7.3	7.1	7.5	6.1
ED	3.1	3.6	3.6	2.4	2.8	3.8	3.0
SE	6.6	6.6	6.7	6.7	6.6	7.2	6.1
LL	17.6	18.0	18.1	16.8	17.3	18.7	15.2
IL	30.8	31.4	29.0	28.9	31.2	29.5	31.6
FL L	7.4	7.8	8.2	7.0	7.5	7.3	6.8
HLL	13.5	13.1	12.6	13.3	13.5	13.2	11.5
TAIL/SVL	2.4	2.3	2.3		1.9	2.2	1.9
HL/SVL	0.2	0.3	0.2	0.2	0.2	0.2	0.2
ES/HL	0.4	0.4	0.4	0.5	0.4	0.5	0.5
HW/HL	0.5	0.5	0.6	0.6	0.6	0.6	0.6
MSR	39	37	38	40	37	40	37
LVSR	9	9	9	9	9	10	9
TVSR	30	28	29	31	28	30	28
SL	4/4	4/4	4/4	4/5	4/4	4/4	4/5
IL	6/6	7/6	6/6	7/7	6/6	6/6	6/6
SC	4/4	4/4	4/4	4/4	4/4	4/4	4/4
LUFT	22	20	21	22	24	22	22
Femoral pores	12/10	10/10	12/12	12/11	13/12	11/10	10/10

characteristics: Prefrontals well separated from the anterior supraocular (versus mostly in contact in *I. bivittata*, *I. microlepidota* and *I. tanganicana*); lower number (34–41) of midbody scales rows (44–47 in *I. grandiceps* and 43–48 in *I. robusta* **sp. nov.**); small, depressed head and pointed snout (versus large robust head and rounded snout in *I. grandiceps* and *I. robusta* **sp. nov.**); four supralabials anterior to the subocular (versus mostly five in *I. grandiceps* and *I. robusta* **sp. nov.**); distinctive occipital scale usually extending posteriorly well beyond the level of the parietals (versus large trapeziform occipital wedged between the parietals, not protruding past parietals in *I. grandiceps* and *I. robusta* **sp. nov.**).

The new species resembles *I. capensis* sensu lato in its narrow, pointed snout, with the prefrontals well separated from the anterior subocular. It differs in that the new species exhibits black spots on the chin shields and gular scales (versus immaculate in *I. capensis* sensu lato) and the absence of a clear upper white dorsolateral stripe that separates the dark black lateral band from the dorsal brown vertebral band (versus present in most *I. capensis* sensu lato).

In the phylogenetic analysis, the uncorrected p distances show that the new species differs by >5.9% for 16S and >12.3% for ND4 sequence divergence from other *Ichnotropis* species (Table 2).

Holotype description (Fig. 25). Adult male measuring 67.7 mm SVL and 160 mm TAIL (2.4 × SVL). Body moderately depressed; head distinctly depressed, almost twice as long as broad (HL 15.8/HW 8.5 mm), its length equivalent to 23.3% of SVL, expanded in the temporal region and very distinct from the neck. Adpressed hind limb just reaching the anterior edge of ear opening. The foot length is longer than the head length (FL 19.2/HL 15.8 mm).

Dorsal head shields very feebly striated and keeled; nostril pierced between three nasals, the supranasals in broad contact behind the rostral; frontonasal as long as broad (2.2 × 2.2 mm); prefrontals much longer than broad (2.7 × 1.5 mm), in broad contact medially, not reaching the anterior supraoculars (separated by a small keeled scale), in contact with the anterior and posterior loreal; frontal more than twice as long as its maximum width between the posterior tips of the prefrontals (4.6 × 2.1 mm), rounded anteriorly and strongly narrowed posteriorly; paired frontoparietals longer than broad (3.0 × 2.0 mm); parietals longer than broad (3.8 × 2.6 mm), extending posteriorly, widely separated by a large interparietal and occipital, the posterior margin extending past the posterior borders of the parietals; three keeled temporal scales bordering the parietal, the first one longest, followed by the second and third (smallest); two enlarged supraoculars, the anterior supraocular slightly longer than the posterior one and longer than its distance from the posterior loreal (2.4 mm vs. 1.5 mm), in contact with the posterior half of the frontal, separated from the posterior loreal by two smaller keeled scales; the anterior supraoculars are preceded by a cluster of five smaller keeled scales, the posterior supraocular is followed by three smaller keeled post-supraocular scales, the two supraoculars are separated from the supraciliaries by a single row of nine small keeled scales. Five supraciliaries, the first two much longer than the others and forming a long oblique suture. Lower nasal in contact with the rostral, first supralabial, and anterior loreal (narrow contact on left side); postnasal small, in contact with the other two nasals, anterior loreal, and frontonasal. Two loreals, the posterior one much larger and divided below; four supralabials anterior to the subocular, whose lower border on the lip is much shorter (3×) than the upper border; three supralabials posterior to subocular; temporal scales strongly keeled; a narrow tympanic shield on the upper anterior corner of the vertically elongate ear opening. Lower eyelid scaly with a median series (4–5) of vertically elongate scales. Six infralabials; five pairs of large chin shields, the first three pairs in median contact; gular scales imbricate; no collar.

Dorsal scales rhombic, strongly keeled and imbricate; laterals smaller and feebly keeled, passing gradually into the smooth, rounded ventral plates, which are broader than long; 39 scales around the middle of the body; ventral plates in nine longitudinal and 30 transverse rows between the fore- and hind limbs; preanal scales irregular; scales on upper surfaces of limbs rhombic, strongly keeled, and imbricate; 12/10 femoral pores on each side; subdigital lamellae pluricarinate and spinulose, 22 under the 4th toe; caudal scales strongly keeled above and below, except those just posterior to the vent, which are smooth.

Colouration. (In life, breeding colouration; Fig. 24A): The dorsum varies from grey on the head and nape to reddish-brown on the dorsum and grey on the tail. The side of the body has a dark black band that originates on the snout and run posteriorly to the tail, where it disappears at the tip. Below this black band is a white stripe that originates on the snout, runs below the eye to the front limb, is less distinct between the fore- and hind limb, and then fades onto the tail. Below this white line is another black stripe that originates on the snout, running along the edges of the supra- and infralabials to the front limbs. The white stripes on the sides of the head and the gular region are pale yellow. Below the black band and white flank stripe (that appears as scattered white and grey spots in places) is an orange band. Limbs are brick red and grey. Chin shields and gular scales have scattered black blotches of varying sizes. The venter is white with scattered black specks. Colouration (in preservative; Fig. 25): Above pale grey-brown; a well-defined broad (covering 3–4 scales at midbody) black dorsolateral band extends from the tip of the snout to the groin; below this black dorsolateral band is a narrow white band (covering one scale at midbody) which extends from the tip of the snout to just posterior to the front limb, fading towards the groin and tail base. Below this white band is another narrow black band extending from the mental, along the edge of the jaw (edge of supra- and infralabials) to just posterior to the forelimb insertion. Flanks bear a light brown band (two scales wide); gular and chin shields with scattered black spots or blotches; limbs dorsally brown and ventrally white; 2–3 white spots on the anterior surfaces of the legs; venter white with scattered black specks.

Paratype and additional material variation. The paratypes are in agreement with the holotype in scalation, with only minor variation: Prefrontal always separate from the anterior supraocular by one scale (except PEM R19905 on right side); frontonasal always separate from the 1st supraciliaries (except in PEM R23409 and PEM R23506); two (rarely three) scales separating anterior supraocular from the posterior loreal; cluster of 3–9 scales in front of the anterior supraocular; single row of 6–9 scales separating the supraoculars from the supraciliaries; 1–4 post-supraoculars; four supraciliaries; 4–5 supralabials; 6–7 infralabials; five chin shields, with first three in contact (PEM R23505 has six chin shields, with the first four in contact on the left side); 9–10 transverse ventral plates; 25–31 longitudinal ventral plates; 34–41 midbody scale rows; 19–24 subdigital lamellae under the 4th toe; 10–13 femoral pores on each thigh. PEM R23409 exhibits some aberrant head scalation in that the anterior loreal seems to be divided, forming a supraloreal that separates the anterior loreal from the frontonasal and the parietal, and the posterior loreal is divided into two scales. Size: Adult specimens varied from 62.7–71.2 mm (mean: 65.3 mm) SVL and 117.0–160.0 mm (mean: 141.2 mm) TAIL. Largest female: 65.1 mm SVL (PEM R19905 – Camp Chiri, Angola); largest male: 71.2 mm SVL (BE_RMCA_Vert.R.17492 – Dundo, Angola). Colouration of all males are in agreement with the holotype. The paratype female (PEM R23531; Fig. 24B) is duller in colouration, almost uniformly reddish-brown dorsally and grey laterally, with no white stripes or black bands.

Distribution. Only recorded from the headwaters of the Lungwebungu and Cuando Rivers in central Angola, northwards to the DRC border (Fig. 19). Some specimens from Mabwe River, Upemba National Park, DRC (IRSNB 7895, 7897, 7907–9, 78728), exhibit the same distinct dark brown to black gular markings and might be assigned to this species. If confirmed, this new species could be more widely distributed than currently thought.

Habitat and natural history. This species was not found to be sympatric with any other *Ichnotropis* species, but it occurs in close geographical proximity to *I. capensis* sensu lato and *I. robusta* **sp. nov.** This species is associated with wet Miombo woodland.

Key to the genus *Ichnotropis* Peters, 1854

1a Snout depressed and pointed, prefrontal separated from anterior supraocular by one or two smaller keeled scales... **2**
1b Snout robust and rounded, prefrontal mostly in contact with anterior supraocular .... **5 (*I. bivittata* group)**
2a 43–47 midbody scale rows, body robust, head broad, adult SVL > 70 mm .... **3 (*I. grandiceps* group)**
2b 25–42 midbody scale rows, body slender, head narrow, adult SVL < 65 mm .... **(*I. capensis* group)**
3a Confined to the drier Zambezian Baikiaea woodlands or Combretum-Vachellia bushveld in western Zambia and the Zambezi Region of Namibia and adjacent Botswana; occurs below 1000 m a.s.l .... ***I. grandiceps***
3b Confined to the Angolan Plateau, which consists of moister Angolan Miombo woodland; occurs above 1300 m a.s.l. .... ***I. robusta* sp. nov.**
4a Long, slender body and head; dark black spots/blotches on chin shields and gular scales, no clear upper white dorsolateral line separating dorsolateral black band from dorsal brown vertebral band .... ***I. longicorpa* sp. nov.**
4b Short body and head; no dark black spots/blotches on chin shields or gular scales, clear white upper dorsolateral line separating black dorsolateral band from dorsal brown vertebral band .... ***I. capensis* sensu lato**
5a ≥ 42 (42–50) midbody scale rows, known only from Mt Moco, Angola... ***I. microlepidota***
5b ≤ 42 (28–42) midbody scale rows **6**
6a Presence of dorsolateral blue or yellow spots in life...**7**
6b No dorsolateral blue or yellow spots, only known from north-eastern DRC..***I. chapini***
7a Prefrontals mostly separated from the anterior supraocular, which is often in contact with the 1st supraciliary; evenly spaced blue dorsolateral spots; occurs in southern DRC, Zambia, Malawi and Tanzania................. ***I. tanganicana***
7b Prefrontal mostly in contact with anterior supraocular, which is always in contact with the 1st supraciliary; closely spaced yellow spots above arm; occurs in Angola, eastern DRC, Republic of the Congo and Gabon.......***I. bivittata***

Discussion

Although *Ichnotropis* species are locally abundant and widely distributed across sub-Saharan Africa, excluding West Africa, the genus remains among the most taxonomically neglected of African lacertids. This historical oversight is likely driven by a combination of strong seasonal activity patterns, which limit detectability outside of peak reproductive periods (Broadley 1967a, 1974, 1979; Jacobsen 1987; this study), and a legacy of taxonomic confusion dating back over a century (Boulenger 1921; Laurent 1952, 1964; van den Berg 2017; Benito et al. 2025). As a result, specimen collections have remained sparse in many regions, and the group's true species richness has long been underestimated.

Through expanded geographic sampling, covering much of the known ranges of *I. bivittata* and *I. capensis*, and the generation of the first genetic data for *I. tanganicana* and *I. grandiceps*, we provided the most comprehensive and geographically inclusive phylogenetic framework for *Ichnotropis* species to date. Species delimitation analyses, combined with a substantially enhanced morphological dataset, support the validity of most currently recognised species (with the exception that we could not validate the phylogenetic status of *I. chapini*) and justify the formal description of two new Angolan endemics: *Ichnotropis robusta* **sp. nov.** and *I. longicorpa* **sp. nov.** These findings underscore the continued importance of integrating molecular and morphological approaches in taxonomic revisions of morphologically conservative lineages.

Conversely, our phylogenetic framework also facilitated the reassessment of several taxonomically ambiguous species and subspecies, many of which had not previously been evaluated using phylogenetic analyses. For instance, although *I. b. pallida* exhibits notable genetic divergence from other *I. bivittata* populations, we conservatively synonymise the subspecies with the nominal form until further data become available. Furthermore, based on our findings, we recommend retaining *I. longipes* and *I. macrolepidota* as synonyms of *I. capensis* sensu lato, due to the absence of consistent diagnostic morphological differences and inclusion of topotypic material in our phylogenetic analyses. Additionally, we propose synonymising *I. c. nigrescens* with *I. bivittata*, and treating *I. overlaeti* as a junior synonym of *I. tanganicana*, based on morphological congruence. Newly collected *Ichnotropis* material from west of the Kabobo Plateau and Upemba National Park in DRC allowed us to reassess the poorly known *I. tanganicana*, previously known only from its type specimen and a vague type locality (Boulenger 1917; Meiri et al. 2018). Our data confirm the species' taxonomic validity, help revise the species description and suggest a broader geographic distribution than previously recognised. As a result, most historical records of *I. bivittata* from East Africa are here reassigned to *I. tanganicana*.

While there was a more comprehensive sampling for *I. capensis* relative to *I. bivittata*, the limited material available for *I. bivittata* (n = 4, including topotypic *I. b. pallida*) exhibited moderate genetic divergence, and species delimitation analyses consistently identified these lineages as distinct. Given the broad unsampled distribution of *I. bivittata*, coupled with the high genetic diversity observed within the available dataset, increased geographic sampling, especially within topographically complex Angola, DRC, Republic of the Congo and Gabon, may reveal additional cryptic diversity. Moreover, our species delimitation analyses recovered multiple putative candidate species within the *I. capensis* sensu lato complex. It must be noted that some of these lineages may correspond to previously described species, such as *I. longipes*, but resolving this will require targeted sampling from type localities or museomics (i.e., historical DNA [hDNA]) to assess potential synonymy or revalidation (McGuire et al. 2018; Raxworthy and Smith 2021; Zacho et al. 2021; Lalueza-Fox 2022; Letsch et al. 2025). Although we were unable to assess the phylogenetic placement of *I. chapini* due to the absence of genetic data, we recommend its provisional assignment to the *I. bivittata* group based on similarities in head morphology and scalation. Until further material becomes available for molecular analysis, we propose retaining *I. chapini* as a valid species.

The species delimitation analyses confirmed the species status of both newly described and previously recognised taxa, less conservative methods also revealed potential cryptic diversity within *I. tanganicana*, *I. bivittata*, *I. longicorpa* **sp. nov.**, and *I. capensis* sensu lato. We caution that single-locus approaches can overestimate species boundaries by conflating intraspecific variation with interspecific divergence, especially under conditions of incomplete lineage sorting or limited geographic sampling (e.g., Carstens et al. 2013; Sukumaran and Knowles 2017). To mitigate this risk, we employed five independent species delimitation methods, enabling cross-validation and allowing us to conservatively interpret only those lineages supported by multiple lines of evidence (morphology, colouration, ecology) as candidate species (e.g., Fujisawa and Barraclough 2013; Zhang et al. 2013; Kapli et al. 2016).

Morphological analyses broadly support the three major clades recovered by the phylogenetic analyses, with diagnostic differences in head shape, scalation, and breeding colouration. These traits are largely consistent across multiple populations, making them valuable for species identification in the field. The *I. capensis*, *I. grandiceps* and *I. bivittata* groups exhibit distinctive morphological characteristics that aid in distinguishing them from each another, even in the absence of genetic data. However, *I. tanganicana* is an exception: It forms a deeply divergent mitochondrial lineage that is sister to all other *Ichnotropis* species in the phylogeny; nevertheless, it remains morphologically similar to all members of the *I. bivittata* group, being thus included as part of this group. The recognition of *I. tanganicana* as a distinct species is supported primarily by molecular divergence, unique geographic distribution, and its distinctive colouration – most notably the presence of evenly spaced blue lateral spots – underscoring the importance of integrating genetic and phenotypic data in resolving cryptic diversity within morphologically conservative lineages.

Biogeographically, *Ichnotropis* shows its highest diversity across the northern and western parts of central and southern Africa, with the Kalahari Basin emerging as a hotspot for species richness for this group. In contrast, eastern Africa is represented by only a single species (i.e., *I. tanganicana*), while South Africa harbours just one taxon from the *I. capensis* complex. These patterns are shaped by regional habitat heterogeneity, historical barriers to gene flow, and likely also by limited historical sampling in large swathes of suitable habitat (Greenbaum et al. 2018).

The description of two new *Ichnotropis* species from Angola contributes to the wave of reptile species discoveries in the region over the past two decades (Conradie et al. 2012, 2020a, 2020b, 2020c; Stanley et al. 2016; Branch et al. 2019, 2021; Marques et al. 2019a, 2019b, 2020, 2022a, 2022b, 2023a, 2023b, 2024; Ceríaco et al. 2020b, 2020c, 2020d, 2024; Hallermann et al. 2020; Lobón-Rovira et al. 2021, 2022, 2025a, 2025b; Parrinha et al. 2021, 2025a, 2025b, 2025c; Wagner et al. 2021; Bates et al. 2023; Röll et al. 2024). Since 2012, Angola's known lacertid diversity has nearly doubled, from 10 to 18 species, mirroring growth in other reptile groups such as skinks and geckos (Conradie 2024). Given that large portions of Angola remain poorly surveyed, further species discoveries are likely to occur within the territory.

The two new *Ichnotropis* species described here were discovered through intensive fieldwork in central and southeastern Angola, regions long underexplored due to decades of civil conflict and the difficult access to these areas (Conradie et al. 2021). Recent herpetological surveys in these areas have yielded numerous new species, expanded faunal records, and have provided comprehensive species inventories (e.g., Conradie et al. 2016, 2020a, 2020b, 2021, 2022a, 2022b, 2023; Nielsen et al. 2020), underscoring the importance of targeted fieldwork and systematic biodiversity assessments in historically inaccessible areas (Tolley et al. 2016). These two newly described *Ichnotropis* species (*I. robusta* **sp. nov.** and *I. longicorpa* **sp. nov.**) are currently considered Angolan endemics, though they may also occur in adjacent regions of DRC and Zambia. Finally, the Angolan highlands and adjacent Miombo woodlands appear particularly significant, harbouring several endemic or near-endemic taxa (Bauer et al. 2023; Becker et al. 2023). These findings align with previous research identifying this region as a hotspot of reptile endemism and support calls for enhanced conservation attention.

Conclusion

This study presents the most comprehensive phylogenetic and taxonomic revision of the genus *Ichnotropis* to date. By integrating mitochondrial and nuclear molecular data, detailed morphological assessments, and broad geographic sampling, we reveal that *Ichnotropis* lizards harbour more diversity than previously recognised. Our findings support the description of two new taxa, indicate multiple potential cryptic species and clarifies the taxonomic status of several historically ambiguous names. The recovered phylogenetic structure and strong geographic partitioning underscore the evolutionary significance of central and southern Africa, particularly the Angolan highlands, as a centre of diversification and endemism for reptiles. This work not only stabilizes the taxonomy of *Ichnotropis*, but also lays a robust foundation for future evolutionary, ecological and conservation studies for this group across its range.

Acknowledgements

This work was made possible through the collaboration and support of numerous individuals and institutions. We thank the Ministry of Environment of the Republic of Angola (MINAMB), particularly Dr. Miguel Xavier, Director of the Instituto Nacional de Biodiversidade e Conservação (INBC), for their institutional collaboration. Material was collected and exported under the following permits issued by MINAMB: 31/GGPCC/2016 and 151/INBAC/MINAMB/2019. We also acknowledge the exceptional logistical assistance provided by Fundação Kissama, especially Vlady Russo.

WC thanks the Wild Bird Trust, which administers the National Geographic Okavango Wilderness Project (2015–2019 National Geographic Society grant), and Chris Brooks, who organized the SAREP Aquatic Biodiversity Surveys of the upper Angola catchments of the Cubango-Okavango River Basin (May 2012) and the lower Cuito and Cuando River Basins (April 2013). We are also grateful to the Natural History Museum of Maputo, which endorsed and provided permits (315/MHN/E.27/2014) to carry out part of this work in Mozambique.

This work received financial and logistical support from several institutions: The National Geographic Society Committee for Research and Exploration (CRE 9281-13); the South African National Biodiversity Institute; the National Research Foundation of South Africa (Grant #92776) for the 2014 Mozambique survey; and Khangela Safaris for camp logistics in 2014. CK thanks and acknowledges Upemba National Park, Forgotten Parks Foundation (DPF), Institut Congolais pour la Conservation de la Nature (ICCN), University of Lubumbashi, and Hankuzi Explorations for their assistance with facilitating the collection of valuable Congolese samples for this study.

JLR is currently supported by Associação BIOPOLIS CIBIO Base FUI 2020–2023 (UIDB1 50027 i2020). This work was also partially supported by the Synthesis+ BE-TAF Project 2022 Grant obtained by JLR. We thank the CTM staff at CIBIO – especially Susana Lopes, Sofia Mourão, and Patrícia Ribeiro – for their dedicated laboratory support.

EG acknowledges Ana Betancourt of the Border Biomedical Research Center (BBRC) Genomics Analysis Core Facility for technical services and facilities. This work was supported by Grant 5U54MD007592 from the National Institute on Minority Health and Health Disparities (NIMHD), part of the US National Institutes of Health (NIH).

We are grateful to Garin Cael (RMCA) and Olivier Pauwels (RBINS) for providing access to relevant material from their herpetological collections. Photographs of key museum specimens were generously provided by: Eugen Behrens (Museo delle Scienze, MUSE), Lauren Vonnahme (American Museum of Natural History, AMNH), Patrick Campbell (Natural History Museum London, NHML), Joshua Mata (The Field Museum of Natural History, FMNH), Matthew Gage (Museum of Comparative Zoology, Harvard University, MCZ), and Frank Tillack (Museum für Naturkunde Berlin, ZMB). Sebastian Kirchhof (Natural History Museum Abu Dhabi, NHMAD) kindly provided additional sequences.

We also thank the following individuals for their assistance in the field and sample collection: Ninda Baptista, Gabriella Bittencourt-Silva, Thomas Branch, William R. Branch, Hanlie Engelbrecht, James Harvey, Timóteo Júlio, Michele Menegon, Götz Neef, and Alex Rebelo. Reuben van Breda extends special thanks to Ed Netherlands, Ash Bullard, Haley Dutton, Bernie Jordaan, Bertha Buiswalelo, Francois Becker, and Louis du Preez for their help in the field, as well as Piet Beytell and Francois Jacobs and their team for facilitating fieldwork in Namibia. Specimens in Namibia were collected under the National Commission of Research, Science and Technology permit AN20191118. We are grateful to the late Don Broadley and Bill Branch for allowing us to incorporate their unpublished data on the genus.

References

Aljanabi SM, Martinez I (1997) Universal and rapid salt-extraction of high quality genomic DNA for PCR-based techniques. Nucleic Acids Research 25: 4692–4693. https://doi.org/10.1093/nar/25.22.4692

Ayres DL, Darling A, Zwickl DJ, Beerli P, Holder MT, Lewis PO, Huelsenbeck JP, Ronquist F, Swofford DL, Cummings MP, Rambaut A, Suchard MA (2019) BEAGLE: An application programming interface and high-performance computing library for statistical phylogenetics. Systematic Biology 61: 170–173. https://doi.org/10.1093/sysbio/syr100

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: 12–28. https://doi.org/10.1080/21564574.2020.1778108

Bates MF, Lobón-Rovira J, Stanley EL, Branch WR, Vaz Pinto P (2023) A new species of blue-eyed *Cordylus* Laurenti, 1768 from the central-western 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 F (2023) Highland reptiles of Angola and Namibia. Namibian Journal of Environment 8: 259–276.

Bauer AM, Childers JL, Broeckhoven C, Mouton PLN (2019) A new *Nucras* Gray, 1838 (Squamata: Lacertidae) from the Strandveld of the Western Cape, South Africa. Zootaxa 4560: 149–163. https://doi.org/10.11646/zootaxa.4560.1.8

Bauer AM, Childers JL, Burger M (2025) The *Nucras* (Squamata: Lacertidae) of the eastern Zambezi River Basin, with the description of a new species from Zambia. Zootaxa 5632: 480–500. https://doi.org/10.11646/zootaxa.5632.3.3

Bauer AM, Murdoch M, Childers JL (2020) A reevaluation of records of sandveld lizards, *Nucras* Gray, 1838 (Squamata: Lacertidae), from northern Namibia. Amphibian and Reptile Conservation 14 (Taxonomy Section): 231–250 (e271).

Becker FS, Baptista NL, Vaz Pinto P, Ernst R, Conradie W (2023) The amphibians of the highlands and escarpments of Angola and Namibia. Namibian Journal of Environment 8: 245–257.

Benito M, Conradie W, Vaz Pinto P, Lobón-Rovira J (2025) A needle in a haystack: Rediscovery and revised description of *Ichnotropis microlepidota* Marx, 1956, from the central highlands of Angola. Zoosystematics and Evolution 101: 887–906. https://doi.org/10.3897/zse.101.136290

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: 37–56.

Bocage JVB (1895) Herpétologie d'Angola et du Congo. Imprimerie Nationale, Lisbon, 203 pp.

Boulenger GA (1887) Catalogue of the Lizards in the British Museum (Natural History). Vol. III. Lacertidae. British Museum, London, I–XII, 118 pp.

Boulenger GA (1917) Descriptions of new lizards of the family Lacertidae. Annals of the Annals and Magazine of Natural History 19: 277–279.

Boulenger GA (1921) Monograph of the Lacertidae. Vol. 2. British Museum, London, 451 pp.

Branch WR (1998) Field Guide to Snakes and Other Reptiles of Southern Africa. 2nd Edition. Struik Publishers, Cape Town, 399 pp.

Branch WR, Conradie W, Vaz Pinto P, Tolley KA (2019) Another Angolan Namib endemic species: A new *Nucras* Gray, 1838 (Squamata: Lacertidae) from south-western Angola. Amphibian and Reptile Conservation 13 (Special Section): 82–95 (e199).

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: 55–82. https://doi.org/10.3897/zse.97.57202

Broadley DG (1967a) The life cycles of two sympatric species of *Ichnotropis* (Sauria: Lacertidae). Zoologica Africana 3: 1–2.

Broadley DG (1967b) A new species of *Ichnotropis* (Sauria: Lacertidae) from the Botswana Caprivi Border. Arnoldia 3: 1–5.

Broadley DG (1974) Field studies on 'annual lizards' of the genus *Ichnotropis*. The Rhodesia Science News 8: 309

Broadley DG (1979) A field study of two sympatric "annual" lizards (genus *Ichnotropis*) in Rhodesia. South African Journal of Zoology 14: 133–138.

Carstens BC, Pelletier TA, Reid NM, Satler JD (2013) How to fail at species delimitation. Molecular Ecology 22: 4369–4383.

Ceríaco LMP, 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: 1–71. https://doi.org/10.5962/bhl.part.11464

Ceríaco LMP, Agarwal I, Marques MP, Bauer AM (2020b) 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: 92–106. https://doi.org/10.11646/zootaxa.4861.1.6

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

Ceríaco LMP, Marques MP, André I, Afonso E, Blackburn DC, Bauer AM (2020d) Illustrated type catalogue of the "lost" herpetological collections of Museu do Dundo, Angola. Bulletin of the Museum of Comparative Zoology 162: 379–440. https://doi.org/10.3099/0027-4100-162.7.379

Ceríaco LMP, 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.

Chernomor O, von Haeseler A, Minh BQ (2016) Terrace aware data structure for phylogenomic inference from supermatrices. Systematic Biology 65: 997–1008. https://doi.org/10.1093/sysbio/syw037

Childers JL, Kirchhof S, Bauer AM (2021) Lizards of a different stripe: Phylogenetics of the *Pedioplanis undata* species complex (Squamata, Lacertidae), with the description of two new species. Zoosystematics and Evolution 97: 249–272. https://doi.org/10.3897/zse.97.61351

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: 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, Nelson Mandela University, Gqeberha, 499 pp.

Conradie W, Baptista NL, Verburgt L, Keates C, Harvey J, Júlio T, Neef G (2021) Contributions to the herpetofauna of the Angolan Okavango-Cuando-Zambezi river drainages. Part 1: Serpentes (snakes). Amphibian and Reptile Conservation 15 (General Section): 244–278 (e292).

Conradie W, Bill, R, Branch WR (2016) The herpetofauna of the Cubango, Cuito, and lower Cuando river catchments of south-eastern Angola. Amphibian and Reptile Conservation 10 (Special Section): 6–36 (e126).

Conradie W, Branch WR, Measey GJ, Tolley KA (2012) Revised phylogeny of sand lizards (*Pedioplanis*) and the description of two new species from south-western Angola. African Journal of Herpetology 60: 91–112. https://doi.org/10.1080/21564574.2012.676079

Conradie W, Deepak V, Keates C, Gower DJ (2020a) 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: 79–107. https://doi.org/10.1080/21564574.2020.1782483

Conradie W, Keates C, Baptista NL, Lobón-Rovira J (2022b) 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, Lobón-Rovira J, Vaz Pinto P, Verburgt L, Baptista NL, Harvey J, Júlio T (2020b) New insights into the taxonomic status, distribution and natural history of de Witte's clicking frog (*Kassinula wittei* Laurent, 1940). African Zoology 55: 311–322. https://doi.org/10.1080/15627020.2020.1821771

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. Amphibian and Reptile Conservation 17 (General Section): 19–56 (e325).

Conradie W, Keates C, Verburgt L, Baptista NL, Harvey J, Júlio T, Neef G (2022a) Contributions to the herpetofauna of the Angolan Okavango- Cuando-Zambezi River drainages. Part 2: Lizards (Sauria), chelonians, and crocodiles. Amphibian and Reptile Conservation 16 (General Section): 181–214 (e322).

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: 435–453. https://doi.org/10.3897/zse.98.86299

de Queiroz K (1998) The general lineage concept of species, species criteria, and the process of speciation: A conceptual unification and terminological recommendations. In: Howard DJ, Berlocher SH

(Eds) Endless Forms: Species and Speciation. Oxford University Press, Oxford, 57–75.

de Witte G-F (1933) Reptiles récoltés au Congo belge par le Dr. H. Schouteden et par M. G.-F. de Witte. Annales du Musée Royal du Congo Belge (Sciences Zoologiques) 3: 53–100.

de Witte G-F, Laurent RF (1942) Liste des Lacertidae du Congo Belge et description d'une espèce nouvelle. Revue de Zoologie et de Botanique Africaines 36: 165–180.

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

Edwards S, Tolley KA, Vanhooydonck B, Measey GJ, Herrel A (2013b) Is dietary niche breadth linked to morphology and performance in Sandveld lizards *Nucras* (Sauria: Lacertidae)? Biological Journal of the Linnean Society 110: 674–688. https://doi.org/10.1111/bij.12148

Edwards S, Vanhooydonck B, Herrel A, Measey GJ, Tolley KA (2012) Convergent evolution associated with habitat decouples phenotype from phylogeny in a clade of lizards. PLoS ONE 7: e51636. https://doi.org/10.1371/journal.pone.0051636

Englender A, Haring E, Kirchhof S, Mayer M (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: 132–143. https://doi.org/10.1111/jzs.12012

Farris JS, Kãllersjö M, Kluge A, Buit C (1994) Testing significance of congruence. Cladistics 10: 315–320. https://doi.org/10.1111/j.1096-0031.1994.tb00181.x

Farris JS, Kãllersjö M, Kluge A, Buit C (1995) Constructing a significance test for incongruence. Systematic Biology 44: 570–572. https://doi.org/10.1093/sysbio/44.4.570

Fujisawa T, Barraclough TG (2013) Delimiting species using single-locus data and the generalized mixed Yule coalescent approach. Systematic Biology 62: 707–724. https://doi.org/10.1093/sysbio/syt033

Greenbaum E, Dowell Beer S, Hughes DF, Wagner P, Anderson CG, Villanueva CO, Malonza PK, Kusamba C, Muninga WM, Aristote MM, Branch WR (2018) Phylogeography of Jackson's forest lizard *Adolfus jacksoni* (Sauria: Lacertidae) reveals cryptic diversity in the highlands of East Africa. Herpetological Monographs 32: 51–68. https://doi.org/10.1655/HERPMONOGRAPHS-D-18-00005.1

Greenbaum E, Villanueva CO, Kusamba C, Aristote MM, Branch WR (2011) A molecular phylogeny of Equatorial African Lacertidae, with the description of a new genus and species from eastern Democratic Republic of the Congo. Zoological Journal of the Linnean Society 163: 913–942. https://doi.org/10.1111/j.1096-3642.2011.00732.x

Haacke WD (1970) New herpetological records from South West Africa. Annals of the Transvaal Museum 26: 277–283.

Hall TA (1999) BioEdit: A user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symposium Series 41: 95–98.

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: 29–78. https://doi.org/10.1080/21564574.2020.1777470

Hellmich W (1957) Die Reptilienausbeute der Hamburgischen Angola-Expedition. Mitteilungen aus dem Hamburger Zoologischen Museum und Institut 55: 39–80.

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

Huelsenbeck J, Rannala B (2004) Frequentist properties of Bayesian posterior probabilities of phylogenetic trees under simple and complex substitution models. Systematic Biology 53: 904–913. https://doi.org/10.1080/10635150490522629

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

Jacobsen NHG, Pietersen EW, Pietersen DW (2010) A preliminary herpetological survey of the Vilanculos Coastal Wildlife Sanctuary on the San Sebastian Peninsula, Vilankulo, Mozambique. Herpetology Notes 3: 181–193.

Kalyaanamoorthy S, Minh BQ, Wong TKF, von Haeseler A, Jermiin LS (2017) ModelFinder: Fast model selection for accurate phylogenetic estimates. Nature Methods 14: 587–589. https://doi.org/10.1038/nmeth.4285

Kapli T, Lutteropp S, Zhang J, Kobert K, Pavlidis P, Stamatakis A, Flouri T (2016) Multi-rate Poisson tree processes for single-locus species delimitation under maximum likelihood and Markov chain Monte Carlo. Bioinformatics 33: 1630–1638. https://doi.org/10.1093/bioinformatics/btx025

Keates C (2024) Herpetofauna. In: Keates C (Ed.) Biodiversity Survey of the Kibara Plateau: Upemba National Park, June – July 2024. Hankuzi Explorations, Unpublished Report, 101 pp.

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

Laurent RF (1952) Batraciens et reptiles récemment acquis par le Musée du Congo. Revue de Zoologie et de Botanique Africaine 44: 198–203.

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

Letsch H, Greve C, Hundsdoerfer AK, Irisarri I, Moore JM, Espeland M, Wanke S, Arifin U, Blom MPK, Corrales C, Donath A, Fritz U, Köhler G, Kück P, Lemer S, Mengual X, Salas NM, Meusemann K, Palandačić A, Printzen C, Sigwart JD, Silva-Brandão KL, Simões M, Stange M, Suh A, Szucsich N, Tilic E, Töpfer T, Böhne A, Janke A, Pauls SU (2025) Type genomics: A framework for integrating genomic data into biodiversity and taxonomic research. Systematic Biology: syaf040. https://doi.org/10.1093/sysbio/syaf040

Lalueza-Fox C (2022) Museomics. Current Biology 32: R1214–R1215. https://doi.org/10.1016/j.cub.2022.09.019

Lobón-Rovira J, Conradie W, Baptista NL, Vaz Pinto P (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, Conradie W, Iglesias DB, Ernst R, Veríssimo L, Baptista N, Vaz Pinto P (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, Heinicke MP, Bauer AM, Conradie W, Vaz Pinto P (2025a) Three new endemic species of Namib day geckos (Gekkonidae: *Rhoptropus*) from the Namibe Province, Angola. Ecology and Evolution 15: e71609. https://doi.org/10.1002/ece3.71609

Lobón-Rovira J, Vaz Pinto P, Keates C, Stanley EL (2025b) Ancient polymorphism, secondary contact, taxonomic inflation or all of them together? Mito-nuclear discordance in the Angolan girdled lizard (Cordylidae: *Cordylus*), with the description of a new species from the central highlands. Zoological Journal of the Linnean Society 205: zlaf112. https://doi.org/10.1093/zoolinnean/zlaf112

Loveridge A (1933) Reports on the scientific results of an expedition to the southwestern highlands of Tanganyika Territory. VII. Herpetology. Bulletin of Museum of Comparative Zoology (Harvard) 74: 197–415.

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: 622–633. https://doi.org/10.1016/j.ympev.2007.04.021

Manaças S (1963) Sáurios de Angola. Memórias da Junta de Investigações do Ultramar, Lisboa, 43, Segunda Série. Estudos de Zoologia 43: 223–240.

Marques MP, Ceríaco LMP, Bandeira S, Pauwels OSG, Bauer AM (2019a) Description of a new long-tailed skink (Scincidae: *Trachylepis*) from Angola and the Democratic Republic of the Congo. Zootaxa 4568: 51–68. https://doi.org/10.11646/zootaxa.4568.1.3

Marques MP, Ceríaco LMP, Blackburn DC, Bauer AM (2018) Diversity and distribution of the amphibians and terrestrial reptiles of Angola: Atlas of historical and bibliographic records (1840–2017). Proceedings of the California Academy of Sciences (Series 4) 65 (Supplement II): 1–501.

Marques MP, Ceríaco LMP, Buehler MD, Bandeira SA, Janota JM, Bauer AM (2020) A revision of the dwarf geckos, genus *Lygodactylus* (Squamata: Gekkonidae), from Angola, with the description of three new species. Zootaxa 4853: 301–352. https://doi.org/10.11646/zootaxa.4853.3.1

Marques MP, Ceríaco LMP, Heinicke MP, Chehouri RM, Conradie W, Tolley KA, Bauer AM (2022a) 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, Ceríaco LMP, Stanley EL, Bandeira SA, Agarwal I, Bauer AM (2019b) A new species of girdled lizard (Squamata: Cordylidae) from the Serra da Neve Inselberg, Namibe Province, southwestern Angola. Zootaxa 4668: 503–524. https://doi.org/10.11646/zootaxa.4668.4.4

Marques MP, Parrhina D, Ceríaco LMP, 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. Vertebrate Zoology 73: 325–343. https://doi.org/10.3897/vz.73.e101329

Marques MP, Parrinha D, Lopes-Lima M, Tiutenko A, Bauer AM, Ceríaco LMP (2024) 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

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

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

Marx H (1956) A new lacertid lizard from Angola. Fieldiana Zoology 39: 5–9.

Mayer W (2013) Kommentierte Lacertiden-Liste für Europa, Afrika, den Nahen Osten inklusive der Arabischen Halbinsel und Asien. L@CERTIDAE 7: 8–141.

McGuire JA, Cotoras DD, O'Connell B, Lawalata SZS, Wang-Claypool CY, Stubbs A, Huang X, Wogan GOU, Hykin SM, Reilly SB, Bi K, Riyanto A, Arida E, Smith LL, Milne H, Streicher JW, Iskandar DT (2018) Squeezing water from a stone: High-throughput sequencing from a 145-year old holotype resolves (barely) a cryptic species problem in flying lizards. PeerJ 6: e4470. https://doi.org/10.7717/peerj.4470

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: 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. https://doi.org/10.1109/GCE.2010.5676129

Minh BQ, Lanfear R, Trifinopoulos J, Schrempf D, Schmidt HA (2021) IQ-TREE Version 2.1.2: Tutorials and Manual Phylogenomic Software by Maximum Likelihood. http://www.iqtree.org/doc/iqtree-doc.pdf [accessed 21 March 2022].

Nguyen L-H, Schmidt HA, Von Haeseler A, Minh BQ (2015) IQ-TREE: A fast and effective stochastic algorithm for estimating maximum likelihood phylogenies. Molecular Biology and Evolution 32: 268–274. https://doi.org/10.1093/molbev/msu300

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

Parrinha D, Marques MP, De Sousa ACA, Bauer AM, Ceríaco LMP (2025b) Buried in the sands of time: A new species of *Sepsina* Bocage, 1866, from Angola (Squamata: Scincidae). Annals of Carnegie Museum 90: 183–193. https://doi.org/10.2992/007.090.0302

Parrinha D, Marques MP, Heinicke MP, Khalid F, Parker KL, Tolley KA, Childers JL, Conradie W, Bauer AM, Ceríaco LMP (2021) A revision of Angolan species in the genus *Pedioplanis* Fitzinger (Squamata: Lacertidae), with the description of a new species. Zootaxa 5032: 001–046. https://doi.org/10.11646/zootaxa.5032.1.1

Parrinha D, Marques MP, Picelli AM, Jordaan A, Bishop-Schouster LJ, Heinicke MP, Bauer AM, Ceríaco LMP (2025c) Two new species of *Pachydactylus* (Squamata: Gekkonidae) from Kaokoveld. Ichthyology & Herpetology 113: 412–432. https://doi.org/10.1643/h2024108

Parrinha D, Marques MP, Tiutenko A, Heinicke MP, Bauer AM, Ceríaco LMP (2025a) A new species of Namib day gecko (Gekkonidae: *Rhoptropus* Peters, 1869) from the Serra da Neve inselberg, southwestern Angola. Zootaxa 5569: 439–458. https://doi.org/10.11646/zootaxa.5569.3.2

Phadima MM, Brammer T, Mussa J, Henrion MYR, Gawa T (2025) *Ichnotropis bivittata* Bocage, 1866, Angolan rough-scaled lizard. African Herp News 87: 22–25.

Pietersen DW, Pietersen EW, Conradie W (2017) Preliminary herpetological survey of the Ngonye Falls and surrounding regions in south-western Zambia. Amphibian and Reptile Conservation 11 (Special Section): 24–43 (e148).

Pietersen DW, Verburgt L, Davies J (2021) Snakes and Other Reptiles of Zambia and Malawi. Struik Nature, Cape Town, 376 pp.

Puillandre N, Brouillet S, Achaz G (2021) ASAP: Assemble species by automatic partitioning. Molecular Ecology Resources 21: 609–620. https://doi.org/10.1111/1755-0998.13281

Puillandre N, Lambert A, Brouillet S, Achaz GJME (2012) ABGD, automatic barcode gap discovery for primary species delimitation. Molecular Ecology 21: 1864–1877. https://doi.org/10.1111/j.1365-294x.2011.05239.x

Rambaut A (2018) FigTree. Tree Figure Drawing Tool Version 1.4.4. http://tree.bio.ed.ac.uk/software/figtree [accessed 31 October 2020].

Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA (2018) Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. Systematic Biology 67: 901–904. https://doi.org/10.1093/sysbio/syy032

Raxworthy CJ, Smith BT (2021) Mining museums for historical DNA: Advances and challenges in museomics. Trends in Ecology & Evolution 36: 1049–1060. https://doi.org/10.1016/j.tree.2021.07.009

Robertson IAD, Chapman BM, Chapman NF (1963) Notes on some reptiles collected in the Rukwa Valley, S.W. Tanganyika. Annals and Magazine of Natural History 5: 421–432.

Röll B, Vaz Pinto P, Lobón-Rovira J (2024) A new species of African diurnal dwarf geckos (Gekkonidae: *Lygodactylus*) from the Lower Guinea rainforest. Zootaxa 5538: 561–574. https://doi.org/10.11646/zootaxa.5538.6.3

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MRBAYES 3.2: Efficient Bayesian phylogenetic inference and model selection across a large model space. Systematics and 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 [accessed 20 November 2023].

Schmidt KP (1919) Contributions to the herpetology of the Belgian Congo based on the collection of the American Congo Expedition, 1909-1915. Pt. I. Turtles, crocodiles, lizards, and chameleons. Bulletin of the American Museum of Natural History 39: 385–624.

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

Spawls S, Howell K, Drewes RC, Ashe J (2002) Field Guide to the Reptiles of East Africa. Princeton University Press, Princeton, NJ, 543 pp.

Spawls S, Howell K, Hinkel H, Menegon M (2018) Field Guide to East African Reptiles. 2nd Edition. Bloomsbury, London, 624 pp.

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

Sukumaran J, Knowles LL (2017) Multispecies coalescent delimits structure, not species. Proceedings of the National Academy of Sciences of the USA 114: 1607–1612. https://doi.org/10.1073/pnas.1607921114

Swofford D L (2003) PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.

Tabachnick BG, Fidell LS (2019) Using Multivariate Statistics (7th ed.). Allyn & Bacon/Pearson Education, California State University, Northridge, CA, 848 pp.

Tamura K, Stecher G, Peterson D, Filipski A, Kumar S (2013) MEGA6: Molecular evolutionary genetics analysis version 6.0. Molecular Biology and Evolution 30: 2725–2729. https://doi.org/10.1093/molbev/mst197

Thompson JD, Higgins DG, Gibson TJ (1994) CLUSTAL W: Improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. Nucleic Acids Research 22: 4673–4680. https://doi.org/10.1093/nar/22.22.4673

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

Tolley KA, Conradie W, Pietersen DW, Weeber J, Burger M, Alexander, G.J. (Eds) (2023) Conservation Status of the Reptiles of South Africa, Eswatini and Lesotho. Suricata 10. South African National Biodiversity Institute, Pretoria, 651 pp.

Uetz P, Freed P, Aguilar R, Reyes F, Kudera J, Hošek J (Eds) (2025) The Reptile Database. http://www.reptile-database.org [accessed 24 March 2025].

Vaidya G, Lohman DJ, Meier R (2011) SequenceMatrix: Concatenation software for the fast assembly of multigene datasets with character set and codon information. Cladistics 27: 171–180. https://doi.org/10.1111/j.1096-0031.2010.00329.x

van Breda RV (2023) Herpetofaunal Survey of the Khaudum–Ngamiland Dispersal Area in Namibia. MSc. Thesis, University of the North-West, Potchefstroom, 97 pp.

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. L@CERTIDAE (Eidechsen Online) 4: 60–138.

Wagner P, Butler B, Ceríaco LMP, Bauer AM (2021) A new species of the *Acanthocercus atricollis* (Smith, 1849) complex (Squamata: Agamidae). Salamandra 57: 449–463.

Wagner P, Greenbaum E, Malonza P, Branch B (2014) Resolving sky island speciation in populations of East African *Adolfus alleni* (Sauria, Lacertidae). Salamandra 50: 1–17.

Xia X (2018). DAMBE7: New and improved tools for data analysis in molecular biology and evolution. Molecular Biology and Evolution 35: 1550–1552. https://doi.org/10.1093/molbev/msy073

Zacho CM, Bager MA, Margaryan A, Gravlund P, Galatius A, Rasmussen AR, Allentoft ME (2021) Uncovering the genomic and metagenomic research potential in old ethanol-preserved snakes. PLoS ONE 16: e0256353. https://doi.org/10.1371/journal.pone.0256353

Zhang J, Kapli P, Pavlidis P, Stamatakis A (2013) A general species delimitation method with applications to phylogenetic placements. Bioinformatics 29: 2869–2876. https://doi.org/10.1093/bioinformatics/btt499

Appendix

List of material examined for the study ($^{+}$examined by William Branch, *examined by Donald Broadley, $^{\#}$photographs only). Museum acronyms: AMNH – American museum of Natural History, BMNH – British Museum (now Natural History Museum, London), CHL - Colecção Herpetológica do Lubango, Angola, DM – Dundo Museum, Angola, NMNW – National Museum Namibia, NMZB – Natural History Museum of Zimbabwe, PEM – Port Elizabeth Museum, TM – Transvaal Museum (now Ditsong National Museum of Natural History), USNM – Smithsonian National Museum of Natural History. Other abbreviations: P series – Pedro Vaz Pinto field series, DRC – Democratic Republic of the Congo, NP – National Park, IR – Integral Reserve.

Ichnotropis bivittata

ANGOLA: $^{\#}$P5-074, P5-075, Alto Cuilo (–10.0853; 19.4624); $^{+}$DM 1854 (*I. b. pallida* – holotype), Boca da Humpata, Huila (–14.9333; 13.5167); $^{+}$BMNH 1906.8.24.34–42, Caconda (–13.7333; 15.0667); P1-318, Cambau (–10.1048; 15.2182); $^{+}$AMNH 47113–7, $^{+}$FMNH 18507 (5851), $^{+}$FMNH 18507 (5855–6), NMZB-UM 16358; Chitau (–11.4333; 17.15); PEM R23530, Cuito town (–12.3278; 16.9067); $^{+}$BMNH 1904.5.2.28 (98), BMNH 1904.5.2.29 (115), *MBL 662a–b (destroyed syntypes), *MBL 663a–b (destroyed syntypes), $^{+,\#}$ZMB 5827 (syntype), Duque de Braganca [= Calandula] (–9.0916; 15.9549); *MBL 661, Huila (destroyed); *MBL 660a–b (destroyed), Lobango (–14.9167; 13.5); CHL0675, Laundo IR (–10.2772; 16.9533); #unvouchered photo, Mussemde (–10.5252; 15.9810); $^{+}$FMNH 74288, Serra do Moco (–12.4167; 15.1833); PEM R17934 (*I. b. pallida*), 7 km East of Humpata (–14.9820; 13.4352). **DRC**: BE_RMCA_Vert.R.14641 (*I. c. nigrescens* – holotype), Bololo (–2.1667; 16.2333); BE_RMCA_Vert.R.14719, Lemfu, Bas-Congo (–5.3; 15.2167); BE_RMCA_Vert.R.15925, BE_RMCA_Vert.R.16240, Bolobo, Village Nolua (–2.1667; 16.2333); BE_RMCA_Vert.R.21138, BE_RMCA_Vert.R.21234, Makaw River, Kasai (–3.4667; 18.3); BE_RMCA_Vert.R.40 (*I. overlaeti* – paratype), Kwango; BE_RMCA_Vert.R.914, Bas Congo; BE_RMCA_Vert.R.979, Kimpana (–4.0990; 17.1378). **GABON**: $^{\#}$iNaturalist 240842482, Lekoko (–22.4262; 13.5546); $^{\#}$iNaturalist 239804857, Lekoko (–22.2228; 13.5076).

Ichnotropis chapini

DRC: BE_RMCA_Vert.R.3656–7, Adra (Kibali-Ituri), 3.5; 30.5); $^{\#}$AMNH 10674 (holotype), Aba (3.8333; 30.1667)

Ichnotropis microlepidota

ANGOLA: $^{+\#}$FMNH 74283–7, Serra do Moco (–12.4167; 15.1478); MHNCUP-REP0983, Serra do Moco (–12.4554; 15.1632).

Ichnotropis tanganicana

DRC: IRSNB 7845(1–2), IRSNB 7848(1–5), Lusinga, Upemba NP (–8.9326; 27.2055); IRSNB 7850, Mukana, marsh near Lusinga, Upemba NP (–8.9202 27.0278); IRSNB 7852(1–3), Kateke River, Upemba NP; IRSNB 7857(1–3), Kakunda River, Upemba NP (–8.8469; 26.7341); IRSNB 7863, IRSNB 7871, Masomb on Grande-Kafwe River, Upemba NP (–9.0833; 27.2); IRSNB 7875(1–2), Kalumengongo River, Upemba NP (–8.9457; 26.9897); PEM R19203, Katwe Camp Kundelungu (–10.565; 27.8586); PEM R28448–9, PEM R28452, PEM R28456, Upemba National Park (–9.0443; 26.9966); BE_RMCA_Vert.R.1289, Mission de Loanza, Katanga (–8.6753; 28.7002); BE_RMCA_Vert.R.1869 (*I. c. nigrescens* – paratype), Luluabourg (–58958; 22.4178); BE_RMCA_Vert.R.20198, Lula (Luisa) (–7.2; 22.4167); BE_RMCA_Vert.R.2367, Kandolo (Sankuru-Kasai) (–5.8111; 21.6952); BE_RMCA_Vert.R.7674, Kansenia (–10.3167; 26.033); BE_RMCA_Vert.R.9691 (*I. overlaeti* – holotype), Kapanga (–8.35; 22.2833); $^{\#}$MUSE-VER 9947, Kindingi, west of Kabobo Plateau (–5.2626; 29.9076); *NMZB-UM 12728, Masombwe, Upemba NP (–9.0833; 27.2). **MALAWI**: *NMZB-UM 24432-3, Misuku Hills (–9.6667 33.55). **TANZANIA**: *NMZB 3217, Msanzi, Ufipa (–8.1698; 31.5212); $^{\#}$MCZ R30836-7, Ipemi, Udzungwa Mountains (–8.3333; 35.9667). **ZAMBIA**: PEM R02817–8, Abercorn [= Mbala] (–8.84; 31.3658); *IRSNB 2666, Mbala (–8.8402; 31.3659); *NMZB 1511, Sakeji Stream (–11.2329; 24.3118).

Ichnotropis grandiceps

BOTSWANA: *NMZB-UM 16278, *USNM 163989–90, 40 km W of Mohembo (–18.2996; 21.4171). **NAMBIA**: RE211206D1/NMNW R12212, Khaudum (–18.2876; 20.9897); TM 30822, Ndobe, 15 km N of Aha Mts. (–19.5783; 20.9978); TM 38609–10, Farm Deo Valente (–18.9348; 18.8448); TM 38404, Caprivi strip, 16 km E of 21 0 E corner beacon, Botswana border (–18.3176; 21.1536). **ZAMBIA**: TM 86237, Sioma Park Headquarters (–16.6689; 23.5675).

Ichnotropis capensis sensu lato

ANGOLA: PEM R20008–9, HALO Cuito Cuanavale campsite & office (–15.1392; 19.1436); PEM R20486–8, western end of M'Pupa airstrip (–17.5119; 20.0431); PEM R21490, middle Longa River (–16.28392; 18.84744); PEM R21843–5, small tributary of Curiri River, 4 km south of Lunge River (–14.6848; 18.6737); PEM R23274–8, Cuanavale River source (–13.0933; 18.8940); PEM R23253–4, Cacundu Falls (–13.77390; 18.75520); PEM R23298, grasslands W of Cuanavale to Samanunga village (–13.0751; 18.88481); PEM R23326–8, MCTA: no number, Cuito River source lake (–12.6894; 18.3601); PEM R23351–3, Culua River source, 6 km SE of Cuito River source (–12.7368; 18.3931); PEM R23370, MCTA: no number, Cuanavale River source (–14.8547; 19.2864); PEM R23414–9, Cuando River source (–13.0034; 19.1275); PEM R23440, MCTA: no number (x2), Cuando River source trap 1 (–13.0039; 19.1281); PEM R23453, MCTA: WC-4584 (plus 1 additional specimen), Quembo River trap 4 (–13.13586; 19.04709); PEM R23489, Quembo River trap 2 (–13.1354; 19.0440); PEM R23493–5, Cuanavale River source lake camp side (–13.0944; 18.8937); PEM R23508–9, amphitheatre at Cuanavale River source (–13.0505; 18.8962); PEM R23521–2, grassland drive west of Cuanavale River source (–13.0135; 18.8170); PEM R23539, Longa River (–14.55956; 18.41419); PEM R23546–8, Quembo River source camp (–13.1456; 19.0457); PEM R27393, MCTA: WC-6796, Cuanavale River source lake (–13.0905; 18.8939); PEM R27394–401, MCTA: WC-6796, Quembo River bridge camp (–13.5275; 19.2806). **BOTSWANA**: *BM 1910.5.30.17, 50 km N of Okwa (–21.9654; 21.9); *LACM 17036–41, Kwai Camp (–19.1609; 23.4645); *NMZB 1158, Tsane (–24.0333; 21.9); *NMZB-UM 13369, Nunga (–18.8051; 25.7381); *NMZB-UM 13670, 10 km W of Gabarone (–24.6464; 25.9119); *NMZB-UM 14471–2, 55 km S of Ghanzi (–22.1964; 21.6500); *NMZB-UM 16189, 30 km E of Magweggana (–18.5450; 23.8227); *NMZB-UM 16276–7, 40 km W of Mohembo (–18.2996; 21.4196); *NMZB-UM 16286–8, 90 km W of Mohembo (–18.2981; 20.9441); *NMZB-UM 16377–8, Kasane (–17.8167; 251.1500); *NMZB-UM 16510, 80 km E of Shakawe (–18.6418; 21.1468); *NMZB-UM 9735, *NMZB-UM 9770–2, 65 km NW of Lephepe (–22.9013; 25.3484); *NMZB-UM 9786, Lephepe (–23.6643; 27.6173). **DRC**: IRSNB 10673 (Adult), IRSNB 10673 (Juvenile), Kasaji, Katanga (–10.3817; 23.4477); IRSNB 78728(1–2), IRSNB 7874, IRSNB 7895(1–2), IRSNB 7897(1–4), IRSNB 7907(1–2), IRSNB 7908(1–3), IRSNB 7909(1–4), NMZB-UM 12719, Mabwe River, Upemba NP (–8.6826; 6.4775); BE_RMCA_Vert.R.4644, M’Pala, Kanzenze region (–10.5197; 25.2126); BE_RMCA_Vert.R.6045, Mukishi, Haut-Lomami (*I. overlaeti* – paratype) (–8.4942; 24.6858); BE_RMCA_Vert.R.678, Lofoi, Katanga (*I. overlaeti* – paratype) (–10.2167; 27.4167); BE_RMCA_Vert.R.7777–92, Dilolo, Lualaba (–10.4667; 22.46667). **MOZAMBIQUE**: PEM R05565, northeastern edge Lake Xingute, Maputo Special Reserve); –26.5072; 31.8172); PEM R15549, PEM R15556–7, 7 km North of Chibuto (–24.6231; 33.5661); PEM R21112–3, Chizavane, Zona Braza Lodge (–25.0137; 34.0375); PEM R24969, Panda (–23.9475; 34.4644; #ZMb 6123, 83857, Lourenzo Marques [= Maputo] (*I. macrolepidota* – syntypes) (–25.9653; 32.5892). **NAMIBIA**: IRSNB 11769, farm Labora, Gobabis district; NMZB-UM 23278, 15 km WSW of Katima Mulilo (–17.6851; 24.0520); RE211206B1/NMNW R11561, RE211206B3/NMNW R11562, Khaudum (–18.2876; 20.9897). **SOUTH-AFRICA**: PEM R08393, Kwangwanase Post Office, Manguzi (–26.9833; 32.7500); PEM R08509, 3 km southeast of Manguzi (–27.0061; 32.7688); PEM R08403, PEM R12003, PEM R12190–3, PEM R12289, PEM R12363, Sihangwane, Tembe Elephant Park (–27.0508; 32.4275); PEM R12365, PEM R12369, Glentig, near Nylstroom. –24.4004; 28.4430); PEM R12371, Pretoria (–25.7500; 28.200); PEM R12372, Honingfontein (–23.2952; 30.0549); PEM R12919, Matubatuba (–28.4053; 32.2138); PEM R24748, Tembe Elephant Park (–27.0217; 32.4583); PEM R25371, Lephalale (–23.6319; 27.6170). **ZAMBIA**: PEM R01999, *NMZB-UM 4440–1, NMZB-UM 4487, Lusaka (–15.1667; 28.1167); PEM R06394–7 (AM 5958), Isoka Boma (–10.1606; 32.6335); PEM R06277, Sakeji School (–11.2333; 24.3114); PEM R12318–21, *NMZB 2824–5, Balovale (–13.5493; 23.1102); PEM R12342, Situnda pan, Liuwa Plains National Park (Kalabo) (–14.6706; 22.6567); PEM R12621–3, Siyengi pan, Liuwa Plains National Park (Kalabo) (–14.8142; 22.9311); PEM R22021–4, Ngonye Falls (–16.6736; 23.5969); *BM.1932.5.3.33, Chibuluma, Numbwa (–14.9783; 27.0619); *FMNH 133029, *NMZB-UM 10064–5, *NMZB-UM 21013, *NMZB-UM 6756, Kalabo, Barotseland (–14.99939; 22.6780); *NMZB 2220–30, *NMZB-UM 11381, *NMZB-UM 9226–35, Livingstone (–17.8520; 25.2585); *NMZB 2823, Lunga Game Reserve (–12.8112; 24.760); *NMZB 3158, Kasusu, Kalomo (–17.0348; 25.6504); *NMZB 10520, *NMZB 10548–53, *NMZB 10576–79, *NMZB 10624, *NMZB 10645–7, *NMZB 10649, *NMZB 10697–701, Hillwood Farm, Ikelenge (–11.2502; 24.3101). **ZIMBABWE**: PEM R12323–4, Marandellas (–18.2000; 31.5500); PEM R12325, PEM R12330, Kutama (–17.7333; 30.4167); PEM R12331–2, Musami (–17.8000; 31.6333); PEM R12335, Driefontein (–19.4172; 30.7135); PEM R12336–7, Salisbury [= Harare] (–17.8361; 31.0408); PEM R12338–9, Plumtree (–20.4906; 27.8033); PEM R12340, Filabusi (–20.5333; 29.2833); *NMZB 10898, Botswana Border Post BB 276, 1 km from Zimbabwe gate (–19.625; 26.125); *NMZB 11488–90, Ngamo Pans, Hwange NP (–19.1125; 27.4626); *NMZB 11885, Kennedy Annexe, Hwange (–18.8624; 27.1673); *NMZB 11890, Wexau Pan, Hwange (–19.1266; 27.3652); *NMZB 11899, Ngweshla Pans, Hwange (–19.0276; 27.1121); *NMZB 12389–92, *NMZB 12395, *NMZB 12398, Mfagaza, Hwange NP (–19.125; 27.375); *NMZB 12401, Marambo Pan, Hwange (–19.5333; 27.58333); *NMZB 12409, Madundumela, Hwange NP (–19.125; 27.125); *NMZB 12436, Vungu Bridge, Gweru (–19.625; 29.625); *NMZB 12587, Mfagaza-Madisevan Pan, Hwange (–19.125; 27.375); *NMZB 12640–47, N of Mbazu, Hwange NP (–19.125; 27.125); *NMZB 12659–66, S of Mbazu, Hwange NP (–19.375; 27.125); *NMZB 12700–6, *NMZB 17207, Verneys Pan, Hwange NP (–189606; 26.8175); *NMZB 12744–5, 8 km W of Verneys Pan, Hwange NP (–18.9655; 26.7426); *NMZB 12810, *NMZB 12836–7, *NMZB 12850, Westwood Ranch, Hwange (–17.9167; 25.5333); *NMZB 13037, Njakwa Pan, Hwange NP; *NMZB 13048, Dina Pan, Hwange (–18.9833; 26.3333); *NMZB 13072, 8 km S of Dina Pan, Hwange, –19.0556; 26.3333); *NMZB 13092, Bembesi Vlei, Hwange (–18.8362; 26.6386); *NMZB 13148–9, Manzimbomvu Pan, Hwange (–18.875; 26.125); *NMZB 13159, 4 km E of Tshamasi Pan, Hwange (–19.125; 26.625); *NMZB 13391, Makona Pan, Hwange (–19.3167; 26.9167); *NMZB 13417, 2 km WSW of Dorama Pan, 19.7402; 26.4156); *NMZB 13432, 2 km S of Matambo Pan, Hwange (–19.6396; 26.4861); *NMZB 13442–4, 5 km SW of Tamasanka Pan, Hwange NP (–19.6486; 26.3328); *NMZB 13466, Tamasanka Pan, Hwange NP (–19.62; 5 26.37); *NMZB 13470, 2 km W of Jazibannini, Hwange NP (–19.375; 26.625); *NMZB 13473, *NMZB 13477–8, 3 km NW of Little Dzivanini, Hwange (–19.8808; 26.4796); *NMZB 13520, 4 km E, Shakwanki, Hwange (–19.1983; 26.3037); *NMZB 13524–6, 1 km W Shakwanki, Hwange NP (–19.1997; 26.2667); NMZB 13581–2, 2.5 km NNW of Ngwahla Pan, Hwange NP (–19.3415; 26.0750); *NMZB 13583–4, Ngwahla Pan, Hwange NP (–19.0276; 27.1121); *NMZB 13591–2, Tamafupa, Hwange NP (–19.3277; 26.0926); *NMZB 13796, Pandamatenga, Hwange NP (–18.5000; 25.6667); *NMZB 9012, Kazuma Depression West (–18.3500; 25.5333); *NMZB 9171, Kazuma Forest Land (–18.3500; 25.5333); *NMZB 9196, Panda Masuie Forest Land (–18.125; 25.625); *NMZB 9523–4, Gokwe (–18.2048; 28.9349).

Supplementary Material 1

Figures S1–S4

Authors: Conradie W, Keates C, Greenbaum E, Lobón-Rovira J, Tolley KA, Benito M, Vaz Pinto P, van Breda RV, Verburgt L (2025)

Data type: .docx

Explanation notes: Figure S1. IQ-TREE Maximum likelihood concatenated phylogeny for *Ichnotropis*. — **Figure S2.** MrBayes Bayesian inference concatenated phylogeny for *Ichnotropis*. — **Figure S3.** IQ-TREE Maximum likelihood mitochondrial genes concatenated phylogeny for *Ichnotropis*. — **Figure S4.** IQ-TREE Maximum likelihood nuclear genes concatenated phylogeny for *Ichnotropis*.

Link: https://doi.org/10.3897/vz.74.e167366.suppl1

Supplementary Material 2

Tables S1–S4

Authors: Conradie W, Keates C, Greenbaum E, Lobón-Rovira J, Tolley KA, Benito M, Vaz Pinto P, van Breda RV, Verburgt L (2025)

Data type: .docx

Explanation notes: Table S1. Primers and PCR conditions used to generate sequences for the study. — **Table S2.** Results of two principal components analysis (PCA) implemented on Angolan *Ichnotropis* (Dataset 1) and multivariate analysis of variance of morphological characters. — **Table S3.** Results of the post hoc pairwise analysis (Tukey's HSD test) using PC scores as input and *Ichnotropis* species as fixed factor. — **Table S4.** Results of the analysis of morphometric differences between *Ichnotropis* spp.

Link: https://doi.org/10.3897/vz.74.e167366.suppl2