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The Angolan bushveld lizards, genus *Heliobolus* Fitzinger, 1843 (Squamata: Lacertidae): Integrative taxonomy and the description of two new species

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Abstract

The genus *Heliobolus* comprises four recognized species, all endemic to sub-Saharan Africa. Of these, only *Heliobolus lugubris* occurs in southern Africa, its distribution extending from Angola in the west to Mozambique in the east and reaching as far south as parts of northern South Africa. Like many of the reptile species that occur in southern Africa, *Heliobolus lugubris* is poorly studied, and preliminary investigation suggested that it may contain cryptic diversity. The present work focusses on the Angolan population of *H. lugubris* and uses an integrative taxonomic approach based on morphological, coloration and DNA sequence data. The results indicate that some of the current and historical specimens of *H. lugubris* from Angola do not correspond to the nominotypical form, and that differences between specimens suggest the presence of two additional species, described here as *Heliobolus bivari* **sp. nov.** from the southernmost xeric/desertic regions and plateau of Namibe Province, southwestern Angola and *H. crawfordi* **sp. nov.** from the Serra da Neve inselberg north through the sub-desert coastal regions of northern Namibe, Benguela, and Kwanza Sul provinces. Nominotypical *Heliobolus lugubris* is confirmed to occur in Cuando Cubango Province, southeastern Angola.

Resumo

O género *Heliobolus* é atualmente composto por quatro espécies, todas estas endémicas da África Subsariana. Das quatro espécies, apenas uma, o *Heliobolus lugubris* ocorre na África Austral, estendendo-se de Angola, a oeste, Moçambique, a leste, para sul até

partes do norte da África do Sul. Como muitas das espécies de répteis que ocorrem no sul de África, o *Heliobolus lugubris* têm sido pouco estudado. Uma investigação preliminar recente sugere que pode conter uma diversidade críptica considerável. O presente trabalho foca-se na população angolana de *H. lugubris* e apresenta uma revisão taxonómica integrativa com base em métodos morfológicos, de coloração e filogenéticos. Os resultados indicam que os registos atuais e históricos dos espécimes de *H. lugubris* no país não correspondem à forma nominotípica, e as diferenças entre exemplares sugere a presença de duas espécies adicionais, descritas aqui como *Heliobolus bivari* **sp. nov.**, que ocorre nas partes mais meridionais das regiões xéricas/desérticas e áreas de planalto do sudoeste de Angola e *H. crawfordi* **sp. nov.**, que ocorre desde o inselberg da Serra da Neve, em direção a norte até às regiões costeiras subdesertas. Confirma-se a ocorrência da espécie nominotipica *Heliobolus lugubris* na província do Cuando Cubango no sudeste de Angola.

Keywords

Angola, endemism, integrative taxonomy, lizards, reptiles

Palavras-chave

Angola, endemismo, lacertídeos, répteis, taxonomia integrativa

Introduction

In Angola, the family Lacertidae is represented by six genera – *Heliobolus* Fitzinger, 1843; *Holaspis* Gray, 1863; *Ichnotropis* Peters, 1854; *Meroles* Gray, 1838; *Nucras* Gray, 1838; and *Pedioplanis* Fitzinger, 1843 (Marques et al. 2018; Branch et al. 2019a) encompassing seventeen species. Four (three *Pedioplanis* and one *Nucras*) of these species have been described in the last decade (Conradie et al. 2012; Branch et al. 2019b; Parrinha et al. 2021). Despite the considerable increase in the number of described taxa, most taxonomic studies incorporating Angolan lacertids suggest that species-level diversity in the country is still underestimated and further taxonomic work is needed to uncover this hidden diversity (Conradie et al. 2012; Branch and Tolley 2017; Marques et al. 2018; Branch et al. 2019a,b; Parrinha et al. 2021). While the Angolan populations of *Pedioplanis* and *Nucras* have been the focus of several recent investigations (Conradie et al. 2012; Branch et al. 2019b; Baptista et al. 2020; Parrinha et al. 2021), the country's populations of *Ichnotropis* and *Heliobolus* still lack thorough taxonomic work. Angolan *Heliobolus* have already been signaled by several authors as potentially comprising undescribed cryptic lineages (Branch and Tolley 2017; Marques et al. 2018; Branch et al. 2019a).

The genus *Heliobolus* includes four currently recognized species (Dubke et al. 2018; Uetz et al. 2022), namely the bushveld lizard, *Heliobolus lugubris* (Smith, 1838), Neumann's Sand Lizard *Heliobolus neumanni* (Tornier, 1905), the Glittering Sand Lizard, *Heliobolus nitidus* (Günther, 1872), and Speke's Sand Lizard, *Heliobolus spekii* (Günther, 1872). Both *H. neumanni* and *H. spekii* are restricted to East Africa, *H. nitidus* occurs in an extensive area in West and Central Africa, while *H. lugubris* is the single representative of the genus in southern Africa, being distributed in southwestern Angola, Namibia, Botswana, Zimbabwe, parts of northern South Africa, and Mozambique (Uetz et al. 2022). *Heliobolus lugubris* was originally described by Smith (1838) as *Lacerta lugubris*, from the type locality "District immediately beyond the northern frontier of the Colony" (probably referring to what is now the Northern Cape Province of South Africa). In Angola, the species has been recorded in the southwestern region, which includes the low elevation areas of Benguela, Namibe, Cunene and Cuando Cubango provinces (Marques et al. 2018). Despite not having been studied in detail, a preliminary phylogenetic analysis (Branch and Tolley 2017) incorporating Angolan material of *H. lugubris sensu lato* supported the presence of distinct lineages within Angolan territory.

As part of ongoing research on the Angolan herpetofauna, we collected new specimens of Angolan *Heliobolus* from several localities across southwestern Angola. With this additional material, it was possible to investigate the taxonomic identity of the *H.* cf. *lugubris* population in the country and to assess the diversity and distribution of the genus in Angola. Based on a combination of morphological, meristic, and coloration characters and DNA sequence data, we found evidence that supports the existence of two undescribed species of *Heliobolus*, closely related to *H. lugubris*, in Angola. In order to stabilize the taxonomy and to provide an improved estimate of the distribution of the genus in southern Africa, we describe these two lineages as new species.

Materials and methods

Material examined

Specimens collected for this study were euthanized following an approved IACUC protocol (Villanova University #1866), preserved in 10% buffered formalin in the field, and transferred to 70% ethanol for long-term storage at the conclusion of field work. Liver tissue was removed before formalin fixation and preserved in either RNAlater

and transferred to 95% ethanol or directly in 95% ethanol for long-term storage (Table 1). For mensural and meristic comparisons, we examined 57 *Heliobolus* specimens deposited in the American Museum of Natural History (**AMNH**), New York, U.S.A.; the California Academy of Sciences (**CAS**), San Francisco, U.S.A.; Museu de História Natural e da Ciência da Universidade do Porto (**MHNC-UP**), Porto, Portugal; Port Elizabeth Museum (**PEM**), at Bayworld, Elizabeth to Gqeberha, South Africa. Additional specimens from the Natural History Museum (**BMNH**), London, England, U.K.; Museu Nacional de Ciencias Naturales (**MNCN**), Madrid, Spain; Musée d'histoire naturelle de La Chaux-de-Fonds (**MHNC**), Chaux-de-Fonds, Switzerland; Muséum National d'histoire naturelle de la Ville de Genève (**MNHG**), Genève, Switzerland; Naturhistorisches Museum Basel (**NMBA**), Basel, Switzerland; Senckenberg Forschungsinstitut und Naturmuseum [or Senckenberg Research Institute and Natural History Museum] (**SMF**), Frankfurt am Main, Germany; Museum für Naturkunde (**ZMB**), Berlin, Germany; Ditsong National Museum of Natural History (**TM**), Pretoria, Gauteng, South Africa; the Instituto Nacional da Biodiversidade e Áreas de Conservação (**INBAC**), Kilamba-Kiaxi, Angola; and the National Museum of Namibia (**NMNW**), Windhoek, Namibia, were also consulted. All specimens examined in this study are listed in the taxonomic accounts below. Information on morphological characters of species that could not be examined, as well as supplemental data, was acquired from the literature (e.g., FitzSimons 1943; Szczerbak 1975; Auerbach 1987; Branch 1998; Dubke et al. 2018).

Locality data are presented in decimal degrees and use the WGS 84 datum. Older records (non-GPS) were mostly derived from Marques et al. (2018) and georeferenced

Table 1. Specimens used for genetic analysis and corresponding GenBank accession numbers for genes used in the study. Locality data are reported in the form of decimal degrees and use the WGS 84 map datum. See Materials and Methods section for collection abbreviations. Institution and field number acronyms not cited in the Material and Methods section as follows: MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.; AMB, Aaron M. Bauer field numbers; FP/KTH/RSP/WP, Krystal Tolley field numbers; MBUR/MB: Marius Burger field numbers; SVN, Stuart V. Nielsen field numbers; WRB/AG, William R. Branch field numbers. All genotyped specimens of *Heliobolus bivari* **sp. nov.** and *H. crawfordi* **sp. nov.** are part of the type series.

	Specimen ID		Locality	Genbank Accession Number			
Species	**Field No.**	**Museum No.**		**16S**	**CO1**	**ND4**	**RAG-1**
Australolacerta australis (Hewitt, 1926)	KTH-569	n/a	SA: Western Cape, Goedemoed-Langeberg	DQ871151	MN015100	HF547725	DQ871208
Heliobolus bivari **sp. nov.**	AG142	PEM R24128	Angola: Namibe, 1 km SE of Farm Mucongo	OP055968		OP057322	OP057281
	AG143	PEM R24129	Angola: Namibe, 1 km SE of Farm Mucongo	OP055969		OP057323	OP057282
	AMB10595	CAS 266276	Angola: Namibe, Virei-Chipumpo	OP055982	OP053373	OP057334	OP057295
	AMB10596	CAS 266277	Angola: Namibe, Virei-Chipumpo	OP055983	OP053374	OP057335	OP057296
	AMB10597	CAS 266278	Angola: Namibe, Virei-Chipumpo	OP055984	OP053375	OP057336	OP057297
	AMB10598	CAS 266279	Angola: Namibe, Virei-Chipumpo	OP055985	OP053376	OP057337	OP057298
	AMB10599	CAS 266280	Angola: Namibe, Virei-Chipumpo	OP055986	OP053377	OP057338	OP057299
	AMB10600	CAS 266281	Angola: Namibe, Virei-Chipumpo	OP055987	OP053378	OP057339	OP057300
	AMB10601	CAS 266282	Angola: Namibe, Virei-Chipumpo	OP055988	OP053379	OP057340	OP057301
	AMB10602	CAS 266283	Angola: Namibe, Virei-Chipumpo	OP055989	OP053380	OP057341	OP057302
	AMB10603	CAS 266284	Angola: Namibe, Virei-Chipumpo	OP055990	OP053381	OP057342	OP057303
	AMB10604	CAS 266285	Angola: Namibe, Virei-Chipumpo	OP055991	OP053382	OP057343	OP057304
	AMB10631	CAS 266286	Angola: Namibe, Virulundo	OP055992	OP053383	OP057344	OP057305
	AMB10633	CAS 266287	Angola: Namibe, Virulundo	OP055993	OP053384	OP057345	OP057306
	KTH09-265	PEM R17965	Angola: Huila, along Humpata-Namibe Rd	OP055998		OP057349	
	KTH09-266	PEM R17966	Angola: Namibe, road to Espiheira	OP055999		OP057350	OP057308

	Specimen ID		Locality	Genbank Accession Number			
Species	**Field No.**	**Museum No.**		**16S**	**CO1**	**ND4**	**RAG-1**
	WRB937	PEM R21626	Angola: Namibe, road to Leba	OP056018			
	WRB938	PEM R21630	Angola: Namibe, Leba Pass road	OP056019		OP057367	OP057321
Heliobolus crawfordi **sp. nov.**	AG11	PEM R24019	Angola: Namibe, road north of Bibala	OP055967			OP057280
	AG17	PEM R24024	Angola: Namibe, road north of Bibala, towards Lola	OP055970			OP057283
	AG24	PEM R24004	Angola: Namibe, 10 km W Lola	OP055971			OP057284
	AMB10285	CAS 266267	Angola: Namibe, Dolondolo	OP055972	OP053363	OP057324	OP057285
	AMB10286	CAS 266268	Angola: Namibe, Dolondolo	OP055973	OP053364	OP057325	OP057286
	AMB10287	CAS 266269	Angola: Namibe, Dolondolo	OP055974	OP053365	OP057326	OP057287
	AMB10289	CAS 266271	Angola: Namibe, Dolondolo	OP055975	OP053366	OP057327	OP057288
	AMB10333	CAS 266273	Angola: Namibe, Dolondolo	OP055976	OP053367	OP057328	OP057289
	AMB10348	CAS 266275	Angola: Namibe, Dolondolo	OP055977	OP053368	OP057329	OP057290
	WRB935	PEM R24025	Angola: Namibe, road north of Bibala towards Lola	OP056017		OP057366	OP057320
Heliobolus lugubris (Smith, 1838)	ABB20	n/a	Namibia: Hardap, Haruchas	JX962910			EF632216
	AMB6975	n/a	Namibia: Kunene, Sesfontein	OP055994			
	FP271A	n/a	SA: Kruger National Park	OP055995		OP057346	
	FP291	n/a	SA: Kruger National Park	OP055996		OP057347	OP057307
	FP295	n/a	SA: Kruger National Park	OP055997		OP057348	
	MB20857	n/a	SA: Northern Cape, Farm Boseekoebaard (SE of Groblershoop)	OP056000		OP057351	
	MB20860	n/a	SA: Northern Cape, Farm Panheuwel, E of Langberge, ENE of Groblershoop	OP056001		OP057352	
	MB20901	n/a	SA: Northern Cape, Farm Boseekoebaard (SE of Groblershoop)	OP056002		OP057353	OP057309
	MB20940	n/a	SA: Northern Cape, 36 km NE of Groblershoop	OP056003		OP057354	
	MB21313	PEM R20956	SA: Northern Cape, Red Sands Country Lodge (14 km SW of Kuruman)	OP056004		OP057355	OP057310
	MB21691	n/a	SA: Mpumalanga, Frischgewaagd (Bobididi) Resettlement, about 20 km S of Steelpoort	OP056005		OP057356	
	MBUR00377	n/a	SA: Limpopo, Makgabeng area, W of Senwabawana (Bochum)	OP056006		OP057357	
	MCZ A28701	MCZ R 193176	Namibia: Erongo, Farm Omandumba	OP056007			MW823306
	MCZ Z37870	MCZ R 184277	Namibia: Kunene, Kamanjab Rest Camp	DQ871141		HF547729	DQ871199
	MCZ Z37893	MCZ R 184282	Namibia: Kunene, Kamanjab Rest Camp	OP056008		OP057358	OP057311
	MCZ Z37894	NMNW 11134	Namibia: Kunene, Kamanjab Rest Camp	DQ871142		HF547730	DQ871200
	MCZ 38795	CAS 234140	SA: Limpopo, Farm Pylkop	OP056009		OP057359	OP057312
	MCZ 38796	CAS 234141	SA: Limpopo, Farm Pylkop	OP056010			OP057313
	RSP275	n/a	SA: Northern Cape, Tswalu Kalahari Reserve	OP056011		OP057360	OP057314

Species	Specimen ID		Locality	Genbank Accession Number			
	Field No.	Museum No.		16S	CO1	ND4	RAG-1
	RSP285	PEM R18582	SA: Northern Cape, Tswalu Kalahari Reserve	OP056012		OP057361	
	RSP339	PEM R18603	SA: Northern Cape, Tswalu Kalahari Reserve	OP056013		OP057362	OP057315
	RSP482	PEM R18642	SA: Limpopo, Venetia Limpopo Nature Reserve			OP057363	OP057316
	SVN364	PEM R19599	SA: Limpopo, Lapalala Reserve	OP056014		OP057364	OP057317
	SVN365	PEM R19562	SA: Limpopo, Lapalala Reserve	OP056015		OP057365	OP057318
	WP037	n/a	Namibia: Sandveld Agricultural Station, 40 km N of Gobabis Omaheke	OP056016			OP057319
Heliobolus spekii (Günther, 1872)	n/a	CAS 198923	Kenya: Rift Valley Province, Kajiado District	AF206608	AF206583		EF632217
Ichnotropis capensis (Smith, 1838)	AMB6007	CAS 209602	SA: KwaZulu-Natal, Kosi Bay	DQ871149	MN015099	MN030223	DQ871206
Lacerta agilis Linnaeus, 1758	n/a	n/a	n/a	DQ494823	MN015108	MN030232	EF632222
Latastia longicaudata (Reuss, 1834)	n/a	n/a	n/a	JX962911	MG700025		EF632229
Meroles reticulatus (Bocage, 1867)	AMB10374	CAS 264771	Angola: Namibe, Amélia Beach	OP055978	OP053369	OP057330	OP057291
	AMB10375	CAS 264772	Angola: Namibe, Amélia Beach	OP055979	OP053370	OP057331	OP057292
	AMB10376	CAS 264773	Angola: Namibe, Amélia Beach	OP055980	OP053371	OP057332	OP057293
	AMB10421	CAS 264782	Angola: Namibe, Curoca River	OP055981	OP053372	OP057333	OP057294
Nucras tessellata (Smith, 1838)	AMB5582	CAS 206723	SA: Northern Cape, Groenriviermond	DQ871143	AF206565	MG846565	HG005257
Pedioplanis namaquensis (Duméril & Bibron, 1839)	AMB7577	n/a	Namibia: 17 km E of Ugab crossing	DQ871098	AF206566	HF547767	DQ871156
Poromera fordii (Hallowell, 1857)	n/a	USNM-Herp: 584231	Republic of the Congo: Lekoumou, Bambama village	AF080370	MH274569		EF632240

using the GEOLocate web application (https://www.geo-locate.org), elevation is reported in meters above sea level.

Phylogenetic methods

We constructed a DNA sequence dataset to estimate phylogenetic relationships among *Heliobolus* cf. *lugubris* samples from Angola, Namibia, and South Africa. The dataset includes 54 ingroup samples: 28 from Angola and 26 from Namibia and South Africa, plus nine lacertid outgroup taxa *Heliobolus spekii*, *Australolacerta australis* (Hewitt, 1926), *Ichnotropis capensis* (Smith, 1838), *Lacerta agilis* Linnaeus, 1758, *Latastia longicaudata* (Reuss, 1834), *Meroles reticulatus* (Bocage, 1867), *Nucras tessellata* (Smith, 1838), *Pedioplanis namaquensis* (Duméril and Bibron, 1839), and *Poromera fordii* (Hallowell, 1857) (Table 1), chosen for broad phylogenetic coverage based on previous phylogenetic analyses of African lacertids (Mayer and Pavlicev 2007; Greenbaum et al. 2011; Edwards et al. 2013). *Heliobolus neumanni* and *H. nitidus* were not available for inclusion in the phylogenetic analysis. Fragments of four mitochondrial and nuclear genes were targeted for sequencing and analysis: 16S (561 bp), CO1 (665 bp), ND4 plus adjacent tRNAs (882 bp) and RAG-1 (1347 bp).

We extracted DNA from ethanol-preserved tissue samples using Qiagen DNeasy tissue kits following the manufacturer's protocol. PCR amplification of target genes was performed using the primers listed in Table 2 and the following standard cycling conditions: 95°C initial denaturation (150 s), followed by 40 cycles of denaturation at 95°C (30 s), annealing at 46–55°C (30 s) and extension at 72°C (60 s), with a 72°C final extension (150 s). Amplified DNA was purified using either agarose gel extraction or Axygen AxyPrep magnetic beads and sequenced at the University of Michigan Advanced Genomics Core or at Macrogen (Amsterdam). Resulting sequences were assembled using MEGA X v.10.0.5 (Kumar et al. 2018), and individual gene alignments were produced using CLUSTALX v.2.1 (Larkin et al. 2007).

The primary phylogenetic analysis used a concatenated alignment including all available genetic data.

Table 2. List of primers used for PCR in this study.

Gene	Primer	Sequence	Direction	Source
16S	16S-A	5′-CGCCTGTTTATCAAAAACAT-3′	Forward	Palumbi (1996)
16S	16S-B	5′-CCGGTCTGAACTCAGATCACGT-3′	Reverse	Palumbi (1996)
CO1	RepCO1F	5′-TNTTMTCAACNAACCACAAAGA-3′	Forward	Nagy et al. (2012)
CO1	RepCO1R1	5′-ACTTCTGGRTGKCCAAARAATCA-3′	Reverse	Nagy et al. (2012)
ND4	ND4-F	5′-CACCTATGACTACCAAAAGCTCATGTAGAAGC-3′	Forward	Arévalo et al. (1994)
ND4	LeuR1	5′-CATTACTTTTACTTGGATTTGCACCA-3′	Reverse	Arévalo et al. (1994)
RAG-1	R13	5′-TCTGAATGGAAATTCAAGCTGTT-3′	Forward	Groth and Barrowclough (1999)
RAG-1	RAG-1-PedF2	5′-GGYGAYRTTGACACAATCCATCCTAT-3′	Forward	Parrinha et al. (2021)
RAG-1	RAG-1-PedR1	5′-GTACTGAGGTGTATCTTGTTGCA-3′	Reverse	Parrinha et al. (2021)
RAG-1	RAG-1-PedR2	5′-CAGCAAAAGCTTTCACTTGAAGT-3′	Reverse	Parrinha et al. (2021)

PartitionFinder v.2.1.1 (Lanfear et al. 2017) was used to identify the best-fitting partitioning scheme and models of evolution under the Akaike Information Criterion (AIC). A total of 11 potential partitions were considered, including 16S, tRNAs, and each codon position for the three protein-coding genes. The best scheme under the AIC used the following subdivisions and models of evolution, which were applied to subsequent analyses: 16S (GTR+I+G), tRNAs (HKY+G), CO1 position 1 (SYM+I), CO1 position 2 (TVM+I), CO1 position 3 (TrN+G), ND4 position 1 (GTR+I+G), ND4 position 2 (TVM+G), ND4 position 3 (TIM+G), RAG-1 position 1 (HKY+I), RAG-1 position 2 (HKY+I), RAG-1 position 3 (SYM+G). Using these partitions, a maximum likelihood (ML) phylogenetic analysis was run using IQ-TREE v.2.1.2 (Nguyen et al. 2014). The primary analysis used all partitions, with branch support assessed using 1000 ultrafast bootstrap replicates (Hoang et al. 2018). Strongly supported nodes were defined as those with bootstrap support (BS) $\geq$ 95%, with moderately supported nodes from 70–90%. Single-gene trees were constructed separately from each alignment (16S, CO1, ND4 + tRNA, and RAG-1) and compared to one another and the concatenated phylogeny to confirm there was no significant discordance in phylogenetic tree topologies. The quality control analyses of each single gene retained the relevant partitions and models used in the primary analysis. We also used MEGA X to calculate uncorrected p-distances for ND4 to provide an estimate of sequence divergence among *Heliobolus* specimens. Pairwise comparisons were made between all pairs of individuals in the dataset.

Morphological methods

Specimens were measured with a digital caliper, and pholidosis was observed through a stereomicroscope. Scale nomenclature, scale counts, and measurements used in the descriptions follow Conradie et al. (2012). We recorded the following 27 characters: snout-vent length (**SVL**), from the snout to the vent; tail length (**TL**), from cloaca to tip of tail, measured only in specimens with complete original tails; head length (**HL**), from tip of snout to anterior tympanum border; head width (**HW**), from the lateral edge of the left parietal to the lateral edge of the right parietal, above the eyes; length of the forelimb (**LFL**), from the elbow to the wrist; length of the hindlimb (**LHL**), measured from knee to heel; inter-limb distance (**ILD**), corresponding to the distance between axillary and inguinal region; body length (**BL**), from the median collar plate to the cloaca; collar-snout distance (**CS**), from the median collar plate to the tip of the snout; number of nasal scales (**NS**); number of collar plates (**CPL**); number of gular scales (**GS**), in a straight line from the symphysis of the chin shields to the median collar plate; number of femoral pores (**FP**); number of midbody scale rows (**MSR**); ventral longitudinal rows (**LVSR**), counted from the axilla to the groin; ventral transverse rows (**TVSR**), counted midway between fore- and hind limbs; number of subdigital lamellae under the fourth toe (**LUFT**); number of supralabials anterior to the subocular (**SL**); number of infralabials (**IL**); number of supraciliaries (**SC**); number of supraoculares (**SO**); number of small granules in front of supraoculars touching frontal and prefrontal (**GrSO**); number of rows of granules between supraoculars and supraciliaries (**GrRows**); contact between parietals (**CPT**); contact between frontoparietals (**CFP**); contact between supranasals (**CSN**); contact between prefrontals (**CPF**).

Results

Phylogenetic relationships

The concatenated phylogeny (Fig. 1) recovers strongly supported relationships at basal nodes within sampled *Heliobolus*. Clades recovered with moderate to strong support in the single gene analyses matched those observed in the concatenated dataset, indicating no significant discordance in the data. *Heliobolus* cf. *lugubris* samples (hereafter referred to as the "*H. lugubris* complex") comprise a strongly supported (BS=99%) monophyletic group sister to *H. spekii* (BS=100%), the only other *Heliobolus* species in the dataset. The *H. lugubris* complex itself includes three strongly supported monophyletic and geographically discrete clades (BS=100% for each clade).

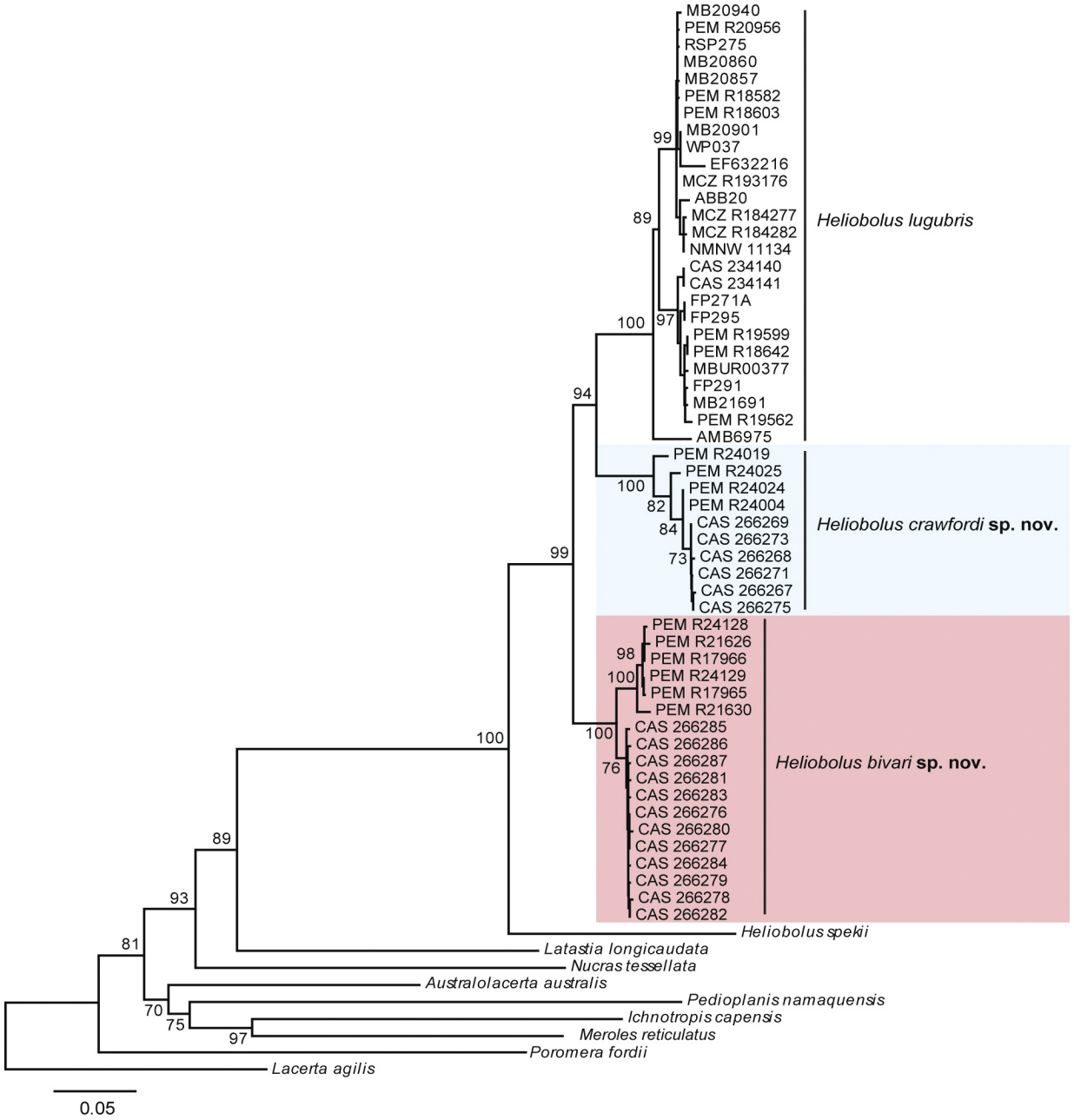

Figure 1. Maximum likelihood phylogeny of the *Heliobolus lugubris* complex based on a concatenated dataset of 16S, CO1, ND4, and RAG-1 sequences. The tree is rooted with exemplar African and Eurasian lacertid taxa. Bootstrap support values are provided at key nodes.

One of these clades includes samples from widespread localities scattered across South Africa and Namibia. There is limited structure within this clade, with one subgroup consisting of a single specimen from Sesfontein in northwestern Namibia, one subgroup consisting of specimens from across Namibia and South Africa (BS=99%), and one subgroup containing individuals from northeastern South Africa (BS=97%). As the type locality of *H. lugubris* is within the central core of the distribution of this clade, we consider it representative of true *H. lugubris*.

The two other clades in the *H. lugubris* complex are endemic to Angola but have allopatric ranges, with one occurring in far southwestern Angola and the other farther north. These two Angolan clades have previously been identified as *H. lugubris* (Branch and Tolley 2017; Marques et al. 2018; Branch et al. 2019a). The northern Angolan clade is recovered as sister to true *H. lugubris* (BS=94%), with the southern Angola clade in turn sister to this grouping. Although there are records from inland areas of southern Angola (Huíla, Cunene, and Cuando Cubango provinces) (Marques et al. 2018), there was no genetic material available from these populations for inclusion in the phylogenetic analysis. Based on the identity of geographically adjacent populations for which we do have genetic data, it is likely that the specimens from Huíla and Cunene provinces represent the southwestern Angolan lineage while the specimen from Cuando Cubango represents true *H. lugubris* [after the acceptance of this manuscript, the Cuando Cubango specimen was ge-

Figure 2. Comparison of the juvenile dorsal pattern between individuals of *Heliobolus bivari* **sp. nov.**, *H. crawfordi* **sp. nov.** and *H. lugubris*. Photos by Werner Conradie and Luis M.P. Ceríaco.

netically confirmed to belong to true *H. lugubris*; W. Conradie, unpubl. data].

The three clades within the *H. lugubris* complex show high sequence divergence between them with uncorrected p-distances for ND4 ranging from 10.2–14.0% when comparing individuals between clades. In contrast, intra-clade values are from 0–4.6%. The inter-clade sequence divergences are comparable to species level divergence values observed between species of African Lacertidae from other genera (Mayer and Pavlicev 2007; Conradie et al. 2012; Edwards et al. 2013; Branch et al. 2019b; Parrinha et al. 2021). As our results suggest that the three major clades in the *H. lugubris* complex form separate genetically distinct and geographically discrete evolutionary lineages, and that each clade possesses diagnostic morphological features as described below, we recognize them herein as distinct species.

Morphology

Mensural and meristic data for the studied species are presented in Table 3. The two new *Heliobolus* species occurring in Angola differ from each other and from *Heliobolus lugubris* from southern Africa most noticeably in coloration patterns, but present very conservative external morphological characters.

One characteristic that can easily differentiate the two new Angolan species and the nominotypical *H. lugubris* is the coloration pattern of juveniles (Fig. 2). In *H. lugubris* the pale vertebral stripe is usually discontinuous (in slightly older specimens it becomes continuous but bears clear evidence that it was originally discontinuous when younger), while in the two new taxa this stripe is always continuous. This coloration pattern is, however, common to both new Angolan species and therefore is not diagnostic between them.

Detailed diagnoses for each species are provided in the taxonomic accounts section.

Systematics

Heliobolus bivari sp. nov.

http://zoobank.org/90F36FAB-4824-43C0-8005-F948D8F68-AD3

Figs 2–7; Tables 3–4

Eremias lugubris [part]: Bocage 1895: 31; Boulenger 1921: 243.
Heliobolus lugubris [part]: Branch 1998: 161; Ceríaco et al. 2016: 56; Marques et al. 2018: 213; Branch et al. 2019a: 317.

Comment. The first records attributable to *Heliobolus bivari* **sp. nov.** are those provided by Bocage (1895) from Capangombe and Maconjo, followed by those of Boulenger (1921) from "Konondoto, Mossamedes". After decades without published records, Ceríaco et al. (2016) and Branch and Tolley (2017) provided additional localities for the species in the Namibe Province. All these records were originally identified as *H. lugubris*. Branch and Tolley (2017) presented the first evidence that the Angolan populations of *Heliobolus*, namely those in Namibe, western Huíla and Benguela provinces, corresponded to two putative new taxa: *Heliobolus* sp. 1 and *Heliobolus* sp. 2, the first of which is referable to *Heliobolus bivari* **sp. nov.**

Table 3. Morphometric and meristic comparisons between *Heliobolus bivari* **sp. nov.**, *Heliobolus crawfordi* **sp. nov.** and *Heliobolus lugubris*. Data presented as "mean [minimum–maximum]", measurements are presented in millimeters (mm). Abbreviations are those described in the Materials and Methods section.

	***H. bivari* sp. nov. (*n*=22)**	***H. crawfordi* sp. nov. (*n*=18)**	***H. lugubris* (*n*=17)**
SVL	54.8 [47.6–62.2]	52.2 [48.2–57.9]	52.3 [45.5–56.9]
TL	125.7 [100.7–162]	121.9 [6–19]	122.2 [106–139]
TL/SVL	2.3 [1.6–2.8]	2.3 [1.7–2.8]	2.3 [2–3]
ILL	27.7 [21.3–32.7]	26 [20.1–32.9]	25.9 [21.8–28.4]
BL	37.6 [31.1–42.9]	36.1 [23.8–42.3]	33 [22.9–36.8]
CSL	19.1 [16.3–22.7]	17.8 [15.7–20.3]	19.1 [16.6–21]
HL	12.8 [10.5–14]	11.8 [10–13.5]	12.7 [10.9–14]
HW	8.6 [7.4–11.9]	7.8 [6–19]	7.7 [4.5–9.2]
LFL	6.6 [5–8.9]	6.1 [5–7.4]	7 [6.3–7.9]
LHL	12.1 [9.8–14.1]	11.8 [10–13.2]	12 [10.7–13.2]
SL	5.5 [4–9]	4.7 [4–8]	5 [4–6]
IL	6.4 [5–7]	6.2 [5–7]	6 [5–8]
NS	3 [3–3]	3 [3–3]	3.7 [3–4]
SC	4.8 [3–7]	4.8 [4–6]	5.7 [5–7]
GrSO	8 [7–10]	15.1 [7–28]	8.3 [5–14]
GrRows	1.3 [1–3]	1.9 [1–3]	1 [1–1]
LVSR	6 [6–6]	6.1 [6–7]	6 [6–6]
TVSR	27 [25–30]	25.4 [24–27]	26.1 [23–28]
MSR	71.5 [64–82]	78 [70–90]	75.3 [64–85]
CP	6.7 [6–8]	7.1 [6–14]	8.5 [6–11]
GS	24.3 [19–29]	21.8 [18–27]	23.1 [19–27]
FP	15.3 [13–19]	13.3 [11–17]	14.3 [12–17]
LUFT	26.6 [21–34]	22 [16–26]	25.3 [23–28]
CPT	Usually in contact (n=16), or in a single point (n=6); rarely without contact (n=3)	Usually without contact (n=15); rarely in contact (n=3)	Usually in contact (n=12); occasionally without contact (n=5)
CFP	Always in contact (n=25)	Always in contact (n=18)	Always in contact (n=17)
CSPN	Always in contact (n=25)	Always in contact (n=18)	Always in contact (n=17)
CPF	Always in contact (n=25)	Always in contact (n=18)	Always in contact (n=17)

Diagnosis (adults). A medium-sized lizard, identified to genus by the following combination of characters: well-developed limbs, slender body, elongated snout, long tail, and a distinct collar on ventral region (FitzSimons 1943; Branch 1998). *Heliobolus bivari* **sp. nov.** can be distinguished from other members of its genus by the following combination of characteristics: (1) stout medium-size body (mean SVL 54.6 mm); (2) long-tailed (mean 123.7 mm), tail more than twice the body length; (3) midbody scale rows 64–82 (mean: 71.5); (4) higher number of subdigital lamellae under the fourth toe (mean: 26.6); (5) parietals usually in contact, rarely separated; (6) cranial shields not ornamented and temporal shield smooth; (7) lateral dark marking through the ear to the posterior margin of the eye faded or totally absent; (8) absence of bright yellow dots ventrolaterally.

Comparison with other *Heliobolus* species. *Heliobolus bivari* **sp. nov.** is distinguished from *H. neumanni* by possessing a higher number of midbody scale rows (64–82 *vs*. 40–42). It is distinguished from *H. nitidus* by possessing a higher number of midbody scale rows (64–82 *vs.* 52–64) and by color pattern (background light-brown to orange-brown above *vs.* background greenish, especially on the flanks). *Heliobolus bivari* **sp. nov.** is distinguished from *H. spekii* by having the cranial shields not ornamented and temporal shield smooth (*vs*. cranial shields ornamented and temporal shield keeled). The morphological differences between *H. bivari* **sp. nov.** and *H. lugubris* are more subtle, possibly corresponding to the close phylogenetic relationship between the two species. Molecular phylogenetics and the interpreted distribution (*H. bivari* **sp. nov.** in southwestern Angola *vs. H. lugubris* in eastern Angola, Namibia, Botswana, Zimbabwe, South Africa, and Mozambique) are the best proxies for identification. However, *H. bivari* **sp. nov.** can be distinguished from *H. lugubris* by the presence of 1–3 rows of granules between the supraoculars and supraciliaries (*vs*. only one row), on average a lower number of collar plates (6.7 [6–8] *vs.* 8.5 [6–11]), and, on average, a higher number of subdigital lamellae under the fourth toe (26.6 [21–34] *vs.* 25.3 [23–28]).

Holotype. An adult female (CAS 266287, field number AMB 10633; Fig. 3), collected in Virulundo [–16.2852°, 12.9419°, 718 m a.s.l.], Namibe Province, Angola, by Luis M.P. Ceríaco, Suzana A. Bandeira, and Ishan Agarwal on 2 December 2016.

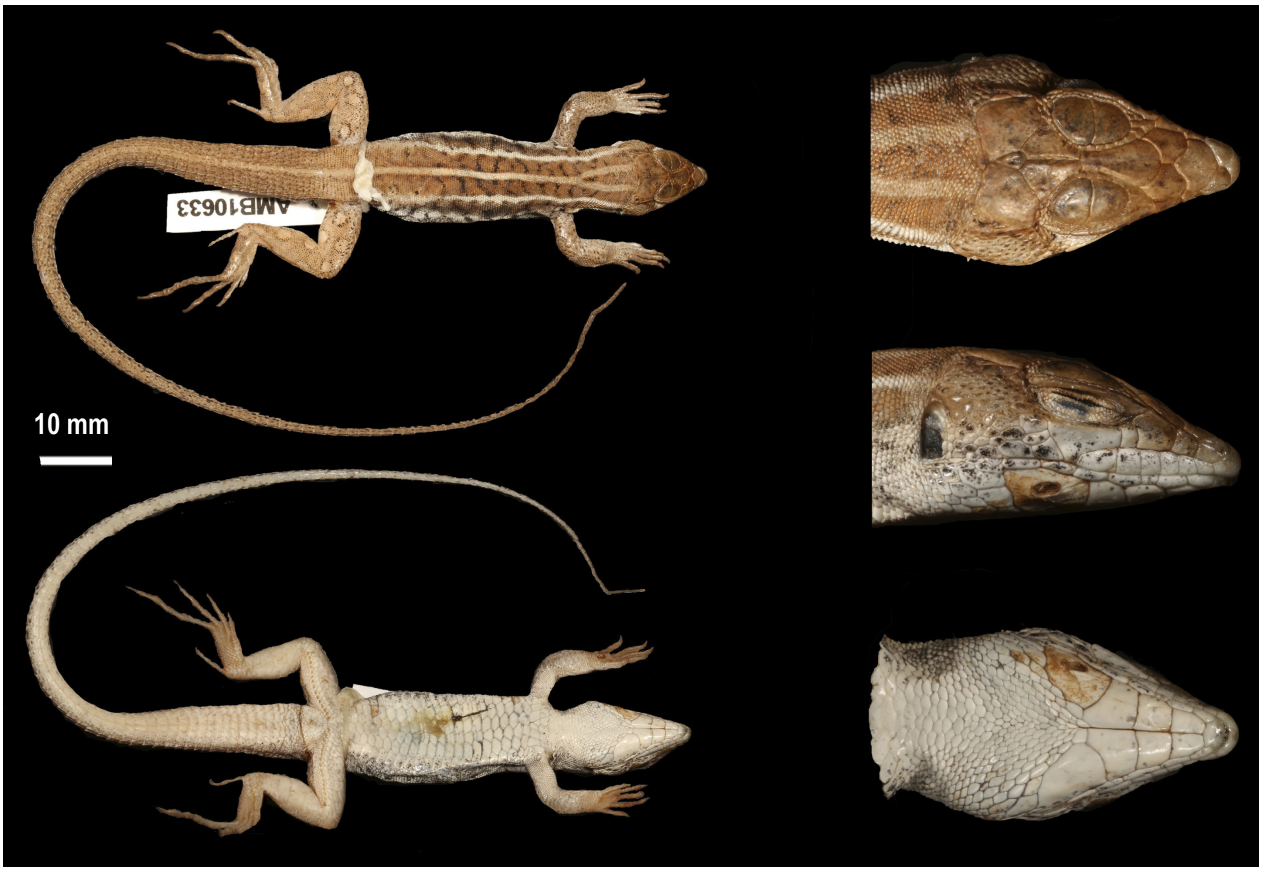

Figure 3. Dorsal and ventral whole-body views (left) and dorsal, lateral, and ventral views of the head (right) of the holotype of *Heliobolus bivari* **sp. nov.** (CAS 266287). Photo by Luis M.P. Ceríaco.

Paratypes. All specimens from Angola. 16 specimens. Huíla Province: An adult female (PEM R17965, field number MBUR 02130), collected at an outcrop by the side of the road at the bottom of the escarpment between Humpata and the limits of Namibe Province [–15.0447°, 13.1594°, 642 m a.s.l.], by William R. Branch, Werner Conradie, John Measey and Krystal A. Tolley on 16 January 2009. Namibe Province: Ten adults, both females and males **(**CAS 266276–266285, field numbers AMB 10595–10604), collected at Virei-Chipumpo [–16.2793°, 12.9584°, 742 m a.s.l.], by Luis M.P. Ceríaco, Suzana A. Bandeira, and Ishan Agarwal, on 1 December 2016; an adult female (CAS 266286, field number AMB 10631), collected at the same locality as the holotype, by same collectors and date; an adult female (PEM R17966, field number MBUR 02299), collected on road from Lake Arco to Espinheira rocky valley [–15.9136°, 12.3952°, 319 m a.s.l.], by William R. Branch, Werner Conradie, John Measey and Krystal A. Tolley, on 23 January 2009; an adult male (PEM R21626, field number ANG 0296), collected 50 km E of Namibe [=Moçâmedes] on main road to Leba [–15.0156°, 12.5550°, 516 m a.s.l.], by William R. Branch, Johan Marais, James Titus-McQuillan, Ninda Baptista, and Pedro Vaz Pinto, on 8 December 2012; an adult male (PEM R21630, field number ANG 0287), collected 7.8 km from the bottom of Leba Pass [–15.0447°, 13.1595°, 642 m a.s.l.], by William R. Branch, Johan Marais, James Titus-McQuillan, Ninda Baptista, and Pedro Vaz Pinto on 8 December 2012; an adult female (PEM R24128, field number AG 142) and an adult male (PEM R24129, field number AG 143), collected 1 km SE of Farm Mucongo [–14.7867°, 12.4961°, 303 m a.s.l.], by William R. Branch, Pedro Vaz Pinto and Ninda Baptista, on 7 November 2015.

Additional material. Huíla Province: Gambos Foster's farm [–15.8500°, 14.6833°, 1189 m a.s.l.] (PEM R22039); Capelongo [–14.4667°, 16.3000°, 1453 m a.s.l.] (AMNH R47034–47036); Mulondo [–15.6500°, 15.2000°, 1156 m a.s.l.] (MNHG 1545.018). Namibe Province: Namibe-Lubango road, 2 km E of Mangueiras, south side of the road [–15.0436°, 13.1600°, 622 m a.s.l.] (CAS 254885); on main road to Leba [–15.0156°, 12.5550°, 516 m a.s.l.] (PEM R21626–21627); 7.8 km from bottom of Leba Pass [–15.0447°, 13.1595°, 642 m a.s.l.] (PEM R21628, 21629, 21631); Konondoto, Mossamedes [=Moçâmedes] [undetermined] (BMNH 1907.6.29.27–31); Caraculo [–15.0167°, 12.6667°, 463 m a.s.l.] (TM 40252–40253); Maconjo [–15.01667°, 13.2°, 865 m a.s.l.] (ZMB 7774). Cunene Province: Ponang Kuma (currently Donguena) [–17.0167°, 14.7167°, 1109 m a.s.l.] (BMNH 1907.6.29.19–26); Mupanda [–17.1333°, 15.7667°, 1114 m a.s.l.] (MHNC 91.0518, MNHG 858.098, NMBA 13357–13358); Calueque [–17.2583°, 14.5750°, 1453 m a.s.l.] (PEM R22038).

Historical localities (no extant specimens). Namibe Province: Maconjo [–15.0167°, 13.2000°, 865 m a.s.l.] (Bocage 1895); Capangombe [–15.1000°, 13.1500°, 553 m a.s.l.] (Bocage 1895). Unknown Locality: Kuangu (BMNH 1905.5.29.15–16).

Table 4. Mensural (in mm) and meristic counts of the holotype and paratypes of *Heliobolus bivari* **sp. nov.** Abbreviations are the same as those described in the Materials and Methods section.

	CAS 266287	**CAS 266276**	**CAS 266277**	**CAS 266278**	**CAS 266279**	**CAS 266280**	**CAS 266281**	**CAS 266282**	**CAS 266283**	**CAS 266284**	**CAS 266285**	**CAS 266286**	**PEM R 17965**	**PEM R 17966**	**PEM R 24128**	**PEM R 24129**	**PEM R 21630**
	Holotype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype
Sex	♀	♂	♀	♀	♀	♀	♀	♀	♂	♀	♂	♀	♀	♂	♀	♀	♂
SVL	57.9	56.1	55.7	52.6	57.1	54	57.4	50.6	47.8	47.7	47.6	53.9	53.6	62.2	58.7	56.0	51.2
TL	162	133	129	141	111	121.0	126	126	108	121	111	133	115.7	100.7	—	147.1	—
TL/SVL	2.8	2.4	2.3	2.7	1.9	2.2	2.2	2.5	2.3	2.5	2.3	2.5	2.2	1.6	—	2.6	—
HL	13.5	13.3	13.5	11.8	13.0	11.0	13.2	11.0	10.5	14.0	11.0	13.7	12.1	14.0	12.7	13.9	13.6
HL/SVL	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.3	0.2	0.3	0.2	0.2	0.2	0.2	0.3
SVL/HL	4.2	4.2	4.1	4.5	4.4	4.9	4.3	4.6	4.5	3.4	4.3	3.9	4.4	4.4	4.6	4.0	3.7
HW	11.9	8.4	9.4	9.7	9.3	8.5	8.9	8.5	7.6	9.4	9.4	8.6	7.5	8.5	7.4	8.0	7.6
ILL	30.6	28.9	30.8	24.6	30.0	23.4	26.9	26.1	30.6	21.3	23.6	25.8	25.5	31.2	32.1	27.8	26.5
BL	42.9	41.0	42.5	38.2	40.0	34.8	39.0	36.3	42.9	31.1	32.5	34.9	35.9	42.9	40.1	35.0	32.5
CSL	22.7	18.0	19.0	21.8	18.2	17.1	18.2	19.5	22.7	18.5	21.8	19.2	17.2	20.2	17.6	20.3	18.4
LFL	6.5	6.8	5.6	8.9	7.2	6.5	7.3	7.5	7.0	7.1	5.0	6.7	5.7	6.5	6.2	6.4	6.0
LHL	9.8	11.2	13.3	13.4	13.1	11.0	10.2	11.4	11.1	11.4	10.0	13.3	11.8	12.8	12.2	12.7	12.9
SL	6 | 6	5 | 5	5 | 5	5 | 5	5 | 4	5 | 4	5 | 4	5 | 9	6 | 7	4 | 5	6 | 5	5 | 7	5 | 5	5 | 5	7 | 5	5 | 5	5 | 4
IL	7 | 7	7 | 7	6 | 7	6 | 7	7 | 6	7 | 6	6 | 6	7 | 7	6 | 7	6 | 6	7 | 7	6 | 7	6 | 6	6 | 6	7 | 7	6 | 6	6 | 6
SC	4 | 5	4	6 | 5	4	4	4 | 4	4 | 5	5 | 5	5 | 5	4 | 5	6 | 5	4 | 5	5 | 5	6 | 6	5 | 5	5 | 5	6 | 5
GrSO	8 | 8	7 | 7	7 | 6	7 | 8	9 | 8	8 | 8	8 | 8	8 | 8	7 | 6	10 | 9	7 | 7	8 | 7	10 | 10	8 | 7	7 | 8	5 | 6	10 | 9
GrRows	1	1	1–2	1	1	1	1	1	1	1	1	1	1	1–2	1–2	1–2	1
MSR	66	64	72	70	82	79	69	—	64	78	72	70	73	87	78	79	81
LVRS	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6
TVRS	25	28	27	25	30	26	28	27	27	26	27	28	25	27	25	24	25
CP	7	8	8	6	7	6	7	8	6	6	10	7	6	7	6	5	7
GS	24	19	23	23	25	23	26	29	20	27	27	26	25	26	28	23	23
FP	15 | 16	14 | 14	13 | 14	14 | 12	13 | 13	13 | 15	16 | 16	16 | 16	19 | 19	15 | 15	14 | 18	13 | 14	16 | 13	17 | 16	14 | 16	17 | 17	18 | 17
LUFT	24	27	—	—	27	27	27	—	—	33	34	26	27	23	27	27	25

Unassigned records (records that could represent *H. bivari* sp. nov.). Angola [undetermined] (MHNC 91.0515–17, 91.0519–23) – presumably a part of Mulondo specimens (Monard 1937).

Description of the Holotype. Individual in good condition. Adult female with a complete original tail (Fig. 3). Body cylindrical (SVL 57.9 mm, TL 162 mm, HL 13.5 mm), relatively stout (SVL/HL 4.3) with robust limbs. Well-defined neck and moderately sized head (HL/SVL 0.23); tail length greater than two and a half times the SVL length (TL/SVL 2.8). Additional measurements are presented in Table 5. Rostral wider than long, visible from above. Nostril pierced between three scales; supranasals in broad contact with each other behind rostral; infranasal in contact with rostral, anterior-most supralabial and anterior loreal; postnasal medium and subquadrangular, placed between the supranasal, infranasal, loreal and frontonasal. Upper head shields flat and smooth. Frontonasal hexagonal, wider than long. Prefrontals in broad contact with each other, the loreals, frontonasal and frontal. Frontal longer than wide, narrower posteriorly, in broad contact with prefrontals anteriorly and frontoparietals posteriorly; separated from supraoculars laterally by a single row of small scales. Paired frontoparietals in broad median contact, touching frontal anteriorly and the parietals and interparietal posteriorly; separated from the posterior supraocular by a single row of small granular scales. Interparietal longer than wide, arrow-shaped. Occipital round. Parietals almost as long as wide, in contact with frontoparietals and interparietal. Two rounded supraoculars in contact with each other, bordered by a group of 13 (right side) and 12 (left side) small granules which are in contact with the prefrontal, frontal, frontoparietals and parietal. One row of small granules between anterior supraocular and supraciliaries, increasing to two rows posterior to supraocular suture. Supraciliaries five, the first longest. Temporal scales irregular, small and granular. One elongated, narrow tympanic shield present on the anterior-dorsal edge of the ear opening. Subocular bordering lip, upper margin much wider than lower. Six supralabials anterior to subocular and two posterior to subocular. Infralabials seven. Lower eyelid scaly with an elongated median transparent patch that is dark-edged. Mental wider than long, in contact with first pair of chin shields and infralabials. Four pairs of chin shields, anterior three pairs in broad medial contact, fourth largest. Gular scales 24 in a straight line between symphysis of the chin shields and median collar plate. Collar free, comprising seven enlarged plates. Ventral scales smooth, in six longitudinal and 25 transverse rows. Precloacal scales homogenous and subequal, with two scales in the center. Femoral pores 15 on right leg and 16 on left leg. Lamellae under fourth toe 24. Dorsal scales small and granular. Upper forelimb and anterior hindlimb covered above by large hexagonal plates; forearm covered above by slightly imbricate and keeled scales, larger than dorsal scales, and below by enlarged plates. Hindlimbs covered above by slightly imbricate and keeled scales, larger than dorsal scales, and below by enlarged plates. Scales on tail diagonally keeled, except for those on ventral side, which are smooth.

Coloration in life. Background coloration was light brown to orange-brown, with three visible and continuous light-yellow to beige dorsal stripes, and a series of transverse dark brown markings between these stripes. Dorsolateral dark brown markings from each side of the flanks through the ear to the posterior margin of the eye faded, more visible between limbs. An interrupted whitish band is visible ventrolaterally. Yellow vertebral stripe dividing on the neck (in a Y-shape) that continues anteriorly to the posterior borders of the parietals and extends posteriorly to the base of the tail, continuous, fading on the proximal portion of the tail. Head uniformly light brown to orange-brown with white labials, with darker speckles on the supralabials which become more pronounced posteriorly. The limbs are also light brown to orange-brown, speckled with a series of yellow to white dots on their dorsal surfaces, these being most noticeable on the hindlimbs. Venter homogeneous dirty white, except the palms and soles, which are orangish; darker speckling is present laterally on the outer row of ventral scales.

Coloration in ethanol. Background color in preserved specimens is light brown to orange-brown on dorsum of head, trunk, legs and tail (Fig. 3). The dorsum presents the same pattern of coloration as in live specimens, with three continuous pale cream stripes between transverse dark markings, with the median pale stripe bifurcating (Y-shape) on the neck and extending posteriorly as a single stripe to the base of the tail. A continuous light to dark brown band extends from the flanks through the ear to the posterior margin of the eye, being most noticeable just in front of the hindlimbs. An interrupted cream band is present on the flanks between the limbs. Cream spots on limbs. Venter cream to dirty white with darker speckling present on the outermost row of ventral scales.

Variation. Variation in scalation and body measurements of the type series is reported in Table 5. The paratypes agree almost entirely with the holotype description, although in six of the paratypes (CAS 266281–266286) the subocular does not reach the lip and, therefore, does not separate the anterior and posterior supralabials. Labial markings are more faded on paratypes. Background colouration varies from orange-brown to light brown, with pale median and dorsolateral stripes. In some specimens, the pale vertebral stripe is bordered laterally by a dark brown longitudinal stripe. Some specimens have a faint to distinct darker brown dorsolateral patch, which extends from the flanks through the ear to the posterior margin of the eye. The yellow vertebral stripe divides on the neck (in a Y-shape) that continues anteriorly to the posterior borders of the parietals and extends posteriorly to the base of the tail, either continuously or interrupted (Fig. 4). Juveniles black above and below, with a continuous yellow vertebral stripe and two broken white-yellow dorsolateral stripes above the arms; tail yellow-orange; symmetrically arranged yellow to orange spots and mark-

Table 5. Mensural (in mm) and meristic counts of the holotype and paratypes of *Heliobolus crawfordi* **sp. nov.** Abbreviations are the same as those described in the Materials and Methods section.

	CAS 266269	**CAS 266267**	**CAS 266268**	**CAS 266271**	**CAS 266273**	**CAS 266275**	**AMNH-R 41567**	**AMNH-R 41570**	**AMNH-R 41587**	**PEM R 21625**	**PEM R 22058**	**PEM R 22059**	**PEM R 24004**	**PEM R 24019**	**PEM R 24024**	**PEM R 24025**	**PEM R 24168**
	Holotype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype
Sex	♂	♀	♀	♀	♂	♀	♀	♀	♀	♀	♀	♀	♀	♂	♂	♂	♂
SVL	51.7	50.9	51.1	49.5	53.3	53.0	53.3	53.1	48.2	53.4	53.9	51.1	57.9	49.5	53.2	49.2	52.8
TL	123	128	127	105	144	152	110.2	92.2	116	—	—	—	—	—	—	—	—
TL/SVL	2.3	2.5	2.5	2.1	2.7	2.8	2.1	1.7	2.4	—	—	—	—	—	—	—	—
HL	13.5	11	12	12.2	11.6	10.7	10	11.2	11.3	12.2	11.5	11.5	13.4	12.2	12.4	11.4	12.4
HL/SVL	0.3	0.2	0.2	0.2	0.2	0.2	0.1	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.3	0.2
SVL/HL	3.8	4.6	4.2	4.1	4.6	4.9	5.3	4.7	4.2	4.3	4.7	4.4	4.3	4.1	4.3	4.3	4.3
HW	9.5	7.4	8.7	7.8	9.6	9.1	6.5	6.5	6.0	7.3	7.4	7.1	8.1	8.1	8.1	7.6	7.4
ILL	24.9	29.8	28.7	32.9	23.2	24.7	25.5	23.2	20.1	27.6	30.3	25.5	30.0	22.3	28.2	25.0	29.5
BL	37.3	40.8	42.3	40.0	35.0	37.0	37.0	36.2	29.7	36.1	36.7	36.6	40.9	23.8	35.1	33.3	34.9
CSL	15.7	16.4	18.4	18.4	17.6	20.2	18.3	20.3	18.1	18	17.9	16.0	15.8	17.0	19.0	16.7	17.7
LFL	5.8	6.6	6.0	6.6	5.1	7.4	5.1	5.0	5.1	6.8	6.2	6.3	6.2	6.5	6.5	5.9	6.0
LHL	11.6	12.3	10.0	12.2	13.1	11.6	12	11.0	10.0	12.4	12.2	11.9	12.3	11.5	12.2	11.8	11.7
SL	4 | 4	4 | 5	4 | 5	5 | 4	4 | 5	5 | 5	4 | 4	5 | 5	4 | 4	4 | 4	5 | 5	5 | 5	5 | 5	5 | 5	5 | 5	8 | 5	5 | 5
IL	7 | 7	6 | 7	6 | 5	7 | 6	6 | 6	6 | 6	5 | 5	7 | 7	5 | 5	6 | 6	6 | 6	6 | 6	7 | 6	7 | 7	7 | 6	6 | 6	5 | 5
SC	5 | 5	5	5 | 5	5 | 5	5 | 5	6 | 6	5 | 5	4 | 4	4 | 4	5 | 4	6 | 6	5 | 5	6 | 5	5 | 6	5 | 5	5 | 5	5 | 5
GrSO	8 | 8	9 | 9	8 | 8	9 | 8	8 | 9	9 | 9	8 | 8	7 | 7	9 | 10	8 | 9	23| 22	12 | 11	12 | 10	11 | 9	12 | 11	8 | 9	10 | 8
GrRows	1	1–2	1	1	1	1	1	1–2	1	1–2	2	2	1–2	1	1	1	1
MSR	70	77	80	90	70	75	76	88	72	69	84	77	77	74	78	67	80
LVRS	6	6	7	6	6	6	6	6	6	6	6	6	6	6	6	6	6
TVRS	24	25	24	26	25	24	27	27	27	24	25	25	27	24	25	24	24
CP	6	8	6	7	7	11	7	5	6	8	6	6	11	8	8	9	6
GS	19	19	18	23	20	21	21	20	20	19	25	25	21	22	26	22	27
FP	14 | 15	16 | 16	13 | 14	13 | 12	16 | 16	16 | 15	15| 17	17 | 17	14 | 14	14 | 14	16 | 18	15 | 17	14 | 14	16 | 17	14 | 14	17 | 16	17 | 17
LUFT	20	16	19	24	20	—	19	24	26	20	25	25	27	23	25	24	27

Figure 4. *Heliobolus bivari* **sp. nov**. in life (CAS 266276). In a sandy riverbed between Virei and Chipumpo, Namibe Province, Angola. Photo by Ishan Agarwal.

Figure 5. Juvenile *Heliobolus bivari* **sp. nov**. in life (specimen not collected) from Bibala [–15.0726°, 13.1128°, 501 m a.s.l.], Namibe Province, Angola. Photo by Rogério Ferreira.

ings on the top of the head and snout; labials present some white markings (Figs 2, 4, 5).

Distribution, habitat and natural history notes. *Heliobolus bivari* **sp. nov.** appears to be restricted to southwestern Angola, occurring in the southernmost parts of the region in the xeric/desertic lowlands (Fig. 6). The presences of records close to Namibia's border might indicate that the species is more widespread in similar habitats and could extend into neighboring Namibia, although this hypothesis requires confirmation. Individuals have been observed basking during daytime on sandy substrate, usually where there is sparse vegetation (e.g., shrubs) or on open sandy plains (Fig. 7). Little is known about the natural history of this species, but its ecological habits and behavior are expected to be similar to other *Heliobolus* species, therefore being oviparous and insectivorous. As commonly observed in juvenile *H. lugubris* individuals, we assume that juveniles of *H. bivari* **sp. nov.** mimic *Anthia* (Carabidae) ground beetles (Huey

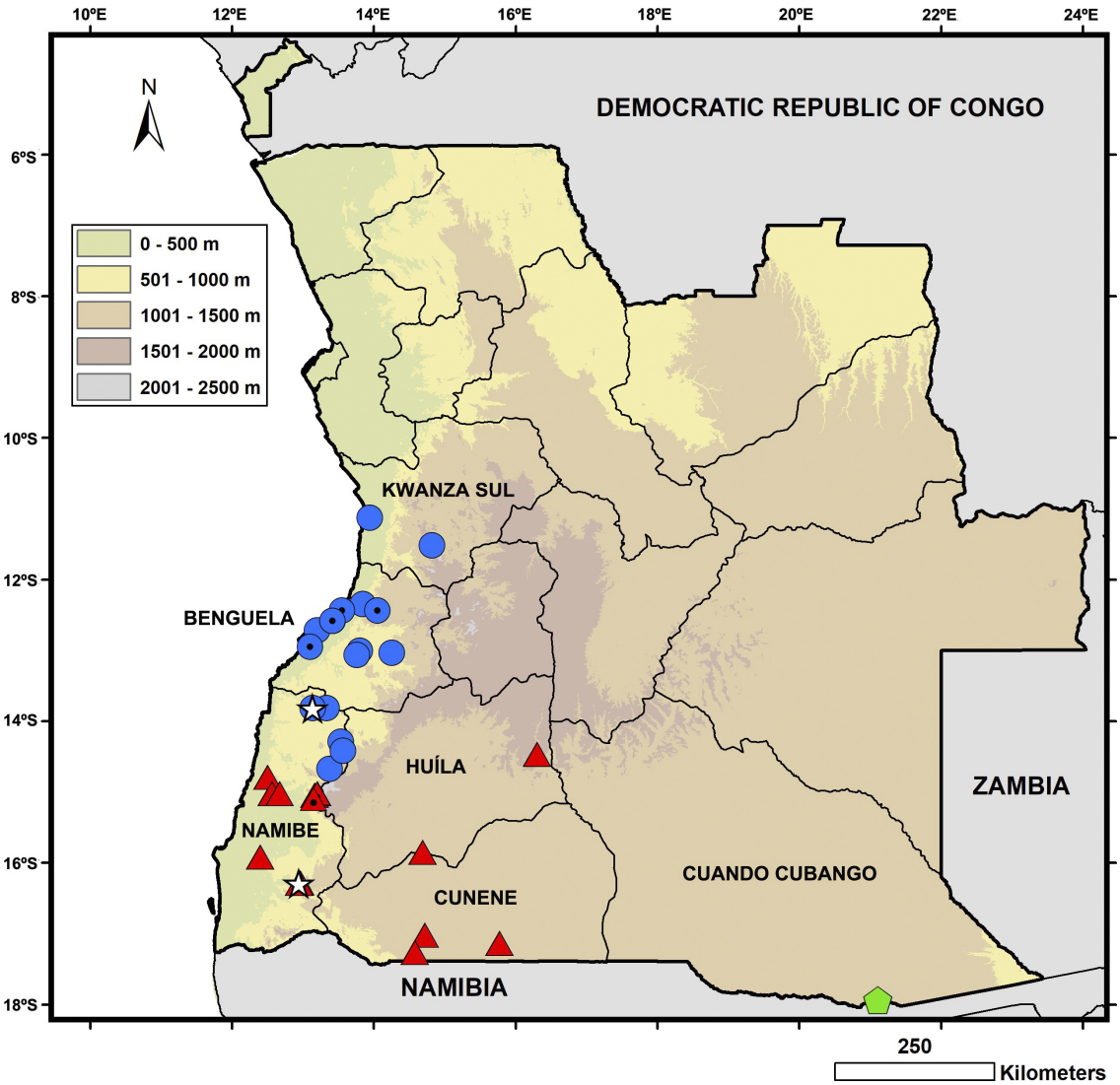

Figure 6. Distribution of *Heliobolus* species in Angola. Blue circles: *H. crawfordi* **sp. nov.**; dotted blue circles: historical records of *H. crawfordi* **sp. nov.**; red triangles: *H. bivari* **sp. nov.**; dotted red triangles: historical records of *H. bivari* **sp. nov.**; white stars: type localities for both species; green pentagon: *H. lugubris*. Colour palate represents elevation as depicted in the legend.

Figure 7. Typical habitat of *Heliobolus bivari* **sp. nov.** Virei, Namibe Province, Angola. Photo by Ishan Agarwal.

Figure 8. Dorsal and ventral whole-body views (left) and dorsal, lateral and ventral views of the head (right) of the holotype of *Heliobolus crawfordi* **sp. nov.** (CAS 266269). Photos by Aaron M. Bauer.

and Pianka 1977; Schmidt 2004), both through their iconic white and yellow markings on a black body, and by adopting an "arched" position when walking, imitating the general shape of a beetle.

Etymology. The species is named after the Portuguese entomologist António Bivar de Sousa (Lisbon, 1946–), a researcher at the recently defunct Instituto de Investigação Científica Tropical (IICT), Lisbon, Portugal. António Bivar de Sousa has had an important role in entomological research in Angola, being one of the main authorities on the country's Lepidoptera. The specific epithet is a patronym in the masculine genitive singular. We propose the English common name of Bivar's bushveld lizard, and the Portuguese common name of lagartixa de Bivar.

Heliobolus crawfordi sp. nov.

http://zoobank.org/7897E091-B803-4849-AD5C-3E690E75-9F24

Figs 2, 6, 8–11; Table 3, 5

Eremias lugubris [part]: Bocage 1867: 221; 1895: 31; Boulenger 1921: 239; Monard 1937: 75; Mertens 1938: 437.

Lamperemias lugubris [part]: Szczerbak 1975: 33.

Heliobolus lugubris [part]: Branch 1998: 161; Marques et al. 2018: 213; Branch et al. 2019a: 317.

Comment. Historical records of *H. lugubris* from Benguela Province (Bocage 1867, 1895; Boulenger 1921; Monard 1937; Mertens 1938; Szczerbak 1975) are all referable to *H. crawfordi* **sp. nov.** Since then, new records have expanded its known distribution to the neighboring province of Kwanza Sul and south into northern Namibe Province.

Diagnosis (adults). A medium-sized lizard, identified to genus by the following combination of characters: well-developed limbs, slender body, elongated snout, long tail, and a distinct collar on ventral region of neck (FitzSimons 1943; Branch 1998). *Heliobolus crawfordi* **sp. nov.** can be distinguished from other members of its genus by the following combination of characteristics: (1) slender body of medium-size, mean SVL 52.2 mm; (2) long-tailed (mean 121.9 mm), tail more than twice body length; (3) midbody scale rows 70–90 (mean: 78); (4) low number of subdigital lamellae under the fourth toe (mean: 22); (5) parietals usually separated; (6) cranial shields not ornamented and temporal shield smooth; (7) lateral dark marking extending through the ear to the posterior margin of the eye; (8) presence of bright yellow dots ventrolaterally.

Comparison with other *Heliobolus* species. *Heliobolus crawfordi* **sp. nov.** is distinguished from *H. neumanni* by possessing a higher number of midbody scale rows (70–90 *vs.* 40–42). *Heliobolus crawfordi* **sp. nov.** is distinguished from *H. nitidus* by possessing a higher number

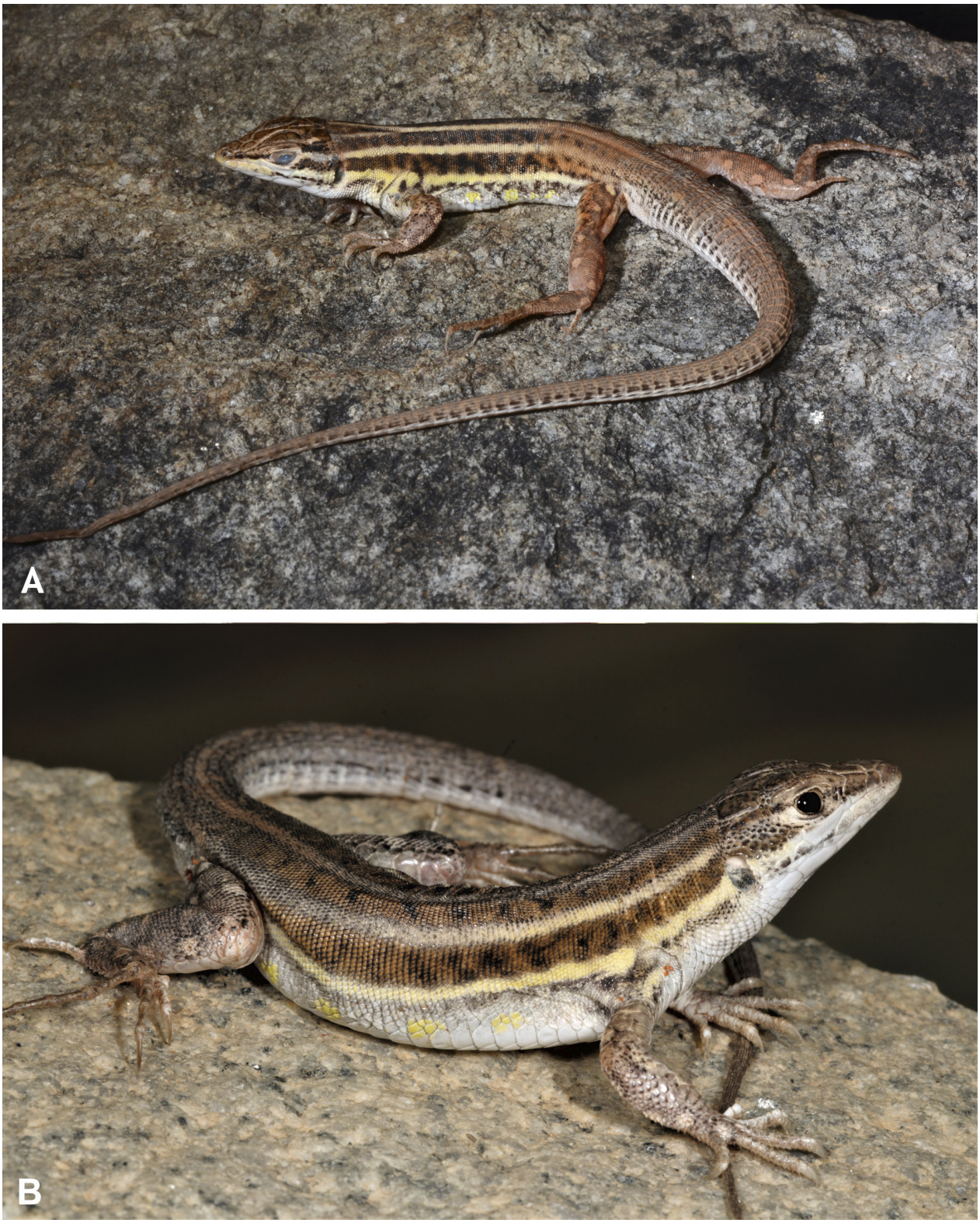

Figure 9. *Heliobolus crawfordi* **sp. nov**. in life. **A** Male holotype (CAS 266269); **B** Female (PEM R21625), from 7 km E of Catengue on road to Cubal [–12.9994°, 13.7986°, 814 m a.s.l.], Benguela Province, Angola. Photos by Luis M.P. Ceríaco (A) and William R. Branch (B).

of midbody scale rows (70–90 *vs.* 52–64) and by color pattern (background light brown to orange-brown above *versus* background greenish, especially on the flanks). *Heliobolus crawfordi* **sp. nov.** is distinguished from *H. spekii* by having the cranial shields not ornamented and temporal shield smooth (*versus* cranial shields ornamented and temporal shield keeled). The morphological differences between *H. crawfordi* **sp. nov.** and *H. lugubris* are much more subtle, indicative of the close phylogenetic relationship between the two species. Molecular data and distribution (*H. crawfordi* **sp. nov.** in western Angola *versus H. lugubris* in south-eastern Angola, Namibia, Bo-

Figure 10. Subadult *Heliobolus crawfordi* **sp. nov.** (CAS 266146) in life, from a sandy road to Quilengues, base of Serra da Neve [–13.8113°, 13.3322°, 587 m a.s.l.], Namibe Province, Angola. Photo by Luis M.P. Ceríaco.

tswana, Zimbabwe, South Africa, and Mozambique) are the best proxies for its identification, as is the presence of bright yellow spots ventrolaterally (absent in *H. lugubris*). *Heliobolus crawfordi* **sp. nov.** can potentially also be distinguished from *H. lugubris* by the presence of 1–3 rows of granules between the supraoculars and supraciliaries (versus only one row), by having a lower average number of collar plates (7.1 [6–14] *vs.* 8.5 [6–11]), a lower number of subdigital lamellae under the fourth toe (22 [16–26] *vs.* 25.3 [23–28]) and having the parietal scales usually separated (*versus* usually in contact). Juveniles of *H. crawfordi* **sp. nov.** can be distinguished from *H. lugubris* by the presence of a continuous white-yellow vertebral stripe (*vs.* a discontinuous vertebral stripe). *Heliobolus crawfordi* **sp. nov.** can be distinguished from *H. bivari* **sp. nov.** by having, on average, a lower number of subdigital lamellae under the fourth toe (22 [16–26] *vs.* 26.6 [21–34]), parietal scales usually separated (*vs.* usually in contact), a lateral dark marking through the ear to the posterior margin of the eye (*vs.* faded or totally absent), and presence of bright yellow spots ventrolaterally (*vs.* absent).

Holotype. An adult male (CAS 266269, field number AMB 10287; Fig. 8), collected in N'Dolondolo (–13.8133°, 13.1362°, 681 m a.s.l.), Namibe Province, Angola, by Luis Ceríaco, Suzana Bandeira, and Ishan Agarwal on 21 November 2016.

Paratypes. All specimens from Angola. 16 specimens. Kwanza Sul Province: An adult male (PEM R24168, field number AG 16.02), collected 2–3 km W of Sumbe-Gabela road [–11.1239°, 13.9406°, 160 m a.s.l.], by William R. Branch, Pedro Vaz Pinto and Ninda Baptista, on 30 October 2015. Benguela Province: Three adult females (AMNH-R 41567, 41570, 41587), collected at Hanha [–11.5167°, 14.8167°, 1397 m a.s.l.], by Herbert Lang and Rudyerd Boulton, on 14 May 1925; an adult female (PEM R21625, field number WC-1881), collected 7 km E of Catengue on road to Cubal [–12.9994°, 13.7986°, 814 m a.s.l.], by William R. Branch, Johan Marais, James Titus-McQuillan, Ninda Baptista, and Pedro Vaz Pinto, on 3 December 2012; two adult females (PEM R22058–22059, field numbers PVP 062–063), collected 30 km NE of Lobito [–12.3411°, 13.8408°, 274 m a.s.l.], by Pedro Vaz Pinto, on 23 October 2013. Namibe Province: Five adults (females and males) (CAS 266267–266268, 266271, 266273, 266275, field numbers AMB 10285–10286, 10289, 10333, 10348), collected at same locality by same collectors as the holotype, on 21 and 23 November 2016; an adult female (PEM R24004, field number AG 024), collected 10 km W of Lola, edge of Bentiaba River, road northwest to Camacuio [–14.2903°, 13.5306°, 802 m a.s.l.], by William R. Branch, Pedro Vaz Pinto and Ninda Baptista, on 2 November 2015; an adult male (PEM R24019, field number AG 011), collected on the road north of Bibala [–14.6708°, 13.3717°, 793 m a.s.l.], by William R. Branch, Pedro Vaz Pinto and Ninda Baptista, on 2 November 2012; two adult males (PEM R24024–24025, field numbers AG 016–017), collected on the road N of Bibala towards Lola [–14.4161°, 13.5647°, 920 m a.s.l.], by William R. Branch, Pedro Vaz Pinto and Ninda Baptista, on 2 November 2015.

Additional material. Benguela Province: Huxe [–12.7167°, 13.2000°, 65 m a.s.l.] (BMNH 1906.8.24.44–45); Benguela [–12.5833°, 13.4167°,

Figure 11. Type locality habitat of *Heliobolus crawfordi* **sp. nov.** on N'Dolondolo, base of Serra da Neve Inselberg, Namibe Province, Angola. Photo by Luis M.P. Ceríaco.

15 m a.s.l.] (MNCN 7946); Catengue [–13.0622°, 13.7561°, 586 m a.s.l.] (PEM R26335); Cubal [–13.0333°, 14.2500°, 921 m a.s.l.] (SMF 25388). Namibe Province: base of Serra da Neve, near Malowe village [–13.8113°, 13.3322°, 879 m a.s.l.] (CAS 266120–266121, 266146; INBAC/LMPC 1221; MHNC-UP/REP 869–871).

Historical localities (no extant specimens). Benguela Province: Benguela [–12.5833°, 13.4167°, 15 m a.s.l.] (Bocage 1867); Catumbela [–12.4333°, 13.5500°, 15 m a.s.l.] (Bocage 1895); Quissange [–12.4333°, 14.0500°, 870 m a.s.l.] (Bocage 1895); Dombe [–12.9500°, 13.1000°, 50 m a.s.l.] (Bocage 1895).

Description of the Holotype. Individual in good condition. Adult male with a complete original tail (Fig. 8). Body cylindrical (SVL 51.7 mm, TL 123 mm, HL 13.5 mm), and relatively elegant (SVL/HL 3.8), with a well-defined neck and moderately sized head (HL/SVL 0.26) and robust limbs; tail length almost two and a half times greater than SVL length (TL/SVL 2.4). Additional measurements are presented in Table 5. Rostral wider than long, visible from above. Nostril pierced between three scales; supranasals in broad contact with each other behind rostral; infranasal in contact with rostral, anterior-most supralabial and anterior loreal; postnasal medium-sized and subquadrangular, placed between the supranasal, infranasal, anterior loreal and frontonasal. Frontonasal hexagonal, wider than long. Prefrontals in broad contact with each other, the anterior loreals, frontonasal and frontal. Frontal longer than wide, narrower posteriorly, in broad contact with prefrontals anteriorly, and frontoparietals posteriorly. Paired frontoparietals in broad contact, touching frontal anteriorly and the parietals and interparietal posteriorly. Interparietal slightly longer than wide. Occipital round. Parietals in narrow contact behind the interparietal, as long as wide, in contact with frontoparietals and interparietal. Two rounded supraoculars in contact with each other, bordered by a group of 14 (right side) and 15 (left side) small granules, which separate the supraoculars from the prefrontal, frontal, frontoparietals and parietals. One row of small granules between anterior supraocular and supraciliaries, increasing to two rows posterior to supraocular suture. Supraciliaries five, the first longest. Temporal scales irregular, small and granular. One elongated tympanic shield present on the antero-dorsal margin of the ear opening. Subocular bordering lip, upper margin much wider than lower. Four supralabials anterior to subocular and two posterior to subocular. Infralabials seven. Lower eyelid scaly with a median transparent patch that is black-edged. Mental wider than long, in contact with first pair of chin shields and infralabials. Four pairs of chin shields, the first three in broad median contact, fourth pair largest. Gular scales 19 in a straight line between symphysis of the chin shields and median collar plate. Collar free, comprising six enlarged plates. Ventral scales smooth, in six longitudinal and 24 transverse rows. Precloacal scales homogeneous and subequal, with two scales in the center. Femoral pores 14 on right leg and 15 on left leg. Lamellae under fourth toe 20. Dorsal scales small and granular. Upper forelimb and anterior of hindlimb covered above by large hexagonal plates; forearm covered above by slightly imbricate and keeled scales, larger than dorsal scales, and below by enlarged plates. Hindlimbs covered above by slightly imbricate and keeled scales, larger than dorsal scales, and below by enlarged plates. Scales on tail diag-

onally keeled, except for those on ventral side, which are smooth or slightly keeled.

Coloration in life. Background coloration is brown to orange-brown with three continuous beige dorsal stripes, with a series of fairly broad transverse dark brown markings between stripes (Fig. 9). Dorsolateral dark brown markings continue through the ear to the posterior margin of the eye. Bright yellow spots present ventrolaterally. Vertebral stripe dividing on the neck (in a Y-shape), extending anteriorly to the posterior margins of the parietals, and extending posteriorly to the lower back, where it fades out. Lower back uniform light orange; tail orange-grey dorsally. A pale ventrolateral band arises on the posterior margin of the subocular, extending posteriorly through the ear to the hindlimb insertion; pale yellow anteriorly, becoming beige posteriorly. Head uniformly light brown. Supralabials yellow with some dark infusions; dark infusions becoming more prominent on subocular and posterior supralabials, forming a narrow dark brown stripe that continues posteriorly to the ear opening. Limbs light brown to orange-brown, speckled with large pale spots dorsally. The venter is homogeneous dirty white, except for the orangish palmar regions of the hands and feet.

Coloration in ethanol. Background color of preserved specimens brown to orange-brown above on dorsum of head, trunk, legs and tail (Fig. 8). The dorsum presents the same pattern of coloration as in live specimens, with three continuous pale cream stripes with short, dark lateral stripes in between, with the median pale stripe bifurcating (Y-shape) on the neck and extending posteriorly as a single stripe to the base of the tail. Dorsolateral dark brown marking continues anteriorly through the ear to the posterior margin of the eye. A beige stripe and yellow blotches are visible ventrolaterally. Cream spots on limbs. Venter cream to dirty white with no markings or speckling.

Variation. Variation in scalation and body measurements of the type series is reported in Table 6. The paratypes agree almost entirely with the holotype description. The presence of the ventrolateral yellow spots is variable from being obvious to faded in some individuals. Juveniles black above and below with a continuous yellow vertebral stripe on the dorsum and two broken stripes above the arms; tail sandy-orange; symmetrically arranged yellow to orange spots and markings on the top of the head and snout, labials present some white markings (Figs 2, 10).

Distribution, habitat and natural history notes. *Heliobolus crawfordi* **sp. nov.** seems to be restricted to the central coastal regions of Angola (Fig. 5). The species is distributed from central Namibe Province to southern Kwanza Sul Province and is widespread in Benguela Province. Similar to *Heliobolus bivari* **sp. nov.** this species is usually observed basking during daytime on the sandy ground, commonly in areas with sparse vegetation (e.g., shrubs) or on open sandy plains (Fig. 11). Little is known about the natural history of this species, but its ecological habits and behavior are expected to be similar to other *Heliobolus* species, being oviparous and insectivorous. As commonly observed in juvenile *H. lugubris* individuals, the juveniles of *H. crawfordi* **sp. nov.** also seem to imitate *Anthia* (Carabidae) ground beetles through their iconic white and yellow markings on a black body, their adopting an "arched" position when walking, and imitating the general shape of a beetle (MPM pers. obs.).

Etymology. The species is named after the Portuguese mammalogist João Crawford-Cabral (Funchal, 1929–2020), a researcher at the former Instituto de Investigação Científica de Angola (IICA), Sá da Bandeira [currently Lubango], Huíla Province, Angola, and the recently defunct Instituto de Investigação Científica Tropical (IICT), Lisbon, Portugal. João Crawford-Cabral played a pivotal role in the establishment and development of the zoological collections of IICA, currently housed at the Instituto Superior de Ciências de Educação (ISCED) in Lubango, Huíla Province, Angola, as well as in the publication of several important syntheses of biogeographic analyses on Angolan vertebrates. The specific epithet is a patronym in the masculine genitive singular. We propose the English common name of Crawford-Cabral's bushveld lizard, and the Portuguese common name of lagartixa de Crawford-Cabral.

Heliobolus lugubris (Smith, 1838)

Figs 5, 12–14

Lacerta lugubris (Smith 1838: 93)
Heliobolus lugubris [part]: Branch 1998: 161; Conradie et al. 2016: 24; Marques et al. 2018: 213.

Comment. This species was described by Smith (1838) based on specimens from "District immediately beyond the northern frontier of the Colony", probably referring to what is now the Northern Cape Province of South Africa. While the species has historically been recorded in Angola (see previous accounts), our current data indicates that the species has a much narrower distribution in the country than previously believed. The first confirmed records of the species in the country are those presented by Conradie et al. (2016) from Dirico region, Cuando Cubango Province, near the Namibian border, although it is possible that the species may occur in other areas in the southeastern part of the country.

Material examined. Cuando Cubango Province: East of Dirico Camp 7 [–17.9361°, 21.1027°, 1018 m a.s.l.] (PEM R21500).

Distribution, habitat and natural history notes. *Heliobolus lugubris* occurs from southeastern Angola, where it has been confirmed only from the extreme south-

Figure 12. Dorsal and ventral whole-body views (left) and dorsal, lateral and ventral views of the head (right) of *Heliobolus lugubris* (PEM R21500). Photos by Werner Conradie.

ernmost part of Cuando Cubango Province, eastwards to Mozambique, reaching as far south as parts of northern South Africa.

Discussion

Southwestern Angola represents a hotspot of diversity (Ceríaco et al. 2016; Marques et al. 2018; Lobón-Rovira et al. 2022) with a high number of new reptile species described from here in the last decade (Conradie et al. 2012; Stanley et al. 2016; Ceríaco et al. 2018, 2020; Branch et al. 2019a, 2019b, 2021; Marques et al. 2019, 2020; Parrinha et al. 2021). There are still, however, several areas in the southwest that remain largely undocumented in terms of biodiversity and that require further surveys and research focus. In the last few years, the Angolan lacertids have been the subject of attention, resulting in the description of four new species (Conradie et al. 2012; Branch et al. 2019b; Baptista et al. 2020; Parrinha et al. 2021). The description of *Heliobolus bivari* **sp. nov.** and *H. crawfordi* **sp. nov.** add to this regional lacertid diversity.

The taxonomy of the genus *Heliobolus* has been stable since the late 19th century. The addition of these two new Angolan species raises the currently known number of bushveld lizards to six, which highlights the importance of new data from field surveys and integrative taxonomic studies, especially for such a morphologically conservative group. *Heliobolus bivari* **sp. nov.** and *H. crawfordi* **sp. nov.**, despite morphological similarity, exhibit a set of subtle morphological characters that can distinguish them, and there is clear ND4 sequence divergence exceeding 10% which easily separates both lineages. It is interesting to note that one of the few consistent physical features differentiating the three Angolan *Heliobolus* species is their coloration patterns, not only of the adults but also of the juveniles. Although coloration in lacertids has traditionally been disregarded as a good diagnostic character for closely related taxa, especially due to the high prevalence of color polymorphism in the family Lacertidae (see Brock et al. 2022) and for the difficulty of objectively differentiating between subtle coloration differences, most recent descriptions of southern African lacertids (all backed by molecular phylogenies) have relied on coloration differences to diagnose the newly described species (Conradie et al. 2012; Branch et al. 2019b; Childers et al. 2021; Parrinha et al. 2021). This situation agrees with the results of Brock et al. (2022) that color polymorphism can be a driver of speciation. More interestingly in this case is the fact that we report here for the first time a clear and diagnostic difference in the coloration of the juvenile specimens. Juvenile *H. lugubris* are known to mimic noxious, acid-spraying carabid beetles of the genus *Anthia* in order to reduce predation (Huey and Pianka 1977) – the juveniles present a dark coloration pattern that strongly resembles the pattern of the beetles and even actively forage with arched backs, mimicking the movement of a beetle. We observed juveniles of *H. crawfordi* **sp. nov.** adopting the same movement "style" and given its close phylogenetic position, it is safe to assume that *H. bivari* **sp. nov,** juveniles also adopt this strategy. Therefore, the coloration differences of the juveniles of

Figure 13. *Heliobolus lugubris* in life. **A** Adult female (PEM R21783) from Alicedale Citrus Estate, Tshipise [–22.5716°, 30.1128°, 586 m a.s.l.], Limpopo Province, South Africa. Photo by William R. Branch. **B** Juvenile *Heliobolus lugubris* (specimen not collected) in life, from Rogella pan, Tswalu Kalahari Reserve [–27.3000°, 22.2296°, 1031 m a.s.l.], Northern Cape Province, South Africa. Photos by Werner Conradie.

H. bivari **sp. nov.** and *H. crawfordi* **sp. nov.** against those of *H. lugubris* may (or may not) represent adaptive mimicry of the local colour variation between populations of *Anthia* beetles. It would be interesting to assess whether the juvenile color patterns of the three *Heliobolus* species correspond to differences in coloration of sympatric taxa and/or populations of these beetles.

Given their interpreted distributions, it appears that the two new species may be allopatric, with *H. bivari* **sp. nov.** restricted to the xeric/desertic lowlands of the south-

Figure 14. Habitat of *Heliobolus lugubris*, west of Dirico, Cuando Cubango Province, Angola. Photo by Werner Conradie.

ernmost parts of Namibe Province, and *H. crawfordi* **sp. nov.** limited to the arid habitats of central coastal regions of the country, from Namibe to Benguela provinces and extending to the southern areas of Kwanza Sul Province.

The ecology, natural history and behavior of the newly described species are expected to be similar to other *Heliobolus* species, being diurnal, oviparous and insectivorous. Despite the lack of detailed information regarding the natural history and ecology for both species, the typical habitat for both species does not appear to be threatened at present, and both are considerably widespread. Following the IUCN Red List guidelines (IUCN Standards and Petitions Committee 2019), both *H. bivari* **sp. nov.** and *H. crawfordi* **sp. nov.** would most likely be considered Least Concern. Despite this, further studies are needed to better assess their distributions, population trends, and conservation status.

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