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A LONG-KNOWN NEW SPECIES OF THE *TRACHYLEPIS MACULILABRIS* SPECIES COMPLEX (SQUAMATA: SCINCIDAE) FROM SOUTH-EASTERN AFRICA

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ABSTRACT

The Eastern African populations of the *Trachylepis maculilabris* species complex, long recognized as a molecularly distinct but taxonomically unresolved lineage, are formally described as a **new species**, *Trachylepis farooqii*. A total of 386 specimens of the *T. maculilabris* complex from across its known range were morphologically examined, and 214 *Trachylepis* specimens were included in the molecular phylogeny. Phylogenetic analysis using mitochondrial (168 and ND2) and nuclear (RAG1) genes recovered the East African populations as a separate lineage. The East African populations also showed a high degree of genetic distance for the 16S, ND2, and RAG1 genes when compared to the most genetically similar species. Haplotype network analysis revealed a clear geographic structuring of haplotypes across regions, with the new species described here restricted to Eastern Africa. *Trachylepis farooqii*, **sp. nov**, can be distinguished phenotypically from *Trachylepis maculilabris* (Gray, 1845) by usually having orange dorsolateral bands. The morphological assessments align with the molecular phylogeny and provide robust evidence for the designation of those Eastern African populations as a new species, increasing the number of *Trachylepis* species in Mozambique to 15.

KEY WORDS: cryptic diversity, East Africa, phylogenetics, systematics, taxonomy, Trachylepis farooqii, sp. nov.

INTRODUCTION

The speckled-lipped skink, Trachylepis maculilabris (Gray, 1845), is one of the most widespread members of its genus in continental Africa, with populations occurring from west and central to coastal South-Eastern Africa (Mausfeld-Lafdhiya et al. 2004; Ceríaco et al. 2016, 2024; Allen et al. 2019). The species was originally described by Gray (1845) based on a specimen from "West Africa" (Fig. 1), and its taxonomic and nomenclatural history is considerably complex (see Broadley 1974a, 2000; Hoogmoed 1974; Ceríaco et al. 2016). Populations of morphologically similar skinks in the Indian Ocean islands, as well as those in the Atlantic Ocean islands of São Tomé and Príncipe, have been associated with T. maculilabris in the past, either being described as subspecies, or considered conspecific or closely related. In the Indian Ocean islands group, Trachylepis comorensis (Peters, 1854) from the Comoro Islands and Madagascar was considered as a subspecies of T. maculilabris by Broadley (1974a). Similarly, the Pemba and Mesale Islands endemic Trachylepis albotaeniata (Boettger, 1913) and the Europa Island endemic Trachylepis infralineata (Boettger, 1913), were also considered as subspecies of T. maculilabris by Broadley (1974a). In the same publication, Broadley (1974a) described Mabuya [=Trachylepis] maculilabris casuarinae, endemic to Casuarina Island, off the north Mozambique coast. Recent works have shown that all of these taxa, even if being part of a clade containing the continental populations of T. maculilabris, are taxonomically distinct from the continental ones (Broadley 2000; Mausfeld-Lafdhiya et al. 2004; Rocha et al. 2010; Lima et al. 2013; Ceríaco et al. 2016, 2024; Weinell et al. 2019; however, see Sanchez et al. 2019, who continue to consider T. infralineata as a subspecies of T. maculilabris). In the Atlantic Ocean, the São Tomé and Príncipe Islands populations were also considered part of T. maculilabris (see Jesus et al. 2005; Rocha et al. 2010), until Ceríaco (2015) and Ceríaco et al. (2016, 2020) elevated them to specific status as Trachylepis adamastor Ceríaco, 2015, on Príncipe Island and Tinhosa Grande Islet, and Trachylepis thomensis Ceríaco, Marques, and Bauer, 2016, on São Tomé Island and its surrounding islets.

The taxonomic and nomenclatural history of continental *T. maculilabris* is also complex. In the second half of the nineteenth century, Bocage (1866) described *Euprepes* anchietae Bocage, 1866, from the Cabinda enclave in Angola, while Peters (1879) described *Euprepes notabilis* Peters, 1879, based on specimens from Cabinda Province and Central Angola. These names quickly fell into the synonymy of *T. maculilabris* (see Bocage 1895; Marques et al. 2018) and were mostly forgotten. In a recent taxonomic revision of the *Trachylepis* of Angola, Ceríaco et al. (2024) designated a neotype for *Euprepes anchietae* (synonymizing it with *T. maculilabris*), but revalidated *Trachylepis notabilis* (Peters, 1879) as a valid species.

In the early twentieth century, Sternfeld (1911) described a species from East Africa that he named Mabuya diesneri boulengeri Sternfeld, 1911. The species would be considered as a subspecies of T. maculilabris by Loveridge (1942, 1953, 1957) until Broadley (1974a) elevated it to a full species, a decision that has been accepted and confirmed by all the subsequent authors who have dealt with the species (Broadley 2000; Weinell et al. 2019; Ceríaco et al. 2024). Later, based on several specimens from northeastern Democratic Republic of the Congo, Sternfeld (1913) described Mabuia maculilabris major. Sternfeld's (1913) work has been signaled as problematic by authors such as Bauer et al. (2003) and Ceríaco et al. (2016), as the author proceeded to describe several varieties of his newly coined subspecies, none of which are nomenclaturally available. The issues regarding Sternfeld's (1913) description will be discussed elsewhere (Ceríaco et al. in prep.). Adding to these nomenclatural conundrums, Mausfeld-Lafdhiya et al. (2004) provided the first molecular evidence supporting the separation of continental T. maculilabris in two main groups, the Eastern African populations and the west African nominotypical form. The authors opted not to take any taxonomic decision and left the putative new species from East Africa unnamed. Several studies confirmed the initial evidence put forward by Mausfeld-Lafdhiya et al. (2004). Rocha et al. (2010) highlighted the cryptic diversity within the T. maculilabris complex, identifying at least three distinct lineages: one occurring on the islands of São Tomé and Príncipe, a second in West Africa, and a third in East Africa. Ceríaco et al. (2016) also noted this differentiation, referring to these populations as the "western-African lineage" or "typical maculilabris" and the "eastern-African lineage." Weinell et al. (2019) found T. maculilabris to be paraphyletic in their maximum likelihood phylogeny, with



Fig. 1.—Holotype of Trachylepis maculilabris (BMNH 1946.8.18.17) from "West Africa." Photos by Patrick Campbell.

one clade comprising populations from Gabon and Angola, and another clade represented by populations from Malawi. Ceríaco et al. (2024) reaffirmed the cryptic diversity of the T. maculilabris complex, identifying "Trachylepis maculilabris 1" as a clade containing the Malawian population and "Trachylepis maculilabris 2" as a clade containing the West African populations. Subsequent authors who have referred to this population also refrained from naming it and continued to call it T. maculilabris (see Spawls et al. 2002, 2018, 2023; Branch et al. 2005; Carretero et al. 2005; Malonza et al. 2006, 2011, 2018; Goldberg 2009; Largen and Spawls 2010; Jungnickel 2012; Conradie et al. 2016; Weinell et al. 2019; Buruwate and Lloyd-Jones 2024; Ceríaco et al. 2024). Regarding the Central and West African T. maculilabris (i.e., the nominotypical form), Allen et al. (2019) found considerable levels of cryptic molecular diversity which may warrant a specific taxonomic status.

With all taxonomic and nomenclatural issues affecting Atlantic and Indian Ocean islands taxa mostly solved and recent advances in our taxonomic understanding and the nomenclatural standing of the continental populations, three main cases remain to be addressed in the *T. maculi*-

labris species complex. These are: (1) the taxonomic status of the cryptic diversity found by Allen et al. (2019) in the West and Central African populations; (2) the relationship between Sternfeld's (1913) M. maculilabris major and these populations; and (3) the taxonomic status of Mausfeld-Lafdhiya et al.'s (2004) Eastern African lineage. It can already be proposed that Sternfeld's *M. maculilabris* major is related to what is currently construed as the nominotypical form of T. maculilabris (i.e., West and Central African populations), and thus may be applicable to one of the lineages found by Allen et al. (2019), but it is not applicable to the Eastern African populations (Ceríaco et al. in prep.). Thus, there are no other available names that can be applied to the Mausfeld-Lafdhiya et al. (2004) Eastern African lineage were it to be elevated to specific status. As part of an ongoing revision of the T. maculilabris species complex, we here review the taxonomy of the East African populations. The recent collection of new specimens in northern Mozambique allowed us to combine the gathered morphological data with newly generated molecular data to better explore the taxonomic identity of this Eastern African form.

MATERIAL AND METHODS

Specimen collection and sampling.-Specimens collected for this study were fixed in the field with 10% buffered formalin and transferred to 70% ethanol for long term preservation. Liver tissue was removed before formalin fixation and preserved in 96-100% ethanol and subsequently transferred to 95% ethanol for storage. For mensural and meristic comparisons, we examined 386 specimens of Trachylepis species (including type specimens of the T. maculilabris species complex, namely T. maculilabris - BMNH 1946.8.18.17 [fig. 1]; T. adamastor - IICT/R 2/1970; T. casuarinae - NMZB-UM 24077; T. comorensis - ZMB 4982; T. notabilis - ZMB 9204, T. principensis - MUHNAC/MB03-000957; and T. thomensis - MUHNAC/MB03-000712) deposited in the collections of the Natural History Museum (BMNH), London, UK; the Instituto de Investigação Científica Tropical (IICT), Lisboa, Portugal; the Museum of Comparative Zoology (MCZ), Harvard University, Cambridge, USA; the Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo, Brazil; the Carnegie Museum of Natural History (CM), Pittsburgh, USA; the Muséum national d'Histoire naturelle (MNHN-RA), Paris, France; the Museu Nacional de História Natural e da Ciência da Universidade de Lisboa (MUHNAC), Lisboa, Portugal; the Natural History Museum of Zimbabwe (NMZB and NMZB-UM), Bulawayo, Zimbabwe; the Museum für Naturkunde (ZMB), Berlin, Germany; and Ditsong National Museum of Natural History (TM), Pretoria, South Africa (for a detailed list see respective taxonomic accounts and Appendices 1 and 2). Specimens listed with the acronym KMH (Kim Howell field series) and AJL are deposited in NMZB. Additional specimens were also examined but only to confirm specific identity (Appendix 2). Information on morphological characters of species and/or type material that could not be examined, as well as supplementary data for all East African Trachylepis species, was obtained from the relevant literature (e.g., Boulenger 1887; Boettger 1913; Schmidt 1919; Laurent 1947, 1954, 1964; Broadley 1974a, 1974b, 2000; Hoogmoed 1974; Branch 1998; Spawls et al. 2002, 2018, 2023; Ceríaco 2015; Ceríaco et al. 2016, 2024; Allen et al. 2017; Weinell and Bauer 2018; Pietersen et al. 2021). Locality data for examined specimens are reported in decimal degrees using the WGS-84 map datum.

Molecular methods.— DNA from new samples obtained in Mozambique was extracted following the protocol described in Fetzner (1999). Polymerase chain reactions (PCR) were performed to amplify portions of two mitochondrial loci and one nuclear locus commonly used in systematic studies. Mitochondrial loci included 16S ribosomal RNA (16S) and a locus containing the proteincoding gene NADH dehydrogenase subunit 2 (ND2); the nuclear locus was the recombination activation protein 1 (RAG1). Thermocycler profiles (PCR) and primers (PCR and sequencing) were the same as described in Weinell et al. (2019). Purification of PCR products was performed with Exonuclease I and Shrimp Alkaline Phosphatase (Thermo Fisher Scientific Inc.). Both strands of each fragment were sequenced using the BigDye Terminator 3.0 cycle Sequencing kit (Applied Biosystems) according to manufacturer's protocol. PCR products were sequenced at Instituto de Ciências Biomédicas da Universidade de São Paulo (São Paulo, Brazil). Novel sequences obtained in this study were deposited in GenBank.

We used Geneious v11.0.2 to de novo assemble and edit novel sequences. We downloaded the sequences of RAG1, ND2, and 16S available on GenBank for the following ingroup taxa: T. maculilabris, T. thomensis, T. sechellensis (Duméril and Bibron, 1839), T. wrightii (Boulenger, 1887), T. affinis (Gray, 1838), T. comorensis, T. adamastor, T. notabilis, T. quinquetaeniata (Lichtenstein, 1823), T. paucisquamis (Hoogmoed, 1978), T. polytropis (Boulenger, 1903), T. margaritifer (Peters, 1854), and T. atlantica (Schmidt, 1945) (Supplementary Table S1). We included Chioninia delalandii (Duméril and Bibron, 1839) as outgroup, as previous analysis recovered this lineage outside Trachylepis (Karin et al. 2016). We aligned each gene individually using MAFFT v7.310 (Katoh and Standley 2013), which was associated with TranslatorX (Abascal et al. 2010) in the case of protein-coding genes (ND2 and RAG1) to prevent shift in the reading frame. As sequence lengths were not standardized, the iterative refinement algorithm L-INS-i was chosen as it is recommended for sets of sequences with conserved domains and large gaps (Katoh et al. 2005). We checked the alignments using SeaView v4 (Gouy et al. 2010), translating protein-coding sequences to check for early stop codons. Sequences that disturbed the alignment were excluded and the remaining sequences realigned. For each locus, we calculated both the pairwise distances between each pair of individuals and the mean distance between groups of species using MEGA11 (Tamura et al. 2021). We used the p-distance method modeled with a gamma distribution, and all positions with less than 95% site coverage were eliminated.

To estimate phylogenetic relationships of the putative new species under maximum likelihood (ML), we concatenated single-locus alignments using SeqKit2 (Shen et al. 2024) and inferred a phylogeny with the final matrix (214 terminals and 2751 bp) using IQTREE v1.6.12 (Nguyen et al. 2014). We partitioned sites by locus and, for proteincoding genes, also by codon positions. The best-fit substitution models, including FreeRate model, were estimated for each partition using ModelFinder (Kalyaanamoorthy et al. 2017; Table 1). We combined both ultrafast bootstrap and SH-aLRT to assess branch support, each with 1,000 replicates, and we considered a clade to be reliable if UF-Boot \ge 95% and SH-aLRT \ge 80% (Guindon et al. 2010; Minh et al. 2013). To better understand the relationship between populations within the T. maculilabris species complex, we inferred haplotype networks from the three genes (16S, ND2, and RAG1) using the TCS method (Clement et al. 2002), as implemented in POPART v.1.7 (Leigh et al.

 TABLE 1. Best-fit substitution models estimated with ModelFinder for each gene and codon position. Rate heterogeneity coded as follows: proportion of invariable sites allowed (+I), discrete Gamma model with 4 rate categories (+G4), FreeRate model with 2 rate categories (+R2).

 ND2
 ND2
 ND2
 RAG1
 RAG1
 RAG1

Model/Gene	168	ND2 1st	ND2 2nd	ND2 3rd	RAG1 1st	RAG1 2nd	RAG1 3rd
Substitution model	TIM2	TPM3	TN	TIM2	НКҮ	НКҮ	TNe
Rate heterogeneity	+I+G4	+G4	+G4	+R2	+I	+I	+R2

2015). The 16S network included 101 sequences, followed by RAG1 with 66 and the ND2 included 59.

Morphological methods.—Specimens were measured with a digital caliper to the nearest 0.1 mm, while lepidosis was observed with the help of a stereomicroscope. Scale nomenclature, scales counts, and measurements used in the descriptions follow Broadley (2000), Ceríaco (2015), Ceríaco et al. (2016, 2024), and Margues et al. (2019). We measured the following 21 characters: snout-vent length (SVL), from tip of snout to the vent; tail length (TL), from cloaca to tip of tail, measured only in specimens with complete, original tails; head height (HH), from the underside of jaw to the top of head; head length (HL), from tip of snout to anterior tympanum border; head width (HW), from the lateral edge of the left parietal to the lateral edge of the right parietal, above the eyes; eye-nostril distance (EN), from the anterior edge of the eve to the posterior nostril border; eye-snout distance (ES), from the anterior edge of the eye to the tip of snout; inter-nostril distance (IN), corresponding to minimum distance between the nostrils; number of scale rows at midbody (MSR); number of scales dorsally (SAD), from the nuchal (excluded from count) to base of the tail (above cloacal slit); number of scales ventrally (SAV), from the mental (excluded from count) to cloacal slit; number of subdigital lamellae under Finger-IV (LUFF); number of subdigital lamellae under Toe-IV (LUFT); number of supraciliaries (SC); number of supralabials (SL), with those widened in subocular position indicated between brackets; type of contact between parietals (CP); contact between frontoparietals (CFP); contact between supranasals (CSN); contact between prefrontals (CPF); number of keels on dorsal scales (KDS); and type of plantar scales (PS), keeled, smooth or spinose. Coloration patterns were reported, and high-resolution photographs of preserved specimens were taken. Measured and scale counted specimens are noted under "Material examined" section in the respective taxonomic accounts. Specimens physically examined (but not measured or scale counted), either directly by the authors, through photos, or by colleagues and whose taxonomic identification was unambiguous, are listed under "Additional material" section in the respective taxonomic accounts.

RESULTS

Phylogenetic relationships.—In our concatenated ML phylogeny (Fig. 2), most species were recovered as monophyletic, with only T. polytropis and T. comorensis as paraphyletic. *Trachylepis atlantica* was recovered as a strongly supported monophyletic group (99.7 SH-aLRT/100 UF-Boot) sister to another well supported clade comprising T. quinquetaeniata and T. margaritifer (90.6/99). In a recent phylogeny for the genus *Trachylepis*, Weinell et al. (2019) recovered T. atlantica as sister to a clade containing several species of the maculilabris group. This difference may be due to the use of nine markers to infer the phylogeny. whereas in the present study we chose to include only the genes available for the East African T. maculilabris. This is corroborated by the tree of Ceríaco et al. (2024), which recovered the same relationships of T. atlantica as in the present work, using the same three genes. Trachylepis quinquetaeniata and T. margaritifer were both recovered as monophyletic with high support (99.3/100 and 86/100, respectively). The monophyletic T. paucisquamis (91.3/100) and T. affinis (100/100) were recovered as sister groups. The clade comprising T. polytropis and T. notabilis was highly supported (96.8/96). However, T. polytropis was recovered as paraphyletic with respect to T. notabilis. Trachylepis wrightii and T. sechellensis formed a strongly supported clade (99/100) sister to the T. maculilabris group.

Within the *T. maculilabris* species complex, we recovered a strongly supported clade (92.9/98) comprising seven individuals from East Africa (Tanzania, Malawi, and Mozambique). Two Malawian individuals were recovered as sister groups with high support (91.6/100) and the three individuals from Mozambique formed a clade. The Tanzanian specimen was recovered as sister to a clade comprising the sequences from Mozambique and Malawi. This East Africa lineage was found as the sister group of the rest of the *T. maculilabris* group with high support (98.9/100).



Fig. 2.—Maximum likelihood concatenated phylogeny of *Trachylepis* based on 16S, ND2, and RAG1 genes, with emphasis on the *T. maculilabris* group. SH-aLRT/UFBoot support values greater than 80/95 are displayed next to nodes. The Eastern African clade is highlighted in gray. Clades with triangles were collapsed for clarity.



Fig. 3.—TCS haplotype network of ND2, 16S, and RAG1 genes for the *Trachylepis maculilabris* species complex. Circle size represents the number of sequences and colors correspond to different areas. Color tones match the regions, with Central Africa in orange, Western Africa in blue, and Eastern Africa in green tones. Mutations are expressed numerically for ND2 and by black circles for RAG1 and 16S.

Trachylepis thomensis was recovered with strong support (99.8/100) and as sister group of the remainder *T. maculilabris* species complex. Both *T. adamastor* (95/100) and *T. boulengeri* (100/100) were found to be monophyletic. However, *T. comorensis* was recovered paraphyletic with respect to *T. boulengeri* and *T. casuarinae*. This positioning of the Indian Ocean island clade within the Central and West African clade was recovered with low support, probably because the data were insufficient to robustly resolve it. We therefore expect that by increasing the phylogenetic signal in future analyses of the genus, the position of the Indian Ocean island clade will be clarified and perhaps embedded within a geographically related clade.

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DNA sequences.—The East African *maculilabris* specimens showed a high relative degree of genetic distance for

the 16S, ND2, and RAG1 genes from the most genetically similar species. For 16S, the Eastern African lineage shows a minimum genetic distance of 1.94% from *T. comorensis* and a maximum of 6.3% from *T. polytropis*. For ND2, it shows a minimum distance of 13.17% from *T. maculilabris* and a maximum of 21% from *T. paucisquamis*. For RAG1, it shows a minimum of 0.61% from *T. boulengeri* and a maximum of 3.48% from *T. margaritifer*. These distances are in line with those reported for the distinction of other species of the genus (Ceriaco et al. 2016, 2024; Marques et al. 2019).

Haplotype networks.—The *T. maculilabris* complex individuals are from 17 distinct geographic areas, each represented by a unique color (Fig. 3). Overall, our analysis reveals a clear geographic structuring of haplotypes across

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	<i>Trachylepis farooqii</i> , sp. nov. (N = 137)	Trachylepis maculilabris (N = 249)
SVL	27–98 (73.1 ± 14.8), N = 134	44.2-92.2 (70.5 ± 8.4)
TL	40–165 (119.4 ± 30.5), N = 72	77.2–191.1 (124.8 ± 23.8)
HW	$10.4-12.8 (11.5 \pm 1.0), N = 4$	6.1–15 (9.8 ± 1.5)
HH	7.6–11.2 (8.7 ± 1.7), N = 4	4.4–10.7 (7.5 ± 1.3)
HL	10.7–21 (16.4 ± 1.6), N = 75	9.0–21.3 (15.1 ± 1.9)
IN	2.5–3.2 (2.7 ± 0.3), N = 4	$1.2-3.2 (2.2 \pm 0.4)$
EN	3.5–4.5 (4.1 ± 0.4), N = 4	2.3-5.3 (3.9 ± 0.6)
ES	6.1–7.3 (6.6 ± 0.5), N = 4	3.4–7.7 (5.9 ± 0.8)
TL/SVL (%)	101.4–270.8 (168.8 ± 28.2), N = 72	108.2–249.0 (180.4 ± 31.3)
HL/SVL (%)	18.8–25.1 (21.4 ± 1.4), N = 75	$16.5-26.3 (21.4 \pm 1.6)$
ES/HL (%)	39.4–41.7 (40.9 ± 1.0), N = 4	25.8-52.8 (39.1 ± 3.0)
HW/HL (%)	67.1–73.7 (71.1 ± 3.1), N = 4	52.4-81.9 (65.2 ± 4.4)
HH/HL (%)	46.7–64.4 (53.7 ± 8.0), N = 4	30.7–65.7 (49.4 ± 4.4)
LUFT	14–21 (N = 136)	14–21
LUFF	14–15 (N = 4)	10–16
MSR	28–36 (N = 129)	29–40
SAD	49–58 (N = 31)	46-64
SAV	55–70 (N = 70)	50–68
KDS	3–9 (N = 135)	3–6
SC	5–7, rarely 3 or 4	5-6
SL (SO)	7 (5), rarely 8 (6)	7 (5)
PS	Smooth	Smooth
СР	SPC (N = 2) or C (N = 2)	Usually C (N= 161) or SPC (N = 81), rarely S (N = 6) or F (N = 1)
CFP	Always C (N = 4)	Usually C (N = 245), rarely F (N = 3) or S (N = 2)
CSN	S (N = 75) or C (N = 41)	Usually SPC (N = 194), sometimes C (N = 39) or S (17)
CPF	Usually S (N = 108), sometimes C (N = 19)	Usually C (N = 139) or SPC (N = 85), sometimes S (N = 25)
Coloration	Dorsum reddish brown to brownish yellow with a pair of orangish dorsolateral bands.	Dorsum olive gray to dark brown, with no dorsolateral bands.

 TABLE 2. Mensural and meristic comparisons between *Trachylepis farooqii*, sp. nov., and *T. maculilabris*. Data presented as minimum-maximum (mean ± standard deviation). Type of contact between head shields coded as follows: in contact (C), in contact at a single point (SPC), separated (S), fused (F).

these regions. The ND2 haplotype network exhibited the greatest diversity, identifying 39 distinct haplotypes, none of which were particularly prevalent. Notably, the green haplotypes from Mozambique are divided into two clusters: one containing a single haplotype with a sequence from *T. boulengeri*, and another comprising two haplotypes with sequences of the Eastern African *T. maculilabris* lineage. In the 16S network, 21 haplotypes were identified, with some standing out, such as one containing 20 sequences predominantly from Cameroon and another with 19 sequences mainly from the Democratic Republic of the Congo. Despite these regional distinctions, a clear

clustering of Eastern African haplotypes is evident. As with ND2, the haplotypes of Eastern African *T. maculi-labris* are exclusive, showing no overlap with sequences from other species, which is consistent with the recovered topology (Fig. 2). Eastern African *T. maculilabris* is represented by three haplotypes, one from Tanzania, another from Mozambique, and the third including specimens from Malawi, Mozambique, and an unspecified location in East Africa. These three haplotypes are grouped together and connected to other haplotypes from East Africa. The RAG1 network revealed only four haplotypes. Again, the five Eastern African *T. maculilabris* sequences are in a single,



Fig. 4.—Holotype of Trachylepis farooqii, sp. nov. (MZUSP L108148) from Naburi, Mozambique. Photos by Luis M. P. Ceríaco.

exclusive haplotype, comprising three sequences from Mozambique and two from Malawi. This haplotype is directly linked to a haplotype containing three *T. boulengeri* sequences from Mozambique.

Morphology.—Morphometric and meristic data for the specimens of *T. maculilabris* from Central/West Africa and those from East Africa are presented in Table 2. Two morphotypes, distinguishable from each other in several consistent characters, were recovered: one in the Eastern Africa specimens and one from Central and West Africa. A detailed diagnosis and comparison are provided in the taxonomic account below.

Species concept.—Based on the combined evidence provided by the morphological data, molecular phylogeny, and

the haplotype networks, we adopt the general lineage species concept (de Queiroz 1999) and describe the Eastern African populations of *T. maculilabris* as a new species.

SYSTEMATIC ZOOLOGY

Class Reptilia Laurenti, 1768 Order Squamata Oppel, 1811 Family Scincidae Gray, 1825 Subfamily Scincinae Gray, 1825 Genus *Trachylepis* Fitzinger, 1843

Trachylepis farooqii, sp. nov.

LSID: urn:lsid:zoobank.org:act:574BB593-5554-4254-9043-457F65BE 5AF (Figs. 4–7A)



Fig. 5.—Holotype in life of Trachylepis farooqii, sp. nov. (MZUSP L108148). Photo by Marco Sena.

Euprepis cf. maculilabris: Mausfeld-Lafdhiya et al. (2004:167).

Mabuia maculilabris: Loveridge (1920: 152, 1923b:956); Barbour and Loveridge (1928:157)

Mabuia maculilabris [part]: Loveridge (1923a:858).

- Mabuya maculilabris [part]: Schmidt (1919:525); Loveridge (1933:312, 1936:310); Spawls and Rotich (1997:70); Broadley (2000:94); Mausfeld et al. (2000:12); Spawls et al. (2002:133); Largen and Spawls (2010:394).
- Mabuya maculilabris comorensis (not Peters): Loveridge (1953:200, 1955:173)
- Mabuya maculilabris maculilabris: Robertson et al. (1963:423); Broadley (1974a:7); Lanza (1990:425); Loveridge (1951:183, 1957: 209); Broadley and Howell (1991:15).

Trachylepis maculilabris [part]: Branch et al. (2005:201); Malonza et al. (2006:103; 2011:152); Goldberg (2009:114); Ceríaco et al. (2016:301); Conradie et al. (2016:174); Spawls et al. (2018:141); Weinell (2019:187); Allen (2019:232); Lyakurwa (2019:12); Pietersen et al. (2021:272); Spawls et al. (2023:256); Ceríaco et al. (2024:82).

Holotype.—An adult male (MZUSP L108148, field number MTR 38383, Fig. 4) collected at Naburi [16.78857S, 38.88581E], Mozambique, by Miguel Trefaut Rodrigues, Renato Sousa Recoder, Marco Aurélio de Sena, Agustin Camacho, Mohamed Harun, Samuel Bila, Francisco Dal Vechio, and Mauro Teixeira Junior on 27 October 2015.

Paratypes.—One adult male (MZUSP L108146, field number MTR 38221) and one adult female (MZUSP L108147, field number MTR 38327), collected at Naburi [16.78857S, 38.88581E], Mozambique, by Miguel Trefaut Rodrigues, Renato Sousa Recoder, Marco Aurélio de Sena, Agustin Camacho, Mohamed Harun, Samuel Bila, Francisco Dal Vechio, and Mauro Teixeira Junior, respectively on 27 and 28 October 2015. One adult male (MNHN-RA 2009.0442, field number 1578I), collected at Cabo Delgado region [10.8388S, 40.1944E], northern Mozambique, by Ivan Ineich on 26 November 2009.

Diagnosis.—A medium-sized skink (max. SVL 98 mm, KMH 11907), with fully developed pentadactyl limbs (Fig. 5); dorsal scales with three to nine keels, commonly 7 (68%); ventral scales smooth; 55–70 SAV; 49–58 SAD; 28-36 MSR; subdigital lamellae smooth; plantar scales smooth; 14-21 LUFT; 14-15 LUFF; supranasals usually separated (65%), sometimes in contact; parietals touching

Mabuya maculilabris maculilabris [part]: Loveridge (1942:342).

[&]quot;Trachylepis maculilabris 1": Ceríaco et al. (2024:7). "Trachylepis maculilabris 4": Sindaco et al. (2012:355). "Trachylepis maculilabris 5": Sindaco et al. (2012:355).

	MZUSP L108148 (Holotype)	MZUSP L108146 (Paratype)	MZUSP L108147 (Paratype)	MNHN-RA 2009.0442 (Paratype)
Sex	Male	Female	Male	Male
SVL	75.6	77.1	86.9	81.3
TL	86.0	-	-	-
HW	11.5	10.4	11.4	12.8
HH	7.6	8.2	7.9	11.2
HL	15.7	14.8	17.0	17.4
IN	2.7	2.6	2.5	3.2
EN	4.2	3.5	4.5	4.1
ES	6.5	6.1	6.7	7.3
TL/SVL (%)	113.8	-	-	-
HL/SVL (%)	20.8	19.2	19.6	21.4
ES/HL (%)	41.4	41.2	39.4	41.7
HW/HL (%)	73.3	70.3	67.1	73.7
HH/HL (%)	48.4	55.4	46.7	64.4
LUFT	16	16	15	18
LUFF	14	15	15	15
MSR	33	33	32	33
SAD	54	57	55	52
SAV	55	57	57	55
KDS	7	7	7	5
SC	5 (left), 7 (right)	6	7	6
SL (SO)	7 (5)	7 (5)	8 (6) and 7 (5)	7 (5)
PS	Smooth	Smooth	Smooth	Smooth
СР	С	SPC	SPC	С
CFP	С	С	С	С
CSN	S	S	SPC	S
CPF	S	SPC	S	S

TABLE 3. Mensural and meristic data for the type series of *Trachylepis farooqii*, sp. nov. Type of contact between head shields coded as follows: in contact (C) in contact at a single point (SPC) separated (S) fused (F)

at a single point or in contact; prefrontals usually separated (85%), sometimes in contact; frontoparietals always in contact; one pair of enlarged nuchal scales; ear opening vertically ovoid and smaller than the eye, lacking subtriangular auricular scales on the anterior margin. One scale row above the window in eyelid. Supralabials seven (rarely eight), the fifth being subocular; three to seven supraciliaries, but three and four being rare; nostril oriented laterally. Dorsum reddish brown with a pair of orange dorsolateral stripes extending from the eye to halfway down the tail (Figs. 5, 6A, 7A); labials grayish brown with dark speckling between scales. Venter cream white to yellow (Fig. 6B) with dark speckling near the flanks and on the first third of the tail. **Description of the holotype.**—A well-preserved adult male with minor ventral injury beneath the left forelimb and some missing scales. Body cylindrical and robust with a poorly defined neck and well-developed pentadactyl limbs; tail long and robust, longer than the SVL, smoothly tapering. Fore- and hind limbs overlap when depressed against the body. SVL 75.6 mm, TL 86 mm, HW 11.5 mm, HL 15.7 mm, with relatively long and prominent snout. Additional measurements are presented in Table 3. Ear opening medium sized, lacking anterior subtriangular auricular scales. Rostral scale visible from above. Nostrils oriented laterally and set posteriorly, so that postnasal effectively borders nostril. Supranasals separated. Frontonasal wider than long, in contact with loreal. Prefrontals irregularly pentagonal, separated from each other, each in



Fig. 6.—Live paratype of *Trachylepis farooqii*, sp. nov. (MNHN-RA 2009.0442) from Cabo Delgado region, northern Mozambique. **A**, fronto-lateral view showing the amber-colored lateral band. **B**, ventral view showing the lemon-yellow venter color. Photos by Ivan Ineich.



Fig. 7.—Live specimens showing the orangish dorsolateral band on *Trachylepis farooqii*, sp. nov., and the lack of dorsolateral band on *T. maculilabris*. **A**, non-collected specimen of *T. farooqii*, sp. nov., from Taratibo, Mozambique; **B**, specimen of *T. maculilabris* from Kalandula, Angola (CAS 263587). Photos by Harith Farooq and Luis M. P. Ceríaco, respectively.



Fig. 8.—Distribution map of *Trachylepis farooqii*, sp. nov., and *T. maculilabris* in Africa. The specimens of *T. farooqii*, sp. nov., used exclusively for molecular analysis are indicated by a blue circle. Green stars denote the type localities. Specimens whose identity has not been confirmed by the authors and whose distribution is close to that of *T. maculilabris* are indicated by a white triangle.

contact with the following head shields: frontonasal, loreal, first and second supraocular, and frontal. Two loreals. Frontal longer than the distance between anterior tip of frontal and tip of snout. Frontal in contact with two supraoculars (second and third) on each side. Two frontoparietals in contact with each other, the frontal, third and fourth supraoculars, parietal, and interparietal. Frontoparietal plus interparietal length slightly shorter than frontal length. Interparietal twice as long as broad, with a visible parietal foramen. Parietals larger than frontoparietals. Parietals in contact. Five supraciliaries on the left side, second largest; seven on the right side. Seven supralabials, fifth being subocular. Eight infralabials. Postmental bordering seven scales (mental, two infralabials on each side and two primary chin shields). Transparent scale present in lower eyelid, as is usual for Trachylepis. Tympanum visible, at same level as mouth. Dorsal scales with seven smooth keels. Ventral scales smooth. MSR 33, SAD 54, SAV 55. Limbs with five digits; scales on palms and soles smooth. Relative length of fingers IV>III>II>V>I, relative length of toes IV>III>V>III>I. Finger-IV lamellae 14, Toe-IV lamellae 16. Dorsum reddish brown with a pair of darker dorsolateral stripes extending from the eye to halfway

down the tail; labials grayish brown with dark speckling between scales. Venter cream white with dark speckling near the flanks and on the first third of the tail.

Coloration in ethanol.—Dorsum of body uniformly brown with a pair of dark dorsolateral stripes. Flanks uniformly brown. Labials grey with light brown vertical spots. Ventral surface white, with brown speckles on the first half of the tail and near the infralabials.

Variation.—Variation in scalation and body measurements among the type series of *Trachylepis farooqii*, sp. nov. is reported in Table 3. Parietals in broad contact (MZUSP L108148, MNHN-RA 2009.0442) or touching at a single point contact (MZUSP L108146, L108147). Supranasals separated (MZUSP L108148, L108146, MNHN-RA 2009.0442) or in contact at a single point (MZUSP L108147). Prefrontals separated (MZUSP L108148, L108147, MNHN-RA 2009.0442) or in contact at a single point (MZUSP L108147, MNHN-RA 2009.0442) or in contact at a single point (MZUSP L108147, MNHN-RA 2009.0442) or in contact at a single point (MZUSP L108146). Supraciliaries 7 (MZUSP L108147), 6 (MZUSP L108146, MNHN-RA 2009.0442) or 5 on the left and 7 on the right (MZUSP L108148). Supralabials 7, with the fifth being subocular (MZUSP



Fig. 9.—Habitat of collected specimens of *Trachylepis farooqii*, sp. nov., in Mozambique. **A**, holotype (MZUSP L108148) locality in Naburi; **B**, paratype (MNHN-RA 2009.0442) locality in Cabo Delgado. Photos by Marco Sena and Ivan Ineich, respectively. L108148, L108146, L108147, MNHN-RA 2009.0442); paratype MZUSP L108147 shows 8 supralabials on the left, with the sixth being subocular. Dorsum brownish yellow and head toasted yellow, sometimes with scattered white speckles between eyes and insertion of forelimbs. There is probably a sexual coloration dimorphism during reproduction with males having a vivid orange lateral band and a lemon-yellow venter, but throat and underside of jaw being white (MNHN-RA 2009.0442; Fig. 6).

Comparison with other Eastern African Trachylepis and members of the T. maculilabris group.—Trachylepis farooqii, sp. nov. differs from all the other Trachylepis species known to occur in Eastern Africa, as follows: it differs from T. albotaeniata by usually having 5-7 supraciliaries (vs. 4 in T. albotaeniata). It differs from T. maculilabris by usually having supranasals and prefrontals separated (vs. usually in contact in T. maculilabris) and dorsolateral bands (vs. no dorsolateral bands in T. maculilabris - see Fig. 7). It differs from T. boulengeri by usually having 5-7 supraciliaries (vs. usually 4, sometimes 5 in T. boulengeri) and light vellow to dark dorsolateral stripes (vs. no dorsal stripes in T. boulengeri). It differs from T. casuarinae by usually having separated prefrontals (vs. usually in contact in T. casuarinae), LUFT 14-21 (vs. 23-24 in T. casuarinae), LUFF 14-15 (vs. 16-17 in T. casuarinae) and dorsolateral stripes (vs. no dorsal stripes in *T. casuarinae*). It differs from T. comorensis by having usually LUFT 14-19, only 6 specimens with LUFT 20–21 (vs. 20–24 in T. comorensis). It differs from T. damarana, T. lacertiformis, T. striata, and T. wahlbergii by having scales on palms and soles smooth (vs. keeled and spinose in the latter). It differs from T. homalocephala and T. margaritifer by usually having 5–7 keels on dorsal scales (vs. 3 keels in the latter). It differs from T. megalura and T. varia by having one scale row above window in eyelid (vs. two scale rows in the latter). It differs from T. depressa by lacking auricular scales (vs. 3–4 lanceolate auricular scales in *T. depressa*).

Distribution.—The current known distribution of *Trachylepis farooqii*, sp. nov., is restricted to South-East Africa, spanning from the Zambezia Province in central Mozambique, delimited in the south from Naburi to Mulanje Mountain in Malawi and extending northwards to southeastern Kenya (Fig. 8). Its range probably encompasses the coastal regions of Somalia, following the continuous coastal dry forest strip, but further data are needed to confirm this assumption.

Habitat and natural history notes.—Found in forest glades, woodland coastal scrub, farmland, and gardens, usually near water sources. It is diurnal, arboreal, and climbs trees, bushes, thin branches, and leaves. It also uses buildings, walls, thatched roofs, rock outcrops, and often climbs coconut palms in coastal areas (Spawls et al. 2018). The holotype (MZUSP L108146) and paratypes (MZUSP L108146, L108147) were found active in miombo wood-

land habitats in the surroundings of Naburi village (Fig. 9). A paratype (MNHN-RA 2009.0442) was collected around a termite mound in a typical miombo vegetal formation. Specimens were also found, but not collected, at the Gilé National Park in sympatry with *T. boulengeri*.

Etymology.—The specific epithet "*farooqii*" is formed in the genitive singular and is masculine. It is given in honor of Harith Omar Morgadinho Farooq (born 1986), Mozambican herpetologist who in the last decade has greatly contributed to uncovering the rich and still poorly known herpetofauna of his country. Harith has also been a strong advocate for the African biodiversity and responsible for training a new generation of Mozambican naturalists. We suggest "Farooq's skink" and "Lagartixa de Farooq" as the English and Portuguese common names for this species, respectively.

DISCUSSION

The Eastern African population of the Trachylepis macu*lilabris* species complex was first suggested to represent a separate evolutionary lineage in the beginning of the 21st century (Mausfeld-Lafdhiya et al. 2004), but the nomenclatural complexity of the group and high morphological similarity between the East African form and the true T. maculilabris of West Africa precluded its proper taxonomic identification until now. An integrative approach, built on the recent advances on the taxonomy and nomenclatural history of the group and combining newly generated molecular data with a large set of morphological data allowed us to unambiguously distinguish T. farooqii, sp. nov., from the other Trachylepis species. The analysis of a large sample of specimens revealed some major differences: the prefrontals and supranasals are usually separated in T. farooqii, sp. nov., whereas they are usually in contact in T. maculilabris, and the dorsolateral orange bands present in T. faroogii, sp. nov., which are absent in T. maculilabris. In addition, the new 16S, ND2, and RAG1 sequences of three specimens, which formed a clade with the specimens previously analyzed and identified as a distinct lineage, allowed the Eastern African form to be recognized as a new species. Further work, however, is still needed in the T. maculilabris species complex to better understand the whole extent of its cryptic diversity, especially amongst the populations that are currently considered to be part of the nominal form in Central and West Africa.

In the last decade, 12 new species of *Trachylepis* have been described, including the insular *T. thomensis* from São Tomé and *T. adamastor* from São Tomé and Príncipe (Ceríaco 2015; Ceríaco et al. 2016), and the West African continental species *T. gonwouoi* Allen, Tapondjou, Welton, and Bauer, 2017, from Cameroon and Republic of the Congo (Allen et al. 2017), *T. raymondlaurenti* Marques, Ceríaco, Bandeira, Pauwels, and Bauer, 2019, from Democratic Republic of the Congo and Angola (Marques et al. 2019), *T. boehmei* Koppetsch, 2020, from Ethiopia (Koppetsch 2020), and *T. attenboroughi, T. bouri, T. hilariae, T. ovahelelo, T. suzanae, T. vunongue*, and *T. wilso-ni* Ceríaco, Marques, Parrinha, Tiutenko, Weinell, Butler, and Bauer, 2024, from Angola (Ceríaco et al. 2024). With this, the description of a new species from Mozambique, Malawi, Tanzania, and Kenya highlights the importance of southeast Africa for studies about the diversification of the genus *Trachylepis*. These descriptions of new species of reptiles in the region, combined with predictions of high discovery potential of lizard species in southeast Africa, show that more fieldwork and herpetological studies are needed for the region to improve our knowledge of the poorly known biodiversity of southeast Africa (Moura and Jetz 2021).

Regarding its conservation, *Trachylepis farooqii*, sp. nov., occurs over a large geographic area, covering Mozambique, Malawi, Tanzania, and dry coastal forests of southeast Kenya. Based on its distribution and the presence of several conservation areas in these territories, such as Gorongosa, Gilé, and Serengeti National Parks, we suggest a conservation status of Least Concern, following the IUCN Red List guidelines (IUCN 2024). However, formal conservation assessments are still needed to formally evaluate *T. farooqii*, sp. nov. conservation status.

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LITERATURE CITED

- ABASCAL, F., R. ZARDOYA, AND M.J. TELFORD. 2010. TranslatorX: multiple alignment of nucleotide sequences guided by amino acid translations. Nucleic Acids Research, 38:W7–W13.
- ALLEN, K.E., W.P. TAPONDJOU, E. GREENBAUM, L.J. WELTON, AND A.M. BAUER. 2019. High levels of hidden phylogenetic structure within Central and West African *Trachylepis* skinks. Salamandra, 55(4):231–241.
- ALLEN, K.E., W.P. TAPONDIOU, L.J. WELTON, AND A.M. BAUER. 2017. A new species of *Trachylepis* (Squamata: Scincidae) from Central Africa and a key to the *Trachylepis* of West and Central Africa. Zootaxa, 4268(2):255–269.
- BARBOUR, T., AND A. LOVERIDGE. 1928. A comparative study of the herpetological faunae of the Uluguru and Usambara Mountains, Tanganyika Territory, with descriptions of new species. Memoires of the Museum of Comparative Zoology, 50:85–265.
- BAUER, A.M., G. SHEA, AND R. GÜNTHER. 2003. An annotated catalogue of the type of scincid lizards (Reptilia, Squamata, Scincidae) in the collection of the Museum für Naturkunde der Humboldt-Universität zu Berlin (ZMB). Mitteilungen aus dem Museum für Naturkunde in Berlin, 79:253–321.
- BOCAGE, J.V.B. 1866. Lista dos reptis das possessões portuguezas d'Africa ocidental que existem no Museu de Lisboa. Jornal de Sciencias Mathematicas, Physicas e Naturaes, 1:37–56.
- —. 1895. Herpétologie d'Angola et du Congo. Ministério da Marinha e das Colónias, Lisbonne. 203 pp. + 20 pl.
- BOETTGER, O. 1913. Reptilien und Amphibien von Madagascar, den Inseln und dem Festland Ostafrikas. Pp. 269–375, *in* Reise in Ostafrika in den Jahren 1903–1905 (A. Voeltzkow, ed.). Wissenschaftliche Ergebnisse. Vol. 3. Systematische Arbeiten. Schweizerbartsche Verlagsbuchhandlung, Nägele und Sproesser, Stuttgart.
- BOULENGER, G.A. 1887. Catalogue of the Lizards in the British Museum (Natural History). Volume 3. Lacertidae, Gerrhosauridae, Scincidae, Anelytropsidae, Dibamidae, Chamaeleontidae. Trustees of the British Museum, London. xii + 575 pp. + 40 pl.
- BRANCH, W.R. 1998. Field Guide to the Snakes and Other Reptiles of Southern Africa, Third Edition. Struik Publishers, Cape Town. 399 pp.
- BRANCH, W.R., M.O. RÖDEL, AND J. MARAIS. 2005. Herpetological survey of the Niassa Game Reserve, northern Mozambique. Part I: Reptiles. Salamandra, 41(4):195–214.
- BROADLEY, D.G. 1974a. A review of the Mabuya maculilabris group in South-Eastern Africa (Sauria: Scincidae). Arnoldia (Rhodesia), 6(23):1–10.
- ———. 1974b. A review of the *Mabuya lacertiformis* complex in Southern Africa. Arnoldia (Rhodesia), 7(18):1–16.
- 2000. A review of the genus *Mabuya* in southeastern Africa (Sauria: Scincidae). African Journal of Herpetology, 49(2):87–110.
- BROADLEY, D.G., AND K.M. HOWELL. 1991. A checklist of the reptiles of Tanzania, with synoptic keys. Syntarsus (Bulawayo), 1:1–70.
- BURUWATE, T.C., AND D.J. LLOYD-JONES. 2024. Amphibian and reptile diversity of Niassa Special Reserve, northern Mozambique. Journal of East African Natural History 113(1):1–18.
- CARRETERO, M.A., D.J. HARRIS, AND S. ROCHA. 2005. Recent observations of reptiles in the Comoro Islands (western Indian Ocean). Herpetological Bulletin, 91:19–28.
- CERIACO, L.M.P. 2015. Lost in the middle of the sea, found in the back of the shelf: a new giant species of *Trachylepis* (Squamata: Scincidae) from Tinhosa Grande islet, Gulf of Guinea. Zootaxa, 3973(3):511–527.
- CERÍACO, L.M.P, J. BERNSTEIN, A.C. SOUSA, M.P. MARQUES, A.M. BAUER, AND S.J. NORDER. 2020. The reptiles of Tinhosa Grande islet (Gulf of Guinea): a taxonomic update and the role of Quaternary sea level fluctuations in their diversification. African Journal of Herpetology, 69(2):200–216.
- CERÍACO, L.M.P., M.P. MARQUES, AND A.M. BAUER. 2016. A review of the genus *Trachylepis* (Sauria: Scincidae) from the Gulf of Guinea, with descriptions of two new species in the *Trachylepis maculi*-

labris (Gray, 1845) species complex. Zootaxa, 4109(3):284-314.

- CERIACO, L.M.P., M.P. MARQUES, D. PARRINHA, A. TIUTENKO, J.L. WEINELL, B.O. BUTLER, AND A.M. BAUER. 2024. The *Trachylepis* (Squamata: Scincidae) of Angola: an integrative taxonomic review with the description of seven new species. Bulletin of the American Museum of Natural History, 465:1–153.
- CLEMENT, M., Q. SNELL, P. WALKE, D. POSADA, AND K. CRANDALL. 2002. TCS: estimating gene genealogies. Proceedings of the 16th International Parallel and Distributed Processing Symposium, 2:184.
- CONRADIE, W., G. BITTENCOURT-SILVA, H.M. ENGELBRECHT, S.P. LOADER, M. MENEGON, C. NANVONAMUQUITXO, M. SCOTT, AND K.A. TOLLEY. 2016. Exploration into the hidden world of Mozambique's sky island forests: new discoveries of reptiles and amphibians. Zoosystematics and Evolution, 92(2):163–180.
- DE QUEIROZ, K. 1999. The general lineage concept of species, species criteria, and the process of speciation. Pp. 57–75, *in* Endless Forms: Species and Speciation (D.J. Howard and S.H. Berlocher, eds.). Oxford University Press, New York.
- FETZNER, J.W. 1999. Extracting high-quality DNA from shed reptile skins: a simplified method. BioTechniques, 26:1052–1054.
- GOLDBERG, S.R. 2009. Notes on reproduction of the speckle-lipped Mabuya, Trachylepis maculilabris (Squamata: Scincidae) from Kenya and Uganda. Bulletin of the Maryland Herpetological Society, 45(4):114–116.
- GOUY, M., S. GUINDON, AND O. GASCUEL. 2010. SeaView version 4: a multiplatform graphical user interface for sequence alignment and phylogenetic tree building. Molecular Biology and Evolution, 27(2):221–224.
- GRAY, J.E. 1845. Catalogue of the Specimens of Lizards in the Collection of the British Museum. Trustees of the British Museum, London. 289 pp.
- GUINDON, S., J. DUFAYARD, V. LEFORT, M. ANISIMOVA, W. HORDIJK, AND O. GASCUEL. 2010. New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of phyml 3.0. Systematic Biology, 59(3):307–321.
- HOOGMOED, M.S. 1974. Ghanese lizards of the genus Mabuya (Scincidae, Sauria, Reptilia). Zoologische Verhandelingen, 138(1):1–62.
- IUCN. 2024. The IUCN Red List of Threatened Species [cited 15 July 2024]. Available from https://www.iucnredlist.org.
- JESUS, J., A. BREHM, AND D.J. HARRIS. 2005. Relationships of scincid lizards (*Mabuya* spp.) from the islands of the Gulf of Guinea based on mtDNA sequence data. Amphibia-Reptilia, 26(4):467–473.
- JUNGNICKEL, J. 2012. Ein Echsen-Kleinbiotop auf der Insel Sansibar. Terraria-Elaphe, 4:14–15.
- KALYAANAMOORTHY, S., B.Q. MINH, T.K. WONG, A. VON HAESELER, AND L.S. JERMIIN. 2017. ModelFinder: fast model selection for accurate phylogenetic estimates. Nature Methods, 14(6):587–589.
- KARIN, B.R., M. METALLINOU, J.L. WEINELL, T.R. JACKMAN, AND A.M. BAUER. 2016. Resolving the higher-order phylogenetic relationships of the circumtropical *Mabuya* group (Squamata: Scincidae): an out-of-Asia diversification. Molecular Phylogenetics and Evolution, 102:220–232.
- KATOH, K., AND D.M. STANDLEY. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Molecular Biology and Evolution, 30(4):772–780.
- KATOH, K., K.I. KUMA, T. MIYATA, AND H. TOH. 2005. Improvement in the accuracy of multiple sequence alignment program MAFFT. Genome Informatics, 16(1):22–33.
- KOPPETSCH, T. 2020. A new species of *Trachylepis* (Squamata: Scincidae) from the Amhara Region, Ethiopia, and a key to the Ethiopian *Trachylepis*. Zootaxa, 4859(1):113–126.
- LANZA, B. 1990 [1988]. Amphibians and reptiles of the Somali Democratic Republic: check list and biogeography. Biogeographia– The Journal of Integrative Biogeography, 14(1):407–465.
- LARGEN, M.J., AND S. SPAWLS. 2010. Amphibians and Reptiles of Ethiopia and Eritrea. Edition Chimaira, Frankfurt. 694 pp.
- LAURENT, R.F. 1947. Notes sur quelques reptiles appartenant à la collection du Musée royal d'Histoire naturelle de Belgique. Bulletin du

Musée royal d'Histoire naturelle de Belgique, 23(16):1–12.

- 1954. Reptiles et batraciens de la région de Dundo (Angola) (Deuxième Note). Publicações Culturais da Companhia de Diamantes de Angola, 9:37–84.
- 1964. Reptiles et amphibiens de l'Angola (Troisième contribution). Publicações Culturais. Companhia de Diamantes de Angola, 67:1–165.
- LEIGH, J.W., AND D. BRYANT. 2015. PopART: full-feature software for haplotype network construction. Methods in Ecology and Evolution, 6(9):1110–1116.
- LIMA, A., D.J. HARRIS, S. ROCHA, A. MIRALLES, F. GLAW, AND M. VENCES. 2013. Phylogenetic relationship of *Trachylepis* skink species from Madagascar and the Seychelles (Squamata: Scincidae). Molecular Phylogenetics and Evolution, 67(3):615–620.
- LOVERIDGE, A. 1920. Notes on East African lizards collected 1915–1919, with description of a new genus and species of skink and new subspecies of gecko. Proceedings of the Zoological Society of London, 90(1–2):131–167.
- . 1923a. A list of the lizards of British territories in East Africa (Uganda, Kenya Colony, Tanganyika, Zanzibar) with keys for the diagnosis of the species. Proceedings of the Zoological Society of London, 1923:841–863.
- ——. 1923b. Notes on East African lizards collected 1920-1923 with the description of two new races of *Agama lionotus*. Proceedings of the Zoological Society of London, 93(4):935–969.
- 1933. Reports on the scientific results of an expedition to the southwestern highlands of Tanganyika Territory. VII. Herpetology. Bulletin of the Museum of Comparative Zoology, 74(7):197–416.
- 1936. Scientific results of an expedition to rain forest regions in Eastern Africa. V. Reptiles. Bulletin of the Museum of Comparative Zoology, 79(5):209–337.
- 1942. Scientific results of a fourth expedition to forested areas in east and central Africa. IV. Reptiles. Bulletin of the Museum of Comparative Zoology, 91(4), 237–373.
- 1951. On reptiles and amphibians from Tanganyika Territory collected by C.J.P. Ionides. Bulletin of the Museum of Comparative Zoology, 106(4):177–204.
- —. 1953. Zoological Results of a fifth expedition to East Africa. III. Reptiles from Nyasaland and Tete. Bulletin of the Museum of Comparative Zoology, 110(3):142–322.
- 1955. On a second collection of reptiles and amphibians taken in Tanganyika Territory by C.C.J.P. Ionides, Esq. Journal of the East African Natural History Society, 22:168–198.
- 1957. Checklist of the reptiles and amphibians of East Africa (Uganda, Kenya, Tanganika, Zanzibar). Bulletin of the Museum of Comparative Zoology, 117:151–362.
- LYAKURWA, J.V., K.M. HOWELL, L.K. MUNISHI, AND A.C. TREYDTE. 2019. Uzungwa Scarp Nature Forest Reserve; a unique hotspot for reptiles in Tanzania. Acta Herpetologica, 14(1):3–14.
- MALONZA, P.K., B.A. BWONG, AND V. MUCHAI. 2011. Kitobo Forest of Kenya, a unique hotspot of herpetofaunal diversity. Acta Herpetologica, 6(2):149–160.
- MALONZA, P.K., D.M. MULWA, J.O. NYAMACHE, AND G. JONES. 2018. Biogeography of the Shimba Hills ecosystem herpetofauna in Kenya. Zoological Research, 39(2):97–104.
- MALONZA, P.K., V.D. WASONGA, V. MUCHAI, D. ROTICH, B.A. BWONG, AND A.M. BAUER. 2006. Diversity and biogeography of herpetofauna of the Tana River Primate National Reserve, Kenya. Journal of East African Natural History, 95(2):95–109.
- MARQUES, M.P., L.M.P. CERÍACO, S. BANDEIRA, O.S.G. PAUWELS, AND A.M. BAUER. 2019. Description of a new long-tailed skink (Scincidae: *Trachylepis*) from Angola and the Democratic Republic of Congo. Zootaxa, 4568(1):51–68.
- MARQUES, M.P., L.M.P. CERÍACO, D.C. BLACKBURN, AND A.M. BAUER. 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 2):1–501.
- MAUSFELD-LAFDHIYA, P., A. SCHMITZ, I. INEICH, AND L. CHIRIO. 2004.

Genetic variation in two African *Euprepis* species (Reptilia, Scincidae), based on maximum–likelihood and Bayesian Analyses: taxonomic and biogeographic conclusions. Bonner zoologische Beiträge, 52:159–177.

- MAUSFELD, P., M. VENCES, A. SCHMITZ, AND M. VEITH. 2000. First data on the molecular phylogeography of scincid lizards of the genus *Mabuya*. Molecular Phylogenetics and Evolution, 17(1):11–14.
- MINH, B.Q., M.A.T. NGUYEN, AND A. VON HAESLER. 2013. Ultrafast approximation for phylogenetic bootstrap. Molecular Biology and Evolution, 30(5):1188–1195.
- MOURA, M.R., AND W. JETZ. 2021. Shortfalls and opportunities in terrestrial vertebrate species discovery. Nature Ecology & Evolution 5:631–639.
- NGUYEN, L.T., H.A. SCHMIDT, A. VON HAESELER, AND B.Q. MINH. 2014. IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. Molecular Biology and Evolution, 32:268–274.
- PETERS, W.C.H. 1879. Neue oder Weniger bekannte Eidechsenarten aus der Familie der Scinciden (*Eumeces güntheri*, *Euprepes* notabilis, Ablepharus rutilus). Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin, 1879(3):35–37.
- PIETERSEN D., L. VERBURGT, AND J. DAVIES. 2021. Snakes and Other Reptiles of Zambia and Malawi. Struik Nature, Cape Town. 376 pp.
- ROBERTSON, I.A.D., B.M. CHAPMAN, AND R.F. CHAPMAN. 1963. Notes on some reptiles collected in the Rukwa Valley, SW Tanganyika. Annals and Magazine of Natural History, 13(5):421–432.
- ROCHA, S., D.J. HARRIS, AND M. CARRETERO. 2010. Genetic diversity and phylogenetic relationships of *Mabuya* spp. (Squamata: Scincidae) from western Indian Ocean islands. Amphibia-Reptilia, 31(3):375–385.
- ROHLAND, N., AND D. REICH. 2012. Cost-effective, high-throughput DNA sequencing libraries for multiplexed target capture. Genome Research, 22(5):939–946.
- SANCHEZ, M., A. CHOEUR, F. BIGNON, AND A. LAUBIN. 2019. Reptiles of the Îles Éparses, Indian Ocean: inventory, distribution, and conservation status. Herpetological Conservation and Biology, 14(2):481– 502.
- SCHMIDT, K.P. 1919. Contributions to the herpetology of the Belgian Congo based on the collection of the American Congo Expedition, 1909–1915. Part I. Turtles, crocodiles, lizards and chameleons; with field notes by Herbert Lang and James P. Chapin. Bulletin of the

American Museum of Natural History, 39:385-624.

- SHEN, W., B. SIPOS, AND L. ZHAO. 2024. SeqKit2: a Swiss army knife for sequence and alignment processing. iMeta, e191.
- SINDACO, R., M. METALLINOU, F. PUPIN, M. FASOLA, AND S. CARRANZA. 2012. Forgotten in the ocean: systematics, biogeography and evolution of the *Trachylepis* skinks of the Socotra Archipelago. Zoologica Scripta, 41:346–362.
- SPAWLS, S., K. HOWELL, R.C. DREWES, AND J. ASHE. 2002. A Field Guide to the Reptiles of East Africa: Kenya, Tanzania, Uganda, Rwanda and Burundi. Academic, London. 543 pp.
- SPAWLS, S., K. HOWELL, H. HINKEL, AND M. MENEGON. 2018. Field Guide to East African Reptiles, Second Edition. Bloomsbury, London. 634 pp.
- SPAWLS, S., A. MOHAMMAD, AND T. MAZUCH. 2023. Handbook of Amphibians and Reptiles of North-east Africa. Bloomsbury Wildlife, London. 640 pp.
- SPAWLS, S., AND D. ROTICH. 1997. An annotated checklist of the lizards of Kenya. Journal of East African Natural History, 86:61–83.
- STERNFELD, R. 1911. Zur Reptilienfauna Deutsch-Ostafrikas. Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin, 1911:245–251.
- . 1913. Reptilia. Pp. 197–279, in Wissenschaftliche Ergebnisse der deutschen Zentral-Afrika-Expedition 1907–1908 unter Führung Adolf Friedrichs, Herzogs zu Mecklenberg. Band IV. Zoologie II. (1912) (H. Schubotz, ed.). Klinkhardt & Biermann, Leipzig.
- TAMURA, K., G. STECHER, AND S. KUMAR. 2021. MEGA 11: Molecular Evolutionary Genetics Analysis Version 11. Molecular Biology and Evolution, 38(7):3022–3027.
- UETZ, P., P. FREED, R. AGUILAR, F. REYES, J. KUDERA, AND J. HOŠEK (EDS.). 2024. The Reptile Database [cited 20 July 2024]. Available from http://www.reptile-database.org.
- WEINELL, J.L., AND A.M. BAUER. 2018. Systematics and phylogeography of the widely distributed African skink *Trachylepis varia* species complex. Molecular Phylogenetics and Evolution, 120:103–117.
- WEINELL, J.L., W.R. BRANCH, T.J. COLSTON, T.R. JACKMAN, A. KUHN, W. CONRADIE, AND A.M. BAUER. 2019. A species-level phylogeny of *Trachylepis* (Scincidae: Mabuyinae) provides insight into their reproductive mode evolution. Molecular Phylogenetics and Evolution, 136:183–195.

APPENDIX 1. Material examined.

List of specimens used in morphological analysis. The coordinates are presented in the [latitude, longitude] format. Specimens used in the molecular analyses are marked with an asterisk (*). (continued on next page)

Trachylepis maculilabris.—ANGOLA. Cabinda Province: Catholic Mission Sanctuary [5.5614S, 12.1779E] (MUHNAC/MB03-001390). Municipal beach (Tafi's Beach) [5.5578S, 12.1779E] (CAS 264215–216). Fortaleza [5.6528S, 12.2481E] (CAS 264217). Malanje Province: Laúca Dam, flooded area [9.7627S, 15.1438E] (MUNHAC/MB03-001353, 001356–1362). Swamp on the edge of corn field, Kalandula [9.0755S, 16.0117E] (CAS 263587). Uíge Province: Forested lagoon in Mucaba mountains [7.2430S, 15.1673E] (MUNHAC/MB03-001401, 001402). Camp site near water pump, E of Ponte, Serra Pingano [7.6829S, 14.9340E] (MUNHAC/MB03-001403). Unknown: MNHN-RA 1896.0203, 1900.0488–0489, 1904.0163, 1904.0017, 1904.0173, 1907.0256.

BENIN. Donga Department: Agougou [9.3833N, 1.4500E] (MNHN-RA 1917.0057-0058, 1917.0060-0060A, 1917.0061-0061A).

CAMEROON. Adamawa Province: Banyo village [6.7800N, 11.8200E] (MNHN-RA 2005.1653–1655). Daré ville [7.0730N, 15.0840E] (MNHN--RA 2005.1719-1720). Dir, east of Ngaoundal [6.3270N, 13.5390E] (MNHN-RA 2005.1726). Doua village (5km from Mboula) [6.6480N, 14.0190E] (MNHN-RA 2005.1727, 2005.1731). Febadi, Tibati-Meïganga intersection with Ngaoundéré [6.5940N, 13.0690E] (MNHN-RA 2005.1975). Fongoi Village (Tchabal Mbabo) [7.2300N, 12.0530E] (MNHN-RA 2005.1748, 2005.2846). Malarba Mayo Tollere, between Banyo and Tibati [6.5980N, 12.1530E] (MNHN-RA 2005.1806–1808). Matakoro, west of Tchabal Munguel [7.5180N, 13.3860E] (MNHN-RA 2005.1799). Mwinkwing, southern shores of Lake Tikar [6.0700N, 11.4100E] (MNHN-RA 2005.1900, 2005.1904, 2005.1907, 2005.1910). Ngam, west of Djohong, Adamaoua [6.7420N, 14.5680E] (MNHN-RA 2005.1915). Ribao, north of Somié [6.5070N, 11.4540E] (MNHN-RA 2005.1953-1954). Sabongari [7.0480N, 12.5140E] (MNHN-RA 2005.1955). Tibati village [6.4790N, 12.6010E] (MNHN-RA 2005.1995–1997). Wadjiri, between Tibati and Doualayel [6.7899N, 12.6449E] (MNHN-RA 2005.1945). Centre Region: Botatango at Ngoya Bitom (gulf of Bafia) [4.4110N, 11.2480E] (MNHN-RA 2005.1707, 2005.1710–1712). Dibang [3.8890N, 10.7150E] (MNHN-RA 2005.1723–1724). Matsari, south of Yoko [5.3540N, 12.2320E] (MNHN-RA 2005.1800– 1801, 2005.1819). Nkolfeb, at the foot of Mbaminkom [3.9600N, 11.4300E] (MNHN-RA 2005.1833-1835). Nkwoljobe, at the foot of Mbaminkom [3.9640N, 11.3620E] (MNHN-RA 2005.1830, 2005.1832). East Region: Bertoua ville [4.5770N, 13.6910E] (MNHN-RA 2005.1690). Kika, east of Moloundou [1.9590N, 15.5820E] (MNHN-RA 2005.1766–1767). Medjo, north of Lomié [3.4630N, 13.4680E] (MNHN-RA 2005.1860–1861). Zoulabot II, south of Lomié [2.8950N, 13.8990E] (MNHN-RA 2005.1973). Littoral Region: Makondo [3.8060N, 10.2780E] (MNHN-RA 2005.1785, 2005.1788). Mouanko [3.6580N, 9.7940E] (MNHN-RA 2005.1896). Northwest Region: Anyajua, above Bello [6.2360N, 10.3940E] (MNHN-RA 2005.1602). Baba II, Bamenda Highlands [5:857N, 10.102E] (MNHN-RA 2005.1611). Bamenda, Col de la route de Bafoussam [5.9614N, 10.1517E] (MNHN-RA 1997.3643). Bamessing [6.0040N, 10.3520E] (MNHN-RA 2005.1624–1625). Benakuma, west of Wum [6.4090N, 9.9180E] (MNHN-RA 2000.5200*, 2005.1677, 2005.1681). Bingo village, Bamenda Highlands [6.1660N, 10.2900E] (MNHN-RA 2005.1692-1693). Jakiri, Bamenda-Nkambe road [6.0550N, 10.6580E] (MNHN-RA 2005.1762). Mbiame, Bamenda Highlands [6.1900N, 10.8490E] (MNHN-RA 2005.1847-1848). Tefo Village, Bamenda Highlands [6.2999N, 10.3699E] (MNHN-RA 2005.2484). South Region: Afan, north-east of Ma'an [2.6360N, 10.8400E] (MNHN-RA 2000.5199*). Bouandjo, south of Ebodje [2.5160N, 9.8280E] (MNHN-RA 2005.1713). Chutes de la Lobé [2.8840N, 9.8980E] (MNHN-RA 2005.1775). Kribi [2.9700N, 9.9150E] (MNHN-RÅ 1999.9461, 2005.1977). Mbebe, 47 km south of Edéa [3.4050N, 10.1170E] (MNHN-RÅ 2005.1844). Southwest Region: Atolo, Mamfe district [6.2500N, 9.4500E] (MNHN-RA 2005.1607-1608). Bambe village, Banyang-Mbo [5.2040N, 9.6300E] (MNHN-RA 2005.1621-1622). Bascheo 2, north of Mamfe [6.1920N, 9.4330E] (MNHN-RA 2005.1614). Bendom, Banyang-Mbo [5.2600N, 9.6900E] (MNHN-RA 2005.1685-1689). Ebamut, Banyang-Mbo [5.1300N, 9.7400E] (MNHN-RA 2005.1732). Ekona Lelu, Mount Cameroon [4.2730N, 9.3040E] (MNHN--RA 2005.1739, 2005.2487). Enyandong village, Banyang-Mbo [5.1110N, 9.7030E] (MNHN-RA 2005.1744-1745, 2005.2489). Eyang Ntui, Mawne Forest Reserve [5.7700N, 9.3990E] (MNHN-RA 2005.1746). Green Valley, west of Batibo [5.7370N, 9.8520E] (MNHN-RA 2005.1756). Kembong, south Mamfe [5.6390N, 9.2370E] (MNHN-RA 2005.1763). Limbé-ville [4.0070N, 9.2060E] (MNHN-RA 2005.1774). Limbo, Banyang-Mbo [5.2400N, 9.7600E] (MNHN-RA 2005.1974). Mende, Takamanda mountains [6.3130N, 9.3640E] (MNHN-RA 2005.1868). Nguti village [5.3500N, 9.4160E] (MNHN-RA 2005.1924–1926). Ossing village, south of Mamfe [5.6200N, 9.3200E] (MNHN-RA 2005.1939). Tafu village, north of Mamfe [5.7700N, 9.5190E] (MNHN-RA 2005.1992). West Region: Befang [5.1500N, 10.1833E] (MNHN-RA 2005.1675–1676). Foumban [5.7295N, 10.8775E] (MNHN-RA 2005.1749). Magba [5.9770N, 11.2320E] (MNHN-RA 2005.1777, 2005.1779, 2005.1781–1782). Mount Mbapit, southwest of Foumbot [5.5210N, 10.6690E] (MNHN-RA 2005.1841). Penka-Michel [5.4720N, 10.2420E] (MNHN-RA 2005.1940, 2005.1951). Santchou [5.2820N, 9.9770E] (MNHN-RA 2005.1957).

CENTRAL AFRICAN REPUBLIC. Bamingui-Bangoran Prefecture: Kaga Poungourou [7.8389N, 20.2312E] (MNHN-RA 1997.2932). Manovo [9.2000N, 20.4833E] (MNHN-RA 1997.2935). Ndélé [8.409167N, 20.653056E] (MNHN-RA 1997.2940). **Bangui Prefecture:** Bangui [4.3733N, 18.5628E] (MNHN-RA 1992.4746, 1994.8635–8636, 1997.2917–2919). **Haut-Mbomou Prefecture:** Mboki [5.3166N, 25.9666E] (MNHN-RA 1997.2936, 1997.2938–2939, 1997.3248). **Kémo Prefecture:** Sibut [5.7333N, 19.0833E] (MNHN-RA 1997.2956). **Lobaye Prefecture:** Ngotto [4.0000N, 17.3500E] (MNHN-RA 1997.2942, 1997.2945–2946). **Lim-Pendé Prefecture:** Paoua [7.25N, 16.4333E] (MNHN-RA 1995.4495, 1997.2952, 1997.4496). **Mambéré-Kadéï Prefecture:** Betbérati [4.2613N, 15.7894E] (MNHN-RA 1997.2921, 1997.2923). **Mbomou Prefecture:** Ouazoua [4.2666N, 22.4166E] (MNHN-RA 1997.2949–2951). Sangba [4.3971N, 18.5499E] (MNHN-RA 1999.8600, 1999.8704–8705). **Nana-Mambéré Prefecture:** Bouar [5.9499N, 15.6000E] (MNHN-RA 1997.2928). **Ombella-M'Poko Prefecture:** Boali [4.8000N, 18.1166E] (MNHN-RA 1995.4477). Yaloké [5.3167N, 17.0833E] (MNHN-RA 1997.2957). Zimba [4.1238N, 18.6186E] (MNHN-RA 1992.4750, 1992.4753, 1992.4756). **Ouham Prefecture:** Kouki [6.9933N, 17.0750E] (MNHN-RA 1995.24462, 1997.2920). Lidjombo [2.6833N, 16.1000E] (MNHN-RA 1997.2933). **Sangha-Mbaéré Prefecture:** Bayanga [2.9167N, 16.2500E] (MNHN-RA 1995.4462, 1997.2920). Lidjombo [2.6833N, 16.1000E] (MNHN-RA 1997.2947). **Prefecture:** Bayanga [2.9167N, 16.2500E] (MNHN-RA 1995.4473). Ndakane (MNHN-RA 1997.3087–3088). Salkapa (MNHN-RA 1997.2953–2954). S.C.A.D. [Société Centre Africaine de Débitage] (MNHN-RA 1995.4498). Gubangui (MNHN-RA 1997.3087–3088). Salkapa (MNHN-RA 1997.2953–2954). S.C.A.D. [Société Centre Africaine de Débitage] (MNHN-RA 1995.4498). Gubangui (MNHN-RA 1995.0316, 1995.0316).

DEMOCRATIC REPUBLIC OF THE CONGO. North Kivu Province: Rutshuru, Lake Kivu region [1.1945S, 29.4368E] (MNHN-RA 1940.0109–0110).

Appendix 1.

(continued from previous page)

REPUBLIC OF THE CONGO. Brazzaville Department: Brazzaville [4.2366S, 15.2540E] (MNHN-RA 1891.0429–0431). Kouilou Department: Pointe-Noire [4.7785S, 11.8232E] (MNHN-RA 1967.0278–0279, 1967.0282).

GABON. Estuaire Province: Denis [0.31694N, 9.36694E] (MNHN-RA 2002.0044–0045). **Haut-Ogooué:** Djouori River [1.6454S, 13.8625E] (MNHN-RA 1998.0694). **Nyanga Province:** Majumba [3.8166S, 11.0166E] (MNHN-RA 1899.0123). **Ogooué-Ivindo Province:** Makokou [0.5666N, 12.8666E] (MNHN-RA 1973.1563–1564).

GUINEA. Nzérékoré Region: Beyla [8.6833N, 8.6333W] (MNHN-RA 1921.0333–0335). Macenta [8.5364N, 9.4764W] (MNHN-RA 1921.0328). N'Zébéla [8.0833N, 9.1W] (MNHN-RA 1921.0330–0332, 1921.0337–0338). N'Zérékoré [7.7143N, 8.3957W] (MNHN-RA 1921.0325–0327). Ziela [7.7127N, 8.3591W] (MNHN-RA 1951.0107). Zouguepo [7.7055N, 8.4072W] (MNHN-RA 1967.0243–0244, 1967.0246). **Region unkown:** Serengbara (MNHN-RA 1951.0103). Toungarata (MNHN-RA 1951.0106). MNHN-RA 1951.0104, 1951.0159.

IVORY COAST. Comoé District: Assinie [5.1350N, 3.2900W] (MNHN-RA 1888.0065). District unkown: MNHN-RA 1967.0238, 1967.0241.

LIBERIA. Nimba County: Mount Nimba, Grassfield savannah [7.5071N, 8.5061W] (MNHN-RA 1998.0660).

SUDAN. Boma: Towot [6.1723N, 34.3831E] (MNHN-RA 1997.6553).

UGANDA. Kasese District: Kasenyi [0.0319S, 30.1486E] (MNHN-RA 1940.0113-0115). District unknown: MNHN-RA 1940.0111-0112.

UNKOWN COUNTRY: "West Africa" (BMNH 1946.8.18.17 - holotype). MNHN-RA 1966.1759, 2001.0167, 2001.0170, 2001.0994.

Trachylepis farooqii, sp. nov.—**KENYA. Kilifi County:** Mariakani [3.8648S, 39.4740E] (NMZB-UM 11357). **Kwale County:** Diani Beach, South of Mombasa [4.2765S, 39.5959E] (AJL 1542).

MOZAMBIQUE. Cabo Delgado Province: Cabo Delgado, Miombo area [10.8388S, 40.1944E] (MNHN-RA 2009.0442 — paratype). Sofala Province: Inhamitanga [18.2156S, 35.1594E] (MZB-UM 21892–21897). Zambezia Province: Naburi [16.78857S, 38.88581E] (MZUSP L108146–108147 — paratypes, L108148 — holotype). Province unknown: BM 57.10.28.11.

MALAWI. Mulanje District: Chisambo, Mlanje [16.0419S, 35.5523E] (UM 25379, 26637–26639). Lujeri [16.0413S, 35.6499E] (NMZB-UM 4210, 4241–4246; MCZ 50750). **Nkhata Bay District:** Limphasa Dambo [11.6566S, 34.2291E] (UM 24668–24677). Nkwadzi Hill Forest [11.6833S, 34.2499E] (UM 24688).

TANZANIA. Dar es Salaam Region: Dar es Salaam [6.8925S, 39.3177E] (NMZB 5936–5938, 8218, 8220; TM 3638). **Lindi Region:** Kilwa [8.9799S, 39.5121E] (MCZ 52442–52443). Lindi District [9.4549S, 38.4696E] (MCZ 50006). Tendaguru [10.0979S, 39.1165E] (BM 1928.10.19.61). **Morogoro Region:** Kimboza Forest [7.0336S, 37.7836E] (NMZB 8247). Lower Kihansi Gorge, Kilombero [8.6187S, 35.8663E] (NMZB 13747–13748; KMH 24011). Mwaya [8.9155S, 36.8245E] (MCZ 30861–30885). **Mtwara Region:** Mikindani [10.2814S, 40.1113E] (MCZ 47605–47606). **Tanga Region:** Amani [5.1002S, 38.6335E] (BM 1971.168–169; TM 13283; UM 5332, 5338). Bombo Forest Reserve [4.8482S, 38.6873E] (KMH 23696). Gendagenda Forest, Handeni [5.5002S, 38.6490E] (NMZB 12169). Kambai Forest Reserve [4.9932S, 38.7011E] (NMZB 14833, 14845, 14852, 14859). Kwangumi Forest Reserve, Tanga [4.9523S, 38.7408E] (NMZB 15392). Magoroto [5.1166S, 38.7499E] (MCZ 47449–47450; UM 7355). Manga Forest Reserve, Muheza [5.0168S, 38.7668E] (KMH 11907; NMZB 14810, 15584–15586). Mlinga Forest Reserve [5.0829S, 38.7499E] (KMH 23430). Mtai West Forest Reserve, Tanga [4.8331S, 38.7669E] (NMZB 15342, 15344–15345). Segoma Forest Reserve [4.9668S, 38.7499E] (MMZB 15618–15619, 15666–15668). Semdoe Forest Reserve, Muheza [4.9679S, 38.7047E] (NMZB 15342, 15344–15345). Segoma Forest Reserve [4.9688S, 38.7499E] (MZB 15618–15619, 15666–15668). Semdoe Forest Reserve, Muheza [4.9679S, 38.7047E] (NMZB 15596–15603). **Pwani Region:** Kazimzumbwi Forest Reserve [6.9071S, 39.0959E] (KMH 22689; NMZB 11287, 11296, 11313, 11319). Mlola Forest, Mafia Island [7.8860S, 39.8244E] (NMZB 11255, 11259, 11262, 11311, 12143). **Unguja South Region:** Jozani Forest, Zanzibar Island [6.2678S, 39.4259E] (BM 1947.1.2.65–67, 1956.1.6.33–36). Makunduchi Road, Zanzibar Island [6.4136S, 39.5529E] (BM 1940.2.2273). **Region unkown:** NMZB 18042.

APPENDIX 2.

Additional material.

Specimens that were physically examined, whose taxonomic identification was unambiguous, but not measured and scale counted. The coordinates are presented in the [latitude, longitude] format.

Trachylepis maculilabris.—ANGOLA. Bengo Province: Ambriz [7.8574S, 13.1182E] (BMNH 1851.1.19.8–11). Benguela Province: Entre Rios, Dep. De Benguela [13.0167S, 14.6333E] (ZSM 99/1953). Cuanza Norte Province: Mucoso bei Dondo [9.5333S, 14.6500E] (ZSM 100/1953). Ndalla Tando (currently N'dalatando) [9.3000S, 14.9167E] (BMNH 1909.10.29.99). Cuanza Sul Province: Cada Amboim, abandoned plantation [10.8672S, 14.3244E] (CAS 263098). Congulu, Amboim [10.8667S, 14.2833E] (BMNH 1936.8.1.612–617). Laúca Dam, flooded area [9.7627S, 15.1438E] (MU-NHAC/MB03-001352, 001354–001355). Quirimbo, 75 km E of Amboim [10.6833S, 14.2667E] (BMNH 1936.8.1.618–619). Huíla Province: Gungue, Rio Kwando [13.7363S, 15.4216E] (AMB 12713–12714). Luanda Province: Quifangondo [8.7667S, 13.4333E] (MNHNL Rep/A/Sc no number). Luanda Norte Province: De Beers, Lucapa [8.4228S, 20.7392E] (PEM R19459, R19463*). Dundo [7.3667S, 20.8333E] (BMNH 1966.250–255; MD 226, 2259, 5085, 5088, 5090, 5092, 5094, 5099, 5103, 5119, 5130, 5142, 5150, 5155, 5164, 5200, 5209). Headwaters of Lovua, North of village Capaia [8.3385S, 20.2425E] (PEM R19459). Muita [7.8000S, 21.4100E] (MD 807, 1076). Luanda Sul Province: Alto Cuila (= Alto Cuilo) [10.0500S, 19.5170E] (MCZ R-74111; MD 5308–5309). Malanje Province: Capana [9.7284S, 15.3459E] (MNHNL Rep/A/Sc 1–36). Duque de Bragança (currently Kalandula) [9.1333S, 16.0667E] (TM 45468). Kalandula Falls [9.0740S, 16.0030E] (CAS 263586). Unknown: AMNH 48710–48726; FMNH 74301; MHNG 1545.015; MNHN-RA 1907.0200, 1907.0256; MHNC-UP/REP 272.

CAMEROON. Centre Region: Bafia, Mbam-et-Inoubou (Centre) [4.755N, 11.224E] (CM S7071). Eséka [3.633N, 10.783E] (CM 60725–60726). Yaounde [3.826N, 11.516E] (CM 14961). South Region: Lolodorf, Océan (Sud) [3.234N, 10.730E] (CM S9334, S9347–9348, S9352–9353, S9357, S9361, S9374, S9376, S9380–9381, S9387, S9389–9390, 15161). Sangmélima, Foulassi, Dja-et-Lobo (Sud) [2.919N, 11.956E] (CM S6702, S6706, S6710, S6723, S6725, S6728, S6734, S6745, S6747, S7032, S8033, S8036–8037).

Supplementary Table S1.

List of the specimens and associated GenBank accession numbers included in the present study for molecular analysis. *(continued on next page)*

Taxa	Voucher	16S	ND2	RAG1
Chioninia delalandii	BMNH 2000.18	MG605667	KX231461	KX231373
Trachylepis affinis	Mausfeld 2000	AF153561	NA	NA
Trachylepis affinis	BYU 62150	MK496067	MK583061	MK542163
Trachylepis affinis	NCSM 88360	MK496066	MK583060	NA
Trachylepis affinis	BYU 62075	MK496065	MK583059	MK542157
Trachylepis affinis	BYU 62125	MK496064	MK583058	MK542166
Trachylepis affinis	BYU 62073	MK496063	MK583057	MK542158
Trachylepis affinis	BYU 62124	MK496062	MK583056	MK542156
Trachylepis affinis	BYU 62131	MK496061	MK583055	MK542161
Trachylepis affinis	BYU 62130	MK496060	MK583054	MK542162
Trachylepis affinis	BYU 62133	MK496059	MK583052	MK542165
Trachylepis affinis	BYU 62102	MK496058	MK583053	MK542160
Trachylepis affinis	BYU 62132	MK496057	MK583051	MK542164
Trachylepis affinis	UWBM 6039	MK496056	MK583050	NA
Trachylepis affinis	MVZ 245340	MK496055	MK583049	MK542154
Trachylepis affinis	MVZ 252607	MK496054	MK583047	NA
Trachylepis affinis	MVZ 252604	MK496053	KY696695	NA
Trachylepis affinis	PEM R-5425	MK791995	NA	MK791859
Trachylepis affinis	PEM R-5340	MK791994	NA	NA
Trachylepis affinis	NCSM 88359	MK791993	MK791972	MK791913
Trachylepis affinis	BYU 62095	MK791992	MK791971	MK791896
Trachylepis affinis	CAS 256857	KX671798	NA	NA
Trachylepis affinis	CAS 256856	KX671797	NA	NA
Trachylepis affinis	CAS 256707	KX671796	NA	NA
Trachylepis affinis	BYU 573608	KY683573	KY696697	NA
Trachylepis affinis	UWBM 6031	KY683572	KY696696	MK542159
Trachylepis affinis	MVZ 252608	KY683571	KY696694	MK542153
Trachylepis affinis	USNM 584239	KY683569	KY696698	NA
Trachylepis affinis	CAS 219357	KU954509	NA	NA
Trachylepis affinis	KUZ 46904	AB028819	NA	NA
Trachylepis affinis	MNHN 2001.0108	AY159122	NA	NA
Trachylepis affinis	MNHN 2002.0746	AY159120	NA	NA
Trachylepis affinis	MNHN 2002.0743	AY159119	NA	NA
Trachylepis affinis	MNHN 2002.0742	AY159118	NA	NA
Trachylepis affinis	CAS 253795	KU954508	NA	NA
Trachylepis affinis	MUHNAC/MB03-000959	KU954499	MT613943	MT613960
Trachylepis affinis	MUHNAC/MB03-001023	NA	MT613944	MT613962
Trachylepis affinis	E18512	NA	MK583064	NA
Trachylepis affinis	SS819	NA	MK583063	NA
Trachylepis affinis	SS822	NA	MK583062	NA
Trachylepis affinis	MVZ 252605	NA	MK583048	MK542167
Trachylepis affinis	MUHNAC/MB03-001024	NA	NA	MT613963
Trachylepis affinis	BYU 62126	NA	NA	MK542155
Trachylepis affinis	PEMField174	NA	NA	MK791860

Supplementary Table S1. (continued from previoust page)

Trachylepis atlantica	MRT 4428	DQ238914	NA	NA	
Trachylepis atlantica	MRT 4427	DQ238913	NA	NA	
Trachylepis atlantica	MRT 4429	DQ238912	NA	NA	
Trachylepis atlantica	BMNH 1888.1.19.20a	AY151467	NA	NA	
Trachylepis atlantica	BMNH 1888.1.19.20	AY151466	NA	NA	
Trachylepis atlantica	BMNH 1888.1.19.19	AY151465	NA	NA	
Trachylepis atlantica	BMNH 1888.1.19.18	AY151464	NA	NA	
Trachylepis atlantica	BMNH 1888.1.19.17	AY151463	NA	NA	
Trachylepis atlantica	MNRJ 7747	AY070362	NA	NA	
Trachylepis boulengeri	PEM R-16179	MK792003	NA	MK791864	
Trachylepis boulengeri	PEM R-15451	MK792002	NA	MK791863	
Trachylepis boulengeri	PEM R-5533	KX231454	KX231470	KX231384	
Trachylepis boulengeri	PEM R-13442	MK792006	NA	NA	
Trachylepis boulengeri	mE1110110	JQ598785	NA	NA	
Trachylepis casuarinae	71Mcaguri	AY151474	NA	NA	
Trachylepis comorensis	ZFMK 62192	AF153565	NA	NA	
Trachylepis comorensis	MH7	HM192758	NA	NA	
Trachylepis comorensis	MH23	HM192757	NA	NA	
Trachylepis comorensis	MH11	HM192756	NA	NA	
Trachylepis comorensis	AJ18	HM192753	NA	NA	
Trachylepis comorensis	AJ12	HM192752	NA	NA	
Trachylepis comorensis	MY1	HM192751	NA	NA	
Trachylepis comorensis	MY12	HM192750	NA	NA	
Trachylepis comorensis	MY37	HM192749	NA	NA	
Trachylepis comorensis	MY51	HM192748	NA	NA	
Trachylepis farooqii, sp. nov.	MZUSP L108146	PQ892219	PV388835	PV388832	
Trachylepis farooqii, sp. nov.	MZUSP L108147	PQ892218	PV388834	PV388831	
Trachylepis farooqii, sp. nov.	MZUSP L108148	PQ892220	PV388836	PV388833	
Trachylepis farooqii, sp. nov.	Mausfeld 2000	AF153574	NA	NA	
Trachylepis farooqii, sp. nov.	PEM R-16325	MK792020	NA	MK791872	
Trachylepis farooqii, sp. nov.	PEM R-9737	MK792019	NA	MK791871	
Trachylepis farooqii, sp. nov.	ZFMK 74514	AY070356	NA	NA	
Trachylepis maculilabris	MVZ 253443	KU954523	NA	MK542238	
Trachylepis maculilabris	MVZ 252621	KU954522	MK583111	MK542237	
Trachylepis maculilabris	MVZ 249750	KU954521	KY696699	MK542226	
Trachylepis maculilabris	MVZ 249749	KU954520	KY696700	NA	
Trachylepis maculilabris	MVZ 249672	KU954519	MK583107	MK542224	
Trachylepis maculilabris	MVZ 245344	KU954518	MK583108	NA	
Trachylepis maculilabris	MVZ 245343	KU954517	NA	NA	
Trachylepis maculilabris	CAS 256254	KU954516	NA	NA	
Trachylepis maculilabris	CAS 253881	KU954515	MK583118	MK542235	
Trachylepis maculilabris	CAS 250828	KU954514	MK583132	MK542229	
Trachylepis maculilabris	CAS 249868	KU954513	MK583116	NA	
Trachylepis maculilabris	CAS 249859	KU954512	MK583114	MK542217	

Supplementary Table S1. (continued from previoust page)

Trachylepis maculilabris	MCZ 188639	MK496143	MK583146	MK542228
Trachylepis maculilabris	UTEP 21821	MK496142	NA	MK542242
Trachylepis maculilabris	UTEP 21820	MK496141	NA	MK542259
Trachylepis maculilabris	UTEP 21818	MK496140	NA	MK542241
Trachylepis maculilabris	UTEP 21816	MK496139	NA	NA
Trachylepis maculilabris	UTEP 21815	MK496138	NA	MK542253
Trachylepis maculilabris	UTEP 21814	MK496137	NA	MK542252
Trachylepis maculilabris	UTEP 21801	MK496136	MK583144	MK542244
Trachylepis maculilabris	UTEP 21829	MK496135	MK583143	NA
Trachylepis maculilabris	UTEP 21828	MK496134	MK583142	MK542248
Trachylepis maculilabris	UTEP 21825	MK496133	MK583140	MK542211
Trachylepis maculilabris	UTEP 21824	MK496132	MK583141	MK542209
Trachylepis maculilabris	UTEP 21827	MK496131	NA	MK542214
Trachylepis maculilabris	UTEP 21822	MK496130	NA	MK542247
Trachylepis maculilabris	UTEP 21819	MK496129	MK583139	MK542257
Trachylepis maculilabris	UTEP 21817	MK496128	MK583138	MK542216
Trachylepis maculilabris	UTEP 21813	MK496127	MK583137	MK542246
Trachylepis maculilabris	UTEP 21809	MK496126	MK583136	MK542210
Trachylepis maculilabris	UTEP 21808	MK496125	MK583135	NA
Trachylepis maculilabris	UTEP 21807	MK496124	MK583134	MK542258
Trachylepis maculilabris	UTEP 21806	MK496123	MK583133	NA
Trachylepis maculilabris	UTEP 21798	MK496122	MK583130	MK542251
Trachylepis maculilabris	UTEP 21826	MK496120	MK583129	NA
Trachylepis maculilabris	UTEP 21812	MK496119	MK583127	MK542255
Trachylepis maculilabris	UTEP 21811	MK496118	MK583128	MK542239
Trachylepis maculilabris	UTEP 21810	MK496117	MK583126	MK542233
Trachylepis maculilabris	UTEP 21804	MK496116	MK583125	MK542215
Trachylepis maculilabris	UTEP 21803	MK496115	MK583124	MK542254
Trachylepis maculilabris	UTEP 21802	MK496114	MK583123	MK542245
Trachylepis maculilabris	UTEP 21800	MK496113	MK583122	MK542243
Trachylepis maculilabris	UTEP 21799	MK496112	MK583121	MK542234
Trachylepis maculilabris	UTEP 21797	MK496111	MK583120	MK542213
Trachylepis maculilabris	CAS 253495	MK496109	MK583117	MK542250
Trachylepis maculilabris	CAS 253268	MK496108	NA	MK542230
Trachylepis maculilabris	CAS 249863	MK496107	MK583115	MK542249
Trachylepis maculilabris	MVZ 252620	MK496103	MK583112	MK542236
Trachylepis maculilabris	MVZ 249747	MK496102	MK583110	MK542225
Trachylepis maculilabris	MVZ 249746	MK496101	MK583109	MK542240
Trachylepis maculilabris	MVZ 245342	MK496099	MK583106	MK542223
Trachylepis maculilabris	BYU 62028	MK496098	NA	MK542219
Trachylepis maculilabris	BYU 62010	MK496097	MK583119	MK542222
Trachylepis maculilabris	BYU 62054	MK496096	MK583105	MK542220
Trachylepis maculilabris	BYU 62014	MK496095	MK583104	MK542227
Trachylepis maculilabris	BYU 62022	MK496094	MK583103	MK542218
Trachylepis maculilabris	BYU 62039	MK496093	MK583102	MK542221
Trachylepis maculilabris	BYU 62031	MK496092	MK583101	MK542212
Trachylepis maculilabris	BYU 62148	MK496091	MK583100	NA
Trachylepis maculilabris	BYU 62101	MK496090	MK583099	MK542231

Supplementary Table S1.

(continued from previoust page)

Trachylepis maculilabris	PEM R-19463	MK792072	MK791975	NA
Trachylepis maculilabris	PEM R-5844	MK792018	NA	MK791870
Trachylepis maculilabris	AMB 9883	MK792017	NA	MK791916
Trachylepis maculilabris	CAS 256792	KX671801	NA	NA
Trachylepis maculilabris	CAS 253882	KX671800	NA	NA
Trachylepis maculilabris	USNM 584344	KY683562	NA	NA
Trachylepis maculilabris	BYU 573505	KY683561	KY696701	NA
Trachylepis maculilabris	MNHN 2000.5200	AY159124	NA	NA
Trachylepis maculilabris	MNHN 2000.5199	AY159123	NA	NA
Trachylepis maculilabris	UTEP 21823	NA	MK583145	MK542256
Trachylepis maculilabris	UTEP 21805	NA	MK583131	MK542232
Trachylepis maculilabris	UWBM 6045	NA	MK583113	NA
Trachylepis maculilabris	MCZ 184557	NA	MK583098	MK542208
Trachylepis margaritifer	ZFMK 68647	AF153575	NA	NA
Trachylepis margaritifer	PEM R-9745	MK792024	NA	MK791874
Trachylepis margaritifer	PEM R-5539	MK792023	NA	MK791873
Trachylepis margaritifer	CAS 234173	MK792022	NA	NA
Trachylepis margaritifer	CAS 234165	MK792021	NA	NA
Trachylepis margaritifer	69Mmarga	AY151473	NA	NA
Trachylepis margaritifer	BYU 47330	DQ238942	NA	NA
Trachylepis notabilis	MUHNAC/MB03-001357	NA	NA	PP074207
Trachylepis notabilis	MUHNAC/MB03-001355	NA	NA	PP074206
Trachylepis paucisquamis	PEM R-4438	MK792031	NA	MK791879
Trachylepis paucisquamis	PEM R-4436	MK792030	NA	MK791878
Trachylepis paucisquamis	UWBM 6041	KX364963	KX365040	NA
Trachylepis paucisquamis	UWBM 6042	KY683565	KY696686	NA
Trachylepis paucisquamis	UWBM 6043	KY683564	KY696685	NA
Trachylepis polytropis	PEM R-5377	MK792033	NA	MK791881
Trachylepis polytropis	PEM R-5443	MK792032	NA	MK791880
Trachylepis polytropis	PEM R-15714	KY683558	NA	NA
Trachylepis adamastor	CAS 238898	KU954511	NA	NA
Trachylepis adamastor	MUHNAC/MB03-000979	KU954503	NA	NA
Trachylepis adamastor	MUHNAC/MB03-000957	KU954502	NA	NA
Trachylepis adamastor	MUHNAC/MB03-000956	KU954501	NA	NA
Trachylepis adamastor	MUHNAC/MB03-000955	KU954500	NA	NA
Trachylepis quinquetaeniata	ZFMK 68646	AF153579	NA	NA
Trachylepis quinquetaeniata	UWBM 6056	MK496151	MK583097	MK542205
Trachylepis quinquetaeniata	UWBM 6053	MK496150	MK583096	MK542202
Trachylepis quinquetaeniata	MVZ 249790	MK496149	MK583095	MK542207
Trachylepis quinquetaeniata	MVZ 249769	MK496148	MK583094	MK542204
Trachylepis quinquetaeniata	MVZ 249760	MK496147	MK583091	MK542201
Trachylepis quinquetaeniata	MVZ 249765	MK496146	MK583090	MK542200
Trachylepis quinquetaeniata	MVZ 249759	MK496145	MK583089	MK542199
Trachylepis quinquetaeniata	MVZ 245356	MK496144	MK583092	NA
-	1	1	1	1

Supplementary Table S1. (continued from previoust page)

Trachylepis quinquetaeniata	TJC1372	MK792041	NA	MK791909
Trachylepis quinquetaeniata	MVZ 249761	KY683557	KY696705	NA
Trachylepis quinquetaeniata	MVZ 249768	KY683556	KY696702	NA
Trachylepis quinquetaeniata	MVZ 249785	KY683555	KY696703	NA
Trachylepis quinquetaeniata	UWBM 6050	KY683554	KY696704	MK542203
Trachylepis quinquetaeniata	FMNH 262234	KC621335	NA	NA
Trachylepis quinquetaeniata	FMNH 262235	DQ238907	NA	NA
Trachylepis quinquetaeniata	FMNH 262236	DQ238906	NA	NA
Trachylepis quinquetaeniata	FMNH 262232	DQ238899	NA	MK791883
Trachylepis quinquetaeniata	BYU 47350	DQ238874	NA	NA
Trachylepis quinquetaeniata	KUZ 45890	AB028789	NA	NA
Trachylepis quinquetaeniata	AMNH 109798	NA	MK583093	MK542206
Trachylepis sechellensis	TRASEY1	MK792042	NA	MK791884
Trachylepis thomensis	562	EU164496	NA	NA
Trachylepis thomensis	543Neves	AY997725	NA	NA
Trachylepis thomensis	574LagoaAzul	AY997724	NA	NA
Trachylepis thomensis	729Rolas	AY997723	NA	NA
Trachylepis thomensis	503STome	AY997722	NA	NA
Trachylepis thomensis	539Neves	AY997721	NA	NA
Trachylepis thomensis	525StCatarina	AY997720	NA	NA
Trachylepis thomensis	517Santana	AY997719	NA	NA
Trachylepis thomensis	512Santana	AY997718	NA	NA
Trachylepis thomensis	511Santana	AY997717	NA	NA
Trachylepis thomensis	508Santana	AY997716	NA	NA
Trachylepis thomensis	733PFurada	AY997715	NA	NA
Trachylepis thomensis	563Rolas	AY997714	NA	NA
Trachylepis thomensis	506Santana	AY997713	NA	NA
Trachylepis thomensis	MUHNAC/MB03-000963	KU954507	NA	MT613961
Trachylepis thomensis	MUHNAC/MB03-000962	KU954506	MT613954	MT613965
Trachylepis thomensis	MUHNAC/MB03-000961	KU954505	MT613955	MT613967
Trachylepis thomensis	MUHNAC/MB03-000960	KU954504	NA	NA
Trachylepis thomensis	CAS 218722	MK792056	NA	MK791890
Trachylepis thomensis	CAS 218821	KU954510	NA	NA
Trachylepis wrightii	MAWR1	AY151472	NA	NA