



# A new species of green-eyed *Cordylus* Laurenti, 1768 from the west-central highlands of Angola, and the rediscovery of *Cordylus angolensis* (Bocage, 1895) (Squamata: Cordylidae)

Michael F. Bates<sup>1,2</sup>, Javier Lobón-Rovira<sup>3,4,5</sup>, Edward L. Stanley<sup>6</sup>, William R. Branch<sup>7,†</sup>, Pedro Vaz Pinto<sup>3,5,8,9</sup>

1 Division of Herpetology, Department of Animal and Plant Systematics, National Museum, P.O. Box 266, Bloemfontein, 9300, South Africa

2 Department of Zoology & Entomology, University of the Free State, P.O. Box 339, Bloemfontein, 9300, South Africa

3 CIBIO/InBio Centro de Investigação em Biodiversidade e Recursos Genéticos, Universidade do Porto, Rua Padre Armando Quintas, Campus de Vairão, 4485-661 Vairão, Portugal

4 Departamento de Biologia, Faculdade de Ciências, Universidade do Porto, 4099-002 Porto, Portugal

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

6 Division of Digital Imaging, Florida Museum of Natural History, University of Florida, Gainesville, FL, 32611, USA

7 Port Elizabeth Museum (Bayworld), P.O. Box 13147, Humewood, Gqeberha, 6013, South Africa

8 TwinLab CIBIO/ISCED, Instituto Superior de Ciências da Educação da Huila, Rua Sarmento Rodrigues s/n, Lubango, Angola

9 Fundação Kissama, Rua 60 Casa 560, Lar do Patriota, Luanda, Angola

† deceased

<https://zoobank.org/09BAF93C-CA7A-46C3-AEA8-1E5074BD691B>

Corresponding author: Michael F. Bates (herp@nasmus.co.za)

Academic editor Uwe Fritz | Received 25 September 2022 | Accepted 26 May 2023 | Published 14 July 2023

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

## Abstract

*Cordylus angolensis* (Bocage, 1895) was described 128 years ago on the basis of a single specimen collected at Caconda in the west-central highlands of Angola. Additional specimens referred to this species were collected at ‘Mombolo’ (also in the central highlands) during the Vernay Angola Expedition in 1925. As the holotype was apparently destroyed in the fire of 1978 at the Museu Bocage in Lisbon and no additional specimens have been collected, its taxonomic status and phylogenetic relationships has remained uncertain. The species has eluded all efforts aimed at its re-discovery in the vicinity of the type locality, with a single specimen from near Condé, north of Mombolo—collected in 1970 by Wulf Haacke—the only other specimen of *Cordylus* known from west-central Angola. Recent field work in the Angolan highlands resulted in the collection of a series of specimens from Taqueta Mountain (west of Caconda), Monte Verde (Sandula, ‘Mombolo’) and Uassamba (Vondo). A phylogenetic analysis, using three mitochondrial and six nuclear genes, indicated the existence of two distinct species-level lineages in the Angolan highlands. These two species are allopatric and morphologically distinct, differing especially in terms of their colour patterns, eye colour and certain scalation characteristics. We therefore confirm that *C. angolensis* is a valid species and designate a neotype, and describe a new species, *Cordylus momboloensis* sp. nov.

## Keywords

Africa, Cordyliformes, distribution, Sauria, taxonomy

## Introduction

*Cordylus* Laurenti, 1768 is the most speciose and geographically widespread genus of girdled lizards (Cordylidae), comprising 21 species of mainly rupicolous lizards that occur from the south-western tip of South Africa northwards through Botswana and Namibia to Angola, and elsewhere to Mozambique, Zimbabwe, Zambia, Malawi, south-eastern Democratic Republic of the Congo, Tanzania and Kenya, with an apparently isolated population in southern Ethiopia (Branch 1998; Broadley and Branch 2002; Branch et al. 2005; Greenbaum et al. 2012; Bates et al. 2014; Stanley et al. 2016; Marques et al. 2019).

*Cordylus* originally encompassed all heavily armoured members of the family Cordylidae, but a phylogenetic analysis by Stanley et al. (2011) revealed that this grouping was paraphyletic and the genus was consequently divided into six genera, five of which were new. *Cordylus* was reduced to only 20 species, with three additional species, *Cordylus marunguensis* Greenbaum et al., 2012, *Cordylus namakuuius* Stanley et al., 2016, and *Cordylus phonolithos* Marques et al., 2019 described subsequently. Two species in the *C. minor* FitzSimons, 1943 group, namely *C. cloetei* Mouton & Van Wyk, 1994 and *C. aridus* Mouton & Van Wyk, 1994, were recently synonymised with *C. minor* (Tolley et al. 2021).

Stanley et al. (2011) identified two geographically distinct clades within *Cordylus*, a predominantly East African group (that also included the Angolan *Cordylus machadoi* Laurent, 1964) containing species found from the South African province of Mpumalanga northwards to Ethiopia (see Broadley and Branch 2002), and a Cape group containing species restricted mainly to the Western and Eastern Cape provinces of South Africa (see Branch 1998; Bates et al. 2014). Within the more northerly East African group, *Cordylus vittifer* (Reichenow, 1887) was recovered as sister to all other species, with *Cordylus jonesii* (Boulenger, 1891), *C. machadoi* and *Cordylus rhodesianus* (Hewitt, 1933) forming a clade sister to the remaining eastern and northern species. Subsequently, more species-rich phylogenies returned the Angolan *C. machadoi* as sister to the East African group (Greenbaum et al. 2012; Stanley et al. 2016; Marques et al. 2019). However, the phylogenetic position of another Angolan species of *Cordylus*, *C. angolensis* Bocage, 1895, remained unknown as the latter was not sampled in any of these studies.

Despite some early reptile and amphibian collecting in Angola during the colonial era (e.g., Bocage 1895; Schmidt 1933; Parker 1936; Monard 1937; Hellmich 1957; Laurent 1964), there were few subsequent collections (e.g., Branch and McCartney 1992) until the first decade of the 21<sup>st</sup> century. Angola has experienced long-lasting political instability and armed conflicts, starting with the Angolan struggle for national liberation (1961–1974), and following independence from Portuguese rule in 1975, by the Angolan Civil War (1975–2002). With the advent of peace and increased security across the country, modern surveys have revealed a very rich herpetological diversity (e.g., Haacke 2008; Huntley 2009, 2011;

Conradie et al. 2012a, 2012b, 2013, 2016, 2020a, 2020b, 2021, 2022a, 2022b; Ceriaco et al. 2014, 2016, 2018, 2020a, 2020b, 2020c, 2021; Branch and Conradie 2015; Stanley et al. 2016; Branch et al. 2017, 2018, 2019a, 2019b, 2021; Branch 2018a; Baptista et al. 2018, 2019a, 2020; Marques et al. 2019, 2020, 2022a, 2022b, 2023; Vaz Pinto et al. 2019, 2021; Hallerman et al. 2020; Nielsen et al. 2020; Lobón-Rovira et al. 2021, 2022a, 2022b, 2022c; Parrinha et al. 2021; Wagner et al. 2021). Historical records of reptiles and amphibians in Angola (1840 to 2017) were recently summarised and mapped by Marques et al. (2018), a checklist of the country's snakes was published by Branch (2018b), and summaries of current knowledge of reptiles and amphibians were produced by Branch et al. (2019c) and Baptista et al. (2019b) respectively.

Four species of *Cordylus* have been recorded from Angola, namely *C. angolensis* and three closely related species restricted to the south-western parts of the country, namely *C. machadoi*, *C. namakuuius* and *C. phonolithos*. Bocage (1895) examined three specimens of Angolan *Cordylus*, all of which he considered similar to *Cordylus cordylus* (Linnaeus, 1758). He described *Zonurus* (= *Cordylus*) *angolensis* on the basis of one of these specimens, sent from Caconda (13°46'S, 15°05'E) in the west-central part of Angola by the Portuguese collector José Alberto de Oliveira Anchieta (1832–1897). The other two specimens without specific localities were assigned to *Z. cordylus*. Perhaps because the description of *Z. angolensis* is contained under the heading “*Zonurus cordylus*” and Bocage (1895: 25) noted that it was “included in our catalogues provisionally under the name *Z. angolensis*” (translated from French), he neglected to mention this species in his subsequent list of type specimens in the Lisbon collection (Bocage 1897). The holotype of *Z. angolensis* is presumed to have been destroyed in the fire of 1978 at the Museu Bocage in Lisbon (Almaça and Neves 1987; Madruga 2011).

Broadley (1965, 1966) split the genus *Cordylus* into two groups on the basis of habitat: an essentially East African group of mainly tree-living species, and a South African-Zimbabwe group of more strongly depressed rupicolous taxa (see also Visser 1971). Although nothing was known about its habitat use, Broadley (1965) assigned *C. angolensis*—presumably on geographical grounds—to the more northerly group of partly arboreal species.

Broadley (1971: 22) considered the taxonomy of the northern forms of *Cordylus* and noted “I have examined the type and only known specimen of *Zonurus angolensis* Bocage from Caconda, Angola, and it is probably synonymous with *C. t. tropidosternum* Cope, having the three outer rows of ventrals keeled and mucronate and the tail almost equal to snout-vent length in spite of the tip being missing.” Broadley and Branch (2002: 10) noted that *C. angolensis* appeared to be a valid species, but “only three or four specimens are available, so this species should be redescribed when more material becomes available from Angola”. The additional specimens they referred to were three lizards from Mombolo in the collection of the American Museum of Natural History (New York) collected in Angola during the Vernay Angola Expedition in

1925 (Bogert 1940) and another specimen (Ditsong National Museum of Natural History [formerly Transvaal Museum], Pretoria) from near Condé further north in the country (D.G. Broadley in litt. 17 April 2009).

Greenbaum et al. (2012) examined three (AMNH R4733–5) Mombolo specimens for which they provided various measurements and scale counts. Although they referred their material to *C. angolensis* because it was similar to Bocage's (1895) holotype with regard to colour pattern, head dimensions, lack of a loreal scale, presence of a small row of scales between the anal plates, and in having similar numbers of transverse rows of ventrals, they noted that their specimens had only 11–12 longitudinal rows of ventrals compared to 16 in the holotype. Reissig (2014) also provided scalation data for '*C. angolensis*', but without reference to museum material, and mapped it at the two localities mentioned above.

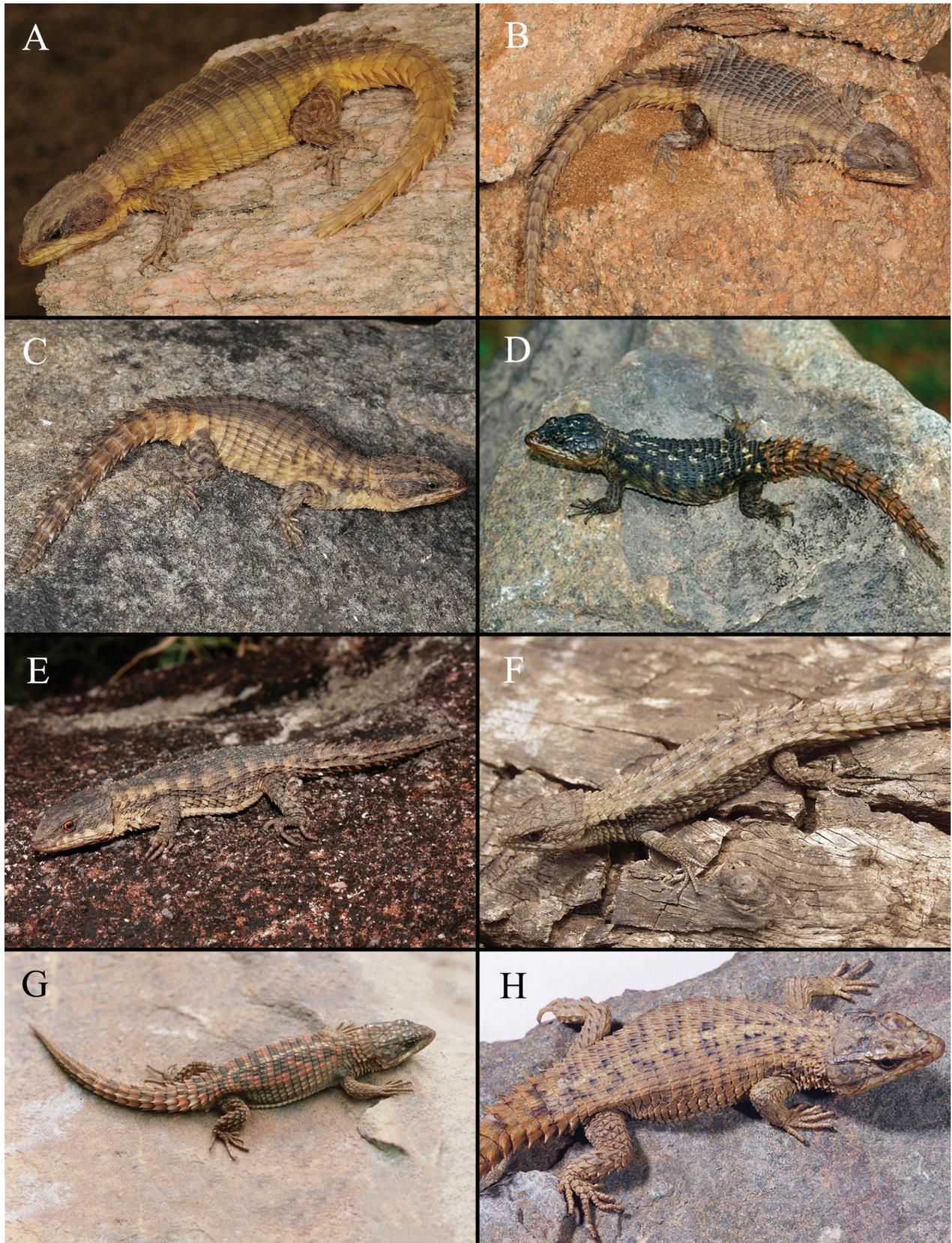
*Cordylus vittifer machadoi* was described by Laurent (1964) on the basis of a male holotype (see fig. 26 in Ceriaco et al. 2020d) and a juvenile paratype (Fig. S1), both collected at an elevation of 1800 m a.s.l. at Leba (15°03'S, 13°16'E) on the Humpata Plateau, Huíla Province, Angola. This locality is about 240 km south-west of Caconda, the type locality of *C. angolensis*. A few additional nearby localities for *C. machadoi* were added by Stanley et al. (2016). Laurent (1964) considered his Angolan lizards to be closely related to South African populations of *C. vittifer* (Figs 1, S2), despite their occurring about 1600 km apart, as they shared the characteristically elongated scales of the first row of transverse dorsals (see FitzSimons 1943, p. 461 and fig. 368; this feature is also present in *C. namakuiyus* and *C. phonolithos*). *Cordylus v. machadoi* was distinguished from other *C. vittifer* on the basis of its greater numbers of longitudinal dorsal scale rows (26–28 versus 20–24) and a narrower rostral scale (2.32–2.34 times wider than deep versus 3–4 times wider). Reichenow (1887), in his original description of *Zonurus vittifer* (Fig. S2), reported only 20–22 longitudinal dorsal scale rows and did not mention the size or shape of the rostral, and it therefore seems that Laurent (1964) was referring to Loveridge (1944a, see table on p. 15) and possibly also FitzSimons (1943) when comparing *machadoi* to *vittifer*. It should be noted that concepts of species boundaries within *Cordylus* around the time of Laurent's (1964) description were very different from what they are now. At that time, biological rather than lineage-based species concepts were often followed, and morphological similarity was used to rank populations, sometimes resulting in morphologically distinct and geographically disparate populations being considered subspecies. Both FitzSimons (1943) and Loveridge (1944a), for example, recognized several subspecies of *C. cordylus*, often isolated, occurring from the Cape Peninsula (*C. c. cordylus*) to as far north as Zimbabwe (i.e., *C. c. rhodesianus* = *C. rhodesianus*) and central Namibia (*C. c. pustulatus* [Peters, 1862] = *Namazonurus pustulatus*); and Loveridge (1944a) considered *Z. angolensis* a subspecies of *C. cordylus*, despite a geographical gap of about 2000 km.

Material from "Damaraland" (north-western Namibia), identified as *Zonurus griseus* Cuvier, 1829 by Pe-

ters (1869) and *Z. cordylus* by Boulenger (1885), was referred to *Cordylus cordylus angolensis* by Loveridge (1944a) and Mertens (1955, 1971), although this region is close to southerly records of *C. namakuiyus* in Angola (Lobón-Rovira et al. 2022b) and *C. cf. machadoi* in adjacent northern Namibia (Stanley et al. 2016). However, the Damaraland material cannot be assigned to any species of *Cordylus* with certainty as Peters (1869) did not provide morphological data, while Boulenger's (1885) description included material (probably *C. cordylus*) from South Africa, and he does not mention the characteristically elongated first row of transverse dorsals that characterises the *C. machadoi* group (*C. machadoi*, *C. namakuiyus*, *C. phonolithos*) and *C. vittifer*. Peters' specimens were probably deposited in the collection of the Museum für Naturkunde der Humboldt-Universität, Berlin, but most Namibian *Cordylus* specimens there are without specific localities and it was not possible to trace any specimens specifically from Damaraland (F. Tillack in litt. 2 February 2012). Mertens (1955, 1971) suggested that "*C. c. pustulatus*" may be a junior synonym of "*C. c. angolensis*", but *N. pustulatus* is in fact morphologically distinct and restricted to central Namibia (Branch 1998).

Monard (1937) referred Bocage's (1895) two Angolan "*C. cordylus*" without localities to *C. vittifer*, but it is not clear why he was of that opinion. Perhaps he had in fact examined some of the Angolan material and had observed the elongated first row of transverse dorsals that characterises *C. vittifer* and the *C. machadoi* group. Nevertheless, Loveridge (1944a) disagreed with Monard and suggested, apparently on the basis of their assumed geographical proximity, that Bocage's *Cordylus* were all referable to *C. c. angolensis*. Loveridge (1944a: 39) also noted that Boulenger's (1897) record of a *Zonurus cordylus* from the Aruwimi River (a tributary of the Congo River) in Democratic Republic of the Congo "may be *angolensis* or else an undescribed form, it certainly would not be typical *cordylus*." Laurent (1964) felt that Monard (1937) could not have assigned the two Angolan specimens (lacking locality details) to *C. vittifer* based on the information presented by Bocage. Bocage's (1895) description of these specimens includes sparse details and the scalation details given do not identify the specimens with certainty as *C. machadoi*, *C. namakuiyus* or *C. phonolithos*. However, the same details do not unequivocally refer these specimens to *C. angolensis* as suggested by Loveridge (1944a), and Bocage's specimens may likely represent the first Angolan records of either *C. machadoi* or *C. namakuiyus*, considering that his main provider of Angolan material, José de Anchieta, collected extensively within the geographical range of these two species, and not *C. phonolithos* (see below) which is restricted to Serra da Neve. The problem is now academic, as these specimens, along with the holotype of *C. angolensis*, were apparently destroyed in the fire at the Museu Bocage in Lisbon in 1978. Although Bocage's description of *C. angolensis* is brief and unillustrated, there is little reason to suggest that his species is synonymous with *C. machadoi*, *C. namakuiyus* or *C. phonolithos*.

A molecular phylogeny conducted by Stanley et al. (2016) on cordylids from south-western Angola deter-



**Figure 1.** Live specimens of various species of *Cordylus*: **A** *C. machadoi* (PEM R25218 – 6 km north of Humpata, Huila Province, Angola; photo: William R. Branch); **B** *C. namakuivus* (PEM R18005 – between Namibe and Omahua lodge, Namibe Province, Angola; photo: William R. Branch); **C** *C. phonolithos* (CAS 263581, holotype – vicinity of N’Dolondolo, Serra da Neve, Namibe Province, Angola; photo: Luis M. P. Ceriaco); **D** *C. rhodesianus* (near Chimoio, Mozambique; photo: David Maguire); **E** *C. tropidosternum* (Kayalekera, Malawi; photo: Luke Verburgt); **F** *C. jonesii* (Umbabat Private Nature Reserve, Mpumalanga Province, South Africa; photo: Darren Pietersen); **G** *C. vittifer* (NMB R8523 – Farm: Dipka 220, Vrede district, Free State Province, South Africa; photo: Michael F. Bates); **H** *C. cordylus* (NMB R8540 – Ha Sehlab, Lesotho; photo: Michael F. Bates). Representatives of all four *Cordylus* clades recovered by the current genetic analysis are included.

mined that *C. machadoi* occurred at high elevations on the Humpata Plateau, while populations in the Pro-Namib, at lower elevations in the more arid western parts, represented a new species, *C. namakuivus*. Morphologically, the latter species differed most notably from *C. machadoi* on account of its extensive osteodermal armour, and possession of a large interparietal scale that completely separates the anterior parietals (in *C. machadoi* the interparietal is small and does not fully separate the anterior parietals). The status of Namibian populations from Baynes and Otjihipa mountains referred to as *C. machadoi* (e.g., Branch 1998; Stanley et al. 2016, as *C. cf. machadoi*) remains unclear as they have not been subjected to genetic analysis, although newly-collected *Cordylus namakuivus* material from the highlands of Iona National Park (2033 m elevation), near the southern border of Angola (Lobón-Rovira et al. 2022b), suggests that the material from Baynes and Otjihipa mountains may belong to this species. Specimens were recently collected in the Otjihipa Mountains and will be subjected to genetic analysis to examine their status (F. Becker pers comm. 2022).

A third species in the *C. machadoi* group, namely *C. phonolithos*, was described by Marques et al. (2019). It was based on a subadult male (holotype) and a juvenile (paratype) collected at Serra da Neve inselberg, north of the other two species and about 200 km west of Caconda. The new species was shown to be the sister species to *C. machadoi* + *C. namakuivus*. The authors named several morphologically diagnostic features that distinguished their new species from the latter two species, but with a larger sample at hand, most of these characters appear to be variable (see below; P. Vaz Pinto and J. Lobón-Rovira, unpubl. data).

Fortunately, the holotype of *C. angolensis* was examined at the Museu Bocage in 1968 by the late Dr Donald Broadley (Natural History Museum, Bulawayo) before it was apparently destroyed in the fire a decade later. Broadley's scale counts agree with data presented by Bocage (1895), but he also recorded additional morphological data (see below). A series of five specimens from Mombolo on the plateau in west-central Angola, collected on 11 September 1925 by H. and A. Chapman during the Vernay Angola Expedition, were initially catalogued at the American Museum of Natural History (New York) as "*Cordylus tropidosternum jonesii*". Although similar to *C. angolensis*, to which they were referred by Broadley and Branch (2002) and Greenbaum et al. (2012), it was evident that these specimens differed with regard to certain scalation characteristics. Differences in morphology between *C. angolensis* and the Mombolo samples mentioned above led us to hypothesise that at least two distinct species were present in the central-western highlands of Angola.

Recent field work in central-western Angola resulted in the collection of a series of specimens from Taqueta Mountain (c. 100 kms west of Caconda), Monte Verde (Sandula, 'Mombolo') and Mount Uassamba (Vondo). In order to examine the evolutionary relationships between these populations, we conducted a phylogenetic analysis using three mitochondrial and six nuclear genes. A de-

tailed morphological evaluation was also conducted, indicating the existence of two distinct species, one of which we refer to *C. angolensis*, while the other represents a new species (initially referred to as *C. 'Mombolo'*) which we describe below.

## Materials and methods

### Molecular analysis

#### Sampling

Between 2016 and 2021, specimens of *Cordylus* were collected across Angola, focusing on the central highlands. A total of 25 specimens, comprising 12 *C. angolensis*-like specimens and 13 specimens of the *C. machadoi* group, were collected as vouchers. Specimens were euthanised by injection of tricaine methanesulfonate (MS222) (Conroy et al. 2009). After euthanasia, specimens were fixed in 10% formalin, after which they were transferred to 70% ethanol for long-term storage in the Museo Nacional de Ciencias Naturales (MNCN), Spain, Port Elizabeth Museum, Gqeberha (PEM), South Africa and Fundação Kissama (FKH), Angola. For phylogenetic analyses, liver or muscle samples were collected and stored in 96% or 99% ethanol. Localities were recorded by Global Positioning System (WGS84 co-ordinate system).

#### Molecular data

Phylogenetic analysis was used to provide a phylogenetic context and support the morphological findings. For that purpose we generated 213 new *Cordylus* sequences from 24 individuals from across Angola following Stanley et al. (2011), summarised in Table 1. DNA was extracted using EasySpin Genomic DNA Tissue Kit (Citomed, Portugal), following the manufacturer's protocols. PCR amplifications were performed to amplify three mitochondrial genes (16S, 12S and ND2) and six nuclear genes (RAG-1, c-mos, BDNF, PRLR, MYH2 and Kif24) following Stanley et al. (2011, 2016). Primer and PCR conditions are presented in Table 2. For phylogenetic comparisons we combined the newly-generated sequences and complemented this with previously published sequence data of 60 *Cordylus* individuals (Stanley et al. 2011, 2016; Greenbaum et al. 2012; Nielsen and Colston 2014; Marques et al. 2019), using *Namazonurus campbelli* (FitzSimons, 1938) as outgroup, and *Pseudocordylus* + *Ouroborus* as sister groups (Stanley et al. 2011; Table 1). Samples of 20 of the 21 known species (excluding only *C. nyikae* Broadley & Mouton, 2000) were included in the analysis. Sequences were cleaned and inspected visually using GENEIOUS Prime v2021.1.1 (<http://www.geneious.com>), and aligned using MUSCLE with the same software. Finally, sequences were concatenated using MESQUITE v3.6 (Madisson and Madisson 2019). All sequences have been deposited in GenBank (Table 1).

**Table 1.** Cordylidae samples included in this study with museum voucher numbers/field numbers and GenBank accession numbers for nine genes. Voucher specimens are indicated with museum accession numbers: CAS – California Academy of Sciences, San Francisco; CHL – Coleção Herpetologica do Lubango; FKH – Fundação Kissama Private Collection, Luanda; MCZ – Museum of Comparative Zoology, Harvard; MNCN – National Museum of Natural Science, Madrid; NMB – National Museum, Bloemfontein; PEM – Port Elizabeth Museum, Gqeberha; UTEP – University of Texas, El Paso. According to W. Conradie (pers. comm. 2022), *C. machadoi* WRB 0040 and 0041 are duplicates of PEM R19782 and R19784 respectively.

Species	Catalogue Number	Field Number	Country/Locality	16S	12S	ND2	PRLR	Kif24	c-mos	RAG-1	MYH2	BDNF	Source
<i>Cordylus angolensis</i> (Neotype)	MNCN 50648	NB 0612	Angola/Taqueda Mtn	OQ869891	OQ869867	OQ869522	OQ869474	OQ869428	OQ867122	OQ869498	OQ869452	OQ869544	This study
<i>C. angolensis</i>	CHL 611	NB 0611	Angola/Taqueda Mtn	OQ869890	OQ869866	OQ869521	OQ869473	OQ869427	OQ867121	OQ869497	OQ869451	OQ869543	This study
<i>C. angolensis</i>	CHL 613	NB 0613	Angola/Taqueda Mtn	OQ869892	OQ869868	OQ869523	OQ869475	OQ869429	OQ867123	OQ869499	OQ869453	OQ869545	This study
<i>C. angolensis</i>	MNCN 50649	NB 0614	Angola/Taqueda Mtn	OQ869893	OQ869869	OQ869524	OQ869476	OQ869430	OQ867124	OQ869500	OQ869454	OQ869546	This study
<i>C. machadoi</i>	—	KTH 09059	Angola/Humpata	HQ167204	KT941132	KT941260	KT941311	KT941234	KT941205	KT941369	HQ167424	KT941168	Stanley et al. (2011)
<i>C. machadoi</i>	PEM R18006	KTH 09056	Angola/Humpata	KT941143	KT941129	—	KT941308	KT941231	KT941202	KT941366	KT941245	KT941165	Stanley et al. (2016)
<i>C. machadoi</i>	PEM R18007	KTH 09057	Angola/Humpata	KT941145	KT941131	KT941259	KT941310	KT941233	KT941204	KT941368	KT941247	KT941167	Stanley et al. (2016)
<i>C. machadoi</i>	PEM R18008	KTH 09058	Angola/Humpata	KT941144	KT941130	KT941258	KT941309	KT941232	KT941203	KT941367	KT941246	KT941166	Stanley et al. (2016)
<i>C. machadoi</i>	PEM R19782	KTH 09006	Angola/Humpata	KT941142	KT941128	—	KT941307	KT941230	KT941201	KT941365	KT941244	KT941164	Stanley et al. (2016)
<i>C. machadoi</i>	PEM R19784	KTH 09005	Angola/Humpata	KT941141	KT941127	KT941257	KT941306	KT941229	KT941200	KT941364	KT941243	KT941163	Stanley et al. (2016)
<i>C. machadoi</i>	CHL 698	NB 0698	Angola/Tundavala	OQ869894	OQ869870	OQ869525	OQ869477	OQ869431	OQ867125	OQ869501	OQ869455	OQ869547	This study
<i>C. machadoi</i>	CHL 699	NB 0699	Angola/Tundavala	OQ869895	OQ869871	OQ869526	OQ869478	OQ869432	OQ867126	OQ869502	OQ869456	OQ869548	This study
<i>C. machadoi</i>	CHL 700	NB 0700	Angola/Tundavala	OQ869896	OQ869872	OQ869527	OQ869479	OQ869433	OQ867127	OQ869503	OQ869457	OQ869549	This study
<i>C. machadoi</i>	CHL 701	NB 0701	Angola/Tundavala	OQ869897	OQ869873	OQ869528	OQ869480	OQ869434	OQ867128	OQ869504	OQ869458	OQ869550	This study
<i>C. machadoi</i>	MNCN 50650	NB 0702	Angola/Tundavala	OQ869898	OQ869874	—	OQ869481	OQ869435	OQ867129	OQ869505	OQ869459	OQ869551	This study
<i>C. machadoi</i>	WRB 0040	—	Angola	JQ389806	JQ389799	—	JQ389851	JQ389812	—	—	—	—	Greenbaum et al. (2012)
<i>C. machadoi</i>	WRB 0041	—	Angola	JQ389807	JQ389800	—	—	—	—	—	—	—	Greenbaum et al. (2012)
<i>C. momboloensis</i> sp. nov.	FKH 0129	P9-17	Angola/Vondo	OQ869904	OQ869880	OQ869534	OQ869487	OQ869441	OQ867135	OQ869511	—	OQ869557	This study
<i>C. momboloensis</i> sp. nov. (Paratype)	FKH 0125	P9-13	Angola/Vondo	OQ869900	OQ869876	OQ869530	OQ869483	OQ869437	OQ867131	OQ869507	OQ869460	OQ869553	This study
<i>C. momboloensis</i> sp. nov. (Paratype)	MNCN 50760	P9-14	Angola/Vondo	OQ869901	OQ869877	OQ869531	OQ869484	OQ869438	OQ867132	OQ869508	OQ869461	OQ869554	This study
<i>C. momboloensis</i> sp. nov. (Paratype)	FKH 0127	P9-15	Angola/Vondo	OQ869902	OQ869878	OQ869532	OQ869485	OQ869439	OQ867133	OQ869509	OQ869462	OQ869555	This study
<i>C. momboloensis</i> sp. nov. (Paratype)	FKH 0128	P9-16	Angola/Vondo	OQ869903	OQ869879	OQ869533	OQ869486	OQ869440	OQ867134	OQ869510	OQ869463	OQ869556	This study
<i>C. momboloensis</i> sp. nov. (Holotype)	PEM R25217	AG16.36	Angola/Mt Verde	OQ869899	OQ869875	OQ869529	OQ869482	OQ869436	OQ867130	OQ869506	—	OQ869552	This study
<i>C. momboloensis</i> sp. nov. (Allotype)	MNCN 50761	P9-140	Angola/Sandula	OQ869905	OQ869881	OQ869535	OQ869488	OQ869442	OQ867136	OQ869512	OQ869464	OQ869558	This study

Species	Catalogue Number	Field Number	Country/Locality	16S	12S	ND2	PRLR	Kif24	c-mos	RAG-1	MYH2	BDNF	Source
<i>C. momboloensis</i> sp. nov.	—	P1-279	Angola/Bocoio	OQ869914	—	—	—	—	—	—	—	—	This study
<i>C. namakuiyus</i>	CAS 254754	—	Angola/near Pico do Azevado	KT941137	KT941123	KT941253	KT941302	KT941225	KT941194	KT941358	KT941239	KT941157	Stanley et al. (2016)
<i>C. namakuiyus</i>	CAS 254755	—	Angola/near Pico do Azevado	KT941138	KT941124	KT941254	KT941303	KT941226	KT941195	KT941359	KT941240	KT941158	Stanley et al. (2016)
<i>C. namakuiyus</i>	CAS 254912	—	Angola/near Caraculo	KT941135	KT941121	KT941251	KT941300	KT941223	KT941192	KT941356	KT941237	KT941155	Stanley et al. (2016)
<i>C. namakuiyus</i>	CAS 256529	—	Angola/near Caraculo	KT941136	KT941122	KT941252	KT941301	KT941224	KT941193	KT941357	KT941238	KT941156	Stanley et al. (2016)
<i>C. namakuiyus</i>	CAS 256530	—	Angola/ near Pico do Azevado	KT941139	KT941125	KT941255	KT941304	KT941227	KT941196	KT941360	KT941241	KT941159	Stanley et al. (2016)
<i>C. namakuiyus</i>	CAS 256531	—	Angola/ near Pico do Azevado	KT941140	KT941126	KT941256	KT941305	KT941228	KT941197	KT941361	KT941242	KT941160	Stanley et al. (2016)
<i>C. namakuiyus</i>	PEM R18005	KTH 09212	Angola/between Namibe and Omauha Lodge	KT941148	KT941134	—	KT941313	KT941236	KT941207	—	KT941250	KT941170	Stanley et al. (2016)
<i>C. namakuiyus</i>	FKH 0262	P9-169	Angola/Chapeu Armado	OQ869908	OQ869884	OQ869537	OQ869491	OQ869445	OQ867139	OQ869515	OQ869467	OQ869561	This study
<i>C. namakuiyus</i>	CHL 609	NB 0609	Angola/Mariquita	OQ869907	OQ869883	—	OQ869490	OQ869444	OQ867138	OQ869514	OQ869466	OQ869560	This study
<i>C. namakuiyus</i>	CHL 616	NB 0616	Angola/Meva	OQ869906	OQ869882	OQ869536	OQ869489	OQ869443	OQ867137	OQ869513	OQ869465	OQ869559	This study
<i>C. phonolithos</i>	AMB 10272	—	Angola/Serra da Neve	MN342160	—	QGN01202	—	—	—	—	—	—	Marques et al. 2019
<i>C. phonolithos</i>	CAS 263581	—	Angola/Serra da Neve	MN342159	—	QGN01201	—	—	—	—	—	—	Marques et al. 2019
<i>C. phonolithos</i>	CHL 848	NB 0848	Angola/Serra da Neve	OQ869909	OQ869885	OQ869538	OQ869492	OQ869446	OQ867140	OQ869516	OQ869468	OQ869562	This study
<i>C. phonolithos</i>	MNCN 50651	NB 0849	Angola/Serra da Neve	OQ869910	OQ869886	OQ869539	OQ869493	OQ869447	OQ867141	OQ869517	OQ869469	OQ869563	This study
<i>C. phonolithos</i>	MNCN 50652	NB 0850	Angola/Serra da Neve	OQ869911	OQ869887	OQ869540	OQ869494	OQ869448	OQ867142	OQ869518	OQ869470	OQ869564	This study
<i>C. phonolithos</i>	CHL 851	NB 0851	Angola/Serra da Neve	OQ869912	OQ869888	OQ869541	OQ869495	OQ869449	OQ867143	OQ869519	OQ869471	OQ869565	This study
<i>C. phonolithos</i>	CHL 852	NB 0852	Angola/Serra da Neve	OQ869913	OQ869889	OQ869542	OQ869496	OQ869450	OQ867144	OQ869520	OQ869472	OQ869566	This study
<i>C. beraducii</i>	JB 6	—	Tanzania	KT941403	KT941400	KT941393	KT941390	JQ389811	KT941187	KT941351	KT941386	KT941150	Stanley et al. (2016)
<i>C. beraducii</i>	JB 7	—	Tanzania	KT941404	KT941401	KT941394	KT941391	—	KT941188	KT941352	KT941387	KT941151	Stanley et al. (2016)
<i>C. beraducii</i>	WRB 0037	—	Tanzania/Mtera	HQ167172	HQ167061	KT941395	HQ167501	HQ167283	KT941189	KT941353	HQ167392	KT941152	Stanley et al. (2011)
<i>C. cordylus</i>	AMB 8168	—	S. Africa/E. Cape	HQ167182	HQ167071	HQ166970	HQ167511	HQ167293	—	—	HQ167402	—	Stanley et al. (2011)
<i>C. cordylus</i>	PEM R17464	—	S. Africa/E. Cape	HQ167190	HQ167079	HQ166978	HQ167519	HQ167301	—	—	HQ167410	—	Stanley et al. (2011)
<i>C. cordylus</i>	PEM R15012	—	S. Africa/E. Cape	HQ167189	HQ167078	HQ166977	HQ167518	HQ167300	—	—	HQ167409	—	Stanley et al. (2011)

Species	Catalogue Number	Field Number	Country/Locality	16S	12S	ND2	PRLR	Kif24	e-mos	RAG-1	MYH2	BDNF	Source
<i>C. cordylus</i>	PEM R17394	—	S. Africa/E. Cape	HQ167232	HQ167121	HQ167015	HQ167561	HQ167343	—	—	HQ167452	—	Stanley et al. (2011)
<i>C. imkeae</i>	MBUR 01795	—	S. Africa/N. Cape	HQ167197	HQ167086	HQ166985	HQ167526	HQ167308	—	—	HQ167417	—	Stanley et al. (2011)
<i>C. imkeae</i>	MBUR 01796	—	S. Africa/N. Cape	HQ167198	HQ167087	HQ166986	HQ167527	HQ167309	KT941191	KT941355	HQ167418	KT941154	Stanley et al. (2011)
<i>C. jonesii</i>	AMB 8310	—	S. Africa/Limpopo	HQ167199	HQ167088	HQ166987	HQ167528	HQ167310	KT941198	KT941362	HQ167419	KT941161	Stanley et al. (2016)
<i>C. jonesii</i>	AMB 8396	—	S. Africa/Limpopo	HQ167200	HQ167089	HQ166988	HQ167529	HQ167311	KT941199	KT941363	HQ167420	KT941162	Stanley et al. (2016)
<i>C. macropholis</i>	AMB 8873	—	S. Africa/W. Cape	HQ167206	HQ167095	HQ166993	HQ167535	HQ167317	—	—	HQ167426	—	Stanley et al. (2011)
<i>C. macropholis</i>	AMB 8874	—	S. Africa/W. Cape	HQ167207	HQ167096	HQ166994	HQ167536	HQ167318	KT941208	KT941371	HQ167427	KT941171	Stanley et al. (2011)
<i>C. marunguensis</i>	EBG 2994	—	DRC/Marungu Mountains	JQ389803	JQ389798	KT941396	JQ389849	JQ389810	KT941209	KT941372	JQ389846	KT941172	Stanley et al. (2016)
<i>C. marunguensis</i>	UTEF 20374	—	DRC/Marungu Mountains	JQ389803	JQ389798	—	JQ389849	JQ389810	—	KU298675	—	—	Greenbaum et al. (2012)
<i>C. marunguensis</i>	UTEF 20375	—	DRC/Marungu Mountains	JQ389802	JQ389797	—	JQ389848	JQ389809	—	—	JQ389846	—	Greenbaum et al. (2012)
<i>C. mclachlani</i>	AMB 8855	—	S. Africa/W. Cape	HQ167208	HQ167097	HQ166995	HQ167537	HQ167319	KT941210	KT941373	HQ167428	KT941173	Stanley et al. (2011)
<i>C. mclachlani</i>	CmclSU 1	—	S. Africa/W. Cape	HQ167209	HQ167098	HQ166996	HQ167538	HQ167320	—	KT941373	HQ167429	—	Stanley et al. (2011)
<i>C. meculae</i>	PEM R16164	—	Mozambique/Mecula	HQ167210	HQ167099	—	HQ167539	HQ167321	KT941413	KT941416	HQ167430	KT941416	Stanley et al. (2016)
<i>C. meculae</i>	PEM R16165	—	Mozambique/Mecula	HQ167211	HQ167100	—	HQ167540	HQ167322	KT941414	KT941417	HQ167431	KT941417	Stanley et al. (2016)
<i>C. meculae</i>	PEM R16202	—	Mozambique/Mecula	HQ167233	HQ167122	—	HQ167562	HQ167344	KT941415	—	HQ167453	KT941418	Stanley et al. (2016)
<i>C. meculae</i>	PEM R16203	—	Mozambique/Mecula	HQ167234	HQ167123	—	HQ167563	HQ167345	—	—	HQ167454	—	Stanley et al. (2016)
<i>C. minor</i>	CminSU	—	S. Africa/N. Cape	HQ167212	HQ167101	HQ166997	HQ167541	HQ167323	—	—	HQ167432	—	Stanley et al. (2011)
<i>C. minor</i>	PEM R16371	—	S. Africa/W. Cape	HQ167169	HQ167058	HQ166958	HQ167498	HQ167280	KT941186	—	HQ167389	KT941149	Stanley et al. (2011)
<i>C. minor</i>	PEM R16376	—	S. Africa/W. Cape	HQ167170	HQ167059	HQ166959	HQ167499	HQ167281	—	—	HQ167390	—	Stanley et al. (2011)
<i>C. niger</i>	AMB 8875	—	S. Africa/W. Cape	HQ167216	HQ167105	HQ166999	HQ167545	HQ167327	—	—	HQ167436	—	Stanley et al. (2011)
<i>C. niger</i>	CnigSU 1	—	S. Africa/W. Cape	HQ167217	HQ167106	HQ167000	HQ167546	HQ167328	KT941211	KT941374	HQ167437	KT941174	Stanley et al. (2011)
<i>C. oelofseni</i>	AMB 8851	—	S. Africa/W. Cape	HQ167218	HQ167107	HQ167001	HQ167547	HQ167329	—	—	HQ167438	—	Stanley et al. (2011)
<i>C. oelofseni</i>	AMB 8860	—	S. Africa/W. Cape	HQ167221	HQ167110	HQ167004	HQ167550	HQ167332	KT941212	KT941375	HQ167441	KT941175	Stanley et al. (2011)
<i>C. oelofseni</i>	AMB 8862	—	S. Africa/W. Cape	HQ167222	HQ167111	HQ167005	HQ167551	HQ167333	—	—	HQ167442	—	Stanley et al. (2011)
<i>C. oelofseni</i>	CoelSU 1	—	S. Africa/W. Cape	HQ167219	HQ167108	HQ167002	HQ167548	HQ167330	KT941213	KT941376	HQ167439	KT941176	Stanley et al. (2011)
<i>C. oelofseni</i>	CoelSU 2	—	S. Africa/W. Cape	HQ167220	HQ167109	HQ167003	HQ167549	HQ167331	—	—	HQ167440	—	Stanley et al. (2011)
<i>C. rhodesianus</i>	ELSPET 4	—	Pet Trade	HQ167230	HQ167119	HQ167013	HQ167559	HQ167341	KT941214	KT941377	HQ167450	KT941177	Stanley et al. (2016)
<i>C. rhodesianus</i>	ELSPET 5	—	Pet Trade	HQ167231	HQ167120	HQ167014	HQ167560	HQ167342	—	—	HQ167451	—	Stanley et al. (2016)
<i>C. rivae</i>	TJC 564	—	Ethiopia	KM242128	KM242126	—	KM242122	KM242118	—	—	KM242124	—	Nielsen and Colston (2014)
<i>C. rivae</i>	TJC 565	—	Ethiopia	KM242129	KM242127	—	KM242123	KM242119	—	—	KM242125	—	Nielsen and Colston (2014)
<i>C. tropidosternum</i>	JB 8	—	Tanzania	KT941405	KT941402	KT941397	KT941392	KT941389	KT941215	KT941378	KT941388	KT941178	Stanley et al. (2016)
<i>C. tropidosternum</i>	WRB 0038	—	Tanzania	HQ167236	HQ167125	—	HQ167565	HQ167347	—	—	HQ167456	—	Stanley et al. (2016)
<i>C. tropidosternum</i>	WRB 0042	—	Tanzania	HQ167235	HQ167124	KT941398	HQ167564	—	KT941216	KT941379	HQ167455	KT941179	Stanley et al. (2016)

Species	Catalogue Number	Field Number	Country/Locality	16S	12S	ND2	PRLR	Kif24	c-mos	RAG-1	MYH2	BDNF	Source
<i>C. ukungensis</i>	WRB 0039	—	Kenya/Uzungwe Mts	HQ167237	HQ167126	KT941399	HQ167566	HQ167348	KT941217	KT941380	HQ167457	KT941180	Stanley et al. (2016)
<i>C. vittifer</i>	AMB 6073	—	S. Africa/ Mpumalanga	HQ167241	HQ167130	HQ167019	HQ167570	HQ167352	KT941218	KT941381	HQ167461	KT941181	Stanley et al. (2011)
<i>C. vittifer</i>	AMB 8274	—	S. Africa/Limpopo	HQ167242	HQ167131	HQ167020	HQ167571	HQ167353	KT941219	KT941382	HQ167462	KT941182	Stanley et al. (2011)
<i>C. vittifer</i>	AMB 8603	—	Eswatini	HQ167243	HQ167132	HQ167021	HQ167572	HQ167354	KT941220	KT941383	HQ167463	KT941183	Stanley et al. (2011)
<i>Namazonurus campbelli</i>	MCZ 27028	—	Namibia	HQ167174	HQ167063	HQ166962	HQ167503	HQ167285	KT941221	KT941384	HQ167394	KT941184	Stanley et al. (2016)
<i>Ouroborus cataphractus</i>	MBUR 01792	—	S. Africa/N. Cape	HQ167177	HQ167066	HQ166965	HQ167506	HQ167288	KT941222	KT941385	HQ167397	KT941185	Stanley et al. (2016)
<i>Pseudocoryphylus melanotus subviridis</i>	NMB R8558	—	S. Africa/KwaZulu-Natal	HQ167268	HQ167157	HQ167046	HQ167597	HQ167379	—	—	HQ167486	—	Stanley et al. (2011)
<i>P. m. subviridis</i>	NMB R8560	—	S. Africa/KwaZulu-Natal	HQ167267	HQ167156	ADO13379	HQ167596	HQ167378	—	—	HQ167485	—	Stanley et al. (2011)

## Phylogenetic analysis

Bayesian inference (BI) and maximum likelihood (ML) analyses were performed with sequence data for 85 specimens using separate analyses for each gene, as well as different analyses for concatenated sets of three mitochondrial genes (ND2, 16S and 12S) and six nuclear genes (RAG-1, c-mos, BDNF, PRLR, MYH2 and Kif24), and all genes combined. The partitioning schemes were determined using PartitionFinder2 (Lanfear et al. 2017) and the best substitution model of sequence evolution was selected using ModelFinder (Kalyaanamoorthy et al. 2017) in IQ-Tree v.1.6.12, with the Bayesian Information Criterion (BIC). We partitioned the combined dataset by gene, as suggested in PartitionFinder2. The best fit substitution models were TN+F+I+G4 (ND2), TPM2u+F+I+G4 (12S), TIM2e+I+G4 (16S), HKY+F+I (RAG-1), TPM2u+F+I (c-mos), K2P+I (BDNF), K2P+G4 (PRLR), K2P+G4 (MYH2) and TNe+I+G4 (Kif24). Phylogenies were constructed based on concatenated data. Bayesian inference analyses were conducted with MrBayes v.3.2.7 (Ronquist et al. 2012) on CIPRES (Miller et al. 2010) with nine partitions of the concatenated dataset, while ML was performed in IQ-Tree v.1.6.12 using “ultrafast” bootstrapping option (Trifinopoulos et al. 2016). The final BI analysis was run for  $10 \times 10^6$  generations of the Metropolis coupled Markov chain Monte Carlo [(MC)3], sampled every 1000 generations. Convergence was assessed by examining the effective sample size (ESS) values using Tracer 1.7 (Rambaut et al. 2014) where all parameter values had ESS values  $>200$ , and 25% of the trees obtained were discarded as burn-in, to generate a 50% majority rule consensus tree in MrBayes. We set the substitution model space with the option lset nst=mixed rates=invgamma. Bootstrap analyses (BS) with 1000 pseudoreplicates were used to evaluate relative branch support. Bootstrap values of 95% or higher were considered as supported (Huelsenbeck and Hillis 1993). Posterior probabilities (PP) were used to assess nodal support, and  $PP \geq 0.95$  was considered strongly supported. Uncorrected pairwise sequence divergences (p-distance) were calculated for ND2 sequences in MEGA v.10.1.7 (Kumar et al. 2018).

The identity of an individual from Morro do Pundo, Bocoio (P1-279 in Table 1), for which only a tail tip was obtained, was determined (as *C. ‘Mombolo’*) using the 16S marker under the conditions as defined above. This sample was not included in the phylogenetic analysis, but its locality was plotted on the distribution map below.

## Morphological evaluation

### Material examined

This study was based on material in the herpetological holdings of the following museums/collections: American Museum of Natural History, New York (AMNH); Ditsong National Museum of Natural History (formerly Transvaal Museum), Pretoria (TM); Florida Museum of

**Table 2.** PCR primer details used for this study.

Gene	Primer	Length (bp)	Sequence	Reference
<b>16S</b>	16Sa	581	5' CGCCTGTTTATCAAAAACAT 3'	Simon et al. (1994)
	16Sb		5' CCGGTCTGAACTCAGATCACGT 3'	
<b>12S</b>	12sf700	459	5' AAACCTGGGATTAGATACCCCACTAT 3'	Stanley et al. (2011)
	12sr600		5' GAGGGTGACGGCGGTGTGT 3'	
<b>ND2</b>	L4437-R	1025	5' AAGCTTTCGGGCCCATACC 3'	Macey et al. (1997)
	H5540-F		5' TTTAGGGCTTTGAAGGC 3'	
	R102		5' CAGCCTAGGTGGGCGATTG 3'	
<b>RAG-1</b>	RAG1_fl1a	1040	5' CAGCTGYAGCCARTACCATAAAAAT 3'	Wiens et al. (2010)
	RAG1_r2		5' CTTTCTAGCAAAAATTTCCATTCAT 3'	
<b>c-mos</b>	G73	407	5' GCGGTAAAGCAGGTGAAGAAA 3'	Wiens et al. (2010)
	G74		5' TGAGCATCCAAAGTCTCCAATC 3'	
<b>BDNF</b>	BDNF_f	732	5' GACCATCCTTTTCTKACTATGGTTATTTTCATACTT 3'	Wiens et al. (2010)
	BDNF_r		5' CTATCTTCCCCTTTTAATGGTCAGTGTACAAAC 3'	
<b>PRLR</b>	PRLRf1	532	5' GACARYGARGACCAGCAACTRATGCC 3'	Townsend et al. (2008)
	PRLRr1		5' GACYTTGTGRACCTTCYACRTAATCCAT 3'	
<b>Kif24</b>	Kif24f	572	5' WGGCTGCTGRAAYTGCTGGTG 3'	Portik et al. (2010)
	Kif24r		5' SAAACGTRTCTCCMAAACGCATCC 3'	
<b>MYH2</b>	MYH2f	765	5' GAACACCAGCCTCATCAACC 3'	Stanley et al. (2011)
	MYH2r		5' TGGTGTCTGCTCCTTCTTC 3'	

Natural History, Gainesville (UF); Museum of Comparative Zoology, Harvard (MCZ); National Museum, Bloemfontein (NMB); Port Elizabeth Museum, Gqeberha (PEM); Museo Nacional de Ciencias Naturales, Madrid (MNCN); Fundação Kissama Private Collection, Luanda (FKH); Coleção Herpologica do Lubango, Lubango (CHL); University of Texas at El Paso, El Paso (UTEP); and Tim Colston's field series, private (TJC). Material examined in detail is listed in the species accounts and in Appendix 1.

### External morphology

Specimens were examined using binocular dissecting microscopes (up to 40 or 48 times magnification). Measurements were performed using digital calipers (0.01 mm) or a ruler (1 mm), often under magnification. Apart from five AMNH specimens from 'Mombolo' and 13 similar new specimens, 140 additional specimens (14 *C. machadoi*, one *C. cf. machadoi* from Namibia, 30 *C. namakuiyus*, seven *C. phonolithos*, 72 *C. vittifer*, five *C. jonesii*, five *C. rhodesianus*, six *C. tropidosternum* [Cope, 1869]) were examined for comparison (Appendix 1). These numbers include specimens for which details of head scalation only were available from photographs (two *C. machadoi*, two *C. namakuiyus*, five *C. phonolithos*; see below). Males were usually identified by their well-developed femoral pores (weakly developed with small or absent secretory plugs in females) and the presence of differentiated femoral scales (absent in females). However, because some females of *C. vittifer* possess differentiated femoral scales (De Waal 1978), all specimens of this species were also dissected and examined for presence of ovaries and/or oviducts in females, and testes and/or sperm ducts in males.

Measurements were performed on the right side of the body unless damaged. The following were measured:

snout-vent length (SVL, from tip of snout to anterior margin of vent, with lizard on its back and flattened); tail length (posterior margin of vent to tail tip, original tails unless indicated); head length (tip of snout to posterior margin of lateral temporals); head width (widest part in the temporal area); head height (midpoint of eye from top of head to bottom of lower jaw); ear length (greatest distance more-or-less dorso-ventally); eye length (excluding small scales around the eye); nostril-eye distance (shortest distance between); eye-ear distance (shortest distance); snout-eye length (tip of snout to anterior margin of eye, excluding small scales around the eye); internarial distance (shortest distance between nostrils); inter-orbital distance (measured between the middle of the eye sockets); snout-arm length (from tip of snout to anterior margin of forelimb); axilla-groin distance (posterior edge of forelimb insertion to anterior edge of hindlimb insertion); forearm (inner part of elbow fold to tip of claw of fourth (longest) finger; 4<sup>th</sup> (longest) toe of hindlimb).

Scale counts were, unless indicated, performed on both sides of each lizard. The following counts were taken: supralabials (all scales bordering the upper lip, excluding the rostral, but including the scale at the corner of the mouth; the second last supralabial is the largest); infralabials (all scales bordering lower lip, excluding the mental, the posterior one situated at the corner of the mouth below and partly behind the posterior supralabial); sublabials (large scales in contact with the infralabials, the posterior one situated near the ear opening below and partly behind the posterior infralabial); number of chin shields in contact with anterior sublabials; supraoculars (large scales); supraciliaries (narrow and elongate scales above the eye and in contact with the much larger supraoculars, excluding tiny granules and postocular scales that may be in contact with the posterior supraocular); lo-

reals; suboculars (all scales bordering eye and in contact with the supralabials, but excluding the preocular and any postoculars; when present, a fourth subocular is invariably situated near the back of the eye); preoculars; rows of gulars between posterior angles of jaws, excluding tiny granules; dorsals, transverse rows (from immediately behind occipitals to vent); dorsals, longitudinal rows (counted midway between fore- and hindlimbs, excluding granular or minute scales on either side if present); ventrals, transverse rows (from axilla to groin; the most anterior row curves anteriorly and the most posterior row curves posteriorly); ventrals, longitudinal rows (counted midway between fore- and hindlimbs; the most lateral row consists of scales generally at least half as wide as the adjacent inner ones; when this row is not clearly distinguishable, the formula ‘12 + 2’ is used, indicating a possible extra row on either side); subdigital lamellae on 4<sup>th</sup> (longest) toe (the most basal scale counted is fully present on the digit); femoral pores; differentiated femoral scales (generation glands).

The interpretation of ‘occipital’ requires explanation. In the genus *Cordylus*, occipitals are typically defined as the scales posterior to, and in contact with, the pair of posterior parietals, plus those scales in contact with the posterior upper temporals [on either side of the posterior parietals] (e.g., FitzSimons 1943). This is quite straightforward in some species, such as *C. vittifer* (Fig. S2), as the occipitals are often distinct, of similar size and present as a more-or-less straight row across the back of the head; and also, in this species, the row of occipitals is followed immediately behind by the first transverse row of dorsals which consists of mostly elongated scales (longer than those of the next row of dorsals) and has the appearance of a collar. However, the interpretation of what comprises occipitals in most species of Angolan *Cordylus* is complicated by the presence of what appear to be incomplete rows of these scales, i.e., rows that start with a scale situated behind the posterior upper temporal, followed by one or more scales on other side (and in contact behind the posterior parietals), but the ‘row’ is then interrupted medially by the intrusion of large scales from the row behind. We refer to the interrupted row as ‘occipitals’ (‘pre-occipitals’ in Stanley et al. 2016) and the undivided row behind, which has some scales in contact with the parietals medially, as ‘post-occipitals’ (Fig. 2). The posterior part of the post-occipitals aligns, more-or-less, with the posterior part of the posterior lateral temporals. In the three species of the *C. machadoi* group, the two rows of ‘occipitals’ are both situated anterior to the ‘collar’ represented by the first transverse row of dorsals, which, as in *C. vittifer*, is easily recognized by its much-elongated scales. In *C. namakuiyus* and *C. phonolithos* the first ‘row’ of occipitals is incomplete, but in *C. machadoi* it is often continuous throughout. The situation is somewhat more difficult to interpret in the two west-central highlands species as neither has the transverse row of much-elongated dorsal scales. In the Taqueta Mountain population of Angolan *Cordylus* (*C. angolensis*) there is a continuous row of occipitals (the next row is considered the first transverse row of

dorsals), the posterior ends of which are more-or-less aligned with the posterior parts of the posterior lateral temporals; but in other populations from the west-central highlands of the country (*C. ‘Mombolo’*) there is a medially-interrupted row of occipitals followed by a row of post-occipitals (posterior edges extending slightly beyond, or aligned with, the posterior edges of posterior lateral temporals).

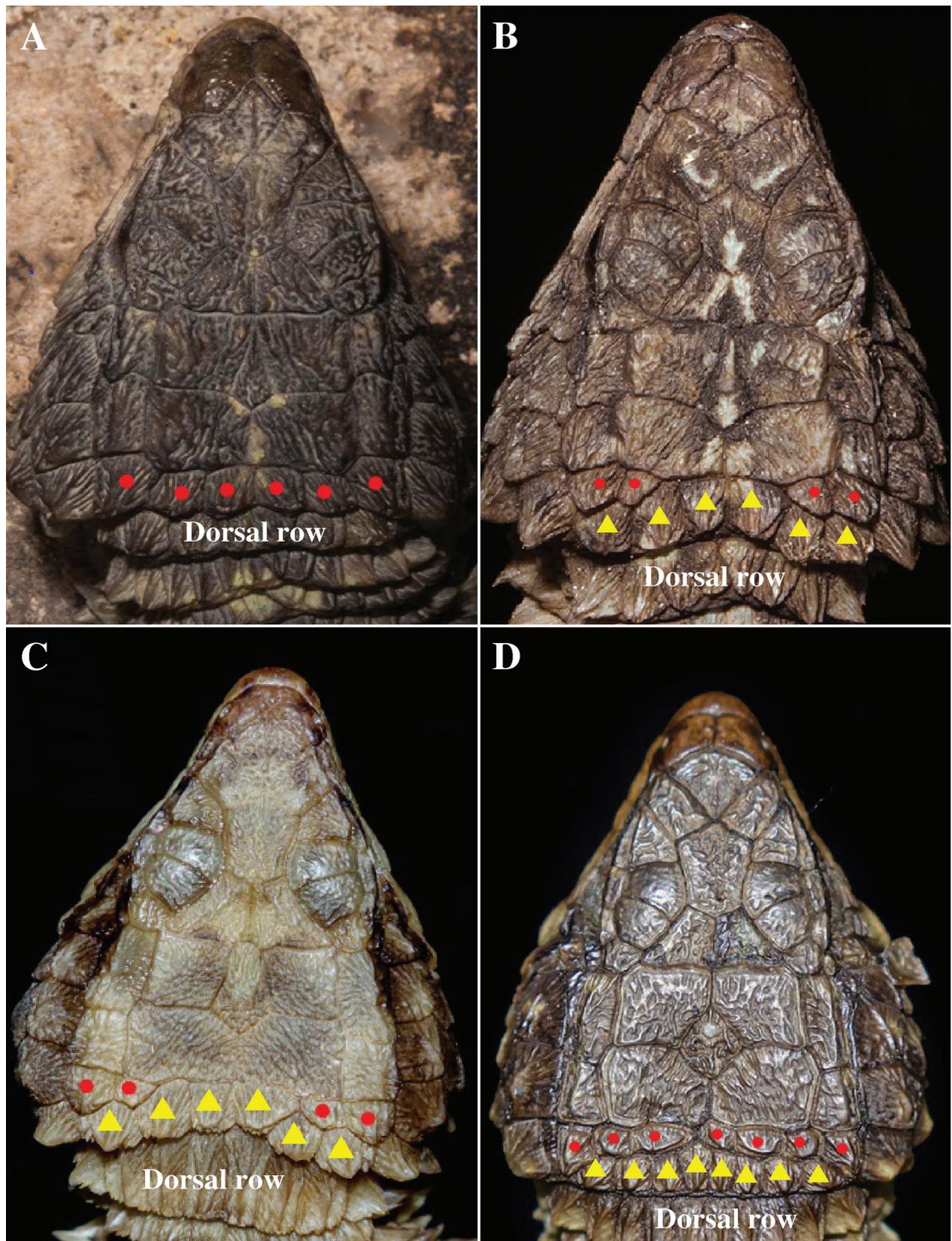
## Comparison with related species

All material referable to *C. angolensis*, as well as that of *C. ‘Mombolo’*, was compared to one another and samples of other Angolan *Cordylus*, namely *C. machadoi*, *C. namakuiyus* and *C. phonolithos* (Fig. 1). Samples of four related, geographically proximate, species, namely *C. tropidosternum*, *C. jonesii*, *C. rhodesianus* and *C. vittifer* (Fig 1; see data and relationships to *C. machadoi* group: Broadley and Branch 2002; Stanley et al. 2011; Marques et al. 2019) were also examined for comparison. As there is uncertainty about the type locality of *C. vittifer* (given as ‘Transvaal’ by Reichenow 1887, but possibly ‘Bethel’ as noted by Bauer et al. 1994) and the species varies considerably in terms of scale characters and colour pattern (e.g., De Waal 1978; Jacobsen 1989), samples were selected from six areas representing its total range, with populations assigned to the three known varieties (A, B, C) where possible (Fig. S3). A number of scalation and body size characters were compared (see below).

In the diagnoses and diagnostic key below, comparative morphological details were derived from: Bocage (1895); FitzSimons (1943); Loveridge (1944a); Laurent (1964); Mouton (1986, 1987); Mouton and Van Wyk (1990, 1994); Broadley and Mouton (2000); Broadley and Branch (2002); Branch et al. (2005); Bates (2007); Greenbaum et al. (2012); Stanley et al. (2016); Marques et al. (2019); and data presented in this paper.

## Osteological analysis

For osteological descriptions of the west-central Angolan cordylid material, microComputed Tomography (CT) datasets of *C. ‘Mombolo’* (AMNH R47333–4 and TM 46476) and *C. angolensis* (MNCN 50648) were produced using Phoenix V|Tome|X M (Nanoscale Research Facility, University of Florida), Phoenix V|Tome|X S (Microscopy and Imaging Facility, American Museum of Natural History) and Zeiss Xradia 510 Versa (Centro de Instrumentación Científica of Granada [CIC], Spain) systems. Separate scans of the head and body were performed to maximize the resolution of the cranial datasets. X-ray settings were modified to maximize resolution, contrast and signal to noise (Table S1). X-ray radiographs were converted to tomograms using filtered back-projection, with Datos|X R (Waygate Technologies) and Reconstructor Scout-and-Scan Control System (Zeiss) software. Comparative CT datasets for the other three species of Angolan *Cordylus* and nine species of east African *Cordylus* were produced at the institutions listed above, or



**Figure 2.** Arrangement of occipitals (red circles) and post-occipitals (yellow triangles) in **A** *Cordylus angolensis* (CHL 611), **B** *C. momboloensis* sp. nov. (MNCN 50760), **C** *C. namakuiyus* (CHL 609), and **D** *C. machadoi* (CHL 700)]. The first transverse row of dorsal scales is labeled. Photos: Pedro Vaz Pinto (A, B), and Timóteo Júlio (C, D).

obtained from [www.morphsource.org](http://www.morphsource.org). All CT data were processed in VGStudioMax 2022.1 (Volume Graphics, Heidelberg, Germany) to digitally isolate individual cra-

nial bones, postcranial skeleton and osteoderms to facilitate osteological descriptions and comparative analysis. Total osteoderm and postcranial skeleton volumes were

recovered for all scanned Angolan cordylid material and the osteoderm/postcranial skeleton volume ratio plotted against SVL to provide an allometric assessment of the degree of armour for each species. All resulting tomogram data are freely available on [www.morphosource.org](http://www.morphosource.org) (Table S1).

## Species assessment

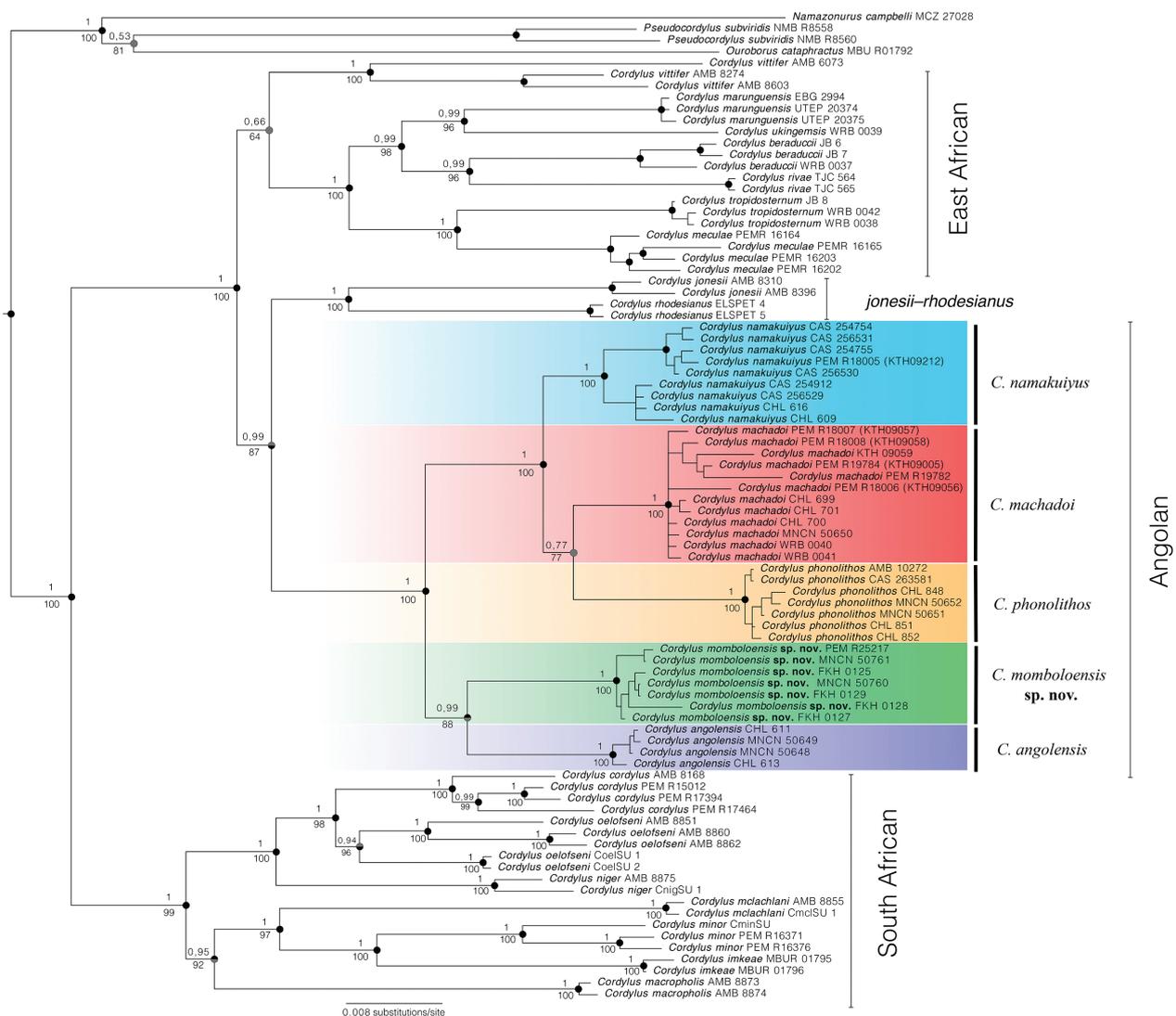
We follow a lineage-based species concept whereby a species is represented by an independently evolving meta-population lineage (Frost and Hillis 1990; de Queiroz 1998, 2007). The species delimitation approach followed in this study is based on an integrative approximation (Vieites et al. 2009; Padial et al. 2010; Lobón-Rovira et al. 2022d), considering as separate species those lineages that are well supported based on phylogenetic, morphological, and biogeographic/ecological differences.

## Results

### Phylogenetic analysis

Both the BI and ML analyses were largely concordant, yielding the same well-supported topology. Phylogenetic analyses demonstrate that Angolan *Cordylus* is sister to the *C. jonesii*–*C. rhodesianus* group (PP: 0.99, BS: 87) (Fig. 3).

Angolan *Cordylus* represents a well-supported monophyletic group (PP: 1, BS: 100), divided into a northern clade, which includes *C. angolensis* from the central highlands of Angola and an undescribed sister species, *C.* ‘Mombolo’, from slightly further north (PP: 0.99, BS: 88), and a southern clade that includes the three species of the *C. machadoi* group (*C. machadoi*, *C. namakuiyus* and *C. phonolithos*). The Taqueta material is referable to *C. angolensis* on the basis of its similarity to the holo-



**Figure 3.** Maximum likelihood (ML) phylogenetic tree for *Cordylus* based on concatenated dataset, with Bayesian inference (BI) support overlaid. Numbers above the key nodes indicate BI posterior probability ( $\geq 0.95$  were considered supported), while below the key nodes indicate ML bootstrap values ( $\geq 95\%$  were considered supported). Major Angolan clades are highlighted in different colours.

**Table 3.** ND2 divergences (uncorrected pairwise distances) between cordylid taxa, including all *Cordylus* from Angola. Bold values depict intraspecific divergences.

	1	2	3	4	5	6	7	8	9
1. <i>Namazonurus campbelli</i>	—								
2. <i>Pseudocordylus m. subviridis</i>	22.46	<b>7.7</b>							
3. <i>Cordylus vittifer</i>	22.12	20.82	<b>11.7</b>						
4. <i>Cordylus jonesii</i>	22.02	20.75	16.54	<b>2.8</b>					
5. <i>Cordylus namakuiyus</i>	22.07	19.50	16.05	16.43	<b>4.3</b>				
6. <i>Cordylus machadoi</i>	23.19	20.27	16.38	16.82	7.57	<b>2.4</b>			
7. <i>Cordylus phonolithos</i>	21.56	18.90	16.77	15.60	9.40	8.94	<b>0.4</b>		
8. <i>Cordylus</i> ‘Mombolo’	22.74	21.25	16.60	16.70	9.85	11.59	12.29	<b>1.1</b>	
9. <i>Cordylus angolensis</i>	22.22	19.82	16.55	15.15	10.85	11.97	11.92	9.22	<b>0.2</b>

type (see below). These clades show large genetic ND2 p-distance between them (~10.00%). The uncorrelated ND2 p-distance found between *C. angolensis* and *C.* ‘Mombolo’ was 9.2% (Table 3) where uncorrelated ND2 p-distance within each taxon was 1.1% or less. Within the southern clade, the minimum uncorrelated ND2 p-distance was 7.6% between the species. *Cordylus machadoi* clusters as sister to the recently described *C. phonolithos* (uncorrelated p-distance: 8.9%; PP: 0.77, BS: 77), leaving the remaining clade of *C. namakuiyus* as sister species of this latter group (PP: 1, BS: 100).

## Morphological evaluation

**Length of scales in the first transverse row of dorsals** (Figs 4, S2). In *C. machadoi*, *C. namakuiyus* and *C. phonolithos*, and *C. vittifer*, all or most of the scales in the first transverse row of dorsals are about 1.5–3 times longer than those in the row behind. In some cases, this row appears as a distinct collar. In *C. angolensis* and *C.* ‘Mombolo’, as well as all other species of *Cordylus* (e.g., FitzSimons 1943; Broadley and Branch 2002), the first transverse row of dorsals is similar to the second, with most or all scales of about the same length.

**Presence or absence of a loreal scale** (Figs 5, 7). A loreal shield (usually distinctly smaller than the preocular) is usually present in most species compared here, as well as *C. cordylus* (see also FitzSimons 1943; Mouton 1987; Bates 2007; Broadley and Branch 2002), but always absent in *C. angolensis* and *C.* ‘Mombolo’. A loreal was absent in eight out of 35 *C. vittifer* variety B (partly fused with preocular on one or both sides of head in two specimens; absent on left side only in one specimen) and partly fused with the preocular on the right side of the head in one (of 18) *C. vittifer* from KwaZulu-Natal.

**Nasal scales** (Figs 5, 7). In all Angolan species, *C. jonesii*, and *C. rhodesianus* the nasal scale is divided posteriorly (i.e., longitudinally), while it is undivided in *C. tropidosternum* (see also Broadley and Branch 2002) and *C. vittifer* (but divided longitudinally in NMB R8768). In a couple of *C.* ‘Mombolo’ (i.e., TM 46476 and right side of PEM R025217) the nostril appears to be in contact with

the preocular. There are also differences in the position of the sulcus – it is situated between the outer center of the nostril and the preocular in *C. angolensis* and *C.* ‘Mombolo’, between the outer center of nostril and loreal in *C. machadoi*, *C. phonolithos* and *C. namakuiyus*, between outer center of nostril and suture between loreal and first supralabial (‘curved sulcus’ according to Broadley and Branch 2002) in *C. rhodesianus*, and is present as a groove (also referred to as a ‘curved sulcus’ by Broadley and Branch 2002) running from above the nostril down to the outer center of the loreal in *C. jonesii*.

**Position of the nostril** (Figs 5, 7). Broadley and Branch (2002) noted that the position of the nostril within the nasal proved to be a useful taxonomic character. The nostril of *C. angolensis* and *C.* ‘Mombolo’ is pierced halfway up the posterior edge of a large, slightly domed nasal, and is well separated from the first supralabial (usually by more than the greatest extent of the nostril). In *C. machadoi*, *C. phonolithos* and *C. namakuiyus* the situation is similar and the nostril is also well separated from the first supralabial – lower edge of nostril separated from first supralabial by a distance of at least  $\frac{3}{4}$  its own diameter, whereas in *C. vittifer* the nostril and first supralabial are in close proximity – usually (87.5%, n = 72) separated by a distance of  $<\frac{1}{2}$  diameter of nostril (first supralabial is in contact with the nostril in two specimens, and in NMB R8864 the nasal rim and first supralabial are fused). In *C. marunguensis* (south-eastern Democratic Republic of the Congo) the nostril is situated centrally on the lower margin of the nasal, separated from the first supralabial by a narrow rim (Greenbaum et al. 2012). In *C. cordylus* the nostril is situated in the lower, posterior part of the nasal, and frequently bordered below by a small scale (FitzSimons 1943; Bates 2007). In *C. jonesii* and *C. rhodesianus* the nostril is pierced centrally in the posterior half of a semi-divided nasal; whereas in *C. tropidosternum* it is pierced in the postero-inferior corner of the nasal and bordered by the first supralabial (Fig. 7; Broadley and Branch 2002).

The position of the nostril relative to the suture between rostral and first supralabial is also informative. In *C. angolensis* and *C.* ‘Mombolo’ the entire nostril is situated posterior to the suture, as is the case in *C. tropidosternum* and *C. vittifer*, whereas in all three species of the *C. machadoi* group at least some part of the nostril is sit-

uated above the suture, which is often also the case with *C. rhodesianus* and *C. jonesii* (Fig. 7; see also Broadley and Branch 2002).

**Texture of sublabial scales** (Figs 5, 6). The sublabials are moderately to deeply corrugated in *C. angolensis*, *C.* ‘Mombolo’, *C. machadoi*, *C. namakuuiyus*, *C. phonolithos* and *C. jonesii*; but the first two pairs of sublabials may be largely smooth in some *C. machadoi* (Fig. 6W–Y) and all sublabials are weakly corrugated in a juvenile *C.* cf. *machadoi* (TM 57561) from Namibia. In *C. vittifer* and *C. rhodesianus* most sublabials are smooth, with only the posterior ones (last and sometimes also second last sublabial; also third last in *C. vittifer*, NMB R8867) distinctly corrugated in some specimens. According to Broadley and Branch (2002) the sublabials are rugose in *C. jonesii* and *C. tropidosternum*, but smooth to feebly rugose in *C. rhodesianus*.

**Relative size of the frontonasal scale** (Fig. 4). In *C. machadoi*, *C. namakuuiyus* and *C. phonolithos* the frontonasal is always larger than either of the prefrontals, whereas it is always smaller in *C.* ‘Mombolo’ and usually smaller in *C. vittifer* (of equal size in NMB R4591, NMB R10301–2, 10329; larger in NMB R8149, 8740; absent in NMB R8866). The frontonasal varies in size in *C. angolensis* (smaller than a prefrontal in three specimens, bigger in two [Fig. 4B, C]), *C. rhodesianus* (smaller than a prefrontal in three specimens, of equal size in NMB R10031, slightly larger in NMB R10034) and *C. jonesii* (smaller in three specimens, larger in NMB R8652, 8655).

**Proximity of the frontonasal to the frontal scale** (Fig. 4). In most species the frontonasal and frontal are usually separated by the prefrontals. However, these scales were in contact in 38% of *C. jonesii* and 29% of *C. rhodesianus* (Broadley and Branch 2002). They were separated in all *C.* ‘Mombolo’ specimens, but in contact in two (Fig. 4A, C) of the five *C. angolensis* examined. This character seems to be quite variable in the *C. machadoi* complex: in *C. machadoi* the frontal and frontonasal are often in good contact, in narrow contact medially in CHL 700, narrowly excluded in TM 40132, and separated by the prefrontals in TM 57561 (*C.* cf. *machadoi*); *C. namakuuiyus*: usually separated by prefrontals but occasionally in contact; *C. phonolithos*: separated in the type series (Marques et al. 2019), but in Fig. 4: equally often in broad contact (R, T, U) or separated by prefrontals (Q, S, V), once in narrow median contact (P). The frontonasal and frontal are occasionally in contact in *C. vittifer*, as they are in one of five specimens of both *C. jonesii* and *C. rhodesianus* examined. In variety A of *C. vittifer* the frontonasal and frontal are often (five out of 12 specimens) separated by one or two (NMB R3825) azygous shields.

**Occipitals and post-occipitals** (Figs 2, 4). In *C. angolensis* there is always a regular, uninterrupted row of six occipitals in broad contact (narrowly medially in CHL 615). In *C.* ‘Mombolo’ a medially-interrupted row (i.e., 2–3 small scales on either side of the head) is always present,

as well as a row of 5–6 post-occipitals. A medially-interrupted row of small occipitals also characterises *C. namakuuiyus* (2–4 on either side of head; plus 6–8 post-occipitals; the holotype has 2–3 occipitals on either side of the head and 7 post-occipitals), and *C. phonolithos* (3–5 occipitals on either side of head; plus 6–7 post-occipitals; the holotype has 4 occipitals on either side of the head, but on the right side there is an additional two scales between the occipitals and the 10 post-occipitals), but in *C. machadoi* there may be a continuous row of 6–8 occipitals, plus a continuous row of 6–8 post-occipitals (Fig. 4), although the holotype has four occipitals on the left and three on the right, narrowly interrupted medially by the fifth (from the left) of seven post-occipitals (Laurent 1964; fig. 26, Ceriaco et al. 2020d), while the paratype (Fig. S1) has 8 ‘occipitals’ and what is best described as four small, narrow, supernumerary scales between them and the posterior parietals. A regular row of six occipitals (occasionally 4, 5, 7 or 8 in *C. vittifer*; 8 in *C. rhodesianus* [NMB R10035]; 5 in *C. jonesii* [NMB R8653]) was present in all specimens examined of the other species. However, in *C. vittifer* var. A, most specimens had two occipitals on either side of the head, and a row of 7–8 post-occipitals.

**Anterior parietals** (Fig. 4). In *C. phonolithos* and most *C. namakuuiyus* the pair of anterior parietals is completely separated by the interparietal, which is therefore in contact with the frontoparietals. However, in two (M, N) of three *C. namakuuiyus* shown in Fig. 4, the interparietal does not separate the anterior parietals (although it almost does in one [N] of these two specimens), it does so only narrowly in AMNH 47316, and it separates most of the anterior parietals in PEM R25218 but a few small adjacent scales are present between interparietal and frontoparietals. The anterior parietals are also completely separated by the interparietal in 11 out of 13 specimens of *C. vittifer* var. A, but in other populations of this species they are usually in contact anteriorly. In other species, including *C. angolensis*, *C.* ‘Mombolo’, *C. machadoi*, *C. jonesii*, *C. rhodesianus* and *C. tropidosternum* (see also Broadley and Branch 2002), the anterior parietals are usually in contact anteriorly. Exceptions (anterior parietals fully separated by interparietal) in material examined: one specimen each of *C. angolensis* and *C.* ‘Mombolo’, TM 57561 (*C.* cf. *machadoi*) from Namibia, three out of 31 specimens of *C. vittifer* var. B, one out of 18 *C. vittifer* from KwaZulu-Natal (in two others a small squarish scale anterior to the interparietal separates the anterior parietals), and one out of five specimens of both *C. jonesii* and *C. rhodesianus*. Marques et al. (2019) indicated that the posterior parietals of *C. phonolithos* were fully separated by a large scale that is also in contact with the interparietal. However, such a scale was absent in all seven specimens (P to V) of this species photographed for Fig. 4.

**Femoral pores and differentiated femoral scales (generation glands)** (Table 4, Table S2). Males of all species have large secretory femoral pores. One male *C. machadoi* (PEM R19782) also has a differentiated scale



**Figure 4.** Dorsal views of the head in Angolan *Cordylus*. *Cordylus angolensis*—A CHL 611, B CHL 615, C MNCN 50649, D CHL 613, E MNCN 50648 (neotype); *C. momboloensis* sp. nov.—F MNCN 50760 (paratype), G FKH 0125 (paratype), H FKH 0127 (paratype), I FKH 0128 (paratype), J FKH 0129, K PEM R25217 (holotype), L MNCN 50761 (allotype); *C. namakuiyus*—M PEM R25218, N CHL 616, O CHL 609; *C. phonolithos*—P CHL 852, Q CHL 1056, R MNCN 50651, S CHL 851, T CHL 1057, U MNCN 50652, V CHL 848; and *C. machadoi*—W CHL 701, X CHL 700, Y PEM R19784. Photos: Pedro Vaz Pinto (A–N, P–V), Timóteo Júlio (O, W–X), and William R. Branch (Y).



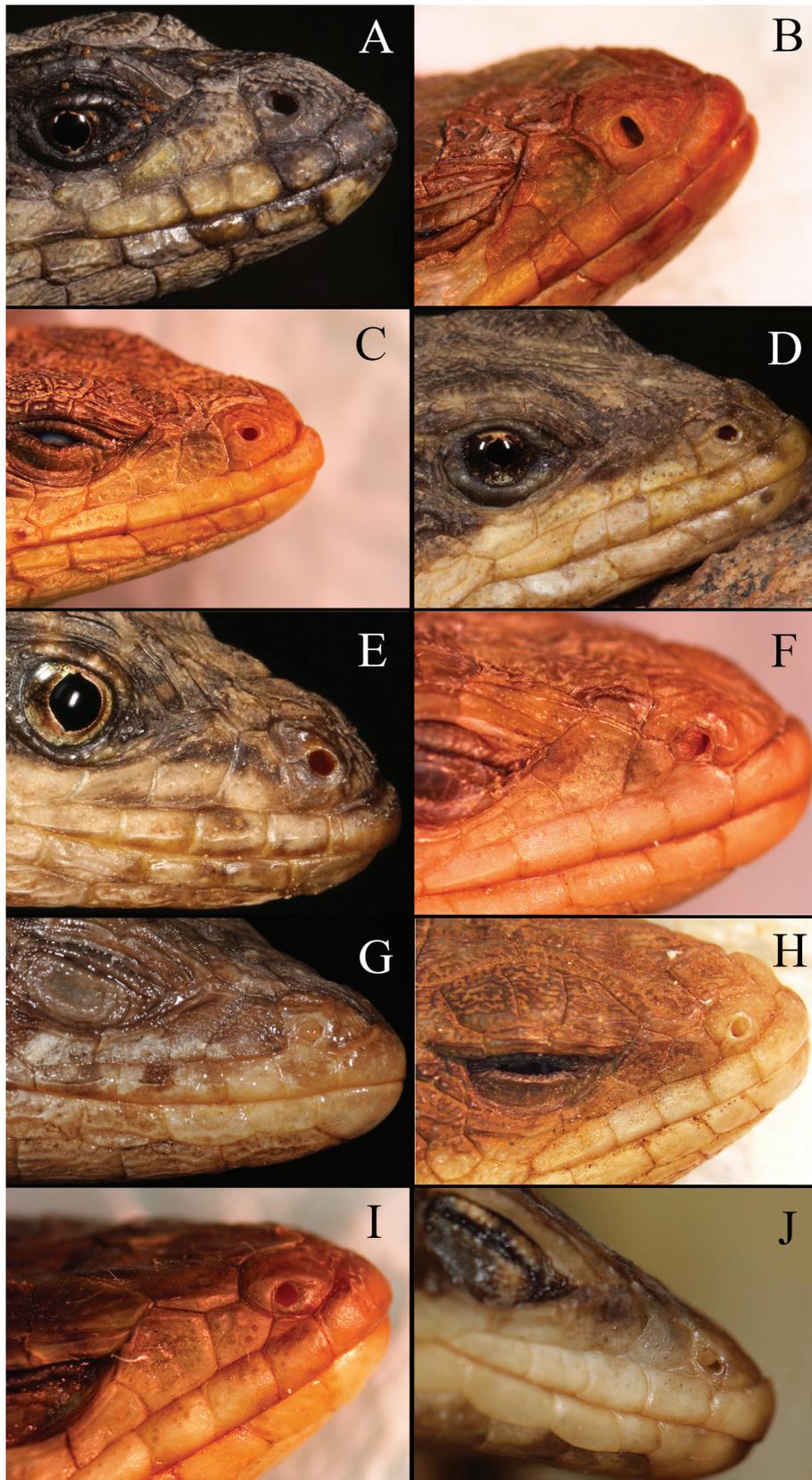
**Figure 5.** Lateral views of the head in Angolan *Cordylus*. *Cordylus angolensis*—A CHL 611, B CHL 615, C MNCN 50649, D CHL 613, E MNCN 50648 (neotype); *C. momboloensis* sp. nov.—F MNCN 50760 (paratype), G FKH 0125 (paratype), H FKH 0127 (paratype), I FKH 0128 (paratype), J FKH 0129, K PEM R25217 (holotype), L MNCN 50761 (allotype); *C. namakuiyus*—M PEM R25218, N CHL 616, O CHL 609; *C. phonalithos*—P CHL 852, Q CHL 1056, R MNCN 50651, S CHL 851, T CHL 1057, U MNCN 50652, V CHL 848; and *C. machadoi*—W CHL 701, X CHL 700, Y PEM R19784. Photos: Pedro Váz Pinto (A–N, P–V), Timóteo Júlio (O, W–X), and William R. Branch (Y).

(possibly a generation gland) on a lateral pre-anal scale at the tail base. In *C. angolensis* males there are 5–6 femoral pores, and 19–25 well-developed generation glands, per thigh; while the one female has 5 pores on the left and 6 on the right (no generation glands). However, in the material assigned to *C. ‘Mombolo’*, males have 5–8 femoral pores with 25–37 generation glands, and females have 4–7 femoral pores (no generation glands). Counts for *C. machadoi* are: femoral pores 5–7 in males and 6–7

females, generation glands in males 10–25; for *C. namakuiyus*: femoral pores 4–6 in males, 4–5 (once 6) in females, generation glands in males 9–18; and *C. phonalithos*: femoral pores 7–8 in males, 7 in female, generation glands in males 16–21. Females of most species usually have small to moderate femoral pores with secretions, but pores vary in *C. vittifer* (var. A and B [Mpumalanga/Eswatini and Limpopo populations]): small, pit-like and apparently non-secretory [of moderate size with secre-



**Figure 6.** Ventral views of the head in Angolan *Cordylus*. *Cordylus angolensis*—A CHL 611, B CHL 615, C MNCN 50649, D CHL 613, E MNCN 50648 (neotype); *C. momboloensis* sp. nov.—F MNCN 50760 (paratype), G FKH 0125 (paratype), H FKH 0127 (paratype), I FKH 0128 (paratype), J FKH 0129, K PEM R25217 (holotype), L MNCN 50761 (allotype); *C. namakuiyus*—M PEM R25218, N CHL 616, O CHL 609; *C. phonolithos*—P CHL 852, Q CHL 1056, R MNCN 50651, S CHL 851, T CHL 1057, U MNCN 50652, V CHL 848; and *C. machadoi*—W CHL 701, X CHL 700, Y PEM R19784. Photos: Pedro Vaz Pinto (A–N, P–V), Timóteo Júlio (O, W–X), and William R. Branch (Y).



**Figure 7.** Arrangement of the nasal shield, nostril and scales of the snout in *Cordylus*: **A** *C. angolensis* (CHL 615 – Taqueta Mountain, Angola); **B** *C. momboloensis* sp. nov. (AMNH R47333 – ‘Mombolo’, Angola); **C** *C. machadoi* (TM 40133 – 1.4 km NE of Humbia, Angola); **D** *C. namakuiyus* (PEM R25218 – 10.4 km S of Rio Mucungo on tar road to Bentiaba, Namibe Province, Angola); **E** *C. phonolithos* (CAS 263581, holotype – vicinity of N’Dolondolo, Serra da Neve, Angola); **F** *C. vittifer* (NMB R8721 – Farm Goede Hoop 182, Mpumalanga Province, South Africa); **G** *C. tropidosternum* (PEM R13288 – Moebase village, Zambesiaca Province, Mozambique); **H** *C. jonesii* (NMB R8656 – Farm Doorenwaard 313, Limpopo Province, South Africa); **I** *C. rhodesianus* (NMB R10034 – York Forest Land, Zimbabwe); **J** *C. cordylus* (NMB R9525 – De Hoop Nature Reserve, Western Cape Province, South Africa). Photos: Javier Lobón-Rovira (A), Michael F. Bates (B, C, F, H, I, J), William R. Branch (D, G), and Luis M. P. Cerriaco (E).

**Table 4.** Comparative meristic data for *Cordylus* from the Angolan clade and various species in the East African clade (including *C. jonesii*–*C. rhodesianus*). The first row of data refers to the range of values, the second row is the mean, and the third row is the standard deviation. For *C. angolensis*, data for the (now lost) holotype, as recorded by Bocage (1895) and Broadley (pers. comm.), was not used in calculations (see discussion in species account), but is indicated in square brackets when it exceeds the ranges recorded here; for *C. phonolithos*, data is for the holotype and paratype (Marques et al. 2019) and two new specimens (MNCN 50651–2). (M = male, F = female, J = juvenile. <sup>-1</sup> means that sample size for a particular character was one less than that indicated in the second column, <sup>-2</sup> means two less, <sup>-3</sup> means three less. \*Includes FKH 0129 in Fig. 4; \*\*Holotype, paratype, and CHL 848, 851, 852, 1056 and MNCN 50652 in Fig. 4).

Species	Sample Size	Gulars in contact with 1 <sup>st</sup> pair chin shields	Gulars b/n angle of jaws	Transverse rows of dorsals	Longitudinal rows of dorsals	Transverse rows of ventrals	Longitudinal rows of ventrals	Lamellae under 4 <sup>th</sup> toe	Lamellae under 4 <sup>th</sup> finger	Femoral pores (total both legs)	Differentiated femoral scales (total both legs)
<i>C. angolensis</i>	5 (4 M, 1 F)	5–6 5.2 ±0.447	20–21 [26] 20.2 ±0.447	24–25 24.4 ±0.548	20–23 [26] 21.2 ±1.30	22–24 [27] 22.8 ±0.837	14 [16]	14	—	M 11–12 F 11	M 38–50 F 0
<i>C. momboloensis</i> sp. nov.	12 (5 M, 7 F)	4–5* <sup>-1</sup> 4.6 ±0.515	16–26 20.2 ±2.66	22–24 22.9 ±0.900	18–23 20.7 ±1.56	22–27 23.9 ±1.78	11–14 12.3 ±0.754	11–15 <sup>-2</sup> 13.1 ±1.10	—	M 10–15 F 8–12	M 53–72 F 0
<i>C. machadoi</i>	12 (7 M, 5 F)	3–5 4.1 ±0.793	18–24 <sup>-1</sup> 20.4 ±1.69	23–27 24.8 ±1.14	22–27 24.8 ±1.66	22–26 23.5 ±1.45	11–18 13.8 ±2.09	10–15 13.7 ±1.44	9–13 11.2 ±1.03	M 11–14 F 12–14	M 20–48 F 0
<i>C. cf. machadoi</i> (Namibia)	1 (1 J)	5	24	23	22	23	14	14	10	J 9	J 0
<i>C. namakuiyus</i>	26 (11 M, 15 F)	3–5 3.6 ±0.697	15–18 <sup>-1</sup> 17.3 ±0.737	22–26 23.6 ±0.852	19–24 22.0 ±1.37	19–23 <sup>-1</sup> 21.5 ±0.770	10–18 13.1 ±1.48	11–15 12.8 ±1.05	9–12 10.7 ±0.962	M 8–12 F 8–12	M 19–36 F 0
<i>C. phonolithos</i>	4 (2 M, 1 F, 1 J)	3–5** 4.4 ±0.787	17–18 17.3 0.500	24–26 25.0 0.816	22–23 22.5 0.577	23 <sup>-2</sup>	16–17 16.5 0.577	14 <sup>-1</sup>	12 <sup>-3</sup>	M 14–15 F 14 J 0	M 33–42 F 0 J 0
<i>C. tropidosternum</i>	6 (3 M, 3 F)	4	23–25 23.5 0.837	27–28 27.3 0.516	19–23 21.0 1.55	23–28 25.3 1.86	12–14 12.3 0.816	13–14 13.3 0.516	12–13 12.3 0.516	M 12 F 0–13	M 16–29 F 0
<i>C. rhodesianus</i>	5 (1 M, 4 F)	2–4 3.00 ±0.707	22–24 23.0 ±0.707	26–28 27.0 ±1.00	22–25 23.6 ±1.14	22–25 22.8 ±1.30	12–14 13.2 ±1.10	12–13 12.2 ±0.447	10–11 10.2 ±0.447	M 14 F 11–12	M 49 F 0
<i>C. jonesii</i>	5 (2 M, 3 F)	3–4 3.2 ±0.447	20–22 20.8 ±0.837	23–24 23.6 ±0.548	19–24 21.4 ±1.95	21–25 23.4 ±1.52	12–14 12.4 ±0.894	13–14 13.4 ±0.548	10–12 11.6 ±0.894	M 11–12 F 8–10	M 10–13 F 0
<i>C. vittifer</i>	72 (35 M, 31 F, 6 J)	2–5 <sup>-1</sup> 3.2 ±0.873	15–24 <sup>-1</sup> 20.6 ±1.63	23–27 25.0 ±0.731	20–27 22.4 ±1.37	21–27 24.2 ±1.40	14–18 15.1 ±1.11	12–16 <sup>-1</sup> 13.5 ±0.734	10–13 <sup>-1</sup> 11.5 ±0.733	M 10–18 F 0–19 J 0–12	M 17–62 F 0–10 J 0–18

tions in NMB R8768 from Mpumalanga]; var. B [Free State] and var. C: large and secretory; KwaZulu-Natal: moderate to large and secretory). Differentiated femoral scales are present in males of all species, but absent in all females except those of *C. vittifer* variety *C. Cordylus jonesii*, *C. rhodesianus* and *C. tropidosternum* all have similar numbers of femoral pores per thigh (3–8) to the Angolan species; but often lower numbers of generation glands per thigh (3–21) (Broadley and Branch 2002), although a couple of specimens examined for the present study had high counts (*C. rhodesianus*: 23–26).

**Ventral scale rows longitudinally** (Table 4, Table S2). All newly-collected specimens of *C. angolensis* have 14 longitudinal rows of ventral scales versus the 11–14 (usually 12–13) in material assigned to *C. ‘Mombolo’*. Bocage (1895) recorded 16 ventral scale rows for the holotype of *C. angolensis*, but he may have included an extra row of small ‘pseudoventrals’ on either side. There was much variation in the other species: 11–18 in *C. machadoi*; 10–18 in *C. namakuiyus*; 16–17 in *C. phonolithos*; 12–14 in *C. tropidosternum*, *C. jonesii* and *C. rhodesianus*, and 14–18 in *C. vittifer* (var. A: 16–18, mean 16.2; KwaZulu-Natal: 14–16, mean 14.3; var. B: 14–16, sometimes 18; var. C: 14).

**Other scale counts** (Table 4, Table S2). There is considerable variation in most other meristic scale characters. Regarding the number of gular scales in contact with the first pair of chin shields, *C. angolensis* (5–6, mean 5.2) and *C. ‘Mombolo’* (4–5, mean 4.5) had the highest counts, and *C. vittifer* var. A had the lowest (2–3, mean 2.3), but these were the only populations that did not overlap in this character.

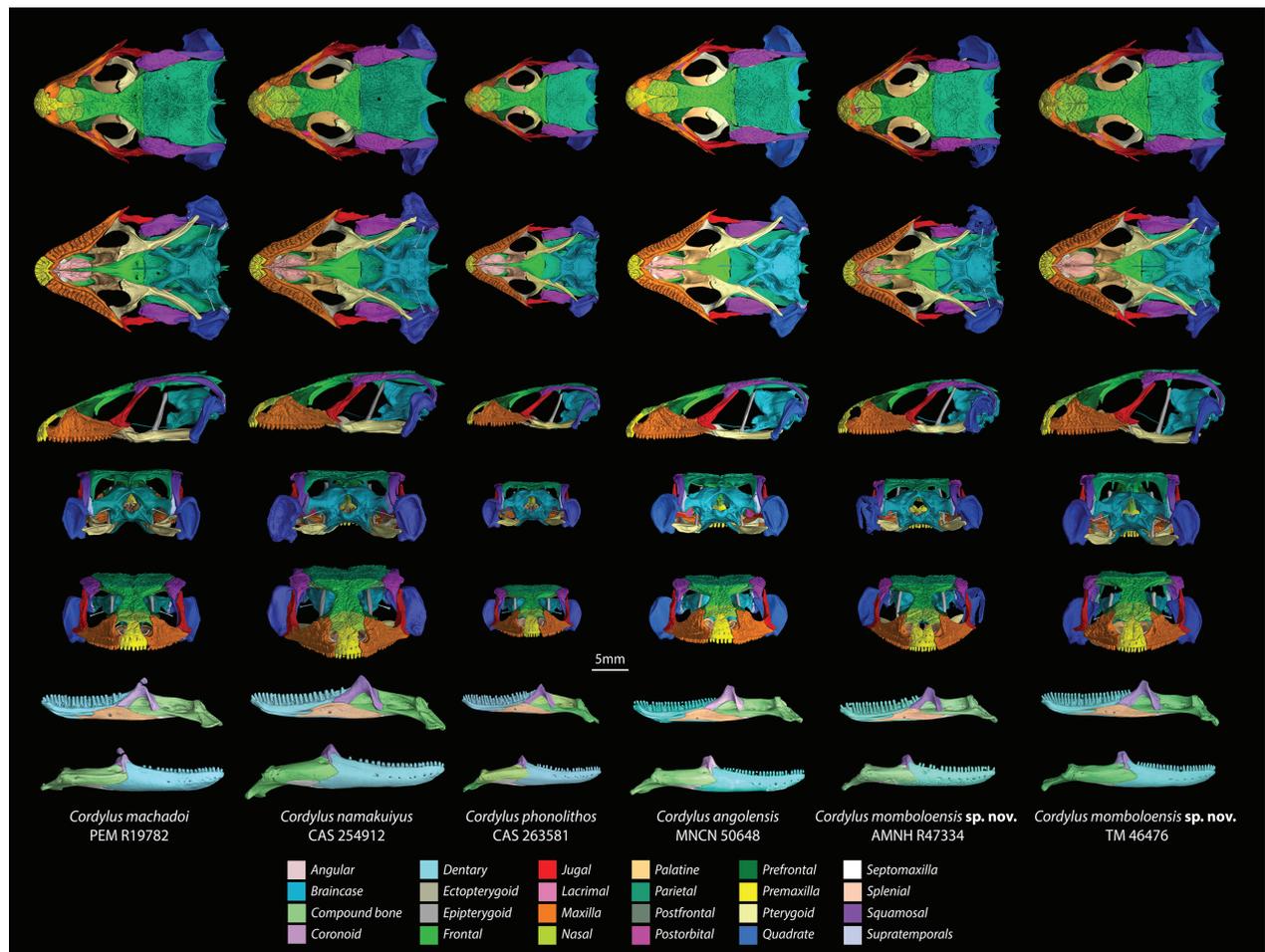
**Colour pattern** (in life; Figs 1, 4, 6 and other figures below). The back of both *C. angolensis* and *C. ‘Mombolo’* is a mixture of pale and dark brown, the darker scales tending to form vague transverse bands. In both species there is always a paired series of irregular, pale, cream-greenish to blue markings/blotches paravertebrally along the back, from the neck to the base of the tail (see figures below). In *C. angolensis* the markings tend to be smaller and less extensive compared to *C. ‘Mombolo’*, which also has more extensive pale markings on the top of the head. The belly is dirty white, but while the throat is of a similar colour in *C. ‘Mombolo’*, it is cream in *C. angolensis*. In *C. machadoi*, *C. namakuiyus* and *C. phonolithos* the central part of the back, top of limbs and top of head are mostly plain medium brown, and the flanks tan to cream-yellow; in the latter two species the flanks are paler, and *C. phonolithos* has vaguely marked, broad, cream dorsolateral stripes. In *C. vittifer* the dorsum is brown to orange-brown, usually with darker markings, and may contain dark (occasionally pale) lateral stripes and/or a pale vertebral stripe (e.g., Bates et al. 2014; Reissig 2014). *Cordylus tropidosternum* is dark brown above, often with pale or darker markings that may form ragged dorsolateral bands; *C. jonesii* is light brown with darker blotches, while *C. rhodesianus* is yellow-brown to black with pale (sometimes bright yel-

low) and dark blotches (Broadley and Branch 2002). The venter of most species is white to cream, but in *C. machadoi* it is sometimes mainly yellow (Fig. S4) or a mixture of yellow and cream, and it may be cream-yellow in *C. namakuiyus*.

**Colour of the iris of the eye** (Fig. 5). This character needs to be photo-recorded using live specimens. In most of the Angolan species (*C. angolensis* and the three species of the *C. machadoi* complex) the iris in life is brown (Fig. 5). However, in *C. ‘Mombolo’* most of it is greenish (blueish-green to some eyes), with a narrow brown ring around the black pupil. This eye colour is a diagnostic feature that easily separates the latter and its sister species *C. angolensis*. Based on colour photographs in Reissig (2014) and Fig. 1, the iris in *C. jonesii*, *C. tropidosternum*, *C. rhodesianus* and *C. vittifer* is brown to orange-brown (distinctly orange in *C. tropidosternum*, Fig. 1E).

**Texture of gular scales** (Fig. 6). Gulars or throat scales are smooth in *C. angolensis* but weakly keeled at least laterally in most *C. ‘Mombolo’* specimens. In one specimen (MNCN 50760) of *C. ‘Mombolo’* most of the gulars are obtusely keeled (Fig. 6). Judging from Fig. 6, the gulars are smooth in *C. machadoi* and *C. phonolithos*, but in *C. namakuiyus* two of the three specimens have obtuse keeling laterally on the throat. Most of the gulars are obtusely keeled in *C. tropidosternum*, smooth in *C. rhodesianus*, while in *C. jonesii* they are smooth mesially but feebly keeled laterally (Broadley and Branch 2002). In *C. vittifer* the gulars are usually smooth except for the lateral ones below the ear openings which are often weakly and obtusely keeled (e.g., holotype, Fig. S2), but all scales may be smooth as in var. C; occasionally the laterals are distinctly keeled, and in a few cases most other gulars are also weakly or even moderately (e.g., NMB R8773) keeled.

**Cranial skeleton** (Fig. 8, Table S3). CT scans of Angolan *Cordylus* and select members of the East African *Cordylus* clade (see Table S1) reveal some consistent skeletal differences between the two morphotypes from west-central Angola. The maxilla of *C. ‘Mombolo’* is deeper and the maxillary process more pronounced than observed in *C. angolensis*, causing a steeper, shorter articulation with the nasals. The posteromedial process of the parietal differs between *C. angolensis* and *C. ‘Mombolo’*, the former having a narrow and biconcave “Y”-shaped projection that articulates with the sagittal crest of the supraoccipital, while the latter’s process is less laterally compressed, forming an “M”-shaped projection. The posteromedial process of the members of the *C. machadoi* complex is variably bifurcated, and the shape of this process is highly variable within these and other species of *Cordylus* (Lang 1991; Stanley et al. 2016). *Cordylus ‘Mombolo’* has nine premaxillary teeth while all other *Cordylus* observed have seven (rarely 6) such teeth. *Cordylus ‘Mombolo’* has 18–20 maxillary and 22–26 dentary teeth, *C. angolensis* has 22 maxillary and 25–26 dentary teeth, *C. machadoi* has 13–17 maxillary and 18–21 dentary teeth,



**Figure 8.** Computed tomography images depicting the cranial osteology of the five species of *Cordylus* from Angola.

*C. namakuiyus* has 15–18 maxillary and 16–22 dentary teeth, and *C. phonolithos* has 19–20 maxillary and 22–23 dentary teeth. Counts for other East African *Cordylus* are 14–20 maxillary, and 16–23 dentary, teeth.

**Osteoderms** (Figs 9, S5). Both *C. angolensis* and *C. ‘Mombolo’* are more heavily armoured than *C. machadoi*, *C. jonesi* and *C. marunguensis*, with a distribution and degree of osteodermal armour similar to that seen in *C. namakuiyus*, *C. rhodesianus*, *C. beraduccii* Broadley and Branch 2002, *C. tropidosternum*, *C. vittifer* and *C. nyikae* (Stanley 2013). It has been hypothesised that the degree of armour in cordylids is linked to microhabitat use, with species living in more exposed environments possessing greater amounts of armour (Stanley 2013). The degree of dermal armour has also been shown to increase allometrically with SVL within cordylid species (Stanley et al. 2016; Broekhoven et al. 2017). Our assessment of Angolan *Cordylus* osteoderm volume (Fig. S5) reveals a strong allometric signal in the relative amount of dermal armour, with larger individuals having a greater osteoderm/postcranial skeleton volume ratio. There are also clear differences in the degree of armourment between the well-armoured *C. namakuiyus* and the more lightly armoured species, *C. machadoi*. When included in the allometry plot (Fig. S5), *C. ‘Mombolo’* and *C. phonolithos* appear to be as robustly armoured as *C. namakuiyus*, while *C.*

*angolensis* appears to occupy an intermediate position between *C. namakuiyus* and *C. machadoi*, though an expanded sampling of ontogenetic series is required before fine-scale diagnostic characters in the degree of armour can be reported.

The morphological and genetic differences mentioned above, together with allopatry, support the recognition of two different species in the *C. angolensis* clade. We take the opportunity below to describe the *C. ‘Mombolo’* lineage as a new species.

## Systematics

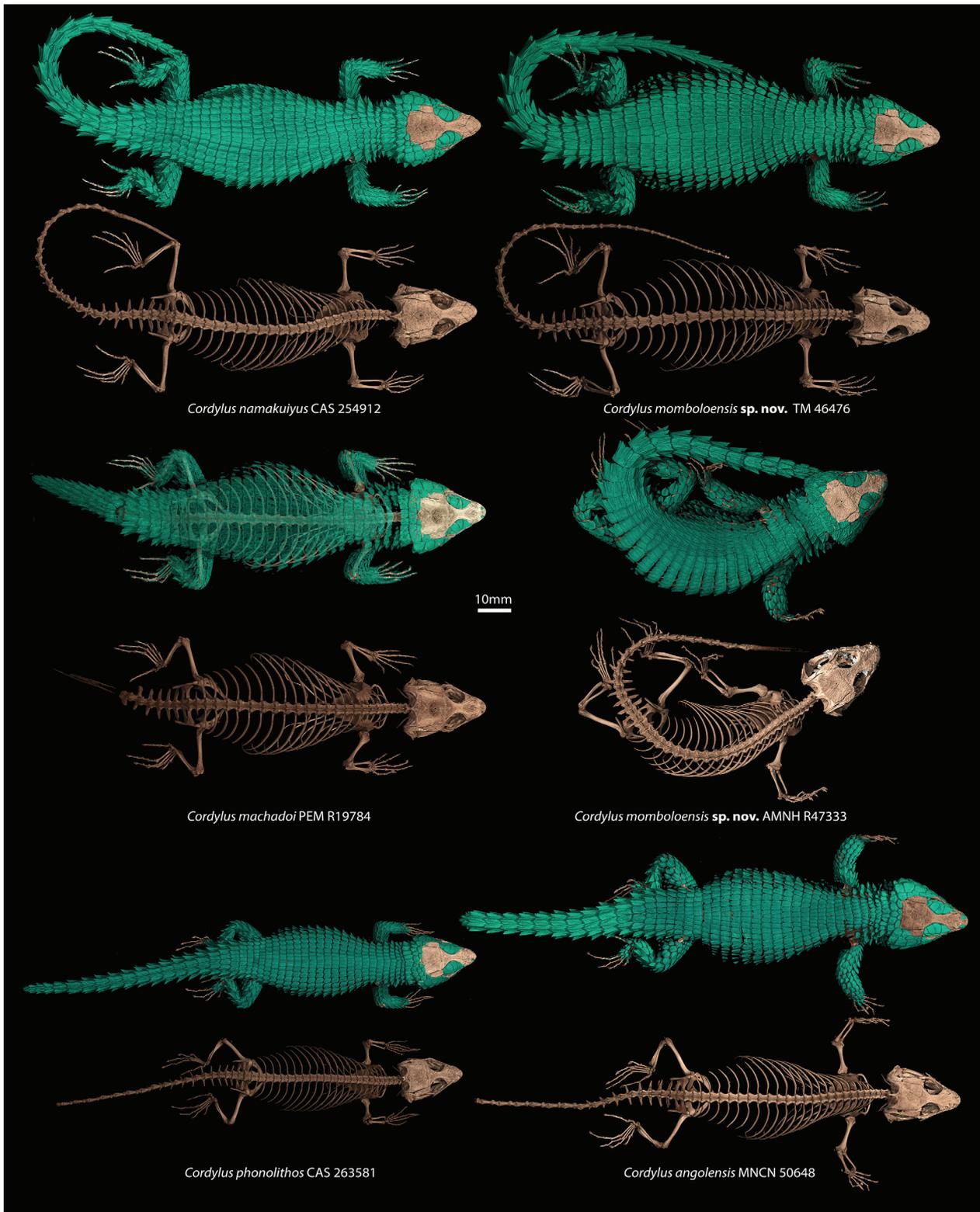
### Squamata: Sauria: Cordylidae

#### *Cordylus angolensis* (Bocage, 1895)

Figs 4–11; Tables 5, 6

Angolan girdled lizard; Lagarto-espinhoso de Angola

**Chresonymy.** *Zonurus angolensis* Bocage, 1895: 25. Type locality. Caconda, Angola.



**Figure 9.** Computed tomography generated images showing the osteology of the five Angolan *Cordylus* species. Osteoderms are highlighted in blue-green.

*Cordylus cordylus angolensis* – Loveridge (1944a: 38); Mertens (1955: 59, 1971: 53).

*Cordylus angolensis* – Visser (1971: 19); Broadley and Branch (2002) partim; Branch et al. (2005) partim; Adolphs (2006: 17); Broadley (1971: 22); Broadley (2006: 1) partim; Stanley et al. (2011: 67) partim; Greenbaum et al. (2012: 32) partim; Caconda; Reissig (2014: 33) partim.

Bocage's (1895) description of a single type specimen (MBL 429, adult male) of *C. angolensis* was fairly terse and he did not provide any illustrations. He described the dorsal parts of the head and back as being a variety of brown and black on a pale tan, with two longitudinal series of small irregular whitish spots along the back, the tail brown, with venter white. Regarding scalation he

noted only that: Internasal (= frontonasal) rhomboid, in contact with the anterior part of the frontal, thus separating the prefrontals; loreal absent; preocular large and in contact with the posterior part of the nasal; nasal large, slightly domed, pierced halfway up the posterior edge; gular with quadrangular scales, smooth, narrow, juxtaposed, of various shapes, and significantly smaller than in *C. cordylus*; dorsals in 26 longitudinal and 24 transverse rows; ventrals in 16 longitudinal and 27 transverse rows; two large pre-anal scales separated on the median line by two small plates; pre-anal pores 6 [presumably number of femoral pores on each thigh]; snout-vent length = 74 mm; tail length = 78 mm (incomplete). Head width/SVL = 24.3%; head length/SVL = 31.1% [based on head and body measurements provided].

In 1968 Dr Donald G. Broadley (in litt., 18 January 2012) examined the holotype (MBL 429) of *C. angolensis* at the Museu Bocage in Lisbon and recorded the following data: nasals in broad contact, loreal absent (fused with preocular); frontal and frontonasal in contact, suboculars 3, supraciliaries 3, gulars 26, dorsals in 24 transverse and 26 longitudinal rows, ventrals in 27 transverse and 16 longitudinal rows, femoral pores 6 on each thigh; outer three rows of ventrals keeled and mucronate; SVL = 78 mm; tail length 74 mm tail (broken). As mentioned earlier, Broadley (1971: 22) noted that the tail of the holotype was “almost equal to snout-vent length in spite of the tip being missing”.

According to Madruga (2011: 4), despite the fire at Museu Bocage in 1978, “many of Bocage’s papers, folder, manuscripts and correspondence still exist today”. From February to April 2012 MFB corresponded with Catarina Madruga (Museu Bocage) who searched through Bocage’s correspondence and notes in the hope of finding information and/or diagrams of the holotype of *C. angolensis*, but nothing was found. The holotype of *C. angolensis* is no longer available, so in order to stabilise the taxonomy we designate a neotype that is in agreement with Bocage’s (1895) description of the species (see above).

The new specimens from Taqueta Mountain were collected about 100 km west of Caconda and are assigned to *C. angolensis* on the basis of their similarity to the holotype as described by Bocage (1895) and Broadley (pers. comm.) (see details above). Their colour patterns are similar, as are several of the scale counts. Bocage (1895) noted that the frontonasal was in contact with the frontal in the holotype; and while this was the case in only two of the five new specimens, this is clearly a variable character. Bocage’s (1895) holotype of *C. angolensis* reportedly had 16 longitudinal rows of ventrals, whereas the Taqueta Mountain specimens examined here all had 14 rows. Such discrepancies probably reflect the likelihood that different observers count these rows differently, e.g., some observers may exclude a poorly differentiated lateral row that others count. A similar problem may occur with regards to the longitudinal rows of dorsals (26 in holotype versus 20–23 in new material), transverse rows of ventrals (27 versus 22–24) and gulars across the throat (26 versus 20–21).

**Neotype.** The holotype (MBL 429) is no longer in existence, and therefore we propose and describe one of the new specimens as neotype: MNCN 50648, an adult male from Taqueta Mountain, Benguela Province, Angola (–13.7778°, 14.1794°; 2112 m a.s.l.) collected 10 August 2017 by Afonso Vaz Pinto and Pedro Vaz Pinto.

**Additional new material.** Adult males: MNCN 50649, CHL 611, CHL 613; adult female: CHL 615. Same collecting information as neotype.

**Diagnosis.** A medium to large rupicolous *Cordylus* with a moderately depressed head and body. Referred to *Cordylus* (rather than any other species of Cordylidae) by the following combination of characters: head distinct from body, two pairs of large and well developed limbs (body serpentiform, head indistinct from body, and limbs rudimentary in *Chamaesaura* Schneider, 1799), scales on back large and keeled (granular in *Platysaurus* Smith, 1844, partly granular in *Pseudocordylus* Smith, 1838 and *Hemicordylus* Smith, 1838), non-spinose occipitals (spinose in *Smaug* Stanley et al., 2011), 23–24 transverse dorsal scale rows (40–43 in *Ninurta* Stanley et al., 2011; 31–46 in *Karusasaurus* Stanley et al., 2011; 15–16 in *Ouroborus* Stanley et al., 2011); loreal absent (present in *Smaug*, *Nirnuta*, *Ouroborus*, *Karusasaurus*, and *Namazonus* Stanley et al., 2011).

*Cordylus angolensis* is distinguishable from other members of its genus by the following combination of characters: (1) back dark brown with a paravertebral series of pale markings; (2) top of head plain brown or with occasional pale blotches; (3) iris of the eye brown; (4) scales of the first transverse row of dorsals similar in appearance to those of the row behind; (5) loreal shield absent; (6) nostril pierced in the posterior part of a large nasal, situated behind the suture of rostral and first supralabial, usually well separated from both the first supralabial and the preocular; (7) a regular row of six enlarged, non-spinose occipitals; (8) Frontonasal separated from the frontal by a pair of prefrontals (each of which usually exceeds it in size) or in contact; (9) Anterior pair of parietals usually in contact anteriorly; (10) dorsolateral and lateral scales may be weakly to moderately spinose; (11) tail spinose, but more weakly so distally; (12) dorsal scale rows transversely 24–25; (13) dorsal scale rows longitudinally 20–23; (14) ventral scale rows transversely 22–24; (15) ventral scale rows longitudinally 14; (16) subdigital lamellae on 4<sup>th</sup> toe 14; (17) femoral pores per thigh 5–6 in males and females; (18) differentiated femoral scales [generation glands] per thigh in males 19–25; (19) premaxillary teeth 7.

Its status as a distinct species is supported by monophyly with high levels of support from a suite of three mitochondrial and six nuclear markers (see above); and it differs from *C. ‘Mombolo’* (see below), the most similar species genetically and morphologically, by an uncorrelated ND2 p-distance of 9.22% (Table 3).

**Comparisons with other *Cordylus* species.** It differs from most other *Cordylus* (except *C. ukingensis* [Love-

ridge, 1932], *C. macropholis* [Boulenger, 1910], and *C. vittifer* [which occasionally has a loreal] in lacking a loreal. It differs from *C. ukingensis* and *C. macropholis* by virtue of its smooth (rarely with a few weak keels on a few scales) versus strongly keeled (even spinose in *C. macropholis*) gulars, as well as by having its nostril pierced near the middle of the posterior part of the nasal scale (versus infero-posteriorly). Differs from *C. tropidosternum* by having smooth versus keeled gulars, and having the nostril well separated from the first supralabial (not in contact or near-contact); from *C. rhodesianus* by having distinctly rugose versus finely rugous to smooth upper head shields, 24–25 versus 25–29 transverse rows of dorsals, and a straight versus curved sulcus dividing the posterior part of the nasal; from *C. jonesii* by having its nostril pierced halfway up the posterior edge of the nasal rather than towards the centre, and a straight versus curved sulcus dividing the posterior part of the nasal; and from *C. marunguensis* which has the nostril pierced centrally on the lower margin of the nasal. Distinguished from *C. vittifer* and *C. machadoi*, *C. namakuiyus* and *C. phonolithos* by always lacking a loreal scale, having most or all scales of the first transverse row of dorsals of similar length (rather than longer) than those of the next row, and by having a pair of paravertebral rows of pale greenish-cream spots or blotches versus a lack of these. Most similar to *C. ‘Mombolo’* (see below).

**Description of the neotype.** MNCN 50648 (Figs 4–6, 8–11; Tables 5, 6). *External morphology:* Head and body moderately depressed. SVL 88.4 mm. Tail 62.8 mm (tip missing), 0.71+ times as long as SVL. Head 24.6 mm, 1.18 times as long as wide (20.9 mm); head depth 10.6 mm, 50.6% head width. Upper head shields coarsely rugose. Nasals in broad contact; frontonasal quadrangular and slightly smaller than a prefrontal; prefrontals in contact with one another (separating frontonasal from frontal), and each one in contact with the frontal, first supraocular, preocular and a large nasal on either side; frontal in contact with first and second supraoculars, followed by a pair of frontoparietals in median contact; interparietal flask-shaped, narrowing and extending anteriorly to completely separate the anterior parietals; each anterior parietal smaller than a posterior parietal; a straight row of six rugose but non-spinose occipitals. Four supraoculars and three supraciliaries. Nasals large, with nostril pierced more-or-less centrally in the posterior part of the scale; nostril separated from preocular by a distance of more than half its diameter, distinctly separated from first supralabial by a distance almost equal to the height of the latter scale (and almost equal to the greatest extent of the nostril); nasal divided posteriorly at the level of the middle of the nostril. Loreal absent. Lower eyelid with 9–10 vertical septa. Three suboculars, well separated from the lip, with another large scale bordering the eye between posterior subocular and postocular. Rostral semi-divided dorsally and about twice as broad as deep; supralabials 6; infralabials 6; sublabials 5. Mental almost twice as broad as long. Gulars vary considerably in size and shape, from rectangular (especially

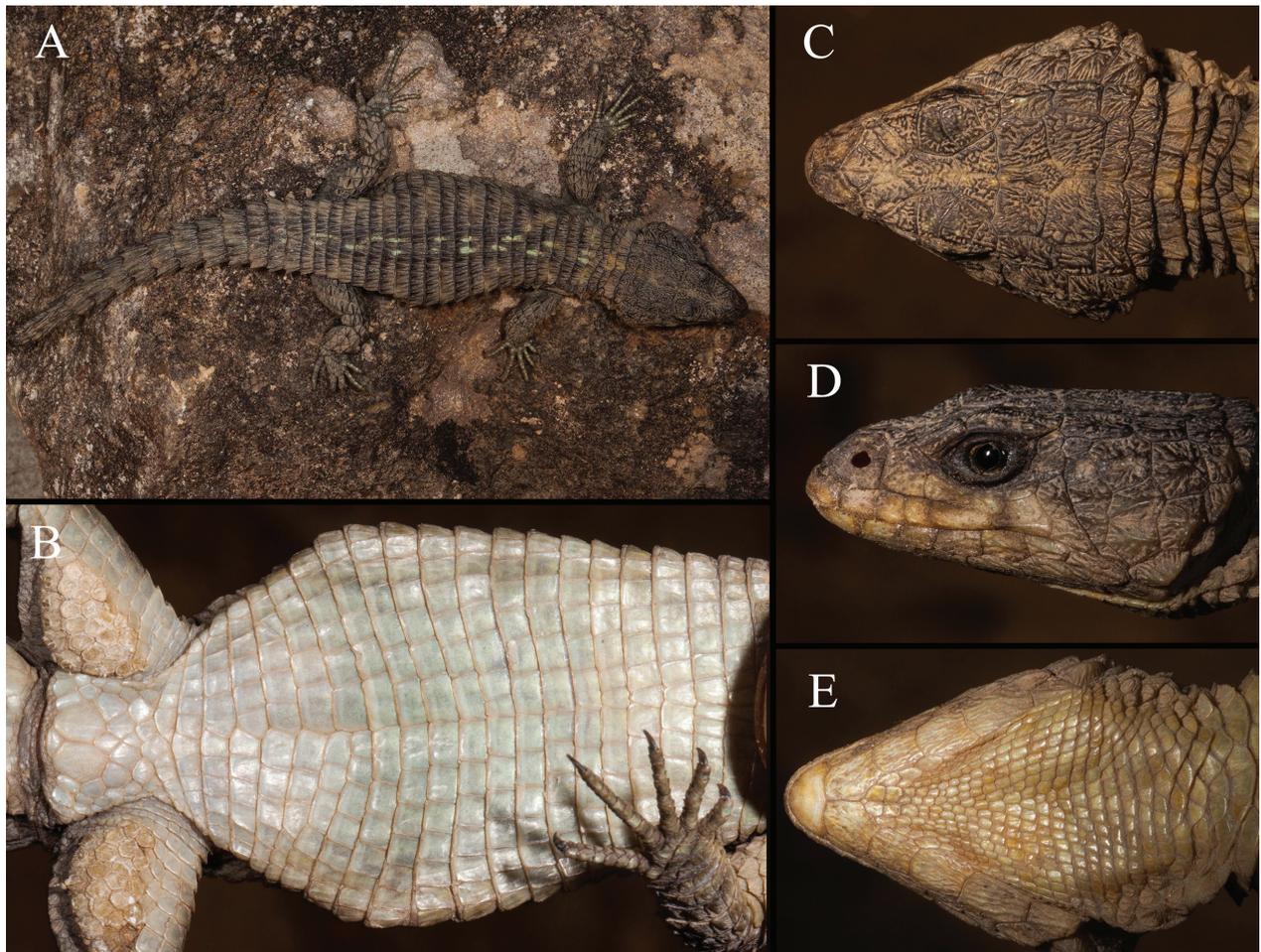
on the sides) to square and oval, mostly smooth (a few centrally have feeble blunt keels medially) and at most subimbricate, forming about 12 transverse rows (from first row in line with angle of jaws to last distinct row posterior to chin shields), and 20 longitudinal rows between posterior angles of jaws; 5 chin shields (including tiny median scale anteriorly) in contact with 1<sup>st</sup> pair of sublabials; two pairs of distinctly enlarged chin shields posterior to these.

Dorsal scales rectangular, rugose, moderately keeled (less so medially), seldom spinose or mucronate, not serrated at the posterior edges; laterals oval, juxtaposed, rugous, sharply keeled and moderately spinose, no additional spines on the free end of scales; dorsals plus laterals in 25 transverse rows and 20 longitudinal rows (vertebral scales slightly smaller); on the central part of the belly the mesial ventrals are rectangular (transversely) and larger than others, the next row on either side with slightly rectangular scales, including the next two rows on either side; ventrals mostly smooth, but 2–3 lateral rows on either side with some obtusely keeled scales; ventrals in 22 transverse and 14 longitudinal rows (plus a row of oval, keeled scales on either side); a pair of enlarged and somewhat oval pre-cloacal plates is followed anteriorly (before the ventrals) by two transverse rows of much smaller irregular scales.

Scales on limbs above are large, strongly keeled and spinose; scales under fourth (longest) toe 14 on left and right feet; femoral pores 6 on left thigh, 5 on right, with distinct plugs of yellowish secretion; differentiated glandular femoral scales on thigh 21 on left, 20 on right. Tail with whorls of large, elongate, strongly keeled, spinose (spines directed backwards and longest superolaterally), weakly serrated, scales; supracaudals strongly keeled throughout most of their length, subcaudals basally distinctly keeled mainly on the distal half. Scales on palms of hands and soles of feet moderately to obtusely keeled; supradigital scales of hands smooth to weakly keeled, of feet smooth to moderately keeled; subdigital scales of hands weakly keeled, of feet moderately keeled.

*Colour:* The colour pattern of the neotype in life is similar to that described for the holotype (see above). The back is a mixture of light and dark brown, with some of the darker markings forming ill-defined transverse bands, and there is a series of greenish-cream blotches, mostly elongated, arranged in close proximity paravertebrally (about eight pairs). Top of the head is a mixture of pale and dark brown, with an ill-defined pale median band longitudinally. The upper parts of the tail are brown, with some keels dark brown. Belly is dirty white and the throat cream. Bocage (1895) recorded the markings on the back as ‘whitish’, but this may have been in reference to preserved material that had faded somewhat.

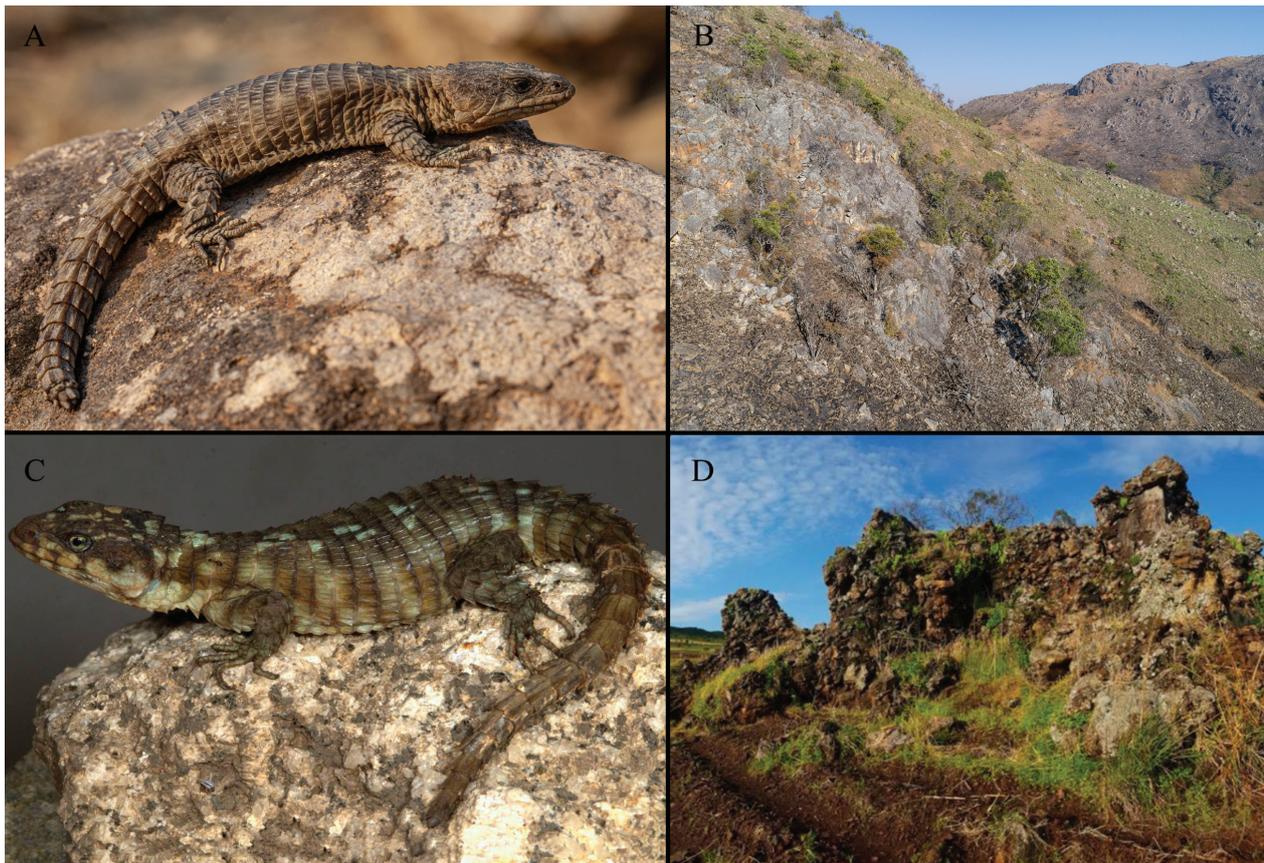
*Cranial skeleton* (Fig. 8, Table S1): Segmented mesh file of MNCN 50648 can be found here <http://tinyurl.com/CordylusAngola>. Morphosource link to tomogram stacks [doi.org/10.17602/M2/M529985](https://doi.org/10.17602/M2/M529985). The scales of the dorsal and temporal regions of the skull and the ventrolateral aspects of the jaws are underlain with rugose osteoderms. These osteoderms fuse to the parietal, frontal and postor-



**Figure 10.** Neotype (MNCN 50648) of *Cordylus angolensis* from Taqueta Mountain, Benguela Province, Angola. **A** dorsal aspect, **B** ventral region, **C** top of the head, **D** left side of the head, **E** ventral side of the head. Photos: Pedro Vaz Pinto.

bital bones, although the mesokinetic and metakinetic joints appear unobstructed and flexible. Lateral maxilla and anterior aspect of the premaxilla lack osteoderms. The parietal is pentagonal, with five osteoderms that underlie the parietal shields fused to its dorsal surface, and a narrow, bifid, 'Y'-shaped medioposterior process that articulates with the sagittal crest of the supraoccipital. Three large osteoderms are fused to the frontal, which is unpaired and clasped by the parietal at its posterolateral edge. The upper temporal fenestra is obscured anteriorly by a large osteoderm fused to the dorsal surface of the postorbital bone, and posteriorly by two unfused rectangular osteoderms that overlie the squamosal. Premaxilla is unpaired and contains seven pleurodont teeth, with a dorsal process that extends posteriorly to intersect the nasals, which themselves overlie the frontal. The maxillae are typically scinciform, with a deeply grooved crista dentalis, a deep fossa that lodges the lacrimal sac, 9 (left) or 11 (right) lateral foramina, and 22 (left) or 23 (right) teeth. Teeth display pleurodont attachment and are unicuspid, with a slight concave surface where they connect with the mandibular teeth. No palpebral is present but the prefrontals possess a small protuberance, forming a shelf that directly underlies the anteriormost superorbital osteoderm. The jugal is triangular in cross-section and asymmetrically T-shaped, with a tapering anterior process and a broad,

truncated posterior process that extends along and past the posterior edge of the maxilla. The lacrimal bone is small, flattened and oval, slightly bicuspid anteriorly, the two processes meeting prefrontal cusps to bracket the lacrimal duct. Pterygoids are edentate and extend back to connect with the quadrates, becoming C-shaped in cross-section posterior to the epipterygoid condyle. The squamosal is curved and blade-like, circular in cross-section anteriorly, becoming flattened posteriorly, where it articulates with the cephalic condyle of the quadrate and the supratemporals. Supratemporals are flattened, ovoid and not fused with the elongate paraoccipital processes. The posterior aspect of the prootic not fully fused with the otooccipital, resulting in a deep groove along the dorsal aspect of the paraoccipital processes. Quadrates very broad with a pronounced ridge and concave region at the lateral edge of the adductor musculus mandibulae posterior origin. The supraoccipital has a strong sagittal crest that extends posteriorly to contact the ventral surface of the medioposterior process of the parietal. The prootic bears an extended alar process and a well-developed, rhomboid crista prootica, and a very weak supratrigeminal process. Basipterygoid processes are well developed and flattened. The lower jaw possesses a large adductor fossa, a highly flattened and medially extended retroarticular process, a medially open Meckelian canal that is



**Figure 11.** *Cordylus angolensis*: live neotype (A) and habitat at the collecting site of Taqueta Mountain, Angola (B); and *C. momboloensis* sp. nov.: live holotype (C) and habitat at the type locality of Sandula, Angola (D). Photos: Pedro Vaz Pinto (A, B), and William R. Branch (C, D).

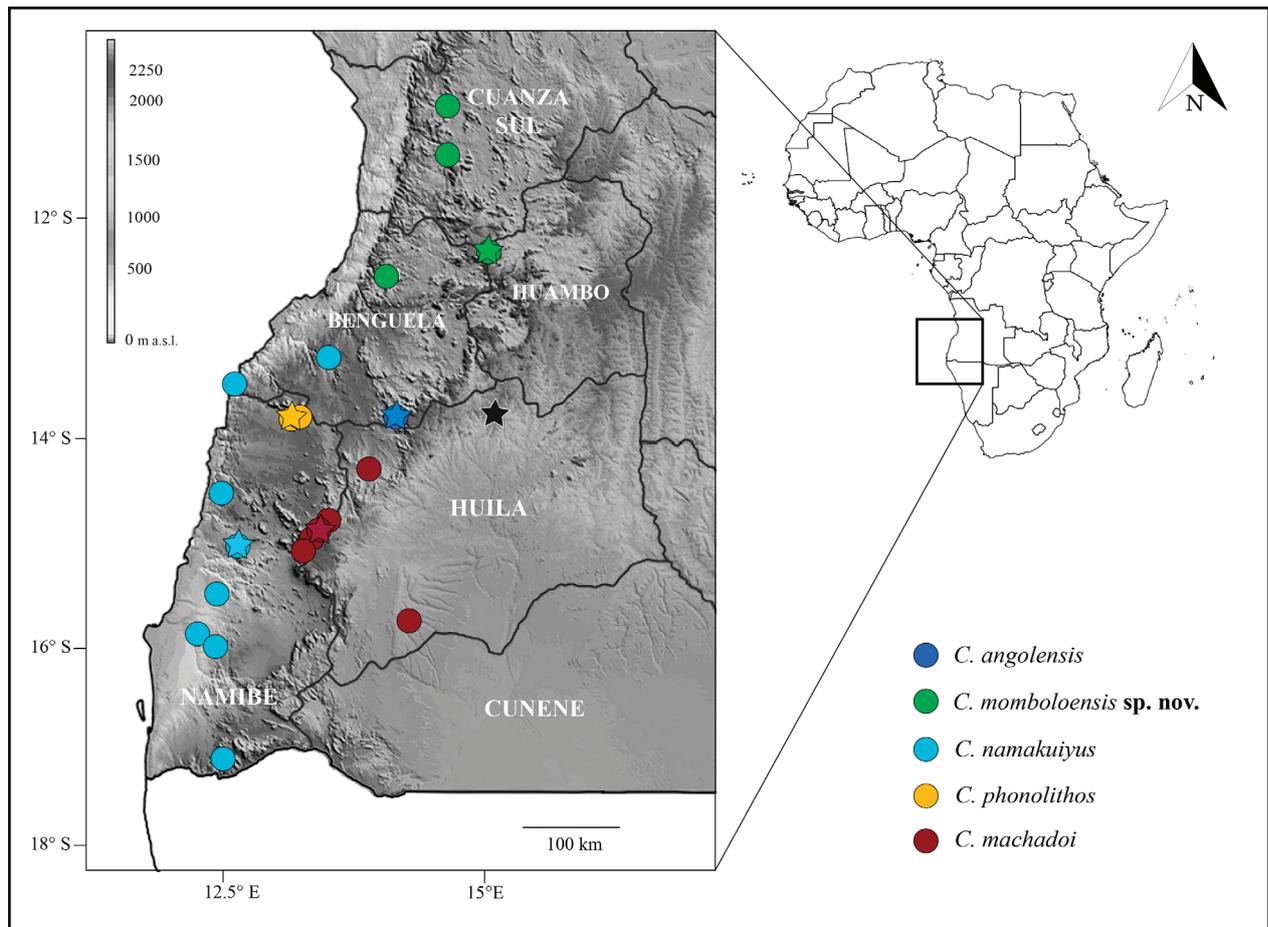
closed posteriorly by a large splenial, and a dentary with a strong subdental shelf; 25 (left) and 27 (right) mandibular teeth, and six dentary foramina.

**Postcranial skeleton:** Segmented mesh file of MNCN 50648 can be found here ([tinyurl.com/Cang1Skel](https://tinyurl.com/Cang1Skel) Morpho-source link to tomogram stack <https://doi.org/10.17602/M2/M529986>). The axial skeleton comprises 26 presacral (eight cervical, three sternal, two xiphisternal, five long asternal ribs with ossified costal cartilage, seven short asternal ribs and one very short pair of ribs immediately anterior to the sacral vertebrae), two sacral and 15 (incomplete, regenerated tail) caudal vertebrae. Cervical ribs 4–6 are distally flattened and bipid, with the ventral processes more elongated. Pubis flattened and curved with a large, ventrally angled pectineal tubercle. Pubic symphysis flattened and triangular, separating the pubes entirely. Hyperischium and hypoischium well developed. Sternal plate broad with no fontanelle. Interclavicle cruciform. Digits three and four on right manus are truncated, but display a typical phalangeal pattern of 2–3–4–5–3 for the manus and 2–3–4–5–4 for the pes.

**Osteoderms:** (Fig. 9) The dorsal trunk is covered in rectangular, dorsomedially keeled, imbricate osteoderms, each roughly three times as long as wide. Dorsal osteoderms are arranged in whorls and become progressively more oval and better separated laterally. The nuchal osteoderms are spined posterior to the tympanic opening. Ventral osteoderms are delicate and plate-like, and con-

centrated in the gular, antero-pectoral and abdominal regions. No precloacal osteoderms. The forelimbs are covered in keeled, imbricate, rhomboid osteoderms, except for the axillary, antecubical and palmar regions, which are unarmoured. The hindlimbs are covered in rhomboid osteoderms, except for the ventral femoral, popliteal and plantar regions. Hindlimb osteoderms are unkeeled on the anterior thigh, and become more spinose posteriorly and distally. The caudal osteoderms are large, robust and arranged in imbricated whorls, feebly keeled and mucronate along the dorsal and ventral aspects, becoming more heavily spined laterally.

**Variation in additional new material.** (Figs 4–6; Tables 5, 6). **External morphology:** Detailed morphometrics and mensural data for the new material is presented in Tables 5–6. All additional material agrees in general with the holotype and neotype, but differs as follows: Less than half the length of the nasals are separated by the frontonasal in CHL 613; frontonasal pentagonal in MNCN 50649; size of the frontonasal varies from much smaller than a prefrontal scale (CHL 613), only slightly smaller (CHL 611), about equal to or only slightly larger (CHL 615) or distinctly larger (MNCN 50649); frontonasal and frontal in narrow (CHL 611) and broad (MNCN 50649) contact, separating frontonasal and frontal. Shape and size of the interparietal varies: usually kite-shaped (with most acute angle anteriorly) and separating more than



**Figure 12.** Geographical distribution of *Cordylus angolensis* (dark blue) and *C. momboloensis* sp. nov. (green) in Angola. The distribution of the three species of the *C. machadoi* group (*C. machadoi* [red], *C. namakuiyus* [pale blue], *C. phonolithos* [yellow]) is also indicated. Type localities are indicated by stars; for *C. angolensis*, the original type locality of Caconda is indicated by a black star, while the neotype locality is indicated by a dark blue star. Locality records are from the present study (see species accounts and Appendix 1) as well as Bocage (1895), Laurent (1964), Stanley et al. (2016), Marques et al. (2019), and Lobón-Rovira et al. (2022b).

three-quarters of the anterior parietals, but rhomboidal (diamond-shaped) and separating only about half the anterior parietals in CHL 615. Occipitals only 7 in MNCN 50649. Nostril pierced in the middle (not posterior part) of the nasal in CHL 611; nostril separated from pre-ocular by a distance varying from less than half its diameter (right side in CHL 613) to about equal thereto (e.g., left side of CHL 613); and nostril separated from first supralabial by more than half the height of the latter and a distance about equal to the first supralabial on the left side in CHL 611 and CHL 613. Supralabials 5 on right side of head in CHL 611. In CHL 613 a small, discrete, triangular scale ('postnasal') is present between the nasal, preocular and first two supralabials on the right side of the head. Rostral undivided, and partly fragmented in MNCN 50649. Mental less than twice as broad as long in CHL 611. Gulars smooth, juxtaposed to subimbricate. Six chin shields (including tiny median one) in contact with first supralabials in CHL 611. Dorsals in 24–25 rows transversely, and 20–23 rows longitudinally. Ventrals in 22–24 rows transversely. Femoral pores 6 on left and right limbs in CHL 613; differentiated glandular femoral scales in males 19–25 per thigh, but absent in female CHL 615.

**Colour:** Similar to that described for the neotype, but CHL 611 and CHL 615 have a few scattered cream markings on the top of the head, and none have a pale median band.

**Size:** Largest male (CHL 611, Taqueta Mountain): SVL 88.5 mm, tail length 73.6 mm (original), total length 162.1 mm, head length (HL) 23.2 mm, head width (HW) 22.1 mm, head height (HH) 10.9 mm. Largest female (CHL 615, Taqueta Mountain): SVL 103.1 mm, tail length 84.1 mm (original), total length 187.2 mm, HL 25.7 mm, HW 22.3 mm, HH 10.3 mm.

**Habitat.** Although no specific habitat information was available in Bocage's (1895) original description, the morphology of this species suggested that it is rupicolous, as are most other congeners (Branch 1998). The type locality of Caconda, where José de Anchieta was based, lies in relatively flat terrain between 1500 and 1700 m a.s.l. The local habitat there today comprises mostly agricultural fields, interspersed with very occasional, scattered, small granite outcrops. In the past, the region of Caconda was probably covered by well-developed miombo woodlands, characterised by dominance of tree species such as *Julbernardia paniculata*, *Brachystegia spiciformis*

**Table 5.** Meristic data for scalation characters in *Cordylus angolensis* and *Cordylus momboloensis* sp. nov. from Angola. When different, the number of scales on the left and right sides of the head are separated by a slash symbol (/). For occipitals, when the row is medially interrupted by post-occipitals, the number of scales on the left and right sides of the head respectively are separated by a plus sign (+).

	<i>Cordylus angolensis</i>						<i>Cordylus momboloensis</i> sp. nov.											
	MNCN 50648 (Neotype)	MNCN 50649	CHL 611	CHL 613	CHL 615	PEM R25217 (Holotype)	MNCN 50760 (Paratype)	FKH 0127 (Paratype)	FKH 0128 (Paratype)	AMN R47333 (Paratype)	MNCN 50761 (Allotype)	FKH 0125 (Paratype)	AMN R47331 (Paratype)	AMN R47332 (Paratype)	AMN R47334 (Paratype)	AMN R47335 (Paratype)	TM 46476	FKH 0129
Sex	Male	Male	Male	Male	Female	Male	Male	Male	Male	Male	Female	Female	Female	Female	Female	Female	Female	Juvenile
Supralabials	6	6	6	6	6	6/5	5/6	6	6	6/5	6	6	5	6	5	5	5/7	6
Infralabials	6	6	6	6	6	6	6	6	6	—	6	6	5/4	6/5	5	5	6	7/6
Sublabials	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5
Supraoculars	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4
Supraciliaries	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
Suboculars	3	3	4/3	3/4	3/4	4/3	3	3	3	3	3	2/3	3	4	3	3	3	3
Occipitals*	6	6	6	6	6	2+3	2+2	3+2	3+2	2+2	2+2	2+3	2+2	2+2	2+2	2+2	2+2	2+2
Post-occipitals	—	—	—	—	—	6	6	5	6	6	6	6	6	6	6	6	6	6
Gulars transversely	20	20	20	20	21	26	19	20	18	19	19	21	22	21	16	18	23	—
Gulars contacting 1 <sup>st</sup> pair sublabials	5	5	6	5	5	5	5	4	—	4	5	5	5	5	4	4	4	5
Dorsals transversely	25	25	24	24	24	22	24	23	22	22	24	24	22	22	23	22	24	—
Dorsals longitudinally	20	20	21	22	23	23	22	21	18	22	22	22	21	21	20	18	20	—
Ventrals transversely	22	23	22	23	24	22	26	25	23	27	25	25	23	23	23	22	22	—
Ventrals longitudinally	14	14	14	14	14	12+2	12	11	14	12	12	12	12+2	12+2	13	13	12+2	—
Scales under 4th toe	14	14	14	14	14	13/14	13	—	—	15	14	14	13	13	11	13	13	—
Femoral pores	6/5	6/5	6/5	6	6/5	7	8/7	8/7	7/6	5	4	5	5	6	0	5	7/5	—
Differentiated femoral scales	21/20	19	21/19	25	0	26/27	30/26	37/35	30/29	30/25	0	0	0	0	0	0	0	—

and *Brachystegia* spp. (Barbosa 1970). Nevertheless, the species has never again been found in the vicinity of Caconda, but was instead found almost 100 km to the west on Taqueta Mountain, at 2112 m a.s.l., where the habitat is typical of the Angolan highlands (Fig. 11B). All specimens were found in cracks and crevices in granite outcrops present on moderate to steep slopes, surrounded by well-developed montane grassland in proximity to Afromontane forest patches in deep ravines.

**Distribution.** Although the original type locality is given as Caconda (Huila Province), efforts over more than one century to rediscover the species at or near that locality have failed. The fact that Anchieta was based at Caconda for more than 20 years (Banha de Andrade 1985), and the holotype appears to be the only specimen collected, suggests that the species was likely rare there in those days possibly due to scarcity of rocky habitat, which subsequently must have been further impacted by human encroachment and use of rocks for construction. Alternatively, the holotype may have also been collected on the mountains criss-crossed by the 19<sup>th</sup> century land routes linking Caconda to the major coastal city of Benguela, a route that was often followed by Anchieta himself and his assistants. While conducting surveys in this region in 2017, and specifically targeting the mountains thought to have been along those historical routes, we made the discovery of a population of *C. angolensis* at Taqueta Mountain. This new locality is currently the only site where this species

Table 6. Mensural data and body ratios of *Cordylus angolensis* and *Cordylus momboloensis* sp. nov. from Angola (r = regenerated tail; w = width; l = length).

	<i>Cordylus angolensis</i>						<i>Cordylus momboloensis</i> sp. nov.										
	MNCN 50648 (Neotype)	MNCN 50649	CHL 611	CHL 613	CHL 615	PEM R25217 (Holotype)	MNCN 50760 (Paratype)	FKH 0127 (Paratype)	FKH 0128 (Paratype)	AMNH R47333 (Paratype)	MNCN 50761 (Allotype)	FKH 0125 (Paratype)	AMNH R47331 (Paratype)	AMNH R47332 (Paratype)	AMNH R47334 (Paratype)	AMNH R47335 (Paratype)	TM 46476
Sex	Male	Male	Male	Male	Female	Male	Male	Male	Male	Male	Female	Female	Female	Female	Female	Female	Female
SVL	88.37	84.99	88.54	82.89	103.07	85.06	90.53	88.68	88.21	76.14	89.53	88.83	87.06	87.11	77.3	60.7	105.97
Tail length	62.78r	66.19	73.64	79.54	84.14	77.48r	88.36	84.43	66.65	66.60r	85.44	85.54	75r	76.59	72.3	56.2	113
Head length	24.61	21.93	23.24	20.54	25.72	25.3	23.07	23.32	22.54	22.34	22.30	22.36	24.64	23.98	20.63	17.10	27.74
Head width	20.86	19.80	22.08	20.01	22.34	21.35	21.33	19.50	19.75	20.70	20.53	20.52	20.29	20.07	19.6	14.50	22.19
Head height	10.56	9.76	10.92	10.71	10.33	9.22	11.93	11.34	9.37	9.28	11.80	11.39	10.40	—	8.15	7.91	10.41
Ear length	7.82	7.14	7.50	5.53	6.96	6.78	6.99	6.96	6.10	6.06	8.80	6.92	6.52	6.65	5.96	—	5.98
Orbital length	4.00	4.89	4.62	4.22	4.16	4.60	4.47	4.29	4.33	4.47	4.41	4.45	3.20	4.89	4.06	—	4.05
Nostril to eye	3.19	3.07	3.79	3.92	4.15	4.67	4.03	3.91	4.31	3.07	2.93	3.58	5.15	4.56	4.46	—	5.41
Eye to ear	11.65	10.32	11.03	11.13	12.08	11.37	10.80	9.26	8.46	9.15	11.34	9.71	11.12	10.12	10.04	—	11.90
Snout to eye	7.15	8.51	8.16	7.25	7.30	9.90	7.99	7.14	7.65	9.14	6.06	6.66	9.82	9.33	8.24	7.16	10.85
Internarial	6.55	4.54	4.92	4.40	4.73	4.95	5.40	4.77	5.02	5.08	5.11	4.94	5.11	4.29	4.84	—	5.64
Interorbital	10.90	10.99	9.04	8.43	8.88	10.6	8.63	8.24	8.78	8.67	10.51	9.50	10.74	9.96	10.63	—	11.76
Snout to arm	32.14	29.80	32.91	30.99	32.47	32.33	35.04	34.13	36.57	31.85	31.28	29.91	32.73	33.99	32.60	25.95	36.72
Axilla to groin	38.23	40.04	35.90	35.40	51.37	36.09	40.15	38.97	35.43	35.01	44.29	44.53	42.84	43.80	33.32	29.66	53.50
Forearm length	15.65	13.05	16.48	14.20	16.84	19.8	18.58	17.90	17.57	—	17.73	17.67	20.90	19.01	19.00	—	23.30
Fourth toe	10.28	11.39	10.38	11.41	12.58	10.22	11.03	12.66	12.65	12.02	11.31	12.16	10.75	10.40	11.11	8.74	11.93
Tail length/SVL	0.710	0.779	0.832	0.960	0.816	0.912	0.976	0.952	0.756	0.875	0.954	0.963	0.861+	0.879	0.935	0.926	1.066
Head length/SVL	0.278	0.258	0.262	0.248	0.250	0.297	0.255	0.263	0.256	0.293	0.249	0.252	0.283	0.275	0.267	0.282	0.262
Head width/SVL	0.236	0.233	0.249	0.241	0.217	0.251	0.236	0.220	0.224	0.272	0.229	0.231	0.233	0.230	0.254	0.239	0.209
Head w/Head l	0.848	0.903	0.950	0.974	0.869	0.845	0.925	0.836	0.876	0.927	0.921	0.918	0.823	0.837	0.950	0.848	0.800
Orbital/Head l	0.163	0.223	0.199	0.205	0.162	0.182	0.194	0.184	0.192	0.200	0.198	0.199	0.130	0.204	0.197	—	0.146
Forearm/SVL	0.177	0.154	0.186	0.171	0.163	0.233	0.205	0.202	0.199	—	0.198	0.199	0.240	0.218	0.246	—	0.220

is known to occur with any certainty (Fig. 12). Nevertheless, it is likely to be present on various rocky hills on the highlands west of Caluquembe, along the ridge of the southern Angolan escarpment, where suitable habitat is present.

**Localities.** Angola: Caconda (−13.7199°, 15.0648°), Taqueta Mountain (−13.7778°, 14.1794°).

**Conservation.** This species is known from only one locality, and little is known about its biology or population trends. Nevertheless, it should be noted that montane habitats in Angolan highlands are currently under anthropogenic pressure due to widespread excessive burning, cutting of remnant forests, and overgrazing of grasslands, all of which may negatively affect the species. The actual range of this species is difficult to infer and threats cannot be fully assessed at this time, but a Data Deficient categorisation, based on IUCN (2022a) Standards and Petitions Committee criteria, may apply.

**Remarks.** It was not possible to locate the specimen of ‘*Zonurus cordylus*’ from Aruwimi (presumably Aruwimi River, a tributary of the Congo River) in northern Democratic Republic of the Congo as documented by Boulenger (1897). However, we reject Loveridge’s (1944a) inclusion of this record under *C. c. angolensis*. If the locality is indeed valid and a population of *Cordylus* does/did occur in the vicinity of this river, it is likely – as suggested by Loveridge (1944a) – to represent an undescribed species. The Aruwimi River enters the Congo River at Basoko and extends eastward to a position north of Bunia (near Nizi) where it continues, as the Nizi River, to the vicinity of Jiba near the western shores of Lake Albert. The nearest other cordylids are *C. tropidosternum* (see map in Greenbaum et al. 2012) from northern Tanzania, about 700 km southeast from the nearest part of the Aruwimi/Nizi River, and Katanga Province (D.R.C.) about 900 km to the south.

### *Cordylus momboloensis* sp. nov.

<https://zoobank.org/F34A7197-A522-4B65-93D0-C6AF3D-40FAEC>

Figs 4–9, 11, 13–15; Tables 5, 6

Mombolo girdled lizard; Lagarto-espinhoso do Mombolo

**Chresonymy.** *Cordylus angolensis* not Bocage, 1895: Broadley and Branch (2002: 10) partim; Branch et al. (2005: 137) partim; Broadley (2006: 1) partim; Stanley et al. (2011: 67) partim; Greenbaum et al. (2012: 32) partim; Mombolo; Reissig (2014: 33 + map) partim; Stanley et al. (2016: 202 + map) partim.

**Holotype.** PEM R25217, an adult male from Sandula (Mombolo), Cuanza Sul Province, Angola (−12.1789°, 15.0292°; 1975 m a.s.l.) collected on 6 November 2016 by William R. Branch, Ninda Baptista and Pedro Vaz Pinto.

**Paratypes.** **Allotype:** MNCN 50761, an adult gravid female from Sandula (Mombolo), Cuanza Sul Province, Angola (−12.1811°, 15.0316°; 2095 m a.s.l.) collected 29 May 2019 by Pedro Vaz Pinto. **Other paratypes:** AMNH R47333 (adult male), AMNH R47331 (adult female), AMNH R47332 (adult female), AMNH R47334 (adult female) and AMNH R47335 (subadult female), all from Mombolo, Angola (exact site unknown, but likely at the Chapman’s farm of Sandula, same co-ordinates as for the holotype) collected on 11 September 1925 by ‘H. Chapman and A. Chapman’ during the Vernay Angola Expedition. MNCN 50760 (male), FKH 0127 (male), FKH 0128 (male), FKH 0125 (female), from Vondo (Uassamba Mountain), Cuanza Sul Province, Angola (−11.2415°, 14.6288°; 1989 m a.s.l.) collected 3 February 2019 by Pedro Vaz Pinto.

**Additional referred material.** TM 46476, an adult female from 3 km W of Condé, Cuanza Sul Province, Angola (about −10.8516°, 14.6387°; 1236 m a.s.l.) collected on 25 May 1974 by Wulf D. Haacke. FKH 0129, a juvenile from Vondo (Uassamba Mountain), Cuanza Sul Province, Angola (−11.2415°, 14.6288°; 1989 m a.s.l.) collected 3 February 2019 by Pedro Vaz Pinto.

**Diagnosis.** (Where variation in additional material falls outside the range of type material, this is indicated in parentheses.) A medium to large rupicolous *Cordylus* with a moderately depressed head and body. Referred to *Cordylus* (rather than any other species of Cordylidae) by the following combination of characters: head distinct from body, two pairs of large and well developed limbs (body serpentiform, head indistinct from body, and limbs rudimentary in *Chamaesaura*), scales on back large and keeled (granular in *Platysaurus*, partly granular in *Pseudocordylus* and *Hemicordylus*), non-spinose occipitals [and post-occipitals] (occipitals spinose in *Smaug*), 23–24 transverse dorsal scale rows (40–43 in *Ninurta*; 31–46 in *Karusasaurus*; 15–16 in *Ouroborus*); loreal absent (present in *Smaug*, *Nirnuta*, *Ouroborus*, *Karusasaurus*, and *Namazonurus*).

*Cordylus momboloensis* sp. nov. is distinguishable from other members of its genus by the following combination of characters: (1) back dark brown with a paravertebral series of pale markings; (2) top of head with pale blotches; (3) iris of the eye mostly pale green (blue-green to some eyes), with a brown ring around the pupil; (4) scales of the first transverse row of dorsals similar in appearance to those of the row behind; (5) loreal shield absent; (6) nostril pierced in the posterior part of a large nasal, situated behind the suture of rostral and first supralabial, always well separated from the first supralabial, and usually separated from the preocular; (7) an interrupted row of non-spinose occipitals consisting of 2–3 scales on either side of head; (8) a row of 5–6 non-spinose post-occipitals, the median scales of which are in contact with the posterior parietals and separate the occipitals; (9) Frontonasal separated from the frontal by a pair of prefrontals, each of which exceeds it in size; (10) Anterior pair of parietals usually in contact anteriorly; (11) dorsolateral

and lateral scales weakly to moderately spinose; (12) tail spinose, more weakly so distally; (13) dorsal scale rows transversely 22–24; (14) dorsal scale rows longitudinally 18–23; (15) ventral scale rows transversely 22–27; (16) ventral scale rows longitudinally 12–13 [rarely 11 or 14]; (17) subdigital lamellae on 4<sup>th</sup> toe 11–15; (18) femoral pores per thigh 5–8 in males, 4–6 in females [rarely 0; 7 on one side in a non-type specimen, TM 46476]; (19) differentiated femoral scales [generation glands] per thigh in males 25–37; (20) premaxillary teeth 9.

Its status as a new species is supported by monophyly with high levels of support from a suite of three mitochondrial and six nuclear markers (see above); and it differs from *C. angolensis*, the most similar species genetically and morphologically, by an uncorrelated ND2 p-distance of 9.22% (Table 3).

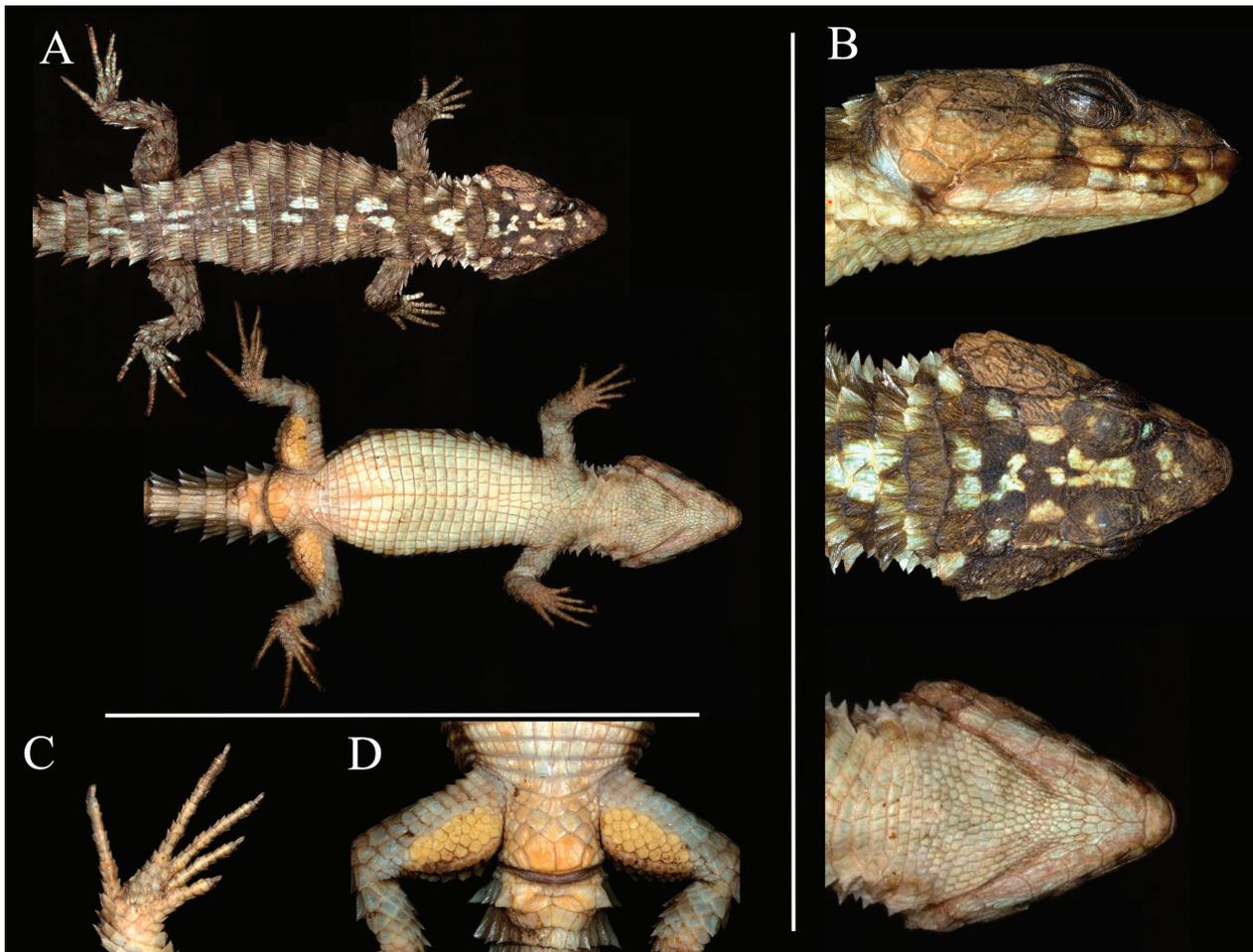
**Comparisons with other *Cordylus* species.** The new species differs from all other *Cordylus* in having nine (rather than seven, rarely six) premaxillary teeth, and from most other congeners (except *C. angolensis*, *C. ukingensis*, *C. macropholis*, and *C. vittifer* [occasionally has a loreal]) in lacking a loreal. It differs from *C. ukingensis* and *C. macropholis* by virtue of its weakly keeled or smooth versus strongly keeled (even spinose in *C. macropholis*) gulars, as well as by having its nostril pierced near the middle of the posterior part of the nasal scale (versus infero-posteriorly). Differs from *C. tropidosternum* by having smooth or weakly keeled versus keeled gulars, and having the nostril well separated from the first supralabial (not in contact or near-contact); from *C. rhodesianus* by having distinctly rugose versus finely rugose to smooth upper head shields, 22–24 versus 25–29 transverse rows of dorsals, and a straight versus curved sulcus dividing the posterior part of the nasal; from *C. jonesii* by having its nostril pierced halfway up the posterior edge of the nasal rather than towards the centre; and a straight versus curved sulcus dividing the posterior part of the nasal; and from *C. marunguensis* which has the nostril pierced centrally on the lower margin of the nasal. Distinguished from *C. vittifer*, *C. machadoi*, *C. namakuiyus* and *C. phonolithos* by always lacking a loreal scale, having most or all scales of the first transverse row of dorsals of similar length (rather than longer) than those of the next row, and by having a pair of paravertebral rows of pale greenish-cream spots or blotches versus a lack of these.

The new species is most similar to *C. angolensis*, but distinguished from it as follows: in live specimens the iris of the eye is largely pale green to blueish-green versus brown; top of head distinctly marked by pale blotches versus mostly plain brown; throat usually dirty white versus cream; a medially-interrupted row of occipital scales (2–3 on either side of head) is present, never forming a continuous row, each scale usually smaller than a post-occipital versus a continuous row of 6 occipitals across the back of the head; lower numbers of ventral scale rows longitudinally (usually 12–13 vs 14); relatively longer forearms (forearm/SVL 0.20–0.25 versus 0.15–0.19); higher numbers of generation glands in males (25–37 per

thigh versus 19–25); and higher numbers of premaxillary teeth (nine versus seven).

**Description of holotype.** PEM R25217 (Figs 4–6, 11, 13, Tables 5, 6). *External morphology:* Head and body moderately depressed. SVL 85.1 mm. Tail 77.5 mm (tip truncated and healed), 91.1% SVL. Head length 25.3 mm, 1.19 times as long as wide (21.4 mm), head depth 9.2 mm, 43.2% head width. Upper head shields coarsely rugose, not striated. Nasals in moderate contact, their posterior halves separated by the frontonasal, which is quadrangular and about half the size of a prefrontal; prefrontals in moderate contact with one another, and contacting the supranasals, preoculars and anterior supraoculars on either side; frontal in contact with first and second supraoculars, followed by a pair of frontoparietals in median contact; interparietal quadrangular, separating posterior one-third of anterior parietals, and anterior one-third of posterior parietals, the latter being distinctly larger than the anterior ones; occipitals two on one side of head, three on the other, interrupted by a slightly curved row of six post-occipitals; occipitals and post-occipitals rugose, occasionally striated but essentially non-spinose. Four supraoculars and three supraciliaries (postocular also in contact with posterior supraocular). Nasals large, with nostril pierced more-or-less centrally in the posterior part of the scale; nostril separated from preocular by a distance of about half its diameter, distinctly separated from first supralabial by a distance of more than half the height of the latter scale (i.e., at least half the greatest extent of the nostril); nasal divided posteriorly at the level of the middle of the nostril, and also divided below the nostril, forming a small postnasal. Loreal absent. Lower eyelid with 6–7 vertically enlarged septa; suboculars 4 left and 3 right, well separated from the lip. Rostral 2.3 times as broad as deep; supralabials on left side six (four anterior to median subocular), right side five (three anterior to median subocular); infralabials 6; sublabials 5. Mental 1.9 times as broad as long; gulars vary considerably in size and shape, from elongate, sometimes rectangular, on the sides of the throat, to squarish, oval and irregular, sometimes pentagonal or hexagonal, smooth and at most subimbricate, forming about 12 transverse rows (from first row in line with angle of jaws to last distinct row posterior to pair of sublabials), and 26 longitudinal rows between posterior angles of jaws; 5 chin shields (including a tiny elongate scale medially) in contact with 1<sup>st</sup> pair of sublabials.

Dorsal scales closely-set but often juxtaposed, rectangular, rugose, moderately keeled (less so on middle of back), some are also weakly spinose dorso-laterally, occasionally weakly serrated at their posterior edges; laterals occasionally subimbricate, often oval, rugose, sharply keeled and moderately spinose, no additional spines or serrations on the free ends of scales; dorsals (including laterals) in 22 transverse rows (excluding one half-row) and 23 longitudinal rows (including row of small vertebral scales which is interrupted at parts); on the central part of the belly the paired rows of mesial ventrals are rectangular (transversely), the next row on either side



**Figure 13.** Holotype (PEM R25217) of *Cordylus momboloensis* sp. nov. from Sandula (Mombolo), Cuanza Sul Province, Angola. **A** dorsal and ventral aspects, **B** lateral (right), dorsal and ventral aspects of the head, **C** underside of the foot, **D** femoral region of the legs. Although not evident because of the way the holotype was photographed, its tail is intact. Photos: Pedro Vaz Pinto.

with only slightly transversely rectangular scales, the others being squarish, with two rows of lateral ventrals on either side consisting of longitudinally-rectangular scales; ventrals mostly smooth, but the outermost lateral row on either side, and an additional row of ‘pseudo-ventrals’ on either side, with some obtusely keeled scales; ventrals in 22 transverse and 12 longitudinal rows (excluding a row of oval, keeled scales on either side best considered ‘pseudo-ventrals’); a pair of enlarged pre-cloacal plates is followed anteriorly (before the ventrals) by 2–3 transverse rows of much smaller plates.

Scales on upper parts of hindlimbs are large, strongly keeled and strongly spinose; scales of forelimbs large, moderately keeled and moderately spinose; scales under fourth (longest) toe 13 on left foot, 14 on right; scales under fourth (longest) finger 10 on left hand, 11 on right; femoral pores 7 on each thigh, of moderate size with distinct plugs of yellowish secretion; differentiated glandular femoral scales on thighs 26 on left, 27 right. Tail whorled, dorsally with large, elongate, rugose, strongly keeled, spinose, weakly serrated scales, with spines directed backwards and longest superolaterally; supracaudals strongly keeled throughout most of their length, subcaudals basally distinctly keeled mainly on the distal half of tail. Scales on palms of hands obtusely keeled,

on soles of feet moderately keeled; supradigital scales of hands weakly keeled, of feet moderately keeled; subdigital scales of hands and feet weakly keeled or smooth.

*Colour of holotype* (in life): The upper parts of the head, back, flanks, limbs and tail were mostly dark brown, with irregular pale or light greenish to blueish-green markings on either side of the midline (about six pairs) and on top of the head; venter whitish to cream; throat dirty white (Fig. 13). After preservation: As above, but back with indications of dark bands, and pale dorsal markings and venter have faded to a dirty white colour.

**Variation in paratypes.** (n = 10). (Figs 4–6, 8–9, 14; Tables 5, 6). Note: In AMNH R47333 the following characters could not be examined as the snout had been crushed/damaged: loreal, septa in eyelid, suboculars, infralabials and mental.

*External morphology:* All paratypes are similar to the holotype, but differ as follows: SVL 76.1–90.5 mm (males), 60.7–89.5 mm (females). Original tail shorter than SVL (87.5–97.6%, n = 9). Head 1.05–1.21 times as long as wide, head height 0.416–0.582 times head width. Nasals in narrow contact in FKH 0125, MNCN 50760 and MNCN 50761 (allotype; posterior three-quarters separated by frontonasal). Frontonasal tiny in AMNH



**Figure 14.** Paratypes of *Cordylus momboloensis* sp. nov. from ‘Mombolo’, Angola (from left: AMNH R47333, R47332, R47331). Photo: Wulf D. Haacke.

R47333, slightly smaller than a prefrontal in FKH 0127, MNCN 50760 and MNCN 50761, about equal in size to a prefrontal in FKH 0125 and FKH 0129; prefrontals in broad contact in MNCN 50760 and FKH 0128, in narrow contact in MNCN 50761; interparietal irregular and separating anterior parietals in FKH 0125, kite-shaped (with most acute angle anteriorly) in MNCN 50760, completely separating posterior parietals in AMNH R47331, completely separating anterior parietals in MNCN 50760, and separating most of the anterior parietals in AMNH R47332 (the anterior part of the interparietal is followed, after a short gap, by an elongate lozenge-shaped scale which separates the anterior extremity of the anterior parietals and contacts the suture between frontoparietals); anterior and posterior parietals similar in size in AMNH R47331, 47333–4. Occipitals 2–3 on either side of head, interrupted medially by the row of post-occipitals; a slightly (AMNH R47335) to distinctly (AMNH R47332–4, MNCN 50760) curved row of six (five in FKH 0128) post-occipitals; nasal not divided below the nostril; a tiny elongate scale is present between the nasal, preocular and first supralabial in AMNH R47332 (nostrils damaged/reamed in AMNH R47334). A few occipitals with weak keels in FKH 0125. Nostril separated from preocular by more than half its diameter on left side of head and less than half on right (FKH 0125, MNCN 50760), about half on left and less than half on the right in FKH 0127–8, and less than half on both sides in FKH 0129; and nostril separated from first supralabial by a distance greater than half

its height on left and equal on right (MNCN 50760), equal to half the distance on the left in FKH 0125, and exceeding the height of the supralabial on the left in FKH 0129. Lower half of preocular with a vertical suture medially in MNCN 50761 (allotype). Lower eyelid with 5–7 vertical septa; suboculars 3–4 (two on left side of head in FKH 0125, usual two posterior scales apparently fused). Rostral 2.21–2.60 times as broad as deep [AMNH only]; supralabials 5–6; infralabials 5–6, but 4 on right side of head of AMNH R47331. Anterior pair of sublabials of FKH 0125 completely separated by a moderate-sized elongate scale that contacts the mental; 4–5 chin shields (including small median scale) in contact with 1<sup>st</sup> pair of sublabials. Mental 1.52–1.75 times as broad as long [AMNH only]; gulars subimbricate to juxtaposed, irregular throughout in FKH 0125, FKH 0127, MNCN 50760 and MNCN 50761 (allotype), a few lateral gulars with obtuse and feeble median keels, but FKH 0125, FKH 0128 and FKH 0129 also have feebly keeled gulars centrally, in 16–22 longitudinal rows between posterior angles of jaws.

Dorsals plus laterals in 22–24 transverse rows and 18–22 longitudinal rows; ventrals in 22–27 transverse and 12–13 [11 in FKH 0128, 14 in AMNH R47333] longitudinal rows (an additional row of ‘pseudo-ventrals’ on either side between ventrals and laterals in AMNH R47331 and 47332 only).

Scales under fourth (longest) toe 11–15, under fourth (longest) finger 10–12 [AMNH only]; femoral pores per thigh 5–8 in males, 4–6 (0 in AMNH R47334) in females;

differentiated glandular femoral scales in males only, 25–37 per thigh. In AMNH R47332 the basal subcaudals are obtusely keeled or smooth. Supradigital scales of hands smooth to moderately keeled, of feet smooth to strongly keeled; in AMNH R47331 subdigital scales of feet strongly keeled and occasionally spinose, especially posteriorly.

*Colour of paratypes (in life):* Colouration of the Sandula and Vondo paratypes was similar to that of the holotype. The belly had a slightly blueish tinge.

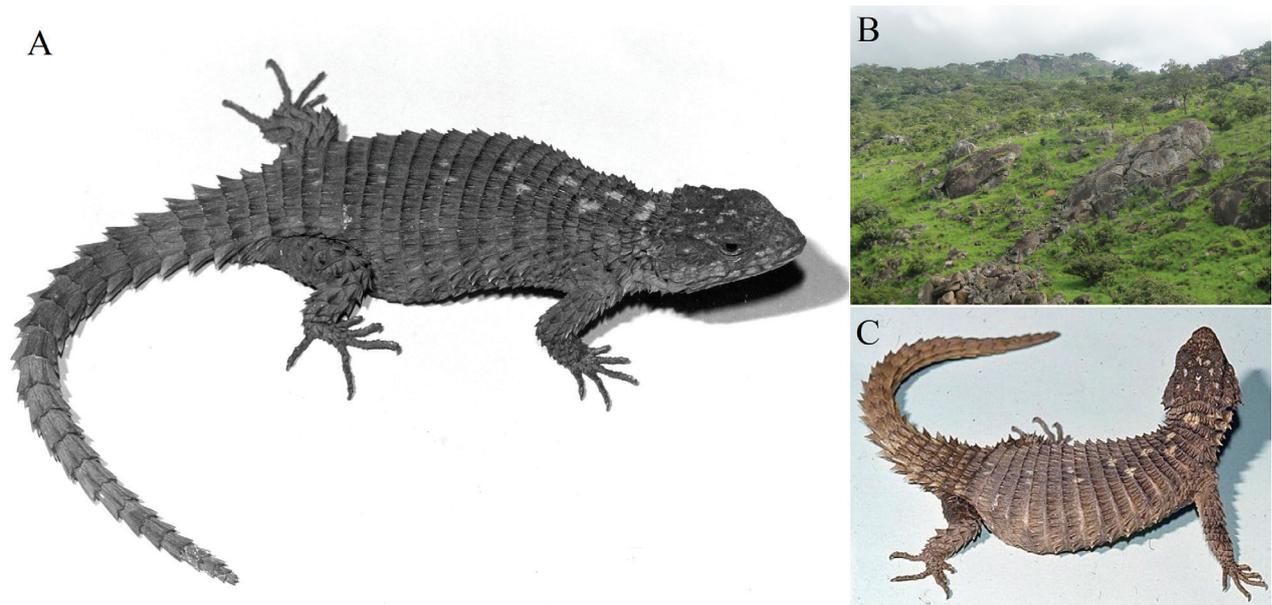
*Colour of paratypes (in preservative):* AMNH R47331 is the most distinctly marked of the old ‘Mombolo’ series (Fig. 14): The upper parts of the head, back, flanks, limbs and tail are medium to dark brown; there are five dark transverse bands across the back from nape to tail, separated by narrower bands of paler colour, including three pairs of large and distinct cream-coloured paravertebral blotches, together with a series of less distinct but similarly pale blotches dorso-laterally; and a few cream spots are present on the top of the head. In the other AMNH specimens the upper parts of the head, back, flanks, limbs and tail are medium to dark brown, but without distinct dark markings or pale spots (pattern may have faded). Venter of all AMNH specimens are cream to pale tan.

*Cranial skeleton:* (Fig. 8; segmented mesh files of paratype AMNH R47334 and TM 46476 can be found here ([tinyurl.com/CangolensisAMNH](https://tinyurl.com/CangolensisAMNH)) and here ([tinyurl.com/CordylusAngola2](https://tinyurl.com/CordylusAngola2)). Morphosource links to tomogram stacks (<https://doi.org/10.17602/M2/M530010> and <https://doi.org/10.17602/M2/M530028>). Consistent characters between both specimens are reported here, with any differences noted. The scales of the dorsal and temporal regions of the skull and the ventrolateral aspects of the jaws overlie rugose osteoderms. These osteoderms fuse to the proximal parietal, frontal and postorbital bones, although the mesokinetic and metakinetic joints appear unobstructed and flexible. Lateral maxilla and anterior aspect of the premaxilla lack osteoderms. The parietal is pentagonal, with five osteoderms that underlie the parietal shields fused to its dorsal surface, and tapers to a bifid medioposterior process, which articulates with the sagittal crest of the supraoccipital. Three large osteoderms are fused to the frontal, which is unpaired and clasped by the parietal at its posterolateral edge. The upper temporal fenestra is obscured anteriorly by a large osteoderm fused to the dorsal surface of the postorbital bone, posteriorly by two unfused rectangular osteoderms that overlie the squamosal. Premaxilla is unpaired and contains nine pleurodont teeth, with a dorsal process that extends posteriorly to intersect the nasals (absent due to damage in AMNH R47334), which themselves overlie the frontal. The maxillae are typically scinciform, with a deeply grooved crista dentalis, a deep fossa that accommodates the lacrimal sac, and 20–21 (TM 46476) to 18–19 (AMNH R47334) teeth. Teeth display pleurodont attachment and are unicuspid, with a slight concave surface where they connect with the mandibular teeth. No palpebral is present but the prefrontals possess a small protuberance, forming a shelf that directly underlies the anteriormost superorbital osteoderm. The jugal is triangular in cross-section and asymmetrical-

ly T-shaped, with a tapering anterior process and a broad, truncated posterior process that extends along and past the posterior edge of the maxilla. The lacrimal bone is small, flattened and oval, slightly bicuspid anteriorly, the two processes meeting prefrontal cusps to bracket the lacrimal duct. Pterygoids are edentate and extend back to connect with the quadrates, becoming C-shaped in cross-section posterior to the epipterygoid condyle. The squamosal is curved and blade-like, circular in cross-section anteriorly, becoming flattened posteriorly, where it articulates with the cephalic condyle of the quadrate and the supratemporals. Supratemporals are laterally flattened, ovoid and not fused with the elongate paraoccipital processes. The posterior aspect of the prootic in the smaller AMNH R47334 is not fully fused with the otooccipital, resulting in a deep groove along the dorsal aspect of the paraoccipital processes. Quadrates very broad with a pronounced ridge and concave region at the entire lateral edge in TM 46476 (right quadrate of AMNH R47334 partially damaged). The supraoccipital has a strong sagittal crest that extends posteriorly to contact the ventral surface of the medioposterior process of the parietal. The prootic bears an extended alar process and a well-developed, rhomboid christa prootica, and a very weak supratrigeminal process. Basipterygoid processes are well developed and flattened. The lower jaw possesses a large adductor fossa, a highly flattened and medially extended retroarticular process, a medially open Meckelian canal that is closed posteriorly by a large splenial, and a dentary with a strong subdental shelf; 22 (AMNH R47334) and 25–26 (TM 46476) mandibular teeth, and 6–7 dentary foramina.

*Postcranial skeleton:* Segmented mesh files of AMNH R47333 and TM 46476 can be found here: [tinyurl.com/CangAMNHskel](https://tinyurl.com/CangAMNHskel) and here [tinyurl.com/Cang2Skel](https://tinyurl.com/Cang2Skel). Morphosource links to tomogram stacks (<https://doi.org/10.17602/M2/M15862> and <https://doi.org/10.17602/M2/M529986>). The axial skeleton is comprised of 25 presacral vertebrae: eight cervical, three sternal, two xiphisternal, five long asternal ribs with ossified costal cartilage, then seven short asternal ribs (the ribs immediately anterior to the sacral vertebrae in AMNH R47333 are highly reduced), two sacral and 24 caudal vertebrae (incomplete, regenerated tail in AMNH R47333). Cervical ribs 4–6 are distally flattened and bipid, with the ventral processes more elongated. Pubis flattened and curved with a large, ventrally-angled pectineal tubercle. Pubic symphysis flattened and triangular, separating the pubes entirely. Hyperischium and hypoischium well developed. Sternal plate broad, lacking a fontanelle. Interclavicle cruciform. Digits display a typical phalangeal pattern of 2–3–4–5–3 for the manus and 2–3–4–5–4 for the pes.

*Osteoderms* (Fig. 9): The dorsal trunk is covered in rectangular, dorsomedially keeled, imbricate osteoderms, each roughly three times longer than its width. The dorsal osteoderms are arranged in whorls, becoming more oval and better separated laterally. The nuchal osteoderms are spined posterior to the tympanic opening. Ventral osteoderms are absent in AMNH R47333, and delicate and plate-like in TM 46476, grading from rhomboid in the gular region to mildly imbricated and cycloid in the pec-



**Figure 15.** A, C Adult female *Cordylus momboloensis* sp. nov. (TM 46476) from 3 km W of Condé, Cuanza Sul Province, Angola. B Habitat shown is in the vicinity of Condé. Photos: Wulf D. Haacke (A, C), and William R. Branch (B).

toral region, square and non-imbricate in the abdominal region, to pentagonal in the cloacal region. The forelimbs are covered in keeled, imbricate, rhomboid osteoderms, except for the axillary, antecubical and palmar regions, which are unarmoured. The hindlimbs are covered in rhomboid osteoderms, except for the ventral femoral, popliteal and plantar regions. Hindlimb osteoderms are unkeeled on the anterior thigh, become more spinose posteriorly and distally. The caudal osteoderms are large, robust and arranged in imbricated whorls, feebly keeled and mucronate along the dorsal and ventral aspects, becoming more heavily spined laterally.

**Variation in additional material** (n = 2). (Figs 4–6, 8–9, 15; Tables 5, 6)

**External morphology:** TM 46476 (female). SVL 106.0 mm. Original tail 106.7% SVL. Head 1.25 times as long as wide, head height 0.469 times head width. Nasals in broad contact. Interparietal bulb-shaped with a long neck, completely separating the anterior parietals. Anterior and posterior parietals similar in size and shape. Nostril in contact with preocular, nasal scale apparently not divided, and no postnasal present. Lower half of preocular with a vertical suture medially, suggesting partial fusion with loreal. Lower eyelid with five vertically enlarged septa. Rostral 2.8 times as broad as deep. Supralabials 5 left, 7 right. Mental 1.49 times as long as broad. Gulars mostly rectangular and obtusely and feebly keeled, imbricate to subimbricate, forming nine transverse rows (from first row in line with angle of jaws to last distinct row posterior to pair of sublabials), and 23 longitudinal rows between posterior angles of jaws. Four chin shields in contact with first pair of sublabials. Dorsals in 24 transverse and 20 longitudinal rows. Ventrals in 22 transverse and 12 (plus one row of ‘pseudo-ventrals’ on either side) longitudinal rows. Pair of cloacal plates preceded by two transverse rows of much smaller plates. Scales under

fourth toe 13 (both sides), under fourth finger 12 (both sides). Femoral pores 7 left, 5 right; no differentiated femoral scales. Subdigital scales of feet strongly keeled and spinose, especially posteriorly.

FKH 0129 (juvenile). Data for head only, see Figs 4–6 and Table 5. Supralabials 6. Infralabials 7 left, 6 right. Suboculars 3. Occipitals 2 on either side of head.

**Colour of additional material** (in life). TM 46476: Upperparts medium brown with a paired series of irregular cream paravertebral blotches from nape to base of tail; top of head with a few small, scattered, cream markings. FKH 0129 was similar to the type series.

**Size.** Largest male (MNCN 50760, Vondo): SVL 90.5 mm, tail length 88.4 mm (original), total length 178.9 mm, head length 23.1 mm, head width 21.3 mm, head height 11.9 mm. Largest female (MNCN 50761 allotype, Vondo): SVL 89.5 mm, tail length 85.4 mm (original), total length 174.9 mm, HL 22.3 mm, HW 20.5 mm, HD 11.8 mm. A non-type female (TM 46476, 3 km W of Condé), referred to this species, measures SVL 106.0 mm, tail length 113 mm (original), total length 219 mm, HL 26.8 mm, HW 22.2 mm, HD 12.7.

**Etymology.** The name ‘momboloensis’ derives from the local name (“m’bolo”) for Mombolo which in Umbundo – main language in central Angola – is applied to bread or staple food. It is a reference to the fact that the region in question consists of a fertile and relatively large highland plateau (surrounded by mountains, in Luanza Sul Province). Most of the available specimens, including the holotype as well as the first series of specimens of this species collected during the Vernay Angola Expedition in 1925, were collected in Mombolo.

**Habitat.** Although no specific habitat information is available for the material housed at the AMNH, it is like-

ly that it may have been obtained at the same site as the recent material from Sandula. At both the Sandula and Vondo localities, the species proved to be rupicolous and specimens were found sheltering inside cracks and crevices in rocky outcrops (igneous rocks in Sandula and granite in Vondo) present in fairly steep slopes above 1900 m a.s.l. (Fig. 11D). The surrounding habitat at Sandula and Vondo is montane grassland. The specimen from Condé was reportedly found in a rock outcrop surrounded by grassland and sparse miombo savannah (see Fig. 15B).

**Distribution.** This species was collected at Sandula (Monte Verde) and Vondo (Mount Uassamba), both in Cuanza Sul Province on high mountain peaks at 1975–2095 m a.s.l., and an individual was briefly observed at Morro do Pundo (−12.4464°, 13.9171°) in Benguela Province, at approximately 1000 m elevation near the town of Bocoio (Fig. 12). The Bocoio specimen quickly disappeared into a deep crevice and only a tail tip was secured. The latter was analysed for 16S and the specimen was referred to this species. The two peaks at Sandula and Vondo are situated about 110 km apart in highlands that include several mountain chains that have never been surveyed before, suggesting that the species is widespread on the west-central Angolan plateau in suitable mountain habitat, while the specimen from 3 km W of Condé places the species further north at elevations of about 1236 m a.s.l. in miombo woodlands (Fig. 12).

The AMNH material was collected by ‘H. Chapman and A. Chapman’ in 1925 and simply labeled as ‘Mombolo’. This location, however, is rather vague as the region of Mombolo covers about 1000 km<sup>2</sup>, and included three farms belonging to the Chapman family. A very detailed discussion on the problems in relation to another rupicolous lizard, *Afroedura bogerti*, collected under identical circumstances ( Loveridge 1944b), is provided by Branch et al. (2017). It can be noted that Hill and Carter (1941) stated that “Boulton and Charles Chapman went to Namba in the Mombolo region.” Two of Chapman’s farms were located on the separate mountain chains of Namba and Monte Verde (Sandula), suggesting that the geographic location could be confidently narrowed down to those two sites. However, several recent surveys conducted on both mountains have so far resulted in *Cordylus* being found only at Sandula, suggesting that this was the original locality where the Chapman specimens were collected.

**Conservation.** Little is known about the biology of this species, but habitat at the four sites where it has been found appears to be relatively undisturbed. Given the current knowledge, if an assessment was to be done, it is likely to result in a classification of Least Concern based on IUCN (2022a) Standards and Petitions Committee criteria.

## Key to the genus *Cordylus* in Angola

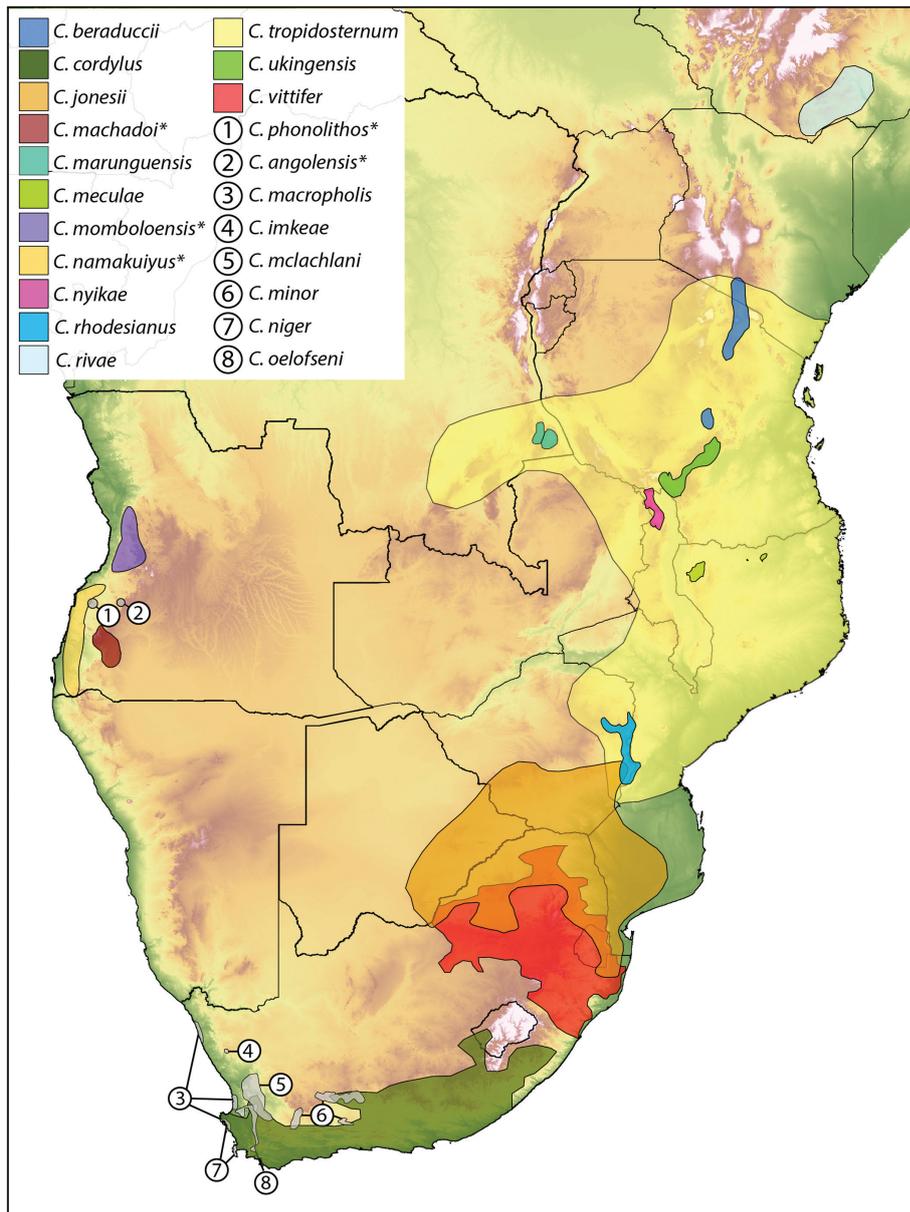
- 1a Loreal present; nostril situated above the suture between rostral and first supralabial; scales of the first transverse row of dorsals mostly elongated .....2
- 1b Loreal absent; nostril situated posterior to suture between rostral and first supralabial; scales of the first transverse row of dorsals not elongated, similar to those of subsequent rows.....4
- 2a Interparietal small, not completely separating the anterior parietals; ventral osteoderms absent.....*C. machadoi*
- 2b Interparietal large and usually in contact with the frontoparietals, separating the anterior parietals; ventral osteoderms present .....3
- 3a Femoral pores in adults 4–6 per leg .....*C. namakuiyus*
- 3b Femoral pores in adults 7–8 per leg .....*C. phonolithos*
- 4a Iris of the eye brown; occipitals in a regular row of six scales; ventral scales in 14 rows longitudinally; generation glands in males 19–25 per leg; forearm/SVL 0.15–0.19.....*C. angolensis*
- 4b Iris of the eye pale green or blue-green; occipitals 2–3 on either side of head, interrupted medially by a row of 5–6 post-occipitals; ventral scales in 12–13 (rarely 11 or 14) rows longitudinally; generation glands in males 25–37 per leg; forearm/SVL 0.20–0.25.....*C. momboloensis* sp. nov.

## Discussion

The most recent phylogeny of the genus *Cordylus* indicated a distinct Angolan clade consisting of three species: *C. machadoi*, *C. namakuiyus* and *C. phonolithos* (Marques et al. 2019). However, the relationship of these species to *C. angolensis* Bocage, 1895 was not established pending the availability of samples. Nevertheless, Stanley et al. (2016) hypothesised that ‘*C. angolensis*’ based on material housed at AMNH (i.e., *C. momboloensis* sp. nov.) was

most closely related to the other species of the Angolan clade (*C. machadoi* group) considering the known strong biogeographic fidelity of the genus *Cordylus* and co-occurrence in this area.

In the present study we analysed lizards from the west-central highlands of Angola and placed them in a phylogenetic context with their congeners, including the three species in the *C. machadoi* group. *Cordylus angolensis* and *C. momboloensis* sp. nov. form a sister clade to the *C. machadoi* group. Within the latter, *C. machadoi* (high elevation escarpment) and *C. phonolithos* (Serra da



**Figure 16.** Geographical distribution of the genus *Cordylus*, restricted to sub-Saharan Africa. In the key, Angolan species are indicated by an asterisk. Polygons for non-Angolan species are reported from IUCN (2022b).

Neve inselberg) group together, rather than *C. machadoi* + *C. namakuiyus* (arid lowlands) as indicated by Marques et al. (2019), but support is weak and therefore relationships within the group remain unresolved. The *C. machadoi*–*C. phonolithos* relationship suggests a once continuous highland population, and therefore the possibility of taxonomic over-inflation (see Tolley et al. 2021) within the *C. machadoi* group should be investigated.

*Cordylus angolensis* and *C. momboloensis* **sp. nov.** are superficially similar species of comparable size, colour pattern and scutellation. Nevertheless, we show that they differ with regard to the arrangement of occipitals/post-occipitals, numbers of ventral scale rows longitudinally, relative forearm length, numbers of generation glands in males, and in terms of eye colour – a character not usually mentioned in cordylid species comparisons (see Diagnosis above). There are also differences between *C. angolensis* and *C. momboloensis* **sp. nov.** with regard to the skeleton and osteoderms: 22–23 maxillary teeth on either side versus 18–21 respectively; premax-

illary teeth 7 versus 9; and in *C. angolensis* the posterior process of the parietal is much longer compared to *C. momboloensis* **sp. nov.** Osteoderm distributions of *C. momboloensis* **sp. nov.** differ between the two specimens scanned, but greater sampling is needed to ascertain whether this is a result of ontogenetic, geographic or stochastic variation.

Our phylogeny agrees largely with that of Stanley et al. (2016) and Marques et al. (2019) in regard to the Cape/South African and East African clades, with one noticeable difference. We found that the Angolan *Cordylus* were most closely related to a *C. jonesii* + *C. rhodesianus* clade, comprising two species which in our analysis fall outside the East African clade. This *C. jonesii* + *C. rhodesianus* grouping is supported by at least one scale character (a posteriorly divided nasal scale). The close relationship of *C. jonesii* + *C. rhodesianus* with the Angolan species may suggest a mechanism as to how the ancestors of the strictly rupicolous Angolan *Cordylus* were able to traverse about 1400 km of non-rocky habitat

and colonise their current territory. *Cordylus jonesi* and *C. rhodesianus* form part of the continuous corridor of the eastern clade, co-occurring with *C. vittifer* in the south and *C. tropidosternum* in the north (Fig. 16). *Cordylus jonesii* has a broader distribution than most *Cordylus* species and, like the similarly widespread *C. tropidosternum*, is an ecologically unusual cordylid, often eschewing the typical cordylid rock-crevice retreat sites for tree bark and hollow tree limbs in mopane woodlands (Branch 1998). If the reduced reliance on rocky habitat seen in *C. jonesii* represents the plesiomorphic condition for this clade, the ancestors of Angolan *Cordylus* may have been able to disperse through the dry woodlands of the southern African Miocene via Botswana, Zimbabwe, Zambia and northern Namibia (Bamford 2000), reverting to obligate rupicolity upon reaching the rocky habitats of the Angolan escarpment and coastal desert. The current diaspora in the northern *Cordylus* clade implies that the intermediate habitat must have become unsuitable following the westwards dispersal, with aridification of the Kalahari in the mid- to late-Miocene providing one explanation of how this isolation could have occurred (Hoetzel et al. 2015).

Recent studies on other rupicolous lizards in the south-western quarter of Angola have indicated similar distribution patterns to *Cordylus*. In both Angolan *Afroedura* and *Cordylus*, the main divide splits one clade in the west-central highlands and one clade widely distributed along the south-western coastal plain and escarpment. The six species of Angolan flat geckos (Branch et al. 2021; Conradie et al. 2022b) show a distribution pattern similar to the five species of *Cordylus* (Fig. 12): in the west-central highlands the *A. bogerti* group is similarly distributed to the *C. angolensis* group, and in the south-western group the other three species of *Afroedura* have a similar distribution to the *C. machadoi* group (high elevations at the top of the southern escarpment: *A. vazpintorum* and *C. machadoi*; Serra da Neve inselberg: *A. praedicta* and *C. phonolithos*; widely distributed on the semi-arid coastal plain: *A. donveae*, *A. vazpintorum*, *C. namakuiyus*). *Hemidactylus benguellensis* is another gecko restricted to south-western Angola (Lobón-Rovira et al. 2021), with a distribution similar to the *C. machadoi* group as its range includes the lowlands (similar to the range of *C. namakuiyus*), highlands (similar to *C. machadoi*) and Serra da Neve (habitat of *C. phonolithos*).

These similar distribution patterns strongly suggest that the same evolutionary forces may have shaped the speciation history of these genera in Angola. The Angolan west-central highlands, corresponds to the marginal mountain chain or ancient massif (Huntley 2019), and includes most of the country's highest peaks and Afro-montane ecosystems. These highlands are recognized as an important centre of biodiversity endemism, as part of a continent-wide archipelago of relic montane grasslands and forests (Huntley 2019). Radiation of saxicolous lizards speciating allopatrically in 'rock islands' has been well documented (e.g., Branch et al. 2021; Conradie et al. 2022b), and our data suggest that the species currently present in the Angolan central highlands, such as *C. angolensis* and *C. momboloensis* sp. nov., represent rela-

tively old lineages, while speciation in the south-western clade is more recent and may not be fully resolved.

Despite several recent studies on the herpetofauna of Angola (see references in Introduction), more surveys will be required to allow an evaluation of the true distribution of both *C. angolensis* and *C. momboloensis* sp. nov., and to investigate the possibility of additional congeners occurring in the country. The highlands of central Angola are still relatively poorly known biologically and barely explored, but it is likely that future work will reveal similar speciation patterns in other rupicolous taxa, which may significantly contribute to a better interpretation of Angolan biogeography in general. Our findings underline the importance of the Angolan west-central highlands in functioning as a regional reservoir of biodiversity, and highlight the need to conserve its highly threatened montane habitats.

## Conclusion

Our evaluation of genetic and morphological data indicates that two species of allopatric, rupicolous *Cordylus*, *C. angolensis* and *C. momboloensis* sp. nov., occur in the west-central highlands of Angola. *Cordylus angolensis* was until now known only from the holotype collected 128 years ago. We also show that these two species form a clade most closely related to the three species of the *C. machadoi* complex in south-western Angola, and together the Angolan assemblage of *Cordylus* is a distinct clade most closely related to east African congeners, especially *C. jonesii* + *C. rhodesianus*.

## Acknowledgements

We thank the following individuals: Agnes Phindane (National Museum, Bloemfontein) for measuring non-Angolan lizards and assisting with calculations of body size; Werner Conradie (Port Elizabeth Museum) for a few measurements on the holotype of *C. momboloensis* sp. nov.; Laurreta Mahlangu (Ditsong National Museum of Natural History, Pretoria), David Kizirian (American Museum of Natural History, New York), and Seth Eiseb and Mathilde Awases (National Museum of Namibia, Windhoek) for loans of Angolan and Namibian *Cordylus* specimens; Afonso Vaz Pinto and Ninda Baptista (Centro de Investigação em Biodiversidade e Recursos Genéticos, Portugal) for field support to collect specimens for this study; the late Wulf Haacke (Pretoria) for information about Angolan collecting localities and for supplying photographic images of Angolan specimens; Frank Tillack (Museum für Naturkunde der Humboldt-Universität, Berlin) for information about the holotype of *C. vittifer* and for supplying photographs of this specimen; Aaron Bauer (Villanova University, Villanova) for providing copies of old literature; René Navarro (University of Cape Town) for preparing the *C. vittifer* map; Luis Verissimo (Catholic University of Angola, Luanda) for information on locality names, habitat and elevations in Angola; Werner Conradie (Port Elizabeth Museum, Bayworld), Krystal Tolley (South African National Biodiversity Institute, Cape Town) and John Measey (Stellenbosch University, Stellenbosch), field

companions of the late WRB in Angola; Alberto Sanchez-Vialas for providing detailed photographs of the neotype of *C. angolensis* and other material deposited at Museo Nacional de Ciencias Naturales, Madrid; Luis Ceriaco for photographs of the holotype of *C. phonolithos*; David Maguire, Darren Pietersen and Luke Verburgt for photographs of live cordylids; and Fatima Linares (Centro de Instrumentación Científica of Granada) for CT scanning of the neotype of *C. angolensis*. JLR was supported by Fundação para a Ciência e Tecnologia (FCT) contract PD/BD/140808/2018 and BIOPOLIS 2022–18. Comparative CT material was produced as part of the NSF oVert TCN (NSF:1701714).

## References

- Adolphs K (2006) *Bibliotheca Cordyliformium*. Squamata Verlag, Sankt Augustin.
- Almacá C, Neves AM (1987) The Museu Bocage and the new series of its Arquivos. *Arquivos do Museu Bocage, Nova Série I*(1): 1–8.
- Bamford MK (2000) Cenozoic macro-plants. In: Partridge TC, Maud RR (Eds) *The Cenozoic of Southern Africa*. Oxford Monographs on Geology and Geophysics 40: 351–356.
- Banha de Andrade AA (1985) O naturalista José de Anchieta (Vol. 24). Instituto de Investigação Científica Tropical, Centro de Estudos de História e Cartografia Antiga, xxiii + 187 pp.
- Baptista N, Antonio T, Branch WR (2018) Amphibians and reptiles of the Tundavala region of the Angolan Escarpment. In: Revermann R, Krewenka KM, Schmiedel U, Olwoch M, Helmschrot J, Jürgens N (Eds) *Climate Change and Adaptive Land Management in Southern Africa – Assessments, Changes, Challenges, and Solutions*. Biodiversity & Ecology, Vol. 6. Klaus Hess Publishers, Göttingen, 397–403. <https://doi.org/10.7809/b-e.00351>
- Baptista N, Antonio T, Branch WR (2019a) The herpetofauna of Bicuar National Park and surroundings, southwestern Angola: A preliminary checklist. *Amphibian & Reptile Conservation* 13: 96–130 (e203).
- Baptista N, Conradie W, Vaz Pinto P, Branch WR (2019b) The amphibians of Angola: Early studies and the current state of knowledge. In: Huntley BJ, Russo V, Lages F, Ferrand N (Eds) *Biodiversity of Angola*. Science & Conservation: A Modern Synthesis. Springer, Cham, 243–281. [https://doi.org/10.1007/978-3-030-03083-4\\_12](https://doi.org/10.1007/978-3-030-03083-4_12)
- 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>
- Barbosa LAG (1970) Carta Fitogeográfica de Angola. Instituto de Investigação Científica de Angola, Luanda, 323 pp.
- Bates MF (2007) First records of the Cape girdled lizard, *Cordylus cordylus* (Linnaeus, 1758), in Lesotho. *Navorsing van die Nasionale Museum, Bloemfontein* 23: 185–195.
- Bates MF, Branch WR, Bauer AM, Burger M, Marais J, Alexander GJ, De Villiers MS (Eds) (2014) *Atlas and Red List of the Reptiles of South Africa, Lesotho and Swaziland*. Suricata 1. South African National Biodiversity Institute, Pretoria, xvii + 485 pp.
- Bauer AM, Lang M, Günther R (1994) An annotated type catalogue of the pygopods, xantusiids, gerrhosaurids and cordylids (Reptilia: Squamata: Pygopodidae, Xantusiidae, Gerrhosauridae and Cordylidae) in the collection of the Zoological Museum, Berlin. *Mitteilungen aus dem Zoologischen Museum in Berlin* 70: 85–92. <https://doi.org/10.1002/mmnz.19940700103>
- Bocage JV Barboza du (1895) *Herpétologie d'Angola et du Congo*. Imprimerie Nationale, Lisbonne, 8, i–xx + 1–203, plates 1–19. <https://doi.org/10.5962/bhl.title.5505>
- Bocage JV Barboza du (1897) *Mamíferos, Reptis e Batrachios d'África de que existem exemplares typicos no Museu de Lisboa*. *Jornal de Sciencias Mathematicas, Physicase Naturae* 1897: 187–206.
- Bogert CM (1940) Herpetological results of the Vernay Angola Expedition with notes on African reptiles in other collections. Part I. Snakes, including an arrangement of African Colubridae. *Bulletin of the American Museum of Natural History* 77: 1–107, 1 plate.
- Boulenger GA (1885) *Catalogue of the lizards in the British Museum (Natural History)*, Volume II. Iguanidae, Xenosauridae, Zonuridae, Anguidae, Anniellidae, Helodermatidae, Varanidae, Xantusiidae, Teiidae, Amphisbaenidae. 2<sup>nd</sup> edition. British Museum, London, i–xiii + 1–497, pls I–XXIV. <https://doi.org/10.5962/bhl.title.53974>
- Boulenger GA (1891) Description of a new lizard of the genus *Zonurus* from the Transvaal. *The Annals and Magazine of Natural History (6<sup>th</sup> Series)* 7: 417. <https://doi.org/10.1080/00222939109460635>
- Boulenger GA (1897) A list of reptiles and batrachians from the Congo Free State, with descriptions of two new snakes. *The Annals and Magazine of Natural History (6<sup>th</sup> series)* 19: 276–281. <https://doi.org/10.1080/00222939708680537>
- Boulenger GA (1910) A revised list of the South African reptiles and batrachians, with synoptic tables, special reference to the specimens in the South African Museum, and descriptions of new species. *Annals of the South African Museum* 5: 455–539.
- Branch B [WR] (1998) *Field Guide to Snakes and other Reptiles of Southern Africa*. Third edition. Struik, Cape Town, 399 pp.
- Branch WR (2018a) Auf Reptiliensuche in der angolanischen Okavango-Wildnis / Herping the Angolan Okavango Wilderness. *Sauria* 40: 25–57.
- Branch WR (2018b) Snakes of Angola: An annotated checklist. *Amphibian & Reptile Conservation* 12: 41–82 (e159).
- Branch WR, Conradie WC (2015) VI. Herpetofauna da região da Lagoa Carumbo/Herpetofauna of the Carumba Lagoon Area. In: Huntley BJ (Ed.) *Relatório sobre a expedição Avaliação Rápida da Biodiversidade de Regio da Lagoa Carumbo, Lunda Norte – Angola/Expedition Report / Rapid Biodiversity Assessment of the Carumba Lagoon Area, Lunda Norte, Angola*. Ministerio do Ambiente, Republica de Angola, Luanda, 194–209.
- Branch WR, McCartney CJ (1992) A report on a small collection of reptiles from southern Angola. *Journal of the Herpetological Association of Africa* 41: 1–3. <https://doi.org/10.1080/04416651.1992.9650346>
- Branch WR, Baptista N, Vaz Pinto P (2018) Angolan amphisbaenians: Rediscovery of *Monopeltis luandae* Gans, 1976, and comment on the type locality of *Monopeltis perplexus* Gans, 1976 (Sauria: Amphisbaenidae). *Herpetological Notes* 11: 603–606.
- Branch WR, Rödel M-O, Marais J (2005) A new species of rupicolous *Cordylus* Laurenti 1768 (Sauria: Cordylidae) from Northern Mozambique. *African Journal of Herpetology* 54: 131–138. <https://doi.org/10.1080/21564574.2005.9635526>
- Branch WR, Baptista N, Keates CW, Edwards S (2019a) Rediscovery, taxonomic status, and phylogenetic relationships of two rare and endemic snakes (Serpentes: Psammophinae) from the southwestern Angolan plateau. *Zootaxa* 4590: 342–366. <https://doi.org/10.11646/zootaxa.4590.3.2>
- Branch WR, Conradie W, Vaz Pinto P, Tolley KA (2019b) Another Angolan Namib endemic species: A new *Nucras* Gray, 1838 (Squamata:

- Lacertidae) from south-western Angola. *Amphibian & Reptile Conservation* 13: 82–95 (e199). <http://doi.org/10.5281/zenodo.3731977>
- Branch WR, Vaz Pinto P, Baptista N, Conradie W (2019c) The reptiles of Angola: History, diversity, endemism and hotspots. In: Huntley BJ, Russo V, Lages F, Ferrant N (Eds) *Biodiversity of Angola. Science & Conservation: A Modern Synthesis*. Springer, Cham, 283–334. [http://doi.org/10.1007/978-3-030-03083-4\\_13](http://doi.org/10.1007/978-3-030-03083-4_13)
- 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. <https://doi.org/10.3897/zse.97.57202>
- Branch WR, Haacke W, Vaz Pinto P, Conradie W, Baptista N, Verburgt L, Verissimo L (2017) Loveridge's Angolan geckos, *Afroedura karroica bogerti* and *Pachydactylus scutatus angolensis* (Sauria, Gekkonidae): New distribution records, comments on type localities and taxonomic status. *Zoosystematics and Evolution* 93: 157–166. <https://doi.org/10.3897/zse.93.10915>
- Broadley DG (1965) Some taxonomic and distributional problems presented by Central African reptiles. *Journal of the Herpetological Association of Rhodesia* 23/24: 19–30. <https://doi.org/10.1080/0440730X.1965.9650547>
- Broadley DG (1966) The herpetology of south-east Africa. PhD Thesis, University of Natal, Pietermaritzburg, South Africa.
- Broadley DG (1971) A reassessment of the northern forms currently assigned to the *Cordylus cordylus* group. *Journal of the Herpetological Association of Africa* 7: 20–22. <https://doi.org/10.1080/04416651.1971.9650787>
- Broadley DG (2006) CITES Standard Reference for the Species of *Cordylus* (Cordylidae, Reptilia): CITES Nomenclature Committee for the 14<sup>th</sup> meeting of the CoP: 10.
- Broadley DG, Branch WR (2002) A review of the small east African *Cordylus* (Sauria: Cordylidae), with the description of a new species. *African Journal of Herpetology* 51: 9–34. <https://doi.org/10.1080/21564574.2002.9635459>
- Broadley DG, Mouton P le FN (2000) A new species of rupicolous *Cordylus* Laurenti from Malawi (Sauria: Cordylidae). *African Journal of Herpetology* 49: 169–172. <https://doi.org/10.1080/21564574.2000.9635443>
- Broeckhoven C, de Kock C, Mouton P le FN (2017) Sexual dimorphism in osteoderm expression and the role of male intrasexual aggression. *Biological Journal of the Linnean Society* 122: 329–339. <https://doi.org/10.1093/biolinnean/blx066>
- Ceríaco LMP, De Sa S dos AC, Bauer AM (2018) The genus *Osteoleamus* (Crocodylidae) in Angola and a new southernmost record for the genus. *Herpetology Notes* 11: 337–341.
- Ceríaco LMP, Marques MP, Bandeira SA (2016) Parque Nacional da Cangandala. Instituto Nacional da Biodiversidade e Áreas de Conservação & Museu Nacional de Historia Natural e da Ciência, Luanda, 95 pp.
- 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/10.11646/zootaxa.4746.1.1>
- Ceríaco LMP, Bauer AM, Blackburn DC, Lavres ACFC (2014) The herpetofauna of the Capanda Dam Region, Malanje, Angola. *Herpetological Review* 45: 667–674.
- Ceríaco LMP, Heinicke MP, Parker KL, Marques MP, Bauer AM (2020b). A review of the African snake-eyed skinks (Scincidae: *Panaspis*) from Angola, with the description of a new species. *Zootaxa* 4747: 77–112. <https://doi.org/10.11646/zootaxa.4747.1.3>
- Ceríaco LMP, Santos BS, Marques MP, Bauer AM, Tiutenko A (2021) Citizen Science meets specimens in old formalin filled jars: A new species of banded rubber frog, genus *Phrynomantis* (Anura, Phrynomeridae) from Angola. *Alytes* 38: 18–48.
- Ceríaco LMP, Tolley KA, Marques MP, Heinicke MP, Bauer AM (2020c) A dwarf among giants: Phylogenetic position of the elusive Angolan adder (*Bitis heraldica*) and biogeographic affinities of Angolan Afromontane regions. *African Journal of Herpetology* 69: 108–118. <https://doi.org/10.1080/21564574.2020.1782484>
- Ceríaco LMP, Marques MP, Andre I, Afonso E, Blackburn DC, Bauer AM (2020d) Illustrated type catalogue of the “lost” herpetological collections of Museu do Dondo, Angola. *Bulletin of the Museum of Comparative Zoology* 162: 379–440. <https://doi.org/10.3099/0027-4100-162.7.379>
- Conradie W, Bills R, Branch WR (2016) The herpetofauna of the Cuito, Cuito, and lower Cuando river catchments of south-eastern Angola. *Amphibian & Reptile Conservation* 10: 6–36 (e126).
- Conradie W, Branch WR, Tolley KA (2013) Fifty shades of grey: Giving colour to the poorly known Angolan ashy reed frog (Hyperoliidae: *Hyperolius cinereus*), with the description of a new species. *Zootaxa* 3635: 201–223. <https://doi.org/10.11646/zootaxa.3635.3.1>
- Conradie W, Branch WR, Measey GJ, Tolley KA (2012a) A new species of *Hyperolius* Rapp, 1842 (Anura: Hyperoliidae) from the Serra de Chela mountains, south-western Angola. *Zootaxa* 3269: 1–17. <https://doi.org/10.11646/zootaxa.3269.1.1>
- 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 (2022a) Taxonomical review of *Prosymna angolensis* Boulenger, 1915 (Elapoidea, Prosymnidae) with the description of two new species. *Zookeys* 1121: 97–143. <https://doi.org/10.3897/zookeys.1121.85693>
- Conradie W, Measey GJ, Branch WR, Tolley KA (2012b) Revised phylogeny of African sand lizards (*Pedioplanis*), with the description of two new species from south-western Angola. *African Journal of Herpetology* 61: 1–22. <https://doi.org/10.1080/21564574.2012.676079>
- Conradie W, Schmitz A, Lobón-Rovira J, Becker FS, Vaz Pinto P, Hauptfleisch ML (2022b) 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>
- Conradie W, Baptista NL, Verburgt L, Keates C, Harvey J, Julio T, Neef G (2021) Contributions to the herpetofauna of the Angolan Okavango-Cuando-Zambezi river drainages. Part 1: Serpentes (snakes). *Amphibian & Reptile Conservation* 15: 244–278 (e292).
- 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>
- Conroy CJ, Papenfuss T, Parker J, Hahn NE (2009) Use of tricaine methanesulfonate (MS222) for euthanasia of reptiles. *Journal of the American Association for Laboratory Animal Science* 48: 28–32.
- Cope ED (1869) Seventh contribution to the herpetology of Tropical America. *Proceedings of the American Philosophical Society* 11: 147–169.

- Cuvier G (1829) Le règne animal distribué d'après son organisation pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Tome II, Les Reptiles. Paris, Déterville, pp. i–xvi, 1–406, plates i–xx.
- 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 Queiroz K (2007) Species concepts and species delimitation. *Systematic Biology* 56: 879–886. <https://doi.org/10.1080/106351507-01701083>
- De Waal SWP (1978) The Squamata (Reptilia) of the Orange Free State, South Africa. *Memoirs van die Nasionale Museum, Bloemfontein* 11: i–iii, 1–160.
- FitzSimons V [F] (1938) Transvaal Museum expedition to South-West Africa and Little Namaqualand, May to August 1937. Reptiles and Amphibians. *Annals of the Transvaal Museum* 19: 153–209.
- FitzSimons VF (1943) The lizards of South Africa. *Transvaal Museum Memoirs* 1: i–xv, 1–528, plates 1–24.
- Frost DR, Hillis DM (1990) Species in concept and practice: Herpetological applications. *Herpetologica* 46: 87–104.
- Greenbaum E, Stanley EL, Kusamba C, Moninga WM, Goldberg SR, Bursey CR (2012) A new species of *Cordylus* (Squamata: Cordylidae) from the Marungu Plateau of south-eastern Democratic Republic of the Congo. *African Journal of Herpetology* 61: 14–39. <https://doi.org/10.1080/21564574.2012.666505>
- Haacke WD (2008) A new leaf-toed gecko (Reptilia: Gekkonidae) from south-west Angola. *African Journal of Herpetology* 57: 85–92. <https://doi.org/10.1080/21564574.2008.9635571>
- Hallermann J, Ceriaco 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 Hamburgischen Zoologischen Museum und Institut* 55: 39–80.
- Hewitt J (1933) Descriptions of some new reptiles and a frog from Rhodesia. *Occasional Papers of the Rhodesian Museum* 2: 45–50, 1 pl.
- Hill ER, Carter TD (1941) The mammals of Angola, Africa. *Bulletin American Museum of Natural History* 78: 1–211.
- Hoetzel S, Dupont LM, Wefer G (2015) Miocene–Pliocene vegetation change in south-western Africa (ODP Site 1081, offshore Namibia). *Palaeogeography, Palaeoclimatology, Palaeoecology* 423: 102–108. <https://doi.org/10.1016/j.palaeo.2015.02.002>
- Huelsenbeck JP, Hillis DM (1993) Success of phylogenetic methods in the four-taxon case. *Systematic Biology* 42: 247–264. <https://doi.org/10.1093/sysbio/42.3.247>
- Huntley B (2009) SANBI/ISCED/UAN Angolan Biodiversity Assessment and Capacity Building Project, Report on Pilot Project. South African National Biodiversity Institute, Cape Town, unpublished report.
- Huntley B (2011) Biodiversity rapid assessment of Lagoa Carumbo area, Lunda Norte, Angola. Preliminary unpublished report on the expedition.
- Huntley BJ (2019). Angola in outline: Physiography, climate and patterns of biodiversity. In: Huntley BJ, Russo V, Lages F, Ferrant N (Eds) *Biodiversity of Angola. Science & Conservation: A Modern Synthesis*. Springer, Cham, 15–42.
- IUCN Standards and Petitions Committee (2022a) Guidelines for using the IUCN Red List Categories and Criteria. Version 15. Prepared by the Standards and Petitions Committee. <https://www.iucnredlist.org/documents/RedListGuidelines.pdf> (accessed 21 June 2022).
- IUCN (2022b) The IUCN Red List of Threatened Species. Version 2022–1. <https://www.iucnredlist.org> (accessed 21 June 2022).
- Jacobsen NHG (1989) A herpetological survey of the Transvaal. PhD Thesis, University of Natal, Durban.
- 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>
- Kumar S, Stecher G, Li M, Knyaz C, Tamura K (2018) MEGA X: Molecular evolutionary genetics analysis across computing platforms. *Molecular Biology and Evolution* 35: 1547–1549. <https://doi.org/10.1093/molbev/msy096>
- LANFEAR R, FRANDSEN PB, WRIGHT AM, SENFELD T, CALCOTT B (2017) PartitionFinder 2: New methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. *Molecular Biology and Evolution* 34: 772–773. <https://doi.org/10.1093/molbev/msw260>
- Lang M (1991) Generic relationships within Cordyliformes (Reptilia: Squamata). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique (Biologie)* 61: 121–188.
- Laurent RF (1964) Reptiles et amphibiens de l'Angola. *Publicações Culturais Companhia de Diamantes de Angola* 67: 1–165.
- Linnaeus C (1758) *Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis*. Tomus I. Regnum Animale. Editio Decima. Laurentius Salvius, Stockholm, 824 pp. <https://doi.org/10.5962/bhl.title.542>
- Lobón-Rovira J, Conradie W, Baptista NL, Vaz Pinto P (2022c) 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: 91–117. <https://doi.org/10.3897/zookeys.1127.84942>
- Lobón-Rovira J, Rocha S, Gower DJ, Perera A, Harris DJ (2022d) The unexpected gecko: A new cryptic species within *Urocotyledon inexpectata* (Stejneger, 1893) from the northern granitic Seychelles. *Zootaxa* 5150: 556–578. <https://doi.org/10.11646/zootaxa.5150.4.5>
- Lobón-Rovira J, Conradie W, Buckley Iglesias D, 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, Conradie W, Vaz Pinto P, Keates C, Edwards S, du Plessis A, Branch WR (2022a) Systematic revision of *Afrogecko ansorgii* (Boulenger, 1907) (Sauria: Gekkonidae) from western Angola. *Zootaxa* 5124: 401–430. <https://doi.org/10.11646/zootaxa.5124.4.1>
- Lobón-Rovira J, Vaz Pinto P, Becker FS, Tolley KA, Measey J, Bennett B, Boon B, Sá S, Conradie W (2022b) An updated herpetofaunal species inventory of Iona National Park in southwestern Angola. *Check List* 18: 289–321. <https://doi.org/10.15560/18.2.289>
- Loveridge A (1932) New reptiles and amphibians from Tanganyika Territory and Kenya Colony. *Bulletin of the Museum of Comparative Zoology at Harvard College* 72: 375–387.

- Loveridge A (1944a) A revision of the African lizards of the family Cordylidae. Bulletin of the Museum of Comparative Zoology at Harvard College 95: 1–118, plates 1–12.
- Loveridge A (1944b) New geckos of the genera *Afroedura*, new genus, and *Pachydactylus* from Angola. American Museum Novitates 1254: 1–4.
- Macey JR, Larson A, Ananjeva NB, Fang Z, Papenfuss TJ (1997) Two novel gene orders and the role of light-strand replication in rearrangement of the vertebrate mitochondrial genome. Molecular Biology and Evolution 14: 91–104. <https://doi.org/10.1093/oxfordjournals.molbev.a025706>
- Maddison WP, Maddison DR (2019) Mesquite: a modular system for evolutionary analysis. Version 3.6. <http://www.mesquiteproject.org>
- Madrugá C (2011) The zoological collection of the Museu de Lisboa and the networks of scientific correspondence and exchange (1858–1898). Conference Proceedings Paper: 4<sup>th</sup> International Conference of the European Society for the History of Science, November 2010. [http://lisboa.academia.edu/CMadruga/Papers/807559/Networks\\_of\\_scientific\\_correspondence\\_and\\_exchange\\_1858-1898](http://lisboa.academia.edu/CMadruga/Papers/807559/Networks_of_scientific_correspondence_and_exchange_1858-1898)
- Marques MP, Ceriaco 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, Ceriaco 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, Ceriaco LMP, Stanley EL, Bandeira SA, Agarwal I, Bauer AM (2019) A new species of girdled lizard (Squamata: Cordylidae) from the Serra da Neve Inselberg, Namibe Province, southwestern Angola. Zootaxa 4668: 503–524. <https://doi.org/10.11646/zootaxa.4668.4.4>
- Marques MP, Ceriaco 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, Parrinha D, Santos BS, Bandeira S, Butler BO, Sousa ACA, 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, Ceriaco LMP, Brennan IG, Heinicke MP, Bauer AM (2023) 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>
- Mertens R (1955) Die Amphibien und Reptilien Südwestafrikas: Aus den Ergebnissen einer im Jahre 1952 ausgeführten Reise. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 490: 1–172.
- Mertens R (1971) Die Herpetofauna Südwest-Afrikas. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 529: 1–110.
- 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>
- Monard A (1937) Contribution a l'herpétologie d'Angola. Arquivos Museu Bocage 8: 1–154.
- Mouton P le FN (1986) Description of a new species of *Cordylus* Laurenti (Reptilia: Cordylidae) from the south-western Cape, South Africa. South African Journal of Zoology 21: 319–324. <https://doi.org/10.1080/02541858.1986.11448006>
- Mouton P le FN (1987) Phenotypic variation among populations of *Cordylus cordylus* (Reptilia: Cordylidae) in the south-western Cape Province, South Africa. African Journal of Zoology 22: 119–129. <https://doi.org/10.1080/02541858.1987.11448032>
- Mouton P le FN, van Wyk JH (1990) Taxonomic status of the melanistic forms of the *Cordylus cordylus* complex (Reptilia: Cordylidae) in the south-western Cape, South Africa. South African Journal of Zoology 25: 31–38. <https://doi.org/10.1080/02541858.1990.11448185>
- Mouton P le FN, van Wyk JH (1994) Taxonomic status of geographical isolates in the *Cordylus minor* complex (Reptilia: Cordylidae): A description of three new species. Journal of the Herpetological Association of Africa 43: 6–18. <https://doi.org/10.1080/04416651.1994.9650376>
- Nielsen SV, Conradie W, Ceriaco LMP, Bauer AM, Heinicke MP, Stanley EL, Blackburn DC (2020) A new species of rain frog (Brevicipidae, *Breviceps*) endemic to Angola. ZooKeys 979: 133–160. <https://doi.org/10.3897/zookeys.979.56863>
- Padial JM, Miralles A, De la Riva I, Vences M (2010) The integrative future of taxonomy. Frontiers in Zoology 7: 1–14. <https://doi.org/10.1186/1742-9994-7-16>
- Parker HW (1936) Dr. Karl Jordan's expedition to south-west Africa and Angola: Herpetological collections. Novitates Zoologicae 40: 115–146.
- Parrinha D, Marques MP, Heinicke MP, Khalid F, Parker KL, Tolley KA, Childers JL, Conradie W, Bauer AM, Ceriaco LMP (2021) A revision of Angolan species in the genus *Pedioplanis* Fitzinger (Squamata: Lacertidae), with the description of a new species. Zootaxa 5032: 1–46. <https://doi.org/10.11646/zootaxa.5032.1.1>
- Peters W (1862) Übersicht einiger von dem, durch seine africanischen Sprachforschungen rühmlichst bekannten, Hrn. Missionär C. H. Hahn bei Neu-Barmen, im Hereroland, an der Westküste von Africa, im 21° südl. Br. gesammelten Amphibien, nebst Beschreibungen der neuen Arten. Monatsberichte der Königlichen Preussischen Akademie der Wissenschaften zu Berlin 1862: 15–26.
- Peters W (1870 [1869]) Förteckning på de af J. Wahlberg i Damaralandet insamlade Reptilierna. Öfversigt af Konglinge Vetenskaps-Akademiens Förhandlingar 26: 657–662.
- Portik D, Bauer AM, Jackman TR (2010) The phylogenetic affinities of *Trachylepis sulcata nigra* and the intraspecific evolution of coastal melanism in the Western rock skink. African Zoology 45: 147–159. <https://doi.org/10.3377/004.045.0217>
- Rambaut A, Suchard MA, Xie D, Drummond AJ (2014) Tracer Version 1.6. Available from: <http://beast.bio.ed.ac.uk/Tracer> (accessed 31 March 2023).
- Reichenow A (1887) Neue Wirbelthiere des Zoologischen Museums in Berlin. Zoologischer Anzeiger 10: 369–372.
- Reissig J (2014) Girdled Lizards and Their Relatives: Natural History, Captive Care and Breeding. Edition Chimaira, Frankfurt am Main, 249 pp.
- 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 choice across a large model space. Software for Systematics and Evolution 61: 539–542. <https://doi.org/10.1093/sysbio/sys029>

- Schmidt KP (1933) The reptiles of the Pulitzer Angola expedition. *Annals of the Carnegie Museum* 22: 1–15, 2 plates. <https://doi.org/10.5962/p.214561>
- Simon C, Frati F, Beckenbach A, Crespi B, Liu H, Flook P (1994) Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. *Annals of the Entomological Society of America* 87: 651–701. <https://doi.org/10.1093/aesa/87.6.651>
- Stanley EL (2013) Systematics and morphological diversification of the Cordylidae (Squamata). PhD Thesis, Richard Gilder Graduate School, American Museum of Natural History, New York, N.Y.
- Stanley EL, Bauer AM, Jackman TR, Branch WR, Mouton P le FN (2011) Between a rock and a hard polytomy: Rapid radiation in the rupicolous girdled lizards (Squamata: Cordylidae). *Molecular Phylogenetics and Evolution* 58: 53–70. <https://doi.org/10.1016/j.ympev.2010.08.024>
- Stanley EL, Ceriaco LMP, Bandeira S, Valerio H, Bates MF, Branch WR (2016) A review of *Cordylus machadoi* (Squamata: Cordylidae) in southwestern Angola, with the description of a new species from the Pro-Namib desert. *Zootaxa* 4061: 201–226. <https://doi.org/10.11646/zootaxa.4061.3.1>
- Tolley KA, Telford NS, Taft JM, Bates MF, Conradie W, Makhubo BG, Alexander GJ (2021) Taxonomic inflation due to inadequate sampling: Are girdled lizards (*Cordylus minor* species complex) from the Great Karoo one and the same? *Biological Journal of the Linnean Society* 135: 1–24. <https://doi.org/10.1093/biolinnean/blab119>
- Townsend TM, Alegre RE, Kelley ST, Wiens JJ, Reeder TW (2008) Rapid development of multiple nuclear loci for phylogenetic analysis using genomic resources: An example from squamate reptiles. *Molecular Phylogenetics and Evolution* 47: 129–142. <https://doi.org/10.1016/j.ympev.2008.01.008>
- Trifinopoulos J, Nguyen LT, von Haeseler A, Minh BQ (2016) W-IQ-TREE: A fast online phylogenetic tool for maximum likelihood analysis. *Nucleic Acids Research* 44: 232–235. <https://doi.org/10.1093/nar/gkw256>
- Vaz Pinto P, Verissimo L, Branch WR (2019) Hiding in the bushes for 110 years: Rediscovery of an iconic Angolan gecko (*Afrogecko ansorgii* Boulenger, 1907, Sauria: Gekkonidae). *Amphibian & Reptile Conservation* 13: 29–41 (e182).
- Vaz Pinto V, Conradie W, Becker F, Lobón-Rovira J (2021) Updated distribution of *Kolekanus plumicaudus* (Sauria: Gekkonidae), with some comments on its natural history. *Herpetology Notes* 14: 1207–1212.
- Vieites DR, Wollenberg KC, Andreone F, Köhler J, Glaw F, Vences M (2009) Vast underestimation of Madagascar's biodiversity evidenced by an integrative amphibian inventory. *Proceedings of the National Academy of Sciences* 106: 8267–8272. <https://doi.org/10.1073/pnas.0810821106>
- Visser J (1971) *Cordylus cordylus* and its races in the Cape Province – A general discussion. *Journal of the Herpetological Association of Africa* 7: 18–20. <https://doi.org/10.1080/04416651.1971.9650786>
- Wagner P, Butler BO, Ceriaco LMP, Bauer AM (2021) A new species of the *Acanthocercus atricollis* complex (Squamata: Agamidae). *Salamandra* 57: 449–463. <https://doi.org/10.5281/zenodo.5614612>
- Wiens JJ, Kuczynski CA, Townsend T, Reeder TW, Mulcahy DG, Sites JW (2010) Combining phylogenomics and fossils in higher-level squamate reptile phylogeny: Molecular data change the placement of fossil taxa. *Systematic Biology* 59: 674–688. <http://doi.org/10.1093/sysbio/syq048>

## Appendix 1

Specimens of *Cordylus* examined for this study: extralimital species and species in the *C. machadoi* group. Localities are listed alphabetically by country or province; for South Africa the farm name is followed by number and magisterial district; museum catalogue numbers are followed in parentheses by mapping co-ordinates or quarter-degree grid cell codes (usage explained in Bates et al. 2014). Elevations are in meters above sea level. Asterisks denote material used only for CT-scanning (see Fig. S5, and <https://www.morphosource.org>).

### *Cordylus beraduccii*

KENYA. 20.4 km North of Kajiado, Rift Valley Province – CAS 198943\* (01°55'45.9"S, 36°37'41.1"E; 0136DC; 1488 m)

### *Cordylus jonesii*

SOUTH AFRICA. Limpopo Province: Doorenwaard 313 Vhembe district – NMB R8652–6 (2229CB); Leysdorp environs – MCZ R14212\* (23°58'58.8"S, 30°31'58.8"E; 2330DC; 733 m).

### *Cordylus machadoi*

ANGOLA. 5 km SSE of Chibemba, Huíla Province – TM 40095–6 (15°47'08"S, 14°06'19"E; 1514CC); 1.4 km NE of Humbia, Namibe Province – TM 40131–3 (14°43'31.6"S, 13°27'38.4"E; 1413CB); 6.3 km N of Humpata, Huíla Province – PEM R18006–8, 19782, 19784 (14°57'42.7"S, 13°20'05.9"E; 1413CD; 2136 m); Nascente do Tchivinguiro, Huíla Province – PEM R18009 (15°01'02.9"S, 13°19'15.2"E; 1513AB; 1688 m); Tchivinguiro (Agronomics School), about 25 km due SSW of Lubango, Huíla Province – MNM 7002 (15°10'S, 13°18'E;

1513AB); Tundavala, Huíla Province – CHL 700–1 (14°50'26.4"S, 13°22'28.8"E; 1413CD; 2239 m); CAS 263578–9\* (14°49'25.9"S, 13°22'52.1"E; 1413CD).

### *Cordylus cf. machadoi*

NAMIBIA. Baynes Mountains, Kunene Region – TM 57561 (1712BA).

### *Cordylus marunguensis*

DEMOCRATIC REPUBLIC OF CONGO. Marungu Mountains, Katanga Province – UTEP 20374\* (07°43'08.1"S, 29°45'52.4"E; 0729DB; 1993 m).

### *Cordylus namakuiyus*

ANGOLA. "Angola" – AMNH R47297–302, 47304–16 [47301\*, 47310\* also used for CT scanning], 47317–21; 1.8 km W of Caraculo, Namibe province – CAS 254912–4\* (15°0'59.4"S, 12°38'31.3"E; 1512BA; 503 m), CAS 256529\* (15°0'57.3"S, 12°38'32.6"E; 1512BA; 509 m); 88 km N of Espinheira, near Iona National Park, Namibe

Province – PEM R18005 (also used for CT-scanning; 15°59'48.5"S, 12°24'24.6"E; 1512CD; 308 m); vicinity of Mariquita Meva, Benguela Province – CHL 609, 616 (13°29'52.0"S, 12°36'17.0"E; 1312BC; 331 m); 35 km NW (by road) of Pico Azevedo, Namibe Province – CAS 254754–5\*, 256530–1\* (15°28'33.2"S, 12°27'45.7"E; 1512AD; 421 m); 10.4 km S of Rio Mucungo on tar road to Bentiaba, Namibe Province – PEM R25218–9 (14°50'31.0"S, 12°25'40.0"E; 1412CD; 369 m); data for first transverse row of dorsals, occipitals, post-occipitals, interparietal/anterior parietals, and ventral rows longitudinally only, not included in Table 4); 49 km ESE of Tombua, Namibe Province – TM 40430 (15°53'S, 12°16'E; 1512CD; 215 m).

### *Cordylus nyikae*

MALAWI. Nyika Plateau, Northern Region – PEM R20120\*, PEM R20121\*.

### *Cordylus phonolithos*

ANGOLA. Namibe Province: Serra da Neve, N'Dolondolo – CAS 263581\* (13°48'24.4"S, 13°08'06.3"E; 1313CC; 754 m); Serra da Neve – CHL 848 (13°46'10.4"S, 13°15'07.2"E; 1313CD; 1715 m); CHL 851 (13°46'23.6"S, 13°14'56.0"E; 1313CC; 1934 m); CHL 852, 1056–7 (13°46'26.6"S, 13°14'51.3"E; 1313CC; 1983 m); MNCN 50651 (13°46'19.7"S, 13°15'03.9"E; 1313CD; 1838 m; female: SVL = 94.5 mm, scales around 15<sup>th</sup> row of caudals = 12); MNCN 50652 (13°46'21.4"S, 13°15'00.4"E; 1313CD; 1883 m; male: SVL = 95.7 mm, scales around 15<sup>th</sup> row of caudals = 8).

### *Cordylus rhodesianus*

ZIMBABWE. Manicaland Province: Nyanga district: Chinaka farm – NMB R10035 (1832BC); Gugurumba – NMB R10031 (1832BC); Inyangani Mountain – NMB R10032–3 (1832BD); Nyanga National Park – CAS 209623\* (18°18'57" S, 32°41'52"E; 1832BC; 1846 m); York Forest Land – NMB R10034 (1832BC).

### *Cordylus rivae*

ETHIOPIA. East of Negelle, Oromia Region – TJC 0564\*.

### *Cordylus tropidosternum*

MALAWI. Chitipa district, near Jembya Forest Reserve, Northern Region – PEM R20121 (1033BA); MOZAMBIQUE, Zambesiaca Province: Moebase village – PEM R13288 (1638DC); east of Moebase village – PEM R13297 (1638DC); 1 km west of Namagure village – PEM R13264–5 (1638DC); Top of Tenge Hill, Capital Iron Ore mine site, Tete, Tete Province – PEM R20599 (1533DB); TANZANIA. Magoroto, East Usambara Mountains, Tanga Region – UF:herp:63302\* (05°06'30.2"S, 38°44'37.3"E; 0538BA; 785 m).

### *Cordylus ukingensis*

TANZANIA. Tandala, Ukinga Mountains, Njombe Region – MCZ R-30761\* (09°23'00"S, 34°14'00"E; 0934AC; 2008 m).

### *Cordylus vittifer* variety A (Free State and Gauteng provinces) (1 in Fig. S3)

SOUTH AFRICA. Free State: Annie's Rust 763, Heilbron district – NMB R3412–3 (2628CC); Baltespoort 998, Vredefort district – NMB R912 (2727AA); Mara 395, Parys district – NMB R3771–2 (2627DC); Mara 855, Vredefort district – NMB R4049, 4054 (2727AD); Van der Walts Rust 1021, Vredefort district – NMB R3825 (2627CC); Gauteng: Bronkhorstspuit, Bronkhorstspuit district – NMB R1603–5 (2528DC); Orange Grove, Johannesburg – MCZ R-14215\* (26°10'01.2"S,

28°04'58.8"E; 2628AA; 1706 m); 2.3 km WSW of Visitors Centre, Suikerbosrand Nature Reserve, Heidelberg district – NMB R8869 (2628AC).

### *Cordylus vittifer* variety B (Free State Province) (2 in Fig. S3)

SOUTH AFRICA. Free State, Vrede district: Berlin 497 – NMB R2420, 2422 (2729AC); Dipka 200 – NMB R3002, 8523 (2729CA); Klipplaat 380 – NMB R2393, 2395 (2728BD); Rouxmenel 896 – NMB R8800 (2729CB); Tygerfontein 240 – NMB R2922, 2925 (2729CB); Uitvlugt 227 – NMB R827, 832 (2729AD); Woudzicht 492 – NMB R2449–50 (2728DB).

### *Cordylus vittifer* variety B (Limpopo Province) (3 in Fig. S3)

SOUTH AFRICA. Limpopo Province: Bloemhof 4, Potgietersrus district – NMB R8865 (2429AA); Entabeni Nature Reserve, Soutpansberg district – NMB R8858–9, 8863–4 (2230CD); Helderfontein 6KS, Potgietersrus district – NMB R8194 (2429AA); Monte Christo 1011, Thabamooop district – NMB R8148–9 (2329DD); Zwartkloof 707, Warmbad district – NMB R8857 (2428CC).

### *Cordylus vittifer* variety B (Mpumalanga Province and Eswatini) (4 in Fig. S3)

SOUTH AFRICA. Mpumalanga: De Goedeverwachting 57, Carolina district – NMB R8290 (2630AA); Desire 563, Pilgrim's Rest 2 district – NMB R8770, 8773 (2430DD); Goede Hoop 182, Ermelo district – NMB R8721–2 (2630BA); Joubertsdal 448, Nelspruit district – NMB R8866 (2530DB); Lochiel 192, Eerstehoek district – NMB R8291 (2630BB); Mount Sheba, Pilgrims Rest 2 district – NMB R8768 (2430DC); Rietfontein 19, Carolina district – NMB R8723 (2630AB); Sabieshoek 200, Pilgrims Rest 2 district – NMB R8727–8 (2530BA); Saddleback Hill, Barberton, Barberton district – NMB R8867 (2531CC); ESOWATINI. Malolotja Nature Reserve – NMB R8868 (2631AA).

### *Cordylus vittifer* variety C (Free State Province) (5 in Fig. S3)

SOUTH AFRICA. Free State, Harrismith district: Tafelberg 'A' 1312 – NMB R8193 (2829AA); Waterfall 1157 – NMB R3077, 3086, 4591–3, 4597 (2829AD).

### *Cordylus vittifer* (KwaZulu-Natal Province) (6 in Fig. S3)

SOUTH AFRICA. KwaZulu-Natal: Dewar 2400, Dundee district – NMB R10324–5 (2830AD); Gcotoli, N of Kranskop, Kranskop district – NMB R8739–40 (2830DD); Honig Krantz 945, Camperdown district – NMB R10306, 10309 (2930DC); Howard 4353, Lions River district – NMB R10315, 10321 (2929BD); Isandlwana, Nqutu district – NMB R8402 (2830BC); Maritz Daal 940, Lions River district – NMB R10311, 10314 (2930AC); Tarzan 13727, Ubombo district – NMB R10323 (2732CA); Upper end of Langefontein 980, Pinetown district – NMB R10304 (2930DB); Farm no. 822, Vryheid district – NMB R10326, 10328 (2831AA); Farm no. 906, Camperdown district – NMB R10301–2 (2930DA); Farm no. 15356, Nhlusane Mountain, Lions River district – NMB R10329 (2929DB).

## Supplementary Material 1

### Figure S1

**Authors:** Bates MF, Lobón-Rovira J, Stanley EL, Branch WR, Vaz Pinto P (2023)

**Data type:** .tif

**Explanation note:** Paratype of *Cordylus machadoi* (MCZ 74120). Dorsal **A**, lateral **B** and ventral **C** aspects of the head; dorsal **D** and ventral **E** aspects of the body. Photos: William R. Branch.

**Copyright notice:** This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

**Link:** <https://doi.org/10.3897/vz.73.e95639.suppl1>

## Supplementary Material 2

### Figure S2

**Authors:** Bates MF, Lobón-Rovira J, Stanley EL, Branch WR, Vaz Pinto P (2023)

**Data type:** .tif

**Explanation note:** Holotype (ZMB 10762) of *Zonurus vittifer*. **A–D** Lateral, ventral and dorsal aspects of the head; **E, F**: dorsal and ventral aspects of the body; **G, H** femoral region of the right and left legs, respectively. Photos: Frank Tillack.

**Copyright notice:** This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

**Link:** <https://doi.org/10.3897/vz.73.e95639.suppl2>

## Supplementary Material 3

### Figure S3

**Authors:** Bates MF, Lobón-Rovira J, Stanley EL, Branch WR, Vaz Pinto P (2023)

**Data type:** .png

**Explanation note:** Geographical distribution of *Cordylus vittifer* in South Africa and Eswatini. Shaded areas depicting the species overall distribution are based on Bates et al. (2014). The different populations for which morphological data is provided are numbered and colour coded: 1 (pink): variety A, Free State and Gauteng provinces, South Africa; 2 (pale green): variety B, Free State Province, South Africa; 3 (yellow): variety B, Limpopo Province, South Africa; 4 (dark green): variety B, Mpumalanga Province, South Africa and Eswatini; 5 (blue): variety C, Free State; 6 (purple): KwaZulu-Natal Province, South Africa.

**Copyright notice:** This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

**Link:** <https://doi.org/10.3897/vz.73.e95639.suppl3>

## Supplementary Material 4

### Figure S4

**Authors:** Bates MF, Lobón-Rovira J, Stanley EL, Branch WR, Vaz Pinto P (2023)

**Data type:** .jpg

**Explanation note:** Ventral aspect of *Cordylus machadoi* (PEM R19784 – 6.3 km north of Humpata, Angola). Photo: William R. Branch.

**Copyright notice:** This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

**Link:** <https://doi.org/10.3897/vz.73.e95639.suppl4>

## Supplementary Material 5

### Figure S5

**Authors:** Bates MF, Lobón-Rovira J, Stanley EL, Branch WR, Vaz Pinto P (2023)

**Data type:** .pdf

**Explanation note:** Allometry plot of relative osteoderm volume (osteoderm-postcranial skeleton volume ratio) against snout-vent length (mm) in Angolan *Cordylus*. **1)** *Cordylus machadoi* PEM R18006, **2)** *C. machadoi* PEM R18009, **3)** *C. machadoi* PEM R19782, **4)** *C. machadoi* PEM R19784, **5)** *C. machadoi* CAS 263579, **6)** *C. machadoi* CAS 263578, **7)** *C. namakuiyus* CAS 254912, **8)** *C. namakuiyus* CAS 254913, **9)** *C. namakuiyus* CAS 254914, **10)** *C. namakuiyus* CAS 254754, **11)** *C. namakuiyus* CAS 254755, **12)** *C. namakuiyus* CAS 56529, **13)** *C. namakuiyus* CAS 56530, **14)** *C. namakuiyus* CAS 256531, **15)** *C. namakuiyus* PEM R18005, **16)** *C. namakuiyus* AMNH R47301, **17)** *C. angolensis* MNCN 50648, **18)** *C. momboloensis* **sp. nov.** AMNH R47333, **19)** *C. momboloensis* **sp. nov.** TM 46476, **20)** *C. phonolithos* CAS 263581. Dotted lines represent hypothetical osteoderm growth pattern of *C. namakuiyus* (blue) and *C. machadoi* (red).

**Copyright notice:** This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

**Link:** <https://doi.org/10.3897/vz.73.e95639.suppl5>

## Supplementary Material 6

### Table S1

**Authors:** Bates MF, Lobón-Rovira J, Stanley EL, Branch WR, Vaz Pinto P (2023)

**Data type:** .xlsx

**Explanation note:** Scan settings and Morphosource DOIs for CT datasets of Angolan *Cordylus* studied in this description. Scan location codes: *NRF-UF* = Nanoscale Research Facility, University of Florida, USA. *MIF-AMNH* = Microscopy Imaging Facility, American Museum of Natural History, New York, USA. *GE-SC* = General Electric Inspection Technologies, LP Technical Solutions Center, San Carlos, California, USA. *CIC* = Centro de Instrumentación Científica of Granada, Spain.

**Copyright notice:** This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

**Link:** <https://doi.org/10.3897/vz.73.e95639.suppl6>

## Supplementary Material 7

### Table S2

**Authors:** Bates MF, Lobón-Rovira J, Stanley EL, Branch WR, Vaz Pinto P (2023)

**Data type:** .xlsx

**Explanation note:** Comparative meristic data for *Cordylus* from the Angolan clade and various species and populations in the East African clade (including *C. jonesii*–*C. rhodesianus*). The first row of data refers to the range of values, the second row is the mean, and the third row is the standard deviation. For *C. phonolithos*, data is for the holotype and paratype (Marques et al. 2019) and two new specimens (MNCN 50651–2). (M = male, F = female, J = juvenile. <sup>-1</sup> means that sample size for a particular character was one less than that indicated in the second column, <sup>-2</sup> means two less, <sup>-3</sup> means three less. \*Includes FKH 0129 in Fig. 4; \*\*Holotype, paratype, and CHL 848, 851, 852, 1056 and MNCN 50652 in Fig. 4).

**Copyright notice:** This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

**Link:** <https://doi.org/10.3897/vz.73.e95639.suppl7>

## Supplementary Material 8

### Table S3

**Authors:** Bates MF, Lobón-Rovira J, Stanley EL, Branch WR, Vaz Pinto P (2023)

**Data type:** .xlsx

**Explanation note:** Premaxillary, maxillary and dentary teeth counts for Angolan and east African *Cordylus*.

**Copyright notice:** This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

**Link:** <https://doi.org/10.3897/vz.73.e95639.suppl8>